

Welcome to

"PARA-SITE: an electronic guide to parasitology"

Produced as an educational initiative of the:

- ASP (Australian Society of Parasitology Inc.);
- UQ (The University of Queensland); and
- ABRS (Australian Biological Resources Study).

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PARA-SITE provides basic information about parasites causing disease in animals and people. It covers information on:

- parasite morphology (fundamental to taxonomy);
- host range (species specificity);
- site of infection (tissue/organ tropism);
- parasite pathogenicity (disease potential);
- modes of transmission (spread of infections);
- differential diagnosis (detection of infections); and
- treatment and control (cure and prevention).



Table of Contents **page**

Foreword . . . . . 3.

Introduction to parasitology . . . . . 10.

Overview . . . . . 11.
Mathematical models . . . . . 21.
Taxonomy . . . . . 36.

Protozoan parasites . . . . . 50.

Amoebae . . . . . 60.
Flagellates . . . . . 94.
Apicomplexa . . . . . 309.
Ciliates . . . . . 618.
Ascetospora . . . . . 755.

Microspora . . . . . 783.

Myxozoa . . . . . 828.

Helminth parasites . . . . . 994.

Nematodes . . . . . 1010.
Acanthocephala . . . . . 1694.
Cestodes . . . . . 1716.
Digenea . . . . . 1865.
Monogenea . . . . . 2020.

Arthropod parasites . . . . . 2069.

Lice . . . . . 2080.
Bugs . . . . . 2176.
Fleas . . . . . 2200.
Flies . . . . . 2271.
Ticks . . . . . 2593.
Mites . . . . . 2755.
Crustaceans . . . . . 2942.
Pentastomes . . . . . 2975.

Diagnostic parasitology . . . . . 2994.

Symptomatology . . . . . 3001.
Direst detection . . . . . 3003.
Indirect demonstration . . . . . 3019.

Parasite control . . . . . 3028.

Drugs . . . . . 3029.
Vaccines . . . . . 3037.
Management . . . . . 3048.

Index . . . . . 3058.

Foreword

In developing this resource, I consider it essential that students get to know the parasite assemblages themselves in order to understand the ways in which they interact with their hosts and cause disease, as well as to understand the logic behind different diagnostic techniques and various treatment and control strategies. By learning basic parasitological information in a clinical context, it is hoped students will develop their skills to:

- diagnose the major parasitic groups in host tissues and organs;
- deduce their modes of transmission from their sites of infection;
- indicate their pathogenicity for different host groups;
- identify boundaries to their distribution and abundance;
- recommend appropriate treatment and control strategies; and
- assess their significance with respect to human and animal health and welfare.

The impetus for this work was provided by the apparent absence of textbooks giving the right degree and mix of biological and clinical information. Many general biology texts only give cursory information on a small range of parasites while most clinical texts concentrate on a few of the most serious parasitic diseases of medical and veterinary significance. At the other end of the spectrum, there are many specialist texts dealing exclusively with individual parasitic groups and the information presented can be overwhelming to students. This electronic resource was designed in an attempt to find some common middle ground between the generalist and specialist texts available. Knowledge of the many different parasite assemblages is essential for their differential diagnosis, treatment and control.

I wrote this resource part-time over a decade, beginning with parasites of medical importance and moving onto parasites of domestic animals and then wildlife, including fish. Parasite genera were selected on the basis of their significance to human and animal health and also as requested by students. Early versions of essays on individual genera were incorporated into teaching materials released to undergraduate students enrolled for a third-level course on parasitology at The University of Queensland. Their feedback was crucial for revision and expansion. A compilation of 30 essays was made available on-line through the Australian Society for Parasitology (ASP) website, an organization that generously provided funds to employ a biological artist to draw new life-cycle diagrams. The preliminary PARA-SITE website proved popular as an educational tool, so the decision was made to expand the e-resource to include more parasites of interest. There are now around 250 parasite genera covered in this revised version. It is hoped that other ASP Fellows and members may add to this resource over the coming years, providing a knowledge bank and legacy for future generations of parasitologists.

Peter O'Donoghue
Brisbane, 2025

Notes on format

Information is summarized for over 250 parasite genera, including protozoa, helminths and arthropods. Each genus is dealt with separately and provides a complete introductory account, so there is some preliminary repetition for closely-related genera (this was done so that each genus could stand-alone when the resource is delivered electronically). The following format has been used throughout.

Genus
Name and type of parasite

Overview
Succinct summary covering parasite identity, basic biology and clinical significance.

Classification:
Taxonomy presented as Domain, Supergroup, Phylum, Class, Order, Family, Genus *et al.*

Please note that parasite taxonomy is constantly changing as new characters sets are explored and incorporated into phylogenetic classification systems. There is no perfectly correct system, merely current opinion. Parasites have conventionally been classified on the basis of phenotypic characters (morphology, biology, hosts), but now advances in molecular biology have allowed extensive genotypic characters (gene sequences, proteins) to be used to infer phylogenetic relationships between taxa. In some cases, genotypic characterization has ratified phenotypic classifications, but in other cases, molecular data has suggested alternative groupings. In this resource, an attempt has been made, where appropriate, to link conventional and contemporary classifications to provide some continuity between old and new schools of thought. Information has been gleaned from numerous electronic sources, as would be available to anyone using contemporary web search engines. It has been kept up-to-date as far as possible, but remember that taxonomy is an ever-changing game.

Parasite biodiversity and host range:
This section introduces that type of parasite being covered, beginning with its main characteristics and ending with its biodiversity (species richness) in the form of a host-parasite species list. These lists are compilations of records retrieved by searching public data-bases and published reviews and papers. Where appropriate, they include synonyms, *species inquirenda*, *nomen dubia* and sometimes species that have since been reassigned to other genera. I have retained as many old records as possible to help guide readers through the complex terrain of species diversity as presented on the internet. I will leave it to specialists to revise listings by lumping or splitting species. During the development of this resource, students requested that I provide common names for hosts rather than just their scientific binomial names to aid recognition (in contradiction to conventional practice). I initially attempted to provide both, but the tables became very cumbersome. I have listed the hosts together with their familial designations to indicate the range of presumptive host specificity (narrow or broad).

Parasite morphology:
This section describes the numbers and types of developmental stages formed by each parasite genus, with information given on size ranges and morphological appearances.

Site of infection:
The anatomical location (tissue tropism) is given for each parasite developmental stage within their various hosts.

Pathogenesis:
The pathogenic potential (virulence) is indicated for infections/infestations, noting major clinical signs and risk factors for disease.

Developmental cycle and mode of transmission:
Details are given on the life-cycles of representative species (note that the life-cycles of most species remain to be determined). The major modes of transmission are indicated: direct v. indirect; horizontal $\pm$ vertical.

Differential diagnosis:
The usual methods for diagnosing infections are reported, together with notes on new or experimental techniques.

Treatment and control:
Therapeutic and prophylactic options for disease control are provided, but specific information (doses, courses, etc) are not stated as treatment should be carried out under professional medical/veterinary supervision. Preventive measures are summarized: covering hygiene, sanitation, disinfection, vector control, vaccination and education, as appropriate.

Table of parasite genera

Parasite genus	Type	Parasitosis (disease)	Major hosts	Page
Entamoeba	Protozoa: amoeba	dysentery, meningoencephalitis	mammals	63
Neoparamoeba/Paramoeba	Protozoa: amoeba	amoebic gill disease	fish	71
Acanthamoeba	Protozoa: amoeba	meningoencephalitis, keratitis	mammals	76
Balamuthia	Protozoa: amoeba	granulomatous encephalitis	mammals	83
Naegleria	Protozoa: amoeba	amoebic meningoencephalitis	mammals	88
Amyloodinium	Protozoa: flagellate	marine velvet	fish	98
Crepidoodinium	Protozoa: flagellate	gill spots	fish	98
Piscinoodinium	Protozoa: flagellate	freshwater velvet	fish	98
Haematodinium	Protozoa: flagellate	bitter crab disease	crabs	107
Ichthyodinium	Protozoa: flagellate	piscine skin lesions	fish	107
Perkinsus	Protozoa: flagellate	shellfish tissue lesions	shellfish	116
Cochlosoma	Protozoa: flagellate	avian enteritis	birds	122
Trichomonas vaginalis	Protozoa: flagellate	vaginitis	primates	128
Trichomonas gallinae	Protozoa: flagellate	canker	birds	136
trichomonads	Protozoa: flagellate	enteritis	reptiles, frogs, fish	144
Tritrichomonas foetus	Protozoa: flagellate	bovine infertility	artiodactyls	156
Histomonas	Protozoa: flagellate	enterohepatitis, blackhead	birds	165
Dientamoeba	Protozoa: flagellate	diarrhoea	mammals	172
Hexamita, Spironucleus	Protozoa: flagellate	pinhead, hole-in-head disease	birds	179
Giardia	Protozoa: flagellate	diarrhoea	mammals	189
Trypanosoma (piscine)	Protozoa: flagellate	subclinical	fish	197
Trypanosoma (reptilian)	Protozoa: flagellate	subclinical	reptiles, amphibia	210
Trypanosoma (avian)	Protozoa: flagellate	Subclinical	birds	223
Trypanosoma brucei	Protozoa: flagellate	sleeping sickness	mammals	233
Trypanosoma cruzi	Protozoa: flagellate	Chagas disease	mammals	242
Trypanosoma evansi	Protozoa: flagellate	surra	mammals	260
Leishmania	Protozoa: flagellate	cutaneous or visceral lesions	mammals	268
Sauroleishmania	Protozoa: flagellate	subclinical	lizards	280
Ichthyobodo (*Costia*)	Protozoa: flagellate	piscine skin lesions	fish	287
Cryptobia	Protozoa: flagellate	piscine skin lesions	fish	294
Trypanoplasma	Protozoa: flagellate	piscine anaemia	fish	301
Cryptosporidium	Protozoa: apicomplexan	diarrhoea	mammals, birds	313
Haemogregarina	Protozoa: apicomplexan	blood parasite	reptiles	324
Hepatozoon	Protozoa: apicomplexan	blood parasite	mammals	337
Klossiella	Protozoa: apicomplexan	kidney lesions	mammals	360
Caryospora	Protozoa: apicomplexan	coccidiosis	mammals	366
Cyclospora	Protozoa: apicomplexan	coccidiosis	mammals	374
Isospora, Cystoisospora	Protozoa: apicomplexan	coccidiosis	mammals, birds	382
Eimeria	Protozoa: apicomplexan	coccidiosis	mammals, birds	399
Goussia	Protozoa: apicomplexan	coccidiosis	fish	440
Sarcocystis (*Frenkelia*)	Protozoa: apicomplexan	tissue cysts, haemorrhages	mammals, birds	452
Besnoitia	Protozoa: apicomplexan	tissue cysts	mammals	473
Neospora	Protozoa: apicomplexan	abortion	mammals	482
Toxoplasma	Protozoa: apicomplexan	tissue cysts, abortion	mammals	490
Hammondia	Protozoa: apicomplexan	tissue cysts	mammals	498
Plasmodium	Protozoa: apicomplexan	malaria, anaemia, fever	mammals	505
Plasmodium	Protozoa: apicomplexan	anaemia	birds	519
Plasmodium	Protozoa: apicomplexan	anaemia	reptiles	535
Haemoproteus	Protozoa: apicomplexan	tissue lesions	birds	563
Leucocytozoon/Akiba	Protozoa: apicomplexan	tissue lesions	birds	581
Babesia	Protozoa: apicomplexan	tick fever	mammals	593
Theileria	Protozoa: apicomplexan	East Coast fever	mammals	605
Balantidium	Protozoa: ciliate	diarrhoea	mammals	620
Chilodonella	Protozoa: ciliate	gill/skin diseases	fish	627
Uronema	Protozoa: ciliate	gill/skin lesions	fish	634
Ichthyophthirius	Protozoa: ciliate	ich, freshwater whitespot	fish	641
Tetrahymena	Protozoa: ciliate	tet, tissue lesions	fish	648

Trichodina	Protozoa: ciliate	piscine skin lesions	fish	658
peritrichs	Protozoa: ciliate	fouling organisms	aquatic	681
Haplosporidium, Minchinia	Protozoa: ascetospora	oyster mortalities	molluscs	757
Bonamia	Protozoa: ascetospora	winter mortality	molluscs	765
Mikrocytos	Protozoa: ascetospora	Denman Island disease	molluscs	771
Marteilia	Protozoa: ascetospora	Abers disease, QX	molluscs	776
Glugea et al. (fish)	Fungi: microspora	tissue lesions	fish	785
Thelohania .. (arthropods)	Fungi: microspora	tissue lesions	arthropods	801
Encephalitozoon (tetrapods)	Fungi: microspora	tissue lesions	tetrapods	815
Myxobolus .. (bivalvulid)	Cnidaria: myxozoa	lesions, whirling disease	fish	831
Kudoa .... (multivalvulid)	Cnidaria: myxozoa	lesions, myoliquefaction	fish	975
Strongyloides	Helminth: nematode	Cochin diarrhoea, larval currens	mammals	1020
Rhabditis, Pelodera	Helminth: nematode	dermatitis	mammals	1029
Trichostrongylus	Helminth: nematode	scours, illthrift	mammals	1036
Haemonchus	Helminth: nematode	scours, anaemia	mammals	1047
Ostertagia	Helminth: nematode	scours, illthrift	mammals	1056
Teladorsagia	Helminth: nematode	scours, illthrift	mammals	1067
Hyostrongylus	Helminth: nematode	diarrhoea, wasting	mammals	1076
Cooperia	Helminth: nematode	scours, illthrift	mammals	1084
Nematodirus	Helminth: nematode	diarrhoea, illthrift	mammals	1093
Ollulanus	Helminth: nematode	gastritis, vomiting, wasting	mammals	1102
Nippostrongylus	Helminth: nematode	verminous pneumonia	mammals	1109
Strongylus	Helminth: nematode	arteritis, anaemia, colic	mammals	1117
Triodontophorus et al.	Helminth: nematode	unthriftiness	mammals	1126
Cyathostomum et al.	Helminth: nematode	equine enteritis	mammals	1134
Chabertia	Helminth: nematode	haemorrhagic enteritis	mammals	1147
Oesophagostomum	Helminth: nematode	diarrhoea, ulcerative colitis	mammals	1154
Stephanurus	Helminth: nematode	hepatic cirrhosis	mammals	1164
Syngamus	Helminth: nematode	gapes, respiratory distress	birds	1171
Ancylostoma	Helminth: nematode	Old World hookworm disease	mammals	1181
Globocephalus	Helminth: nematode	hookworm disease	mammals	1191
Uncinaria	Helminth: nematode	hookworm disease	mammals	1198
Necator	Helminth: nematode	New World hookworm disease	mammals	1206
Bunostomum	Helminth: nematode	hookworm disease	mammals	1214
Gaigeria	Helminth: nematode	hookworm disease	mammals	1222
Dictylocaulus	Helminth: nematode	husk, respiratory disease	mammals	1229
Metastrongylus	Helminth: nematode	bronchitis	mammals	1237
Protostrongylus	Helminth: nematode	pulmonary lesions	mammals	1245
Muellerius	Helminth: nematode	pulmonary lesions	mammals	1253
Parelaphostrongylus	Helminth: nematode	brainworm, moose illness	mammals	1261
Elaphostrongylus	Helminth: nematode	neurological and muscle lesions	mammals	1269
Aelurostrongylus	Helminth: nematode	respiratory disease	mammals	1277
Angiostrongylus	Helminth: nematode	neural lesions	mammals	1285
Parastrongylus	Helminth: nematode	meningoencephalitis	mammals	1293
Filaroides	Helminth: nematode	respiratory disease	mammals	1303
Oslerus	Helminth: nematode	respiratory disease	mammals	1312
Ascaris	Helminth: nematode	gut obstruction	mammals	1319
Parascaris	Helminth: nematode	illthrift	mammals	1328
Toxascaris	Helminth: nematode	illthrift	mammals	1335
Toxocara	Helminth: nematode	illthrift, larval migrans	mammals	1342
Anisakis	Helminth: nematode	enteric lesions	mammals, fish	1352
Heterakis	Helminth: nematode	emaciation	birds	1365
Ascaridia	Helminth: nematode	diarrhoea, anaemia	birds	1375
Oxyuris	Helminth: nematode	perianal pruritus	mammals	1383
Enterobius	Helminth: nematode	perianal pruritus	mammals	1390
Passalurus	Helminth: nematode	enteritis	mammals	1398
Syphacia	Helminth: nematode	enteritis	mammals	1404
Aspiculuris	Helminth: nematode	enteritis	mammals	1414
Habronema, Draschia	Helminth: nematode	summer sores	mammals	1421
Tetrameres	Helminth: nematode	anaemia	mammals	1430

Gongylonema	Helminth: nematode	regurgitation	mammals, birds	1442
Spirocerca	Helminth: nematode	vomiting, anorexia	mammals, birds	1451
Cylicospirura et al.	Helminth: nematode	stomach lesions	mammals	1459
Ascarops, Physocephalus	Helminth: nematode	inappetence	mammals	1466
Acuaria et al.	Helminth: nematode	oesophagitis	birds	1476
Thelazia	Helminth: nematode	conjunctivitis	mammals	1494
Oxyspirura	Helminth: nematode	opthalmitis	birds	1502
Physaloptera	Helminth: nematode	vomiting, anorexia	mammals	1512
Gnathostoma	Helminth: nematode	larval migrans	mammals	1527
Parafilaria	Helminth: nematode	skin bleeding lesions	mammals	1538
Stephanofilaria	Helminth: nematode	dermatitis	mammals	1545
Onchocerca	Helminth: nematode	river blindness	mammals	1552
Wuchereria	Helminth: nematode	lymphatic filariasis	mammals	1562
Brugia	Helminth: nematode	lymphatic filariasis	mammals	1571
Mansonella	Helminth: nematode	subcutaneous filariasis	mammals	1580
Dipetalonema et al.	Helminth: nematode	dermatitis	mammals	1590
Dirofilaria	Helminth: nematode	heartworm disease	mammals	1602
Loa	Helminth: nematode	subcutaneous Calabar swellings	mammals	1614
Setaria	Helminth: nematode	neurological disease	mammals	1622
Camallanus	Helminth: nematode	enteritis	fish	1631
Dracunculus	Helminth: nematode	guinea worm, skin lesions	mammals	1643
Trichuris	Helminth: nematode	rectal prolapse	mammals	1650
Capillaria et al.	Helminth: nematode	tissue lesions	mammals, birds, fish	1659
Trichinella	Helminth: nematode	muscle lesions	mammals	1685
Macracanthorhynchus	Helminth: acanthocephala	enteritis	mammals	1696
Oncicola	Helminth: acanthocephala	enteritis	mammals	1702
Polymorphus	Helminth: acanthocephala	enteritis	birds	1708
Taenia (incl. *Multiceps*)	Helminth: cestode	cysticercosis, coenurosis, gid	mammals	1720
Echinococcus	Helminth: cestode	hydatid disease	mammals	1734
Anoplocephala et al.	Helminth: cestode	colic	mammals	1742
Dipylidium	Helminth: cestode	enteritis	mammals	1755
Amoebotaenia	Helminth: cestode	enteritis	birds	1763
Choanotaenia	Helminth: cestode	reduced growth	birds	1769
Davainea	Helminth: cestode	enteritis	birds, mammals	1780
Raillietina	Helminth: cestode	nodular tapeworm disease	birds, mammals	1789
Hymenolepis	Helminth: cestode	enteritis	mammals, birds	1807
Diphyllobothrium et al.	Helminth: cestode	enteritis	mammals, fish	1831
Spirometra	Helminth: cestode	tissue lesions	mammals, fish	1843
Bothriocephalus	Helminth: cestode	enteritis	fish	1854
Fasciola	Helminth: digenea	hepatic fibrosis	mammals	1869
Fasciolopsis	Helminth: digenea	enteritis	mammals	1877
Echinostoma	Helminth: digenea	diarrhoea	mammals, birds	1884
Paramphistomum	Helminth: digenea	enteritis	mammals	1907
Gastrodiscoides	Helminth: digenea	enteritis	mammals	1921
Opisthorchis	Helminth: digenea	hepatic fibrosis	mammals	1929
Clonorchis	Helminth: digenea	hepatic cirrhosis	mammals	1938
Metorchis	Helminth: digenea	hepatic fibrosis	mammals	1946
Heterophyes	Helminth: digenea	diarrhoea	mammals	1954
Metagonimus	Helminth: digenea	diarrhoea	mammals	1962
Dicrocoelium	Helminth: digenea	anaemia, cirrhosis	mammals	1981
Paragonimus	Helminth: digenea	respiratory/neurological	mammals	1990
Schistosoma	Helminth: digenea	bilharzia	mammals	1999
Trichobilharzia et al.	Helminth: digenea	dermatitis, swimmer's itch	birds, mammals	2010
Gyrodactylus	Helminth: monogenea	dermal ulceration	fish	2022
Dactylogyrus	Helminth: monogenea	respiratory signs	fish	2040
Benedenia	Helminth: monogenea	skin lesions	fish	2062
Haematopinus	Insect: louse	dermatitis	mammals	2084
Linognathus	Insect: louse	skin lesions	mammals	2091
Solenoptes	Insect: louse	skin lesions	mammals	2098
Pediculus	Insect: louse	pediculosis	mammals	2104

Pthirus	Insect: louse	pthiriasis, crabs	mammals	2110
Trichodectes	Insect: louse	skin lesions	mammals	2116
Bovicola, Damaliia	Insect: louse	pruritus, dermatitis	mammals	2123
Felicola	Insect: louse	dermatitis	mammals	2132
Lipeurus et al.	Insect: louse	restlessness	birds	2139
Menopon et al.	Insect: louse	restlessness	birds	2157
Heterodoxus	Insect: louse	pruritus, dermatitis	mammals	2170
Cimex	Insect: bug	skin lesions	mammals	2178
Triatoma et al.	Insect: bug	skin lesions	mammals	2185
Pulex	Insect: flea	irritation, dermatitis	mammals	2203
Echidnophaga	Insect: flea	irritation, dermatitis	birds, mammals	2211
Ctenocephalides	Insect: flea	pruritus, dermatitis	mammals	2220
Xenopsylla	Insect: flea	pruritus	mammals	2229
Spilopsyllus	Insect: flea	irritation, skin lesions	mammals	2237
Tunga	Insect: flea	nodular/ulcerated skin lesions	mammals	2244
Ceratophyllus	Insect: flea	pruritus, dermatitis	mammals, birds	2253
Nosopsyllus	Insect: flea	pruritus, dermatitis	mammals, birds	2263
Culex, Aedes, Mansonia	Insect: mosquito	annoyance, blood loss	mammals, birds	2278
Anopheles	Insect: mosquito	annoyance, blood loss	mammals, birds	2305
Culicoides	Insect: midge	pruritus, hypersensitivity	mammals, birds	2317
Simulium	Insect: fly	annoyance, pruritus	mammals, birds	2335
Phlebotomus, Lutzomyia	Insect: fly	irritation, pruritus, wheals	mammals	2357
Tabanus et al.	Insect: fly	irritation	mammals	2369
Glossina	Insect: fly	irritation, hypersensitivity	mammals	2400
Melophagus	Insect: fly	anaemia, reduced productivity	mammals	2410
Hippobosca	Insect: fly	irritation	mammals	2417
Musca	Insect: fly	annoyance	mammals	2424
Stomoxys	Insect: fly	annoyance, allergy	mammals	2433
Haematobia	Insect: fly	annoyance	mammals	2441
Lucilia, Calliphora	Insect: fly	myiasis (flystrike)	mammals	2449
Cochliomyia, Chrysomya	Insect: fly	myiasis screw-worm)	mammals	2463
Cordylobia	Insect: fly	obligate furuncular myiasis	mammals	2474
Sarcophaga	Insect: fly	furuncular myiases	mammals	2482
Wohlfahrtia	Insect: fly	furuncular myiases	mammals	2498
Dermatobia	Insect: fly	cutaneous myiasis	mammals	2506
Oestrus	Insect: fly	nasopharyngeal myiases	mammals	2514
Hypoderma	Insect: fly	subcutaneous myiases, warbles	mammals	2522
Gasterophilus	Insect: fly	stomatitis, ulceration	mammals	2531
Argas	Arachnid: tick	irritation, anaemia	birds, mammals	2543
Ornithodorus	Arachnid: tick	anaemia, toxicosis	mammals	2555
Otobius	Arachnid: tick	irritation, otitis	mammals	2570
Ixodes	Arachnid: tick	anaemia, toxicosis, paralysis	mammals, birds	2577
Rhipicephalus (*Boophilus*)	Arachnid: tick	trauma, toxicosis	mammals	2618
Haemaphysalis	Arachnid: tick	trauma, toxicosis	mammals, birds	2647
Amblyomma (*Aponomma*)	Arachnid: tick	trauma, toxicosis	mammals, reptiles	2678
Bothriocroton	Arachnid: tick	trauma, toxicosis	reptiles, mammals	2714
Dermacentor	Arachnid: tick	trauma, toxicosis	mammals	2723
Hyalomma	Arachnid: tick	trauma, toxicosis	mammals	2739
Ornithonyssus	Arachnid: mite	dermatitis, anaemia	birds, mammals	2557
Dermanyssus	Arachnid: mite	irritation, anaemia	birds, mammals	2766
Pneumonyssus	Arachnid: mite	nodular lung lesions, rhinitis	mammals	2774
Raillietia	Arachnid: mite	vestibular disease	mammals	2781
Sternostoma	Arachnid: mite	respiratory signs	birds	2787
Varroa	Arachnid: mite	bee mortalities	insects	2795
Demodex	Arachnid: mite	demodectic mange	mammals	2805
Cheyletiella	Arachnid: mite	scaly dermatitis	mammals	2815
Myobia	Arachnid: mite	myobiic mange	mammals	2822
Psorobia, Psorergates	Arachnid: mite	psorergatic mange	mammals	2829
Trombicula et al.	Arachnid: mite	dermatitis	mammals, birds	2837
Psoroptes	Arachnid: mite	psoroptic mange, ear canker	mammals	2850

Otodectes	Arachnid: mite	otitis	mammals	2857
Chorioptes	Arachnid: mite	chorioptic mange	mammals	2864
Sarcoptes	Arachnid: mite	sarcoptic mange, scabies	mammals	2871
Notoedres	Arachnid: mite	notoedric mange	mammals	2880
Trixacarus	Arachnid: mite	mange	mammals	2888
Cytodites	Arachnid: mite	air sacculitis	birds	2894
Lynxacarus	Arachnid: mite	pruritus, unkempt coats	mammals	2900
Leporacarus	Arachnid: mite	dermatitis	mammals	2907
Chirodiscoides	Arachnid: mite	dermatitis	mammals	2914
Myocoptes	Arachnid: mite	myocoptic mange	mammals	2921
Knemidocoptes	Arachnid: mite	depluming itch, scaly leg	birds	2928
Laminosioptes	Arachnid: mite	carcase lesions	birds	2936
Lernaea	Crustacea: copepod	gill/skin lesions	fish	2944
Ergasilus	Crustacea: copepod	gill lesions	fish	2953
Argulus	Crustacea: branchiura	gill/skin lesions	fish	2965
Porocephalus, Armillifer	Crustacea: pentastome	respiratory signs	reptiles	2977
Linguatula	Crustacea: pentastome	respiratory signs	mammals	2987

Introduction to Parasitology

Parasitism is the most common way of life; more than 50% of all animal species are parasites. Parasites occur in all animal species, and they may have a profound effect on the health of people, domestic animals and wildlife. Parasitology is the study of parasitism; a multidisciplinary subject covering many topics including morphology, taxonomy, biology, behaviour, life-cycles, pathogenesis, epidemiology, ecology, physiology, biochemistry, genetics and molecular biology, as well as the diagnosis, immunology and treatment of infections.

Parasites live at the expense of their hosts whereas other symbiotes may be mutualists (living in mutual benefit with host) or commensals (living without benefit or detriment to host). Parasites may infect the gastrointestinal tracts or circulatory systems of their hosts; they may invade different tissues and organs or they may live on the external surfaces of their hosts. Many infections may be asymptomatic whereas others may cause acute (transient) or chronic (persistent) clinical diseases ranging markedly in severity (mild to fatal). Parasitic infections may cause mortality (foetal, neonatal, adult death), morbidity (disease manifest by enteritis, fever, anaemia, etc.), production losses (reduced meat, milk, fibre production), and tissue lesions (reduced marketability of product). Despite many advances in parasite treatment and control, infections still persist due to many factors, including urbanization (crowding together); more intensive farming systems, greater translocation of animals, further land and marine development, inadequate effluent disposal, emergence of parasite drug resistance, and spread of vector insecticide resistance.

Parasite assemblages

Many types of organisms have adopted a parasitic mode of existence; that is, they require a host for their own survival. Three major groups of parasites are recognized: protozoa (belonging to the kingdom Protista), and helminths and arthropods (belonging to the kingdom Animalia, or Metazoa).

Protozoa: Over 10,000 species of single-celled protozoa have been described in the gut, blood or tissues of vertebrate and invertebrate hosts. Parasitic flagellates cause enteric diseases such as giardiasis, urogenital diseases such as trichomoniasis, systemic diseases such as sleeping sickness, and tissue diseases such as Chagas' disease and kala azar. Parasitic amoebae cause dysentery, meningoencephalitis and corneal lesions. Spore-forming sporozoa cause many serious diseases: Apicomplexa cause coccidiosis, malaria and tick fevers; Microspora parasitize fish and insects; and Ascetospora cause seasonal mortalities in oysters. Parasitic ciliates cause diarrhoea or lesions in humans and animals while commensal species cause serious fouling problems in aquaculture.

Helminths: Around 50,000 species of multicellular helminths (worms) have been described from a wide range of hosts. Roundworms (nematodes) cause much morbidity and mortality in humans and animals throughout the world. Serious infections include filiariases, hookworm and threadworm diseases. Larval and adult tapeworms (cestodes) may be found in many vertebrate hosts. Some species do not cause clinical disease whereas others may cause severe weight loss, diarrhoea, abdominal pain or space-occupying lesions. Flukes (trematodes) include many important species such as sheep liver fluke and human schistosomes or blood flukes.

Arthropods: Thousands of arthropods are parasitic at some stage in their life-cycles. Many cause serious diseases and limit agricultural productivity. Parasitic insects include biting and sucking lice which may cause skin lesions or anaemia, fleas which may cause allergic dermatitis, and various flies which suck blood as adults or produce larvae which feed on host tissues. Parasitic arachnids include ticks which feed on blood and may cause anaemia or paralysis and mites which feed on skin and may cause mild itching, hair loss or severe mange.

Overview of parasitology

Parasitism

Three general environments are available for life as we know it: terrestrial, aquatic and biotic. By definition, parasites are those animals which occupy the last niche, i.e. live in or on another species, their host. Parasitism is a form of symbiosis, an intimate relationship between two different species. There is a biochemical interaction between host and parasite; i.e. they recognise each other, ultimately at the molecular level, and host tissues are stimulated to react in some way. This explains why parasitism may lead to disease, but not always. It is often a life-long relationship for the parasite, which cannot survive without its host. While it is often claimed (even by definition) that a parasite must damage its host in some way (to distinguish parasitism from commensalism and mutualism), in practice this can be impossible to establish, because we know so little about most symbiotic relationships; certainly, many human parasitic infections are asymptomatic (which is not the same as non-pathogenic).

Origins

Parasitism must have arisen very early in the history of life on Earth, when primordial microorganisms learnt to survive inside other cells which they had invaded either passively (e.g. by phagocytosis) or actively (e.g. by penetration). When multicellular organisms with alimentary tracts appeared, they would have inevitably (accidentally or intentionally) eaten free-living microorganisms (and, later, free-living helminths). Ingested animals that managed to survive in this new environment would have appreciated the nutrient-rich environment; energy saved in looking for food could then be diverted to proliferating and resisting the host's efforts to dislodge them. With time, these parasites became so adapted to life in the host; they "forgot" how to survive outside. However, to succeed, they still needed to produce offspring that could negotiate the outside world to find new hosts.

Not surprisingly, all parasitic animals have free-living counterparts to which they are clearly related, and the greatest diversity of parasites is still found within the alimentary tracts of "higher" animals. As host species diverged with evolution, they "carried" with them their parasites. It is virtually the rule today that parasitic protozoa and helminths found in any vertebrate species have almost identical relatives in related vertebrates, and most of them are exquisitely host-specific. For example, the two common amoebae of the human colon, *Entamoeba histolytica* and *E. coli*, have almost identical relatives within a wide range of vertebrate hosts. There is even *E. moshkovskii*, a species that has been found only in sewers, which probably evolved from parasitic species! *E. gingivalis* occurs only in the human mouth, and has lost its cystic stage, presumably because trophozoites are so efficient at transferring between hosts. The same occurs with helminths, e.g. the roundworm of the human small intestine, *Ascaris lumbricoides*, has counterparts in pigs, dogs, cats, flying foxes, elephants, dolphins and many other mammals.

Once established in the host intestine, some parasites "learned" to invade the gut mucosa and deeper tissues, or to survive in the guts of predators that consumed their original hosts. Involvement of invertebrate "micropredators" in such life-cycles could then have led to parasite transmission via blood or tissue ingestion. Other parasites, in their infective stages, developed the ability to invade via the skin. It is not too difficult to conceptualise how complex life-cycles, utilizing a range of different hosts, might have arisen. Many examples of "missing links" in parasite evolution can still be found today; although far more are well-and-truly extinct. It is misleading to think of extant protozoan or helminth species as "primitive", for they have been evolving as long as all other species, including *Homo sapiens*, and utilise sophisticated survival mechanisms that we are only beginning to understand.

Parasitism clearly has advantages over independent existence, for parasites greatly outnumber free-living animals, both in terms of individuals and species; from an evolutionary viewpoint, it is the ultimate life-style. The obvious benefit to the parasite is that its host provides, *gratis*, a relatively stable, nourishing home. The energy saved in seeking food, shelter and transport is then concentrated on reproducing and evading host defence mechanisms, which are provoked in virtually every case, although not always obviously.

Fields of study

Medical Parasitology is the study of those organisms which parasitise humans. According to the definition above, parasites could include the viruses, bacteria, fungi, protozoa and metazoans (multicellular organisms) which infect their host species. However, for historical reasons (and because they are NOT classed as animals), the first three have been incorporated into the discipline of Microbiology. Parasitology claims those protozoa (unicellular animals), helminths (worms) and arthropods (insects and arachnids) whose existence depends on the availability of host animals, i.e. they are obligate parasites. Some rare parasites are called facultative, because they can survive and reproduce without a host, but very few that infect humans belong to this group (e.g. free-living amoebae). While we could argue about whether certain insects and mites are "temporary parasites" or "micro-predators", insects as a group belong to the discipline of Entomology, while ticks and mites are the concern of Acarology. Another crude way of distinguishing these is to label them ectoparasites (living on the host body surface), in contrast to the endoparasites (which live inside the host). The major contribution of insects in Parasitology is as vectors of several infections, although several are true parasites in their own right.

The disciplines also differ in ways other than taxonomic boundaries. In Microbiology, while morphology or staining properties (e.g. with Gram's stain) are important in the basic categorisation of the organisms, species identification generally depends on culturing and identifying specific enzymatic reactions, antigenic configurations or DNA sequences; i.e. the test-tube is important. In Parasitology, morphological recognition remains foremost, so that parasites (or their vectors) are still identified on characteristic shapes and sizes; i.e. the microscope rules supreme. Subspeciation or strain-typing is less well-developed, and may depend on molecular configurations or host-specificity. Culture has been a basic tool in Microbiology almost from its inception, and cell-culture is especially important in Virology (where viruses are not observed directly, but initially recognised by their effects on cultured cells). In Parasitology, culture was for a long time virtually impossible for most organisms, including protozoa. Nevertheless, in recent years, technical advances have allowed the *in vitro* cultivation of increasing numbers of parasite species, including even some helminths, although this is a procedure still in its infancy and used largely in research, rather than for routine clinical diagnosis. Advances in molecular biology are revolutionising all the biological sciences, including Parasitology. However, the organisms still must be identified initially on their morphology, and this is the basis of most parasite diagnoses made in clinical pathology laboratories.

Every known species (living and extinct) is assigned a unique combination of genus and species names which, by convention, are printed in italics or underlined. Infections with parasites are often indicated by the abbreviated genus name plus the suffix -osis. Some authorities use the suffix -iasis if the infection causes disease, but this distinction is often meaningless or impossible to establish. Purists argue that -osis belongs to species names derived from Greek, while those with Latin parentage deserve -iasis (it becomes tricky if you don't know the name's origins). Either can be used, depending on which sounds better (although a recent international convention aims to standardise all this), and we must be tolerant of the many exceptions, e.g. tuberculosis (mycobacteriosis), malaria (plasmodiosis), elephantiasis (lymphatic filariasis, or filariosis). If more than one parasite belongs in the genus, then the species name may be added to qualify the infection, *e.g.* schistosomiasis mansoni (not italicised).

Life-cycles

While parasites are adapted to living in or on their hosts, they can only survive by producing offspring capable of finding new hosts. The key to understanding their dispersal through the world is through knowledge of their life-cycles or modes of transmission, involving many aspects of parasite biology, reproduction and epidemiology.

Protozoa, in their motile, feeding, growing, asexually-multiplying forms are known as trophozoites (*trophe* = nutrition; *zooite* = minute animal). These are adapted for existence in the host and, generally, are unable to survive the rigours of life outside. Under appropriate conditions, which we do not yet understand, some trophozoites of gut protozoa coat themselves in a protective shell and shut down metabolically, to become cysts. These are designed to survive in the outside world long enough to reach new hosts. In the most highly-evolved protozoa (apicomplexans), which are obligate intracellular parasites, asexual division of the trophozoite (schizogony; *schizein* = to divide, or split; *-gony* = reproduction) leads to the generation of many merozoites (*meros* = piece, segment) which then invade other host cells. Eventually, instead of undergoing further schizogony, merozoites undergo sexual reproduction (gamogony) developing into either macrogametocytes (female) or microgametocytes (male). Fertilisation results in the formation of a zygote, termed an oocyst (= egg-cyst), which is designed to survive in the outside world so that it may infect another host. The ripe (sporulated) oocyst contains infective "seeds" known as sporozoites, which arise during its maturation (sporogony = generation of spores).

The metazoan parasites (multi-celled worms and arthropods) generally are dioecious, i.e. adults occur as separate males and females. Tapeworms and most flukes are the exceptions (hermaphrodites). After copulation, females produce fertile eggs, each containing an embryo. This undergoes embryonation developing into a juvenile or larva which will hatch out under suitable conditions. The egg may be the infective stage, or larvae may develop in the outside world to infectivity, or larvae may develop further in one or more intermediate hosts before they are able to reinfect their definitive hosts. Because their larvae must develop outside the host, adult helminths cannot multiply directly within a host (in stark contrast to protozoa which can proliferate to large numbers).

Many parasites complete their developmental cycle in a single host species (monoxenous life-cycles) while others require multiple host species (heteroxenous life-cycles). When multiple hosts are involved, the definitive host is that species in which the adult (or sexual) form of the parasite occurs, whereas the intermediate host is the species which supports the development and/or multiplication of the non-sexual, or larval (for helminths), stages of the parasite. Intermediate hosts which physically carry the infective stage from one host to another are also termed vectors; they are mechanical vectors if they simply transmit the parasite (unchanged and non-multiplied), and cyclical vectors if they also function as true intermediate hosts that support essential development and/or proliferation of the parasite. Intermediary hosts may be optional in some helminth life-cycles; the parasite might not undergo essential development in them, although it may increase in size. These paratenic hosts carry parasites through food chains to the definitive host, ensuring successful transmission even when the hosts are thinly dispersed through the environment. Some parasites exhibit low specificity for their definitive and/or intermediate hosts and so can develop in a range of animal species.

A zoonosis is a human infection caused by an organism which occurs naturally in other animals, known as reservoirs of infection. Most parasite life-cycles that are known have only been worked out quite recently; i.e. within the last 100 years. Information is therefore fragmentary, and many ambiguities exist. We could argue about whether the mosquito genus *Anopheles* or the primate species *Homo sapiens* is the definitive host for malaria parasites as gamogony in initiated in the human but culminates in fertilization in the mosquito.

Host specificity

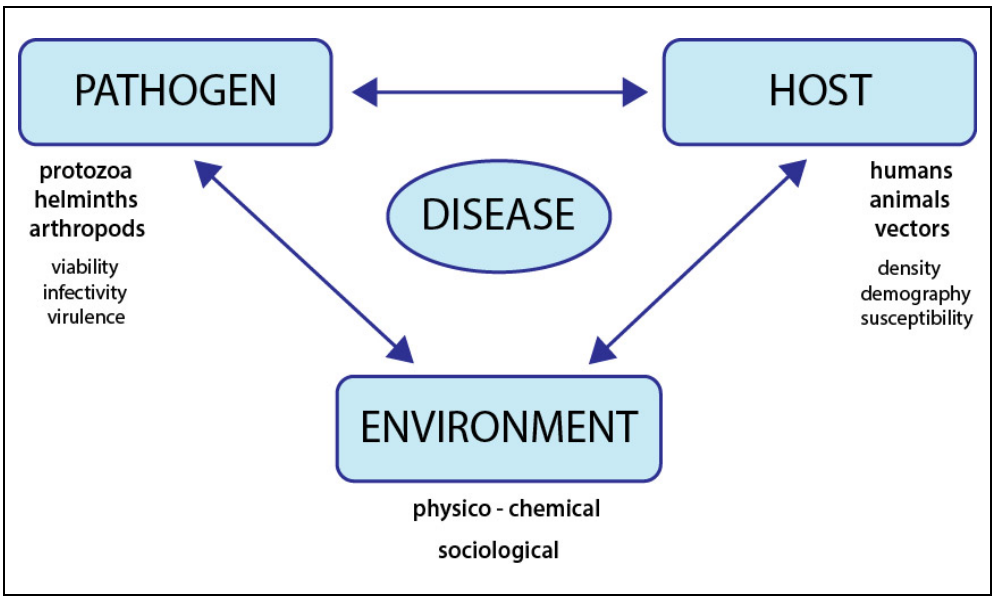
Parasites can be very particular about which host species they will use; this can apply to definitive as well as intermediate hosts. A parasite that is specific for a single host species is said to be oioxenous, one that parasitizes closely-related hosts is stenoxenous, while one that parasitizes unrelated hosts is euryxenous. Host-specificity is determined by a complex of factors, some obvious and others still obscure. The first requirement is that the prospective host shares its environment with the parasite (ecological specificity); e.g. parasites of dolphins might not have much luck infecting humans who don't live near the sea (although modern food transport networks have changed this!). Secondly, host behaviour must expose it to the parasite (ethological specificity); e.g. people who eat dolphin food (fish) may acquire parasites intended for dolphins. Finally, once the parasite comes into contact with the host, it must recognise appropriate cues and feel comfortable within its new surroundings (physiological specificity); e.g. if a parasite of dolphins thinks it is in a large fish or a dolphin when it arrives in the human gut, it may then behave accordingly. Obviously, this last determinant of host-specificity is the one we understand least.

Parasites interact with host secretions and surfaces and membranes: they must recognise and respond to molecular configurations (receptors/ligands). Detection of subtle variations in metabolites allows them to follow road-maps; they need to make critical changes in behaviour and development according to changes in host physiology/behaviour (neural/endocrine cues?); and they must be satisfied with their diet (host intestinal contents, blood and/or tissues). Clearly, all these combinations are unique for each host species, and vary even among individuals within a species, within an individual host throughout its own life-cycle and even throughout a 24-hour day. Likewise, each population of parasites is heterogeneous, so some individuals succumb very easily if in the wrong host ("losers") whereas others persist and may come close to full development ("pioneers"). This is the driving force of evolution, and parasites are the most rapidly evolving animals.

Epidemiology

This is the descriptive and analytical study of how diseases or infective organisms are distributed in human populations. A parasite is endemic to a geographical region if it is sustained by transmission amongst people living there. An infection maintained in animal populations is enzootic (which must apply to all zoonoses), although this term is going out of fashion. An infection acquired locally (usually in an endemic region) is autochthonous. Infected people who bring an organism into a non-endemic area are labelled imported cases; should the parasite then transfer to another person in that region, the secondary case becomes an introduced infection. If the parasite establishes in the new population, it becomes newly-endemic.

Many workers recognize an 'epidemiological triad' of inter-connected factors required for infectious disease outbreaks: viz; the pathogen must be present; susceptible hosts must be present; and environmental conditions must support the viability of both. The manifold interactions between these major determinants influences disease prevalence, distribution, severity (morbidity and mortality) and transmission. Disease control programmes should address all arms of the triad to ensure interventions are integrated, appropriate and effective. For example, treating whole communities with drugs may seem effective over the short-term, but it does not provide the hosts with any lasting protection and does not decontaminate the environment so hosts become re-infected.



The level of infection in a population is measured by prevalence and incidence. Prevalence refers to the prevailing level of a condition within a defined population, and is best applied to conditions without a clearly identifiable onset, such as most helminthic infections, chronic toxoplasmosis, Chagas' disease (or malignant, degenerative or metabolic diseases). It is measured by a single study of a population over a brief time-period (cross-sectional survey). Incidence refers to the number of new cases acquired per unit of population per unit of time, and is more meaningful for acute, short events (incidents), with an identifiable beginning (or end!) e.g. many viral infections, acute malaria (or deaths, or accidents). It can be measured only by monitoring a population over a sufficient period or time (longitudinal study) and determining the rate increase or decrease. Obviously, the incidence, prevalence and duration of a particular condition are closely and simply inter-related. An epidemic occurs when the incidence of new cases significantly exceeds the usual rate; if the disease is protracted, this will be reflected by an increase in prevalence as well.

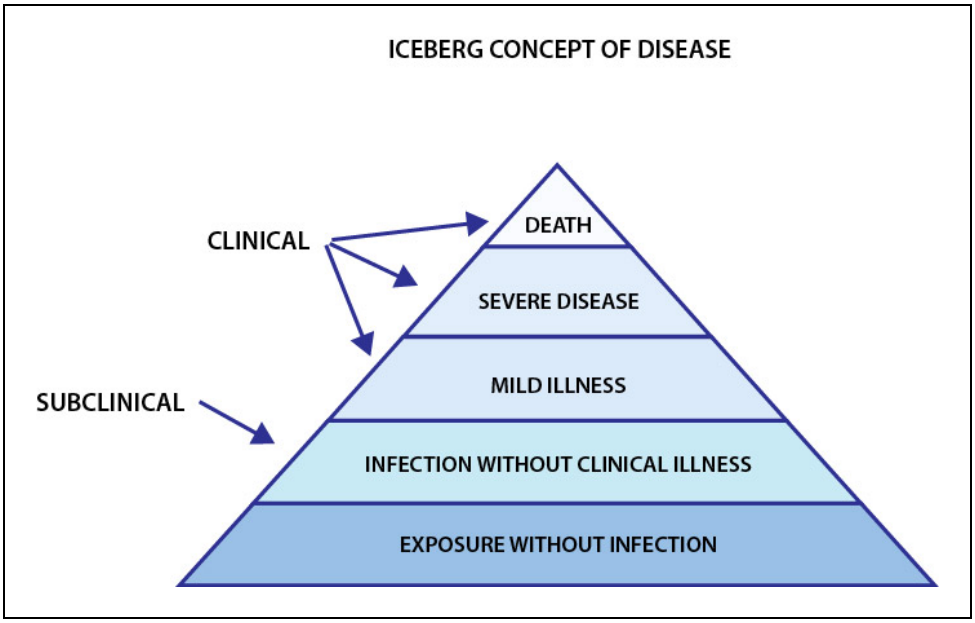
Quantitation of infection

Infective organisms have been categorized as either microparasites, which multiply directly within the host (all the microbes, plus protozoa) or macroparasites, which generally cannot multiply in the host; their numbers depend on how many infective eggs or larvae are taken on board. Ectoparasites do not happily fit into this classification, for they are clearly "macro", but often can multiply to huge populations on the one host. However, their development may be considered "external", as they usually reside outside the host on the surface. The term "infestation", sometimes used for macroparasitic infections, is going out of fashion, but can be applied to contaminated inanimate objects, e.g. a house infested with fleas, or bushland infested with ticks.

Infection with microparasites is an all-or-none situation; you either have measles, influenza, bubonic plague, toxoplasmosis, giardiasis, etc., or you don't. It is not often possible, or necessary, to quantify reliably the intensity of such an infection (number of organisms on board a host). In many instances, the severity of disease is not reliably related to the numbers of parasites detectable in blood, tissues or secretions (a notable exception is malaria, in which the percentage of infected red cells can be estimated and sometimes is important clinically). In the case of helminths and arthropods, which are generally visible macroscopically as discrete individuals, the number of organisms is meaningful, because it can be measured and does influence the likelihood or severity of disease. Therefore, in epidemiological studies of macroparasitic infections, their intensity becomes important, in addition to incidence and prevalence. Virtually all population studies have shown that the intensity of infection does not follow a normal distribution, but exhibits an "aggregated" or "over-dispersed" pattern: a small number of hosts harbour most of the parasites, whereas most individuals carry few or no parasites (characterised mathematically as a "negative binomial distribution").

Clinical and pathological considerations

While, by definition, a parasite should evoke a host reaction, there need not be any obvious adverse effects because, in the great majority of cases, infected individuals exhibit little evidence of disease. In many cases, it can be difficult or impossible to determine whether an organism is a parasite or commensal (e.g. many intestinal protozoa, and worms). However, other parasite infections do cause serious disease, to such an extent that they become major public health problems. It is generally assumed that the longer a parasite and its host species have co-evolved, i.e. have had time to adapt to each other, the less pathogenic the infection becomes. On the other hand, infections with parasites that are poorly adapted to humans, i.e. zoonoses, are more likely to cause serious disease. Some believe parasite virulence and host resistance tend towards enzootic stability over time as it is not in the best interest of either partner to kill the other, despite considerable evidence for the escalating 'arms race' observed between parasite aggressiveness and host immunity. More recently, others have noted a negative correlation between parasite virulence and transmission suggesting a 'trade-off hypothesis' between these factors (increased virulence results in decreased transmission). However, there are many exceptions to these "rules". Remember, clinicians generally only see those individuals who develop disease; there may be many more who remain well, even though infected. Clinicians often liken this scenario to observing an "iceberg" – they generally only see the tip-of-the-iceberg (hosts with disease) while the bulk remains hidden (hosts with subclinical infections, asymptomatic carriers).

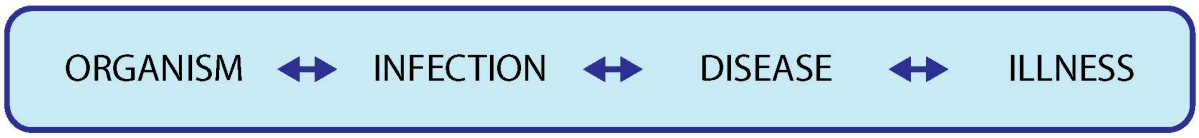


The development of disease depends on both host factors **(**susceptibility/resistance**)** and parasite factors (pathogenicity/virulence). Hosts have been shown to be more susceptible to disease by virtue of their age (neonates and geriatrics), gender (females, mainly during pregnancy and lactation), nutritional state (malnourished), physiological state ('stressed' hosts) and immunological competency (greater in immuno-suppressed or immuno-compromised hosts). From the parasite perspective, the major important determinant for the development of disease is parasite pathogenicity (or virulence), i.e. capacity to induce disease, including the inter-related factors of invasiveness (motility, enzyme secretion, presence of specific tissue receptors, induction of phagocytosis), fecundity (rate of producing offspring), means of egress from host, stimulation and/or suppression of immunity and inflammation, production of exo- and endo-toxins and resistance to host defences. Such virulence-determinants often correlate directly with the parasite's capacity to survive and reproduce, and they also may adversely affect host survival and fecundity. There often appears to be a negative correlation between parasite virulence and parasite transmission, where increasing virulence comes at the cost of decreasing parasite survival and thus transmission (Trade-off Hypothesis). Parasitism applies a pressure on host populations that selects out more resistant individuals; it has even been argued that parasites serve to improve the fitness of their host species (Red Queen Hypothesis), and were a major influence in the evolution of sex! However, genetic changes that increase resistance to infection often handicap the host in other ways, generating a dynamic equilibrium between protection against infection and susceptibility to other diseases (balanced polymorphism). There is no doubt that infectious organisms exert a powerful and continuous evolutionary pressure on host populations (and vice versa).

Parasitic diseases

In the field of infectious diseases, it is conceptually important not to confuse aetiological agents with their effects on the host. An infection occurs when an organism, i.e. the parasite, is found in its host. Some experts don't like to label this an infection, unless there is evidence of a response in host tissues; this applies particularly to commensal organisms, which normally occur on human skin or in the gastrointestinal tract, but which cause disease only when they breach the surface barriers. Infection is a host-organism interaction; it cannot exist without a host. Presence of infective organisms in the environment, e.g. in food, on fomites or in water, is not infection, but contamination (or "infestation"). For instance, we should not talk about "infected water supplies".

Moreover, an infection is not the same as a disease, which is a pathological change in the host, i.e. abnormalities induced in tissues by direct mechano-chemical damage and/or release of toxins and/or inflammatory mediators. Illness occurs when the host suffers the effects of the disease and becomes a patient, i.e. complains of symptoms (subjective, felt by the patient) which interfere with normal life, and perhaps manifests clinical signs (objective, detectable by the doctor), always with psychosocial undertones and ramifications. This is summarised as follows:



Where you start in the above sequence depends on whether you are the parasite or the patient! The illness is what the patient complains about to the doctor (often with judicious prompting), the disease is what the clinician may detect on physical examination (and the pathologist confirms in laboratory tests or at autopsy), and the causative organism (or its products, or antibodies to it) is what the diagnostic laboratory usually seeks and identifies. In any particular patient, all of these apparent components might be totally unrelated, so that linking them together becomes a major and still unresolved difficulty, even in some very common infections. Such distinctions may seem pedantic, but their appreciation helps in understanding stages in the evolution of an infectious disease, and is important to minimise confusion. Many people are infected; in fact, every one of us has at some time harboured at least one parasite species, and most of the world's people carry many parasites most of the time. However, relatively few are diseased, and not all of them suffer illness. Infections without illness are called subclinical or asymptomatic. Note that this does not mean being free of disease.

The interval between exposure to infection and the onset of illness is known as the incubation, latent or pre-patent period or phase. Some authorities define this period as the time from exposure to the time of becoming infective to others, but not all agree with this. Others define the latent period as the time from exposure to the first occurrence of recognisable specific manifestations, be they symptoms, signs, positive serology or other laboratory findings; if for symptoms, then it is called the incubation period. With many parasitic infections in endemic areas, these definitions may be of little use clinically, because people are repeatedly being exposed to infection.

An infection is patent when direct evidence of the organism can be detected, e.g. in the patient's faeces, blood or secretions, regardless of whether symptoms have appeared. Some infections may be patent but subclinical; others may cause illness, yet not be patent. However, the individual who has patent infection is essential to transmission of the organism, because it can then be transferred directly to other hosts, to vectors, or into the environment, where it may need to develop through stages to infectivity. Obviously, the detection of patency depends on the sensitivity of the test being used to identify the organism.

Often, indirect evidence of infection is the best that can be offered by the diagnostic laboratory, in the form of circulating antibodies generated against antigens of the infecting organism. Apart from the issues of specificity and sensitivity, another difficulty common to all antibody tests is distinguishing between ongoing, active infection and recently resolved or past infection. In other cases, serology may be even less adequate, for the simple reason that a test has not been developed, and the infection is known as cryptic. In some infections, specific monoclonal antibodies can be used to identify parasite antigens, and the polymerase chain reaction is becoming increasingly available to identify nucleotide sequences from infective organisms, although the limitations of these technological advances have not been well-established.

Usually, disease results predominantly from the host's efforts to deal with the parasite, involving immunological and other less well understood responses to an organism which refuses to go away, and which utilises effective strategies to avoid being damaged. The principles (and even details) of host responses to infecting organisms apply equally to microbial and parasitic infections and, as we learn more about the precise mechanisms, the more difficult it becomes, in the clinical context, to justify the separation of these groups of pathogens. Obviously, viruses may succumb more readily than worm larvae to protective mechanisms involving antibodies, complement, lymphocytes, phagocytes and other effector cells and molecules, but all infections initially trigger similar basic repertoires of responses. A major discriminating influence is whether the organisms are intra- or extra-cellular,

which partly determines the class of MHC molecules with which they interact. The minute parasitic protozoa that multiply in host cells have much in common with viruses, so that host responses to these infections and the resulting diseases can be so similar that, clinically, they may be indistinguishable.

Furthermore, patients have only a limited range of symptoms to complain about, so that generally it is impossible to diagnose the causative organism from the clinical features. However, a careful history, taken to evaluate the likelihood of exposure to specific parasites, often narrows the range of options (differential diagnosis), and indicates the specimens which should be sent to the laboratory for definitive diagnosis. This can be much cheaper (and much more satisfying for the clinician - and the patient) than running a battery of tests blindly, and is essential for effective treatment and suitable preventive measures.

Parasitological parameters

Parasitic infections can be studied from many angles: we can focus on the parasites, their hosts, the environments they share and the ways in which they interact. People working in this field come from numerous backgrounds, including zoology, physiology, biochemistry, immunology, molecular biology, pharmacology, ecology, economics, anthropology, sociology, engineering, agriculture, education, mathematics and, of course, human and veterinary medicine. Specific disciplines focus on specific aspects, thus parasitological knowledge may be fragmentary. In order to obtain (retain) a holistic overview, many parasitologists use a parametric approach to organize information. The following headings have proven useful:

- AETIOLOGY (study of causative agent: in this case, the parasitic organism): colloquial and scientific (binomial) species name, broad group e.g. amoeba, nematode; stages occurring in humans (larva, cyst, trophozoite etc.); approximate size/shape.

- LIFE-CYCLE (summary of biology): Hosts – definitive, intermediate, paratenic; anatomical locations and sites of multiplication; development and survival in intermediate host/environment.

- EPIDEMIOLOGY (dispersal in populations): Distribution, worldwide and in endemic areas; prevalence, by age, sex, occupation (demographics); transmission into and out of hosts; ecological determinants, i.e. geography, climate, vectors, human behaviour and resources (housing, hygiene, sanitation, nutrition, occupation, animal reservoirs, medical facilities, preventive and control measures).

- PATHOGENESIS (dispersal within host; mechanisms of disease): sites affected; mechanical and/or chemical damage; local and systemic host responses (acute and chronic); effectiveness of immunity; effects on transmission; host resistance/susceptibility.

- CLINICAL MANIFESTATIONS (how patient affected): logical extension of knowledge on pathogenesis; know mainly which organ system(s) involved and how manifests; symptoms and signs.

- DIAGNOSIS (how detected): specimens required; how and when collected, preserved, transported; how examined in laboratory; reliability of results (sensitivity, specificity, predictive values); safety aspects (i.e. infectivity of clinical specimens, their handling and disposal).

- TREATMENT (therapy): Is it necessary? effective? safe? Types of drugs, dosages, spectrum of activity, modes of action; contra-indications, side-effects; compliance; susceptibility/resistance

- PREVENTION/CONTROL (prophylaxis/intervention/management): public health concerns (individual, family, community: who is at risk?); chemoprophylaxis (necessary under what conditions?); interruption of transmission; behaviour modification; patient/community education; prospective/retrospective screening programmes, vaccination (availability, strategies); environment/food/water contamination, purification/disinfection.

Students and practitioners should always remember that parasitology demands good comprehensive knowledge of at least two biological entities, the parasites and their hosts. Only by studying both in concert can we begin to understand the complex interactions between them, particularly those resulting in disease.

MATHEMATICAL MODELS OF POPULATION BIOLOGY

Living organisms occur in discrete populations, often delimited by specific ecological and/or ethological boundaries. When scientists study organismal biology, at some point they need to consider population structure. Population biology is a quantitative science, whereby the dynamics and kinetics of population distribution, abundance and growth are measured (as prevalence, incidence, density, concentration, intensity, etc.). Many mathematical models have been developed to describe population structures based on past and current trends, and then used to predict future trends.

Co-existence

Scientists recognize many different levels of biological organization, from the miniscule to the majestic. Living things range from single-celled organisms (simple, but by no means primitive) to multicellular organisms (with cellular specialization to form complex tissues and organs). We also recognize several levels of collective co-existence, where organisms live together in:

- populations (all the individuals of a species within a given area);
- communities (all species of living organisms within a given area);
- ecosystems (all living things within a given area, together with all the non-living components in that area with which life interacts); and the
- biosphere (all the environments on Earth inhabited by life).

Ecology is the study of interactions between organisms and their environments; a holistic science involving many disciplines. Ecologists seek to understand organismal biodiversity, distribution and abundance (species richness, temporal and spatial variation) with respect to biotic and abiotic (environmental) influences.

Ecosystem ecology emphasizes energy flow and chemical cycling among the various biotic and abiotic components.

Community ecology deals with the interactions between the whole array of species in a community, including competition, predation, herbivory, symbiosis, and disease.

Population ecology concentrates mainly on factors that affect how many individuals of a particular species live in an area.

The study of parasite ecology is complicated by the fact that it involves two populations:

- that of the parasite; and
- that of the host.

It is not enough to know how the temporal and spatial distribution and abundance of the parasite changes without considering host population dynamics, kinetics and demography. For example, how many hosts are infected, how severe/intense are the infections, are infected hosts delimited by age, gender, behaviour, etc.?

It is important that interactions between the two populations be carefully examined; basically in order to answer the following question: Do the partner organisms gain benefit or detriment from the interaction? The answer effectively defines the inter-species biological relationship between the two organisms.

In this instance, parasitism is defined as a type of relationship beneficial to the parasite but detrimental to the host (see following Table for different types of relationships).

Type of relationship	Organism 1 (usually larger)	Organism 2 (usually smaller)	Examples
SYMBIOSIS ("living together") (direct contact between organisms) (usually long term)			
mutualism	host benefits	symbiont benefits	ruminants/ciliates
cleaning symbiosis	host benefits	cleaner benefits	fish/cleaner wrasse
commensalism	host unaffected	commensal benefits	reptiles/trichomonads
phoresis	host unaffected	phoront benefits	mollusc/anemone
inquilinism	host unaffected	inquiline benefits	worm tubes/bacteria
neutralism	host unaffected	symbiont unaffected	difficult to prove
parasitism	host harmed	parasite benefits	humans/nematodes
parasitoidism	host harmed	parasitoid benefits	caterpillar/wasp larva
amensalism	unaffected	harmed	mould/bacteria
OTHER ECOLOGICAL INTERACTIONS (direct/indirect contact) (often short term)			
PREDATION (involving feeding, consumption)			
herbivory	herbivore benefits	plant harmed	ruminants/grass
carnivorism	predator benefits	prey harmed	felids/rodents
INTERSPECIFIC COMPETITION (interference/exploitative/apparent/scramble competition) (competitive exclusion, niche differentiation, local extinction, change in community structures)			
competition	harmed	harmed	lions/cheetahs
synnecrosis	killed	killed	extinctions
DECEPTION (crypsis (hard to see), mimesis (masquerade), motion dazzle)			
mimicry	unaffected	mimic benefits	wasp/moth
camouflage	unaffected	benefits	leaf/katydid

It is essential that the type of relationship be determined in order to select the most appropriate methodology to quantitate and model population growth over time, for example:

- predator-prey populations are best examined by Lotka-Volterra models;
- unconstrained microbial growth by exponential models;
- constrained growth by logistic models;
- microparasites by SIR models; and
- macroparasites by HPW models.

Population ecology

Population ecology is the study of populations in relation to the environment, including abiotic/biotic influences on population density, distribution, age structure, and size. Demography is the study of the vital statistics of populations and how they change over time. Populations wax and wane in size as individuals join (births and immigration) and leave (deaths and emigration). The population growth rate ordinarily refers to the change in population over a specific time period expressed as a percentage of the number of individuals in the population at the beginning of that period; given by the formula:

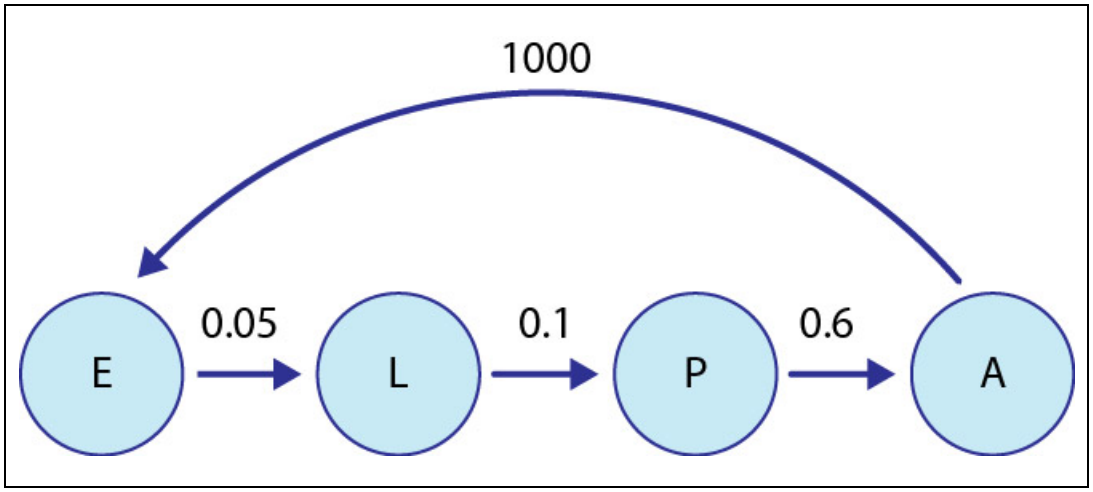
Growth rate = [(births + immigration) - (deaths + emigration)] / population

The survival pattern of a population can be summarized in a life table, best constructed by following the fate of a specific cohort (a group of individuals of the same age) from birth until death. For example, the following hypothetical life table may apply to flea populations, showing the survival of the different developmental stages over time.

Time period	Developmental stage	Number alive
1	Eggs (E)	10,000
2	Larvae (L)	500
3	Pupae (P)	50
4	Adults (A)*#	30

*The male:female ratio of adult fleas is 1:1
#Adult female fleas lay a total of 2,000 eggs

Stage-structured diagrams can be used to depict the life-cycles of organisms, with arrows connecting different stages showing the proportion of the population transitioning between those stages within any single time interval. For example, the stage-structured life-cycle model based on data from the hypothetical flea life table would be:



Simultaneous equations (SEs) can be developed to model population structures, allowing the calculation of the numbers of individuals within particular stages over time. The relevant SEs for the hypothetical flea model from time t to time $t+1$ would be:

$E_{t+1} = 0\,E_t + 0\,L_t + 0\,P_t + 1{,}000\,A_t$ [which simplifies to = $1{,}000\,A_t$]
$L_{t+1} = 0.05\,E_t + 0\,L_t + 0\,P_t + 0\,A_t$ [which simplifies to = $0.05\,E_t$]
$P_{t+1} = 0\,E_t + 0.1\,L_t + 0\,P_t + 0\,A_t$ [which simplifies to = $0.1\,L_t$]
$A_{t+1} = 0\,E_t + 0\,L_t + 0.6\,P_t + 0\,A_t$ [which simplifies to = $0.6\,P_t$]

The constants derived for the SEs can be incorporated into a transition matrix (delete letters but retain numbers) so that matrix operations can be used to streamline mathematical calculations. The 4x4 transition matrix for the hypothetical flea model would be:

$$\begin{pmatrix} 0 & 0 & 0 & 1{,}000 \\ 0.05 & 0 & 0 & 0 \\ 0 & 0.1 & 0 & 0 \\ 0 & 0 & 0.6 & 0 \end{pmatrix}$$

The transition matrix can be used to determine the numbers of individuals within each life cycle stage over time. For example, if you currently have 1000 eggs, 100 larvae, 50 pupae and 10 adult fleas, you can use the transition matrix to determine how many of each stage you will have after each time period has passed (begin with t = 0), calculated as follows:

$$\begin{pmatrix} 0 & 0 & 0 & 1{,}000 \\ 0.05 & 0 & 0 & 0 \\ 0 & 0.1 & 0 & 0 \\ 0 & 0 & 0.6 & 0 \end{pmatrix}$$

t=0	t=1	t=2	t=3
1000	10000	30000	6000
100	50	500	1500
50	10	5	50
10	30	6	3

t=1	t=2	t=3	t=4
10000	30000	6000	3000
50	500	1500	300
10	5	50	150
30	6	3	30

Thus, after four time periods, there will be 3000 eggs, 300 larvae, 150 pupae and 30 adult fleas.

Numerous mathematical processes can be applied to quantitate the numbers of individuals within a population, but they require sound knowledge of population developmental biology as well as reasonable counts or estimates of current population numbers. More frequently, models developed for populations of single species of organisms are based on their growth rates (calculated from births, deaths, immigrations, and emigrations). Two common models describe exponential growth (where population size is unconstrained as resources are unlimited) and logistic growth (where population size is constrained to a carrying capacity due to resource limitations).

Exponential model of population growth

The exponential model describes population growth in an idealized, unlimited environment. While this may not frequently occur naturally, it can be used to examine the capacity for a species to increase in population size and the conditions for that to occur. Population growth rate is based on influx (births and immigration) and efflux (deaths and emigration). The population increases in size when birth rates exceed death rates, and when immigrations exceed emigrations. If we ignore migrations for simplicity's sake (as in closed populations), we can express the change in population size mathematically as:

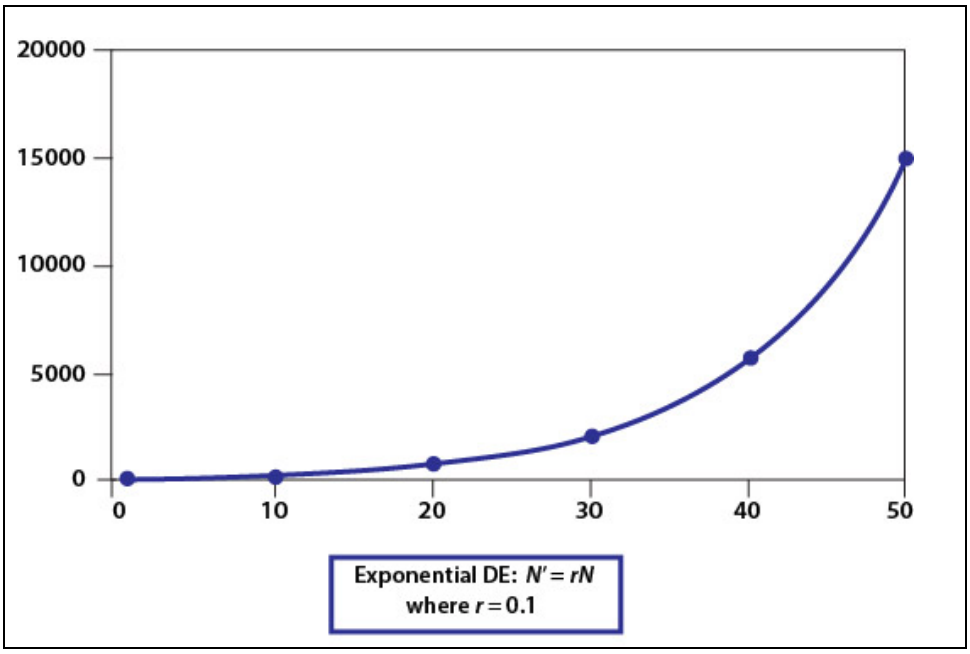
$\Delta N/\Delta t = B - D$ where ΔN = change in population size;
Δt = time interval;
B = births; and
D = deaths.

Births and deaths can also be expressed as "per capita rates", by calculating the average number occurring per individual during the specified time period. For example, if there are 34 births per year in a population of 1,000 individuals, the annual per capita birth rate, b = 34/1000 (= 0.034). This rate can be used to calculate the expected number of births per year in a population of any size by using the formula $B = bN$. Similarly, if there are 24 deaths in the population over the same period, the annual per capita death (mortality) rate, m = 24/1000 (= 0.024), and $D = mN$. The equation for population change over time can be simplified as:

$\Delta N/\Delta t = bN - mN = (b - m)N$

The birth and death rates can be amalgamated into the "per capita rate of increase (r)" [= (b - m)]. Obviously, the population is growing when $r > 0$, declining when $r < 0$, and stable when $r = 0$. The equation for change in population size is therefore simplified to:

$\Delta N/\Delta t = rN$ [expressed as $dN/dt = rN$ or $N' = rN$ using differential calculus]



This differential equation (DE) states that the rate of change of the population (N') depends on the growth rate (r) and the current population size (N). The solution to this differential equation is the exponential function:

$N = Ae^{rt}$ [proven by differentiating the function to give $N' = r.Ae^{rt} = rN$]

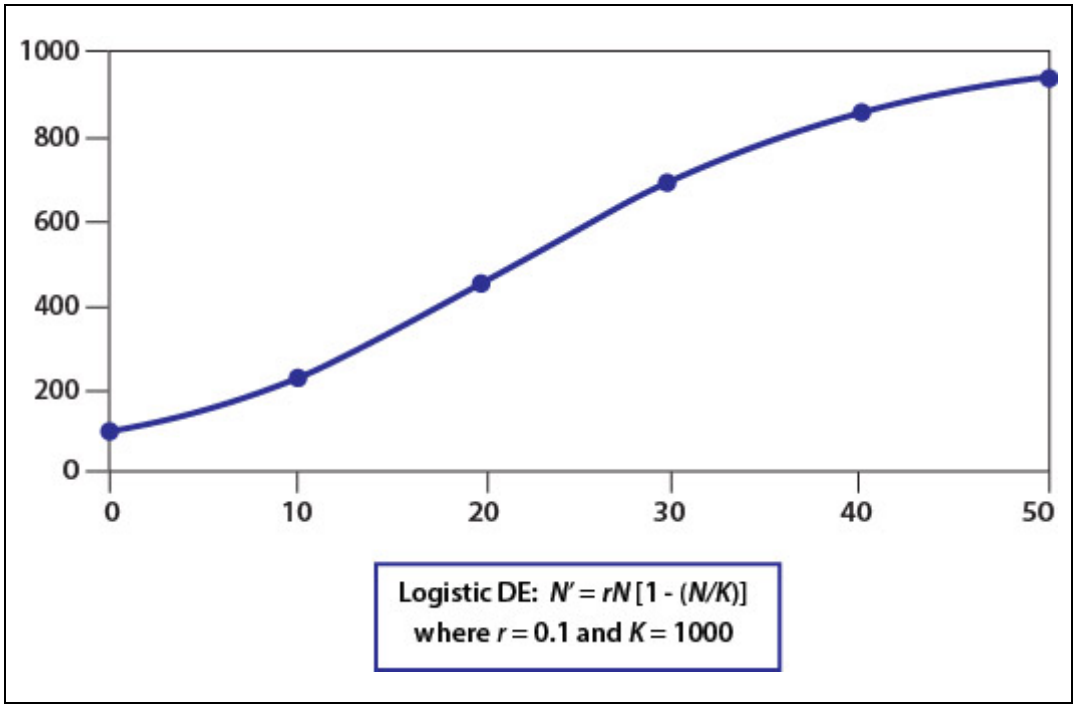
Under ideal conditions, population growth can become exponential. Births exceed deaths, so the population grows and accumulates more new individuals per unit of time when it is large. When population size is plotted over time, exponential growth is seen as a characteristic J-curve (increase becoming steeper with time). J-shaped curves are characteristic of populations that are introduced into new or unfilled environments (especially in the microscopic world of microbes).

Logistic model of population growth

In most natural systems, resources are limited therefore population growth is constrained. The logistic model of population growth incorporates the concept of 'carrying capacity' to account for limited resources. As population density increases, each individual has access to a smaller share of the total resources available. Ultimately, there is an upper limit to population size; the 'carrying capacity' defined as the maximum stable population size that a particular environment can support. Carrying capacity is not fixed but varies over time and space. Energy limitation often determines carrying capacity, although other factors, such as shelters, refuges, nutrients, water, breeding sites etc, can be limiting. If individuals cannot obtain sufficient resources to reproduce, the per capita birth rate (b) will decline. If they cannot find and consume enough energy to maintain themselves, the per capita death rate (m) may increase. A decrease in b or an increase in m results in a lower per capita rate of increase (r). In the logistic population growth model, growth declines as carrying capacity is reached.

Mathematically, the logistic model begins with the equation for exponential growth, adding an expression that reduces the rate of increase as N increases. If the carrying capacity is K, then $(K - N)$ is the number of additional individuals the environment can accommodate, and $(K - N)/K$ is the fraction of K that is still available for population growth. Multiplying r by this fraction gives the growth rate of the population as:

$dN/dt = rN\,[(K - N)/K]$ [alternatively expressed as $N' = rN\,[1 - (N/K)]$



When N is small compared to K, the term $[(K - N)/K]$ is large and the rate of increase is steep. But when N is large and approaches K as resources become limited, the term $[(K - N)/K]$ is small and so is the rate of population growth. When N is plotted over time, the logistic model of population growth produces an S-shaped (sigmoid) curve. Population growth rate slows dramatically as N approaches K.

The solution to the logistic differential equation is the function:

$$N(t) = K.N_o / [N_o + (K - N_o)\, e^{-rt}]$$

In practice, knowledge of this function is not required to calculate new population sizes as the DE can be solved approximately using Euler's method where the new population size (N_{new}) can be calculated by knowing the old population size (N_{old}) and the rate of change (N') of the population over known time steps (h):

$$N_{new} = N_{old} + N'.h$$

***r/K* selection theory**

The fitness of a species can be fundamentally enhanced by two different strategies: fast reproduction (multiplication, replication) or prolonged development (long-life, stability). These strategies are not independent, but form a continuum from one extreme to another for different species. How much one species invests in one strategy over the other depends on the selective environment, and in biology is called *r/K* selection. The mathematical principles are derived from the logistic growth model of population biology which indicates the traits that favour either quantity or quality of offspring in a species. That is, *r*-selected species invest in reproduction (quantity) while *K*-selected species invest in prolonged development and long-life (quality).

$$dN/dt = rN\,[(K - N)/K]$$

where r = growth rate (reproduction) (quantity)
K = carrying capacity (development) (quality)
N = population size, and
t = time

***r*-selected species**	***K*-selected species**
population grows exponentially (abundant resources) but never reaches carrying capacity (predators, droughts, etc)	population approaching carrying capacity, slow growth due to competition for limited resources
colonizers (opportunists)	competitors
unstable environments	stable environments
exploit less-crowded ecological niches	strong competitors in crowded niches
small organisms	large organisms
short-lived	long-lived
weak competitors	strong competitors
numerous offspring	few offspring
offspring with low probability of survival	offspring with high probability of survival
little parental care	significant parental care
fast maturation	slow maturation
rapid dispersal	slow dispersal
broad range	territorial
Examples: bacteria, protists, insects, weeds, rodents	Examples: terns, whales, elephants, trees, humans

Epidemiology

Epidemiology literally translates from Greek terms to mean "the study of what is upon the people", suggesting that it applies only to human populations. However, the term is widely used in zoology (sometimes supplanted by the term epizootiology), botany and microbiology. Epidemiology is the study of factors affecting the health and illness of populations. It provides a quantitative foundation for evidence-based medicine for identifying risk factors for disease and determining optimal treatment approaches. Studies may be conducted on communicable (infectious) diseases (caused by viruses, bacteria, fungi, protozoa, helminths, and arthropods) and non-communicable diseases (usually classified as inflammatory, cardiovascular, neoplastic, genetic, developmental, endocrine, nutritional, autoimmune, traumatic, senescence, iatrogenic, or idiopathic in origin). Diseases may be evident in a population as sporadic (occasional), endemic (established/persistent), epidemic (outbreak) or pandemic (global in distribution) diseases.

To study the occurrence, spread and control of diseases, epidemiologists employ a range of study designs generally categorized as descriptive (observational), analytic (testing for significant relationships) and experimental (testing treatments and other interventions). Generally speaking, epidemiologists study relationships between cause (exposure) and effect (morbidity and mortality). Morbidity is defined as the incidence of illness, and mortality as the incidence of death. Public health agencies often combine these measurements into a single equation:

$$DALY = YLD + YLL$$

where DALY = Disability Adjusted Life Years (combined burden);
YLD = Years Life lost due to Disability (morbidity burden); and
YLL = Years Life Lost due to premature death (mortality burden).

Assessments of the impact of disease are based on measurements of its distribution and abundance within a population (incorporating spatial and temporal variation), including:

- prevalence (cross-sectional study of population at selected point or period)
  [if 70 people were infected from a population of 100 examined in July, prevalence = 70%]

- incidence (longitudinal study of population over specified time)
  [if prevalence is 70% in July and 80% in October, incidence = + 10% (increased by 10% over 3 months)]
  [Note, can have negative incidence, when prevalence decreases over time]

- intensity/severity (different categories, often qualitative, sometimes quantitative)
  [disease severity based on range of symptoms/signs, often supported by clinical parameters]
  [infection intensity = number of organisms per infected host]
  [Note, mean infection intensity is different from mean parasite abundance (the latter may include uninfected hosts)]

These parameters may exhibit longitudinal fluctuations (variation over days, weeks, months or years) due to a wide variety of factors (demographic, socioeconomic, behavioural, geographic, and climatic). For example, climatic changes associated with global warming are predicted to cause many diseases to increase in incidence, distribution and severity (due to host translocations, greater susceptibility/diminished resistance, expanded ranges and enhanced survival of pathogens and vectors, ineffective/inappropriate treatment/control). Establishing cause and effect can be problematic, so several guidelines (non-prescriptive criteria) have been proposed for assessing evidence of causation (the Bradford-Hill criteria), involving:

- Strength (a small association does not mean that there is not a causal effect);
- Consistency (replication by different persons in different places with different samples);
- Specificity (the more specific the association, the greater the probability);
- Temporality (the effect must occur after the cause, and include any expected delays);
- Biological gradient (higher exposure should generally lead to higher incidence);
- Plausibility (there should be a plausible mechanism to explain the relationship); and
- Coherence (correlation between field and laboratory findings).

There are four main types of epidemiological studies: case series, case controls, cohorts and outbreaks.

1. Case series describe the experience of a single patient, or a group of patients with a similar diagnosis. They are purely descriptive and often rely on an astute clinician identifying an unusual feature of a patient's disease and formulating a hypothesis. Analytical studies are then done to investigate possible causal factors.

2. Case control studies involve matching cases with disease to comparable controls without disease (from the same local population), and then looking back through time at potential exposures both populations may have encountered. A 2 x 2 matrix is constructed, displaying exposed cases (A), exposed controls (B), unexposed cases (C) and unexposed controls (D).

	CASES	CONTROLS
EXPOSED	A	B
UNEXPOSED	C	D

The parameter used to measure association is the odds ratio (OR), which is the ratio of the odds of exposure in the cases (A/C) to the odds of exposure in the controls (B/D), that is,

$$OR = (AD) / (BC)$$

If OR >> 1, then the conclusion is "those with the disease are more likely to have been exposed".
If OR ~ 1, then exposure and disease were probably not associated.
If OR << 1, this suggests that exposure may have been protective in the causation of disease.

Case control studies are usually faster and more cost effective than cohort studies, but are sensitive to bias (such as recall and selection bias).

3. Cohort studies select subjects based on their exposure status, and then follows them forward through time to assess their outcome status. The results are tabulated in a 2x2 matrix:

	CASES	CONTROLS
EXPOSED	A	B
UNEXPOSED	C	D

The parameter generated to measure association is the relative risk (RR) which is the ratio of the incidence of disease in the exposed group (A/(A+B)) to that in the unexposed group (C/(C+D)), that is,

$$RR = (A/(A+B)) / (C/(C+D))$$

If RR >> 1, then the conclusion is "those with the exposure were more likely to develop disease".
If RR ~ 1, then there was no association.
If RR << 1, then exposure may have even been protective.

Prospective cohort studies have many benefits over retrospective case control studies. The RR is a more powerful effect measure than the OR, as the OR is just an estimation of the RR, since true incidence cannot be calculated in a case control study where subjects are selected based on disease status. Temporality can be established in a prospective study, and confounders are more easily controlled for. However, cohort studies are more costly, and there is a greater chance of losing subjects to follow-up based on the long time period over which the cohort is followed.

4. Outbreak investigations. A disease outbreak is a classification used in epidemiology to describe the sudden appearance, or sudden increase in incidence, of a disease in a specified group or population. Local outbreaks may be confined to a small area or village, while epidemics are outbreaks affecting regions or countries, and pandemics are global disease outbreaks. Outbreaks may originate from single point sources or from multiple common sources. Exposure to infections may be irregular, periodic or continuous and may involve contact with environmental sources (water, food or air-borne), zoonotic (animal-to-human) and anthropogenic (human-to-human) sources. Several modes of transmission are commonly recognized for infectious diseases: venereal, faecal-oral, aerosol, predator-prey, and vector-borne transmission.

When investigating outbreaks, epidemiologists have developed a number of widely accepted steps; these include:

- verify the diagnosis,
- confirm the existence of the outbreak above background levels,
- define inclusion criteria (what constitutes a case),
- conduct descriptive assessment (time, place, people),
- develop a hypothesis (causes?),
- test hypothesis (collect and analyse data),
- refine hypothesis as appropriate and carry out further study,
- develop and implement control and prevention systems, and
- release findings to greater community.

Mathematical epidemiological models

Biological systems are inherently complex, with many interactions occurring between their component parts, some conspicuous but most cryptic. Nonetheless, many attempts have been made to develop mathematical models to reliably monitor and predict disease distribution and abundance. Simulation models are vital to governments and public health agencies to prepare and respond to disease outbreaks through resource allocation, infrastructure development, preparedness training and public education. While such models have frequently been used in sciences such as physics and engineering, they have only relatively recently been applied to infectious diseases. This has necessitated the development of a specific vocabulary to define parameters as well as adopting a de-constructivist approach to identify integral components and mathematical relationships.

Parasite populations

Infectious disease models distinguish between ‘microparasites’ and ‘macroparasites’ *sensu latu*. Microparasites are infectious disease agents which reproduce directly, often at very high rates, within the host. They are generally small, have short generation times, and usually produce long-lasting immunity against re-infection. The duration of infection is usually short relative to the life span of the host, so infections are typically transient. On the other hand, macroparasites have no direct reproduction within the definitive host, producing transmission stages that pass from the host to complete their life-cycle. They are typically large and have longer generation times, which can often be a significant fraction of the host’s life expectancy. Immunity tends to be of relatively short duration once the parasites are removed, and infections are often persistent, with hosts being continually re-infected. Thus, two types of models have been developed for host-parasite interactions:

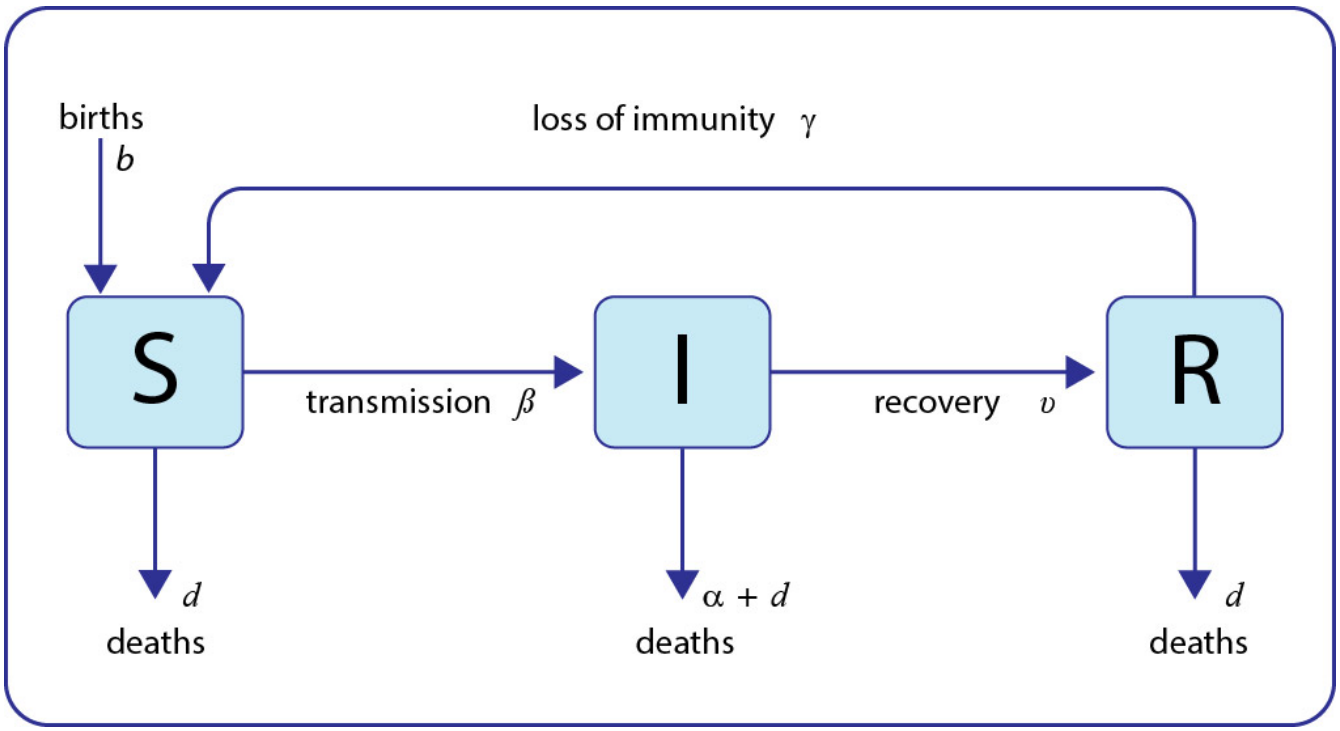
- Microparasite models (usually involving acute, transient, multiplicative infections)
- Macroparasite models (usually involving chronic, prolonged, cumulative infections)

Microparasite models

Microparasites, in the broadest sense, include viral, bacterial and protozoan pathogens. These micro-organisms reproduce quickly, reach very high intensities within individual hosts, cause acute transient infections (short duration compared to host life span), are often limited by host immune responses, and recovered individuals may develop protective immunity against re-infection.

Mathematical models developed for microparasites actually model changes in the number of infections (that is, number of hosts infected), rather than the number of parasites present. The SIR model classifies the total host population (N) into three subpopulations, containing susceptible (S), infected (I) or recovered/resistant (R) individuals, without accounting for within-host abundance/intensity.

Population dynamics of microparasites are driven largely by the rate of transmission between hosts (β), the rate of recovery of infected hosts (ν) and the rate at which any immunity is lost (γ). The model can also take into account changes in host populations, including births (b, all newborns being susceptible) and deaths due to natural causes (d) as well as deaths due to parasitic disease (α). A concept map of the SIR model is shown below.



[An interactive microparasite model is available via Populus (free download at www.cbs.umn.edu/populus/)]

Populations are quantitated as:

N = total host population (number)
S = susceptible host subpopulation
I = infected host subpopulation
R = recovered (immune) host subpopulation

Changes in SIR populations depend on host variables, namely:

b = host birth rate
d = host death rate (natural mortality)

Changes also depend on parasite variables, including:

α = disease-induced mortality rate
β = between-host transmission rate
ν = recovery rate
γ = rate of immunity loss

Movement between S, I and R states are modelled by a series of differential equations (DEs), whereby numbers change over time, that is, dS/dt, dI/dt, dR/dt. Such changes are said to be instantaneous (not discrete) rates of change. When there is no change in rate (for instance, $dS/dt = 0$), that population is stable; but when the rate is > 0 or < 0, the population increases or decreases, respectively.

The DEs differ according to whether transmission is density-dependent (DD) or frequency-dependent (FD). DD transmission considers that infections occur in direct proportion to the number of encounters between susceptible and infected individuals, which is simply the product of their densities (SI). FD transmission recognizes that mixing of the population is not homogeneous and that many individuals have limited numbers of contacts. The frequency of susceptible hosts (S/N) therefore determines the number of transmissions rather than the absolute density (S).

The DEs for the SIR-DD model are:

$$dS/dt = b(S+I+R) - dS - \beta SI + \gamma R$$ [in the SIR-FD model, βSI is replaced with $(\beta SI)/N$]

$$dI/dt = \beta SI - (\alpha+d+\nu)I$$

$$dR/dt = \nu I - (d+\gamma)R$$

The equations can be integrated to obtain the net reproductive rate of disease:

$$R_0 = (\beta S)/(\alpha+d+\nu)$$

Note the effects on R_0 due to:

- variation in parasite transmission [affecting the term βS ($\uparrow$ infections, $\uparrow R_0$)]; and
- the life span of infections [affecting the term $1/(\alpha+d+\nu)$ ($\uparrow$ mortality of host or parasite, $\downarrow R_0$)].

For disease to persist, R_0 must exceed 1, so we can set $R_0 = 1$ to get the threshold susceptible-host population density to sustain the parasite, that is:

$$S_T = (\alpha+d+\nu)/\beta$$

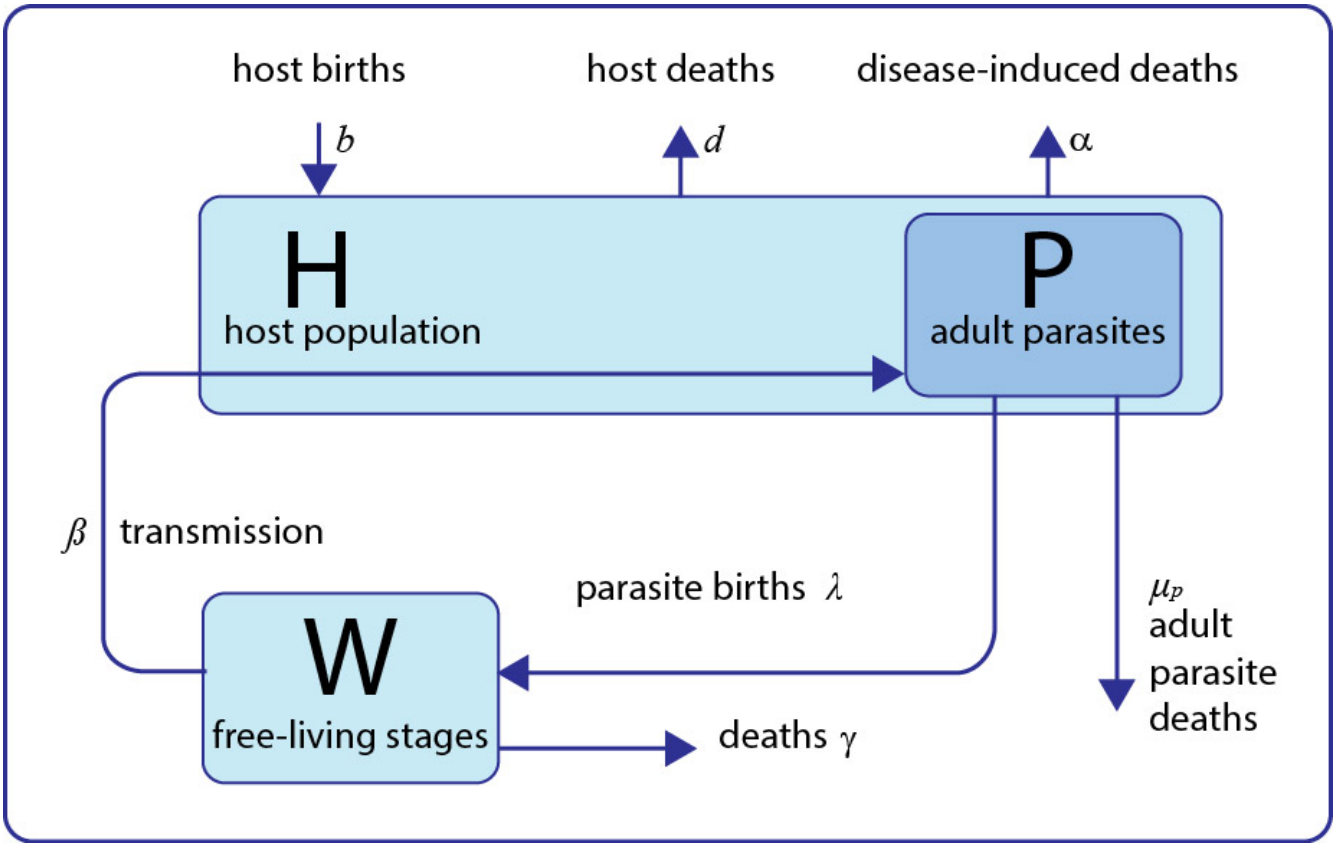
The implication is that the disease will go extinct unless $S > S_T$

Macroparasite Models

Macroparasites generally include helminths and arthropods which usually cause chronic and persistent infections. Disease severity depends on the number of parasites present which in turn depends on exposure to free-living infective stages. Infections are often over-dispersed, as a small fraction of the host population may harbour most of the parasites.

It is not sufficient to divide the host population into *S*, *I* or *R* classes, as macroparasite models must track the intensity of infection in individual hosts (often by assuming a probability distribution for parasite loads). Models take into account host population size (*H*) as well as populations of adult parasites (*P*) (inside hosts) and free-living stages (*W*) (outside hosts).

The Anderson & May (A&M) model characterizes between-host variation in parasite burdens with a negative binomial distribution. The decoupled A&M model is a simplified version whereby infective stages are assumed to be short-lived and at equilibrium. The Dobson & Hudson (D&H) model includes a hypobiotic stage of arrested parasite development following infection, before maturation of adult parasites affect host vitality. A concept map for the A&M macroparasite model with direct transmission is shown below:



[An interactive macroparasite model is available via Populus (free download at www.cbs.umn.edu/populus/)]

Parameters used in the model include:

H = total host population size (numbers)
P = total parasite population size (total numbers of adults)
W = population of free-living infective stages (eggs and larvae)

Host parameters include:

b = host birth rate (/time)
d = host death rate (natural mortality) (/time)

Parasite parameters involve:

α = disease-induced mortality rate (/parasite/time)
β = transmission rate per host contact (/host/time)
λ = birth rate of parasite eggs or larvae (/time)
κ = negative binomial aggregation parameter (a dimensionless constant inversely proportional to assumed parasite aggregation among hosts)
μ_P = natural mortality rate of adult parasites (/time)
γ = infective stage mortality rate (/time)

The DEs for movement between H, P and W states in the A&M model are:

$$dH/dt = (b-d)H - \alpha P$$

$$dP/dt = \beta WH - (\mu_P+d+\alpha)P - \alpha P^2/H[(k+1)/k]$$

$$dW/dt = \lambda P - \gamma W - \beta WH$$

The equations can be integrated to obtain the net reproductive rate of disease:

$$R_0 = (\beta\lambda H)/(\mu_P + d + \alpha)(\gamma+\beta H)$$

Note the effects on R_0 due to variation in:

- parasite fecundity [affecting the term $\beta\lambda$] (↑ fecundity, ↑ R_0);
- the life span of infections [affecting the term $1/(\mu_P + d + \alpha)$] (↑ mortality of host or parasite, ↓ R_0); and
- the life span of free-living stages [affecting the term $1/(\gamma+\beta H)$] (↑ parasite mortality, ↓ R_0).

Host and parasite populations may reach equilibrium if $\lambda - (\mu_P+d+\alpha) > (b-d).[(\kappa+1)/\kappa]$

If so, the parasite is capable of regulating host populations to an equilibrium where $P/H = (b-d)/\alpha$

If not, but $\lambda - (\mu_P+d+\alpha) > 0$, then hosts grow at an exponential rate (< disease-free rate).

If not, but $\lambda - (\mu_P+d+\alpha) < 0$, then the parasite cannot be maintained.

Parasite biodiversity and community structures

The distribution and abundance of parasites depends on many biotic and abiotic factors. Traditional measures of parasite biodiversity are species richness (number of species present), relative abundance (numbers present) and distribution (temporal and spatial). However, when examining host-parasite communities, other aspects must be considered: including host range (definitive, intermediate and/or paratenic hosts, including vectors) and host specificity (especially phylospecificity involving obligate, facultative, opportunistic, preferred or permissive hosts). Because parasites adversely affect their hosts, information is also required on their pathogenicity (infectivity, virulence) and immunological interactions (influencing host susceptibility/resistance).

All qualitative and quantitative measures of ecological indices are based on the recognition of individual species (both parasites and hosts), traditionally determined using a constellation of characters encompassing structural and biological variation (morphotypes, biotypes, culture requirements, viability, transmission, growth and developmental cycles) and more recently, genetic variation (subspecies, strains, variants, serotypes, zymodemes, genotypes, clades). If the traditional definition of a species is given as their genetic exclusivity (i.e. living in reproductive isolation), it is notable that the complete developmental cycles of many parasites is unknown, and few interbreeding experiments have ever been attempted. It is therefore often quite subjective as to whether any variation between isolates should be considered inter-specific (separating species) or intra-specific (within species). The recognition of individual species is essential for any quantitative ecological studies as all metrics are based on either prevalence (presence or absence) of parasite species within host species, their abundance or intensity (numbers of parasites present in individual hosts) or their relative abundance or relative intensity (mean values for populations).

Ecological studies may be conducted at several different levels: involving single or multiple parasite populations within single individual hosts, single host populations or multiple host populations. By definition,

- ‘infra-population’ studies involve one parasite species in one host individual,
- ‘infra-community’ studies involve all parasite species in one host individual,
- ‘component community’ studies involve all parasite species found in one host population, and
- ‘compound community’ (or metapopulation) studies involve all parasite species in all host species within a given area.

Analyses of prevalence and/or abundance data are used to reveal:

- patterns of dominance (core versus satellite species, prevalence-abundance interactions),
- dispersion and aggregation (variance to mean ratio (VMR) and derivatives, rank-abundance plots, species abundance models such as niche pre-emption),
- biodiversity complexity, involving species richness (contingency tables of co-existence, Jaccard’s coefficient, Sorensen’s coefficient),
- relative abundance influencing evenness and heterogeneity (Shannon’s diversity index (H’), Simpson’s diversity index (DI) and derivatives),
- host range and specificity (phylospecificity (Rohde’s indices, Poulin & Mouillot’s index), beta-specificity, phylobetaspecificity), and
- community structures based on similarity/dissimilarity matrices (covariance, nestedness, and cluster analyses).

Meta-population studies also allow observations to be made on:

- the type of diversity (alpha-, beta- or gamma-diversity),
- host-parasite relationships (co-speciation, host switching, ecological fitting), and
- environmental relationships (analyses of variance, correlation/regression analyses, principal components analyses, correspondence analyses involving biotic/abiotic factors such as season, location, climate, host demography).

Taxonomic classification of parasites

Taxonomic classification systems are intended to show phylogenetic relationships between life-forms, reflecting their evolution by descent. Many taxonomic characters have been used to show differences and similarities between organisms, moving from conventional phenotypic characters (such as morphology, biology, geography) to contemporary genotypic characters (DNA and protein characterization). After several centuries of considered debate and informed revision, the taxonomic classification of organisms now generally adheres to a three-domain system: recognizing the Archaea, Eubacteria and Eukaryota as profoundly different organisms, nonetheless with common ancestry. Four kingdoms of Eukaryota ('true-nucleated' organisms) are generally recognized: the Protista, Fungi, Animalia and Plantae. Parasites are found in each kingdom.

Kingdom: Protista (unicellular eukaryotes)
Subkingdom: Protozoa (motile protists)

Supergroup: Excavata (with conspicuous ventral feeding groove)

Group: Metamonad (amitochondriate flagellates with karyomastigonts)

Phylum: Fornicata (diplomonads)
Order: Diplomonadida (with 1-2 karyomastigonts (each with 4 basal bodies/flagella associated with nucleus))
Family: Hexamitidae (2 karyomastigonts arranged in binary axial symmetry)
Giardia vertebrates, small intestines, direct (faecal-oral)
Hexamita (+ *Spironucleus*), vertebrates, intestines/organs/skin, direct (faecal-oral, water-borne)

Phylum: Parabasalia (anaerobic flagellates with parabasal body supporting Golgi cisternae or dictyosome, trichomonads, hypermastigids, retortamonads)
Class: Hypermastigia (Cristamonadea) (with multiple flagella)
Order: Trichomonadida (with 3-5 anterior flagella, and single recurrent flagellum)
Family: Monocercomonadidae (simplest forms, costa absent, most without undulating membrane, some aflagellate)
Histomonas birds, caeca/liver, direct (+ nematode PH)
Dientamoeba humans/rodents, gut, direct (faecal-oral)
Family: Trichomonadidae (stout axostyle, costa present, supporting undulating membrane)
Trichomonas mammals/birds, gut/urogenital tract, direct
Family: Cochlosomatidae (cells with anterior adhesive disc, lateral groove, 6 flagella, axostyle)
Cochlosoma birds, intestines, direct

Group: Discoba (diverse group supported robustly by molecular studies)

Phylum: Heterolobosea (diverse group, incl. amoebo-flagellates, most form cysts or clusters of fruiting bodies)
Order: Schizopyrenida (no fruiting bodies)
Family: Vahlkampfidae (eruptive limax amoeboid form cylindrical, most form temporary flagellated stages)
Naegleria human, CNS, opportunist (normally free-living)

Phylum: Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass: Prokinetoplastina (small group supported by molecular studies)
Family: Ichthyobodonidae (2 heterodynamic flagella arising from pocket that continues as a groove)
Ichthyobodo (= *Costia*) fish, gills/skin, direct (water)
Subclass: Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order: Parabodonida (biflagellated, recurrent flagellum attached or free)
Family: Parabodonidae (Cryptobiidae, Trypanoplasmatidae) (epizoic or endozoic in invertebrates and/or fish)
Cryptobia fish, gills/skin, direct (water)
Trypanoplasma fish, blood, indirect (leech vector)
Order: Trypanosomatida (parasitic, single anterior flagellum, often forming undulating membrane)
Family: Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)
Trypanosoma vertebrates, blood/tissues, indirect (fly/bug vectors)
Leishmania vertebrates, tissues, indirect (sandfly vectors)

Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria)

Group: Alveolata (with cortical alveoli)

Phylum: Protalveolata (incl. perkinsids parasitic in molluscs)
Class: Perkinsea (parasitic in marine bivalves and abalone, form biflagellated zoospores)
Order: Perkinsorida (with characters of class)
Family: Perkinsidae (with characters of order)
Perkinsus shellfish, tissues, direct (water-borne)

Phylum: Dinoflagellata (with unique mesokaryotic nuclei (lacking histones), autotrophs and heterotrophs)
Class: Blastodiniophyceae (extracellular athecate parasites of zooplankton, algae, crustacea and fish)
Order: Blastodiniales (uninucleate trophonts with chloroplasts)
Family: Oodiniaceae (trophont fusiform with rhizoid-like invasive organelle)
Amyloodinium/Crepidoodinium/Piscinoodinium fish, skin, direct (water)
Class: Syndiniophyceae (multinucleate plasmodial trophonts)
Order: Syndiniales (parasitic in copepods, appendicularians, crabs, radiolaria and fish eggs)
Family: Syndiniaceae (multinucleate trophonts without chloroplasts)
Haematodinium/Ichthyodinium crustaceans, fish, tissues, direct (water)

Phylum: Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))

Class: Gregarinomorphea (gregarines, gamogony and sporogony in aquatic hosts, trophonts with specialized attachment apparatus, epimerite or mucron, syzygy)
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)
Family: Cryptosporidiidae (oocysts with 4 naked sporozoites, mucosal parasites in vertebrates)
Cryptosporidium vertebrates, intestines/stomach/lungs, direct (faecal-oral)

Class: Coccidiomorphea [Conoidasida] (with conoid)
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)

Suborder: Adeleina (syzygy, 1-4 microgametes)
Family: Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)
Haemogregarina reptiles/amphibia/fish, tissues/blood, indirect (leech/arthropod vectors)
Hepatozoon mammals/birds/reptiles, tissues/blood, indirect (ingestion of arthropod vector)
Family: Klossiellidae (zygote inactive, sporocysts formed (rather than oocysts))
Klossiella mammals, kidney, direct

Suborder: Eimeriorina (no syzygy, many microgametes)
Family: Eimeriidae (monoxenous, endogenous intracellular merogony and gamogony, exogenous sporogony)
Caryospora birds/reptiles/mammals, gut, direct (faecal-oral)
Cyclospora mammals/reptiles, gut, direct (faecal-oral)
Isospora (+ *Atoxoplasma*), birds/reptiles, intestines, direct (faecal-oral)
Eimeria non-carnivorous vertebrates, intestines + tissues, direct (faecal-oral)
Epieimeria fish, gut/intestines, direct (faecal-oral, water)
Goussia fish, gut, direct (faecal-oral, water)
Family: Sarcocystidae (heteroxenous, oocysts with two sporocysts, tissue cyst formation in intermediate hosts)
Subfamily: Cystoisosporinae (monozoic cysts in paratenic transport hosts, sporocysts without Stieda bodies)
Cystoisospora carnivores/omnivores, gut/tissues, direct/indirect
Subfamily: Sarcocystinae (metrocytes present in cysts, simple/elaborate cyst walls)
Sarcocystis mammals/birds/reptiles, gut/muscles, indirect (predator-prey)
Frenkelia birds/mammals/reptiles, gut/tissues, indirect (predator-prey)
Subfamily: Toxoplasmatinae (metrocytes not present, thin cyst walls)
Besnoita mammals/reptiles, gut/tissues, indirect (predator-prey)
Hammondia mammals, gut/tissues, indirect (predator-prey)
Neospora dogs/herbivores, gut/muscles/CNS, indirect (predator-prey)
Toxoplasma cats/vertebrates, gut/muscles/CNS, indirect (predator-prey + vertical)

Class: Aconoidasida (without conoid)

Order: Haemosporida (pleomorphic stages in blood of vertebrates, insect vectors. motile zygote (ookinete))
Family: Plasmodiidae (schizogony in tissues then blood cells, gamonts in blood cells, haemozoin pigment)
Plasmodium mammals/birds/reptiles, liver/erythrocytes, indirect (mosquito vectors)
Family: Haemoproteidae (schizogony in tissues, gamonts in blood cells, haemozoin pigment)
Haemoproteus birds, endothelia/erythrocytes, indirect (hippoboscid fly vectors)
Family: Leucocytozoidae (schizogony in tissues, gamonts in blood cells, no haemozoin pigment)
Leucocytozoon (+ *Akiba*), birds, tissues/leucocytes, indirect (simuliid fly vectors)

Order: Piroplasmida (pear-shaped stages in blood cells of vertebrates, tick vectors)
Family: Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission in ticks)
Babesia mammals, erythrocytes, indirect (ixodid tick vectors)
Family: Theileriidae (merogony in leucocytes then erythrocytes, trans-stadial transmission in ticks)
Theileria ruminants, leucocytes/erythrocytes, indirect (ixodid tick vectors)

Phylum: Ciliophora (with cilia, nuclear dualism, pellicular alveoli, reproductive conjugation)
Subphylum: Intramacronucleata (microtubules occur inside macronuclear envelope during division))

Class: Litostomatea (simple mouths, special somatic kineties)
Subclass: Trichostomatia (endosymbionts, holotrichous ciliation)
Order: Vestibuliferida (distinct oral depression (= vestibulum))
Family: Balantidiidae (monoxenous symbiotes, in vertebrates, sometimes histophagous)
Balantidium pigs/primates, large intestine, direct (faecal-oral)

Class: Phyllopharyngea (cytopharynx with leaf-like phyllae)
Subclass: Phyllopharyngia (cyrtos, ventral cilia)
Order: Chlamydodontida (body dorsoventrally flattened, ventral cilia thigmotactic)
Family: Chilodonellidae (reniform body dorsoventrally flattened, two fields of dorsal ciliary rows)
Chilodonella fish, gills/skin, direct (water)

Class: Oligohymenophorea (distinct oral ciliature, comprising right paroral membrane and 3 left membranelles)

Subclass: Scuticociliatia (with scuticum or scuticovestige)
Order: Philasterida (short paroral dikinetid membrane)
Family: Uronematidae (membranelles aligned with long axis, anterior pole non-ciliated)
Uronema fish, tissues, opportunist (normally free-living)

Subclass: Hymenostomatida (right paroral dikinetid plus 1-3 left polykinetids)
Order: Hymenostomatida (preoral suture, somatic monokinetids)
Suborder: Ophryoglenina (with organelle of Lieberkuhn (watchglass organelle))
Family: Ichthyophthiriidae (monoxenous ectoparasites, form encysted tomonts which release swarmers/theronts)
Ichthyophthirius (+ *Cryptocaryon*), fish, skin/gills, direct (water)
Suborder: Tetrahymenina (organelle of Lieberkuhn absent)
Family: Tetrahymenidae (pyriform body, longitudinal ciliary rows)
Tetrahymena fish, skin/gills/organs, direct (water)

Subclass: Peritrichia (lacking somatic kineties, oral cilia extend from infundibulum)
Order: Mobilida (mature trophont mobile, aboral holdfast organelle)
Family: Trichodinidae (stout cylindrical body, posterior adhesive disc with denticular ring)
Trichodina fish, skin/gills, direct (water)
Order: Sessilida (attached to substrate with scopula (specialized flattened thigmotactic area) with or without stalk)
Family: Epistylididae (scopula produces noncontractile stalk, retractile lip encircles elevated peristomial disc)
Apiosoma fish, skin/gills, direct (water)
Epistylis fish/crustacea, exoskeleton, direct (water)
Family: Scyphidiidae (solitary ciliates, attached by scopula)
Riboscyphidia syn *Scyphidia* fish/crustacea, exoskeleton, direct (water)
Ambiphrya fish/crustacea, exoskeleton, direct (water)
Family: Vorticellidae (solitary, gregarious or colonial, retractile stalks with central myoneme)
Vorticella fish/crustacea, exoskeleton, direct (water)
Carchesium fish/crustacea, exoskeleton, direct (water)
Family: Zoothamniidae (solitary or colonial, retractile stalks with shared myonemes)
Genus: *Zoothamnium* fish/crustacea, exoskeleton, direct (water)

Group: Rhizaria (various amoebae and flagellates)
Division: Cercozoa (biflagellated and/or amoeboid, usually with filopodia, plus Ascetospora)

Phylum: Ascetospora (haplosporidian and paramyxean parasites forming unique spores)

Class: Haplosporea (haplosporosomes present)
Order: Haplosporida (spore with one sporoplasm, spore orifice covered externally by operculum or internally by diaphragm)
Family: Haplosporididae (spores with operculum)
Haplosporidium/Minchinia/Urosporidium oysters, tissues, direct
Bonamia oysters, haemocytes, direct

Class: Paramyxea (form unique multicellular spores with cells enclosed within each other)
Order: Marteilida (internal cleavage of secondary cells then sporonts)
Family: Marteiliidae (sporonts contain 2-4 tricellular spores)
Marteilia oysters, tissues, direct
incertae sedis "Microcells" (uninucleate microcells, no spores, no plasmodia, no haplosporosomes)
Mikrocytos oysters, tissues, direct?

Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)

Phylum: Amoebozoa (locomotion by noneruptive pseudopodia, asexual development)

Subphylum: Conosa (archamoebae & mycetozoa, many flagellated forms, flagellar root with microtubular cone)
Class: Archamoebae (amoebae (no flagellates), cysts rounded, uni-/multi-nucleate, amitochondriate)
Family: Entamoebidae (uninucleate amoeboid forms, symbiotic in digestive tract of vertebrates)
Entamoeba mammals, colon (liver/brain), direct (faecal-oral)

Subphylum: Lobosa (with lobose pseudopodia)
Class: Discosea/Flabellinea (flattened forms, protoplasmic flow polyaxial)
Order: Dactylopodida (tapering finger-like subpseudopodia (= dactylopodia), most do not form cysts)
Family: Vexilliferidae (long slender subpseudopodia, spiny appearance, many with glycostyles/scales on cell surface, paramoebids with parasomes (Nebenkorper) near nucleus)
Neoparamoeba/Paramoeba fish, gills, direct (water)
Class: Longamoebea (flattened elongated cells with pointed subpseudopodia)
Order: Centramoebida (finely-tapering subpseudopodia (= acanthopodia), most form cysts)
Family: Acanthamoebidae (trophozoites flattened, prominent subpseudopodia, cysts stellate)
Acanthamoeba human, CNS, direct (water)
Balamuthia mammals, CNS, direct (soil/water)

Group: Opisthokonta (stages with single posterior flagellum)

Subgroup: Nucletmycea (Holomycota, fungi and relatives)

Kingdom: Fungi (with chitinous walls, includes microsporidia)
Division: Microsporidia (form unicellular spores, with coiled polar tubes, amitochondriate, all parasitic)

Class: Microsporea (polar filament well-formed, oval spores)
Order: Microsporida (polaroplast present)
Suborder: Apansporoblastina (sporophorous vesicle absent)
Family: Nosematidae (all stages diplokaryotic)
Nosema insects (bees), tissues, direct?
Family: Unikaryonidae (all stages unikaryotic, in cell cytoplasm or in parasitophorous vacuole)
Encephalitozoon mammals, tissues, direct?
Enterocytozoon mammals, gut, direct?
Suborder: Pansporoblastina (sporophorous vesicle present)
Family: Glugeidae (all stages unikaryotic, numerous sporoblasts formed in vesicles)
Glugea fish, tissues, direct?
Pleistophora fish, muscles, direct (water)
Trachipleistophora fish, tissues, direct?
Pseudoloma fish, nervous system, direct (water, carnivorism
Family: Thelohaniidae (meronts diplokaryotic, spores unikaryotic, 8 spores formed in each vesicle)
Thelohania crustaceans/insects, tissues, direct?

Group: Holozoa (metazoans, filasterans, ichthyosporeans, choanomonads)

Kingdom: Metazoa (Animalia) (multicellular eukaryotes, heterotrophs, notably animals)

Phylum: Cnidaria (diploblastic, radial symmetry, cnidocytes with nematocysts, sea anemones, corals, jellyfish, hydrozoa, myxozoa)

Subphylum: Myxozoa (form multicellular valved spores with polar filaments)
Class: Myxosporea (spores with 1-2 sporoplasms, 1-6 polar capsules)
Order: Bivalvulida (spores with two valves)
Suborder: Platysporina (polar capsules in sutural plane)
Family: Myxobolidae (spores flattened, suture forms elevated ridge, one polar capsule smaller than the other)
Myxobolus fish, tissues, direct + indirect?
Order: Multivalvulida (radially symmetrical spores, 3-7 valves, 3-7 polar capsules grouped together at apex)
Family: Kudoidae (four valves and polar capsules, mainly histozoic in muscles of marine fish)
Kudoa fish, muscles, direct/indirect?
Family: Trilosporidae (three valves and polar capsules, coelozoic/histozoic in marine fish)
Unicapsula fish, muscles, direct/indirect?

Group: Protostomia (triploblastic, spiral cleavage)

Subgroup: Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)

Phylum: Platyhelminthes (flatworms, acoelomate, free-living/parasitic, most parasites hermaphroditic, prominent attachment organs)

Clade: Neodermata (syncytial tegument = neodermis)

Class: Trematoda (flukes, most with dorsoventrally flattened bodies, sac-like gut)

Subclass: Digenea (two or more hosts (one a mollusc), cycle involves larval miracidium, sac-like sporocyst/redia stages in snail, cercariae/metacercariae)
Order: Diplostomatida (most 'strigeids', blood and intestinal flukes mainly of tetrapods, some fish, infection usually by cercerial penetration)
Suborder: Diplostomata (furcocercous (fork-tailed) cercariae)
Superfamily: Schistosomatoidea (parasites in fish and tetrapod DH, miracidium penetrates gastropod, bivalve, annelid IH, sporocysts formed, fork-tailed cercariae, penetrates DH)
Family: Schistosomatidae (blood flukes, cylindrical bodies, in blood vessels of alimentary/urinary tract, separate sexes, male with gynaecophoric canal to hold female)
Schistosoma mammals/birds, blood vessels, indirect (freshwater snail IH)
Trichobilharzia, Austrobilharzia birds, blood vessels, indirect (snail vectors)
Order: Plagiorchiida ('echinostomatids', plagiorchiids', mainly fish hosts, some tetrapods, infection often by ingestion of cercariae or metacercariae)
Suborder: Pronocephalata (fish, tetrapod DH, gastropod IH, sporocyst and redia formed; simple-tailed cercariae, encysts in open, metacercariae eaten by DH)
Superfamily: Paramphistomoidea (rumen flukes, miracidium penetrates gastropod IH)
Family: Paramphistomidae (thick fleshy worms, conical shape, ventral sucker near posterior end, redial with appendages, cercariae with two eyespots)
Paramphistomum cattle/sheep, rumen/reticulum, indirect (planorbid snail IH)
Gastrodiscoides pig/humans, large intestine, indirect (snail IH)
Suborder: Echinostomata (fish, tetrapod DH, miracidium penetrates gastropod IH, redia formed, simple-tailed cercariae, encysts in open or in second IH, metacercariae eaten by DH)
Superfamily: Echinostomatoidea (slender worms, adult with collar of peglike spines)
Family: Echinostomidae (in piscivores, acetabulum near oral sucker, rediae with appendages, cercariae without eyespots and with simple tail, miracidia with one pair protonephridia)
Echinostoma birds/mammals, gut, indirect (snail IH-1, molluscs/planaria/fish/tadpoles IH-2)
Family: Fasciolidae (large leaf-shaped flukes, in herbivores, conical anterior end, ventral sucker at level of shoulders)
Fasciola mammals, liver, indirect (freshwater snail IH)
Fasciolopsis man/pig, intestines, indirect (planorbid snail IH)
Suborder: Opisthorchiata (fish, tetrapod DH, egg eaten by gastropod IH, rediae formed, simple-tailed cercariae, encysts in second IH, metacercariae eaten by DH)

Superfamily: Opisthorchioidea (small-medium flukes, often spinose, piscivorous DH)
Family: Heterophyidae (tiny pyriform flukes, in intestines of mammals/birds, two IH (snails and fishes/frogs))
Heterophyes carnivores, intestines, indirect (fw snail IH-1, fw fish IH-2)
Metagonimus dogs/cats/pigs/humans, small intestines, indirect (snail IH-1, fish IH-2)
Family: Opisthorchidae (medium leaf-shaped flukes, in bile ducts of mammals, rediae without appendages, cercariae with two eyespots, metacercariae in second IH)
Opisthorchis piscivorous mammals, liver, indirect (fw snail IH-1, fw fish IH-2)
Clonorchis carnivores, liver, indirect (fw snail IH-1, fw fish IH-2)
Metorchis cat/dog/fox/seal, liver, indirect (snail IH-1, fish IH-2)
Suborder: Xiphidiata (xiphidiocercariae with penetrating stylet in anterior margin of oral sucker)
Superfamily: Gorgoderoidea (fish or tetrapod DH, miracidia penetrate gastropod, bivalve IH, sporocysts and rediae formed, simple-tailed cercariae with stylet, encysts in open or in second IH, metacercariae eaten by DH)
Family: Dicrocoeliidae (small lancet-like flukes, eggs ingested by snails, no redial stage, two-three IH)
Dicrocoelium ruminants, liver, indirect (terrestrial snail IH-1, ant IH-2)
Family: Paragonimidae (thick oval flukes, scale-like spines, miracidia, snail IH-1, crustacean/insect IH-2)
Paragonimus carnivores, lungs, indirect (fw snail IH-1, fw crustaceans IH-2)

Class: Monogenea (monoxenous ectoparasites, sac-like gut, hermaphroditic, direct cycles, oncomiracidium with 3 ciliary bands)
Order: Monopisthocotylea (posterior haptor comprising a single symmetrical attachment unit, no haptoral clamps)
Family: Gyrodactylidae (small worms, posterior haptor with pair of large central hooks and 16 small marginal hooks; viviparous, sometimes hyperviviparity (Russian nested dolls))
Gyrodactylus fish, skin/fins/gills, direct (water)
Family: Dactylogyridae (small worms, posterior haptor with 2 pairs large ventral anchors and 14 small marginal hooks, oviparous)
Dactylogyrus fish, gills, direct (water)
Family: Capsalidae (large worms, haptor with pair anterior suckers and two pairs of posterior hooks)
Benedenia fish, skin/gills, direct (water)

Class: Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass: Eucestoda (larvae hexacanth (with six hooks))

Order: Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)
Family: Taeniidae (tapeworms of carnivores/humans, scolex often armed, proglottids with unpaired reproductive organs and single genital pore, fluid-filled cystic metacestodes)
Taenia carnivores/omnivores, intestines/tissues, indirect (predator-prey)
Multiceps dog/herbivores, muscle/brain, indirect (predator-prey)
Echinococcus dogs/omnivores, gut/tissues, indirect (predator-prey)
Family: Anoplocephalidae (tapeworms of hoofed animals, scolex unarmed, cysticercoid in arthropods)
Anoplocephala, Anaplocephaloides, Equinia, Moniezia, Thysaniezia
herbivores, intestines, indirect (soil mite/insect IH)
Family: Dipylidiidae (armed scolex, proglottids with paired reproductive organs and two lateral genital pores)
Dipylidium dog/cat, small intestines, indirect (flea/louse IH)
Family: Dilepididae (tapeworms of dog/cat and fowl, armed scolex, genital pores alternate, cysticercoid larva)
Amoebotaenia birds, small intestines, indirect (earthworms IH)
Choanotaenia birds, small intestines, indirect (beetle/fly IH)
Family: Davaineidae (tapeworms of birds, large rostellum with hammer-shaped hooks and spiny suckers)
Davainea birds, small intestines, indirect (terrestrial mollusc IH)
Raillietina birds, small intestines, indirect (ants/beetles/cockroaches IH)
Family: Hymenolepididae (tapeworms of birds/rodents/humans, slender strobilia, 1-4 testes, cysticercoid larva)
Hymenolepis mammals/birds, small intestines, indirect (arthropod/annelid/mollusc IH)

Order: Diphyllobothriidea (= Pseudophyllidea) (aquatic host species, unarmed scolex, with two grooves (bothria), genital organs and pores centrally placed, indirect cycles with two IH)
Family: Diphyllobothriidae (eggs release coracidium, more than one IH (procercoid in copepods, pleroceroids in frogs and other aquatic vertebrates) and often PHs)
Diphyllobothrium piscivorous mammals, small intestines, indirect (copepod IH-1/fw fish IH-2)
Dibothriocephalus piscivorous mammals, small intestines, indirect (copepod IH-1/fw fish IH-2)
Spirometra carnivores, small intestines, indirect (copepod IH-1/frogs IH-2)

Order: Bothriocephalidea (aquatic hosts (fish, amphibians), 2 bothria)
Family: Bothriocephalidae (eggs, hexacanth coracidia, procercoid larvae in copepods)
Bothriocephalus fish, intestines, indirect (copepod IH-1)
Schyzocotyle fish, intestines, indirect (copepod IH-1)

Clade: Gnathifera (small cuticular jaws, except Acanthocephala)
Group: Syndermata (eutelic syncytial epidermis)

Phylum: Acanthocephala (thorny-headed worms, pseudocoelomate, unsegmented, anterior retractable proboscis with numerous hooks, lack gut, indirect cycles, eggs with acanthor, acanthella develops in arthropod IH (or PH))
Class: Archiacanthocephala (oval thick-shelled eggs, body wall lacunar canals dorsal & ventral (or just dorsal))

Order: Oligacanthorhynchida (proboscis subspherical, short rows of several hooks, protonephridial organs present)
Family: Oligacanthorhynchidae (single family)
Macracanthorhynchus pig, small intestines, indirect (beetle IH)
Oncicola cats/foxes/dingoes, small intestines, indirect (beetle IH + bird PHs)
Class: Palaeacanthocephala (elongate eggs, sometimes with polar thickenings, body wall lacunar canals lateral)
Order: Polymorphida (trunk wrinkled, proboscis bulbous/cylindrical, with numerous hooks in alternating rows)
Family: Polymorphidae (spinose trunk, proboscis bulbous, double-walled proboscis receptacle)
Polymorphus ducks, small intestines, indirect (copepod IH)

Subgroup: Ecdysozoa (cuticle moulted = ecdysis)

Clade: Nematoidea (collagenous cuticle without microvilli)

Phylum: Nematoda (unsegmented, pseudocoelomate roundworms, hydrostatic skeleton, tubular digestive tract, longitudinal musculature, dioecious, free-living/symbiotic species)

Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)

Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)

Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)

Superfamily: Trichinelloidea (oesophagus with short muscular anterior portion and long glandular posterior portion)
Family: Trichinellidae (males with copulatory pseudobursae, spicules absent, viviparous, juveniles and adults can occur in same host, juveniles intracellular in skeletal muscle nurse cell)
Trichinella mammals, small intestines/muscles, direct (carnivorism)
Family: Trichuridae (whipworms, sudden transition in width, slender anteriorly, barrel-shaped eggs with polar plugs)
Trichuris mammals, caeca, direct (faecal-oral)
Family: Capillariidae (gradual transition in width, in gut/respiratory tract of mammals/birds, eggs with polar plugs)
Capillaria (*Eucoleus*) mammals/birds, various tissues, direct (faecal-oral) + earthworm PH
Pseudocapillaria fish, intestines, direct (water) + indirect oligochaete PHs

Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)

Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, setae absent on females, single testis in males, cuticle 2-4 layers, oesophagus divided into bulbs)

Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)

Infraorder: Rhabditomorpha ('rod'shaped' buccal cavity)

Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Family: Rhabditidae (protandrous hermaphrodite (male becomes female), parasitic and free-living generations)
Rhabditis animals, skin, direct (faecal-oral, transdermal)
Pelodera animals, skin, direct (faecal-oral, transdermal)

Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, some birds)
Family: Ancylostomatidae (hookworms, large buccal capsule bent dorsally, armed with teeth/cutting plates, infection usually by percutaneous/transdermal penetration of infective L3)
Ancylostoma humans/dogs/cats, small intestines, direct (faecal-oral, transdermal)
Globocephalus pigs, small intestines, direct (faecal-oral)
Uncinaria dogs/foxes/cats, small intestines, direct (faecal-oral)
Necator humans/pigs, small intestines, direct (faecal-oral, transdermal)
Bunostomum ruminants, small intestines, direct (transdermal, faecal-oral)
Gaigeria sheep, small intestines, direct (transdermal)
Family: Metastrongylidae (infection of pigs by ingestion of earthworm/molluscan IH carrying L3)
Metastrongylus pigs, lungs, indirect (molluscan IH)
Family: Protostrongylidae (infection of ruminants by ingestion of earthworm/molluscan IH carrying L3)
Protostrongylus sheep/goats, lungs, indirect (mollusc IH)
Muellerius sheep/goats, lungs, indirect (mollusc IH)
Parelaphostrongylus cervids, brain, indirect (snail IH)
Elaphostrongylus cervids, muscles, indirect (snail IH)
Family: Angiostrongylidae (no buccal cavity, infection of vertebrates by ingestion of earthworm/molluscan IH)
Aelurostrongylus cats, lungs, indirect (mollusc IH) + PHs
Angiostrongylus dog, rat, lungs, blood vessels, indirect (mollusc IH) + PHs
Parastrongylus rat, pulmonary artery, indirect (mollusc IH) + PHs
Family: Filaroididae (direct cycle, infection of carnivores by ingestion of L1)
Filaroides dogs/mustelids, lungs, direct (faecal-oral)
Oslerus dogs, trachea, direct (faecal-oral)
Family: Strongylidae (strongyles, large buccal capsules, often with teeth/leaf crown, infection by ingestion of L3three pairs of branches in dorsal ray, equid hosts,)
Subfamily: Strongylinae (large strongyles, red-worms, globular buccal capsules)
Strongylus equines, caecum/colon, direct (faecal-oral)
Subfamily: Cyathostominae (small strongyles, cylindrical buccal capsule)
Cyathostomum equines, caecum/colon, direct (faecal-oral)
Poteriostomum equines, caecum/colon, direct (faecal-oral)
Triodontophorus equines, caecum/colon, direct (faecal-oral)
Oesophagodontus equines, caecum/colon, direct (faecal-oral)
Craterostomum equines, caecum/colon, direct (faecal-oral)
Family: Chabertiidae (nodular worms, two pairs of branches in dorsal ray)
Chabertia ruminants, caecum/colon, direct (faecal-oral)
Oesophagostomum ruminants/pigs/humans, caecum/colon, direct (faecal-oral)
Family: Stephanuridae (kidney-worm, in pigs)
Stephanurus pig, kidneys, direct (faecal-oral, transdermal) + earthworm PHs
Family: Syngamidae (gapeworm, in trachea of birds and mammals)
Syngamus birds, trachea, direct (faecal-oral) + earthworm/mollusc PHs
Family: Trichostrongylidae ((hair-like trichostrongyles, found in gut, infection by ingestion of L3, oesophagus lacking bulb, bursate males, lips reduced/absent, females lay thin-shelled eggs in morula stage, direct cycles)
Trichostrongylus herbivorous mammals/birds, gut, direct (faecal-oral)
Haemonchus ruminants, abomasum, direct (faecal-oral)
Ostertagia cattle, abomasum, direct (faecal-oral)
Teladorsagia sheep/goats, abomasum, direct (faecal-oral)
Cooperia ruminants, small intestines, direct (faecal-oral)
Nematodirus ruminants, small intestines, direct (faecal-oral)
Hyostrongylus pig, stomach, direct (faecal-oral)
Family: Dictylocaulidae (lung worms, direct cycle, infection by ingestion of L3)
Dictylocaulus ruminants/equids/camelids, lungs, direct (faecal-oral)
Family: Ollulanidae (head with spiral coil, female tail with cusps, viviparous (develop to L3 in uterus))
Ollulanus cat/fox/pig, stomach, direct (ingestion of vomitus)
Family: Heligmosomatidae (adults filiform, reddish in colour, direct cycle)
Nippostrongylus rodents, small intestines, direct (percutaneous)

Suborder: Spirurina (mostly parasitic, males often with coiled tail)
Incertae sedis

Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Family: Dracunculidae (buccal capsule reduced, female highly enlarged, filled with L1)
Dracunculus humans, subcutaneous tissues, indirect (copepod IH)

Infraorder: Ascaridomorpha (large roundworms, mouth opening surrounded by three large lips, numerous caudal papillae)

Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, direct cycle but larvae undertake hepato-pulmonary migration)
Family: Ascarididae (large pale roundworms, in terrestrial mammals)
- *Ascaris* humans/pigs, small intestines, direct (faecal-oral)
- *Parascaris* horses, small intestines, direct (faecal-oral)
- *Toxascaris* dogs/foxes/cats, small intestines, direct (+ PHs)
- *Toxocara* dogs/cats/bovids, small intestines, direct (vertical + faecal-oral) + PHs

Family: Anisakidae (large stout worms, in marine mammals/fishes/birds)
- *Anisakis* dolphins/whales, gut, indirect (copepod IH) + fish PHs

Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by ingestion of eggs)
Family: Heterakidae (worms with lateral alae, oesophagus with rounded terminal bulb)
- *Heterakis* birds, caeca, direct (faecal-oral) + earthworm PHs

Family: Ascaridiidae (slender club-shaped oesophagus without rounded terminal bulb)
- *Ascaridia* birds, small intestines, direct (faecal-oral) +earthworm PHs

Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)

Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Family: Gnathostomidae (swollen anterior head bulb, covered with rows of hooks, two lateral lips, four cervical sacs)
- *Gnathostoma* cats/pigs, stomach, indirect (copepod IH) + vertebrate PHs

Infraorder: Oxyuridomorpha (small pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)

Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Family: Oxyuridae (direct cycle, females deposit sticky eggs around anus, infection by ingestion of egg)
- *Oxyuris* horse, large intestines, direct (faecal-oral)
- *Enterobius* humans, large intestines, direct (faecal-oral)
- *Passalurus* rabbits, large intestines, direct (faecal-oral)
- *Syphacia* rodents, large intestines, direct (faecal-oral)

Family: Heteroxynematidae (direct cycle, females deposit eggs in faeces, infection by ingestion of egg/larva)
- *Aspiculuris* rodents, large intestines, direct (faecal-oral)

Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)

Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Family: Acuariidae (cephalic cordons, grooved cuticular structures)
- *Acuaria* birds, gizzard, indirect (water fleas/grasshoppers/beetles IH)
- *Dispharynx* birds, gizzard, indirect (water fleas/grasshoppers/beetles IH)

Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal prominence/tooth, ovoviviparous, L1-L3 in copepod)
Family: Camallanidae (buccal capsule well-developed, with pair sclerotized valves, male with caudal alae)
- *Camallanus* fish, intestines, indirect (copepod IH)

Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect subcutaneous/intermuscular tissues, blood vessels or lymphatic systems of hosts, indirect cycles with arthropod IH)
Family: Filariidae (numerous anterior papillae and cuticular ridges, lay eggs with L1 already fully formed)
- *Parafilaria* horses/cattle, connective tissue, indirect (muscid flies IH)
- *Stephanofilaria* cattle, skin, indirect (buffalo flies IH)

Family: Onchocercidae (adults loose in tissues or in nodules, viviparous (live birth of L1 microfilariae))
- *Onchocerca* humans/cattle/horses, connective tissue, indirect (ceratopogonid/simuliid IH)
- *Wuchereria* humans, lymphatics, indirect (mosquito IH)
- *Brugia* humans/cats, lymphatics, indirect (mosquito IH)
- *Mansonella* humans, body cavities, indirect (midges IH)
- *Dipetalonema* dogs/camelids/humans, connective tissue, indirect (fleas/lice IH)
- *Acanthocheilonema* dogs/camelids/humans, connective tissue, indirect (fleas/lice IH)
- *Dirofilaria* dogs/cats/humans, heart, indirect (mosquito IH)
- *Loa* humans, subcutaneous, indirect (fly IH)
- *Setaria* sheep/cattle/horses, peritoneum/eye/scrotum, indirect (mosquito IH)

Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Family: Habronematidae (pharynx with dorsal and ventral tooth, indirect cycle involving ingestion of fly)
Habronema horses, stomach, indirect (muscid flies IH)
Draschia horses, stomach, indirect (muscid flies IH)
Family: Tetrameridae (extravagant sexual dimorphism, females swollen, coloured bright red)
Tetrameres birds, proventriculus, indirect (water fleas/grasshoppers IH)

Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Family: Physalopteridae (two large lateral pseudolabia, armed with teeth, lips with basal collar, caudal alae on males)
Physaloptera cats, stomach, indirect (crickets IH) + vertebrate PHs

Superfamily: Spiruroidea ((oesophagus divided into anterior muscular and posterior glandular portions, never with bulb, coiled tail in males, two spicules invariably dissimilar, indirect cycles, arthropod IHs, two prominent trilobed lips (pseudolabia), infect oesophagus/stomach (crop/gizzard))
Family: Gongylonematidae (anterior cuticle covered with large bosses or irregular scutes arranged in 8 rows)
Gongylonema cattle/sheep, oesophagus, indirect (beetle/cockroach IH)
Family: Spirocercidae (stout pink-red worm, well-developed buccal capsule, with 6 rudimentary lips)
Spirocerca dog, oesophagus/aorta, indirect (beetle IH) + vertebrate PHs
Ascarops pigs, stomach, indirect (beetles IH) + vertebrate PHs
Physocephalus pigs, stomach, indirect (beetles IH) + vertebrate PHs
Cylicospirura cats/foxes/dasyurids, stomach, indirect (beetle IH)
Cyathospirura cats/foxes/dasyurids, stomach, indirect (beetle IH)

Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Family: Thelaziidae (hexagonal mouth, lacking lips, conspicuous transverse anterior striations, live on surface of eye)
Thelazia cattle/horses, conjunctiva, indirect (muscid flies IH)
Oxyspirura birds, eye, indirect (cockroaches IH)

Suborder: Tylenchina (fungal, plant and animal parasites)

Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))

Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)
Family: Strongyloididae (threadworms, parasitic parthenogenetic females, free-living sexual generations)
Strongyloides mammals/birds, small intestines, direct (faecal-oral + transmammary)

Clade: Panarthropoda (with haemocoel, ventrolateral appendages)

Phylum: Arthropoda (coelomate metameric invertebrate animals, chitinous exoskeleton, segmented body, jointed limbs, moults (ecdyses) between instars, metamorphosis common)

Subphylum: Chelicerata (2 tagmata (cephalothorax + abdomen), chelicera, no antennae)

Class: Arachnida (spiders, scorpions, ticks, mites, two tagmata, 4 pairs of legs, no antennae, slit sensilla, incomplete metamorphosis)

Subclass: Acari (Acarina) (ticks & mites, segmentation inconspicuous/absent, sac-like body, mouth and appendages on capitulum)

Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)

Order: Ixodida (= Metastigmata) (ticks, macroscopic, spiracles/stigmata posterior to legs, hypostome toothed, exposed, obligate blood-feeding ectoparasites of vertebrates)
Family: Argasidae (soft ticks, lack dorsal scutum, capitulum covered by body, hide in cracks/crevices)
Argas birds, skin, direct
Ornithodorus mammals, skin, direct
Otobius mammals, ears, direct

Family: Ixodidae (hard ticks, with dorsal scutum, capitulum projects anteriorly, attach and feed on 1, 2 or 3 hosts)
Ixodes mammals/birds, skin, direct
Rhipicephalus (*Boophilus*) mammals, skin, direct
Haemaphysalis mammals, skin, direct
Amblyomma (incl. *Aponomma p.p.*) mammals/reptiles, skin, direct
Bothriocroton (incl. *Aponomma p.p.*) reptiles/mammals, skin, direct
Dermacentor mammals, skin, direct
Hyalomma mammals, skin, direct

Order: Mesostigmata (gamesid mites, legs grouped anteriorly, spiracles/stigmata between second and fourth legs)
Family: Macronyssidae (large blood-sucking ectoparasites, only protonymph and adults feed, relatively long legs)
Ornithonyssus birds, skin/feathers, direct
Family: Dermanyssidae (large blood-feeding ectoparasites, greyish-white bodies becoming red when engorged)
Dermanyssus mammals/birds, skin/feathers, direct
Family: Halarachnidae (obligate parasites in respiratory tracts or ears of mammals)
Pneumonyssoides dogs/primates, nasal passages/sinuses, direct
Family: Raillietiidae (parasitic in ears of mammals)
Raillietia mammals, ears, direct
Family: Rhinonyssidae (parasites of nasopharynx of birds)
Sternostoma birds, nasal passages, direct
Family: Varroidae (bee mites, flat button shape, red-brown colouration, suck haemolymph)
Varroa bees, cuticle, direct

Superorder: Acariformes (diverse mites, without posterior stigmata)

Order: Prostigmata [Trombidiformes] (with stigmata on capitulum, distinct setae on body/legs)

Family: Demodecidae (small follicle mites, elongate cigar-shaped body, 4 pairs stumpy legs at front of body)
Demodex mammals, hairs, direct
Family: Cheyletiellidae (predatory and parasitic mites, body with waist, palps enlarged, legs terminate in combs)
Cheyletiella dogs/cats/rabbits, skin, direct
Family: Myobiidae (parasitic on fur-bearing mammals, esp. bats, body with lateral bulges)
Myobia mice, skin/hair, direct
Family: Psorergatidae (body circular, legs regularly spaced, long posterior setae, legs with inward-curved spines)
Psorobia, Psorergates sheep, skin, direct
Family: Trombiculidae (only larval stages parasitic, nymphs and adults free-living)
Trombicula, Eutrombicula, Neotrombicula, Leptotrombicula
mammals/birds, skin, direct

Order: Astigmata [Sarcoptiformes] (mange mites, without spiracles, respire through body surface, first two pairs of legs separated from posterior pairs, lack claws, with sucker-like modifications)

Family: Psoroptidae (non-burrowing mites, oval bodies, third and fourth pairs of legs project beyond body margin)
Psoroptes ruminants/horses/rabbits, skin, direct
Otodectes cats/dogs/foxes/ferrets, ear, direct
Chorioptes horses/sheep/cattle, skin, direct
Family: Sarcoptidae (burrowing mites, circular bodies, third and fourth legs do not project beyond body margin)
Sarcoptes humans/dogs, skin, direct
Notoedres cats/rabbits/rats, skin, direct
Trixacarus guinea pigs, skin, direct
Family: Ctyoditidae (respiratory parasites of birds, chelicerae absent, palps fused to form sucking organ)
Cytodites birds, air sacs, direct
Family: Listrophoridae (parasitic on fur-bearing mammals, distinct dorsal shield, legs modified for grasping hairs)
Lynxacarus cats, skin, direct
Leporacarus rabbits/hares, skin, direct
Chirodiscoides guinea pigs, skin, direct
Family: Myocoptidae (parasitic on fur of rodents, anterior legs pincer-like)
Myocoptes mice, skin/hair, direct
Family: Knemidokoptidae (burrowing scaly leg and face mites, round body, no dorsal spines, short stubby legs)
Knemidocoptes, Neoknemidocoptes birds, skin, direct
Family: Laminosioptidae (small mites, smooth elongated body, few setae, affect muscles of birds)
Laminosioptes birds, subcutaneous tissues, direct

Subphylum: Crustacea (chitinous cuticle, gills, 2 pairs antennae, mouthparts comprise pair mandibles and 2 pairs maxillae, segments with pair biramous extremities (podia), metamorphosis involving larval nauplius/zoea)

Class: Maxillipoda (nauplius with maxillipodan eye, 5 cephalic, 6 thoracic and usually 4 abdominal segments plus telson)

Subclass: Copepoda (elongate body, thorax with 7 somites (first few fused with head to form cephalothorax), gradual metamorphosis with series of copepodid instars succeeding naupliar instars, some ectoparasitic forms)

Order: Cyclopoida (antennules short with 10-16 articles, buccal cavity open)
Family: Lernaeidae (females insert anterior attachment organ into host tissues, develop paired egg sacs, free-swimming naupliar stage, five copepodid stages and adults on hosts)
Lernaea fish, gills, direct (water)
Order: Poecilostomatoida (simple parasitic forms of fishes to bizarre symbiotic forms of invertebrates)
Family: Ergasilidae (antennae modified into powerful organs of prehension, parasitic in freshwater and marine fishes)
Ergasilus fish, gills, direct (water)

Subclass: Branchiura (head with flattened bilobed cephalic fold, antennae reduced, carapace expands laterally to form respiratory alae, blood suckers on fish)

Order: Argulidea (single order)
Family: Argulidae (fish lice, discoid body, attaches using hooks/suckers/barbs, stylus inserted to feed on blood)
Argulus fish, skin/gills, direct

Subclass: Pentastomatida (tongue worms, crustacean-related parasites, lost virtually all appendages, elongate, segmented, anterior end with mouth and two pairs of tiny claws (penta-stome appearance))

Order: Porocephalida (horizontally-aligned hooks, posterior genital openings)
Family: Porocephalidae (cylindrical adults, parasites of snakes)
Porocephalus, Armillifer snakes, respiratory passages, indirect (rodent IH)
Order: Cephalobaenida (obliquely-paired hooks, medial genital openings)
Family: Linguatulidae (spatulate adults, parasites of mammals)
Linguatula mammals, respiratory passages, indirect (mammalian IH)

Subphylum: Hexapoda (3 tagmata (head+thorax+abdomen), 3 pairs uniramous legs, whole-limb mandibles)

Class: Insecta (three body regions (head, thorax, abdomen), ectognathous mouthparts (bases lie outside head capsule), six legs, single pair antennae, free-living and parasitic species)

Subclass: Pterygota (with wings)

Infraclass: Neoptera (wings fold back over body)

Superorder: Hemipterodea (= Exopterygota) (young resemble adults, have externally developing wings, piercing/sucking mouthparts)

Order: Hemiptera (true bugs/aphids/scale insects, mouthparts with stylet-like mandibles/maxillae, gradual metamorphosis)
Suborder: Heteroptera (some plant-feeders, some predatory on other arthropods, some blood-feeders on vertebrates)
Family: Cimicidae (small wingless bugs, incl. bedbugs, blood feeders on animals)
Cimex mammals/birds, skin, direct
Family: Reduviidae (large winged cone-nose/kissing/assassin bugs, incl. triatome bugs, blood feeders on animals)
Triatoma, Panstrongylus, Rhodnius mammals, skin, direct

Order: Phthiraptera (lice, small wingless insects, permanent obligate ectoparasites, dorsoventrally flattened, stout legs and claws, incomplete metamorphosis (eggs, nymphs, adults))

Suborder: Anoplura (sucking lice, narrow pointed head, pierce skin and feed on fluids (solenophagy))
Family: Haematopinidae (short-nosed lice, ectoparasites of domestic animals, claws on ends of legs of similar size)
Haematopinus horses/cattle/pig, skin/hair, direct
Family: Linognathidae (long-nosed lice, claws on first leg smaller than those on other legs)
Linognathus ruminants/dogs/foxes, skin/hair, direct
Solenoptes cattle, skin/hair, direct

Family: Pediculidae (head/body lice of primates)
Pediculus primates, skin/hair, direct
Family: Pthiridae (pubic lice of primates)
Pthirus humans, skin/hair, direct

Suborder: Mallophaga (= wool-eating) (chewing lice, broad rounded head, feed on keratin, host/site specific)

Superfamily: Ischnocera (without maxillary palps, prominent filiform antennae, keratin feeders (hairs/feathers))
Family: Trichodectidae (parasitize mammals, 3-segmented antennae, single claw on tarsi)
Trichodectes dogs, skin/hair, direct
Bovicola, Damalinia sheep/cattle/horses, skin/fleece/hair, direct
Felicola cats, skin/hair, direct
Family: Philopteridae (parasitize birds, five-segmented antennae, paired claws on tarsi)
Lipeurus, Goniocotes birds, skin/feathers, direct

Superfamily: Amblycera (with maxillary palps, large rounded heads, 4-segmented antennae in antennal grooves)
Family: Menoponidae (parasitize birds)
Menopon, Menacanthus birds, skin/feathers, direct
Family: Boopiidae (parasitize mammals/marsupials)
Heterodoxus dogs/macropods, skin/hair, direct

Superorder: Holometabola (= Endopterygota) (young do not resemble adults, holometabolous (complete) development, with internally developing wings)

Group: Panorpoid (complex of orders)

Order: Siphonaptera (fleas, wingless (=-aptera), adults feed on blood ("siphon-), laterally compressed, third pair of legs adapted for jumping, complete metamorphosis with vermiform larvae, pupation in silk cocoons)
Family: Pulicidae (parasites of mammals)
Pulex humans/dogs/cats, skin, direct
Echidnophaga mammals/birds, skin, direct
Ctenocephalides dogs/cats/humans, skin, direct
Xenopsylla rats/dogs/cats/humans, skin, direct
Spilopsyllus rabbit, skin, direct
Family: Ceratophyllidae (parasites of small rodents and birds)
Ceratophyllus small rodents/birds/humans, skin, direct
Nosopsyllus rats, skin, direct
Family: Tungidae (chigoes/jiggers/chiggers/chique/sand fleas, females burrow under skin, enclosed in sinus)
Tunga mammals, skin, direct

Order: Diptera (true flies, midges, mosquitoes, with single pair of membranous forewings (diptera), hindwings modified into halteres, complete metamorphosis with vermiform larvae)

Suborder: Nematocera (small midges/mosquitoes, long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs)
Family: Culicidae (mosquitoes, elongate mouthparts form proboscis, slender wings with scales on veins/margins)
Subfamily: Culicinae (scutellum with trilobed posterior margin, scaly abdomen, larva with prominent air-tube)
Culex, Aedes, Mansonia mammals/birds, skin, direct
Subfamily: Anophelinae (scutellum rounded or straight, abdominal sternites lack scales, larva lacks air-tube)
Anopheles mammals/birds, skin, direct
Family: Ceratopogonidae (small biting midges/sand flies, narrow spotted wings, maritime species associated with mangroves/swamps; native species associated with freshwater; introduced species associated with dung)
Culicoides mammals/birds, skin, direct
Family: Simuliidae (small black flies/buffalo gnats, characteristic humped backs, wings not patterned or hairy)
Simulium, Austrosimulium mammals/birds, skin, direct
Family: Psychodidae (moth flies/sand flies, incl. phlebotomines, characteristically hairy bodies and wings)
Phlebotomus/Lutzomyia mammals/birds, skin, direct

Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy))

Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))
Family: Tabanidae (large stout horse/deer/March flies, often brightly coloured, painful bite, daytime feeders)
Tabanus, Chrysops, Haematopota mammals, skin, direct

Infraorder: Muscomorpha **(**Cyclorrhapha) (small-medium sized flies, sponging/biting mouthparts, cyclorrhaphous (circular-seamed) pupa, larva lacks sclerotized head capsule, short pendulous antennae composed of 3 segments usually with feather-like arista, some cause larval myiases)
Division: Schizophora (head with frontal suture (lunule))
Section: Calyptratae (calypters cover halteres)
Family: Glossinidae (tsetse flies, biting mouthparts, characteristic proboscis bulb, both sexes blood-feeders)
Glossina mammals, skin, direct
Family: Hippoboscidae (flat/louse flies, leathery abdomen, piercing mouthparts, strong claws on feet)
Melophagus sheep, skin/fleece, direct
Hippobosca mammals, skin, direct
Family: Muscidae (house/bush/stable/buffalo flies, nuisance flies, synanthropic (associated with human activity))
Subfamily: Muscinae (with sucking mouthparts adapted to feeding on decaying organic matter)
Musca mammals, nonparasitic
Subfamily: Stomoxinae (with elongate biting mouthparts adapted to blood feeding)
Stomoxys mammals, skin, direct
Haematobia bovines, skin, direct
Family: Calliphoridae (blow flies, often metallic, larvae cause myiases (flystrike/screw-worm infestation))
Lucilia (primary), *Calliphora* (secondary)
mammals, skin/subcutaneous tissues, direct
Cochliomyia (primary screw-worm) *Chrysomya* (Old World screw-worm, primary/secondary))
mammals, skin/subcutaneous tissues, direct
Cordylobia (tumbu fly) mammals, skin/subcutaneous tissues, direct
Family: Sarcophagidae (flesh flies, not metallic, breed in excrement/carrion/decomposing organic matter)
Sarcophaga mammals, skin/subcutaneous tissues, direct
Wohlfahrtia mammals, skin/subcutaneous tissues, direct
Family: Oestridae (large hairy bot flies, third larval stage or bot resemble small sausages, larvae cause myiases)
Subfamily: Cuterebrinae (skin bot flies)
Dermatobia cattle/humans, skin, direct
Subfamily: Oestrinae (head maggots)
Oestrus sheep, nasal sinuses, direct
Subfamily: Hypodermatinae (cattle grubs, ox warbles, heel flies)
Hypoderma cattle, subcutaneous tissues, direct
Subfamily: Gasterophilinae (stomach bots)
Gasterophilus equines, stomach, direct

PROTISTA

PROTOZOAN PARASITES

Protozoa are eukaryotic organisms (with a membrane-bound nucleus) which exist as structurally and functionally independent individual cells (= unicellular); including those species which are gregarious or form colonies. None have adopted multicellular somatic organisation characteristic of metazoan organisms. Instead, they have developed relatively complex subcellular features (membranes and organelles) which enable them to survive the rigours of their environments. The unicellular protozoa comprise multiple diverse assemblages, containing motile protozoal protists as well as non-motile algal and fungal protists. Early classification schemes recognized the higher taxon Protozoa (with a capital 'P'), but this was later subsumed to the descriptor protozoa (with a small 'p') in deference to the recognition of Protista (or Protoctista) as a collective group, although most composite members have now been integrated with other eukaryotes into several supergroups (viz. Excavata, SAR and Amorphea).

Protists exhibit enormous diversity in form and function. They are ubiquitous as free-living organisms in terrestrial and aquatic habitats and as symbionts (commensals, mutualists or parasites) of most animals and many plants. The diversity of protistan organisms is well appreciated both in terms of their structural heterogeneity, as well as their species richness and zoogeographic/biogeographic distribution. Most protists are microscopic organisms - only a few grow to a size large enough to be visible to the naked eye. Protistan cells (and indeed all individual metazoan cells) are constrained to microscopic sizes because of the small distances over which macromolecules may be transported for metabolic purposes (all parts of the cell must be accessible). The microscopic cell is therefore the basic unit of life. Individual protistan cells display all the same essential life activities as higher metazoan eukaryotes: they move about to feed, breed and survive.

Protista may be autotrophic (produce their own organic molecules), heterotrophic (derive organic molecules from external sources) or even mixotrophic (alternating between internal and external sources). Phototrophs (or photoautotrophs) synthesize their own organic molecules with energy derived from photosynthesis, while osmotrophs (or saprotrophs) take up dissolved nutrients across their cell membranes by passive and active transport or by pinocytosis. Phagotrophs (or holotrophs) ingest particulate material and use metabolic processes (catabolic decomposition and anabolic synthesis) to derive energy and organic molecules. They may be filter-feeders with simple-to-sophisticated oral structures to sweep food towards the mouth or they may be predatory (actively preying on other organisms) - being bactivorous (ingest bacteria), algivorous (ingest algae), herbivorous (ingest plant material), carnivorous (ingest other microscopic protists or zooplankton) or even histophagous (parasites invading and eating the tissues of larger organisms).

All eukaryotic cells are chimeric; they contain genetic information from multiple ancestral lineages. Modern molecular genealogies have generated complex pictures of eukaryote genomes where ancient lateral gene transfers have tangled their evolutionary history. All eukaryotes have a true nucleus (= 'eu-karyon') whereby the genetic material is enclosed by a membrane - in contrast to archae- and eu-bacteria (formerly referred to collectively, but incorrectly, as 'prokaryotes') where the genetic material lies directly in the cytoplasm. The nuclear membrane of eukaryotic cells is confluent with other endomembrane systems, including endoplasmic reticulum (serving as a scaffold for ribosomes – the sites of protein synthesis) and dictyosomes (Golgi bodies where proteins are processed and packaged). Structural support is provided by cytoskeletal elements (microtubules and microfilaments) which are also involved in motility, by means of undulipodia (including flagella and cilia) or pseudopodia (involving temporary cellular extensions and cytoplasmic streaming), feeding (phagocytosis and pinocytosis) and nuclear division (nuclear spindle formation).

The serial endosymbiosis theory (SET) posits that eukaryotic cells serially acquired various endomembrane and organellar systems from endosymbiotic bacteria over long evolutionary history. Indeed, molecular biological studies have indicated that mitochondria may have originated from α-proteobacteria (similar to rickettsias) and chloroplasts from cyanobacteria. Not all extant protozoa possess the 'full' complement of eukaryotic organelles (some lack dictyosomes, some lack mitochondria, etc.), thus their variable possession of such components makes them basal in eukaryote evolution, or intermediary between bacterial domains and eukaryotes (in some cases, making them the perfect missing links).

Classification schemes

The name ‘proto-zoa’ literally means ‘first animals’ and early classification systems grouped the protozoa with members of the animal kingdom due to their many similarities to eukaryotic metazoan cells. However, they were recognized as a discrete assemblage on the basis of their unicellularity and were assigned to the taxon Protozoa which was considered basal to the Metazoa (they are invariably figured as the trunk of the animal tree of life - befitting their name as the ‘first animals’). Nonetheless, the members of the subkingdom Protozoa are quite disparate. Indeed, the taxon has never been considered a natural assemblage of organisms but rather one of convenience. Various classification schemes have been proposed for protozoan organisms. Since its inception in the 1880’s, the Butschlian scheme has dominated whereby four major assemblages were recognized on the basis of their locomotion using specialized subcellular and cytoskeletal features:

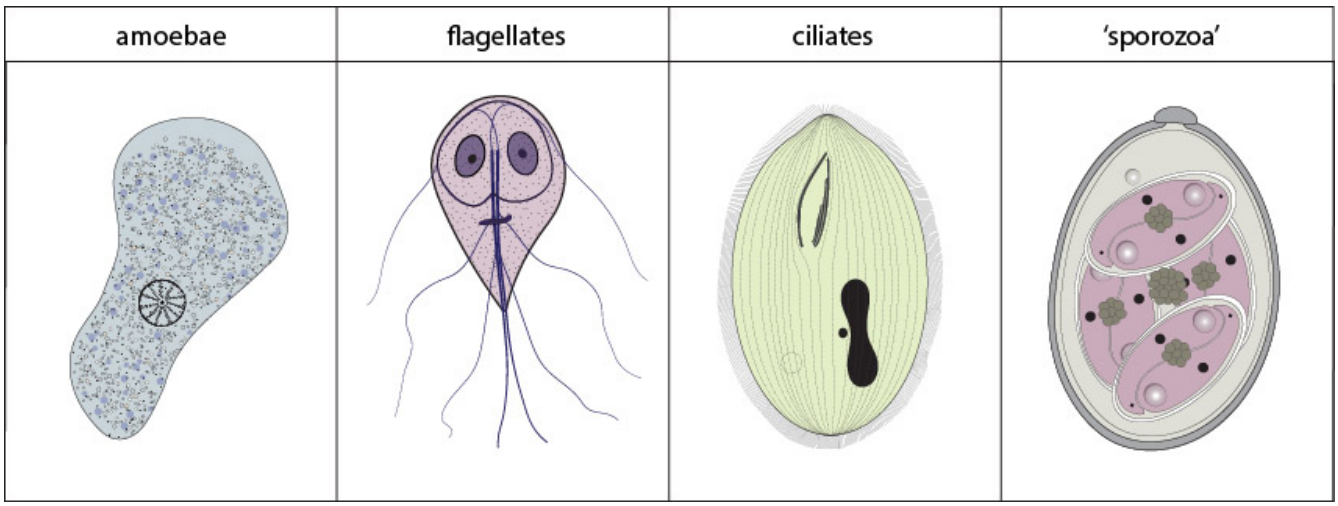
- Sarcodina (amoebae) use pseudopodia (singular: pseudopodium) to creep or crawl over solid substrates. Pseudopodia (or ‘false feet’) are temporary thread-like or balloon-like extensions of the cell membrane into which the protoplasm streams. Similar amoeboid motion has been observed in cells of many life-forms, especially phagocytic cells (e.g. human macrophages).

- Mastigophora (flagellates) use elongate flagella* (singular: flagellum) which undulate to propel the cell through liquid environments. Flagella are ‘whip-like’ extensions of the cell membrane with an inner core of microtubules arranged in a specific 2+9 configuration (2 single central microtubules surrounded by 9 peripheral doublets). This configuration is conserved throughout eukaryotic biology, many organisms produce flagellated cells (e.g. human spermatozoa).

- Infusoria (ciliates) use numerous small cilia* (singular: cilium) which undulate in waves allowing cells to swim in fluids. Cilia are ‘hair-like’ extensions of the cell membrane similar in construction to flagella but with interconnecting basal elements facilitating synchronous movement. Ciliated cells are found in specialized tissues and organs in many other higher life-forms (e.g. human bronchial epithelial cells).

- Sporozoa (‘spore-formers’) were originally recognized not on the basis of their locomotion, but because they all formed non-motile spores as transmission stages. Recent studies, however, have shown that many pre-spore stages move using tiny undulating ridges or waves in the cell membrane imparting a forward gliding motion, but the actual mechanisms involved are not yet known.

*The flagella and cilia of eukaryotes ‘undulate’ (dynein-walking along microtubules) rather than ‘rotate’ like the flagella of archae-/eu-bacterial organisms. Some authorities therefore reserve the term ‘flagellum’ for bacteria and recommend the term ‘cilium’ for eukaryotes, while others favour the collective term ‘undulipodia’ for eukaryotic flagella and cilia.



More recently, many attempts have been made to reconcile the members of these basic but disparate groups into a small number of phyla formally recognized in a consensus classification system. A range of phenotypic characters were used to classify organisms: including morphological (cellular/subcellular, light/electron microscopic); behavioural (*in vivo* host specificity, life cycle, distribution, *in vitro* cultivation requirements); and biochemical (metabolic respiration/digestion, drug sensitivity/resistance, molecular structure/function) characteristics. Several decades ago, the Society of Protozoologists published a revised classification system (Levine *et al*., 1980) and an illustrated guide (Lee *et al*., 1985) to the Protozoa; recognizing eight main phyla, principally on the basis of morphology.

- Sarcomastigophora (flagellates and amoebae) — most free-living, some symbiotic
- Labyrinthomorpha (cells glide on ectoplasmic network) — parasitic on marine algae
- Ciliophora (ciliates, dikaryotic) — most free-living, some symbiotic
- Apicomplexa ('sporozoa', apical complex present) — parasitic in vertebrates/invertebrates
- Microspora (unicellular spores with polar tubes) — parasitic in vertebrates/invertebrates
- Haplosporidia (spores without polar capsules) — parasitic mainly in oysters
- Paramyxea (unique cells within cells configuration) — parasitic mainly in oysters
- Myxozoa (multicellular spores with polar capsules) — parasitic mainly in fish

Over the last two decades, classification schemes have adopted a broader perspective to encompass all unicellular protistan organisms, including traditional protozoal, algal and fungal groups as well as their intermediates. Ultrastructural studies identified many new assemblages with distinctive subcellular features (organelles, membranes and cytoskeletal elements), and contemporary molecular biological studies on gene and protein sequences are now facilitating comparative analyses and the construction of phylogenetic trees whose topologies better reflect evolutionary relationships. The Society of Protozoologists revised their guide to the protozoa (Lee *et al*., 2000) with the recognition of some 40 protistan phyla on the basis of genotypic and phenotypic characters. Lower taxonomic groupings (families, genera and species) are often well supported by comparative genotypic analyses, while their higher taxonomic affinities (orders, classes, phyla) are slowly being resolved amidst some controversy. The Society (now the International Society of Protistologists) recently published a revised classification of eukaryotes (Adl *et al*., 2012, 2018) integrating unicellular and multicellular organisms into several supergroups [note that the taxonomic rank of the assemblages (phylum, class, order, etc.) varies widely according to author, so they are ranked here using dot-points rather than with names to provide an uncluttered overview]:

Domain: Eukaryota (membrane-bound nucleus)

- Supergroup: Excavata (with conspicuous ventral feeding groove)
  - • Metamonad (amitochondriate flagellates with karyomastigonts)
    - •• Fornicata (diplomonads)
    - •• Parabasalia (trichomonads, hypermastigids, retortamonads)
    - •• Preaxostyla (oxymonads)
  - • Discoba (diverse group supported robustly by molecular studies)
    - ••• Heterolobosea (amoebo-flagellates, schizopyrenids or vahlkampfids
    - ••• Euglenozoa (euglenids and kinetoplastids)

- Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria)
  - • Stramenopiles (with heterokont/dissimilar flagella)
    - •• Opalina (opalescent symbiotes in amphibians)
  - • Alveolata (with cortical alveoli)
    - •• Protalveolata (incl. perkinsids parasitic in molluscs)
    - •• Dinoflagellata (mesokaryotic nuclei, autotrophs and heterotrophs)
    - •• Ciliophora (nuclear dualism, hair-like cilia, conjugation)
    - •• Apicomplexa (with apical complex organelles)
  - • Rhizaria (various amoebae and flagellates
    - •• Cercozoa (biflagellated and/or amoeboid, usually with filopodia, plus ascetospora (haplosporidia, paramyxea))
    - •• Retaria (amoebae with reticulopodia (Foraminifera) or axopodia (Radiolaria))

- Supergroup: Amorphea (unikonts, with single flagellum, or nonflagellated amoebae)

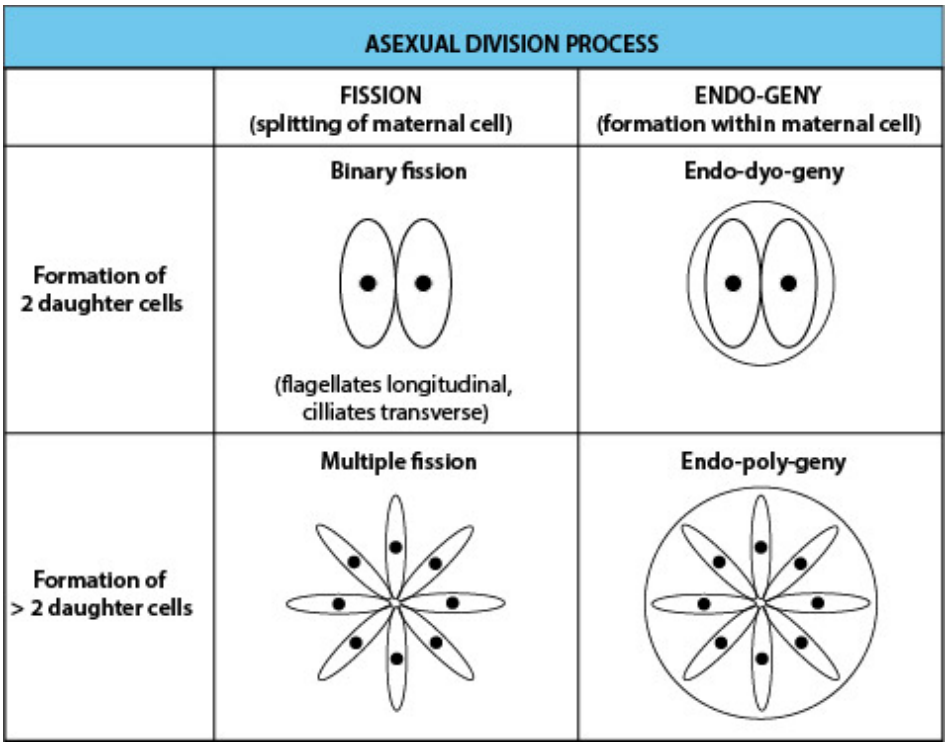
• Amoebozoa			(naked/testate amoebae, noneruptive variable pseudopodia)
	•• Tubulinea		(produce tubular subcylindrical pseudopodia)
	•• Discosea		(never produce tubular pseudopodia)
	•• Archamoebae		(amitochondriate but with nonaerobic organelles)
	•• Gracilipodia		(produce short conical or fine hair-like subpseudopodia)
• Opisthokonta			(stages with single posterior flagellum)
	•• Nucletmycea		(Holomycota, fungi and relatives)
		••• Nuclearia	(round amoebae with filopodia)
		••• Fungi	(fungi, with chitinous walls; incl. microsporidia)
	•• Holozoa		(metazoans, filasterans, ichthyosporeans, choanomonads)
		••• Metazoa	(multicellular heterotrophs, notably animals (incl. myxozoa))

Biodiversity

Protozoan biodiversity (or species richness) includes counts (estimates) of some 32,000 extant (living) species and another 34,000 extinct (fossil) species (especially foraminifera). Of those alive today, some 21,000 species occur as free-living organisms in aquatic or terrestrial environments, whereas the remaining 11,000 species are parasitic in vertebrate and invertebrate hosts. There are approximately 6,900 flagellate species (1,800 parasitic, 5,100 free-living), 11,550 amoebae species (250 parasitic, 11,300 free-living), 7,200 ciliate species (2,500 parasitic, 4,700 free-living) and 5,600 sporozoan species (all parasitic). Estimates of protozoan parasite biodiversity vary considerably because little is known about the host range and specificity of most parasites. Some host species harbour only one or a few protozoan species, while others have many. Some parasite species only occur in one host species, while other parasites have a broad host range. The potential number of parasitic species (N) depends on the number of available host species (A), their host specificity (B = average number of protozoan species per host species) and their host range (C = average number of host species per protozoan species); according to the formula $N = AB/C$. Estimates of N can vary 100-fold because estimates of B and C may vary by as much as 50-fold.

Protozoal diseases

Protists have enormous proliferative/multiplicative potential. While animals and plants divide asexually by open mitosis (extranuclear spindle, with pole bodies), most protists divide by closed mitosis (nuclear envelope does not breakdown, but contains internal spindles), with the exception of parabasalids and dinoflagellates (closed mitosis with external spindles). Protists can divide asexually by splitting (binary or multiple fission) or internal division (endogeny or plasmotomy). Many species are also able to reproduce sexually, either forming conjugated pairs which exchange nuclei (e.g. ciliates) or forming separate male and female gametes (gamogony) which recombine (syngamy) to form zygotes (e.g. apicomplexans).



Parasite pathogenicity (virulence) and disease severity is often positively correlated with their proliferative potential. Protozoan species which quickly multiply within host tissues cause acute transient severe diseases (rapid-onset, high-intensity, short duration). The parasites often exhibit exponential growth until specific host immune responses develop and act against infections (sterile immunity leading to eradication, concomitant or premunitive immunity leading to reduction but not elimination). In most vertebrate hosts, adaptive/acquired immune responses (humoral and cell-mediated) become most effective approximately one week after primary infection. During this time, the parasites may cause significant damage to host cells and tissues leading to overt clinical disease. Some protozoa, however, encyst within host tissues giving rise to chronic protracted diseases.

Host pathology is generally indicated by the four cardinal signs of inflammation: rubor (redness), calor (heat), tumor (swelling) and dolor (pain) due to the hyperaemia and extravasation of phagocytes associated with innate immunity. Inflammation may be focal, local or systemic (indicated by the suffix '-itis', e.g. inflammation of the heart is called carditis, that of the brain encephalitis, etc) and it may be accompanied by other systemic responses (e.g. fever due to the release of endogenous pyrogens which act on the hypothalamic thermostat; ischaemia due to collapse of the microcirculation; circulatory shock due to peripheral constriction to divert blood to vital organs in viscera; toxic shock due to endo- or exo-toxins; hypersensitivities due to hysterical immune responses, etc.).

Disease symptoms (described to clinician) and signs (observed by clinician) depend largely on the host compartment or tissue systems involved. Infections may occur in extracellular compartments (lumen-dwelling or interstitial parasites) but most protozoan species, at some stage, occupy intracellular locations (ultimately causing cell lysis thus structural and functional pathology). Protozoan parasites infecting the gastro-intestinal tract may be lumen-dwelling, mucosal-browsers or invasive in epithelial or subepithelial locations. Their presence causes local inflammation (gastritis and/or enteritis) resulting in vomiting and/or diarrhoea. Protozoa infecting the vascular system (fluid or cellular components) often cause haemolytic anaemia and fever. Parasites infecting specific tissues or organs often cause space-occupying lesions and ultimately organ malfunction.

Life-cycles

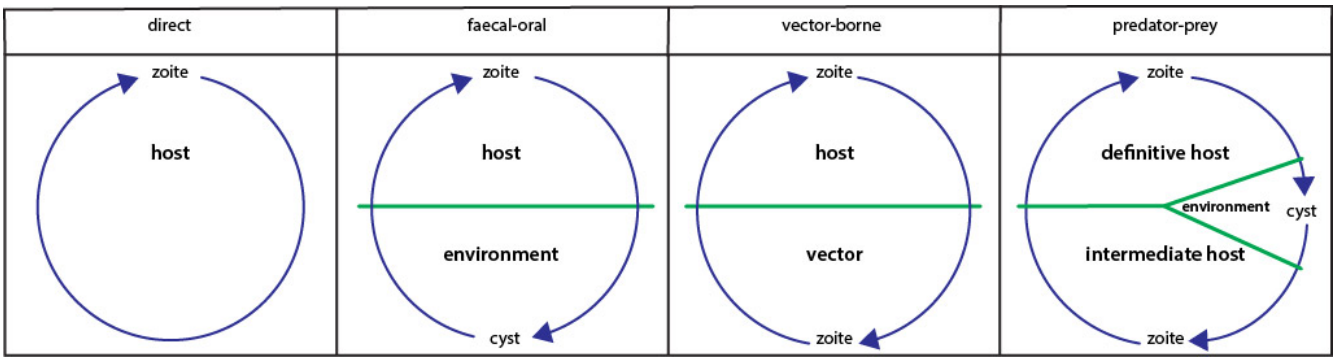
Protozoan developmental stages occurring within hosts generally consist of feeding trophozoites, and they may be found intracellularly (within host cells) or extracellularly (in hollow organs, body fluids or interstitial spaces between cells). While trophozoites are ideally suited to their parasitic mode of existence, they are not very resistant to external environmental conditions and do not survive long outside of their hosts. To move from host-to-host, protozoan parasites use one of four main modes of transmission: direct, faecal-oral, vector-borne and predator-prey transmission.

- direct transmission of trophozoites through intimate body contact, such as sexual transmission (e.g. *Trichomonas* spp. flagellates causing trichomoniasis in humans and bovine infertility in cattle).

- faecal-oral transmission of environmentally-resistant cyst stages passed in faeces of one host and ingested with food/water by another (e.g. *Entamoeba histolytica*, *Giardia duodenalis* and *Balantidium coli* all form faecal cysts which are ingested by new hosts leading to amoebic dysentery, giardiasis and balantidiasis, respectively).

- vector-borne transmission of trophozoites taken up by blood-sucking arthropods (insects or arachnids) and passed to new hosts when they next feed (e.g. *Trypanosoma brucei* flagellates transmitted by tsetse flies to humans where they cause sleeping sickness, *Plasmodium* spp. haemosporidia transmitted by mosquitoes to humans where they cause malaria).

- predator-prey transmission of zoites encysted within the tissues of a prey animal (e.g. herbivore) being eaten by a predator (carnivore) which subsequently sheds spores into the environment to be ingested by new prey animals (e.g. tissue cysts of the sporozoan *Toxoplasma gondii* being ingested by cats, and tissue cysts of the microsporidian *Thelohania* spp. being ingested by crustaceans).

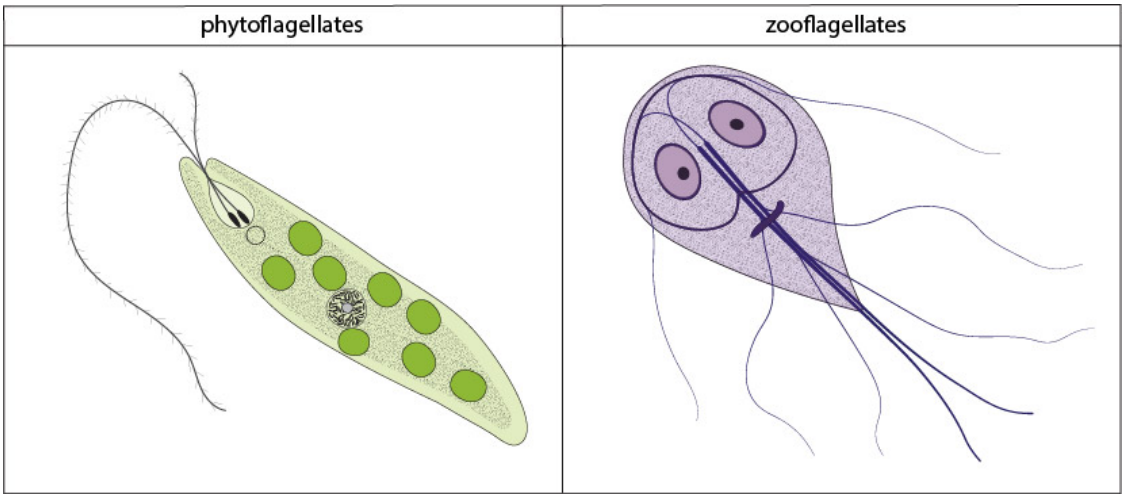


Overview of major protozoan groups parasitizing animals

Flagellates and amoebae are considered to be closely related, because some amoebae form transient flagellated stages (to aid in dispersal) and some flagellates exhibit intermittent amoeboid motion. Two groups of flagellates are recognized on the basis of the presence or absence of chloroplasts:

- Phytoflagellates with chloroplasts derive energy by photosynthesis. Most are free-living aquatic organisms and some exhibit periodic blooms (e.g. red tides). Others contain potent neurotoxins and cause paralytic shellfish poisoning.

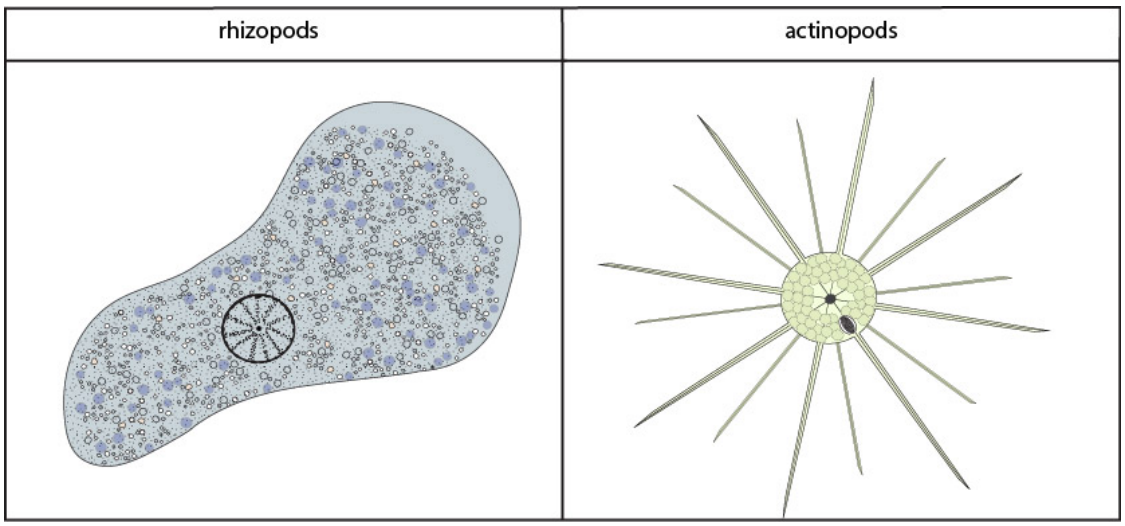
- Zooflagellates without chloroplasts derive energy by the absorption of nutrients or the ingestion of food particles. Many species occur as free-living aquatic organisms whereas others live in insects and some vertebrates as symbiotes, commensals or parasites (several species cause major human diseases such as sleeping sickness, Chagas' disease, kala azar and diarrhoea).



Two groups of amoebae are recognized on the basis of the types of pseudopodia formed with or without regular microtubule arrays:

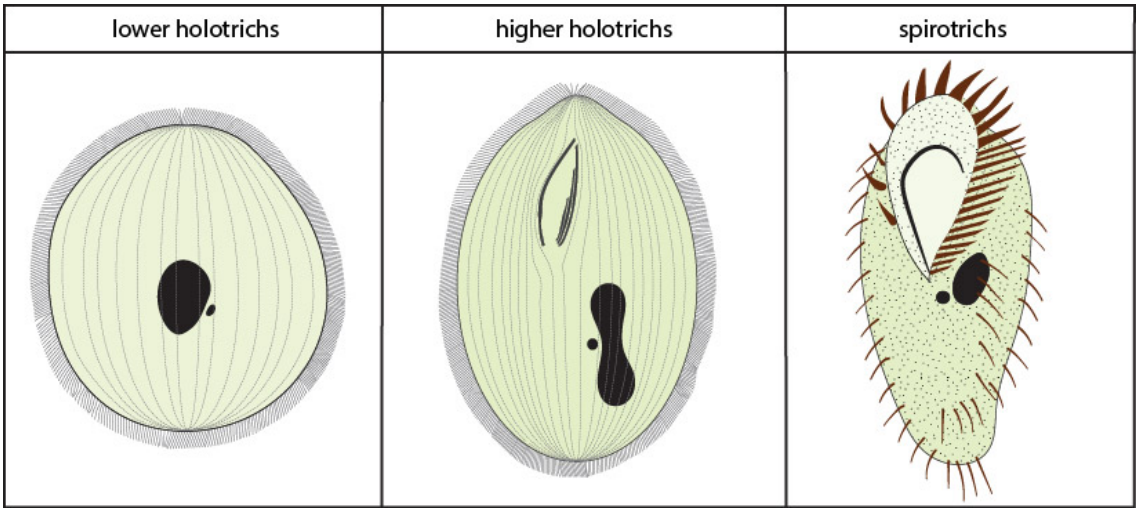
- Rhizopod amoebae produce broad lobopodia, fine filopodia or net-like reticulopodia which do not contain regular microtubule arrays. Many aquatic species contribute to water quality by consuming bacteria and algae whereas terrestrial species contribute to soil health via nutrient cycling. Some species, such as foraminifera, build unique tests (shells) which contribute to fossil records.

- Actinopod amoebae form radial axopodia which are stiffened by internal arrays of microtubules arising from an organizing centre. All species are free-living planktonic organisms, marine species known as radiolaria, and freshwater species known as heliozoa (or sun animalcules).



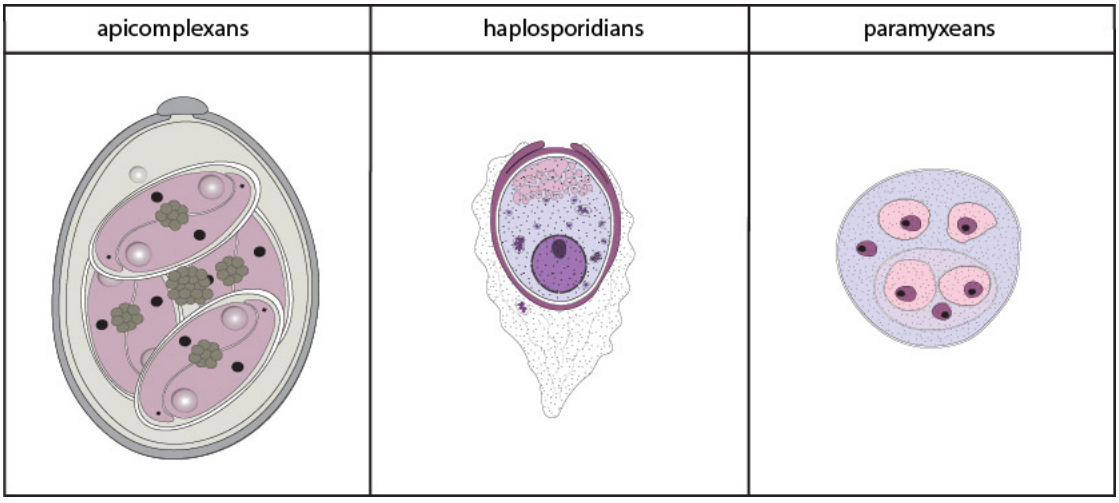
The ciliates are regarded to be quite separate from other groups, more because they possess two types of nuclei (vegetative macronuclei and reproductive micronuclei) than because they possess cilia. Three groups are recognized on the basis of their patterns of somatic (body) and buccal (oral) ciliature:

- Lower holotrichs have simple body and oral ciliature. Most are free-living aquatic species but some are highly specialized symbionts aiding cellulose digestion in herbivores.
- Higher holotrichs have simple body ciliature but more specialized oral ciliature forming membranelles. Most occur as free-living aquatic organisms but some live as commensals or parasites in a range of animals.
- Spirotrichs have reduced body ciliated but well-developed oral ciliature forming an adoral zone of membranelles. The majority are bactivores living in aquatic and terrestrial habitats.



All sporozoa are obligate parasites, they form temporary non-motile spores which contain infective cells. Three major groups are recognized on the basis of different spore morphology:

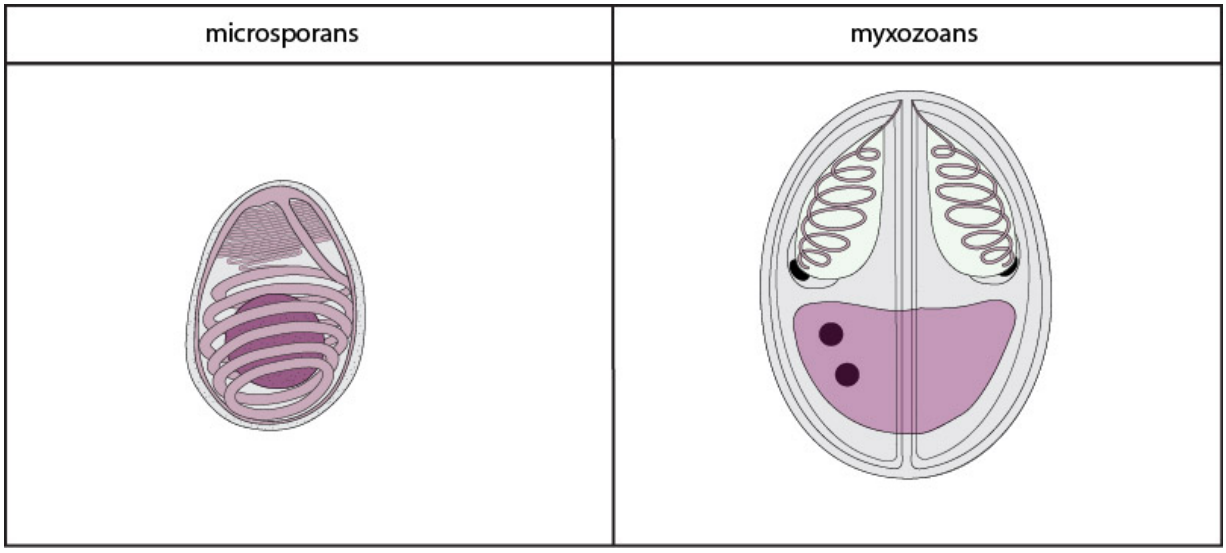
- Apicomplexan parasites form distinctive oocysts containing infective sporozoites. Many species occur only in invertebrates whereas others may infect vertebrates causing severe diseases (such as malaria, tick fever, diarrhoea or abortion).
- Haplosporidian parasites form unicellular spores without polar filaments in the tissues of aquatic invertebrates. They cause significant morbidity and mortality in oysters throughout the world.
- Paramyxean parasites form unique spore-within-spore arrangements within the tissues of bivalves and polychaetes. They cause QX and Aber disease in oysters



Another two sporozoa-like groups were long considered to be protistan parasites, but contemporary studies have shown them to belong to different kingdoms: microsporidian parasites belonging to the kingdom Fungi, and myxosporean parasites belonging to the kingdom Metazoa (Animalia).

- Microsporidian parasites form unicellular spores containing coiled polar tubes used to infect host cells. Most species infect invertebrates (especially insects) although some form cysts in vertebrates (mainly fish).

- Myxosporean parasites form multicellular spores containing capsulogenic and sporoplasmic cells enclosed within valvulogenic cells. All species are found as coelozoic or histozoic parasites of marine and freshwater fishes; some causing debilitating diseases and tissues lesions.

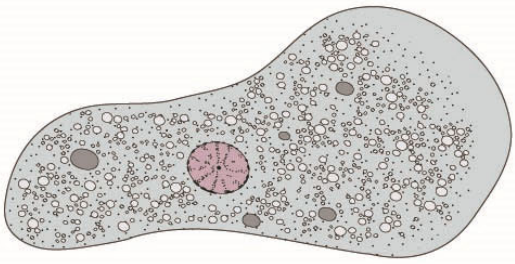


Protista
(amoebae)

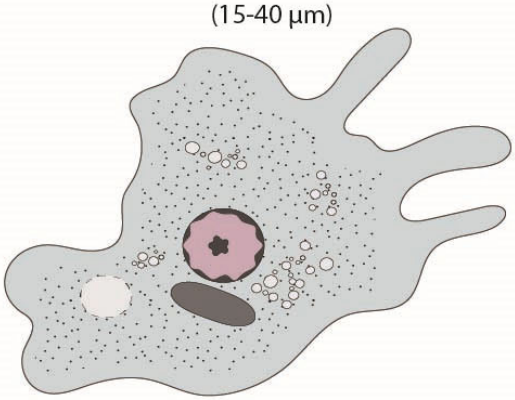
Amoebae

trophozoites

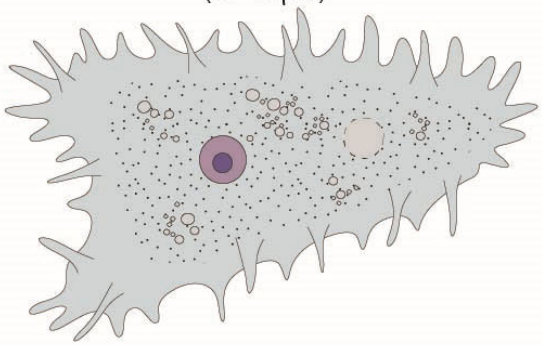
Entamoeba
(10-40 µm)



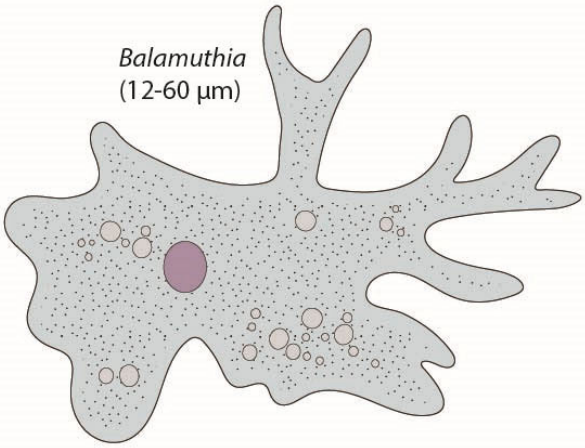
Paramoeba
(15-40 µm)



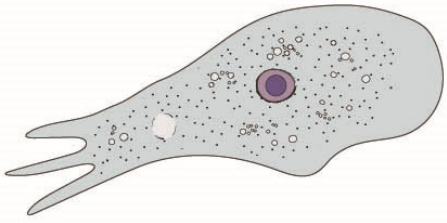
Acanthamoeba
(15-40 µm)



Balamuthia
(12-60 µm)



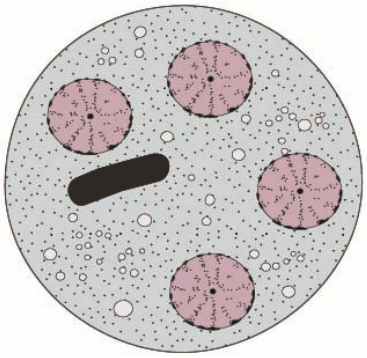
Naegleria
(10-15 µm)



Amoebae

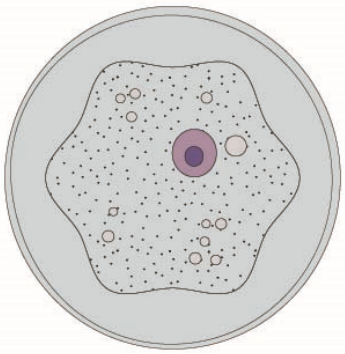
cysts

Entamoeba
(10-16 µm)

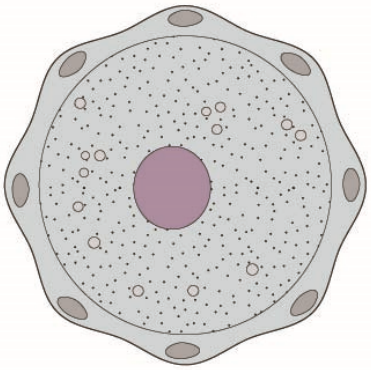


Paramoeba
no cyst formation

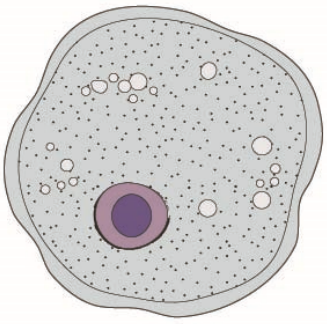
Acanthamoeba
(10-20 µm)



Balamuthia
(6-30 µm)



Naegleria
(10-20 µm)



Entamoeba
(protist: amoeba)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Protists which move and feed using pseudopodia (false feet) are known as amoebae. Rather than forming a monophyletic group, amoebae are divided into three major disparate groups: Heterolobosea (supergroup Excavata), Rhizaria (supergroup SAR) and Amoebozoa (supergroup Amorphea). The latter contains four classes of amoebae differing in their types of pseudopodia and organelles: Tubulinea, Discosea, Gracilipodia and Archamoebae. The parasite *Entamoeba* belongs to the archamoebae which form broad pseudopodia but do not produce fruiting bodies like mycetozoa (slime molds). They are naked amoebae (without tests or shells) and have simple life-cycles (without temporary flagellated stages). Most archamoebae are parasites or endocommensals in the digestive tracts of arthropod or vertebrate hosts. They form motile feeding trophozoites with single broad lobopodia and are transmitted between hosts by environmentally resistant cysts. Individual species are differentiated on the basis of cyst morphology and nuclear structure, although many have a vesicular nucleus with a central endosome. Infections by the species *E. histolytica* may cause amoebic dysentery and secondary 'abscesses' in humans.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Phylum: Amoebozoa (locomotion by noneruptive pseudopodia, asexual development)
Subphylum: Conosa (archamoebae & mycetozoa, many flagellated forms, flagellar root with microtubular cone)
Class: Archamoebae (amoebae (no flagellates), cysts rounded, uni-/multi-nucleate, amitochondriate)
Family: Entamoebidae (uninucleate amoeboid forms, symbiotic in digestive tract of vertebrates)
Genus: *Entamoeba* (parasitic in digestive tracts of vertebrates)
Species: *E. histolytica* (causes amoebic dysentery in humans and primates)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Amoebae form pseudopodia to move and feed. Several types of amoebae are recognized on the basis of differences in their biology and morphology, with recent molecular phylogenetic studies supporting their classification into three major disparate phyla: Heterolobosea (supergroup Excavata), Amoebozoa (supergroup Amorphea) and Rhizaria (supergroup SAR). Most species are free-living in aquatic and terrestrial habitats where they feed on other micro-organisms, but several species have become symbiotic in metazoan organisms as endocommensals or opportunistic-facultative parasites (representatives tabulated below).

Higher taxonomy	Class/Order	Family	Genus	Hosts	Tissues (disease)*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: **Discoba** (diverse group supported robustly by molecular studies)					
Phylum: Heterolobosea (amoebo-flagellates, most form cysts)	O: Schizopyrenida (no fruiting bodies)	Vahlkampfidae (eruptive limax pseudopodia, flagellated stages)	*Naegleria*	mammals	central nervous system (PAM)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)					
Phylum: **Amoebozoa** (locomotion by noneruptive pseudopodia, asexual development)					
Subphylum: Conosa (archamoebae & mycetozoa)	C: Archamoebae (amitochondriate, rounded cysts)	Entamoebidae (uninucleate, endozoic)	*Entamoeba*	mammals	colon (dysentery), central nervous system (SAM)
Subphylum: Lobosa (lobose amoebae)	C: Discosea (flattened forms, protoplasmic flow polyaxial)	Vexilliferidae (dactylopodia, parasomes)	*Paramoeba* *Neoparamoeba*	fish	gills (AGD)
	C: Longamoebea (flattened elongated cells, stellate cysts)	Acanthamoebidae (acanthopodial subpseudopodia)	*Acanthamoeba, Balamuthia*	mammals	central nervous system (GAE)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups robustly supported by molecular studies)					
Group: **Rhizaria** (amoebae with fine pseudopodia in simple, branching or anastomosing patterns)					
Phylum: Cercozoa	Filosa (with filopodia, naked or testate)			free-living (aquatic, terrestrial)	

Phylum: Endomyxa	heterotrophic amoeboid or plasmodial cells	free-living, some parasitoids
Phylum: Retaria	Foraminifera (with reticulopodia), Radiolaria (with axopodia)	free-living (aquatic)

*PAM = primary amoebic meningoencephalitis; SAM = secondary amoebic meningoencephalitis; GAE = granulomatous amoebic encephalitis; AGD = amoebic gill disease.

Amoebae that move using noneruptive pseudopodia are placed in the phylum Amoebozoa, either in the subphylum Lobosa (with lobose pseudopodia) or Conosa (with microtubular cones). Conose amoebozoans include the Mycetozoa (slime molds with fruiting bodies) and the unique Archamoebae, thought to be 'ancient' as they lack mitochondria and dictyosomes (Golgi bodies) but possess mitosomes (presumably modified/reduced mitochondria). Most archamoebae are parasites or endocommensals in the digestive tracts of arthropod or vertebrate hosts. They are naked amoebae (without tests or shells) and have simple life-cycles (without temporary flagellated stages). They form motile feeding trophozoites with single broad lobopodia and most form environmentally resistant cysts to facilitate transmission and dispersal. Some 50 *Entamoeba* spp. have been described primarily in mammals and a few in birds, reptiles and fish. Four basic groups are recognized on the basis of parasite morphology: those not forming cysts and those forming uninucleate, quadrinucleate or octonucleate cysts. In many instances, these morphotypic groupings were supported by molecular phylogenetic studies. *Entamoeba histolytica* is predominantly found in primates (including humans) and occasionally in dogs, cats, cattle, pigs and rodents. This species may cause amoebic dysentery in humans as well as extra-intestinal amoebic abscesses in soft tissues. The parasite has a worldwide distribution and is prevalent in tropical and subtropical countries (estimated prevalence as high as one tenth of the world's population, with 100,000 deaths annually). It is readily confused with *Entamoeba dispar*, a species which is identical in appearance but is not considered to be pathogenic (although it has recently been found in some diarrhoeic patients). The species *E. hartmanni* was originally thought to be a 'small race' of *E. histolytica*, but it has not been associated with disease. Another species *Entamoeba polecki* has occasionally been found in association with disease in pigs, monkeys and rarely humans. The species *Entamoeba moshkovskii* was originally only found in sewage, but it has also recently been found in symptomatic patients. *E. gingivalis* is found in the oral cavity of humans, sometimes in individuals with gum disease. The nonpathogenic species *E. coli* is commonly found in humans throughout the world. *Entamoeba invadens* is considered to be a serious pathogen of reptiles, especially in captive snakes and lizards. Other enteric amoebae found in humans, *Iodamoeba butschlii*, *Endolimax nana* and *Dientamoeba fragilis* (now considered to be a flagellate), are still considered to be nonpathogenic endocommensals.

***Entamoeba* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
species with quadrinucleate mature cysts (*E. histolytica*-like group)				
E. anatis	Anseriformes: anatid (ducks); Otidiformes: otidid (bustards)	caecum	enteritis	South Africa, Asia, North America
E. bangladeshi	Primates: hominid (human)	large intestines	nonpathogenic	Bangladesh
E. ctenopharyngodoni	freshwater Cypriniformes: cyprinid (grass carp)	rectum	nonpathogenic	China
E. curens	Anura: ranid (pond frogs), bufonid (toads)	large intestines		India
E. dispar	Primates: hominid (human, chimpanzee), cercopithecid (red-tailed monkey, langurs, leaf monkeys, mandrill), atelid (woolly monkey), pitheciid (white-faced saki), hylobatid (siamang)	large intestines	nonpathogenic (but found in some patients with diarrhoea)	worldwide
E. ecuadoriensis	sewage	-	-	Ecuador
E. equi	Perissodactyla: equid (horse)	large intestines	enteritis	South America
E. hartmanni (syn. *E. minuta p.p., minutissima, tenuis*)	Primates: hominid (human), atelid (howler monkeys, woolly monkeys), cercopithecid (langurs, leaf monkeys, mandrill)	large intestines	nonpathogenic	worldwide
E. histolytica (syn. *E. africana, brasiliensis, caudata, dysenteriae, minuta p.p., nipponica, schaudinni, tetragena, venaticum*)	Primates: hominid (human), cercopithecid (langurs, colobus, leaf monkeys, rhesus, Barbary macaque, pig-tailed macaque, mandrill, patas monkey, DeBrazza's monkey, vervet monkey, grivet monkey, green monkey, white-nosed monkey, Campbell's monkey, Celebes crested macaque), atelid (howler monkey, spider monkeys, woolly monkeys), callitrichid (tamarins), lemurid (brown lemur); occasionally Carnivora: canid (dog), felid (cat); Artiodactyla: suid (pig), bovid (cattle); Rodentia: murid (rats, mice)	large intestines (may spread to soft tissues, esp. liver, brain)	dysentery, ulceration, abscesses	worldwide
E. ilowaiskii	Anura: ranid (pond frogs)	large intestines	pathogenic	unknown
E. insolita	Testudines: testudinid (tortoise)	large intestines	enteritis	unknown

E. invadens (syn. *E. serpentis*)	Serpentes: pythonid (African rock python, Indian python, blood python), colubrid (mussurana, indigo snake, black racer, eastern racer, Brazilian bird snake, Brazilian smooth snake, viperine snake, grass snake, king snake, garter snake, pond snake, striped house snake, water snakes); boid (tree boa, slender, boa constrictor, anaconda), elapid (spitting cobra, black-and-white cobra, black-necked cobra), viperid (copperhead, Gaboon viper, night adder); Sauria: anguid (slow-worm), lacertid (wall lizards), varanid (Komodo dragon, Bengal monitor, water monitor, lace monitor), scincid (blue-tongued skink), iguanid (green iguana), diplodactylid (crested geckos), sphenodontid (tuatara); Testudines: testudinid (red-footed tortoise, spider tortoise, giant tortoise), kinosternid (loggerhead musk turtle), emydid (wood turtle, painted turtle, box turtles), cheloniid (loggerhead sea turtle, green sea turtle); Crocodilia: crocodylid (crocodiles), alligatorid (alligator)	intestines (may spread to soft tissues)	regurgitation, diarrhoea, tissue invasion	worldwide
E. knowlesi	Testudines: emydid (box turtle), platysternid (big-headed turtle)	large intestines	nonpathogenic	Asia
E. lagopodis	Anseriformes: anatid (ducks); Galliformes: phasianid (ptarmigans)	caecum	nonpathogenic	unknown
E. moshkovskii	sewage, recently in Primates: hominid (human)	large intestines	nonpathogenic (but found in some patients with diarrhoea)	Europe, North America, Africa, India, Australia
E. nuttali (syn. *E. ateles, cynomolgi, duboscqi*)	Primates: hominid (chimpanzee), cercopithecid (rhesus, macaques, baboon), plus experimental infection in Rodentia: cricetid (hamster)	large intestines	enteritis (may spread to soft tissues)	Japan, China, Sri Lanka
E. pyrrhogaster	Anura: ranid (pond frogs), bufonid (toads); Urodela: salamandrid (fire newts, crested newts)	large intestines	nonpathogenic	Asia
E. ranarum	Anura: ranid (pond frogs), Urodela: ambystomatid (mole salamander)	large intestines (may spread to soft tissues)	enteritis, extraintestinal lesions	worldwide
E. salpae	marine Perciformes: sparid (Salema porgy)	gut	nonpathogenic	Europe
E. terrapinae	Testudines: emydid (painted turtle)	colon	nonpathogenic	worldwide
E. testudinis	Testudines: testudinid (tortoises), emydid (painted turtle)	colon	nonpathogenic	unknown
E. varani	Sauria: varanid (Nile monitor)	colon	nonpathogenic	Africa
species with uninucleate mature cysts (*E. bovis*-like group)				
E. antelocaprae	Artiodactyla: bovid (antelope)	large intestines	lesions, inflammation	Americas
E. bovis	Artiodactyla: bovid (cattle, buffalo)	large intestines	nonpathogenic	Africa
E. bubalis	Artiodactyla: bovid (buffalo)	large intestines	nonpathogenic	Philippines
E. chattoni	Primates: cercopithecid (macaques, rhesus), occasionally hominid (human)	large intestines	nonpathogenic	Africa
E. dilimani (syn. *E. debliecki p.p.*)	Artiodactyla: bovid (goat)	large intestines	nonpathogenic	Philippines
E. gadi	marine Gadiformes: gadid (pollock)	rectum	nonpathogenic	North America
E. nezumia	marine Gadiformes: macrourid (grenadier)	stomach, intestines	nonpathogenic	North Atlantic
E. ovis (syn. *E. debliecki p.p.*)	Artiodactyla: bovid (sheep, goat)	large intestines	nonpathogenic	worldwide

E. pimelodi	freshwater Siluriformes: pimelodid (catfish)	gut	nonpathogenic	South America
E. polecki (syn. *E. debliecki p.p.*)	Artiodactyla: suid (pig), bovid (cattle, sheep, goat); Primates: cercopithecid (macaques, langur), callitrichid (tamarins); occasionally hominid (human)	large intestines	subclinical, occasionally diarrhoea	South-East Asia, Americas, Europe, Middle-East
E. suis (syn. *E. debliecki p.p.*)	Artiodactyla: suid (pig)	large intestines	nonpathogenic	Asia, Europe, Americas
E. struthionis	Struthioniformes: struthionid (ostrich)	large intestines	nonpathogenic	Europe
species with octonucleate mature cysts (*E. coli*-like group)				
E. chiropteris	Chiroptera: vespertilionid (lesser Asiatic yellow bat)	large intestines	nonpathogenic	India
E. citelli	Rodentia: sciurid (squirrel)	large intestines	nonpathogenic	unknown
E. cobayae (syn. *E. caviae*)	Rodentia: caviid (guinea pig)	large intestines	nonpathogenic	worldwide
E. coli (syn. *E. hominis, loeschi*)	Primates: hominid (human), atelid (howler monkeys, woolly monkeys), cercopithecid (langurs, redtail monkey, mandrill)	large intestines	nonpathogenic	worldwide
E. criceti	Rodentia: cricetid (hamster)	large intestines	nonpathogenic	unknown
E. cuniculi	Lagomorpha: leporid (rabbit)	large intestines	nonpathogenic	Russia, Korea
E. dipodomysi	Rodentia: heteromyid (kangaroo rat)	large intestines	nonpathogenic	North America
E. flaviviridis	Sauria: phyllodactylid (wall geckos), scincid (mabuya skinks)	intestines	nonpathogenic	Sudan
E. funambulae	Rodentia: sciurid (palm squirrel)	large intestines	nonpathogenic	India
E. gallinarum	Galliformes: phasianid (fowl)	caecum	nonpathogenic	worldwide
E. lacerticoli	Sauria: xantusiid (night lizard), iguanid (desert iguana, fence lizard, side-blotched lizard, zebra-tailed lizard, chuckwalla)	intestines	nonpathogenic	North America
E. marmotae	Rodentia: sciurid (marmot)	large intestines	nonpathogenic	unknown
E. muris (syn. *E. ratti*)	Rodentia: murid (rats, mice), cricetid (hamster)	large intestines, caecum	nonpathogenic	worldwide
E. wenyoni	Artiodactyla: bovid (goat), camelid (camel)	large intestines	nonpathogenic	unknown
species with cysts (number of nuclei unknown)				
E. chiangraiensis	freshwater Synbranchiformes: synbranchid (Asian swamp eel)	gut	nonpathogenic	Asia
species without cysts (*E. gingivalis*-like group)				
E. barreti	Testudines: chelydrid (snapping turtles)	colon	nonpathogenic	unknown
E. caprae	Artiodactyla: bovid (goat)	large intestines	nonpathogenic	unknown
E. gedoelsti (syn. *E. intestinalis*)	Perissodactyla: equid (horse)	caecum, large intestines	nonpathogenic	unknown
E. gingivalis (syn. *E. buccalis, canibuccalis, equibuccalis, maxillaris, suigingivalis*)	Primates: hominid (human), cercopithecid (macaques); Artiodactyla: suid (pig), Perissodactyla: equid (horse); Carnivora: canid (dog), felid (cat)	oral cavity	nonpathogenic (but found in some humans with gum disease)	worldwide
E. molae	marine Tetraodontiformes: molid (sunfish)	hindgut	nonpathogenic	North America
species for which cyst formation is uncertain				
E. synodontis	freshwater Siluriformes: mochokid (wahrindi)	gut	nonpathogenic	Africa

Parasite morphology: The parasite alternates between two different developmental stages: trophozoites and cysts. The trophozoites are irregular in shape measuring from 10-40 µm in diameter and contain a vesicular nucleus with a central endosome (karyosome), peripheral chromatin and radial achromatic fibrils (imparting a 'cart-wheel' appearance). Trophozoites have granular cytoplasm containing food vacuoles and invasive forms commonly engulf host erythrocytes. The trophozoites move by protoplasmic streaming and form single clear broad pseudopodia (lobopodia). The cysts are spherical measuring 10-16 µm in diameter and contain four nuclei when mature. Immature cysts may also contain a characteristic oblong chromatoid bar formed by semicrystalline aggregations of ribosomes.

Site of infection: Most *Entamoeba* spp. have been detected in the large intestines of their vertebrate hosts, often ranging from the caecum to the rectum. Several species have also been found in extra-intestinal locations, particularly soft tissues such as the liver and brain. *E. histolytica* trophozoites generally reside in the lumen of the large intestines but they may invade the colonic mucosa, perforate the gut and cause extra-intestinal lesions in other organs (especially liver, lungs and brain). Cysts are not formed in host tissues but are passed in faeces to the external environment.

Pathogenesis: In most infections, trophozoites stay confined to the gut lumen (effectively behaving as commensals) and do not cause any disease manifestations (asymptomatic). However, under certain conditions (still to be determined), *E. histolytica* trophozoites may adhere to colonic epithelial cells (using galactose-specific lectin receptors) and then invade the mucosa. This results in mild to severe clinical signs involving diarrhoea, amoebic dysentery (with mucus and blood), abdominal pain, weight loss and fatigue. Disease onset may be gradual over weeks, while disease duration may be persistent becoming worse with time. Invasion of the gut mucosa may cause flask-shaped erosive ulcers ('amoebomas') resulting in amoebic colitis. Trophozoites involved in tissue invasion are often observed to have ingested host erythrocytes. Parasite enzymes (such as cysteine proteases, lipases and amoebapores (pore-forming proteins)), normally used for digestive processes, may also cause lysis, necrosis and apoptosis of host cells. The species name '*histo-lytica'* literally means 'tissue-destroyer'. Considerable variation has been observed in the pathogenicity (virulence) of different isolates, with multiple mechanisms being implicated, including parasite adherence, multiplication, phagocytosis, cytolysis and immunomodulation. Invasive strains are resistant to complement-mediated lysis, but provoke cell-mediated inflammatory responses involving neutrophils and macrophages. Some infections may progress to extra-intestinal involvement when trophozoites penetrate the submucosa and disseminate via the circulation or lymphatics to other organs; mainly the liver via the portal circulation, but sometimes the lungs and occasionally the brain, heart, spleen or skin (*E. histolytica* causes SAM, secondary amoebic meningoencephalitis). The parasites may form space-occupying lesions or amoebic 'abscesses' up to several centimetres in diameter (not conventional abscesses as they are bacteriologically sterile). Liver disease is characterized by fever, hepatomegaly and abdominal pain. Ulcers and 'abscesses may perforate the lining of the infected organ and rupture into the peritoneum, pleural cavity or pericardium causing complicated infections, hyperaemia, acute inflammation with predominantly neutrophils, septicaemia and fatalities.

Developmental cycle and mode of transmission: Infections undergo faecal-oral transmission between hosts via the contamination of food and water by cysts from infected hosts and their subsequent ingestion by new susceptible hosts. *E. histolytica* trophozoites passing posteriad condense into spherical precysts (containing chromatoidal bars) which then mature into cysts (containing four nuclei). The cysts are very resistant to environmental conditions and may survive for months in suitable moist conditions, especially in the tropics. When cysts are ingested with contaminated food or water, excystation occurs within hours in the intestines and multiple trophozoites emerge from each cyst (nuclear division and cytokinesis may produce eight emergent trophozoites). The trophozoites colonize the large intestines over days where they feed and divide by binary fission. Rapid population growth may occur culminating in disease although the clinical course of infection generally becomes progressively worse over weeks. Most infections have been traced to human sources of infection, as many infected people are asymptomatic cyst-shedders who act as reservoir hosts. Nonetheless, zoonotic transmission from companion animals and vermin has been implicated epidemiologically, and coprophagous insects may help disseminate infections by mechanical transmission of cysts to food.

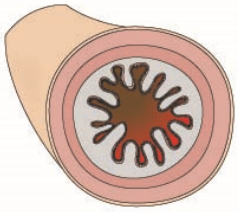
Differential diagnosis: Infections are conventionally diagnosed by repeated stool examinations for motile trophozoites and non-motile cysts. *E. histolytica* trophozoites may be detected by direct microscopy of fresh warm aliquots mixed with saline, but they rapidly lose their motility in aged, cooled or refrigerated samples. Similarly, aspirates of 'abscesses' must be examined quickly to detect haematophagous trophozoites. Amoebae can be cultured in various axenic or xenic (monophasic or diphasic) media to amplify their numbers. Most often, faecal samples are fixed to comply with transport and laboratory occupational health and safety requirements. Cysts can be concentrated from samples (ethyl acetate, formol-ether techniques) stained with iodine, or detected in permanent faecal smears stained with Trichrome or iron haematoxylin. Considerable expertise is required to differentiate pathogenic species from harmless commensals on the basis of nuclear and cyst morphology. Because cyst excretion can be intermittent, multiple faecal samples should be examined before amoebic infections can be ruled out. *E. histolytica, E. dispar, E. polecki* and *E. moshkovskii* all form medium-sized cysts with four nuclei, and can only be reliably differentiated by molecular characterization (isoenzymes, antigens or nucleotide sequences). *E. hartmanni* forms smaller cysts with four nuclei and *E. coli* forms larger cysts with up to eight nuclei. Serological tests for specific host antibodies (complement fixation, agglutination, fluorescence, and enzyme immuno-assays) have been developed to help diagnose invasive and/or extra-intestinal infections, but they cannot be used to detect asymptomatic carriers as lumen-only infections rarely elicit immunological responses. Monoclonal antibodies have been incorporated into several copro-antigen test kits, and immuno-chromatographic assays have been used to type parasite antigens. Isoenzyme electrophoresis (notably glucose phosphate isomerase, hexokinase, malic enzyme, and phosphoglucomutase zymodemes) have previously been used to differentiate amoebae species, but have now been superseded by polymerase chain reaction (PCR) amplification of unique nucleotide sequences (notably genes encoding rRNA or membrane antigens).

Human enteric amoebae	Cyst diameter	Number of nuclei per cyst	Nuclear characteristics	Erythrophagocytosis

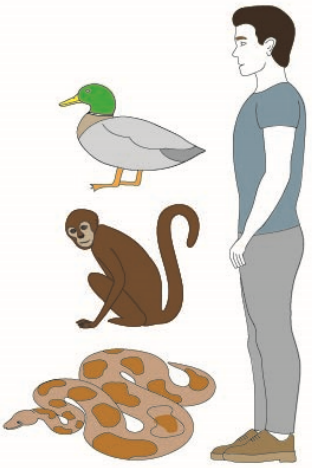
Entamoeba histolytica	10-15 µm	4	cartwheel	present in invasive forms
Entamoeba dispar	10-15 µm	4	cartwheel	absent
Entamoeba moshkovskii	10-15 µm	4	cartwheel	absent
Entamoeba polecki	10-15 µm	4	cartwheel	absent
Entamoeba hartmanni	5-9 µm	4	cartwheel	absent
Entamoeba coli	15-30 µm	8	cartwheel	absent
Iodamoeba butschlii	9-15 µm	1	granular endosome	absent
Endolimax nana	6-9 µm	1	endosome halo	absent
Dientamoeba fragilis	no cyst		now considered to be a flagellate	

Treatment and control: Patients may be treated with luminal, hepatic and/or tissue amoebicides as warranted, although complete cure is difficult to attain. Older drugs such as emetine and dehydroemetine are still used intramuscularly, while oral 5-nitroimidazole formulations (metronidazole, tinidazole and ornidazole) are effective tissue amoebicides, sometimes in association with tetracycline. Chloroquine has been shown to kill amoebae in liver lesions but not elsewhere. Large hepatic ‘abscesses’ may require surgical drainage of the ‘anchovy-sauce’ pus. Paromomycin, diloxanide and iodoquinol have been used to treat luminal and asymptomatic infections. Disease has been strongly associated with poor sanitation, especially with respect to disposal of human faeces and the quality of water supplies. High infection rates have been found in orphanages, mental institutions, military camps and amongst lower socio-economic groups living in crowded conditions. Disease may be more severe in populations that subsist primarily on high carbohydrate and low protein diets. Control may be facilitated by maintaining high standards of hygiene, especially for those involved in food handling and preparation. Food should be protected from flies and cockroaches, and potable water supplies should be treated (filtration and/or chlorination). Water and sewer systems should be properly maintained and sewage treatment or faecal waste disposal/containment should be used to reduce environmental contamination.

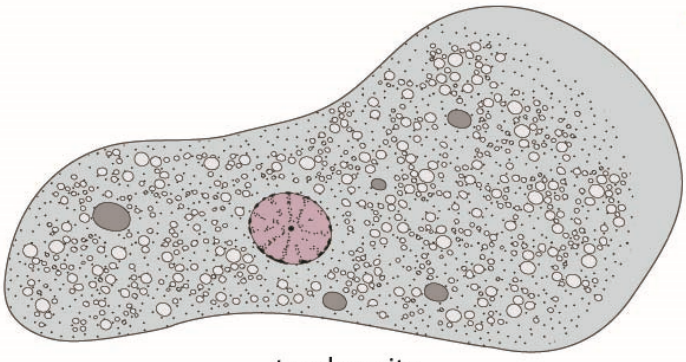
Entamoeba



colon
(dysentery, ulceration, hepatic abscesses, secondary amoebic meningoencephalitis)



Vertebrate Hosts
(mammals, some reptiles, birds))



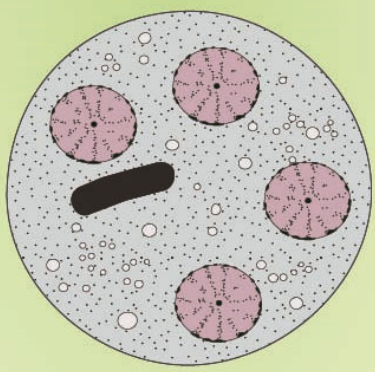
single clear lopopod

trophozoite
(10-40 µm)



cysts ingested

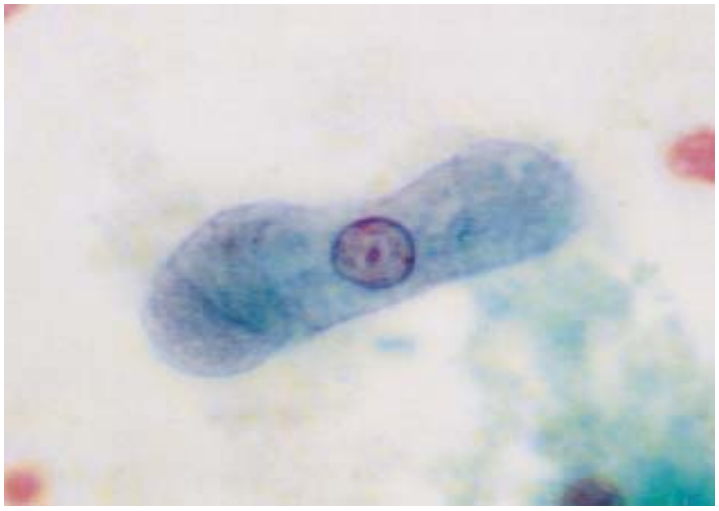
cysts excreted in faeces



often with chromatoid bar

cyst
(10-16 µm)

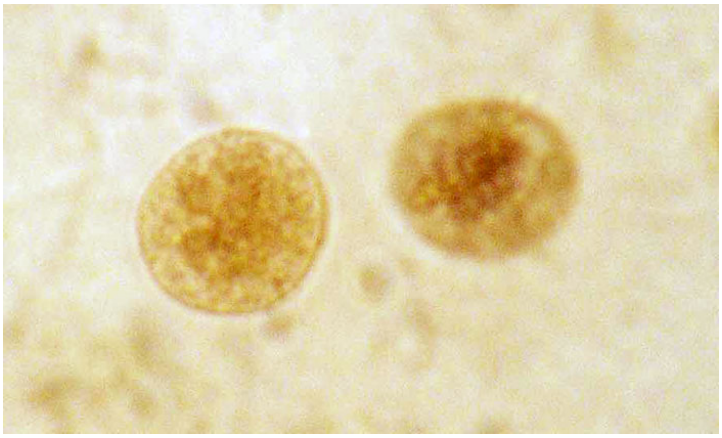
faecal-oral transmission
via contaminated food/water



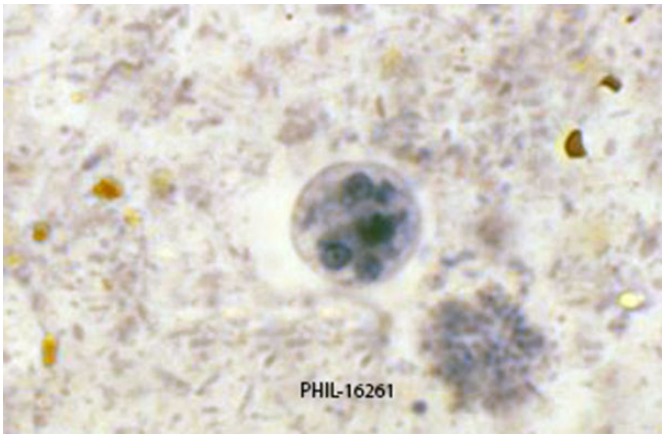
Entamoeba trophozoite



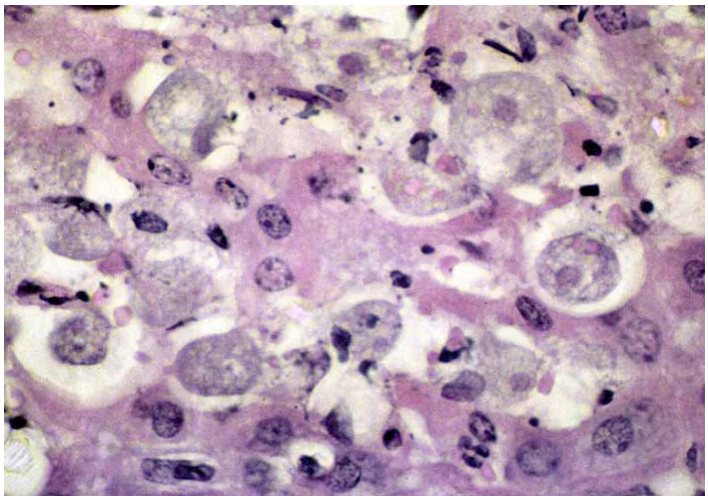
Entamoeba trophozoite



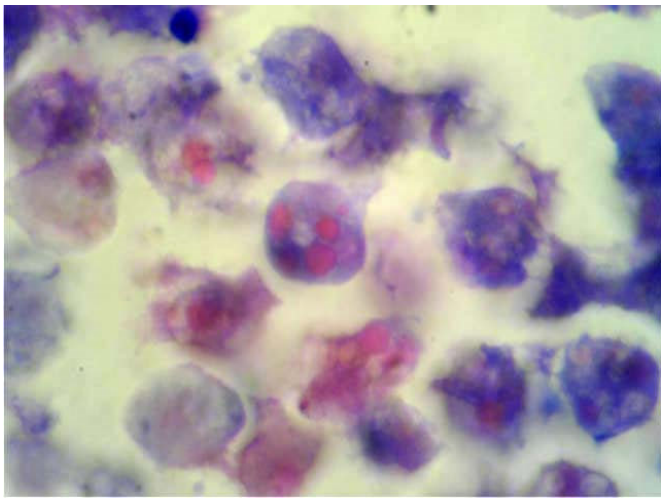
Entamoeba cysts



Entamoeba cyst



Entamoeba liver lesion



Entamoeba brain lesion

Neoparamoeba/Paramoeba
(protist: amoeba)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Protists which move and feed using pseudopodia (false feet) are known as amoebae. Rather than forming a monophyletic group, amoebae are divided into three major disparate groups: Heterolobosea (supergroup Excavata), Rhizaria (supergroup SAR) and Amoebozoa (supergroup Amorphea). The latter contains four classes of amoebae differing in their types of pseudopodia and organelles: Tubulinea, Discosea, Gracilipodia and Archamoebae. Discosean amoebae are flattened in profile and form broad lobopodia. Vexilliferid amoebae form digitiform (finger-like) subpseudopodia (dactylopodia) emerging from the cell-wide lobopodium and most species have a fibrillar surface layer (glycocalyx) with embedded scales. Most species do not form cysts and are found as free-living aquatic organisms, although some can be opportunistic pathogens of marine hosts. The paramoebae are characterized by the presence of parasomes (Nebenkorper) which are semi-crystalline folded arrays on minicircle DNA in the kinetoplasts (mitochondria) of eukaryotic endosymbionts. Several species have been linked to disease and death in marine fish and invertebrates. *Neoparamoeba perurans* is currently recognized as the aetiological agent of amoebic gill disease (AGD) principally of salmonids, although other species (*N. pemaquidensis*, *N. branchiphila*) may be associated with diseases.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Phylum: Amoebozoa (locomotion by noneruptive pseudopodia, asexual development)
Subphylum: Lobosa (with lobose pseudopodia)
Class: Discosea/Flabellinea (flattened forms, protoplasmic flow polyaxial)
Order: Dactylopodida (tapering finger-like subpseudopodia (= dactylopodia), most do not form cysts)
Family: Vexilliferidae (long slender subpseudopodia, spiny appearance, many with glycostyles/scales on cell surface, paramoebids with parasomes (Nebenkorper) near nucleus)
Genus: *Neoparamoeba/Paramoeba* (parasitic on gills of fish, trophozoites without scales)
Species: various species (cause amoebic gill disease (AGD), mainly in salmonids)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Amoebae form pseudopodia to move and feed. Several types of amoebae are recognized on the basis of differences in their biology and morphology, with recent molecular phylogenetic studies supporting their classification into three major disparate phyla: Heterolobosea (supergroup Excavata), Amoebozoa (supergroup Amorphea) and Rhizaria (supergroup SAR). Most species are free-living in aquatic and terrestrial habitats where they feed on other micro-organisms, but several species have become symbiotic in metazoan organisms as endocommensals or opportunistic-facultative parasites (representatives tabulated below).

Higher taxonomy	Class/Order	Family	Genus	Hosts	Tissues (disease)*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: **Discoba** (diverse group supported robustly by molecular studies)					
Phylum: Heterolobosea (amoebo-flagellates, most form cysts)	O: Schizopyrenida (no fruiting bodies)	Vahlkampfidae (eruptive limax pseudopodia, flagellated stages)	*Naegleria*	mammals	central nervous system (PAM)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)					
Phylum: **Amoebozoa** (locomotion by noneruptive pseudopodia, asexual development)					
Subphylum: Conosa (archamoebae & mycetozoa)	C: Archamoebae (amitochondriate, rounded cysts)	Entamoebidae (uninucleate, endozoic)	*Entamoeba*	mammals	colon (dysentery), central nervous system (SAM)
Subphylum: Lobosa (lobose amoebae)	C: Discosea (flattened forms, protoplasmic flow polyaxial)	Vexilliferidae (dactylopodia, parasomes)	*Paramoeba* *Neoparamoeba*	fish	gills (AGD)
	C: Longamoebea (flattened elongated cells, stellate cysts)	Acanthamoebidae (acanthopodial subpseudopodia)	*Acanthamoeba, Balamuthia*	mammals	central nervous system (GAE)

Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups robustly supported by molecular studies)		
Group: **Rhizaria** (amoebae with fine pseudopodia in simple, branching or anastomosing patterns)		
Phylum: Cercozoa	Filosa (with filopodia, naked or testate)	free-living (aquatic, terrestrial)
Phylum: Endomyxa	heterotrophic amoeboid or plasmodial cells	free-living, some parasitoids
Phylum: Retaria	Foraminifera (with reticulopodia), Radiolaria (with axopodia)	free-living (aquatic)

*PAM = primary amoebic meningoencephalitis; SAM = secondary amoebic meningoencephalitis; GAE = granulomatous amoebic encephalitis; AGD = amoebic gill disease.

Amoebae that move using noneruptive pseudopodia are placed in the phylum Amoebozoa, either in the subphylum Lobosa (with lobose pseudopodia) or Conosa (with microtubular cones). Lobose amoebozoans include the Dactylopodida with finger-like subpseudopodia (= dactylopodia) and the Centramoebida with finely-tapering subpseudopodia (= acanthopodia). Vexilliferids are spiny dactylopodid amoebae most of which do not form cysts. They include the paramoebae which are characterized by the possession of parasomes (Nebenkorper) adjacent to the nucleus. They are naked amoebae (without tests or shells) and have simple life-cycles (without temporary flagellated stages). Paramoebae are found free-living in marine waters throughout the world, particularly in areas with high levels of nutrients such as tidal marshes, intertidal zones and marine sediments. Several species have been found as opportunistic pathogens in fish, particularly in association with amoebic gill disease (AGD) in salmonids. The causative agent of AGD may not be a single species but an assemblage of similar species. Amoebae recovered from affected fish were initially identified morphologically as *Paramoeba pemaquidensis*, and later reassigned to the genus *Neoparamoeba* when it was found they lacked surface scales. Molecular studies using 18S rRNA gene sequences then led to the differentiation and characterization of *N. pemaquidensis* and *N. branchiphila* from the gills of affected fish, but their role in AGD aetiology was presumptive. Recent molecular studies, including fluorescent *in situ* hybridization (FISH), demonstrated the aetiological agent of AGD to be the novel species *N. perurans* and this work has been validated by parasite culture and experimental transmission studies (thus fulfilling Koch's postulates). Infections are found predominantly in cultured salmonids, including sea-caged Atlantic salmon and rainbow trout in Tasmania, pen-reared coho in USA and Canada and chinook salmon in New Zealand. Several *Paramoeba* species have also been found in association with mass mortalities in crabs, sea urchins and lobsters, predominantly in North America.

Protozoan species	Hosts	Sites	Disease	Geographic location
Neoparamoeba branchiphila	Salmoniformes: salmonid (Atlantic salmon)	gills	AGD?	Australia
Neoparamoeba pemaquidensis	Salmoniformes: salmonid (Atlantic salmon, rainbow trout, brown trout), Pleuronectiformes: pleuronectid (flounder), Scombriformes: gempylid (barracouta), Perciformes: serranid (seabass, seabream), Syngnathiformes: syngnathid (seahorses)	gills	AGD?	Australia, North America, Europe
Neoparamoeba perurans	Salmoniformes: salmonid (Atlantic salmon, coho, chinook, rainbow trout), Pleuronectiformes: pleuronectid (turbot), Osmeriformes: plecoglossid (ayu)	gills	amoebic gill disease (AGD)	Australia, New Zealand, North and South America, Europe
Paramoeba invadens	Echinodermata: echinoid (sea urchins)	radial nerve/water vascular canal tissues	mass mortality	North America
Paramoeba pernicosa	Crustacea: portunid (blue crab, rock crab, European green crab)	haemal spaces, connective tissue, organs	gray crab disease	North America
Paramoeba sp.	Crustacea: nephropid (lobster)	nervous system, muscles, gills	red tail, limp lobster	North America

Parasite morphology: These small lobose amoebae have only been found as trophozoites (cyst formation does not occur) and they lack the well-organized cell surface structures of other vexilliferids (such as hexagonal glycostyles or surface scales). The trophozoites are subspherical measuring from 15-40 μm in length although they can range in size from 10-75 μm. They form numerous (up to 50) digitiform pseudopodia when floating and mammiliform pseudopodia when adherent to substrates. Trophozoites have an extensively flattened hyaline zone with an irregular anterior margin, and occasionally conical pseudopodia projecting forwards. The trophozoites contain a single vesicular nucleus (5-7 μm in diameter) with a large central endosome as well as one or more intracellular perinuclear bodies (2-5 μm) known as parasomes (or secondary nuclei, Nebenkorper, amphisomes) which have recently been found to be folded arrays of minicircle DNA in the kinetoplast of eukaryotic endosymbionts known as *Perkinsiella amoebae*-like organisms (PLOs) related to the marine flagellates *Ichthyobodo*.

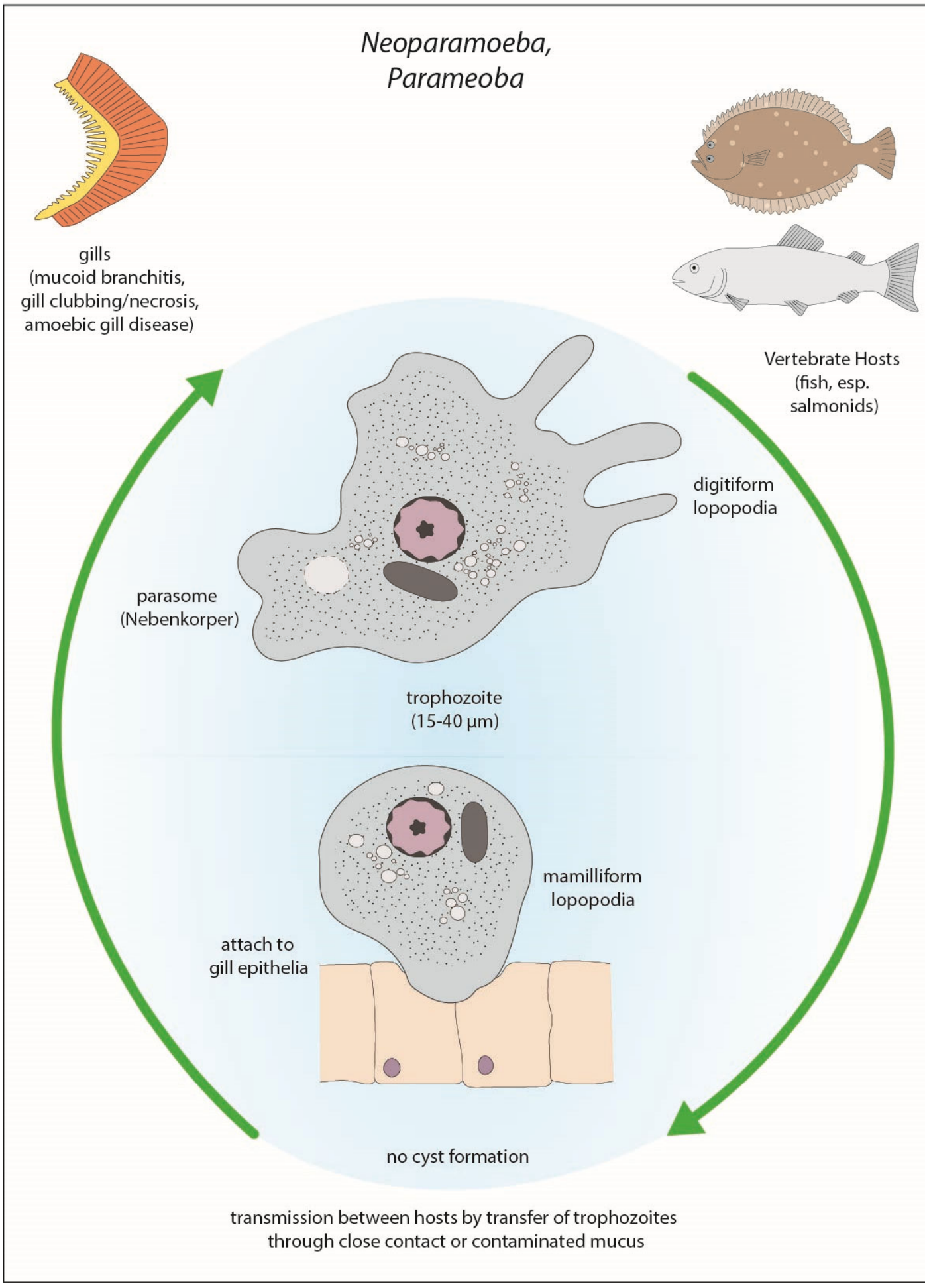
Site of infection: In fish, amoebae attach themselves to the surfaces of the gills and rarely penetrate the epithelium. In blue crabs, amoebae were found haemal spaces, connective tissues, muscles, hepatopancreas and in heavy infections, in the central nervous system. In sea urchins, amoebae were widespread in all tissues but consistently localized in radial nerve/water vascular canal tissue. In lobster, amoebae were frequently detected in the central nervous system but also in the gills and muscles.

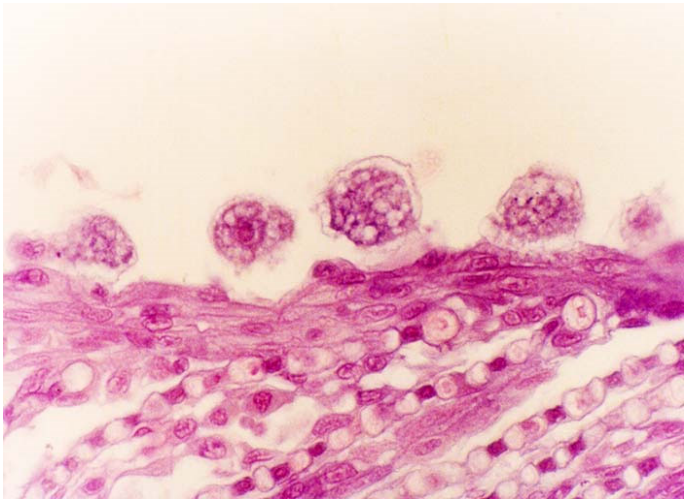
Pathogenesis: In fish, the attachment of amoebae to the gill epithelia resulted in extensive epithelial hyperplasia and hypertrophy with proliferation of amoebae in multifocal lesions. Fish became lethargic and displayed respiratory distress with flared opercula and behavioural changes, such as accumulating at the surface, reduced feeding and sometimes reversed postures (ventral side up). There was extensive mucus on the gills (mucoid branchitis) with clubbed necrotic gill filaments developing focal white-grey patches in heavy infections, conditions drastically reducing gill function and possibly predisposing to secondary bacterial infections. Histologically, there was prominent epithelial hyperplasia and fusion of distal portions of the secondary lamellae, often resulting in the formation of large interlamellar vesicles. Mortalities up to 50% have been reported. Fish vary greatly in their susceptibility to AGD, with Atlantic salmon and rainbow trout being most susceptible. Fish with existing gill lesions due to jellyfish damage, clubbing and necrosis gill syndrome are often rapidly colonized by amoebae with severe outcomes. In crabs, clinical signs included tissue displacement and lysis (esp. hemocytes) with significant decreases in haemocyanin contributing to the grayish appearance of the ventral exoskeleton (hence the name gray crab disease). In sea urchins, parasites were associated with significant decreases in coelomocytes and mass mortalities. In lobsters, amoebae were associated with lethargy and coagulopathy (‘limp lobster’) and morbid lobster frequently had red discolouration (gaffkemia) typical of ‘red tail’.

Developmental cycle and mode of transmission: The amoebae are normally free-living marine organisms but they can opportunistically infect fish (termed amphizoic). AGD is transmitted horizontally when mucus containing amoebae sloughs off infected gills into the water column and amoebae are then free to colonize the gills of other fish. Attachment to the gills is facilitated by lectin/glycoconjugated bonds and characteristic gill lesions appear 2-4 days later and dramatically increase by day 7. Infections are most prevalent during late summer and autumn, in seawater at temperatures of 8-9°C or above, and in seawater with high salinity (>32 ppt (parts per thousand)), although infections have been found at 7.2 ppt. Infections in crabs may also be transmitted by the consumption of moribund or dead crabs.

Differential diagnosis: AGD is diagnosed by the detection of large numbers of amoebae in fresh wet mounts of gills, although they can be difficult to differentiate from epithelial cells. Amoebae can be found in stained histological sections (especially using periodic acid-Schiff’s (PAS) reagent), but their numbers may be reduced due to detachment from gill surfaces during fixation and processing. Nuclei and parasomes are readily visible using Feulgen DNA stains. Polyclonal antibodies have been developed to immunolabel amoebae in sections, but they exhibit cross-reactivity between different species. Amoebae can be cultured *in vitro* from clinical samples, either by malt yeast agar with seawater overlaid or on salmon embryo cell lines. Different amoebae species are relatively similar morphologically - they are best differentiated by PCR amplification of 18S rRNA gene sequences.

Treatment and control: Outbreaks of AGD in tanks and pens have been associated with high stocking densities (overcrowding), microfouling and biofouling (often due to overfeeding and organic enrichment), stagnant water (poor flow), warm water (12-20ºC) and high salinity (>32 ppt). Conventional external treatments of affected fish with formalin, chelated copper, diquat, malachite green and chloramine were not preventive or curative. The most effective treatment was freshwater bathing of diseased fish for 2-6 hours which provided symptomatic relief and substantially reduced the number of amoebae (good for land-based tanks, but difficult for sea-based netpens). Bath treatment with hydrogen peroxide (100-200 ppm for 1-2 hours) also reduced numbers of amoebae but there was a narrow safety margin before toxicity problems arose. Aquaculture enterprises have adopted various management strategies in attempts to prevent and/or control outbreaks of AGD, with some successes attributed to keeping fish cohorts separated at different sites (rather than co-mingled), reducing stocking densities, and positioning sea-cages further apart and in estuarine waters with lower salinity.


Neoparamoeba,
Parameoba
gills
(mucoid branchitis,
gill clubbing/necrosis,
amoebic gill disease)
Vertebrate Hosts
(fish, esp.
salmonids)
digitiform
lopopodia
parasome
(Nebenkorper)
trophozoite
(15-40 µm)
mamilliform
lopopodia
attach to
gill epithelia
no cyst formation
transmission between hosts by transfer of trophozoites
through close contact or contaminated mucus



Neoparamoeba trophozoites on fish gills

Acanthamoeba
(protist: amoeba)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Protists which move and feed using pseudopodia (false feet) are known as amoebae. Rather than forming a monophyletic group, amoebae are divided into three major disparate groups: Heterolobosea (supergroup Excavata), Rhizaria (supergroup SAR) and Amoebozoa (supergroup Amorphea). The latter contains four classes of amoebae differing in their types of pseudopodia and organelles: Tubulinea, Discosea, Gracilipodia and Archamoebae. Discosean amoebae are flattened in profile and form broad lobopodia. Acanthamoebae form finely-tapering subpseudopodia (acanthopodia) emerging from the cell-wide lobopodium and they exhibit sluggish motility. Most species form cysts and are found as free-living organisms, although some species are considered to be 'amphizoic' due to their ability to live as both free-living organisms and parasitic pathogens. Most free-living species live in aquatic or terrestrial environments where they feed on bacteria, fungi and other protozoa. Several *Acanthamoeba* species, however, are facultative/opportunistic parasites primarily in the central nervous system, skin and lungs of humans and animals, and the cornea of humans.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Phylum: Amoebozoa (locomotion by noneruptive pseudopodia, asexual development)
Subphylum: Lobosa (with lobose pseudopodia)
Class: Longamoebea (flattened elongated cells with pointed subpseudopodia)
Order: Centramoebida (finely-tapering subpseudopodia (= acanthopodia), most form cysts)
Family: Acanthamoebidae (trophozoites flattened, prominent subpseudopodia, cysts stellate)
Genus: *Acanthamoeba* (free-living in terrestrial and aquatic environments, some species opportunistic parasites)
Species: various species cause granulomatous amoebic encephalitis and cutaneous acanthamoebiasis in humans and animals, and amoebic keratitis in humans

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Amoebae form pseudopodia to move and feed. Several types of amoebae are recognized on the basis of differences in their biology and morphology, with recent molecular phylogenetic studies supporting their classification into three major disparate phyla: Heterolobosea (supergroup Excavata), Amoebozoa (supergroup Amorphea) and Rhizaria (supergroup SAR). Most species are free-living in aquatic and terrestrial habitats where they feed on other micro-organisms, but several species have become symbiotic in metazoan organisms as endocommensals or opportunistic-facultative parasites (representatives tabulated below).

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Phylum: Heterolobosea (amoebo-flagellates, most form cysts)	O: Schizopyrenida (no fruiting bodies)	Vahlkampfidae (eruptive limax pseudopodia, flagellated stages)	*Naegleria*	mammals	central nervous system (PAM)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)					
Phylum: **Amoebozoa** (locomotion by noneruptive pseudopodia, asexual development)					
Subphylum: Conosa (archamoebae & mycetozoa)	C: Archamoebae (amitochondriate, rounded cysts)	Entamoebidae (uninucleate, endozoic)	*Entamoeba*	mammals	colon (dysentery), central nervous system (SAM)
Subphylum: Lobosa (lobose amoebae)	C: Discosea (flattened forms, protoplasmic flow polyaxial)	Vexilliferidae (dactylopodia, parasomes)	*Paramoeba* *Neoparamoeba*	fish	gills (AGD)
	C: Longamoebea (flattened elongated cells, stellate cysts)	Acanthamoebidae (acanthopodial subpseudopodia)	*Acanthamoeba, Balamuthia*	mammals	central nervous system (GAE)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups robustly supported by molecular studies)					
Group: **Rhizaria** (amoebae with fine pseudopodia in simple, branching or anastomosing patterns)					

Phylum: Cercozoa	Filosa (with filopodia, naked or testate)	free-living (aquatic, terrestrial)
Phylum: Endomyxa	heterotrophic amoeboid or plasmodial cells	free-living, some parasitoids
Phylum: Retaria	Foraminifera (with reticulopodia), Radiolaria (with axopodia)	free-living (aquatic)

*PAM = primary amoebic meningoencephalitis; SAM = secondary amoebic meningoencephalitis;
GAE = granulomatous amoebic encephalitis; AGD = amoebic gill disease.

Amoebae that move using noneruptive pseudopodia are placed in the phylum Amoebozoa, either in the subphylum Lobosa (with lobose pseudopodia) or Conosa (with microtubular cones). Lobose amoebozoans include the Dactylopodida with finger-like subpseudopodia (= dactylopodia) and the Centramoebida with finely-tapering subpseudopodia (= acanthopodia). Acanthamoebae are flattened centramoebid amoebae which form stellate cysts. They are naked (without tests or shells) and have simple life-cycles (without temporary flagellated stages), most being free-living amoebae (FLA) abundant in aquatic and terrestrial environments. Some FLA species are amphizoic and may opportunistically infect vertebrate hosts, usually causing neurological conditions. Primary meningoencephalitis (PAM) is caused by *Naegleria* spp. while granulomatous amoebic encephalitis (GAE) is caused by *Acanthamoeba*, *Balamuthia* or *Sappinia* spp. [note that secondary amoebic meningoencephalitis (SAM) is caused by extraintestinal infections by the parasite *Entamoeba histolytica*]. FLA do not form a natural assemblage but have been split by recent molecular studies into different phyla: *Naegleria* being classified within the Heterolobosea (amoebo-flagellates), and *Acanthamoeba*, *Balamuthia* and *Sappinia* within the Amoebozoa (noneruptive pseudopodia) [together with the parasite *Entamoeba*]. Early studies often did not differentiate between the genera *Acanthamoeba* and *Hartmannella* (and sometimes even *Naegleria*), so the validity of many initial case reports remains questionable. *Acanthamoeba* spp. have since been found to be one of the most prevalent protozoa found around the world. They have been isolated from soil, dust, air, freshwater, seawater, sediments, vegetation and as contaminants in bacterial, yeast and mammalian cell cultures. Around 26 species have been described, 15 being recorded as opportunistic pathogens in mammals, birds, reptiles, amphibians and fish. Serological studies have detected antibodies against *Acanthamoeba* spp. in up to 80% of human populations, indicating a much greater prevalence of exposure than the low (rare) incidence of clinical disease would suggest. Recently, nuclear (Rns) or mitochondrial (rns) ribosomal RNA gene sequencing have been used to identify various genotypes from clinical and environmental samples (encoded T1-T20). Genotypes T7, T8, T9, T17 and T18 belong to group I; genotypes T3, T4, T11, T13 and T19 to group II; and genotypes T1, T2, T5, T6, T10, T12 and T15 to group III. Some genotypes remain to be grouped morphologically (T16, T20) and some species remain to be genotyped (e.g. *A. echinulata*). In addition, several genotypes have been detected that are not referable to named species, while other genotypes may represent several species (especially T4), Most genotypes have been recovered from environmental samples, while a growing number are being associated with clinical disease in humans and animals. Genotypes recovered from hosts but not referable to known *Acanthamoeba* spp. include T1, T6, T13 and T17 from clinical samples; T14 from human faeces; and T20 from the internal organs of a toucan.

***Acanthamoeba* species**	**Genotype (rDNA)**	**Cyst morphotype**	**Hosts**	**Location**	**Clinical signs**
un-named species	T1	II	humans	brain	encephalitis
A. palestinensis	T2	III	humans	eye, brain	keratitis, encephalitis
A. griffini	T3	II	humans	eye	keratitis
A. castellanii	T4	II	humans	eye, brain, skin, lung, prostate, bone, muscle, sinus	keratitis, encephalitis, cutaneous lesions
A. lugdunensis	T4	II	humans	eye	keratitis
A. polyphaga	T4	II	humans, fish^{+}	eye, brain	keratitis, encephalitis
A. rhysodes	T4	II	humans	eye, brain	keratitis, encephalitis
A. triangularis	T4	II	humans	eye	keratitis
A. lenticulata	T5	III	humans	eye, brain	keratitis, encephalitis
un-named species	T6	III	humans	eye	keratitis
*A. astronyxis**	T7	I	humans	brain, adrenal, lymph node, sinus, thyroid, skin	encephalitis
A. culbertsoni	T10	III	humans	eye, brain, liver, spleen, uterus, skin	keratitis, encephalitis
A. hatchetti	T11	II	humans	eye	keratitis
A. quina	T11	II	humans	eye	keratitis
A. healyi	T12	III	humans	eye, brain	keratitis, encephalitis
un-named species	T13	II	humans	eye	keratitis
A. jacobsi	T15	III	humans	eye	keratitis

un-named species	T17	I	humans	eye, brain	keratitis, encephalitis
A. byersi	T18	I	humans	brain, skin	encephalitis, cutaneous lesions

*This record is considered by some to represent a case of culture contamination.
[+]Trophozoites recorded from gills, urinary bladder, spleen, gall bladder and blood of freshwater fish (white sucker, common shiner, blue tilapia, largemouth bass, striped bass, channel catfish, carp, goldfish and rainbow trout)

Experimental infections by *Acanthamoeba* spp. have been established in a range of animals (mice, rats, hamsters, rabbits, pigs) to model disease (both AK and GAE). Naturally acquired infections have also been detected in gorillas (GAE), cattle (GAE, lungs, faeces, some involving genotype T4), water buffalo (lungs), sheep (GAE), horses (placentitis due to *A. hatchetti*), dogs (GAE due to *A. castellanii* and *A. culbertsoni*, as well as un-named species in lungs and viscera), cats (AK due to T4), muskrats (faeces), ground squirrels (gut), rabbits (liver, *A. polyphaga*), kangaroos (GAE), birds (*A. polyphaga* in intestines of turkeys, genotypes T4 and T5 in cornea of sparrowhawks, T20 in internal organs of toucan, un-named species in faeces of ducks and gulls and intestines of pigeons), reptiles (faeces of snakes and lizards), amphibians (faeces of toads and frogs) and fish (gills, spleen, urinary bladder and blood of wild caught and ornamental freshwater species). Free-living species which have not been associated with disease include: *A. astronyxis* (group I, genotype T7), *A. comandoni* (I, T9), *A. divionensis* (II, T4), *A. echinulata* (I), *A. mauritaniensis* (II, T4), *A. micheli* (II, T19), *A. paradivionensis* (II, T4), *A. pearcei* (I, T3), *A. pustulosa* (III, T2), *A. royreba* (III, T4), *A. stevensoni* (II, T11), *A. terricola* (II, T4), *A. tubiashi* (I, T8) as well as genotypes T16 and T17. Free-living species have been isolated from soil and water samples; including coastal seawater, freshwater lakes, streams, rivers, swimming pools, thermal springs, power plants and sewage works.

Many *Acanthamoeba* spp. have also been found to harbour microbial endosymbionts (*Candidatus Caedibacter acanthamoebae, Candidatus Odyssella thessalonicensis, Candidatus Paracaedibacter acanthamoebae, Candidatus Paracaedibacter symbiosus, Comamonas acidovorans, Legionella pneumophila, Pseudomonas aeruginosa*, megavirus, mimivirus and pandoravirus) [note that the term *Candidatus* is used to denote interim taxonomic status for bacteria that cannot be maintained in culture], as well as supporting the development and multiplication of other bacterial species (*Aeromonas, Afipia felis, Bacillus cereus, Bartonella, Burkholderia picketti, Campylobacter jejuni, Chlamydia pneumoniae, Coxiella burnetii, Cytophaga, Escherichia coli 0157, Flavobacterium, Francisella tularensis, Helicobacter pylori, Listeria monocytogenes, Mycobacterium avium, Mycobacterium leprae, Pasteurella multocida, Prevotella intermedia, Porphyromonas gingivalis, Rickettsia, Salmonella enterica, Salmonella typhyimurium, Shigella, Simkania negevensis, Staphylococcus aureus, Vibrio cholera* and *Waddlia chondrophila*).

Parasite morphology: Acanthamoebae form two developmental stages: motile feeding trophozoites and dormant resting cysts (they do not form temporary flagellated stages). Trophozoites range in size from 15-40 µm, contain a single nucleus with a large central dense nucleolus, a contractile vacuole and form numerous spiny pseudopodia (acanthopodia). Cysts are uninucleate and bound by a proteinaceous ectocyst wall and a cellulosic endocyst wall. The cysts are roughly ovoid, range from 10-20 µm in diameter and are frequently wrinkled and stellate in appearance. Individual *Acanthamoeba* species were initially classified according to cyst size and shape into three morphotypes: group I forming large cysts (>18 µm) with smooth ectocysts and stellate endocysts meeting radially at operculate pores; group II forming medium cysts (<18 µm) with wrinkled ectocysts and stellate to polygonal endocysts; and group III forming smaller cysts (<15 µm) with smooth ectocysts and spherical endocysts. Subsequent studies, however, found that these characters varied according to encystation and/or culture conditions.

Site of infection: Amoebae (both trophozoites and cysts) have been found in various organs; including the skin, upper respiratory tract, brain, liver, kidneys, adrenals, prostate, lymph nodes, bone marrow and pancreas of humans, primates and some domestic animals, as well as in the eyes but only in humans.

Pathogenesis: Most free-living amoebae are active predators feeding on bacteria, algae, yeasts and other protistans in their aquatic or terrestrial environments by phagocytosis or engulfment through pseudopod, food cup and/or food vacuole formation. In addition, some are able to take up soluble nutrients through pinocytosis and/or membrane transporters. Several *Acanthamoeba* spp. are regarded to be opportunistic parasites when they infect vertebrate hosts, often by taking advantage of temporary weaknesses in host immunity (such as traumatic lesions in immune barriers or suppressed innate or adaptive immune responses). Infections have been associated with three disease syndromes: amoebic keratitis (AK) exclusive to humans; granulomatous amoebic encephalitis (GAE) in humans and wild and domestic animals (such as horses, canines, bovines, ovines, monkeys, gorillas, and kangaroos) and cutaneous acanthamoebiasis (CA) reported in humans, canines, gorillas and several monkey species, often alongside GAE. The T4 genotype has frequently been associated with clinical disease in humans, including AK, GAE, CA and even disseminated infections involving the nasal passages, sinuses, lungs and gut. In addition, genotypes T3 and T11 (rarely T2, T5, T6 and T15) may cause AK; and genotypes T1, T10 and T12 (rarely T2, T5, T7 and T17) may cause GAE. If amoebae gain access to the body via the skin, CA can develop and persist over months being characterized by firm, non-tender erythematous nodules on the skin that drain a purulent exudate and can become ulcerated. Amoebae may invade the brain via haematogenous spread from the skin or directly via the upper respiratory tract, especially through the nasal mucosa to the olfactory bulb. GAE is a late-onset, protracted and usually fatal disease of the central nervous system (CNS) with a variable incubation period of several weeks to months. GAE is characterized by

inflammatory necrosis of the brain due to parasite infiltrates and activity (esp. secretion of proteases) and host immune responses (proinflammatory) resulting in brain swelling, haemorrhagic necrosis, fibrin thrombi and neuronal damage. The description 'granulomatous' refers to the masses of immune cells that form at sites of infection or inflammation. Multifocal lesions present in the brain stem, midbrain, corpus callosum, and cerebellum. Symptoms include fever, headaches, stiff neck, aphasia, hemiparesis, changes in mental state (confusion, hallucinations, personality changes, irritability, sleep disturbances and decreased consciousness), vomiting, nausea, focal neurologic deficits, cranial nerve palsies, increased cranial pressure, seizures and coma, eventually leading to death. Moderate to severe oedema occurs in the cerebral hemispheres, and a chronic exudate consisting of inflammatory cells is present over the cortex. Trophozoites and cysts are scattered throughout neurological tissues, and occasionally other organs (liver, kidneys, adrenals, lungs). Multinucleated giant cells form granulomas around colonies of amoebae in immuno-competent patients; but this response is mild or completely absent in immuno-compromised hosts. Tissue damage may be caused directly by feeding trophozoites, induced by pro-inflammatory cytokine responses, or both. Dissemination to the lungs can occur and leads to pneumonitis. AK is a progressive sight-threatening corneal infection and is common amongst contact-lens wearers or people who have sustained corneal trauma. Amoebae invade the corneal epithelium and breech Bowman's membrane penetrating to the underlying collagenous stroma which they invade using collagenases. Trophozoites cluster around the corneal nerves producing radial keratoneuritis and severe pain. Other symptoms include radial neuritis, eyelid ptosis, photophobia, corneal opacity, blurred vision, lacrimation, conjunctival hyperaemia, epithelial ulcers, ring-like stromal infiltrates and scleritis. AK has not been found to lead to systemic infection or death, but is complicated by cataracts, increased intraocular pressure and hypopyon (inflamed anterior chamber) such that eye-sight can be threatened. GAE and CA are generally contracted by chronically ill patients (associated with diabetes, alcoholism and dialysis) or immuno-compromised individuals (due to congenital or acquired immunodeficiencies or immunosuppressive therapy for cancer or transplantation), whereas AK patients and most infected animals are immunocompetent. Pathogenicity has been associated directly with parasite adhesins, invasion, phagocytosis, acanthopodia activity, cytolytic enzyme production (phospholipases metalloproteinases, glycosidases, elastases, collagenases, myelinases, fibrinolytic enzymes, ecto-ATPases, neuroaminidases, superoxide dismutases), plasminogen activation, acanthaporin (pore-forming toxin); and indirectly with physiological tolerance (osmolarity, temperature, pH), biofilms, chemotaxis, drug resistance, cellular differentiation, cyst formation and host immunity (various cytokines, host cell apoptosis).

Developmental cycle and mode of transmission: Acanthamoebae are prevalent throughout the world in aquatic and terrestrial habitats, being found in raw and potable freshwater sources, seawater, sediments, soil, dust, air, sewage and numerous engineered facilities (swimming pools, spas, air-conditioning units, dialysis units, dental treatment units, eyewash stations). Infections occur when hosts come into direct contact with organisms in water and soil sources, and possibly associated aerosols. Organisms may enter the skin through cuts, wounds or abrasions, infect the nasal mucosa by inhalation or contact with contaminated water (immersion while bathing) or infect the eye by direct contact (often with contact lenses or cases washed in contaminated water). *Acanthamoeba* cysts are formed when environmental conditions become adverse for trophozoites (e.g. desiccation, food deprivation, pH and temperature extremes) and they excyst when conditions improve. The released trophozoites feed, grow and multiply asexually by mitotic division (binary fission). Trophozoites are the infective stage, but both cystic and trophic forms can enter the host, and both stages can be isolated from diseased and healthy individuals. There is no evidence to implicate horizontal transmission from one person to another or from one species to another.

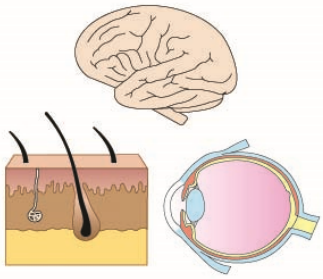
Differential diagnosis: Microscopic examination of biopsy samples (skin, brain, cornea, cerebrospinal fluid, bronchoalveolar lavage) is conventionally used to detect characteristic trophozoites and cysts; either in wet mounts, cytospin preparations or stained smears. Organisms may be stained using haematoxylin and eosin, trichrome, periodic acid-Schiff's or Gomori methenamine silver stains. Other identification techniques include chemofluorescent staining (Calcofluor, acridine orange), immunoflourescent or immunoperoxidase antibody labelling, confocal microscopy as well as organism cultivation (monoxenic plates/flasks, axenic media culture or tissue culture on mammalian cell monolayers). Ophthalmologic examination can reveal dendriform patterns on the epithelium of the cornea. DNA extracted from tissue samples has also been successfully screened by polymerase chain reaction (PCR) amplification of nuclear and/or mitochondrial ribosomal RNA gene sequences. Genotyping at these loci is recommended for molecular epidemiology. For GAE, a lumbar puncture for a cerebrospinal fluid examination can be performed, which does not test for the presence of amoebae but for elevated white blood cell counts, reduced glucose levels and elevated protein levels. CT scans are usually performed before lumbar puncture to ensure the technique is not contraindicated because of the risk of herniation. Regrettably, most cases of GAE are diagnosed post-mortem.

Treatment and control: Prognosis is poor for GAE and CA patients, primarily due to the low efficacy of current diagnostic methods, the inefficiency of current drugs, cyst formation within host tissues and the compromised immunity of most patients. Nonetheless, GAE has been successfully treated with various antimicrobial multi-drug regimens guided by *in vitro* antibiotic sensitivity testing. Drugs have included various combinations of cotrimoxazole, clotrimazole, fluconazole, flucytosine, isethionate, itraconazole, ketoconazole, pentamidine, sulfadiazine, amphotericin B, rifampin, miconazole, paromomycin, polymyxin and trimethoprim-sulfamethoxazole. Topical chlorhexidine and ketoconazole have been used to treat skin lesions in CA.

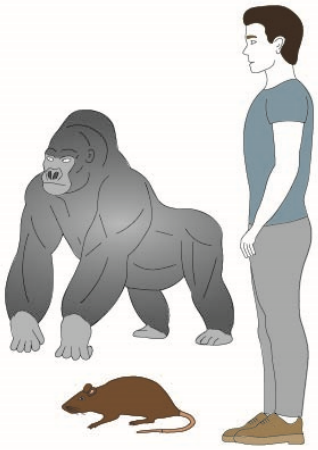
Early diagnosis is vital for a successful treatment of AK as cysts are highly resistant to therapy. Propamidine, micronazole nitrate and neomycin have been used successfully in combination, as have cationic antiseptics (chlorhexidine or polyhexamethylene

biguanide) with diamides (propamidine or hexamidine). The duration of the therapy is a minimum of 3-4 weeks but may require up to 6-12 months. If drugs prove unsuccessful, the infected cornea can be debrided and a penetrating keratoplasty performed. Prevention of AK revolves around the proper sanitation of contact lenses and their cases which are major sources of the disease. Decontamination in hydrogen peroxide solutions has proven effective. Sterile solutions must be used to clean and store lenses. Avoiding complete contact with acanthamoebae is difficult because they are ubiquitous and prevalent in the environment. Cysts are resistant to most biocides, antibiotics and routine water chlorination procedures, and they have been shown to remain viable for years in water at low temperatures. Precautions should be taken when swimming or bathing in untreated waters (avoid facial immersion and inhalation of water or aerosols). Patient cohorts most at risk (immunocompromised individuals) should avoid potentially contaminated sites and undergo regular health monitoring.

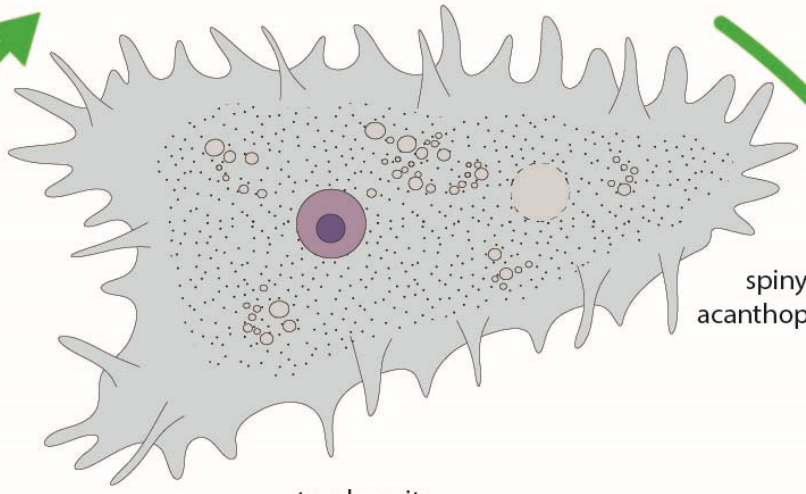
Acanthamoeba



skin, brain, eye
(cutaneous lesions,
amoebic keratitis,
granulomatous amoebic
encephalitis)



Vertebrate Hosts
(mammals, some
other animals)

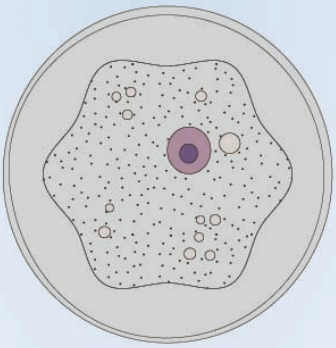


spiny
acanthopodia

trophozoite
(15-40 µm)

exystment in contact
with skin/cornea

cyst formation in
external environment



often stellate
in appearance

cyst
(10-20 µm)

many species free-living in terrestrial and aquatic habitats,
some opportunistic/facultative parasites
(transmission by contact when bathing)



Acanthamoeba trophozoite



Acanthamoeba cysts



Acanthamoeba brain lesion

Balamuthia
(protist: amoeba)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Protists which move and feed using pseudopodia (false feet) are known as amoebae. Rather than forming a monophyletic group, amoebae are divided into three major disparate groups: Heterolobosea (supergroup Excavata), Rhizaria (supergroup SAR) and Amoebozoa (supergroup Amorphea). The latter contains four classes of amoebae differing in their types of pseudopodia and organelles: Tubulinea, Discosea, Gracilipodia and Archamoebae. Tubulinid amoebae form tubular subcylindrical pseudopodia and the cells may be testate (surrounded by a shell) or naked. Discosean amoebae are flattened in profile and form broad lobopodia. Acanthamoebae form finely-tapering subpseudopodia (acanthopodia) emerging from the cell-wide lobopodium and they exhibit sluggish motility. Most species form cysts and are found as free-living organisms. *Balamuthia* was originally classified as a leptomyxid amoebae exhibiting limax, plasmodial, reticulated and/or polyaxial pseudopodia, but molecular studies have found it to be closely related to *Acanthamoeba*. The single species, *Balamuthia mandrillaris*, normally exists as a free-living amoeba in soil and aquatic environments, but can opportunistically infect humans and animals causing granulomatous amoebic encephalitis (GAE).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Phylum: Amoebozoa (locomotion by noneruptive pseudopodia, asexual development)
Subphylum: Lobosa (with lobose pseudopodia)
Class: Longamoebea (flattened elongated cells with pointed subpseudopodia)
Order: Centramoebida (finely-tapering subpseudopodia (= acanthopodia), most form cysts)
Family: Acanthamoebidae (trophozoites flattened, prominent subpseudopodia, cysts stellate)
Genus: *Balamuthia* (free-living in terrestrial environments, sometimes opportunistically parasitic)
Species: *B. mandrillaris* (causes granulomatous amoebic encephalitis, disseminated disease or skin lesions in humans)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Amoebae form pseudopodia to move and feed. Several types of amoebae are recognized on the basis of differences in their biology and morphology, with recent molecular phylogenetic studies supporting their classification into three major disparate phyla: Heterolobosea (supergroup Excavata), Amoebozoa (supergroup Amorphea) and Rhizaria (supergroup SAR). Most species are free-living in aquatic and terrestrial habitats where they feed on other micro-organisms, but several species have become symbiotic in metazoan organisms as endocommensals or opportunistic-facultative parasites (representatives tabulated below).

Higher taxonomy	Class/Order	Family	Genus	Hosts	Tissues (disease)*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: **Discoba** (diverse group supported robustly by molecular studies)					
Phylum: Heterolobosea (amoebo-flagellates, most form cysts)	O: Schizopyrenida (no fruiting bodies)	Vahlkampfidae (eruptive limax pseudopodia, flagellated stages)	*Naegleria*	mammals	central nervous system (PAM)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)					
Phylum: **Amoebozoa** (locomotion by noneruptive pseudopodia, asexual development)					
Subphylum: Conosa (archamoebae & mycetozoa)	C: Archamoebae (amitochondriate, rounded cysts)	Entamoebidae (uninucleate, endozoic)	*Entamoeba*	mammals	colon (dysentery), central nervous system (SAM)
Subphylum: Lobosa (lobose amoebae)	C: Discosea (flattened forms, protoplasmic flow polyaxial)	Vexilliferidae (dactylopodia, parasomes)	*Paramoeba* *Neoparamoeba*	fish	gills (AGD)
	C: Longamoebea (flattened elongated cells, stellate cysts)	Acanthamoebidae (acanthopodial subpseudopodia)	*Acanthamoeba, Balamuthia*	mammals	central nervous system (GAE)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups robustly supported by molecular studies)					
Group: **Rhizaria** (amoebae with fine pseudopodia in simple, branching or anastomosing patterns)					

Phylum: Cercozoa	Filosa (with filopodia, naked or testate)	free-living (aquatic, terrestrial)
Phylum: Endomyxa	heterotrophic amoeboid or plasmodial cells	free-living, some parasitoids
Phylum: Retaria	Foraminifera (with reticulopodia), Radiolaria (with axopodia)	free-living (aquatic)

*PAM = primary amoebic meningoencephalitis; SAM = secondary amoebic meningoencephalitis; GAE = granulomatous amoebic encephalitis; AGD = amoebic gill disease.

Amoebae that move using noneruptive pseudopodia are placed in the phylum Amoebozoa, either in the subphylum Lobosa (with lobose pseudopodia) or Conosa (with microtubular cones). Lobose amoebozoans include the Dactylopodida with finger-like subpseudopodia (= dactylopodia) and the Centramoebida with finely-tapering subpseudopodia (= acanthopodia). Acanthamoebae are flattened centramoebid amoebae which form stellate cysts. They are naked (without tests or shells) and have simple life-cycles (without temporary flagellated stages), most being free-living amoebae (FLA) abundant in aquatic and terrestrial environments. Some FLA species are amphizoic and may opportunistically infect vertebrate hosts, usually causing neurological conditions. Primary meningoencephalitis (PAM) is caused by *Naegleria* spp. while granulomatous amoebic encephalitis (GAE) is caused by *Acanthamoeba*, *Balamuthia* or *Sappinia* spp. [note that secondary amoebic meningoencephalitis (SAM) is caused by extraintestinal infections by the parasite *Entamoeba histolytica*]. FLA do not form a natural assemblage but have been split by recent molecular studies into different phyla: *Naegleria* being classified within the Heterolobosea (amoebo-flagellates), and *Acanthamoeba*, *Balamuthia* and *Sappinia* within the Amoebozoa (noneruptive pseudopodia) [together with the parasite *Entamoeba*]. *Balamuthia* was first thought to be a leptomyxid amoebae on the basis of its thick-walled cyst and pleomorphic pseudopodia: the latter being limax (monopodial slug-like movement), plasmodial (multinucleate), reticulated (fibrous network) and/or polyaxial (movement on more than one axis). However, molecular phylogenetic studies have firmly placed *Balamuthia* as a close relative of acanthamoebae rather than other leptomyxids. *Balamuthia mandrillaris* was originally isolated from a mandrill baboon (hence the specific epithet). It was subsequently discovered to be a free-living amoebae commonly found in soil and dust, but which can opportunistically infect humans, horses, sheep and dogs but is most often seen in non-human primates. There are no intermediate hosts in the life cycle and there is no evidence that animals are reservoirs for human infections. The amoeba has a worldwide distribution and can infect both immuno-competent and immuno-suppressed hosts; notably humans with HIV/AIDS or those undergoing immuno-suppressive treatment.

***Balamuthia* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
B. mandrillaris	Primates: hominid (human, gorilla, orangutan), hylobatid (gibbon), cercopithecid (colobus monkey, baboon); Carnivora: canid (dog); Perissodactyla: equid (horse); Artiodactyla: bovid (sheep)	brain, lungs, spleen, kidneys, adrenals, skin	granulomatous encephalitis	Europe, Americas, Australia, Asia

Parasite morphology: This amoeba forms two developmental stages; vegetative trophozoites and dormant cysts (it does not form a temporary flagellated stage). The trophozoites are 12-60 µm in diameter and most are uninucleate with an unusually large dense vesicular nucleus generally containing one large central nucleolus (although more than one nucleolus may occur). They often contain multiple nuclear-like bodies which are spherical, 2-4 µm in diameter, have a large dense central body and are found near the tips of extended pseudopodia. The shape of the trophic form is variable; sometimes appearing rounded with no pseudopodia, but often extended in a thread-like configuration with multiple and extended pseudopodia. Cysts are polygonal or spherical measuring 6-30 µm in diameter and wrinkled in appearance. They are bound by a three-layered cyst wall lacking pores; composed of a thick inner (endocyst) wall, a wrinkled outer (ectocyst) wall and an amorphous fibrillar middle (mesocyst) wall.

Site of infection: Amoebae (trophozoites and cysts) infect the skin or lungs and may spread haematogenously thereafter to the central nervous system or disseminate to other organs such as the kidneys, adrenal glands, pancreas and thyroid. There is also some evidence to suggest amoebae may invade the brain via the olfactory nerve.

Pathogenesis: Infection of the skin leads to localised dermal ulcerations which can be very slow to heal or simply fail to do so. Nasopharyngeal infections may lead to pneumonitis and subsequently spread to the brain causing granulomatous amoebic encephalitis (GAE), sometimes known specifically as *Balamuthia* amoebic encephalitis (BAE). *Balamuthia* characteristically exhibits slow growth and spread to the nervous system may take from several weeks up to two years. Symptoms are insidious and are often not recognised in the early stages of infection. Symptoms of the sub-acute stage include headache, seizures, nausea, stiff neck and increased cerebrospinal fluid in the brain. GAE is a chronic condition with high mortality due to the formation of haemorrhagic necrotising lesions in brain tissue, particularly in perivascular spaces. The description ‘granulomatous’ refers to the masses of immune cells that form at sites of infection or inflammation. Symptoms include focal paralysis, seizures, facial paralysis, difficulty in swallowing and double vision. Changes in clinical parameters include elevated levels of protein and leukocytes in cerebrospinal fluid and blood as well as decreased levels of glucose. Infections occur in both immuno-compromised and immuno-competent individuals, particularly in children and the elderly. Unlike other free-living amoebae which opportunistically infect

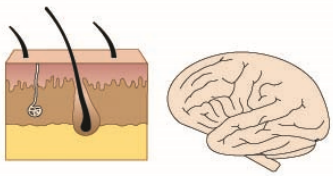
animals, *Balamuthia* cannot be grown in cultures containing only bacteria as a food source – the amoebae require eukaryotic cells and thrive in tissue cell cultures, especially those containing human brain microvascular endothelial cells. *Balamuthia* binds preferentially to collagen-1, laminin-1 and fibronectin in the extracellular matrix resulting in the production of 'food cups' allow them to feed on cells. Infections have also been shown to induce production of the cytokine IL-6 by brain endothelial cells leading to inflammatory responses which worsen the condition. Other putative virulence factors involve metalloprotease activity leading to degradation of the extracellular matrix (particularly collagen-1 and -3, elastin and plasminogen) and an increase in pathology associated with decreased tissue structure and function.

Developmental cycle and mode of transmission: *B. mandrillaris* is a free-living amoeba found most commonly in soil and at times in aquatic environments. Trophozoites feed mainly on other protozoa but lack of food induces encystment. Infections are thought to be acquired by hosts either by trophozoites invading cuts, wounds or abrasions in the skin and then entering the bloodstream or by cysts being inhaled into the upper respiratory tract. Zoonotic transmission has been considered as non-human primates are commonly affected by *B. mandrillaris* but there is no evidence as yet to suggest that animals act as reservoirs of infection. There is little evidence for human-to-human transmission and most cases occur as solitary infections not constrained by geography.

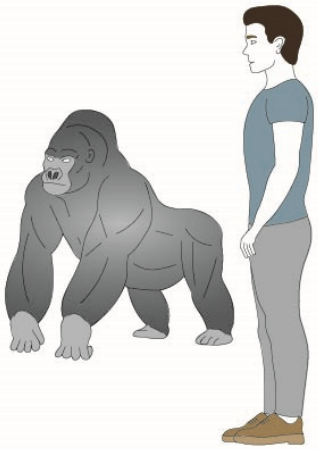
Differential diagnosis: Most cases are fatal and are diagnosed post-mortem. Cysts and trophozoites can be identified via microscopic examination of fixed and stained histological sections, or by immunofluorescent-antibody labelling using a specific antiserum (anti-*Balamuthia* antibodies raised in rabbits). Host antibodies have been detected in serum samples by enzyme immunoassays and DNA has been amplified from clinical samples by polymerase chain reaction (PCR) amplification of ribosomal RNA gene sequences. Radiological imaging techniques (CT and MRI scans) have also been used to identify symptomatic lesions in the brain. Unlike the other free-living amoebae that can cause meningo-encephalitis, *Balamuthia* is difficult to isolate and culture from cerebrospinal fluid. Instead, amoebae may be recovered from brain biopsy material cultured in the presence of mammalian cells.

Treatment and control: A major problem associated with therapy is the ability of *Balamuthia* to form cysts which are highly resistant to physical and chemical stresses. The triple layered cell wall presents a significant barrier to antimicrobials and it is highly likely that cysts may reactivate following chemotherapy leading to a recurrence of infection. Multiple drugs have been tested against trophozoites for the treatment of infections, with variable success reported for amphotericin B, zaithromycin, fluconazole, flucytosine, pentamidine and propamidine isethionates, miltefosine and sulfa drugs. Unfortunately, many have undesirable side effects when used for prolonged periods and new, less toxic drugs are required. Chemotherapy has also been complemented by immuno-therapy using specific antibodies raised against *Balamuthia* isolates. Good prognosis relies heavily upon early diagnosis and timely treatment, especially of low dose infections involving amoebae strains of low virulence. Prevention involves reducing transmission potential by avoiding contact with potential sources (using gloves when working with soil and not immersing the head when swimming or bathing in untreated waters).

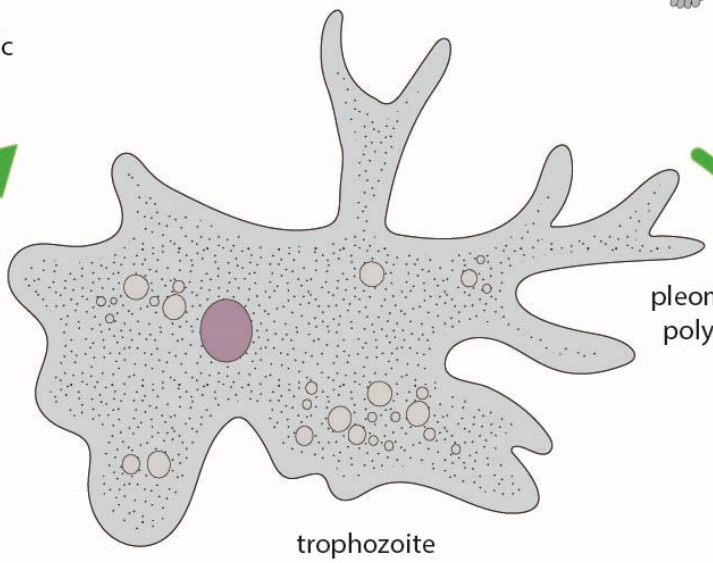
Balamuthia



skin, brain
(dermal ulcers,
granulomatous amoebic
encephalitis)



Vertebrate Hosts
(mammals, esp.
primates)

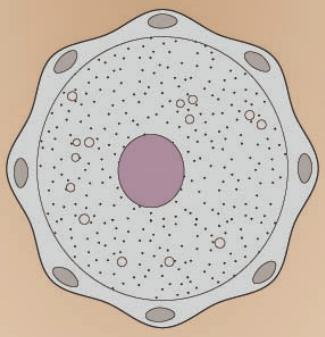


pleomorphic
polypodia

trophozoite
(12-60 µm)

exystment in contact
with skin

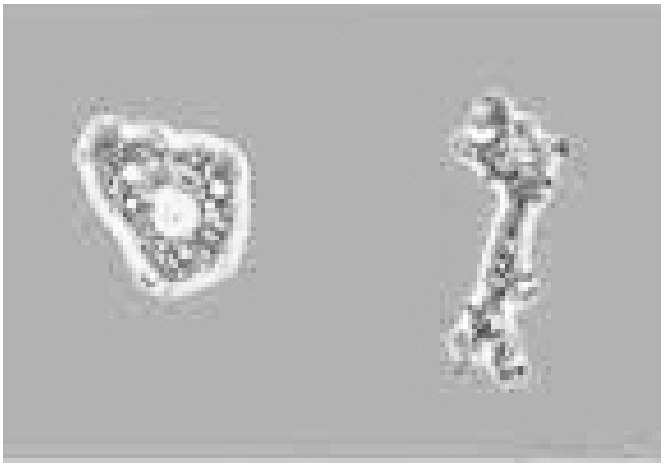
cyst formation in
external environment



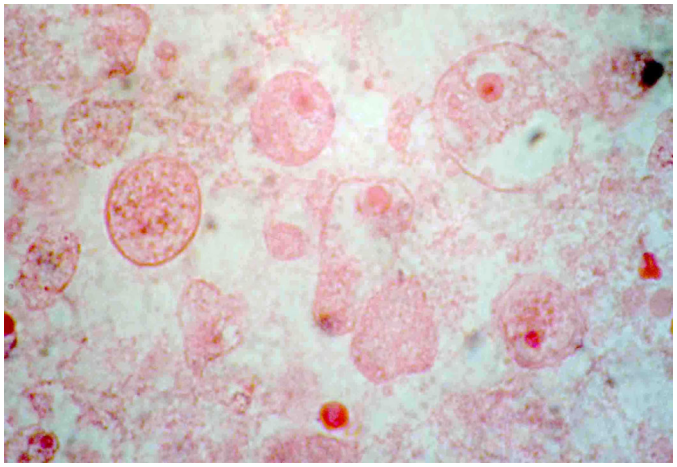
often with
wrinkled
exocyst wall

cyst
(6-30 µm)

usually free-living in terrestrial and aquatic habitats,
occasionally opportunistically parasitic
(transmission by contact with soil)



Balamuthia trophozoites



Balamuthia brain lesion



Balamuthia cyst

Naegleria
(protist: amoeba)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Protists which move and feed using pseudopodia (false feet) are known as amoebae. Rather than forming a monophyletic group, amoebae are divided into three major disparate groups: Heterolobosea (supergroup Excavata), Rhizaria (supergroup SAR) and Amoebozoa (supergroup Amorphea). Heterolobosean amoebae form cylindrical trophozoites with eruptive limax pseudopodia. They have also been shown to have an alternate flagellated stage in their developmental cycle, although molecular phylogenetic studies have included some taxa which lack either an amoeboid or a flagellated stage. This group includes the acrasid mycetozoans (slime moulds) which form fruiting bodies and vahlkampfiid amoebae (schizopyrenids) which do not form fruiting bodies. They all form environmentally-resistant cysts. Most species are found as bactivores in soil, water or faeces, and several species are able to opportunistically infect the central nervous system of vertebrate hosts. *Naegleria fowleri* usually lives in warm freshwater environments but can invade the human body through the nasal mucosa and cause primary amoebic meningoencephalitis (PAM).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Discoba (diverse group supported robustly by molecular studies)
Phylum: Heterolobosea (diverse group, incl. amoebo-flagellates, most form cysts or clusters of fruiting bodies)
Order: Schizopyrenida (no fruiting bodies)
Family: Vahlkampfidae (eruptive limax amoeboid form cylindrical, most form temporary flagellated stages)
Genus: *Naegleria* (free-living amoebae in terrestrial/aquatic habitats, some opportunistically parasitic)
Species: *N. fowleri* (causes primary amoebic meningoencephalitis in humans)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Amoebae form pseudopodia to move and feed. Several types of amoebae are recognized on the basis of differences in their biology and morphology, with recent molecular phylogenetic studies supporting their classification into three major disparate phyla: Heterolobosea (supergroup Excavata), Amoebozoa (supergroup Amorphea) and Rhizaria (supergroup SAR). Most species are free-living in aquatic and terrestrial habitats where they feed on other micro-organisms, but several species have become symbiotic in metazoan organisms as endocommensals or opportunistic-facultative parasites (representatives tabulated below).

Higher taxonomy	Class/Order	Family	Genus	Hosts	Tissues (disease)*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: **Discoba** (diverse group supported robustly by molecular studies)					
Phylum: Heterolobosea (amoebo-flagellates, most form cysts)	O: Schizopyrenida (no fruiting bodies)	Vahlkampfidae (eruptive limax pseudopodia, flagellated stages)	*Naegleria*	mammals	central nervous system (PAM)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)					
Phylum: **Amoebozoa** (locomotion by noneruptive pseudopodia, asexual development)					
Subphylum: Conosa (archamoebae & mycetozoa)	C: Archamoebae (amitochondriate, rounded cysts)	Entamoebidae (uninucleate, endozoic)	*Entamoeba*	mammals	colon (dysentery), central nervous system (SAM)
Subphylum: Lobosa (lobose amoebae)	C: Discosea (flattened forms, protoplasmic flow polyaxial)	Vexilliferidae (dactylopodia, parasomes)	*Paramoeba* *Neoparamoeba*	fish	gills (AGD)
	C: Longamoebea (flattened elongated cells, stellate cysts)	Acanthamoebidae (acanthopodial subpseudopodia)	*Acanthamoeba, Balamuthia*	mammals	central nervous system (GAE)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups robustly supported by molecular studies)					
Group: **Rhizaria** (amoebae with fine pseudopodia in simple, branching or anastomosing patterns)					
Phylum: Cercozoa	Filosa (with filopodia, naked or testate)			free-living (aquatic, terrestrial)	
Phylum: Endomyxa	heterotrophic amoeboid or plasmodial cells			free-living, some parasitoids	

Phylum: Retaria	Foraminifera (with reticulopodia), Radiolaria (with axopodia)	free-living (aquatic)

*PAM = primary amoebic meningoencephalitis; SAM = secondary amoebic meningoencephalitis; GAE = granulomatous amoebic encephalitis; AGD = amoebic gill disease.

The Heterolobosea has a diverse membership, most forming cysts or fruiting bodies, but their grouping is supported robustly by molecular studies. The phylum includes the schizopyrenids or amoebo-flagellates; i.e. amoebae that form temporary flagellated stages for dispersal. The vahlkampfids are naked amoebae (without tests or shells) that form eruptive 'limax' pseudopodia; most species being free-living amoebae (FLA) in aquatic and terrestrial environments. Some FLA species are amphizoic and may opportunistically infect vertebrate hosts, usually causing neurological conditions. Primary meningoencephalitis (PAM) is caused by *Naegleria* spp. while granulomatous amoebic encephalitis (GAE) is caused by *Acanthamoeba*, *Balamuthia* or *Sappinia* spp. [note that secondary amoebic meningoencephalitis (SAM) is caused by extraintestinal infections by the parasite *Entamoeba histolytica*]. FLA do not form a natural assemblage but have been split by recent molecular studies into different phyla: *Naegleria* being classified within the Heterolobosea (amoebo-flagellates), and *Acanthamoeba*, *Balamuthia* and *Sappinia* within the Amoebozoa (noneruptive pseudopodia) [together with the parasite *Entamoeba*]. Around 50 *Naegleria* spp. have been described throughout the world as free-living amoebae primarily from freshwater sources. While several species have been isolated from various vertebrate hosts, only *Naegleria fowleri* has been associated with disease in humans, especially children. Clinical infections were first encountered in Australia where *N. fowleri* was associated with public water supplies, but infections have now been found in many countries in association with warm waters such as heated swimming pools, geothermal springs, tropical lakes, above-ground pipelines and discharged industrial cooling water.

***Naegleria* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
N. aerobia	Experimental infections in Rodentia: murid (mice), caviid (guinea pig)	brain, skin, viscera	encephalitis	various laboratories
N. australiensis	Experimental infections in Rodentia: murid (mice)	brain	encephalitis	various laboratories
N. fowleri	Primates: hominid (human), Perissodactyla: tapirid (tapir); Artiodactyla: bovid (cattle); plus experimental infections in Primates: cercopithecids (macaques, rhesus), Rodentia: murid (mice), caviid (guinea pigs), cricetid (cotton rat, muskrat) sciurid (squirrels); Artiodactyla: bovid (sheep); Lagomorpha: leporid (rabbits)	brain	encephalitis	cosmopolitan
N. italica	Experimental infections in Rodentia: murid (mice)	brain	encephalitis	various laboratories
N. philippinensis	Experimental infections in Rodentia: murid (mice)	brain	encephalitis	various laboratories

Compared to the number of *Naegleria* spp. and isolates described from environmental samples, only a small number have been recovered from naturally infected hosts. *N. fowleri* has been associated with clinical disease in humans, cattle and a tapir, although experimental infections have been established in a range of laboratory, domestic and wild animals. Several other *Naegleria* spp. have been found to experimentally infect laboratory animals, *N. gruberi* has been recovered from the intestinal contents of freshwater fish while un-named species have been detected in the brain and liver of mice and rabbits. Nonetheless, natural infections may be more widespread than previously thought as evidenced by the recent molecular characterization of *Naegleria* isolates from the brain, gills, liver, spleen, kidney and skin of 12 species of freshwater fishes which resulted in the detection of ten novel genotypes and eight genotypes referable to the species *N. australiensis, N. pagei, N. fultoni* and *N. clarki*. Indeed, serological studies have detected antibodies against *Naegleria* antigens in a wide variety of wild mammals; including raccoons, opossums and various rodents. Other species recovered from freshwater and wet soils include *N. americana, N. andersoni, N. angularis, N. antarctica, N. arctica, N. byersi, N. canariensis, N. carteri, N. chilensis, N. clarki, N. dobsoni, N. dunnebackei, N. endoi, N. fultoni, N. galeacystis, N. gallica, N. gruberi, N. indonesiensis, N. jadini, N. jamiesoni, N. johanseni, N. laresi, N. lovaniensis, N. martinezi, N. mexicana, N. minor, N. morganensis, N. neoantarctica, N. neochilensis, N. neodobsoni, N. neopolaris, N. niuginiensis, N. pagei, N. paradobsoni, N. peruana, N. polaris, N. pringsheimi, N. pussardi, N. robinsoni, N. schusteri, N. spitzbergenensis, N. sturti, N.*

tenerifensis and *N. tihangensis.* No endosymbiotic bacteria have been detected in environmental or clinical isolates of *Naegleria* spp.

Parasite morphology: *Naegleria* spp. have three morphological stages in their life cycle: amoeboid trophozoites, flagellated trophozoites (amoebo-flagellates) and cysts. Under adverse environmental conditions, including cold or dry environments, the parasite will encyst in order to survive. Cysts are ovoid measuring 8-12 μm in diameter and are bound by a porous wall of 1-2 layers, depending on the species. The pores are large and plugged with mucus. Regenerated trophozoites emerge through the pores when environmental conditions allow. Amoeboid trophozoites predominate as motile feeding and dividing stages. They are pleomorphic and constantly changing shape, from thin elongate forms to robust round forms. When rounded, *Naegleria fowleri* trophozoites measure 10-15 μm in diameter. They are uninucleate and have a characteristic dense nucleolus surrounded by a large transparent nuclear halo. They have a granular cytoplasm containing numerous vacuoles and they often form peripheral 'food cups' used to engulf bacteria, yeasts or cellular debris as a nutrient source, as well as providing an attachment mechanism. Trophozoites exhibit a limax (slug-like) monopodial pattern of movement, wherein they extend finger-like lobopodia to move forward. Trophozoites reproduce by binary fission to produce two identical offspring. Amoeboid trophozoites may also form temporary bi-flagellated stages 10-20 μm in length which act as non-feeding non-dividing dispersal forms in aquatic media.

Site of infection: *Naegleria fowleri* infects the central nervous system, initially the olfactory and frontal lobes but progressing through perivascular regions to the base of the brain, the brain stem and the cerebellum. A single case was also reported where amoebae were detected in an immuno-compromised patient outside the brain in lesions in the stomach, intestines, lymph nodes and lungs. Cyst formation has not been reported in host tissues.

Pathogenesis: *Naegleria* species and strains vary markedly in their infectivity and pathogenicity so many infections may be asymptomatic and go unnoticed. Indeed, *Naegleria* amoebae (including *N. fowleri*) have been isolated from the nasal mucosa of healthy asymptomatic individuals. However, invasive infections by *N. fowleri* most often result in fulminant (sudden and severe) central nervous system disease, and eventually death. Once the organism has gained access to the brain, strains with a low level of pathogenicity consume nerve tissue in a piecemeal fashion, using food cups. In contrast, highly pathogenic strains apparently absorb the hosts' nervous tissue by releasing cytolytic enzymes to lyse cells thus allowing the amoebae to consume the cellular debris. It is this process that leads to the disease known as primary amoebic meningoencephalitis (PAM), a combination of cell lysis and inflammation involving brain tissues and the surrounding meninges. Onset of symptoms occurs within days of exposure, and includes severe headache, nausea and vomiting, stiff neck, variable fever of (38.5-41°C) and behavioural abnormalities. Thus far, most infections have involved children and the disease PAM has almost invariably proven fatal after 1-2 weeks.

Developmental cycle and mode of transmission: Infections are acquired when amoeboid trophozoites and cysts in water come into contact with the olfactory epithelium of the nasal mucosa. Trophozoites penetrate the epithelium and track along the olfactory nerve crossing the cribriform plate to the olfactory bulb in the subarachnoid space. From there, trophozoites are free to move throughout the rest of the central nervous system. Obviously, infections are more likely in people who spend a long time swimming, bathing or submerging their heads regularly in water, particularly untreated warm water sources (including shallow pools, spas and geothermal springs). Thermotolerant amoebae thrive in warm waters (*N. fowleri* grows fastest at 42°C) and they can tolerate suboptimal chlorine disinfection. Children are more at risk as they are likely to spend more time splashing and diving in water. There is also some evidence to suggest that *Naegleria* cysts may also be inhaled as dust formed from dried freshwater lakes, although *N. fowleri* cysts have been shown to have poor resistance to desiccation and thus only rarely occurs in soil.

Differential diagnosis: Presentation with meningitis-like symptoms is the first indicator of PAM. A recent history of immersion in freshwater could alert a physician to consider the possibility of *Naegleria* infection. Direct diagnosis may be made by microscopic examination of brain biopsy material of cerebrospinal fluid (CSF) for motile amoebae. Samples mounted in a drop of distilled water may further aid identification, as *Naegleria* trophozoites quickly become flagellated when exposed to water (as opposed to those of *Acanthamoeba*). Amoebae can also be cultured on agar plates spread with bacteria incubated at 37°C for 24 hours. Serological (ELISA) and molecular (PCR) tests have recently been developed to aid diagnosis but are used mainly for research. Molecular characterization techniques have been used to explore genotypic variation between and within species. Isoenzyme electrophoresis, restriction fragment length polymorphism (RFLP) and randomly amplified polymorphic DNA (RAPD) analyses led to the recognition of three major geographic variants of *N. fowleri* (European, Oceanic and American), but subsequent studies using ribosomal RNA gene sequences have so far identified six major genotype groups; three corresponding to geographic regions but another three being more widespread.

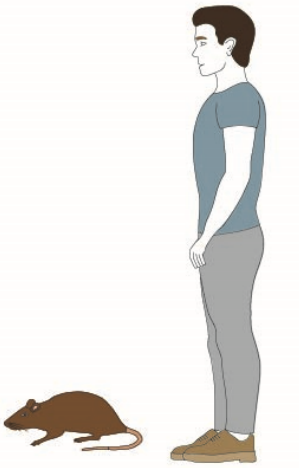
Treatment and control: The currently accepted treatment for infection with *Naegleria fowleri* is aggressive treatment with high doses of intravenous and intrathecal amphotericin B, and in some cases miconazole. PAM is generally fatal within 1–2 weeks of infection, thus early diagnosis is essential for successful treatment. Meningitis is a relatively common condition; however, *Naegleria*

fowleri as a cause of these symptoms is rare. It is therefore unlikely to be suspected and diagnosed early enough for effective treatment. Doctors need to be aware of the risk of infection and public education campaigns should be mounted in high-risk areas (such as around hot springs and warm pools). Signs should warn bathers not to immerse their heads and to avoid diving, splashing and inhaling mists. Swimming pools and spas should be regularly chlorinated (at appropriate dosages) and monitored for the presence of amoebae. Chlorine has been shown to kill all life-cycle stages of *N. fowleri* if thoroughly mixed into water supplies, and chloramination has been shown to be most effective.

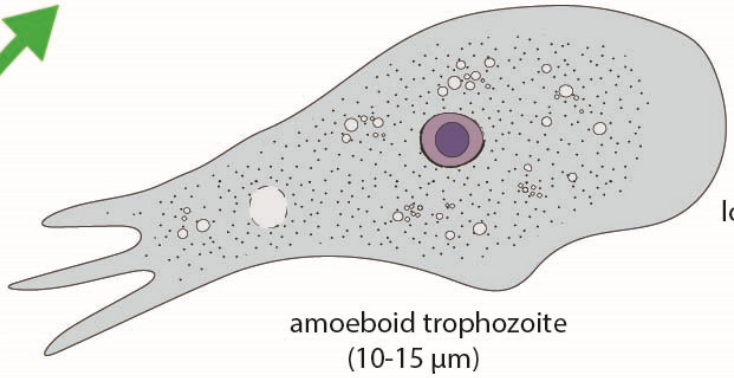
Naegleria



nasal mucosa, brain
(cell lysis, inflammation,
primary amoebic
meningoencephalitis)



Vertebrate Hosts
(mammals, some
other animals)



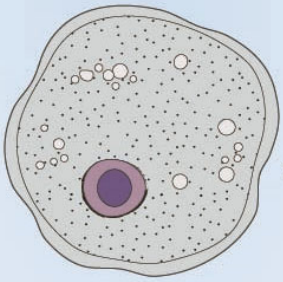
leading
'limax'
lobopodia

trailing
filopodia

amoeboid trophozoite
(10-15 µm)

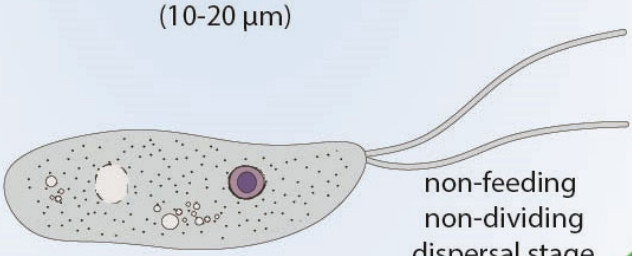
exystment in contact
with nasal mucosa

cyst formation in
external environment



porous
cyst wall

cyst
(10-20 µm)



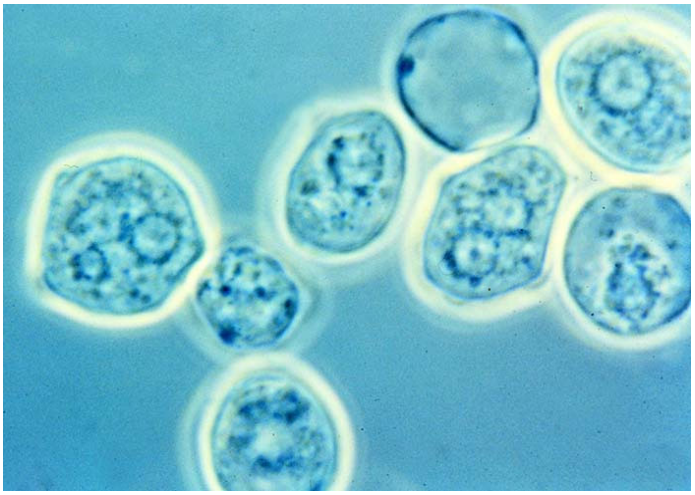
non-feeding
non-dividing
dispersal stage

unique biflagellated
trophozoite (10-20 µm)

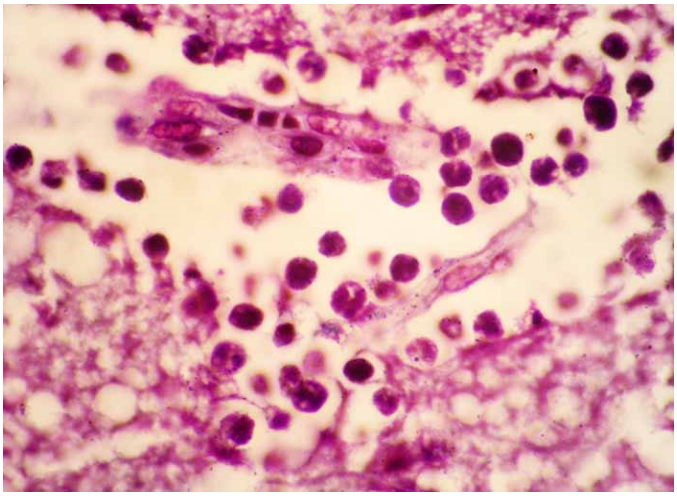
many species free-living in aquatic and terrestrial habitats,
some opportunistically parasitic
(transmission by contact when bathing)



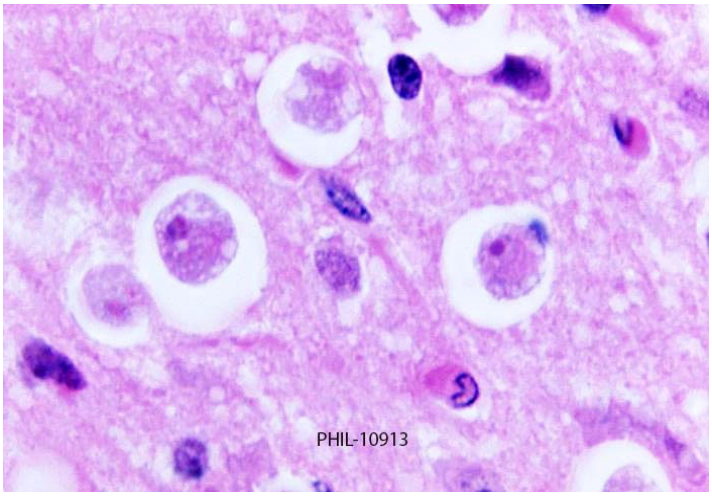
Naegleria trophozoites



Naegleria cysts



Naegleria brain lesion



Naegleria brain lesion

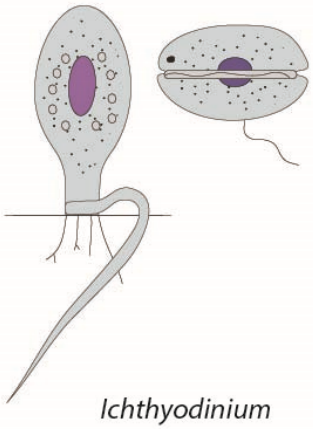
Protista
(flagellates)

Dinoflagellates

Amyloodinium

trophont (< 150 µm)

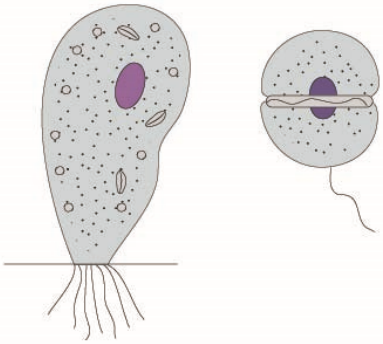
dinospore (5-20 µm)



Piscinoodinium

trophont (< 160 µm)

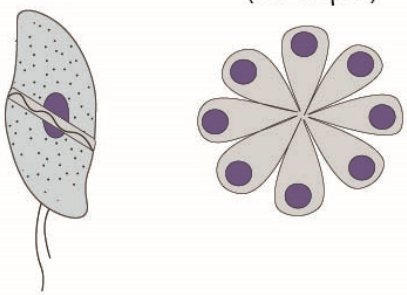
dinospore (5-20 µm)



Ichthyodinium

dinospore (8-12 µm)

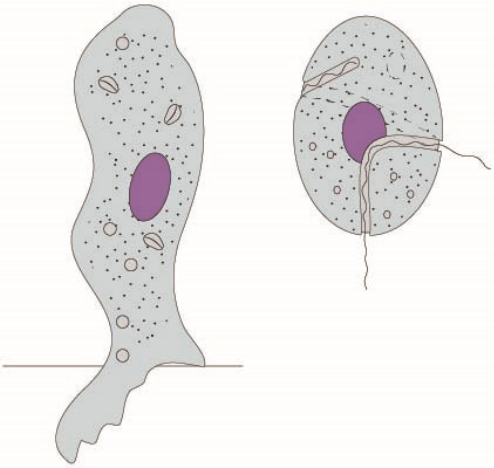
schizonts (20-40 µm)



Crepidoodinium

trophont (< 700 µm)

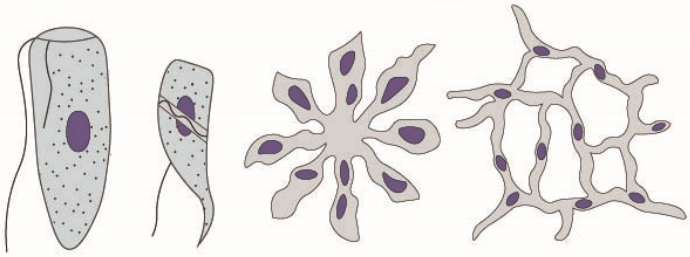
dinospore (5-20 µm)



Haematodinium

dinospores (7-14 µm)

multinucleate plasmodia (6-200 µm)

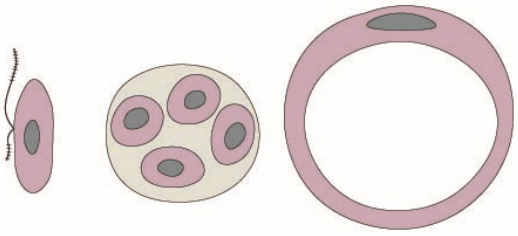


incertae sedis: Perkinsus

zoospore (4-6 µm)

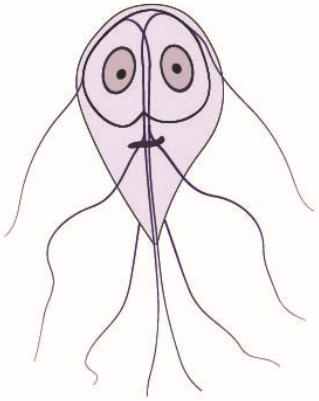
schizont (15-100 µm)

zoosporangia (30-200 µm)

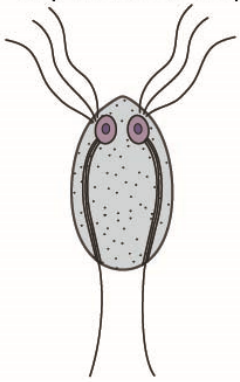


Diplomonad flagellates

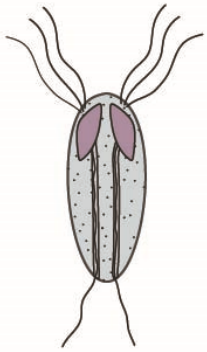
Giardia
trophozoite (10-30 µm)



Hexamita
trophozoite (3-22 µm)

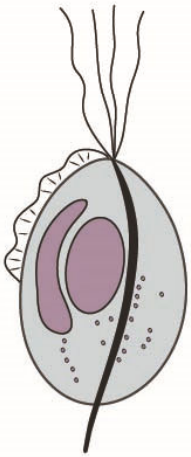


Spironucleus
trophozoite (5-20 µm)

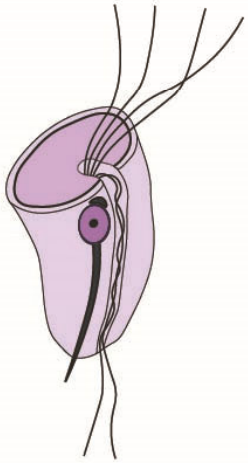


Parabasalid flagellates

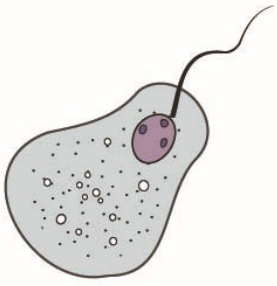
Trichomonas
trophozoite (7-32 µm)



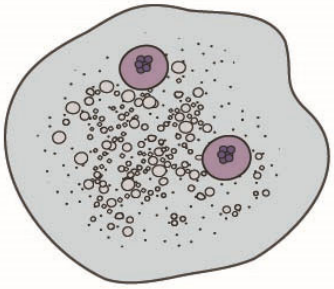
Cochlosoma
trophozoite (5-20 µm)

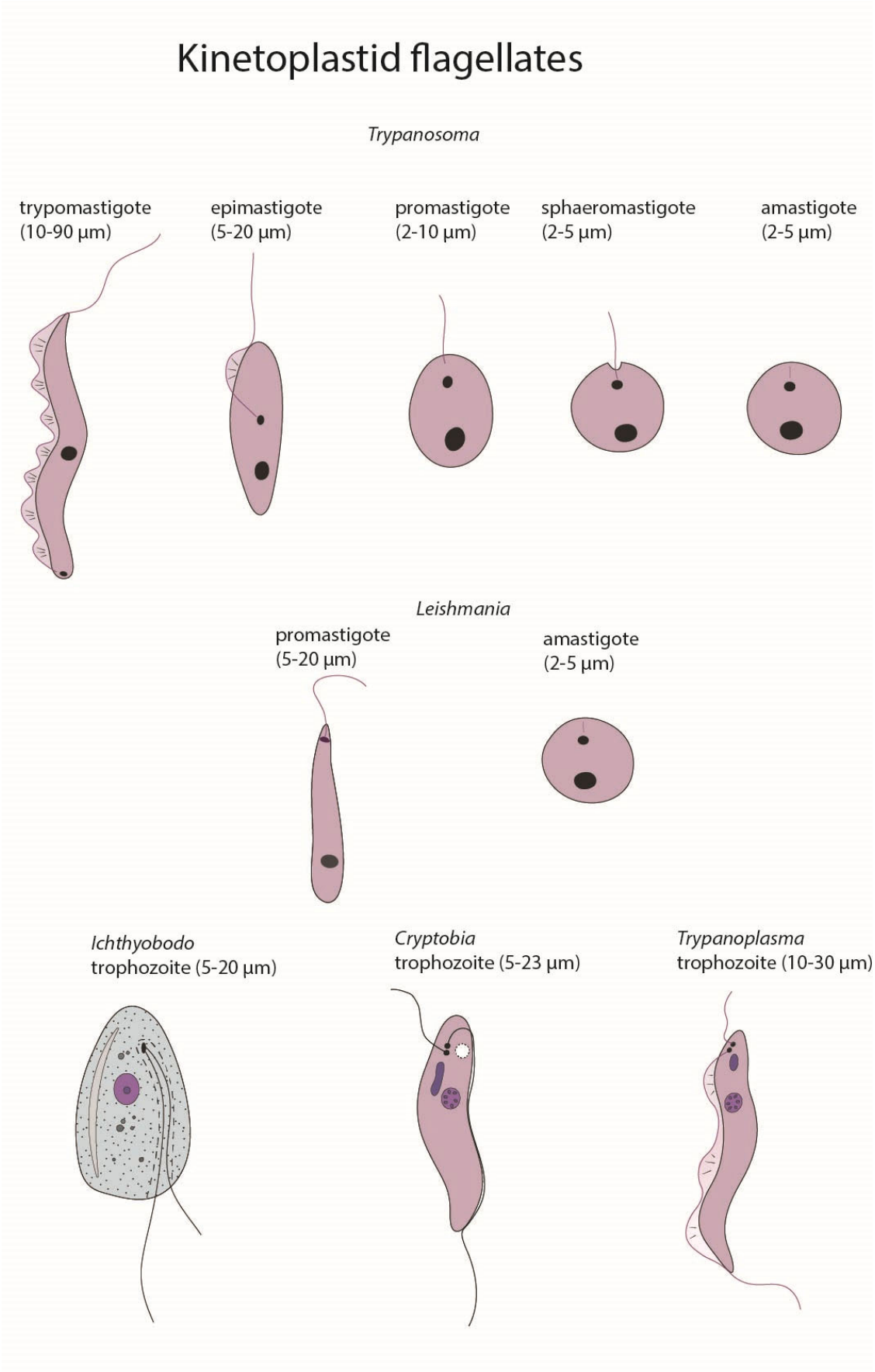


Histomonas
trophozoite (5-30 µm)



Dientamoeba
trophozoite (4-40 µm)




Kinetoplastid flagellates
Trypanosoma
trypomastigote
(10-90 µm)
epimastigote
(5-20 µm)
promastigote
(2-10 µm)
sphaeromastigote
(2-5 µm)
amastigote
(2-5 µm)
Leishmania
promastigote
(5-20 µm)
amastigote
(2-5 µm)
Ichthyobodo
trophozoite (5-20 µm)
Cryptobia
trophozoite (5-23 µm)
Trypanoplasma
trophozoite (10-30 µm)

Amyloodinium, Crepidoodinium, Piscinoodinium
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Phytoflagellates possess chloroplasts, which require sunlight to function, so most species are free-living aquatic organisms. Dinoflagellates have a distinctive haploid nucleus (dinokaryon) where the chromosomes remain condensed during interphase and are evident as beaded strands due to low levels of histones and associated proteins (condition termed 'mesokaryotic'). Many dinoflagellates form characteristic free-swimming dinospores (thecate and/or pigmented) and various species have been associated with coloured tides/blooms, bioluminescence and even neurotoxicity in mammals (paralytic shellfish poisoning). Some species, however, are heterotrophic and parasitic in marine animals; including the blastodinids which form uninucleate trophonts (with chloroplasts) attached to the skin of fish where they may cause surface lesions (such as velvet disease).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria)
Group: Alveolata (with cortical alveoli)
Phylum: Dinoflagellata (with unique mesokaryotic nuclei (lacking histones), autotrophs and heterotrophs)
Class: Blastodiniophyceae (extracellular athecate parasites of zooplankton, algae, crustacea and fish)
Order: Blastodiniales (uninucleate trophonts with chloroplasts)
Family: Oodiniaceae (trophont fusiform with rhizoid-like invasive organelle)
Genus: *Amyloodinium* (parasitic on skin of fish)
Genus: *Crepidoodinium* (parasitic on skin of fish)
Genus: *Piscinoodinium* (parasitic on skin of fish)
Species: various species cause lesions in fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					

Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

The group Alveolata in the supergroup SAR is characterized by the possession of cortical membranous alveoli (vesicles or sacs) underlying and supporting the cell wall, and includes many otherwise disparate groups comprising 3 large assemblages (Apicomplexa, Ciliophora, Dinoflagellata) and 6 smaller taxa (Acavomonidia, Chromerida, Colpodellida, Colponemidia, Perkinsozoa and Voromonadida). The phylum Dinoflagellata comprises a diverse group of aquatic organisms, with many free-living species being important in food chains either as producers (autotrophs) or consumers (heterotrophs), some being endosymbiotic in invertebrates (e.g. in photosynthetic corals) and some being parasitic mainly in invertebrates but also a few vertebrates (fish). Dinoflagellates have a distinctive haploid nucleus (dinokaryon) where the chromosomes remain condensed during interphase and are evident as beaded strands due to low levels of histones and associated proteins (condition termed 'mesokaryotic'). Many dinoflagellates contain chloroplasts so early classification systems have used either botanical or zoological nomenclature, whereas recent molecular phylogenetic studies on eukaryotes have recognized and characterized cognate groups and provided appropriate names. Trophonts (or dinospores) of most species have an unequal heterodynamic pair of flagella; one ribbon-like and lying in equatorial furrow (girdle or cingulum) and the other directed posteriorly and often lying in a longitudinal ventral furrow (sulcus). Many species have thecate dinospores encased in armour composed of cellulosic plates; the anterior section is termed the epitheca (epicone in unarmoured species) and the posterior section is called the hypotheca (hypocone). Most species have unique membranous cytoplasmic organelles called pusules which are thought to be associated with osmoregulatory or excretory function. Many species have coloured chloroplasts and/or coloured pigments, some even exhibiting bioluminescence when disturbed by wind, wave or boat wakes. Several pigmented species bloom under suitable environmental conditions and cause 'red tides' and some pigments are neurotoxic to mammals when concentrated in the tissues of fish or filter-feeding shellfish (causing PSP 'paralytic shellfish poisoning'). Exemplars of toxic dinoflagellates are tabulated below (for interest only):

Toxic dinoflagellates	Toxin	Transvector	Effect
Prorocentrum	venerupin	shellfish	human hepatotoxicity
Dinophysis	okadaic acid	shellfish	human enterotoxicity
Pyrodinium	saxitoxin	shellfish	human neurotoxicity (PSP)
Protogonyaulax	saxitoxin	shellfish	human neurotoxicity (PSP)
Gymnodinium	saxitoxin	shellfish	human neurotoxicity (PSP) & fish kills
Ptychodiscus	brevetoxin	shellfish	human neurotoxicity & fish kills
Peridinium	glenodinine	-	fish kills
Gambierdiscus	ciguatoxin	fish	ciguatera

Over 4,000 dinoflagellate species are recognized in 550 genera: the majority being free-living autotrophs in pelagic or neritic surface waters. However, some 140 species from 5 families are heterotrophic and parasitic in aquatic hosts: including Oodinidae

(e.g. *Amyloodinium, Piscinoodinium* and *Crepidoodinium* on skin and gills of fish); Syndinidae (e.g. *Ichthyodinium* and *Hematodinium* in tissues of fish and crabs); Chytriodinidae (e.g. *Chytriodinium* on eggs of copepods and shrimps); Paradinidae (e.g. *Paradinium* in body cavities of copepods); and Ellobiopsidae (e.g. *Ellobiopsis* and *Thalassomyces* on exoskeletons of crustacea). Genera parasitic on fish and in shellfish that are covered in this document are tabulated below.

Taxon	Genus	Hosts	Site	Transmission
Class: Blastodiniophyceae† (uninucleate trophonts, often with chloroplasts)				
Order: Blastodiniales† (ectoparasitic on zooplankton, algae, crustacea and fish)				
Oodinidae (trophonts with rhizoid-like holdfast organelles, gymnospores)	*Amyloodinium*	fish	skin	direct (water)
	Crepidoodinium	fish	skin	direct (water)
	Piscinoodinium	fish	skin	direct (water)
Class: Syndiniophyceae (multinucleate trophonts, without chloroplasts)				
Order: Syndiniales (endoparasitic in copepods, appendicularians, crabs, radiolaria and fish eggs)				
Syndinidae (plasmodial trophonts, dinospores not of *Gymnodinium* type)	*Hematodinium*	decapods	tissues	direct (water)
	Ichthyodinium	fish	tissues	direct (water)

†In recent classifications, these names are no longer valid, and the genera are considered *incertae sedis* in the Dinoflagellata.

Ectoparasitic oodinid dinoflagellates found on fish were often first identified as *Oodinium* spp., but this genus has now been reserved for species found on tunicates and polychaetes which form sac-like trophonts without rhizoid-like attachment organelles, stomopodes, chloroplasts or starch granules. Those species infecting fish have subsequently been transferred to new genera (*Amyloodinium*, *Piscinoodinium* and *Crepidoodinium*) which all form elongate trophonts with elaborate rhizoid-like holdfast organelles attached to host cells, but differ in their host range, tissue tropism, pathogenicity, trophont size, rhizoid type, and vary in their possession of peduncles, stomopodes, chloroplasts, alveolar plates, tomont (palmella) cyst walls, dinospore (gymnospore) size and stigma (eyespots): tabulated as follows:

Character	Dinoflagellate genera ectoparasitic on fish		
	Amyloodinium	***Piscinoodinium***	***Crepidoodinium***
Hosts	marine fish	freshwater fish	marine/estuarine fish
Site of infection	skin, gills	skin, gills	gills
Trophont shape	pyriform	pyriform	fusiform
Trophont size	up to 150 µm	80-160 µm	up to 670-820 µm
Peduncle (stalk)	short	short	absent
Holdfast projections	long filiform	rod-like	finger-like
Attachment to host cells	penetrate cells	penetrate cells	do not penetrate cells
Tentacle-like stomopode	present	absent	absent
Chloroplasts	absent	present	present
Alveoli	with plates	without plates	without plates
Cytoplasm	not spongy	not spongy	spongy
Starch grains	present	present	present
Tomont (palmella) division	with common cyst wall	without common envelope	?
Number of dinospores	up to 256	up to 256	up to 2048
Dinospore stigma (eyespot)	present	absent	absent

Infections by *Amyloodinium* and *Piscinoodinium* species may cause superficial discolourations of fish skin (condition known as velvet disease) with attached trophonts leading to host cell destruction and superficial lesions. Infections occur in marine and freshwater fish respectively, particularly in species used in aquaculture and aquarium industries. Infections by *Crepidoodinium* species are less invasive and confined to the gills of several marine and estuarine fish species, although their presence may possibly interfere with respiratory function.

Parasite species	Hosts	Location (disease)	Gymnospores	Distribution
Amyloodinium ocellatum (syn. *Oodinium*)	marine and brackish-water fish – Acanthuriformes: acanthurid (doctorfish tang, Atlantic blue tang), sciaenid (silver croaker, spot croaker, Atlantic croaker, southern kingcroaker, northern kingcroaker, sand seatrout, spotted seatrout, squeteague, red	gills, eyes, skin, fins, sometimes internal organs (velvet disease)	10-15 x 8-15 µm	cosmopolitan

	rum, banded drum, striped drum, cubbyu, meagre); Anguilliformes: ophichthid (speckled worm eel, shrimp eel); Aulopiformes: synodontid (inshore lizardfish); Batrachoidiformes: batrachoidid (Gulf toadfish, midshipman fish); Blenniformes: blenniid (striped blenny, feather blenny, freckled blenny); Carangiformes: carangid (blue runner, crevalle jack, horse-eye jack, leather jack, Atlantic bumper, pilot fish, Florida pompano, permit, greater yellowtail); Cichliformes: cichlid (Mozambique tilapia); Clupeiformes: dorosomatid (scaled sardine), engraulid (bay anchovy); Cyprinodontiformes: fundulid (saltmarsh topminnow), poeciliid (western mosquitofish); Gadiformes: morid (southern codling); Gobiesociformes: gobiesocid (skilletfish); Gobiiformes: eleotrid (spiny-cheek sleeper), gobiid (frillfin goby, naked goby, code goby, clown goby, pink wormfish), oxudercid (violet goby); Holocentriformes: holocentrid (squirrelfish); Kurtiformes: apogonid (flamefish); Labriformes: labrid (bluehead wrasse), scarid (blue parrotfish); Moroniformes: ephippid (Atlantic spadefish), moronid (striped bass, European seabass); Mugiliformes: mugilid (flathead grey mullet); Myliobatiformes: dasyatid (Atlantic stingray); Perciformes: centrarchid (bluegill), chaetodontid (foureye butterflyfish), epinephelid (rock hind, red grouper, snowy grouper), gerreid (silver mojarra), haemulid (porkfish, redmouth grunt, grey grunt, banana grunt, Spanish grunt, white grunt, blue-striped grunt), latid (barramundi), lobotid (Atlantic tripletail), lutjanid (mutton snapper, schoolmaster snapper, northern red snapper, grey snapper, dog snapper, lane snapper, yellowtail snapper), pomacanthid (gray angelfish, French angelfish), pomacentrid (sergeant major, marine clownfish), pomatomid (bluefish), serranid (rock sea bass, black sea bass, graysby, pygmy sea bass, belted sandfish, white-spotted soapfish, greater soapfish), sparid (gilthead sea bream, white sea bream, two-banded sea bream, sharpsnout sea bream, sheepshead, pinfish, porgy); Pleuronectiformes: achirid (lined sole, hogchoker), cynoglossid (blackcheek tonguefish), paralichthyid (bay whiff, fringed flounder, southern flounder), soleid (Senegalese sole); Scombriformes: stromateid (silver pomfret); Scorpaeniformes: scorpaenid (barbfish), triglid (northern searobin, striped searobin, bluespotted searobin, bighead searobin); Siluriformes: ariid (hardhead catfish, gafftopsail catfish); Syngnathiformes: syngnathid (lined seahorse, chain pipefish); Tetraodontiformes: balistid (green triggerfish), diodontid (striped burrfish, spotfin porcupinefish), monacanthid (orange			

	filefish, plainhead filefish), ostraciid (scrawled cowfish, buffalo trunkfish), tetraodontid (northern puffer, least puffer, Caribbean sharpnose puffer)			
Piscinoodinium pillulare (syn. *Oodinium pillularis, O. limneticum*)	tropical freshwater aquaria fish - Anabantiformes: osphronemid (Siamese fighting fish, paradise fish); Characiformes: characid (tetras); Cypriniformes: cyprinid (goldfish, zebrafish, barbs, danios, Crucian carp, common carp, sunbleak, tench), Cyprinodontiformes: poeciliid (guppies, mollies, platys, swordtails); Urodela: ambystomatid (axolotyl larvae); Anura: ranid (tadpoles of European common brown frogs and moor frogs)	gills, skin, fins, nasal cavity, eye orbit (velvet disease)	10-19 x 7-12 µm	cosmopolitan (aquaria, cultures)
Crepidoodinium cyprinodontum	estuarine Cyprinodontiformes: cyprinodontid (sheepshead minnow), fundulid (mummichog, spotfin killifish, striped killifish, rainwater killifish)	gills	5-9 x 2-5 µm	North America
Crepidoodinium australe	estuarine Perciformes: sillaginid (sand whiting)	gills	17 x 12 µm	Australia

Parasite morphology: The dinoflagellates *Amyloodinium*, *Piscinoodinium* and *Crepidoodinium* spp. each form 3 different types of morphological stages during their development: trophonts, tomonts and spores (each stage having acquired a variety of names over history). The trophonts (sometimes known as trophozoites) attach to host cells, beginning as small ovoid stages around 20-30 µm in diameter but then growing to becoming elongate fusiform to pyriform stages varying in size from 80-820 x 50-80 µm according to species: *Amyloodinium* ranging up to 150 µm, *Piscinoodinium* from 80-160 µm, and *Crepidoodinium* up to 670-820 µm. The trophonts are enclosed in cellulosic walls that are often rugose (with longitudinal furrows) and usually projecting perpendicularly from the host cell surface with the attached end narrowed slightly, and in the case of *Amyloodinium* and *Piscinoodinium* containing a short stalk (peduncle). They vary in colour from green-brown due to the presence of chloroplasts (in *Piscinoodinium* and *Crepidoodinium*) or remain colourless (*Amyloodinium* without chloroplasts). It should be noted that some *Piscinoodinium* isolates apparently lacking chloroplasts had elaborate membranous organelles associated with starch granules in a manner similar to that of chloroplast thylakoids, suggesting they may be degenerated chloroplasts. The trophonts were sessile and attached to the surface of host epithelial cells by discoid holdfast organelles with several elongate anchor-like projections (called rhizoids). *Amyloodinium* and *Piscinoodinium* have filiform or rod-like projections that penetrate host cells, while *Crepidoodinium* have finger-like projections that do not penetrate host cells. *Amyloodinium* also had a special tentacle-like stomopode extending basally which appears to be involved in feeding. All trophonts had well developed pusules (non-contractile vacuoles) involved in osmoregulation and/or excretion. Mature trophonts detach from the host and become spherical as they encyst to form tomont (palmella) stages which are reproductive stages as they undergo a series of internal divisions (palintomy) either within a common cystic envelope (*Amyloodinium*) or the old envelope dissolves after each division (*Piscinoodinium*). The tomonts grow up to 100-200 µm in size and they produce and release numerous free-swimming spores (known as swarmers, zoospores or dinospores which resemble those of the free-living genus *Gymnodinium,* hence the frequent use of the name gymnospores). Tomonts of *Amyloodinium* and *Piscinoodinium* may release up to 256 spores, whereas those of *Crepidoodinium* may release up to 2,048 spores. The spores have an armoured cellulosic wall and are ovoid with a somewhat flattened hamburger-shape ranging in size from 5-19 x 2-15 µm. They are biflagellated with 2 flagella: one transverse flagellum lying in an equatorial furrow (girdle or cingulum); and one longitudinal flagellum directed posteriorly and lying in a ventral furrow (sulcus). The spores often have small ventral pseudopodial projection that is used for host attachment, and the spores of *Amyloodinium* also possess a dark-coloured eyespot (stigma).

Site of infection: *Amyloodinium* and *Piscinoodinium* have ectoparasitic trophonts with rhizoid projections penetrating host epithelial cells, commonly on the gills, skin or fins of fish, but sometimes on the eyes and oropharyngeal cavity. *Amyloodinium* is cosmopolitan in brackish and seawater environments in temperate and tropical areas and has a broad host range, being found on some 123 fish species (the only dinoflagellate capable of infecting teleosts and elasmobranchs). *Piscinoodinium* is found in freshwater environments and has been recorded on almost 20 fish species, particularly small species involved in the aquarium trade. In contrast, trophonts of *Crepidoodinium* spp. do not have projections penetrating host cells but attach themselves to gill epithelia in some 6 species of estuarine fishes.

Pathogenesis: Infections by ectoparasitic trophonts may cause a skin condition known as velvet disease (sometimes called gold dust or rust disease). *Amyloodinium* causes marine velvet (amyloodinosis, previously known as oodiniosis) and *Piscinoodinium* causes freshwater velvet (piscinoodiniosis). The skin of infected fishes takes on a cream, gold or rust-coloured dusty appearance that varies in intensity with the density of attached trophonts. Skin discolouration may develop over several days to weeks with patches

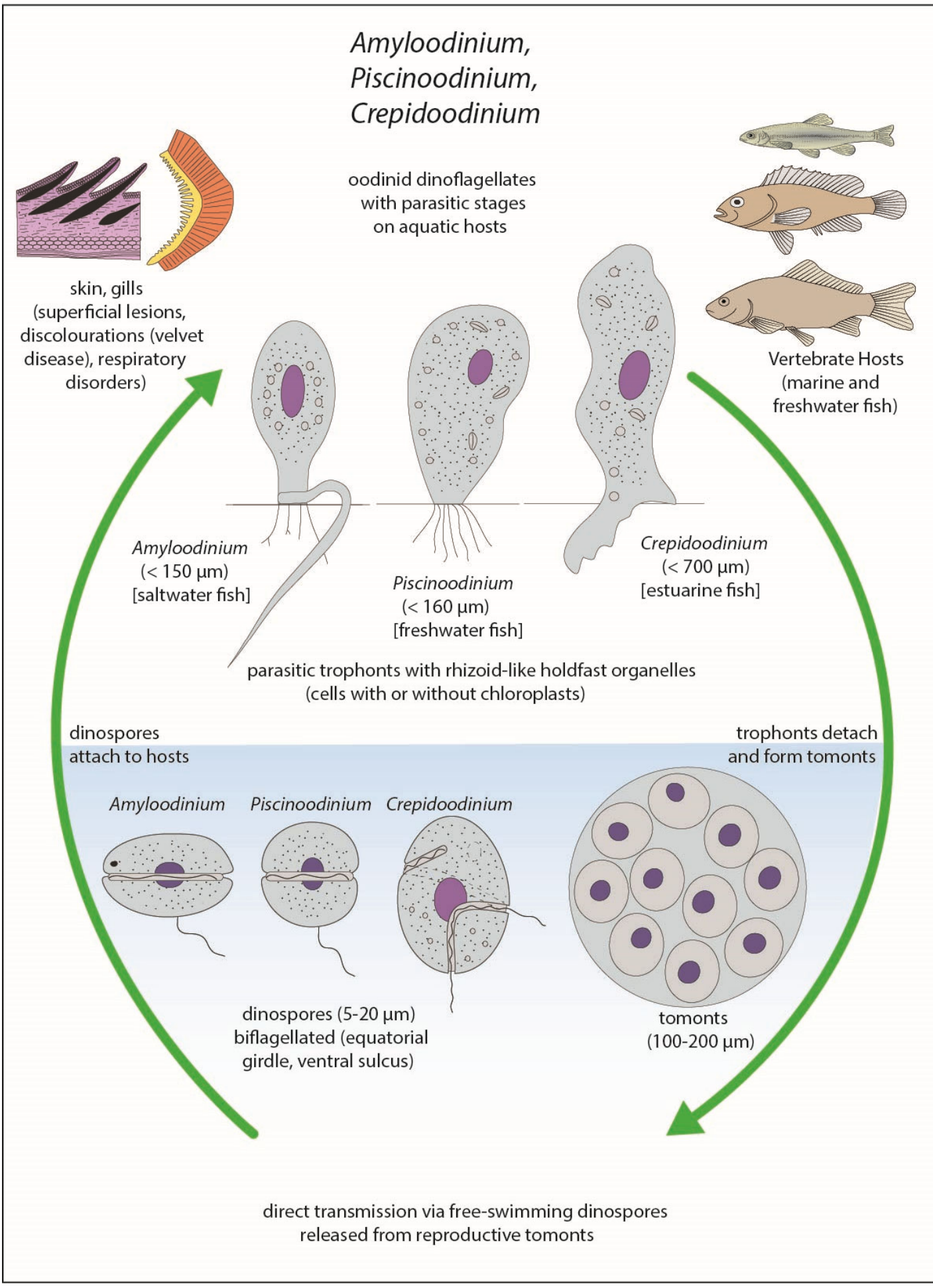
progressing to more dense films which may eventually present as a contiguous finely granular layer over the whole body and fins. Although attached trophonts are essentially sessile, they constantly twist and turn as their rhizoid projections penetrate epithelia slowly damaging and destroying cells causing focal lesions. Infections elicit moderate-to-intense tissue reactions with inflammation, haemorrhages, epithelial hyperplasia and necrosis. The gills may become swollen, oedematous and have excessive mucus production making breathing difficult. Infected fish experience discomfort and often show behavioural changes, such as rubbing against solid objects with jerky ('flashing') movements, clamping the fins against the body, and dyspnoea with rapid laboured breathing and gathering at the water surface gasping for air. In heavy advanced infections, the skin may begin to peel off and fish become lethargic, anorexic, lose weight and die. The causes of death may involve various combinations of respiratory insufficiency, metabolic depletion, osmoregulatory impairment, and secondary microbial infections due to epithelial disruptions. Velvet is highly contagious and thrives on fish stressed by captivity or other factors (especially poor water quality due to over-feeding, over-crowding or poor oxygenation). Infections constitute serious problems for both aquaculture and mariculture enterprises, particularly lagoon-based valliculture and inland brackish-water farming where shallow beds and poor water circulation allows parasites to proliferate over the warmer months. Infections may occur in all fish life stages, although there is some evidence to suggest that some fish may develop protective immunity after repeated or protracted exposure. Infections by *Crepidoodinium* spp. are confined to the gills of estuarine fish but the trophonts attached to gill filaments do not have rhizoid projections that penetrate and destroy host cells. Most infections are benign, and the organism is often considered to be a symphoriont rather than a parasite. However, further studies are required to determine whether heavy or persistent infections cause or predispose to gill lesions that may compromise respiratory function.

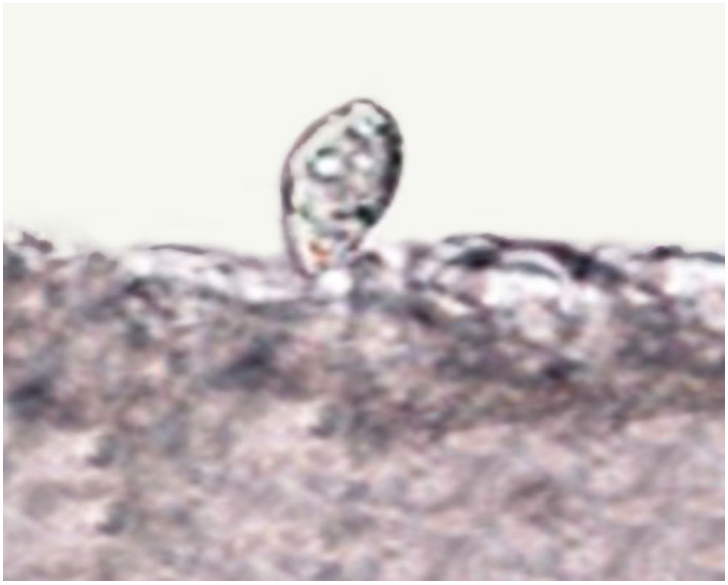
Developmental cycle and mode of transmission: These ectoparasitic dinoflagellates have similar life-cycles, involving attached feeding trophonts, detached reproductive tomonts, and free-swimming planktonic dinospores. Fish become infected when biflagellated dinospores in the water column attach themselves to epithelial surfaces using ventral pseudopodial projections. Once attached, they transform into sac-like trophonts with elaborate holdfast organelles which are disc-like with rhizoid projections attached to the cell surface or penetrating the host cell. The trophonts feed and grow, maturing in 2-6 days. When mature, the trophonts detach from the host and drop to the benthos where they round up transforming into ovoid tomonts. These stages are encysted and surrounded by a cellulosic wall, which thickens and provides good protection against unfavourable environmental conditions. The tomonts are reproductive stages and they undergo a series of asexual divisions by repeated binary fission (first division being longitudinal, and successive divisions occurring regularly and perpendicular to each other). Division may occur within a common cystic envelope, or the old envelope may dissolve after each division. In 2-4 days, tomonts produce numerous dinospores (up to 256 or more) which are released through tears or ruptures in the tomont wall. The dinospores are motile biflagellated dispersive stages which swim around in the water column. Transmission is direct and facilitated by the dinospores which are infective to susceptible fish for several days but will die if they do not find a host in that time. Once attached to a new host, the dinospore transforms into a trophont within 5-20 minutes. The duration of the life-cycle is temperature dependent, as is trophont size and tomont fecundity, and can range from 3-20 days. Parasite prevalence and abundance is greatest following rapid exponential growth in the warm months over summer.

Differential diagnosis: Infections may be suspected when fish exhibit flashing or gaping behaviours by rubbing against solid objects or struggling to breathe. Diagnoses are generally made by the visual detection of trophonts attached to the skin surface, best conducted using oblique light sources in darkened conditions. Green-brown parasites may be seen imparting a metallic yellow to velvet dusty sheen to the skin (and not as discrete white spots like those formed by ectoparasitic ciliates). Small fish may be anaesthetized and examined directly at low power under a dissecting microscope (the gills can also be examined by gently lifting opercular structures). Alternatively, skin scrapings and gill filament snips can be collected as biopsy or necropsy samples and wet mounts examined at higher powers under a compound microscope (often using Lugol's iodine to stain the starch-containing trophonts a dark brown to black colour). It is recommended that necropsy samples be collected and examined as soon as practicable, as trophonts usually detach shortly after host death. Several research studies have developed immunological tests (enzyme-linked immunosorbent assays) to detect specific host antibodies against parasite antigens, and elevated antibody titres have been associated with the development of some protective immunity. Molecular biological techniques have also been used to detect dinoflagellates in water and tissue samples by polymerase chain reaction (PCR) amplification of nuclear gene sequences (especially ribosomal RNA genes).

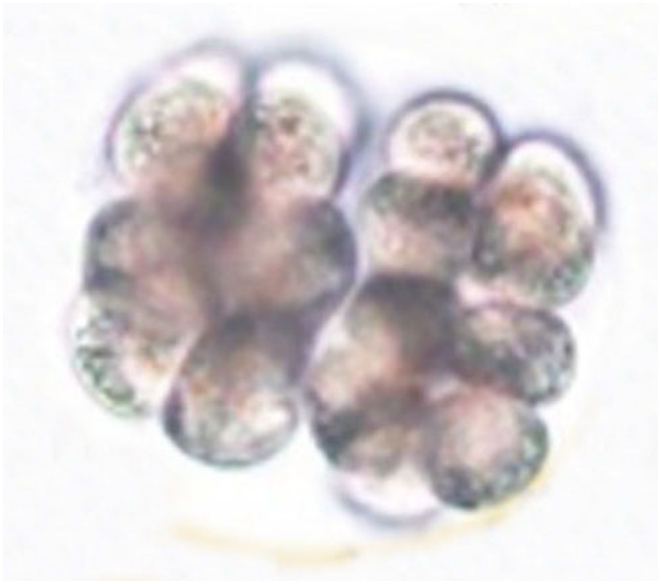
Treatment and control: Infections by ectoparasitic dinoflagellates have been successfully controlled in closed culture systems (including aquaria) by water treatment (disinfection and/or filtration) and by manipulating water quality (chemical/physical characteristics). The life-cycle stages most affected by chemical treatment are the free-living dinospores, while attached trophonts and encysted tomonts are more resistant to treatment. A range of antiprotozoal and algacidal chemicals have proven effective; including acriflavine (or trypaflavine), chloroquine, formalin, hydrogen peroxide, copper sulphate and a large number of broad-spectrum cocktail treatments are commercially available (involving mixtures of formaldehyde, cupramine, sulfathiazole, nitrofurantoin, nitrofural, quinacrine dihydrochloride, malachite green, and copper sulphate). It is important to treat infections as soon as practicable (to counter exponential growth), and to increase water aeration during treatment (to assist respiration in the case of gill infections). Fish with open sores may also benefit from antibiotic treatment for secondary bacterial infections. Caution should be exercised as some chemicals can be toxic to certain fish species (especially loaches, pufferfish, mormyrids, stingrays, and catfish) and many are lethal to aquatic invertebrates (including shrimp and snails). Studies have shown that alterations in water temperature,

salinity and light levels for several days-weeks may help control infections, provided resident fish can tolerate such changes. Raising the water temperature to 29°C has been shown to speed up the parasite life-cycle, adding salt to freshwater aquaria or subjecting marine species to freshwater baths may help combat infections, and covering tanks to exclude ambient light stops parasite species with chloroplasts from accessing alternate photosynthetic pathways. When all else fails, recourse can be taken to removing all fish from aquaria, tanks or ponds for at least 7 days after which time all dinoflagellates will be dead. Other management strategies designed to prevent the spread on infections include regular screening, isolation and quarantine of new stock (particularly introduced wild fish), avoiding stress situations which may diminish natural or acquired immunity (such as inappropriate diet, poor water quality, inadequate aeration, fluctuating water chemistry/temperature, overcrowding, and aggressive behaviours such as fighting/bullying), effective water filtration, improved sanitation (disinfection of shared equipment) and preventing cross-contamination (dinospores can be spread by strong winds in aerosol droplets generated by farm equipment servicing contiguous ponds/tanks). Obviously, control programmes are difficult to implement in large-scale facilities utilizing natural aquatic features, such as coastal lagoons, fiords, estuarine swamps, inland lakes, ponds and rivers, some of which have experienced intermittent or periodic outbreaks. A case may be made for intensive studies on vaccine development as it has been consistently observed that many fish species surviving infections develop some protective immunity to subsequent challenge.

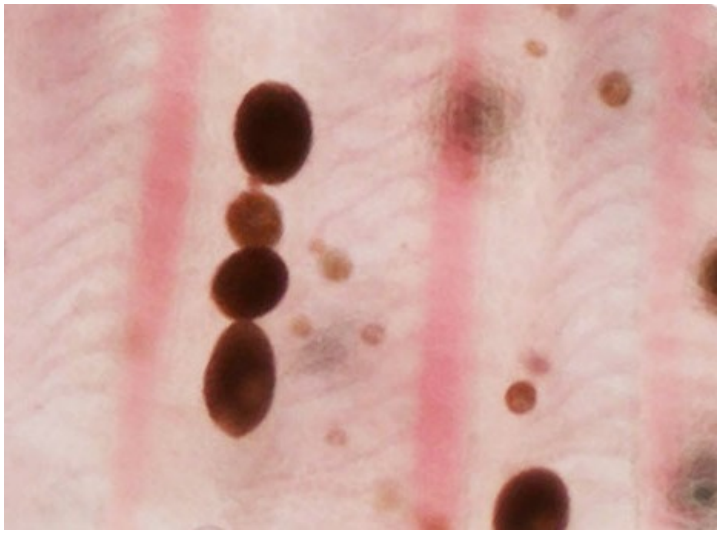

Amyloodinium,
Piscinoodinium,
Crepidoodinium
oodinid dinoflagellates
with parasitic stages
on aquatic hosts
skin, gills
(superficial lesions,
discolourations (velvet
disease), respiratory
disorders)
Vertebrate Hosts
(marine and
freshwater fish)
Amyloodinium
(< 150 µm)
[saltwater fish]
Piscinoodinium
(< 160 µm)
[freshwater fish]
Crepidoodinium
(< 700 µm)
[estuarine fish]
parasitic trophonts with rhizoid-like holdfast organelles
(cells with or without chloroplasts)
dinospores
attach to hosts
trophonts detach
and form tomonts
Amyloodinium
Piscinoodinium
Crepidoodinium
dinospores (5-20 µm)
biflagellated (equatorial
girdle, ventral sulcus)
tomonts
(100-200 µm)
direct transmission via free-swimming dinospores
released from reproductive tomonts



Amyloodinium trophont on fish gill



Amyloodinium tomonts in fish tank



Piscinoodinium trophonts on fish gills

Hematodinium/Ichthyodinium
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Phytoflagellates possess chloroplasts, which require sunlight to function, so most species are free-living aquatic organisms. Dinoflagellates have a distinctive haploid nucleus (dinokaryon) where the chromosomes remain condensed during interphase and are evident as beaded strands due to low levels of histones and associated proteins (condition termed 'mesokaryotic'). Many dinoflagellates form characteristic free-swimming dinospores (thecate and/or pigmented) and various species have been associated with coloured tides/blooms, bioluminescence and even neurotoxicity in mammals (paralytic shellfish poisoning). Some species, however, are heterotrophic and parasitic in marine animals, including the syndinids which form multinucleated plasmodial trophonts (without chloroplasts) in the tissues of crustacea and fish.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria)
Group: Alveolata (with cortical alveoli)
Phylum: Dinoflagellata (with unique mesokaryotic nuclei (lacking histones), autotrophs and heterotrophs)
Class: Syndiniophyceae (multinucleate plasmodial trophonts)
Order: Syndiniales (parasitic in copepods, appendicularians, crabs, radiolaria and fish eggs)
Family: Syndiniaceae (multinucleate trophonts without chloroplasts)
Genus: *Hematodinium* (parasitic in tissues of decapod crustaceans)
Genus: *Ichthyodinium* (parasitic in eggs of fish)
Species: various species cause lesions in fish and shellfish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum:	Order: Diplomonadida	Hexamitidae	*Giardia*	vertebrates	direct (f-o)

Fornicata (diplomonads)	(1-2 karyomastigonts)	(2 karyomastigonts with binary axial symmetry)		(gut)	
			Hexamita Spironucleus	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

The group Alveolata in the supergroup SAR is characterized by the possession of cortical membranous alveoli (vesicles or sacs) underlying and supporting the cell wall, and includes many otherwise disparate groups comprising 3 large assemblages (Apicomplexa, Ciliophora, Dinoflagellata) and 6 smaller taxa (Acavomonidia, Chromerida, Colpodellida, Colponemidia, Perkinsozoa and Voromonadida). The phylum Dinoflagellata comprises a diverse group of aquatic organisms, with many free-living species being important in food chains either as producers (autotrophs) or consumers (heterotrophs), some being endosymbiotic in invertebrates (e.g. in photosynthetic corals) and some being parasitic mainly in invertebrates but also a few vertebrates (fish). Dinoflagellates have a distinctive haploid nucleus (dinokaryon) where the chromosomes remain condensed during interphase and are evident as beaded strands due to low levels of histones and associated proteins (condition termed 'mesokaryotic'). Many dinoflagellates contain chloroplasts so early classification systems have used either botanical or zoological nomenclature, whereas recent molecular phylogenetic studies on eukaryotes have recognized and characterized cognate groups and provided appropriate names. Trophonts (or dinospores) of most species have an unequal heterodynamic pair of flagella; one ribbon-like and lying in equatorial furrow (girdle or cingulum) and the other directed posteriorly and often lying in a longitudinal ventral furrow (sulcus). Many species have thecate dinospores encased in armour composed of cellulosic plates; the anterior section is termed the epitheca (epicone in unarmoured species) and the posterior section is called the hypotheca (hypocone). Most species have unique membranous cytoplasmic organelles called pusules which are thought to be associated with osmoregulatory or excretory function. Many species have coloured chloroplasts and/or coloured pigments, some even exhibiting bioluminescence when disturbed by wind, wave or boat wakes. Several pigmented species bloom under suitable environmental conditions and cause 'red tides' and some pigments are neurotoxic to mammals when concentrated in the tissues of fish or filter-feeding shellfish (causing PSP 'paralytic shellfish poisoning'). Exemplars of toxic dinoflagellates are tabulated below (for interest only):

Toxic dinoflagellates	Toxin	Transvector	Effect
Prorocentrum	venerupin	shellfish	human hepatotoxicity
Dinophysis	okadaic acid	shellfish	human enterotoxicity
Pyrodinium	saxitoxin	shellfish	human neurotoxicity (PSP)
Protogonyaulax	saxitoxin	shellfish	human neurotoxicity (PSP)
Gymnodinium	saxitoxin	shellfish	human neurotoxicity (PSP) & fish kills
Ptychodiscus	brevetoxin	shellfish	human neurotoxicity & fish kills
Peridinium	glenodinine	-	fish kills
Gambierdiscus	ciguatoxin	fish	ciguatera

Over 4,000 dinoflagellate species are recognized in 550 genera: the majority being free-living autotrophs in pelagic or neritic surface waters. However, some 140 species from 5 families are heterotrophic and parasitic in aquatic hosts: including Oodinidae (e.g. *Amylodinium, Piscinoodinium* and *Crepidoodinium* on skin and gills of fish); Syndinidae (e.g. *Ichthyodinium* and

Hematodinium in tissues of fish and crabs); Chytriodinidae (e.g. *Chytriodinium* on eggs of copepods and shrimps); Paradinidae (e.g. *Paradinium* in body cavities of copepods); and Ellobiopsidae (e.g. *Ellobiopsis* and *Thalassomyces* on exoskeletons of crustacea). Genera parasitic on fish and in shellfish that are covered in this document are tabulated below.

Taxon	Genus	Hosts	Site	Transmission
Class: Blastodiniophyceae† (uninucleate trophonts, often with chloroplasts)				
Order: Blastodiniales† (ectoparasitic on zooplankton, algae, crustacea and fish)				
Oodinidae (trophonts with rhizoid-like holdfast organelles, gymnospores)	*Amyloodinium*	fish	skin	direct (water)
	Crepidoodinium	fish	skin	direct (water)
	Piscinoodinium	fish	skin	direct (water)
Class: Syndiniophyceae (multinucleate trophonts, without chloroplasts)				
Order: Syndiniales (endoparasitic in copepods, appendicularians, crabs, radiolaria and fish eggs)				
Syndinidae (plasmodial trophonts, dinospores not of *Gymnodinium* type)	*Hematodinium*	decapods	tissues	direct (water)
	Ichthyodinium	fish	tissues	direct (water)

†In recent classifications, these names are no longer valid, and the genera are considered *incertae sedis* in the Dinoflagellata.

Molecular biological studies on environmental and clinical isolates have shown that endobiotic parasites belonging to the Syndiniales include at least 5 major marine alveolate groups (MALV I-V), sometimes given interchangeably as Syndiniales I-V): namely, MALV I infecting ciliates and fish (including *Ichthyodinium*); MALV II infecting dinoflagellates and radiolarians; MALV III recovered from the environment; MALV IV infecting metazoans (including *Hematodinium* infecting crabs); and MALV V recovered from the environment. Endoparasitic syndinid dinoflagellates form multinucleate plasmodial trophonts (without chloroplasts) in the tissues of their hosts, which then produce free-swimming biflagellated dinospores (not of the *Gymnodinium* type). *Ichthyodinium* parasitizes embryos and larvae of marine fin fish living and reproducing in the ichthyoplankton primarily in tropical and warm-temperate oceanic ecosystems. There have been several suggestions to transfer *Ichthyodinium* to Perkinsoidea on the basis of some similarities in parasite morphology and biology (nuclei without the typical dinoflagellate appearance, presence of rhoptry-like structures, possible pseudo-conoid, biflagellated spores, and schizogony), but they have not been supported by subsequent molecular analyses of small and large subunit ribosomal RNA genes. *Hematodinium* parasitizes the haemolymph and haemocoels of marine decapod crustaceans (crabs, lobsters, and some shrimp) around the world, with heavy infestations imparting a stringent taste to the flesh (termed bitter crab syndrome). The parasites form a series of dividing stages in internal organs, including amoeboid, filamentous and arachnoidal trophonts (schizonts), gorgonlocks and clump colonies, and finally arachnoidal sporonts which produce free-swimming dinospores. Molecular characterization studies have detected some genetic differences between isolates from different crustacean species and from different oceanic regions, but further studies are required to determine whether they are intra- or inter-specific differences.

Parasite species	Hosts	Location (disease)	Dinospores	Distribution
Genus *Ichthyodinium* (amoeboid trophonts growing to multinucleate plasmodia)				
I. chabelardi	marine fish: Anguilliformes: anguillid (European eel); Carangiformes: carangid (Atlantic horse mackerel); Clupeiformes: alosid (European pilchard), engraulid (European anchovy); Gadiformes: gadid (Atlantic cod, blue whiting); Perciformes: serranid (leopard coral grouper), sparid (gilthead bream, bogue); Pleuronectiformes: scophthalmid (turbot); Scombriformes: scombrid (Atlantic mackerel, yellowfin tuna, Pacific bluefin tuna); Stomiiformes: sternoptychid (bristlemouth)	vitelline sacs in eggs, larvae	8-12 µm	Eurasia
Genus *Hematodinium* (parasitic in tissues of decapodid crustaceans)				
H. australis	Decapoda: portunid (blue swimmer crab, sand crab, mud crab), trapeziid (coral/guard crab)	haemolymph, haemal spaces		Australia
H. perezi	Decapoda: carcinid (European green crab, Pennant's swimming crab), cancrid (Jonah crab, Atlantic rock crab, brown crab), ovalipid (lady crab), polybiid (harbour crab, velvet crab), portunid (Atlantic blue crab, Asian blue crab), varunid (mud-flat crab)	haemal sinuses, haemocytes, soft tissues (bitter crab disease)	macrospores 12-14 µm microspores 7-9 µm	Atlantic, Pacific, North Sea
H. spp. (unidentified isolates, including novel? genotypes)	Decapoda: cancrid (brown crab, Jonah crab, Atlantic rock crab), epialtid (common spider crab, longnose spider crab), lithodid (scarlet king crab, red king crab, blue king crab), menippid (Florida stone crab),	haemal sinuses, haemocytes		Atlantic, Pacific, North Sea

	munidid (rugose squat lobster), nephropid (Norway lobster), oregoniid (inshore tanner crab, triangle tanner crab, grooved tanner crab, snow crab, great spider crab, contracted crab), ovalipid (lady crab), pagurid (common hermit crab, Prideaux's hermit crab), palaemonid (ridgetsail prawn), panopeid (flatback mud crab, saltmarsh mud crab, Say mud crab), penaeid (giant tiger prawn), polybiid (velvet crab), portunid (lesser blue crab, mud crab), trapeziid (coral crab, guard crab)			

Parasite morphology: These endoparasitic dinoflagellates form at least 4 different types of stages during their development: uninucleate trophonts (amoeboid and/or filamentous); multinucleate trophonts (including stages described as arachnoid trophonts, plasmodia, schizonts, and sometimes gorgonlocks and clump colonies); sporonts (arachnoid) with sporoblasts forming prespores; and free-swimming biflagellated zoospores (dinospores). *Ichthyodinium* first appears as uninucleate amoeboid trophonts 8-20 µm long with condensed chromatin in the nucleus (dinokaryon-like) and cytoplasmic trichocysts (thought to be involved in attachment). The trophonts are vegetative and undergo division (plasmotomy) involving at most 3 schizont generations forming multinucleate plasmodia. Primordial schizonts are formed when trophonts divide by multiple mitotic divisions without subsequent cytoplasmic division to form large multinucleated stages 100-140 µm. The schizont cytoplasm then forms cylindrical projections around each nucleus, with the resultant cells budding from the rest. These cells were initially cylindrical or racquet-shaped measuring around 20 µm in length. In some host species, they formed secondary schizonts by undergoing successive longitudinal bipartitions, but the posterior poles of the daughter cells remained attached, so they assumed a rosette shape. The secondary schizonts then formed long cords (up to 1-2 mm) of successive groups of 8 cells before releasing cylindrical-oblong cells (note that some studies have failed to find secondary schizonts, rosettes or cords in several host species). The products of the previous schizont generations then formed the last schizont generation where the cells became spherical after a series of divisions producing numerous (sometimes thousands) small (20-24 µm in diameter) uninucleate zoosporangia. When released into water, the sporangia underwent 1-2 divisions producing free-swimming dinospores. Note that in some studies, zoosporangia were not observed as the spherical cells transformed directly into dinospores. The dinospores did not have a *Gymnodinium*-like configuration but had a wide shallow slanted cingulum (not deep and equatorial) and a shallow ventral sulcus (not pronounced). The dinospores ranged in size from 8-12 x 4-5 µm and possessed 2 smooth flagella which were spherical in cross-section (typical dinoflagellates have a ribbon-like transverse flagellum with a flattened cross-section due to the possession of an axoneme along the outer edge and a contractile fiber (often referred to as a striated strand) along the inner edge). The dinospores possessed alveolate pellicles and contained trichocysts and some apical complex organelles (rhoptries and microtubules). *Hematodinium* also formed uninucleate trophonts (initially filamentous then rounded amoeboid stages) that developed into large amorphous multinucleate trophonts (known as arachnoid trophonts or schizonts) which then formed arachnoid sporonts producing sporoblasts, prespores and finally dinospores. The trophonts were small rounded stages measuring 6-18 µm in diameter with a single dinokaryon nucleus with chromatin condensed as small beads. They formed large amorphous multinucleate plasmodia 20-48 µm which were vermiform with 2-20 nuclei in *H. perezi* or ovoid with 2-5 nuclei in *H. australis.* The sporonts were found to produce 2 types of naked (athecate) gymnodinoid dinospores, macro-spores measuring 12-14 µm long and micro-spores measuring 7-9 µm long. *In vitro* culture studies also revealed the presence of several intermediate stages, with arachnoid trophonts giving rise to smaller schizonts which transform into polypodial (tentacular) 'gorgonlocks' colonies which then round up to form clump colonies giving rise to further trophonts.

Site of infection: Endoparasitic stages of *Ichthyodinium* are found within the vitelline (yolk) sacs in eggs and larvae of fin fish while those of *Hematodinium* are found within the haemolymph or haemocoels of internal organs (hepatopancreas, heart, gills, muscle) of marine decapods (crabs, lobster, and some shrimp). Infections by *Ichthyodinium* have been recorded in the eggs and/or larvae of some 14 species of fin fish belonging to 10 different families from the Mediterranean Sea and the Atlantic and Pacific Oceans. Infections by *Haematodinium* spp. have been found in some 38 crustacean species around the world, including economically-important species such as edible crabs from Europe, tanner and snow crabs from the northern Pacific and Atlantic Oceans, blue crabs from the Atlantic, lobsters from Norway, and swimming and mud crabs from Asia and Russia.

Pathogenesis: Both genera of endoparasitic dinoflagellates may cause morbidity and mortality in their respective hosts. *Ichthyodinium* stages in the yolk sacs of fish eggs and larvae have been associated with their subsequent destruction (the condition sometimes referred to as parasitic castration, even though infections do not destroy the gonads). Instead, heavy infections cause discolouration (opacities) and distention of the yolk sacs leading to their rupture before or after hatching resulting in the death of the eggs or larvae. Epizootics have been recorded in various fishes, both wild and farmed species, often accompanied by drastic reductions in their reproduction success (low egg hatching rates, poor larval survival). The highest rates of infection have been observed in the winter and early spring in cold-water fish species but in the warmer months in temperate and tropical fish species. In either case, infections are intimately linked to the breeding cycles of the resident fish species as parasites only infect eggs shortly after spawning (allegedly through weaknesses in the eggshell, possibly sperm tracts). It has been suggested that global climate change leading to rising ocean temperatures may facilitate expansions in the host and geographic ranges of the parasites, affecting

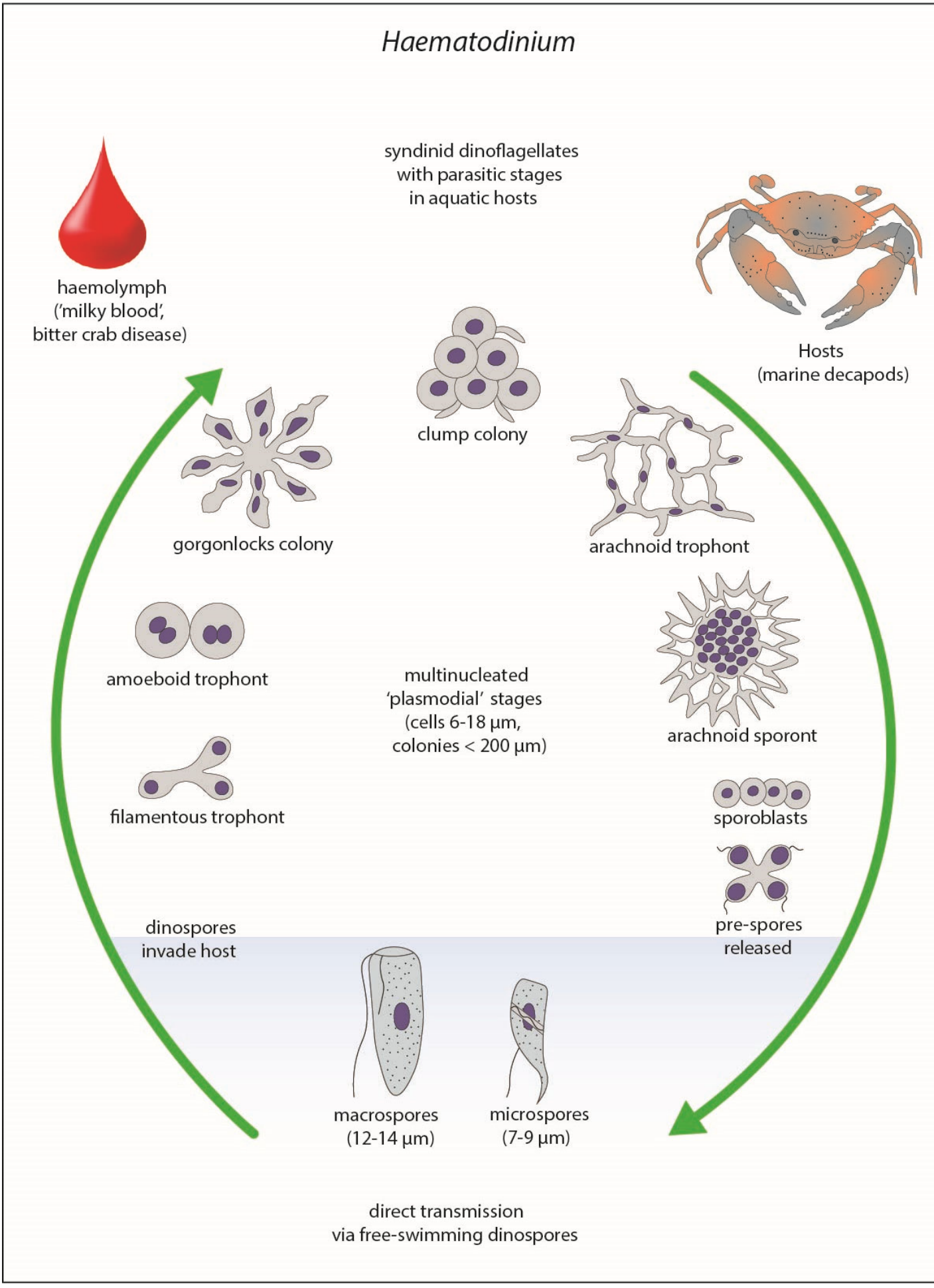
commercial fishing industries or preventing the establishment of stable seed stocks for aquaculture. *Hematodinium* undergoing massive proliferation in the haemolymph and tissues of marine decapods cause a series of physiological and pathological changes resulting in functional deficits contributing to mortality. The haemolymph becomes opalescent or milky-white in colour, slow to clot and exhibits dramatic reductions in haemocytes (sometimes absent). Infections have been associated with milky blood disease in cultured swimming crabs, yellow water disease in cultured mud crabs, and milky shrimp disease in prawn aquaculture. Infected animals undergo significant detrimental biochemical changes, involving nutrient depletion and reduced levels of haemolymph proteins (including haemocyanin and glycogen) with lowered oxygen-carrying capacity of the haemolymph but elevated rates of oxygen consumption within tissues. Nearly all major organs and tissues exhibit cellular damage and necrosis, with dilation of haemal sinuses, pressure necrosis in spongy connective tissues, lysis of hepatopancreatic tubules, muscular degeneration, discoloured shells and respiratory dysfunction due to loss of gill epithelial cells, lamellar distention, fusion and clubbing (swelling), loss of trabecular cells and haemocyte infiltrations. Infected crustaceans become lethargic with drooping limbs and mouthparts, lose weight and have short survival times in captivity. The main cause of death is attributed to disruption of gas transport and tissue anoxia caused by massive proliferation of the parasites, and some crabs are also thought to die from metabolic exhaustion. A key feature of many infections is the condition known as bitter crab disease, which occurs when cooked muscles take on a chalky texture and an astringent after-taste that makes them unmarketable. The bitter taste of cooked crabs may be due to the dinoflagellates themselves or their metabolites. Small numbers of diseased crabs have been shown to render entire batches of crabs unpalatable if they are processed together. Infections have also been associated with immunosuppression as evidenced by alterations in gene expression and regulation, with pronounced haemocytopenia hindering normal immune responses (clotting, phagocytosis, encapsulation of foreign material, production of antibiotic factors) and facilitating secondary bacterial infections resulting in septicaemia (commonly associated with stress in crustaceans). Epidemics have been recorded in commercially-fished decapod species resulting in significant economic losses, particularly around bays and fjords in northern America.

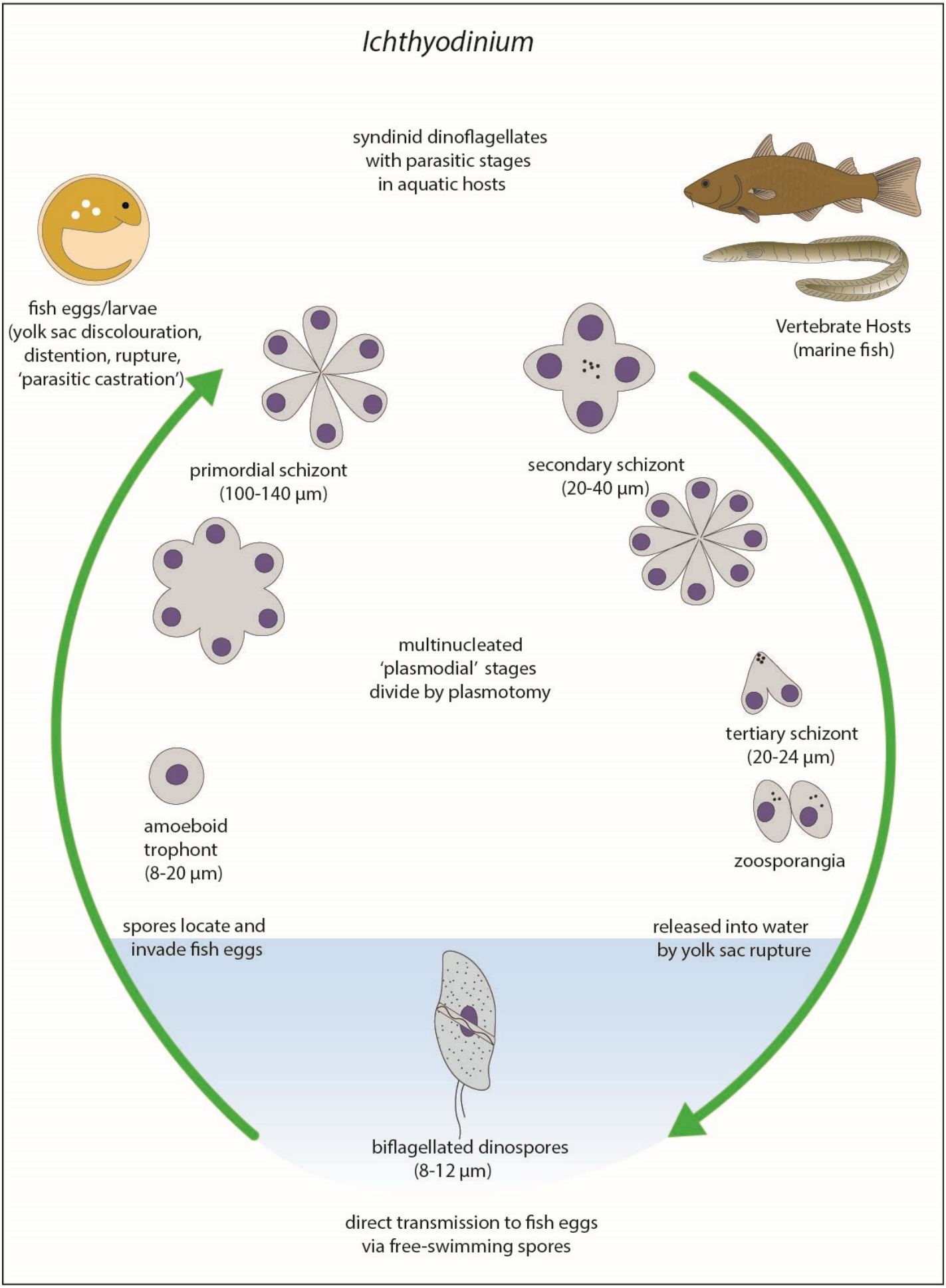
Developmental cycle and mode of transmission: Few complete life-cycles have been determined but they involve dinospore attachment or ingestion, the development of endoparasitic vegetative trophonts forming large amorphous plasmodia that give rise to free-swimming spores as the main transmissive stages. The invasive stages of *Ichthyodinium* form small amoeboid mononuclear cells in the yolk sacs of fish eggs (evident after gastrulation). The trophonts grow and undergo several cycles of schizogony (dividing by plasmotomy) to form multinucleate plasmodia (schizonts) that eventually release cells that either form zoosporangia or directly divide to form biflagellated dinospores. Molecular biological studies have detected parasite DNA in fertilized fish eggs, fish larvae, and rearing water, but not in the gonads of the parent fish nor in smaller fish used as feed. Infections have been detected in fish eggs as early as 2-8 hours after spawning, and free-swimming dinospores have been detected several days later in lysed fish eggs or larvae. Dinospores have been observed as early as 2 hours after yolk sac rupture and they are actively free-swimming for several days but die unless they invade new fish eggs. Epidemiological studies initially suggested that *Ichthyodinium* infected adult fish from benthic prey and then spread vertically through gametes, but there is now overwhelming evidence to refute this. Transmission occurs horizontally when free-swimming dinospores infect fish eggs soon after spawning. Freshly spawned eggs transferred to containers of sterilized seawater do not become infected, but if the eggs are left in rearing water for at least one hour they become infected. *Hematodinium* also undergoes a complex developmental cycle whereby dinospores invade the haemolymph in their decapod hosts and form filamentous and then amoeboid trophonts which proliferate through arachnoid trophonts (interconnected plasmodial colonies) that eventually form syncytial arachnoid sporonts which release sporoblasts and/or pansporoblasts that develop to prespores then motile dinospores. Some isolates have also been observed to undergo an alternative developmental pathway when arachnoid sporonts in the late stages of development release pansporoblasts (or multinucleated schizonts) that formed gorgonlocks (filamentous) colonies that underwent segmentation and formed clump colonies which developed directly to arachnoid trophonts. Studies on lobsters revealed cycles involving fusion of macro- and micro-spores to form filamentous trophonts which developed directly to gorgonlocks and then clump colonies to produce more arachnoid trophonts. In all cases, transmission between hosts was achieved by water-borne free-swimming dinospores, although some studies demonstrated that the experimental transfer of trophonts and plasmodia may lead to infections in recipient hosts although transmission between crabs by feeding (scavenging, predation or cannibalism) were not highly successful. Epidemiological studies revealed that most *Hematodinium* infections were seasonal, although the patterns differed according to host species, type of fisheries and geographic location. Infection peaks were observed in the summer and autumn in boreal regions, but in winter in temperate regions. Parasite development occurred over a wide temperature range (best between 8-15°C) and outbreaks were often associated with high salinity waters (above 18 parts per thousand (ppt)) with some evidence to suggest dinospores lost viability promptly in low salinity water (< 15 ppt). Infections generally took 9-12 months to develop and there were strong associations with moulting cycles (most prevalent post-moult). Outbreaks have been associated with rising water temperatures which stimulate moulting activity. Most outbreaks have been confined to sites with unique hydrologic features (such as fjords or poorly draining estuaries with shallow sills), areas with salinity > 11 ppt and stressful conditions such as seasonal hypoxia or predation pressure. However, some outbreaks have also occurred in more open ocean regions in crabs from depths > 250 meters.

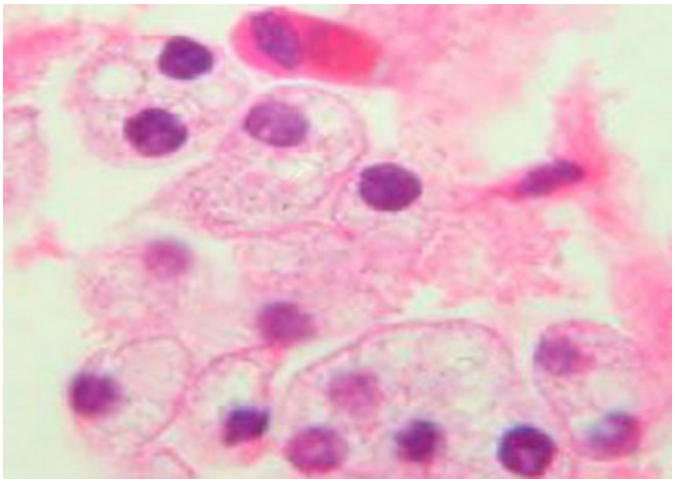
Differential diagnosis: Clinical infections may be indicated by unique discolourations of host tissues which may then be confirmed by the direct detection of endoparasitic developmental stages by microscopic examination or by molecular probes. *Ichthyodinium* developmental stages cause dark opacities in the yolk sacs of fish eggs or larvae which can be observed by visual examination. Microscopic examination of excised samples (aspirates, smears, squashes, sections) reveals the presence of numerous ovoid trophonts, schizonts and/or dinospores depending on the stage of infection. Molecular biological techniques have also been used to

detect parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences, notably small subunit (SSU) ribosomal RNA (rRNA) and internal transcribed spacer (ITS) regions). Phylogenetic studies have suggested there may be 2 species of *Ichthyodinium*: with *I. chabelardi* found in European fish populations; and a slightly different genotype found in some Asian fish populations (leopard coral grouper and yellowfin tuna). However, further studies are required to characterize these and additional isolates. *Hematodinium* infections may cause darker red colouration of the carapace and pale pink colouration of the appendage joints of infected decapods (cooked appearance) and the haemolymph appears cloudy and opaque ('milky'). Microscopic examination of wet mounts or smears of haemolymph or histological sections of haemal spaces in tissues reveals the presence of various parasitic stages (uninucleate trophonts, multinucleate plasmodia, sporonts and developing spores depending on the stage of infection). Parasites stain relatively well with Jenner-Giemsa or other blood stains, and often have distinctive dinokaryon nuclei (with condensed chromatin) and multinucleate stages tend to have a 'frothy' cytoplasm. Researchers have developed immunological tools (fluorescent-antibody tests) to detect infections in Norway lobsters, which appear to be quite sensitive, but little is known about their specificity. Molecular biological techniques have been used to detect parasites in clinical and environmental samples by PCR amplification of nuclear gene sequences (SSU rRNA, ITS). Phylogenetic studies have confirmed the differentiation of *H. australis* from *H. perezi*, but have also suggested that 3 genotypes of *H. perezi* may occur varying in host range and geographic location: including a generalist clade containing isolates from tanner crabs, king crabs, green crabs, contracted crabs, hermit crabs and lobsters from the North Atlantic and North Pacific Oceans; a small clade containing isolates from snow crabs from Canada, lobsters from Norway, brown crabs and hermit crabs from Europe; and another small clade containing isolates from harbour crabs from Europe, Atlantic blue crabs from eastern North America, and Asian blue crabs and mud crabs from China. Further studies are required to determine the extent of the genetic variation between isolates.

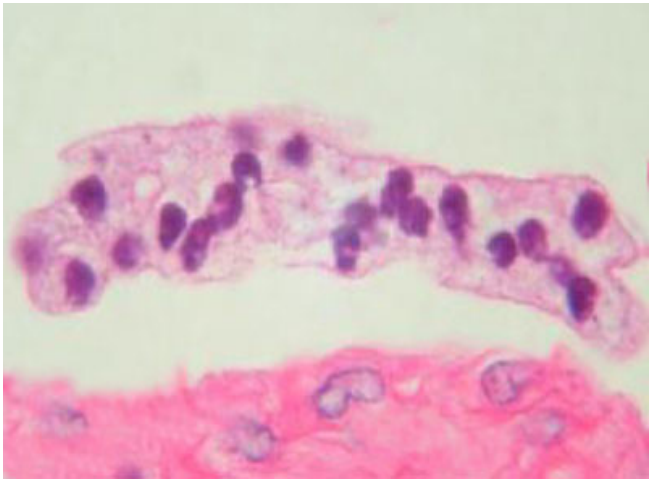
Treatment and control: Infections by endoparasitic dinoflagellates are difficult to control as there are no effective chemotherapeutic agents available and preventive strategies based on hygiene can only be implemented in some aquaculture enterprises and not in wild fisheries. *Ichthyodinium* has been detected sporadically in wild fish (especially in sardines and mackerel) but has proven to be a pest species on some fish farms. Infections in fish eggs and larvae are prevalent during spawning seasons, so it is imperative that broodstock be regularly screened for infections to prevent outbreaks. Studies have shown that maintaining good water quality and incubating fertilized eggs and rearing broodstock in disinfected seawater (oxidant-treated (ozone) or UV-sterilized) prevented the horizontal transfer of infections. *Hematodinium* infections have been found in a variety of marine decapods, both in wild and cultured stocks. Several studies have found that chemotherapy with broad-spectrum antibiotics helped crabs survive infections, but the most effective measures for controlling infections in mariculture involved regular screening (of both cultured and co-habitating sentinel species), quarantine (isolation of infected stocks), limiting translocations of live animals, avoiding polyculture pond systems (infections can occur in co-cultured shrimp as well as wild sympatric crabs and prawns), harvesting animals in winter (when fewer crabs are infected and meat is more marketable), and culling or removing dead animals (preferentially disposing of them through onshore fertilizer processing plants, and not using infected crabs for bait). Following outbreaks, some success has also been reported rebuilding populations from lightly infected stock (but not from heavily infected animals).


Haematodinium
syndinid dinoflagellates
with parasitic stages
in aquatic hosts
haemolymph
('milky blood',
bitter crab disease)
Hosts
(marine decapods)
clump colony
gorgonlocks colony
arachnoid trophont
amoeboid trophont
multinucleated
'plasmodial' stages
(cells 6-18 µm,
colonies < 200 µm)
arachnoid sporont
filamentous trophont
sporoblasts
pre-spores
released
dinospores
invade host
macrospores
(12-14 µm)
microspores
(7-9 µm)
direct transmission
via free-swimming dinospores

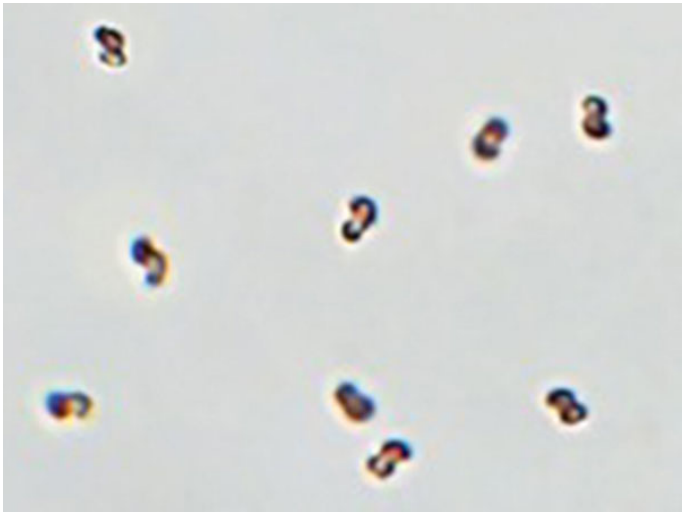

Ichthyodinium
syndinid dinoflagellates
with parasitic stages
in aquatic hosts
fish eggs/larvae
(yolk sac discolouration,
distention, rupture,
'parasitic castration')
Vertebrate Hosts
(marine fish)
primordial schizont
(100-140 µm)
secondary schizont
(20-40 µm)
multinucleated
'plasmodial' stages
divide by plasmotomy
tertiary schizont
(20-24 µm)
amoeboid
trophont
(8-20 µm)
zoosporangia
spores locate and
invade fish eggs
released into water
by yolk sac rupture
biflagellated dinospores
(8-12 µm)
direct transmission to fish eggs
via free-swimming spores



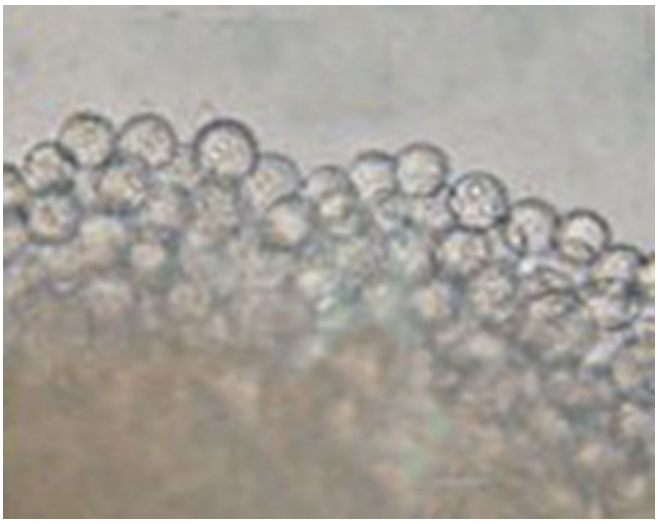
Haematodinium trophonts in haemolymph of crab



Haematodinium colony in crab tissues



Haematodinium dinospores



Ichthyodinium trophonts in fish egg

Perkinsus
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). One small alveolate group comprises the Perkinsozoa (Protalveolata) which includes the unique perkinsids that parasitize molluscs. Perkinsids form endogenous vacuolated trophonts in the tissues of bivalves and abalone and exogenous biflagellated zoospores with apicomplexan and dinoflagellate affinities. Infections have caused significant mortalities in commercial and wild shellfish populations.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria)
Group: Alveolata (with cortical alveoli)
Phylum: Perkinsozoa/Protalveolata (perkinsids parasitic in molluscs)
Class: Perkinsea (parasitic in marine bivalves and abalone, form biflagellated zoospores)
Order: Perkinsorida (with characters of class)
Family: Perkinsidae (with characters of order)
Genus: *Perkinsus* (parasitic in tissues of abalone)
Species: various species cause lesions and mortalities in shellfish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates	direct (f-o)

parabasal body)		membrane)		(gut)	
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

The group Alveolata in the supergroup SAR is characterized by the possession of cortical membranous alveoli (vesicles or sacs) underlying and supporting the cell wall, and includes many otherwise disparate groups comprising 3 large assemblages (Apicomplexa, Ciliophora, Dinoflagellata) and 6 smaller taxa (Acavomonidia, Chromerida, Colpodellida, Colponemidia, Perkinsozoa and Voromonadida). The phylum Perkinsozoa (syn. Protalveolata) was erected to accommodate members of the unique dinoflagellate-like genus *Perkinsus* which are parasitic in marine molluscs, but which form planktonic biflagellated zoospores involved in transmission. Classification of the group has a convoluted history. The causative agent for a disease in oysters was first reported as a fungus belonging to the genus *Dermocystidium*. It was subsequently placed in various fungal and protozoal groups depending on which phenotypic characters were used. Ultrastructural studies then revealed the presence of subpellicular membranes, micropores and putative (incomplete) conoids in trophonts and it was renamed *Perkinsus* and transferred to the phylum Apicomplexa. More recently, however, molecular biological studies on several independent genes suggested strong affinities between *Perkinsus* and dinoflagellates; with both groups assigned to the clade Alveolata. Several *Perkinsus* spp. have been described as parasites of gastropods and bivalves, especially abalone, oysters and clams. Infections were first linked to massive oyster mortalities in the Gulf of Mexico and subsequently to mortalities (or die-back) in gastropods (abalone) and other bivalves (oysters and clams) around the world. Recent surveys have revealed perkinsids to be common parasites in numerous bivalve species, especially in tropical waters.

***Perkinsus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
P. beihaiensis	Bivalvia: ostreid (Hong Kong oyster, Suminoe oyster), pteriid (Akoya pearl oyster, blacklip pearl oyster)	connective tissues, gut epithelia, digestive gland	lesions	China
P. chesapeaki (syn. *P. andrewsi*)	Bivalvia: myid (soft-shell clam), solecurtid (saltwater clam), tellinid (Baltic clam), venereid (hard clam), cardiid (small giant clam, crocus clam), ostreid (eastern oyster)	gills	-	United States
P. honshuensis	Bivalvia: venerid (Manila clam, variegated carpet shell clam)	connective tissues, digestive gland	-	Asia
P. karlssoni (dubious record)	Bivalvia: pectinid (bay scallop)	cultured soft tissues	-	Canada (hatchery)
P. marinus (syn. *Dermocystidium marinum, Labyrinthomyxa marina*)	Bivalvia: ostreid (eastern oyster, mangrove cupped oyster); Gastropoda: pyramidellid (impressed odostome sea snail, ectoparasitic on eastern oysters)	soft tissues	mortalities	Atlantic, Gulf of Mexico
P. mediterraneus	Bivalvia: ostreid (European flay oyster)	soft tissues	-	Europe
P. olseni (syn. *P. atlanticus*)	Gastropoda: haliotid (blacklip abalone, greenlip balone, whirling abalone, staircase abalone), Bivalvia: arcid (ark cockle), chamid (reflexed jewel box), venerid (New Zealand little neck clam, Palourde clam, Manila clam,	soft tissues	pustular lesions, mortalities	Pacific, Atlantic, Mediterranean

	pullet carpet shell)			
P. qugwadi	Bivalvia: pectinid (Japanese weathervane scallop)	internal tissues	mortalities	Canada

Parasite morphology: *Perkinsus* spp. form 4 different morphological stages during their development, each stage given different names over time; namely, trophozoites (aplanospores, meronts); schizonts (sporangia, tomonts, rosettes); zoosporangia (including prezoosporangia or hypnospores); and zoospores (considered to be equivalent to dinoflagellate dinospores). Trophozoites are ovoid stages measuring 2-20 µm in diameter that may be found throughout molluscan tissues. Smaller forms are also often observed within phagosomes of haemocytes. Mature trophozoites (10-20 µm) have a large eccentric vacuole occupying up to 90% of the cell volume, thereby displacing the nucleus to the cell periphery and producing a typical signet-ring appearance. The vacuole sometimes contains a large polymorphic inclusion body (termed a vacuoplast), and the nucleus contains a prominent nucleolus. Parasites undergo asexual multiplication (vegetative proliferation known as palintomy) whereby mature trophozoites undergo successive bipartitioning (alternating karyokinesis and cytokinesis) to form schizonts ranging in diameter from 15-100 µm (usually < 25 µm). Schizonts contain 2-64 (usually 8-32) daughter trophozoites which often stay together in a rosette-like arrangement inside a dense wall 2-4 µm thick. The contained trophozoites are coccoid or cuneiform in shape measuring 2-4 µm along their long axis. They are liberated when the wall ruptures allowing them to invade adjacent tissues where they grow becoming larger and developing vacuoles. When trophozoites are trapped in anoxic tissues from dead or dying hosts, or cultured in fluid thioglycolate medium, they become enlarged and appear as thick-walled ovoid prezoosporangia measuring 30-80 µm in diameter (some extremes up to 480 µm). When these stages are released into seawater, they differentiate into flask-shaped zoosporangia with 1-2 lateral discharge tubes and undergo zoosporulation by successive karyokinesis and cytokinesis producing hundreds of zoospores. Zoospores are biflagellated ellipsoidal uninucleate cells measuring 4-6 x 2-3 µm, and they contain several cytoplasmic vacuoles, lateral mitochondria, and a rudimentary apical complex with a conoid, polar ring, subpellicular microtubules (up to 39), micronemes and rhoptries (similar to that possessed by apicomplexan parasites). The 2 flagella are inserted laterally, with the longer anterior flagellum bearing a row of long filamentous mastigonemes (tinsels) and the shorter posterior flagellum being naked. Mature zoospores escape from zoosporangia via the discharge tube, and they may initiate infection in new hosts via epithelia of the gills, mantle or gut.

Site of infection: Screening surveys have detected *Perkinsus* spp. in over 67 molluscan species, with clinical infections found primarily in bivalves (oysters) and gastropods (abalone) from temperate and tropical regions in Atlantic, Pacific and Mediterranean waters. Trophozoites have been detected in stomach and intestinal epithelial cells, digestive gland epithelia, haemocytes, adductor muscles, and connective tissues associated with viscera, mantle and gills.

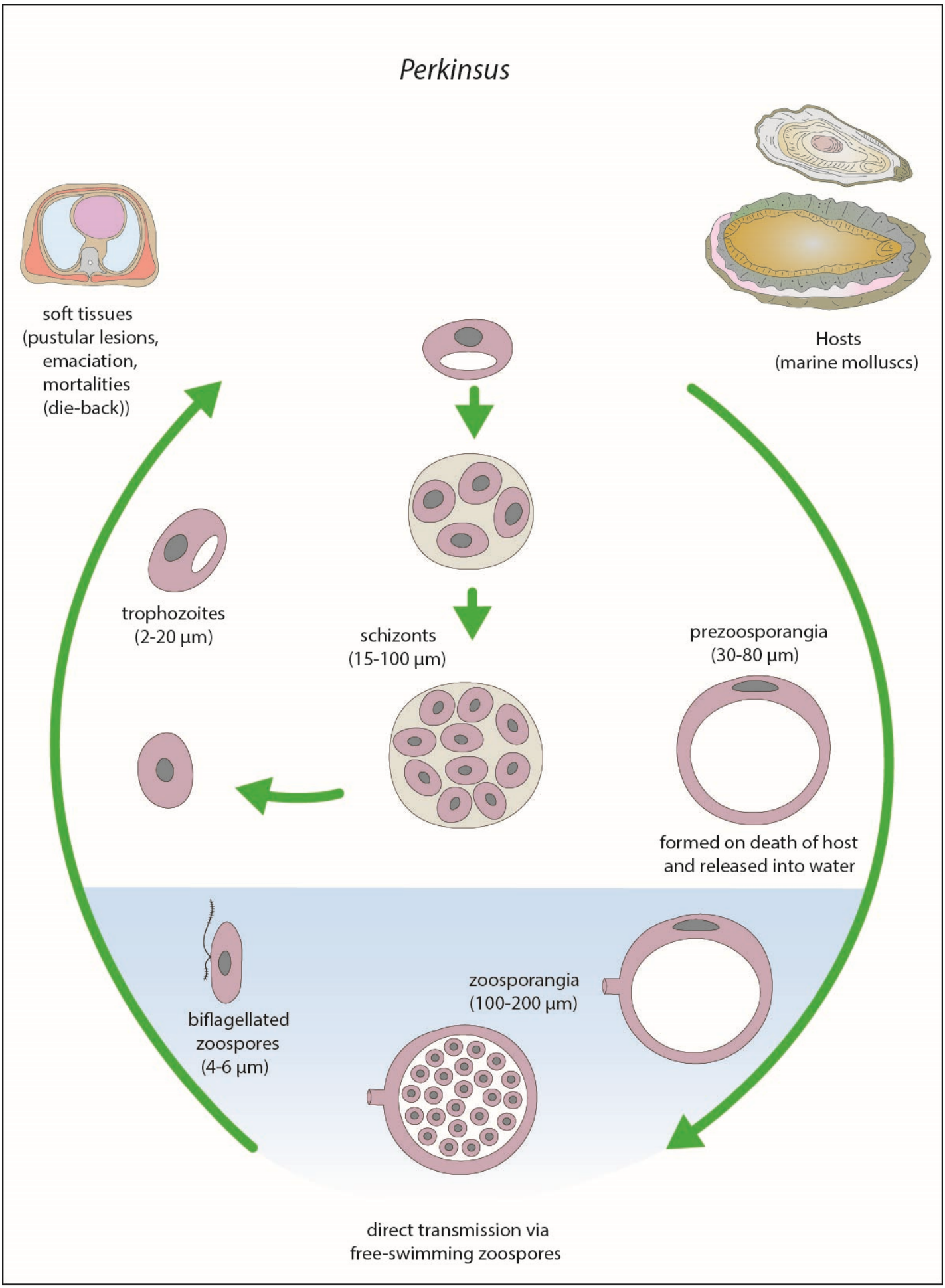
Pathogenesis: Clinical infections have been detected in conjunction with mass mortalities in cultured oysters as well as population declines (die-back) in wild shellfish. The disease is generally known as perkinsosis (although *P. marinus* infections in oysters were initially known as ‘dermo’) and is characterized by gross signs of severe emaciation, digestive gland pallor, pustular-like lesions in soft tissues, shrinkage of the mantle from the shell, retarded growth and inhibition of gonad development. Trophozoites invading host tissues evoke haemocytic infiltrates of epithelia, connective tissue, muscle fascicles and blood spaces, with parasites occurring both within haemocytes and free within tissues. While haemocytes may actively phagocytose parasites, they are not destroyed but rather multiply within haemocytes ultimately causing their lysis (thus contributing to the systemic spread of infections). Advanced infections are characterized by extensive haemocyte activation and recruitment, with concomitant exuberant production of oxygen intermediates (free oxygen radicals). Host cells in the immediate vicinity are destroyed leading to structural losses through focal necrotic and/or inflammatory lesions. Pathogenesis appears to be associated with various host-parasite molecular interactions involving agglutinins (enhancing phagocytosis) and the release of enzymes (facilitating tissue invasion and necrosis) and antiproteases (inhibiting humoral responses). The lesions sometimes become so extensive that they appear as cream-yellow pustular abscesses up to 10 mm in diameter, making the flesh unacceptable for marketing. Infections spread and damage gut epithelia, adductor muscles, connective tissues throughout the viscera and gills, and sometimes occlude haemolymph sinuses. Molluscs become moribund and lose condition with reduced growth, weight loss and even impaired fecundity due to depleted energy reserves. Heavy infections have been associated with high mortalities in specific regions, both within cultured shellfish and in wild populations. Disease outbreaks have often been reported in conjunction with stressors affecting host susceptibility to infection, including the weakened condition of hosts following spawning, pollution and reduced water quality leading to hypoxia, over-crowding and poor nutritional status.

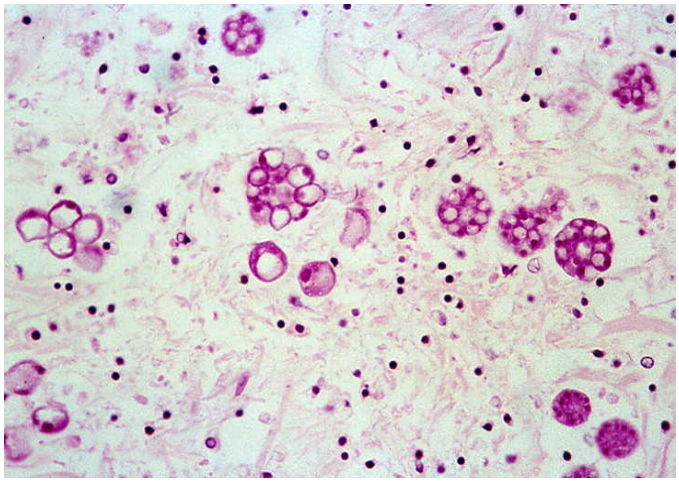
Developmental cycle and mode of transmission: These enigmatic organisms have life-cycles involving the repeated schizogonous multiplication of endoparasitic trophozoites in the tissues of live molluscs, followed by the liberation of free-swimming biflagellated zoospores from zoosporangia forming when lesions rupture or when hosts die. Trophozoites invade tissues and grown from small uninucleate ovoid stages to larger vacuolated forms which have a typical signet-ring appearance due to peripheral displacement of the nucleus by the eccentric vacuole. Mature trophozoites then multiply by forming schizonts which exhibit successive internal partitioning (alternating nuclear and cytoplasmic divisions) to form numerous (2-64) round to wedge-shaped trophozoites which are liberated when the mother schizont ruptures. The parasites may undergo multiple cycles of schizogony in live hosts leading to heavy

disseminated infections. When the host dies and infected tissues decompose becoming anoxic, trophozoites transform into large ovoid prezoosporangia. This transformation also occurs *in vitro* when infected tissues are cultured in thioglycolate medium. When prezoosporangia are then released into seawater, they differentiate into flask-shaped zoosporangia within which numerous biflagellated zoospores develop by palintomy over 4 days. The zoospores are liberated into the marine environment through discharge tubes which develop in the sides of the zoosporangia. The free-swimming zoospores may then infect new hosts with the primary portal of entry apparently being the gut epithelium, although it may also occur via epithelia of the gills, labial palps and mantle. The zoospores lose their flagella when they invade host tissues and round up to become small trophozoites, thus completing the cycle. Transmission between hosts is therefore direct and may be accomplished without vectors or alternative hosts. However, it is also thought that trophozoites multiplying within live hosts may also be released by diapedesis and in faeces, and may constitute a source of infection for hosts in the immediate vicinity (thus accounting for the rapid spread of infections in beds/racks of live oysters). There are also some suggestions that scavengers may be involved in the dissemination of infections as prezoosporangia have been detected in the faeces of fish, oyster drills and crabs feeding on dead or moribund oysters. One study also suggested that *P. marinus* found in pyramidellid snails ectoparasitic on oysters may be injected during feeding or contaminate the surrounding water. Epizootiological studies have consistently shown correlations between parasite development, prevalence, intensity and geographic distribution, particularly with respect to water temperature and salinity. More infections and disease have been associated with warmer temperatures (over 20°C for at least one month) and higher salinities (over 15 parts per thousand), often manifesting in annual seasonal patterns of infection and disease (peaking in summer).

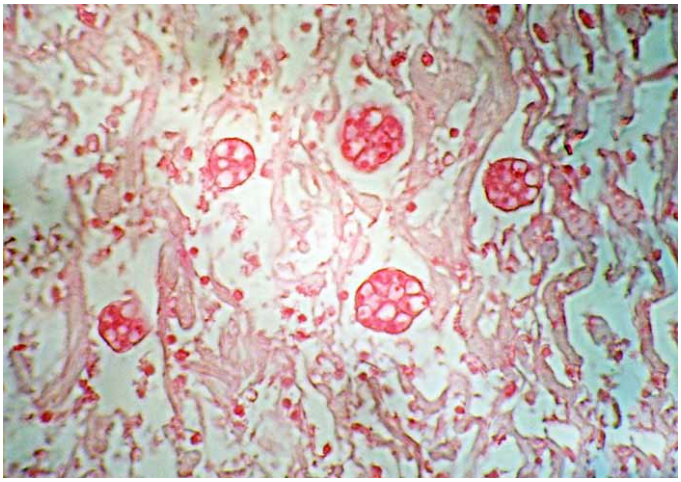
Differential diagnosis: Infections are generally detected postmortem by the light microscopic observation of vacuolated trophozoites in tissue sections taken from moribund shellfish or those with visible cyst-like pustular lesions. Alternatively, prezoosporangial stages may be detected in tissue samples cultured for several hours-days in fluid thioglycolate medium (FTM) or Ray's FTM supplemented with nystatin (RFTM). These stages stained well with Lugol's iodine and were evident as large blue-black spheres. Cultures may be incubated for as little as 4-8 hours but are often extended up to 7 days to promote better growth and development. Prezoosporangia are induced to transform to zoospore-producing zoosporangia by transferring them from RFTM to seawater. Various agencies recommend culturing postmortem samples from the heart, rectum, mantle and gills (sometimes antemortem samples of haemolymph) and semi-quantitating the results by counting the numbers of organisms and ranking them numerically (1-5) for infections ranging from very light to heavy. Researchers have also successfully raised polyclonal and monoclonal antibodies against prezoosporangia and incorporated them into fluorescent and enzyme immuno-assays to detect infections, but encountered some problems with specificity and cross-reactivity against some dinoflagellate species. More recently, molecular biological techniques have been used with considerable success to detect infections and examine parasite phylogenetic relationships following the polymerase chain reaction (PCR) amplification of several DNA sequences (small and large subunit ribosomal RNA plus internal transcribed spacers regions, and type I actin genes).

Treatment and control: Experimental studies on controlling infections in cultured oysters revealed some apparent benefits (reduced mortality and lesion scores) using bath treatments with chlorine, cycloheximide, N-halamine disinfectants, freshwater flushes, and water filtration followed by ultraviolet irradiation. However, such treatments are impractical under field conditions, and prezoosporangial stages have been found to have a high tolerance to chlorine, low temperatures and low pH. Control has therefore relied primarily on modifying shellfish management and culture procedures to reduce the incidence and spread on infections. Recommended strategies include regular and intensive monitoring (particularly over summer), the removal of infected stock, the isolation of seed stock, transplanting seeds from low salinity areas to higher salinity grow-out areas, avoiding over-crowding, harvest early if infections detected before mass mortalities occur, avoiding "shucking" shellfish over commercial beds, and fallow beds after harvest. Several mathematical models based on host, parasite and environmental factors have been devised to help growers predict and avoid outbreaks. There has also been some success in selectively breeding resistant hosts, including allochthonous species, triploid oysters, hybrid scallops, and first-generation scallop progeny, most of which grow faster but are not as fecund (although some say they taste better as they have higher glycogen contents due to gametogenesis arrest).


Perkinsus
soft tissues
(pustular lesions,
emaciation,
mortalities
(die-back))
Hosts
(marine molluscs)
trophozoites
(2-20 µm)
schizonts
(15-100 µm)
prezoosporangia
(30-80 µm)
formed on death of host
and released into water
biflagellated
zoospores
(4-6 µm)
zoosporangia
(100-200 µm)
direct transmission via
free-swimming zoospores



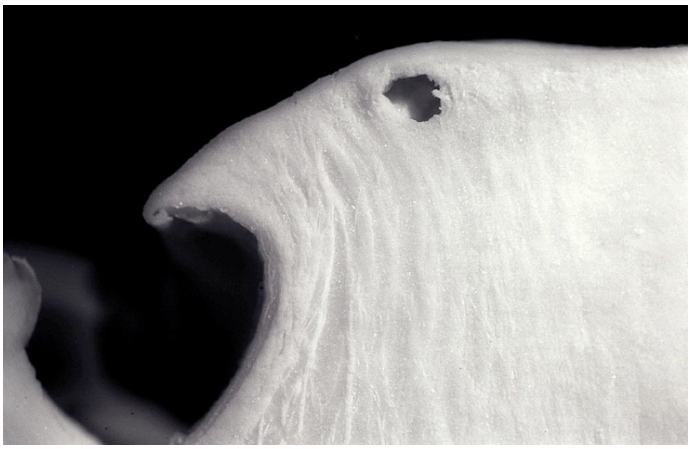
Perkinsus trophozoites in abalone muscle



Perkinsus trophozoites in abalone muscle



Perkinsus pustules in abalone muscle



Perkinsus lesion in abalone muscle

Cochlosoma
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Parabasalid flagellates have conspicuous parabasal bodies which have been shown to be dictyosomes (Golgi bodies) connected by striated fibres to the flagellar basal body. Hypermastigids (cristamonads) have multiple flagella arranged in tufts, plates or rows, including the trichomonads which have a tuft of anterior flagella plus a recurrent flagellum free or associated with the cell body forming an undulating membrane. Most *Cochlosoma* species are parasitic in the intestines of birds and the trophozoites have an anterior adhesive disc, lateral grooves and the mastigont system comprises six flagella, an axostyle and a parabasal body.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Metamonad (amitochondriate flagellates with karyomastigonts)
Phylum: Parabasalia (anaerobic flagellates with parabasal body supporting Golgi cisternae or dictyosome, trichomonads, hypermastigids, retortamonads)
Class: Trichomonadea (single mastigont, comb-like structure absent, infrakinetosomal body absent)
Order: Trichomonadida (lamelliform undulating membrane, B-type costa)
Family: Trichomonadidae (5-6 flagella, cone-like axostyle)
Genus: *Cochlosoma* (parasitic in intestines of birds)
Species: various species cause enteritis in birds

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae	*Cochlosoma*	birds	direct (f-o)

		(anterior adhesive disc)		(gut)	
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Metamonads are a group of excavates (with ventral feeding groove) that have several subcellular elements associated with their flagella forming a unique mastigont (an ultrastructural complex of organelles and cytoskeletal fibrils (incl. dictyosomes (Golgi bodies), centrioles (basal bodies) and a microtubular axostyle)). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Most metamonads are amitochondriate but have retained reduced organelles of mitochondrial origin (fornicates containing mitosomes while parabasalians possess hydrogenosomes). Members of the phylum Parabasalia typically possess parabasal bodies adjacent to Golgi bodies (dictyosomes), and have microtubular arrays forming a conspicuous pelta-axostyle complex (cap-like pelta and a cone- or tube-like longitudinal axostyle). Six parabasalid classes are currently recognized on the basis of morphological, biological and molecular phylogenetic studies. Cells in three classes (Trichomonadea, Tritrichomonadea, Hypotrichomonadea) bear single mastigonts (set of kinetosomes (basal bodies) and associated appendages – ancestral unit comprising 4 kinetosomes) with flagella arranged in an anterior tuft, but many have one recurrent flagellum forming an undulating membrane (lamelliform or rail-type) supported by a costa (A- or B-type) and sometimes a basal comb-like structure and/or infrakinetosomal body. Many species are symbiotic (mutualists, commensals or parasites) in animals, although some are free-living in moist habitats. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Cells in another three classes (Cristamonadea, Trichonymphea, Spirotrichonymphea) have more complex structures, often with multiple mastigonts bearing hundreds to thousands of flagella. Most were previously assigned to the now-defunct group Hypermastigida, and they are primarily found as symbionts (mutualists) in insects (mostly termites).

Family	**Key characters to 'trichomonad' families in vertebrates***						**Representative genera**
	Number of flagella	**Undulating membrane**	**Costa**	**Axostyle**	**Comb-like structure**	**Infra-kinetosomal body**	
Class Trichomonadea (single karyomastigont)							
Order Trichomonadida (with costa) (endobiotic in vertebrates (mammals, birds, reptiles, amphibia) and invertebrates)							
Trichomonadidae	5-6	lamelliform	B-type	cone-like	absent	absent	*Cochlosoma, Trichomonas, Trichomitopsis, Tetratrichomonas, Pentatrichomonas*
Order Honigbergiellida (without costa) (endobiotic in vertebrates (mammals, reptiles, amphibia))							
Hexamastigidae	5-6	absent	absent	cone-like	absent	absent	*Hexamastix*
Class Tritrichomonadea (uninucleate to binucleate)							
Order Tritrichomonadida (endobiotic in vertebrates (mammals, birds, reptiles, amphibia, fish))							

Tritrichomonadidae	4-5	rail-type	A-type	tube-like	present	present	*Tritrichomonas*
Simplicimonidae	4	absent	absent	tube-like	present	present	*Simplicimonas*
Monocercomonidae	4	absent	absent	cone-like	present	present	*Monocercomonas*
Dientamoebidae	0-4	absent	absent	cone-like	absent	absent	*Dientamoeba, Histomonas*
Class Hypotrichomonadea (single karyomastigont)							
Order Hypotrichomonadida (endobiotic in vertebrates (reptiles, amphibia, mammals) and invertebrates)							
Hypotrichomonidae	4	lamelliform	A-type	cone-like	present	absent	*Trichomitus, Hypotrichomonas*

*Taxa found only in invertebrate hosts (such as termites and cockroaches) are not listed

The class Trichomonadea contains a diverse range of cells with single karyomastigonts giving rise to 2-6 flagella, with one being recurrent but lacking a comb-like structure and infrakinetosomal body. Two orders are recognized: Honigbergiella (undulating membrane absent or lamelliform without supporting costa); and Trichomonadida (most with lamelliform undulating membrane supported by B-type costa and stout cone-like axostyles). The family Trichomonadida contains some 10 genera (*Cochlosoma, Lacusteria, Pentatrichomonas, Pentatrichomonoides, Pseudotrichomonas, Pseudotrypanosoma, Tetratrichomonas, Trichomitopsis, Trichomonas* and *Trichomonoides*) which vary in their cellular, organellar and flagellar configurations, zoogeography (host ranges), and biological characteristics (heterotrophs ranging from mutualists to commensals to parasites). The genus *Cochlosoma* contains robust conical-ovoid cells with 6 flagella, an anterior adhesive disc and lateral groove and prominent protruding axostyle. Some 5 species have been described as endoparasites in the intestines of birds and shrews, with at least one species causing enteritis in domestic poultry and waterfowl, particularly in North America.

Parasite species†	**Size (µm)**	**Vertebrate Hosts**	**Location**	**Clinical signs**	**Distribution**
Class: **Trichomonadea** (single karyomastigont) [4-6F-CLS-IKB(+CA in most genera, TA or reduced in others)]					
Order: Trichomonadida [5-6F+LUM+BC]					
Family: Trichomonadidae [+CA]					
Cochlosoma (anterior adhesive disc, lateral groove) [6F-UM-C+CA]					
Cochlosoma anatis (syn. *C. rostratum*)	6-12 x 4-7	Anseriformes: anatid (mallard, muscovy, pintail, shoveler, lesser scaup), Galliformes: phasianid (turkey, chicken)	caecum, large intestines, cloaca	enteritis, runting	worldwide
Cochlosoma picae	5-8 x 3-5	Passeriformes: corvid (American magpie)	cloaca		North America
Cochlosoma soricis	9-12 x 4-7	Eulipotyphla: soricid (vagrant shrew, American water shrew)	intestines		North America
Cochlosoma striatum		Galliformes: phasianid (ruffed grouse)			North America
Cochlosoma turdi	4-8 x 2-5	Passeriformes: turdid (American robin, incl. eastern robin)	cloaca		North America
Cochlosoma sp.		Galliformes: phasianid (quail), Passeriformes: fringillid (finches), estrildid (parrot-finches); Chiroptera (bats)			mostly North America

†Coding: + = present; - = absent; #F = total number of flagella; UM = undulating membrane; LUM = lamelliform undulating membrane; C = costa; BC = B-type costa; CA = cone-like axostyle (*Trichomonas*-type); TA = tube-like axostyle (*Tritrichomonas*-type); CLS = comb-like structure; IKB = infrakinetosomal body.

Parasite morphology: *Cochlosoma* spp. only form one developmental stage: trophic forms known as trophozoites. These small flagellated stages have asymmetrical ovoid-pyriform bodies that are broader anteriorly and narrower posteriorly. Trophozoites usually measure from 5-10 µm in length but those of some species range up to 18 µm long. The anterior end is obliquely truncated by a prominent cup-like adhesive disc from which a lateral groove extends along one side. Trophozoites are uninucleate with a single subspherical nucleus situated near the centre of the body. The anterior nucleus adjoins a prominent parabasal apparatus, consisting of a Golgi complex and a solitary parabasal fiber extending posteriad. Trophozoites possess 6 flagella which arise from the anterior end of the cell and vary in length. One flagellum is recurrent and is attached along the length of the cell body by an undulating membrane but extends free at the posterior end. The undulating membrane runs along the lateral groove and is supported by a conspicuous costa with type B periodicity. Four flagella are free and emerge anterolaterally from the lateral groove. The sixth flagellum emerges from a basal body on the dorsal side of the body, independent of the basal body complex of the other flagella. A thin axostyle originates near the anterior basal bodies and passes longitudinally through the cell protruding posteriorly. Most *Cochlosoma* spp. also possess variable numbers of double membrane-bound organelles (similar to hydrogenosomes) throughout the cytoplasm (differences in type and number sometimes used to differentiate species). Several studies have noted the rare occurrence

of non-flagellated ovoid stages, and while it has been suggested that they may be 'pseudocyst' stages, further confirmatory studies are required.

Site of infection: Infections by *Cochlosoma* spp. have been recorded mainly in birds and occasionally in mammals. Some 5 parasite species have been detected in over 20 species of birds belonging to 4 passerine families (corvids, estrildids, fringillids, turdids) and 2 non-passerine families (anatids, phasianids), and at least 2 species have been found in mammals (shrews and bats). Flagellates are found extracellularly within the digestive tract, particularly the large intestines, caeca and cloaca, and sometimes the small intestines. Most infections have been detected in North America, but one species (*C. anatis*) has been found worldwide.

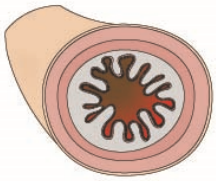
Pathogenesis: Most infections are asymptomatic, but some have been associated with outbreaks of diarrhoea in turkeys and ducks and mortalities in finches. Trophozoites may occur free in the lumen of the intestines, but they can attach themselves by suction to surface epithelia using their adhesive discs. Attachment leaves distinctive marks on host cells resulting in microscopic inflammatory lesions. This may cause catarrhal enteritis in wild and domestic turkey poults and ducklings that is characterized by the excretion of yellow-stained or moist bulky droppings with progressive dehydration, lethargy, ruffled feathers, runting and some mortalities amongst nestlings. While most infections in adult finches are subclinical, young birds are highly susceptible to severe diarrhoeal disease with high mortalities. It should also be noted that many clinical cases involve concomitant infections with other intestinal pathogens, notably coccidia, *Hexamita* and *Salmonella*, which often confounds the aetiology of disease.

Developmental cycle and mode of transmission: Observations on *Cochlosoma anatis* have revealed a simple monoxenous (one-host) life-cycle whereby trophozoites reproduce asexually by longitudinal binary fission within the host intestines. Despite the occasional reported of nonflagellated pseudocyst stages in some hosts, little is known about how parasites are transmitted from host-to-host. Studies on faecal-oral transmission have been unequivocal, but there have been reports of oral transmission by experimental inoculation suggesting young animals may become infected when fed by infected parents. Indeed, adult animals appear to be resistant to clinical infections but can act as long-term carriers. Further studies are required to demonstrate transmission cycles.

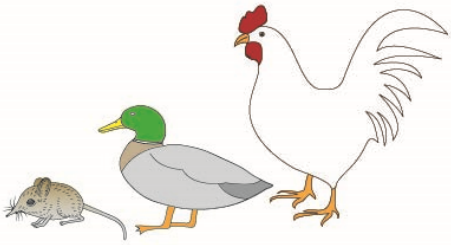
Differential diagnosis: The diagnosis of infections on clinical grounds is confounded by the nonspecificity of any signs observed as they may be caused by numerous other enteric infections and conditions. Infections are diagnosed by the direct microscopic detection and identification of motile trophozoites in fresh samples of faeces or intestinal scrapings taken soon after host death. Trophozoites may be observed swimming in a characteristic rotary (corkscrew) pattern, and are best observed using microscopic illumination systems that introduce diffraction (winding down the condenser or closing the diaphragm) or contrast (phase-contrast or interference-contrast) into fresh wet smear samples. Attempts to counter-stain or fix trophozoites in samples do not work well as the cells rapidly lose motility, die, lyse or simply do not take up stains. Recourse may be made to examining histological sections of infected tissues, but parasites can be hard to detect in mucosal epithelia. Transmission and scanning electron microscopy have been used to examine internal and topographical ultrastructural features of harvested trophozoites preserved in suitable fixatives. More recently, molecular biological techniques have been used to detect parasites in clinical samples, and even in house flies (*Musca domestica*), by the polymerase chain reaction (PCR) amplification of mitochondrial (16S ribosomal RNA) gene sequences.

Treatment and control: Infections in birds have been treated effectively by the application of nitroimidazole (metronidazole, ronidazole) or organoarsenic compounds (nitarsone) administered in their drinking water, but these drugs are not registered for in commercial poultry due to concerns about bioaccumulation and harmful residues. Infections may be controlled by instituting good husbandry practices to reduce flock contamination and maintain host health (such as regular monitoring, quarantining sick or new birds, providing good nutrition and clean water, prompt waste removal, and decontaminating fomites and equipment.

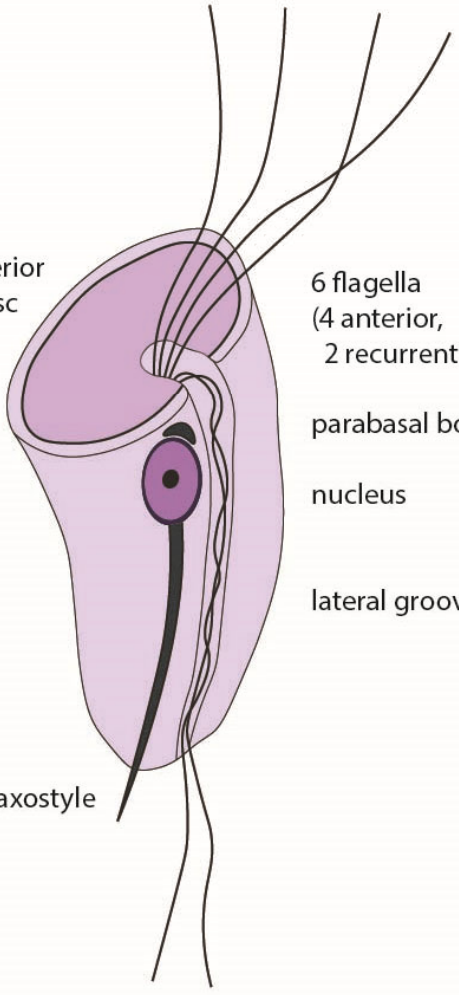
Cochlosoma



intestines
(catarrhal enteritis,
diarrhoea, poor
condition)



Vertebrate Hosts
(birds, esp. poultry,
waterfowl), some
mammals (shrews)



unique anterior
adhesive disc

6 flagella
(4 anterior,
2 recurrent)

parabasal body

nucleus

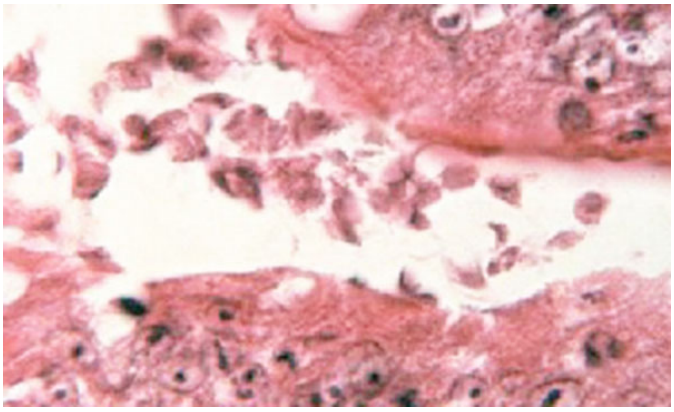
lateral groove

axostyle

trophozoites
(5-18 µm)

no cyst formation

direct transmission presumably by transfer of trophozoites
via close contact (flocking, grooming, nesting, allo-feeding)

 *Cochlosoma* trophozoites	

Trichomonas vaginalis
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Parabasalid flagellates are anaerobic amitochondriate protists which have distinctive parabasal bodies (dictyosomes) adjacent to flagellar basal bodies (kinetosomes) and an axostyle-pelta complex providing structural support. Trichomonads are a major constituent group and most have 4-6 apical flagella, one being recurrent and often forming an undulating membrane supported by a costa. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Many *Trichomonas* spp. have been reassigned to different genera based on the number of free anterior flagella e.g. *Tritrichomonas*, *Tetratrichomonas* and *Pentatrichomonas* having 3, 4 and 5 anterior flagella respectively. Confusingly, the name *Trichomonas* has been retained for some species with 4 anterior flagella (mainly those in man, some rodents and birds). Most trichomonad species are endocommensals in mammals, birds, reptiles and insects but several species are parasitic in the alimentary or urogenital tracts of man and domestic animals.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Metamonad (amitochondriate flagellates with karyomastigonts)
Phylum: Parabasalia (anaerobic flagellates with parabasal body supporting Golgi cisternae or dictyosome, trichomonads, hypermastigids, retortamonads)
Class: Trichomonadea (single mastigont, comb-like structure absent, infrakinetosomal body absent)
Order: Trichomonadida (lamelliform undulating membrane, B-type costa)
Family: Trichomonadidae (5-6 flagella, cone-like axostyle)
Genus: *Trichomonas* (parasites/commensals in tubular organs of vertebrates)
Species: *T. vaginalis* (causes vaginitis in humans)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)

body)		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Metamonads are a group of excavates (with ventral feeding groove) that have several subcellular elements associated with their flagella forming a unique mastigont (an ultrastructural complex of organelles and cytoskeletal fibrils (incl. dictyosomes (Golgi bodies), centrioles (basal bodies) and a microtubular axostyle)). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Most metamonads are amitochondriate but have retained reduced organelles of mitochondrial origin (fornicates containing mitosomes while parabasalians possess hydrogenosomes). Members of the phylum Parabasalia typically possess parabasal bodies adjacent to Golgi bodies (dictyosomes), and have microtubular arrays forming a conspicuous pelta-axostyle complex (cap-like pelta and a cone- or tube-like longitudinal axostyle). Six parabasalid classes are currently recognized on the basis of morphological, biological and molecular phylogenetic studies. Cells in three classes (Trichomonadea, Tritrichomonadea, Hypotrichomonadea) bear single mastigonts (set of kinetosomes (basal bodies) and associated appendages – ancestral unit comprising 4 kinetosomes) with flagella arranged in an anterior tuft, but many have one recurrent flagellum forming an undulating membrane (lamelliform or rail-type) supported by a costa (A- or B-type) and sometimes a basal comb-like structure and/or infrakinetosomal body. Many species are symbiotic (mutualists, commensals or parasites) in animals, although some are free-living in moist habitats. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Cells in another three classes (Cristamonadea, Trichonymphea, Spirotrichonymphea) have more complex structures, often with multiple mastigonts bearing hundreds to thousands of flagella. Most were previously assigned to the now-defunct group Hypermastigida and they are primarily found as symbionts (mutualists) in insects (mostly termites).

Trichomonad taxonomy can be very confusing as many *Trichomonas* spp. have now been reassigned to sister genera based on the number of anterior flagella e.g. *Tritrichomonas*, *Tetratrichomonas* and *Pentatrichomonas* having 3, 4 and 5 anterior flagella respectively. Confusingly, the name *Trichomonas* has been retained for some species with 4 anterior flagella (mainly those in man, some rodents and birds). Recent ultrastructural and molecular biological studies have also led to the placement of the genus *Tritrichomonas* into a separate class (Tritrichomonadea) as the cells contain unique comb-like structures and infrakinetosomal bodies at the bases of their recurrent flagella (both lacking in members of the class Trichomonadea). Several genera (*Hypotrichomonas* and *Trichomitus*) were assigned to another class (Hypotrichomonadea) as their cells contained comb-like structures but lacked infrakinetosomal bodies.

Family	**Key characters to 'trichomonad' families in vertebrates***						**Representative genera**
	Number of	**Undulating membrane**	**Costa**	**Axostyle**	**Comb-like**	**Infra-kinetosomal**	

	flagella				structure	body	
Class Tritrichomonadea (uninucleate to binucleate)							
Order Tritrichomonadida (endobiotic in vertebrates (mammals, birds, reptiles, amphibia, fish))							
Tritrichomonadidae	4-5	rail-type	A-type	tube-like	present	present	*Tritrichomonas*
Simplicimonidae	4	absent	absent	tube-like	present	present	*Simplicimonas*
Monocercomonidae	4	absent	absent	cone-like	present	present	*Monocercomonas*
Dientamoebidae	0-4	absent	absent	cone-like	absent	absent	*Dientamoeba, Histomonas*
Class Trichomonadea (single karyomastigont)							
Order Trichomonadida (with costa) (endobiotic in vertebrates (mammals, birds, reptiles, amphibia) and invertebrates)							
Trichomonadidae	5-6	lamelliform	B-type	cone-like	absent	absent	*Cochlosoma, Trichomonas, Trichomitopsis, Tetratrichomonas, Pentatrichomonas*
Order Honigbergiellida (without costa) (endobiotic in vertebrates (mammals, reptiles, amphibia))							
Hexamastigidae	5-6	absent	absent	cone-like	absent	absent	*Hexamastix*
Class Hypotrichomonadea (single karyomastigont)							
Order Hypotrichomonadida (endobiotic in vertebrates (reptiles, amphibia, mammals) and invertebrates)							
Hypotrichomonidae	4	lamelliform	A-type	cone-like	present	absent	*Trichomitus, Hypotrichomonas*

*Taxa found exclusively in invertebrate hosts (such as termites and cockroaches) are not listed.

The class Trichomonadea contains a diverse range of cells with single karyomastigonts giving rise to 2-6 flagella, with one being recurrent but lacking a comb-like structure and infrakinetosomal body. Two orders are recognized: Honigbergiella (undulating membrane absent or lamelliform without supporting costa); and Trichomonadida (most with lamelliform undulating membrane supported by B-type costa and stout cone-like axostyles). The family Trichomonadida contains some 10 genera (*Cochlosoma, Lacusteria, Pentatrichomonas, Pentatrichomonoides, Pseudotrichomonas, Pseudotrypanosoma, Tetratrichomonas, Trichomitopsis, Trichomonas* and *Trichomonoides*) which vary in their cellular, organellar and flagellar configurations, zoogeography (host ranges), and biological characteristics (heterotrophs ranging from mutualists to commensals to parasites). Trichomonads (*sensu latu* = in the broadest sense) usually exhibit strong site specificity (tissue tropism) and occur in the alimentary, urogenital or respiratory tracts of their hosts, where they may cause very different types of disease. Several specialized species living in the urogenital tracts of vertebrates may cause severe inflammatory diseases, with *Trichomonas vaginalis* causing vaginitis in humans, and *Tritrichomonas foetus* causing bovine infertility. A few species living in the upper respiratory and alimentary tracts of birds may cause life-threatening diseases, including *Trichomonas gallinae* causing canker in birds. In contrast, those inhabiting the intestinal tracts of vertebrate and invertebrate hosts are often considered to be symbiotes or commensals (rather than parasites) as most infections appear benign. Rather than try to cover trichomonad biodiversity and their disparate clinical significance in one comprehensive section, it has been elected to showcase representatives in 4 separate sections, targeting:

- urogenital infections by *Trichomonas vaginalis* in humans;
- urogenital infections by *Tritrichomas foetus* in cattle;
- oral infections by *Trichomonas gallinae* in birds; and
- enteric infections by *Trichomonas, Tetratrichomonas* and *Pentatrichomonas* spp. in a wide range of hosts.

The species *Trichomonas vaginalis* infects the urogenital tracts of human hosts around the world, being found on every continent and during every season. Transmission occurs when trophozoites are transferred between males and females during coitus. Infections in males are generally asymptomatic but they act as carriers, while infections in females may cause clinical disease ranging from vaginitis to endometritis, with some linking infections to infertility and cervical cancer.

Parasite species	Size (µm)	Vertebrate Hosts	Location	Clinical signs	Distribution
Class: **Trichomonadea** (single karyomastigont) [4-6F-CLS-IKB(+CA in most genera, TA or reduced in others)]†					
Order: Trichomonadida [5-6F+LUM+BC]					
Family: Trichomonadidae [+CA]					
Genus: *Trichomonas* [5F(=4A+R)-RF]					
Trichomonas vaginalis [+AF]	4-32 x 2-15	Primates: hominid (human), plus experimental infections in cercopithecid (macaques), cebid (squirrel monkey); Rodentia: murid (mice)	urogenital system (atypically respiratory tract)	vaginitis, urethritis, endometritis	worldwide

†Coding: + = present; - = absent; #F = total number of flagella; #A = number of anterior flagella; R = recurrent flagellum; RF = recurrent flagellum extending posteriorly as free flagellum; LUM = lamelliform undulating membrane; BC = B-type costa; AF = axostyle protrudes posteriorly; CA = cone-like axostyle (*Trichomonas*-type); TA = tube-like axostyle (*Tritrichomonas*-type); CLS = comb-like structure; IKB = infrakinetosomal body.

Parasite morphology: *Trichomonas vaginalis* only forms one developmental stage, trophic forms known as trophozoites which are multi-flagellated. Under unfavourable growth conditions, these stages can round up and internalize their flagella. It has been suggested by some that these rounded stages may be 'pseudocysts', but most workers consider them to be degenerate forms as none have been observed to give rise to normal motile forms. Trophozoites have oval-pyriform bodies ranging from 7-32 μm in length by 5-12 μm in width depending on their state of nutrition. Those cultured in the presence of abundant food become rotund, while those cultured in less favourable conditions become thin and spatulate. Trophozoites may also appear more pleomorphic becoming amoeboid when in contact with host cells. All intact stages are uninucleate with a prominent anterior nucleus surrounded by a porous nuclear envelope. The nucleus is located just posterior or adjacent to a distinctive parabasal body formed by dictyosomes (Golgi complexes). The nucleus and parabasal body are associated with small dense basal bodies (kinetosomes) forming a single karyomastigont unit (ancestral unit with 4 kinetosomes). The kinetosomes give rise to 4 flagella which project forwards forming an anterior tuft some 8-15 μm in length. In *T. vaginalis*, a separate kinetosome gives rise to a fifth flagellum which is recurrent (directed posteriad) and attached longitudinally to the cell body forming an undulating membrane that terminates before reaching the posterior end of the cell. The undulating membrane is lamelliform in appearance (rather than rail-like) and it is underpinned by a slender elongate rod-like structure in the cell cytoplasm known as the costa, which is striated with a periodicity known as B-type (rather than A-type). Functional flagella impart motion and free cells typically exhibit a forward spiralling motion, with the undulating membrane imparting a quivering/shimmering appearance to the cell body. Trophozoites also possess a slender longitudinal hyaline rod-like structure known as an axostyle which is composed of concentric rows of microtubules forming a cone (rather than a tube). The axostyle begins near the nucleus and runs posteriorly through the cell body, sometimes protruding through the posterior end and terminating in a sharp point. Trichomonads are anaerobic and do not have mitochondria, but rather possess membrane-bound organelles known as hydrogenosomes (formerly called siderophil granules) often located in rows along the axostyle. Hydrogenosomes are energy-producing organelles that generate molecular hydrogen (by metabolizing pyruvate to acetate and carbon dioxide producing ATP by substrate-level phosphorylation with release of hydrogen ions).

Site of infection: Trophozoites of *T. vaginalis* are extracellular parasites located within the reproductive organs of humans; occurring in the urethra, vagina, cervix and uterus in women, and the urethra, prostate, seminal vesicles and epididymis of men. Trophozoites may occur free-swimming within the lumina of the tubular organs, but they may also attach temporarily to the surface of epithelial cells by small or large lateral outgrowths that are amoeboid in appearance. *T. vaginalis* is cosmopolitan in distribution and may be found in human populations throughout the world.

Pathogenesis: Infections by *Trichomonas vaginalis* usually occur in sexually active people and may result in asymptomatic carriage, especially in males, to causing acute or chronic clinical disease (trichomoniasis), with women exhibiting signs from mild vaginal discomfort and dyspareunia (painful intercourse) to severe incapacitating illness. Trophozoites inhabit reproductive organs where they may obtain nutrients for growth and survival, but they also interact with host epithelial cells producing a range of pathologies. They are strict amitochondriate anaerobes that uses hydrogenosomes to produce energy by metabolising carbohydrates or utilizing amino acids. Trophozoites thrive in acidic conditions (pH 4-6) which stimulates their growth and multiplication by longitudinal division. Parasites move using their cytoskeletal elements (microtubules, microfilaments) to interact with epithelial cells, employing a range of adhesion proteins for cell-to-cell adhesion (specific ligand-carbohydrate reactions which can also invoke parasite amoeboid transformation with the development of cellular extensions/interdigitations), cell-to-basement membrane binding (laminin-binding proteins), and extracellular matrix adhesion (fibronectin receptors). Attached parasites secrete cytotoxic enzymes (lysosomal hydrolases, cysteine proteases) which degrade host cells causing their desquamation, detachment, membrane perforation and lysis. Cellular debris is then ingested by the parasites. Feeding cells are also able to ingest resident bacteria, yeasts, and even host blood cells by phagocytosis, and they may also be ingested by host monocytes. When underlying capillary beds are exposed, trophozoites specifically target erythrocytes for iron and lipid acquisition by releasing haemolytic factors (adhesins, perforins) which facilitate erythrolysis and also direct erythrophagocytosis. Many of these molecular interactions stimulate the production of proinflammatory and chemotactic cytokines from epithelial cells and resident immune cells, including the recruitment of neutrophils which aggravate clinical signs.

In women, *T. vaginalis* is well-adapted to the variable vaginal micro-environment with around 50% of infections being asymptomatic but the remaining 50% causing clinical disease, with cyclic symptoms and signs worsening around menses (menstruation) due to changes in host tissues (sloughing epithelia), fluids (mucus, serum), cells (microbial flora, blood cells), macromolecules (lipids, carbohydrates, proteins) and chemistry (notably pH). Menstrual flow is thought to be more conducive to nutrient and iron uptake by parasites, and trophozoites have developed efficient mechanisms to cope with oxidative stress (heat shock proteins, P-glycoproteins). Trichomoniasis is principally a disease of women in their reproductive years, with clinical manifestations rarely observed before menarche or after menopause. A wide range of symptoms have been reported, but many are commonly seen in other sexually transmitted diseases (STDs). Disease severity has been associated with differences in parasite pathogenicity (strain virulence), intensity of infection, site of infection within the urogenital system, as well as host susceptibility, hormone levels, and resident vaginal flora (esp. lactobacilli). The prepatent (incubation) period usually ranges from 4-28 days, and acute infections often subside over weeks to become chronic with the abatement of symptoms but their occasional recurrence. Once

established, infections may persist in women for extended periods (weeks, months, sometimes years). Clinical infections usually cause flagrant vaginitis (significant degeneration, irritation and inflammation of the vagina) with local cellular immune responses (leucocyte infiltrations) resulting in erythema (redness), pruritus (itching), burning sensations, mucopurulent (yellow-green) frothy discharge (occasionally with blood, but leukorrhea discharge only in acute infections) and foul-smelling odours (exacerbated by the production of molecular hydrogen by parasite hydrogenosomes). The vaginal mucosa may develop a speckled appearance due to the occurrence of small punctate haemorrhagic spots, and sexual intercourse may become painful or difficult (dyspareunia). Parasites may cause irritation of the vulva resulting in erythema, oedema and diffuse vulvitis with copious leukorrhea. Infections may also extend to the cervix with women developing cervicitis, cervical erosion and sometimes colpitis macularis (strawberry cervix) formed by punctate haemorrhagic lesions (evident by colposcopy). Recent studies have also cautiously linked chronic infections to an increased incidence of cervical cancer. Parasites may continue to ascend the genital tract migrating through the cervix into the uterus causing inflammation (endometritis) with long-standing infections associated with atypical pelvic inflammatory disease and possible infertility problems (due to the generation of a uterus 'hostile' to implantation). Infections may occasionally invade the urinary system causing urethritis and cystitis with lower abdominal pain and dysuria (painful or difficult urination). Other infrequent complications include adnexitis (inflammation of uterine appendages such as fallopian tubes and ovaries), and pyosalpinx (pus-filled fallopian tubes). Women infected during pregnancy are predisposed to premature rupture of the placenta, premature labour, and low birth-weight infants. Parasites may also be transmitted to newborns as they pass through the birth canal of infected mothers, sometimes resulting in urinary tract infections in female infants and rarely pneumonia-like pulmonary infections.

Infections in men are usually transient and do not persist for long (10 days or less). Most infections (around 90%) are asymptomatic but the men may still act as carriers. Some infections do produce mild symptomatic disease (indistinguishable from other causes of non-gonococcal urethritis) while a smaller number develop acute disease characterized by urethritis with scanty clear to mucopurulent discharge, dysuria, mild pruritus or burning sensation immediately after sexual intercourse (or urination). Infrequent complications include balanoposthitis (inflammation of the glans and foreskin), prostatitis, epididymitis, epididymo-orchitis, and possibly infertility. Although the course of infection in men is self-limiting, the parasites do not appear to elicit strong protective immune responses in their hosts. Re-infection can occur with the renewal of clinical disease, particularly in women. Immunological studies have shown that trichomonads may evade host immune responses by a number of mechanisms; including the modification of surface proteins (via antigenic shedding, antigenic variation, and antigenic shift); secreting proteins to modify host immunoglobulins (both secretory and serum antibodies) and complement (activating alternate pathways); and masking themselves with host proteins (by molecular mimicry and surface coating). Epidemiological studies have revealed risk factors for infection include sexual activity, particularly unprotected sex, promiscuity and prostitution, poor feminine hygiene, and other sexually-transmitted diseases (STDs). Indeed, *T. vaginalis* infections increase the risk of human immunodeficiency virus (HIV) transmission by causing mucosal damage and facilitating viral entry. Trichomoniasis has been reported in all racial, ethnic and socioeconomic groups around the world, with some regional geographic variation (more common in Africa). The World Health Organization considers trichomoniasis to be one of the most common STDs, with an estimated prevalence approaching 200 million and an annual incidence of several million new cases yearly.

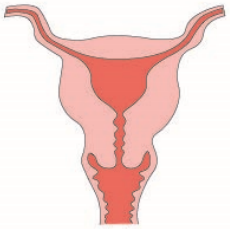
Developmental cycle and mode of transmission: The trichomonad *T. vaginalis* has a simple direct life-cycle involving flagellated trophozoites that replicate asexually by longitudinal binary fission. The parasites have considerable proliferative potential, exhibiting exponential (binary) growth every few hours under favourable conditions. Reproduction involves the duplication of locomotory organelles and the development of 2 attractophores flanking the nucleus which subsequently become poles for division. The nuclear membrane is retained, and microtubules extend into the nucleus attaching to chromosomal centromeres. The extranuclear spindle (paradesmose) elongates and the daughter cells separate. Trophozoites reside within the urogenital tract and are unable to survive for long outside hosts. They do not form cysts, and some nonflagellated rounded forms originally thought to be 'pseudocysts' are now considered to be degenerate transient forms which cannot recover. Transmission therefore involves the direct transfer of live trophozoites between the urogenital tracts of hosts, the vast majority occurring via sexual intercourse. Occasionally, nonsexual transmission has been observed involving contaminated douche nozzles, specula or toilet seats, as well as to infants and virginal females via soiled clothing, toweling or sanitary products. Live trophozoites have been found in urine and semen after several hours of exposure to air and in swimming pool water, and trophozoites may remain viable in culture after 24 hours post-inoculation on damp fomites. Vertical transmission may also occur either during the birth process when the baby transits the birth canal, or infants become contaminated by urinary or vaginal secretions from infected women.

Differential diagnosis: The diagnosis of clinical infections by symptomatology alone is confounded by the nonspecificity of symptoms/signs as many other urogenital infections or conditions may cause similar manifestations (notably odiferous exudates). Definitive diagnosis is therefore made by the direct demonstration of motile trophozoites in vaginal, urethral or prostatic secretions by microscopy or by *in vitro* culture. Wet mounts should be examined immediately as parasites only remain motile for short periods (10 minutes) when exposed to air. Motile trophozoites move with a characteristic jerky forward rotary motion and their undulating membranes impart of shimmering appearance to the cell body. Unstained trophozoites are best observed under suboptimal illumination (condenser down or diaphragm closed to introduce diffraction) or using high contrast systems (phase-contrast or differential interference contrast, e.g. Nomarski). Alternatively, a small number of stains may be used to visualize organisms, especially Giemsa or Papanicolaou (Pap) stains, as well as a few fluorochrome stains. Fixed smears can also be examined following

staining to help differentiate rounded forms of parasites from polymorphonuclear leucocytes. Suitable stains have included haematoxylin, Giemsa, acridine orange, Leishmans, periodic acid-Schiff, Fontana and Pap stains, many of which also allow gynaecological screening for cytologic abnormalities. A range of *in vitro* culture systems have been developed to amplify trichomonads from clinical samples, with broth cultures or InPouch cultures in liquid media being the most effective. Trichomonads lack the ability to synthesize many macromolecules *de novo* (particularly purines, pyrimidines and many lipids), so liquid culture media need to include all essential macromolecules, vitamins and minerals (especially serum providing lipids, amino acids, fatty acids, iron and trace metals). Suitable media include Kupferberg medium, Diamond's TYM medium (trypticase-yeast-maltose), Diamond's TYI-S-33 medium (trypticase-yeast-iron with foetal calf serum and vitamin 107-Tween 80 mix), Trichosel medium, Linstead's semi-defined medium (modified CMRL 1066 medium) and Linstead's chemically defined media (DL7, DL8). Culture is often laborious and tedious, with results only becoming available after 2-7 days. Studies have shown that trophozoites can be grown on various cell lines (e.g. McCoy cells) in serum-free tissue culture, but such processes are not routinely available due to cost. Some studies, however, indicated that tissue culture could be used to examine parasite virulence factors, such as haemolytic activity, adherence and cytotoxicity. Experimental animal models have been used for *in vivo* culture in monkeys, hamsters, guinea pigs, rats, mice, cattle, and dogs, but most were poor models which did not mimic disease. Nevertheless, some promising results were obtained in squirrel monkeys (sustained symptomatic disease and horizontal transmission, but some confusion with indigenous trichomonads) and mice (intravaginal inoculation producing disease but usually requiring pre-oestrogenization, intraperitoneal inoculation linked to virulence as evident by visceral organ necrosis, and subcutaneous inoculation linked to virulence as evident by abscess formation). Various immunological techniques have been used to detect specific host antibodies to trichomonad antigens, including gel diffusion, complement fixation, agglutination, fluorescence and enzyme immunoassays which varied in both sensitivity and specificity by reacting with variety of antigenic markers. Monoclonal antibodies have also been developed and used in agglutination, fluorescence and enzyme immunoassays to detect parasite antigens in clinical samples. More recently, molecular biological techniques have been used to characterize parasites in clinical samples following the amplification of nuclear gene sequences (18S ribosomal RNA, ferrodoxin, beta-tubulin, adhesion protein genes, and a highly-repetitive 2-kb DNA sequence) by conventional, nested and real-time polymerase chain reaction (PCR) techniques, and dot-blot DNA hybridization assays using radioactive isotopes or fluorochrome labels.

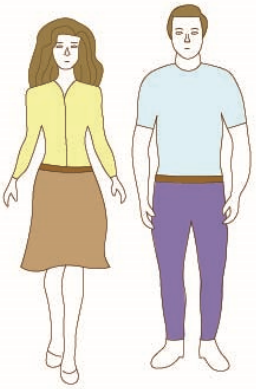
Treatment and control: Clinical infections may be treated using drugs effective against anaerobic bacteria and protozoa, notably the nitroimidazole drug (metronidazole) and derivatives (tinidazole, ornidazole, secnidazole, flunidazole, nimorazole and carnidazole). Some trichomonacidal activity has also be found using aromatic polyenes (hamycin), some antibiotics (paromomycin, anisomycin, purpuromycin), nitrothiazole derivatives (niridazole), nitrothiazolyls (nitazoxanide), nitrofurans (furazolidone, nifaratel), a microtubule-inhibitor (mebendazole) and some salt solutions (sodium nitrite, sodium nitroprusside, Roussin's black salt), but their activity was variable and many exhibited adverse side-effects. Nitroimidazoles are usually given orally, although some formulations are available as topical vaginal medications (creams and gels) or pessaries. Metronidazole is well tolerated despite its metallic taste, but alcohol consumption is contraindicated due to antabuse-like side-effects (ethanol sensitivity) and other adverse reactions (nausea, vomiting, headache, insomnia, dizziness, drowsiness, rash). In addition, metronidazole should not be administered to pregnant women in the first trimester as it may cross the placenta causing problems. Instead, pregnant women with severe symptoms are best treated with intravaginal pessaries containing clotrimazole, povidone-iodine, nonoxynol-9 or arsenical compounds. The treatment of disease in neonates (babies infected during birth) is often curtailed as most infections resolve after 3-6 weeks as maternal oestrogen levels wane. Regrettably, there are growing numbers of treatment failures (4-10%), either due to non-compliance or reinfection, but more usually due to the emergence of drug-resistant strains of parasites. Metronidazole is a pro-drug which is reduced by the enzyme pyruvate: ferredoxin oxidoreductase (PFOR) to yield cytotoxic nitro radical anions that interfere with parasite DNA synthesis. Resistance to metronidazole may be aerobic involving oxygen-scavenging pathways and ferredoxin or anaerobic involving the reduction or cessation of PFOR and hydrogenase activity. A range of preventive measures have been adopted to reduce the transmission of infections, including regular health screening and treatment of patients and sexual partners, practicing safe sex (using condoms), abstinence or monogamy, maintaining high standards of feminine hygiene, and using suppositories and alkaline douches to lower vaginal pH and reduce symptoms. Many countries have instigated public awareness and health education campaigns targeting sexually-transmitted diseases. The prospects for vaccine appear to be poor because natural infections do not induce long-term immune protection despite the demonstration of specific antibodies (serum and mucosal) and some local inflammatory responses. Both humoral and cellular responses rapidly wane (within 6 months), particularly after treatment, and hosts are susceptible to re-infection and disease. The parasites have also been shown to have adopted many different immuno-evasion tactics, involving antigenic variation, molecular mimicry and coating themselves in host molecules. Nevertheless, several vaccine trials were conducted with mixed results. Patients with refractory infections that were inoculated with heat-inactivated trophozoites exhibited some clinical improvement, as did those inoculated with heat-inactivated 'abnormal strains' of lactobacilli isolated from clinical cases. The apparent cross-protection afforded by the latter studies was thought to be due to microbial interactions favouring resident flora that were inhibitory to parasite growth. Experiments on a mouse model found that subcutaneous injections of whole trophozoites with and without adjuvants prior to their oestrogenization and prebiotic vaginal inoculation with lactobacilli led to the resolution of some infections and the development of some protection in vaccinated mice, suggesting the trichomonad-bacterial interactions could be further exploited for therapeutic and prophylactic purposes.

Trichomonas vaginalis

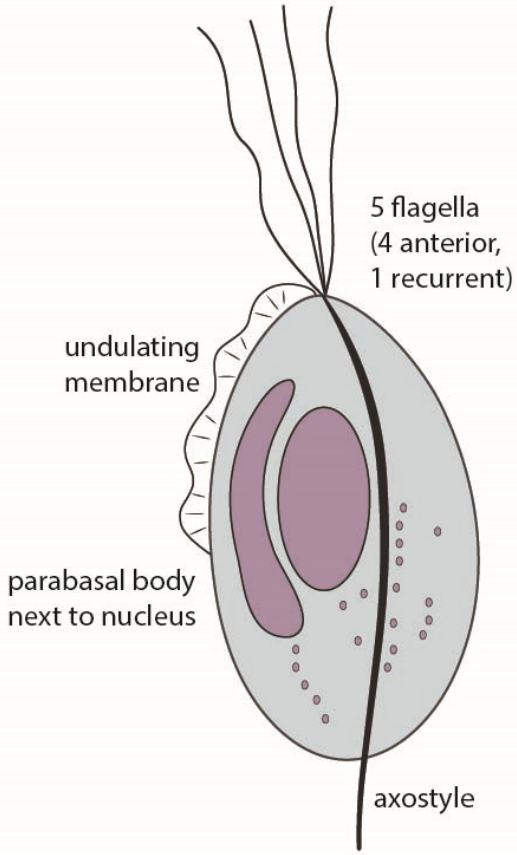


urogenital tract
(vaginitis, urethritis,
endometritis,
infertility?)

division by
longitudinal
binary fission



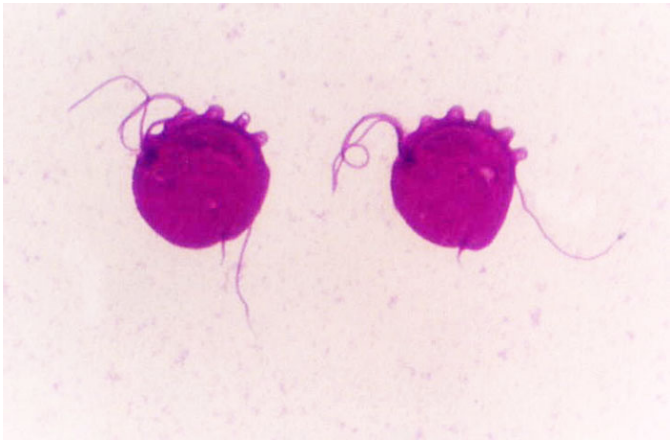
Vertebrate Hosts
(humans)



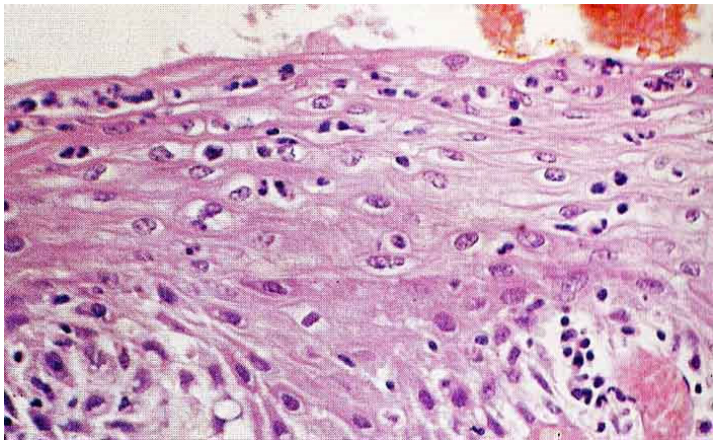
trophozoites
(7-32 µm)

no cyst formation

direct transmission by transfer of trophozoites
during coitus, occasionally via contaminated fomites,
or during parturition



Trichomonas vaginalis trophozoites



Trichomonas vaginalis vaginitis

Trichomonas gallinae
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Parabasalid flagellates are anaerobic amitochondriate protists which have distinctive parabasal bodies (dictyosomes) adjacent to flagellar basal bodies (kinetosomes) and an axostyle-pelta complex providing structural support. Trichomonads are a major constituent group and most have 4-6 apical flagella, one being recurrent and often forming an undulating membrane supported by a costa. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Many *Trichomonas* spp. have been reassigned to different genera based on the number of free anterior flagella e.g. *Tritrichomonas*, *Tetratrichomonas* and *Pentatrichomonas* having 3, 4 and 5 anterior flagella respectively. Confusingly, the name *Trichomonas* has been retained for some species with 4 anterior flagella (mainly those in man, some rodents and birds). Most trichomonad species are endocommensals in mammals, birds, reptiles and insects but several species are parasitic in the alimentary or urogenital tracts of man and domestic animals.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Metamonad (amitochondriate flagellates with karyomastigonts)
Phylum: Parabasalia (anaerobic flagellates with parabasal body supporting Golgi cisternae or dictyosome, trichomonads, hypermastigids, retortamonads)
Class: Trichomonadea (single mastigont, comb-like structure absent, infrakinetosomal body absent)
Order: Trichomonadida (lamelliform undulating membrane, B-type costa)
Family: Trichomonadidae (5-6 flagella, cone-like axostyle)
Genus: *Trichomonas* (parasites/commensals in tubular organs of vertebrates)
Species: *T. gallinae* (causes canker in birds)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)

body)		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Metamonads are a group of excavates (with ventral feeding groove) that have several subcellular elements associated with their flagella forming a unique mastigont (an ultrastructural complex of organelles and cytoskeletal fibrils (incl. dictyosomes (Golgi bodies), centrioles (basal bodies) and a microtubular axostyle)). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Most metamonads are amitochondriate but have retained reduced organelles of mitochondrial origin (fornicates containing mitosomes while parabasalians possess hydrogenosomes). Members of the phylum Parabasalia typically possess parabasal bodies adjacent to Golgi bodies (dictyosomes), and have microtubular arrays forming a conspicuous pelta-axostyle complex (cap-like pelta and a cone- or tube-like longitudinal axostyle). Six parabasalid classes are currently recognized on the basis of morphological, biological and molecular phylogenetic studies. Cells in three classes (Trichomonadea, Tritrichomonadea, Hypotrichomonadea) bear single mastigonts (set of kinetosomes (basal bodies) and associated appendages – ancestral unit comprising 4 kinetosomes) with flagella arranged in an anterior tuft, but many have one recurrent flagellum forming an undulating membrane (lamelliform or rail-type) supported by a costa (A- or B-type) and sometimes a basal comb-like structure and/or infrakinetosomal body. Many species are symbiotic (mutualists, commensals or parasites) in animals, although some are free-living in moist habitats. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Cells in another three classes (Cristamonadea, Trichonymphea, Spirotrichonymphea) have more complex structures, often with multiple mastigonts bearing hundreds to thousands of flagella. Most were previously assigned to the now-defunct group Hypermastigida and they are primarily found as symbionts (mutualists) in insects (mostly termites).

Trichomonad taxonomy can be very confusing as many *Trichomonas* spp. have now been reassigned to sister genera based on the number of anterior flagella e.g. *Tritrichomonas*, *Tetratrichomonas* and *Pentatrichomonas* having 3, 4 and 5 anterior flagella respectively. Confusingly, the name *Trichomonas* has been retained for some species with 4 anterior flagella (mainly those in man, some rodents and birds). Recent ultrastructural and molecular biological studies have also led to the placement of the genus *Tritrichomonas* into a separate class (Tritrichomonadea) as the cells contain unique comb-like structures and infrakinetosomal bodies at the bases of their recurrent flagella (both lacking in members of the class Trichomonadea). Several genera (*Hypotrichomonas* and *Trichomitus*) were assigned to another class (Hypotrichomonadea) as their cells contained comb-like structures but lacked infrakinetosomal bodies.

Family	**Key characters to 'trichomonad' families in vertebrates***						**Representative genera**
	Number of	**Undulating membrane**	**Costa**	**Axostyle**	**Comb-like**	**Infra-kinetosomal**	

	flagella				structure	body	
Class Tritrichomonadea (uninucleate to binucleate)							
Order Tritrichomonadida (endobiotic in vertebrates (mammals, birds, reptiles, amphibia, fish))							
Tritrichomonadidae	4-5	rail-type	A-type	tube-like	present	present	*Tritrichomonas*
Simplicimonidae	4	absent	absent	tube-like	present	present	*Simplicimonas*
Monocercomonidae	4	absent	absent	cone-like	present	present	*Monocercomonas*
Dientamoebidae	0-4	absent	absent	cone-like	absent	absent	*Dientamoeba, Histomonas*
Class Trichomonadea (single karyomastigont)							
Order Trichomonadida (with costa) (endobiotic in vertebrates (mammals, birds, reptiles, amphibia) and invertebrates)							
Trichomonadidae	5-6	lamelliform	B-type	cone-like	absent	absent	*Cochlosoma, Trichomonas, Trichomitopsis, Tetratrichomonas, Pentatrichomonas*
Order Honigbergiellida (without costa) (endobiotic in vertebrates (mammals, reptiles, amphibia))							
Hexamastigidae	5-6	absent	absent	cone-like	absent	absent	*Hexamastix*
Class Hypotrichomonadea (single karyomastigont)							
Order Hypotrichomonadida (endobiotic in vertebrates (reptiles, amphibia, mammals) and invertebrates)							
Hypotrichomonidae	4	lamelliform	A-type	cone-like	present	absent	*Trichomitus, Hypotrichomonas*

*Taxa found exclusively in invertebrate hosts (such as termites and cockroaches) are not listed.

The class Trichomonadea contains a diverse range of cells with single karyomastigonts giving rise to 2-6 flagella, with one being recurrent but lacking a comb-like structure and infrakinetosomal body. Two orders are recognized: Honigbergiella (undulating membrane absent or lamelliform without supporting costa); and Trichomonadida (most with lamelliform undulating membrane supported by B-type costa and stout cone-like axostyles). The family Trichomonadida contains some 10 genera (*Cochlosoma, Lacusteria, Pentatrichomonas, Pentatrichomonoides, Pseudotrichomonas, Pseudotrypanosoma, Tetratrichomonas, Trichomitopsis, Trichomonas* and *Trichomonoides*) which vary in their cellular, organellar and flagellar configurations, zoogeography (host ranges), and biological characteristics (heterotrophs ranging from mutualists to commensals to parasites). Trichomonads (*sensu latu* = in the broadest sense) usually exhibit strong site specificity (tissue tropism) and occur in the alimentary, urogenital or respiratory tracts of their hosts, where they may cause very different types of disease. Several specialized species living in the urogenital tracts of vertebrates may cause severe inflammatory diseases, with *Trichomonas vaginalis* causing vaginitis in humans, and *Tritrichomonas foetus* causing bovine infertility. A few species living in the upper respiratory and alimentary tracts of birds may cause life-threatening diseases, including *Trichomonas gallinae* causing canker in birds. In contrast, those inhabiting the intestinal tracts of vertebrate and invertebrate hosts are often considered to be symbiotes or commensals (rather than parasites) as most infections appear benign. Rather than try to cover trichomonad biodiversity and their disparate clinical significance in one comprehensive section, it has been elected to showcase representatives in 4 separate sections, targeting:

- urogenital infections by *Tritrichomas foetus* in cattle;
- urogenital infections by *Trichomonas vaginalis* in humans;
- oral infections by *Trichomonas gallinae* in birds; and
- enteric infections by *Trichomonas, Tetratrichomonas* and *Pentatrichomonas* spp. in a wide range of hosts.

While numerous *Trichomonas* spp. have been detected in the alimentary tracts of birds, most occur below the level of the stomach (in the intestines) and only a few infect organs above the stomach (oral cavity, throat). One species in particular, *Trichomonas gallinae*, has been associated with severe necrotizing caseous lesions in the upper digestive tract causing a condition commonly known as canker. Infections have been reported in various bird species around the world, notably in juvenile pigeons (squabs) but also including domestic poultry (turkey poults, chickens) as well as aviary birds (budgerigars, parrots).

Parasite species	Size (µm)	Vertebrate Hosts	Location	Clinical signs	Distribution
Class: **Trichomonadea** (single karyomastigont) [4-6F-CLS-IKB(+CA in most genera, TA or reduced in others)]†					
Order: Trichomonadida [5-6F+LUM+BC]					
Family: Trichomonadidae [+CA]					
Trichomonas [5F(=4A+R)+LUM-RF]					
Trichomonas gallinae (syn. *Cercomonas gallinae, C. hepaticum,*	5-20 x 2-9	Columbiformes (rock pigeon, wood pigeon, white-crowned pigeon, band-tailed pigeon, pink pigeon,	upper digestive tract (mouth, pharynx,	canker (roup, frounce),	worldwide

Trichomonas columbae) [+AF]		Seychelles blue-pigeon, Eurasian collared dove, ring turtle-dove, Madagascar turtle-dove, Indian dove, spotted dove, red-eyed dove, laughing dove, zebra dove, mourning dove, Galapagos dove, white-winged dove, white-bellied dove, ground dove, white-tipped dove), Accipitriformes (bald eagle, black kite, Egyptian vulture, shikra, African goshawk, rufous-chested sparrowhawk, Cooper's hawk, western marsh-harrier, northern goshawk, gray hawk, red-shouldered hawk, red-tailed hawk, Eurasian buzzard, golden eagle, Bonelli's eagle, booted eagle, secretary-bird), Falconiformes (Cooper's hawk, red-tailed hawk, red-shouldered hawk, golden eagle, lesser kestrel, Eurasian kestrel, American kestrel, red-necked falcon, merlin, lanner falcon, saker falcon, gyrfalcon, peregrine falcon, sparrow hawk, duck hawk), Strigiformes (barn owl, scops owl, screech-owl, horned-owl, eagle-owls, tawny owl, barred owl, little owl, boobook), Gruiformes (rails); Passeriformes (finches, canaries, sparrows, jays, crows, currawong, magpie, ravens, mockingbirds), Psittaciformes (lorikeets, budgerigars, cockateil, tovi parakeets), Cuculiformes (channel bill cuckoo), Caprimulgiformes (frogmouth), Anseriformes (ducks, geese), rarely Galliformes (chickens, turkeys, bobwhite quail), Charadriiformes (gull); plus experimental subcutaneous assays in mice	oesophagus, proventriculus, crop), liver, lungs	necrotizing lesion	
Trichomonas gypaetinii		Accipitriformes (bearded vulture, Egyptian vulture, black vulture)	upper digestive tract	non-pathogenic	Europe
Trichomonas stableri	slender 13 x 6, rounded 8 x 6	Columbiformes: columbid (pigeons)	oral cavity, oesophagus	caseo-necrotic lesions	North America

†Coding: + = present; - = absent; #F = total number of flagella; #A = number of anterior flagella; R = recurrent flagellum; RF = recurrent flagellum extending posteriorly as free flagellum; LUM = lamelliform undulating membrane; BC = B-type costa; AF = axostyle protrudes posteriorly; CA = cone-like axostyle (*Trichomonas*-type); TA = tube-like axostyle (*Tritrichomonas*-type); CLS = comb-like structure; IKB = infrakinetosomal body.

Parasite morphology: *Trichomonas gallinae* forms motile trophic stages known as trophozoites which possess 5 flagella. Trophozoites have ovoid to pyriform bodies ranging from 5-12 µm in length, with well-fed forms becoming robust and extending up to 20 µm in length. Cells possess a single prominent nucleus located anteriorly adjacent to a distinctive parabasal body formed by dictyosomes (Golgi complexes). The nucleus and parabasal body are associated with small dense basal bodies (kinetosomes) forming a single karyomastigont unit (ancestral unit with 4 kinetosomes). The kinetosomes give rise to 4 flagella which project forwards forming an anterior tuft around 8-10 µm in length. In *T. gallinae*, a separate kinetosome gives rise to a fifth flagellum which is recurrent (directed posteriad) and attached longitudinally to the cell body forming a short undulating membrane that does not reach the end of the body. The undulating membrane is lamelliform in appearance (rather than rail-like) and is underpinned by a slender elongate rod-like structure in the cell cytoplasm known as the costa, which is striated with a periodicity known as B-type (rather than A-type). Trophozoites swim with a characteristic jerky forward motion, and the undulating membrane imparts a quivering/shimmering appearance to the cell body. Trophozoites also possess a slender longitudinal hyaline rod-like structure

known as an axostyle which is composed of concentric rows of microtubules forming a cone (rather than a tube). The axostyle begins near the nucleus and runs posteriorly through the cell body, protruding through the posterior end and terminating in a sharp point. Trichomonads are anaerobic and do not have mitochondria, but rather possess membrane-bound organelles known as hydrogenosomes (formerly called siderophil granules) often located in rows along the axostyle. *T. gallinae* does not form true encapsulated cysts, but cells may sometimes round up and lose their flagella and undulating membranes. This generally occurs under unfavourable conditions, and has been observed to be reversible. These stages have been called 'pseudocysts' and they are thought to behave as resistant forms under stressful environmental conditions.

Site of infection: Trophozoites are usually found in the upper alimentary tract (mouth cavity, pharynx, oesophagus, proventriculus, crop) and nasal cavities of birds, sometimes penetrating to underlying organs (liver, lungs, heart, pancreas). In juvenile pigeons (squabs), infection may be seen at the umbilicus and can track up into the liver via the falciform ligament connection. Infections have been recorded mainly Columbiformes (> 20 species of pigeons/doves), birds of prey (> 40 species of eagles, hawks, falcons, vultures and owls), as well as in several Psittaciformes (lorikeets, budgerigars, parakeets), Passeriformes (finches, canaries, sparrows, corvids, mockingbirds), Gruiformes (rails), Cuculiformes (cuckoos), and Anseriformes (ducks, geese), but rarely in Galliformes (chickens, turkeys, bobwhite quail) and Charadriiformes (gulls).

Pathogenesis: Infections may cause clinical disease (trichomoniasis) in the upper digestive and respiratory tracts of birds, varying in severity from mild mucosal inflammation to caseous areas that block the oesophageal lumen and prove fatal. The disease is often canker, but is also known as frounce in raptors, or roup in columbiforms and psittaciforms. Trophozoites occur free in the lumina of the tubular organs as well as browsing and attaching to mucosal surfaces where they cause diffuse cellulitis and inflammation with increasing numbers of heterophils. The parasites may then invade underlying tissues causing rounded lesions with spur-like projections that coalesce to form ulcerative and exudative lesions. The lesions may become necrotic with thick caseous masses (composed of fibrin, inflammatory cells, bacteria and trichomonads) that can block passages (mouth, pharynx, oesophagus, crop, sometimes proventriculus and conjunctival sac). Some parasite strains also create diphtheritic membranes associated with fibrinous lesions in internal organs such as pharynx, lungs, liver and peritoneum. Affected birds exhibit depression, drowsiness, listlessness, weakness, ruffled and matted feathers, and have greenish exudates from the beak and/or yellow cheesy caseous masses (canker) around the beak, eyes or nasal passages. Nasal and oral exudation may impair breathing (with dyspnoea) and feeding (with dysphagia, excessive salivation, swallowing difficulties, sometimes regurgitation) leading to anorexia, weight loss, emaciation, inability to stand or maintain balance, increased thirst, swollen faces, pendulous crops, sometimes diarrhoea, and even death (as early as 4 days after infection, but usually around 3 weeks). The severity of infection depends on differences in host susceptibility, the intensity of infection, the stage of infection (acute/chronic) and strain differences in parasite virulence, some strains notably causing systemic disease by invading internal organs (liver, lungs, pericardium, air sacs, pancreas) occasionally forming abscesses (liver, lungs). Clinical infections occur mainly in young birds, especially pigeon squabs, although many birds recover from disease but may remain asymptomatic carriers. Birds harbouring light infections or infections by avirulent strains appear to develop some protective (premunitive) immunity against disease which wanes after infections are lost. Humoral and cellular immune responses appear to be involved following the phagocytosis of parasites by leucocytes, leading to the production of serum and secretory antibodies, and lymphocytic infiltrates. The worldwide distribution of disease closely mirrors that of rock pigeons which are considered to be principal hosts responsible for most dissemination. Clinical disease occurs more frequently in spring and summer months and is thought to be associated with peak periods of bird reproduction (including courtship, nesting and feeding nestlings).

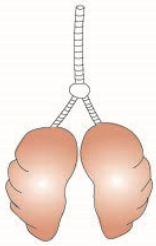
Developmental cycle and mode of transmission: Trichomonads have simple direct life-cycles involving the multiplication of trophozoites by longitudinal binary fission and their transmission to new hosts by contact or contaminated food or water. The parasites do not form true cysts, but rounded nonflagellated pseudocysts may also be involved in transmission cycles. Parasites are very sensitive to desiccation and survive poorly in the external environment, but trophozoites have been found to remain viable for up to 5 days in moist grains and for several hours in water sources (depending on salinity). Studies have indicated that the minimal infective dose may be as small as a single trophozoite. Birds come into direct contact with each other when billing during courtship, when cross-feeding, and when feeding nestlings with maternal crop milk or regurgitated food. Birds with oral or throat lesions often have difficulty swallowing large pieces of grain and may drop them where they are taken up by other birds. Birds of prey have been found to become infected by feeding on infected prey where trophozoites may survive for up to 48 hours after host death. Risk factors for clinical infections include high bird population densities (especially overcrowding in caged birds), poor hygiene (particularly of food and water sources), and concomitant infections (notably pigeon circovirus). Epidemiological studies have also shown that the prevalence of infections in wild birds is greatest during hot dry weather, possibly due to more birds gathering at fewer water holes.

Differential diagnosis: Clinical infections are strongly suggested by the occurrence of characteristic caseous (canker) lesions in the oral/nasal cavities of birds, but there may be some confusion with other pathological conditions (such as nonspecific pharyngoesophagitis, vitamin A deficiency, sialoliths (salivary stones)) or other infectious diseases (poxviruses, fungi, *Capillaria* nematodes), particularly those involving granuloma formation (e.g. tuberculosis, mycoplasmosis, salmonellosis, coligranuloma). Definitive diagnosis is made by the direct microscopic detection of motile trophozoites in exudates or scrapings collected from

birds. Wet mounts are generally prepared from swabs collected from the oral cavity and examined unstained by high contrast bright-field microscopy or by dark-field, phase-contrast or interference-contrast microscopy. Smears may also be prepared and stained with Giemsa, silver, iron haematoxylin, malachite green, methylene blue, or acradine orange. Host tissues may also be collected at autopsy and histological sections examined after staining with haematoxylin and eosin, Giemsa or periodic acid-Schiff stains. Several studies have also developed immunohistochemical stains using polyclonal or monoclonal antibodies labelled with fluorochromes or enzymes. Parasites may be readily cultured *in vitro* using a variety of liquid/semiliquid media at 37-40°C, but essential macromolecules, vitamins and minerals need to be included as trophozoites lack the ability to synthesize many materials *de novo*. Suitable media include Diamond's TYI media, Trichosel medium, medium 199 and Hollander fluid (HF) medium, most with serum supplements to provide lipids, fatty acids, iron and trace metals. A range of tissue cultures have also been used to support trichomonad growth, including chick liver cells, monkey kidney cells, chicken hepatocellular carcinoma cell (LMH) monolayers, and Japanese quail fibrosarcoma cell (QT-35) monolayers. Experimental studies have been used to examine parasite pathogenicity following the subcutaneous inoculation of known numbers of axenically cultured trophozoites and then measuring lesion size 6 days later. An enzyme immunoassay has been developed to help diagnose infections in poultry by the detection of specific host antibodies against parasite antigens. More recently, a range of molecular biological techniques have been used to detect and characterize trichomonads in clinical samples by isoenzyme electrophoresis, Western blot analyses, restriction enzyme analyses and the polymerase chain reaction (PCR) amplification of nuclear gene sequences (large and small subunit ribosomal RNA, internal transcribed spacers, alpha-tubulin, iron-hydrogenase) and fluorochrome- or chromogenic-based *in situ* hybridization (ISH) assays.

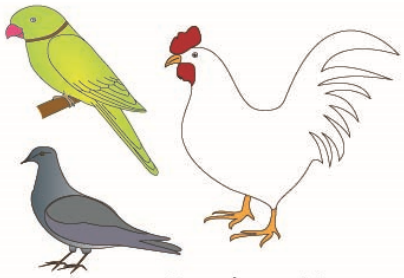
Treatment and control: A variety of chemotherapeutic agents have been used to treat clinical infections in birds, initially involving adding stringents, disinfectants or antibiotics to drinking water or topically to mouth and throat of affected birds, and subsequently using antiparasitic drugs as water or food additives or as systemic formulations. In particular, good results were achieved using nitroimidazole drugs (metronidazole, carnidazole, ronidazole, dimetridazole) which exhibit selective toxicity for anaerobic bacteria and protozoa. These drugs are usually well tolerated but they may cause some adverse side-effects and toxicity problems (e.g. dimetridazole). There are also growing instances of treatment failures due to the emergence of drug-resistant parasite strains due to subtherapeutic dosing and sustained prophylactic use. Recent studies have indicated that some synthetic polyphenolic/flavonoid compounds (chalcones) may be used to treat infections. In all instances, however, large caseous masses do not respond to treatment and recourse is often made to their surgical removal. A variety of preventive measures have been employed to reduce sources of infection and limit transmission. Regular health surveillance and treatment can help prevent the introduction of infections in commercial flocks and aviaries, especially when new or translocated birds are isolated in quarantine. Barrier systems and screens should be used around bird holding facilities to deny access to potential carriers (wild birds), and birds of prey should be prevented from hunting urban pigeons. Strict hygiene and sanitation may be used to limit environmental contamination by avoiding communal food and water sources, regularly cleaning feeders and water containers using bleach disinfectants, and thoroughly drying washed fomites, cages and buildings. Good husbandry practices should be used to keep birds in optimal nutrition in non-crowded stress-free conditions to stop them from becoming more susceptible to infection and disease.

Trichomonas gallinae

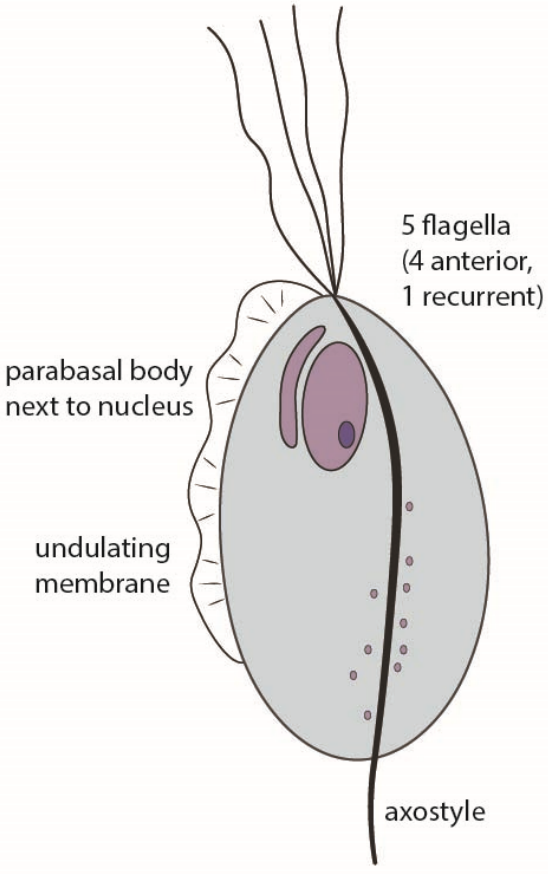


upper alimentary tract
(necrotizing caseous
lesions (canker))

division by
longitudinal
binary fission



Vertebrate Hosts
(birds)



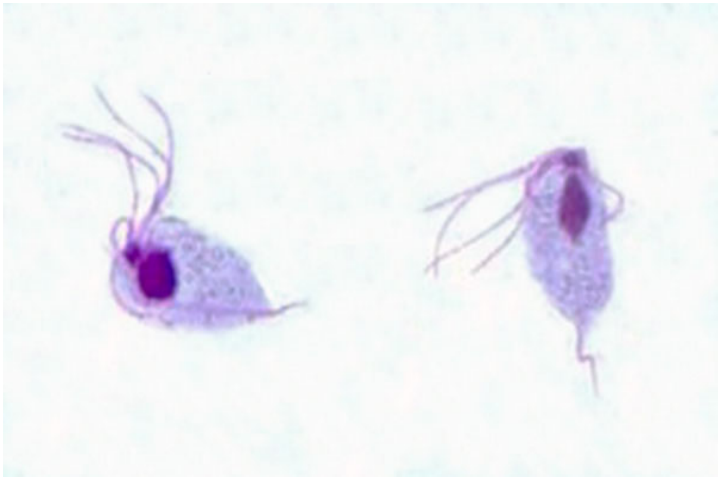
trophozoites
(5-20 µm)

no cyst formation

direct transmission by transfer of trophozoites
during close contact or via contaminated fomites



Trichomonas gallinae trophozoites



Trichomonas gallinae trophozoites

Trichomonads (enteric species in mammals, birds, reptiles, amphibia, fish, invertebrates)
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Parabasalid flagellates are anaerobic amitochondriate protists which have distinctive parabasal bodies (dictyosomes) adjacent to flagellar basal bodies (kinetosomes) and an axostyle-pelta complex providing structural support. Trichomonads are a major constituent group and most have 4-6 apical flagella, one being recurrent and often forming an undulating membrane supported by a costa. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Many *Trichomonas* spp. have been reassigned to different genera based on the number of free anterior flagella e.g. *Tritrichomonas*, *Tetratrichomonas* and *Pentatrichomonas* having 3, 4 and 5 anterior flagella respectively. Confusingly, the name *Trichomonas* has been retained for some species with 4 anterior flagella (mainly those in man, some rodents and birds). Most trichomonad species are endocommensals in mammals, birds, reptiles and insects but several species are parasitic in the alimentary or urogenital tracts of man and domestic animals.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Metamonad (amitochondriate flagellates with karyomastigonts)
Phylum: Parabasalia (anaerobic flagellates with parabasal body supporting Golgi cisternae or dictyosome, trichomonads, hypermastigids, retortamonads)
Class: Trichomonadea (single mastigont, comb-like structure absent, infrakinetosomal body absent)
Order: Trichomonadida (lamelliform undulating membrane, B-type costa)
Family: Trichomonadidae (5-6 flagella, cone-like axostyle)
Genus: *Trichomonas* (parasites/commensals in tubular organs of vertebrates)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae	*Trichomonas*	vertebrates	direct (f-o, v)

		(stout axostyle, costa, undulating membrane)		(urogenital tract, gut)	
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Metamonads are a group of excavates (with ventral feeding groove) that have several subcellular elements associated with their flagella forming a unique mastigont (an ultrastructural complex of organelles and cytoskeletal fibrils (incl. dictyosomes (Golgi bodies), centrioles (basal bodies) and a microtubular axostyle)). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Most metamonads are amitochondriate but have retained reduced organelles of mitochondrial origin (fornicates containing mitosomes while parabasalians possess hydrogenosomes). Members of the phylum Parabasalia typically possess parabasal bodies adjacent to Golgi bodies (dictyosomes), and have microtubular arrays forming a conspicuous pelta-axostyle complex (cap-like pelta and a cone- or tube-like longitudinal axostyle). Six parabasalid classes are currently recognized on the basis of morphological, biological and molecular phylogenetic studies. Cells in three classes (Trichomonadea, Tritrichomonadea, Hypotrichomonadea) bear single mastigonts (set of kinetosomes (basal bodies) and associated appendages – ancestral unit comprising 4 kinetosomes) with flagella arranged in an anterior tuft, but many have one recurrent flagellum forming an undulating membrane (lamelliform or rail-type) supported by a costa (A- or B-type) and sometimes a basal comb-like structure and/or infrakinetosomal body. Many species are symbiotic (mutualists, commensals or parasites) in animals, although some are free-living in moist habitats. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Cells in another three classes (Cristamonadea, Trichonymphea, Spirotrichonymphea) have more complex structures, often with multiple mastigonts bearing hundreds to thousands of flagella. Most were previously assigned to the now-defunct group Hypermastigida and they are primarily found as symbionts (mutualists) in insects (mostly termites).

Trichomonad taxonomy can be very confusing as many *Trichomonas* spp. have now been reassigned to sister genera based on the number of anterior flagella e.g. *Tritrichomonas*, *Tetratrichomonas* and *Pentatrichomonas* having 3, 4 and 5 anterior flagella respectively. Confusingly, the name *Trichomonas* has been retained for some species with 4 anterior flagella (mainly those in man, some rodents and birds). Recent ultrastructural and molecular biological studies have also led to the placement of the genus *Tritrichomonas* into a separate class (Tritrichomonadea) as the cells contain unique comb-like structures and infrakinetosomal bodies at the bases of their recurrent flagella (both lacking in members of the class Trichomonadea). Several genera (*Hypotrichomonas* and *Trichomitus*) were assigned to another class (Hypotrichomonadea) as their cells contained comb-like structures but lacked infrakinetosomal bodies.

Family	**Key characters to 'trichomonad' families in vertebrates***						**Representative genera**
	Number of flagella	**Undulating membrane**	**Costa**	**Axostyle**	**Comb-like structure**	**Infra-kinetosomal body**	

Class Tritrichomonadea (uninucleate to binucleate)							
Order Tritrichomonadida (endobiotic in vertebrates (mammals, birds, reptiles, amphibia, fish))							
Tritrichomonadidae	4-5	rail-type	A-type	tube-like	present	present	*Tritrichomonas*
Simplicimonidae	4	absent	absent	tube-like	present	present	*Simplicimonas*
Monocercomonidae	4	absent	absent	cone-like	present	present	*Monocercomonas*
Dientamoebidae	0-4	absent	absent	cone-like	absent	absent	*Dientamoeba, Histomonas*
Class Trichomonadea (single karyomastigont)							
Order Trichomonadida (with costa) (endobiotic in vertebrates (mammals, birds, reptiles, amphibia) and invertebrates)							
Trichomonadidae	5-6	lamelliform	B-type	cone-like	absent	absent	*Cochlosoma, Trichomonas, Trichomitopsis, Tetratrichomonas, Pentatrichomonas*
Order Honigbergiellida (without costa) (endobiotic in vertebrates (mammals, reptiles, amphibia))							
Hexamastigidae	5-6	absent	absent	cone-like	absent	absent	*Hexamastix*
Class Hypotrichomonadea (single karyomastigont)							
Order Hypotrichomonadida (endobiotic in vertebrates (reptiles, amphibia, mammals) and invertebrates)							
Hypotrichomonidae	4	lamelliform	A-type	cone-like	present	absent	*Trichomitus, Hypotrichomonas*

*Taxa found exclusively in invertebrate hosts (such as termites and cockroaches) are not listed.

The class Trichomonadea contains a diverse range of cells with single karyomastigonts giving rise to 2-6 flagella, with one being recurrent but lacking a comb-like structure and infrakinetosomal body. Two orders are recognized: Honigbergiella (undulating membrane absent or lamelliform without supporting costa); and Trichomonadida (most with lamelliform undulating membrane supported by B-type costa and stout cone-like axostyles). The family Trichomonadida contains some 10 genera (*Cochlosoma, Lacusteria, Pentatrichomonas, Pentatrichomonoides, Pseudotrichomonas, Pseudotrypanosoma, Tetratrichomonas, Trichomitopsis, Trichomonas* and *Trichomonoides*) which vary in their cellular, organellar and flagellar configurations, zoogeography (host ranges), and biological characteristics (heterotrophs ranging from mutualists to commensals to parasites). Trichomonads (*sensu latu* = in the broadest sense) usually exhibit strong site specificity (tissue tropism) and occur in the alimentary, urogenital or respiratory tracts of their hosts, where they may cause very different types of disease. Several specialized species living in the urogenital tracts of vertebrates may cause severe inflammatory diseases, with *Trichomonas vaginalis* causing vaginitis in humans, and *Tritrichomonas foetus* causing bovine infertility. A few species living in the upper respiratory and alimentary tracts of birds may cause life-threatening diseases, including *Trichomonas gallinae* causing canker in birds. In contrast, those inhabiting the intestinal tracts of vertebrate and invertebrate hosts are often considered to be symbiotes or commensals (rather than parasites) as most infections appear benign. Rather than try to cover trichomonad biodiversity and their disparate clinical significance in one comprehensive section, it has been elected to showcase representatives in 4 separate sections, targeting:

- urogenital infections by *Tritrichomas foetus* in cattle;
- urogenital infections by *Trichomonas vaginalis* in humans;
- oral infections by *Trichomonas gallinae* in birds; and
- enteric infections by *Trichomonas, Tetratrichomonas* and *Pentatrichomonas* spp. in a wide range of hosts.

A large number of trichomonad species have been reported in the digestive tracts from a wide range of vertebrates (mammals, birds, reptiles, amphibia, fish) and invertebrates (wood-eating termites and cockroaches, leeches, snails). Most infections have not been associated with clinical disease and many trichomonads are considered to be harmless commensals or symbiotes (even mutualists in insects). While trichomonads are often encountered in clinical samples, they are generally regarded to be incidental detections unrelated to aetiology. Nonetheless, several species have tentatively been associated with mild clinical signs in a small number of hosts, including *Trichomonas tenax* and *Pentatrichomonas hominis* in humans, and *Tetratrichomonas gallinarum* in birds.

Parasite species†	**Size (µm)**	**Vertebrate Hosts**	**Location**	**Clinical signs**	**Distribution**
Class: **Trichomonadea** (single karyomastigont) [4-6F-CLS-IKB(+CA in most genera, TA or reduced in others)]					
Order: Trichomonadida [5-6F+LUM+BC]					
Family: Trichomonadidae [+CA]					
Trichomonas [5F(=4A+R)+LUM-RF+BC]					
Trichomonas agilis	10-14 x 7-9	Isoptera: kalotermitid (termite *Calotermes brouni*)	hindgut		New Zealand

Trichomonas alexeieffi		Sauria: anguid (slow worm)			Europe
Trichomonas anthropopitheci		Primates: hominid (chimpanzee)			Africa
Trichomonas aotus		Primates: aotid (three-striped night monkey)	intestines		Americas
Trichomonas aragaoi		Edentata: myrmecophagid (southern tamandua)			South America
Trichomonas aulacodi		Rodentia: thryonomyid (greater cane rat)			Africa
Trichomonas avium		Gruiformes: aramid (cayenne wood rail); Cuculiformes: cuculid (ani, guira cuckoo); Piciformes: galbulid (nunbird)			Americas
Trichomonas boae		Serpentes: boid (boa constrictor)			South America
Trichomonas bonasae		Galliformes: tetraonid (ruffed grouse)			Europe
Trichomonas bramae		Strigiformes: strigid (spotted owlet)			Asia
Trichomonas brevicollis		Isoptera: kalotermitid (termite *Calcaritermes brevicollis*)	hindgut		Central America
Trichomonas brixi [+AF]	4-11 x 2-8	Carnivora: canid (dog), felid (cat)	oral cavity		Europe
Trichomonas cartagensis		Isoptera: kalotermitid (termite *Glyptotermes contracticornis*)	hindgut		Central America
Trichomonas chagasi		Rodentia: caviid (rock cavy)			South America
Trichomonas chordeilis		Caprimulgiformes: caprimulgid (night hawk)			Americas
Trichomonas coccyzi		Cuculiformes: cuculid (yellow-bellied cuckoo)			Americas
Trichomonas corvus		Passeriformes: corvid (eastern American crow)			North America
Trichomonas costulata [+RF+AF]+costula		Isoptera: kalotermitid (termite *Cryptotermes havilandi*)	hindgut		India, Brazil
Trichomonas cryptonucleata		Rodentia: sciurid (woodchuck)			North America
Trichomonas cynomysi		Rodentia: sciurid (prairie-dog)			North America
Trichomonas digranula		Rodentia: sciurid (woodchuck)			North America
Trichomonas duboscqui		Anura: discoglossid (painted frog)			Europe
Trichomonas equibuccalis [+AF]	6-9 x 6	Perissodactyla: equid (horse, donkey)	mouth	non-pathogenic	worldwide
Trichomonas flagelliphora		Rodentia: caviid (guinea pig)			
Trichomonas frugivori		Rodentia: murid (black rat)			India
Trichomonas fulicae		Gruiformes: rallid (American coot)			Americas
Trichomonas gallinae	covered in separate section				
Trichomonas gigantea		Isoptera: archotermopsid (termite, *Porotermes adamsoni*)	hindgut		Australia
Trichomonas hegneri		Galliformes: tetraonid (European partridge), phasianid (California quail)			Europe, North America
Trichomonas hoarei		Pelecaniformes: phalacrocoracid (cormorant)			Africa
Trichomonas holmgreni		Isoptera: kalotermitid (termite *Neotermes holmgreni*)	hindgut		Central America
Trichomonas iowensis		Caprimulgiformes: caprimulgid			Americas

		(night hawk)			
Trichomonas labella		Isoptera: termitid (termite *Microtermes hispaniolae*)	hindgut		Central America
Trichomonas lacertae		Sauria: scincid (golden skink), xantusiid (desert night lizard), agamid (starred agama), lacertid (land lizard, wall lizard, green lizard), iguanid (crested desert lizard, chuckawalla lizard, brush lizard, zebra-tailed lizard, collared lizard, horned lizard, sand lizard)			Eurasia, Africa, Americas
Trichomonas lanceolata		Caprimulgiformes: caprimulgid (nacunda nightjar)			Africa
Trichomonas landei		Charadriiformes: scolopacid (sanderling)			North America
Trichomonas lavieri		Rodentia: cricetid (pine vole)			North America
Trichomonas leucuri		Rodentia: hystricid (Indian crested porcupine)	caecum		India
Trichomonas lighti		Isoptera: termitid (termites *Amitermes minimus, emersoni, silvestrianus, coachellae, wheeleri*)	hindgut		North America
Trichomonas limacis		Gastropoda: limacid (land snail)			Europe
Trichomonas linearis		Isoptera: termitid (termite *Orthognathotermes wheeleri*)	hindgut		Americas
Trichomonas mabuiae		Sauria: scincid (golden skink)			Asia
Trichomonas macropi		Diprotodontia: macropodid (kangaroo, rock kangaroo, Woodward wallaroo, black-faced kangaroo, great grey kangaroo, black tree kangaroo)			Australia
Trichomonas macrostoma		Isoptera: hodotermitid (termite *Hodotermes mossambicus*)	hindgut		Africa
Trichomonas megastoma		Rodentia: erethiozontid (hairy tree porcupine)			Americas
Trichomonas muris		Rodentia: murid (house mouse, wood mouse, brown rat), sciurid (ground squirrel, thirteen-striped ground squirrel), cricetid (bank vole, field mouse, white-footed mouse)			Americas, Eurasia
Trichomonas mystromyis		Rodentia: murid (white-tailed rat)			Europe
Trichomonas ninaekohlyakimovi		Clitellata: hirudinid (leech)			Europe
Trichomonas ortyxis		Galliformes: tetraonid (European partridge), phasianid (valley quail)			Europe, North America
Trichomonas oti		Strigiformes: strigid (screech owl)			Americas
Trichomonas parva		Rodentia: murid (brown rat, house mouse)			Europe
Trichomonas phasiani		Galliformes: phasianid (ring-necked pheasant, bobwhite quail)	intestines	diarrhoea, dehydration	Europe
Trichomonas pisobiae		Charadriiformes: scolopacid (least sandpiper, pectoral sandpiper, semipalmated sandpiper)			North America
Trichomonas porzanae		Gruiformes: rallid (sora rail)			North

					America
Trichomonas sanguisugae		Clitellata: hirudinid (horse leech)			Europe
Trichomonas sigalasi		Charadriiformes: scolopacid (dunlin)			Holarctic
Trichomonas singhii		Rodentia: murid (gerbil)			India
Trichomonas tapiri		Perissodactyla: tapirid (tapir)			Americas
Trichomonas tatusi		Edentata: dasypodid (nine-banded armadillo)			Americas
Trichomonas tenax (syn. *Trichomonas buccalis*) [-RF+AF]	4-16 x 2-15	Primates: hominid (human), rarely Carnivora: canid (dog), plus experimental infection in Primates: cercopithecid (macaques); Carnivora: felid (cat), Rodentia: murid (mice)	oral cavity, submaxillary glands (atypically respiratory tract)	periodontal disease, pleural empyema	worldwide
Trichomonas termitidis (possibly *Trichomonoides trypanoides*)		Isoptera: rhinotermitid (termites *Rhinotermes, Schedorhinotermes*)	hindgut		
Trichomonas termopsidis [+AF]	11-55 x 7-29	Isoptera: archotermopsid (termites *Zootermopsis angusticollis, nevadensis, laticeps*)	hindgut		North America
Trichomonas tritonis		Urodela: salamandrid (marbled newt)			Europe
Trichomonas vaginalis	covered in separate section				
Trichomonas vermiformis		Isoptera: hodotermitid (termite *Anacanthotermes murgabicus*)	hindgut		Africa
Trichomonas vitali		Anura: bufonid (cane toad)			Americas
Trichomonas wenrichi		Rodentia: sciurid (woodchuck)			North America
Trichomonas sp.		Perciformes: sparid (salema porgy)	intestines		Europe
Trichomitopsis [5F(=4A+R)+RF+BC+UM+A]					
Trichomitopsis termitis (syn. *Trichomonas termitis*)	30-83 x 15-64	Isoptera: archotermopsid (termite *Archotermopsis wroughtoni*)	hindgut		India
Tetratrichomonas (possible syn. *Trichomonoides*) [5F(=4A+R)+RF] (pseudocyst formation)					
Tetratrichomonas anatis (syn. *Trichomonas*)	13-27 x 8-18	Anseriformes: anatid (ducks)	posterior intestines	non-pathogenic	worldwide
Tetratrichomonas anseris (syn. *Trichomonas*)	8-14 x 4-7	Anseriformes: anatid (goose)	caecum	non-pathogenic	worldwide
Tetratrichomonas brumpti (syn. *Trichomonas*)		Testudines: testudinid (Ceylon terrapin, radiated tortoise, African spurred tortoise, Chaco tortoise)	digestive tract	non-pathogenic	Eurasia, Africa
Tetratrichomonas buttreyi		Artiodactyla: suid (pig)	large intestines	non-pathogenic	Europe
Tetratrichomonas canistomae (syn. *Trichomonas*)	7-12 x 3-4	Carnivora: canid (dog)	oral cavity	non-pathogenic	North America, Europe
Tetratrichomonas didelphidis (syn. *Trichomonas*)	5-11 x 3-9	Didelphimorpha: didelphid (opossum)	intestines	non-pathogenic	Americas
Tetratrichomonas felistomae (syn. *Trichomonas*)	6-11 x 3-4	Carnivora: felid (cat)	oral cavity	non-pathogenic	North America
Tetratrichomonas gallinarum (syn. *Trichomonas,*	6-15 x 3-10	Galliformes: phasianid (chickens, turkeys, guineafowl, quail, chukar, pheasant),	caecum, liver (atypically human	mostly asymptomatic, possibly	worldwide

Trichomonas pullorum) [+RF+AF]		Anseriformes: anatid (ducks, geese), plus experimental subcutaneous assays in Rodentia: murid (mice), atypical infection in Primates: hominid (human)	respiratory tract)	typhlo-hepatitis	
Tetratrichomonas macacovaginae (syn. *Trichomonas*)		Primates: cercopithecid (rhesus monkey)	vagina		Asia
Tetratrichomonas microti (syn. *Trichomonas*)	4-9	Rodentia: murid (rats, mice), cricetid (hamsters, voles)	large intestines	non-pathogenic	worldwide
Tetratrichomonas ovis (syn. *Trichomonas, Ditrichomonas ovis*) [+RF+AF]	6-9 x 4-8	Artiodactyla: bovid (sheep)	rumen, caecum	non-pathogenic	North America
Tetratrichomonas pavlovi (syn. *Trichomonas, Trichomonas bovis*)	11-12 x 6-7	Artiodactyla: bovid (cattle)	caecum	non-pathogenic	Europe
Tetratrichomonas prowazeki (syn. *Trichomonas*)		Clitellata: hirudinid (horse leech); Perciformes: sparid (sea bream); Urodela: salamandrid (giant newt, common newt, salamander, northern crested newt); Anura: discoglossid (midwife toad), leptodactylid (swamp frog), ranid (pond frogs), bufonid (toads); Crocodila: crocodylid (marsh crocodile); Serpentes: colubrid (grass snakes, garter snakes)			India, Americas, Eurasia
Pentatrichomonas [6F(=5A+R)+RF+BC]					
Pentatrichomonas alleni		Passeriformes: corvid (Himalayan crow)	alimentary tract	non-pathogenic	Himalayas
Pentatrichomonas capellae	8-14 x 4-9	Charadriiformes: charadriid (snipe)	caecum		
Pentatrichomonas centropi	7-14 x 5-12	Cuculiformes: cuculid (crow pheasant)	caecum		
Pentatrichomonas hominis (syn. *Cercomonas hominis, Monocercomonas hominis, Trichomonas intestinalis, Pentatrichomonas felis, Trichomonas felis*) [+RF+AF]	6-20 x 3-14	Primates: hominid (human), callitrichid (marmoset), cercopithecid (macaques); Artiodactyla: suid (pig), bovid (cattle, water buffalo, goat); Carnivora: canid (dog); felid (cat); Rodentia: caviid (guinea pig); Serpentes: boid (boa); Strigiformes: strigid (owl); plus experimental infections in Rodentia: murid (rats, mice), cricetid (hamster)	large intestines (atypically respiratory tract)	non-pathogenic	worldwide
Pentatrichomonas ketupae [*nomen nudum*]	7-136 x 6-11	Strigiformes: strigid (brown fish owl)	intestines	non-pathogenic	India
Pentatrichomonas lobivanellae [*nomen nudum*]	6-13 x 4-8	Charadriiformes: charadriid (red-wattled lapwing)	caecum	non-pathogenic	India
Class: **Hypotrichomonadea** (single mastigont) [4F+CLS-IKB+LUM+AC+CA]					
Order: Hypotrichomonadida (as for class)					
Family: Hypotrichomonadidae (syn. Trichomitidae) (2 genera)					
Hypotrichomonas					
Hypotrichomonas	10-35	Serpentes: boid (boa), colubrid	intestines		Americas,

acosta		(indigo snake, racers, hog-nosed snakes, rat snakes, king snakes, grass snakes, garter snakes, gopher snakes), helodermatid (beaded lizards); Testudines (turtle)			Africa
Hypotrichomonas hemidactyli		Sauria: gekkonid (house gecko)			India
Hypotrichomonas osmaniae		Sauria: varanid (monitor lizard)			India
Hypotrichomonas venkataramiahii		Sauria: varanid (monitor lizard)			India
Trichomitus [4F(=3A+R)+RF+UM+AC]					
Trichomitus batrachorum (syn *Tritrichomonas, Trichomonas, T. natricis*)	10-15	Anura: ranid (edible frog, Indian bullfrog, common frog, green frog), hylid (European tree frog), pipid (clawed frog), bufonid (natterjack toad, Asiatic toad, common toad); Urodela: ambystomatid (mole salamanders), salamandrid (salamanders, crested newts); Serpentes: colubrid (grass snakes, gopher snakes, garter snakes); Sauria: iguanid (horned lizard), lacertids (green lizards), scincid (skink lizard), gekkonid (Leschenault's leaf-toed gecko); Serpentes: colubrid (long-nosed snake); plus molecular detection in Artiodactyla: suid (pig)	intestines		worldwide
Trichomitus fecalis [+AF]	5-14 x 4-6	Primates: hominid (human), plus experimental infection in Anura (tadpoles, frogs)	faeces		North America
Trichomitus marmotae (syn. *Trichomonas*)	10-15	Rodentia: sciurid (squirrels, woodchuck)			North America
Trichomitus rotunda [+AF]	7-12 x 4-8	Artiodactyla: suid (pig)	caecum, colon	non-pathogenic	worldwide
Trichomitus trypanoides (syn. *Trichomonas trypanoides*) [+AF]	16	Isoptera: rhinotermitid (termites *Reticulitermes lucifugus, tibialis, flavipes*)	hindgut		North America
Trichomitus wenyoni (syn. *Tritrichomonas*)	4-16	Rodentia: murid (rats, mice), cricetid (hamster); Primates: cercopithecid (macaques)	large intestines	non-pathogenic	worldwide

†Coding: + = present; - = absent; #F = total number of flagella; #A = number of anterior flagella; R = recurrent flagellum; RF = recurrent flagellum extending posteriorly as free flagellum; UM = undulating membrane; LUM = lamelliform undulating membrane; RUM = rail-type undulating membrane; C = costa; AC = A-type costa; BC = B-type costa; A = axostyle; AF = axostyle protrudes posteriorly; CA = cone-like axostyle (*Trichomonas*-type); TA = tube-like axostyle (*Tritrichomonas*-type); CLS = comb-like structure; IKB = infrakinetosomal body.

Parasite morphology: Trichomonads forms motile trophic stages (trophozoites) that have multiple flagella: *Trichomonas* and *Tetratrichomonas* spp. having 4 anterior flagella plus a recurrent flagellum, and *Pentatrichomonas* having 5 (sometimes 3 or 4) anterior flagella plus a recurrent flagellum. Trophozoites usually have thin elongate pyriform bodies ranging from 5-20 µm in length (6-15 µm for *Tetratrichomonas gallinarum*, 5-16 µm for *Trichomonas tenax,* 8- 20 µm for *Pentatrichomonas hominis).* All stages contain a single prominent anterior nucleus located adjacent to a distinctive parabasal body formed by dictyosomes (Golgi complexes). The nucleus and parabasal body are associated with small dense basal bodies (kinetosomes) forming a single karyomastigont unit (ancestral unit with 4 kinetosomes). The kinetosomes give rise to the anterior tuft of flagella which projects forwards for 5-15 µm. An independent neighbouring kinetosome gives rise to the recurrent flagellum (directed posteriad) which is attached longitudinally to the cell body forming an undulating membrane. The recurrent flagellum of *Trichomonas* spp. does not extend beyond the posterior margin of the cell, while that of *Tetratrichomonas* and *Pentatrichomonas* spp. projects beyond the posterior margin as a free flagellum. The undulating membrane is lamelliform in appearance (rather than rail-like) and it is

underpinned by a slender elongate rod-like structure in the cell cytoplasm known as the costa, which is striated with a periodicity known as B-type (rather than A-type). Trophozoites swim in fluids with a distinctive wobbly jerky movement, with the undulating membrane imparting a quivering/shimmering appearance to the cell body. Trophozoites also possess a slender longitudinal hyaline rod-like structure known as an axostyle which is composed of concentric rows of microtubules forming a cone (rather than a tube). The axostyle begins near the nucleus and runs posteriorly through the cell body, protruding through the posterior end and terminating in a sharp point. The axostyle is often lined with unique membrane-bound structures known as hydrogenosomes (formerly called siderophil granules) which are anaerobic energy-producing organelles that generate molecular hydrogen (by metabolizing pyruvate to acetate and carbon dioxide producing ATP by substrate-level phosphorylation with release of hydrogen ions). Trichomonads do not form encapsulated cysts, although some cells (particularly *Tetratrichomonas* spp.) may round up and lose their flagella forming what has been called pseudocysts. Some regard these stages to be resistant transmissive forms while others consider them to simply be degenerate forms.

Site of infection: Trichomonads occur in the digestive tracts of a wide range of animals, with *Trichomonas* spp. recorded in 10 families of birds, 16 families of mammals, 6 families of reptiles, 3 families of amphibia, 5 families of termites, one leech family, and one snail family; *Tetratrichomonas* spp. in 8 mammal families, 2 bird families, 3 reptile families, 5 amphibian families, one fish family, and one leech family; and *Pentatrichomonas* spp. in 10 mammal families, 4 bird families, and one reptile family. Most species are considered to be harmless commensals in vertebrates or mutualistic symbiotes in insects. Several species, however, have tentatively been associated with clinical disease in a few hosts, including *Trichomonas tenax* and *Pentatrichomonas hominis* in humans, and *Tetratrichomonas gallinarum* in birds. Trophozoites are found within the lumina of tubular organs: *Trichomonas tenax* in the mouths of humans (between the teeth, in pus pockets, tooth cavities, tartar, tonsillar crypts), rarely in the trachea and lungs; *Pentatrichomonas hominis* in the large intestines and caecum of humans, sometimes in the stomach; and *Tetratrichomonas gallinarum* in the large intestines of poultry (chickens, turkeys, guinea fowl, quail, ducks, geese).

Pathogenesis: Most infections are asymptomatic and have not been associated with any clinical disease, even when trophozoites are present in abundance in the lumen of the digestive tract. Infections by a few species have occasionally been linked with clinical conditions involving irritation and inflammation of mucosal membranes when trophozoites contact epithelial surfaces, sometimes invading atypical locations. The species *Tetratrichomonas gallinarum* usually causes latent infections in the large intestines of poultry, but may sometimes cause lesions in the caecum and liver with microvillous atrophy, papule formation and necrotic enteritis resulting in diarrhoea with yellow frothy liquid caecal exudates. The parasite is regarded as a potential causative agent of enterohepatitis especially in turkeys, and infections are thought to aggravate other disease conditions (such as histomoniasis and typhlohepatitis in galliform birds). Infections in ducks have been associated with reduced egg production and increased mortalities in female birds. The species *Trichomonas tenax* is often reported as a harmless commensal in the mouth of humans, feeding on microorganisms and cellular debris. However, trophozoites invading the respiratory system have been associated with debilitating pulmonary diseases (bronchiectasis, abscesses, and possibly carcinomas) in individuals with poor dental hygiene, malnutrition and alcoholism. The species *Pentatrichomonas hominis* is usually regarded to be an endocommensal in the large intestines of humans, but when parasites invade the respiratory tract by aspiration or through bronchoenteral fistulas, they may cause necrotizing pulmonary abscesses and pleural effusions. Atypical infections by *Trichomonas vaginalis* and *Tritrichomonas foetus* have been recorded in the respiratory tract of patients with empyema and pulmonary diseases (such as acute respiratory distress syndrome).

Developmental cycle and mode of transmission: Trichomonads have simple monoxenous (one-host) life cycles involving the asexual multiplication of trophozoites within hosts and their transmission to new susceptible hosts by intimate contact or the ingestion of recently contaminated food or water. The parasites do not form true encapsulated cysts, and only a few species (particularly *Tetratrichomonas* spp.) form rounded nonflagellated stages (called pseudocysts) that are either degenerate forms or may be environmentally-resistant forms. Trophozoites divide by longitudinal binary fission and they do not survive for long outside of host tissues. Nonetheless, a few experimental studies have found that trophozoites expelled from hosts may survive in moist food and drinking water for several hours. Infections by *Tetratrichomonas gallinarum* are thought to be transmitted via the consumption of contaminated food and water, and experimental infections have been achieved by oral and cloacal inoculation. Trophozoites of *Trichomonas tenax* cannot survive passage through the stomach of humans, so most transmission occurs by direct oral contact, such as kissing or sharing eating/drinking utensils. Trophozoites of *Pentatrichomonas hominis* are excreted in human faecal samples thus supporting faecal-oral transmission but only involving freshly contaminated food or water. Trophozoites have recently been detected in or on filth flies suggesting the possibility of passive transport by paratenic hosts, but only within the small window of opportunity of limited trophozoites survival.

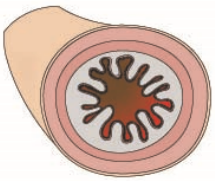
Differential diagnosis: Infections are conventionally diagnosed by the microscopic detection of trichomonads in clinical samples. Motile trophozoites may be detected in wet mounts of excretions, exudates, tissue swabs, impressions or scrapings by high-contrast bright-field, phase-contrast or interference-contrast microscopy. Live parasites move with a characteristic jerky rolling motion and the undulating membrane gives a shimmering appearance to the cell body. Trophozoites may also be detected in fixed smears following staining with Giemsa, silver, iron haematoxylin, malachite green, methylene blue, or acradine orange, but fixation often causes cells to condense or lyse. Tissue samples may also be collected at necropsy and histological sections examined for parasites

after staining with haematoxylin and eosin, Giemsa, periodic acid-Schiff or immunohistochemical stains using polyclonal or monoclonal antibodies. Trophozoites may also be cultured *in vitro* from clinical samples by anaerobic cultivation in axenic or monoxenic liquid/semiliquid media, such as Diamond's medium or InPouch TF media culture kits. Some trichomonad species have also been grown on cell lines maintained in tissue cultures: e.g. *Tetratrichomonas gallinarum* grows on monkey kidney cells, chicken liver (LMH) cells or quail (QT35) fibroblasts. Enzyme immunoassays have been developed to detect specific host antibodies against *Tetratrichomonas gallinarum* in poultry, and modern molecular biological techniques have been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (large and small subunit ribosomal RNA and internal transcribed spacers 1 and 2). Molecular characterization has led to the recognition of 5 groups (A-E) and 11 subgroups (A1, A2, B1, B2, B3, C1, C2, C3, D1, D2, E) amongst *Tetratrichomonas gallinarum* isolates.

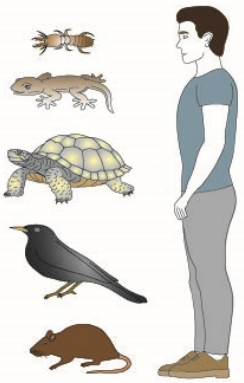
Treatment and control: Clinical infections have generally responded well to chemotherapy using nitroimidazole drugs (metronidazole, dimetridazole), although their application may cause some adverse side-effects and there are growing concerns about the emergence of drug-resistant strains of parasites. Preventive measures designed to minimize contamination and reduce the risk of transmission basically involves regular health monitoring, quarantine, strict hygiene and sanitation, water treatment, food hygiene, and good husbandry (maintaining nutrition and avoiding stressors). Management practices in commercial poultry production should include regularly changing feed and water, cleaning containers and drying fomites in holding facilities, separating cohorts without co-mingling, and avoiding stressors (such as over-crowding, poor nutrition and concomitant infections). In humans, better oral hygiene is recommended to control the spread of *Trichomonas tenax*, and proper sanitation, water treatment and good food hygiene should be employed to prevent the faecal-oral transmission of *Pentatrichomonas hominis.*

Pentatrichomonas (6 flagella)*
Tetratrichomonas (5 flagella)*
Trichomitopsis (5 flagella)*
Trichomonas (5 flagella)*
Trichomitus (4 flagella)*

*one flagellum recurrent and
forming undulating membrane



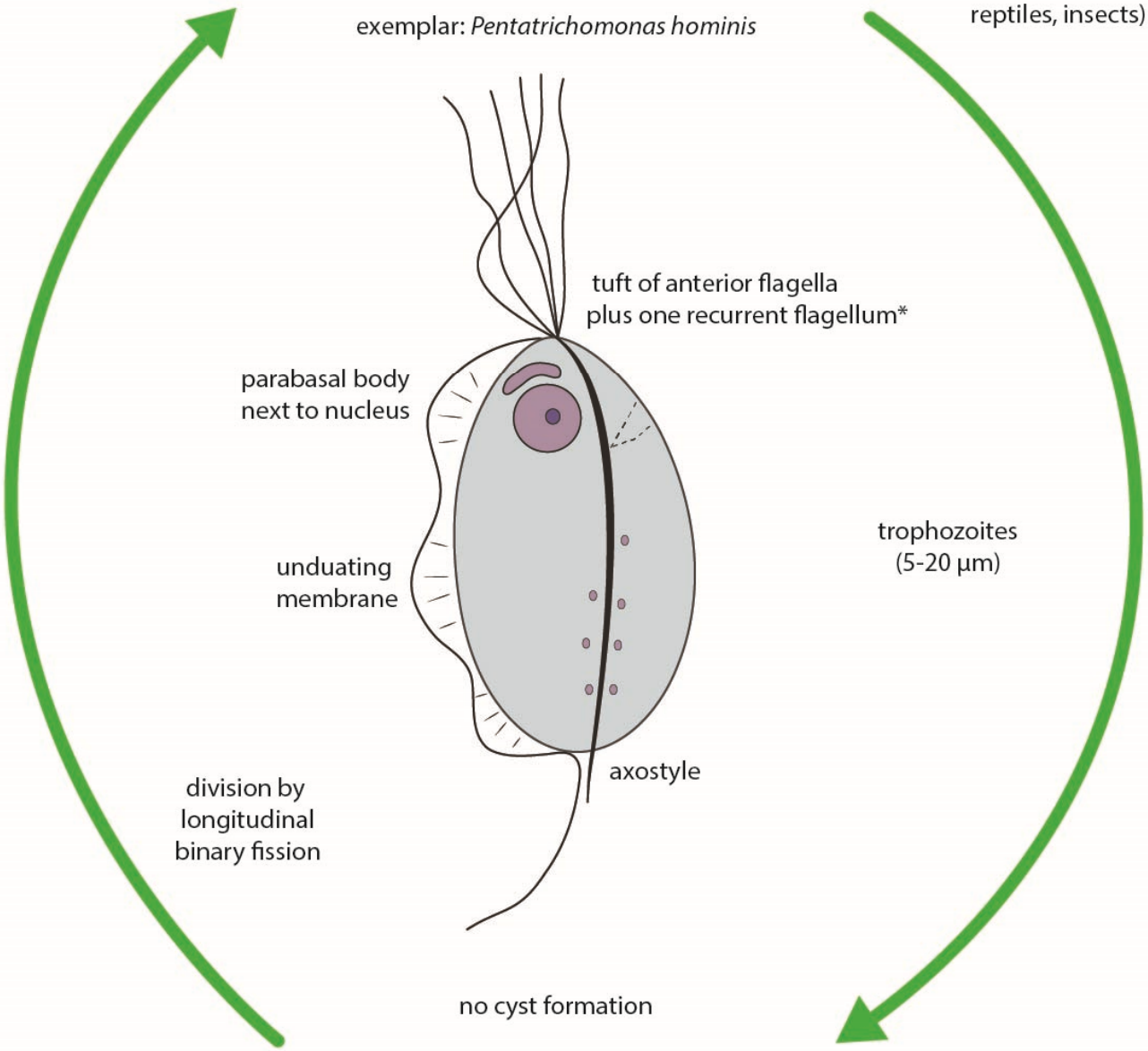
alimentary tract
(rare gut pertubations)



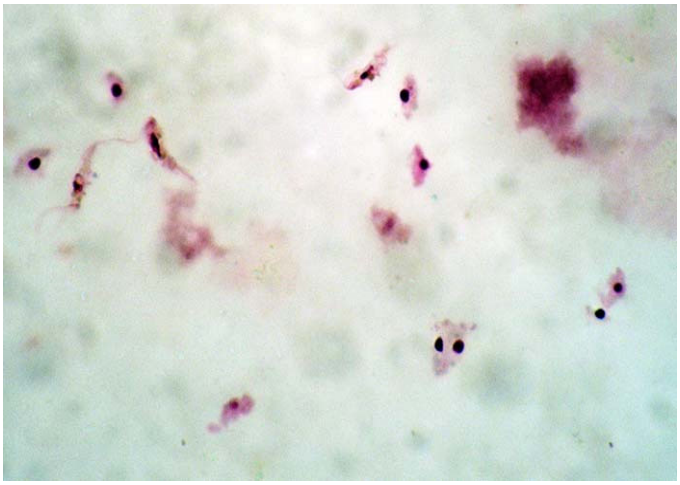
Hosts
(mammals, birds,
reptiles, insects)

most species not associated with disease
(often considered to be endocommensals)

exemplar: *Pentatrichomonas hominis*



direct transmission by transfer of trophozoites
during close contact (courtship, grooming, allo-feeding)
or possibly via contaminated fomites



Trichomonas trophozoites from termite hindgut



Trichomonas trophozoite from snake gut

Tritrichomonas foetus
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Parabasalid flagellates are anaerobic amitochondriate protists which have distinctive parabasal bodies (dictyosomes) adjacent to flagellar basal bodies (kinetosomes) and an axostyle-pelta complex providing structural support. Trichomonads are a major constituent group and most have 4-6 apical flagella, one being recurrent and often forming an undulating membrane supported by a costa. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Many *Trichomonas* spp. have been reassigned to different genera based on the number of free anterior flagella e.g. *Tritrichomonas*, *Tetratrichomonas* and *Pentatrichomonas* having 3, 4 and 5 anterior flagella respectively. Recent studies have reassigned *Tritrichomonas* spp. to a novel class based on ultrastructural features and genotypic differences. The species *Tritrichomonas foetus* has variously been associated with bovine abortion and infertility, chronic diarrhoea in cats and subclinical infections in pigs.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Metamonad (amitochondriate flagellates with karyomastigonts)
Phylum: Parabasalia (anaerobic flagellates with parabasal body supporting Golgi cisternae or dictyosome, trichomonads, hypermastigids, retortamonads)
Class: Tritrichomonadea (single mastigont, comb-like structure, infrakinetosomal body)
Order: Tritrichomonadida (variable possession of undulating membrane and costa)
Family: Tritrichomonadidae (4-5 flagella, rail-type undulating membrane, A-type costa, tube-like axostyle)
Genus: *Tritrichomonas* (parasites/commensals in tubular organs of vertebrates)
Species: *T. foetus* (causes abortion and infertility in cattle)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae	*Trichomonas*	vertebrates	direct (f-o, v)

		(stout axostyle, costa, undulating membrane)		(urogenital tract, gut)	
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Metamonads are a group of excavates (with ventral feeding groove) that have several subcellular elements associated with their flagella forming a unique mastigont (an ultrastructural complex of organelles and cytoskeletal fibrils (incl. dictyosomes (Golgi bodies), centrioles (basal bodies) and a microtubular axostyle)). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Most metamonads are amitochondriate but have retained reduced organelles of mitochondrial origin (fornicates containing mitosomes while parabasalians possess hydrogenosomes). Members of the phylum Parabasalia typically possess parabasal bodies adjacent to Golgi bodies (dictyosomes), and have microtubular arrays forming a conspicuous pelta-axostyle complex (cap-like pelta and a cone- or tube-like longitudinal axostyle). Six parabasalid classes are currently recognized on the basis of morphological, biological and molecular phylogenetic studies. Cells in three classes (Trichomonadea, Tritrichomonadea, Hypotrichomonadea) bear single mastigonts (set of kinetosomes (basal bodies) and associated appendages – ancestral unit comprising 4 kinetosomes) with flagella arranged in an anterior tuft, but many have one recurrent flagellum forming an undulating membrane (lamelliform or rail-type) supported by a costa (A- or B-type) and sometimes a basal comb-like structure and/or infrakinetosomal body. Many species are symbiotic (mutualists, commensals or parasites) in animals, although some are free-living in moist habitats. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Cells in another three classes (Cristamonadea, Trichonymphea, Spirotrichonymphea) have more complex structures, often with multiple mastigonts bearing hundreds to thousands of flagella. Most were previously assigned to the now-defunct group Hypermastigida and they are primarily found as symbionts (mutualists) in insects (mostly termites).

Trichomonad taxonomy can be very confusing as many *Trichomonas* spp. have now been reassigned to sister genera based on the number of anterior flagella e.g. *Tritrichomonas*, *Tetratrichomonas* and *Pentatrichomonas* having 3, 4 and 5 anterior flagella respectively. Confusingly, the name *Trichomonas* has been retained for some species with 4 anterior flagella (mainly those in man, some rodents and birds). Recent ultrastructural and molecular biological studies have also led to the placement of the genus *Tritrichomonas* into a separate class (Tritrichomonadea) as the cells contain unique comb-like structures and infrakinetosomal bodies at the bases of their recurrent flagella (both lacking in members of the class Trichomonadea). Several genera (*Hypotrichomonas* and *Trichomitus*) were assigned to another class (Hypotrichomonadea) as their cells contained comb-like structures but lacked infrakinetosomal bodies.

Family	**Key characters to 'trichomonad' families in vertebrates***						**Representative genera**
	Number of flagella	**Undulating membrane**	**Costa**	**Axostyle**	**Comb-like structure**	**Infra-kinetosomal body**	

Class Tritrichomonadea (uninucleate to binucleate)							
Order Tritrichomonadida (endobiotic in vertebrates (mammals, birds, reptiles, amphibia, fish))							
Tritrichomonadidae	4-5	rail-type	A-type	tube-like	present	present	*Tritrichomonas*
Simplicimonidae	4	absent	absent	tube-like	present	present	*Simplicimonas*
Monocercomonidae	4	absent	absent	cone-like	present	present	*Monocercomonas*
Dientamoebidae	0-4	absent	absent	cone-like	absent	absent	*Dientamoeba, Histomonas*
Class Trichomonadea (single karyomastigont)							
Order Trichomonadida (with costa) (endobiotic in vertebrates (mammals, birds, reptiles, amphibia) and invertebrates)							
Trichomonadidae	5-6	lamelliform	B-type	cone-like	absent	absent	*Cochlosoma, Trichomonas, Trichomitopsis, Tetratrichomonas, Pentatrichomonas*
Order Honigbergiellida (without costa) (endobiotic in vertebrates (mammals, reptiles, amphibia))							
Hexamastigidae	5-6	absent	absent	cone-like	absent	absent	*Hexamastix*
Class Hypotrichomonadea (single karyomastigont)							
Order Hypotrichomonadida (endobiotic in vertebrates (reptiles, amphibia, mammals) and invertebrates)							
Hypotrichomonidae	4	lamelliform	A-type	cone-like	present	absent	*Trichomitus, Hypotrichomonas*

*Taxa found exclusively in invertebrate hosts (such as termites and cockroaches) are not listed.

Trichomonads (*sensu latu* = in the broadest sense) usually exhibit strong site specificity (tissue tropism) and occur in the alimentary, urogenital or respiratory tracts of their hosts, where they may cause very different types of disease. Several specialized species living in the urogenital tracts of vertebrates may cause severe inflammatory diseases, with *Trichomonas vaginalis* causing vaginitis in humans, and *Tritrichomonas foetus* causing bovine infertility. A few species living in the upper respiratory and alimentary tracts of birds may cause life-threatening diseases, including *Trichomonas gallinae* causing canker in birds. In contrast, those inhabiting the intestinal tracts of vertebrate and invertebrate hosts are often considered to be symbiotes or commensals (rather than parasites) as most infections appear benign. Rather than try to cover trichomonad biodiversity and their disparate clinical significance in one comprehensive section, it has been elected to showcase representatives in 4 separate sections, targeting:

- urogenital infections by *Tritrichomas foetus* in cattle;
- urogenital infections by *Trichomonas vaginalis* in humans;
- oral infections by *Trichomonas gallinae* in birds; and
- enteric infections by *Trichomonas, Tetratrichomonas* and *Pentatrichomonas* spp. in a wide range of hosts.

The genus *Tritrichomonas* was separated from other trichomonads initially on the basis of ultrastructural studies, notably involving the possession of different undulating membranes (rail-type), costae (A-type), axostyles (tube-like) and the presence of comb-like structures and infrakinetosomal bodies. Molecular characterization studies, however, revealed that many of these characters were not apomorphic but plesiomorphic, with many related taxa varying considerably in their structural complexity, and often demonstrating reductive evolution by lacking (or having lost) various features. The novel class Tritrichomonadea was erected to accommodate a diverse range of cells with 1-2 nuclei and 0-5 flagella but otherwise varying in their possession of various cytoskeletal, membranous and cytoplasmic elements. The order Tritrichomonadida contains 4 families: one family with 'trichomonad' features (Tritrichomonadidae (genus *Tritrichomonas*) with uninucleate cells, 4-5 flagella, rail-type undulating membranes, A-type costae, tube-like axostyles); and 3 families with greatly simplified structures (Dientamoebidae syn. Protrichomonadinae (4 genera: *Dientamoeba, Histomonas, Parahistomonas, Protrichomonas*) with uni- to bi-nucleate cells, 0-4 flagella, cone-like axostyles (if present), but lacking undulating membranes, costae, comb-like structures and infrakinetosomal bodies; Monocercomonadidae (one genus *Monocercomonas*) with uninucleate cells, 4 flagella, marginal plates, cone-like axostyles, but lacking undulating membranes and costae; and Simplicimonadidae (one genus *Simplicimonas*) with uninucleate cells, 4 flagella, marginal plates, tube-like axostyles, but lacking undulating membranes and costae). Most cognate species have been recorded as symbiotes (mutualists, commensals or parasites) of insects, but a few species infect vertebrate hosts, including humans and domestic animals.

Around 16 *Tritrichomonas* spp. have been found in the alimentary tracts of their mammalian, avian or amphibian hosts, but one species, *Tritrichomonas foetus,* also occurs in the urogenital tract of cattle. Infections by *Tritrichomonas foetus* are of considerable veterinary importance as they are responsible for serious economic losses in many cattle breeding areas throughout the world by causing reproductive failure. However, recent molecular phylogenetic studies have cast doubt on the host specificity, site of infection and pathogenicity of *Tritrichomonas foetus*. Genetic characterization studies have detected almost identical genotypes in other tissues and organs of non-bovine hosts: notably, the digestive tracts of diarrhoeic cats and dogs and asymptomatic pigs. Isolates identified as *Tritrichomonas suis* from the digestive tracts of pigs have been shown to be genetically similar to

Tritrichomonas foetus isolates from the urogenital tracts of cattle by random amplified polymorphic DNA (RAPD) and restriction fragment length polymorphism (RFLP) analyses as well as by sequencing at 11 loci covering ribosomal RNA (rRNA), including internal transcribed spacer regions 1 and 2, cysteine proteases (CP) 1, 2, 4, 5, 6, 7 and 9 and malate dehydrogenase 1, although small differences were evident at two other loci (CP8 and elongation factor 1-alpha (EF-1α)). On the basis of their genetic similarities, many authors now consider these species to be synonymous. In addition, other studies have shown isolates from diarrhoeic cats to be genetically similar to *Tritrichomonas foetus* isolates from cattle at 11 loci covering internal transcribed spacer region 2 of rRNA, EF-1α, CP 1, 2, 4, 5, 6, 7, 8 and 9, and malate dehydrogenase 1 (MDH1). It was initially suggested the cat isolates be named *Tritrichomonas blagburni* but some consider there were not enough differences for speciation from *Tritrichomonas foetus*. Information on the resultant *Tritrichomonas foetus* complex has therefore been partitioned into three groups corresponding to symptomatic urogenital infections in cattle, symptomatic intestinal infections in cats and asymptomatic intestinal infections in pigs.

Parasite species†	**Size (µm)**	**Vertebrate Hosts**	**Location**	**Clinical signs**	**Distribution**
Class: **Tritrichomonadea** (uninucleate to binucleate) [0-5F+RUM+AC+CLS+IKB+CA/TA]					
Order: Tritrichomonadida (as for class)					
Family: Tritrichomonadidae (uninucleate, suprakinetosomal body present) [4-5F+TA] (1 genus)					
Tritrichomonas [4F(=3A+R)+RF+AC]					
Tritrichomonas foetus (syn. *Trichomonas foetus*) complex					
Tritrichomonas foetus (cattle isolates) [+AF]	8-25 x 3-15	Artiodactyla: bovid (cattle), rarely cervid (roe deer), camelid (camel); Perissodactyla: equid (horse), plus experimental infection in Rodentia: murid (mice, rats), caviid (guinea pigs); Lagomorpha: leporid (rabbit); Carnivora: canid (dog), felid (cat); Artiodactyla: bovid (goat, sheep), suid (pig): Primates: cercopithecid (macaques); Aves: Galliformes (chickens, turkeys); atypical infection in Primates: hominid (human)	uterus, prepuce (atypically human respiratory tract)	vaginitis, abortion, infertility	worldwide
Tritrichomonas foetus (syn. *Tritrichomonas blagburni*) (cat isolates) [+AF]	10-25 x 3-15	Carnivora: felid (cat), canid (dog), plus paratenic transport in Mollusca: gastropod (slugs)	ileum, caecum, colon	diarrhoea	Europe, North America, Australia, Asia
Tritrichomonas foetus (syn. *Tritrichomonas suis, Trichomonas suis*) (pig isolates) [+AF]	9-16 x 2-6	Artiodactyla: suid (pig), plus experimental infection in bovid (cattle)	nasal cavity, stomach, caecum, colon	non-pathogenic (but has induced abortion experimentally in pigs)	worldwide
other *Tritrichomonas* species					
Tritrichomonas augusta (syn. *Trichomonas*)		Urodela: cryptobranchid (hell-bender), salamandrid (giant newt, common newt, spotted salamander), ambystomid (marbled salamander, tiger salamander), plethodontid (red-backed salamander, slimy salamander, dusky salamander); Anura: bufonid (Fowler's toad), pelobatid (spadefoot frog), ranid (bullfrog, southern leopard frog, leopard frog, yellow-legged frog, Pacific coast frog), hylid (tree frog, swamp tree frog)	intestines		worldwide
Tritrichomonas beckeri	4-8 x 2-5	Cuculiformes: cuculid (yellow-billed cuckoo)	large intestines	non-pathogenic	Americas
Tritrichomonas caviae (syn. *Trichomonas*)	10-22	Rodentia: caviid (guinea pig)	caecum, colon	non-pathogenic	worldwide

Tritrichomonas eberthi (syn. *Trichomonas eberthi*) [+AF]	8-14 x 4-7	Galliformes: phasianid (chickens, turkeys); Anseriformes: anatid (ducks)	caecum	non-pathogenic	worldwide
Tritrichomonas enteris	6-12 x 5-6	Artiodactyla: bovid (cattle)	colon	non-pathogenic	Europe, India
Tritrichomonas equi (syn. *Trichomonas faecalis, equi*)	10-11 x 5-6	Perissodactyla: equid (horse, donkey)	caecum, colon	diarrhoea, colitis	worldwide
Tritrichomonas floridanae (syn. *Trichomonas*)	7-12 x 3-7	Galliformes: tetraonid (partridge), phasianid (valley quail, bobwhite quail, California quail)	caecum	non-pathogenic	North America
Tritrichomonas gigantica	7-22 x 3-10	Galliformes: phasianid (quail)	caecum	non-pathogenic	nr
Tritrichomonas indica [*nomen nudum*]	9-18 x 5-14	Galliformes: phasianid (black-breasted quail)	caecum	non-pathogenic	India
Tritrichomonas minuta (syn. *Trichomonas*)	4-9	Rodentia: murid (rats, mice), cricetid (hamster)	large intestines	non-pathogenic	worldwide
Tritrichomonas mobilensis	7-11 x 1-3	Primates: cebid (squirrel monkey)	large intestines	non-pathogenic	widespread in laboratory colonies
Tritrichomonas muris (syn. *Trichomonas criceti*)	12-20	Rodentia: murid (rats, mice), cricetid (voles, hamster)	large intestines	non-pathogenic	worldwide
Tritrichomonas nonconforma		Sauria: dactyloid (anoles)	cloaca		Cuba
Tritrichomonas pondicerianae [*nomen nudum*]	9-17 x 8-13	Galliformes: phasianid (grey partridge)	caecum	non-pathogenic	India
Tritrichomonas rotunda		Artiodactyla: suid (pig)	large intestines	non-pathogenic	Europe
Tritrichomonas simhii		Anura: ranid (pond frog)			India

†Coding: + = present; - = absent; #F = total number of flagella; #A = number of anterior flagella; R = recurrent flagellum; RF = recurrent flagellum extending posteriorly as free flagellum; RUM = rail-type undulating membrane; AC = A-type costa; AF = axostyle protrudes posteriorly; CA = cone-like axostyle (*Trichomonas*-type); TA = tube-like axostyle (*Tritrichomonas*-type); CLS = comb-like structure; IKB = infrakinetosomal body.

Parasite morphology: *Tritrichomonas foetus* forms motile trophic developmental stages known as trophozoites which are multi-flagellated. The parasites do not form true encapsulated cysts, but under unfavourable growth conditions, some cells can round up and lose their flagella. It has been suggested that these stages may be 'pseudocysts', but most workers consider them to be degenerate forms as none have been observed to give rise to normal motile forms. Trophozoites have spindle-pyriform bodies ranging from 8-25 μm in length by 3-15 μm in width depending on their state of nutrition. Those cultured in the presence of abundant food become rotund, while those cultured in less favourable conditions become thin and spatulate. All intact stages are uninucleate with a prominent anterior ovoid nucleus located adjacent to a distinctive sausage-shaped parabasal body formed by dictyosomes (Golgi complexes). The nucleus and parabasal body are associated with small dense basal bodies (kinetosomes) forming a single karyomastigont unit (ancestral unit with 4 kinetosomes). The kinetosomes give rise to 3 flagella which project forwards forming an anterior tuft some 8-15 μm in length. In *Tritrichomonas foetus*, the fourth kinetosome gives rise to a recurrent flagellum (directed posteriad) that is attached longitudinally to the cell body forming an undulating membrane. The recurrent flagellum runs the whole length of the body and extends beyond the posterior margin as a free flagellum. The undulating membrane is rail-like in appearance (rather than lamelliform) and it is underpinned by a slender elongate rod-like structure in the cell cytoplasm known as the costa, which is striated with a periodicity known as A-type (rather than B-type). Functional flagella impart motion and free cells typically exhibit a forward spiralling motion, with the undulating membrane imparting a quivering/shimmering appearance to the cell body. Trophozoites also possess a slender longitudinal hyaline rod-like structure known as an axostyle which is composed of concentric rows of microtubules forming a tube (rather than a cone). The axostyle begins near the nucleus and runs posteriorly through the cell body, protruding through the posterior end and terminating in a sharp point. Tritrichomonads also possess a unique comb-like structure and infrakinetosomal body (both structures lacking in typical trichomonads). Tritrichomonads (like all trichomonads) are anaerobic and do not have mitochondria, but rather possess membrane-bound organelles known as hydrogenosomes (formerly called siderophil granules) that are located along the axostyle, appearing as a 'chromatic ring' under the light microscope and as osmiophilic granules under the transmission electron microscope. Hydrogenosomes are energy-producing organelles that generate molecular hydrogen (by metabolizing pyruvate to acetate and carbon dioxide producing ATP by substrate-level phosphorylation with release of hydrogen ions).

Site of infection: *Tritrichomonas foetus* has been recorded primarily in the urogenital tract of cattle, but may also occur in the alimentary tracts of cats and pigs. In cattle, trophozoites are usually found in cows in the vagina, although they may colonize the

surface of the entire genital system (vagina, cervix, endometrium, oviducts) and even migrate to the uterus. Parasites may be found in the preputial cavity of bulls on the surface of the stratified squamous epithelium of the penis and proximal foreskin, although some infections may extend to the seminal vesicles, epididymis and testes. In cats, trophozoites occur in the mucosal lining of the ileum, caecum, colon and rectum (especially on the surface of the colon and in colonic crypts), and rarely in the urogenital tract. In pigs, parasites have been detected in the nasal cavities, stomach and intestines. Other *Tritrichomonas* spp. have been described from the alimentary tracts of rodents (rats, mice, hamsters, guinea pigs, voles), equids (horse, donkey), primates (squirrel monkey) as well as some birds (cuckoos, chickens, turkeys, partridge, quail, ducks), lizards (anoles), and amphibians (newts, salamanders, toads and frogs).

Pathogenesis: Infections by members of the *Tritrichomonas foetus* complex have been associated with symptomatic urogenital infections in cattle, symptomatic intestinal infections in cats and asymptomatic intestinal infections in pigs (infections in different host species are thought to be due to different parasite genotypes). Trophozoites lack cytostomes but capture food through the cell surface by pinocytosis and phagocytosis resulting in the accumulation of cytoplasmic food vacuoles of variable sizes. The parasites feed on solutes and particulate material (including bacteria) within the lumina of tubular organs or in contact with mucosal surfaces. While light infections may remain asymptomatic or subclinical, the presence of growing numbers of parasites may cause significant tissue irritation and inflammation with attendant pathologies.

Infections in cattle by *Tritrichomonas foetus* s.s. are of considerable veterinary importance as they cause bovine tritrichomoniasis, a sexually transmitted disease, resulting in serious economic losses mainly in extensively-managed herds due to reproductive failure (abortion, endometritis and infertility). Cows recently infected may develop mild vaginitis, cervicitis or endometritis, with few overt clinical signs other than mucopurulent vaginal discharges. Most infections are self-limiting and parasites are cleared from the vagina and uterus of non-pregnant heifers after 6-16 weeks, but hosts do not develop any long-lasting immunity. In pregnant cows, infections do not interfere with fertilization, implantation or early foetal development, but they can result in foetuses being lost early in gestation with resorption or abortion (typically around 2-3 months, rarely 4). Abortions may be missed by producers who think that the cows simply had not conceived. Most cows recover but some may retain foetal material which becomes macerated or mummified leading to pyometra, chronic endometritis and temporary infertility. A few cows may remain infected throughout pregnancy and into the following breeding season, but such carrier cows are rare. Disease is typically associated with lowered fertility in infected herds, with poor pregnancy rates, many services per conception, long calving intervals, extended calving periods, calf crop reduction, and wide variation in weaning weights. The severity of disease has been found to depend on differences in parasite virulence (strain variation), the intensity of infection, the mechanical action of parasites on mucosal surfaces, their feeding activities involving the secretion of enzymes, pinocytosis and phagocytosis, host susceptibility and the extent of changes to the intrauterine environment. Infections in bulls usually do not cause any clinical signs of disease, although some animals develop inflammation of the penis (balanitis) with small nodules and preputial discharges. Infections often become chronic and bulls may act as asymptomatic carriers for years. This presents a problem for artificial insemination programs, because most techniques used to cryopreserve flagellated sperm also cryopreserve flagellated trophozoites. Risk factors for infection include age (infections accumulate in bulls > 4 years old), herd size (higher prevalence in larger herds), high bull:cow ratios (more sexual contacts), multiple bulls in service (more cross-infections), cohort co-mingling (more transmission) and breed susceptibility (higher prevalence in *Bos taurus* (esp. Angus, Charolais, Hereford and Simmental breeds) than in *Bos indicus* or hybrids).

Infections in cats by *Tritrichomonas foetus* s.l. (syn. *T. blagburni*) have been associated with lymphocytic and plasmacytic inflammation of the colon resulting in colitis (large bowel diarrhoea) with increased frequency of defaecation of semi-formed to liquid faeces sometimes containing fresh blood or mucus. Faeces are often yellow-green in colour, gassy and malodourous. The diarrhoea may be chronic or intermittent and may range from mild to intractable. Animals may also exhibit faecal incontinence, tenesmus, flatulence, abdominal pain, anal irritation, and sometimes systemic signs such as anorexia, vomiting, depression and weight loss. The course of infection waxes and wanes over several weeks but may persist for 5-24 months. Most cats go into clinical remission but still act as asymptomatic carriers, while some may relapse for short periods with worse diarrhoea. Risk factors include age (mainly a disease of kittens and young cats < 12 months of age), breed (pedigree cats, particularly Siamese and Bengal), population density (catteries, cat shelters, breeding centres), attendance at cat shows, and concurrent enteric infections. Infections in pigs by *Tritrichomonas foetus* s.l. (syn. *T. suis*) are asymptomatic with the organisms essentially considered to be harmless endocommensals.

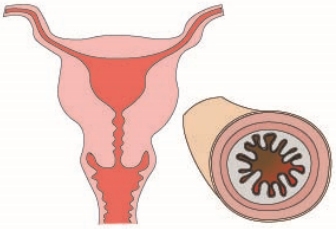
Developmental cycle and mode of transmission: Tritrichomonads have simple life-cycles involving the asexual multiplication of trophozoites in host organs and their transmission to new susceptible hosts by direct contact. They do not form environmentally-resistant cysts and the trophozoites do not survive for long outside of hosts in aerobic conditions. The trophozoites of some species do round up and lose their flagella forming stages known as pseudocysts, but it has not been established whether they are resistant or degenerate forms. Trophozoites multiply by longitudinal binary fission in which the nuclear membrane persists during division (type of mitosis known as cryptopleuromitosis). Parasites may rapidly form large populations by exponential (binary) growth when conditions are optimal. Infections in cattle are transmitted sexually mainly by natural mating (coitus), but sometimes mechanically during artificial insemination or vaginal examination. While parasites may survive semen cryopreservation (especially if samples are contaminated with preputial fluids), transmission via artificial insemination is rare. Bulls are the primary reservoirs for infection and

may be long-term (even life-long) carriers. Cows become immune to re-infection, at least for the breeding season in which they were infected. Infections in cats are spread by direct contact (licking, grooming, nursing) and by faecal-oral transmission when shared litterboxes allow parasites from faeces to be transferred to the paws and fur of other cats to be ingested during grooming. Trophozoites have been found to live in wet cat faeces for 3 days and in contaminated cat food for 5 days. Experimental studies have also shown that terrestrial slugs (leopard and yellow cellar slugs) fed on spiked cat food shed viable trophozoites in their faeces and thus may act as paratenic hosts for the dispersal of cat isolates. The prepatent period for infections in cats ranged from 2-7 days and infections were found to persist in cats for up to 200 days. Infections in pigs are thought to be transmitted through direct contact as well as the faecal-oral contamination of fomites.

Differential diagnosis: Tritrichomoniasis may be indicated as a cause of reproductive failure in cattle based on clinical history, signs of early abortion, and apparent infertility with repeated returns to service or irregular oestrous cycles. Infections are then confirmed by the detection of trophozoites in clinical samples by microscopy, culture or molecular techniques. Motile organisms may be detected in preputial smegma, cervico-vaginal mucus, pyometra discharges, uterine washings, placental fluid, and sometimes from stomach contents of aborted foetuses. Samples may be collected using swabs, brushes, scrapers, insemination pipettes, straws, gauze sponges or aspiration syringes, and dilute samples may be concentrated by centrifugation. Parasite numbers fluctuate in cows during their oestrous cycles with higher numbers found a few days before oestrus. Samples from cats best include freshly-voided or manually-extracted faeces, rectal swabs, or colon flushes. Many routine microbiological techniques (such as fixed smears, coprological sedimentation or floatation) destroy the fragile trophozoites, so it is best to prepare fresh wet smears for high-contrast brightfield, phase-contrast or interference-contrast microscopy. Motile parasites may be identified by their characteristic patterns of motility, involving jerky tumbling motions of cells that appear to shimmer due to rapid movements of their undulating membranes. If required, smears can be stained with Giemsa, silver, iron haematoxylin, malachite green, methylene blue, or acridine orange, but fixation using chemicals, heat or desiccation usually causes cells to contract or lyse. Post-mortem tissue samples can be processed for histological examination following staining with haematoxylin and eosin, Giemsa or periodic acid-Schiff-reagents. Trophozoites may be cultured *in vitro* in semi-defined liquid media (Diamond's media, modified Diamond's media, or InPouch TF selective media) for several days at 25-37°C (trophozoites require added nutrients as they cannot synthesize some macromolecules de novo). Parasites have also been grown on various tissue culture cell lines where they exhibit some cytotoxicity (highly toxic to human cervical (HeLa) cells, bovine lymphosarcoma (BL-3) cells, moderate toxicity to Vero cells, African green monkey kidney cells, and apoptotic to bovine vaginal epithelial (BVEC) cells, and porcine intestinal epithelial (IPEC) cells). Several immunoserological tests (agglutination, haemolytic and enzyme immunoassays) have been developed to detect host antibodies in serum or cervicovaginal mucus, but they generally only detected transient responses. Monoclonal antibodies were also produced and used for the immunohistochemical localization of parasites in host tissues. A murine intradermal test was used to test for virulence by measuring skin lesions after the inoculation of known numbers of fixed cultured trophozoites. More recently, modern molecular biological techniques have been applied to the detection and characterization of parasite isolates by restriction fragment length polymorphism analyses, random amplified polymorphic DNA analyses, *in situ* hybridization (ISH) using fluorochrome- or chromogenic-probes, and direct gene sequencing following the polymerase chain reaction (PCR) amplification of various gene sequences (including small and large subunit ribosomal RNA and internal transcribed spacers 1 and 2, cysteine proteases (CP) 1, 2, 4, 5, 6, 7, 8, 9, cytosolic malate dehydrogenase (MDH1), and elongation factor 1-alpha (EF-1α)). Different genotypes of *Tritrichomonas foetus* have been detected in cattle, cats and swine.

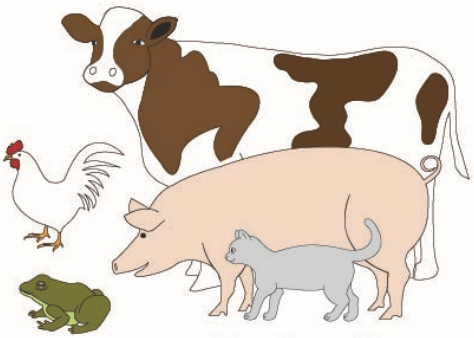
Treatment and control: Options for the treatment and prevention of tritrichomoniasis depend largely on the types and numbers of hosts to be treated. Chemotherapy is rarely attempted in cattle as it is tedious, expensive and only partially effective. Systemic treatments with nitroimidazoles (metronidazole, dimetridazole) often produce adverse side-effects and have led to the emergence of drug-resistant parasite populations. Preputial infections in bulls may respond to treatment with imidazole (ipronidazole) salves or ointments, but many persistent infections become entrenched in the inner genital tubes and testes making them refractory to treatment. Effective control depends on management strategies to detect and cull bulls and cows before their introduction into herds or breeding. Infected animals may be identified by periodic testing and all new and replacement livestock should be screened whilst in quarantine isolation. It is often recommended that bulls be replaced after 4 seasons as younger bulls are better able to eradicate infections whereas they accumulate in older animals. Artificial insemination programs may be used to avoid infections, but only when donor animals are thoroughly screened. Pregnancy testing should be used to identify fertile cows as soon as practicable and infertile animals should be investigated before returned to service. Some producers reduce their breeding seasons to < 4 months for logistic reasons. Good husbandry includes proper nutrition and sanitation as well as avoiding stressful conditions (such as over-crowding, co-mingling herds, and concomitant infections). Several studies have developed experimental vaccines using whole parasites and purified extracts to help eliminate infections before foetal loss, but without necessarily avoiding parasite colonization in the first 40 days. Some vaccines have shown promise, particularly those stimulating strong mucosal responses involving secretory antibodies (IgA, IgG1) and milder systemic responses (IgG2, IgG1). Infections in cats have responded well to treatment with nitroimidazoles (metronidazole, tinidazole, ronidazole), aminoglycosides (paromomycin), benzimidazoles (fenbendazole), nitrofurans (furazolidone), and thiazolides (nitazoxanide), but with some adverse side effects including neurological toxicity. It is recommended that all cats in contact be treated to help eradicate infections in catteries. The adoption of preventive measures designed to reduce transmission should include separating cohorts, limiting contact between cats, strict hygiene and sanitation, disinfecting fomites, equipment, and feeding containers, excluding invertebrates (e.g. slugs and snails) and providing clean food and water. Infections in pigs are asymptomatic and are not treated.

Tritrichomonas

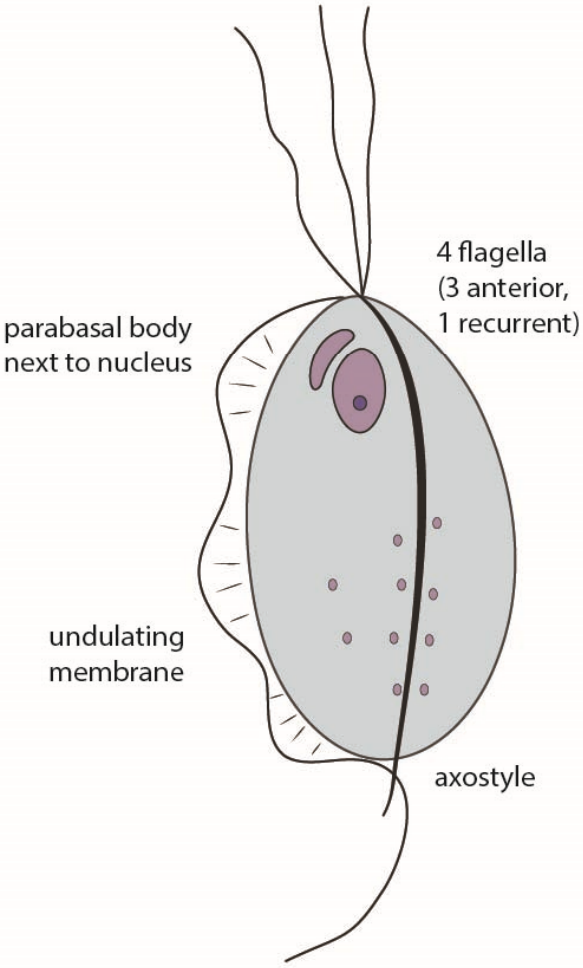


urogenital tract, gut
(vaginitis, endometritis,
abortion, infertility,
rarely diarrhoea)

division by
longitudinal
binary fission



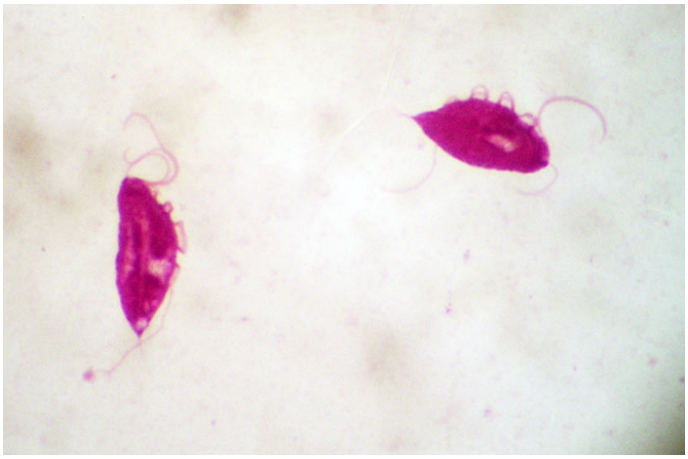
Vertebrate Hosts
(mammals, birds,
amphibians)



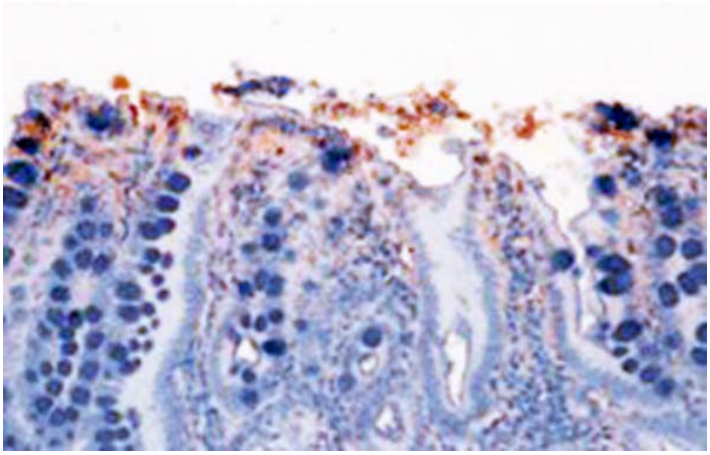
trophozoites
(8-25 µm)

no cyst formation

direct transmission by transfer of trophozoites
by close contact (coitus, parturition, parental care)
or via contaminated fomites



Tritrichomonas foetus trophozoites



Tritrichomonas foetus uterine inflammation

Histomonas
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Parabasalid flagellates are anaerobic amitochondriate protists which have distinctive parabasal bodies (dictyosomes) adjacent to flagellar basal bodies (kinetosomes) and an axostyle-pelta complex providing structural support. Trichomonads are a major constituent group and most have 4-6 apical flagella, one being recurrent and often forming an undulating membrane supported by a costa. Dientamoebids, however, do not have recurrent flagella or associated structures (histomonads have only one flagellum and *Dientamoeba* have none). Most are parasites of insects although a few species infect domestic animals. They do not form cysts so horizontal transmission involves direct contact, and sometimes other hosts. Histomonads parasitize galliform birds and use caecal nematodes as intermediate hosts and earthworms as paratenic hosts. One species (*H. meleagridis*) causes severe disease in turkey poults when aflagellate amoeboid stages invade host tissues.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Metamonad (amitochondriate flagellates with karyomastigonts)
Phylum: Parabasalia (anaerobic flagellates with parabasal body supporting Golgi cisternae or dictyosome, trichomonads, hypermastigids, retortamonads)
Class: Tritrichomonadea (single mastigont, comb-like structure, infrakinetosomal body)
Order: Tritrichominadida (variable possession of undulating membrane and costa)
Family: Dientamoebidae (0-4 flagella, undulating membrane absent, costa absent, cone-like axostyle, comb-like structure absent, infrakinetosomal body absent)
Genus: *Histomonas* (parasitic in caeca/liver of birds)
Species: *H. meleagridis* (causes histomoniasis (infectious enterohepatitis or blackhead disease) in turkeys)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)

body)		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Metamonads are a group of excavates (with ventral feeding groove) that have several subcellular elements associated with their flagella forming a unique mastigont (an ultrastructural complex of organelles and cytoskeletal fibrils (incl. dictyosomes (Golgi bodies), centrioles (basal bodies) and a microtubular axostyle)). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Most metamonads are amitochondriate but have retained reduced organelles of mitochondrial origin (fornicates containing mitosomes while parabasalians possess hydrogenosomes). Members of the phylum Parabasalia typically possess parabasal bodies adjacent to Golgi bodies (dictyosomes), and have microtubular arrays forming a conspicuous pelta-axostyle complex (cap-like pelta and a cone- or tube-like longitudinal axostyle). Six parabasalid classes are currently recognized on the basis of morphological, biological and molecular phylogenetic studies. Cells in three classes (Trichomonadea, Tritrichomonadea, Hypotrichomonadea) bear single mastigonts (set of kinetosomes (basal bodies) and associated appendages – ancestral unit comprising 4 kinetosomes) with flagella arranged in an anterior tuft, but many have one recurrent flagellum forming an undulating membrane (lamelliform or rail-type) supported by a costa (A- or B-type) and sometimes a basal comb-like structure and/or infrakinetosomal body. Many species are symbiotic (mutualists, commensals or parasites) in animals, although some are free-living in moist habitats. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Cells in another three classes (Cristamonadea, Trichonymphea, Spirotrichonymphea) have more complex structures, often with multiple mastigonts bearing hundreds to thousands of flagella. Most were previously assigned to the now-defunct group Hypermastigida and they are primarily found as symbionts (mutualists) in insects (mostly termites).

Family	**Key characters to 'trichomonad' families in vertebrates***						**Representative genera**
	Number of flagella	**Undulating membrane**	**Costa**	**Axostyle**	**Comb-like structure**	**Infra-kinetosomal body**	
Class Trichomonadea (single karyomastigont)							
Order Trichomonadida (with costa) (endobiotic in vertebrates (mammals, birds, reptiles, amphibia) and invertebrates)							
Trichomonadidae	5-6	lamelliform	B-type	cone-like	absent	absent	*Cochlosoma, Trichomonas, Trichomitopsis, Tetratrichomonas, Pentatrichomonas*
Order Honigbergiellida (without costa) (endobiotic in vertebrates (mammals, reptiles, amphibia))							

Hexamastigidae	5-6	absent	absent	cone-like	absent	absent	*Hexamastix*
Class Tritrichomonadea (uninucleate to binucleate)							
Order Tritrichomonadida (endobiotic in vertebrates (mammals, birds, reptiles, amphibia, fish))							
Tritrichomonadidae	4-5	rail-type	A-type	tube-like	present	present	*Tritrichomonas*
Simplicimonidae	4	absent	absent	tube-like	present	present	*Simplicimonas*
Monocercomonidae	4	absent	absent	cone-like	present	present	*Monocercomonas*
Dientamoebidae	0-4	absent	absent	cone-like	absent	absent	*Dientamoeba, Histomonas*
Class Hypotrichomonadea (single karyomastigont)							
Order Hypotrichomonadida (endobiotic in vertebrates (reptiles, amphibia, mammals) and invertebrates)							
Hypotrichomonidae	4	lamelliform	A-type	cone-like	present	absent	*Trichomitus, Hypotrichomonas*

*Taxa found only in invertebrate hosts (such as termites and cockroaches) are not listed

The genus *Tritrichomonas* was separated from other trichomonads initially on the basis of ultrastructural studies, notably involving the possession of different undulating membranes (rail-type), costae (A-type), axostyles (tube-like) and the presence of comb-like structures and infrakinetosomal bodies. Molecular characterization studies, however, revealed that many of these characters were not apomorphic but plesiomorphic, with many related taxa varying considerably in their structural complexity, and often demonstrating reductive evolution by lacking (or having lost) various features. The novel class Tritrichomonadea was erected to accommodate a diverse range of cells with 1-2 nuclei and 0-5 flagella, but otherwise varying in their possession of various cytoskeletal, membranous and cytoplasmic elements. The order Tritrichomonadida contains 4 families: one family with 'trichomonad' features (Tritrichomonadidae (genus *Tritrichomonas*) with uninucleate cells, 4-5 flagella, rail-type undulating membranes, A-type costae, tube-like axostyles); and 3 families with greatly simplified structures (Dientamoebidae syn. Protrichomonadinae (4 genera: *Dientamoeba, Histomonas, Parahistomonas, Protrichomonas*) with uni- to bi-nucleate cells, 0-4 flagella, cone-like axostyles (if present), but lacking undulating membranes, costae, comb-like structures and infrakinetosomal bodies; Monocercomonadidae (one genus *Monocercomonas*) with uninucleate cells, 4 flagella, marginal plates, cone-like axostyles, but lacking undulating membranes and costae; and Simplicimonadidae (one genus *Simplicimonas*) with uninucleate cells, 4 flagella, marginal plates, tube-like axostyles, but lacking undulating membranes and costae). Most cognate species have been recorded as symbiotes (mutualists, commensals or parasites) of insects, but a few species infect vertebrate hosts, including humans and domestic animals.

The genus *Histomonas* contains 2 species which form uninucleate cells within the caeca of avian hosts, mostly galliforms. One species (*H. meleagridis*) forms flagellated lumen forms (trophozoites with one flagellum) as well as non-flagellated tissue forms (rounded trophozoites). Transmission between birds occurs when tissue forms infect caecal nematodes as paratenic hosts and are transferred to new hosts within nematode eggs. The species *Histomonas meleagridis* causes severe disease in birds, sometimes known as blackhead. Infections are cosmopolitan and prevalent in gallinaceous fowl, esp. young turkeys (up to 14 weeks of age) and chickens (up to 16 weeks of age). Infections also occur in peafowl, grouse and pheasant, but reports in non-galliform birds, such as ostriches, are rare and ducks and geese have proven refractory to experimental infection. The other species (*H. wenrichi*) only forms flagellated lumen forms (trophozoites with 4 flagella), and transmission is thought to involve contamination of food and water.

Parasite species	**Length (µm)**	**Vertebrate Hosts**	**Location**	**Clinical signs**	**Distribution**
Class: **Tritrichomonadea** (uninucleate to binucleate) [0-5F±RUM+AC+CLS+IKB+CA/TA]†					
Order: Tritrichomonadida (as for class)					
Family: Dientamoebidae (uninucleate to binucleate, marginal plate present) [0-4F-UM-C±CA-CLS-IKB]					
Histomonas (flagellated lumen form, sometimes aflagellar tissue form, caecal nematode vector) [0-4F]					
Histomonas meleagridis (syn. *Amoeba*) [0-2F]	6-20	Galliformes: phasianid (turkeys, chickens, chukar, pheasant, quail, grouse, jungle fowl, guinea fowl, peafowl), occasionally Struthioniformes: struthionid (ostriches) [plus invertebrate vector Nematoda: ascaridid (caecal worm *Heterakis gallinarum*), the eggs of which may also be ingested by paratenic hosts: Clitellata: lumbricid (earthworms); Diptera:	caeca (spreading to liver, spleen, kidney, lungs)	anorexia, diarrhoea, depression, ruffled feathers, blackened skin around head (blackhead) (or chronic wasting disease)	worldwide

		muscid (houseflies)]			
Histomonas wenrichi (syn. *Parahistomonas*) [4F]	9-30	Galliformes: phasianid (turkeys, chickens, pheasant)	caeca	non-pathogenic	

†Coding: + = present; - = absent; #F = total number of flagella; UM = undulating membrane; RUM = rail-type undulating membrane; C = costa; AC = A-type costa; CA = cone-like axostyle (*Trichomonas*-type); TA = tube-like axostyle (*Tritrichomonas*-type); CLS = comb-like structure; IKB = infrakinetosomal body.

Parasite morphology: Histomonads form 2 different types of developmental stages: flagellated trophozoites and non-flagellated amoeboid forms (sometimes with small but distinct lobose pseudopodia). All stages are uninucleate and pleomorphic in shape (often rounded, sometimes spindle-shaped) ranging in size from 5-30 μm for trophozoites and 8-19 μm for amoeboid forms. The nucleus is ovoid and located eccentrically adjacent to a V-shaped parabasal body formed by dictyosomes (Golgi complexes) and flagellar basal bodies (kinetosomes). The kinetosomes give rise to eukaryotic flagella (with 2 central microtubules and 9 peripheral doublets) which extend from the anterior margin of the cells for 2-8 μm. *H. meleagridis* trophozoites possess one short flagellum, while those of *H. wenrichi* have 4 longer flagella. Trophozoites also possess a longitudinal rod-like structure called an axostyle that is composed of concentric rows of microtubules forming a cone (rather than a tube). Histomonads are anaerobic and do not have mitochondria, but rather possess membrane-bound organelles known as hydrogenosomes (formerly called siderophil granules) that are located along the axostyle. Hydrogenosomes are energy-producing organelles that generate molecular hydrogen (by metabolizing pyruvate to acetate and carbon dioxide producing ATP by substrate-level phosphorylation with release of hydrogen ions). Histomonads do not form true encapsulated cysts, but some cells round up and lose their flagella apparently forming small so-called 'resistant' stages 4-11 μm in diameter with an eosinophilic cytoplasm.

Site of infection: Infections are found in galliform birds (turkeys, chickens, chukar, pheasant, quail, grouse, jungle fowl, guinea fowl, peafowl), and occasionally in struthioniform birds (ostriches). Trophozoites infect the caecum while invasive forms can penetrate the epithelium and be disseminated to the liver and other organs (e.g. spleen, kidney, lungs). Parasites may also be taken up by caecal nematodes (*Heterakis gallinarum*) where they infect the ovaries and then worm eggs. Infected worm eggs may be ingested and transported by invertebrate paratenic hosts, including earthworms and houseflies.

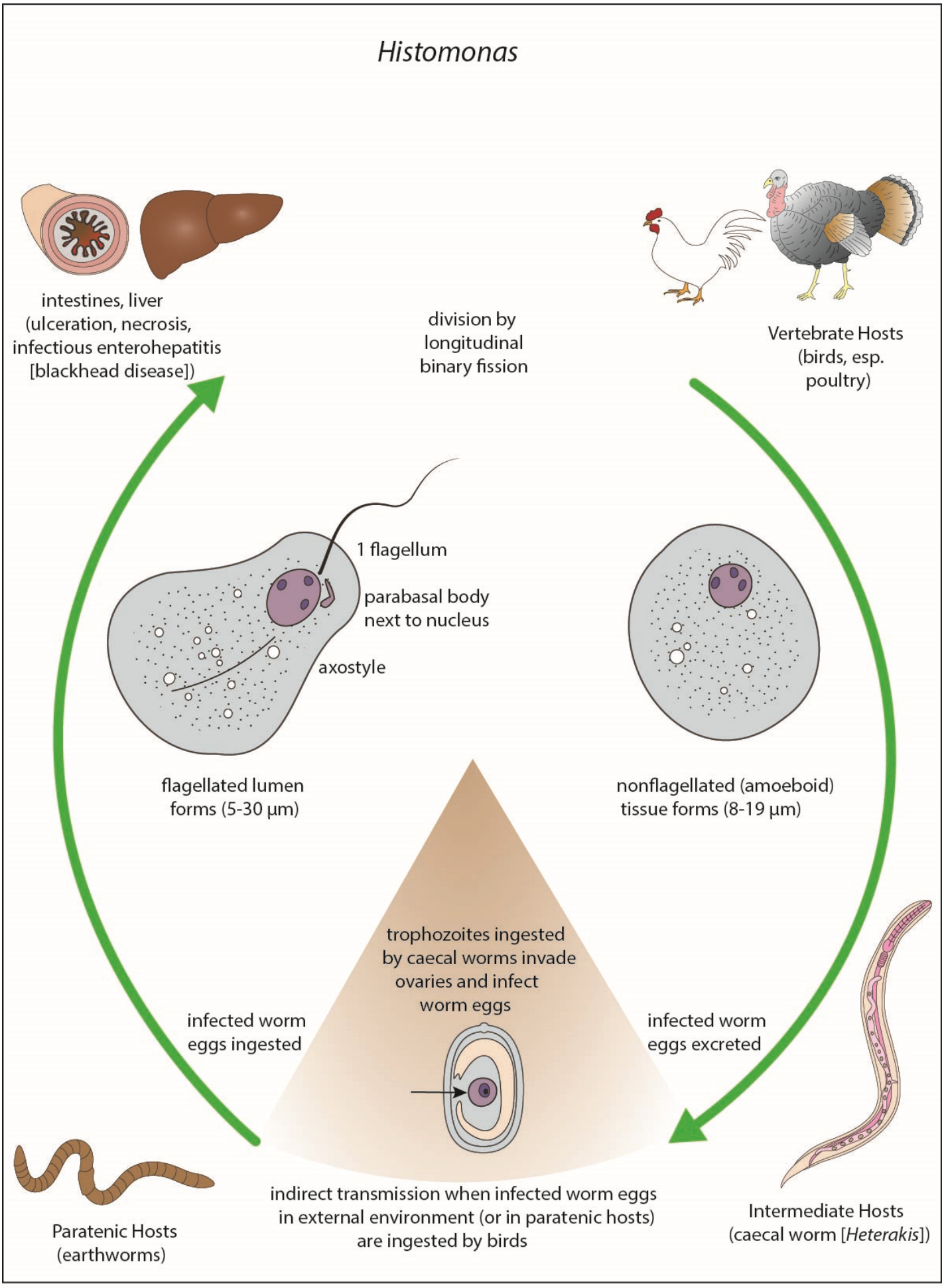
Pathogenesis: Infections in birds may be asymptomatic, subclinical or cause severe clinical disease known as histomoniasis, infectious enterohepatitis, necrotizing typhlohepatitis or 'blackhead', especially in turkey poults. The severity of disease varies according to differences in host susceptibility, intensity of infection, parasite virulence, frequency of exposure, and concomitant infections (co-infections by histomonads and bacteria (e.g. *Escherichia coli, Clostridium perfringens*) predispose to disease). Histomonad trophozoites feed on solutes and particulate material in the caecal mucosa, while amoeboid forms invade tissues and feed on host tissues. Trophozoites first infect the caecal wall causing small punctate ulcers in which the organisms multiply. The ulcers grow and coalesce resulting in the mucosa becoming inflamed, thickened and necrotic, with dysbiosis causing increased permeability. The caeca become grossly enlarged and haemorrhagic, eventually developing a hard caseous adherent core. Amoeboid stages may then penetrate the mucosa and pass along the portal circulation to the liver and other organs (lung, kidney and spleen in severe cases, sometimes pancreas, heart, brain and bursa). Parasites cause necrotic foci which grow peripherally to produce characteristic (pathognomic) circular depressed lesions up to 1 cm in diameter. The lesions appear as yellow-green necrotic areas with grey peripheral margins and radial streaks (commonly known as 'bulls-eye target' lesions). Lesions are characterized by hyperaemia, haemorrhages, necrosis, serous exudates and infiltrations of macrophages, lymphocytes and multinucleated giant cells. Infected birds exhibit reduced food intake, reduced weight gain, increased thirst, depression, drooping wings, ruffled feathers, yellowish diarrhoea, blackened heads (often due to secondary bacterial infection), and death. Clinical signs may develop within 7-12 days of infection, and most mortalities occur 1-2 weeks later. Surviving birds recover as the necrotic lesions are repaired by lymphocytic cells and fibroblasts, often with scarring. The caseous caecal plug contracts and is expelled allowing the caeca to return to normal size. Recovered birds exhibit a strong protective immunity (involving humoral and cellular responses) but may continue to harbour organisms for some time (premunition). Young turkeys rapidly succumb to infection (mortalities sometimes reaching 80-100%), whereas older birds develop a chronic wasting disease. Chickens and other birds are more resistant to the pathogenic effects of the parasite but may harbour subclinical infections and act as reservoirs of infections for turkeys.

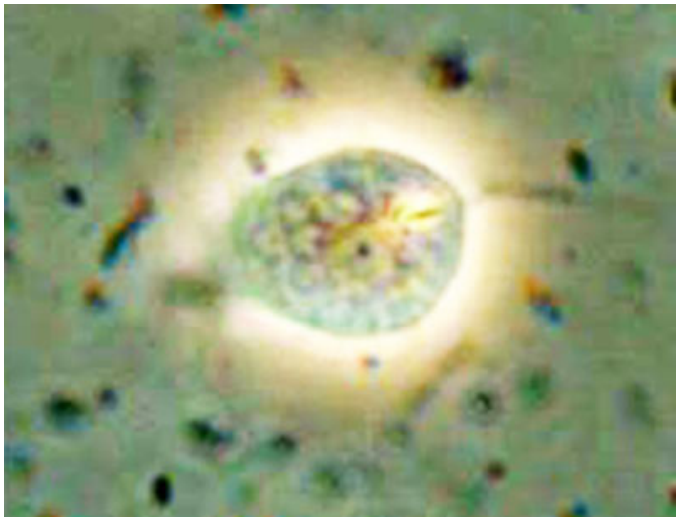
Developmental cycle and mode of transmission: Histomonads do not form environmentally-resistant cysts, with both trophozoites and amoeboid forms being fragile and not surviving long outside of host (only up to 6 hours on feathers and feed, and up to 9 hours in nonchlorinated water and faecal droppings). It was early discovered that caecal worms (*Heterakis gallinarum*) may be involved in transmission cycles as workers were unable to initiate disease in the absence of caecal worms. It was found that histomonads had adopted a unique mode of transmission using caecal nematodes as intermediate hosts. Nematodes feeding on infected host tissues ingest histomonads which then invade their ovaries and infect developing worm eggs. The nematodes then pass infected eggs which are excreted in host faeces. The worm eggs, and their hitch-hiking histomonads, may survive for long periods in the external environment before they are taken up by foraging birds. Once ingested, the worm eggs hatch in the intestines, releasing both worm larvae and histomonads to initiate infections. Chickens are excellent hosts for caecal worms and act as reservoirs of infection, while

other birds are poor hosts for caecal worms, but may still act as asymptomatic carriers of infection. It has also been demonstrated that infected worm eggs may be taken up by a small number of invertebrates (including earthworms, houseflies, darkling beetles, and lesser mealworms) which act as paratenic (transport) hosts. Infected worm eggs may survive in these hosts for some time (up to 2 years in earthworms) and remain infective to birds feeding on paratenic hosts. Indeed, infections can accumulate in earthworms and be transmitted to birds, especially following periods of rain when earthworms come to the soil surface and are readily consumed. There is also some evidence that histomonads may be directly transmitted between birds, not by oral infection (as they rarely survive the low pH of the ventriculus unless protected within worm ova), but by the phenomenon of cloacal drinking which transfers materials from the vent area into the caeca through waves of reverse peristalsis (this is a natural process in turkeys whereby the cloaca is stimulated to take up materials from the environment to help build the immune system). Horizontal transmission is thought to be aided by comingling and close contact (huddling behaviour) by turkeys, particularly on moist litters.

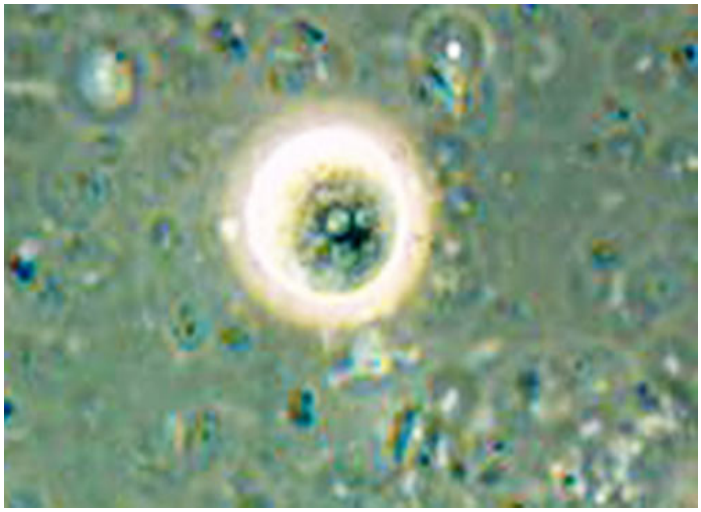
Differential diagnosis: Infections are frequently diagnosed on the basis of history, clinical signs and necropsy findings (especially the pathognomonic 'bulls-eye target' lesions). Faecal samples and mucosal scrapings can be examined for live parasites using wet mounts, warm stages and high contrast microscopy. Tissue samples taken at necropsy may be processed for histological examination for lesions containing clusters of histomonads following staining with haematoxylin and eosin, periodic acid-Schiffs, Giemsa and Grocott's silver stains. Histomonads can be cultured *in vitro* from suspect caecal and liver samples using Dwyer's medium or modified medium 199 with serum supplements. Parasites have also been cultured *in vivo* in turkeys by the intracloacal inoculation of infected liver, caecal tissues or suspensions of cultivated trophozoites. Immunological techniques (enzyme immunoassays) have been developed to detect specific host antibodies and parasite antigens in clinical samples, but their sensitivity and specificity are unknown. More recently, molecular biological techniques have been used to diagnose infections and characterize parasite isolates following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (18S ribosomal RNA, internal transcribed spacers (ITS) 1 and 2, beta-tubulin, alpha-actinin 1, RNA polymerase II subunit RPB1).

Treatment and control: A range of chemicals have been used to treat histomonad infections in poultry. Early studies using trivalent arsenicals (arsenious acid, atoxyl, neoarsphenamine, tryparsamide) and pentavalent arsenicals (nitarsone, carbasone, roxarsone) gave inconsistent results, while subsequent studies using nitroimidazoles (dimetridazole, metronidazole, ornidazole, tinidazole), nitrofurans (furazolidone), thiametroimidines (enheptin-T) and thiazoles (nithiazide, nitrothiazole) were more effective, although some resistance to metronidazole was observed. However, many drugs are no longer used as feed additives in poultry production due to concerns over toxicities and food residues. There are few other candidates, although an aminoglycoside antibiotic (paromomycin) exhibited reasonable prophylactic activity and some phytochemicals (herbal extracts, dietary supplements) gave good *in vitro* results but not *in vivo.* Fortunately, anthelmintic treatment with benzimidazoles (mebendazole, albendazole, fenbendazole) are very effective against caecal nematode infections, therefore depriving histomonads of their major mode of transmission. Routine treatment of commercial poultry flocks with anthelmintics has drastically reduced the incidence of histomoniasis. Preventive measures employed to further reduce parasite transmission include regular health surveillance (screening birds, quarantining new introductions, culling infected birds, burning or burying bodies), strict hygiene (disinfecting equipment, feeders, waterers, roosts), good sanitation (remove contaminated litter, avoid damp soils), biosecurity (excluding paratenic hosts), and good husbandry (separate cohorts, avoid co-mingling (especially of chickens and turkeys) and reduce stressors (maintain nutrition and avoid over-crowding). Experimental vaccination studies have shown some promise with parasite strains attenuated by serial passage producing some protection when administered orally or cloacally, but no commercial vaccines have yet been developed.

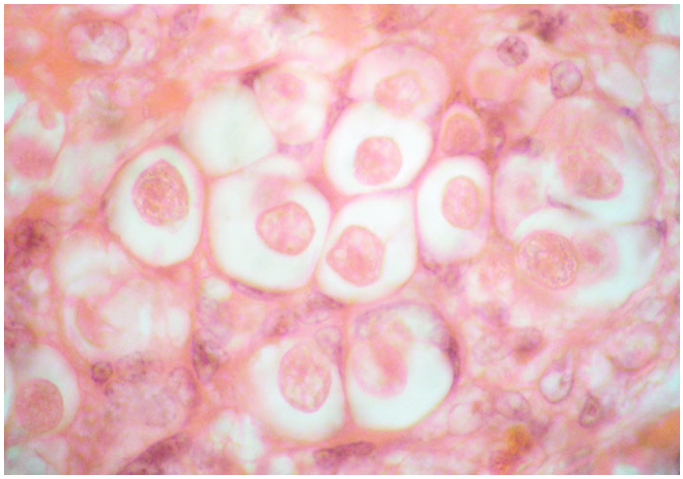

Histomonas
intestines, liver
(ulceration, necrosis,
infectious enterohepatitis
[blackhead disease])
division by
longitudinal
binary fission
Vertebrate Hosts
(birds, esp.
poultry)
1 flagellum
parabasal body
next to nucleus
axostyle
flagellated lumen
forms (5-30 µm)
nonflagellated (amoeboid)
tissue forms (8-19 µm)
trophozoites ingested
by caecal worms invade
ovaries and infect
worm eggs
infected worm
eggs ingested
infected worm
eggs excreted
Paratenic Hosts
(earthworms)
indirect transmission when infected worm eggs
in external environment (or in paratenic hosts)
are ingested by birds
Intermediate Hosts
(caecal worm [Heterakis])



Histomonas flagellated trophozoite



Histomonas amoeboid trophozoite



Histomonas liver lesion in chicken

Dientamoeba
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Parabasalid flagellates are anaerobic amitochondriate protists which have distinctive parabasal bodies (dictyosomes) adjacent to flagellar basal bodies (kinetosomes) and an axostyle-pelta complex providing structural support. Trichomonads are a major constituent group and most have 4-6 apical flagella, one being recurrent and often forming an undulating membrane supported by a costa. Dientamoebids, however, do not have recurrent flagella or associated structures (histomonads have only one flagellum and *Dientamoeba* have none). Most are parasites of insects although a few species infect domestic animals. *Dientamoeba* are small nonflagellated binucleate amoebae that have been shown to have trichomonad affinities due to the presence of a parabasal apparatus (basal body and axostyle lacking), a paradesmosome as part of an extranuclear spindle originating from attractophores, and hydrogenosomes (modified mitochondria). The species *D. fragilis* is frequently found in humans and may cause enteritis and diarrhoea.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Metamonad (amitochondriate flagellates with karyomastigonts)
Phylum: Parabasalia (anaerobic flagellates with parabasal body supporting Golgi cisternae or dictyosome, trichomonads, hypermastigids, retortamonads)
Class: Tritrichomonadea (single mastigont, comb-like structure, infrakinetosomal body)
Order: Tritrichominadida (variable possession of undulating membrane and costa)
Family: Dientamoebidae (0-4 flagella, undulating membrane absent, costa absent, cone-like axostyle, comb-like structure absent, infrakinetosomal body absent)
Genus: *Dientamoeba* (symbiotic in gut of humans/rodents)
Species: *D. fragilis* (may cause diarrhoea in humans)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)

body)		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Metamonads are a group of excavates (with ventral feeding groove) that have several subcellular elements associated with their flagella forming a unique mastigont (an ultrastructural complex of organelles and cytoskeletal fibrils (incl. dictyosomes (Golgi bodies), centrioles (basal bodies) and a microtubular axostyle)). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Most metamonads are amitochondriate but have retained reduced organelles of mitochondrial origin (fornicates containing mitosomes while parabasalians possess hydrogenosomes). Members of the phylum Parabasalia typically possess parabasal bodies adjacent to Golgi bodies (dictyosomes), and have microtubular arrays forming a conspicuous pelta-axostyle complex (cap-like pelta and a cone- or tube-like longitudinal axostyle). Six parabasalid classes are currently recognized on the basis of morphological, biological and molecular phylogenetic studies. Cells in three classes (Trichomonadea, Tritrichomonadea, Hypotrichomonadea) bear single mastigonts (set of kinetosomes (basal bodies) and associated appendages – ancestral unit comprising 4 kinetosomes) with flagella arranged in an anterior tuft, but many have one recurrent flagellum forming an undulating membrane (lamelliform or rail-type) supported by a costa (A- or B-type) and sometimes a basal comb-like structure and/or infrakinetosomal body. Many species are symbiotic (mutualists, commensals or parasites) in animals, although some are free-living in moist habitats. Most species have simple life cycles with longitudinal binary fission of motile-flagellated or rounded tissue-phase cells (only a few species form cysts). Cells in another three classes (Cristamonadea, Trichonymphea, Spirotrichonymphea) have more complex structures, often with multiple mastigonts bearing hundreds to thousands of flagella. Most were previously assigned to the now-defunct group Hypermastigida and they are primarily found as symbionts (mutualists) in insects (mostly termites).

Family	**Key characters to 'trichomonad' families in vertebrates***						**Representative genera**
	Number of flagella	**Undulating membrane**	**Costa**	**Axostyle**	**Comb-like structure**	**Infra-kinetosomal body**	
Class Trichomonadea (single karyomastigont)							
Order Trichomonadida (with costa) (endobiotic in vertebrates (mammals, birds, reptiles, amphibia) and invertebrates)							
Trichomonadidae	5-6	lamelliform	B-type	cone-like	absent	absent	*Cochlosoma, Trichomonas, Trichomitopsis, Tetratrichomonas, Pentatrichomonas*
Order Honigbergiellida (without costa) (endobiotic in vertebrates (mammals, reptiles, amphibia))							

Hexamastigidae	5-6	absent	absent	cone-like	absent	absent	*Hexamastix*
Class Tritrichomonadea (uninucleate to binucleate)							
Order Tritrichomonadida (endobiotic in vertebrates (mammals, birds, reptiles, amphibia, fish))							
Tritrichomonadidae	4-5	rail-type	A-type	tube-like	present	present	*Tritrichomonas*
Simplicimonidae	4	absent	absent	tube-like	present	present	*Simplicimonas*
Monocercomonidae	4	absent	absent	cone-like	present	present	*Monocercomonas*
Dientamoebidae	0-4	absent	absent	cone-like	absent	absent	*Dientamoeba, Histomonas*
Class Hypotrichomonadea (single karyomastigont)							
Order Hypotrichomonadida (endobiotic in vertebrates (reptiles, amphibia, mammals) and invertebrates)							
Hypotrichomonidae	4	lamelliform	A-type	cone-like	present	absent	*Trichomitus, Hypotrichomonas*

*Taxa found only in invertebrate hosts (such as termites and cockroaches) are not listed

The genus *Tritrichomonas* was separated from other trichomonads initially on the basis of ultrastructural studies, notably involving the possession of different undulating membranes (rail-type), costae (A-type), axostyles (tube-like) and the presence of comb-like structures and infrakinetosomal bodies. Molecular characterization studies, however, revealed that many of these characters were not apomorphic but plesiomorphic, with many related taxa varying considerably in their structural complexity, and often demonstrating reductive evolution by lacking (or having lost) various features. The novel class Tritrichomonadea was erected to accommodate a diverse range of cells with 1-2 nuclei and 0-5 flagella but otherwise varying in their possession of various cytoskeletal, membranous and cytoplasmic elements. The order Tritrichomonadida contains 4 families: one family with 'trichomonad' features (Tritrichomonadidae (genus *Tritrichomonas*) with uninucleate cells, 4-5 flagella, rail-type undulating membranes, A-type costae, tube-like axostyles); and 3 families with greatly simplified structures (Dientamoebidae syn. Protrichomonadinae (4 genera: *Dientamoeba, Histomonas, Parahistomonas, Protrichomonas*) with uni- to bi-nucleate cells, 0-4 flagella, cone-like axostyles if present, but lacking undulating membranes, costae, comb-like structures and infrakinetosomal bodies; Monocercomonadidae (one genus *Monocercomonas*) with uninucleate cells, 4 flagella, marginal plates, cone-like axostyles, but lacking undulating membranes and costae; and Simplicimonadidae (one genus *Simplicimonas*) with uninucleate cells, 4 flagella, marginal plates, tube-like axostyles, but lacking undulating membranes and costae). Most cognate species have been recorded as symbiotes (mutualists, commensals or parasites) of insects, but a few species infect vertebrate hosts, including humans and domestic animals.

The genus *Dientamoeba* contains one species (*D. fragilis*) which forms uni- or bi-nucleate non-flagellated stages in the lower alimentary tracts of humans and pigs, although experimental infections have been established in sheep and monkeys. There is ongoing debate as to the clinical significance of the organism, with some regarding it to be a nonpathogenic endocommensal while others consider it to be a sporadic cause of chronic diarrhoea and fatigue in humans.

Parasite species	**Length (µm)**	**Vertebrate Hosts**	**Location**	**Clinical signs**	**Distribution**
Class: **Tritrichomonadea** (uninucleate to binucleate) [0-5F+RUM+AC+CLS+IKB+CA/TA]†					
Order: Tritrichomonadida (as for class)					
Family: Dientamoebidae (syn. Protrichomonadidae) (uninucleate to binucleate, marginal plate present [0-4F-UM-C+CA-CLS-IKB]					
Dientamoeba (aflagellar lumen forms, binucleate or uninucleate)					
Dientamoeba fragilis [0F]	3.5-12	Primates: hominid (human, gorilla); Artiodactyla: suid (pig); experimentally in Artiodactyla: bovid (sheep), Rodentia: murid (mice, rats); Primates: cercopithecid (baboon, macaques)	colon	diarrhoea	worldwide

†Coding: + = present; - = absent; #F = total number of flagella; UM = undulating membrane; RUM = rail-type undulating membrane; C = costa; AC = A-type costa; CA = cone-like axostyle (*Trichomonas*-type); TA = tube-like axostyle (*Tritrichomonas*-type); CLS = comb-like structure; IKB = infrakinetosomal body.

Parasite morphology: *Dientamoeba fragilis* forms motile vegetative stages known as trophozoites, which are variable in size (ranging from 3.5-12 µm in length but sometimes being as large as 20-40 µm). They are usually rounded in shape, but motile forms may appear fan-shaped due to the possession of small hyaline irregularly-lobed pseudopodia. These parasites lack flagella, undulating membranes, costae, and axostyles, but are nonetheless classified with the tritrichomonads on the basis of ultrastructural and molecular studies. Trophozoites often have a highly vacuolated cytoplasm with large food vacuoles, inclusion bodies and granules. They also contain multiple osmiophilic membrane-bound bodies known as hydrogenosomes, which are energy-producing organelles that generate molecular hydrogen (by metabolizing pyruvate to acetate and carbon dioxide producing ATP by substrate-

level phosphorylation with release of hydrogen ions). The majority of the trophozoites are binucleate with 2 eccentric nuclei measuring 1-3 µm in diameter, although some mononucleate stages may be recently divided cells. The nuclei contain 3-8 granules imparting a fragmented appearance without peripheral chromatin. An extracellular spindle lies between the nuclei, and numerous dictyosomes (Golgi complexes) cover the filaments. The parasites have not been observed to form true cysts in humans, but cyst formation has been reported in laboratory mice. The cysts were rounded and encapsulated by a filamentous cyst wall with a peritrophic space between the enclosed parasite and the dense outer shell.

Site of infection: Infections in humans are confined to the large intestines, ranging from the caecum to the rectum, but most frequently in the proximal colon and appendix where trophozoites infect mucosal crypts beneath the epithelium. Infections in other primates, pigs, sheep and rodents are localized in the lower digestive tract.

Pathogenesis: *Dientamoeba fragilis* was initially considered to be a harmless commensal as the majority of infections (up to 90%) were found in people that did not have any clinical symptoms. Nonetheless, the organism was sometimes found as the only putative aetiological agent present in patients with mild gastrointestinal complaints. Trophozoites feed on bacteria within the gut by phagocytosis but they do not invade host tissues. They digest material in food vacuoles and eliminate wastes by exocytosis. The presence of motile feeding stages may cause local irritation with eosinophilic inflammatory responses. Clinical symptoms and signs include loose stools or diarrhoea (often mucoid, sometimes watery, sometimes with blood), abdominal pain, tenderness, cramping, nausea, vomiting, low grade fever, fatigue, anorexia, weight loss and failure to thrive in children. Persistent infections have also been associated with malnutrition, dehydration, appendicitis and rarely pruritic skin rashes. Dientamoebiasis may be acute (over 2 weeks) or chronic (up to 2 years) and a common misdiagnosis is irritable bowel syndrome or colitis (similar symptoms). Clinical infections are more prevalent in children (< 10 years of age), in males, during spring and summer, and in populations living in crowded conditions with poor hygiene (e.g. developing countries). Epidemiological observations have indicated that many infections are coincident with enterobiasis, caused by the pinworm (*Enterobius vermicularis*).

Developmental cycle and mode of transmission: The transmission cycle has yet to be established. Trophozoites occur in the lumen of the large intestine, where they multiply via binary fission, and are shed in faeces. This suggests faecal-oral transmission may occur, but trophozoites do not survive for long in faeces and cyst formation has not been demonstrated in natural infections in humans (only sometimes in experimentally-infected laboratory mice). Transmission may involve contact with contaminated fomites or the ingestion of contaminated food or water, but such routes remain to be confirmed. It has also been postulated that intermediate or paratenic invertebrates may act as alternate hosts or vectors for transmission, notably pinworms (*Enterobius vermicularis*) which show high co-infection rates, or possibly roundworms (*Ascaris lumbricoides*). However, these conjectures remain speculative as no definitive studies have yet been conducted (anecdotal evidence at best).

Differential diagnosis: Infections cannot be diagnosed on clinical grounds as most are asymptomatic and any evident clinical signs mimic those of irritable bowel syndrome or colitis. Differential diagnosis is afforded by the direct microscopic detection of fractile rounded parasites in faecal samples or gut content. Trophozoites are able to survive and move in fresh faeces, but they are sensitive to aerobic exposure and dissociate when placed in saline, tap water or distilled water. Conventional coprological techniques are ineffective as trophozoites are destroyed by formol-ether concentration and do not survive prolonged sedimentation/floatation techniques. Microscopy is usually conducted on fresh wet mounts or on permanently stained smears of unformed or formed stools. It is recommended that multiple (preferably sequential) stool samples be examined as the parasite shedding is highly variable. Trophozoites vary greatly in size and their nuclear structures cannot be seen in saline preparations. Wet mounts can be counter-stained with crystal violet haematoxylin, while fixed smears may be stained with Giemsa or Field's stain. Alternatively, faecal samples can be fixed prior to microscopy using polyvinyl alcohol (PVA), modified Schaudinn's, phenol-alcohol-formalin, or sodium acetate-acetic acid-formalin (SAF) fixatives (but not merthiolate-iodine-formalin as it is not very stable and does not stain nuclei) followed by staining with Mayer's haemalum, iron-haematoxylin, celestine blue, Wheatley's trichrome or Lawless' stain. Trophozoites may also be cultured *in vitro* in rice starch media or in xenic culture using very dilute samples. An indirect fluorescent-antibody test was developed to detect parasites in preserved faecal samples but exhibited low sensitivity. More recently, molecular biological techniques have been used to detect and characterize parasites in clinical samples following conventional and real-time (RT) polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit ribosomal RNA).

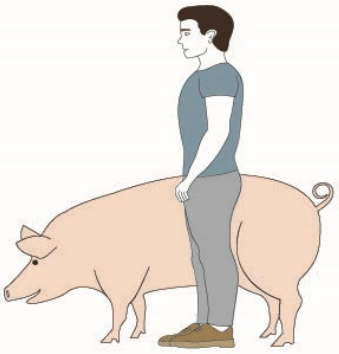
Treatment and control: A range of drugs have been used in attempts to treat clinical infections, including organoarsenics (carbarsone, diphetarsone), tetracycline antibiotics (tetracycline, doxycycline), aminoglycoside antibiotics (paromomycin), macrolide antibiotics (erythromycin), quinolines (nitroxoline, iodoquinol) and nitroimidazoles (metronidazole, secnidazole, tinidazole and ornidazole). The most effective were metronidazole, iodoquinol, tetracycline, and paromomycin, but their application frequently caused side-effects such as abdominal cramping, nausea and rash. There are also a growing number of treatment failures using metronidazole due to the emergence of drug-resistance parasite strains. It is recommended that treated individuals be re-tested several weeks after therapy, and that other family members in close contact be tested and treated if required. It is also suggested that patients be examined for pinworm infections (*Enterobius vermicularis*) and treated with anthelmintics if required. Various common-

sense preventive measures may be used to reduce the risks of transmission: including strict personal hygiene (frequently washing hands, especially before eating or handling foods), proper sanitation (clean toilets, hygienic disposal or disinfection of nappies), water treatment (filtration/chlorination, or boil water from untreated sources), and food hygiene (avoid foods fertilized with nightsoil (human waste), wash foods in clean water, and cook thoroughly).

Dientamoeba

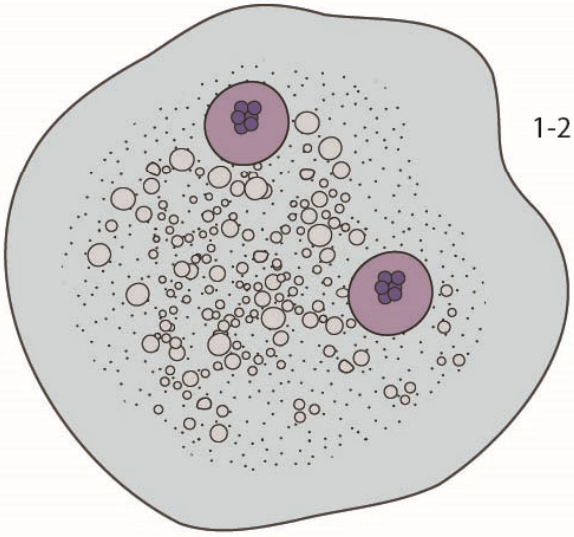


intestines
(enteritis, diarrhoea)



Vertebrate Hosts
(mammals)

division by
longitudinal
binary fission



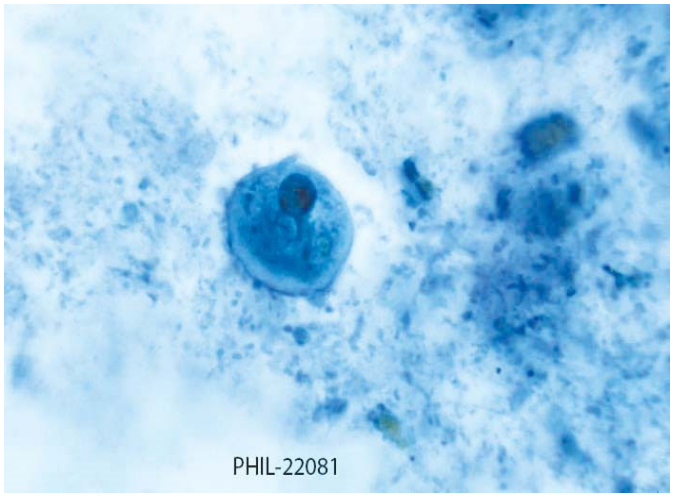
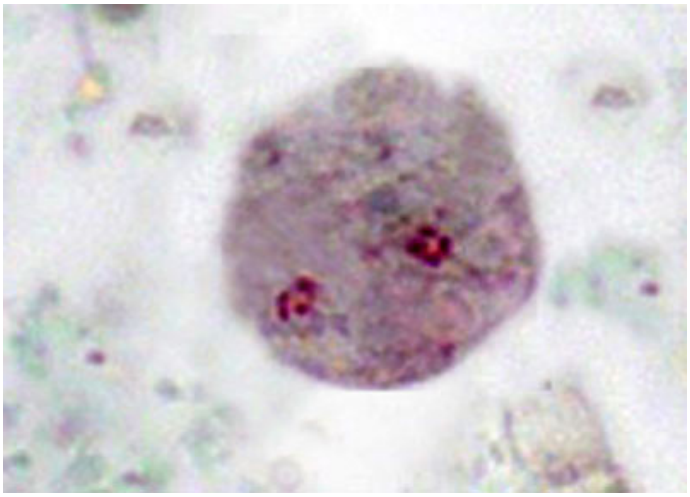
1-2 nuclei

amoeboid
nonflagellated
stage

trophozoites
(4-40 µm)

no cyst formation

transmission unknown
(speculated to involve close contact
or contaminated fomites)

	
Dientamoeba trophozoite	*Dientamoeba* trophozoite

Hexamita* and *Spironucleus
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Diplomonads have complex nucleus-associated karyomastigonts and are defined by the possession of two nuclei and unique bilateral symmetry (diplozoic appearance). They typically form reproductive cysts (each containing four nuclei) which facilitate their transmission between hosts. Hexamitids are parasites or commensals in mammals, birds, reptiles and fish. All species are characterized by their pyriform shape and bilateral symmetry with two equal nuclei lying side by side, two intracytoplasmic granular axonemes and 6-8 flagella. *Hexamita* and *Spironucleus* species are parasitic in the intestines of vertebrates and insects and several species cause enteric diseases in birds and fish.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Metamonad (amitochondriate flagellates with karyomastigonts)
Phylum: Fornicata (diplomonads)
Order: Diplomonadida (with 1-2 karyomastigonts (each with 4 basal bodies/flagella associated with nucleus))
Family: Hexamitidae (2 karyomastigonts arranged in binary axial symmetry)
Genus: *Hexamita* and *Spironucleus* (parasitic in small intestines/organs/skin of vertebrates and insects)
Species. various species cause hexamitosis in birds or fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)

Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Metamonads are a group of excavates (with ventral feeding groove) that have several subcellular elements associated with their flagella forming a unique mastigont (an ultrastructural complex of organelles and cytoskeletal fibrils (incl. dictyosomes (Golgi bodies), centrioles (basal bodies) and a microtubular axostyle)). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Most metamonads are amitochondriate but have retained reduced organelles of mitochondrial origin (fornicates containing mitosomes while parabasalians possess hydrogenosomes). Members of the phylum Fornicata are characterized by the possession of a distinct feeding groove or cytopharyngeal tube. Two classes are recognized: Eupharyngea commonly found in the digestive tracts of animals; and Carpediemonadea found in anaerobic intertidal sediments. The class Eupharyngea contains 2 orders: Diplomonadida with paired karyomastigonts; and Retortamonadida with single karyomastigonts. The diplomonads (meaning 'double monads') are binucleate and most species are found in the alimentary tracts of vertebrate hosts, although several free-living species occur in organically rich waters. Diplomonads typically form reproductive cysts (each containing 4 nuclei) to facilitate their transmission. Their motile vegetative forms (trophozoites) contain 1-2 kinetids, each with 4 kinetosomes but sometimes not all flagellated, and at least one flagellum per kinetid is directed posteriorly and may be associated with the cytopharyngeal tube or groove. Two families are generally recognized, 'monozoic' Enteromonadidae containing *Enteromonas*, *Caviomonas* and *Trimitus*; and 'diplozoic' Hexamitidae containing the genera *Giardia, Hexamita*, *Spironucleus*, *Trepomonas* and *Octomitus*. Some consider the enteromonads to be a regressive group with progressive reduction in the number of flagella while others consider them to be ancestral giving rise to the diplozoic hexamitids through the failure of cytokinesis. More recently, it was proposed that the order Diplomonadida be replaced by two new orders, Distomatida (containing *Trepomonas*, *Hexamita* and *Spironucleus*) and Giardiida (containing *Giardia* and *Octomitus*), both in a novel subclass Diplozoa. Differences in the placement of families and genera within the Diplomonadida (or Fornicata) remain to be reconciled.

Family	**Genus**	**Hosts**	**Pathogenicity**
Enteromonadidae (monozoic)	*Enteromonas*	mammals	nonpathogenic
	Trimitus	frogs, reptiles, fish, insects	nonpathogenic
	Caviomonas	rodents	nonpathogenic
Hexamitidae (diplozoic)	*Trepomonas*	frogs, fish, tortoises	nonpathogenic
	Octomitus	frogs, rodents	nonpathogenic
	Spironucleus	rodents, birds, fish	pathogenic in birds, fish
	Hexamita	birds, frogs, fish, tortoises, insects	pathogenic in birds, fish, tortoises
	Giardia	mammals, birds, frogs, reptiles	pathogenic in mammals, birds

The genera *Hexamita* and *Spironucleus* infect a wide range of vertebrate hosts, with some species causing enteric and/or systemic diseases in birds, fish and reptiles. It is often difficult to differentiate between these genera using morphological criteria because the pyriform trophozoites change shape prior to division (rounding up to become more spherical). Many species have been transferred between genera which has led to considerable taxonomic confusion. Nonetheless, ultrastructural and

molecular characterization studies have confirmed that the genera should be kept separate rather than merged. Both genera form cells with 2 karyomastigonts, thus possessing 8 flagella (6 anterior flagella used for locomotion and 2 recurrent flagella in longitudinal canals (flagellar pockets)). The genus *Hexamita* forms cells with elongate-spherical bodies, large cytostomes, spherical nuclei with shallow kinetosomal pockets, kinetosomal complexes located anterolaterally, and the recurrent flagella associated with the surface of the nuclei. In contrast, the genus *Spironucleus* forms cells with pyriform bodies, smaller cytostomes, elongated nuclei with deep kinetosomal pockets, kinetosomal complexes located anteromedially, and the recurrent flagella passing between the nuclei. Both genera form cysts which are passed into the external environment contaminating food and water supplies. Molecular characterization studies are now being used to determine phylogenetic relationships between clinical isolates, but it is apparent that more detailed morphotypic and more extensive genotypic studies are required to help resolve the current taxonomic confusion. Several species are recognized as significant pathogens causing clinical disease in their hosts: including *Spironucleus salmonis* causing enteritis in salmonid fishes, *Spironucleus meleagridis* causing enteritis in galliform birds, *Spironucleus vortens* causing hole-in-the-head lesions in aquarium fishes, *Spironucleus muris* causing digestive problems in rodents, and *Hexamita parva* causing tubulointerstitial nephritis in tortoises.

Parasite species	Size (µm)	Vertebrate Hosts	Location	Clinical signs	Distribution
Family: **Hexamitidae** (with functional feeding apparatus)					
Genus: ***Hexamita*** (pyriform body with 2 tube-like cytopharynxes run through body)					
H. africanus		freshwater Siluriformes: mochokid (wahrindi)	stomach, intestines		Africa
H. axostylus	8-10 x 5-10	Cypriniformes: cyprinid (yellowtail)	posterior intestine		China
H. capellani (syn. *capelani*)		marine Gadiformes: gadid (poor cod)	intestines		Europe
H. capsularis		Cypriniformes: cyprinid (yellowfin)	intestines		China
H. cryptocerci		Blattodea: blaberid (wood-feeding roach)	hindgut		North America
H. furcata		free-living			Europe
H. giganti	10-14 x 10-14	Cypriniformes: cyprinid (yellowtail)	posterior intestine		China
H. gigas		Clitellata: haemopid (horse-leech)	gut		Europe
H. globulus	4-6 x 4-6	Cypriniformes: cyprinid (yellowtail, yellow-tailed pomfret)	posterior intestine		China
H. gracilima		free-living in water			Europe
H. guanqiaoensis		Cypriniformes: cyprinid (smallscale yellowfin)	intestines		China
H. gyrans		free-living in water			Europe
H. hemiculteri	9-12 x 4-7	Cypriniformes: cyprinid (sharpbelly)	posterior intestine		China
H. hollandei		free-living in water			Europe
H. honghuensis	8-10 x 5-9	Cypriniformes: cyprinid (yellowtail, yellow-tailed pomfret)	posterior intestine		China
H. inflata (= *Bodo inflatus*)		free-living in water			Europe
H. insana		free-living in water			Europe
H. intestinalis		Anura: ranid (pond frogs), hylid (peepers), bufonid (toads); Urodela: ambystomatid (mole salamanders), plethodontid (dusky salamanders), salamandrid (crested newts)			North America, Eurasia
H. jiangxiensis	8-11 x 3-6	Cypriniformes: cyprinid (grass carp)	posterior intestine		China
H. liangzihuensis		Cypriniformes: cyprinid (smallscale yellowfin, xenocyprinids)	intestines		China
H. longifila		free-living in water			Europe
H. longiformis	32-40 x 3-5	Cypriniformes: cyprinid (yellowtail, yellow-tailed pomfret)	posterior intestine		China
H. megalobramae	8-10 x 4-7	Cypriniformes: cyprinid (Wuchang bream, goldfish, qingbo)	posterior intestine		China
H. minor		free-living in water			Europe
H. motellae		marine Gadiformes: lotid (shore rockling)	intestines		Europe

H. mutabilis		free-living in water/soil			Europe
H. nelsoni	8-16 x 3-8	Bivalvia: ostreid (eastern oyster, Pacific oyster, Sydney rock oyster, Olympia oyster, European flat oyster)	stomach		Europe, North America, Australia
H. nobilis	12-17 x 9-12	Cypriniformes: cyprinid (yellowtail, yellow-tailed pomfret)	posterior intestine		China
H. nodulosa (= *Bodo nodulosus*)		free-living in water			Europe
H. ophiocephala	8-11 x 4-5	Anabantiformes: channid (northern snakehead)	caecum, posterior intestine		China
H. oviformis	12-17 x 7-11	Cypriniformes: cyprinid (yellowtail)	posterior intestine		China
H. parva	3-4	Testudines: testudinid (yellow-footed tortoise, red-eared slider, leopard tortoise, Forsten's tortoise, Chaco tortoise, Asian forest tortoise), emydid (eastern box turtle, diamondback terrapin, wood turtle, pond turtles, American box turtles), geoemydid (Asian spiny turtle, Asian box turtle, leaf turtles, spotted turtle); Anura: ranid (pond frogs), bufonid (toads); Urodela: ambystomatid (mole salamanders), plethodontid (dusky salamanders), salamandrid (crested newts), Sauria: chameleonid (veiled chameleon, common chameleon, panther chameleon), gekkonid (African fat-tailed gecko), agamid (frilled dragon), scincid (broad-headed skink)	intestines, kidneys	nephritis	worldwide
H. periplanetae (syn. *Octomitus*)		Blattodea: blattid (cockroaches)	gut		Europe
H. pitheci (syn. *Octomitus*)		Primates: cercopithecid (rhesus macaque)	intestines, gall bladder		Asia
H. polymorphola	9-14 x 4-7	Cypriniformes: cyprinid (yellowtail)	posterior intestine		China
H. pulcher		Rodentia: sciurid (thirteen-lined ground squirrel)	caecum		North America
H. rodiformis	15-22 x 4-5	Cypriniformes: cyprinid (yellowtail, yellow-tailed pomfret)	posterior intestine		China
H. rostrata (now *Urophagus*)		free-living in water			Europe
H. salpae		marine Perciformes (salema porgy)			
H. spiralis		free-living in water			Europe
H. symphysodonis		Cichliformes: cichlid (blue discus)	intestines		Europe
H. skujai		free-living in water			Europe
H. truncatus		free-living in water			Europe
H. truttae	7-12 x 3-6	freshwater Cichliformes: cichlid (angelfish, banded cichlid), Cypriniformes: cyprinid (goldfish, barbs, golden rudd), Cyprinodontiformes: poeciliid (least killifish, mosquitofish), Characiformes: characid (black widow tetra)	gut, gallbladder		
H. variformis		Cypriniformes: cyprinid (grass carp, yellowfin)	intestines		China
H. vesiformis	7-9 x 5-7	Cypriniformes: cyprinid (yellowtail)	posterior intestine		China

H. wuchangensis	8-9 x 3-4	Cypriniformes: cyprinid (yellowtail)	posterior intestine		China
Genus: ***Spironucleus*** (elongate body with 2 tube-like cytopharynxes run through body) [8F]					
S. anguillae (syn. *S. mirabilis*)		freshwater Anguilliformes: anguillid (eels)	intestines		Eurasia
S. barkhanus	6-20 x 4-14	marine Salmoniformes: salmonid (Atlantic salmon, Arctic char, grayling)	intestines, liver, spleen, kidneys	enteritis, lesions	Europe
S. carassii	7-9 x 3-4	Cypriniformes: cyprinid (goldfish, Eurasian carp, crucian carp)	posterior intestine		Eurasia
S. columbae		Columbiformes: columbid (pigeons)	intestines		
S. ctenopharyngodoni	7-9 x 3-4	Cypriniformes: cyprinid (grass carp)	posterior intestine		China
S. elegans (syn. *Hexamita sinensis?*)	5-11 x 2-5	freshwater Anura: ranid (frogs); Urodela: salamandrid (salamanders); Cypriniformes: cyprinid (grass carp); Cichliformes: cichlid (angelfish)	lower intestines, rectum	emaciation	France
S. granularis		Cypriniformes: cyprinid (yellowfin)	intestines		China
S. meleagridis (syn. *Hexamita*)	8 x 3	Galliformes: phasianid (peafowl, turkey, pheasant, quail, chukar partridge)	intestines		worldwide
S. minutus		Cypriniformes: cyprinid (yellowfin)	intestines		China
S. mobilis		Anguilliformes: anguillid (eel)			Asia
S. muris	7-9 x 2-3	Rodentia: murid (rats, mice, hamsters)	small intestines, caecum	digestive disorders	worldwide
S. phycidis (syn. *Hexamita*)		marine Gadiformes: lotid (shore rockling)	intestines		Europe
S. salmonicida (separated from *S. barkhanus* on basis of molecular studies and pathogenicity)		Marine Salmoniformes: salmonid (Arctic char, Atlantic salmon, brown trout); plus aquarium fish?	muscles, organs	abscesses	Europe
S. salmonis (syn. *Octomitus, Hexamita*)	7-14 x 3-10 cysts 10 x 7	freshwater and marine Salmoniformes: salmonid (brown trout, rainbow trout, brook trout, lake trout, steelhead trout, grayling, coho salmon); Gadiformes: gadid (Atlantic cod), lotid (burbot)	intestines, other organs	enteritis	Eurasia, North America
S. salpae (syn. *Hexamita*)		marine Perciformes: sparid (salema porgy)	intestines		Europe
S. sinensis	10-12 x 5-7	Cypriniformes: cyprinid (yellowtail)	posterior intestine		China
S. torosus (syn. *torosa*)	10-19 x 3-13	marine Gadiformes: gadid (Atlantic cod, haddock, saithe, merling), lotid (burbot, cusk, fourbeard rockling)	lower intestines		Canada, Europe
S. vortens	5-21 x 3-11	Cichliformes: cichlid (freshwater angelfish, red discus); Cypriniformes: cyprinid (ide)	gastro-intestinal tract, head	hole-in-head disease, lateral line erosion	North America, Europe
S. xenocyprini (syn. *Hexamita*)		freshwater Cypriniformes: cyprinid (xenocyprinids, smallscale yellowfin)	intestines		China

Parasite morphology: Hexamitids (*Hexamita* and *Spironucleus*) form 2 different types of stages in their developmental cycles: namely flagellated trophozoites and encapsulated cysts. While trophozoites of the 2 genera do exhibit some structural differences, they are remarkably similar in morphology. They are dorsoventrally flattened and oval-pyriform in shape but become rounded just before they divide. They range in size from 3-22 µm in length by 2-13 µm in width depending on the species. Trophozoites exhibit binary axial symmetry in that they possess 2 round-elongate anterior nuclei that are laterally apposed. Each nucleus is adjacent to a cluster of 4 flagellar basal bodies (kinetosomes) collectively forming a karyomastigont unit. The kinetosomes in each cluster are arranged in 2 pairs, with 2 anterior (K1, K2) and 2 posterior (K3, R). Each kinetosome gives rise to a flagellum (eukaryotic-type, with 2 central microtubules and 9 peripheral doublets), 3 flagella (K1-3) project forwards from the cell body, while the fourth

flagellum (R) is recurrent and passes through the body in a flagellar pocket emerging posteriorly as a free flagellum. Each trophozoite therefore has paired karyomastigonts collectively giving rise to 8 flagella (6 anterior and 2 recurrent). The recurrent flagella are also associated with 2 long cytopharynxes running longitudinally through body and opening as cytostomes at the posterior end. Trophozoites lack mitochondria, dictyosomes (Golgi bodies) and microbodies, but possess glycogen granules as their main carbohydrate storage products. The genus *Hexamita* forms cells with elongate-spherical bodies, tube-like cytopharynxes with large funnel-like cytostomes, spherical nuclei with shallow kinetosomal pockets, kinetosomal complexes located anterolaterally, and the recurrent flagella associated with the surface of the nuclei. The genus *Spironucleus* forms cells with pyriform bodies (some tapering to caudal projections), narrow cytopharyngeal tubes with smaller cytostomes (not funnel-like), elongated nuclei (often sausage U-shaped) with deep kinetosomal pockets, kinetosomal complexes located anteromedially, and the recurrent flagella passing between the nuclei. Some species (e.g. *Spironucleus vortens*) have complex adorned surfaces while others (e.g. *S. salmonis, S. barkhanus, S. salmonicida*) are unadorned. Both genera form cysts which are rarely observed. The cysts are ovoid, measuring 10 x 7 μm, thick-walled and possess 2-4 nuclei, glycogen rosettes and flagellar sheaths comprising partially dissembled microtubular ribbons and striated rootlet fibres.

Site of infection: Some 19 *Spironucleus* spp. have been described, 16 species in fish (both marine and freshwater), 2 in birds and 1 in mammals, while 48 *Hexamita* spp. have been recorded; 26 species in fish, 2 in mammals, 1 in reptiles, 1 in amphibia, 1 in oysters, 1 in leeches, 2 in insects, and 14 free-living species in water and soils. Trophozoites of both genera occur extracellularly in the gastrointestinal tract, often in the upper intestines and pyloric region, sometimes in the gall bladder, caecum or rectum, but they may also occur in internal organs or in lesions on the skin. Infections in fish generally involve the intestines and sometimes internal organs, while infections in birds and mammals are confined to the small intestines and caeca.

Pathogenesis: Most hexamitid infections are asymptomatic or subclinical and have not been associated with any clinical disease, but infections by a few species (particularly heavy infections) may cause mild to severe disease: e.g. *Spironucleus salmonis* causing enteritis in salmonid fishes, *Spironucleus vortens* causing hole-in-the-head lesions in aquarium fishes, *Spironucleus meleagridis* causing enteritis in galliform birds, *Spironucleus muris* causing digestive problems in rodents, and *Hexamita parva* causing tubulointerstitial nephritis in tortoises. The parasites feed on solutes, particulate material and even bacteria by cytostomal endocytosis and phagocytosis, some cells becoming intimately associated with host cells suggesting they may feed on host tissues. Infections may cause irritation, inflammation and cellular destruction leading to organ dysfunction. Infections in birds cause bulbous fluid-filled dilatations of the small intestine (especially duodenum and upper jejunum) and the crypts become filled with parasites which attach to epithelial cells by their posterior flagella. This results in catarrhal enteritis (disease known as hexamitosis or spironucleosis) with profuse watery (sometimes yellowish) diarrhoea, cachexia, rapid weight loss without loss of appetite, emaciation, ruffled appearance with dry unkempt feathers, listlessness, weakness, and death (birds may die in coma or convulsions). Surviving birds develop some protective immunity to infection and disease but may be stunted in growth. Asymptomatic infections in adult birds may be protracted such that they act as long-term reservoirs of infection. Infections in rodents cause duodenal inflammation with the crypts becoming cystic and filled with trophozoites resulting in diarrhoea, weight loss, listlessness and weakness. Persistent infections in the kidneys of tortoises may cause tubular dilation, epithelial destruction, metastatic calcification, hyaline casts and tubulointerstitial nephritis, with the excretion of unusually concentrated urine smelling strongly of ammonia. Infections in fish may cause intestinal and/or systemic disease, the severity of which depends on parasite pathogenicity, intensity of infection, host susceptibility and tissues affected. Intestinal infections (e.g. *S. salmonis* in upper intestines, *S. elegans* in lower intestines, *S. torosa* in rectum) are often chronic but may cause damage to the mucosal epithelia resulting in catarrhal enteritis, yellowish watery or gelatinous intestinal contents, pale stringy faeces, faecal pseudocasts, excessive mucus, ascites with abdominal distension, intestinal haemorrhages, red haemorrhagic vent, anaemia, pale gills, weakness, weight loss, anorexia, emaciation with retention of large head ('pinhead' disease) and sometimes exophthalmia and/or dark body coloration. Systemic infections occur when trophozoites secrete histolytic enzymes facilitating their invasion into a variety of tissues/organs (blood, heart, liver, gall bladder, spleen kidney, eye, brain, mesenteries, abdominal cavity, musculo-skeletal system and skin). Many systemic infections are acute with rampant cellular destruction, necrosis, inflammation and congestion. Organ-specific pathologies include kidney necrosis, renal tubule atrophy, anaemia, oedema, ascites, hepatocellular necrosis, cholecystitis, cholangiohepatitis, perihepatitis, encephalitis, meningitis, dermatitis, fin discolouration, fibrosis, granuloma formation, haemorrhages, ulceration, abscess formation, skin lesions releasing yellow strings of mucus, head and lateral line erosion (hole-in-head syndrome), and cartilaginous erosions leading to locomotory disorders (corkscrew motion, swimming on one side). Infections have occasionally been associated with low reproduction rates due to the reduced hatchability of eggs and higher mortalities in young fry. Disease is rarely found in wild fish populations but can commonly occur in cultured fish when subject to stressful conditions. Predisposing factors include inadequate diet, low oxygen content, poor sanitation, over-crowding, transportation, smoltification, poor water quality, changes in temperature, concomitant infections and reduced immunocompetence. Sporadic outbreaks have been reported in many aquarium fish, with different species varying considerably in their susceptibility, but young fish (fry, fingerlings, yearlings and smolts) being most susceptible.

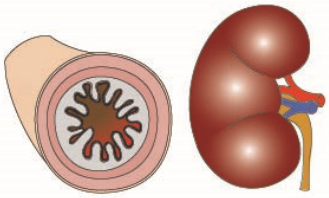
Developmental cycle and mode of transmission: Hexamitids form motile trophozoites that multiply by binary fission within vertebrate hosts, with some ultimately forming encapsulated cysts that are passed in host excretions. Infections are be transmitted between hosts by the ingestion of cysts or trophozoites passed into the external environment where they contaminate food and water

sources. Trophozoites are highly susceptible to external environmental conditions but may survive passage between hosts involved in intimate associations. Cysts are highly resistant to external environmental conditions and may survive for long periods in contaminated food and water supplies. Infections in birds and mammals typically exhibit faecal-oral transmission where cysts excreted with host faeces are ingested by new susceptible hosts. Many birds may act as long-term carriers and persistently shed cysts in their droppings. Infections in fish undergo horizontal transmission in water when stages (cysts and trophozoites) are shed in faeces, mucus strings or from haemorrhagic lesions and ingested by new hosts. It has been suggested that mucus and/or faecal material protected trophozoites from osmotic stress in aquatic environments. Infections are more prevalent in cultured fish, particularly those co-habiting aquaria.

Differential diagnosis: Some infections may be suspected on clinical grounds, mostly those causing gross lesions, such as pinhead or hole-in-head disfigurement in fish. However, most clinical infections cause nonspecific signs which could be attributed to a range of other aetiological agents. Diagnosis is conventionally confirmed by the direct detection of hexamitids in clinical samples. Parasites are usually identified by observations of motility patterns, body morphometrics (shape, size) and subcellular features (notably number and location of flagella) using high-contrast bright-field, phase-contrast or interference-contrast microscopy. It is advised that viscous media (Protoslo, methyl cellulose) be used to prepare wet mounts to slow down energetic trophozoites. Clinical samples from birds, mammals, reptiles or fish usually include fresh faeces or gastrointestinal content, while those from fish may also include skin scrapings, gut scrapings, blood smears, impression smears or tissue imprints of internal organs. Blood samples may be subject to microhaematocrit tube centrifugation to concentrate trophozoites in the buffy coat layer. Smears may be fixed and stained with Giemsa, while fixed tissues may be processed for histological examination after staining with haematoxylin and eosin, Giemsa or periodic acid Schiff's reagent. Several in vitro culture techniques have been used to grow *Spironucleus salmonis* in balanced organic medium (199) supplemented with serum and lactalbumin hydrolysate, Eagle's minimum essential medium (MEM) supplemented with foetal bovine serum, or TYI-33 medium supplemented with bile. Isolates of *S. meleagridis* have also been grown in the allantoic cavities of developing chicken and turkey embryos. An enzyme immunoassay was developed to detect host antibodies against *Spironucleus barkhaus* in Atlantic salmon, but little is known about test sensitivity or specificity. More recently, molecular biological techniques have been used to detect, identify and characterize isolates from a range of hosts by the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit ribosomal RNA, alpha-tubulin, and glutamate dehydrogenase 1 (GDH1).

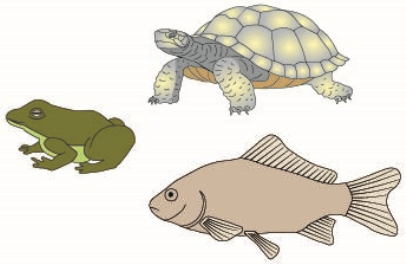
Treatment and control: Different strategies have been used to treat and control infections depending on the hosts involved. Infections in birds may be treated with nitroimidazoles (dimetridazole, metronidazole) given in feed or drinking water for several days, but their application may cause some adverse side-effects. There are also growing concerns about their toxicity and residue levels (particularly in commercial production flocks) and the potential for the development of drug resistance by parasites. It is often recommended that concurrent antibiotic treatment (e.g. oxytetracycline, chlortetracycline) be used to help control secondary bacterial infections. Preventive measures depend on regular health surveillance (testing, quarantine, culling), strict hygiene (disinfect equipment and fomites, water treatment, clean foods), good sanitation (remove litter, use raised or wiremesh floors), biosecurity (prevent contact with wild birds, personnel to take precautions) and sensible husbandry (separate host species and cohorts, avoid over-crowding, provide good nutrition, treat concomitant infections). Infections in mice that have become problematic in rodent colonies have proven difficult to treat, with the administration of metronidazole, fenbendazole or both in food, water or medicated gels not clearing infections. Some efforts to establish parasite-free colonies based on regular testing and culling infected individuals were not completely successful due to false-negative tests due to low parasite burdens or intermittent shedding. It was found necessary to re-derive mouse colonies from scratch to completely eliminate parasites. Clinical infections in the renal and urinary systems of tortoises responded well to oral dosing (via stomach tube) with metronidazole or ronidazole, although some treatments induced vomiting in several individuals. Infections in fish have been treated with a variety of chemicals administered either as bath treatments or added to foodstuffs, including the anti-protozoal nitroimidazoles (metronidazole, benznidazole, ronidazole, secnidazole, dimetridazole), nitrofurans (furazolidone), nitrothiazoles (enheptin-A), phenanthrolines (entobex), antibiotic aminoglycosides (aminosidine) and chlortetracyclines (aureomycin), and even some anthelmintics (albendazole, diethylcarbamazine, nitroscanate). Magnesium sulphate has also been used as a purgative to expel flagellates from the intestines of salmonids. The efficacy of chemical treatment was highly variable depending on host species, age cohorts, host stressors (dietary, physiological, immunological), culture conditions (facilities, crowding), concomitant infections and parasite species/strains. Producers often make recourse to preventive strategies to reduce parasite prevalence and transmission in aquaculture systems. Infections are usually controlled by avoiding the introduction of parasites (through regular testing, quarantine and culling), reducing contamination (good sanitation, cleaning tanks, gravel beds and filters), maintaining water quality (regular flushing, removing accumulated wastes, avoiding fluctuations in temperature, dissolved oxygen and pH), and providing good husbandry (separating cohorts, sensible stocking rates, good nutrition). Infections have become less problematic in salmonid hatcheries since the implementation of moist pellet diets.

Hexamita

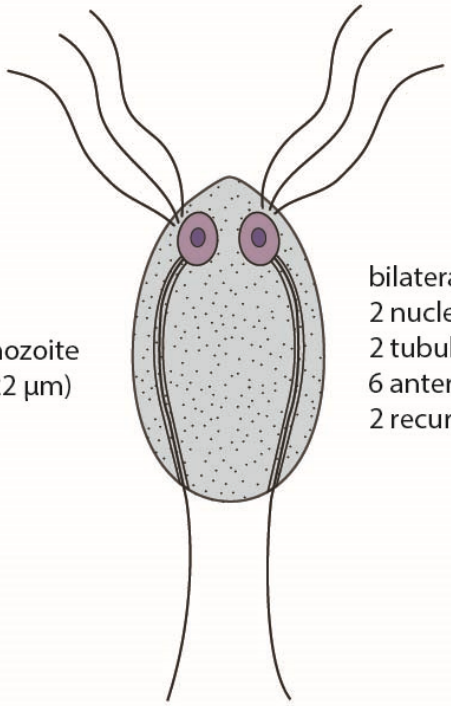


intestines, kidney
(diarrhoea, nephritis)

division by
longitudinal
binary fission



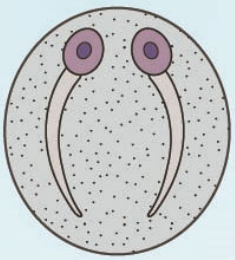
Vertebrate Hosts
(fish, tortoises, frogs)



trophozoite
(3-22 µm)

bilateral symmetry
2 nuclei
2 tubular cytopharynxes
6 anterior flagella
2 recurrent flagella

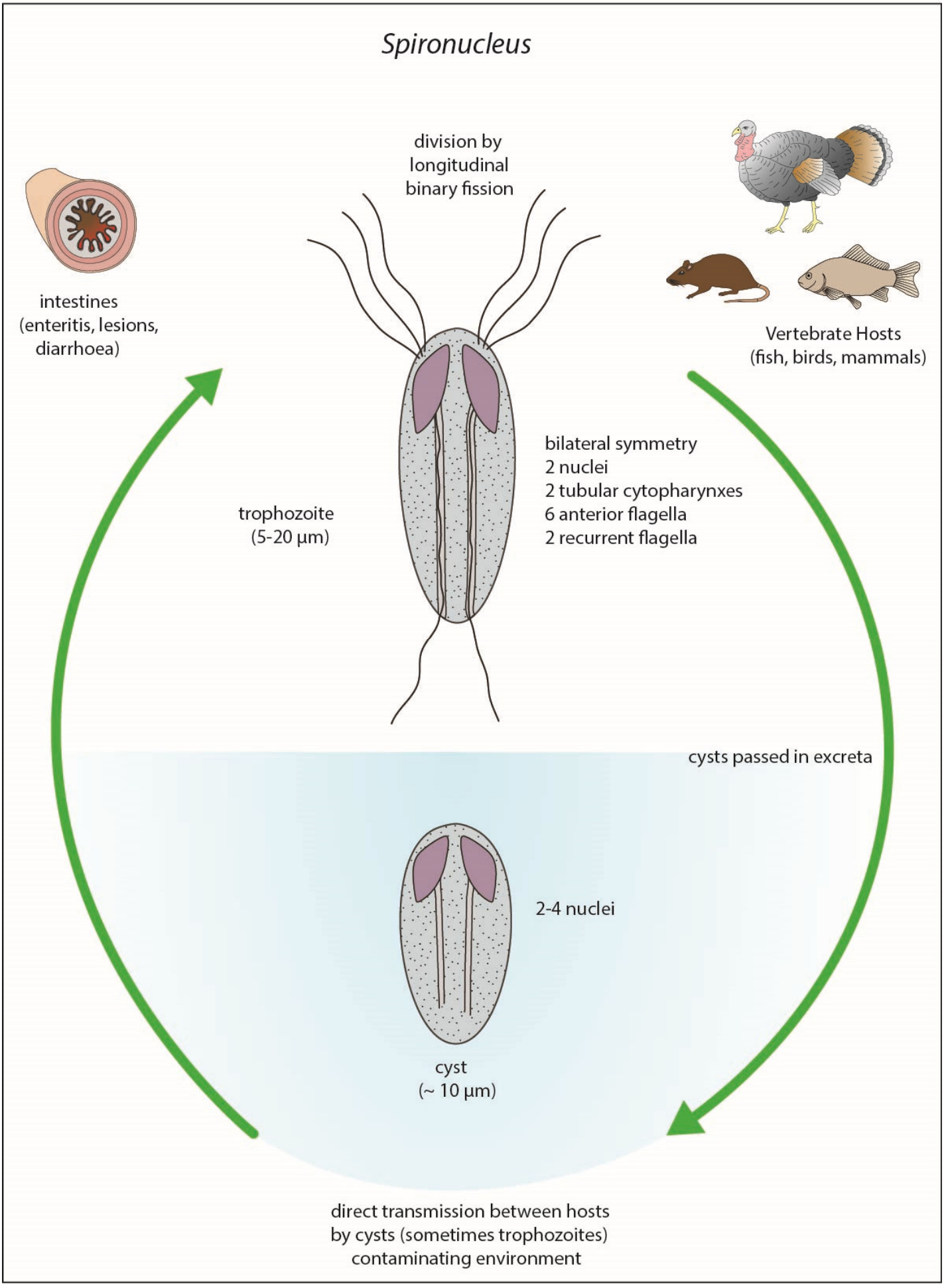
cysts passed in excreta

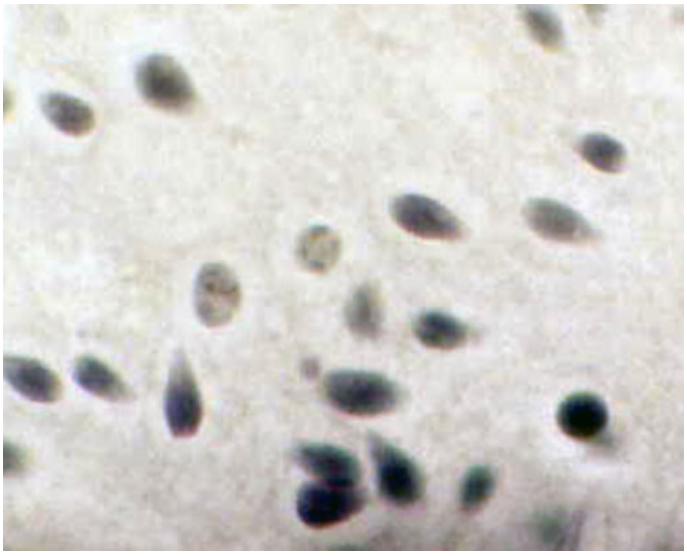


2-4 nuclei

cyst
(~ 10 µm)

direct transmission between hosts
by cysts (sometimes trophozoites)
contaminating environment

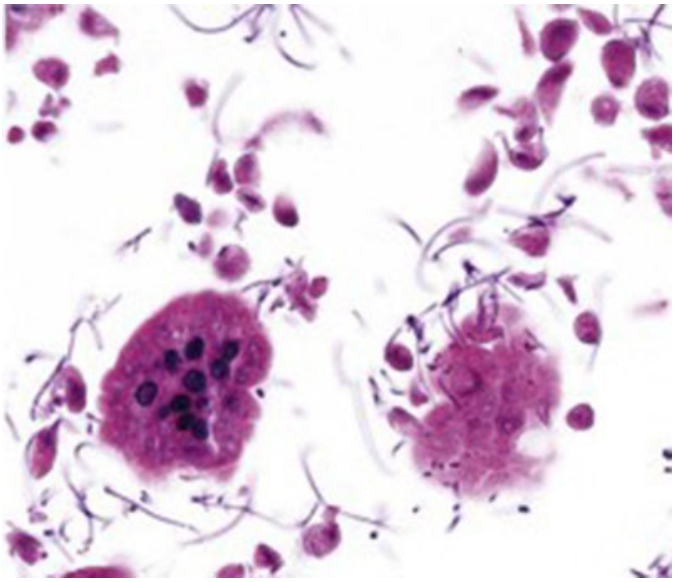

Spironucleus
division by
longitudinal
binary fission
intestines
(enteritis, lesions,
diarrhoea)
Vertebrate Hosts
(fish, birds, mammals)
trophozoite
(5-20 µm)
bilateral symmetry
2 nuclei
2 tubular cytopharynxes
6 anterior flagella
2 recurrent flagella
cysts passed in excreta
2-4 nuclei
cyst
(~ 10 µm)
direct transmission between hosts
by cysts (sometimes trophozoites)
contaminating environment



Hexamita trophozoites



Hexamita trophozoite



Spironucleus trophozoites in gut

Giardia
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Diplomonads have complex nucleus-associated karyomastigonts and are defined by the possession of two nuclei and unique bilateral symmetry (diplozoic appearance). They typically form reproductive cysts (each containing four nuclei) which facilitate their transmission between hosts. Hexamitids are parasites or commensals in mammals, birds, reptiles and fish. Several parasitic species cause severe clinical disease in man and domestic animals. All species are characterized by their pyriform shape and bilateral symmetry with two equal nuclei lying side by side, two intracytoplasmic granular axonemes and 6-8 flagella. The species *G. duodenalis* causes acute watery diarrhoea in humans and other animals, and protracted infections may lead to failure-to-thrive syndrome in infants.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Metamonad (amitochondriate flagellates with karyomastigonts)
Phylum: Fornicata (diplomonads)
Order: Diplomonadida (with 1-2 karyomastigonts (each with 4 basal bodies/flagella associated with nucleus))
Family: Hexamitidae (2 karyomastigonts arranged in binary axial symmetry)
Genus: *Giardia* (parasitic in digestive tracts of vertebrates)
Species: *G. duodenalis* (causes giardiasis (diarrhoea) in vertebrates)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)

Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Metamonads are a group of excavates (with ventral feeding groove) that have several subcellular elements associated with their flagella forming a unique mastigont (an ultrastructural complex of organelles and cytoskeletal fibrils (incl. dictyosomes (Golgi bodies), centrioles (basal bodies) and a microtubular axostyle)). The metamonads comprise fornicates (diplomonads), parabasalians (trichomonads, hypermastigids, retortamonads) and preaxostylans (oxymonads). Most metamonads are amitochondriate but have retained reduced organelles of mitochondrial origin (fornicates containing mitosomes while parabasalians possess hydrogenosomes). Members of the phylum Fornicata are characterized by the possession of a distinct feeding groove or cytopharyngeal tube. Two classes are recognized: Eupharyngea commonly found in the digestive tracts of animals; and Carpediemonadea found in anaerobic intertidal sediments. The class Eupharyngea contains 2 orders: Diplomonadida with paired karyomastigonts; and Retortamonadida with single karyomastigonts. The diplomonads (meaning 'double monads') are binucleate and most species are found in the alimentary tracts of vertebrate hosts, although several free-living species occur in organically rich waters. Diplomonads typically form reproductive cysts (each containing 4 nuclei) to facilitate their transmission. Their motile vegetative forms (trophozoites) contain 1-2 kinetids, each with 4 kinetosomes but sometimes not all flagellated, and at least one flagellum per kinetid is directed posteriorly and may be associated with the cytopharyngeal tube or groove. Two families are generally recognized, 'monozoic' Enteromonadidae containing *Enteromonas*, *Caviomonas* and *Trimitus*; and 'diplozoic' Hexamitidae containing the genera *Giardia, Hexamita*, *Spironucleus*, *Trepomonas* and *Octomitus*. Some consider the enteromonads to be a regressive group with progressive reduction in the number of flagella while others consider them to be ancestral giving rise to the diplozoic hexamitids through the failure of cytokinesis. More recently, it was proposed that the order Diplomonadida be replaced by two new orders, Distomatida (containing *Trepomonas*, *Hexamita* and *Spironucleus*) and Giardiida (containing *Giardia* and *Octomitus*), both in a novel subclass Diplozoa. Differences in the placement of families and genera within the Diplomonadida (or Fornicata) remain to be reconciled.

Family	**Genus**	**Hosts**	**Pathogenicity**
Enteromonadidae	*Enteromonas*	mammals	nonpathogenic
	Trimitus	frogs, reptiles, fish, insects	nonpathogenic
	Caviomonas	rodents	nonpathogenic
Hexamitidae	*Trepomonas*	frogs, fish, tortoises	nonpathogenic
	Octomitus	frogs, rodents	nonpathogenic
	Spironucleus	rodents, birds, fish	pathogenic in birds, fish
	Hexamita	birds, frogs, fish, insects	pathogenic in birds, fish
	Giardia	mammals, birds, frogs, reptiles	pathogenic in mammals, birds

Giardia-like flagellates were first observed in humans by Antony van Leeuwenhoek as early as 1681 but they remained unnamed until 1859 when the name *Cercomonas intestinalis* was proposed by Lambl. Unfortunately, the species name had been used previously in 1850 when revising *Bodo* and *Cercomonas* species. A similar parasite found in rabbits in 1875 was named *Hexamita duodenalis*. The genus name *Giardia* was proposed by Kunstler in 1882 for flagellates in tadpoles, although Blanchard later

suggested in 1888 that the genus name be *Lamblia*. Applying the rules of the International Code of Zoological Nomenclature regarding precedence, the name of the species in humans (if identical to that in rabbits) is *G. duodenalis*, although the synonyms *G. intestinalis* and enigmatically *G. lamblia* are still used by some agencies (especially in medical textbooks). The genus *Giardia* is characterized by cells that form binucleate pyriform trophozoites with 2 adjacent karyomastigonts, a ventral adhesive disc, 2 longitudinal axonemes and 2 tangential median bodies, as well as non-flagellated membrane-bound cysts possessing 4 nuclei.

Infections have been detected in numerous host species around the world, sometimes in association with enteric disease (known as giardiasis). The prevalence of giardiasis in humans is greater in developing rather than developed countries, particularly in pre-school and school children (surveys in developing countries ranging from 10-70% compared to 1-6% in developed countries). Infections have been recorded in many domestic and wild animal species, but most reports have not identified the species involved or have simply ascribed them to particular morphotypes. Although some 50 *Giardia* spp. have been described on the basis of host occurrence, many are morphologically indistinguishable. Early comparative studies recognized three species groups on the basis of trophozoite morphology: thin elongate trophozoites with long club-shaped median bodies assigned to the *G. agilis* group found mainly in amphibians; short stout trophozoites with small round median bodies belonging to the *G. muris* group found mainly in rodents (but also birds and reptiles); and medium-sized pyriform trophozoites with claw-shaped median bodies belonging to the *G. duodenalis* group found mainly in mammals (but also birds and reptiles). Currently, another two intermediary morpho-groups are recognized: comprising *G. microti* from muskrats and voles, and *G. ardeae* and *G. psittaci* from birds. Host specificity within each group remains contested. Epidemiological studies have frequently suggested zoonotic and water-borne transmission between mammals. Indeed, common regional names for the disease often suggest animal or water sources of human infection (e.g. beaver fever, backpacker's malady, traveler's diarrhoea). While experimental infections are difficult to perform due to biological, technical and ethical concerns, cross-transmission studies should be attempted where possible to determine the host ranges for clinical isolates. Alternatively, clinical and environmental isolates may be genetically characterized and cross-matched, akin to genetic 'fingerprinting'.

Molecular characterization techniques have identified a range of genotypes which vary in their host occurrence, host specificity and zoonotic potential. It is particularly noteworthy that multiple genotypes have been detected in individual hosts, suggesting parasite infrapopulations retain genetic heterogeneity rather than clonal dominance. Genes used to characterize types have included small subunit ribosomal RNA, glutamate dehydrogenase, triose-phosphate isomerase, elongation factor 1 alpha, variant surface protein and beta-giardin. Three main zoonotic genotypes of *G. duodenalis* have been found in humans (designated A1, A2, B3) while a growing number of other genotypes have been found in domestic animals and wildlife. Dogs and cats may harbour zoonotic genotypes (A and B) as well as species-specific genotypes (C and D for dogs and cats, F for cats only). All *Giardia* positive dogs and cats must therefore be suspected of carrying potentially zoonotic genotypes and treated accordingly. Cattle and other ruminants may also carry non-zoonotic genotypes (E) as may rats (G). When considering host records of infection, it should be remembered that many early works are confounded by incomplete descriptions or generic identifications only, while more recent molecular studies recognized many genotypes, only some of which have been assigned to particular species. In an attempt to redress this situation, it has recently been proposed that some genotypes be afforded separate species status (namely, assemblage A = *G. duodenalis*, B = *G. enterica*, C (or C/D) = *G. canis*, E = *G. bovis*, F = *G. cati*, G = *G. simondi*).

Parasite species	Hosts	Trophozoite size (and features)	Distribution
G. duodenalis (= assemblage A)	Primates: hominid (human, gorilla), atelid (southern brown howler monkey); Carnivora: canid (dog, red fox, coyote, African painted dog, wolf), felid (cat, jaguar), phocid (grey seal, harp seal, harbor seal, hooded seal), otariid (Australian sea lion); Artiodactyla: bovid (cattle, water buffalo, muskox, sheep, goat, camelid (alpaca), cervid (moose, fallow deer, reindeer, red deer, roe deer, white-tailed deer), suid (pig); delphinid (common dolphin), phocoenid (harbour porpoise), balaenopterid (minke whale); Perissodactyla: equid (horse); Rodentia: murid (mice), mustelid (ferret), castorid (beaver), chinchillid (chinchilla); Lagomorpha: leporid (rabbit); Dasyuromorphia: dasyurid (common planigale); Diprotodontia: macropodid (red kangaroo, western grey kangaroo, Parma wallaby, tammar wallaby, swamp wallaby, yellow-footed rock-wallaby, quokka), potoroid (long-nosed potoroo, rufous rat-kangaroo), phascolarctid (koala); vombatid (southern hairy-nosed wombat); phalangerid (common brushtail possum, mountain brushtail possum); Peramelemorphia: peramelid (quenda); Dasyuromorphia: dasyurid (Tasmanian devil); Galliformes: phasianid (chicken); Anseriformes: anatid (common eider); Charadriiformes: larid	12-15 x 6-8 µm (claw-shaped median bodies)	worldwide

	(herring gull, gull), Lamniformes: lamnid (mako shark); Perciformes: latid (barramundi), sparid (black bream), sciaenid (mulloway), lutjanid (snapper); Mugiliformes: mugilid (sea mullet; Sauria: lacertid (Iberian rock lizard); Bivalvia: tellinid (*Macoma* clams)		
G. enterica (= assemblage B)	Primates: hominid (human, chimpanzee, gorilla), cercopithecid (mandrill, macaque, Japanese macaque, vervet monkey, red colobus monkey), callitrichid (pygmy marmoset, cotton-top mandarin); Artiodactyla: bovid (cattle, muskox, sheep, gazelle), cervid (red deer, roe deer), suid (pig), delphinid (common dolphin, Atlantic white-sided dolphin, Risso's dolphin), phocoenid (harbour porpoise); Perissodactyla: equid (horse); Carnivora: canid (dog, red fox, coyote, African painted dog, wolf), felid (cat), phocid (grey seal, harp seal, harbor seal), otariid (Australian sea lion); Rodentia: castorid (beaver), cricetid (muskrat), chinchillid (chinchilla), mustelid (ferret), caviid (guinea pig), capromyid (Desmarest's hutia); Hyracoidea: procaviid (rock hyrax); Lagomorpha: leporid (rabbit); Diprotodontia: macropodid (red kangaroo, Parma wallaby, tammar wallaby, western grey kangaroo); Dasyuromorphia: dasyurid (tiger quoll, Tasmanian devil); Galliformes: phasianid (chicken); Struthioniformes: struthionid (ostrich); Charadriiformes: larid (herring gull, gull); Anseriformes: anatid (common eider); Perciformes: latid (barramundi), sparid (black bream), sciaenid (mulloway), lutjanid (snapper); Mugiliformes: mugilid (sea mullet); Osmeriformes: galaxiid (western minnow); Lamniformes: lamnid (mako shark), alopiid (thresher shark); Sauria (lacertid (Iberian rock lizard)	12-15 x 6-8 µm (claw-shaped median bodies)	worldwide
G. canis (= assemblages C/D)	Carnivora: canid (dog, fox, coyote, African painted dog), felid (cat), phocid (harbour seal); Artiodactyla: bovid (cattle), suid (pig), kogiid (pygmy sperm whale), delphinid (striped dolphin); Rodentia: chinchillid (chinchilla), murid (mice, bush rat); Diprotodontia: macropodid (kangaroo); Peramelemorphia: peramelid (southern brown bandicoot); rarely Primates: hominid (human)	12-15 x 6-8 µm (claw-shaped median bodies)	worldwide
G. bovis (= assemblage E)	Artiodactyla: bovid (cattle, yak, water buffalo, sheep, goat), cervid (fallow deer, moose), camelid (alpaca), suid (pig); Perissodactyla: equid (horse); Carnivora: canid (dog, fox), felid (cat); Primates: hominid (human), cercopithecid (red colobus monkey); Rodentia: murid (ash-grey mouse), Peramelemorphia: peramelid (southern brown bandicoot); Perciformes: latid (barramundi), sciaenid (mulloway); Sauria: lacertid (Bocage's wall lizard)	12-15 x 6-8 µm (claw-shaped median bodies)	worldwide
G. cati (= assemblage F)	Carnivora: felid (cat, lion): Rodentia: murid (bush rat); rarely Primates: hominid (human); Artiodactyla: phocoenid (harbour porpoise), delphinid (striped dolphin)	12-15 x 6-8 µm (claw-shaped median bodies)	worldwide
G. simoni (= assemblage G)	Rodentia: murid (rats, mice), castorid (beaver)	12-15 x 6-8 µm (claw-shaped median bodies)	Europe, Australia
Assemblage H (un-named)	Carnivora: phocid (grey seal, harbor seal); Charadriiformes: larid (gull)	not determined	North America
G. peramelis (= quenda genotype)	Peramelemorphia: peramelid (southern brown bandicoot)	not determined	Australia
G. muris	Rodentia: murid (mice, rats, gerbil), cricetid (hamster, common vole)	9-12 x 5-7 µm (rounded median bodies)	worldwide
G. cricetidarum	Rodentia: cricetid (Djungarian hamster, Campbell's dwarf hamster, golden hamster)	12-18 x 8-12 µm (round median bodies)	China
G. microti	Rodentia: cricetid (California vole, muskrat); Perciformes: latid (barramundi)	12-15 x 6-8 µm (cysts with 2	North America

		trophozoites)	
G. ardeae	Pelecaniformes: ardeid (grey heron, Cocoi heron, rufous heron, black-crowned night heron, great blue heron), threskiornithid (glossy ibis); Accipitriformes: cathartid (turkey vulture); Suliformes: anhingid (American darter)	10 x 6.5 µm (round-rod median bodies)	North America
G. psittaci	Psittaciformes: psittaculid (budgerigar), psittacid (barred parakeet)	14 x 6 µm (claw-shaped median bodies, lack flange/groove)	Central and North America
G. agilis	Anura: pipid (toads), ranid (frogs) [tadpoles]	20-30 x 4-5 µm (club-shaped median bodies)	Americas, Africa, Europe
G. varani	Sauria: varanid (Nile monitor, Bengal monitor)	12-16 x 8-10 µm (median bodies rare)	Asia, India (North America?)

Other *Giardia* species that have been described (prior to molecular characterization techniques becoming available) include: *G. wenyoni* from Primates: lorisid (slender loris), *G. bradypi* from Pilosa: bradypodid (pale-throated sloth), *G. caprae* from Artiodactyla: bovid (goat, sheep), *G. equii* from Perissodactyla: equid (horse), *G. dasi* from Carnivora: viverrid (palm civet), *G. hegneri* from Carnivora: viverrid (Malay civet), *G. irarae* from Carnivora: mustelid (tayra), *G. suricatae* from Carnivora: herpestid (meerkat), *G. otomyis* from Rodentia: murid (South African vlei rat), *G. beckeri* from Rodentia: sciurid (ground squirrel), *G. caviae* from Rodentia: caviid (guinea-pig), *G. chinchillae* from Rodentia: chinchillid (chinchilla), *G. viscaciae* from Rodentia: chinchillid (viscacha), *G. ondatrae* from Rodentia: cricetid (muskrat), *G. pitymysi* from Rodentia: cricetid (Savi's pine vole), *G. botauri* from Pelecaniformes: ardeid (American bittern), *G. floridae* from Pelecaniformes: ardeid (little blue heron) *G. herodiadis* from Pelecaniformes: ardeid (intermediate egret), *G. hyderabadensis* from Pelecaniformes: ardeid (cattle egret), *G. nycticori* from Pelecaniformes: ardeid (black-crowned night heron), *G. pseudoardeae* from Pelecaniformes: ardeid (great blue heron), *G. beltrani* from Passeriformes: passerid (house sparrow), *G. marginalis* from Passeriformes: lariid (red-backed shrike), *G. melospizae* from Passeriformes: passerellid (swamp sparrow), *G. sturnellae* from Passeriformes: icterid (western meadowlark), *G. recurvirostrae* from Charadriiformes: recurvirostrid (avocet), *G. sanguinis* from Accipitriformes: accipitrid (black-winged kite), *G. tucani* from Piciformes: ramphastid (Ariel toucan), *G. serpentis* from Serpentes: viperid (Cape viper), and *G. denticis* [possibly *Hexamita*] from Perciformes: sparid (Carpenter seabream). In one extraordinary case, *Giardia* trophozoites were even detected inside the mouth and anterior gut of hookworms (*Ancylostoma caninum*) recovered from a dog (probably the result of accidental uptake rather than an instance of hyperparasitism).

Parasite morphology: *Giardia* parasites form two developmental stages: trophozoites and cysts. The trophozoites are pyriform (10-30 µm long) and appear to have bilateral symmetry due to the possession of two adjacent karyomastigonts (nuclear-flagellar basal body units). Each trophozoite therefore possesses two nuclei (which are identical) and eight flagella (two anterior, two lateral, two ventral and two caudal). The trophozoites also have a prominent ventral adhesive disc, two longitudinal axonemes and two tangential curved median bodies. Cysts are ovoid to ellipsoid (11-14 µm in length by 7-10 µm in width), membrane-bound (sometimes imparting a halo-appearance) and contain four nuclei, axonemes and median bodies.

Site of infection: Flagellated trophozoites are found in the small intestines of their hosts, especially the duodenum. Trophozoites have been observed swimming with a distinct corkscrew motion in luminal content as well as adhering to the gut mucosal surface with their ventral adhesive discs (when they detach, they leave distinct oval impressions in the microvillous layer). Trophozoites are occasionally passed together with cysts in stool samples, but the trophozoites do not survive long in the external environment (unlike cysts which are very hardy).

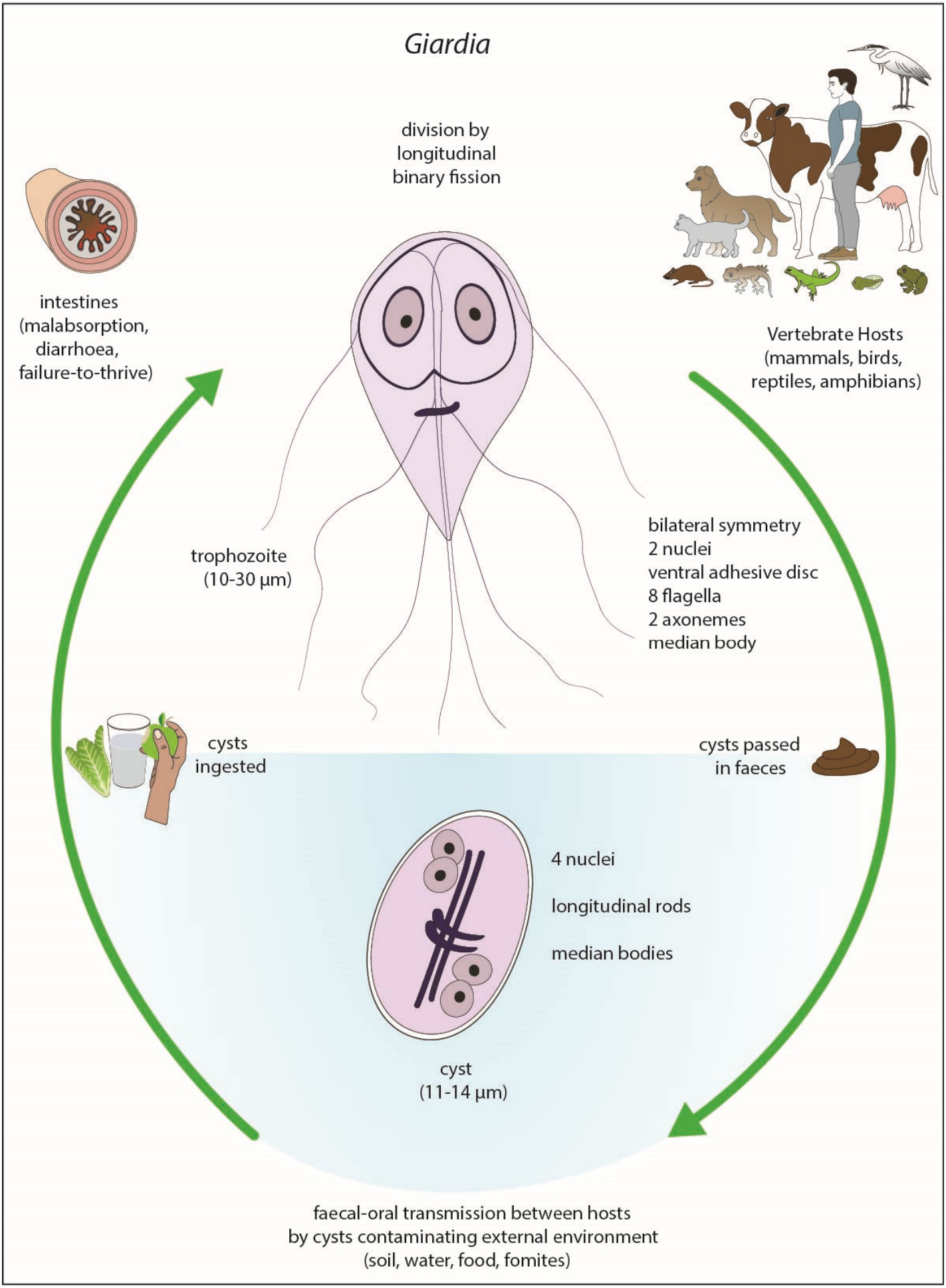
Pathogenesis: *Giardia* spp. may cause asymptomatic infections, acute transient diarrhoea for 1-2 weeks or chronic protracted diarrhoea for more than two weeks. Infections interfere with the normal absorptive functioning of the small intestines, thereby causing osmotic overload of the large intestines resulting in watery or foul-smelling mucoid diarrhoea that may be acute, chronic or intermittent. Attached parasites may physically blanket the small intestinal mucosa significantly reducing the surface area for absorption. Infections damage and increase the turnover rate of epithelial cells culminating in villous atrophy which further reduces the surface area for absorption. Various parasite products have been shown to have detrimental effects on intestinal mucosal cells; including the induction of apoptosis, disruption of the microvillous layer (brush border), disruption of tight cell junctions, and increased membrane permeability. These factors contribute to malabsorption of fats and other nutrients resulting in watery diarrhoea and steatorrhea accompanied by dehydration, intestinal pain (bloating and cramps), flatulence, malaise and sometimes headache. Many patients also become lactose intolerant over the course of infection. Most clinical infections are self-limiting and resolve spontaneously but some persist for months with intermittent diarrhoea (frothy yellow or greasy foul-smelling stools), weight loss, retarded growth and ‘failure-to-thrive’ syndrome. Chronic infections have also been associated with food allergies, arthritis, chronic

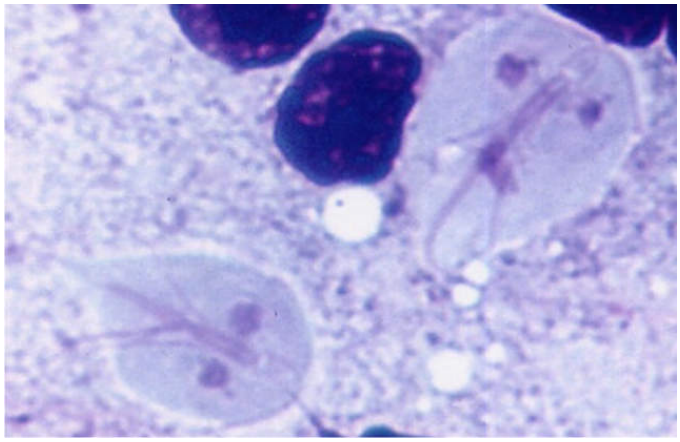
fatigue and irritable bowel syndrome. Young individuals are most susceptible to clinical infections and focal outbreaks are common in child day-care centres and among intensively-reared and housed young animals. Not all infected individuals, however, develop clinical signs but may remain asymptomatic carriers excreting cysts contributing to environmental contamination.

Developmental cycle and mode of transmission: Infections are passed between hosts by the faecal-oral transmission of encysted parasite stages. When trophozoites pass through the colon, they form non-flagellated cysts which are excreted and contaminate the environment. The cysts are said to be reproductive in that they undergo nuclear division as they mature becoming quadrinucleate. Cysts passed in host faeces are immediately infectious. Following their ingestion by a new host, they excyst in the small intestine releasing two trophozoites which attach to the microvillous layer (brush border) of the intestinal epithelial cells (beneath the mucus layer). The trophozoites subsequently feed and multiply asexually by binary fission (a type of mitosis). Excystation stimuli include various post-gastric digestive conditions (bile salts, enzymes, pH, microaerophilic conditions, etc.). Most infections are transmitted accidentally by 'hand-to mouth' contact whereby faecal contaminants on fomites (objects) are transferred to the mouth (e.g. contaminated fingers, utensils, clothing, etc.). The cysts are quite resistant to external environmental conditions and can survive for months, particularly in cool moist conditions. The cysts also contaminate water supplies and cause infections when subsequently ingested with drinking water or the consumption of food-stuffs diluted or washed with contaminated water. *Giardia* cysts have been detected on many food types, including fruit, vegetables, dairy products, meat and shellfish. Infections have also been associated with recreational water use, including swimming pools, lakes and water-theme parks. Many countries have recorded marked seasonal differences in the occurrence of giardiasis, with latitudinal variation depending on both climatic conditions (shown to be conducive to cyst survival) and animal husbandry practices (when susceptible neonates are most abundant). Disease was more prevalent in the rainy season in tropical countries, during autumn in subtropical countries and during spring in countries with temperate climates.

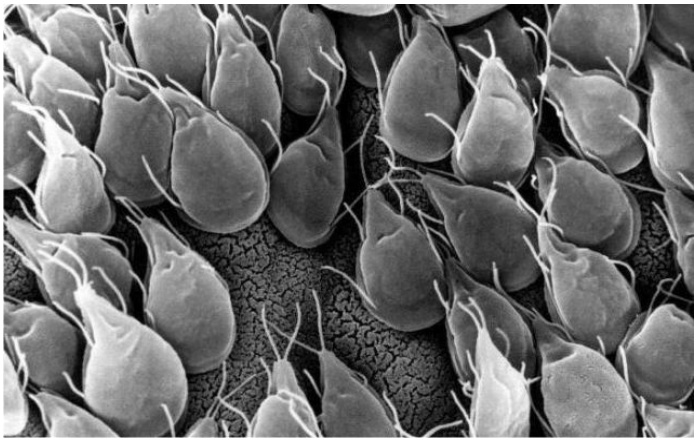
Differential diagnosis: Distinctive cysts of the parasite may be detected by routine coprological examination of faecal smears stained with iodine, trichrome or iron haematoxylin, or by microscopy of faecal concentrates prepared by sedimentation/flotation techniques. The sensitivities of these diagnostic tests are poor due to the intermittent excretion of the small cysts, so multiple faecal samples should be examined over several days. Endoscopic techniques (gastroscopy through to duodenum) have been used in chronic cases to detect trophozoites in intestinal aspirates or biopsy material. A string test has also been used to recover and examine bile-stained mucus for trophozoites. More recently, sensitive and specific immunological techniques (enzyme immuno-assays, immuno-chromatography, and fluorescent-labelling) have been developed to detect parasite antigens in faecal preparations (copro-antigen tests). Monoclonal antibody immuno-reagents are also used in many countries to detect cysts in environmental samples (water sources and food preparations) using immuno-magnetic separation techniques, enzyme immuno-assays or fluorescent-activated cell sorting. Many countries have now introduced molecular diagnostic tools to genotype isolates using polymerase chain reaction (PCR) techniques to amplify parasite DNA [small subunit ribosomal RNA (*18S rRNA*), glutamate dehydrogenase (*gdh*), triose phosphate isomerase (*tpi*), beta-giardin (*bg*), elongation factor 1-alpha (*ef1a*) and variable surface protein (*vsp*) genes], thus allowing the molecular epidemiology of infections to be investigated.

Treatment and control: Metronidazole is the drug of choice for giardiasis despite mild side-effects (such as nausea), but it should not be used in pregnant women due to the risk of birth defects. Recently, there are growing problems with the emergence of metronidazole-resistant parasite strains in several countries. Other nitroimidazole derivatives (tinidazole), nitrofurans (furazolidone), acridine drugs (quinacrine) and microtubule inhibitor anthelmintics (albendazole, fenbendazole, febantel) have been reported effective. Conventional water treatment procedures (filtration and chlorination) are not wholly effective against *Giardia* cysts as they are quite small and resistant to many chemical disinfectants. Control depends largely on good sanitation, proper effluent disposal and effective water treatment (well-maintained sand filtration or microfiltration, optimum chlorination or ozonation, boil water alerts during outbreaks). Hygienic conditions should be maintained, particularly where susceptible hosts are crowded together in intensive facilities (daycare centres, nursing homes, kennels, dairies, etc.). Giardiasis is a notifiable disease in many developed countries, with outbreaks eliciting actionable investigations and interventions by public health agencies. This facilitates better risk assessment, disease management, health education, public awareness and more effective prevention and control programs.

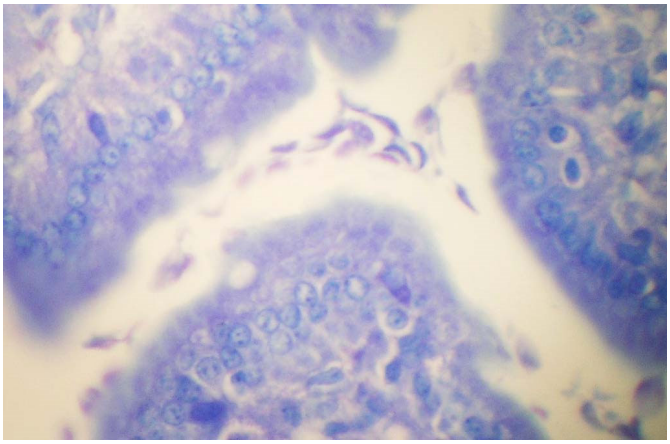

Giardia
division by
longitudinal
binary fission
intestines
(malabsorption,
diarrhoea,
failure-to-thrive)
Vertebrate Hosts
(mammals, birds,
reptiles, amphibians)
trophozoite
(10-30 µm)
bilateral symmetry
2 nuclei
ventral adhesive disc
8 flagella
2 axonemes
median body
cysts
ingested
cysts passed
in faeces
4 nuclei
longitudinal rods
median bodies
cyst
(11-14 µm)
faecal-oral transmission between hosts
by cysts contaminating external environment
(soil, water, food, fomites)



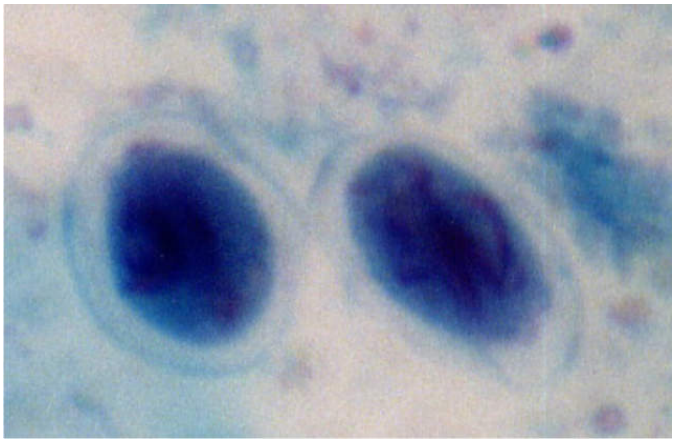
Giardia trophozoites



Giardia trophozoites on gut wall



Giardia trophozoites in gut kumen



Giardia cysts in faeces

Trypanosoma (fish species)
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Trypanosomes have a single flagellum and they form 4 main developmental stages: trypomastigotes (with a posterior kinetoplast and an emergent flagellum forming a long undulating membrane); epimastigotes (with an anterior kinetoplast and an emergent flagellum forming a short undulating membrane); promastigotes (with an anterior kinetoplast and a short emergent flagellum, but no undulating membrane); and amastigotes (with a kinetoplast but no emergent flagellum or undulating membrane). Many trypanosome species are parasitic only in insects whereas others are transmitted by invertebrate vectors to a wide range of vertebrate hosts, including freshwater and marine fish. Piscine trypanosomes are transmitted by leech vectors and infections are generally nonpathogenic although several species may cause anaemia and anorexia in cultured fish.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Discoba (diverse group supported robustly by molecular studies)
Phylum: Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass: Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order: Trypanosomatida (parasitic, single anterior flagellum, often forming undulating membrane)
Family: Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)
Genus: *Trypanosoma* (vector-borne haemoparasites)
Species: various species cause infections in fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates	direct (f-o)

parabasal body)		membrane)		(gut)	
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans are a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)
	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*).

Trypanosomatids are dixenous (2-host) parasites with indirect transmission cycles between vertebrates and invertebrate vectors. *Trypanosoma* spp. form trypo- and/or a-mastigote stages in the blood/tissues of vertebrate hosts, and epi- or pro-mastigote stages in invertebrate haematophagous vectors. Infections have been found in a range of vertebrate species (mammals, birds, reptiles, amphibians and fish) with many different types of haematophagous invertebrates (leeches, bugs, flies, fleas) implicated as vectors or paratenic hosts. Recent molecular phylogenetic studies have validated the separation of mammalian salivarian and stercorarian trypanosomes, but indicated complex placements for trypanosomes from non-mammalian hosts, despite earlier suggestions that they be assigned to separate subgenera. Many clades have been identified, most associated with particular vertebrate or invertebrate hosts, or both, suggesting that 'host-fitting' rather than 'co-speciation' has been the principal mechanism for trypanosome evolution. Comparative phylogenetic studies have shown trypanosomes from fish clustered together with those from tortoises (both groups being transmitted by aquatic leeches). Fish trypanosomes have previously been allocated to two large groupings, comprising pleomorphic (polymorphic) and monomorphic species. The trypomastigotes of monomorphic species are more or less consistent in morphology for each species with little variation in size and/or shape/index (length:width ratio). Those of pleomorphic species demonstrate considerable variation in size, shape index, position of internal organelles (kinetoplast and nucleus), presence/absence of nuclear karyosome, surface striations and/or cytoplasmic granules, architecture of undulating membrane and length of free flagellum. Many pleomorphic species apparently undergo sequential development involving 'young', 'intermediate' and 'adult' forms generally becoming larger and more complex in structure, but often with mensural (morphometric) overlap. It was earlier suggested that pleomorphic trypanosomes of fish be allocated to a distinct *Trypanosoma* subgenus called *Haematomonas*, but molecular phylogenetic studies do not support their separate classification from other piscine trypanosomes. Different species have been identified in bony and cartilaginous fishes as well as from freshwater and marine fish (with a few recorded in estuarine or brackish water species), but little information is available on their actual host specificity. To date, the only known vectors of piscine trypanosomes have been leeches as determined by field observations, dissections and some experimental studies.

***Trypanosoma* species**	**Mastigote length (µm)**	**Hosts [disease]**	**Vectors**	**Distribution**
Species in freshwater fish				
T. abeli		Siluriformes: loricariid (armoured catfish)		South America
T. abramidis		Cypriniformes: cyprinid (common bream, blue bream, white bream, common roach)		Eurasia
T. acanthobramae		Cypriniformes: cyprinid (Tigris bream)		Iraq
T. acerinae	33-49	Perciformes: percid (Eurasian ruffe); Cypriniformes: leuciscid (minnows)	Clitellata: glossiphoniid (*Hemiclepsis marginata*)	Eurasia, North America
T. affonsoi	58	Siluriformes: loricariid (armoured catfish)		Brazil
T. albopunctatus	23-41	Siluriformes: loricariid (pleco catfish)		Brazil
T. alhussaini		Siluriformes: clariid (African sharptooth catfish)		Africa
T. aligaricus		Anabantiformes: channid (spotted snakehead) [anaemia]		India
T. amurense	23-32	Scorpaeniformes: cottid (Kessler's sculpin, Amur sculpin)		Asia
T. anabasi		Anabantiformes: anabantid (climbing perch)		India
T. andradesilvae		Siluriformes: clariid (African sharptooth catfish)		Mozambique
T. anguillicola	35-40	Anguilliformes: anguillid (giant mottled eel, long-finned eel, speckled longfin eel)		Australasia
T. anurum	25-33	Acipenseriformes: acipenserid (Japanese sturgeon)		China

T. anusi		Siluriformes: loricariid (cascudo viola)		Brazil
T. aori		Siluriformes: bagrid (Gangetic mystus)		India
T. arabica		Siluriformes: silurid (Tigris catfish)		Iraq
T. aristichthysi	32	Cypriniformes: cyprinid (bighead carp)		China
T. armeti		Synbranchiformes: mastacembelid (zig-zag eel)		India
T. ataevi		Gobiiformes: gobiid (ratan goby, Kessler's goby, monkey goby, Caspian tadpole goby)		Eurasia
T. atti		Siluriformes: silurid (helicopter catfish)		India
T. aurangabadense		Synbranchiformes: mastacembelid (zig-zag eel)		India
T. azoubeli		Siluriformes: loricariid (armoured catfish)		South America
T. baigulensis		Cypriniformes: cyprinid (reba carp, chela carp)		India
T. bancrofti	27-50	Siluriformes: plotosid (eeltail catfish)		Australia
T. barbae/barbi		Cypriniformes: cyprinid (common barbel)		Europe
T. barretoi	36	Siluriformes: loricariid (armoured catfish)		Brazil
T. barrosi	54	Siluriformes: loricariid (suckermouth catfish)		Brazil
T. basrensis		Cypriniformes: cyprinid (Tigris asp)		Iraq
T. batai		Cypriniformes: cyprinid (bata)		India
T. batrachi		Siluriformes: clariid (walking catfish, broadhead catfish) [anaemia]		India, Asia
T. batrachocephali		Gobiiformes: gobiid (toad goby)		Russia
T. bengalensis	17	Siluriformes: bagrid (Day's mystus)		India
T. birmanii	57	Siluriformes: loricariid (Commerson's pleco)		Brazil
T. blenclini		Blenniformes: blenniid (horned blenny), clinid (snaky clipfish)		Atlantic
T. bliccae		Cypriniformes: cyprinid (common bream, blue bream, bronze bream, common roach)		Eurasia
T. bourouli		Synbranchiformes: synbranchid (marbled swamp eel)		Brazil
T. breindli (syn. *T. laverani nom. preocc.*)		Cypriniformes: cyprinid (bleak)		Europe
T. cancili		Beloniformes: belonid (freshwater garfish)		India
T. carasobarbi		Cypriniformes: cyprinid (Mesopotamian himri)		Iraq
T. carassii (syn. *T. nikitini, scardinii, tincae, T. wincheniense, winitschenkae*)	15-40	Cypriniformes: cyprinid (common carp, crucian carp, goldfish, asp, tench, ide, rudd, common bream, blue bream, common roach), cobitid (spined loach, Siberian spined loach, weatherfish); Esociformes: esocid (northern pike); Perciformes: percid (European perch, ruffe); Salmoniformes: salmonid (Baikal black grayling, Arctic charr); Scorpaeniformes: cottid (Kessler's sculpin) [anaemia]	Clitellata: piscicolid (*Piscicola geometra*), glossiphoniid (*Hemiclepsis marginata*)	Eurasia
T. catostomi	50	Cypriniformes: catostomid (white sucker)		North America
T. chagasi		Siluriformes: loricariid (suckermouthed catfish)		Brazil
T. channai	23-44	Anabantiformes: channid (spotted snakehead)		India
T. chaudhuryi		Cichliformes: cichlid (Mozambique tilapia)		Africa
T. cheni		Anabantiformes: channid (northern snakehead)		China
T. chetostomi	27-35	Siluriformes: loricariid (catfish)		Brazil
T. choudhuryi		Cichliformes: cichlid (Mozambique tilapia)		India
T. clariae		Siluriformes: clariid (walking catfish, broadhead catfish)		India, Asia
T. cobitis (syn. *T. barbatulae, elegans, langeroni, occidentalis, phoxini*)	25-47	Cypriniformes: cyprinid (crucian carp, gudgeon), cobitid (spined loach), leuciscid (common minnow, Eurasian minnow), nemacheilid (stone loach); Scorpaeniformes: cottid (inland riffle sculpin, torrent sculpin, European bullhead, weatherfish), gasterosteid (three-spined stickleback, nine-spine stickleback)	Clitellata: glossiphoniid (*Hemiclepsis marginata*)	Eurasia, North America

		[emaciation]		
T. colisi		Anabantiformes: osphronemid (banded gourami)		India
T. commersoni		Siluriformes: loricariid (Commerson's pleco)		Brazil
T. ctenopharyngodoni		Cypriniformes: cyprinid (grass carp)		China
T. cyanophilum		Cichliformes: cichlid (redbelly tilapia)		Africa
T. cyprinioni		Cypriniformes: cyprinid (kangal fish)		Iraq
T. danilewskyi (possible synonym of *T. carassii*)	15-40	Cypriniformes: cyprinid (common carp, crucian carp, goldfish, tench, barbel, Malabar danio, common shiner), catostomid (white sucker); Perciformes: percid (rainbow darter); Siluriformes: heteropneustid (Asian stinging catfish), ictalurid (brown bullhead); Anguilliformes: anguillid (European eel) [anaemia]	Clitellata: piscicolid (*Piscicola geometra*), glossiphoniid (*Hemiclepsis marginata*)	Eurasia
T. dogieli		Cypriniformes: cyprinid (ide, white-finned gudgeon, Cherskii's thicklip gudgeon); Gobiiformes: gobiid (gobies)		Asia
T. dominguesi	31	Siluriformes: loricariid (armoured catfish)		Brazil
T. dorbygnii	35-48	Siluriformes: doradid (marbled thorny catfish)		Brazil
T. elongatus		Anabantiformes: channid (spotted snakehead)		India
T. ezenami		Salmoniformes: salmonid (brown trout)		Atlantic
T. ferreirae	50-62	Characiformes: characid (tetras)		Brazil
T. francirochai	45	Siluriformes: loricariid (franciroch catfish)		Brazil
T. fulvidraco		Siluriformes: bagrid (yellowhead catfish)		China
T. gachuii		Anabantiformes: channid (dwarf snakehead)		India
T. gadrii		Siluriformes: clariid (walking catfish)		India
T. ganderi		Cypriniformes: cyprinid (largelip labeo)		Africa
T. gandhei		Cypriniformes: cyprinid (carp)		West Africa
T. garrae		Cypriniformes: cyprinid (red garra)		Iraq
T. gasimagomedovi		Anabantiformes: channid (dwarf snakehead); Scorpaeniformes: gasterosteid (Ukrainian stickleback)		Asia
T. gerraroi		Cichliformes: cichlid (Mozambique tilapia)		Africa
T. godavariense		Anabantiformes: channid spotted snakehead)		Asia
T. gracile		Cypriniformes: cyprinid (koi carp)		Eurasia
T. granulosum	20-80	Anguilliformes: anguillid (European eel)	Clitellata: piscicolid (*Piscicola geometra*), glossiphoniid (*Hemiclepsis marginata*)	Europe
T. gorbygnii		Siluriformes: doradid (thorny catfish)		South America
T. guaibensis		Siluriformes: loricariid Commerson's pleco, whiptail catfish)		Brazil
T. hypostomi	25-40	Siluriformes: loricariid (gold speckled pleco)		Brazil
T. iheringi	42	Siluriformes: doradid (marbled spiny catfish)		Brazil
T. immanis	105-132	Siluriformes: loricariid (whiptail catfish)		Brazil
T. inexpectata (syn. *T. leucisci*)		Cypriniformes: cyprinid (orfe, dace, roach)		Eurasia
T. itoi	26	Siluriformes: loricariid (unspecified catfish)		Brazil
T. lamanoi	57	Siluriformes: loricariid (suckermouth catfish)		Brazil
T. langeroni		Scorpaeniformes: cottid (European bullhead)		Europe
T. larai	32-47	Characiformes: prochilodontid (prochilos)		South America
T. latinucleata		Siluriformes: silurid (Amur catfish)		Asia
T. limae	67	Characiformes: erythrinid (trairao)		Brazil
T. liocassis		Siluriformes: bagrid (Ussuri catfish)		Asia
T. lopesi	32	Siluriformes: loricariid (northeast Brazilian pleco)		Brazil
T. loricariae	20	Siluriformes: loricariid (unspecified catfish)		Brazil

T. lotai		Gadiformes: lotid (burbot)		Europe
T. luciopercae		Perciformes: percid (zander, Volga zander)		Eurasia
T. macrodonis	48	Characiformes: erythrinid (wolf fish)		Brazil
T. magdalenae		Cichliformes: cichlid (Krauss' cichlid)		South America
T. magna		Scorpaeniformes: cottid (stone sculpin, deepwater sculpin, pallid sculpin)		Russia
T. maguri		Siluriformes: clariid (walking catfish), bagrid (striped dwarf catfish) [anaemia]		India
T. malopteruri	39	Siluriformes: malapterurid (electric catfish)		Africa
T. mansouri		Cichliformes: cichlid (redbelly tilapia)		Africa
T, marathwadense		Cypriniformes: cyprinid (brown mahseer)		Asia
T. margaritiferi	22-46	Siluriformes: loricariid (yellow-spotted hypostomus)		Brazil
T. markewitschi		Siluriformes: silurid (wels catfish)		Asia
T. mastacembeli		Synbranchiformes: mastacembelid (zigzag eel)		India
T. micropteri		Perciformes: centrarchid (largemouth bass)		China
T. minutum	25	Cypriniformes: cyprinid (lake skygazer)		China
T. mrigali		Cypriniformes: cyprinid (mrigal carp)		India
T. mukasai	25-50	Cichliformes: cichlid (thinface cichlid, Alluaud's haplo, purpleface largemouth, yellowbelly bream, cinereus haplo, Lake Victoria cichlid, blue Victoria mouthbrooder, banded tilapia, three-spotted tilapia, Nile tilapia, Singida tilapia, Mozambique tilapia, Victoria tilapia); Siluriformes: bagrid (semutundu), clariid (African sharptooth catfish, snake catfish), clareotid (Zambezi grunter), mochokid (spotted squeaker, upside-down catfish), nemacheilid (Kashmir triplophysa-loach), schilbeid (silver catfish); Cypriniformes: cyprinid (crucian carp, sattar snowtrout); Osteoglossiformes: mormyrid (elephant-snout fish)		Africa
T. mukundi		Siluriformes: heteropneustid (Asian stinging catfish)		India
T. murtii		Synbranchiformes: mastacembelid (zigzag eel)		Asia
T. mylopharyngodoni	44	Cypriniformes: cyprinid (black carp)		China
T. mysti		Siluriformes: bagrid (Gangetic mystus)		India
T. mystuii		Siluriformes: bagrid (Tigris mystus)		Iraq
T. nandi		Perciformes: nandid (Gangetic leaffish)		India
T. napolesi		Cichliformes: cichlid (Mozambique tilapia)		East Africa
T. neinavana	33-38	Cypriniformes: cyprinid (shabout)		Iraq
T. notopteri		Osteoglossiformes: notopterid (bronze featherback)		Asia
T. nupelianus	18	Siluriformes: loricariid (black armoured catfish)		Brazil
T. orientalis		Cypriniformes: cyprinid (spotted steed, stone moroko); Siluriformes: silurid (Amur catfish)		Asia
T. pancali		Synbranchiformes: mastacembelid (barred spiny eel)		India
T. parasiluri		Siluriformes: silurid (Amur catfish)		Asia
T. pelligrini		Anabantiformes: osphronemid (fork-tailed paradisefish)		Asia
T. percae	18-57	Perciformes: percid (European perch, yellow perch); Salmoniformes: salmonid (brook trout)	Clitellata: piscicolid (*Piscicola geometra*), glossiphoniid (*Hemiclepsis marginata*)	North America, Eurasia
T. petenuscii	50	Siluriformes: loricariid (unspecified armoured catfish)		Brazil

T. phaleri	12- 89	Amiiformes: amiid (bowfin)	Clitellata: glossiphoniid (*Desserobdella phalera*)	North America
T. piavae	44	Characiformes: characid (tetras)		Brazil
T. pingi		Cypriniformes: cyprinid (goldfish)		China
T. pintoi	45	Siluriformes: loricariid (armoured catfish)		Brazil
T. piracicaboe	36-42	Siluriformes: loricariid (cascudo espada)		Brazil
T. piscidium		Anabantiformes: osphronemid (banded gourami)		India
T. plecostomi	20-38	Siluriformes: loricariid (armoured catfish)		Brazil
T. pradoi	20-48	Siluriformes: loricariid (cascudo)		Brazil
T. pseudobagri		Siluriformes: bagrid (unspecified catfish)		Asia
T. punctati	34	Anabantiformes: channid (spotted snakehead)		India
T. puntii		Cypriniformes: cyprinid (kolus barb)		India
T. qadrii		Siluriformes: clariid (walking catfish)		Asia
T. rayi		Cypriniformes: cyprinid (minnow)		Europe
T. rebeloi		Cichliformes: cichlid (Mozambique tilapia)		East Africa
T. regani	21-53	Siluriformes: loricariid (giant white-spot pleco)		Brazil
T. remaki (possible synonym of *T. schulmani*)	bimorphic: 10-25, 45-70	Esociformes: esocid (northern pike); Cypriniformes: cyprinid (ide, tench, common roach)	Clitellata: piscicolid (*Piscicola geometra*), glossiphoniid (*Hemiclepsis marginata*)	Eurasia, North America
T. rohilkhandae		Anabantiformes: channid (spotted snakehead)		India
T. roulei		Synbranchiformes: synbranchid (Asian swamp eel)		Asia
T. rupicola		Cypriniformes: nemacheilid (stone loach)		Asia
T. saccobranchi		Siluriformes: heteropneustid (Asian stinging catfish)		India
T. salihi		Siluriformes: sisorid (Tigris cat)		Iraq
T. sauli		Anabantiformes: channid (spotted snakehead)		India
T. schulmani		Esociformes: esocid (northern pike)		Asia
T. serranoi		Cichliformes: cichlid (Mozambique tilapia)		East Africa
T. siluri		Siluriformes: silurid (Amur catfish)		Asia
T. simondi		Siluriformes: claroteid (giraffe catfish)		Africa
T. singhii		Siluriformes: heteropneustid (Asian stinging catfish)		Asia
T. sinipercae		Perciformes: sinipercid (mandarin fish)		China
T. splendorei (syn. *T. rhamdiae*)	40-48	Siluriformes: heptapterid (silver catfish, South American catfish)		South America
T. squalli		Cypriniformes: cyprinid (ide)		Europe
T. stigmai		Cypriniformes: cyprinid (pool barb)		India
T. striati (syn. *T. ophiocephali*)	32-54	Anabantiformes: channid (northern snakehead, striped snakehead)		Asia
T. striatum	27-30	Siluriformes: bagrid (Braschikow's catfish)		China
T. strigaticeps	21-23	Siluriformes: loricariid (cascudo pintado)		Brazil
T. synodontis		Siluriformes: mochokid (mandi, onespot squeaker)		Africa
T. tandoni		Siluriformes: silurid (helicopter catfish)		Asia
T. tchangi		Centrarchiformes: sinipercid (bigeye mandarin fish)		China
T. tobeyi		Siluriformes: clariid (Angolan walking catfish)		West Africa
T. toddi		Siluriformes: clariid (Angolan walking catfish, mudfish)		Africa
T. trichogasteri		Anabantiformes: osphronemid (banded gourami, three-spot gourami)		Asia
T. venustissimum	72	Siluriformes: loricariid (suckermouth catfish)		Brazil
T. vittati		Siluriformes: clariid (walking catfish, striped dwarf catfish) [anaemia]		India

T. wangi		Cypriniformes: cyprinid (rainbow gudgeon)		China
T. zilli		Cichliformes: cichlid (Guinean tilapia)		Africa
T. zungaroi	62	Siluriformes: pimelodid (gilded catfish)		Brazil
Species in marine fish				
T. aulopi		Aulopiformes: aulopid (Sergeant baker)		Australia
T. balistes		Tetraodontiformes: balistid (grey triggerfish)		Caribbean
T. burresoni		Anguilliformes: anguillid (American eel)		North America
T. callionymi	65-70 striated	Callionymiformes: callionymid (common dragonet)		European Atlantic
T. cataphracti (*nomen nudem*)		Scorpaeniformes: agonid (pogge)		England
T. caulopsettae	26-95	Pleuronectiformes: pleuronectid (large scald flounder, New Zealand sand flounder)		New Zealand
T. cephalacanthi	24-32	Syngnathiformes: dactylopterid (flying gurnard)		West Africa
T. coelorhynchii		Perciformes: haemulid (javelin fish); Gadiformes: morid (red codling)		New Zealand
T. congiopodi		Scorpaeniformes: congiopodid (southern pigfish)		New Zealand
T. cotti	45-55 striated	Scorpaeniformes: cottid (long-spined bullhead)	Clitellata: piscicolid (*Calliobdella punctata*)	European Atlantic
T. delagei	21-33 nonstriated	Blenniiformes: blenniid (shanny)		Northeast Atlantic
T. dohrni	37-41 nonstriated	Pleuronectiformes: soleid (whiskered sole)		Mediterranean
T. epinepheli	9-28	Perciformes: latid (barramundi), serranid (tiger grouper, humpback grouper)		China
T. froesi		Mugiliformes: mugilid (Lebranche mullet)		West Atlantic
T. gobii	38-56 nonstriated	Gobiiformes: gobiid (black goby)		European Atlantic
T. heptatreti	56-98	Myxiniformes: myxinid (broadgilled hagfish)		New Zealand
T. laternae	44-57 nonstriated	Pleuronectiformes: pleuronectid (lefteye flounder)		Northeast Atlantic
T. lotae		Gadiformes: lotid (burbot)		Europe
T. mugilicola (= *mugicola*)	30	Mugiliformes: mugilid (flathead grey mullet); Pleuronectiformes: achirid (hogchoker)		Mexico, Africa
T. mugili		Mugiliformes: mugilid (Lebranche mullet)		Brazil
T. murmanense	32-94 striated	Scorpaeniformes: anarhichadid (Atlantic wolffish, spotted wolffish, northern wolffish), cottid (longhorn sculpin, shorthorn sculpin), cyclopterid (Atlantic spiny lumpfish), liparid (Atlantic snailfish, polka-dot snailfish); Anguilliformes: anguillid (American eel); Gadiformes: gadid (Atlantic cod, polar cod, Atlantic tomcod, saithe), macrourid (roughhead grenadier), phycid (longfin hake, white hake); Labriformes: labrid (cunner); Perciformes: cottid (Arctic hookear sculpin), zoarcid (Newfoundland eelpout, Arctic eelpout, checker eelpout, ocean pout); Pleuronectiformes: pleuronectid (winter flounder, witch flounder, yellowtail flounder, American plaice, Atlantic halibut, Greenland halibut) [anaemia, emaciation]	Clitellata: piscicolid (*Johanssonia arctica*)	North Atlantic, Arctic
T. myoxocephali	41-49 striated	Scorpaeniformes: cottid (longhorn sculpin)		North Atlantic, Arctic
T. nudigobii (syn. *T. capigobii, blenniclini,* on molecular grounds)	bimorphic: 25-46, 55-98	Gobiiformes: gobiid (barehead goby); Blenniiformes: blenniid (horned blenny), clinid (snaky klipfish, agile klipfish, bluntnose klipfish, bull klipfish)	Clitellata: piscicolid (*Zeylani-cobdella*	South Africa

			arugamensis)	
T. pacifica		Pleuronectiformes: pleuronectid (English sole)		East Pacific
T. parapercis		Trachiniformes: pinguipedid (blue cod)		New Zealand
T. platessae (syn. *T. bothi, flesi, limandae*)	23-38 nonstriated	Pleuronectiformes: pleuronectid (European plaice, European flounder, common dab, long rough dab), scophthalmid (brill)		Northeast Atlantic
T. pleuronectidium (syn. *T. aeglefini*)	40-74 striated	Gadiformes: gadid (Atlantic cod, poor cod, haddock, pollock, saithe, Norway pout), lotid (cusk, common ling, fourbeard rockling, American plaice), merlucciid (European hake), phycid (greater forkbeard); Scorpaeniformes: triglid (grey gurnard); Pleuronectiformes: pleuronectid (European flounder, European plaice, witch, common dab, lemon sole), scophthalmid (megrim)	Clitellata: piscicolid (*Calliobdella nodulifera*)	Northeast Atlantic
T. pulchra	40-52	Perciformes: serranid (seaperch)		Australia
T. radiale		Anguilliformes: muraenid (spotted moray)		Atlantic
T. scorpaenae	65-70 nonstriated	Scorpaeniformes: scorpaenid (small red scorpionfish)		Mediterranean
T. senegalense	45 striated	Scorpaeniformes: triglid (streaked gurnard)		West Africa
T. soleae	32-47 striated	Pleuronectiformes: soleid (common sole)	Clitellata: piscicolid (*Calliobdella punctata, Hemibdella soleae*)	Northeast Atlantic
T. sphaeroidis		Tetraodontiformes: tetraodontid (bandtail puffer)		West Africa
T. triglae	54-62 nonstriated	Scorpaeniformes: triglid (streaked gurnard, tub gurnard, grey gurnard)		Mediterranean
T. tripterygium	36-85	Blenniiformes: tripteryglid (variable triplefin, black-faced blenny), clinid (orange clinid)		New Zealand
T. yakimovi	31-36 nonstriated	Syngnathiformes: syngnathid (greater pipefish)		Mediterranean
T. zeugopteri (*nomen nudem*)		Pleuronectiformes: scophthalmid (common topknot)		England
Species in marine elasmobranchs (cartilaginous fishes)				
T. boissoni	45-67	Rhinopristiformes: zanobatid (striped panray)		East Atlantic
T. carchariasi	35-70	Lamniformes: odontaspidid (sand sharks)		Australia
T. gargantua	67-131	Rajiformes: rajid (New Zealand rough skate)		New Zealand
T. giganteum	100-130	Rajiformes: rajid (long-nosed skate)	Clitellata: piscicolid (*Pontobdella muricata*)	Mediterranean
T. haploblephari	20-112	Carcharhiniformes: scyliorhinid (dark shyshark, puffadder shyshark, leopard catshark)		South Africa
T. harriottae	24-38	Chimaeriformes: rhinochimaerid (narrownose chimaera)		Cape Verde Islands
T. humboldti	78-93	Carcharhiniformes: scyliorhinid (Chilean catshark)		Chile
T. mackerrasi	118-125	Orectolobiformes: hemisculliid (epaulette shark)		Australia
T. marplatensis	60-65	Rajiformes: arhynchobatid (softnose skate)		Argentina
T. rajae (syn. *T. variabile*)	55-80	Rajiformes: rajid (common skate, winter skate, little skate, thorny skate, starry ray, mosaic ray, thornback ray, small-eyed ray) [anaemia]	Clitellata: piscicolid (*Pontobdella muricata*)	European Atlantic, Mediterranean
T. scyllii	54-75	Carcharhiniformes: scyliorhinid (large-spotted dogfish, lesser spotted dogfish)	Clitellata: piscicolid (*Pontobdella muricata*)	Northeast Atlantic
T. squalii		Squaliformes: squalid (spurdog)		Northeast Atlantic
T. taeniurae	50-55	Myliobatiformes: dasyatid (blue-spotted ribbontail ray)		Australia

T. torpedinis		Torpediniformes: torpedinid (marbled electric ray)		European Atlantic

Parasite morphology: Piscine trypanosomes form several different developmental stages in their hosts: trypomastigotes in fish and epimastigotes (sometimes sphaeromastigotes, rarely amastigotes, promastigotes and metacyclic trypomastigotes) in leeches. Species were originally identified on the basis of differences in host occurrence (zoogeography) and parasite morphology (morphometrics, presence/absence of granules/striations) but considerable variation has been observed within these characters for many species (variable host specificity, parasite pleomorphy). More recently, molecular techniques (proteins, DNA) have been used to characterize species and indicate phylogenetic relationships. All stages have an oval-round kinetoplast (containing mitochondrial DNA) located separately from the cell nucleus and the flagellar basal body (complex of microtubules) is located adjacent to the kinetoplast. The basal body gives rise to a single flagellum which emerges from the cell in all stages except amastigotes. Observation of live organisms indicates that they move in the direction of the free flagellum, so that cellular aspect has been designated anterior. This sometimes causes confusion when considering the orientation of trypomastigotes which have a long flagellum often mistakenly termed recurrent or trailing when in fact it extends forwards (in contrast to bodonids such as *Cryptobia* and *Trypanoplasma* which do have a recurrent flagellum directed posteriorly). Trypomastigotes are long and slender ranging from 20-90 μm in length and 1-10 μm in width. The kinetoplast is located posterior to the cell nucleus and the emergent flagellum is attached to the cell body forming a long undulating membrane before extending freely beyond the anterior margin. The trypomastigotes of most piscine species are monomorphic (e.g. *T. danilewskyi*), although those of some species may be pleomorphic (e.g. *T. murmanense* with small, intermediate and large forms). They have well-developed cytostomes (mouths) located subapically near the nucleus and they usually possess numerous dense granules juxtaposed to the cytopharyngeal tube. The cell body is membrane-bound with a thin fibrillar surface coat, which in some species bears longitudinal striations. Epimastigotes are elongate ranging in size from 8-26 by 1-4 μm (sometimes comprising short thick forms, long thick forms and longer slender forms). The kinetoplast is located anterior to the cell nucleus and the emergent flagellum is attached to the cell body forming a short undulating membrane before extending freely beyond the anterior margin. Sphaeromastigotes are rounded stages ranging from 3-7 μm in diameter that have an anterior kinetoplast and a short free flagellum emerging from a small depressed pocket. Amastigotes are small rounded stages ranging from 5-7 μm in diameter that do not have emergent flagella or undulating membranes. A few studies have also reported the rare occurrence of promastigotes (kinetoplast anterior to nucleus) and possibly early metacyclic (infective) trypomastigotes (with kinetoplast posterior to nucleus) in leeches.

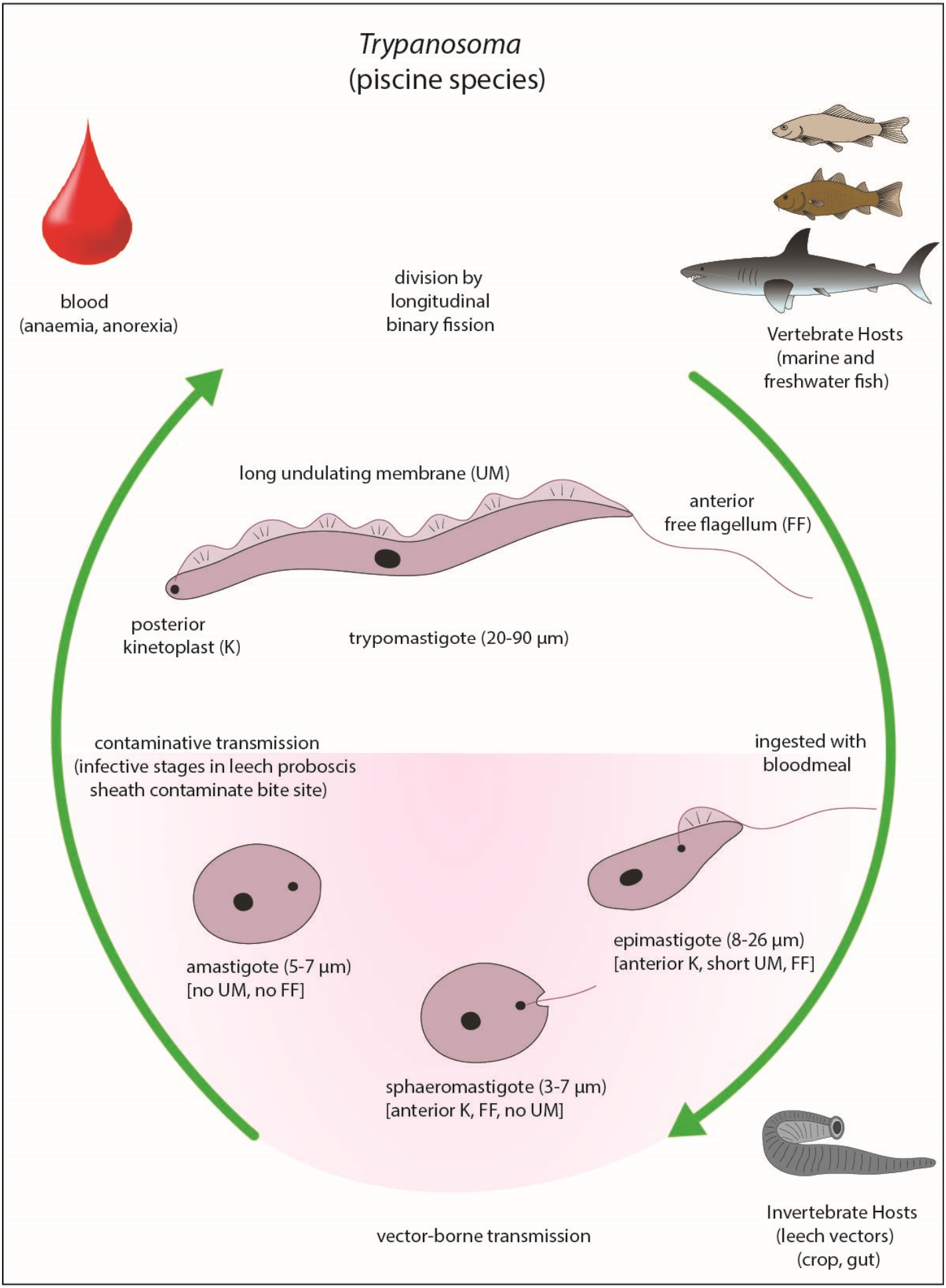
Site of infection: Trypomastigotes occur as extracellular organisms in the blood stream of their fish hosts. Over 200 species have been described in almost 300 fish species: with 165 parasite species reported in 181 freshwater fish species belonging to 48 families in 19 orders (esp. cyprinids and catfish), and 51 parasite species found in 115 marine fish species belonging to 49 families in 24 orders (esp. flounder, but also including some cartilaginous fishes). *Trypanosoma* epimastigotes, sphaeromastigotes and amastigotes infect the crop and intestines of leech vectors, while metacyclic trypomastigotes invade the proboscis sheath. Infections have been demonstrated in 9 leech species: 2 glossiphoniid and one piscicolid species recovered from freshwater fish, and 6 piscicolid species from marine fish.

Pathogenesis: Trypanosomes feed on host fluids by absorbing nutrients through their surface membranes and digesting proteins, carbohydrates and fats by enzyme systems within their protoplasm. Most infections in the blood of fishes have not been associated with any clinical disease, although several species are thought to be responsible for mild anaemia in their hosts, due partly to haemolysis and exacerbated by haemodilution. For example, infections by *T. danilewskyi* may cause progressive anaemia in goldfish resulting in anorexia, poor condition and even death. Infections by *T. murmanense* were found to cause chronic disease with low parasitaemias and low mortalities in goldfish, barramundi, eels, grouper, and tilapia. The severity of anaemia was often correlated to the degree of parasitaemia, with numerous parasites causing greater reductions in haematocrit (packed cell volume), lower erythrocyte counts, and reduced haemoglobin levels. While the parasites were located extracellularly in the host circulation, experimental studies have shown that some trypomastigote excretory-secretory products were able to lyse host erythrocytes in the absence of antibodies. Clinical signs observed in fish have included inappetence with reduced feeding sometimes leading to emaciation, weakness and lethargy. The anorexia was found to involve low food movement through the intestines, mucosal alterations affecting digestion and absorption, increases in appetite-suppressing hormones (cholecystokinin/gastrin), and elevations in the pro-inflammatory cytokines (interleukin-1) altering gut motility. Infected fish may also develop splenomegaly, darkening of the body, exophthalmia, scale loss and respiratory disorders due to gill epithelial hyperplasia, hypertrophy and vacuolation, mucus cell hypertrophy and thrombi formation. There may be some congestion in internal organs (brain, liver, spleen, kidney) due to cellular necrosis, haemorrhages, haemosiderin deposits and melanomacrophage aggregates. There appears to be little innate or acquired immunity to infection, although some fish developed neutralizing antibodies but their trypanocidal lytic activity was lost after several weeks-months. Young fish are more susceptible to clinical disease, while adults often appear to be refractory. However, older fish often harbour small but persistent infections but do not develop disease, suggesting that some premunitive immunity (rather than sterile immunity) may be involved. Infections in freshwater fish exhibit seasonal fluctuations in prevalence and intensity, with more parasites found in warmer months, possibly due to increased fish susceptibility or greater leech activity or both. Infections are also more prevalent in fish that spend more time in shallower waters near vegetation where leeches dwell.

Developmental cycle and mode of transmission: Fish trypanosomes are transmitted by haematophagous leech vectors. The parasites multiply asexually in both vertebrate and invertebrate hosts by symmetrogenic (rather than homothetogenic) binary fission involving the production of a new flagellum, division of the kinetoplast, karyokinesis, and transverse constriction of the midbody culminating in cytokinesis. Fish become infected via leech bites when infective stages are released into the circulation where they develop into trypomastigotes which feed and multiply. Leeches become infected when they feed on host blood and ingest trypomastigotes which undergo cyclic changes forming different multiplicative stages before the formation of infective metatrypanosomes (process termed metacyclogenesis). Three basic developmental patterns have been observed: two in freshwater leeches and one in marine leeches. Some freshwater species (e.g. *T. acerinae, T. abramidis, T. barbi, T. percae, T. remaki, T. squalii*) multiply and develop exclusively in the crop with metacyclic stages migrating forwards (or being regurgitated) as the leech feeds, while other species (e.g. *T. carassii, T. cobitis, T. danilewskyi, T. granulosum, T. phaleri, T. phoxini*) multiply in the crop and intestines (forming epimastigotes, sometimes sphaeromastigotes) before eventual invasion of the proboscis sheath by infective metatrypanosomes which contaminate bite sites. In marine species (e.g. *T. cotti, T. soleae, T. murmanene*), ingested trypomastigotes lose their flagella and divide as amastigotes, then sphaeromastigotes and epimastigotes in the crop and intestines before developing into infective stages in the proboscis sheath.

Differential diagnosis: Trypomastigotes can be detected by microscopic examination of blood either in wet mounts or stained smears. Microhaematocrit tube centrifugation can also be used to concentrated trypomastigotes from blood where they band with the buffy coat layer. Piscine trypanosomes have also been cultured on a variety of blood-agar media where they usually multiply as epimastigotes by binary fission and sometimes multiple fission. Leeches may also be examined for developmental stages by microscopy of squash preparations or histological sections. Molecular biological techniques have been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA, glycosomal glyceraldehyde-3-phosphate dehydrogenase).

Treatment and control: There is no specific chemotherapy available for trypanosome infections in fish, although some chemical bath treatments have reduced infection levels in cultured fish, the most effective for catfish being ethanolic extracts of *Aloe vera* leaves or *Artemisia annua* leaves, and less effective treatments involving diamidines (diminazene aceturate) and even some anthelmintics (praziquantel). Some reports have indicated that thiazole water conditioners or crystal violet disinfectants may help reduce infections in aquarium fish. A range of trypanocidal drugs effective against infections in mammals have yet to be tested against infections in fish. Preventive measures in aquaculture are based around reducing transmission rates to fish by excluding leech vectors, either by chemical treatments of infested fish (trichlorphon baths) or by clearing ponds of vegetation (which support leech populations). Preliminary immunological studies have shown some promise for the potential immuno-modulation of infections. Infected fish have been found to produce antibodies with activity against trypanosomes, but they did not persist. Nonetheless, passive immunization experiments showed antibodies purified from infected fish were able to confer some protection to recipient challenged fish. While some parasite proteins (calreticulin, glycoprotein 63) have been implicated in immuno-evasion strategies (avoiding complement lysis and macrophage phagocytosis), other proteins (beta-tubulin, hepcidin) stimulated protective immune responses in naïve fish. It should be re-iterated that most infections in fish remain asymptomatic despite the persistence of blood stages, so that any acquired immunity may be premunitive. Care should be taken in all control programs not to upset this delicate enzootic stability between hosts and parasites.


Trypanosoma
(piscine species)
blood
(anaemia, anorexia)
division by
longitudinal
binary fission
Vertebrate Hosts
(marine and
freshwater fish)
long undulating membrane (UM)
anterior
free flagellum (FF)
posterior
kinetoplast (K)
trypomastigote (20-90 µm)
contaminative transmission
(infective stages in leech proboscis
sheath contaminate bite site)
ingested with
bloodmeal
amastigote (5-7 µm)
[no UM, no FF]
epimastigote (8-26 µm)
[anterior K, short UM, FF]
sphaeromastigote (3-7 µm)
[anterior K, FF, no UM]
vector-borne transmission
Invertebrate Hosts
(leech vectors)
(crop, gut)



Trypanosoma trypomastigite in fish blood

Trypanosoma (reptile and amphibian species)
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Trypanosomes have a single flagellum and they form four main developmental stages: trypomastigotes (with a posterior kinetoplast and an emergent flagellum forming a long undulating membrane); epimastigotes (with an anterior kinetoplast and an emergent flagellum forming a short undulating membrane); promastigotes (with an anterior kinetoplast and a short emergent flagellum, but no undulating membrane); and amastigotes (with a kinetoplast but no emergent flagellum or undulating membrane). Many trypanosome species are parasitic only in insects whereas others are transmitted by invertebrate vectors to a wide range of vertebrate hosts, including reptiles and amphibians. Trypanosomes in aquatic poikilotherm (cold-blooded) hosts are often transmitted by leeches or mosquitoes, while those of terrestrial poikilotherms are transmitted by sandflies and bugs. Few infections have been associated with clinical disease.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Excavata (with conspicuous ventral feeding groove)
Group:	Discoba (diverse group supported robustly by molecular studies)
Phylum:	Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class:	Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass:	Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order:	Trypanosomatida (parasitic, single anterior flagellum, often forming undulating membrane)
Family:	Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)
Genus:	*Trypanosoma* (vector-borne haemoparasites)
Species:	various species cause infections in reptiles and amphibia

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia	Order: Trichomonadida (3-5 anterior flagella plus	Monocercomonadidae (costa absent, most	*Histomonas*	birds (gut, liver)	direct (f-o)

(with parabasal body)	recurrent flagellum)	without undulating membrane)	*Dientamoeba*	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans are a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)
	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*).

Trypanosomatids are dixenous (2-host) parasites with indirect transmission cycles between vertebrates and invertebrate vectors. *Trypanosoma* spp. form trypo- and/or a-mastigote stages in the blood/tissues of vertebrate hosts, and epi- or pro-mastigote stages in invertebrate haematophagous vectors. Infections have been found in a range of vertebrate species (mammals, birds, reptiles, amphibians and fish) with many different types of haematophagous invertebrates (leeches, bugs, flies, fleas) implicated as vectors or paratenic hosts. Recent molecular phylogenetic studies have validated the separation of mammalian salivarian and stercorarian trypanosomes, but indicated complex placements for trypanosomes from non-mammalian hosts, despite earlier suggestions that they be assigned to separate subgenera (*Trypanomorpha* for those in birds, *Trypanosoma* for those in amphibians, and *Haematomonas* for those in fish). Many clades have been identified, most associated with particular vertebrate or invertebrate hosts, or both, suggesting that 'host-fitting' rather than 'co-speciation' has been the principal mechanism for trypanosome evolution. Comparative phylogenetic studies have shown trypanosomes from major reptilian groups (chelonians, crocodilians and lizards) were polyphyletic and separated into distant clades. Trypanosomes from tortoises clustered together with those from fish (both groups being transmitted by aquatic leeches), whereas trypanosomes from crocodiles (transmitted by tsetse flies) were closest to avian trypanosomes. Trypanosomes from varanid, phrynosomatid and gekkonid lizards clustered together whereas those from chameleons grouped with anuran trypanosomes.

***Trypanosoma* species**	**Mastigote length (µm)**	**Hosts [disease]**	**Vectors**	**Distribution**
Species in lizards				
T. anolisi	19-42	Sauria: dactyloid (slender anole, bridled anole, giant green anole, tropical anole, ghost anole)		Panama, Belize
T. betschii	20-32	Sauria: gerrhosaurid (Madagascar girdled lizard)		Madagascar
T. boueti	18-33	Sauria: scincid (African striped skink, Guinea mabuya, speckle-lipped mabuya)	Diptera: psychodid sand-fly (*Sergentomyia bedfordi*)	West and East Africa
T. chamaeleonis		Sauria: chamaeleonid (Mediterranean chameleon, graceful chameleon)		Sudan
T. cnemaspi	19-32	Sauria: gekkonid (Barbour's gecko, flathead leaf-toed gecko)		Tanzania
T. cordyli	32-62	Sauria: cordylid (East African spiny-tailed lizard)		Tanzania
T. domerguei	19-29	Sauria: oplurid (collared iguana)		Madagascar
T. egerniae	22-28	Sauria: scincid (Cunningham's skink, tree-crevice skink)		Australia
T. fairchildi	36-59	Sauria: dactyloid (bighead anole)		Panama
T. gallyi		Sauria: eublepharid (African fat-tailed gecko)		Africa
T. garnhami	18-39	Sauria: gekkonid (Brooke's house gecko)	Hemiptera: reduviid (*Rhodnius prolixus*); Ixodida: argasid (*Ornithodoros parkeri*)	Kenya
T. gekkonis	42-59	Sauria: gekkonid (Tokay gecko)		Thailand
T. gerrhonoti	50-70	Sauria: anguid (southern alligator lizard)	Diptera: psychodid (*Lutzomyia vexator*)	North America
T. gonatodi	34-47	Sauria: sphaerodactylid (yellow-headed gecko)		Panama

T. kimbozae	25-49	Sauria: gekkonid (flathead leaf-toed gecko)		Tanzania
T. leschnaulti	56-60	Sauria: gekkonid (Leschenault's leaf-toed gecko)		Sri Lanka
T. lygodactyli	25-39	Sauria: gekkonid (flathead leaf-toed gecko, dwarf yellow-headed gecko, Cape dwarf gecko)		Tanzania
T. martini (syn. *T. mabuiae*)	dimorphic: 19-40, 17-25	Sauria: scincid (speckle-lipped skink, red-sided skink, striped skink, five-lined skink, Guinea mabuya)		Africa
T. mochli		Sauria: scincid (fire skink)		Congo
T. ndumoensis	24-45	Sauria: cordylid (Limpopo girdled lizard)		South Africa
T. ocumarensis		Sauria: phyllodactylid (turnip-tailed gecko)		Africa
T. pertenue	15-42	Sauria: gekkonid (termite hill gecko)		India
T. perroteti		Sauria: scincid (red-sided skink)		Africa
T. petteri	43-50	Sauria: gekkonid (Madagascar day gecko)		Madagascar
T. phlebotomi (possible syn. *T. hemidactyli*)		Sauria: gekkonid (common house gecko)	Diptera: psychodid (*Sergentomyia babu,* earlier misidentified as *Phlebotomus minutus*)	India
T. phylluri	36-48	Sauria: carphodactylid (broad-tailed gecko)		Australia
T. platydactyli	26-39	Sauria: phyllodactylid (common wall gecko(, gekkonid (Kotschy's gecko, grey thin-toed gecko, Turkestan thin-toed gecko, Caspian bent-toed gecko)	Diptera: psychodid (*Sergentomyia minuta, Phlebotomus parroti*)	Tunisia, Malta, Italy, France
T. plicae	49-64	Sauria: tropidurid (blue-lipped tree lizard)		Brazil
T. plicaplicae	26-45	Sauria: tropidurid (collared tree lizard)		Guyana
T. poinsetti	31-42	Sauria: phrynosomatid (crevice spiny lizard)		North America
T. rudolphi		Sauria: scincid (agile skink)		Americas
T. ryukyuense	26-45	Sauria: eublepharid (Kuroiwa's leopard gecko)		Japan
T. scelopori	35-47	Sauria: phrynosomatid (western fence lizard), crotaphytid (eastern collared lizard)	Diptera: psychodid (*Lutzomyia vexator*)	North America
T. scincorum	17-34	Sauria: scincid (many-striped skink, bronze grass skink, spotted forest skink, Sabah slender skink)		Asia
T. serveti	20-45	Sauria: phrynosomatid (Teapen rosebelly lizard, rose-bellied lizard), dactyloid (greater scaly anole, bridled anole, dappled anole, slender anole), corytophanid (Hernandez's helmeted basilisk)		Mexico
T. striatae	25-34	Sauria: scincid (striped skink, speckle-lipped skink)		Tanzania
T. superciliosae	87-124	Sauria: tropidurid (diving lizard)		Brazil
T. takydromi	25-48	Sauria: lacertid (Asian grass lizard, green grass lizard)		Japan
T. thecadactyli	19-24	Sauria: phyllodactylid (turnip-tailed gecko)	Diptera: psychodid (*Lutzomyia trinidadensis*)	Panama
T. therezieni	28-33	Sauria: chamaeleonid (short-horned chameleon, Malagasy giant chameleon, carpet chameleon, warty chameleon, Parson's chameleon) [experimental fatalities]	Diptera: culicid (*Culex pipiens*)	Madagascar
T. tokoloshi	29-54	Sauria: cordylid (Zoutpansberg girdled lizard)		South Africa
T. torrealbai	27-38	Sauria: sphaerodactylid (Estado Aragua		Venezuela

		gecko, Margarita leaf-toed gecko)		
T. turcici	28-35	Sauria: gekkonid (Mediterranean house gecko)		Iraq
T. uluguruensis	25-49	Sauria: gekkonid (flathead leaf-toed gecko, dwarf-yellow-headed gecko, Cape dwarf gecko, turquoise dwarf gecko)		Tanzania
T. urosauri	29-38	Sauria: phrynosomatid (long-tailed brush lizard)		North America
T. varani		Sauria: varanid (Nile monitor, savannah monitor)	Diptera: psychodid (*Phlebotomus duboscqi*)	Senegal
T. zonuri	22-36	Sauria: cordylid (Cape girdled lizard)		Tanzania
Species in snakes				
T. brazili	40-79	Serpentes: colubrid (olive keelback, Wagler's snake)	Clitellata: glossiphoniid (*Placobdella brasiliensis, catenigera*)	Brazil
T. butantanense		Serpentes: colubrid (Wagler's snake), viperid (crossed pit viper, tropical rattlesnake)		Brazil
T. cascavelli		Serpentes: viperid (tropical rattlesnake)		America
T. closeli	82-122	Serpentes: colubrid (African brown water snake, Smith's African water snake)		West Africa
T. constrictor	54-82	Serpentes: boid (Bolivian short-tailed boa)		Brazil
T. enhydris		Serpentes: colubrid (buff-striped keelback, rainbow water snake)		Asia
T. erythrolampri	28-34	Serpentes: colubrid (Aesculapian false coral snake)		South America
T. floridana	38-49	Serpentes: colubrid (eastern green water snake, Florida banded water snake)		North America
T. haranti	20-21	Serpentes: pseudoxyrhophiid (lateral water snake)		Madagascar
T. hogei	36-47	Serpentes: colubrid (Brazilian bird snake)	Clitellata: glossiphoniid (*Haementeria lutzi*)	Brazil
T. hydrae	31-41	Serpentes: colubrid (banded water snake, western ribbon snake, Texas rat snake)	Clitellata: glossiphoniid (*Placobdella parasitica*)	North America
T. manguinhensis	64-77	Serpentes: colubrid (Wagler's snake)		Brazil
T. mattogrossense	49-53	Serpentes: colubrid (false water cobra)		South America
T. merremii	64-77	Serpentes: colubrid (Wagler's snake)		Brazil
T. najae	50	Serpentes: elapid (black-necked spitting cobra)		Sudan
T. phylodriasi		Serpentes: colubrid (Paraguay green racer), viperid (crossed pit viper)		South America
T. primeti	dimorphic: 82-105, 44-57	Serpentes: colubrid (checkered keelback), homalopsid (Chinese water snake)		Vietnam
T. psammophis		Serpentes: psammophiid (olive grass snake)		Africa
T. rostellata		Serpentes: homalopsid (rice paddy snake)		Asia
T. salamantae	60-73	Serpentes: boid (Paraguayan rainbow boa)	Diptera: culicid (*Culex dolosus*)	Brazil
T. sebae		Serpentes: boid (Central African rock python)		Africa
T. thamnophis	53-66	Serpentes: colubrid (common garter snake)		Canada
T. tortilis		Serpentes: (homalopsid (Chinese water snake)		Asia

T. voltariae	42	Serpentes: elapid (black-necked spitting cobra)		Ghana
T. yaegeri	46-80	Serpentes: viperid (western cottonmouth)		North America
Species in crocodiles				
T. cecili	62-84	Crocodilia: alligatorid (spectacled caiman)		Brazil
T. grayi [syn. *kochi*]	58-87	Crocodilia: crocodylid (Nile crocodile); Sauria: varanid (savannah monitor)	Diptera: glossinid (*Glossina palpalis, pallidipes, fuscipes, tachinoides*)	Central Africa
T. ralphi		Crocodilia: alligatorid (spectacled caiman, Yacare caiman, black caiman)		Brazil
T. terena		Crocodilia: alligatorid (Yacare caiman)		Brazil, Venezuela
Species in turtles				
T. balithaensis	30-35	Testudines: trionychid (Indian flapshell turtle)	Clitellata: glossiphoniid (*Helobdella nociva*)	India
T. chelodinae	34-43	Testudines: chelid (eastern long-necked turtle, eastern short-necked turtle, Brisbane short-necked turtle, saw-shelled turtle, Krefft's turtle, northern snapping turtle)		Australia
T. chrysemydis	47-50	Testudines: emydid (painted turtle, northern map turtle(, chelydrid (common snapping turtle), trionychid (smooth softshell turtle, spiny softshell turtle, Florida softshell turtle)	Clitellata: glossiphoniid (*Placobdella multilineata, ornata, rugosa, parasitica*)	North America
T. damoniae	32	Testudines: geoemydid (Chinese pond turtle)		Asia
T. gangetica	34-37	Testudines: trionychid (Indian softshell turtle)		India
T. leroyi	59	Testudines: testudinid (Home's hingeback tortoise)		Senegal
T. lissemysi		Testudines: trionychid (Indian softshell turtle)		Asia
T. mocambicum		Testudines: pelomedusid (Upemba mud turtle, Okavango mud turtle, variable mud turtle, East African black mud turtle)		Africa
T. neitzi		Testudines: pelomedusid (serrated hinged terrapin)		Africa
T. platemysi		Testudines: chelid (twist-necked turtle)		South America
T. pontyi	47	Testudines: pelomedusid (East African black mud turtle)		Africa
T. sheppardi		Testudines: pelomedusid (serrated hinged terrapin)		Africa
T. testudinis		Testudines: cheloniid (green sea turtle)		South America
T. vittatae	25-70	Testudines: trionychid (Indian flapshell turtle)	Clitellata: glossiphoniid (*Glossosiphonia* sp.), hirudinid (*Poecilobdella granulosa*)	Sri Lanka

Over 70 trypanosome species have been recorded in amphibian hosts, not only from adult frogs and toads, but often from their tadpole stages. Although it was proposed that anuran species be allocated to a separate *Trypanosoma* subgenus, provisionally called *Trypanosoma*, their classification apart from other trypanosomes has not been supported by molecular phylogenetic studies. Instead, anuran trypanosomes appear to be polyphyletic and interwoven with other species from birds, reptiles and fish. Early workers also recognized six different types (A-F) of trypanosomes in anuran hosts on the basis of trypomastigote morphology.

Trypanosoma	**Mastigote**	**Hosts**	**Vectors**	**Distribution**

species	length (µm) (Type)*			
Species in frogs/toads				
T. andersoni	47-72	Anura: hylid (grey tree frog, spring peeper)		North America
T. arcei (syn. *T. ocellati*?)	40 (A)	Anura: leptodactylid (butter frog)		South America
T. aurorae		Anura: ranid (red-legged frog)		
T. belli	25-41 (D)	Anura: ranid (European common brown frog, edible frog)		China
T. bocagei	71 (B)	Anura: bufonid (African common toad, Asian common toad, Asiatic toad, European toad, Berber toad), ranid (common green frog, Hose's frog), dicroglossid (rice field frog)	Diptera: psychodid (*Phlebotomus squamirostris*), and mosquito?	Africa, East Asia
T. bufophlebotomi		Anura: bufonid (California toad), ranid (American bullfrog)	Diptera: psychodid (*Lutzomyia vexator*)	North America
T. borelli (syn. *T. hylae*)	20-80 (A)	Anura: hylid (red-snouted tree frog, European tree frog), dicroglossid (Indian bullfrog)		Brazil, Europe
T. boyli		Anura: hylid (foothill yellow-legged frog)		North America
T. canadensis		Anura: ranid (northern leopard frog)	Clitellata: glossiphoniid (*Placobdella* sp.)	Canada
T. chattoni (syn. *T. celestinoi*?)	18-25 (F)	Anura: ranid (northern leopard frog, southern leopard frog, Hose's frog, American bullfrog, common green frog, Ryukya tip-nosed frog, crab-eating frog, rice field frog), ptychadenid (Mascarene grass frog), ceratophryid (Argentine horned frog), hylid (European tree frog, white-banded tree frog, waxy monkey tree frog), phrynobatrachid (Natal dwarf puddle frog), leptodactylid (butter frog), bufonid (Asian common toad, Argentine common toad)		Americas, Eurasia, Africa
T. clamatae	33-42 D)	Anura: ranid (northern green frog)		North America
T. clelandi (syn. *T. tasmaniensis*)	41-58 (D)	Anura: limnodynastid (ornate burrowing frog, spotted marsh frog)		Australia
T. diamondi		Anura: ranid (northern leopard frog)		Mexico
T. fallisi		Anura: bufonid (American toad)		Canada
T. galbae		Anura: ranid (Mexican cascades frog, Montezuma leopard frog)		North America
T. gaumontis	15-21 (D)	Anura: bufonid (America toad), ranid (northern leopard frog)		North America
T. grande		Anura: ranid (northern leopard frog)		North America
T. grandicolor	84-151	Anura: pipid (African clawed frog)		Africa
T. grylli	~30-40 (E)	Anura: hylid (southern cricket frog, grey tree frog, spring peeper)		North America
T. hosei		Anura: ranid (Hose's frog)		Asia
T. inopinatum (syn. *T. undulans, elegans, hendersoni*)	12-54 (D)	Anura: ranid (edible frog, common grass frog, northern leopard frog, American bullfrog, Gunther's Amoy frog), dicroglossid (Indian bullfrog, Indian green frog, rice field frog), alytid (Mediterranean painted frog), bufonid (African toad)	Clitellata: glossiphoniid (*Helobdella algira*)	Africa, Europe, Russia, India, Canada
T. ishigakiense		Anura: dicroglossid (rice field frog)		Asia
T. karyozeukton	trimorphic 60-134 (D)	Anura: bufonid (African toad), hylid (southern cricket frog), dicroglossid (crowned bullfrog), ptychadenid (South African sharp-nosed frog)		Africa
T. lavalia	31-36 (D)	Anura: bufonid (American toad)		North America

T. leptodactyli	30-54 (D)	Anura: leptodactylid (butter frog, Vizcachera's white-lipped frog, Bolivian toad-frog), ceratophryid (Argentine horned frog), hylid (black-lined pond frog)	Clitellata: glossiphoniid (*Placobdella braziliensis, catenigera, Glossiphonia complanata*)	South America
T. loricatum	42-48 (C)	Anura: ranid (edible frog, common green frog, dark-spotted frog, gold-spotted pond frog, Gunther's frog, Galam white-lipped frog, Hose's frog), dicroglossid (Indian bullfrog, rice field frog), ptychadenid (South African sharp-nosed frog, Mascarene grass frog), hyperoliid (marbled rush frog), bufonid (African toad)		Eurasia, North America
T. malabaricum		Anura: ranid (fungoid frog)		India
T. mega	72 (D)	Anura: bufonid (Africa toad), ptychadenid (South African sharp-nosed frog), dicroglossid (rice field frog), pyxicephalid (warty frog), hylid (veined tree frog)		Africa
T. miyagii		Anura: ranid (Taurus frog, Okinawa tip-nosed frog)		Asia
T. montezumae		Anura: ranid (Montezuma leopard frog, Mexican cascades frog, Amazon River frog)		Americas
T. montrealis	45-68 (D)	Anura: bufonid (American toad)		North America
T. nagasakiense		Anura: hylid (Japanese tree frog)		Asia
T. nelspruitense	44-70 (D)	Anura: pyxicephalid (Angola river frog, Drakenberg river frog)		South Africa
T. neveulemairei	125-145 (D)	Anura: ranid (edible frog)		Europe
T. ocellati		Anura: leptodactylid (butter frog)		South America
T. parroti	65 (D)	Anura: alytid (Mediterranean painted frog)		Africa
T. parvum	11-14 (D)	Anura: microhylid (noisy cross frog), ranid (green frog)		North America
T. pipientis	52-82 (D)	Anura: ranid (northern leopard frog, wood frog)	Clitellata: glossiphoniid (*Placobdella phalera*)	North America
T. pseudopodium		Anura: bufonid (American toad)		North America
T. raksasa		Anura: ranid (common green frog)		Asia
T. ranarum [type II (flat spiralled form)]	71 (B)	Anura: ranid (northern leopard frog, northern green frog, edible frog, American bullfrog, mink frog, wood frog)		North America, Eurasia
T. rifae		Anura: bufonid (African toad)		Africa
T. rotatorium (syn. *T. sanguinis, T. ranarum p.p.* (simple membranous form), *costatum*)	43-62 (A)	Anura: bufonid (common toad, southern toad, European green toad, African toad, Argentine toad, Fowler's toad, Woodhouse's toad, Texas toad), alytid (midwife toad), aromobatid (yellow-throated frig), arthroleptid (forest tree frog), ceratophryid (Argentine horned frog, Paraguay horned frog, Budgett's frog), dicroglossid (green pond frog, golden frog, skittering frog, rice field frog, Javan wart frog, African tigrine frog), hylid (giant leaf frog, European tree frog, bird-voiced tree frog, emerald-eyed tree frog, green tree frog, gray tree frog, ridged tree frog, veined tree frog, southern chorus frog, Brimley's chorus frog, spring peeper, waxy monkey tree frog, paradoxical frog), hyperoliid (African reed	Clitellata: glossiphoniid (*Batracobdella picta, Glossiphonia complanata, Haementeria lutzi, Helobdella algira, nociva, Hemiclepis marginata, Placobdella ceylonica, marginata*), hirudinid (*Hirudo medicinalis),* macrobdellid (*Macrobdella ditetra*), piscicolid	Eurasia, West Africa, South America

		frog), leptodactylid (butter frog, rufous frog, Dumeril's striped frog, Cei's white-lipped frog, Gunther's white-lipped frog, Vizcachera's white-lipped frog, Bolivian toad-frog), limnodynastid (spotted grass frog), microhylid (red narrow-mouthed frog), pipid (African clawed frog), ptychadenid (Perret's grassland frog, Uganda grassland frog, Dakar grassland frog, Mascarene grass frog, sharp-nosed frog), pyxicephalid (Cape river frog), ranid (common green frog, common brown frog, edible frog, peeping frog, yellow frog, mink frog, white-lipped frog, wood frog, marsh frog, ringed frog, laughing frog, spring frog, green pond frog, black-spotted frog, Gunther's Amoy frog, Hose's frog, common bullfrog, American bullfrog); Urodela: plethodontid (ensatina salamander)	(*Piscicola geometra*); Diptera: culicid (*Culex territans, Aedes aegypti*)	
T. rugosae		Anura: ranid (wrinkled frog)		Asia
T. schmidti	100 (D)	Anura: ranid (southern leopard frog, Northern leopard frog), bufonid (American toad)		North America
T. sergenti	41 (E)	Anura: alytid (painted frog)		Africa
T. somalense sp. inq.		Anura: bufonid (African toad)		Africa
T. systoma		Anura: microhylid (marbled balloon frog)		India
T. taprobanicum		Anura: microhylid (painted globular frog)		India
T. tsanezomiyatai		Anura: ranid (wrinkled frog)		Asia
T. tsukanotoi		Anura: ranid (red-eared frog), dicroglossid (Namie's frog, Indian cricket frog)		Asia
T. tumida	18-35 (E)	Anura: pyxicephalid (Nutt's River frog)		East Africa
Species in salamanders/newts				
T. ambystomae	51-84	Urodela: ambystomatid (Jefferson salamander, silvery salamander, blue-spotted salamander, spotted salamander, Tremblay's salamander), salamandrid (rough-skinned newt)	Clitellata: erpobdellid (*Erpobdella* sp.)	North America
T. barbari		Urodela: salamandrid (California newt)		North America
T. cryptobranchi		Urodela: cryptobranchid (eastern hellbender salamander)		North America
T. diemyctyli	45-80	Urodela: salamandrid (vermilion-spotted newt, eastern newt)	Clitellata: glossiphoniid (*Batrachobdella picta, Placobdella parasitica*)	North America
T. granulosae	41-59	Urodela: salamandrid (rough-skinned newt)		North America
T. ogawai		Urodela: salamandrid (Jefferson salamander, blue-spotted salamander, spotted salamander)		North America
T. tritonis	57-80	Urodela: salamandrid (fire-bellied newt)		Japan

*Trypomastigote morphology: group A (body flattened, sheet-like), B (body flattened, not sheet-like), C (body thick, ellipsoidal), D (body elongate, pointed), E (body pyriform), and F (body spherical).

Parasite morphology: Reptilian trypanosomes may form up to 6 different morphological stages in their developmental cycles: with trypomastigotes invariably being found in vertebrate blood; while a variety of stages (promastigotes, amastigotes, sphaeromastigotes, epimastigotes, and metacyclic trypomastigotes) occur within their invertebrate vectors. Trypomastigotes usually appear as long slender cells (20-90 x 1-10 µm) with a single ovoid central nucleus and a smaller oval-round kinetoplast (containing mitochondrial DNA) located posterior to the cell nucleus. Flagellar basal bodies (complex of microtubules) are located adjacent to the kinetoplast and they give rise to a single long flagellum that emerges and runs forwards along the body forming an undulating membrane but projecting freely anteriorly (it is not a recurrent or trailing flagellum like that formed by *Trypanoplasma* and *Cryptobia* spp.). In reptilian blood, trypomastigotes usually exhibit 2 developmental forms: slender and stumpy forms. Most stages

are slender forms which proliferate in the bloodstream and are thought to exhibit surface antigenic variation to evade host immunity. Stumpy forms, in contrast, are non-proliferative and adapted for transmission. In amphibian blood, trypomastigotes have been allocated to 6 different types whose bodies are flattened (A = sheet-like, B = not sheet-like), ellipsoidal (C), elongate (D), pyriform (E) or spherical (F). The different stages found in vectors include ellipsoidal promastigotes with a posterior kinetoplast and a short emergent flagellum that does not form an undulating membrane, rounded amastigotes without an emergent flagellum, rounded sphaeromastigotes (possibly divisional stages) with a short emergent flagellum, ovoid epimastigotes with an anterior kinetoplast and an emergent flagellum that forms a short undulating membrane, and broad stocky metacyclic trypomastigotes (infective stages) with a posterior kinetoplast and an emergent flagellum forming a long undulating membrane.

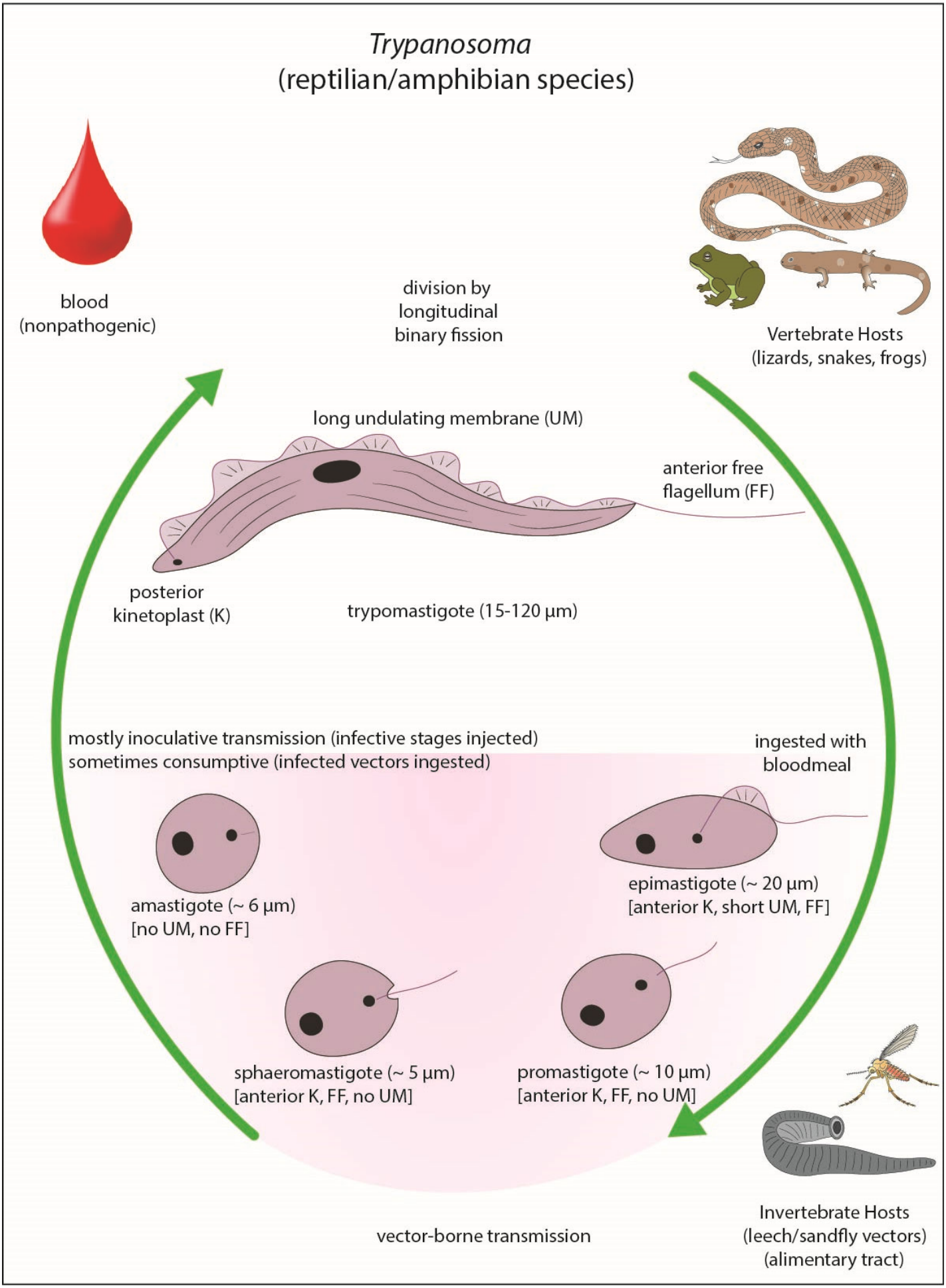
Site of infection: Infections in reptiles typically involve trypomastigote developmental stages swimming free in the circulatory system, although there are rare reports of epimastigote or amastigote stages found in host tissues. A total of 90 parasite species have been described in 130 reptilian hosts: including 47 species reported from 76 lizard species (from 18 families), 25 species from 28 snake species (6 families), 4 species from 4 crocodile species (2 families), and 14 species from 22 testudine species (8 families). Another 60 parasite species have been described from 140 amphibian hosts: including 52 parasite species from 126 anuran species (16 families), and 8 species from 14 salamander species (4 families). Infections in invertebrate vectors may involve several different developmental stages (promastigotes, amastigotes, sphaeromastigotes, epimastigotes and metacyclic (infective) trypanosomes), mainly in the stomach and crop of leeches, or the gut of dipteran vectors. A wide range of invertebrate vectors have been found: including 8 dipteran species (1 culicid, 7 psychodid), 1 hemipteran species (reduviid) and 1 ixodid species (argasid) for infections in lizards; 4 leech species (glossiphoniid) and 1 dipteran species (culicid) for infections in snakes; 4 dipteran species (glossinids) for infections in crocodiles; 7 leech species (6 glossiphoniid, 1 hirudinid) for infections in turtles; 16 leech species (12 glossiphoniid, 1 erpobdellid, 1 hirudinid, 1 macrobdellid, 1 piscicolid) and 4 dipteran species (2 culicid, 2 psychodid) for infections in amphibians.

Pathogenesis: Natural infections by *Trypanosoma* spp. have not been associated with any clinical disease in reptiles and amphibians. While some hosts exhibited mild clinical signs and even some haematological perturbations, the changes were vague and nonspecific and could not be directly attributed to trypanosome infections as the hosts often suffered from other infections or disease conditions. Under experimental conditions, infections were found to cause severe disease when blood from chameleons infected with *T. therezieni* was experimentally inoculated into sibling chameleon species resulting in massive parasitaemias, pulmonary emboli and some fatalities.

Developmental cycle and mode of transmission: In vertebrates, trypomastigotes feed by absorbing nutrients through their surface membranes and multiply by asexual symmetrogenic binary fission involving the replication of organelles, then karyokinesis followed by transverse midbody cytokinesis. While there are some rare early reports of transmission occurring between lizards via cannibalism, studies have demonstrated that infections are usually transmitted between reptilian hosts by invertebrate vectors, which act as secondary hosts in which parasites undergo asexual development forming a variety of different developmental stages. Vector-borne transmission occurs primarily via the bite of haematophagous arthropods and leeches, although some trypanosome species may be transmitted by the ingestion of infected arthropods. Molecular phylogenetic studies have shown that trypanosomes from tortoises clustered together with those from fish (both groups being transmitted by aquatic leeches), whereas trypanosomes from crocodiles (transmitted by tsetse flies) were closest to avian trypanosomes. Trypanosomes from varanid, phrynosomatid and gekkonid lizards clustered together (transmitted by flies, bugs, ticks), whereas those from chameleons (transmitted by mosquitoes) grouped with anuran trypanosomes (transmitted by leeches). In leech vectors, ingested trypomastigotes form epimastigotes in crop or stomach which multiply by binary fission and form metacyclic trypomastigotes that are injected into new hosts via leech bites (inoculative transmission). Development generally takes 14-34 days depending on the species involved and the prevailing water temperatures (faster in warmer conditions). In tsetse fly vectors for crocodilian *T. grayi*, ingested trypomastigotes form epimastigotes in the midgut, divide and enter the hindgut where they transform into metacyclic trypomastigotes that are transmitted to crocodiles when they consume fly vectors (consumptive transmission). Infections in terrestrial reptiles involve other dipteran vectors and follow a more complex developmental sequence, with ingested trypomastigotes forming promastigotes or amastigotes within hyaline cysts in the midgut, then sphaeromastigotes and finally infective epimastigotes in the hindgut which are transmitted to new vertebrate hosts when they ingest vectors during feeding or grooming (consumptive transmission). Development in the vector may take as little as 5 days.

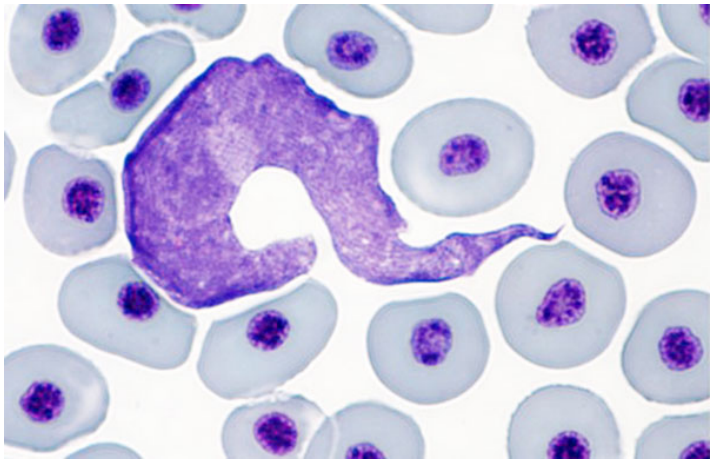
Differential diagnosis: Infections are conventionally diagnosed in reptiles and amphibians by the microscopic detection of trypomastigotes in samples of peripheral or heart blood collected into anti-coagulants. Wet mounts may be examined by high-contrast microscopy to detect motile extracellular trypomastigotes swimming around in blood, or fixed smears may be examined after staining with Giemsa or Leishman's stains. Alternatively, buffy coat layers may be examined for parasites following centrifugation in tubes or haematocrit straws. Invertebrate vectors may be examined for parasite developmental stages by microscopy of squash preparations or fixed histological sections. Parasites may be cultured *in vitro* in various media, including biphasic blood agar, Novy-MacNeal-Nicolle (NNN) media, Diamond's saline-neopeptone-blood (SNB-9) or Ponselle's hypotonic medium. Modern molecular biological techniques have been used to detect and characterize parasite isolates following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA).

Treatment and control: Infections in reptiles and amphibians do not cause clinical disease and therefore do not require treatment. If infections are a cause of concern to herpetologists in zoo or captive collections, it is recommended that some form of vector control be instituted to reduce the risks of transmission, with chemical bath treatments (e.g. trichlorphon) being effective against aquatic leeches, and topical insecticides and/or acaricides used to treat terrestrial hosts for ectoparasitic arthropods.


Trypanosoma
(reptilian/amphibian species)
blood
(nonpathogenic)
division by
longitudinal
binary fission
Vertebrate Hosts
(lizards, snakes, frogs)
long undulating membrane (UM)
anterior free
flagellum (FF)
posterior
kinetoplast (K)
trypomastigote (15-120 µm)
mostly inoculative transmission (infective stages injected)
sometimes consumptive (infected vectors ingested)
ingested with
bloodmeal
amastigote (~ 6 µm)
[no UM, no FF]
epimastigote (~ 20 µm)
[anterior K, short UM, FF]
sphaeromastigote (~ 5 µm)
[anterior K, FF, no UM]
promastigote (~ 10 µm)
[anterior K, FF, no UM]
Invertebrate Hosts
(leech/sandfly vectors)
(alimentary tract)
vector-borne transmission



Trypanosoma trypomastigote in tortoise blood



Trypanosoma trypomastigote in frog blood

Trypanosoma (avian species)
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Trypanosomes have a single flagellum and they form four main developmental stages: trypomastigotes (with a posterior kinetoplast and an emergent flagellum forming a long undulating membrane); epimastigotes (with an anterior kinetoplast and an emergent flagellum forming a short undulating membrane); promastigotes (with an anterior kinetoplast and a short emergent flagellum, but no undulating membrane); and amastigotes (with a kinetoplast but no emergent flagellum or undulating membrane). Many trypanosome species are parasitic only in insects whereas others are transmitted by invertebrate vectors to a wide range of vertebrate hosts, including birds. Avian trypanosomes have been shown to be transmitted by dipteran insects (mosquitoes, hippoboscids, black flies, sand flies) to a range of birds, particularly songbirds and raptors, but few infections have been associated with clinical disease.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Discoba (diverse group supported robustly by molecular studies)
Phylum: Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass: Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order: Trypanosomatida (parasitic, single anterior flagellum, often forming undulating membrane)
Family: Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)
Genus: *Trypanosoma* (vector-borne haemoparasites)
Species: various species cause infections in birds

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia	Order: Trichomonadida (3-5 anterior flagella plus	Monocercomonadidae (costa absent, most	*Histomonas*	birds (gut, liver)	direct (f-o)

(with parabasal body)	recurrent flagellum)	without undulating membrane)	*Dientamoeba*	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans comprise a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)
	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*).

Trypanosomatids are dixenous (2-host) parasites with indirect transmission cycles between vertebrates and invertebrate vectors. *Trypanosoma* spp. form trypo- and/or a-mastigote stages in the blood/tissues of vertebrate hosts, and epi- or pro-mastigote stages in invertebrate haematophagous vectors. Infections have been found in a range of vertebrate species (mammals, birds, reptiles, amphibians and fish) with many different types of haematophagous invertebrates (leeches, bugs, flies, fleas) implicated as vectors or paratenic hosts. Recent molecular phylogenetic studies have validated the separation of mammalian salivarian and stercorarian trypanosomes, but indicated complex placements for trypanosomes from non-mammalian hosts, despite earlier suggestions that they be assigned to separate subgenera. Many clades have been identified, most associated with particular vertebrate or invertebrate hosts, or both, suggesting that 'host-fitting' rather than 'co-speciation' has been the principal mechanism for trypanosome evolution. Several trypanosome species in birds resembled those in mammals belonging to the subgenus *T. Megatrypanum,* but rather than amalgamate both host groups, it was tentatively proposed to group the species from birds into a separate subgenus called *T. Trypanomorpha* (comprising large species including *T. avium, paddae, hannae, confusum, corvi, numidae, gallinarum, macfiei* and *delhiense*). Another three morpho-groups were identified: small trypanosomes (e.g. *T. franchinii, langeroni, guyanense*); broad stumpy trypanosomes (*T. calmettei, caprimulgi, cristatae, ixobrychi, laverani, turdoides, lagonostictae*); and a few species with terminal kinetoplasts (*T. fiadeiroi, lobivanelli, oenae, everetti*). However, molecular phylogenetic studies have not validated any of these groupings for bird trypanosomes, but have suggested much more conservatism that their host range suggests. While over 100 bird trypanosome species have been described (predominantly on the basis of host occurrence), genotypic characterization studies have found many belong to just three clades, each with around four lineages. Clade A comprised species of small-medium trypanosomes with narrow kinetoplasts (< 500 nm) from songbirds and raptors and contained lineages VI, VII, VIII and IX (the latter lineage referable to *T. bennetti*) apparently transmitted by the ingestion of biting midges. Clade B comprised species of larger striated trypanosomes with narrow kinetoplasts from songbirds, raptors, hippoboscid flies and mosquitos and contained lineages I, XII, V (referable to *T. culicavium* which is transmitted to insectivorous passerines by the ingestion of culicine mosquitos) and IV (referable to *T. corvi* which is transmitted to songbirds and raptors by the ingestion of hippoboscid flies). Clade C comprised species of large striated trypanosomes with wide kinetoplasts (> 500 nm) from songbirds, raptors, mosquitos, black flies, hippoboscid flies and sand flies and contained lineages II, III, X and XI (the latter two lineages referable to *T. avium* which is transmitted to songbirds, owls and raptors by black fly ingestion or contamination). Clearly, many more avian trypanosome species remain to be characterized by molecular studies on isolates not only from birds but also from their putative vectors.

***Trypanosoma* species**	**Mastigote length (µm)**	**Hosts**	**Vectors**	**Distribution**
T. abelsalazari		Passeriformes: sturnid (purple starling)		Africa
T. aguedaferreirae		Galliformes: phasianid (double-spurred spurfowl)		Africa
T. anellobiae	30-35	Passeriformes: meliphagid (little wattlebird)		Australia
T. ardeae		Pelecaniformes: ardeid (yellow-crowned night heron, cocoi heron, little blue heron)		Americas
T. asturinulae		Accipitriformes: accipitrid (lizard buzzard)		Africa
T. avium	26-29 striated	Accipitriformes: accipitrid (lesser spotted eagle); Anseriformes: anatid (mallard, northern pintail), Coraciiformes: alcedinid (African pygmy kingfisher), coraciid (European roller); Columbiformes: columbid (mourning dove); Cuculiformes: cuculid	Diptera: simuliid (*Eusimulium securiforme, Metacnephia lyra, Obuchovia albella, Odagmia ornata*, *erganica, Simulium*	Europe, Africa

		(black-billed cuckoo); Falconiformes: falconid (common kestrel); Galliformes: phasianid (rock partridge, Ahanta spurfowl); Passeriformes: bombycillid (cedar waxwing), cardinalid (rose-breasted grosbeak), cisticolid (grey-backed camaroptera), corvid (rook, fish crow, western jackdaw, blue jay), fringillid (canary, purple finch, chaffinch), hirundinid (barn swallow), icterid (red-winged blackbird, bobolink, Baltimore oriole, campo troupial, red-breasted meadowlark), meliphagid (regent honeyeater), mimid (grey catbird), nectariniid (olive sunbird, little green sunbird), parid (boreal chickadee), parulid (American redstart, common yellowthroat, yellow warbler, Tennessee warbler, Canada warbler, yellow-rumped warbler, chestnut-sided warbler, black-and-white warbler, Cape May warbler, Magnolia warbler, MacGillivray's warbler, Wilson's warbler), passerellid (dark-eyed junco, song sparrow, swamp sparrow, chipping sparrow, white-throated sparrow), passerid (house sparrow, northern grey-headed sparrow), ploceid (village weaver, Vieillot's black weaver), pycnonotid (common bulbul, yellow-bellied greenbul, red-whiskered bulbul, little greenbul), turdid (American robin, eastern bluebird, veery, hermit thrush, Swainson's thrush), tyrranid (western flycatcher, olive-sided flycatcher, willow flycatcher, pygmy tyrant), vireonid (red-eyed vireo); Pelecaniformes: ardeid (little blue heron, snowy egret, black-crowned night heron); Piciformes: picid (northern flicker, downy woodpecker); Strigiformes: strigid (tawny owl, long-eared owl)	*aureum, latipes, rugglesi, vernum*, *Tetisimulium coarctata, alajensis*), hippoboscid (*Stilbometopa podopostyla, impressa, Ornithomyia avicularia*)	
T. bakeri		Psittaciformes: psittacid (blossom-headed parakeet)	Diptera: ceratopogonid (*Culicoides nuberculosus*)	Asia
T. balfouri		Psittaciformes: psittacid (blue-crowned parakeet); Passeriformes: thraupid (red-crested cardinal)		South America
T. bennetti		Falconiformes: falconid (American kestrel)		North America
T. bouffardi	19-53 striated	Passeriformes: estrildid (lavender waxbill, black-rumped waxbill, bronze mannikin, red-cheeked cordonbleu, cut-throat finch, red-billed firefinch), ploceid (black-headed weaver, black-necked weaver, red bishop), viduid (village indigobird)		Africa, Europe
T. bramae		Strigiformes: strigid (spotted owlet)		Asia
T. brimonti		Passeriformes: pycnonotid (light-vented bulbul)		Asia
T. brumpti		Falconiformes: falconid (American		North America

(syn. *T. langeroni nom. preocc.*)		kestrel)		
T. bycanistis		Bucerotiformes: bucerotid (trumpeter hornbill)		Africa
T. calmettei		Galliformes: phasianid (junglefowl)		Africa
T. caprimulgi		Caprimulgiformes: caprimulgid (long-tailed nightjar)		Africa
T. catharistae		Cathartiformes: cathartid (black vulture)		Americas
T. centropi		Cuculiformes: cuculid (greater coucal)		Asia
T. chlamydoderae		Passeriformes: ptilorhynchid (great bowerbird)		Australia
T. chaubaudi	42-49	Passeriformes: estrildid (orange-cheeked waxbill)		Africa
T. columbae		Columbiformes: columbid (rock dove)		Europe
T. confusum (possibly a synonym of *T. avium*)		Passeriformes: turdid (thrushes, jays), muscicapid (robins), meliphagid (honey-suckers)	Diptera: simuliid (*Helodon decemarticulatus, Simulium* sp.)	North America
T. corvi	striated	Passeriformes: corvid (rook, house crow, western jackdaw, rufous treepie), turdid (common blackbird); Accipitriformes: accipitrid (Eurasian sparrowhawk)	Diptera: simuliid (*Simulium latipes*), hippoboscid (*Ornithomyia avicularia*)	Eurasia
T. cotylei		Passeriformes: hirundinid (sand martin)		Eurasia, North America
T. cristatae		Musophagiformes; musophagid (great blue turaco)		Africa
T. cuculi		Cuculiformes: cuculid (Indian cuckoo)		India
T. culicavium	40-41	Passeriformes: fringillid (canary), (flycatchers, canaries), muscicapid (collared flycatcher)	Diptera: culicid (*Culex pipiens, modestus, quinquefasciatus*)	Europe
T. cypseli		Apodiformes: apodid (common swift)		Eurasia
T. dabbenei		Passeriformes: formicariid (short-tailed antthrush)		South America
T. dafilae		Anseriformes: anatid (northern pintail duck)		Europe
T. davidmolyneuxi	13-18	Passeriformes: estrildid (common waxbill, orange-cheeked waxbill)		Africa
T. delhiense		Passeriformes: estrildid (Indian silverbill)		India
T. dschunkowskii		Passeriformes: corvid (Eurasian jay)		Eurasia
T. eudyptulae	36-52	Sphenisciformes: spheniscid (little penguin)		Australia
T. eurystomi		Coraciiformes: coraciid (rollers)		Africa
T. everetti	16-20	Passeriformes: estrildid (common waxbill, orange-cheeked waxbill, black-rumped waxbill), fringillid (finch), muscicapid (flycatchers), nectariniid (sunbirds), ploceid (weavers), pycnonotid (bulbuls), sturnid (starlings), zosteropid (white-eyes); Bucerotiformes: bucerotid (hoopoes), Coraciiformes: coraciid (kingfishers)		Africa
T. faridi		Passeriformes: fringillid (Eurasian bullfinch)		Europe
T. fiadeiroi		Accipitriformes: accipitrid (lizard buzzard)		Africa
T. fradei		Coraciiformes: coraciid (broad-billed (roller)		Africa
T. franchinii		Passeriformes: fumariid (great rufous		South America

(= *franchinianus*)		woodcreeper)		
T. francolini		Galliformes: phasianid (double-spurred spurfowl)		Africa
T. fringillinarum		Passeriformes: fringillid (Eurasian chaffinch, common chaffinch, common redpoll)		Eurasia
T. fulicae		Gruiformes: rallid (Eurasian coot)		Eurasia
T. gallinarum	26-29	Galliformes: phasianid (Uganda fowl)		Africa, Asia
T. garruli		Passeriformes: corvid (black-headed jay)		Asia
T. gentilinii	32-40	Passeriformes: estrildid (orange-cheeked waxbill)		Africa
T. grewali		Passeriformes: estrildid (scaly-breasted munia)		Asia
T. guyanense		Accipitriformes: accipitrid (savanna hawk)		South America
T. gymnochidis		Passeriformes: passerid (yellow-throated sparrow)		Asia
T. hannae		Columbiformes: columbid (rock dove)	Diptera: hippoboscid (*Lynchia maura*)	India
T. ixobrychi		Pelecaniformes: ardeid (little bittern)		Africa
T. johnstoni		Passeriformes: estrildid (common waxbill)		Africa
T. knowlesi		Passeriformes: estrildid (Indian silverbill)		India
T. kremeri	50	Passeriformes: estrildid (orange-cheeked waxbill)		Africa
T. lagopodis		Galliformes: phasianid (ptarmigan)		North America
T. lagonstictae		Passeriformes: estrildid (red-billed firefinch)		Africa
T. langeronianus		Falconiformes: falconid (American kestrel)		South America
T. lanii		Passeriformes: laniid (long-tailed shrike)		Asia
T. laverani		Passeriformes: fringillid (American goldfinch), mimid (brown thrasher)		North America
T. liothricis		Passeriformes: leiothrichid (red-billed leiothrix)		Asia
T. lobivanelli		Charadriiformes: charadriid (red-wattled lapwing)		India
T. loxiae		Passeriformes: fringillid (red crossbill, canary, finch)	Diptera: culicid (*Culex pipiens, Aedes argenteus*)	Africa
T. macfiei		Passeriformes: fringillid (canary)		Europe
T. mathisi		Passeriformes: hirundinid (barn swallow)		Europe
T. mayae		Passeriformes: passerid (house sparrow)		Europe
T. mesnili		Accipitriformes: accipitrid (red-shouldered hawk, savanna hawk)		South America
T. milvi		Accipitriformes: accipitrid (black kite)		Eurasia
T. moruoni		Passeriformes: muscicapid (Oriental magpie-robin)		Asia
T. myzanthae	19-24	Passeriformes: meliphagid (noisy miner)		Australia
T. noctuae	26-60	Strigiformes: strigid (little owl)	Diptera: culicid (*Culex pipiens*)	Europe
T. notophoyxis		Pelecaniformes: ardeid (white-faced heron)		Australia
T. numidae		Galliformes: numidid (helmeted guineafowl), phasianid (chicken)	Diptera: simuliid (*Simulium adersi, impucane, nyasalandicum,*	Africa

			vorax)	
T. nycticoracis		Pelecaniformes (black-crowned night heron)		Eurasia
T. oenae		Columbiformes: columbid (Namaqua dove)		Africa
T. ontarioensis		Passeriformes: corvid (American crow), fringillid (canary); Galliformes: phasianid (ruffed grouse, chicken); Psittaciformes: psittaculid (budgerigar)		North America
T. paddae		Passeriformes: estrildid (red-billed firefinch, Java sparrow, black-rumped waxbill), fringillid (canary, serin), thraupid (glistening-green tanager)		Eurasia, Americas
T. pedrozi		Galliformes: cracid (bare-faced curassow)		South America
T. phedinae		Passeriformes: hirundinid (Mascarene martin)		Mauritius
T. polyplectri		Galliformes: phasianid (Germain's peacock pheasant)		Asia
T. pycnonoti		Passeriformes: pycnonotid (common bulbul)		Africa
T. queleae		Passeriformes: ploceid (red-billed quelea)		Africa
T. santadiasi		Strigiformes: strigid (northern white-faced owl)		Africa
T. schistochlamydis		Passeriformes: thraupid (cinnamon tanager)		South America
T. syrnii		Strigiformes: strigid (tawny owl)		Europe
T. thiersi		Caprimulgiformes: caprimulgid (European nightjar)		Europe
T. thomasbancrofti	28-43	Passeriformes: acrocephalid (Eurasian reed warbler), estrildid (zebra finch), fringillid (canary), hirundinid (barn swallow, sand martin), meliphagid (regent honeyeater), phylloscopid (wood warbler, common chiffchaff), sylviid (Eurasian blackcap)	Diptera: culicid (*Culex pipiens, molestus, quinquefasciatus*), hippoboscid (*Ornithomya fringillina*)	Europe, Australia
T. tinami		Tinamiformes: tinamid (cinereous tinamou, great tinamou)		South America
T. turdoides		Passeriformes: leiothrichid (jungle babbler)		India
T. uraguayensis		Passeriformes: fringillid (finch)		South America
T. urolonchae		Passeriformes: estrildid (white-rumped munia)		Asia
T. viduae		Passeriformes: viduid (pin-tailed whydah)		Africa
T. ziemanni		Coraciiformes: coraciid (broad-billed roller)		Africa
T. zonotrichae		Passeriformes: passerellid (rufous-collared sparrow)		Americas

Parasite morphology: Avian *Trypanosoma* spp. form 2 different types of developmental stages: trypomastigotes in birds; and epimastigotes in invertebrate vectors. Trypomastigotes are pleomorphic depending on the species and the stage of development, but most forms are elongate and slender ranging from 20-90 μm in length and 1-10 μm in width. They contain a central ovoid basophilic nucleus as well as a smaller rounded kinetoplast (containing mitochondrial DNA) located behind the host cell nucleus. Flagellar basal bodies (microtubular arrays) are located adjacent to the kinetoplast and give rise to a single long flagellum that emerges and runs along the body surface forming a long undulating membrane before extending freely beyond the cell margin. This margin is the anterior end of the cell as live observations show the parasites moving in the direction of the flagellum (the flagellum is not recurrent or trailing like that of the bodonids *Cryptobia* and *Trypanoplasma*). The cell surface is often striated in appearance with so-called myonemes extending longitudinally or spirally along the body (e.g. *T. avium* complex). Epimastigotes are smaller

cells (5-20 μm long) that have a central nucleus, an anterior kinetoplast and a short emergent flagellum that forms a short undulating membrane.

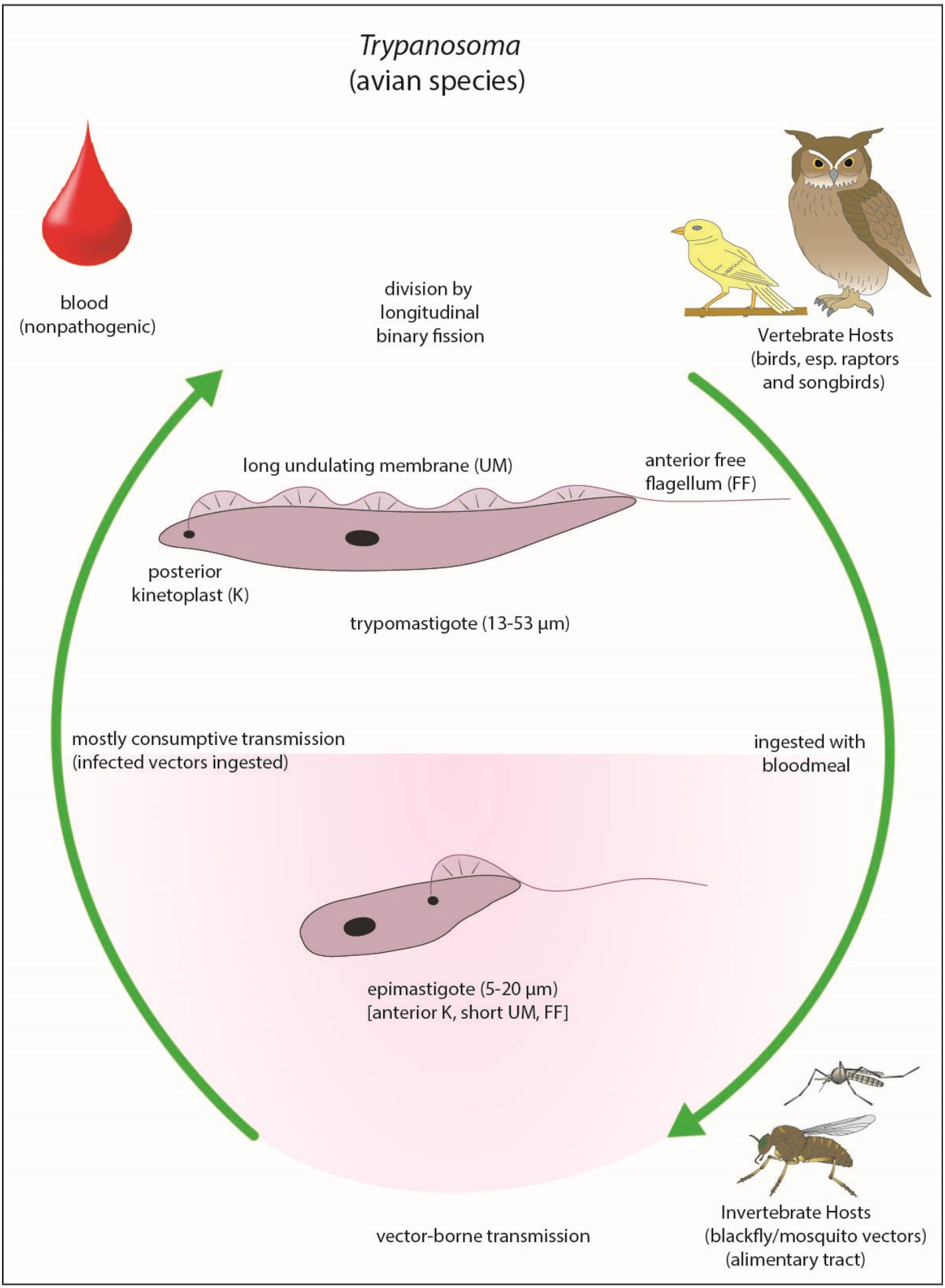
Site of infection: In birds, trypomastigotes are found extracellularly in the circulatory system of their hosts. A total of 93 *Trypanosoma* spp. have been described from 154 bird species, including 61 non-passerine species belonging to 24 families in 21 orders, and 120 passerine species belonging to 33 families. In the invertebrate vectors, epimastigotes are found extracellularly within the hindgut and midgut. Vectors for avian *Trypanosoma* spp. have included 26 dipteran species belonging to 4 families (mainly simuliids, but also some culicids, hippoboscids and one ceratopogonid).

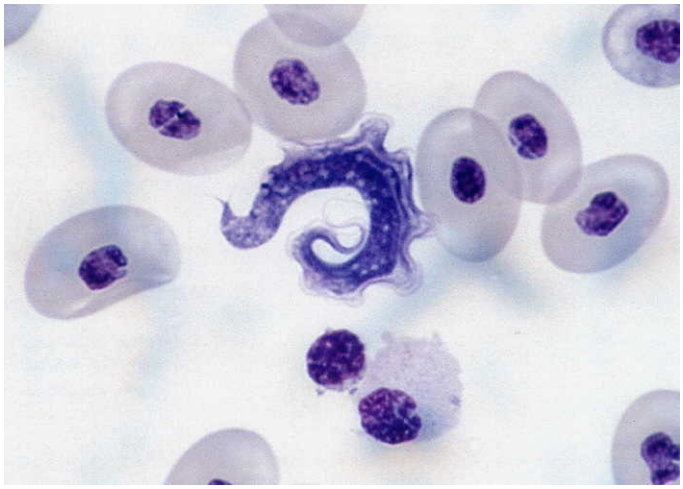
Pathogenesis: Natural infections by avian trypanosomes are considered to be nonpathogenic as they have not been associated with any specific clinical disease. Although some bird hosts may have exhibited clinical signs or haemodynamic disturbances, they were often attributable to concomitant infections or existing disease conditions. Nevertheless, some experimental infections in aviary birds have been associated with chronic disease characterized by progressive splenomegaly, myositis and myocarditis.

Developmental cycle and mode of transmission: Avian trypanosomes have cyclic heteroxenous (2-host) life-cycles with vector-borne transmission involving haematophagous dipteran insects (simuliid blackflies, culicid mosquitoes, hippoboscid louse-flies, and ceratopogonid biting midges). Trypomastigotes swim freely in bird blood where they feed by absorption of nutrients across their surface membranes and multiply asexually by binary fission involving organelle replication, karyokinesis and then transverse cytokinesis. Vectors acquire infections by ingesting trypomastigotes while feeding on bird blood. The parasites are localized in the hindgut where they form rosettes of dividing stages by binary and multiple fission, eventually releasing free epimastigotes that may stay in the hindgut, move forward to the midgut or become localized on the stomodeal valve. Transmission to birds does not occur via vector bite but rather by birds ingesting vectors when feeding or grooming (i.e. consumptive transmission rather than inoculative transmission). Several studies have also implicated transmission via bird conjunctival contamination by vector urine droplets, possibly the consequence of prediuresis (the excretion of water by the vector to concentrate the bloodmeal).

Differential diagnosis: Infections are normally detected in birds by the direct microscopic demonstration of trypomastigotes in blood samples (peripheral or heart blood collected into anticoagulant). Wet mounts may be examined by high-contrast microscopy looking for motile parasites thrashing between blood cells, or fixed smears may be examined after staining with Giemsa or Leichman's stains. Trypomastigotes may also be concentrated from blood samples into the buffy coat layer by centrifugation in capillary or haematocrit tubes. Infections in vectors are usually revealed by examining squash preparations or histological sections. Parasites may be cultured in vitro in a variety of media, including biphasic blood agar with RPMI liquid media or Schneider's *Drosophila* medium with foetal calf serum. Molecular biological techniques have recently been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA, internal transcribed spacer regions 1 and 2, and glycosomal glyceraldehyde 3-phosphate dehydrogenase).

Treatment and control: Infections are nonpathogenic in birds so chemotherapy is not required. If infections are of concern to managers of captive bird collections in zoos or aviaries, measures may be instituted to prevent the spread of infections by excluding potential vectors using physical or chemical barriers in holding facilities or applying topical or systemic insecticides to birds at risk.


Trypanosoma
(avian species)
blood
(nonpathogenic)
division by
longitudinal
binary fission
Vertebrate Hosts
(birds, esp. raptors
and songbirds)
long undulating membrane (UM)
anterior free
flagellum (FF)
posterior
kinetoplast (K)
trypomastigote (13-53 µm)
mostly consumptive transmission
(infected vectors ingested)
ingested with
bloodmeal
epimastigote (5-20 µm)
[anterior K, short UM, FF]
vector-borne transmission
Invertebrate Hosts
(blackfly/mosquito vectors)
(alimentary tract)



Trypanosoma trypomastigote in bird blood

Trypanosoma brucei
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Trypanosomes have a single flagellum and they form four main developmental stages: trypomastigotes (with a posterior kinetoplast and an emergent flagellum forming a long undulating membrane); epimastigotes (with an anterior kinetoplast and an emergent flagellum forming a short undulating membrane); promastigotes (with an anterior kinetoplast and a short emergent flagellum, but no undulating membrane); and amastigotes (with a kinetoplast but no emergent flagellum or undulating membrane). Many trypanosome species are parasitic only in insects whereas others are transmitted by invertebrate vectors to a wide range of vertebrate hosts. Three main groups infect the blood and/or tissues of humans and animals causing severe clinical diseases: including the cyclic salivarian trypanosomes which undergo anterior station (foregut) development in the insect vector and are transmitted via saliva to the blood of vertebrate hosts (e.g. tsetse flies transmit *T. brucei* which causes sleeping sickness in humans and nagana in cattle).

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Excavata (with conspicuous ventral feeding groove)
Group:	Discoba (diverse group supported robustly by molecular studies)
Phylum:	Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class:	Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass:	Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order:	Trypanosomatida (parasitic, single anterior flagellum, often forming undulating membrane)
Family:	Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)
Genus:	*Trypanosoma* (vector-borne haemoparasites)
Species:	*T. brucei* (causes sleeping sickness in humans and nagana in cattle)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum:	Order: Trichomonadida	Monocercomonadidae	*Histomonas*	birds	direct (f-o)

Parabasalia (with parabasal body)	(3-5 anterior flagella plus recurrent flagellum)	(costa absent, most without undulating membrane)		(gut, liver)	
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans comprise a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)

	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*).

Trypanosomatids are dixenous (2-host) parasites with indirect transmission cycles between vertebrates and invertebrate vectors. *Trypanosoma* spp. form trypo- and/or a-mastigote stages in the blood/tissues of vertebrate hosts, and epi- or pro-mastigote stages in invertebrate haematophagous vectors. Infections have been found in a range of vertebrate species (mammals, birds, reptiles, amphibians and fish) with many different types of haematophagous invertebrates (leeches, bugs, flies, fleas) implicated as vectors or paratenic hosts. The species found in mammals have been grouped into two Sections (convenient groups without formal taxonomic rank) primarily on the basis of their developmental cycles in their vectors and their modes of transmission. Each Section contains several subgenera, as follows:

Section: Stercoraria (posterior station development in vector, contaminative transmission)

- *T.* (*Megatrypanum*), large trypanosomes with kinetoplast close to nucleus;
- *T.* (*Herpetosoma*), medium trypanosomes with subterminal kinetoplast;
- *T.* (*Schizotrypanum*), small C-shaped trypanosomes with voluminous terminal kinetoplast;

Section: Salivaria (anterior station development in vector, inoculative (some mechanical) transmission);

- *T.* (*Duttonella*), former *vivax*-group, monomorphic forms with large terminal kinetoplast;
- *T.* (*Nannomonas*), former *congolense*-group, small forms with medium marginal kinetoplast;
- *T.* (*Trypanozoon*), former *brucei*-group, pleomorphic forms with small subterminal kinetoplast;
- *T.* (*Pycnomonas*), former *suis*-subgroup, stout monomorphic forms with small subterminal kinetoplast.

Recent molecular phylogenetic studies have validated the separation of mammalian salivarian and stercorarian trypanosomes, but indicated complex placements for trypanosomes from non-mammalian hosts, despite earlier suggestions that they be assigned to separate subgenera (*Trypanomorpha* for those in birds, *Trypanosoma* for those in amphibians, and *Haematomonas* for those in fish). Many clades have been identified, most associated with particular vertebrate or invertebrate hosts, or both, suggesting that 'host-fitting' rather than 'co-speciation' has been the principal mechanism for trypanosome evolution. Comparative studies have found many differences between trypanosomes of aquatic and terrestrial hosts, with several clades found for species in freshwater fishes, marine fishes, amphibians, tortoises and platypuses (all thought to be transmitted by leech vectors). *T. brucei* belongs to the salivarian trypanosomes which exhibit continuous multiplication in the mammalian host and develop in the anterior station in tsetse fly vectors with inoculative transmission (except for *T. evansi* and *T. equiperdum* which are transmitted mechanically by biting flies or by contact). Four salivarian subgenera are recognized: *Duttonella* comprising monomorphic trypanosomes with a large kinetoplast (*T. vivax, T. uniforme*); *Nannomonas* comprising small trypanosomes with a medium-sized kinetoplast (e.g. *T. congolense, T. simiae*); *Pycnomonas* comprising thick monomorphic forms with a small kinetoplast (*T. suis*); and *Trypanozoon* comprising pleomorphic (stumpy to slender) forms with a small kinetoplast (*T. brucei, T. evansi, T. equiperdum*). Species belonging to the former two subgenera develop in the proboscis or midgut of their vectors while those of the latter two subgenera undergo development in the midgut and salivary glands (except for *T. evansi* and *T. equiperdum* which are transmitted mechanically). Three closely-related subspecies of *T. brucei* are found: *T. b. brucei* which is primarily parasitic in native antelopes and other wild ruminants (asymptomatic carriers, trypanotolerant) but infects introduced domestic animals; *T. b. rhodesiense* which causes acute disease in humans in East Africa; and *T. b. gambiense* which produces a much more chronic disease in humans in West Africa. Other species are also found in ruminants, horses and pigs. Salivarian trypanosomes are confined to tropical Africa, corresponding in distribution with their tsetse fly vectors. Of the ~30 *Glossina* species/subspecies, eight are major vectors of sleeping sickness. The trypanosomes transmitted mechanically by biting flies or by coitus have a more global distribution.

***Trypanosoma* species**	**Mastigote length (µm)**	**Hosts**	**Disease**	**Vectors**	**Distribution**

CYCLIC TRANSMISSION (development within vector)					
SALIVARIA (free flagellum present or absent, kinetoplast terminal or subterminal, posterior end blunt, reproduction in mammalian host continuous, taking place in trypomastigote stages, development in vector (with formation of metatrypanosomes) in anterior station (except in mechanical inoculators), transmission inoculative (except for *T. equiperdum*)					
Subgenus: ***Duttonella*** (trypanosomes of former *vivax*-group, monomorphic forms with free flagellum, rounded posterior end, large kinetoplast usually terminal, development in vector (*Glossina*) in proboscis)					
T. (*D.*) *uniforme*	12-20	Artiodactyla: bovid (cattle, African buffalo, sheep, goat, waterbuck, harnessed bushbuck, sitatunga), giraffid (giraffe)	variable pathogenicity	Diptera: glossinid (*Glossina fuscipes, palpalis*)	East and Central Africa
T. (*D.*) *vivax* [type species] [incl. subspp. *vivax, viennei*] (syn. *T. angolense, bovis, caprae, cazalboui*)	18-31	Artiodactyla: bovid (cattle, African buffalo, sheep, goat, impala, hartebeest, western hartebeest, Lichtenstein's hartebeest, blue wildebeest, topi, common eland, nyala, southern reedbuck, Bohor reedbuck, common duiker, red forest duiker, yellow-backed duiker, Thomson's gazelle, roan antelope, sable antelope, waterbuck, puku, suni, oribi, steenbok, harnessed bushbuck, sitatunga, greater kudu), camelid (camel), suid (warthog); giraffid (giraffe, reticulated giraffe), cervid (white-tailed deer); Perissodactyla: equid (horse, donkey, mule, plains zebra); Carnivora: canid (dog), felid (lion); Rodentia: murid (mouse); Primates: hominid (human)	nagana, souma	Diptera: glossinid (*Glossina austeni, brevipalpis, fuscipes, longipalpis, morsitans, pallidipes, palpalis, swynnertoni, tachinoides, vanhoofi*) plus mechanical transmission by Diptera: tabanid (*Tabanus, Stomoxys* spp.) in New World	tropical Africa
Subgenus: ***Nannomonas*** (trypanosomes of former *congolense*-group, small forms without free flagellum, medium kinetoplast typically marginal, development in vector (*Glossina*) in midgut and proboscis)					
T. (*N.*) *congolense* [type species] (syn. T. *berghei*, *celii*, *dimorphon*, *frobenius*, *mossoense, multiforme* p.p., *nanum*, *pecorum*, *ruandae*, *somaliense*, *urundiense*)	8-24	Artiodactyla: bovid (cattle, African buffalo, goat, sheep, impala, hartebeest, Lichtenstein's hartebeest, common duiker, red forest duiker, yellow-backed duiker, blue wildebeest, topi, Grant's gazelle, Thomson's gazelle, roan antelope, sable antelope, waterbuck, kob, puku, dik-dik, suni, klipspringer, steenbok, southern reedbuck, common eland, nyala, sitatunga, greater kudu), camelid (dromedary), giraffid (giraffe, reticulated giraffe), suid (pig, warthog, red river hog, bushpig); Perissodactyla (horse, donkey, mule, plains zebra); Proboscidea: elephantid (African elephant); Carnivora: canid (dog, hyena), felid (lion); Lagomorpha: leporid (rabbit); Rodentia: murid (rat)	nagana	Diptera: glossinid (*Glossina austeni, brevipalpis, fuscipes, longipalpis, morsitans, pallidipes, palpalis, swynnertoni, tachinoides, vanhoofi*)	tropical Africa
T. (*N.*) *godfreyi*	9-22	Artiodactyla: suid (warthog)	nr	Diptera: glossinid (*Glossina morsitans, pallidipes*)	West Africa

T. (*N.*) *montgomeryi*	10-21	Artiodactyla: bovid (cattle, sheep); suid (pig); Carnivora: canid (dog); Perissodactyla: equid (horse)	nr	Diptera: glossinid (*Glossina morsitans*)	Central Africa
T. (*N.*) *simiae* (syn. *T. ignotum, porci, rhodhaini*)	12-26	Artiodactyla: suid (pig, desert warthog), bovid (cattle); camelid (dromedary); Perissodactyla: equid (horse)	acute porcine trypanosomiasis	Diptera: glossinid (*Glossina austeni, brevipalpis, fusca, fuscipes, fuscipleuris, longipalpis, morsitans, pallidipes. palpalis, tabaniformis, tachinoides, vanhoofi*) plus mechanical transmission by biting flies (*Haematopota*, *Stomoxys*)	tropical Africa
Subgenus: ***Trypanozoon*** (trypanosomes of former *brucei*-group including *brucei*- and *evansi*-subgroups represented by pleomorphic forms (slender, intermediate, stumpy) with or without free flagellum, small kinetoplast subterminal, development in vector (*Glossina*) in midgut and salivary glands, but other species transmitted mechanically without development in vectors (*T. evansi*) or by contact between hosts (*T. equiperdum*))					
T. (*T.*) *brucei brucei* [type species] (syn. *T. anceps, dukei, multiforme p.p., pecaudi, togolense, ugandae*)	11-39	Artiodactyla: bovid (various antelope, cattle, sheep, goat), suid (pig, warthog); Perissodactyla: equid (horse, donkey); Proboscidea: elephantid (African elephant); Carnivora: canid (dog, hyena), felid (cat, lion)	nagana	savanna Diptera: glossinid (*Glossina brevipalpis, fuscipes, longipalpis, morsitans, pallidipes, palpalis, swynnertoni, tachinoides*)	tropical Africa
T. (*T.*) *brucei gambiense* (syn. *T. ugandense, castellanii, hominis, fordii, nepveui, tullochii, rovumense, nigeriense*)	12-35	Primates: hominid (human), cercopithecid (mangabey, white-nosed monkey); Artiodactyla: bovid (cattle, African buffalo, sheep, goat, impala, common wildebeest, black wildebeest, hartebeest, Lichtenstein's hartebeest, topi, roan antelope, sable antelope, waterbuck, puku, oribi, steenbok, southern reedbuck, common duiker, common eland, harnessed bushbuck, sitatunga, greater kudu, kob), camelid (dromedary), suid (pig, desert warthog); Perissodactyla: equid (horse, donkey, mule, plains zebra); Carnivora: canid (dog), hyaenid (spotted hyena), felid (cat, lion), viverrid (genet, civet); Rodentia: murid (rat), caviid (guinea pig), hystricid (porcupine)	sleeping sickness (chronic form)	riverine/forest Diptera: glossinid (*Glossina fuscipes, morsitans, palpalis, swynnertoni tachinoides*)	West and Central Africa
T. (*T.*) *brucei rhodesiense*	12-42	Primates: hominid (humans); Artiodactyla: bovid (cattle, bushbuck, waterbuck, hartebeest, antelope), suid (warthog); Carnivora: canid (dog, hyena), felid (lion); Rodentia: murid (rats)	sleeping sickness (acute form)	savanna Diptera: glossinid (*Glossina morsitans, pallidipes, swynnertoni*)	East and Central Africa

Subgenus: ***Pycnomonas*** (trypanosomes of former *brucei*-group, *suis*-subgroup, represented by stout monomorphic forms with short free flagellum and small subterminal kinetoplast, development in vector (*Glossina*) in midgut and salivary glands)					
T. (*P.*) *suis* [type species]	8-19	Artiodactyla: suid (pig, warthog)	variable pathogenicity	Diptera: glossinid (*Glossina brevipalpis, vanhoofi*)	tropical Africa
Unplaced (but forming a distinct Australian clade)					
T. copemani	30-45	Diprotodontia: phascolarctid (koala), vombatid (wombat), potoroid (potoroo, woylie), macropodid (quokka), peramelid (bandicoot), dasyurid (quoll), phalangerid (brush-tailed possum)	low	Ixodida: ixodid? (*Ixodes australiensis*)	Australia
T. gilletti	42?	Diprotodontia: phascolarctid (koala)	low		Australia
T. vegrandis	7-11	Diprotodontia: phascolarctid (koala), potoroid (woylie), macropodid (grey kangaroo, tammar wallaby), dasyurid (quoll), peramelid (bandicoot); Chiroptera: vespertilionid (wattled bat, long-eared bat), pteropodid (flying fox)			Australia

Parasite morphology: The parasite forms trypomastigotes in vertebrate hosts and epimastigotes in the insect vector. The trypomastigotes (with posterior kinetoplast and emergent flagellum forming an undulating membrane) of the salivarian trypanosome species are pleomorphic in size ranging from 8-42 µm in length by 1-3 µm in width. They occur as elongate slender dividing forms (with long free flagellum) or stumpy non-dividing infective (metacyclic) forms (with no free flagellum). The epimastigotes (with anterior kinetoplast and short undulating membrane) are also variable in size ranging from 10-35 µm in length by 1-3 µm in width.

Site of infection: The parasites undergo anterior station development in their invertebrate vectors and salivarian transmission (via vector saliva) to vertebrates where trypomastigotes are found extracellularly in the blood and lymph (including lymph nodes and spleen) although they may invade the central nervous system and other tissues. Some 13 salivarian species have been described in 82 mammalian species belonging to 27 families in 9 orders (artiodactylans, perissodactylans, proboscideans, carnivores, lagomorphs, rodents, marsupials, chiropterans, and primates). Their dipteran vectors have so far included 13 species of tsetse flies in which parasite development occurred.

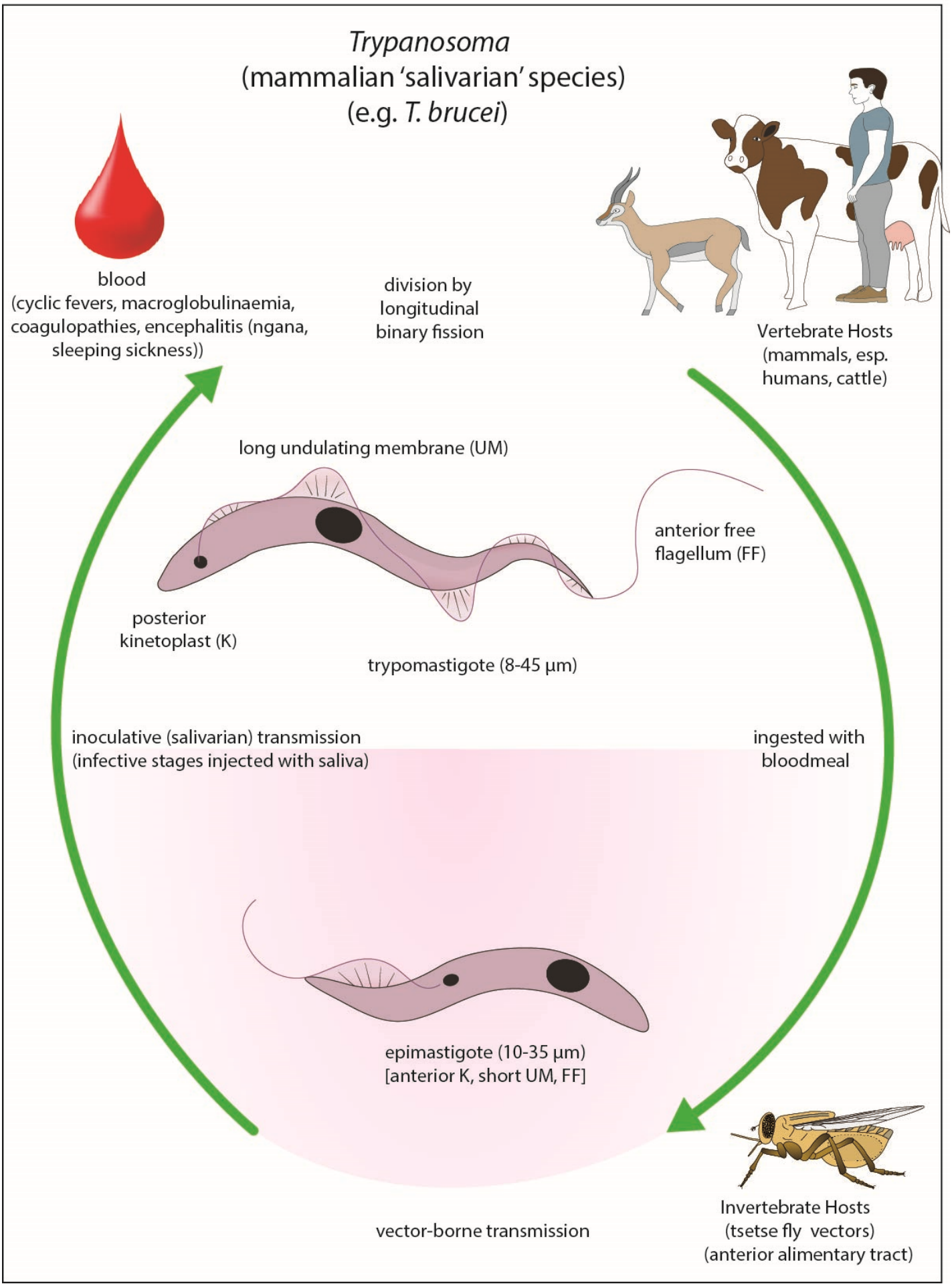
Pathogenesis: The disease in humans is known as Old World (African) trypanosomiasis or human African trypanosomiasis (HAT). Although there are many regional common names given depending on the parasite subspecies and hosts involved, the disease is often called sleeping sickness in humans, and nagana in animals. Parasites injected into the host by the insect vector first cause an inflammatory reaction characterized by a localized tender reddish swelling (known as a chancre). Trypanosomes then multiply in the plasma and interstitial fluid causing acute to subacute febrile illness. *T. b. gambiense* is responsible for most infections in humans (~90%) causing Gambian or West African sleeping sickness, while *T. b. rhodesiense* is generally considered a zoonotic disease with humans as accidental hosts but developing Rhodesian or East African sleeping sickness. *T. b. rhodesiense* infections in humans usually cause acute systemic disease over several weeks with haemolymphatic involvement, swollen lymph nodes, fever and rapid weight loss. *T. b. gambiense* usually causes chronic disease over several months with neurological involvement, meningoencephalitis, lethargy and coma (hence sleeping sickness). A classic sign of *T. b. gambiense* infection is the enlargement of the cervical lymph glands at the back of the neck (known as Winterbottom's sign). Parasite development occurs in cyclic waves moderated by host immune responses. Trypanosomes have a glycoprotein coat on the outer surface of the cell membrane which is highly antigenic and leads to the production of host antibodies which act, together with complement, to lyse parasites. Trypanosomes, however, repeatedly change the molecular arrangement of the coat so some individuals avoid immune destruction and divide to produce a new wave of infection. This antigenic variation is under genetic control and while synthesis of successive variant surface glycoproteins does not occur in a fixed sequence, it is not entirely random. The repeated cycles of host antibody production and parasite destruction leads to cyclic fevers, macroglobulinaemia, microvascular damage, coagulopathy, and perivascular inflammation. There are often two stages of disease: an early haemo-lymphatic stage I with nonspecific symptoms such as fever, anaemia, headache, and lethargy; and a later meningo-encephalitic stage II when parasites have penetrated the blood-brain barrier (within weeks for *T. b. rhodesiense* or up to years for *T. b. gambiense*) causing meningoencephalitis, severe headaches, altered circadian rhythms (night-time insomnia and day-time somnolence), muscle twitches, ataxia, weight loss, psychiatric problems (confusion, irritability, anxiety, hallucinations, delirium), seizures, coma and death. In animals, the clinical course of *T. b.*

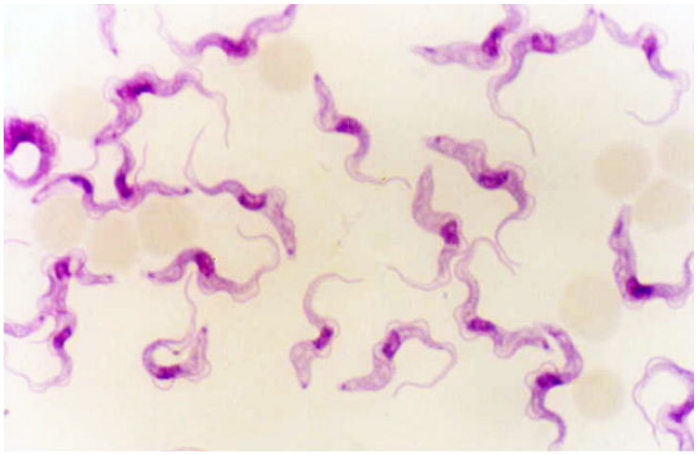
brucei infections depends on the susceptibility of the host species. Horses and dogs are particularly susceptible and may succumb within 2-3 weeks Cattle and pigs are more refractory to disease and may survive for several months. Clinical signs include anaemia, fever, oedema and progressive paralysis. Native animal species (antelope and other wild ruminants) are trypanotolerant and may act as asymptomatic carriers. Humans have been shown to resist infections by other *Trypanosoma* spp. by serum-mediated lysis of the parasites; involving apolipoprotein (apoL1) lytic factors and haptoglobin-like protein (hpr) receptors. *T. b. rhodesiense* avoids lysis through the expression of a serum resistance-associated (*sra*) gene that neutralizes the lytic activity of apoL1. *T. b. gambiense* does not contain the *sra* gene, but resists lysis possibly by the reduced expression of the hpr receptor.

Developmental cycle and mode of transmission: All salivarian trypanosomes are transmitted by tsetse fly vectors (*Glossina* spp.). Metacyclic trypomastigotes ingested during feeding transform into procyclic trypomastigotes in the midgut. These stages migrate through gut membranes and invade the salivary glands over 12-30 days where they transform into epimastigotes which undergo anterior station development to produce infective metacyclic trypomastigotes in the proboscis which are injected during feeding (inoculative transmission). Infections can be transmitted to new susceptible hosts over the entire lifespans of infected flies (around 3 months). Disease distribution mirrors that of the tsetse fly vectors, but is nonetheless patchy with discrete foci, and cases outside the tsetse fly belt are usually imported. Tsetse flies bite and feed sporadically during the day and rest in shaded sites. They find hosts by following carbon dioxide expiratory plumes from animals and use visual cues to land on appropriate feeding sites. Infections by *T. b. gambiense* account for around 95% of human cases and occur in tropical forest of West and Central Africa (separated by the Great Rift Valley) where they are mainly transmitted by tsetse flies belonging to the *palpalis* complex (*G. palpalis, G. fuscipes, G. tachinoides*). Infections by *T. b rhodesiense* occur in savannah areas of East and Southern Africa where they are transmitted by tsetse flies belonging to both the *morsitans* complex (*G. morsitans, G. pallipes, G. swynnertoni*) and the palpalis complex (*G. fuscipes, G. tachinoides*). In addition to vector-borne transmission, there are occasional reports of infections being transmitted horizontally via blood transfusions, or vertically via transplacental passage from mother to foetus. Several species in the New World are also thought to undergo mechanical transmission by tabanid flies (*Tabanus, Stomoxys, Haematopota*).

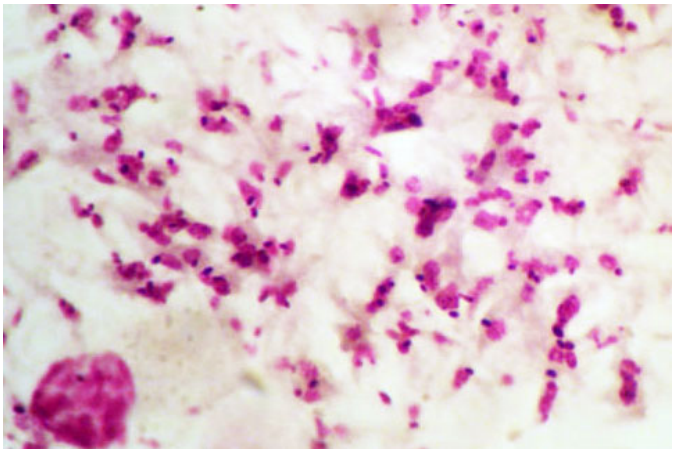
Differential diagnosis: Infections were conventionally diagnosed by the direct detection of parasites in blood, bone marrow, lymph or cerebrospinal fluid by microscopic examination before or after centrifugation. Infections by *T. b. rhodesiense* are often characterized by high parasitaemia, while those by *T. b. gambiense* exhibit intermittent cyclic parasitaemia. The routine examination of wet blood films or stained blood smears is best supplemented by various concentration techniques, such as microhaematocrit tube centrifugation, mini-anion-exchange centrifugation, buffy coat extraction, or fluorochrome staining. It is important that the kinetics (time course) of infection be determined as the treatments for stage I and II diseases are radically different (drugs for stage I cannot cross the blood-brain barrier and those for stage II are extremely toxic). Confirmation of stage II disease may be afforded by examination of cerebrospinal fluid obtained by lumbar puncture for parasites, leucocytes and sometimes increased protein content. *In vitro* cultivation has proven difficult and *in vivo* inoculation into laboratory animals yields variable results. More recently, a variety of immunoserological tests have been developed to detect host antibodies using fluorescent, agglutination or enzyme markers. Card-agglutination and dot-spot tests are available for field use. Molecular characterization techniques utilizing polymerase chain reaction (PCR) amplification of parasite DNA have yielded good results in species/strain differentiation using particular sequences (e.g. serum resistance-associated (*sra*) gene that enables *T. b. rhodesiense* to survive in humans, *T. b. gambiense*-specific glycoprotein (TgsGP), glycosomal glyceraldehyde phosphate dehydrogenase (gGAPDH) as well as small subunit (SSU), large subunit (LSU) and internal transcribed spacer (ITS) regions of ribosomal DNA).

Treatment and control: Historically, arsenical drugs have been used to treat trypanosomiasis despite major toxicity problems (causing up to 5% mortality in patients). A combination of suramin and tryparsamide was used to treat African sleeping sickness for decades, and mapharside was widely used in experimental trypanosomiasis. At present, only five drugs are used to treat human infections. Suramin and pentamidine are used to treat stage I infections by *T. b. rhodesiense* and *T. b. gambiense* in humans respectively, while eflornithine is used alone or in combination with nifurtimox to treat stage II infections by *T. b. gambiense*, and melarsoprol to treat stage II infections by *T. b. rhodesiense.* Drug discovery projects are investigating new formulations for the treatment of infections in humans (e.g. fexinidazole, benzoxaboroles) as well as mechanisms involved in drug bioavailability and brain penetration (e.g. dicationic diamidines). Drugs that are routinely used to treat trypanosomiasis in animals include diminazine aceturate (berenil), isometamidium, homidium bromide, homidium chloride or pyrithidium bromide in ruminants and pigs, quinapyramine sulphate or suramin in horses and camels, and quinapyramine methylsulphate or isometamidium in dogs. Prevention involves avoiding being bitten by tsetse flies, but this can be difficult as they are persistent daytime feeders and can bite through thin clothing. Control measures based on vector eradication (using insecticidal sprays (ground or aerial spraying), fly traps, clearing vegetation or release of sterile male flies) and managing wild game reservoirs of infection (by fencing, culling or creating wildlife corridors) have proven partially effective. Some recent success has been recorded in breeding trypanotolerant domestic livestock (e.g. Ndama cattle). The widespread adoption of various control programs in the tsetse belt of Africa led to a decline in the incidence of human infections several decades ago, but a breakdown of those programs resulted in a resurgence of infections in the late twentieth century. Renewed efforts over the last decade have reduced the prevalence of disease and it is hoped that sustainable programs will help control disease for the 60 million people considered to be at risk of infection.


Trypanosoma
(mammalian 'salivarian' species)
(e.g. *T. brucei*)
blood
(cyclic fevers, macroglobulinaemia, coagulopathies, encephalitis (ngana, sleeping sickness))
division by longitudinal binary fission
Vertebrate Hosts
(mammals, esp. humans, cattle)
long undulating membrane (UM)
anterior free flagellum (FF)
posterior kinetoplast (K)
trypomastigote (8-45 µm)
inoculative (salivarian) transmission
(infective stages injected with saliva)
ingested with bloodmeal
epimastigote (10-35 µm)
[anterior K, short UM, FF]
vector-borne transmission
Invertebrate Hosts
(tsetse fly vectors)
(anterior alimentary tract)



Trypanosoma brucei trypomastigotes in cow blood



Trypanosoma brucei epimastigotes in tsetse fly



Glossina tstetse fly vectors for *Trypanosoma brucei*

Trypanosoma cruzi
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Trypanosomes have a single flagellum and they form four main developmental stages: trypomastigotes (with a posterior kinetoplast and an emergent flagellum forming a long undulating membrane); epimastigotes (with an anterior kinetoplast and an emergent flagellum forming a short undulating membrane); promastigotes (with an anterior kinetoplast and a short emergent flagellum, but no undulating membrane); and amastigotes (with a kinetoplast but no emergent flagellum or undulating membrane). Many trypanosome species are parasitic only in insects whereas others are transmitted by insect vectors to a wide range of vertebrate hosts. Three main groups infect the blood and/or tissues of humans and animals causing severe clinical diseases: including the cyclic stercorarian trypanosomes which undergo posterior station (hindgut) development in vectors and are transmitted via faecal contamination of bite site to infect blood and tissues of vertebrate hosts (e.g. reduviid bugs transmit *T. cruzi* which causes Chagas' disease in humans).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Discoba (diverse group supported robustly by molecular studies)
Phylum: Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass: Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order: Trypanosomatida (parasitic, single anterior flagellum, often forming undulating membrane)
Family: Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)
Genus: *Trypanosoma* (vector-borne haemoparasites)
Species: *T. cruzi* (causes Chagas' disease in humans)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum:	Order: Trichomonadida	Monocercomonadidae	*Histomonas*	birds	direct (f-o)

Parabasalia (with parabasal body)	(3-5 anterior flagella plus recurrent flagellum)	(costa absent, most without undulating membrane)		(gut, liver)	
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium Crepidoodinium Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans comprise a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)

	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*).

Trypanosomatids are dixenous (2-host) parasites with indirect transmission cycles between vertebrates and invertebrate vectors. *Trypanosoma* spp. form trypo- and/or a-mastigote stages in the blood/tissues of vertebrate hosts, and epi- or pro-mastigote stages in invertebrate haematophagous vectors. Infections have been found in a range of vertebrate species (mammals, birds, reptiles, amphibians and fish) with many different types of haematophagous invertebrates (leeches, bugs, flies, fleas) implicated as vectors or paratenic hosts. The species found in mammals have been grouped into two Sections (convenient groups without formal taxonomic rank) primarily on the basis of their developmental cycles in their vectors and their modes of transmission. Each Section contains several subgenera, as follows:

Section: Stercoraria (posterior station development in vector, contaminative transmission)

- *T.* (*Megatrypanum*), large trypanosomes with kinetoplast close to nucleus;
- *T.* (*Herpetosoma*), medium trypanosomes with subterminal kinetoplast;
- *T.* (*Schizotrypanum*), small C-shaped trypanosomes with voluminous terminal kinetoplast;

Section: Salivaria (anterior station development in vector, inoculative (some mechanical) transmission);

- *T.* (*Duttonella*), former *vivax*-group, monomorphic forms with large terminal kinetoplast;
- *T.* (*Nannomonas*), former *congolense*-group, small forms with medium marginal kinetoplast;
- *T.* (*Trypanozoon*), former *brucei*-group, pleomorphic forms with small subterminal kinetoplast;
- *T.* (*Pycnomonas*), former *suis*-subgroup, stout monomorphic forms with small subterminal kinetoplast.

Recent molecular phylogenetic studies have validated the separation of mammalian salivarian and stercorarian trypanosomes, but indicated complex placements for trypanosomes from non-mammalian hosts, despite earlier suggestions that they be assigned to separate subgenera (*Trypanomorpha* for those in birds, *Trypanosoma* for those in amphibians, and *Haematomonas* for those in fish). Many clades have been identified, most associated with particular vertebrate or invertebrate hosts, or both, suggesting that 'host-fitting' rather than 'co-speciation' has been the principal mechanism for trypanosome evolution. Comparative studies have found many differences between trypanosomes of aquatic and terrestrial hosts, with several clades found for species in freshwater fishes, marine fishes, amphibians, tortoises and platypuses (all thought to be transmitted by leech vectors). *T. cruzi* belongs to the stercorarian trypanosomes which exhibit discontinuous multiplication in the mammalian host and develop in the posterior station in vectors with contaminative transmission (except for *T. rangeli* which also undergoes anterior station development and inoculative transmission). Three stercorarian subgenera are recognized: *Megatrypanum* comprising large trypanosomes with the kinetoplast close to the nucleus (e.g. *T. theileri*); *Herpetosoma* comprising medium-sized trypanosomes with a subterminal kinetoplast (e.g. *T. lewisi*); and *Schizotrypanum* comprising small trypanosomes with a large kinetoplast near the posterior pole (e.g. *T. cruzi*). The parasites utilize a range of invertebrate vectors, including reduviid bugs, biting flies, sheep ked and rat fleas. *T. cruzi* and *T. rangeli* are found throughout the Americas where reduviid bugs are prevalent, while other stercorarian species with other vectors have a broader global distribution. Over 40 *T.* (*Megatrypanum*) species have been described from ruminants, carnivores, marsupials, bats, monkeys, edentates and rodents; some 64 *T.* (*Herpetosoma*) species from rodents, lagomorphs, primates, bats, carnivores, marsupials and xenarthrans; and 18 *T.* (*Schizotrypanum*) species from primates (including humans), carnivores, marsupials, edentates, lagomorphs and rodents throughout the New World and numerous bats around the world. *T.* (*S.*) *cruzi* causes serious disease in humans throughout South and Central America and many mammal species, including companion and wild animals, act as reservoirs of infection. Recent estimates on the prevalence of Chagas' disease range as high as 8-14 million people, despite considerable efforts made around the turn of the century to prevent infections.

***Trypanosoma* species**	**Mastigote length (µm)**	**Hosts**	**Disease**	**Vectors**	**Distribution**

CYCLIC TRANSMISSION (development within vector)					
STERCORARIA (free flagellum present, kinetoplast large and not terminal, posterior end pointed, reproduction in mammalian host discontinuous, typically taking place in amastigote or epimastigote stages, development in vector (with formation of metatrypanosomes) in posterior station, transmission contaminative (except for *T. rangeli* where it is anterior station and inoculative transmission))					
Subgenus: ***Megatrypanum*** (large trypanosomes, kinetoplast typically close to nucleus and far from posterior end of body, mammalian species show similarities with amphibian and reptilian species)					
T. (*M.*) *amilcari* (*lapsus T. amileari*)		Rodentia: cricetid (Brazilian colilargo)			Brazil
T. (*M.*) *binneyi*	54-79	Monotremata: ornithorhynchid (platypus)	non-pathogenic		Australia
T. (*M.*) *cervi*	40-61	Artiodactyla: cervid (elk/wapiti, white-tailed deer, mule deer, reindeer, moose)	non-pathogenic		North America
T. (*M.*) *conorhini* (syn. *T. boylei*)	36-62	Rodentia: murids (black rat, house mouse); Primates: cercopithecid (macaque)	non-pathogenic	Hemiptera: reduviid (*Triatoma rubrofasciata*)	tropical Asia, Africa, Polynesia
T. (*M.*) *cyclops*	33-49	Primates: cercopithecid (southern pig-tailed macaque, crab-eating macaque), rarely hominid (human)	low		Southeast Asia
T. (*M.*) *devei*	39-46	Primates: callitrichid (golden-handed tamarin, brown-mantled tamarin, saddleback tamarin)	non-pathogenic		South America
T. (*M.*) *freitasi*	49-52	Didelphimorphia: didelphid (white-eared opossum)	non-pathogenic		South America
T. (*M.*) *helogalei* [incl. subspp. *ichneumoni, helogalei*]	38-54	Carnivora: herpestid (common dwarf mongoose, Egyptian mongoose)	non-pathogenic	Hemiptera: reduviid (*Rhodinus prolixus*), cimicid (*Cimex lectularius*)	Africa
T. (*M.*) *heybergi* (syn. *T. thomasi*)	25-30	Chiroptera: nycterid (hairy slit-faced bat)	non-pathogenic	Diptera: culicid (*Aedes?*), Parasitiformes: macronyssid (*Ornithonyssus*)	West and East Africa
T. (*M.*) *hoarei*	25-44	Eulipotyphla: soricid (ornate shrew, American water shrew, Trowbridge's shrew, vagrant shrew)	non-pathogenic		North America
T. (*M.*) *incertum*	20-29	Chiroptera: vespertilionid (common pipistrelle)	non-pathogenic		England
T. (*M.*) *ingens* (syn. *T. schoenebeckei, tragelaphi p.p.*)	72-130	Artiodactyla: bovid (cattle, zebu, waterbuck, puku, suni, oribi, southern reedbuck, common duiker, harnessed bushbuck, sitatunga), tragulids (Java mouse deer)	non-pathogenic		tropical Africa, Asia
T. (*M.*) *irangiense*	54-61	Primates: lorisid (potto, Prince Demidoff's bushbaby)	non-pathogenic		Central Africa
T. (*M.*) *irwini*	32-39	Diprotodontia: phascolarctid (koala)	low		Australia

T. (*M.*) *lambrechti*	42-57	Primates: atelid (Columbian red howler), cebid (capuchins), pithecid (black-bearded saki, white-faced saki, collared titi monkey)	non-pathogenic		South America
T. (*M.*) *legeri*	26-51	Pilosa: myrmecophagid (southern tamandua, giant anteater), bradypodid (brown-throated sloth), choleopodid (Hoffmann's two-toed sloth)	non-pathogenic		Central America
T. (*M.*) *leleupi*	35-45	Chiroptera: hipposiderid (Sundevall's roundleaf bat)	non-pathogenic	Hemiptera: cimicid (*Stricticimex brevispinosus, Afrocimex leleupi*)	West Africa
T. (*M.*) *leonidasdeanei*	34-74	Chiroptera: emballonurid (greater sac-winged bat)	non-pathogenic	Diptera: psychodid (*Lutzomyia vespertilionis*)	Central America
T. (*M.*) *lizae*	20-45	Chiroptera: hipposiderid (cyclops roundleaf bat)	non-pathogenic		Africa
T. (*M.*) *lucknovi*		Primates: cercopithecid (rhesus macaque)			Africa
T. (*M.*) *magnusi*	27	Chiroptera: vespertilionid (common pipistrelle), emballonurid (naked-rumped tomb bat)	non-pathogenic		Africa, Europe, Asia
T. (*M.*) *mazamarum*	36-85	Artiodactyla: cervids (brocket deer)	non-pathogenic		South America
T. (*M.*) *megachiropterorum*	32	Chiroptera: pteropodid (Pacific flying fox)	non-pathogenic		Oceania
T. (*M.*) *megadermae*	40	Chiroptera: megadermatid (yellow-winged bat), rhinopomatid (lesser mouse-tailed bat)	non-pathogenic		Sudan
T. (*M.*) *melophagium* (syn. *T. woodcocki*)	25-70	Artiodactyla: bovid (sheep)	non-pathogenic	Diptera: hippoboscid (*Melophagus ovinus*)	worldwide
T. (*M.*) *minasense*	28-48	Primates: callitrichid (black-tufted marmoset, white-headed marmoset), pitheciid (titi), cebid (squirrel monkey, capuchin), atelid (woolly monkey)	non-pathogenic		South America
T. (*M.*) *mojiguaci*		Didelphimorphia: didelphid (mouse opossum)			South America
T. (*M.*) *morinorum*	37-45	Chiroptera: hipposiderid (trident bat)	non-pathogenic		West Africa
T. (*M.*) *mpapuense*	29-35	Chiroptera: nycterid (slit-faced bat)	non-pathogenic		Africa
T. (*M.*) *pessoai*	24-37	Chiroptera: phyllostomid (common vampire bat, Seba's short-tailed bat)	non-pathogenic		South and Central America
T. (*M.*) *pestanai*	30-42	Carnivora: mustelid (European badger)	non-pathogenic	Siphonaptera: ceratophyllid (*Paraceras melis*)	Eurasian
T. (*M.*) *phyllotis*	47	Rodentia: cricetid (Darwin's leaf-eared mouse)	non-pathogenic	Diptera: psychodid (*Phlebotomus noguchii*)	South America

T. (*M.*) *pifanoi*	31-54	Chiroptera: phyllostomid (great fruit-eating bat, greater spear-nosed bat)	non-pathogenic	Hemiptera: reduviid (*Triatoma*)	South America
T. (*M.*) *rhinopoma*	31	Chiroptera: rhinopomatid (lesser mouse-tailed bat)	non-pathogenic		Sudan
T. (*M.*) *rochasilvai*		Rodentia: cricetid (large-headed rice rat)			South America
T. (*M.*) *samueli*		Didelphimorphia: didelphid (gray short-tailed opossum)			South America
T. (*M.*) *scotophila*	31	Chiroptera: vespertilionid (greater Asiatic yellow bat)	non-pathogenic		IndoChina
T. (*M.*) *talpae*	21-38	Eulipotyphla: talpid (European mole)	non-pathogenic	Siphonaptera: hystrichopsyllid (*Palaeopsylla minor, Histrichopsylla talpae*)?	Europe
T. (*M.*) *theileri* [type species] (syn. *T. americanum*, *cephalophi, falchawi, franki, himalayanum, lingardi, muktesari, rutherfordi, scheini, tragelaphi p.p., transvaaliense, wrublewskii*)	12-120	Artiodactyla: bovids (cattle, zebu, water buffalo, European bison, suni, greater kudu, steenbok, reedbuck, common duiker, Eurasian moose), camelid (camels), cervid (red deer), tragulid (water chevrotain)	non-pathogenic	Diptera: tabanid (*Tabanus glaucopis, striatus, bromius, Haematopota pluvialis, Hybomitra ciureai, Pangonia, Chrysops*), hippoboscid (*Lipoptenia fortisetosa, cervi, Hippobosca maculata, rufipes*), psychodid (*Phlebotomus perniciosus*), culicid (*Aedes excricians, cataphylla, cantans, cinereus, annulipes, punctor, stictus, vexans, aegypti, Anopheles claviger, plumbeus, maculipennis, Culex annulatus, pipiens, Culiseta annulata, Mansonia richardii*); Ixodida: ixodid (*Hyalomma aegyptum*)	worldwide
T. (*M.*) *theodori*	30-42	Artiodactyla: bovids (goat)	non-pathogenic	Diptera: hippoboscid (*Lipoptena capreoli*)	Middle-East
T. (*M.*) *thylacis*	30-44	Diprotodontia: peramelid (southern brown bandicoot)	non-pathogenic		Australia
T. (*M.*) *trinaperronei*		Artiodactyla: cervid (white-tailed deer)	non-pathogenic	Diptera: hippoboscid (*Lipoptenia mazamae*)	Americas
T. (*M.*) *zeledoni*	36-56	Rodentia: heteromyid (Salvin's spiny pocket mouse)	non-pathogenic		Central America
Subgenus: ***Herpetosoma*** (medium trypanosomes, subterminal kinetoplast far from posterior end of body, mammalian host reproduction in amastigote and/or epimastigote stages)					
T. (*H.*) *acomys*	50	Rodentia: murid (Cairo spiny mouse, golden spiny mouse)	non-pathogenic	Siphonaptera: pulicid (*Parapulex chephrensis*)	Sudan, Middle-East
T. (*H.*) *acouchii* (syn. *T. itriagoi*)	29-44	Rodentia: dasyproctid (Azara's agouti, brown agouti, red acouchi)	non-pathogenic		West Africa, South and Central America
T. (*H.*) *advieri*	22-30	Primates: atelid (red-	non-		West Africa

		faced spider monkey)	pathogenic		
T. (*H.*) *aenomysi*	41	Rodentia: murid (common rufous-nosed rat)	non-pathogenic		West Africa
T. (*H.*) *akodoni*	19-22	Rodentia: cricetid (blackish grass mouse)	non-pathogenic		South America
T. (*H.*) *arvicoli*	nr	Rodentia: cricetid (European water vole)	non-pathogenic		Russia
T. (*H.*) *assintis*		Rodentia: murid (house mouse)			Middle-East
T. (*H.*) *avicularis* (syn. *T. arvicanthi, guisthaui*)	24	Rodentia: murid (Barbary striped grass mouse)	non-pathogenic	Siphonaptera: leptopsyllid (*Leptopsylla*), ceratophyllid (*Nosopsyllus*), hystrichopsyllid (*Stenoponia*?)	Africa
T. (*H.*) *bandicotti*	24-36	Rodentia: murid (greater bandicoot rat, short-tailed bandicoot rat)	non-pathogenic	Siphonaptera: pulicid (*Xenopsylla astia*)	India
T. (*H.*) *blanchardi* (syn. *T. eliomys*)	25-35	Rodentia: glirid (garden dormouse, European edible dormouse)	non-pathogenic	Siphonaptera: ceratophyllid (*Myoxopsylla laverani*)	Europe
T. (*H.*) *brodeni*	25-34	Eulipotyphla: soricid (four-toed elephant shrew)	non-pathogenic		Africa
T. (*H.*) *countinhoi*	32-42	Rodentia: cuniculid (lowland paca)	non-pathogenic		South America
T. (*H.*) *crocidurae*	25-34	Eulipotyphla: soricid (common shrew, greater white-toothed shrew)	non-pathogenic	Siphonaptera: ctenophthalmid (*Ctenophthalmus agyrtes*)	Europe
T. (*H.*) *dendromysi*	30-33	Rodentia: dendromyid (tree mouse)	non-pathogenic		Congo
T. (*H.*) *denysi* (syn. *T. anomaluri*)	37-48	Rodentia: anomalurid (Lord Derby's scaly-tailed squirrel)	non-pathogenic		West Africa
T. (*H.*) *diasi*	40-45	Chiroptera: phyllostomid (great fruit-eating bat, Pallas's long-tongued bat)	non-pathogenic		South America
T. (*H.*) *dressei*	31-35	Rodentia: murid (African tree rat)	non-pathogenic		Congo
T. (*H.*) *ellobii*	nr	Rodentia: cricetid (northern mole vole)	non-pathogenic		Russia
T. (*H.*) *evotomys* [incl. subspp. *evotomys, kudickei, clethrionomi*]	21-32	Rodentia: cricetid (southern red-backed vole, northern red-backed vole, bank vole)	non-pathogenic	Siphonaptera: ceratophyllid (*Ceratophyllus penicilliger, Nosopsyllus fasciatus*), ctenophthalmid (*Ctenophthalmus agyrtes*)	Eurasia, North America
T. (*H.*) *ferriolli*		Rodentia: cricetid (terraced rice rat)			South America
T. (*H.*) *forettinii*	30-32	Rodentia: cricetid (Brazilian pygmy rice rat)	non-pathogenic		South America
T. (*H.*) *graphiuri*	24-27	Rodentia: glirid (woodland dormouse)	non-pathogenic		West Africa
T. (*H.*) *grosi* (syn. *T. apodemi, korssaki*)	21-28	Rodentia: murid (yellow-necked mouse, wood mice, striped field	non-pathogenic	Siphonaptera: ctenophthalmid (*Ctenophthalmus*	Eurasia

		mouse)		*agyrtes, congener*)	
T. (*H.*) *indicum*	18-34	Rodentia: sciurid (Indian palm squirrel); Artiodactyla: bovid (cattle)	non-pathogenic		India
T. (*H.*) *leeuwenhoeki*	43-46	Pilosa: choloepodid (Hoffmann's two-toed sloth), bradypodid (brown-throated sloth)	non-pathogenic		Central America
T. (*H.*) *lemmi*		Rodentia: cricteid (Norway lemming)			Europe
T. (*H.*) *lewisi* [type species] (syn. *T. duttoni p.p., eburneense, longocaudense, murinum*, *rattorum*)	21-37	Rodentia: murid (black rat, brown rat, Annandale's rat, Maclear's rat, Turkestan rat, Anderson's white-bellied rat, rice field rat, Malayan field rat, Polynesian rat, bush rat, Moluccan prehensile-tailed rat, house mouse, Jackson's soft-furred mouse, Natal multimammate mouse, southern multimammate mouse), nesomyid (Gambian pouched rat); Lagomorpha: leporid (cottontail rabbit)	non-pathogenic	Siphonaptera: ceratophyllid (*Nosopsyllus fasciatus, Ceratophyllus hirudinis*), pulicid (*Ctenocephalides canis, Pulex irritans Xenopsylla cheopis*), leptopsyllid (*Leptopsylla senis*); Phthiraptera: haematopinid (*Haemotopinus spinulosus*)	worldwide
T. (*H.*) *lineatum*	16-21	Chiroptera: phyllostomid (white-lined broad-nosed bat)	non-pathogenic		South America
T. (*H.*) *longiflagellum*		Chiroptera: emballonurid (naked-rumped tomb bat)			Iraq
T. (*H.*) *magnusi*		Chiroptera: emballonurid (naked-rumped tomb bat), vespertilionid (Kuhl's pipistrelle)			Iraq
T. (*H.*) *mesnilibrimonti*	30-41	Pilosa: choloepodid (Linnaeus's two-toed sloth)	non-pathogenic		South America
T. (*H.*) *mariae*	21	Rodentia: cricetid (large vesper mouse, Brazilian colilargo)	non-pathogenic	Siphonaptera: pulicid (*Xenopsylla cheopis*), rhopalopsyllid (*Polygenis*)	South America
T. (*H.*) *microti* [incl. subspp. *microti, arvali, nearcticum*]	20-32	Rodentia: cricetid (common vole, eastern meadow vole, prairie vole, California vole, short-tailed field vole, tundra vole)	non-pathogenic	Siphonaptera: ceratophyllid (*Nosopsyllus fasciatus*), ctenophthalmid (*Ctenophthalmus agyrtes*)	Eurasia, North America
T. (*H.*) *musculi* [syn. *T. duttoni p.p.*]	28-32	Rodentia: murid (house mouse, brown rat)	non-pathogenic	Siphonaptera: ceratophyllid (*Ceratophyllus hirundinis, Nosopsyllus*), ctenophthalmid (*Ctenophthalmus*), leptopsyllid (*Leptopsylla*)	Europe, Africa, Americas
T. (*H.*) *mycetae* (syn.	29-37	Primates: atelid (Columbian red howler,	non-pathogenic		South America

T. *forestali*)		red-handed howler, black howler)			
T. (*H.*) *myocastori*	31-80	Rodentia: echimyid (nutria)	non-pathogenic		South America
T. (*H.*) *myoxi*	nr	Rodentia: glirid (hazel dormouse)	non-pathogenic		Europe
T. (*H.*) *myrmecophagae*	49	Pilosa: myrmecophagid (giant anteater)	non-pathogenic	Hemiptera: reduviid (*Rhodnius prolixus*)	South America
T. (*H.*) *nabiasi* (syn. *T. cuniculi, leporissylvaticus*)	21-34	Lagomorpha: leporid (European rabbit, mountain cottontail, desert cottontail, eastern cottontail)	non-pathogenic	Siphonaptera: pulicid (*Spilopsyllus cuniculi*)	worldwide
T. (*H.*) *neotomae* (syn. *T. woodi*)	22-34	Rodentia: cricetid (white-throated woodrat, dusky-footed woodrat, desert woodrat)	non-pathogenic	Siphonaptera: ceratophyllid (*Orchopeas howardi*)	North America
T. (*H.*) *ochotoni*	nr	Lagomorpha: ochotonid (Pallas's pika)	non-pathogenic		Russia
T. (*H.*) *otospermophili* [incl. subspp. *otospermophili, spermophili*] (syn. *T. citelli, iowense, hixsoni, schalaschnikovi*)	25-40	Rodentia: sciurid (California ground squirrel, Franklin's ground squirrel, Richardson's ground squirrel, thirteen-lined ground squirrel, speckled ground squirrel, little ground squirrel, yellow ground squirrel, russet ground squirrel, long-tailed ground squirrel)	non-pathogenic	Siphonaptera: ceratophyllid (*Opisocrostis bruneri*)	Eurasia, North America
T. (*H.*) *palawanense*		Rodentia: murid (Palawan spiny rat)			Philippines
T. (*H.*) *parkeri* [incl. subspp. *parkeri, marmoti*]	27-33	Rodentia: sciurid (yellow-bellied marmot, alpine marmot)	non-pathogenic		North America, Asia
T. (*H.*) *pattolii* (syn. *T. agouchyi*)		Rodentia: dasyproctid (Azara's agouti)			South America
T. (*H.*) *perodictici*	25-45	Primates: galagid (brown greater galago, Prince Demidoff's bushbaby), lorisid (potto)	non-pathogenic		Africa
T. (*H.*) *peromysci*	23-37	Rodentia: cricetid (brush mouse, deermouse, California deermouse, Mexican deermouse, Pinyon mouse)	non-pathogenic		North and Central America
T. (*H.*) *petrodromi* [incl. subspp. *petrodromi, chitali*]	32-41	Macroscelidea: macroscelidid (short-snouted elephant shrew, four-toed elephant shrew)	non-pathogenic		East and Central Africa
T. (*H.*) *pitymydis*	20-30	Rodentia: cricetid (alpine pine vole)	non-pathogenic		Europe
T. (*H.*) *preguici*	45	Pilosa: choloepodid (Hoffmann's two-toed sloth)	non-pathogenic		Central America
T. (*H.*) *primatum*	28-36	Primates: hominids (chimpanzee, gorilla), cercopithecid (mustached guenon)	non-pathogenic		West Africa
T. (*H.*) *rabinowitschi* (syn. *T. criceti,*	17-42	Rodentia: cricetid (European hamster, grey	non-pathogenic	Siphonaptera: pulicid (*Ctenocephalides*	Eurasia

cricetuli, zabolotnyi)		dwarf hamster, Chinese striped hamster, Eversmann's hamster, giant rat-headed hamster)		*canis*), ctenophthalmid (*Ctenophthalmus*), ceratophyllid (*Nosopsyllus fasciatus*)	
T. (*H.*) *rangeli* (syn. *T. aroarii, cebus, escomeli, guatemalense*)	25-37	Primates: hominids (human), cebid (blond capuchin, tufted capuchin, Columbian white-faced capuchin, black-capped squirrel monkey), atelid (spider monkey), aotid (night monkey), callitrichid (marmoset); Pilosa: bradypodid (brown-throated sloth), choloepodid (Hoffmann's two-toed sloth), myrmecophagid (southern tamandua); Carnivora: canid (dog), felid (cat), procyonid (raccoon, coati, kinkajou), mustelid (tayra); Didelphimorphia: didelphid (common opossum, white-eared opossum, grey four-eyed opossum); Rodentia: murid (rat, mouse), caviid (guinea pig), sciurid (squirrel)	non-pathogenic	Hemiptera: reduviid (*Rhodnius prolixus, brethesi, colombiensis, dalessandroi, domesticus, ecuadorensis, milesei, nasutus, neglectus, neivai, pallescens, paraensis, pictipes, robustus, stali, Triatoma dimidiata, infestans, nitida, patagonica, phyllosomae, protracta, vitticeps, Panstrongylus geniculatus, herreri, megistus, Cavernicola hemipterus, pilosa, Triatoma dimidiata, infestans, nitidia, phyllostomae, Mepraia spinolai*); cimicid (*Cimex lectularius, hemipterus*)	South and Central America
T. (*H.*) *renjifoi*	21-33	Rodentia: echimyid (Guyenne spiny rat)	non-pathogenic		South America
T. (*H.*) *saimiri*	25-36	Primates: cebid (common squirrel monkey, black-capped squirrel monkey)	non-pathogenic	Hemiptera: reduviid (*Rhodnius prolixus, Panstrongylus megistus*)	South America
T. (*H.*) *sciuri*	41	Rodentia: sciurid (Congo rope squirrel, Gambian sun squirrel)	non-pathogenic	Siphonaptera: ceratophyllid (*Nosophyllus alladinis*)	West Africa
T. (*H.*) *sigmodoni*	16-25	Rodentia: cricetid (hispid cotton rat)	non-pathogenic		North and Central America
T. (*H.*) *siqueirai*		Rodentia: echimyid (black-spined Atlantic tree-rat)			South America
T. (*H.*) *soricis*	17	Eulipotyphla: soricid (vagrant shrew)	non-pathogenic		North America
T. (*H.*) *tamiasi*	37-39	Rodentia: sciurid (eastern chipmunk)	non-pathogenic	Siphonaptera: ceratophyllid (*Megabothris acerbus, quirini*), hystrichopsyllid (*Tamiophila grandis*))	North America
T. (*H.*) *ulanovi* (syn. *T. berestnev*i, *pygere*thmi)		Rodentia: dipodid (great jerboa, small five-toed jerboa, William's jerboa, greater fat-tailed jerboa)	non-pathogenic		Iran
T. (*H.*) *xeri*	33	Rodentia: sciurid (striped ground squirrel)	non-pathogenic		West Africa
T. (*H.*) *zapi*	26-37	Rodentia: dipodid (meadow jumping	non-pathogenic	Siphonaptera: ceratophyllid	North America

		mouse, western jumping mouse, Pacific jumping mouse)		(*Megabothris abantis*)	
Subgenus: ***Schizotrypanum*** (small C-shaped trypanosomes, voluminous kinetoplast near short pointed posterior end of body, mammalian host reproduction in amastigote and/or epimastigote stages, intracellular development in vertebrate cells, transmitted by haematophagous hemipterans (triatomine and cimicid bugs), homogenous assemblage of morphologically indistinguishable species)					
T. (*S.*) *cruzi* [type species] (syn. *T. deanei*, *minanense, rhesii*, *triatomae*, *vickersae*)	12-30	Primates: hominid (human), atelid (brown woolly monkey, red-handed howler, black howler, Columbian red howler, spider monkey), callitrichid (brown-mantled tamarin, black-mantled tamarin, red-crested tamarin, cottonhead tamarin, common marmoset, black-tufted marmoset, silvery marmoset, pygmy marmoset), cebid (tufted capuchin, white-fronted capuchin, Columbian white-faced capuchin, black-capped squirrel monkey, Guianan squirrel monkey), cercopithecid (rhesus macaque), pithecid (black-fronted titi monkey, bald uakari); Didelphimorphia: didelphid (common opossum, grey opossum, grey short-tailed opossum, grey four-eyed opossum, big-eared opossum, woolly opossum, brown four-eyed opossum, big lutrine opossum, agile gracile opossum, white-bellied fat-tailed mouse opossum, Alston's mouse opossum, Robinson's mouse opossum); Pilosa: bradypodid (three-toed sloth), myrmecophagid (southern tamandua); Cingulata: chlamyphorid (pichi, six-banded armadillo, southern three-banded armadillo, northern naked-tailed armadillo, southern naked-tailed armadillo, big hairy armadillo, screaming hairy armadillo), dasypodid (nine-banded armadillo, greater long-nosed	Chagas' disease	Hemiptera: reduviid (*Triatoma brasiliensis, barberi, carrioni, dimidiata, gerstaeckeri, guasayana, hegneri, infestans, lecticularia, longipennis, maculata, neotomae, pallidipennis, patagonica, phyllosoma, protracta, rubida, rubrofasciata, rubrovaria, sanguisuga, sordida, tibiamaculata, vitticeps, Panstrongylus chinai, lignarius, megistus, geniculatus, herreri, rufotuberculatus, Rhodnius ecuadoriensis, neglectus, prolixus, pallescens, pictipes, Eratyrus cuspidatus;* plus reports in *Cavernicola, Dipetalogaster, Neotriatoma, Parabelminus* and *Psammolestes* spp.)	southern North America, Central and South America

		armadillo, southern long-nosed armadillo, Yepe's mulita); Lagomorpha: leporid (European rabbit, eastern cottontail); Rodentia: caviid (guinea pig, Brazilian guinea pig, Spix's yellow-toothed cavy, southern mountain cavy), cricetid (brush mouse, Pinyon mouse, montane grass mouse, scaly-footed water rat, dusky-footed woodrat, southern plains woodrat, white-throated woodrat, pack rat, large-headed rice rat, terraced rice rat, hairy-tailed akodont), ctenomyid (Tucuman tuco-tuco), cuniculid (lowland paca), dasyproctid (red-rumped agouti, Azara's agouti, Brazilian agouti), echimyid (drab Atlantic tree-rat, Guyenne spiny rat), erethizontid (Bahia porcupine, brown hairy dwarf porcupine, Mexican hairy dwarf porcupine, Brazilian porcupine, Andean porcupine), murid (Mongolian gerbil, black rat, brown rat, Natal multimammate mouse, house mouse), octodontid (common degu), sciurid (antelope squirrel, red-tailed squirrel, Brazilian squirrel, Bolivian squirrel, white-tailed prairie dog), Artiodactyla: suid (pig); Chiroptera: emballonurid (lesser dog-like bat, proboscis bat, greater sac-winged bat), molossid (black mastiff bat, Mexican free-tailed bat, white-striped free-tailed bat), noctilionid (lesser bulldog bat), phyllostomid (common vampire bat, spectral bat, tent-making bat, golden bat, little big-eared bat, greater spear-nosed bat, lesser spear-nosed bat, pale spear-nosed bat, Goldman's nectar bat,			

		great fruit-eating bat, Gervais's fruit-eating bat, Jamaican fruit bat, Seba's short-tailed bat, Pallas's long-tongued bat), vespertilionid (big-eared brown bat, free-tailed bat, black bonneted bat, dwarf bonneted bat, Brazilian brown bat, Argentine brown bat, black myotis, red myotis, Chilean myotis); Carnivora: canid (dog, culpeo, grey fox, hoary fox, South American gray fox, crab-eating fox), felid (cat), mephitid (striped skunk, hooded skunk), mustelid (tayra, lesser grison, greater grison), procyonid (white-nosed coati, South American coati, raccoon, ringtail)			
T. (*S.*) *aunawa*		Chiroptera: miniopterid (great bent-winged bat)			Indonesia
T. (*S.*) *assiutis*		Rodentia: murid (house mouse)			Egypt
T. (*S.*) *erneyi*		Chiroptera: molossid (free-tailed bat)	non-pathogenic		East Africa
T. (*S.*) *hendricki*		Chiroptera: vespertilionid (big brown bat)	non-pathogenic	Hemiptera: cimicid (*Cimex brevis*)	Americas
T. (*S.*) *hipposideri*	14-21	Chiroptera: hipposiderid (bicolored roundleaf bat)	non-pathogenic		Australia
T. (*S.*) *janseni*		Didelphimorphia: didelphid (big-eared opossum)			Brazil
T. (*S.*) *lesourdi*	19	Primates: atelid (red-faced spider monkey)	non-pathogenic		South America
T. (*S.*) *livingstonei*	32	Chiroptera: rhinolophid (Lander's horseshoe bat), hipposiderid (Sundevall's roundleaf bat)	non-pathogenic		Africa
T. (*S.*) *myoti*	?	Chiroptera: vespertilionid (little brown bat)	non-pathogenic	Hemiptera: cimicid (*Cimex brevis*)	North America
T. (*S.*) *noyesi*	two forms 8, 25	Diprotodontia: potoroid (bettong), macropodid (grey kangaroo, hare-wallaby), phalangerid (brush-tailed possum)	non-pathogenic		Australia
T. (*S.*) *pecarii*		Artiodactyla: tayassuid (collared peccary)			Americas
T. (*S.*) *phyllostomae* (possible synonym of *T. cruzi*)	15-24	Chiroptera: phyllostomid (greater spear-nosed bat, Seba's short-tailed bat)	non-pathogenic	Hemiptera: reduviid (*Triatoma infestans*, *Cavernicola pilosa, Panstrongylus geniculatus*), cimicid (*Cimex hemipterus*); Ixodida: argasid	South and Central America

				(*Ornithodorus moubata*?)	
T. (*S.*) *prowazeki*	21	Primates: pitheciid (uakari)	non-pathogenic		originally from Brazil
T. (*S.*) *pteropi*	26-32	Chiroptera: pteropodid (black flying fox)	non-pathogenic		Australia
T. (*S.*) *sanmartini* (possible synonym of *T. cruzi*)	17-24	Primates: cebid (common squirrel monkey)	non-pathogenic	Hemiptera: reduviid (*Rhodnius prolixus*)	South America
T. (*S.*) *vespertilionis* (syn. *T. dionisii, nicolleorum, pipistrelli*)	10-24	Chiroptera: emballonurid (gland-tailed free-tailed bat), hipposiderid (Sundevall's roundleaf bat), miniopterid (common bent-wing bat), molossid (black bonneted bat, western mastiff bat, velvety free-tailed bat, black mastiff bat, Mexican free-tailed bat, northern free-tailed bat, broad-eared bat), mormoopid (Davy's naked-backed bat, Allen's common mustached bat), noctilionid (greater bulldog bat), phyllostomid (common vampire bat, Ipanema bat, Pallas's long-tongued bat, greater spear-nosed bat, tailed tailless bat, Seba's short-tailed bat, California leaf-nosed bat), vespertilionid (small big-eared brown bat, tropical big-eared brown bat, lesser mouse-eared bat, pallid bat, common noctule, common pipistrelle, slender-winged pipistrelle, Kuhl's pipistrelle, serotine bat, Ognev's serotine, Rafinesque's big-eared bat, southern yellow bat, diminutive serotine, big brown bat, eastern red bat, hoary bat, Natterer's bat, black myotis, canyon bat, cave myotis, Arizona myotis, Yuma myotis); Rodentia: murid (house mouse)	non-pathogenic	Hemiptera: cimicid (*Cimex pipistrelli*, *lectularus*), reduviid (*Rhodinus prolixus, Panstrongylus megistus*, *Triatoma megista*?); Ixodida: argasid (*Ornithodorus moubata*?)	Africa, Eurasia, Iran, South America
T. (*S.*) *wauwau*		Chiroptera: mormoopid (naked-backed bat)	non-pathogenic		South and Central America

Parasite morphology: Three developmental stages are usually formed: trypomastigotes, amastigotes and epimastigotes. Trypomastigotes are elongate thin stages with a posterior kinetoplast and an undulating membrane along the length of the body. They are often curved in shape ranging from 15-55 µm in length by 1-4 µm in width. Trypomastigotes undergo a maturation process

known as metacyclogenesis whereby they become smaller and broader as they become infective metacyclic forms (sometimes known as metatrypanosomes). Amastigotes are small rounded non-flagellated cells with an eccentric nucleus and kinetoplast. These cells are among the smallest known eukaryotic cells ranging from 1.5-4.0 µm in diameter. Epimastigotes are long thin cells with an anterior kinetoplast, a short undulating membrane and a long free flagellum. They are pleomorphic in shape and range in size from 10-30 µm in length by 1-4 µm in width. Occasionally, rounded sphaeromastigotes have been described for some species as transient divisional stages with rounded bodies, anterior kinetoplasts and a short flagellum emerging from a flagellar pocket.

Site of infection: Parasites undergo posterior station (hindgut) development in their invertebrate vectors and stercorarian transmission by faecal contamination to vertebrates. Amastigotes are found within vertebrate hosts in many different tissues. Host cells most frequently invaded are reticuloendothelial cells of the spleen, liver and lymphatics and cells in cardiac, smooth and skeletal musculature. The amastigotes divide repeatedly ultimately lysing the host cell and infecting neighbouring cells, sometimes resulting in cyst-like colonies (called pseudocysts) in muscle cells. Some amastigotes give rise to haematozoic trypomastigotes which circulate in the blood. A total of 125 stercorarian *Trypanosoma* spp. have been described in over 240 mammalian host species belonging to 48 families in 12 orders (mainly bats, rodents and primates, but also some artiodactylans, carnivores, opossums, shrews, marsupials, pilosans, and a few lagomorphs, cingulates and monotremes). Trypomastigotes ingested by vectors transform into epimastigotes which multiply in the gut. Around 130 arthropod species have been found to act as vectors for stercorarian trypanosomes: including 66 hemipteran species (mostly reduviids, and some cimicids), 33 dipteran species (culicids, hippoboscids, psychodids, and some tabanids), 26 fleas (ceratophyllids, ctenophthalmids, hystrichopsyllids, leptopsyllids, pulicids, and rhopalopsyllids), 2 ticks (argasid and ixodid), one mite (macronyssid), and one louse (haematopinid).

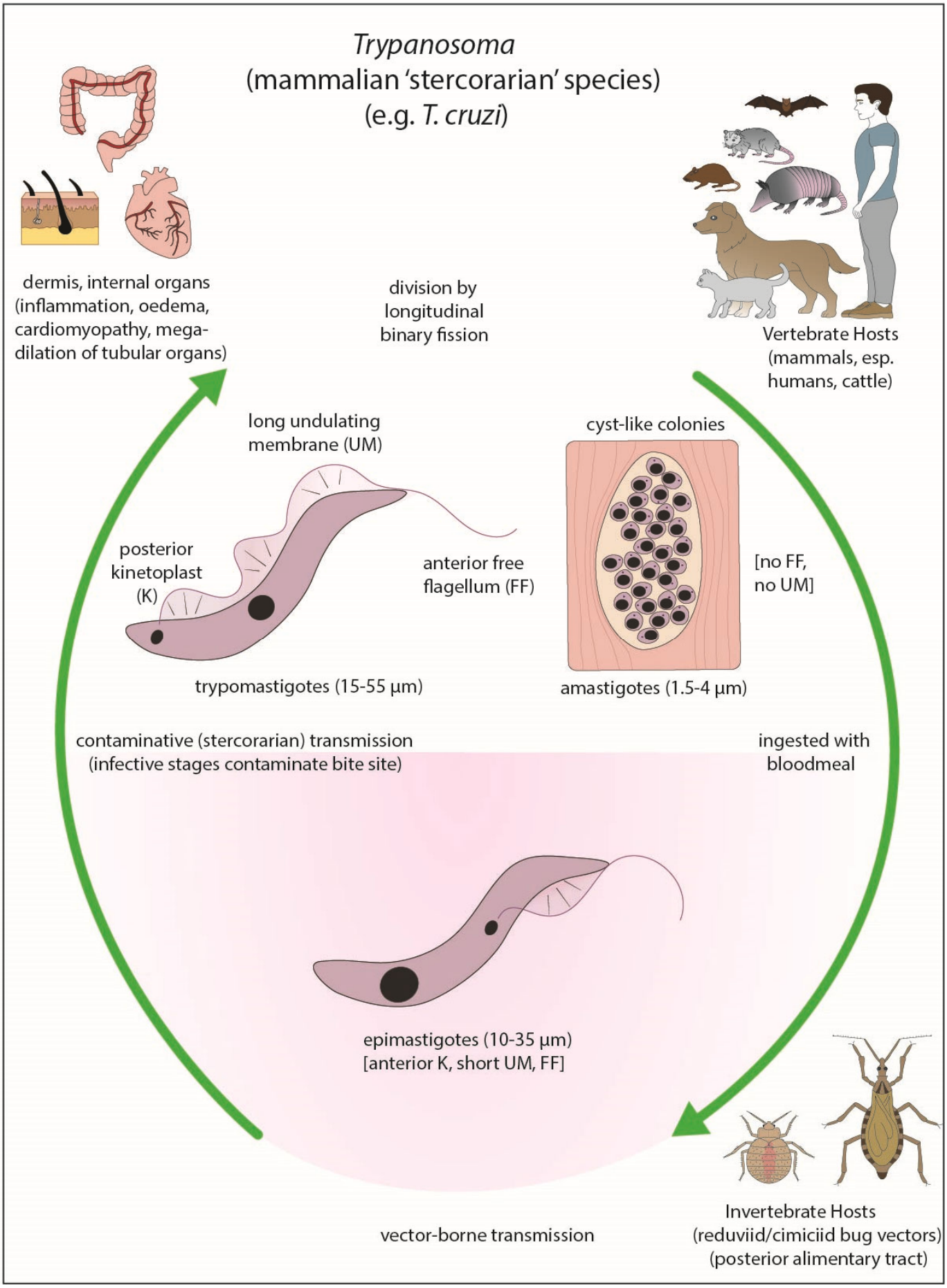
Pathogenesis: *T. cruzi* causes New World (or American) trypanosomiasis (AT), a chronic condition commonly known as Chagas' disease. Most infections may cause few or no symptoms, but acute symptoms may develop particularly in children. The first sign is often acute inflammation and swelling of the skin at the site of infection (lesion called a chagoma). If this involves the conjunctiva of the eye, unilateral orbital oedema (known as Romana's sign) may develop. Amastigotes infect many cells, either actively or by phagocytosis, and undergo proliferation causing cell lysis and tissue lesions. Acute clinical signs include inflammation, fever, hepatosplenomegaly, lymphadenopathy, cardiac arrhythmia and general malaise. If the acute stage of infection is not treated, then patients enter a chronic stage which is initially asymptomatic. Amastigotes continue to multiply in host cells and spread throughout the body via the lymphatics and circulation to most tissues and organs, especially histiocytes, adipocytes, myocardial fibres and autonomic ganglia in the gastro-intestinal tract. Most infected patients continue in this state for the remainder of their lives. However, around a third develop serious clinical manifestations 10-30 years after infection, particularly involving significant organ enlargement and pathology in the heart and intestines. The myocardium may contain large pseudocysts of amastigotes without any surrounding inflammation as well as destroyed myocardial cells with lymphocyte, macrophage and plasma cell infiltrates forming 'microabscesses' that later become fibrotic. The heart undergoes marked hypertrophy and dilatation, with the left ventricular wall becoming so thin as to be transilluminable. Chronic infections are characterized by palpitations (colloquially known in Brazil as baticum), arrhythmias, myositis, thromboses, chest pain, cardiac failure and 'megaviscera syndrome' (dilation of tubular organs, especially the oesophagus and colon). Different *T. cruzi* strains often produce different clinical presentations: e.g. group I strains (rare north of the Amazon basin) usually produce cardiac but not digestive tract lesions; while group II strains may produce both (including meningoencephalopathy in HIV-AIDS patients). Clinical and experimental studies have revealed many complex immune interactions between hosts and parasites. *T. cruzi* amastigotes may infect any nucleated mammalian cell and multiply intracellularly within parasitophorous vacuoles or free in the cytoplasm. Infections have been shown to stimulate many innate and acquired (adaptive) host immune responses, but the parasites are masters at immune evasion and persist for years. While around 90% of infected persons recover from acute infections, they are not immune but continue to have low parasitaemia for indefinite periods. Nonetheless, the prospect of inducing strong host protection has fuelled the search for a vaccine, although differences in parasite virulence and host susceptibility have confounded many studies in laboratory animal models. Most infections by other stercorarian species in animals (domesticated and wild species) are cryptic and do not cause clinical disease, including the *T. theileri* group (*T. theileri, T. melophagium, T. cervi, T. trinaperronei*) in livestock.

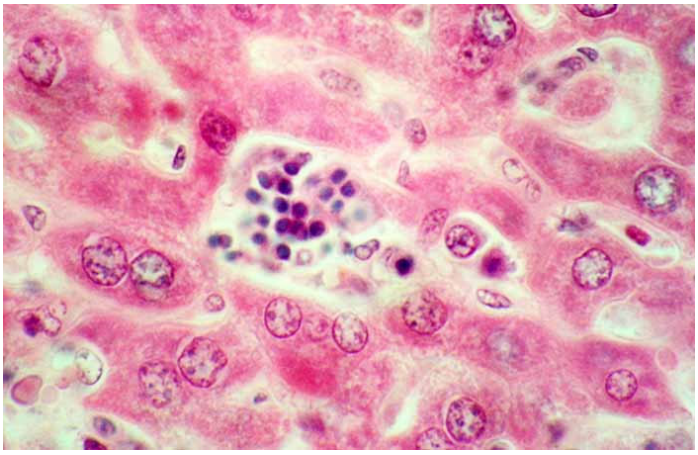
Developmental cycle and mode of transmission: Infections by *T. cruzi* are transmitted by blood-sucking reduviid bugs belonging to the subfamily Triatominae, commonly known as assassin- or kissing-bugs because they often feed around the lips of sleeping persons. The disease is often associated with poverty, because the bugs live in cracks in the mud walls of houses in poor areas. The parasites undergo posterior station (stercorarian) development where epimastigotes develop in the hindgut and metacyclic trypomastigotes are passed in the bug faeces during or after feeding (contaminative transmission). The parasites enter the vertebrate host through the bite site, scratched skin or through mucous membranes rubbed with contaminated fingers. Various regional cultural practices facilitate transmission, including children playing with triatomine bugs, native populations eating bugs with hot sauce, using bug faeces in folklore remedies for warts, or consuming bug-infested sugarcane juice or palm fruit juice. In vertebrate hosts, invading trypomastigotes transform into amastigotes which multiply within host cells giving rise to haematozoic trypomastigotes which are taken up by feeding vectors. Infections by *T. cruzi* and *T. rangeli* are transmitted by reduviid bugs whereas *T. theileri*, *T. melophagium* and *T. lewisi* are transmitted by tabanid flies, sheep ked and rat fleas, respectively. Infections in humans have occasionally been shown to be transmitted horizontally through organ or blood transfusion or sharing intravenous needles for recreational drug use, and sometimes vertically by crossing the placenta and invading developing foetuses. The incubation period in

vectors ranges from 10-30 days, while that in vertebrate hosts ranges from 5-42 days. Infections in animals by members of the *T. theileri* group have been shown to be transmitted by ingesting infected vectors, by the contamination of skin abrasions, mucous membranes or bite sites by vector faeces (aided by the process of prediuresis where the vector voids water to concentrate their bloodmeals), and possibly by transplacental transfer in some bovids and cervids.

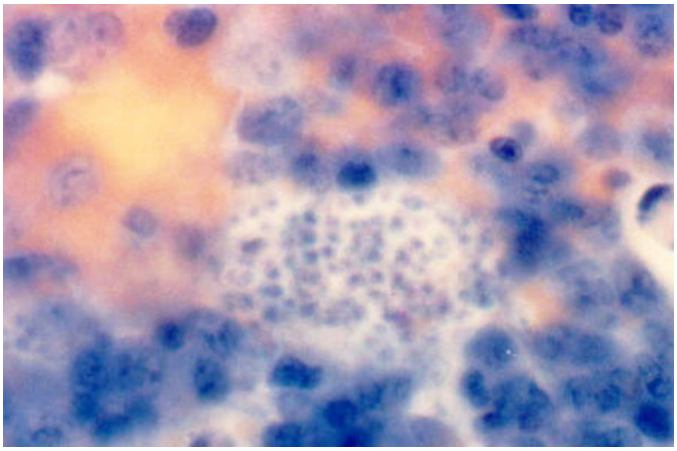
Differential diagnosis: Trypanosomes may be detected in blood, lymph, cerebrospinal fluid or biopsy tissues before or after laboratory culture. The parasites grow well *in vitro* in a range of media (especially nutrient agar-blood mixtures) and they readily infect laboratory mice. In the past, xenodiagnosis has also been used where clean laboratory-reared reduviid bugs are allowed to feed on patients and then examined several weeks later for parasites. A range of immunoserological tests (complement fixation, haemagglutination, immunofluorescence, enzyme immuno-assays and rapid diagnostic tests) have been developed to detect host antibodies and more recently, polymerase chain reaction (PCR) techniques have been used to amplify parasite DNA from clinical samples. Molecular characterization studies have identified various biodemes, zymodemes, schizodemes and genetic lineages which have been grouped into *T. cruzi* I (mainly in wild mammals and sylvan triatomines), *T. cruzi* II (usually in humans) and other non-grouped strains. Sequences examined have included ribosomal DNA, internal transcribed spacers, mitochondrial (kinetoplast) cytochrome B, mini-exon genes and microsatellites (tandem array repetitive DNA).

Treatment and control: Infections do not respond well to chemotherapy due to the 'hidden' intracellular location of the amastigotes. Nifurtimox, benznidazole, allopurinol, pentamidine, melarsoprol, eflornithine and suramin have been reported to reduce the severity of some early-stage infections but some have serious adverse and toxic side-effects and are not effective against chronic infections. Cure rates are low and successful treatment requires hospitalization or careful monitoring of the patient. It is regrettable that only around 1% of patients are ever treated for Chagas' disease, due to the lack of early intervention, effective treatment and affordable healthcare. Control measures based on vector eradication using residual insecticidal sprays, paints or fumigant canisters have proven partially effective but expensive. Houses may be sprayed with pyrethroids such as deltamethrin, cyhalothrin or cyfluthrin and then monitored long-term for bug re-infestations. Prevention includes eliminating potential bug habitats by repairing cracked walls and using better building products and techniques, as well as avoiding bug bites through the use of insecticide-impregnated bed nets.


Trypanosoma
(mammalian 'stercorarian' species)
(e.g. *T. cruzi*)
dermis, internal organs
(inflammation, oedema,
cardiomyopathy, mega-
dilation of tubular organs)
division by
longitudinal
binary fission
Vertebrate Hosts
(mammals, esp.
humans, cattle)
long undulating
membrane (UM)
posterior
kinetoplast
(K)
anterior free
flagellum (FF)
trypomastigotes (15-55 µm)
cyst-like colonies
[no FF,
no UM]
amastigotes (1.5-4 µm)
contaminative (stercorarian) transmission
(infective stages contaminate bite site)
ingested with
bloodmeal
epimastigotes (10-35 µm)
[anterior K, short UM, FF]
vector-borne transmission
Invertebrate Hosts
(reduviid/cimiciid bug vectors)
(posterior alimentary tract)



Trypanosoma cruzi amastigotes in human liver



Trypanosoma cruzi amastigotes in human spleen



Reduviid bug vector for *Trypanosoma cruzi*

Trypanosoma evansi
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Trypanosomes have a single flagellum and they form four main developmental stages: trypomastigotes (with a posterior kinetoplast and an emergent flagellum forming a long undulating membrane); epimastigotes (with an anterior kinetoplast and an emergent flagellum forming a short undulating membrane); promastigotes (with an anterior kinetoplast and a short emergent flagellum, but no undulating membrane); and amastigotes (with a kinetoplast but no emergent flagellum or undulating membrane). Many trypanosome species are parasitic only in insects whereas others are transmitted by insect vectors to a wide range of vertebrate hosts. Three main groups infect the blood and/or tissues of humans and animals causing severe clinical diseases: including the noncyclic trypanosomes which undergo 'mechanical' transmission by biting flies/bats (no development in vector) or by venereal transmission.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Discoba (diverse group supported robustly by molecular studies)
Phylum: Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass: Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order: Trypanosomatida (parasitic, single anterior flagellum, often forming undulating membrane)
Family: Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)
Genus: *Trypanosoma* (vector-borne haemoparasites)
Species: *T. evansi* (causes surra in animals)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia	Order: Trichomonadida (3-5 anterior flagella plus	Monocercomonadidae (costa absent, most	*Histomonas*	birds (gut, liver)	direct (f-o)

(with parabasal body)	recurrent flagellum)	without undulating membrane)	*Dientamoeba*	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans comprise a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)
	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*).

Trypanosomatids are dixenous (2-host) parasites with indirect transmission cycles between vertebrates and invertebrate vectors. *Trypanosoma* spp. form trypo- and/or a-mastigote stages in the blood/tissues of vertebrate hosts, and epi- or pro-mastigote stages in invertebrate haematophagous vectors. Infections have been found in a range of vertebrate species (mammals, birds, reptiles, amphibians and fish) with many different types of haematophagous invertebrates (leeches, bugs, flies, fleas) implicated as vectors or paratenic hosts. The species found in mammals have been grouped into two Sections (convenient groups without formal taxonomic rank) primarily on the basis of their developmental cycles in their vectors and their modes of transmission. Each Section contains several subgenera, as follows:

Section: Stercoraria (posterior station development in vector, contaminative transmission)

- *T.* (*Megatrypanum*), large trypanosomes with kinetoplast close to nucleus;
- *T.* (*Herpetosoma*), medium trypanosomes with subterminal kinetoplast;
- *T.* (*Schizotrypanum*), small C-shaped trypanosomes with voluminous terminal kinetoplast;

Section: Salivaria (anterior station development in vector, inoculative (some mechanical) transmission);

- *T.* (*Duttonella*), former *vivax*-group, monomorphic forms with large terminal kinetoplast;
- *T.* (*Nannomonas*), former *congolense*-group, small forms with medium marginal kinetoplast;
- *T.* (*Trypanozoon*), former *brucei*-group, pleomorphic forms with small subterminal kinetoplast;
- *T.* (*Pycnomonas*), former *suis*-subgroup, stout monomorphic forms with small subterminal kinetoplast.

Recent molecular phylogenetic studies have validated the separation of mammalian salivarian and stercorarian trypanosomes, but indicated complex placements for trypanosomes from non-mammalian hosts, despite earlier suggestions that they be assigned to separate subgenera (*Trypanomorpha* for those in birds, *Trypanosoma* for those in amphibians, and *Haematomonas* for those in fish). Many clades have been identified, most associated with particular vertebrate or invertebrate hosts, or both, suggesting that 'host-fitting' rather than 'co-speciation' has been the principal mechanism for trypanosome evolution. Comparative studies have found many differences between trypanosomes of aquatic and terrestrial hosts, with several clades found for species in freshwater fishes, marine fishes, amphibians, tortoises and platypuses (all thought to be transmitted by leech vectors). *T. brucei* belongs to the salivarian trypanosomes which exhibit continuous multiplication in the mammalian host and develop in the anterior station in tsetse fly vectors with inoculative transmission (except for *T. evansi* and *T. equiperdum* which are transmitted mechanically by biting flies or by contact). Four salivarian subgenera are recognized: *Duttonella* comprising monomorphic trypanosomes with a large kinetoplast (*T. vivax, T. uniforme*); *Nannomonas* comprising small trypanosomes with a medium-sized kinetoplast (e.g. *T. congolense, T. simiae*); *Pycnomonas* comprising thick monomorphic forms with a small kinetoplast (*T. suis*); and *Trypanozoon* comprising pleomorphic (stumpy to slender) forms with a small kinetoplast (*T. brucei, T. evansi, T. equiperdum*). Species belonging to the former two subgenera develop in the proboscis or midgut of their vectors while those of the latter two subgenera undergo development in the midgut and salivary glands (except for *T. evansi* and *T. equiperdum* which are transmitted mechanically by biting flies or via coitus, respectively).

The species *T. evansi* is thought to be derived from *T. brucei brucei* but is no longer able to undergo development in insect vectors due to the loss of genetic material (maxicircles of kinetoplastic mitochondrial DNA). Instead, T. *evansi* relies on mechanical transmission between hosts via biting flies (passive transfer of blood stages as no development occurs in the flies). Infections exhibit a broad host specificity for vertebrates with severe disease developing in permissive hosts, notably camels, horses and dogs, while other domestic and wild ungulates, carnivores and rodents are more refractory to disease. The disease has many regional names, including surra (meaning 'rotten'), murrina, dehab ('fly'), mbori, guifar, dioufar, menchaca or dubla ('emaciated'), yudleye/yudle ('aimless movement'), dukhan, salaf/salef, tahaga, su-auru, purana ('chronic'), tibarsa ('three-year disease'), makhi ki bimari ('horsefly disease'), peste-boba/derrengadera ('limping'), and mal de caderas ('paralysis'). Infections may be transmitted mechanically by various biting flies, including species in the genera *Tabanus*, *Stomoxys*, *Lyparosia*, *Haematopota,* and *Chrysops*. In

the New World, infections may also be transmitted via the bites of vampire bats, which may also act as vertebrate hosts for infections. The species *T. equiperdum* does not utilize invertebrate vectors (not even mechanically), but is transmitted between horses via coitus causing a disease known as dourine.

***Trypanosoma* spp.**	**Mastigote length (µm)**	**Vertebrate hosts**	**Disease**	**Transmission**	**Distribution**
NON-CYCLIC TRANSMISSION (no parasite development within vector)					
MECHANICA (mechanical transmission)					
Subgenus: *Trypanozoon* (trypanosomes of former *brucei*-group including *brucei*- and *evansi*-subgroups represented by pleomorphic forms (slender, intermediate, stumpy) with or without free flagellum, small kinetoplast subterminal, development in vector (*Glossina*) in midgut and salivary glands, but other species transmitted mechanically without development in vectors (*T. evansi*) or by contact between hosts (*T. equiperdum*))					
T. (*T.*) *evansi* (syn. *T. aegyptum, annamense, cameli, equinum, elmassiana, hippicum, kirdanii, marocanum, soudanense, suaurii, venezuelense*)	15-33	Artiodactyla: camelid (Bactrian camel, dromedary, llama, alpaca, guanico); bovid (African buffalo, water buffalo, cattle, sheep, mouflon, goat, gazelle, saiga antelope), suid (pig), tayassuid (collared peccary, white-lipped peccary), cervid (sambar deer, rusa deer, hog deer, barking deer, chital/spotted deer, white-tailed deer, brocket deer); Perissodactyla: equid (horse, ass/donkey, mule), tapirid (Asian tapir), rhinocerotid (Sumatran rhinoceros); Proboscidea: elephantid (Indian elephant); Cingulata: dasypodid (armadillo); Lagomorpha: leporid (rabbit, black nap hare), ochotonid (Pallas's pika); Didelphimorphia: didelphid (opossum, short-tailed opossum); Rodentia: murid (rat, tanezumi rat, long-tailed giant rat, chestnut white-bellied rat, red spiny rat, bandicoot rat, New World mouse), cricetid (hamster, Japanese grass vole), caviid (capybara, lesser capybara, guinea pig); Carnivora: canid (dog, wild dog, wolf, red fox, Bengal fox, Azara's fox, golden jackal), hyaenid (hyena), felid (cat, woodcat, leopard, jaguar, tiger, ocelot), herpestid (small Indian mongoose, Javan mongoose), mustelid (ferret-badger), viverrid (civet cat), ursid (Himalayan black bear), procyonid (South American coati); Diprotodontia: macropodid (agile wallaby, dusky pademelon); Chiroptera: phyllostomid (Latin America vampire bat, broad-nosed bat, short-tailed bat), vespertilionid (mouse-eared bat); Primates: atelid (Colombian red howler monkey, ursine howler), cercopithecid (rhesus macaque), hominid (orangutan); Galliformes: phasianid (chicken)	surra, murrina	Diptera: tabanid (*Tabanus*, *Stomoxys*, *Lyperosia*, *Haematopota, Chrysops*) plus Chiroptera: phyllostomid vampire bats in New World (*Desmodus rotundus*)	Asia, India, North Africa, Americas
T. (*T.*) *equiperdum* (syn. *T. equi, rougeti*)	15-36	Perissodactyla: equid (horse, donkey, mule); plus experimental infections in Lagomorpha: leporid (rabbit), Carnivora: canid (dog); Rodentia: murid (rat, mouse)	dourine	coitus	North Africa, Eurasia, Americas

Parasite morphology: *T. evansi* and *T. equiperdum* belong to a small group of trypanosomes apparently related to *T. brucei* but considered to be 'petite mutants' due to the loss of genetic material (kinetoplast DNA maxicircles) required for cyclic development in tsetse flies (unable to transform into procyclic stages). Due to this loss, they only form blood stages (trypomastigotes) in vertebrates. Trypomastigotes are elongate slender stages ranging in length from 15-36 µm. They have a central ovoid basophilic nucleus as well as another smaller basophilic organelle (containing mitochondrial DNA) known as the kinetoplast which is located subterminally posterior to the nucleus. Flagellar basal bodies (microtubular complexes) are located adjacent to the kinetoplast and give rise to a long flagellum which emerges and runs the length of the body forming a conspicuous undulating membrane before extending freely beyond the cell margin. Observations of live motile parasites show they move in the direction of the free flagellum so that cellular aspect is designated anterior (the flagellum is not recurrent or trailing like that of the bodonids *Cryptobia* and *Trypanoplasma*). During their development, some trypomastigotes form slightly smaller intermediate forms with the kinetoplast located almost terminally and the free flagellum being shorter (but not as small as the stumpy metacyclic forms observed for other *Trypanosoma* spp.). Transmission and culture experiments have sometimes induced profound pleomorphic changes in trypomastigotes involving size disparities, abnormal growth patterns and the development of dyskinetoplasty. A few experimental studies (notably on carnivores and primates) have also described the occasional appearance of sphaeromastigote-like (rounded with short emergent flagellum) and amastigote-like (rounded with non-emergent flagellum) stages (usually in organ smears), but it is not known whether they represented true developmental stages or were degenerate forms.

Site of infection: Trypomastigotes are extracellular parasites usually found intravascularly in the circulatory system of vertebrates, but they may sometimes invade host tissues and organs where they are found in extravascular fluids (including lymph and spinal fluid). The species *T. evansi* has a broad host specificity, with infections found in 78 mammalian species, including ungulates (perissodactyls, artiodactyls), elephants, carnivores, marsupials, opossums, cingulates, lagomorphs, rodents, bats, and primates. Trypomastigotes may also be found contaminating the mouthparts of various secondary hosts which act as mechanical paratenic vectors, mostly tabanid flies (*Tabanus*, *Stomoxys*, *Lyperosia*, *Haematopota, Chrysops*) but occasionally phyllostomid vampire bats (*Desmodus rotundus*). Infections by the species *T. equiperdum* are found primarily in the tissues of equine hosts, rarely in the blood, and trypomastigotes are present in genital secretions of both infected males and females (no vectors are involved).

Pathogenesis: Infections by *T. evansi* vary markedly in their severity depending on host susceptibility (due to species, breed, age, nutritional and immune status) and parasite pathogenicity (strain variation, intensity of infection). Infections cause severe disease in permissive hosts, especially camels, horses and dogs, while other domestic and wild ungulates, carnivores and rodents are more resistant to disease manifestations. Trypomastigote stages occur in the blood where they grow and divide by binary fission, sometimes causing high parasitaemias. However, these stages differ from other African trypanosomes in that they are also able to invade host tissues, including the nervous system. Infections may therefore occur in intra- and extra-vascular fluids and elicit a range of clinical signs which can result in high mortality in some hosts, but more chronic production-limiting diseases in others. Infections of the nervous system may mimic those occurring in sleeping sickness (caused by *T. brucei*). There are many regional names for the disease(s) caused by *T. evansi* (and its many synonyms) reflecting clinical observations, including surra (meaning 'rotten'), murrina, dehab ('fly'), mbori, guifar, dioufar, menchaca or dubla ('emaciated'), yudleye/yudle ('aimless movement'), dukhan, salaf/salef, tahaga, su-auru, purana ('chronic'), tibarsa ('three-year disease'), makhi ki bimari ('horsefly disease'), peste-boba or derrengadera ('limping'), and mal de caderas ('paralysis'). When disease is apparent, it may manifest as acute, subacute or chronic disease. Infections in camels, horses and dogs may have a short incubation period of 1-4 weeks producing acute disease and even death over 2-8 weeks (esp. dogs and horses) or becoming chronic and persisting for 2-3 years (esp. camels). Clinical signs include fever, anaemia, jaundice, pale mucous membranes with petechial or ecchymotic haemorrhages (incl. eyelids of horses) and anterior chamber of eye (horses and dogs) producing ocular signs with conjunctivitis, lachrymation, keratitis and corneal opacities (trypanosomes can be found in gelatinous material from inner canthus). Animals develop ventral oedema involving the abdomen, brisket, legs scrotum and udders (also head and larynx in dogs), highly coloured urine (odiferous in camels) and sometimes transient local or general cutaneous eruption (in horses). They exhibit progressive loss of condition with weakness, lethargy, staring hair, weight loss with cachexia and emaciation (so-called 'living skeletons') despite variable loss of appetite, and marked loss of productivity (meat, milk, power and even abortion in pregnant animals). Infections may lead to neurological signs with alterations in locomotion (forelimb incoordination and hindlimb paresis, known as mal de caderas in horses) and sometimes periodic convulsions prior to death. Animals may die unexpectedly or develop delirium and struggle for hours. All age groups may be affected, but most clinical infections start around weaning. Parasites often exhibit antigenic variation of their surface glycoproteins to evade host immune responses, which contributes to frequent relapses of parasitaemia and remittent clinical signs. Infections have also been associated with immunosuppressive effects that may influence intercurrent diseases or interfere with vaccination campaigns. Nonetheless, animals in endemic regions may develop some resistance to disease but continue to act as asymptomatic or subclinical carriers. Resistance appears to involve both innate (complement, macrophages) and adaptive (humoral and cell-mediated) responses leading to premunitive immunity. Infections in other herbivores are less severe, often persisting as latent-chronic infections making the hosts carriers or reservoirs of infection. Bovids are usually refractory to disease, but some strains in cattle and buffalo in India appear to be more virulent sometimes causing clinical signs including hyperthermia, anaemia, oedema (legs), weight loss, production losses (meat, milk, draught power), neurological signs (usually meningoencephalitis), dyspnoea, recumbency, abortion and sometimes death. Cervids exhibit variable signs, ranging from subacute to acute and fatal, and pigs are highly susceptible to infection but not disease. Infections in Asian elephants have been associated with severe symptoms, fever, anorexia, oedema of face,

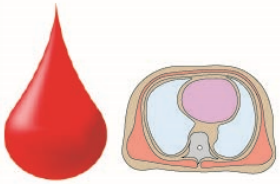
trunk, neck, brisket, lower abdomen and limbs, weakness and restlessness. Experimental transmission studies have also shown that macropod marsupials are very susceptible to infection and disease, with several kangaroo and wallaby species developing acute life-threatening diseases. Infections are occasionally detected in humans but they rarely cause disease as most possess natural trypanolytic proteins (apolipoprotein L1). Infections by *T. equiperdum* cause a disease in equids known as dourine characterized by fever, local oedema of the genitalia and mammary glands, oedematous cutaneous plaques, anaemia, ocular lesions, facial and lip paralysis, incoordination, paraplegia and emaciation, with periodic exacerbation and relapse. Infections in horses are often fatal, but spontaneous recoveries do occur although animals generally remain as latent carriers. Donkeys and mules are more resistant to infections and disease than horses but may also act as asymptomatic carriers.

Developmental cycle and mode of transmission: Trypomastigote stages feed on nutrients in intravascular and extravascular fluids by absorption across their surface membranes. They divide asexually by transverse binary fission involving the replication of organelles followed by karyokinesis and then cytokinesis. Infections by *T. evansi* are usually transmitted mechanically via contamination of the mouthparts of biting tabanid flies, and sometimes via contaminated mouthparts of vampire bats in the New World. The parasites do not undergo further development in these vectors so they are not considered to be true intermediate hosts but rather paratenic transport hosts. Other minor transmission routes have occasionally been reported, including oral transmission to carnivores consuming infected prey, vertical transmission in some hosts (transplacental or transmammary), and even iatrogenic transmission (when butchering animals). In contrast, the species *T. equiperdum* does not utilize invertebrate vectors (not even mechanically), but is transmitted exclusively between horses via coitus (not during every copulation). The incubation periods and duration of the diseases vary considerably between host and parasite species.

Differential diagnosis: Infections may be indicated in some animals by the occurrence of various clinical signs, such as *T. evansi* causing emaciation (surra) or neurological conditions (mal de caderas), or *T. equiperdum* causing oedematous cutaneous plaques (dourine) in horses, but other conditions cannot be discounted. Diagnosis is therefore made by the direct microscopic demonstration of parasites in host fluids (blood, lymph, cerebrospinal fluid) or centrifugal concentrates. Wet mounts may be examined by high-contrast microscopy for live motile trypanosomes, or fixed smears examined after staining with Giemsa or Leishman's stains. Unfortunately, test sensitivities are generally low as parasites may be sequestered extravascularly in host tissues rather than being abundant in the circulation. Parasites may be cultivated *in vitro* using various axenic media (e.g. Hirumi's modified Iscove's medium-9) although *T. equiperdum* appears to prefer soft agarose underlays. Parasites can also be propagated *in vivo* in laboratory mice, rats or rabbits, although some isolates do not readily adapt. A range of serological tests (complement fixation, immunofluorescence, agglutination, enzyme immunoassays) have been developed to detect specific host antibodies against crude and refined parasite antigens, but it is often difficult to distinguish between recent and chronic infections. Molecular biological techniques have been used to detect and characterize parasite isolates following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA, internal transcribed spacer regions, and some maxicircle DNA regions).

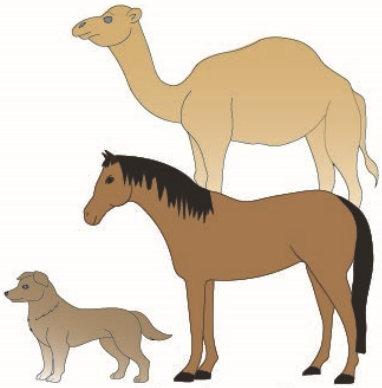
Treatment and control: A range of drugs have been used to treat clinical infections in animals, including trypanocides (quinapyramine, isometamidium chloride, suramin, cymelarsan), diamidines (diminazene aceturate) and even arsenic-based anthelmintics (melarsomine). Treatments have exhibited variable efficacies in different hosts (e.g. diminazene aceturate often ineffective in cattle, horses, pigs and elephants), and the incidence of drug-resistant strains of parasites appears to be increasing. Infections are deemed notifiable diseases in many countries with legislation governing the importation of livestock, diagnosis, quarantine, chemotherapy and chemoprophylaxis. There are no vaccines available as immunological responses are confounded by rapid changes in parasite surface coat antigens (variable surface glycoproteins). Preventive control measures adopted for *T. evansi* are based around controlling vector populations (using physical barriers, chemical insecticides or biological agents), while those adopted for *T. equiperdum* involve selecting uninfected horses for mating or promoting good hygiene during assisted matings. In many situations, the only effective control is achieved by culling infected animals.

Trypanosoma
(mammalian 'mechanica' species)
(e.g. *T. evansi, T. equiperdum*)

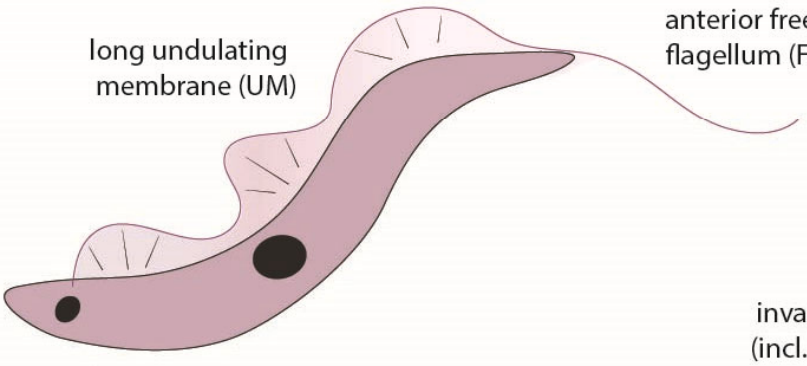


blood, tissues
(fever, anaemia,
jaundice, oedema
(surra))

division by
longitudinal
binary fission



Vertebrate Hosts
(mammals)



long undulating
membrane (UM)

anterior free
flagellum (FF)

posterior
kinetoplast (K)

invade tissues
(incl. central
nervous system)

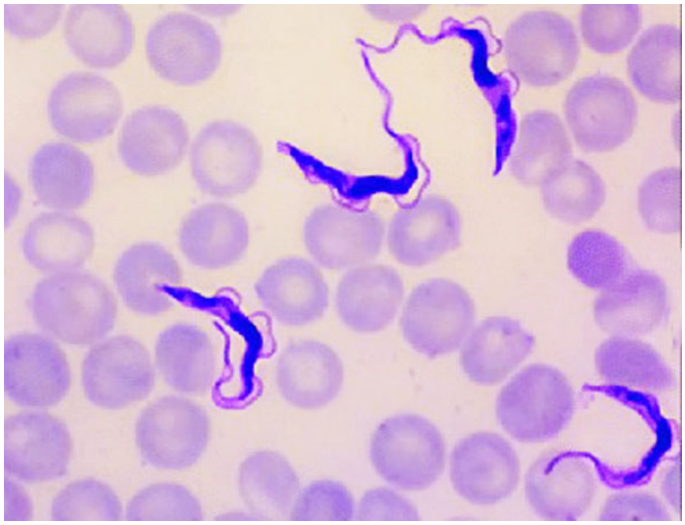
trypomastigote (15-36 µm)



T. evansi
mechanical transmission between hosts when
trypomastigotes contaminate mouthparts
of tabanid flies (sometimes vampire bats)



T. equiperdum
venereal transmission between equine
hosts via coitus



Trypanosoma evansi trypomastigotes

***Leishmania* (mammals)**
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Trypanosomes have a single flagellum and they form four main developmental stages: trypomastigotes (with a posterior kinetoplast and an emergent flagellum forming a long undulating membrane); epimastigotes (with an anterior kinetoplast and an emergent flagellum forming a short undulating membrane); promastigotes (with an anterior kinetoplast and a short emergent flagellum, but no undulating membrane); and amastigotes (with a kinetoplast but no emergent flagellum or undulating membrane). Many trypanosome species are parasitic only in insects whereas others are transmitted by insect vectors to a wide range of vertebrate hosts. Three main groups infect the blood and/or tissues of humans and animals causing severe clinical diseases: including the leishmanias which develop in the foregut of insect vectors and are transmitted via bite to the tissues of vertebrate hosts (e.g. sand flies transmit *Leishmania* spp. causing cutaneous, mucocutaneous or visceral disease in humans and animals).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Discoba (diverse group supported robustly by molecular studies)
Phylum: Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass: Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order: Trypanosomatida (parasitic, single anterior flagellum, often forming undulating membrane)
Family: Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)
Genus: *Leishmania* (vector-borne tissue parasites)
Species: various species cause cutaneous, mucocutaneous or visceral leishmaniasis in humans

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia	Order: Trichomonadida (3-5 anterior flagella plus	Monocercomonadidae (costa absent, most	*Histomonas*	birds (gut, liver)	direct (f-o)

(with parabasal body)	recurrent flagellum)	without undulating membrane)	*Dientamoeba*	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans comprise a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)
	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*). Trypanosomatids are dixenous (2-host) parasites with indirect transmission cycles between vertebrates and invertebrate vectors. *Leishmania* spp. form amastigote stages in the tissues of vertebrate hosts, and promastigote stages in invertebrate haematophagous vectors. Infections have been found in a range of vertebrate hosts (mammals and reptiles) with several types of diptera (sandflies) implicated as vectors. Infections in mammals are most commonly found in humans, dogs and rodents. Infections are confined to tropical areas; different parasite species being found in the Old World (Middle-East and Africa) and the New World (Central and South America). However, the recent discovery of *Leishmania* in macropodid marsupials in northern Australia indicates broader zoogeographic boundaries for parasites, hosts and vectors than previously thought.

Infections in humans have been reported for centuries (as early as the 1500s) with Spanish colonists and others describing skin ulcers in South America, the Middle-East and India (conditions known variously as valley sickness, Andean disease, uta, espundia, Chiclero ulcer, Aleppo boil, Delhi boil, salek, forest yaws and dum dum fever). Leishmaniasis is currently endemic in almost 100 countries and some 350 million people are at risk, with around 2 million new cases each year. Most cases of cutaneous leishmaniasis occur in Iran, Afghanistan, Syria, Saudi Arabia, Brazil and Peru, while most cases of visceral leishmaniasis are found in Bangladesh, Brazil, India and Sudan. *Leishmania* spp. were initially identified on the basis of biological (host/vector specificity, geographic distribution), clinical (symptoms/signs, tissue tropism) and immunological (antigenic) variation, as the very small parasites were remarkably similar morphologically. The classification of *Leishmania* species is complex and several systems have been proposed based on phenotypic and genotypic traits (although most do not advocate formal taxonomic ranks).

- Categorization by clinical disease:
  - Cutaneous leishmaniasis (localized, diffuse (disseminated), leishmaniasis recidivans, or post–kala-azar dermal leishmaniasis) arising from infection of macrophages in the dermis;
  - Mucocutaneous leishmaniasis arising from infection of macrophages in the naso-oropharyngeal mucosa; and
  - Visceral leishmaniasis (kala-azar, or black fever) arising from infection of macrophages throughout reticulo-endothelial system of vertebrate hosts.

- Categorization by geographic occurrence:
  - Old World (Eastern Hemisphere) leishmaniasis, caused by species found in Africa, Asia, Middle East, Mediterranean and India (cutaneous or visceral disease caused by various species complexes in the *L. Leishmania* subgenus [e.g. *L.* (*L.*) *tropica*, *L.* (*L.*) *major* and *L.* (*L.*) *aethiopica*, as well as *L.* (*L.*) *infantum* and *L.* (*L.*) *donovani*]; and
  - New World (Western Hemisphere) leishmaniasis, caused by species found in Central and South America (cutaneous, mucocutaneous and visceral disease caused by species belonging either to the *L.* (*L.*) *mexicana* complex [e.g. *L.* (*L.*) *mexicana*, *L.* (*L.*) *amazonensis* and *L.* (*L.*) *venezuelensis*] or to several species complexes in the *L. Viannia* subgenus [e.g. *L.* (*V.*) *braziliensis*, *L.* (*V.*) *guyanensis*, *L.* (*V.*) *panamensis* and *L.* (*V.*) *peruviana*]).

- Categorization by vector:
  - *Phlebotomus* sand fly vectors (in Old World);
  - *Lutzomyia* sand fly vectors (in New World).

- Categorization by vector tissue tropism:
  - Hypopylarian (hindgut) development in sandfly with transmission via vector consumption (comprises 'primitive' species in lizards e.g. *L. agamae, L. ceramodactyli*);
  - Peripylarian (hindgut then foregut) development in sandfly with inoculative transmission (comprises some lizard parasites of Old World (*L. adleri, L. tarentolae*) but dominated by *L.* (*L.*) *braziliensis* complex of Western Hemisphere); and
  - Suprapylarian (midgut and foregut) development in sandfly with inoculative transmission (comprises species causing cutaneous lesions in New World (*L.* (*L.*) *mexicana* and *L.* (*V.*) *hertigi* complexes) and Old World (*L.* (*L.*) *tropica* complex) or visceral disease in New and Old World (*L.* (*L.*) *donovani* complex).

- Categorization by subgenus:

- Species in mammals with suprapylarian development in sand flies were classified together in the subgenus *L. Leishmania* (generally in the Paleotropics, with the exception of the '*L.* (*L.*) *mexicana'* species complex);
- Species in mammals with peripylarian development in sand flies were allocated to the subgenus *L. Viannia* (generally located in the Neotropics); and
- Species in lizards with hypopylarian development in sand flies were grouped in the subgenus *L. Sauroleishmania* (generally confined to the Old World).

- Categorization by molecular characteristics:
  - Protein and isoenzyme characterization studies indicated that infections in humans and some animals were often highly complex consisting of multiple strains or subspecies (possibly even hybrids), therefore infections have been referred to as species complexes (comprising closely related species).
  - Recent phylogenetic studies have identified three major *Leishmania* clades referable to different subgenera: *L. Viannia* species causing New World cutaneous and mucocutaneous leishmaniasis and undergoing peripylarian development in *Lutzomyia* sandflies; *L. Leishmania* species causing New and Old World cutaneous and visceral leishmaniasis and undergoing suprapylarian development in *Phlebotomus* sandflies; and an intermediary *L. Sauroleishmania* group undergoing hypopylarian development in sand flies and infecting Old World lizards when the vectors are ingested.

Most conventional *Leishmania* spp. have been classified within species complexes within these subgenera. In the Old World, four *L.* (*Leishmania*) complexes are recognized: the 'donovani' complex (comprising *L.* (*L.*) *donovani*, *L.* (*L.*) *infantum* and *L.* (*L.*) *archibaldi*); the 'tropica' complex (*L.* (*L.*) *tropica* and *L.* (*L.*) *killicki*); the 'major' complex (*L.* (*L.*) *major*); and the 'aethiopica' complex (*L.* (*L.*) *aethiopica*). In the New World, four *L.* (*Viannia*) complexes are recognized: the 'Brazilian' complex (comprising *L.* (*V.*) *braziliensis* and *L.* (*V.*) *peruviana*); the 'Guayanian' complex (*L.* (*V.*) *panamensis*, *L.* (*V.*) *guayensis* and *L.* (*V.*) *shawi*); the 'naiffi' complex (*L.* (*V.*) *naiffi*); and the 'lainsoni' complex (*L.* (*V.*) *lainsoni*); as well as two *L.* (*Leishmania*) complexes: the 'Mexican' complex (*L.* (*L.*) *mexicana*, *L.* (*L.*) *amazonensis*, *L.* (*L.*) *garnhami*, *L.* (*L.*) *venezuelensis*, *L.* (*L.*) *forattinii* and *L.* (*L.*) *pifanoi*) and a member of the 'donovani' complex (*L.* (*L.*) *chagasi*). A fourth subgenus has recently been added: *L.* (*Mundinia*) comprising the 'enrietti' complex causing cutaneous and visceral lesions in humans and animals and undergoing suprapylarian development in sand flies and biting midges.

***Leishmania* species**	**Vertebrate hosts**	**Disease**	**Vectors**	**Distribution**
CUTANEOUS (and MUCOCUTANEOUS) LEISHMANIASIS				
Subgenus *Leishmania*				
'*mexicana'* complex				
L. (*L.*) *mexicana* (syn. *L. diffusa, pifanoi*)	Primates: hominid (human), Didelphimorphia: didelphid (common opossum, common black-eared opossum, big-eared opossum, Mexican mouse-opossum, Robinson's mouse opossum); Rodentia: caviid (guinea pig), cricetid (short-tailed cane mouse, big-eared climbing rat, Sumichrast's vesper rat, hispid cotton rat, large-headed rice rat, Brazilian pygmy rice rat, Syrian hamster), cuniculid (lowland paca), dasyproctid (Azara's agouti, Central American agouti), echimyid (Guyenne spiny rat, Tome's spiny rat, Atlantic bamboo rat), heteromyid (Gaumer's spiny pocket mouse, Trinidad spiny pocket mouse, Desmarest's spiny pocket mouse), murid (house mouse, wistar rat, Mongolian gerbil)	chicleros ulcer, cutaneous	Diptera: psychodid (*Lutzomyia anthopora, ayacuchensis, columbia, cruciata, diabolica, migonei, olmeca, ovallesi, panamensis, shannoni, ylephiletor, flaviscutellata*)	Americas
L. (*L.*) *amazonensis*	Primates: hominid (human); Didelphimorphia: didelphid (common opossum, white-eared opossum, brown four-eyed opossum, grey four-eyed opossum, Tate's woolly mouse opossum, woolly mouse opossum, Linnaeus's mouse opossum); Rodentia: cricetid	diffuse, cutaneous	Diptera: psychodid (*Lutzomyia flaviscutellata, longipalpis, nuneztovari, olmeca, reducta*)	South America

	(common bristly mouse, scaly-footed water rat, large-headed rice rat, unicolored rice rat, MacConnell's rice rat), dasyproctid (agouti), echimyid (Guyenne spiny rat); Carnivora: canid (crab-eating fox), felid (cat)			
L. (*L.*) *venezuelensis*	Primates: hominid (human); Carnivora: felid (cat)	cutaneous	Diptera: psychodid (*Lutzomyia olmeca, rangeliana*)	Venezuela
L. (*L.*) *garnhami*	Primates: hominid (human); Didelphimorphia: didelphid (common opossum)	cutaneous	Diptera: psychodid (*Lutzomyia youngi*)	Central America
L. (*L.*) *forattinii*	Didelphimorphia: didelphid (big-eared opossum); Rodentia: cricetid (rice rat)	cutaneous	Diptera: psychodid (*Lutzomyia ayrosai, yuilli*)	Brazil
'*tropica'* complex				
L. (*L.*) *tropica*	Primates: hominid (human), Carnivora: canid (dog); Rodentia: murid (dwarf gerbil, unstriped grass mouse, Mullah spiny mouse)	dry cutaneous	Diptera: psychodid (*Phlebotomus aculeatus, arabicus, chabaudi, guggisbergi, rossi, saevus, sergenti*)	Middle-East, India, Aia, Africa
L. (*L.*) *killicki*	Primates: hominid (human); Rodentia: ctenodactylid (common gundi), murid (mouse)	cutaneous	Diptera: psychodid (*Phlebotomus sergenti*)	North Africa
'*major'* complex				
L. (*L.*) *major*	Primates: hominid (human); Carnivora: canid (dog); Rodentia: dipodid (jerboa), murid (great gerbil, Indian gerbil, Indian desert jird, Libyan jird, sand rat, unstriped grass mouse, house mouse), sciurid (ground squirrel)	wet cutaneous, oriental sore	Diptera: psychodid (*Phlebotomus andrejevi, ansarii, caucasicus, duboscqi, mongolensis, papatasi*)	Africa, Asia, India
'*aethiopica'* complex				
L. (*L.*) *aethiopica*	Primates: hominid (human); Hyracoidea: procaviid (rock hyrax, yellow-spotted rock hyrax)	chronic oriental sore, diffuse or dry cutaneous	Diptera: psychodid (*Phlebotomus longipes, pedifer, sergenti*)	Ethiopia, Kenya
unplaced				
L. (*L.*) *arabica*	Rodentia: murid (fat sand rat)	cutaneous		Middle-East
L. (*L.*) *aristidesi*	Didelphimorphia: didelphid (Robinson's mouse opossum); Rodentia: cricetid (large-headed rice rat), cuniculid (lowland paca), echimyid (Tome's spiny rat)	cutaneous	Diptera: psychodid (*Lutzomyia olmeca*)	Panama
L. (*L.*) *deanei* (now *Porcisia*)	Rodentia: erethizontid (Brazilian porcupine, Andean porcupine)	cutaneous	Diptera: psychodid (*Lutzomyia furcata*)	Brazil
L. (*L.*) *gerbilli*	Rodentia: murid (great gerbil)	cutaneous		Eurasia
L. (*L.*) *herreri*	Pilosa: bradypodid (brown-throated sloth), choloepodid (Hoffmann's two-toed sloth)	cutaneous	Diptera: psychodid (*Lutzomyia* sp.)	South America
L. (*L.*) *hertigi* (now *Porcisia*)	Rodentia: erethizontid (Brazilian porcupine, Andean porcupine)	cutaneous		Panama, Costa Rica
L. (*L.*) *turanica*	Primates: hominid (human), and unspecified monkey; Rodentia: murid (great gerbil, Mongolian gerbil, short-tailed bandicoot rat, house mouse), cricetid (golden hamster, Chinese striped hamster)	cutaneous	Diptera: psychodid (*Phlebotomus mongolensis, andrejevi, papatasi, arabicus*)	Eurasia
Subgenus *Viannia*				
'*braziliensis'* complex				
L. (*V.*) *braziliensis* (syn. *L. wrightii*)	Primates: hominid (human); Didelphimorphia: didelphid	espundia, cutaneous,	Diptera: psychodid (*Lutzomyia ayrozai,*	Central and South America

	(common opossum, white-eared opossum, agile gracile opossum, bare-tailed woolly opossum, woolly mouse opossum, Tate's woolly mouse opossum): Pilosa: bradypodid (brown-throated sloth), choloepodid (Hoffmann's two-toed sloth, Linnaeus's two-toed sloth); Rodentia: cricetid (large-headed rice rat, unicolored rice rat, black-footed pygmy rice rat, montane grass mouse), murid (black rat); Carnivora: canid (dog); Perissodactyla: equid (horse)	mucocutaneous	*carrerai, columbiana, complexa, cruciata, davisi, edwardsi, fischeri, gomezi, intermedia, llanosmartini, migonei, neivai, nuneztovari, ovallesi, panamensis, paraensis, pescei, pessoai, pia, shawi, spinicrassa, tejadai, townsedni, trinidadensis, ylephiletor, youngi, yucumensis, wellcomei, whitmani*)	
L. (*V.*) *peruviana*	Primates: hominid (human); Carnivora: canid (dog); Rodentia: cricetid (South American field mouse, Andean leaf-eared mouse); Didelphimorphia: didelphid (Andean white-eared opossum, white-eared opossum)	uta, cutaneous	Diptera: psychodid (*Lutzomyia ayacuchensis, peruensis, verrucarum*)	Peru, Bolivia
'*quayanensis'* complex				
L. (*V.*) *panamensis*	Primates: hominid (human), aotid (three-striped night monkey), callitrichid (Geoffroy's tamarin); Pilosa: bradypodid (brown-throated sloth), choloepodid (Hoffmann's two-toed sloth); Carnivora: canid (dog), procyonid (northern olingo, South American coati, kinkajou); Rodentia: echimyid (Tome's spiny rat, armoured rat)	cutaneous	Diptera: psychodid (*Lutzomyia cruciata, gomezi, hartmanni, panamensis, sanguinaria, trapidoi, ylephiletor, yuilli, Psychodopygus panamensis*)	Panama, Costa Rica
L. (*V.*) *guyanensis*	Primates: hominid (human); Pilosa: choloepodid (two-toed sloth), myrmecophagid (southern tamandua); Didelphimorphia: didelphid (common opossum, grey slender opossum)	cutaneous, mucocutaneous, pian bois	Diptera: psychodid (*Lutzomyia anduzei, ayacuchensis, longiflocosa, migonei, shawi, umbratilis, whitmani*)	Brazil, Columbia
L. (*V.*) *shawi*	Primates: hominid (human), cebid (tufted capuchin), pithecid (black-bearded saki); Pilosa: bradypodid (pale-throated sloth), choloepodid (Linnaeus's two-toed sloth); Carnivora: procyonid (South American coati)	cutaneous	Diptera: psychodid (*Lutzomyia whitmani*)	Brazil
'*naiffi'* complex				
L. (*V.*) *naiffi*	Primates: hominid (human); Cingulata: dasypodid (nine-banded armadillo); Rodentia: echimyid (Foster's punare)	cutaneous	Diptera: psychodid (*Lutzomyia amazonensis, antunesi, ayrozai, davisi, gomezi,hirsuta, paraensis, shawi, sordelli, squamiventris, tortura, trapidoi, Psychodopygus amazonensis, Nyssomyia anduzei*)	Brazil, French Guiana
'*lainsoni'* complex				
L. (*V.*) *lainsoni*	Primates: hominid (human); Rodentia: cuniculid (lowland paca)	cutaneous	Diptera: psychodid (*Lutzomyia nuneztovari, ubiquitalis, velascoi*)	Brazil
unplaced				
L. (*V.*) *colombiensis*	Primates: hominid (human); Pilosa: choloepodid (Hoffmann's two-toed	cutaneous	Diptera: psychodid (*Lutzomyia hartmanni,*	Columbia

	sloth); Rodentia: sciurid (red-tailed squirrel)		*gomezi, panamensis*)	
L. (*V.*) *equatorensis*	Primates: hominid (human); Pilosa: choloepodid (Hoffmann's two-toed sloth); Rodentia: sciurid (red-tailed squirrel)	cutaneous	Diptera: psychodid (*Lutzomyia hartmanni*)	Ecuador
L. (*V.*) *lindenbergi*	Primates: hominid (human)	cutaneous	Diptera: psychodid (*Lutzomyia antunesi*)	Brazil
Subgenus *Mundinia*				
'*enriettii'* complex				
L. (*M.*) *chancei*	Primates: hominid (human)	cutaneous		Africa
L. (*M.*) *enriettii*	Rodentia: caviid (guinea pig, Brazilian guinea pig), cricetid (hamster)	cutaneous	Diptera: psychodid (*Lutzomyia longipalpis, gomezi*, *correalmai, migonei, monticula*), ceratopogonid biting midges (*Culicoides sonorensis*)	South America
L. (*M.*) *macropodum (syn. L. australiensis*)	Diprotodontia: macropodid (red kangaroo, northern wallaroo, black wallaroo, agile wallaby)	cutaneous	Diptera: ceratopogonid (*Forcipomyia* (*Lasiohelea*), *Culicoides sonorensis*), psychodid (*Lutzomyia migonei*)	Australia
L. (*M.*) *martiniquensis*	Primates: hominid (human); Rodentia: murid (mouse); Artiodactyla: bovid (cattle); Perissodactyla: equid (horse)	diffuse cutaneous, visceral	Diptera: ceratopogonid (*Culicoides peregrinus, sonorensis),* psychodid *(Phlebotomus argentipes*)	Martinique, Thailand, Africa, Europe, North America
L. (*M.*) *orientalis* (syn. *L. 'siamensis'*)	Primates: hominid (humans)	cutaneous, visceral	Diptera: psychodid *(Phlebotomus argentipes, Sergentomyia gemmea, iyengari*), ceratopogonid (*Culicoides sonorensis),*	Asia
L. (*M.*) *procaviensis*	Hyracoidea: procaviid (rock hyrax)	(from nose)		Africa
VISCERAL LEISHMANIASIS				
Leishmania subgenus				
'donovani' complex				
L. (*L.*) *donovani*	Primates: hominid (human); Carnivora: canid (dog, red fox); Didelphimorphia: didelphid (common opossum, Virginia opossum); Diprotodontia: phalangerid (common brushtail possum, common ringtail possum); Rodentia: murid (black-tailed gerbil, Persian jird, unstriped grass mouse, Guinea multimammate mouse)	kala azar, dum-dum fever, Old World visceral	Diptera: psychodid (*Phlebotomus argentipes, celiae, longiductus, martini, orientalis, rodhaini, vansomerenae*)	India, Asia, Africa, South America
L. (*L.*) *archibaldi* (probable synonym of *L. donovani*)	Primates: hominid (human); Carnivora: canid (dog), felid (serval), viverrid (genet): Rodentia: murid (rat)	visceral	Diptera: psychodid (*Phlebotomus orientalis*)	Africa
L. (*L.*) *infantum*	Primates: hominid (human); Carnivora: canid (dog, raccoon dog, wolf, golden jackal, red fox), felid (cat, European wildcat, Iberian lynx), herpestid (Egyptian mongoose), mustelid (stone marten, pine marten, weasel, European mink, polecat, European badger), viverrid (common genet); Lagomorpha: leporid (European rabbit, European hare, Iberian hare); Eulipotyphla: erinaceid (European hedgehog), soricid (greater white-	infantile, visceral, cutaneous, mucocutaneous	Diptera: psychodid (*Phlebotomus alexandri, ariasi, balcanicus, celiae, chinensis, galileus, halepensis, kandelakii, langeroni, longicuspis, longiductus, major, martini, neglectus, orientalis, perfiliewi, perniciosus, sichuanensis, smirnovi, syriacus, tobbi, transcaucasicus, turanicus, wui, Lutzomyia*	Asia, Middle-East, Europe, Africa, South America

	toothed shrew); Didelphimorphia: didelphid (common opossum, white-eared opossum, big-eared opossum); Chiroptera: miniopterid (Schreiber's bat); Rodentia: cricetid (golden hamster, grey dwarf hamster), glirid (edible dormouse, garden dormouse), murid (house mouse, Algerian mouse, yellow-necked mouse, wood mouse, black rat, brown rat, fat sand rat, thin sand rat, great gerbil, Indian gerbil, Libyan jird, Persian jird), sciurid (red squirrel)		*almerioi, antunesi, cruzi, evansi, forattinii, longipalpis, mignoei, pseudolongipalpis, sallesi*)	
L. (*L.*) *chagasi* (probable synonym of *L. infantum*)	Primates: hominid (human); Carnivora: canid (dog, hoary fox, crab-eating fox), felid (cat); Didelphimorphia: didelphid (common opossum)	New World visceral, cutaneous	Diptera: psychodid (*Lutzomyia antunesi, andyzei,cruciata, ovallesi, longipalpis, cruzi, evansi*)	South and Central America

Parasite morphology: Two developmental stages are formed: amastigotes and promastigotes. The amastigotes are small spherical cells ranging from 2-5 µm in diameter. They are non-flagellated cells but the cytoplasm contains a flagellar sac and a non-emergent vestigial flagellum. The nucleus and kinetoplast are surrounded by a small ring of vacuolated cytoplasm and the cells are among the smallest nucleated cells known. Promastigotes are thin elongate cells with an anterior kinetoplast and an emergent free flagellum. They are generally lance-like in shape and range in size from 5-20 µm in length by 1.5-3.5 µm in width. Different parasite species are generally not differentiated by morphological differences, but rather on the basis of geographical, biological and clinical features.

Site of infection: In vertebrates, amastigotes invade macrophage cells of the reticuloendothelial and lymphoid systems of the skin, nasopharynx or viscera depending on the parasite species. The parasites survive within phagosomes in host cells but resist digestion by lysosomal enzymes. They multiply and grow, ultimately rupturing the host cell and releasing stages to infect new macrophages, including those which circulate in the blood (monocytes). Around 36 *Leishmania* spp. have been described from mammals: with 32 species causing cutaneous/mucocutaneous lesions in 90 mammalian species belonging to 28 families in 10 orders (mostly rodents, but also carnivores, artiodactylans, armadillos, opossums, marsupials, hyraxes, horses, sloths and primates), and another 4 species causing visceral infections in 52 mammalian species belonging to 15 families in 8 orders (mainly carnivores and rodents, but also opossums, lagomorphs, marsupials, shrews, bats and humans). In insect vectors, promastigotes develop in the gut undergoing a process known as metacyclogenesis (involving the expression of different surface lipoproteins), with procyclic promastigotes attached to the gut wall, and metacyclic promastigotes maturing as the infective stages. A total of 114 insect species have been found to act as vectors: including 111 species of psychodid sandflies (mainly *Lutzomyia* and *Phlebotomus* spp. and a few *Nyssomyia, Psychodopygus* and *Sergentomyia* spp.) and 3 species of ceratopogonid biting midges (*Culicoides, Forcipomyia* (*Lasiohelea*)).

Pathogenesis: *Leishmania* amastigotes live in the reticulo-endothelial cells of vertebrate hosts and are not destroyed by proteolytic enzymes. Here they feed and replicate, ultimately causing host cell lysis. The parasites cause three distinct types of clinical disease: cutaneous, mucocutaneous and visceral leishmaniasis resulting from replication of the parasites in macrophages of the dermis, nasopharynx or visceral tissues. Old World (muco)cutaneous leishmaniasis is caused mainly by *L.* (*L.*) *major*, *L.* (*L.*) *tropica, L.* (*L.*) *aethiopica, L.* (*L.*) *infantum* and *L.* (*L.*) *donovani* (the last 2 species may also cause visceral disease), while New World (muco)cutaneous leishmaniasis is caused primarily *L.* (*V.*) *braziliensis*, *L.* (*V.*) *columbiensis*, *L.* (*L.*) *mexicana*, *L.* (V.) *lainsoni*, *L.* (*L.*) *garnhami*, *L.* (*L.*) *amazonensis*, *L.* (*V.*) *panamensis*, *L.* (*V.*) *guyanensis*, *L.* (*V.*) *peruviana* and *L.* (*L.*) *infantum* (the latter may also cause visceral leishmaniasis). Disease occurs mainly in those living or working in endemic areas, and outbreaks have been associated with military training and infrastructural development projects as well as travellers visiting scenic or remote locations. In the Old World, the disease occurs mainly in semi-arid and desert regions and is known by various common names depending on species and region, including oriental sore, Aleppo boil, Jericho boil, Baghdad boil, Balkh sore, Penjdeh sore, Briska button, Bouton de Crete and Bouton D'Orient. In the New World, the disease occurs mainly in forested areas and is known as uta, espundia, Chiclero'e ulcer, pain bois and forest yaws. Infections generally involve only one or a few lesions at the bite site; they do not spread to other sites. Active lesions appear as open sores or ulcers with raised borders and pronounced inflammation, occasionally developing into nodular and rarely verrucous lesions. The incubation period varies from one week to several months, and most lesions heal spontaneously within 6 months to 3 years, leaving the host with solid protective immunity to re-infection. However, under certain conditions (esp. immuno-compromised hosts), some infections (e.g. *L.* (*L.*) *aethiopica*) may spread giving rise to diffuse (disseminated) cutaneous leishmaniasis (not unlike leprosy in appearance) that does not resolve spontaneously. Infections by

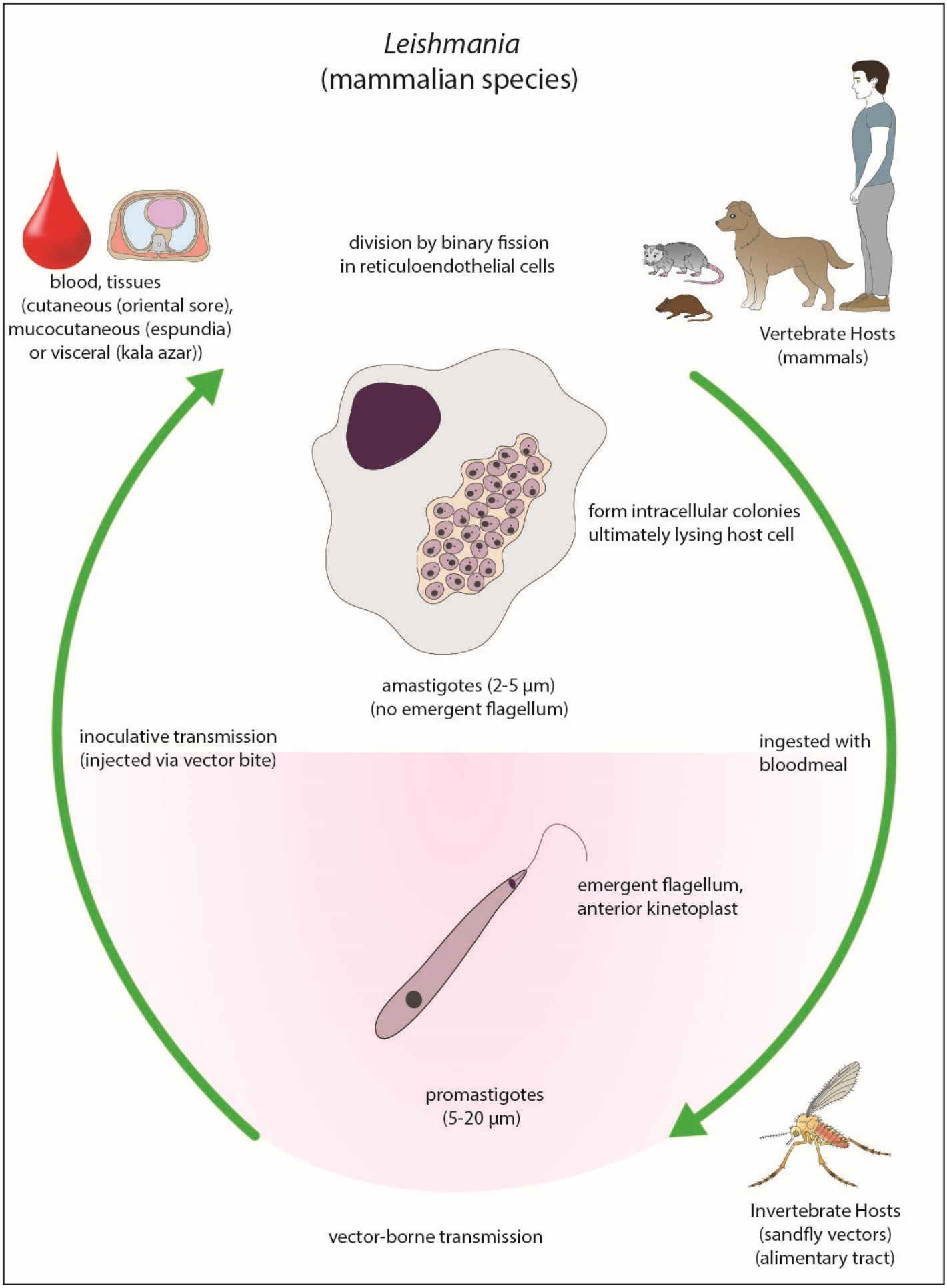
L. (*V.*) *braziliensis* are also often confined to single skin lesions, but sometimes they spread to the mucocutaneous junction in the pharynx and may cause severe destructive nasopharyngeal lesions developing over 5-20 years. Cutaneous infections by *L.* (*V.*) *guyanensis* may also spread to cause mucocutaneous lesions, and there is evidence to suggest that strains infected with endozoic *Leishmania* RNA virus 1 are more virulent due to their enhanced survival in the face of intense host inflammatory responses. Some patients may also develop a chronic cutaneous form of disease called post-kala-azar dermal leishmaniasis which requires prolonged treatment. Visceral leishmaniasis (known as kala-azar, black fever or dumdum fever) is caused by *L.* (*L.*) *donovani* and *L.* (*L.*) *infantum* when infected macrophages congregate in the viscera, notably the liver and spleen, producing leucopoenia, thrombocytopenia, hepatosplenomegaly, lymphadenopathy, oedema, ascites and anaemia. It is a slow but progressive illness, with bouts of irregularly recurring fever, malaise and weight loss and is invariably fatal, unless treated. The incubation period is usually 2-6 months, but has been found to range from as little as 10 days up to several years. Hosts are more susceptible to leishmaniasis when stressed and immunocompromised; due to congenital or acquired immunodeficiencies (esp. HIV-infection), immunosuppressive chemotherapy, and even malnutrition. Hosts are also more prone to concomitant bacterial infections, including tuberculosis, pneumonia and dysentery. The prevalence of leishmaniasis increases initially with host age and then plateaus, likely due to the acquisition of protective immunity. Clusters of disease are also seen within households, likely due to the short flight range of the sandfly vectors. Infections in dogs may be apparent as a progressive wasting disease characterized by weight loss, fever, anorexia, exercise intolerance, non-pruritic skin lesions, lymphadenopathy, lameness and epistaxis.

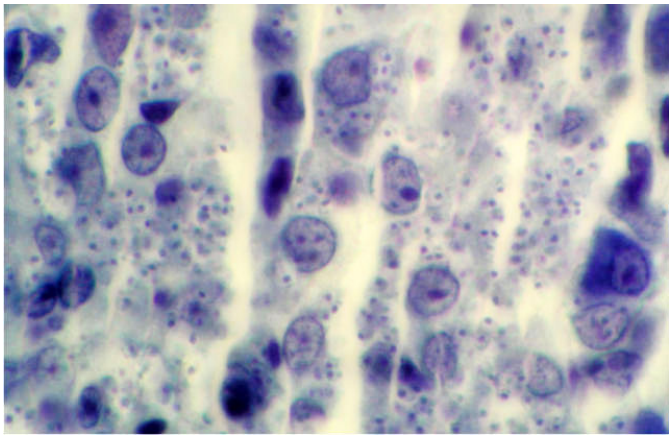
Developmental cycle and mode of transmission: *Leishmania* spp. undergo vector-borne transmission between vertebrate hosts. Epidemiologically, there are three different cycles of infection involving humans: a primitive or sylvatic cycle involving zoonotic transmission to humans from wildlife; a secondary or peri-domestic cycle involving zoonotic transmission from domestic animals; and a tertiary or anthroponotic cycle between humans. The spread of infections depends not only on the degree of contact between humans and animals, but to a greater extent on the abundance, distribution, specificity and competence of the vectors. Most *Leishmania* spp. are transmitted by blood-sucking sand flies belonging to the subfamily Phlebotominae in the dipteran family Psychodidae. These sand flies are small (2.0-3.5 mm long) and have lanceolate wings and tiny hairs covering their bodies. They occur on all continents (except Antarctica), but only two of the six genera are main vectors for leishmaniasis; the genus *Lutzomyia* in the New World (59 out of some 500 species implicated as vectors) and the genus *Phlebotomus* in the Old World (45 out of some 300 species). Only the females feed on blood which is required for them to complete their reproductive cycles, but they may also take up lymph and other extravascular fluids. Amastigotes ingested during feeding transform to procyclic promastigotes and attach to the midgut-hindgut wall where they multiply by binary fission and develop into metacyclic infective promastigotes over 6-20 days. The parasites migrate forward to the foregut and pharynx where they produce a partial or complete blockage of the sucking apparatus. When the sandfly next attempts to feed, it 'clears its throat' and regurgitates a bolus of metacyclic promastigotes into the bite wound. Promastigotes injected into vertebrate hosts are phagocytosed and develop into amastigotes within 24 hours. The recent discovery of an alternative dipteran vector, *Forcipomyia* (*Lasiohelea*) midges, for the *Leishmania* species found in macropodids in Australia reinforces the need for transmission cycles to be definitively determined for many isolates. Promastigotes injected into vertebrate hosts have numerous lipophosphoglycan molecules on their membranes which enables them to resist lysis as well as adhere to macrophage membranes facilitating their phagocytosis. The parasites are resistant to intracellular enzyme degradation and persist within parasitophorous vacuoles formed by fusion of phagosomes with lysosomes. They transform to amastigote stages which undergo massive asexual multiplication, ultimately lysing the host cell releasing amastigotes which infect other host cells. On occasion, infections can be transmitted horizontally between vertebrate hosts by contaminated needles, blood transfusions, organ transplantation, venereal contact and possibly vertically by crossing the placenta.

Differential diagnosis: Amastigotes may be detected microscopically in biopsy material taken from the dermis, bone marrow, spleen, liver, or lymph nodes (parasites are rarely demonstrated in peripheral blood). Intracellular stages are best visualized in tissue smears using Giemsa's or Leishman's stains, but most microscopic techniques have poor limits of detection, sensitivity and specificity. Infections in vectors may be detected by microscopic examination of gut squash preparations or histological sections. Parasites may be isolated and amplified in number as promastigotes by *in vitro* culture in enriched media (such as nutrient agar-blood mixtures) or by experimental inoculation *in vivo* into laboratory animal models (immunosuppressed or susceptible rodent strains). Such culture techniques, however, are time-consuming, costly, technically demanding and may give false negative results for many reasons. Various immunoserological tests have been developed to detect host antibodies against infection (including immunodiffusion, immunoelectrophoresis, agglutination, immunofluorescence and enzyme immunoassays), but there are difficulties in detecting cutaneous infections (due to poor host responses), establishing the time course of infection (distinguishing between recent and chronic infections) and differentially diagnosing infections (discriminating between different parasite species). A range of crude, subcellular and recombinant antigens have been used with varying sensitivities and specificities. Attempts to develop immunological tests to detect parasite antigens in host samples have been thwarted by considerable cross-reactivity with circulating immune complexes, serum amyloid, rheumatoid factor and reactive immunoglobulins (including auto-antibodies). Delayed hypersensitivity is characteristic of cutaneous forms of leishmaniasis and several skin tests (Montenegro reaction test, leishmanin skin test) have been used to screen populations for exposure, although their use for visceral leishmaniasis has proven contradictory. Parasite isolates have been analysed using various protein characterization techniques, including isoenzyme analyses, polyacrylamide gel electrophoresis and immunoblotting. Modern molecular characterization techniques have used the polymerase chain reaction (PCR) to detect restriction fragment length polymorphisms (RFLP), random amplified polymorphic DNA (RAPD), and to amplify specific gene sequences (parasite DNA) from host samples; including small subunit (18S) ribosomal RNA, internal

transcribed spacers, mini-exon gene repeats, microsatellites (maxi- and mini-circles of kinetoplast DNA), beta-tubulin, glycoproteins, heat-shock proteins, cysteine proteases, and mitochondrial cytochrome b.

Treatment and control: Some cutaneous infections require no treatment as lesions may heal within several months. Systemic therapy (intravenous, intramuscular, intralesional) with pentavalent antimonials (sodium stibogluconate or meglumine antimonate) is the treatment of choice for disfiguring and visceral infections. The development of antimonial drug resistance, however, is a growing problem in many endemic areas, including South America, India and the Middle-East. Pentamidine or amphotericin B can be used if antimonials are ineffective, and miltefosine and aminosidine (paromomycin) have shown promise as treatment options, especially when combined with immunotherapy using the tumour-necrosis factor-alpha (TNF-α) inhibitor pentoxifylline. The purine analogue allopurinol has also shown good efficacy against infections in dogs, as many of the others are nephrotoxic. All courses of treatments should be long-term to achieve not only clinical remission but also elimination of the parasites, otherwise relapses may occur. Many human enterprises are conducive to the spread of infections; including urbanization, pet ownership, deforestation, agriculture, migration and tourism. Preventive measures include protection from sand fly bites but this can be difficult as they are so small that they can penetrate most mosquito nets. Reducing the size of reservoir host populations (especially dogs) has proven beneficial in many endemic urban areas. Many cutaneous infections, however, are acquired in forests away from human habitation, as the reservoir hosts are wild animals (esp. rodents). The prevention of sand fly bites in forest areas is almost impossible but may be minimized by the use of protective clothing, insect repellents and insecticidal sprays in houses. In several endemic areas, dogs fitted with deltamethrin-impregnated collars were partly protected from sand fly bites and they exhibited low rates of infection. Considerable research has been conducted on the development of a protective vaccine, prompted by observations that many clinical cases resolve spontaneously leaving the hosts resistant to re-infection. Indeed, vaccination through ‘leishmanization’ has long been practised around the Middle-East (for centuries according to ancient texts), whereby children are inoculated in innocuous sites with viable *L. major* parasites taken from a mildly infected individual. Several combination vaccines are currently undergoing clinical trials, but research has been hampered by our lack of knowledge about host-parasite immune interactions, particularly with respect to immuno-evasion mechanisms. Results derived from laboratory animal models have implicated both innate and acquired (adaptive) immune responses in the acquisition of protection, particularly cell-mediated responses involving helper (CD4 Th) and cytotoxic (CD8 Tc) T-cells and cytokines stimulating Th1 (pro-inflammatory) responses.

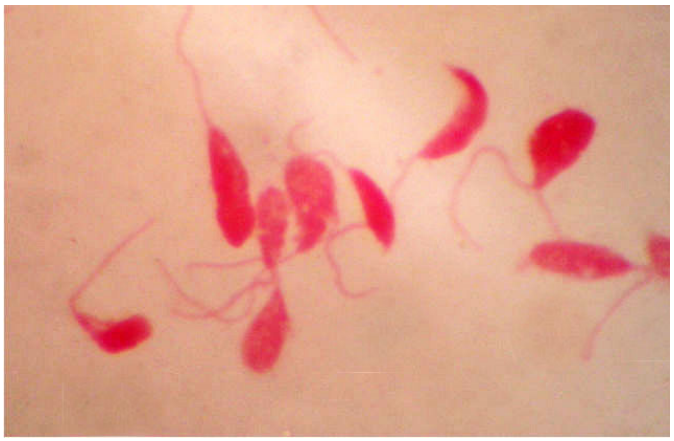

Leishmania
(mammalian species)
blood, tissues
(cutaneous (oriental sore),
mucocutaneous (espundia)
or visceral (kala azar))
division by binary fission
in reticuloendothelial cells
Vertebrate Hosts
(mammals)
form intracellular colonies
ultimately lysing host cell
amastigotes (2-5 µm)
(no emergent flagellum)
inoculative transmission
(injected via vector bite)
ingested with
bloodmeal
emergent flagellum,
anterior kinetoplast
promastigotes
(5-20 µm)
Invertebrate Hosts
(sandfly vectors)
(alimentary tract)
vector-borne transmission



Leishmania amastigotes in liver



Cutaneous leishmaniasis



Leishmania promastigotes in sandfly gut



Phlebotomus sandfly vector for *Leishmania*

***Leishmania* (*Sauroleishmania*) (reptiles)**
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Trypanosomes have a single flagellum and they form four main developmental stages: trypomastigotes (with a posterior kinetoplast and an emergent flagellum forming a long undulating membrane); epimastigotes (with an anterior kinetoplast and an emergent flagellum forming a short undulating membrane); promastigotes (with an anterior kinetoplast and a short emergent flagellum, but no undulating membrane); and amastigotes (with a kinetoplast but no emergent flagellum or undulating membrane). Many trypanosome species are parasitic only in insects whereas others are transmitted by insect vectors to a wide range of vertebrate hosts. Three main groups infect the blood and/or tissues of humans and animals causing severe clinical diseases: including the leishmanias which develop in the foregut of insect vectors and are transmitted via bite to the tissues of vertebrate hosts (e.g. sand flies transmit *L. Sauroleishmania* spp. to lizards).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Discoba (diverse group supported robustly by molecular studies)
Phylum: Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass: Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order: Trypanosomatida (parasitic, single anterior flagellum, often forming undulating membrane)
Family: Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)
Genus: *Leishmania* (*Sauroleishmania*) (vector-borne tissue parasites)
Species: various species infect lizards

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia	Order: Trichomonadida (3-5 anterior flagella plus	Monocercomonadidae (costa absent, most	*Histomonas*	birds (gut, liver)	direct (f-o)

(with parabasal body)	recurrent flagellum)	without undulating membrane)	*Dientamoeba*	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans comprise a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)
	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*).

Trypanosomatids are dixenous (2-host) parasites with indirect transmission cycles between vertebrates and invertebrate vectors. *Leishmania* spp. form amastigote stages in the tissues of their vertebrate hosts, and promastigote stages in invertebrate haematophagous vectors. Species of *Leishmania* in lizards appear to be restricted to the Old World, with the exception of *L. henrici* in the Caribbean. The genus *Sauroleishmania* was originally proposed to include *Leishmania* species infecting reptiles (lizards) rather than mammals, but molecular phylogenetic studies have indicated that it be ranked at the subgeneric rather than the generic level. Nonetheless, there appear to be many differences between leishmanial parasites of mammals and reptiles, including variations in host range and specificity (involving both vertebrate and invertebrate hosts), developmental cycles, modes of transmission, tissue tropism, parasite antigens, isoenzymes and nucleic acids.

***Leishmania* species**	**Hosts**	**Location**	**Vectors**	**Distribution**
Subgenus: *Sauroleishmania*				
L. (*S.*) *adleri*	lacertid (fringe-toed lizard, green lizard, southern long-tailed lizard); Rodentia: cricetid (golden hamster)	blood, skin	Diptera: psychodid (*Sergentomyia clydei*)	Africa
L. (*S.*) *agamae*	agamid (steppe agama, roughtail rock agama)	blood	Diptera: psychodid (*Phlebotomus papatasi, caucasicus, Sergentomyia sintoni*)	Mediterranean
L. (*S.*) *ceramodactyli*	gekkonid (Doria's comb-fingered gecko)	blood	Diptera: psychodid (*Phlebotomus papatasi, caucasicus, Sergentomyia sintoni*)	Mediterranean
L. (*S.*) *gymnodactyli*	gekkonid (comb-toed gecko, Caspian bent-toed gecko, grey thin-toed gecko, frog-eyed gecko), agamid (steppe agama, Caucasian agama, secret toadhead agama, sunwatcher toadhead agama, Lichtenstein's toadhead agama, Radde's toadhead agama), anguid (sheltopusik), lacertid (small-spotted lizard, sand racerunner, striped racerunner, reticulate racerunner, rapid racerunner, Aralo-Caspian racerunner), scincid (ribbon-sided skink, Schneider's skink, golden grass skink); Serpentes: colubrid (common cliff racer, spotted desert racer, dwarf racer), psammophiid (Schokari sand racer), viperid (saw-scaled viper)	blood	Diptera: psychodid (*Phlebotomus papatasi, caucasicus, Sergentomyia sintoni, arpaciensis, clydei, grecovi*)	Russia
L. (*S.*) *hemidactyli*	gekkonid (Gleadow's house gecko, Brooke's house gecko)	blood		India
L. (*S.*) *hoogstraali*	gekkonid (Mediterranean house gecko)	blood	Diptera: psychodid (*Sergentomyia clydei*)	Sudan
L. (*S.*) *platycephala*	gekkonids (flathead leaf-toed gecko, Barbour's gecko)	red and white blood cells	Diptera: psychodid (*Sergentomyia* sp., *Lutzomyia vexator*)	Tanzania
L. (*S.*) *tarentolae*	gekkonids (Moorish gecko, white-spotted wall gecko, Kotschy's gecko)	red and white blood cells, spleen	Diptera: psychodid (*Phlebotomus papatasi, Sergentomyia antennata* (*minuta*),	Mediterranean

			parroti)	
L. (*S.*) *zuckermani*	gekkonids (Turner's thick-toed gecko)	red blood cells -		South Africa
Incertae sedis (uncertain subgeneric placement)				
L. chamaeleonis	chamaeleonid (common chameleon, Cape dwarf chameleon)	cloaca, intestines		Middle-East, Africa
L. davidi	teiid (rainbow whiptail)	cloaca, large intestines		Americas
L. gulikae	agamid (Caucasian agama)	blood		Middle-East
L. henrici	dactyloid (leopard anole, green anole)	blood, cloaca		Caribbean
L. nicollei (syn. *L. helioscopi, phrynocephali*)	agamid (steppe agama, sunwatcher toadhead agama, secret toadhead agama)	blood		Middle-East
L. senegalensis	phyllodactylid (ringed wall gecko)	blood		Africa
L. sofieffi	agamid (spotted toadhead agama, secret toadhead agama)	blood		Middle-East
L. zmeevi	lacertid (reticulate racerunner, Aralo-Caspian racerunner)	blood	Diptera: psychodid (*Phlebotomus papatasi, Sergentomyia sintoni*)	Russia

Parasite morphology: Sauroleishmanias form 2 different types of developmental stages: amastigotes and promastigotes. Amastigotes are small spherical cells ranging from 1-5 µm in diameter (they are among the smallest eukaryotic (nucleated) cells known). They are located intracellularly in vacuoles within the cytoplasm of host cells, sometimes occurring in groups of up to 3-10 cells. Amastigotes are not flagellated but they contain a flagellar sac and a non-emergent vestigial flagellum. They have a rounded central nucleus and a smaller adjacent kinetoplast (containing mitochondrial DNA) surrounded by a small ring of vacuolated cytoplasm. Promastigotes are elongate slender cells ranging in size from 5-20 x 1.5-3.5 µm. They occur as extracellular stages and have a single emergent flagellum that undulates freely from the anterior cell surface (it is not recurrent and does not form an undulating membrane). The flagellum arises from a small dense kinetoplast located anterior to the central cell nucleus. Promastigotes develop from short procyclic forms to long thin metacyclic forms, sometimes involving intermediary forms described as thin nectomonads with short flagella, small leptomonads with long flagellum and short stout haptomonads with short leaf-shaped flagella attached to the vector gut wall.

Site of infection: In reptiles, promastigotes may be found extracellularly in the bloodstream while amastigotes occur as intracellular stages in circulating blood cells (erythrocytes, thrombocytes, monocytes) or phagocytes (macrophages, histiocytes and precursors) within host tissues (skin or viscera). A total of 17 parasites species have been described in reptilian hosts, including 42 lizard species from 9 families (agamids, lacertids, gekkonids, teiids, chamaeleonids, dactyloids, phyllodactylids, scincids) and 5 snake species from 3 families (colubrid, psammophiid, viperid). In vectors, promastigotes develop within the gut either in the posterior station (hypopylarian) or the anterior station (peripylarian). Some 9 species of psychodid sandflies have been found to act as vectors for reptilian leishmanias, including 2 *Phlebotomus* spp., 6 *Sergentomyia* spp. and one *Lutzomyia* sp.

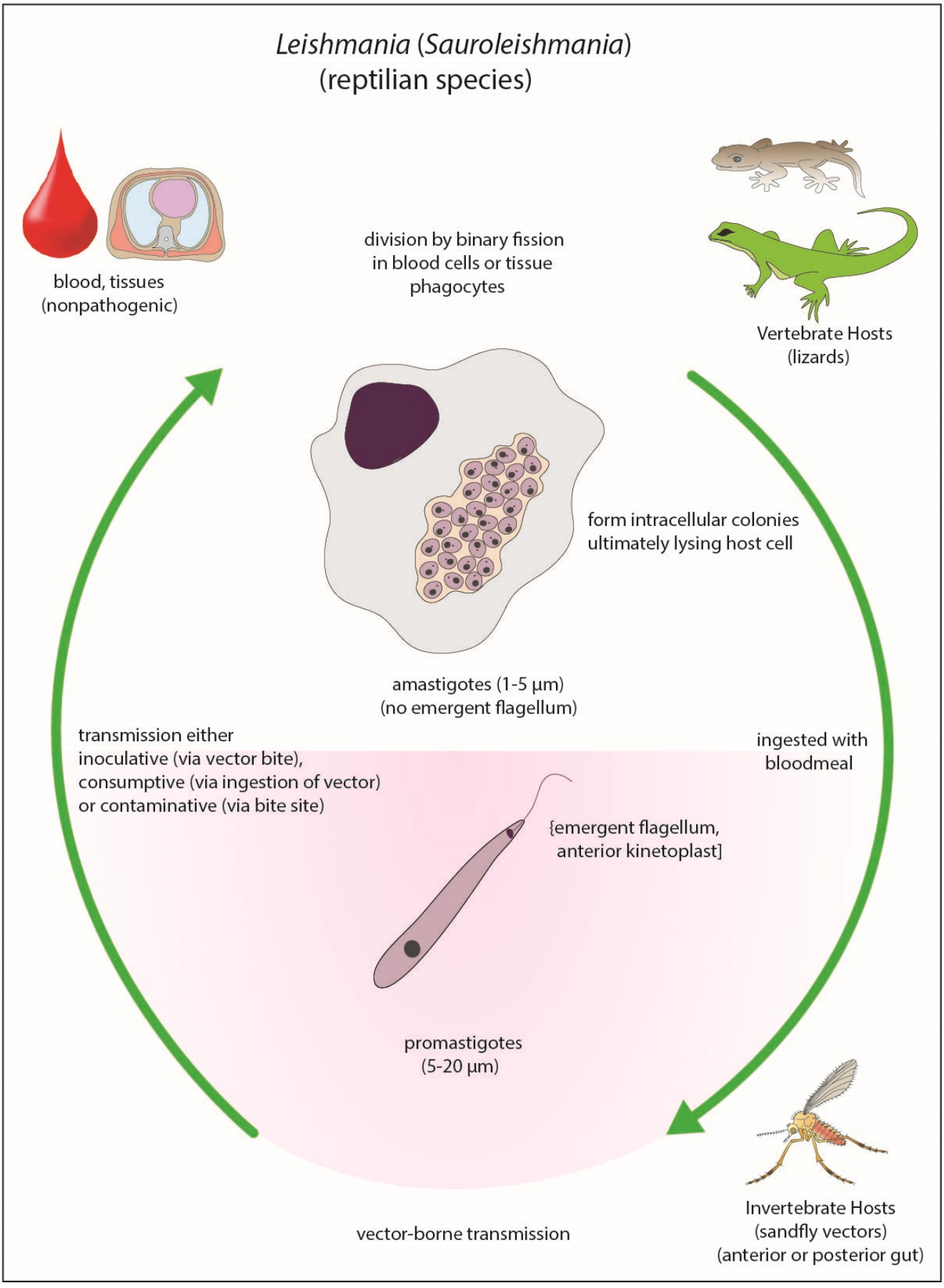
Pathogenesis: Metacyclic infective promastigotes that invade vertebrate host tissues have numerous lipophosphoglycan molecules on their membranes which enables them to resist lysis as well as to adhere to macrophage membranes facilitating their phagocytosis. They transform into amastigotes within parasitophorous vacuoles formed by fusion of phagosomes with lysosomes where they are resistant to digestion by lysozymal enzyme. The amastigotes feed, grow and multiply by asexual division, ultimately rupturing the host cell to release new infective stages**.** Despite their eventual destructive effects on host cells, they do not cause enough cumulative damage to manifest as clinical disease and infections in reptiles are asymptomatic (subclinical at the very least). Experimental transmission studies have shown that the parasites often persist in small numbers and/or in cryptic locations as latent or chronic infections.

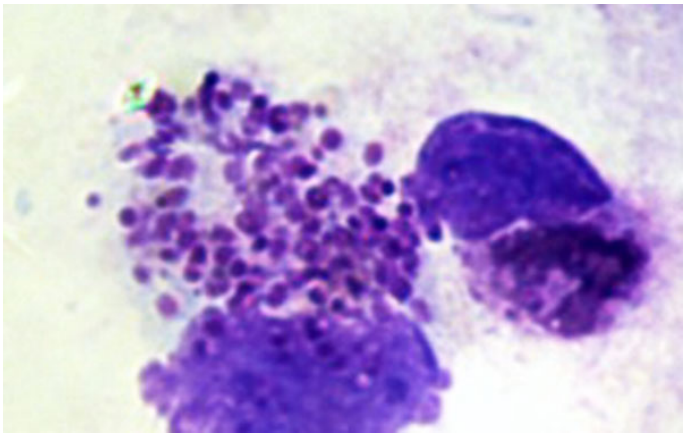
Developmental cycle and mode of transmission: *Sauroleishmania* spp. have heteroxenous (2-host) life-cycles involving blood and tissue stages in reptiles being taken up by haematophagous (blood-feeding) sandfly vectors where infective stages develop in the gut. Vector-borne transmission to reptiles occurs by the ingestion of vectors (consumptive transmission), via contamination by vector faeces (stercorarian transmission) or by vector bite (inoculative transmission). All vectors for reptilian leishmanias belong to the subfamily Phlebotominae in the dipteran family Psychodidae. These sand flies are small (2.0-3.5 mm long) and have lanceolate wings and tiny hairs covering their bodies. Adult female flies feed on vertebrate blood to obtain the nutrients required to complete their reproductive cycles. Amastigotes ingested during feeding transform in the gut into promastigotes which multiply by binary

fission (development from procyclic to metacyclic forms sometimes proceeding through several intermediary stages). Development in the vector gut occurs either in the posterior station (hypopylarian) or anterior station (peripylarian). Promastigotes of hypopylarian species multiply predominantly in the abdominal hindgut, thus implicating transmission by vector faeces or by ingestion of the vector. Promastigotes of peripylarian species multiply primarily in the abdominal midgut and then move forward to the thoracic midgut, oesophagus, pharynx and head, thus implicating transmission by vector bite. Metacyclic promastigotes invading reptiles are taken up by phagocytic cells where they transform into amastigotes and undergo asexual proliferation.

Differential diagnosis: Most infections in reptiles have been detected by isolating promastigotes in culture, indeed many species are only known from cultural forms (which are very similar). Promastigotes grow well *in vitro* in cultures containing enriched media (particularly nutrient agar-blood mixtures). Cultures may be seeded with samples of heart blood, peripheral blood or lacerated tissues from reptiles, as well as gut contents of sandfly vectors. Amastigotes may sometimes be detected by the microscopic examination of blood smears, tissue impression smears or histological sections after staining with Giemsa or Leishman's stains. Several immunoserological tests (fluorescent-antibody tests) have been developed to detect host antibodies against infection in some reptiles, but host responses to cutaneous infections are often poor and most tests could not distinguish between recent and chronic infections. Parasite isolates have been analysed using various protein characterization techniques, including isoenzyme analyses, polyacrylamide gel electrophoresis and immunoblotting, but they have not been adapted for diagnostic use. Modern molecular characterization techniques have used the polymerase chain reaction (PCR) to amplify specific gene sequences (parasite DNA) from host samples; including small subunit (18S) ribosomal RNA (rRNA), internal transcribed spacer regions, and RNA polymerase II large subunit genes.

Treatment and control: Infections in reptiles are asymptomatic and do not require treatment. Various preventive measures may be used in captive reptile colonies to minimize the risks of spreading infections by protecting animals from sandflies using physical barriers, chemical insecticides or biological control programs.


Leishmania (*Sauroleishmania*)
(reptilian species)
blood, tissues
(nonpathogenic)
division by binary fission
in blood cells or tissue
phagocytes
Vertebrate Hosts
(lizards)
form intracellular colonies
ultimately lysing host cell
amastigotes (1-5 µm)
(no emergent flagellum)
transmission either
inoculative (via vector bite),
consumptive (via ingestion of vector)
or contaminative (via bite site)
ingested with
bloodmeal
{emergent flagellum,
anterior kinetoplast]
promastigotes
(5-20 µm)
Invertebrate Hosts
(sandfly vectors)
(anterior or posterior gut)
vector-borne transmission

	
Sauroleishmania amastigotes in lizard tissues	*Sauroleishmania* promastigote in sandfly gut

***Ichthyobodo* (= *Costia*)**
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Ichthyobodonids include members of the genus *Ichthyobodo* (syn. *Costia*) which have two heterodynamic flagella and are parasitic on fish.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Discoba (diverse group supported robustly by molecular studies)
Phylum: Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass: Prokinetoplastina (small group supported by molecular studies)
Family: Ichthyobodonidae (2 heterodynamic flagella arising from pocket that continues as a groove)
Genus: *Ichthyobodo* (= *Costia*) (parasitic on gills/skin of fish)
Species: *I. necator* (*C. necatrix*) (causes surface lesions on fish)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae (anterior adhesive disc)	*Cochlosoma*	birds (gut)	direct (f-o)

Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans comprise a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)
	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina

represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*). Species belonging to the genus *Ichthyobodo* are common cosmopolitan ectoparasites of fishes; mostly on freshwater fish (esp. farmed and ornamental species) but they have also been observed on salmonids reared in estuaries as well as on strictly marine species. Ectoparasitic species were originally assigned to the genus *Bodo*, but were subsequently transferred to a new genus *Costia* which unfortunately was found to be preoccupied so they were transferred to another new genus *Ichthyobodo*. Initially, all infections were thought to be due to the species *Icthyobodo necator* (syn. *Costia necatrix*), but recent studies suggest there are two species in freshwater fish (differing in size) and another in marine fish (different attachment disc and cytostome process). Molecular characterization studies performed on parasite isolates have identified multiple lineages, strains and substrains, and it has been suggested that there may be at least 9 putative 'genotypic' species.

Parasite species (and clade)	**Mastigote length (µm)**	**Hosts**	**Location (disease)**	**Distribution**
Family BODONIDAE (comprising free-living and parasitic genera)				
Genus *Ichthyobodo* (ectoparasites with free-swimming stage alternating with attached feeding stage)				
I. necator (syn. *Bodo necator, Costia necatrix*) (= lineage A, sp. I)	5-20	freshwater Salmoniformes: salmonid (brown trout, rainbow trout, brook trout, Atlantic salmon, chum salmon, pink salmon, sockeye salmon, masu salmon); Acipenseriformes: acipenserid (sterlet sturgeon); Anguilliformes: anguillid (European eel); Cypriniformes: cyprinid (common carp, goldfish, tench, barbs); Cyprinodontiformes: poeciliid (green swordtail, platyfish, guppy, molly); Cichliformes: cichlid (banded tilapia, blackchin tilapia, large African mouthbreeder, Mozambique tilapia, dwarf cichlid, southern mouthbrooder); Perciformes: percid (silver perch, European perch, pike-perch, spotted wolffish); Scorpaeniformes: gasterosteid (three-spined stickleback); Moroniformes: moronid (sunshine bass); Siluriformes: ictalurid (channel catfish); marine Clupeiformes: clupeid (scaly mackerel); Gadiformes: gadid (Atlantic cod); Mugiliformes: mugilid (mullet); Pleuronectiformes: paralichthyid (Japanese flounder), pleuronectid (turbot, European plaice, winter flounder)	skin, fins, gills (epidermal degenerative changes)	worldwide
I. hippoglossi	9-14	marine Pleuronectiformes: pleuronectid (Atlantic halibut)	skin, gills	Europe
I. nitschei (syn. *Tetramitus*) (= lineage B2.1?, spp. VII, VIII)		freshwater Cypriniformes: cyprinid (goldfish); Siluriformes: ictalurid (channel catfish); marine Pleuronectiformes: paralichthyid (Japanese flounder)	skin	Eurasia
I. pyriformis (syn. *Costia*) [may be small form of *I. necator*]	9-14	freshwater Salmoniformes: salmonid (rainbow trout, brook trout, golden trout, char)	skin	North America
I. salmonis (= lineage B1, sp. II)	9-13	euryhaline Salmoniformes: salmonid (Atlantic salmon)	gills, skin	Norway
Un-named isolates				
Ichthyobodo spp.	8-14	marine Salmoniformes: salmonid (Atlantic salmon, chinook salmon, chum salmon); Tetraodontiformes: tetraodontid (tiger puffer); Pleuronectiformes: paralichthyid (olive flounder, summer flounder), pleuronectid (European plaice, winter flounder, common dab, Atlantic halibut), scophthalmid (turbot); Gadiformes: gadid (Atlantic cod, haddock); Gobiiformes: gobiid (two-spotted goby); Centrarchiformes: oplegnathid (spotted	skin, fins, gills	worldwide

		knifejaw); Clupeiformes: dorosomatid (Bali sardinella); Labriformes: labrid (corkwing wrasse, ballan wrasse, cuckoo wrasse, goldsinny wrasse, rainbow wrasse, rock cook); Moroniformes: ephippid (Atlantic spadefish), moronid (European seabass); Mugiliformes: mugilid (flathead grey mullet, Lebranche mullet); Scorpaeniformes: gasterosteid (three-spined stickleback), scorpaenid (black rockfish); Spariformes: sparid (gilt-head bream)		
Ichthyobodo sp. (= lineage B1, sp. III)	9-10	euryhaline Salmoniformes: salmonid (Japanese masu salmon, chum salmon)	fins, skin	Asia
Ichthyobodo sp. (= lineage B3, sp. IV)		marine Gadiformes: gadid (Atlantic cod)	gills, skin	Europe
Ichthyobodo sp. (= lineage B2.2, sp. V)		freshwater Moroniformes: moronid (hybrid striped bass)	skin, gills	North America
Ichthyobodo sp. (= lineage B2.2, sp. VI)		freshwater Cichliformes: cichlid (dwarf cichlid)	skin	North America (ex. Brazil)
Ichthyobodo sp. (= sp. IX)		freshwater Salmoniformes: salmonid (rainbow trout)	skin	North America

Parasite morphology: *Ichthyobodo* spp. form 2 morphologically different developmental stages: free-swimming trophozoites and attached ectoparasitic trophonts. Both forms contain a long tubular mitochondrion with numerous nucleoids so there are many small kinetoplasts scattered throughout the cells. The free-living forms are highly motile, swimming with a rapid-spinning but non-directional manner. They range in size from 8-20 x 9-16 µm and are oval-spherical in shape (sometimes comma-shaped) with a small anterior cytostomal protrusion (nose- or lip-like). Most cells are biflagellated with 2 heterodynamic (unequal) flagella arising from a flagellar pocket under the cytostomal protrusion that opens antero-ventrally into a longitudinal groove extending along the cell. One flagellum is short while the other is long and recurrent (trailing) but not adherent to the cell body (it does not form an undulating membrane). Early reports of cells with 4 flagella were considered to be predivisional forms, but recent studies have described *I. salmonis* cells with 4 flagella (comprising 2 pairs of unequal length). The cell is uninucleate with a single central rounded nucleus surrounded by several large pale vacuoles. A pale bent rod-like structure (axostyle) runs along the cell margin from the anterior protrusion to the posterior body. The cytoplasm contains numerous kinetoplasts varying in number within and between species: e.g. 25-113 for *I. necator* and 23-68 for *I. salmonis*. The attached forms (trophozoites) are non-motile ectoparasites anchored to host cells by small attachment discs at their anterior pointed ends through which a cytostome canal supported by microtubules penetrates into the cytoplasm. The attachment disc often differs between freshwater and marine isolates (being smooth in seawater and ridged in freshwater), but it is not known whether these are intra- or inter-specific variations or related to habitat. The cells range in size from 10-17 x 5-11 µm and are pyriform in shape with the attached pointed end containing the axostyle which extends posteriorly along the cell margin lateral to the flagellar pocket. The cells contain inconspicuous (non-emergent) flagella located in the longitudinal groove which is readily seen and sometimes forms a Y-shape with the flagellar pocket. Trophozoites appear to be elastic and often elongate stretching the cytostome to the midbody. The cell membrane comprises 2 membranous layers with a middle fibrillar layer, and the nuclear membrane also with 2 layers and single nucleolus. The cytoplasm contains numerous kinetoplasts varying in number: e.g. 52-87 for *I. necator* and 21-46 for *I. salmonis*. While multiple species may exist according to genotypic studies, the morphotypic differentiation of species is difficult due to the pleomorphy of both free and attached stages. Recent studies have shown that marine *I. salmonis* cells are generally thinner than freshwater *I. necator* cells, their attachment region is smooth rather than jagged, and they possess 2 lateral spine-like projections.

Site of infection: Free-living stages swim around in the water column and may browse over substrates and sediments. The attached stages are ectoparasitic on fish and may be found on the gills (usually on the tips of secondary gill lamellae) and skin (often on the cuff of skin sheltered by the operculum, the pectoral and pelvic fins, and the area adjacent to the dorsal fin – trophozoites not normally found anterior to operculum). Infections have occasionally been reported in association with fish roe, and there are rare reports of flagellated cells feeding on detached decaying cells and scales in tanks and ponds (one worker even suggesting they were saprophagous stages). *Ichthyobodo* spp. are common ectoparasites on fish; frequently found on freshwater fish (farmed and ornamental species) but also on salmonids reared in estuaries as well as on strictly marine species. Their taxonomic classification is complicated as phenotypic studies (parasite morphology, host occurrence) suggest the existence of several species, while genotypic studies (gene sequences) have identified multiple lineages, strains and substrains, so far suggesting that 9 species may exist (most un-named). To date, infections have been detected in over 50 species of fish, including 19 species of freshwater fish belonging to 7 families in 7 orders, and 31 species of marine fish belonging to 16 families in 12 orders.

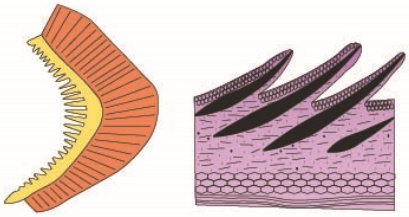
Pathogenesis: *Icthyobodo* spp. feed on epithelial tissues by attaching to cells, penetrating them with a cytostomal canal supported by tubular fibrils and ingesting cell contents, and possibly even secreting digestive enzymes or toxic substances. Infections may cause clinical disease in fish (known as ichthyobodiosis, formerly costiasis) characterized by skin irritation, excess mucus production, flashing and rubbing behaviours and respiratory difficulties. Skin infections may lead to epithelial hyperplasia, Malpighian cell hyperplasia, goblet cell depletion, mucus secretion, cell necrosis, oedema, spongiosis, cloudy greyish discolourations, vacuolization and sloughing of the epidermis and damaged fins. Heavily infected fish often scrape themselves against substrates and rub against immersed objects or the sides of tanks. Gill infections may lead to epithelial hyperplasia, necrosis, mucus secretion, oedema, clubbing of filaments and lamellae, blood vessel collapse, melanomacrophage infiltrates and breathing difficulties. Heavily infected fish often swim near the surface, have difficulty maintaining upright position and swim erratically with occasional 'flashing' behaviour (rolling over exposing pale bellies). Cumulatively, infected fish become lethargic, listless, anorexic, and even emaciated before dying (most deaths due to osmoregulatory problems with haemodilution. Fish may become heavily infected within 1-2 weeks of infection and mortalities peak around 4-8 weeks. Disease is usually more severe in young fish, in malnourished fish, and in stressed fish (due to crowding, capture, translocation, competition with older fish or sudden changes in water quality, especially warmer water temperatures). The parasites are able to survive a wide range of environmental conditions, including temperature, salinity and pH ranges. They may cause significant problems in the culture of young salmonids and cyprinids, especially in hatcheries where fish occur in high numbers, and outbreaks are frequently associated with aquaria, culture ponds and fish in cage cultures.

Developmental cycle and mode of transmission: The parasites have simple direct life-cycles involving free-swimming stages that actively locate fish hosts and attach to their external surfaces to feed. Under favourable conditions, free-living stages divide by longitudinal binary fission (predivision stages are usually larger and may have up to 4 flagella). Studies have shown that these motile stages multiply rapidly when water temperatures are between 10-25°C and that cells die at temperatures above 30°C. It has been suggested that cells may encyst under adverse environmental conditions to facilitate survival, and a few studies have reported inert non-flagellated stages when water temperatures dropped below 8°C, but typical environmentally-resistant membrane-bound cysts have not been observed. When in contact with fish hosts, free-swimming stages use their flagella for site selection and then attach using small flat ventral discs through which cytostomal connections are made to the host cell cytoplasm. Feeding trophozoites detach when replete or disturbed and flagella emerge or develop from their flagellar pockets and longitudinal grooves to restore motility. Infections are therefore water-borne with contamination by free-swimming (and dividing) stages arising from the surfaces of infected fish. The potential sources of infection depend greatly on the host specificities of the *Ichthyobodo* spp. which have yet to be determined. Some of the putative species have only been found in a few related hosts (stenoxenous), while others have been found in a broader range of hosts (euryxenous), albeit limited to sympatric species within specific aquatic habitats (freshwater, euryhaline or marine). Nonetheless, aquaculture facilities may become contaminated by the ingress of feral fishes, and some workers think that amphibian larvae (salamanders, frogs, toads) may also be potential sources of infection. Outbreaks are common in recirculating aquaculture systems, particularly hatcheries where fish are reared in small crowded conditions. Fish also appear to be more susceptible to clinical disease when stressed (and thus immuno-compromised) due to capture, handling, crowding, poor diet, and sudden changes in environment and water quality. Little is known about the immunology of infections although it is thought that recovered fish develop some degree of protective immunity against subsequent disease.

Differential diagnosis: Infections may be indicated by clinical signs of skin irritation, greyish cloudy lesions and behavioural changes, but must be confirmed by the microscopic detection of trophozoites in clinical samples (skin scrapings, mucus, gill snips). Specimens may be detected in wet mounts, fixed smears or histological sections, particularly after staining with iron haematoxylin, carmine or periodic acid-Schiff's reagent, although trophozoites are fragile and may rupture during processing. Molecular biological techniques have been used to detect and characterize isolates following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA and internal transcribed spacer regions). However, further studies are required to determine whether the different lineages or strains detected represent discrete species or species-complexes.

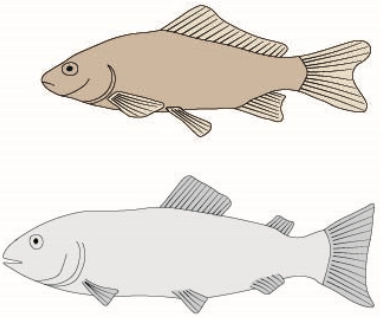
Treatment and control: Clinical infections in cultured and aquarium fish have been successfully treated using chemical bath treatments (formalin, acetic acid, copper sulphate, malachite green, pyridylmercuric acetate) as well as foodstuffs medicated with parasiticidal drugs (metronidazole, secnidazole, triclabendazole), although over 30 other drugs proved ineffective. Various control measures have also been used to decontaminate holding facilities by treating water with chemicals (methylene blue, quinine hydrochloride, malachite green, potassium permanganate, aureomycin, globucid, lysol) or draining, drying and disinfecting ponds or tanks with quicklime or chloride of lime before restocking. Several studies also eliminated parasites from tanks by raising the water temperature to 32°C for several days. Care should also be taken to avoid stressful and crowded conditions to reduce the risk of severe infections.

Ichthyobodo (syn. *Costia*)

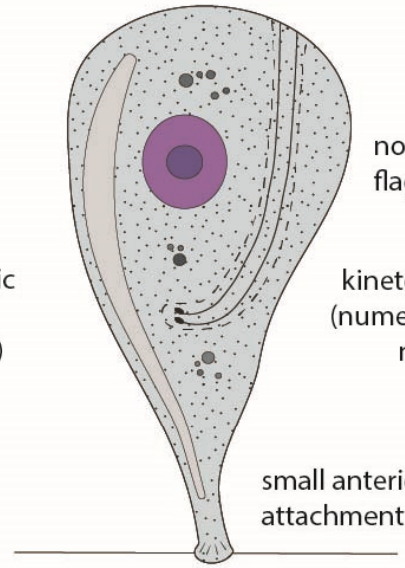


gills, skin
(lesions, respiratory disorders, emaciation)

multiply by longitudinal binary fission



Vertebrate Hosts
(mainly freshwater fish)



no emergent flagella

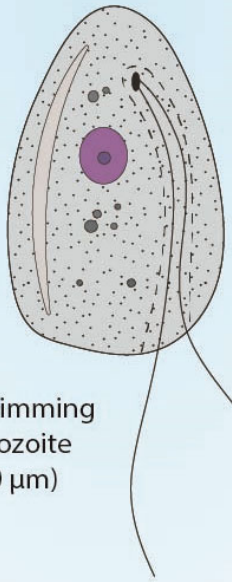
ectoparasitic trophont (10-17 µm)

kinetoplast fragmented (numerous mitochondrial nucleoids)

small anterior attachment disc

attach to host

detach from host



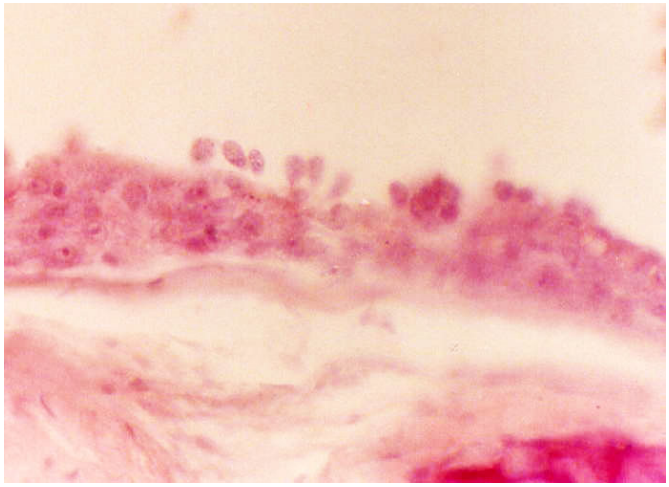
longitudinal axostyle

2 heterodynamic (unequal) flagella

flagellar pocket continues as longitudinal groove

free-swimming trophozoite (5-20 µm)

direct transmission via trophozoites actively seeking hosts in water column



Ichthyobodo trophonts



Ichthyobodo trophont

Cryptobia
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Parabodonids include members of the genus *Cryptobia* which are parasitic for fish, being epizoic on the gills and skin or endozoic in the gut.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Discoba (diverse group supported robustly by molecular studies)
Phylum: Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass: Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order: Parabodonida (biflagellated, recurrent flagellum attached or free)
Family: Parabodonidae (Cryptobiidae, Trypanoplasmatidae) (epizoic or endozoic in invertebrates and/or fish)
Genus: *Cryptobia* (parasitic on gills/skin of fish, direct cycles)
Species: various species cause infections in fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae	*Cochlosoma*	birds	direct (f-o)

		(anterior adhesive disc)		(gut)	
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans comprise a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)
	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic

and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*). The genus *Cryptobia* was originally proposed for biflagellated organisms in the reproductive systems of snails, but was later expanded to include similar organisms in other invertebrates as well as some aquatic vertebrates. The genus *Trypanoplasma* was originally proposed for biflagellated organisms in the blood of freshwater fishes and the crops of leeches. Some workers consider *Trypanoplasma* to be a junior synonym of *Cryptobia*, while others regard them as separate subgenera. Recent molecular phylogenetic studies have suggested that they should continue to be considered as separate genera, with epizoic/endozoic species (thought to undergo direct transmission) being retained within the genus *Cryptobia,* and haemozoic species (thought to undergo indirect transmission via leech vectors) forming the genus *Trypanoplasma* (note that many species have been shuffled between these genera). The genus *Cryptobia* is an enigmatic diverse assemblage of species described from a wide variety of hosts (including marine and freshwater fish, terrestrial and aquatic snails, platyhelminths, chaetognaths, leeches, reef geckos, and mole crickets) as well as several free-living aquatic representatives. [Note that molecular characterization studies have led to the transfer of several *Cryptobia* spp. originally described as free-living bactivorous zooflagellates from anoxic marine sediments to special excavate taxa (including *Carpediomonas* and *Jakoba*)]. Most *Cryptobia* infections in fish appear to be nonpathogenic, but several species have been associated with diseases of the gills, guts and sometimes internal organs.

***Cryptobia* species**	**Mastigote length (µm)**	**Hosts**	**Location (disease)**	**Distribution**
Non-haematozoic (ectoparasitic on gills or body surface, or endoparasitic in intestines), direct transmission				
C. agitans	5-12	freshwater Perciformes: centrarchid (bluegill, white crappie, black crappie); Cypriniformes: cyprinid (bighead carp, silver carp, grass carp, goldfish)	gills (cryptobiosis)	Eurasia, Africa, North America
C. agitata	5-8	freshwater Cypriniformes: cyprinid (bighead carp, silver carp)	gills, body	China
C. antedonae		marine Crinoidea: antedonid (rosy feather star)	coelomic fluid	Europe
C. bialata		brackish water (free-living)		Australia
C. branchialis (syn. *C. agitata, concava, rebae, indica*)	12-23	freshwater/estuarine Cypriniformes: cyprinid (carp, grass carp, bighead carp, silver carp, goldfish, olive barb, golden shiner); Cichliformes: cichlid (Nile tilapia); Gonorynchiformes: channid (milkfish); Perciformes: centrarchid (white crappie, black crappie), percid (fantail darter); Siluriformes: clariid (African sharptooth catfish), ictalurid (channel catfish, brown bullhead); Spariformes: sparid (sea bream)	gills, body (cryptobiosis)	Europe, Asia, Africa, North America
C. carinariae		marine Gastropoda: carinariid (*Carinaria mediterranae*)	spermatheca	Europe
C. carassii		freshwater Cypriniformes: cyprinid (goldfish)	body	Europe
C. catastomi		freshwater Cypriniformes: catostomid (white sucker)	body	North America
C. congeri		marine Anguilliformes: congrid (European conger)	stomach	Atlantic
C. coryphaenoideana		marine Gadiformes: macrourid (Pacific grenadier)	stomach	North America
C. dahli	10-20	marine Scorpaeniformes: cyclopterid (lumpfish)	gut, bladder (nonpathogenic)	Europe
C. dendrocoeli		freshwater Platyhelminthes: dendrocoelid (*Dendrocoelum lacteum*), planariid (*Planaria albissima*)	gut	Europe
C. desertorum		terrestrial Gastropoda: helicid (*Helix desertorum*)	seminal vesicle	Africa
C. eilatica		marine Spariformes: sparid (seabream)	gills	Red Sea
C. geccorum	15-23	terrestrial Sauria: sphaerodactylid (reef gecko)	gut	North America
C. gryllotalpae	10-26	terrestrial Orthoptera: gryllotalpid (European mole cricket)	intestines	Europe

C. helicis		terrestrial Gastropoda: polygyrid (*Helix albolabris*, *tridentata*), helicid (*Helix pomatia*), discid (*Helix alternata*)	seminal vesicles	Europe
C. helicognae		terrestrial Gastropoda: helicid (*Helix pomatia*)	seminal vesicle	Europe
C. indistincta		freshwater Cypriniformes: cyprinid (carp)	body	Eurasia
C. innominata		terrestrial Gastropoda: polygyriid (*Triodopsis tridentata*)	spermatheca	Europe
C. intestinalis	8-19	marine Spariformes: sparid (bogue)	oesophagus, stomach	Mediterranean, Adriatic
C. isidorae		freshwater Gastropoda: planorbid (*Isidora tropica*)	seminal receptacle	Africa
C. iubilans	19	freshwater Cichliformes: cichlid (Texas cichlid, firemouth cichlid, convict cichlid, Jack Dempsey, blue discus); Siluriformes: clariid (vundu, African sharptooth catfish)	gut, internal organs (weight loss, death)	Mexico, Europe, Africa, North America
C. liberia		brackish water (free-living)		Australia
C. limnorum		freshwater Gastropoda: lymnaeid (*Limnaea stagnalis, palustris*)	seminal vesicle	Europe
C. makeevi		euryhaline Salmoniformes: salmonid (pink salmon, chum salmon)	body, gills	Asia
C. rupestre		terrestrial Gastropoda: helicid (*Helix singula*)	seminal vesicle	Europe
C. sagittae	60-100	marine Sagittoidea: sagittid arrowworm (*Sagitta bipunctata*)	midgut	Atlantic
C. stilbia		marine Argentiniformes: bathylagid (smoothtongue)	stomach	Mexico
C. trematomi		marine Perciformes: notothniid (emerald rockcod)	stomach, intestines	Africa
C. trochearum		terrestrial Gastropoda: helicid (*Helix* spp.)	seminal vesicle	Europe
C. udonellae	12-15	marine Platyhelminthes: udonellid (*Udonella murmanica*)	excretory channels	Russia
C. vaginalis		freshwater Clitellata (leeches): haemopid (*Haemopis sanguisuga*), hirundinid (*Hirudo medicinalis*)	vagina	Europe
C. ventriculi		marine Scorpaeniformes: cyclopterid (lumpfish)	body	Atlantic

Parasite morphology: *Cryptobia* spp. only form one developmental stage: elongate biflagellated trophozoites. These cells have oval-elongate tapering (broader anteriorly) bodies (sometimes ribbon-like) ranging in size from 5-23 x 2-6 μm depending on the species (e.g. *C. branchialis* 7-23 x 2-6 μm, *C. iubilans* 5-12 x 3-6 μm). Trophozoites contain a single central ovoid nucleus and a smaller oval-elongate kinetoplast (containing mitochondrial DNA) located nearby. Adjacent flagellar basal bodies (microtubular complexes) give rise to 2 heterodynamic (unequal) flagella emerging anteriorly from a flagellar pocket, with the shorter anterior flagellum being free, while the longer flagellum is recurrent (trailing) and attached to the cell body for most of its length before extending freely from the posterior end. The recurrent flagellum does not form a permanent undulating membrane, but it draws out the pellicle when it beats giving the appearance of a narrow undulating membrane (in contrast, the recurrent flagellum of *Trypanoplasma* spp. form prominent undulating membranes). Trophozoites also possess a large anterior contractile vacuole for fluid regulation within the cell.

Site of infection: Trophozoites are usually detected in association with aquatic hosts, many being ectozoic on the skin or gills and several being endozoic in the intestines, although some occur in terrestrial invertebrates and a few are free-living in brackish water. [Note that organisms that are endozoic in the blood (= haemozoic) have been transferred to the genus *Trypanoplasma* (and are considered separately in next section)). A total of 34 parasite species have been described from a wide variety of hosts, including 26 species of freshwater fish (from 10 families), 7 species of marine fish (from 6 families), 11 species of terrestrial and aquatic snails (from 6 families), 3 platyhelminth species, 2 leech species, one arrowworm species, one crinoid species, one gecko species and one cricket species.

Pathogenesis: Infections by most *Cryptobia* spp. remain asymptomatic or subclinical, but a few species may cause a mild clinical disease (known as cryptobiosis) involving the gills, skin or alimentary tracts of fish. Trophozoites attach to host epithelia by the tip or free portion of the recurrent flagellum expanding to form a ridged ledge. The parasites feed on solutes and small suspended organic materials in the water column or associated with host mucosal membranes. Infections by *C. branchialis* and *C. agitans* on the skin or gills of fish may cause skin abnormalities, discolourations or deformities, excessive mucus production, scale loss, chronic inflammation, gill congestion, hyperaemia, anaemia, respiratory difficulties, anorexia, weight loss and eventually death (mostly in

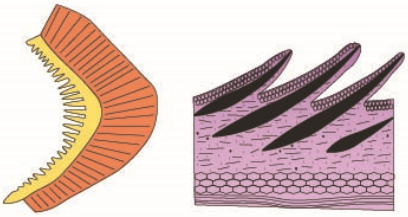
cultured carp, goldfish and catfish). Infected fish are more prone to secondary bacterial infections leading to pale or red skin patches and fin rot. Infections by *C. iubilans* in the stomach and/or intestines of fish can cause multifocal granulomatous inflammation resulting in lethargy, anorexia, stunted growth, emaciation and death (mostly in cichlids). Infections may sometimes spread to visceral organs (liver, spleen, kidney) not by gut perforation, but more likely by intracellular uptake by macrophage-like cells. Infections appear to be more prevalent and severe in young fish, small fish and stressed fish (inadequate diet, poor water quality, crowded conditions and concomitant infections).

Developmental cycle and mode of transmission: Trophozoites multiply asexually by longitudinal binary fission and those of parasitic species have been found to survive free-swimming in aquaria for up to 2 days. Ectozoic species, such as *C. branchialis,* are transmitted directly between fish by the transfer of trophozoites through close body contact or via flagellates in the water column. Infections are particularly prevalent in small aquaria or tanks sharing reticulated water as well as crowded cultures where fish cohabit for protracted periods. Endozoic species, such as *C. iubilans,* are transmitted directly between fish via the faecal contamination of water by trophozoites which subsequently invade new hosts. Experimental studies have also shown that some infections in cichlids may be transmitted by cannibalism when infected tissues are consumed. This led to the suggestion that piscivory or scavenging may be involved in transmission cycles, and it was even proposed that *C. dahli* from lumpfish may be transmitted via prey animals (pelagic crustaceans, annelids, jellyfish) acting as secondary hosts, although this remains to be proven.

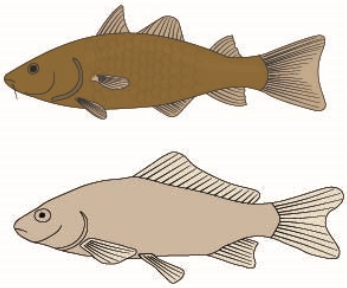
Differential diagnosis: A preliminary diagnosis may be afforded based on clinical signs and history, but infections need to be confirmed by the direct microscopic detection of trophozoites in clinical samples (skin/mucus scrapings, excised gills, gut content, mucosal scrapings, faeces or organ impression smears). Wet mounts may be examined by high-contrast microscopy looking for motile trophozoites, or fixed smears or histological sections may be examined after staining with Giemsa, iron haematoxylin, carmine or periodic acid-Schiff's reagent. Molecular biological techniques have been used to characterize several parasite isolates following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA).

Treatment and control: Ectozoic infections in fish responded reasonably well to bath treatments in various chemicals, including solutions of formalin, malachite green, chloride of lime, copper sulphate, and iron sulphate. However, similar treatments did not work against endozoic infections. Several studies have found that treatment of fish with some nitroimidazoles (dimetridazole) or thiazoles (nitrothiazole) did reduce but not eliminate endozoic parasite burdens. Various preventive measures have been recommended to reduce parasite transmission between fish, including screening new stock, isolating infected individuals for treatment or culling, promptly removing carcases from tanks, disinfecting holding facilities, using treated water and keeping fish healthy in stress-free conditions (by providing proper nutrition and good water quality, avoiding crowding and over-handling, and treating any concomitant infections).

Cryptobia



gills, skin
(discolourations,
congestion)
(some endozoic
in gut)



Vertebrate Hosts
(marine and
freshwater fish)

divide by longitudinal
binary fission

2 flagella
(one subapical,
one recurrent)

subapical
kinetoplast

anterior
contractile
vacuole

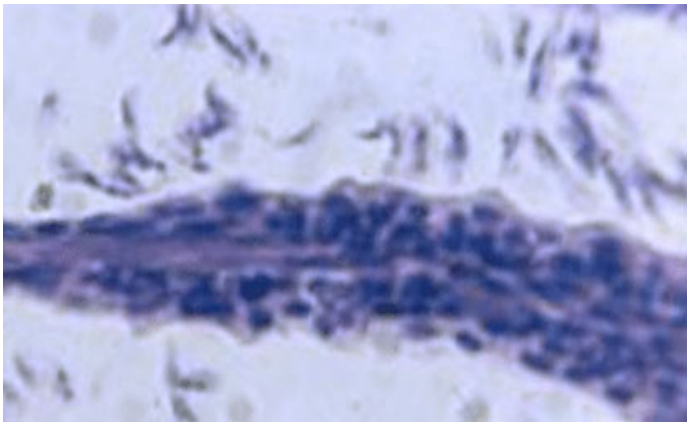
free-swimming stages
become parasitic by
attaching to host cells
using the free portion
of recurrent flagellum

recurrent flagellum attached
to cell body but does not form
an undulating membrane

trophozoite
(5-23 µm)

no cyst formation

direct transmission via trophozoites
actively seeking hosts in water column

	
Cryptobia trophozoites on fish gill	*Cryptobia* trophozoite

Trypanoplasma
(protist: flagellate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). Flagellates are protists that swim using one or more flagella (undulipodia); each arising from a small centriole (basal body, kinetosome) and having a microtubular axoneme core (2+9 configuration). Rather than forming a monophyletic group, flagellates are divided into several disparate groups: metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). Most kinetoplastids are parasitic in vertebrate or invertebrate hosts (some in plants) whereas the remainder are free-living aquatic organisms. All species are characterized by the possession of extranuclear DNA in the form of a kinetoplast, a unique structure formed by massed DNA (circles or lattice) within the single large mitochondrion near the flagellar basal body. The flagellates reproduce by longitudinal binary fission and parasitic species may have simple monoxenous (one-host) or more complicated heteroxenous (two-host) life cycles involving different developmental stages. Parabodonids include members of the genus *Trypanoplasma* which are parasitic in the blood of fishes and are transmitted by leech vectors.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Excavata (with conspicuous ventral feeding groove)
Group: Discoba (diverse group supported robustly by molecular studies)
Phylum: Euglenozoa (flagella inserted in anterior pocket, some heterotrophs, some autotrophs (with chloroplasts))
Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)
Subclass: Metakinetoplastina (large polyphyletic group supported by molecular studies)
Order: Parabodonida (biflagellated, recurrent flagellum attached or free)
Family: Parabodonidae (Cryptobiidae, Trypanoplasmatidae) (epizoic or endozoic in invertebrates and/or fish)
Genus: *Trypanoplasma* (parasitic in blood of fish, indirect cycles involving leeches)
Species: various species cause anaemia in fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Flagellated species have one or more flagella with an internal microtubular core (in a characteristic 2+9 configuration comprising 2 single central microtubules and 9 peripheral doublets) anchored to a submembranous protein structure (known variously as a centriole, basal body, kinetosome or blepharoplast). Many types of flagellated cells have been described and recent phylogenetic studies have classified them into several disparate groups: including the metamonads (amitochondriate flagellates), heteroloboseans (amoeboflagellates), euglenozoans (euglenids and kinetoplastids), stramenopiles (heterokonts), alveolates (dinoflagellates) and cercozoans (biflagellates). While most flagellated protists are free-living organisms swimming and feeding in aquatic environments, representatives of several groups have developed symbiotic relationships with various hosts; some being endoparasitic in vertebrates (notably anaerobic metamonads in tubular organs, and heterotrophic euglenozoans occurring in blood or tissues), and some being parasitic in invertebrates (alveolates in crustacean tissues) (representatives tabulated below).

Higher taxonomy	Class or order	Family	Genera	Hosts (tissues)	Trans-mission*
Supergroup: Excavata (with conspicuous ventral feeding groove)					
Group: Metamonad (amitochondriate flagellates with karyomastigonts)					
Phylum: Fornicata (diplomonads)	Order: Diplomonadida (1-2 karyomastigonts)	Hexamitidae (2 karyomastigonts with binary axial symmetry)	*Giardia*	vertebrates (gut)	direct (f-o)
			Hexamita *Spironucleus*	vertebrates (tissues)	direct (f-o, w)
Phylum: Parabasalia (with parabasal body)	Order: Trichomonadida (3-5 anterior flagella plus recurrent flagellum)	Monocercomonadidae (costa absent, most without undulating membrane)	*Histomonas*	birds (gut, liver)	direct (f-o)
			Dientamoeba	vertebrates (gut)	direct (f-o)
		Trichomonadidae (stout axostyle, costa, undulating membrane)	*Trichomonas*	vertebrates (urogenital tract, gut)	direct (f-o, v)
		Cochlosomatidae	*Cochlosoma*	birds	direct (f-o)

		(anterior adhesive disc)		(gut)	
Group: Discoba (diverse group supported robustly by molecular studies)					
Phylum: Euglenozoa (flagella inserted in anterior pocket, heterotrophs, autotrophs)	Class: Kinetoplastea (heterotrophs, with extranuclear DNA (= kinetoplast) associated with mitochondrion)	Ichthyobodonidae (flagellar pocket continues as groove)	*Ichthyobodo* (= *Costia*)	fish (gills, skin)	direct (w)
		Parabodonidae (epizoic or endozoic)	*Cryptobia*	fish (gills, skin)	direct (w)
			Trypanoplasma	fish (blood)	indirect (v-b)
		Trypanosomatidae (monogenetic forms in insects/plants, digenetic forms in vertebrates & arthropods)	*Trypanosoma*	vertebrates (blood, tissues)	indirect (v-b)
			Leishmania	vertebrates (blood, tissues)	indirect (v-b)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria) (3 groups unified by molecular studies)					
Group: Alveolata (with cortical alveoli)					
Phylum: Dinoflagellata (with unique mesokaryotic nuclei)	Order: Blastodiniales (uninucleate trophonts with chloroplasts)	Oodiniaceae (trophont with rhizoid-like invasive organelle)	*Amyloodinium* *Crepidoodinium* *Piscinoodinium*	fish (skin)	direct (w)
	Order: Syndiniales (multinucleate plasmodial trophonts)	Syndiniaceae (without chloroplasts)	*Haematodinium* *Ichthyodinium*	crustaceans, fish (tissues)	direct (w)
Phylum: Perkinsozoa (parasitic)	Order: Perkinsorida (released trophonts form biflagellated zoospores)	Perkinsidae (incomplete conoid)	*Perkinsus*	gastropods, bivalves (tissues)	direct (w)

*f-o = faecal-oral transmission; v-b = vector-borne transmission, w = water-borne transmission; v = venereal transmission

Euglenozoans comprise a large group of excavates (with ventral feeding groove), most with 1-2 flagella inserted into an anterior pocket. Many species are free-living aquatic autotrophs possessing chloroplasts while others are free-living or symbiotic heterotrophs feeding on solutes, particles and even other organisms. Kinetoplastids are characterised by the possession of a kinetoplast (containing mitochondrial DNA separate from nuclear DNA), a flagellar pocket, basal bodies with three microtubular roots and paraxonemal (paraxial or paraflagellar) rods, and asexual multiplication by longitudinal binary fission. The unique kinetoplast is formed by massed DNA (circles or lattice) usually closely associated with the flagellar basal body (eukinetoplastic) although some species may be polykinetoplastic (with several kinetoplasts) or pankinetoplastic (irregular kDNA) and some mutants even dyskinetoplastic (without a kinetoplast). Two major kinetoplastid groups are recognized: bodonids with two flagella (most being free-living bactivores in aquatic/terrestrial habitats); and trypanosomes with a single flagellum (most being parasites of animals or plants with monoxenous or dixenous life-cycles). Different kinetoplastid assemblages exhibit increasing morphological/ultrastructural complexity in their cellular organization thought to reflect evolutionary grades or clines. Amastigotes are simple non-flagellated cells, choano-, pro- and opistho-mastigotes are flagellated cells with elongate flagella, while epi- and trypo-mastigotes are flagellated cells with undulating membranes. Most kinetoplastids have amastigote and promastigote developmental stages but monoxenous parasites of insects (e.g. *Crithidia*, *Herpetomonas*) do not have more elaborate forms whereas dixenous parasites of plants or animals with invertebrate vectors (e.g. *Trypanosoma, Leishmania*) do have more morphologically complex forms such as epimastigotes and trypomastigotes.

Traditional classification	Molecular classification	Genera	No. spp.	Vertebrate hosts	Transmission (vectors)
F: Trypanosomatidae	SC: Metakinetoplastina F: Trypanosomatidae	*Trypanosoma*	537	mammals, reptiles, frogs, birds, fish	indirect (arthropods, leeches)
		Leishmania	53	mammals, lizards	indirect (sand flies)
F: Bodonidae	SC: Metakinetoplastina F: Parabodonidae	*Cryptobia, Trypanoplasma*	79	fish	direct or indirect (leeches)
	SC: Prokinetoplastina F: Ichthyobodonidae	*Ichthyobodo* (*Costia*)	5	fish	direct

Conventional taxonomic classification systems divide the kinetoplastids into 2 groups: the free-living bi-flagellated Bodonina; and the parasitic uni-flagellated Trypanosomatina. Over 600 species have been described on the basis of multiple phenotypic characters (host occurrence, geographic distribution, vectors, transmission cycles, morphology, development, pathogenicity, culture requirements, etc.). Modern molecular characterization studies, however, have shown that many traditional groups are polyphyletic

and composed of numerous clades. Contemporary phylogenetic classifications recognize 2 main lineages: the Prokinetoplastina represented by 2 diverse genera (*Ichthyobodo* biflagellates ectoparasitic on freshwater and marine fishes, and *Perkinsela* (= *Perkinsiella*) aflagellates endosymbiotic (as parasomes or parasome-like organisms (PLOs)) in amoeba *Paramoeba* and *Neoparamoeba*); and the Metakinetoplastina containing 4 groups, including free-living aquatic eu-bodonids (with one genus *Bodo*), free-living neo-bodonids (with 10 genera, including *Rhynchomonas*), free-living or commensal/parasitic para-bodonids (with 5 genera, including *Cryptobia, Trypanoplasma*), and the parasitic trypanosomatids (containing some 39 genera, including *Trypanosoma* and *Leishmania*). The genus *Cryptobia* was originally proposed for biflagellated organisms in the reproductive systems of snails, but was later expanded to include similar organisms in other invertebrates as well as some aquatic vertebrates. The genus *Trypanoplasma* was originally proposed for biflagellated organisms in the blood of freshwater fishes and the crops of leeches. Some workers consider *Trypanoplasma* to be a junior synonym of *Cryptobia*, while others regard them as separate subgenera. Recent molecular phylogenetic studies have suggested that they should continue to be considered as separate genera, with epizoic/endozoic species (thought to undergo direct transmission) being retained within the genus *Cryptobia,* and haemozoic species (thought to undergo indirect transmission via leech vectors) forming the genus *Trypanoplasma* (note that many species have been transferred between genera). Some 45 *Trypanoplasma* species have been recorded in fish, most in freshwater fish but 4 species in marine fish and one in abalone. The host specificity of all species is uncertain. Several species (*T. salmositica, T. borreli* and *T. bullocki*) cause disease (anaemia and lesions in haematopoietic tissues) and mortality in many fish species throughout the world.

***Trypanoplasma* species**	**Mastigote length (µm)**	**Hosts**	**Location (disease)**	**Vectors**	**Distribution**
Species in freshwater fish					
T. abramidis		Cypriniformes: cyprinid (common bream)	blood		Eurasia
T. acipenseris		Acipenseriformes: acipenserid (beluga sturgeon, bastard sturgeon, sterlet, starry sturgeon, Persian sturgeon, Darya sturgeon)	blood		Eurasia
T. alii		Cypriniformes: cyprinid (red garra)	blood		Iraq
T. al-jaferi		Siluriformes: bagrid (Tigris mystus)	blood		Iraq
T. barbi		Cypriniformes: cyprinid (common barbel)	blood		Europe
T. bliccae		Cypriniformes: cyprinid (white bream)	blood		Asia
T. borreli (syn. *T. carassii, cyprini, keysselitzi, kharbulaewi, tincae*)	20-25	Cypriniformes: cyprinid (common carp, Eurasian carp, crucian carp, grass carp, goldfish, common rudd, red-eye, tench), catostomid (white sucker), leuciscid (common minnow)	blood (anaemia, peritonitis)	Clitellata (leeches): glossiphonid (*Hemiclepsis marginata*), piscicolid (*Piscicola geometra*)	Eurasia, North America
T. capoetobramae		Cypriniformes: cyprinid (Chu sharpray)	blood		Russia
T. cataractae	17	Cypriniformes: cyprinid (longnose dace, eastern blacknose dace, cutlips minnow, central stoneroller)	blood	Clitellata: piscicolid leech (*Cystobranchus virginicus*)	North America
T. catastomi	30-43	Cypriniformes: catostomid (white sucker, longnose sucker)	blood		Canada
T. cavacius	15-20	Siluriformes: bagrid (Gangetic mystus)	blood		India
T. chongqingensis	53	Cypriniformes: cobitid (pond loach)	blood		Asia
T. clariae		Siluriformes: clariid (broadhead catfish)	blood		Asia
T. cotti		Scorpaeniformes: cottid (Baikal yellowfin, longfin Baikal sculpin, vitim sculpin, flathead sculpin, rough sculpin, eurystome sculpin, Godlewski's sculpin, long-spined	blood	Clitellata: piscicolid leech (*Calliobdella punctata*)	Russia

		bullhead)			
T. erythroculteri		Cypriniformes: cyprinid (lake skygazer)	blood		Asia
T. flesi nomen nudum		Pleuronectiformes: pleuronectid (European flounder)	blood		Europe
T. gandei	53	Cypriniformes: cyprinid (macrostome carp)	blood		Africa
T. guernei		Scorpaeniformes: cottid (European bullhead)	blood		Europe
T. gurneyorum		Esociformes: esocid (northern pike), Salmoniformes: salmonid (lake whitefish, lake charr)	blood		Eurasia, North America
T. krishnamurthyi	15-28	Siluriformes: bagrid (Gangetic mystus)	blood		India
T. litoralis		Perciformes: percid (European perch); Scorpaeniformes: cottid Baikal yellowfin)	blood		Russia
T. lomakini		Scorpaeniformes: cottid Baikal yellowfin)	blood		Caspian
T. lynchi	8-25	Scorpaeniformes: cottid (torrent sculpin, coastrange sculpin)	blood		North America
T. makeevi		Salmoniformes: salmonid (chum salmon, pink salmon)	blood, spleen		Russia
T. markewitschi		Anguilliformes: anguillid (European eel)	blood		Europe
T. megalobrami		Cypriniformes: cyprinid (Wuchang bream)	blood		Asia
T. mirabilis		Cypriniformes: cyprinid (Caucasian scraper)	blood		Asia
T. misgurni		Cypriniformes: cobitid (loach)	blood		China
T. neghmei		Pleuronectiformes: pleuronectid (Chilean flounder, fine flounder)	blood		South America
T. ninaekohlyakimovi		Siluriformes: silurid (wels catfish)	blood		Eurasia
T. pseudobagri		Siluriformes: bagrid (yellowhead catfish)	blood		China
T. pseudocaphirhynchi		Acipenseriformes: acipenserid (sturgeon)	blood		Russia
T. rutili		Cypriniformes: cyprinid (roach)	blood		Russia
T. salihi		Siluriformes: (Tigris cat)	blood		Iraq
T. salmositica (syn. *T. lynchi, Cryptobia*)	6-25	Salmoniformes: salmonid (coho salmon, chum salmon, pink salmon, masu salmon, sockeye salmon, brown trout, rainbow trout, brook trout, mountain whitefish); Cypriniformes: cyprinid (longnose dace), catostomid (Klamath largescale sucker); Scorpaeniformes: cottid (torrent sculpin, coastrange sculpin, inland riffle sculpin, paiute sculpin, reticulate sculpin, mottled sculpin, prickly sculpin), gasterosteid (three-spined stickleback)	blood (anaemia, ascites)	Clitellata: piscicolid leech (*Piscicola salmositica*) plus occasional direct transmission	North America
T. sarcocheilichthysi		Cypriniformes: cyprinid (rainbow gudgeon)	blood		China
T. seenghali	15-33	Siluriformes: bagrid (giant river catfish)	blood		India
T. varium		Cypriniformes: nemacheilid (stone loach), cobitid (spined loach, weatherfish)	blood	Clitellata: glossiphonid leech (*Hemiclepsis*	Europe

				marginata),	
T. vidyai	15-30	Siluriformes: bagrid (giant river catfish)	blood		India
T. willoughbii (syn. *T. truttae, valentini*)	20-40	Salmoniformes: salmonid (brown trout, Windermere charr)	blood		Europe
T. zaiki		Scorpaeniformes: cottid (multiradiate sculpin, vitim sculpin, flathead sculpin, big red sculpin, deepwater sculpin)			Russia
Species in marine fish and shellfish					
T. abalonensis	12	Gastropoda: haliotid (variously-coloured abalone)	blood		Asia
T. beckeri	43-165	Scorpaeniformes: cottid (cabezon)	blood	Clitellata: piscicolid leech (*Malmiana diminuta*)	North America
T. bullocki (syn. *T. newingtoniensis*)	11-30	Pleuronectiformes: pleuronectid (winter flounder, American smooth flounder, American plaice), paralichthyid (summer flounder, southern flounder), achirid (hogchoker); Acanthuriformes: sciaenid (Atlantic croaker); Batrachoidiformes: batrachoidid (oyster toadfish); Cyprinodontiformes: fundulid (mummichog, striped killifish)	blood (anaemia)	Clitellata: piscicolid leech (*Calliobdella vivida*)	North America
T. parmae	12-15	Perciformes: pomacentrid (white-ear)	blood		Australia

Parasite morphology: *Trypanoplasma* spp. only form one type of developmental stage, namely biflagellated trophozoites. These cells are elongate slender stages ranging in size from 10-30 x 2-6 μm, with a broader anterior end and a pointed posterior end. They possess a single central rounded nucleus, an elongate-oval anterior kinetoplast (containing mitochondrial DNA) and 2 subapical flagellar basal bodies (microtubule complexes) giving rise to 2 heterodynamic (unequal) flagella from a small flagellar pocket. One flagellum is short and extends free anteriorly, while the other is very long and recurrent (trailing) being attached along the cell body to form an undulating membrane before extending free posteriorly. The trophozoites often exhibit some pleomorphic variation and several studies have recognized several different morphotypes: type I comprising long forms with long undulating membranes; type II being intermediary forms with small undulating membranes; and type III apparently being small newly-divided forms with very small inconspicuous undulating membranes. Contractile vacuoles have only been observed in blood forms of one species, *T. salmositica*.

Site of infection: Trophozoites are usually found in the circulatory system of fish, where they occur as extracellular parasites swimming in the plasma. A total of 45 parasite species have been described: including 41 species found in 83 species of freshwater fish belonging to 16 families (notably cyprinids and sculpins); 4 species found in 12 species of marine fish belonging to 8 families (particularly flounder) and another species in a marine gastropod (abalone). Trophozoites have also been found in the upper alimentary tract of leech vectors where they occur as extracellular parasites in the crop and proboscis sheath. Infections have been found in 7 leech species, including 2 marine piscicolid species, 4 freshwater piscicolid species and one freshwater glossiphonid species.

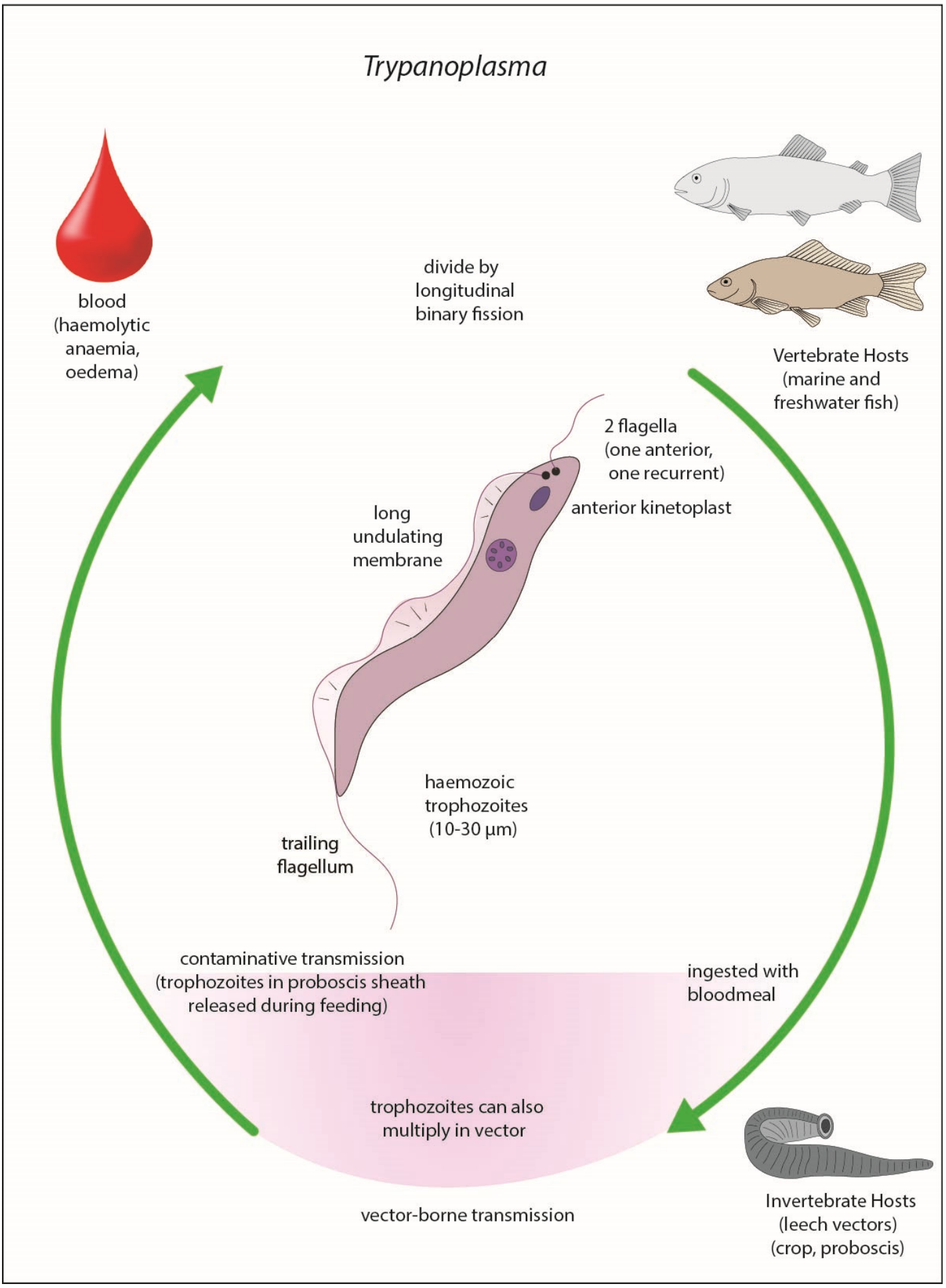
Pathogenesis: Infections by most parasite species are asymptomatic or subclinical, but several species have been associated with clinical disease, particularly in juvenile salmonids in hatcheries, occasionally in fish held in estuarine or marine sea-cages, and also in wild sexually-mature salmon (pre- and post-spawning). Trophozoites in the bloodstream feed on nutrients taken up across their membranes and they are thought to release various secretory/excretory products, including proteases (cysteine protease and metalloprotease) which act as histolytic enzymes causing lesions. Haemolysins are also released when trophozoites are lysed by complement fixation. Heavy haemozoic infection may cause intravascular and extravascular haemolysis either directly or following immune complex formation. This results in progressive haemolytic anaemia (microcytic and hypochromic) exacerbated by haemodilution (through general oedema). Other clinical signs observed in fish include hepatomegaly, splenomegaly, ascites, abdominal distention, exophthalmia (protrusion of eyeballs), anorexia, poor growth, lethargy, emaciation, compromised swimming

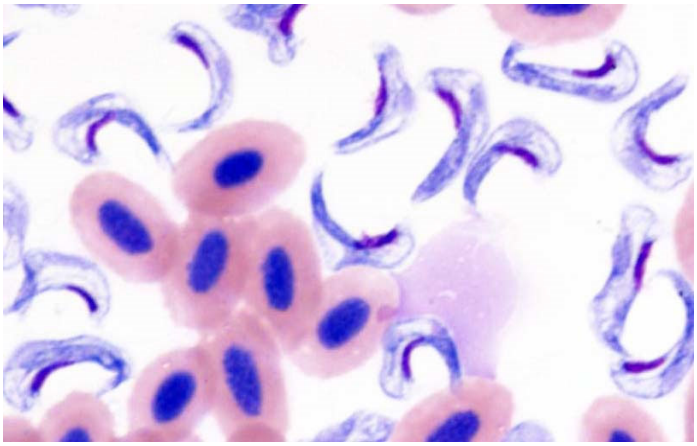
performance and some mortalities. Death has usually been associated with loss of osmoregulatory control, although infected fish are more sensitive to poor water quality and environmental hypoxia. Histopathological changes in dead fish include haemorrhagic foci, cellular necrosis, ulcerative lesions, inflammation, mononuclear cellular infiltrates, congested blood vessels, and occlusion of capillaries by parasites. Disease may become apparent within several weeks in fish in cold waters, but earlier in fish in warmer waters. The severity of disease has been found to be influenced by parasite factors (species/strain virulence, intensity of infection), host factors (age, nutritional state, physiological stress) and environmental factors (culture conditions, water quality, temperature, crowding). Immunological studies have shown there is some innate resistance to infection (involving complement lysis, neutralization of parasite proteases, and enhanced respiratory burst activities of circulating granulocytes) as well as some acquired immunity (involving humoral (agglutinating, neutralizing and complement-fixing antibodies) and cellular responses (phagocytes and lymphocytes). Fish developed some protection against subsequent challenge and studies found that the passive transfer of lymphocytes and plasma from recovered fish conferred protection on naive fish.

Developmental cycle and mode of transmission: Life-cycles have only been determined for some 7 *Trypanoplasma* spp. which all used haematophagous aquatic leeches as vectors for the transmission of infections between fish. The parasites undergo asexual multiplication in both the vertebrate and invertebrate hosts, but only one life-cycle stage is involved (trophozoites). Leeches act as more than mechanical paratenic (transport) hosts as the parasites undergo multiplication, but they are not true biological vectors as the parasites do not undergo any cyclic developmental processes, such as that exhibited by trypanosomes undergoing metacyclogenesis to form metacyclic infective stages. Even though some early studies tentatively described slender forms in leeches as putative 'metacyclic' forms, similar forms occur in fish and in cultures. Parasites multiply in the blood of fish by binary fission whereby nuclei and organelles (kinetoplast, flagella) are replicated before cytokinesis. Two divisional processes have been observed: one involving symmetric division of rounded maternal cells with the formation of similar daughter cells each inheriting an old and a new flagellum (e.g. *T. catostomi*); and another involving asymmetric division of slender maternal cells with formation of dissimilar daughter cells where the slender sibling retains both maternal flagella (e.g. *T. salmositica*). In leeches, the parasites divide by binary fission within 24 hours in the crop and slender forms accumulate in the proboscis sheath and may be transmitted to fish when the leech next feeds. The prepatent period ranges from 1-5 days and appears to be dependent on temperature (taking longer at lower temperatures). Experimental studies have also shown that some haemozoic infections may be transmitted directly between fish kept in tanks without leeches. Infections were transmitted to uninfected fish co-mingling or separated by wire mesh in the same tank. Live parasites were found in mucus on the body surface and may be transmitted to uninfected fish by mucus strands. Trophozoites may be released to the body surface from blisters or ulcers but how they are taken up by new hosts is unknown.

Differential diagnosis: Infections are diagnosed by the microscopic detection of trophozoites in blood samples preferably collected into anticoagulant. Wet mounts of whole blood, serum samples from clotted blood, buffy coat layers harvested by centrifugation, or ascites fluid are best examined by high-contrast microscopy for motile flagellates, while fixed smears can be examined by bright-field microscopy after staining with Giemsa or Leishman's stains. Parasites are readily cultured *in vitro* using semi-solid or liquid media, including biphasic blood agar (NNN or SNB-9), Ponselle's medium, Hank's solution or minimum essential medium (MEM) with heat-inactivated foetal calf serum. Explosive growth of *T. salmositica* occurs when trace amounts of fresh plasma from sexually-mature trout are added to media, but continuous culture appears to attenuate strains as they lose their virulence and sometimes infectivity for fish. Several immunoserological techniques (neutralization, agglutination, immunofluorescence and enzyme immunoassays) have been developed to detect specific host antibodies against *T. salmositica* antigens. Molecular biological techniques have recently been used to detect and characterize parasite isolates following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA, and some repetitive DNA fragments), precipitating major revisions of the parabodonid genera and species (major reshuffling of taxa between the genera *Cryptobia* and *Trypanoplasma*).

Treatment and control: There is currently no effective chemotherapeutic treatment for haemozoic infections by *Trypanoplasma* spp. in fish. Conventional trypanocidal drugs (suramin, berenil, antrycide) had little effect, although isometamidium chloride (samorin) injections gave variable results. Treatments with various antibiotics (penicillin, streptomycin, amphotericin) were purported to have some effect, while treatment with crystal violet (triphenylmethane dye) had some *in vitro* effects but exhibited *in vivo* toxicity problems. Preventive control programmes are based around vector control (reducing leech populations by chemical treatment and clearing vegetation used as substrates for cocoons) and maintaining healthy fish in stress-free conditions (proper nutrition, good water quality, avoid over-handling and over-crowding, and treating concomitant infections). Because infections have been found to be influenced by temperature, some control has been credited to acclimating fish to warmer waters (above 20°C). Experimental studies indicated that fish were able to moderate infections by innate and acquired immune responses resulting in parasite lysis, with complement, antibodies and phagocytes playing a pivotal role in protection. This prompted studies on vaccine development and some success was reported in protecting salmonids against *T. salmosticia* infection by vaccination with live attenuated cultured strains (up to 2 years protection in some instances). Monoclonal antibodies raised against surface membrane epitopes of *T. salmositica* were also found to be therapeutic when injected into fish with acute infections.


Trypanoplasma
blood
(haemolytic
anaemia,
oedema)
divide by
longitudinal
binary fission
Vertebrate Hosts
(marine and
freshwater fish)
2 flagella
(one anterior,
one recurrent)
anterior kinetoplast
long
undulating
membrane
haemozoic
trophozoites
(10-30 µm)
trailing
flagellum
contaminative transmission
(trophozoites in proboscis sheath
released during feeding)
ingested with
bloodmeal
trophozoites can also
multiply in vector
vector-borne transmission
Invertebrate Hosts
(leech vectors)
(crop, proboscis)



Trypanoplasma trophozoites

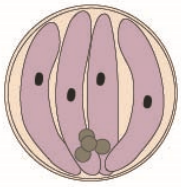


Protista
(apicomplexans)

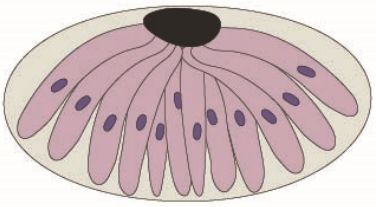
Apicomplexa

enteric oocysts

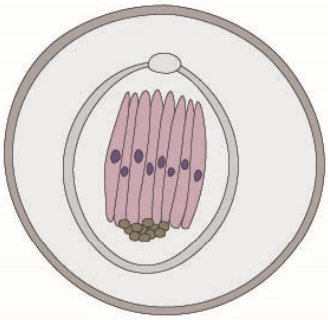
Cryptosporidium
(5-7 µm)



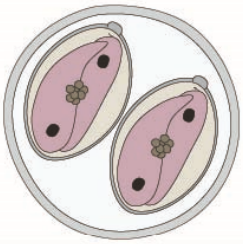
Klossiella
(18-24 µm)



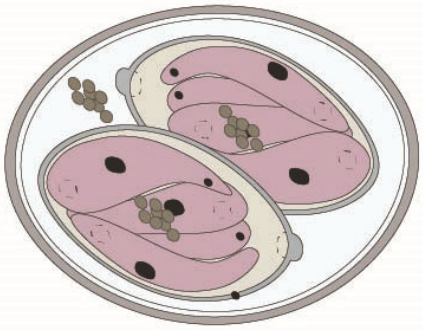
Caryospora
(10-43 µm)



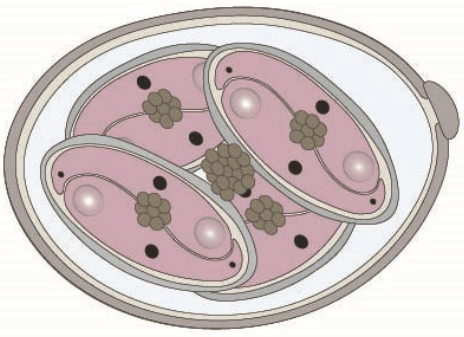
Cyclospora
(7-10 µm)



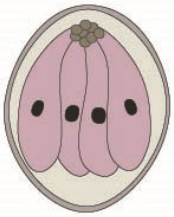
Isospora
(10-40 µm)



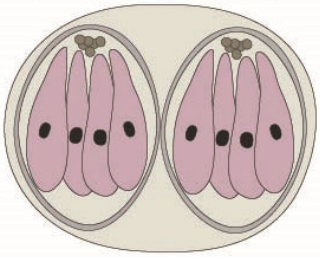
Eimeria
(10-40 µm)



Sarcocystis
(13-19 µm)



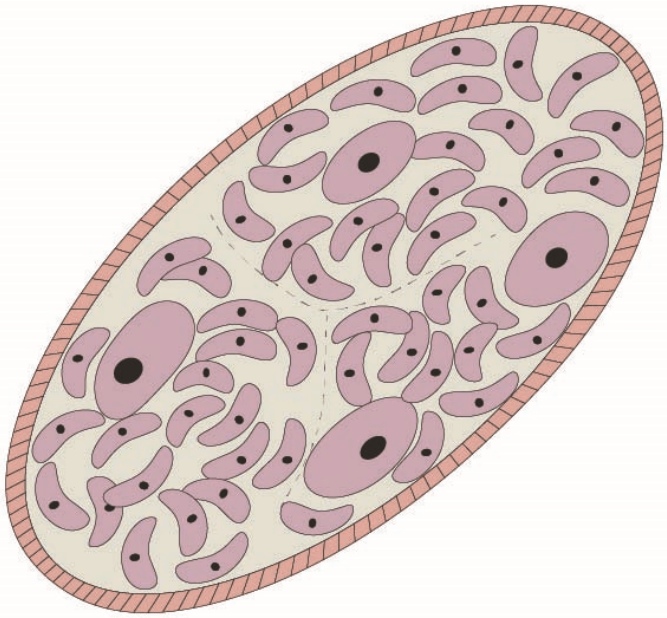
Toxoplasma/Hammondia/Neospora
/Besnoita (9-17 µm)



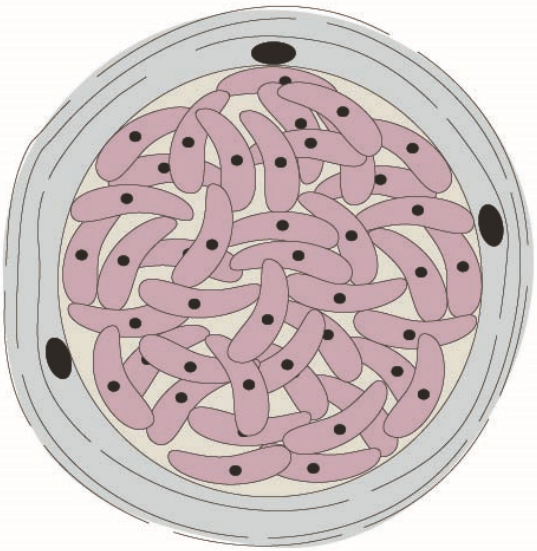
Apicomplexa

tissue cysts

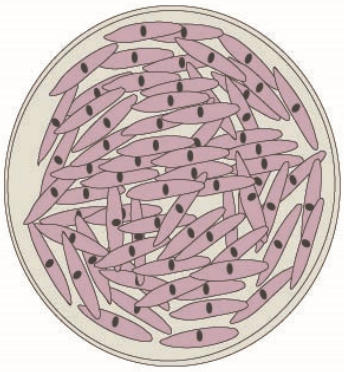
Sarcocystis
(30 µm - 1 cm)



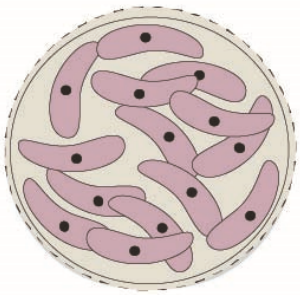
Besnoitia
(200 µm - 5 mm)



Toxoplasma/Hammondia
(10-340 µm)



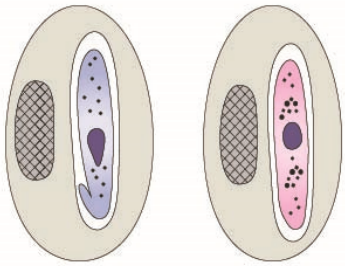
Neospora
(10-100 µm)



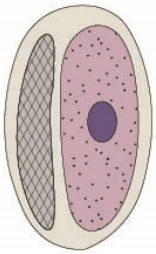
Apicomplexa

haematozoa

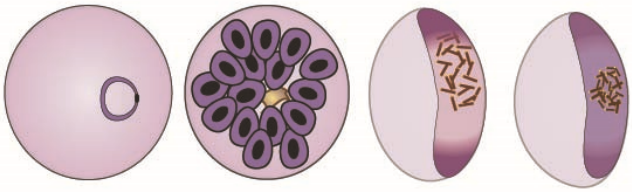
Haemogregarina
(8-15 µm)



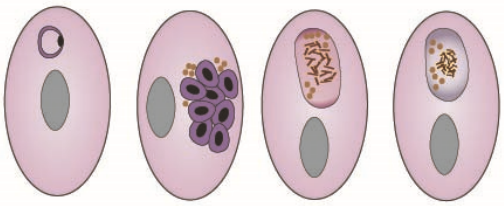
Hepatozoon
(9-12 µm)



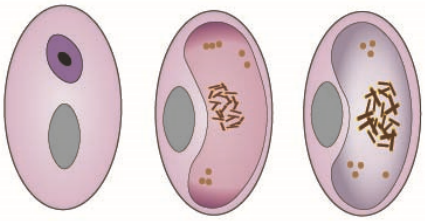
Plasmodium (mammal)
(1-14 µm)



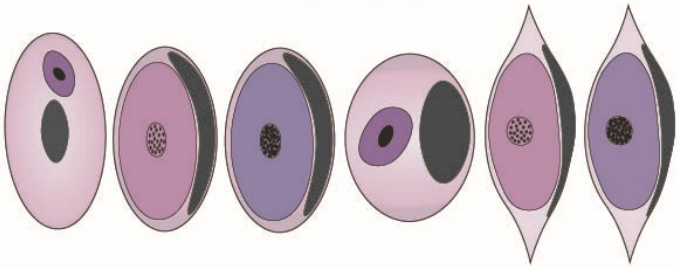
Plasmodium (non-mammalian)
(1-10 µm)



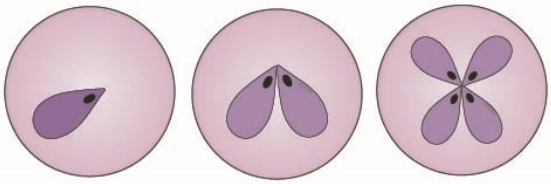
Haemoproteus
(5-24 µm)



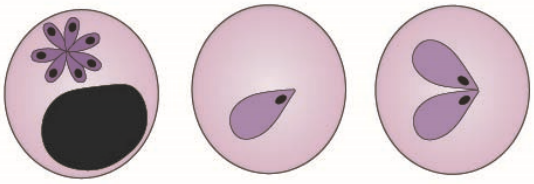
Leucocytozoon
(2-22 µm)



Babesia
(1-4 µm)



Theileria
(1-25 µm)



Cryptosporidium
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. *Cryptosporidium* is a unique genus closely related to the gregarines (parasites of invertebrates) although it was previously grouped with the coccidia as they form non-motile resistant oocysts containing infective sporozoites. Cryptosporidia are monoxenous (one-host) parasites in the digestive and/or respiratory tracts of vertebrate hosts. The parasites develop within the brush border (microvillous layer) of host epithelial cells (not in the host cell proper). Endogenous stages have a prominent attachment organelle and they are located within parasitophorous vacuoles formed by a complete covering of microvilli (intracellular yet extracytoplasmic location). They undergo cyclic asexual merogony (schizogony) followed by gamogony (male microgametes fertilize female macrogametes) resulting in the formation of small oocysts which undergo exogenous sporulation (forming 4 naked sporozoites not contained within sporocysts). Over 60 genotypes have been identified, some in association with mild to severe clinical disease in humans and domestic animals.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Gregarinomorphea (gregarines, gamogony and sporogony in aquatic hosts, trophonts with specialized attachment apparatus, epimerite or mucron, syzygy)
Subclass:	Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)
Family:	Cryptosporidiidae (oocysts with 4 naked sporozoites)
Genus:	*Cryptosporidium* (mucosal parasites in vertebrates)
Species:	various species cause cryptosporidiosis in mammals, birds, reptiles and fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are

heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Cryptosporidium was previously grouped with the coccidia as they form oocysts (albeit unusual in that they contained 4 naked sporozoites and no sporocysts), but recent biological and molecular phylogenetic studies have indicated that they are more closely related to gregarines than to coccidia. Given that some *Cryptosporidium* spp. have been found to form novel extracellular stages and others appear to be able to complete cyclic development in the absence of a host, the genus *Cryptosporidium* has formally been transferred to a new subclass Cryptogregaria in the class Gregarinomorphea. Cryptosporidia are monoxenous (one-host) parasites in the digestive and/or respiratory tracts of vertebrate hosts. The parasites develop within the brush border (microvillous layer) of host epithelial cells (not in the host cell proper). Endogenous stages have a prominent attachment organelle and they are located within parasitophorous vacuoles formed by a complete covering of microvilli (intracellular yet extracytoplasmic location).

Infections have been detected throughout the world in numerous species of mammals, birds, reptiles and fish. Parasite species were originally described primarily on the basis of host occurrence, site of infection, type of disease and, occasionally, differences in oocyst morphometrics. Epidemiological and experimental cross-transmission studies, however, suggested that different parasite species were specific for individual vertebrate classes rather than individual host species. More recently, molecular characterization studies conducted on clinical isolates have identified a range of genotypes (and subgenotypes) that vary markedly in their host specificity; some being highly specific for individual mammalian species (e.g. *C. viatorum*) while others were found in multiple host species (e.g. *C. parvum*). Genetic markers used for parasite characterization have included the small subunit (18S) of nuclear ribosomal DNA (SSU rDNA), second internal transcribed spacer of rDNA (ITS-2), 70 kDa heat shock protein (hsp-70), *Cryptosporidium* oocyst wall protein (cowp), thrombospondin-related adhesive protein (TRAP), actin, β-tubulin, 60 kDa glycoprotein (gp60), 47 kDa protein (cp47), 56 kDa transmembrane protein (cp56), mucin-like protein (mucin1), serine repeat antigen (msc6-7), microsatellite loci (ML1 and ML2) and a T-rich gene fragment (chrom3T). In many instances, it has proven difficult to reconcile genotypes with individual species. Many genotypes have been found (> 125 in hosts, and more in environmental water samples) but most have not been formally named as species. In addition, several named species, notably from early descriptions, have yet to be genotyped, and probably never will be. Despite these confounding elements, molecular epidemiological studies have shown strong correlations between specific parasite genotypes (and subgenotypes) and their anthroponotic, zoonotic and epizootic disease potential and have facilitated tracing of many disease outbreaks.

***Cryptosporidium* species**	**Oocyst size (µm)**	**Hosts**	**Location (clinical signs)**	**Distribution**
C. abrahamseni (= piscine genotype 7)	3.8 x 3.2	Characiformes: characid (redeye tetra, neon tetra)	intestines	Australia
C. alticolis	5.4 x 4.9	Rodentia: cricetid (common vole, meadow vole)	intestines	Europe
C. andersoni (= *C. muris* genotype A)	7.4 x 5.8	Artiodactyla: bovid (cattle, yak, European bison, sheep, mountain goat), camelid (camel); Rodentia: cricetid (golden hamster, Campbell's dwarf hamster, Djungarian hamster), sciurid (steppe marmot, eastern chipmunk), murid (multimammate mice, mouse, lesser gerbil, Mongolian gerbil, bushy-tailed jird, Tristam's jird); Primates: hominid (human); Galliformes: phasianid (crested partridge)	gastric (chronic)	worldwide
C. apodemi	4.2 x 4.0	Rodentia: murid (striped field mouse, yellow-necked mouse)	enteric	Europe
C. avium (= avian genotype V)	6.3 x 4.9	Psittaciformes: psittaculid (red-crowned parakeet, rosy-faced lovebird, budgerigar), psittacid (blue-fronted amazon), cacatuid (cockateil, Major Mitchell's cockatoo); Galliformes: phasianid (chicken)	intestines	Eurasia, Americas
C. baileyi	6.2 x 4.6	Galliformes: phasianid (chicken, brown quail, Japanese quail, turkey, pheasant, chukar partridge); Anseriformes: anatid (ducks, goose); Gruiformes: gruid (whooping crane, white-naped crane); Passeriformes: ploceid (golden-backed weaver), pycnonotid (gray-bellied bulbul), alaudid (crested lark), estrilid (Gouldian finch, zebra finch, Java sparrow), icterid (crested oropendola, red-rumped cocique), leiothrichid (red-billed leiothrix), sturnid (common myna), corvid (black-billed magpie), thraupid (saffron finch); Suliformes: phalacrocoracid (cormorant): Struthioniformes: struthionid (ostrich); Falconiformes: falconid (falcons); Accipitriformes: cathartid (black vulture); Charadriiformes: larid (black-headed gull); Psittaciformes: cacatuid (cockateil), psittacid (red-crowned amazon); Strigiformes: strigid (scops owl); Piciformes: ramphastid (channel-billed toucan); Rodentia: sciurid (eastern chipmunk, eastern grey squirrel)	enteric, respiratory (acute)	worldwide
C. bollandi (= piscine genotype II)	3.1 x 2.8	Cichliformes: cichlid (oscar, angelfish); Characiformes: characid (neon tetra); Mugiliformes: mugilid (flathead grey mullet)	stomach	North America
C. bovis (= bovine genotype B)	4.9 x 4.6	Artiodactyla: bovid (cattle, African buffalo, sheep), Carnivora: canid (fox); Primates: hominid	enteric (chronic)	worldwide

		(mountain gorilla)		
C. canis (= dog genotype)	5.0 x 4.7	Carnivora: canid (dog, coyote, fox, red fox), ursid (black bear); Primates: hominid (human)	enteric (acute)	worldwide
C. (*Piscicryptosporidium*) *cichlidis*	4.3 x 3.3	Cichliformes: cichlid (blue tilapia, Nile tilapia, redbelly tilapia); Cyprinodontiformes: poeciliid (guppy); Characiformes: characid (neon tetra)	gastric	Middle-East
C. cuniculus (= rabbit genotype)	5.2 x 4.6	Lagomorpha: leporid (rabbit); Rodentia: murid (gerbil, mice), Diprotodontia: macropodid (eastern grey kangaroo); Primates: hominid (human)	enteric (acute)	Australia, China, Europe
C. ditrichi	4.7 x 4.2	Rodentia: murid (yellow-necked mouse, mouse, wood mouse, striped field mouse); Primates: hominid (human)	enteric	Europe
C. ducismarci (= tortoise genotype II)	5.0 x 4.8	Testudines: testudinid (radiated tortoise, pancake tortoise, leopard tortoise, Greek tortoise, Hermann's tortoise, Russian tortoise, Egyptian tortoise, marginated tortoise); Serpentes: pythonid (ball python); Sauria: chamaeleonid (veiled chameleon)	nd	Europe
C. erinacei (= hedgehog genotype)	4.9 x 4.4	Eulipotyphla: erinaceid (European hedgehog, four-toed hedgehog); Perissodactyla: equid (horse); Primates: hominid (human)	enteric (chronic)	Europe
C. fayeri (= marsupial genotype I)	5.0 x 4.3	Diprotodontia: macropodid (yellow-footed rock wallaby, red kangaroo, grey kangaroos), phascolarctid (koala); Peramelemorphia: peramelid (western-barred bandicoot); Dasyuromorphia: dasyurid (Tasmanian devil); Didelphimorphia: didelphid (Virginia opossum); Artiodactyla: bovid (sheep); Primates: hominid (human)	enteric (acute)	Australia
C. felis (= cat genotype)	5.0 x 4.5	Carnivora: felid (cat); Artiodactyla: suid (pig); Primates: hominid (human), cercopithecid (rhesus macaque)	enteric (acute)	Americas, Africa, Europe
C. fragile	6.2 x 5.5	Anura: bufonid (black-spined toad)	gastric (chronic)	Asia
C. galli (incl. *C. 'blagburni'*) (= finch genotype I)	8.2 x 6.3	Passeriformes: fringillid (canary, gold finch, pine grosbeak, fife canary, gloster), estrildid (zebra finch, chocolate parson finch, painted firetail finch, munia, chestnut finch, Gouldian finch), thraupid (red-cowled cardinal, lesser seed-finch, saffron finch, slate-coloured seedeater), leiothrichid (silver-eared mesia), bombycillid (Bohemian waxwing), cardinalid (green-winged saltator), turdid (rufous-bellied thrush); Psittaciformes: psittaculid (turquoise parrot), cacatuid (cockateil); Galliformes: phasianid (chicken, hazel hen, grouse, capercaillie); Bucerotiformes: bucerotid (rhinoceros hornbill); Phoenicopteriformes: phoenicopterid (Cuban flamingo); Dasyuromorphia: dasyurid (Tasmanian devil);	gastric (chronic)	Europe, Australia
C. homai		Rodentia: caviid (guinea pig)	respiratory? (acute)	Australia
C. hominis (= human genotype I)	5.2 x 4.9	Primates: hominid (human), cercopithecid (rhesus macaque, olive baboon); Sirenia: dugongid (dugong); Artiodactyla: bovid (cattle, sheep, goat), suid (pig); Diprotodontia: macropodid (rock-wallaby, eastern grey kangaroo); Anseriformes: anatid (Canada goose); Columbiformes: columbid (rock pigeon); Cypriniformes: cyprinid (goldfish)	enteric (acute-chronic)	worldwide
C. huwi (= piscine genotype I)	4.6 x 4.2	Cyprinodontiformes: poecilid (guppy); Cypriniformes: cyprinid (tiger barb); Characiformes: characid (neon tetra)	stomach (chronic)	Australia
C. macropodum (= marsupial genotype II)	5.4 x 4.9	Diprotodontia: macropodid (grey kangaroos, red kangaroo, rock-wallaby, swamp wallaby), phascolarctid (koala)	enteric (acute)	Australia

C. meleagridis	5.2 x 4.6	Galliformes: phasianid (turkey, chicken, red-legged partridge); Psittaciformes: psittaculid (Indian ring-necked parrot, rose-ringed parakeet), cacatuid (cockateil), bombycillid (Bohemian waxwing); Columbiformes: columbid (fan-tailed pigeon, rufous turtle dove); Anseriformes: anatid (ducks); Primates: hominid (human, mountain gorilla); Carnivora: canid (dog), Lagomorpha: leporid (rabbit); Diprotodontia: macropodid (brush-tailed rock-wallaby); Rodentia: murid (mice, deer mouse, rats); Artiodactyla: suid (pig), bovid (cattle)	enteric (acute)	worldwide
C. microti	4.3 x 4.1	Rodentia: cricetid (common vole, meadow vole)	intestines	Europe
C. molnari	4.7 x 4.5	Cypriniformes: cyprinid (bream, goldfish, fringe barb, Eurasian carp), gyrinocheilid (golden algae-eater); Cyprinodontiformes: apaniid (Arabian toothcarp), poecilid (guppy); Cichliformes: cichlid (oscar, altum angelfish); Moroniformes: moronid (European sea bass); Perciformes: monodactylid (butter bream); opistognathid (yellowhead jawfish), percichthyid (Murray cod), pomacanthid (red stripe angelfish), pomacentrid (orange clownfish, azure damselfish, green chromis), serranid (peach fairy basslet, Madder seaperch), sparid (gilt-head sea bream); Acanthuriformes: acanthurid (bristletooth tang, wedgetail blue tang, Tomini surgeonfish, blue surgeonfish); Esociformes: esocid (northern pike); Siluriformes: mochokid (blotched upsidedown catfish)	stomach (chronic)	Europe, Australia
C. muris (= *C. muris* genotype B)	8.4 x 6.3	Rodentia: murid (mouse, Algerian mouse, spiny mouse, wood mouse, multimammate mice, brown rat), sciurid (eastern grey squirrel, Siberian chipmunk), cricetid (golden hamster, desert hamster, Campbell's dwarf hamster, Djungarian hamster, Roborovski hamster, bank vole, Brandt's vole), spalacid (East African mole-rat), caviid (guinea pig, Patagonian mara); Lagomorpha: leporid (rabbit); Hyracoidea: procaviid (rock hyrax); Carnivora: felid (cat), canid (dog, coyote), phocid (ringed seal); Peramelemorphia: thylacomyid (greater bilby), Dasyuromorphia: dasyurid (Tasmanian devil); Primates: hominid (human, mountain gorilla), cercopithecid (crab-eating macaque), lorisid (Sunda slow loris); Artiodactyla: bovid (cattle, goat, sheep, Cuvier's gazelle), camelid (camel), giraffid (reticulated giraffe), suid (pig); Perissodactyla: equid (horse); Caprimulgiformes: podargid (tawny frogmouth); Struthioniformes: struthionid (ostrich); plus pseudo-parasitism (passive food-borne transmission?) Serpentes: boid (boa constrictor), colubrid (black rat snake, yellow rat snake, corn snake), pythonid (ball python), elapid (taipan); Sauria: varanid (crocodile monitor); Anura: ceratophryid (Argentine horned frog)	gastric (chronic)	worldwide
C. myocastoris (= coypu genotype)	5.0 x 4.8	Rodentia: echimyid (nutria)	intestines	Europe
C. nasoris (syn. *C. nasorum*) (not genotyped) (considered *nomen nudum*)	4.3 x 3.2	Perciformes: acanthurid (lipstick tang)	enteric (chronic)	North America
C. occultus (= *C. suis*-like genotype	5.2 x 4.9	Rodentia: murid (brown rat, Tanezumi rat, house mouse, Mongolian gerbil); Artiodactyla: bovid	intestines	Eurasia, Americas,

and *C. parvum* VF383)		(cattle, yak, water buffalo); Primates: hominid (human)		Australia
C. ornithophilus (= avian genotype II)	6.1 x 5.1	Struthioniformes: struthionid (ostrich); Galliformes: phasianid (chicken), Anseriformes: anatid (goose); Psittaciformes: cacatuid (cockateil, galah, Major Mitchell cockatoo), psittacid (sun conure, white-eyed parakeet), psittaculid (eclectus parrot, Alexandrine parrot, princess parrot)	intestines	Eurasia, South America, Australia
C. parvum (= *C. parvum* mouse genotype I)	5.2 x 4.6	Artiodactyla: bovid (cattle, sheep, blue wildebeest, slender-horned gazelle, bongo antelope, eland, yak, sable antelope), suid (pig), camelid (alpaca), cervid (swamp deer, roe deer, red deer, sika deer); Perissodactyla: equid (horse); Carnivora: canid (dog, raccoon dog, red fox, gray wolf), mephitid (skunk); Lagomorpha: leporid (rabbit); Rodentia: sciurid (eastern grey squirrel, Siberian chipmunk, marmot), murid (mouse, Algerian mouse, wood mouse, yellow-necked mouse, deer mouse, black rat), caviid (capybara), cricetid (vole, golden hamster, Djungarian hamster, Campbell's dwarf hamster, southern red-backed vole); Chiroptera: vespertilionid (mouse-eared bat, big brown bat); Eulipotyphla: erinaceid (European hedgehog); Cetacea: delphinid (striped dolphin, bottlenose dolphin); Diprotodontia: macropodid (red kangaroo, rock-wallaby), phascolarctid (koala); Primates: hominid (human, mountain gorilla), cercopithecid (gray langur, purple-faced langur, rhesus macaque); Anseriformes: anatid (Canada goose); Ciconiiformes: ciconiid (white stork); Falconiformes: falconid (gyrfalcon); Gruiformes: rallid (Eurasian coot); Psittaciformes: cacatuid (cockateil); Passeriformes: estrildid (Bengalese finch); Charadriiformes: chionid (stone curlew); Testudines: testudinid (marginated tortoise); Sauria: gekkonid (gecko, leopard gecko), iguanid (green iguana), varanid (monitor); Carangiformes: carangid (mackerel scad); Cichliformes: cichlid (Nile tilapia); Clupeiformes: clupeid (Atlantic herring, pilchard), engraulid (European anchovy); Cypriniformes: cyprinid (common roach, goldfish, Java barb); Esociformes: esocid (northern pike); Gadiformes: gadid (Atlantic cod), lotid (blue ling); Perciformes: latid (barramundi), percid (European perch), sillaginid (golden whiting); Salmoniformes: salmonid (Arctic char, common whitefish, rainbow trout, brown trout); Scombriformes: scombrid (chub mackerel, Atlantic mackerel)	enteric, gastric in some fish (acute-chronic)	worldwide
C. pestis (= genotype C or *C. parvum* bovine genotype II)	4-5	Primates: hominid (human); Rodentia: murid (mouse); Artiodactyla: bovid (cattle)	enteric (acute- chronic)	worldwide
C. proliferans (= *C. muris* strain TS03)	7.7 x 5.3	Rodentia: murid (mouse, spiny mouse, multimammate mice, Tristam's jird, bushy-tailed jird, lesser gerbil, Mongolian gerbil), cricetid (Brandt's vole), sciurid (gray squirrel), spalacid (mole-rat); Perissodactyla: equid (donkey, horse), bovid (African buffalo)	gastric (chronic)	Eurasia, Africa, Americas
C. proventriculi (= avian genotype III)	7.4 x 5.8	Psittaciformes: cacatuid (cockateil)	proventriculus, ventriculus	Australia
C. ratti (= rat genotype 1)	4.9 x 4.7	Rodentia: murid (brown rat)	enteric	Europe
C. (*Piscicryptosporidium*)	2.9	Anabantiformes: osphronemid (gourami);	gastric	Middle-East,

reichenbachklinkei		Cichliformes: cichlid (freshwater angelfish, oscar); Characiformes: characid (neon tetra)		Asia
C. rubeyi (= genotype Sbey03c)	4.7 x 4.3	Rodentia: sciurid (California ground squirrel, prairie dog)	enteric (chronic)	North America
C. ryanae (= deer-like genotype)	3.7 x 3.2	Artiodactyla: bovid (cattle, water buffalo?, zebu?)	enteric (chronic)	worldwide
C. scophthalmi (not genotyped)	4.4 x 3.9	Pleuronectiformes: scophthalmid (turbot)	enteric (chronic)	Europe
C. scrofarum (= pig genotype II)	5.2 x 4.8	Artiodactyla: suid (pig); Rodentia: murid (brown rat, Asian house rat); rarely Primates: hominid (human); Perciformes: sillaginid (western school whiting)	enteric (chronic)	worldwide
C. serpentis	6.2 x 5.3	Serpentes: elapid (death adder, tiger snake, taipan), viperid (Bornmueller's viper, mountain viper, Nikolski viper, diamondback rattlesnake, timber rattlesnake, tropical rattlesnake, jararaca, jararacussu), colubrid (rat snakes, bull snake, king snakes, pine snake, fox snake, milk snake, leaf-nosed snake, corn snake), boid (tree boas, boa constrictor, rainbow boas, green anaconda, viper boa, rosy boa), pythonid (ball python, green python, Burmese python, Boelen's python, rock python); Sauria: agamid (bearded dragon, frilled lizard), chamaeleonid (Madagascar chameleon, mountain chameleon), gekkonid (gargoyle gecko, leopard gecko), scincid (skink), varanid (desert monitor, emerald monitor, Nile monitor, Savannah monitor); Artiodactyla: bovid (cattle); Rodentia: murid (mouse)	gastric (chronic)	worldwide
C. suis (= pig genotype I)	4.6 x 4.2	Artiodactyla: suid (pig), bovid (cattle, sheep); Rodentia: murid (mice, Asian house rat); Primates: hominid (human)	enteric	Europe, Australia
C. testudinis (= tortoise genotype I)	6.4 x 5.9	Testudines: testudinid (radiated tortoise, Chaco tortoise, serrated tortoise, leopard tortoise, Greek tortoise, Hermann's tortoise, Russian tortoise, marginated tortoise, Indian star tortoise); Serpentes: pythonid (ball python)	nd	Europe
C. tyzzeri (= mouse genotype I)	4.6 x 4.2	Rodentia: murid (mouse, yellow-necked mouse, brown rat, Asian house rat), cricetid (voles); Chiroptera: vespertilionid (large-footed bat); Carnivora: felid (cat, black leopard), ailurid (lesser panda); Artiodactyla: suid (pig), bovid (American bison, Barbary sheep, takin); rarely Primates: hominid (human); Serpentes: boid (boa constrictor, emerald tree boa), colubrid (black rat snake, king snake, corn snake, fox snake, milk snake), elapid (red-bellied black snake), pythonid (ball python, Woma python); Sauria: varanid (mangrove monitor)	enteric (chronic)	worldwide
C. ubiquitum (= deer genotype)	5.0 x 4.7	Artiodactyla: bovid (sheep, goat, cattle, impala, blesbok, African buffalo, nyala, alpine ibex, mouflon), cervid (swamp deer, roe deer, red deer, sika deer, white-tail deer); Diprotodontia: macropodid (rock-wallaby); Carnivora: procyonid (raccoon); Rodentia: murid (mouse, deer mouse, gerbil), sciurid (American red squirrel, Eurasian red squirrel, eastern grey squirrel, fox squirrel, eastern chipmunk, woodchuck), castorid (beaver), erethizontid (prehensile-tailed porcupine); Primates: hominid (human)	enteric (acute)	worldwide
C. varanii (syn. *C. saurophilum*) (= desert monitor	4.8 x 4.7	Sauria: varanid (desert monitor, emerald monitor), agamid (bearded dragon), chameleonid (mountain chameleon, veiled chameleon), gekkonid (African	enteric (chronic)	worldwide

genotype)		fat-tailed gecko, gargoyle gecko, leopard gecko), gerrhosaurid (plated lizard), iguanid (green iguana), lacertid (green lizard), scincid (ocellated skink, Schneider's skink, skink); Serpentes: boid (boa constrictor, viper boa), colubrid (black rat snake, bull snake, corn snake, pine snake, milk snake), pythonid (green python)		
C. viatorum	5.4 x 4.7	Primates: hominid (human)	enteric (acute)	Europe (ex: India, Africa, Central America)
C. wrairi	5.4 x 4.6	Rodentia: caviid (guinea pig), sciurid (ground squirrel), murid (mouse); Artiodactyla: bovid (cattle, sheep)	enteric (chronic)	North America, Europe
C. xiaoi (= *C. bovis*-like genotype) (syn. *C. agni*)	3.9 x 3.4	Artiodactyla: bovid (sheep, goat, yak), Diprotodontia: macropodid (western grey kangaroo); Perciformes: sillaginid (western school whiting)	enteric (chronic)	Eurasia, Africa, North America, Australia

Parasite morphology: The parasites form three developmental stages: meronts, gamonts and oocysts. Endogenous developmental stages appear as small basophilic bodies (3-6 µm) attached to the luminal surface of host epithelial cells (epicellular location). These stages are located within parasitophorous vacuoles formed by a covering of microvilli (intracellular but extracytoplasmic) and developing parasites form a prominent lamellated feeding organelle at the site of attachment to the host cell at the base of the vacuole. Meronts divide internally to form multiple merozoites while gamonts mature to form uninucleate macrogametocytes (female) and multinucleate microgametocytes (male). Exogenous oocysts appear as ovoid membrane-bound phase-bright bodies (5-7 x 4-6 µm) containing four sporozoites and an eccentric residual body (sporocysts are not formed). Since the development of *in vitro* cultivation techniques for *Cryptosporidium*, several observations have been made reinforcing the belief suggested by molecular phylogenetic analyses that these parasites are gregarines rather than coccidia. In addition to their epicellular location, epimerite-like feeding organelle, myzocytosis-like feeding mechanism and zoite structural heterogeneity, cryptosporidial stages were found to survive and multiply extracellularly (even in biofilms), move using a gregarine-like gliding motion and undergo syzygy (pairing) prior to gamogony.

Site of infection: Most parasite species infect the small intestines of their hosts (mammals) whereas others infect the respiratory tract (birds) or stomach (reptiles). The parasites undergo several cycles of asexual merogonous development before gamonts are formed. After fertilization, the oocysts mature in the gut and are usually infective as soon as they are excreted from the host.

Pathogenesis: Infections vary markedly in their presentation ranging from asymptomatic to mild acute to severe chronic disease. Endogenous intestinal stages may cause microvillus destruction, villus atrophy, impaired glucose and electrolyte transport, impaired carbohydrate and protein digestion manifesting in malabsorptive and maldigestive disease. Most clinical infections in immunocompetent individuals involve transient acute disease characterized by profuse watery foul-smelling diarrhoea or acute respiratory signs, anorexia, depression, ill-thrift and occasionally death. Neonates and malnourished individuals are most susceptible, whereas older animals become resistant (immune) to infection. Infections may persist in immunocompromised individuals (those with congenital or acquired immunodeficiencies or those undergoing immunosuppressive therapy) resulting in protracted chronic disease which may prove fatal (especially in AIDS patients). In contrast, infections in reptiles (and possibly fish) cause chronic gastritis typified by postprandial regurgitation.

Developmental cycle and mode of transmission: Oocysts excreted by infected hosts contaminate the environment and initiate infections when ingested by susceptible hosts (faecal-oral transmission). This direct transmission cycle may involve the contamination of fomites, water and/or food sources. Some (thin-walled) oocysts are thought to be auto-infective and may excyst in the same host. Parasites undergo two cycles of asexual development (type I and type II merogony) followed by sexual development (gamogony), fertilization (oocyst formation) and sporozoite differentiation (sporogony). Most infections are transmitted by fomites between individuals held in close confinement, such as in child day-care centres, hospitals, zoos, and intensive animal rearing facilities. In addition, oocysts are being detected with increased frequency in treated and untreated water supplies. Many water-borne outbreaks of public health significance have been reported involving contamination of potable and recreational waters (lakes, pools, water parks) by sewage and/or agricultural waste. While conventional methods of water treatment (filtration and chlorination) may reduce contamination levels (quantified by log removal and concentration-time parameters), the small tough oocysts are quite resistant and enough persist to pose a significant problem for water providers. Food-borne transmission has also been recorded (involving milk, cider, salads, sausages), probably attributable to contaminated water being used in food production.

Differential diagnosis: Infections are conventionally diagnosed by the detection of oocysts in smears or concentrates of faecal material or respiratory exudates. Unstained oocysts may be confused with yeasts but they are acid-fast and stain well with basic fuchsin stains. Alternatively, phase-contrast or differential interference contrast microscopy can be used to reveal internal oocyst features, as can vital dyes (DAPI) and fluorescent nucleic acid stains (MPR71059). Although some parasite species can be cultured *in vitro* (in tissue cultures) or *in vivo* (in laboratory or neonatal domestic animals), considerable variation has been observed in parasite infectivity and growth. More success has been reported in detecting oocysts in clinical and environmental samples using specific monoclonal antibodies for immunomagnetic separation or as fluorescent markers for microscopy or flow cytometry. Researchers have also developed several highly sensitive techniques using polymerase chain reaction (PCR) amplification of partial gene sequences followed by electrophoretic fingerprinting (e.g. nested PCR, PCR-RFLP, RT-qPCR. Community epidemiological studies rely on molecular genotyping (and subgenotyping) of clinical and environmental isolates to indicate their anthroponotic and zoonotic potential.

Treatment and control: There is currently no effective chemotherapeutic treatment for cryptosporidiosis, although variable success has been reported using paromomycin, nitazoxanide, tylosin and azithromycin. Supportive treatment by oral or parenteral rehydration may help alleviate symptoms. Some promising results have been obtained using hyperimmune bovine colostrum for passive immunotherapy. Control measures include identification of the source of infection, isolation of infected individuals, maintaining high standards of hygiene, proper effluent disposal, water treatment and disinfection of contaminated surfaces. The oocysts are highly resistant to external environmental conditions and they can survive many commonly used drinking water disinfectants. The oocysts are also very small and may not be removed by inefficient water filtration. Public health authorities recommend boiling water during outbreak situations and also more regularly for high-risk patients groups (such as HIV-positive individuals).

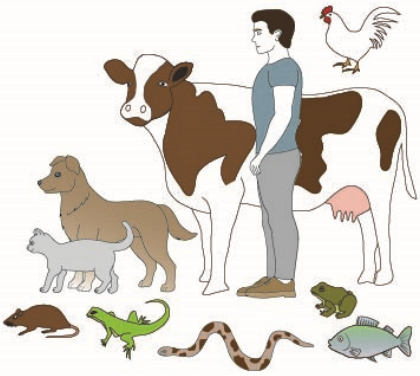
Cryptosporidium

monoxenous (1-host) cycle



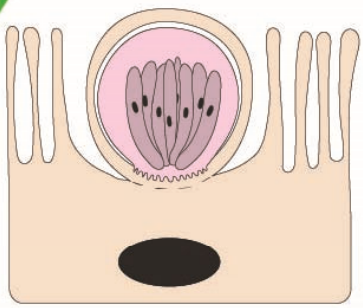
intestines
(malabsorption,
watery diarrhoea)

unique feeder organelle
and parasitophorous vacuole
(epicellular, yet extracytoplasmic)

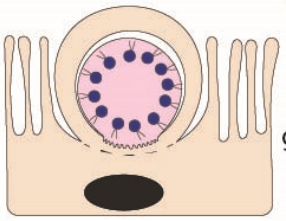


Definitive Hosts
(mammals, birds,
reptiles, fish,
amphibians)

meronts
(3-6 µm)

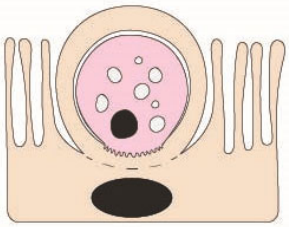


asexual multiplication
(merogony) (several cycles)



micro-
gamont
(male)

sexual reproduction
(gamogony)



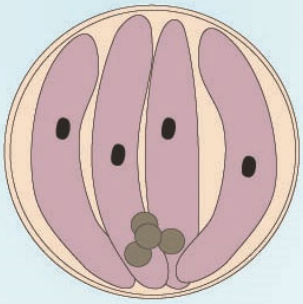
macro-
gamont
(female)



oocysts
ingested

oocysts shed
in faeces

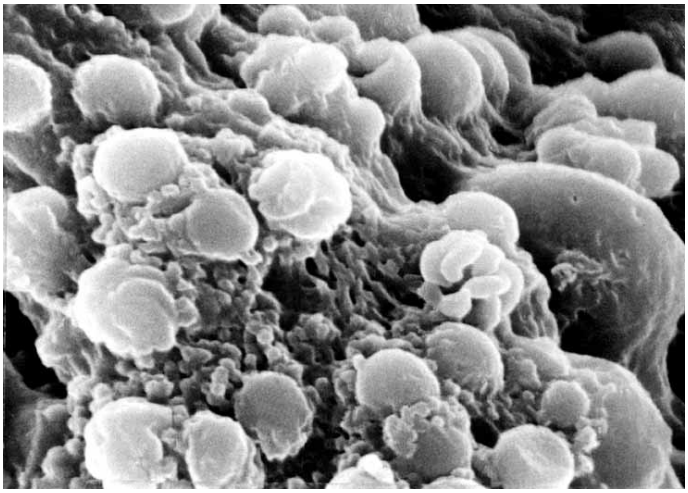




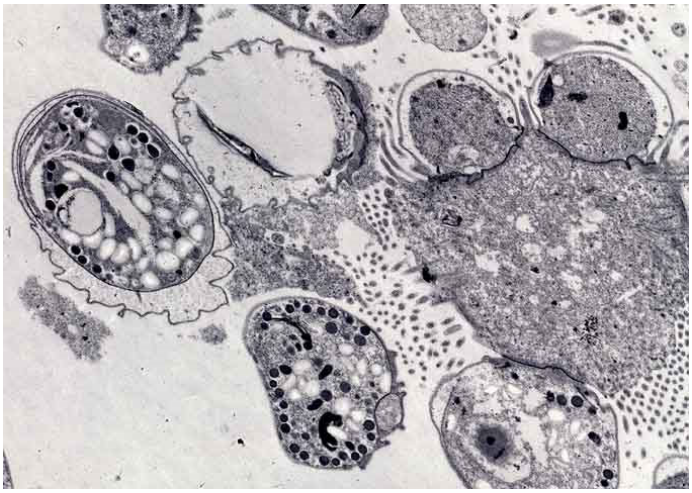
4 naked sporozoites
(no sporocyst)

oocysts
(5-7 µm)

faecal-oral transmission between hosts
via oocysts contaminating environment,
including food/water sources



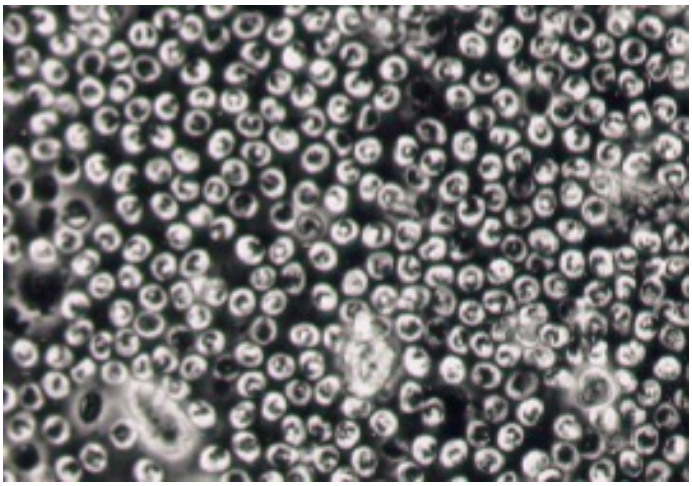
Cryptosporidium endogenous stages (sEM)



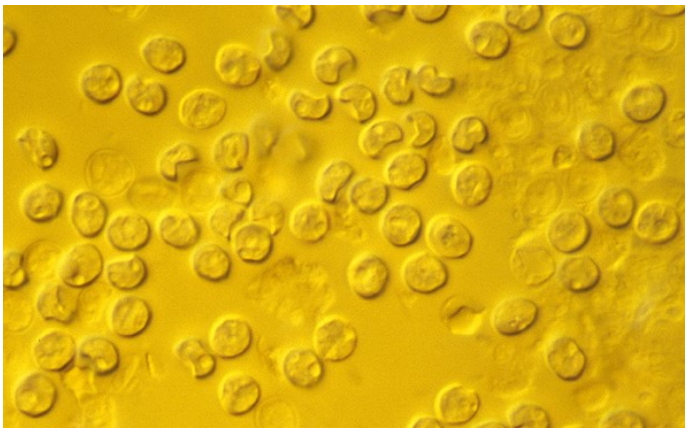
Cryptosporidium endogenous stages (tEM)



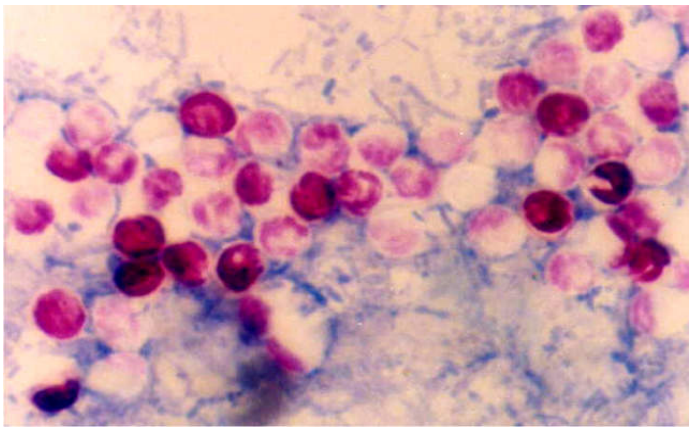
Cryptosporidium endogenous stages on mouse gut



Cryptosporidium oocysts in snake faeces



Cryptosporidium oocysts in faecal float



Cryptosporidium oocysts in faecal smear

Haemogregarina
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia (including the blood parasites paradoxically known as 'haemogregarines') in marine and terrestrial animals; and eimeriid coccidia in vertebrates. Haemogregarines are heteroxenous (2-host) parasites where merogony (= schizogony) and gamogony occurs in the vascular system of a vertebrate host while sporogony occurs in a haematophagous invertebrate host (vector). They are common blood parasites in reptiles and some occur in fish, amphibians, birds and mammals. Four main assemblages are recognized: haemogregarinids, karyolysids, hepatozoids and dactylosomatids. Haemogregarinids (*Haemogregarina*, *Cyrilia* and *Desseria*) produce oocysts with naked sporozoites in the guts of leech vectors. Vertebrates (mainly aquatic animals) are infected by vector bite, and schizogony occurs in host erythrocytes (although infected cells tend to be sequestered in viscera) prior to the development of intraerythrocytic gamonts. Infections are generally considered to be nonpathogenic, even when high parasitaemias are present. Given the paucity of information on the developmental biology of most species, it has been suggested that all members of the genus *Haemogregarina* in snakes, crocodiles, lizards, amphibians, birds and mammals (but not tortoises or fish) be transferred to the genus *Hepatozoon* pending determination of their vectors and developmental cycles.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Adeleina (syzygy, 1-4 microgametes)
Family:	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)
Genus:	*Haemogregarina* (vector-borne haemoparasites)
Species:	various species cause infections in blood/tissues of reptiles/amphibia/fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia

are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as 'haemogregarines' in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Haemogregarines are heteroxenous (2-host) parasites where merogony (= schizogony) and gamogony occurs in the vascular system of a vertebrate intermediate host while fertilization and sporogony occurs in a haematophagous invertebrate definitive host (vector). They are common blood parasites in reptiles and fish and some occur in amphibians, birds and mammals. Infections are generally considered to be nonpathogenic, even when high parasitaemias are present. Haemogregarines are classified together with other coccidia, specifically with the adeleorine coccidia in marine and terrestrial animals. These parasites undergo sexual reproduction involving the formation of macro- and micro-gametes which associate pairwise in syzygy so comparatively few microgametes are produced (usually 1-4). The resultant zygote forms an oocyst containing infective sporozoites which are

transmitted to vertebrates when infected vectors are eaten (consumptive) or when they feed on vertebrate blood (inoculative). Over 450 haemogregarine species have been described in vertebrate blood, most records being confined to the detection of intra-erythrocytic stages (almost exclusively gamonts) which do not produce haemozoin pigment. Numerous species were described simply on the basis of host occurrence but little is known about their actual host specificity or developmental cycles. Despite early confusion, there has been growing acceptance of the recent classification of haemogregarines into four families: Haemogregarinidae containing the genera *Haemogregarina*, *Cyrilia* and *Desseria*; Hepatozoidae containing the genus *Hepatozoon;* Karyolysidae containing the genera *Karyolysus* and *Hemolivia*; and Dactylosomatidae containing the genera *Dactylosoma* and *Babesiosoma* (in addition to 3 other adeleine families: Adeleidae, Klossiellidae and Legerellidae). It has been suggested that the chelonian (tortoise) haemogregarines be regarded as *Haemogregarina sensu stricto* (*s.s.*, in the strictest sense) whereas fish haemogregarines be classified as *Desseria* or *Cyrilia* or left as *Haemogregarina sensu lato* (*s.l.*, in the broadest sense). It was also suggested that all members of the genus *Haemogregarina* in reptiles (snakes, crocodiles, lizards), amphibians, birds and mammals be transferred to the genus *Hepatozoon* pending determination of their vectors and studies on their developmental cycles. All haemogregarines use vertebrates as intermediate hosts for cyclic merogony (often forming macro- then micro-merozoites) in tissues and gamont development in blood cells (mostly red, sometimes white, blood cells). Gamogony is completed in invertebrate definitive hosts (leeches, acarines or dipterans) followed by fertilization and oocyst formation in the gut or haemocoel. The oocysts undergo sporogony resulting in sporozoites lying directly within oocysts (for Dactylosomatidae), within sporocysts (for Hepatozoidae), within tissues (for Haemogregarinidae) or within eggs (for Karyolysidae). The four families are currently differentiated as follows:

- Haemogregarinids produce oocysts with naked sporozoites in the gut of leech vectors, vertebrates are infected by vector bite, and schizogony occurs in host erythrocytes (although infected cells tend to be sequestered in viscera prior to the development of intraerythrocytic gamonts); genera comprise *Haemogregarina s.s.* in turtles and *Haemogregarina s.l., Desseria* and *Cyrilia* in fish.
- Hepatozoids produce oocysts containing numerous sporocysts in the gut or haemocoel of various vectors (leeches, insects, acarines), vertebrates are infected by ingesting vectors, and schizogony occurs in vascular endothelial cells in host tissues (cystic stages also observed contributing to chronic infections and possible paratenic transport); the genus *Hepatozoon* occurs in mammals, reptiles (crocodiles, snakes, lizards), amphibians and birds.
- Karyolysids produce sporokinetes and motile spores in the gut and ova of mite vectors, vertebrates are infected by ingesting mites, and schizogony occurs in host vascular endothelial cells; genera comprise *Karyolysus* and *Hemolivia* in reptiles and amphibians.
- Dactylosomatids produce oocysts which bud sporozoites directly within epithelial cells in the intestines of leech vectors, vertebrates are infected presumably by vector bite and schizogony occurs in host erythrocytes; genera comprise *Dactylosoma* and *Babesiosoma* in reptiles, amphibians and fish.

Family	**Genus**	**No. species**	**Site of development in vertebrate**		**Vertebrate hosts**	**Invertebrate vector**
			meronts	**gamonts**		
Haemogregarinidae	*Haemogregarina*	*s.s.* 38; *s.l.* 42	erythrocytes	erythrocytes	*s.s.* in turtles; *s.l.* in fish	leeches
	Cyrilia	3	erythrocytes	erythrocytes	fish	leeches
	Desseria	35	exo-erythrocytic	erythrocytes	fish	leeches
Hepatozoidae	*Hepatozoon*	341*	viscera	erythrocytes, leucocytes	mammals, reptiles, birds, frogs, fish	leeches, arthropods
Karyolysidae	*Hemolivia*	4	RE cells	erythrocytes	lizards, tortoises, toads	ticks
	Karyolysus	11	viscera ± erythrocytes	erythrocytes	lizards, frogs	mites
Dactylosomatidae	*Dactylosoma*	10	erythrocytes	erythrocytes	reptiles, amphibians, fish	leeches
	Babesiosoma	12	erythrocytes	erythrocytes	fish, amphibians	leeches

*Includes some 200 former *Haemogregarina* spp. from crocodiles, snakes, lizards, amphibians and birds following their mass transfer to the genus *Hepatozoon* pending further characterization

Early phylogenetic studies used cladistics analyses of multiple phenotypic characters (morphology, biology) to reveal several clades apparently associated with different vectors (notably ticks, flies and leeches) rather than particular vertebrate hosts, thus suggesting vector-first evolution. However, such patterns may have arisen due to the environments in which the hosts occurred; e.g. marine hosts with leeches, and terrestrial hosts with ticks or flies. Molecular phylogenetic studies using small subunit (SSU) ribosomal RNA sequences revealed any associations between haemogregarines and their vertebrate hosts to be polyphyletic with many mixed clades associated with parasites in snakes, lizards, amphibians and mammals. Detailed analyses revealed five major clades: two *Hepatozoon* clades (clade A associated with carnivores and clade C with reptiles and frogs) separated by an

intermediary *Hemolivia* clade in lizards, and two distant clades, one containing *Haemogregarina* species from tortoises and the other containing *Dactylosoma/Babesiosoma* species from fish and frogs. The five major clades were also well separated with respect to vectors: the former three clades using ticks and flies as vectors and the latter two using leeches. The *Hepatozoon* species in mammals (clade A) were more closely related to *Karyolysus* species from lizards, while the *Hepatozoon* species in frogs and reptiles (clade C) were more closely related to *Hemolivia* species from tortoises and lizards. Several interesting biological associations were evident between polyphyletic clades. *Haemogregarina* s.s. and dactylosome clades use leech vectors without sporocyst formation, and they only formed micro-merozoites in their turtle, frog or fish hosts. In contrast, members of the *Hepatozoon*, *Karyolysus* and *Hemolivia* clades use tick vectors with sporocyst (or sporokinete) formation, and they formed macro-merozoites in their mammal or reptile hosts.

Haemogregarina spp. have been described from a wide variety of vertebrate hosts; including reptiles (chelonians, crocodiles, snakes, lizards), amphibians (toads, frogs, salamanders), fish, and birds. The type species (*H. stepanowi*) infects chelonians and leeches, so the genus *Haemogregarina s.s*. is considered to contain all species in chelonians, although it has yet to be unequivocally shown that they all have leech vectors in which oocysts produce 8 naked sporozoites. Species of *Haemogregarina s.s.* have been found around the world in a range of freshwater turtles and terrestrial tortoises. Other species infecting fish have been classified as *Haemogregarina s.l.* as little is known about their vectors and sporogonic cycles. Many haemogregarines have been found in bony fish from marine habitats as diverse as intertidal rock pools to submarine canyons, and several species have also been detected in cartilaginous fishes, such as sharks, skates and rays. A smaller number of species have been found in bony fish from freshwater habitats as diverse as ditches, rivers and lakes, with several species are found in catadromous or anadromous fish (such as eels and some salmonids) which spend some of their life-cycles at sea. The taxonomic classification of haemogregarines in lizards, snakes, crocodilians and birds is confounded because not enough information is known about their developmental cycles, especially sporogonic development in their vectors (required for assignment to correct family and genus). Every *Haemogregarina* spp. described from non-chelonian reptiles, amphibians and birds for which sporogonic development was subsequently discovered, had multisporocystic oocysts and they were consequently transferred to the genus *Hepatozoon* in keeping with generic defining characters. It was further suggested that all other *Haemogregarina* spp. from non-chelonian reptiles, amphibians and birds (around 200 species) be similarly transferred to the genus *Hepatozoon* pending identification of their vectors and developmental cycles. This follows the earlier precedents of mass transfers of *Haemogregarina* spp. described from birds and mammals, as well as many non-avian *Leucocytozoon* spp., to the genus *Hepatozoon*. The situation is far from clear, and the various public databases continue to list many *Haemogregarina* spp. from non-chelonian reptiles and amphibians. In this document, those species are listed under the genus *Hepatozoon* (origins and status indicated by synonyms).

***Haemogregarina* species**	**Gamont dimensions (µm)**	**Hosts**	**Location***	**Vectors**	**Distribution**
Haemogregarina s.s. (species in Testudines, with leech vectors)					
H. bagensis	25-30 x 4-5	geoemydid (Spanish pond turtle)	rbc		Tunisia
H. balli	8-14.5 x 3-6.5	chelydrids (snapping turtle), emydid (spotted turtle, painted turtle); geoemydid (Mediterranean pond turtle)	rbc	Hirudinea: glossiphoniid (*Placobdella parasitica, ornata*)	Canada
H. billeti (syn. *H. choudhuryi, gangetica, laverani, malabarica, mesnili, vittatae, xavieri*)	8-9.6 x 2-4.8, elongate forms 17-26	trionychid (softshell turtles, flapshell turtles), emydid (pond turtles)	rbc	Hirudinea: glossiphoniid (*Helobdella nociva*)	India, Sri Lanka
H. bongaonensis	6.5-13.6 x 1.3-4.4	trionychid (softshell turtle)	rbc		India
H. botuliformis	16 x 6	geoemydid (Chinese pond turtle)	rbc		China
H. chelodinae (syn. *H. clelandi, H. dentata*)	7-12 x 7-9	chelid (eastern long-necked turtle, northern snake-necked turtle, broad-shelled river turtle, Murray River turtle, Krefft's turtle, saw-shelled turtle, northern snapping turtle)	rbc		Australia
H. chinemydis	17-19 x 4-5	geoemydid (Chinese pond turtle)	rbc		China
H. clelandi	7-20 x 4-12	chelid (snake-necked turtles)	rbc		Australia
H. clemmydis		emydid (spotted turtle), trionychid (flapshell turtle), geoemydid (Japanese pond turtle)	rbc		Japan

H. cuorae	16-18 x 2-3	geoemydid (Asian box turtle)	rbc		China
H. dimorphon		testudinid (tortoise)	rbc		
H. emydae	8 x 4	trionychid (Chinese softshell turtle)	rbc		Japan
H. fitzsimonsi [molecular evidence suggests close relationship with *Hepatozoon*]	17-18 x 3-4	testudinid (Bell's hinged tortoise, angulate tortoise, leopard tortoise)	rbc	Acari: ixodid (*Amblyomma sylvaticum, A. marmoreum*)	South Africa
H. galeata	11-13 x 5	trionychid (Chinese softshell turtle)	rbc		China
H. ganapatii	6-11.5 x 3-4.5	trionychid (flapshell turtle)	rbc		India
H. hubeiensis		trionychid (Chinese softshell turtle)	rbc		China
H. hydromedusae		chelid (snake-necked turtle)	rbc		Australia
H. ibera		testudinid (tortoise)	rbc		Europe
H. labbei		emydid (spotted turtle), chelid (twist-necked turtle)	rbc		South America
H. macrochelysi		chelydrid (alligator snapping turtle)	rbc		North America
H. maputensis		pelomedusid (side-necked turtle)	rbc		Africa
H. nicorae	10	geoemydid (Indian black turtle)	rbc	Hirudinea: ozobranchid (*Ozobranchus shipleyi*)	India, Sri Lanka
H. parvula		testudinid (Bell's hinged tortoise)	rbc		South Africa
H. pellegrini	two forms: 15-19 x 6-9, 11-15 x 4-6	geoemydid (Mekong snail-eating turtle), platysternid (big-headed turtle)	rbc		Thailand, China, Vietnam
H. pelusiensi	12.5-24 x 3.4-9	geoemydid (Caspian turtle), pelomedusid (serrated hinged terrapin)	rbc	Hirudinea: glossiphoniid (*Placobdella multistrigata*)	South Africa
H. podocnemis		podocnemidid (yellow-spotted Amazon River turtle)	rbc		South America
H. pseudemydis		emydid (sliders, cooters, box turtle, map turtle), kinosternid (eastern mud turtle), chelydrid (common snapping turtle), trionychid (spiny softshell turtle)	rbc, wbc	Hirudinea: glossiphoniid (*Placobdella parasitica*)	Central and North America
H. rara	15 x 2-3	geoemydid (Chinese pond turtle)	rbc		East Asia
H. reichenowi		trionychid (softshell turtle)	rbc		Africa
H. sacaliae	12-15 x 6-8	geoemydid (four-eyed turtle)	rbc		Vietnam
H. sinensis	11-12 x 4-5	trionychid (Chinese softshell turtle)	rbc	Hirudinea (*Mooreotorix cotylifer*)	China
H. stepanowi [type species]	29-37 x 3-5.5	emydid (European pond turtle, Sicilian pond turtle, painted turtle, Blanding's turtle, river cooter, Big Bend slider), chelydrid (common snapping turtle), testudinid (hinge-back tortoise, marginated tortoise), kinosternid (mud turtle, musk turtles), trionychid (softshell turtles)	rbc	Hirudinea: glossiphoniid (*Placobdella catenigera, costata*)	Europe, North America, Africa

H. stepanowiana	18-20 x 5	geoemydid (Chinese pond turtle)	rbc		South-East Asia
H. sternotheri		pelomedusid (side-necked turtle)	rbc		Africa
H. striata		trionychid (Aubry's flapshell turtle)	rbc		Africa
H. sundarbanensis		trionychid (Indian flapshell turtle)	rbc		India
H. testudinis	11-13 x 5-6	testudinid (Asian forest tortoise)	rbc		Indo-Malaysia
H. trionyxis		trionychid (African softshell turtle)	rbc		Africa
Haemogregarina s.l. (species in fish; with leech and isopod vectors)					
species in marine fish producing 2 or more gamonts per erythrocyte ('schizo-haemogregarines')					
H. bigemina (syn. *H. fragilis, Desseria fragilis*)	paired gamonts 10 x 2	Acanthuriformes: acanthurid (surgeonfish, tangs); Anguilliformes: muraenid (morays); Aulopiformes: synodontid (lizardfish); Beloniformes: belonid (needlefish), hemiramphid (halfbeaks); Blenniformes: blenniid (shanny, tompot, Montagu's blenny), clinid (bluntnose klipfish, highfin klipfish, orange clinid); Carangiformes: carangid (trevallies, amberjack), coryphaenid (dolphinfish), rachycentrid (kingfish); Cypriniformes: cyprinid (bream); Gobiiformes: gobiid (gobies); Istiophoriformes: istiophorid (sailfish), sphyraenid (barracuda); Labriformes: labrid (wrasse), scarid (parrotfish); ; Mugiliformes: mugilid (mullet); Perciformes: gerreid (mojarras), haemulid (grunts), kyphosid (chub), lutjanid (snapper, emperor), malacanthid (tilefish), mullid (goatfish), percid (perch), pomacanthid (angelfish), pomacentrid (sergeant-major); serranid (seabass, groupers); Scombriformes: scombrid (frigate tuna, mackerel); Scorpaeniformes: cottid (sculpins); Spariformes: sparid (porgies); Tetraodontiformes: balistid (triggerfish); Trachiniformes: pinguipedid (sandperch)	rbc, wbc	Isopoda: gnathiid (*Gnathia maxillaris, aureamaculosa*?)	Europe, North America, South Africa, Red Sea, South Pacific
H. polypartita	16 gamonts	Gobiiformes: gobiid (rock goby)	rbc		Europe
H. quadrigemina	4 gamonts 18 x 17	Callionymiformes: callionymid (common dragonet)	rbc		France
H. rubrimarensis	paired gamonts 12 x 1.5	Acanthuriformes: acanthurid (surgeonfish); Labriformes: scarid (parrotfish)	rbc		Red Sea
H. sachai	paired gamonts 5.5-10.9 x 1.1-2.0	Pleuronectiformes: scophthalmid (turbot)	wbc, rbc (myeloid leucosis)		Scotland
H. simondi	4, 6, 8 gamonts 9-19 x 1.5-3.6	Pleuronectiformes: soleid (common sole)	rbc, wbc	Hirudinea: piscicolid (*Hemibdella solea*), Copepoda:	Europe

				pennellid (*Lernaeocera*)	
species in marine fish producing one gamont per erythrocyte (with or without polar cap))					
H. balistapi		Tetraodontiformes: balistid (lagoon triggerfish)	rbc	Isopoda: gnathiid (*Gnathia aureamaculosa*)	Australia
H. bathysauri	13.8-17.6 x 3.3-4.3	Aulopiformes: synodontid (lizardfish)	rbc		Cape Verde Islands
H. binucleata		Callionymiformes: callionymid (dragonet)	rbc		England
H. blanchardi		Gobiiformes: gobiid (goby)	rbc		Europe
H. callionymi		Callionymiformes: callionymid (dragonet)	rbc		Europe
H. clavata	32 x 2.5	Pleuronectiformes: soleid (common sole)	rbc		Europe
H. coelorhynchi	polar caps	Gadiformes: macrourid (javelin fish), morid (cod)	rbc		New Zealand
H. curvata	6.3-7.9 x 0.9-2.3	Blenniformes: blenniid (horned blenny), clinid (bluntnose klipfish)	rbc	Hirudinea: piscicolid (*Zeylanicobdella arugamensis*)	South Africa
H. gobii		Gobiiformes: gobiid (goby)	rbc		Europe
H. hartochi		Gobiiformes: gobiid (goby)	rbc		Europe
H. hoplichthys	12.6 x 3.8, with polar cap	Scorpaeniformes: platycephalid (flathead)	rbc		New Zealand
H. koppiensis	6.1-9.8 x 2.0-3.6	Tetraodontiformes: tetraodontid (pufferfish)	rbc		South Africa
H. labri		Labriformes: labrid (wrasse)	rbc		Europe
H. leptoscopi	polar caps	Trachiniformes: uranoscopid (stargazer)	rbc		New Zealand
H. marzinowskii		Gobiiformes: gobiid (black goby)	rbc		Mediterranean
H. michaeljohnstoni	13.8-16.7 x 3.2-3.3	Ophidiiformes: ophidiid (brotulas)	rbc		Cape Verde Islands
H. minuta		Gobiiformes: gobiid (sand goby)	rbc		Mediterranean
H. parmae		Perciformes: pomacentrid (damselfish)	rbc		Australia
H. platessae (syn. *H. achiri, bothi, flesi, laternae*)	7.7 x 1.4	Pleuronectiformes: paralichthyid (flounder), pleuronectid (European plaice), scophthalmid (turbot), soleid (common sole)	rbc		France, North America
H. pollachii		Gadiformes: gadid (cod)	rbc		Europe
H. roelofsi		Scorpaeniformes: scorpaenid (black rockfish)	rbc		North America
H. rovignensis		Scorpaeniformes: triglid (streaked gurnard)	rbc		Africa
H. salariasi		Blenniformes: blenniid (blenny)	rbc		Fiji
H. scorpaenae		Scorpaeniformes: scorpaenid (scorpionfish)	rbc		Europe
H. tetraodontis	7.5-8.5 x 1-1.5	Tetraodontiformes: tetraodontid (pufferfish)	rbc		Australia
H. wladimirovi		Gobiiformes: gobiid (goby)	rbc		Europe
H. yakimovikohli		Gobiiformes: gobiid (goby)	rbc		Europe
species in marine cartilaginous fish (Chondrichthyes)					
H. carchariasi	34	Lamniformes: odontaspidid (sand tiger shark)	rbc		Australia
H. delagei	11.3 x 3.7 some polar caps	Rajiformes: rajid (skates); Squaliformes: squalid (dogfish sharks)	rbc		?
H. hemiscyllii	22-23.5 x 7-9.5	Orectolobiformes: hemiscylliid (epaulette shark)	rbc		Australia
species in freshwater fish					

H. acipenseris	5.9 x 2.4	Acipenseriformes: acipenserid (sturgeon)	rbc		Volga River
H. daviesensis		Ceratodontiformes: lepidosirenid (South American lungfish)	rbc		South America
H. escoi (syn. *Hepatozoon, Leucocytogregarina*)		Esociformes: esocid (pickerel)	rbc		Europe
H. majeedi		Cypriniformes: cyprinid (binni)	rbc		Middle-East
H. meridianus		Mugiliformes: mugilid (mullet)	rbc		Middle-East
H. thyrsoideae		Anguilliformes: anguillid (eels)	rbc		India

*rbc = red blood cells (erythrocytes), wbc = white blood cells (leucocytes)

Haemogregarines from fish that have been shown to form 16 or more sporozoites in leech vectors (Glossiphonidae and Piscicolidae) have been allocated to the genera *Cyrilia* (with erythrocytic merogony) and *Desseria* (with exo-erythrocytic merogony, although the exact location of schizogony has not been determined for many species and infected blood cells may be sequestered in visceral organs).

Parasite species	**Gamont dimensions (µm)**	**Hosts**	**Location**	**Vectors**	**Distribution**
Genus ***Cyrilia*** (merogony and gamogony in blood of freshwater fish, glossiphonid leech vectors)					
C. lignieresi (syn. *C. gomesi*) [type species]		Synbranchiformes: synbranchid (swamp eel)	wbc, rbc	Hirudinea: glossiphoniid (*Haementeria lutzi*)	Central and South America
C. nili (syn. *Desseria nili*)		Anabantiformes: channid (obscure snakehead); Cichliformes: cichlid (tilapia); Siluriformes: bagrid (catfish)	rbc	Hirudinea: glossiphoniid (*Batracobdelloides tricarinata*)	Africa
C. uncinata	24.6 x 5.7, polar caps	Scorpaeniformes: zoarcid (eelpout)	rbc	Hirudinea: piscicolid (*Johanssonia* sp.)	North America
Genus ***Desseria*** (merogony in tissues, gamogony in blood of fish, piscicolid leech vectors)					
species in freshwater teleost fishes					
D. baueri		Scorpaeniformes: cottid (sculpins)	rbc		Asia
D. catostomi	14.5 x 4.5	Cypriniformes: catostomid (suckers)	rbc		North America
D. colisa		Anabantiformes: osphronemid (gouramis)	rbc		West Bengal
D. cotti (syn. *Haemogregarina*)		Scorpaeniformes: cottid (sculpins)	rbc		Europe
D. irkalukpiki	17.2 x 3.2	Salmoniformes: salmonid (char)	rbc		Canada
D. lepidosirensis (syn. *Hg. bertoni*)	capsule	Ceratodontiformes: lepidosirenid (lungfish)	rbc		South America
D. ninakohlyakimovae		Cypriniformes: cyprinid (barbels)	rbc		Europe
D. parasiluri		Siluriformes: bagrid (catfish)	rbc		Asia
D. tilapiae		Cichliformes: cichlid (tilapia)	rbc		Africa
D. turkestanica		Siluriformes: bagrid (catfish)	rbc		Asia
D. vltavensis	12.5 x 3.4	Perciformes: percid (European perch)	rbc		Czechoslovakia
species in marine teleost fishes					
D. acanthoclini (syn. *Hepatozoon*)		Perciformes: plesiopid (roundheads, New Zealand rockfish)	rbc		New Zealand
D. aeglefini (syn. *Hg. urophysis*)	8-14.9 x 1.4-4.4, with polar cap	Gadiformes: gadid (haddock, cod, pollock), merlucciid (hake)	rbc		Northwest Atlantic
D. anarhichadis	polar caps	Scorpaeniformes: anarhichadid	rbc	Hirudinea: piscicolid	Europe

		(wolffish)		(*Platybdella anarrhichae*)	
D. brevoortiae		Clupeiformes: clupeid (menhaden)	rbc		North America
D. cataphracti		Scorpaeniformes: agonid (hooknoses)	rbc		Europe
D. dakarensis		Perciformes: haemulid (grunts)	rbc		Europe
D. georgianae (syn. *Haemogregarina*)		Perciformes: bathydraconid (Antarctic dragonfish)	rbc		Antarctica
D. gilbertiae		Perciformes: latid (seaperch)	rbc		Australia
D. harriottae	7.4-9.6 x 2.7-3.5	Chimaeriformes: rhinochimaerid (narrownose chimaera)	rbc		Cape Verde Islands
D. leptocotti (syn. *Hg. reolofsi*)	6.1-2.1	Scorpaeniformes: cottid (Pacific staghorn sculpin), sebastid (rockfish)	rbc		North America, South Africa
D. londoni	capsule	Blenniformes: blenniid (blennies)	rbc		Europe
D. marshalllairdi	10.1-14.9 x 3-3.9	Gadiformes: macrourid (rattails, grenadiers); Notacanthiformes: halosaurid (abyssmal halosaur)	rbc		Cape Verde Islands, North America
D. mavori		Scorpaeniformes: zoarcid (ocean pout)	rbc		North America
D. moringa		Anguilliformes: muraenid (spotted moray eel)	rbc		South America
D. mugili		Gobiiformes: gobiid (gobies); Mugiliformes: mugilid (mullet)	rbc		South America
D. myoxocephali [type species]	7.8 x 2.4	Scorpaeniformes: agonid (sculpins)	rbc	Hirudinea: piscicolid (*Malmiana nuda, scorpii*)	Northwest Atlantic
D. nototheniiae		Perciformes: nototheniid (cod icefish)	rbc		Antarctic
D. rovignensis	polar cap	Scorpaeniformes: trigilid (gurnard)	rbc		Italy
D. thyrsoideae		Anguilliformes: muraenid (moray eel)	rbc		India
D. zei		Zeiformes: zeid (dories)	rbc		South Africa
D. zeugopteri		Pleuronectiformes: scophthalmid (turbot)	rbc		Europe
species in marine cartilaginous fishes					
D. dasyatis (syn. *Haemogregarina*)		Myliobatiformes: dasyatid (southern stingray)	rbc		North America
D. heterodonti		Heterodontiformes: heterodontid (bullhead shark)	rbc		Asia
D. torpedinis (syn. *Hg. lobianci*)		Torpediniformes: torpedinid (electric rays)	rbc		Europe

Parasite morphology: Haemogregarines form 4 different types of developmental stages: meronts and gamonts in intermediate hosts; and gametes and oocysts in definitive hosts (vectors). Meronts (sometimes called schizonts) appear as rounded basophilic bodies ranging in size from 9-24 µm that are located intracellularly in erythrocytes (*Haemogregarina*, *Cyrilia*) or host viscera (*Desseria*). They undergo internal division to form several (2-8 for *Haemogregarina* and *Cyrilia*, 12-25 for *Desseria*) slender merozoites ranging in size from 9-13 x 2-3 µm. A few early descriptions reported some larger schizonts with up to 70-140 merozoites, but they have not been observed since. Gamonts appear as broad fusiform bodies usually located intracellularly within host erythrocytes (sometimes with more than one gamont per erythrocyte), although they may occasionally be detected in leucocytes or extracellularly in blood smears. They may be crescent-, sausage- or club-shaped, range in size from 8-15 x 2-7 µm, and some appear to have small polar caps. Intra-erythrocytic gamonts are often larger that the host cell nucleus and usually displace it laterally. Gamonts have a single conspicuous nucleus, which is generally discrete and central, but sometimes may be diffuse or

fragmented. Microgamonts (male) have club-shaped nuclei tapering posteriorly, the cytoplasm stains blue with red inclusions, and many possess a short-recurved tail. Macrogamonts (female) have a central rounded nucleus, the cytoplasm stains blue with flocculent material, and they do not possess tails. While many haemogregarine species have been described solely on the basis of host occurrence and gamont morphology, their correct allocation to genera is dependent on differentiating oocysts formed in invertebrate vectors (data lacking for most species). In the vector, ingested gamonts form macrogametocytes (female) and microgametocytes (male) which associate pairwise (syzygy) and develop into anisogamous (dissimilar) gametes. Macrogametes remain as single rounded cells, while microgametocytes lose their tails and produce 1-4 microgametes, most reported to have a single terminal flagellum (although those of some species appear to have no flagella, and other rarely 2 flagella). Fertilization produces a non-motile zygote that begins oocyst formation within a flexible membrane, young undifferentiated oocysts being subspherical (6-9 x 5-8 µm) and growing in size as they mature (10-22 x 8-15 µm). Parasite species that form 4-16 (usually 8) naked sporozoites (not enclosed within sporocysts) have been allocated to the genus *Haemogregarina* (*s.s.* in turtles, s.l. in fish), while those that form 16 or more sporozoites have been allocated to the genera *Cyrilia* and *Desseria* (genera differentiated on the basis of the site of merogony in fish: erythrocytic in *Cyrilia,* and exo-erythrocytic in *Desseria*). The sporozoites are elongate (8-14 x 3-6 µm) tapering posteriorly, and possess a central nucleus and several crystalloid inclusion bodies. Ultrastructural studies have demonstrated the presence of typical apicomplexan organelles in various developmental stages: with most containing polar rings and micropores, and all non-gamete stages bearing an anterior conoid. The cells possessed cristate mitochondria but lacked amylopectin granules (present in *Hepatozoon*).

Site of infection: Hundreds of haemogregarine species have been described from a wide range of vertebrate hosts, including reptiles, amphibians, fish, birds and mammals. Over time, studies on parasite developmental cycles indicated that several genera may be involved. It was suggested that haemogregarines from mammals, birds, snakes, lizards, crocodiles and amphibians be transferred *en masse* to the genus *Hepatozoon* pending further studies. This left haemogregarines in tortoises as members of the genus *Haemogregarina s.s.* (*sensu stricto*, in the strictest sense), while haemogregarines of fish were left in the genus *Haemogregarina sensu lato* (*s.l.*, in the broadest sense) or allocated to the sibling genera *Cyrilia* or *Desseria.* Both *Haemogregarina* and *Cyrilia* spp. form erythrocytic meronts, while *Desseria* spp. form exo-erythrocytic meronts. Infected blood cells often become trapped or sequestered in visceral organs, including the liver, lungs, spleen, bone marrow and occasionally the heart and brain. Gamonts of all 3 genera are then found within erythrocytes (sometimes leucocytes) of their chelonian or piscine hosts. Some 35 species of *Haemogregarina s.s.* have been recorded in around 50 tortoise species (belonging to 10 families). Around 38 species of *Haemogregarina s.l.* have been reported in fish, including 32 species in marine fish belonging to 65 species (in 49 families in 25 orders), and 6 species in freshwater fish belonging to 6 species (in 6 families in 6 orders). Three *Cyrilia* spp. have been found in freshwater fish belonging to 5 species (in 5 families in 5 orders), and 35 *Desseria* spp. have been reported, with 24 species occurring in marine fish belonging to 31 species (in 26 families in 15 orders) and 11 species in freshwater fish belonging to 9 species (in 9 families in 8 orders). In those species for which vectors have been determined, gametogony and oocyst formation occur in the gut epithelia of aquatic invertebrate hosts, predominantly leeches, but including some isopods and rarely copepods.

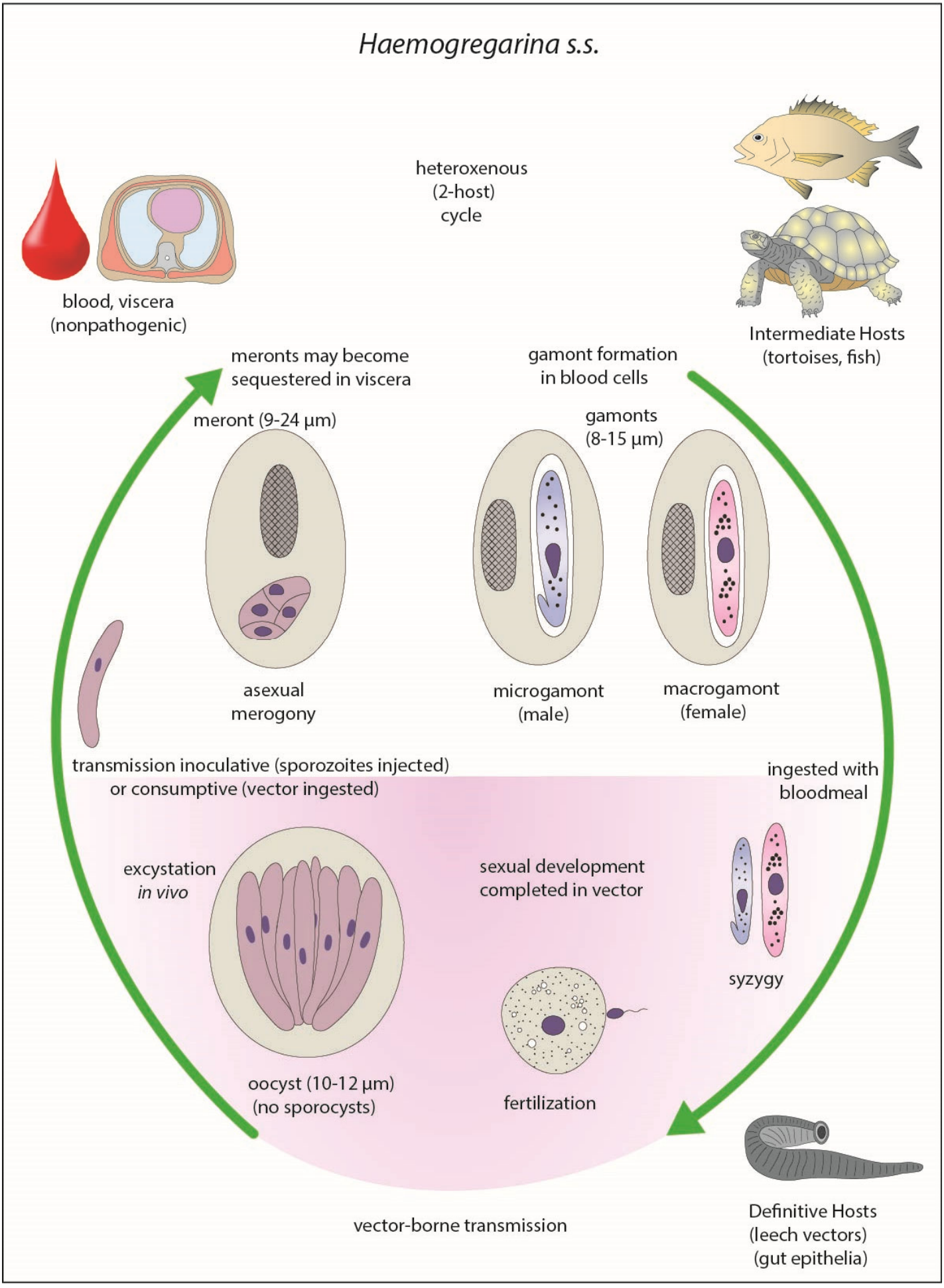
Pathogenesis: Infections by haemogregarines in vertebrates have not been associated with any specific clinical disease, neither during the asexual merogonous proliferation of parasites in blood cells or tissues, nor during the carriage of gamonts in blood cells (even when some parasitaemias exceed 30%). While merogony ultimately leads to host cell lysis to release the contained merozoites, the extent of damage to the host appears to be minimal and usually does not lead to clinical signs. Gamonts that develop in host erythrocytes may persist for long periods and while they may cause variation in erythrocyte morphology (modest hypertrophy, turgidity and nuclear displacement), they are not thought to cause significant haemolysis. Nevertheless, several studies have reported changes in haematological parameters in a few hosts (mainly freshwater fish), but they have often been contradictory, e.g. red cell counts decreased in sturgeon but elevated in other species, and variable but inconsistent white cell counts in several species (esp. lymphocytes, neutrophils and monocytes). Long-standing infections in pond turtles in a European zoo were linked to poor health, general weakness, anorexia, skin haemorrhages, visceral hyperaemia (lungs, liver, kidneys, spleen), reduced hematocrits, and shell lesions often with secondary bacterial or fungal infections. It has often been suggested that subclinical infections in fish may still affect fish health, growth and survival, even resulting in reduced productivity in commercial fisheries and aquaria (particularly in fish stressed by poor water quality and crowded conditions). Some leucocyte infections in cultured marine fish (mostly turbot) have been associated with a proliferative disease (myeloid leucosis or lymphoma-like condition), with lesions comprised entirely of encapsulated aggregates of merozoites or infected macrophages embedded in granulomatous tissue.

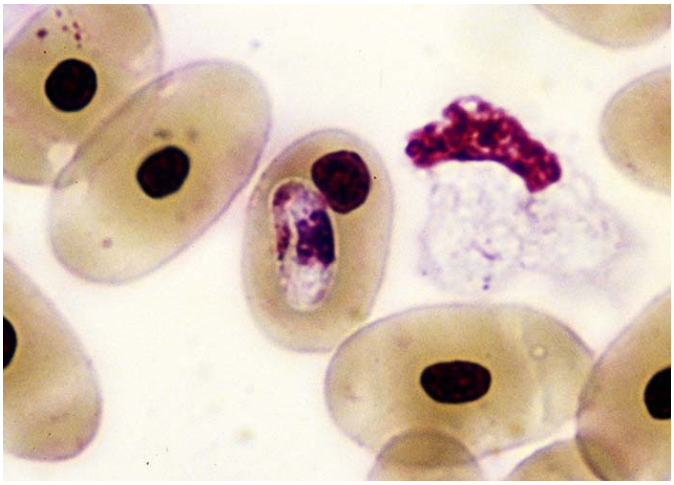
Developmental cycle and mode of transmission: The complete developmental cycles have only been determined for a handful of haemogregarine species, but they have involved obligative heteroxenous (2-host) life-cycles with asexual merogony and gamont formation occurring in the vascular system of vertebrate hosts (intermediate hosts) and sexual gamogony and oocyst formation occurring in the gut of haematophagous invertebrate hosts (vectors or definitive hosts). Vertebrate hosts become infected when sporozoites invade tissues where they form intracellular meronts (schizonts) within blood cells or vascular endothelial cells. An intracellular pre-meront (or trophozoite) stage has occasionally been observed for some species. Most *Haemogregarina* and *Cyrilia* spp. infect erythrocytes, although some species may also infect leucocytes. Infected cells tend to be sequestered in visceral organs. *Desseria* spp. infect endothelial cells in various host tissues. The parasites proliferate asexually by endogenous division (an internal budding process) with meronts producing numerous merozoites. Studies have implicated multiple meront generations in the parasite

proliferative cycles, with some species forming macro-meronts producing small numbers of large merozoites, and other species forming micro-meronts producing larger numbers of smaller merozoites. Several studies have indicated that some species with persistent tissue-phase meronts may possibly be transmitted horizontally between vertebrate hosts by predation (when infected fish are eaten by larger predators), but such transmission remains to be proven. Eventually, merozoites invade erythroblasts or erythrocytes and develop into gamonts, with many studies also describing pre-gamont stages. Haemogregarines have been allocated to 2 broad groups depending on whether cells undergo division immediately before gamont formation: with 'schizo-haemogregarines' or those of the '*bigemina*-group' dividing to form paired (or multiples of two) undifferentiated gamonts; and those of the '*rovignensis*-group' not dividing but forming single monomorphic or sexually dimorphic gamonts, some with deeply staining polar caps. The intra-erythrocytic gamonts are infective to haematophagous vectors (mainly leeches, and some isopods and copepods) when they feed on host blood. The gamonts differentiate in the gut and undergo extracellular gametogenesis often on the microvillous surface of epithelial cells. Female macrogametocytes and male microgametocytes pair up (in syzygy) and form single 'egg-like' macrogametes and several 'sperm-like' microgametes. Fertilization occurs by gamete fusion resulting in a non-motile zygote that initiates oocyst formation within a flexible membrane (rather than a heavy oocyst wall like enteric coccidia). Developing oocysts undergo sporogony forming multiple sporozoites that are not enclosed within secondary cysts (sporocysts) but lie 'naked' within the oocyst. *Haemogregarina* spp. form oocysts with 4-16 (usually 8) naked sporozoites, while *Cyrilia* and *Desseria* spp. form oocysts with more than 16 sporozoites. The oocysts excyst endogenously releasing sporozoites which may be found in various vector tissues, especially the salivary glands. Sporozoites from some species are also thought to undergo one round of merogonous division in vector tissues. The sporozoites and/or merozoites are infective to vertebrate hosts, with transmission being inoculative (sporozoites/merozoites injected during feeding) or consumptive (infected vector eaten during grooming). Some fish haemogregarines have demonstrated strong seasonal patterns of infection, with heavy infections developing in marine hosts when temperatures were higher in spring and summer, while heavy infections developed in freshwater hosts when water temperatures were lower. Besides water temperature, other factors influencing parasite distribution and abundance including host and vector biogeography and population densities, migratory behaviours, and host stress factors (relating to nutritional state and spawning behaviours).

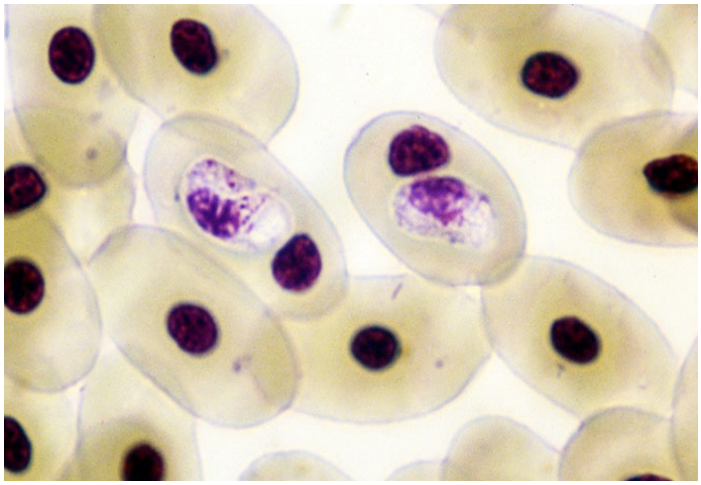
Differential diagnosis: Infections in turtles and fish are predominantly asymptomatic and resistant parasite stages are not voided from hosts. Parasites are usually detected incidentally by the microscopic detection of characteristic intra-erythrocytic gamonts in blood smears stained with Giemsa. Specific and generic identification based solely on gamont morphology is not possible as *Haemogregarina*, *Cyrilia* and *Desseria* spp. form similar gamonts which often includes sexual dimorphism. Meronts (schizonts) are usually detected by the microscopic examination of blood smears and histological sections. *Haemogregarina* and *Cyrilia* spp. form intra-erythrocytic meronts, while *Desseria* spp. form exo-erythrocytic schizonts, but the sequestration of infected cells in host tissues can confound the actual site of infection. Infections in leeches are usually detected by the microscopic examination of fresh squash preparations or fixed histological sections of gut epithelia looking for developing oocysts. Mature oocysts of *Haemogregarina* spp. form oocysts with 4-16 (usually 8) naked sporozoites, while *Cyrilia* and *Desseria* spp. form oocysts with more than 16 naked sporozoites. More recently, molecular biological techniques have also been used to characterize parasites and infer phylogenetic relationships by the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA).

Treatment and control: Treatment is generally not required as most infections are benign and do not produce clinical disease, so there are few historical reports involving chemotherapy. However, several captive turtles with shell lesions had concomitant haemogregarine infections that were tentatively linked to anaemia, low haemoglobin, basophilia, eosinophilia, heterophilia and azurophilia. Haemogregarine numbers declined in some turtles following combination therapies involving the systemic application of antiprotozoals (metronidazole), anthelmintics (albendazole, mebendazole) and antibiotics (enrofloxacin) together with debridement and scrubbing of lesions with disinfectants. Various preventive measures were instituted in captive or culture facilities to eliminate potential sources of infection (routine pond cleaning, vector control) and ensure healthy rearing conditions to avoid chronic host stress and hence susceptibility (avoid over-handling and over-crowding, maintain water quality, and provide good nutrition without contributing to organic enrichment). The eventual elimination of long-standing haemogregarine infections in some zoo turtle collections was attributed to the regular mechanical removal of leeches.


Haemogregarina s.s.
heteroxenous
(2-host)
cycle
blood, viscera
(nonpathogenic)
Intermediate Hosts
(tortoises, fish)
meronts may become
sequestered in viscera
gamont formation
in blood cells
meront (9-24 µm)
gamonts
(8-15 µm)
asexual
merogony
microgamont
(male)
macrogamont
(female)
transmission inoculative (sporozoites injected)
or consumptive (vector ingested)
ingested with
bloodmeal
excystation
in vivo
sexual development
completed in vector
syzygy
oocyst (10-12 µm)
(no sporocysts)
fertilization
vector-borne transmission
Definitive Hosts
(leech vectors)
(gut epithelia)



Haemogregarina s.s. gamont in tortoise blood



Haemogregarina s.s. gamonts in tortoise blood

Hepatozoon
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia (including the blood parasites paradoxically known as 'haemogregarines') in marine and terrestrial animals; and eimeriid coccidia in vertebrates. Haemogregarines are heteroxenous (2-host) parasites where merogony and gamogony occurs in the vascular system of a vertebrate host while sporogony occurs in a haematophagous invertebrate host (vector). They are common blood parasites in reptiles and some occur in fish, amphibians, birds and mammals. Four main assemblages are recognized: haemogregarinids, karyolysids, hepatozoids and dactylosomatids. Hepatozoids (*Hepatozoon*) produce oocysts containing numerous sporocysts in the gut or haemocoel of various vectors (leeches, insects, acarines). Vertebrates are infected by ingesting vectors, and merogony (= schizogony) occurs in vascular endothelial cells prior to the formation of gamonts in erythrocytes and/or leucocytes. Cystic stages have been associated with tissue lesions and may contribute to persistent infections. Given the paucity of information on the developmental biology of most species, it has been suggested that all members of the genus *Haemogregarina* in snakes, crocodiles, lizards, amphibians, birds and mammals (but not tortoises or fish) be transferred to the genus *Hepatozoon* pending determination of their vectors and developmental cycles.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Adeleina (syzygy, 1-4 microgametes)
Family:	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)
Genus:	*Hepatozoon* (vector-borne tissue parasites)
Species:	various species cause infections in rodents and domestic animals

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia

are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as 'haemogregarines' in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Haemogregarines are heteroxenous (2-host) parasites where merogony (= schizogony) and gamogony occurs in the vascular system of a vertebrate intermediate host while fertilization and sporogony occurs in a haematophagous invertebrate definitive host (vector). They are common blood parasites in reptiles and fish and some occur in amphibians, birds and mammals. Infections are generally considered to be nonpathogenic, even when high parasitaemias are present. Haemogregarines are classified together with other coccidia, specifically with the adeleorine coccidia in marine and terrestrial animals. These parasites undergo sexual reproduction involving the formation of macro- and micro-gametes which associate pairwise in syzygy so comparatively few microgametes are produced (usually 1-4). The resultant zygote forms an oocyst containing infective sporozoites which are

transmitted to vertebrates when infected vectors are eaten (consumptive) or when they feed on vertebrate blood (inoculative). Over 450 haemogregarine species have been described in vertebrate blood, most records being confined to the detection of intra-erythrocytic stages (almost exclusively gamonts) which do not produce haemozoin pigment. Numerous species were described simply on the basis of host occurrence but little is known about their actual host specificity or developmental cycles. Despite early confusion, there has been growing acceptance of the recent classification of haemogregarines into four families: Haemogregarinidae containing the genera *Haemogregarina*, *Cyrilia* and *Desseria*; Hepatozoidae containing the genus *Hepatozoon;* Karyolysidae containing the genera *Karyolysus* and *Hemolivia*; and Dactylosomatidae containing the genera *Dactylosoma* and *Babesiosoma* (in addition to 3 other adeleine families: Adeleidae, Klossiellidae and Legerellidae). It has been suggested that the chelonian (tortoise) haemogregarines be regarded as *Haemogregarina sensu stricto* (*s.s.*, in the strictest sense) whereas fish haemogregarines be classified as *Desseria* or *Cyrilia* or left as *Haemogregarina sensu lato* (*s.l.*, in the broadest sense). It was also suggested that all members of the genus *Haemogregarina* in non-chelonian reptiles (snakes, crocodiles, lizards), amphibians, birds and mammals be transferred to the genus *Hepatozoon* pending determination of their vectors and studies on their developmental cycles. All haemogregarines use vertebrates as intermediate hosts for cyclic merogony (often forming macro- then micro-merozoites) in tissues and gamont development in blood cells (mostly red, sometimes white, blood cells). Gamogony is completed in invertebrate definitive hosts (leeches, acarines or dipterans) followed by fertilization and oocyst formation in the gut or haemocoel. The oocysts undergo sporogony resulting in sporozoites lying directly within oocysts (for Dactylosomatidae), within sporocysts (for Hepatozoidae), within tissues (for Haemogregarinidae) or within eggs (for Karyolysidae). The four families are currently differentiated as follows:

- Haemogregarinids produce oocysts with naked sporozoites in the gut of leech vectors, vertebrates are infected by vector bite, and schizogony occurs in host erythrocytes (although infected cells tend to be sequestered in viscera prior to the development of intraerythrocytic gamonts); genera comprise *Haemogregarina s.s.* in turtles and *Haemogregarina s.l., Desseria* and *Cyrilia* in fish.
- Hepatozoids produce oocysts containing numerous sporocysts in the gut or haemocoel of various vectors (leeches, insects, acarines), vertebrates are infected by ingesting vectors, and schizogony occurs in vascular endothelial cells in host tissues (cystic stages also observed contributing to chronic infections and possible paratenic transport); the genus *Hepatozoon* occurs in mammals, reptiles (crocodiles, snakes, lizards), amphibians and birds.
- Karyolysids produce sporokinetes and motile spores in the gut and ova of mite vectors, vertebrates are infected by ingesting mites, and schizogony occurs in host vascular endothelial cells; genera comprise *Karyolysus* and *Hemolivia* in reptiles and amphibians.
- Dactylosomatids produce oocysts which bud sporozoites directly within epithelial cells in the intestines of leech vectors, vertebrates are infected presumably by vector bite and schizogony occurs in host erythrocytes; genera comprise *Dactylosoma* and *Babesiosoma* in reptiles, amphibians and fish.

Family	**Genus**	**No. species**	**Site of development in vertebrate**		**Vertebrate hosts**	**Invertebrate vector**
			meronts	**gamonts**		
Haemogregarinidae	*Haemogregarina*	*s.s.* 38; *s.l.* 42	erythrocytes	erythrocytes	*s.s.* in turtles; *s.l.* in fish	leeches
	Cyrilia	3	erythrocytes	erythrocytes	fish	leeches
	Desseria	35	exo-erythrocytic	erythrocytes	fish	leeches
Hepatozoidae	*Hepatozoon*	341*	viscera	erythrocytes, leucocytes	mammals, reptiles, birds, frogs, fish	leeches, arthropods
Karyolysidae	*Hemolivia*	4	RE cells	erythrocytes	lizards, tortoises, toads	ticks
	Karyolysus	11	viscera ± erythrocytes	erythrocytes	lizards, frogs	mites
Dactylosomatidae	*Dactylosoma*	10	erythrocytes	erythrocytes	reptiles, amphibians, fish	leeches
	Babesiosoma	12	erythrocytes	erythrocytes	fish, amphibians	leeches

*Includes some 200 former *Haemogregarina* spp. from crocodiles, snakes, lizards, amphibians and birds following their mass transfer to the genus *Hepatozoon* pending further characterization

Early phylogenetic studies used cladistics analyses of multiple phenotypic characters (morphology, biology) to reveal several clades apparently associated with different vectors (notably ticks, flies and leeches) rather than particular vertebrate hosts, thus suggesting vector-first evolution. However, such patterns may have arisen due to the environments in which the hosts occurred; e.g. marine hosts with leeches, and terrestrial hosts with ticks or flies. Molecular phylogenetic studies using small subunit (18S) ribosomal RNA sequences revealed any associations between haemogregarines and their vertebrate hosts to be polyphyletic with many mixed clades associated with parasites in snakes, lizards, amphibians and mammals. Detailed analyses revealed five major clades: two *Hepatozoon* clades (clade A associated with carnivores and clade C with reptiles and frogs) separated by an

intermediary *Hemolivia* clade in lizards, and two distant clades, one containing *Haemogregarina* species from tortoises and the other containing *Dactylosoma/Babesiosoma* species from fish and frogs. The five major clades were also well separated with respect to vectors: the former three clades using ticks and flies as vectors and the latter two using leeches. The *Hepatozoon* species in mammals (clade A) were more closely related to *Karyolysus* species from lizards, while the *Hepatozoon* species in frogs and reptiles (clade C) were more closely related to *Hemolivia* species from tortoises and lizards. Several interesting biological associations were evident between polyphyletic clades. *Haemogregarina* s.s. and dactylosome clades use leech vectors without sporocyst formation, and they only formed micro-merozoites in their turtle, frog or fish hosts. In contrast, members of the *Hepatozoon*, *Karyolysus* and *Hemolivia* clades use tick vectors with sporocyst (or sporokinete) formation, and they formed macro-merozoites in their mammal or reptile hosts. Given that *Hepatozoon* did not form a single monophyletic group, it was recently suggested that species from reptiles, amphibians, marsupials, birds and rodents that are transmitted solely by biting insects be transferred to a new genus *Bartazoon*. However, subsequent studies indicated that this genus was not well-supported, so many workers do not recognize *Bartazoon* over *Hepatozoon*.

Infections by *Hepatozoon* spp. have been recorded in tropical and subtropical areas in various vertebrate (reptiles, amphibians, birds, mammals), mostly by the detection of gamonts within erythrocytes and/or leucocytes and the absence of merogonic division in peripheral blood. Instead, merogony occurs with endothelial cells in host tissues, sometimes persisting as cystic forms (monozoic or dizoic) thus contributing to chronic infections (and potentially paratenic transport). For those few species in which the vectors have been determined, transmission from vertebrate to invertebrate occurs during vector blood-feeding, while transmission from invertebrate to vertebrate occurs by the consumption of infected vectors (and not by inoculation through vector bite). Invertebrate vectors have included acarines (mites, ticks), insects (fleas mosquitoes, bugs) and leeches, in which large multisporocystic oocysts are formed within their internal tissues (whereas *Haemogregarina* spp. have leech vectors in which small asporocystic oocysts are formed). Regrettably, the vectors and sporogonous cycles for many species are not known, so their generic placement is uncertain. Studies conducted on several *Haemogregarina* spp. from snakes, lizards and birds revealed that they had arthropod vectors and formed multisporocystic oocysts, so it was suggested that they be transferred to the genus *Hepatozoon.* It was further suggested that all *Haemogregarina* spp. from non-chelonian reptiles and birds (around 200 species) be similarly transferred to the genus *Hepatozoon* pending identification of their vectors and developmental cycles. This follows the earlier precedents of mass transfers of *Haemogregarina* spp. described from birds and mammals, as well as many non-avian *Leucocytozoon* spp., to the genus *Hepatozoon*. To date, over 340 putative *Hepatozoon* spp. have been described, with 509 spp. in mammals, 139 spp. in snakes, 76 spp. in lizards, 6 spp. in crocodiles, 1. sp. in tortoise, 49 spp. in amphibians and 20 spp. in birds. In the following species lists, synonyms have been provided to provide context to the origins and taxonomic status of the *Hepatozoon* spp.

***Hepatozoon* species**	**Gamont dimensions (µm)**	**Hosts**	**Location* (disease)**	**Vectors**	**Distribution**
species in mammals (Mammalia)					
H. acomys		Rodentia: murid (spiny mice)	rbc		Africa, Middle-East
H. akodoni (syn. *Haemogregarina, Leucocytozoon*)		Rodentia: murid (grass mouse)	wbc		South America
H. alactagae (syn. *H. alactaguli*)		Rodentia: dipodid (five-toed jerboa, northern three-toed jerboa, thick-tailed three-toed jerboa, dwarf fat-tailed jerboa)	rbc		Asia
H. americanum	8.8 x 3.9	Carnivora: canid (dogs, coyotes, foxes)	wbc	Acari: ixodid (*Amblyomma maculatum*)	North America, Brazil
H. arvalis (syn. *Leucocytogregarina*)		Rodentia: murid (African grass rat)	wbc		Africa
H. arvicanthis (syn. *H. arvicanthidis*)		Rodentia: murid (African grass rat)	wbc		Africa
H. arvicolae (syn. *Karyolysus*)		Rodentia: cricetid (water vole)	blood cells		Eurasia
H. balfouri (syn. *Haemogregarina, H. jaculi*)		Rodentia: dipodid (jerboas)	wbc (pathogenic experimentally)	Acari: laelapid (*Haemolelaps aegyptius, longipes, centrocarpus*)	North Africa
H. canis (syn. *Leucocytozoon, Leucocytogregarina,*	11 x 4.3	Carnivora: canid (dog, coyote, black-backed jackal, golden jackal,	wbc (fever, anaemia,	Acari: ixodid (*Rhipicephalus sanguineus,*	Europe, Middle-East, Far East,

Haemogregarina, H. rotundata, chattoni, pattoni, Microbesnoitia leoni)		crab-eating fox, red fox, hoary fox, Pampas fox, spotted hyena); procyonid (coati), viverrid (Asian palm civet), felid (cat, cheetah, lion, leopard); Perissodactyla: tapirid (tapir); Didelphimorphia: didelphid (white-eared opossum)	weight loss, splenomegaly, paralysis?)	*decoloratus, microplus, Amblyomma cajennense, maculatum, ovale, sculptum, Haemaphysalis concinna, flava, longicornis, Ixodes ricinus*)	Africa, Americas
H. citellicolum (syn. *Leucocytozoon*)		Rodentia: sciurid (ground squirrel)	wbc		North America
H. criceti (syn. *Leucocytogregarina*)		Rodentia: cricetid (European hamster)	wbc	Acari: laelapid (*Laelaps echidninus*)	Eurasia
H. cricetomysi		Rodentia: nesomyid (Gambian pouched rat)	rbc		Africa
H. cuniculi (syn. *Leucocytogregarina*)		Lagomorpha: leporid (rabbit)	wbc		Europe
H. darjeelingensis		Rodentia: sciurid (flying squirrel)	rbc		Asia
H. dasyuri (syn. *Haemogregarina*)		Dasyuromorphia: dasyurid (eastern quoll)	rbc		Australia
H. dendromi (syn. *H. dendromysi, dendromusi*)		Rodentia: nesomyid (African climbing mouse)	rbc		Africa
H. didelphydis (syn. *Haemogregarina*)		Didelphimorphia: didelphid (American opossum, brown four-eyed opossum, gray four-eyed opossum)	rbc		Americas
H. dolichomorphon		Rodentia: anomalurid (long-eared flying mouse)	wbc		Africa
H. epsteini		Rodentia: murid (brown rat)	wbc		cosmopolitan
H. erhardovae		Rodentia: cricetid (bank vole)	wbc	Siphonaptera: pulicid (*Xenopsylla cheopis*), hystrichopsyllid (*Ctenophthalmus agyrtes, assimilis*), ceratophyllid (*Nosopsyllus fasciatus*)	Eurasia
H. felis (syn. *H. felisdomesticae, Haemogregarina felis-domesticae, Leucocytozoon felis-domestici*)	10.5 x 4.7	Carnivora: felid (cat, wildcat, serval, leopard cat, iriomote cat, jaguar, lion, tiger, caracal, puma, Eurasian lynx)	wbc	Acari: ixodid (*Rhipicephalus sanguineus*)	India, Europe, Americas, Africa
H. funambuli (syn. *Leucocytozoon*)		Rodentia: sciurid (palm squirrel)	wbc		Indo-Asia
H. gaetulum (syn. *H. getulum*)		Rodentia: sciurid (Barbary ground squirrel)	wbc		North Africa
H. gerbilli (syn. *Haemogregarina*)		Rodentia: murid (great gerbil, Indian gerbil, Libyan jird)	rbc	Phthiraptera: haematopinid (*Haematopinus stephensi*)	Asia
H. graomysi		Rodentia: cricetid (gray leaf-eared mouse)	rbc		South America
H. griseisciuri		Rodentia: sciurid	wbc	Acari: laelapid	North

		(eastern grey squirrel)		(*Echinolelaps echidninus*), haemogamasid (*Euhaemogamasus ambulans, Haemogamasus reidi*)	America
H. hoogstraali		Afrosoricida: tenrecid (lowland streaked tenrec)	rbc		Madagascar
H. insectivorae		Eulipotyphla: soricid (common shrew, bicoloured shrew)	wbc		Eurasia
H. krampitzi (syn. *H. microti p.p.*)		Rodentia: cricetid (tundra vole)	wbc		Europe, Asia, North America
H. leporis (syn. *Leucocytozoon*)		Lagomorpha: leporid (Indian hare)	wbc		Indo-Asia
H. leptosoma		Rodentia: cricetid (deer mouse, brush mouse)	wbc		North America
H. luiperdjie		Carnivora: felid (leopard)	wbc		Africa
H. lusitanicum		Rodentia: glirid (garden dormouse)	wbc		Eurasia
H. mereschkowskii		Rodentia: sciurid (speckled ground squirrel, Caucasian ground squirrel)	wbc		Eastern Europe
H. metachiri (syn. *Haemogregarina*)		Didelphimorphia: didelphid (quica opossum)	rbc		South America
H. microti (syn. *H. lavieri, micratai, sylvatici, Haemogregarina*)		Rodentia: cricetid (field vole); dipodid (Severtzov's jerboa); murid (wood mouse, yellow-necked mouse, broad-toothed field mouse); plus exptl. infection in cricetid (bank vole)	wbc	Acari: laelapid (*Laelaps agilis*)	Europe, North Africa
H. muris (syn. *H. innoxia, perniciosus, ratti, Haemogregarina, H. ratti, Leucocytozoon, L. ratti, Leucocytogregarina innoxia*) [type species]		Rodentia: murid (rats, Tullberg's soft-furred mouse)	wbc (pathogenic experimentally)	Acari: laelapid (*Laelaps echidninus*)	cosmopolitan
H. mustelis	nd	Carnivora: mustelid (Siberian polecat)	macrophages		Eurasia, North America
H. musculi (syn. *Leucocytozoon, Leucocytogregarina*)		Rodentia: murid (house mouse)	wbc		cosmopolitan
H. normani		Rodentia: anomalurid (long-eared flying mouse)	wbc		Africa
H. peramelis (syn. *Haemogregarina*)		Peramelemorphia: peramelid (long-nosed bandicoot)	blood plasma		Australia
H. perniciosum		Rodentia: murid (laboratory white rat)	liver, wbc	Acari: laelapid (*Echinolaelaps echidninus*)	North America
H. peromysci		Rodentia: cricetid (brush	wbc		North

(syn. *H. muris p.p.*)		mouse, rock deermouse)			America
H. petauri (syn. *Haemogregarina*)		Diprotodontia: petaurid (sugar glider)	rbc		Australia
H. pitymysi		Rodentia: cricetid (Savi's pine vole)	wbc	Phthiraptera: hoplopleurid (*Hoplopleura acanthopus*); Siphonaptera: ceratophyllid (*Ceratophyllus fasciata*), hystrichopsyllid (*Typhlopsylla assimilis*)	Europe
H. plicatum (syn. *Leucocytogregarina*)		Hyracoidea (unspecified hyrax); Rodentia: ctenodactylid (Spoeke's pectinator)	wbc		East Africa
H. procyonis	10.9 x 5.4	Carnivora: procyonid (raccoon, crab-eating raccoon, South American coati)	monocytes		Americas
H. sciuri (syn. *Haemogregarina*)		Rodentia: sciurid (red squirrel)	wbc	Siphonaptera: ceratophyllid (*Orchopeas wickhami*)	Eurasia
H. sylvatici (syn. *Haemogregarina*)		Rodentia: cricetid (grey red-backed vole), murid (striped field mouse)		Acari: laelapid (*Laelaps agilis*)	North America
H. ursi	10.9 x 3.3	Carnivora: ursid (Japanese black bear, sloth bear)	wbc	Acari: ixodid (*Haemaphysalis flava*, *japonica*)	Japan
species in snakes (Serpentes)					
H. aegypti	13-16 x 2.5-3	colubrid (diadem snake)	lung capillary endothelial cells, rbc	Diptera: culicid (*Culex pipiens*)	Egypt
H. algiri (syn. *Haemogregarina*)		colubrid (rat snake)	rbc		Middle-East
H. amethystina (syn. *Haemogregarina*)		boid (scrub python)	rbc		Australia
H. ancistrodoni (syn. *Haemogregarina*)		viperid (cottonmouth)	rbc		North America
H. arantesi (syn. *Haemogregarina, H. butantanensis*)		colubrid (Wagler's snake, common green racer)	rbc		South America
H. aspidomorphi (syn. *Haemogregarina*)		elapid (white-crowned snake, tiger snake, slaty-grey snake)	rbc		Australasia
H. australis (syn. *Haemogregarina*)		elapid (king brown snake)	rbc		Australia
H. ayorgbor	11-13 x 2-3.5	pythonid (ball pythons) [mice as IH?]	rbc	Diptera: culicid (*Culex quinquefasciatus*)	Africa
H. bancrofti (syn. *Haemogregarina, Karyolysus*)		elapid (spotted back snake, king brown snake, tiger snake)	rbc		Australia
H. bengalensis (syn. *Haemogregarina*)		colubrid (buff-striped keelback)	rbc		Asia
H. bicarinati (syn. *Haemogregarina*)		colubrid (sipos)	rbc		South America
H. bipileata (syn. *Haemogregarina*)		elapid (monocled cobra)	rbc		South Asia

H. bitis (syn. *Haemogregarina*)		viperid (puff adder)	rbc		Africa
H. boigae (syn. *Haemogregarina*)		colubrid (green tree snake, brown tree snake)	rbc		Australia
H. boodoni (syn. *Haemogregarina*)		colubrid (African house snake)	rbc		Africa
H. bornandi (syn. *Haemogregarina*)		colubrid (grass snake)	rbc		Eurasia
H. bradfordi (syn. *Haemogregarina*)		colubrid (banded water snake)	rbc		North America
H. brendae (syn. *Haemogregarina*)		colubrid (short-snouted grass snake)	rbc		Africa, Asia
H. brumpti (syn. *Haemogregarina*)		colubrid (pine snake)	rbc		North America
H. bungari (syn. *Haemogregarina, Laverania*)		elapid (banded krait)	rbc		India, Asia
H. calligaster (syn. *Haemogregarina*)		colubrid (northern tree snake)	rbc		Australia
H. cantliei (syn. *Haemogregarina*)		boid (sand boa)	rbc		South America
H. capsulata (syn. *Haemogregarina*)		viperid (tropical rattlesnake)	rbc		South America
H. carinacauda	23-25 x 5-6	colubrid (Wied's keelback)	rbc	Hirudinea: glossiphoniid (*Haememteria lutzi*)	Brazil
H. cenchridis (syn. *Haemogregarina*)		boid (rainbow boa)	rbc		South America
H. cevapii	15-20 x 2-4	viperid (neotropical rattle snake)	rbc		South America
H. chartusica (syn. *Haemogregarina*)		colubrid (spotted desert racer)	rbc		West Asia
H. chironii (syn. *Haemogregarina*)		colubrid (Boettger's sipo)	rbc		South America
H. colubri (syn. *Haemogregarina*)		colubrid (false coral, spotted desert racer, Asian racer, Aesculapian snake)	rbc		South America, South Asia
H. confusus	14-17 x 3.5-5	colubrid (eastern racer)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. corallus (syn. *Haemogregarina*)		boid (Amazon tree boa)	rbc		South America
H. coronellae (syn. *Haemogregarina*)		colubrid (southern smooth snake)	rbc		Europe
H. crotali (syn. *Haemogregarina, Karyolysus*)		viperid (diamondback rattlesnake, tropical rattlesnake)	rbc		North and South America
H. crotaphopeltis (syn. *Haemogregarina*)		colubrid (herald snake)	rbc		Africa
H. cuestensis	14-19 x 2-5	viperid (neotropical rattle snake)	rbc		South America
H. cyclagrasi (syn. *Haemogregarina*)		colubrid (false water cobra)	rbc		South America
H. darwiniensis (syn. *Haemogregarina*)		elapid (king brown snake)	rbc		Australia
H. dendrophidis (syn. *Haemogregarina, Karyolysus*)		colubrid (green tree snake)	rbc		Australia
H. denisoniae (syn. *Haemogregarina*)		elapid (northern small-eyed snake, marsh snake, red-bellied black snake, tiger snake)	rbc		Australia

H. digueti (syn. *Haemogregarina*)		viperid (massasauga)	rbc		North America
H. dogieli (syn. *Haemogregarina*)		viperid (Gaboon viper)	rbc		Africa
H. domerguei	14 x 3	lamprophiid (Madagascar night snake); transmissible to lamprophiid (blonde hognose); pythonid (African rock python); Sauria: lacertid (common wall lizard, ruin lizard, viviparous lizard), oplurid (Madagascar swift)	rbc	Diptera: culicid (*Culex pipiens, Anopheles stephensi*)	Madagascar
H. drymobii (syn. *Haemogregarina*)		colubrid (Rio tropical racer)	rbc		South America
H. echisi (syn. *Haemogregarina*)		viperid (saw-scaled viper)	rbc		Indo-Asia
H. eidsvoldensis (syn. *Haemogregarina*)		elapid (king brown snake)	rbc		Australia
H. enswerae (syn. *Haemogregarina*)		elapid (forest cobra)	rbc		Africa
H. eristavi (syn. *Haemogregarina*)		viperid (blunt-nosed viper)	rbc		Middle-East
H. fasciatae	16-18 x 3-5	colubrid (banded water snake, green water snake)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. florulentusi (syn. *Haemogregarina*)		colubrid (flowered racer)	rbc		North Africa
H. franchinii (syn. *Haemogregarina*)		pythonid (Indian python)	rbc		South Asia
H. fuscus (syn. *Haemogregarina*)		pythonid (brown water python)	rbc		Australia
H. fusifex	9.2-17.3 x 2.3-8.1	boid (boa constrictor)	rbc	Acari: ixodid (*Amblyomma dissimile*), exptl. in Diptera: culicid (*Culex tarsalis, Aedes togoi*)	North America
H. garnhami (syn. *Haemogregarina*)		psammophiid (Schokari sand racer)	rbc		Egypt
H. ghaffari		viperid (Sahara sand viper)	rbc	Diptera: culicid (*Culex pipiens*)	Egypt
H. gigas (syn. *Haemogregarina*)		colubrid (false water cobra)	rbc		South America
H. gightiensis (syn. *Haemogregarina*)		colubrid (awl-headed snake)	rbc		North Africa, Middle-East
H. guangdongense		colubrid (Chinese ratsnake), exptl. infection in colubrid (Asiatic water snake, radiated ratsnake) homalopsid (Chinese water snake)	rbc		Asia
H. guttata	10-17 x 3.5-6	colubrid (corn snake)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. hassleri (syn. *Haemogregarina*)		colubrid (burrowing snake)	rbc		South America
H. horridus	13-17 x 4-6	viperid (timber rattlesnake)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. imperatoris (syn. *Haemogregarina*)		boid (common boa)	rbc		South America

H. jararacussu (syn. *Haemogregarina*)		viperid (jararacussu, Neuwied's lancehead)	rbc		South America
H. joannoni (syn. *Haemogregarina*)		lamprophiid (false smooth snake)	rbc		Mediterranean
H. juxtanuclearis (syn. *Haemogregarina, Karyolysus*)		boid (boa constrictor)	rbc		Americas
H. laevicolis (syn. *Haemogregarina*)		colubrid (sipos)	rbc		South America
H. lahillei (syn. *Haemogregarina*)		colubrid (grass snake, brown water snake)	rbc		Eurasia, North America
H. lebetina (syn. *Haemogregarina*)		viperid (blunt-nosed viper)	rbc		Middle-East
H. leimadophis (syn. *Haemogregarina*)		dipsadid (penarol snake)	rbc		South America
H. lermensis (syn. *Haemogregarina*)		colubrid (garter snake)	rbc		North America
H. luehi (syn. *Haemogregarina*)		boid (tree boas)	rbc		South America
H. luisieri (syn. *Haemogregarina*)		colubrid (horseshoe whipsnake)	rbc		Mediterranean
H. lutzi (syn. *Haemogregarina*)		boid (green anaconda)	rbc		South America
H. malpoloni (syn. *Haemogregarina*)		psammophiid (Montpellier snake)	rbc		Mediterranean
H. manceauxi (syn. *Haemogregarina*)		colubrid (horseshoe whipsnake)	rbc		Mediterranean
H. mansoni (syn. *Haemogregarina*)	13-16 x 4-6	colubrid (whipsnake)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. massardi	15-20 x 2-4	viperid (neotropical rattle snake)	rbc		South America
H. matruhensis (syn. *Haemogregarina*)		psammophiid (Schokari sand racer)	rbc	Diptera: culicid (*Culex pipiens*)	Egypt
H. megalocystis (syn. *Haemogregarina*)		pythonid (carpet python)	rbc		Australasia
H. mehlhorni	17.2 x 5.4	viperid (saw-scaled viper)	rbc	Diptera: culicid (*Culex pipiens*)	Egypt
H. migonei (syn. *Haemogregarina*)		colubrid (false water cobra)	rbc		South America
H. miliaris (syn. *Haemogregarina*)	13-14 x 3-3.5	colubrid (common water snake)	rbc	Hirudinea: glossiphoniid (*Haementeria lutzi*)	Brazil
H. minchini		colubrid (herald snake)	rbc		Africa
H. mirabilis (syn. *Haemogregarina*)		colubrid (water snakes, tree snakes)	rbc	Hirudinea: cylicobdellid (*Hirudinaria granulosa*)	India
H. mocassini (syn. *Haemogregarina*)	14-18 x 4-6	viperid (water moccasin)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. modesta (syn. *Haemogregarina*)		colubrid (modest groundsnake)	rbc		South America
H. moreliae (syn. *Haemogregarina*)		pythonid (carpet python)	rbc		Australasia
H. mucosus		colubrid (Oriental rat snake)	rbc		Asia
H. musotae (syn. *Haemogregarina*)		lamprophiid (striped house snake, Seychelles house snake)	rbc		Africa
H. najae (syn. *Haemogregarina*)	14-18 x 3.5-6	elapid (Indian cobra)	rbc	Diptera: culicid (*Culex pipiens*)	India
H. pallida		colubrid (Amazon	rbc		South

(syn. *Haemogregarina*)		coastal house snake)			America
H. pefilievi (syn. *Haemogregarina*)		viperid (saw-scaled viper)	rbc		Middle-East, Central Asia
H. perrieri (syn. *Haemogregarina*)		viperid (Neuwied's lancehead)	rbc		South America
H. phisalix (syn. *Haemogregarina*)		pythonid (black-tailed python)	rbc		Indo-Asia
H. phylodriasi (syn. *Haemogregarina*)		colubrid (green racers)	rbc		South America
H. pictiventris	11-16 x 4-6	colubrid (banded water snake)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. pigmentata (syn. *Haemogregarina*)		psammophiid (steppe ribbon racer)	rbc		Asia
H. pituophis (syn. *Haemogregarina*)		colubrid (pine snake, bullsnake)	rbc		North America
H. plimmeri (syn. *Haemogregarina*)	10-15 x 2.5-4.5	viperid (jararaca, lancehead)	rbc	Diptera: culicid (*Culex dolosus*)	Brazil
H. pococki (syn. *Haemogregarina*)		pythonid (black-tailed python, carpet python)	rbc		Australasia
H. poecilogyrus (syn. *Haemogregarina*)		dipsadid (penarol snake)	rbc		South America
H. polytopis	10-15 x 3-6	colubrid (eastern racers)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. priapus	17-20 x 3.5-6	colubrid (eastern racers)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. prolata (syn. *Haemogregarina*)		colubrid (spotted whip snake)	rbc		Asia
H. pseudechis (syn. *Haemogregarina*)		elapid (red-bellied black snake, king brown snake)	rbc		Australia
H. pseudoboae (syn. *Haemogregarina*)		colubrid (black false boa)	rbc		South America
H. pullatus (syn. *Haemogregarina*)		colubrid (caninana)	rbc		Mesoamerica
H. punctatus	12-16 x 4-6	colubrid (ringneck snake)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. pythonis (syn. *Haemogregarina, H. amethystina p.p., colubri p.p., reichenowi, shattocki p.p., Danilewskya*)		pythonid (reticulated python, black-tailed python, rock python, carpet python, amethystine python, green tree python)	rbc		Australasia
H. rarefaciens (syn. *Haemogregarina*)	11-18 x 2.5-9	colubrid (Indigo snake); plus exptl. infections boid (boa constrictor); colubrid (gopher snake)	rbc, wbc	exptl. in Diptera: culicid (*Aedes sierrensis, Anopheles albimanus, Culex tarsalis*)	North America
H. refringens (syn. *Haemogregarina*)		lamprophiid (mole snake)	rbc		South Africa
H. robertsonae (syn. *Haemogregarina*)		pythonid (ball python, rock python)	rbc		Africa
H. rojasi (syn. *Haemogregarina*)		viperid (crossed pit viper), colubrid (Wagler's snake)	rbc		South America
H. romani (syn. *Haemogregarina*)		viperid (tropical rattlesnake)	rbc		South America
H. roulei (syn. *Haemogregarina*)		viperid (crossed pit viper)	rbc		South America
H. samboni (syn. *Haemogregarina*)		viperid (asp viper, blunt-nosed viper)	rbc		South Europe, North Africa
H. sauritus	13-19 x 2.5-	colubrid (southern	rbc	Diptera: culicid	North

	5.5	ribbon snake, eastern racers, black rat snake, corn snake, garter snake, ringneck snake); viperid (timber rattlesnake)		(*Aedes aegypti*)	America
H. sebai (syn. *Haemogregarina*)		pythonid (African rock python)	rbc		Africa
H. seligmanni (syn. *Haemogregarina*)		viperid (bushmaster)	rbc		South America
H. seminatrici	14-20 x 3-5	colubrid (swamp snake)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. serpentium (syn. *Haemogregarina, Drepanidium, Karyolysus*)		boid (green anaconda, boa constrictor), colubrid (savannah hunter, indigo snake, caninana, false fer-de-lance, green racer, tropical racer), viperid (lancehead, rattlesnakes)	rbc		Americas
H. seurati	12-16 x 3-5	viperid (horned viper)	rbc	Diptera: culicid (*Culex pipiens*)	North Africa
H. shattocki (syn. *Haemogregarina*)		pythonid (carpet python, amethystine python), elapid (tiger snake, spotted black snake)	rbc		Australasia
H. sipedon	19 x 3.7	colubrid (northern water snake)	rbc	Diptera: culicid (*Culex pipiens, territans*), then frogs (Anura: ranid (*Rana pipiens*)	Canada
H. sirtalis	17-22 x 3-6	colubrid (garter snake, ribbon snake, eastern racers, banded water snake)	rbc	exptl. in Diptera: culicid (*Aedes aegypti*), then frogs (Anura: ranid (*Rana*)	North America
H. sistruri	12.6-15.8 x 4.7-6.3	viperid (ground rattlesnake)	rbc	Diptera: culicid (*Aedes aegypti*)	North America
H. stegonoti (syn. *Haemogregarina*)		colubrid (slatey-grey snake)	rbc		Australia
H. strigatus (syn. *Haemogregarina*)	14-18 x 6-8	colubrid (coastal house snake)	rbc	Diptera: culicid (*Culex dolosus, fatigans*)	Brazil
H. terzii (syn. *Haemogregarina*)		boid (boa constrictor)	rbc		Americas
H. thamnophis (syn. *Haemogregarina*)		colubrid (garter snakes)	rbc		North America
H. tigrinae (syn. *Haemogregarina*)		colubrid (tiger keelback, four-lined ratsnake), viperid (Siberian pit viper)	rbc		Asia
H. trumata (syn. *Haemogregarina*)		colubrid (Dahl's whip snake)	rbc		Middle-East
H. tucumanensis (syn. *Haemogregarina*)		viperid (crossed pit viper), colubrid (green racer)	rbc		South America
H. viperini (syn. *Karyolysus*)		colubrid (viperine snake)	rbc		Mediterranean
H. vubirizi (syn. *Haemogregarina*)		lamprophiid (Congo file snake)	rbc		Africa
H. wardi (syn. *Haemogregarina*)		colubrid (chain kingsnake)	rbc		North America
H. weissi (syn. *Haemogregarina*)		elapid (Egyptian cobra)	rbc		North Africa
H. zambiensis		colubrid (boomslang)	rbc		Africa

(syn. *Haemogregarina*)					
H. zamenis (syn. *Haemogregarina*)		colubrid (horseshoe whip snake, oriental ratsnake, golden tree snake)	rbc		Mediterranean, South Asia
H. zumpti (syn. *Haemogregarina*)		elapid (black mamba)	rbc		Africa
species in lizards (Sauria)					
H. ameivae (syn. *Haemogregarina*)		teiid (green ameiva)	rbc		South America
H. amphisbaena (syn. *Haemogregarina*)		amphisbaenid (red worm lizard)	rbc		Eurasia
H. annularis (syn. *Haemogregarina*)		phyllodactylid (ringed wall gecko)	rbc		Africa
H. argantis		agamid (Mozambique agama), phyllodactylid (wall gecko)	rbc	Acari: argasid (*Argas brumpti*)	Africa
H. babudierii (syn. *Haemogregarina*)		lacertid (ruin lizard, wall lizard, European green lizard)	rbc		Europe
H. berestnewi (syn. *Karyolysus*)		lacertid (European green lizard)	rbc		Europe
H. bicapsulata (syn. *Haemogregarina*)		lacertid (common wall lizard)	rbc		Europe
H. borreli (syn. *Haemogregarina*)		varanid (desert monitor)	rbc		Africa, Asia
H. boskiani (syn. *Haemogregarina*)		lacertid (fringe-toed lizard)	rbc		North Africa, West Asia
H. breinlii (syn. *Haemogregarina*)	14-16 x 1.5-2.5	varanid (black-headed monitor, lace goanna, sand goanna)	rbc	Diptera: culicid (*Culex fatigans*)	Australia
H. burneti		phyllodactylid (European common gecko)	rbc		Mediterranean
H. camarai (syn. *Haemogregarina*)		varanid (rock monitor)	rbc		Africa
H. capsensis (syn. *Haemogregarina*)		lacertid (fringe-fingered lizards)	rbc		Africa, Eurasia
H. carlosi (syn. *Haemogregarina, H. minuta, Schellackia*)		lacertid (ocellated lizard)	rbc		Europe
H. chabaudi		chamaeleonid (chameleons)	rbc		Africa, Eurasia
H. chamaeleonis (syn. *Haemogregarina*)		chamaeleonid (common chameleon, African chameleon)	rbc		Africa
H. cheissini (syn. *Haemogregarina*)		agamid (Caucasian agama)	rbc		Caucasus
H. cnemidophori (syn. *Haemogregarina*)		teiid (rainbow whiptail)	rbc		Americas
H. ctenosaurae (syn. *Haemogregarina*)		iguanid (spinytail iguana)	rbc		Mexico
H. cunninghami (syn. *Haemogregarina*)		scincid (Cunningham's skink, tree skink)	rbc		Australia
H. curvirostris (syn. *Haemogregarina*)		lacertid (ocellated lizard)	rbc		Europe
H. dolichopyrena (syn. *Haemogregarina*)		gekkonid (Caspian thin-toed gecko)	rbc		West Asia
H. egerniae (syn. *Haemogregarina*)		scincid (Cunningham's skink, tree skink)	rbc		Australia
H. eremiae (syn. *Haemogregarina*)		lacertid (racerunners)	rbc		Eurasia
H. eumecei		scincid (Berber skink)	rbc		North

(syn. *Haemogregarina*)					Africa, West Asia
H. gilruthi (syn. *Haemogregarina*)		varanid (black-headed monitor)	rbc		Australia
H. gouldii (syn. *Haemogregarina, Karyolysus*)		varanid (sand goanna)	rbc		Australia
H. gracilis (syn. *Haemogregarina, Karyolysus*)	18-22.5 x 0.9-1.4	scincid (rainbow skink)	rbc	Diptera: culicid (*Culex pipiens*)	Sudan
H. hamata (syn. *Haemogregarina*)		lacertid (Jackson's forest lizard), scincid (speckle-lipped skink)	rbc		Africa
H. heteronotae (syn. *Haemogregarina*)		gekkonid (Bynoe's gecko)	rbc		Australia
H. hinuliae (syn. *Haemogregarina*)		scincid (golden water skink)	rbc		Australia
H. iguanae (syn. *Haemogregarina*)		iguanid (green iguana, lesser Antillean iguana), teiid (gold tegu)	rbc		Americas, Caribbean
H. jakimovi (syn. *Haemogregarina*)		agamid (toadhead agamas)	rbc		Eurasia
H. johnstoni (syn. *Haemogregarina*)		varanid (lace goanna, sand goanna)	rbc		Australia
H. kisrae	12-15 x 2-5.5	agamid (star lizard)	rbc	Acari: ixodid (*Hyalomma aegyptium*)	Middle-East
H. lygosomarum (syn. *Haemogregarina*)	13.6-16.8 x 4.2-6.3	scincid (Moko skink)	rbc, liver, spleen	Acari: macronyssid (*Ophionyssus scincorum*)	New Zealand
H. mabuiae (syn. *Haemogregarina*)		scincid (bridled skink)	rbc		Middle-East
H. malacitensis (syn. *Haemogregarina*)		lacertid (wall lizard)	rbc		Mediterranean
H. marceaui (syn. *Haemogregarina*)		lacertid (wall lizard)	rbc		Europe
H. mellisselensis (syn. *Haemogregarina*)		lacertid (Dalmatian wall lizard)	rbc		Mediterranean
H. mesnili	15-17 x 4-7	gekkonid (dwarf gecko)	rbc	Diptera: culicid (*Culex fatigans, Aedes albopictus, Stegomyia albopicta*)	Vietnam
H. missoni (syn. *Haemogregarina*)		teiid (gold tegu)	rbc		South America
H. nana (syn. *Haemogregarina*)		lacertid (common wall lizard, Italian wall lizard)	rbc		Mediterranean
H. nicollei (syn. *Haemogregarina*)		lacertid (ocellated lizard)	rbc		North Africa
H. nobrei (syn. *Haemogregarina*)		lacertid (common wall lizard)	rbc		Mediterranean
H. obscura (syn. *Haemogregarina*)		scincid (Cunningham's skink)	rbc		Australia
H. octosporei	17.3-19.5 x 3.8-4.9	scincid (keeled Indian mabuya)	rbc	Acari: macronyssid (*Ophionyssus* sp.)	India
H. ophisauri (syn. *Haemogregarina*)		anguid (European legless lizard)	rbc		Eurasia
H. palmeri (syn. *Haemogregarina*)		agamid (Australian water dragon)	rbc		Australia
H. paradoxa (syn. *Haemogregarina*)		varanid (rock monitor)	rbc		Africa
H. pavlovskyi		gekkonid (Turkestan	rbc		West Asia

(syn. *Haemogregarina*)		thin-toed gecko, Transcaspian bent-toed gecko, wonder gecko)			
H. percomsi (syn. *Haemogregarina*)		agamid (rock agama)	rbc		Asia
H. petrishtchewae (syn. *Haemogregarina*)		agamid (Lichtenstein's toadhead agama)	rbc		Eurasia
H. phyllodactyli (syn. *Haemogregarina*)		phyllodactylid (South American leaf-toed gecko)	rbc		South America
H. platydactyli (syn. *Haemogregarina*)		phyllodactylid (common wall gecko)	rbc		Mediterranean
H. procteri (syn. *Haemogregarina*)		phyllodactylid (Elisa's leaf-toed gecko)	rbc		Middle-East
H. prodhoni		oplurid (Madagascar swift)	wbc		Madagascar
H. psammodromi (syn. *Haemogregarina, H. lusitanica, pallida*)		lacertid (large psammadromus)	rbc, wbc		Mediterranean
H. ramadani (syn. *Haemogregarina*)		lacertid (Bosc's fringe-toed lizard)	rbc		Egypt
H. salimbeni (syn. *Haemogregarina*)		teiid (black tegu)	rbc		South America
H. sauromali	10-21 x 3.3-7.7	iguanid (chuckwallas)	rbc, wbc	Acari: acarid (*Hirstiella* sp.)	Mexico
H. schaudinni (syn. *Haemogregarina*)		lacertid (ocellated lizard)	rbc		North Africa
H. sergentium (syn. *Haemogregarina*)		scincid (ocellated skink)	rbc		Mediterranean, India
H. sinimbui (syn. *Haemogregarina*)		iguanid (green iguana)	rbc		Central and South America
H. taeniolati (syn. *Haemogregarina*)		scincid (copper-tailed skink)	rbc		Australia
H. thomsoni (syn. *Haemogregarina*)		agamid (tuberculated agama, steppe agama)	rbc		Indo-China
H. tiliquae (syn. *Haemogregarina*)		scincid (blue-tongued skink)	rbc		Australia
H. toddi (syn. *Haemogregarina*)		varanid (Nile monitor)	rbc		Africa
H. triatomae (syn. *Haemogregarina*)		teiid (tiger lizard); tropidurid (Amazon lava lizard)	rbc	Hemiptera: reduviid (*Triatoma subrovaria*)	Central and South America
H. tuatarae	12.5-16.7 x 3.3-4.4	Rhynchocephalia: sphenodontid (tuatara)	rbc		New Zealand
H. tupinambis (syn. *Haemogregarina, H. caranii*)	14.5-19 x 5-8	teiid (golden tegu)	rbc	Diptera: culicid (*Culex fatigans*)	Brazil
H. turcomanica (syn. *Haemogregarina, H. agamae*)		agamid (rock agama, toad-headed agama)	rbc		Central and West Asia
H. varani (syn. *Haemogregarina*)		varanid (savannah monitor, desert monitor, Nile monitor, Komodo dragon)	rbc		Africa, Indonesia
H. varanicola (syn. *Haemogregarina, Karyolysus*)		varanid (lace goanna, black-headed monitor, Gould's goanna, Asian water monitor)	rbc		Australasia
H. veloxi (syn. *Haemogregarina*)		lacertid (rapid fringe-toed lizard)	rbc		Central Asia
H. waltairensis		agamid (Oriental garden	rbc		India

(syn. *Haemogregarina*)		lizard)			
species in crocodiles (Crocodilia)					
H. caimani (syn. *Haemogregarina, H. brasiliensis*)	16.2-25 x 2.5-4	alligatorid (broad-snouted caiman, white caiman)	rbc	Diptera: culicid (*Culex dolosus, fatigans*)	Brazil
H. crocodilinorum (syn. *Haemogregarina*)	8-11 x 4-6	crocodylid (African dwarf crocodile); alligatorid (American alligator)	rbc	Hirudinea: glossiphoniid (*Placobdella multilineata*)	North America
H. hankini (syn. *Haemogregarina*)		gavialid (gharial)	rbc		India
H. pettiti (syn. *Haemogregarina*)	18-25 x 2.5-5	crocodylid (Nile crocodile)	rbc	Diptera: glossinid (*Glossina palpalis*)	Senegal
H. serrei (syn. *Haemogregarina*)		alligatorid (caiman)	rbc		South America
H. sheppardi (syn. *Haemogregarina*)		crocodylid (Nile crocodile)	rbc		North Africa
species in tortoises (Testudines)					
H. mauritanicum (syn. *Haemogregarina, Coelomoplasma hyalomma*)		testudinid (Greek tortoise)	rbc	Acari: ixodid (*Hyalomma aegyptium*)	Europe
species in amphibians (Anura)					
H. aegyptia (syn. *Haemogregarina*)	12-15 x 6-9	bufonid (African toad)	rbc		Egypt, Sudan
H. aguai (syn. *Karyolysus aquai, Haemogregarina, H. minima*)		bufonid (cane toad)	rbc		North America
H. andamanensis (syn. *Haemogregarina*)	14.5 x 3.5	ranid (skipper frog)	rbc		India
H. arabica (syn. *Haemogregarina*)		bufonid (Dhofar toad)	rbc		Arabia
H. assiuticus (syn. *Haemogregarina*)	30-38 x 3-5	bufonid (African toad)	rbc		Egypt
H. aurorae (syn. *Haemogregarina*)		ranid (red-legged frog)	rbc		North America
H. berestneffi (syn. *Haemogregarina*)	16-28 x 3-6	ranid (grass frog, green pond frog, skipper frog), dicroglossid (Asian bullfrog)	rbc		Sri Lanka, India
H. boueti (syn. *Haemogregarina, H. boneti*)	16-26 x 3-6	bufonid (African toad, Asian toad)	rbc		Egypt, Guinea-Bissau
H. boyli (syn. *Haemogregarina*)	8-17 x 4-6	ranid (yellow-legged frog)	rbc		North America
H. bufonis (syn. *Haemogregarina, Plasmodium bufonis*)		Anura: bufonid (American toad)	rbc		North America
H. catesbianae (syn. *Haemogregarina*)		ranid (American bullfrog)	rbc	Diptera: culicid (*Culex territans*)	North America
H. cayennensis (syn. *Haemogregarina*)		bufonid (cane toad)	rbc		
H. clamatae (syn. *Haemogregarina, Karyolysus*)		ranid (green frog, leopard frog, American bullfrog)	rbc		North America
H. darlingi (syn. *Haemogregarina*)		bufonid (cane toad)	rbc		
H. epuluensis (syn. *Haemogregarina*)		ptychadenid (South African sharp-nosed frog)	rbc		Africa
H. faiyumensis	13-17 x 4-5	bufonid (African toad)	rbc		Egypt

(syn. *Haemogregarina*)					
H. francai (syn. *Haemogregarina*)	18-20 x 2-3	bufonid (African toad)	rbc		Egypt
H. froilanoi (syn. *Haemogregarina*)	16-21 x 6-8	bufonid (African toad)	rbc		Angola
H. hijaziensis (syn. *Haemogregarina*)		bufonid (Arabian toad)	rbc		Arabia
H. hortai (syn. *Haemogregarina*)		ranid (edible frog)	rbc		Europe
H. hyperolii (syn. *Haemogregarina*)		hyperoliid (reed frog)	rbc		Africa
H. involucrum	19-26 x 4-6	hyperoliid (reed frog)	rbc		South Africa
H. ixoxo	12-17 x 6-9	bufonid (Garman's toad, guttural toad, striped toad)	rbc		South Africa
H. kaloulae (syn. *Haemogregarina*)	16 x 3.6	microhylid (Asian narrowmouth toad)	rbc		India
H. lavieri (syn. *Haemogregarina*)	20	bufonid (African toad)	rbc		Congo
H. legeri (syn. *Haemogregarina*)		bufonid (cane toad)	rbc		
H. leptodactyli (syn. *Leucocytozoon ranarum, Haemogregarina, H. heteronucleata, ranarum*)		leptodactylid (butter frog, smoky jungle frog)	rbc		South America
H. maculatus (syn. *Haemogregarina*)	16.5 x 3.3	rhacophorid (Indian tree frog)	rbc		India
H. magna (syn. *Haemogregarina, H. ranarum p.p., Drepanidium magnum, krusei, Danilewskya krusei*)	12-18 x 4-6	ranid (green frog, rice field frog, leopard frog, marsh frog), dicroglossid (Asian bullfrog)	rbc		Europe, India
H. magni (syn. *Haemogregarina*)	21-26 x 5-9	bufonid (African toad)	rbc		Egypt
H. medinensis (syn. *Haemogregarina*)		ranid (marsh frog)	rbc		Europe
H. moloensis (syn. *Haemogregarina*)	18 x 8	bufonid (toads)	rbc		Kenya
H. neireti (syn. *Haemogregarina*)		ptychadenid (grassland frogs)	rbc		Africa
H. nucleobisecans (syn. *Haemogregarina*)	14.4 x 3	bufonid (Himalaya toad, Asian toad, spotted toad)	rbc		India
H. nutti (syn. *Haemogregarina, Pseudohaemogregarina*)		pyxicephalid (Nutt's river frog)	rbc		Europe
H. pattoni (syn. *Haemogregarina*)		dicroglossid (Indian five-fingered frog)	rbc		India
H. perinucleophilum (syn. *Haemogregarina*)	11.1 x 3.1	dicroglossid (Asian bullfrog)	rbc		India
H. pestanae (syn. *Haemogregarina, H. pistanea*)	12-17 x 4-5	bufonid (African toad)	rbc		Egypt, Guinea-Bissau
H. pulchra (syn. *Haemogregarina*)	15.4 x 3	microhylid (chubby frog)	rbc		India
H. scheini (syn. *Haemogregarina*)		dicroglossid (Asian bullfrog)	rbc		South Asia
H. seychellensis		Gymnophiona: grandisoniid (Stejneger's caecilian)	rbc		Seychelles
H. shirikenimori		Urodela: salamandrid	rbc		Japan

(syn. *Haemogregarina*)		(sword-tail newt)			
H. systoma (syn. *Haemogregarina*)	15.3 x 3.9	microhylid (lesser balloon frog)	rbc		India
H. temporariae (syn. *Haemogregarina, Nematopsis*)		ranid (European grass frog)	rbc		Europe
H. tenuis	11-17 x 4-7	hyperoliid (greater leaf-folding frog, reed frog)	rbc		South Africa
H. theileri (syn. *Haemogregarina, Pseudohaemogregarina ranae*)		pyxicephalid (Angola river frog, Drakensberg River frog, pixie frog)	rbc		Africa
H. thori	11-17 x 4-7	hyperoliid (marbled reed frog)	rbc		South Africa
H. tonkinensis (syn. *Haemogregarina*)		bufonid (Asian toad)	rbc		South Asia
H. tunisiensis (syn. *Haemogregarina*)	12-15 x 8	bufonid (Berber toad)	rbc		Tunisia
species in birds					
H. albatrossi	13 x 6.1	Procellariiformes: diomedeid (albatrosses)	wbc		Southern Ocean
H. aragaoi (syn. *Haemogregarina*)		Passeriformes: thraupid (yellow-billed cardinal)			South America
H. atticorae (syn. *Haemogregarina*)	7.9-9.9 x 3.3-3.9	Passeriformes: hirundinid (South African cliff swallow, tawny-headed swallow, blue-and-white swallow, southern rough-winged swallow, western house martin)	wbc	Acari: argasid (*Ornithodoros peringueyi*); Siphonaptera: pulicid (*Xenopsylla trispinis*)	South Africa, South America
H. columbae (syn. *Haemogregarina*)		Columbiformes: columbid (pigeon)	rbc		Eurasia
H. estrildus	8.8 x 3.7	Passeriformes: estrildid (bronze mannikin)	wbc		Zambia
H. kiwii	9.8-13.5 x 6.2-8.3	Apterygiformes: apterygid (kiwi)	wbc		New Zealand
H. lanis	7.8 x 3.6	Passeriformes: laniid (fiscal shrike)	wbc		Africa
H. malacotinus	10.8 x 5.1	Passeriformes: malaconotid (black-backed puffback)	wbc		Africa
H. neophrontis (syn. *Leucocytogregarina, Leucocytozoon, Toxoplasma, H. adiei, monachus*)	9.6 x 4.6	Accipitriformes: accipitrid (hooded vulture, lappet-faced vulture, white-backed vulture, Egyptian vulture, tawny eagle, red-tailed hawk, black kite, osprey)	wbc		Africa
H. numidis	9.5 x 5.3	Galliformes: phasianid (helmeted guineafowl)	wbc		Africa
H. paroariae (syn. *Haemogregarina, H. brachyspizae*)		Passeriformes: passerellid (Andean sparrow), thraupid (red-cowled cardinal)	wbc		South America
H. parus	9.8-10.6 x 3.6-4.4	Passeriformes: parid (chickadees, titmice)	wbc		North America, Europe
H. passeris	7.9 x 3.9	Passeriformes: ploceid (scaly-feathered weaver)	wbc		Africa
H. pintoi		Accipitriformes:	wbc		Americas

(syn. *Haemogregarina*)		accipitrid (turkey vulture)			
H. pittae	10.6 x 3.7	Passeriformes: pittid (blue-banded pitta)	wbc		Borneo
H. prionopis	10.6 x 6.1	Passeriformes: vangid (white-crested (helmetshrike)	wbc		Africa
H. rhamphocoeli (syn. *Haemogregarina, H. tanagrae*)		Passeriformes: thraupid (scarlet tanager, palm tanager)	wbc		South America
H. sylvae	9.2 x 3.5	Passeriformes: sylviid (chesnut-vented warbler)	wbc		South Africa
H. travassosi (syn. *Haemogregarina*)		Passeriformes: thamnophilid (great antshrike)	wbc		Americas
H. zosteropis	8.3 x 3.3	Passeriformes: zosteropid (Orange River white-eye)	wbc		South Africa

*rbc = red blood cells (erythrocytes); wbc = white blood cells (leucocytes)

Parasite morphology: *Hepatozoon* spp. form 4 different types of developmental stages: meronts in the viscera and gamonts in blood cells of vertebrates; and gametes and oocysts in invertebrate vectors. Meronts (often called schizonts) appear as ovoid basophilic stages (around 30 μm in diameter) in vascular endothelial cells in various tissues of vertebrates. The meronts undergo internal (endogenous) division to form merozoites, with 2 patterns of division observed: one type producing 2-4 large robust macro-merozoites; and the other forming over 20 smaller slender micro-merozoites arranged around the periphery (imparting a 'wheelspoke' appearance). Persistent cysts containing 1 or 2 merozoites (sometimes called cystozoites) have also been observed in host organs for several *Hepatozoon* spp. (but are absent in *Haemogregarina* spp.). All species then form elliptical gamonts (9-12 x 4-6 μm) in white blood cells (mainly neutrophils, rarely monocytes) and sometimes in red blood cells. Gamonts are enveloped in a thick membrane and are usually located in the centre of the cell causing lateral displacement of the lobulated host cell nucleus. The gamonts themselves possess a central compact nucleus that stains dark red with Giemsa while the cytoplasm stains blue. Gamonts ingested by vectors form sexually dimorphic gametocytes (8-11 x 3-5 μm) which are associated pairwise (in syzygy), with female macrogametocytes maturing into robust unicellular macrogametes, and male microgametocytes dividing to produce 1-4 slender uni-flagellated microgametes. Fertilization produces non-motile zygotes that undergo sporogonous development to form large oocysts (200-300 x 150-300 μm) containing numerous (50-70) sporocysts, each of which contains 4-16 or more sporozoites (10-14 x 3-4 μm). Ultrastructural studies have revealed the presence of polar rings, micropores and cristate mitochondria in all stages, anterior conoids in all non-gamete stages, crystalloid bodies in sporozoites, and variable numbers of amylopectin granules (the latter absent in *Haemogregarina* spp.).

Site of infection: In vertebrate hosts, meronts (schizonts) develop in a variety of tissues and organs, including the liver, spleen, kidneys, lymph nodes, bone marrow, heart, lung and muscles. Monozoic or dizoic cysts have also been observed in similar tissues for several parasite species. Gamonts are found in host blood cells, infecting polymorphonuclear leucocytes, and sometimes erythrocytes. Over 340 *Hepatozoon* spp. have been described, which includes some 200 former *Haemogregarina* spp. from non-chelonian reptiles, amphibians and birds. Some 50 parasite species have been reported in 89 mammalian species (belonging to 24 families in 11 orders, mostly carnivores and rodents), almost 140 parasite species in 140 snake species (belonging to 9 families, mostly colubrids), 76 parasite species in 72 lizard species (belonging to 13 families, mainly lacertids), 6 species in 7 crocodile species (belonging to 3 families), one species in a tortoise (testudinid), 49 species in 49 amphibian species (21 species in 12 toad species, 26 species in 31 frog species belonging to 8 families, one species in a salamander and one in a caecilian), and 20 parasite species in 34 bird species (belonging to 18 families in 6 orders, mostly passeriforms and accipitriforms). Of the 340 putative species, the life-cycles have only been determined for some 61 species, all of them utilizing arthropods or leeches as vectors. The parasites completed gametogony in the guts of the vectors, resulting in the formation of polysporocystic oocysts which were found in the haemocoel, Malpighian tubules, stomach, intestines and caeca of the invertebrate hosts. Vectors identified for parasites in mammals included ixodid ticks, laelapid and haemogamasid mites, haematopinid and hoplopleurid lice, and pulicid, hystrichopsyllid and ceratophyllid fleas; those for parasites in snakes included culicid mosquitoes, ixodid ticks, glossiphoniid and cylicobdellid leeches; those for parasites in lizards included culicid mosquitoes, reduviid bugs, acarid and macronyssid mites, argasid and ixodid ticks; those for parasites in crocodiles included glossophoniid leeches, glossinid tsetse flies and culicid mosquitoes; those for the parasites in tortoises were ixodid ticks; those for parasites in amphibians were culicid mosquitoes; and those for parasites in birds included argasid ticks and pulicid fleas.

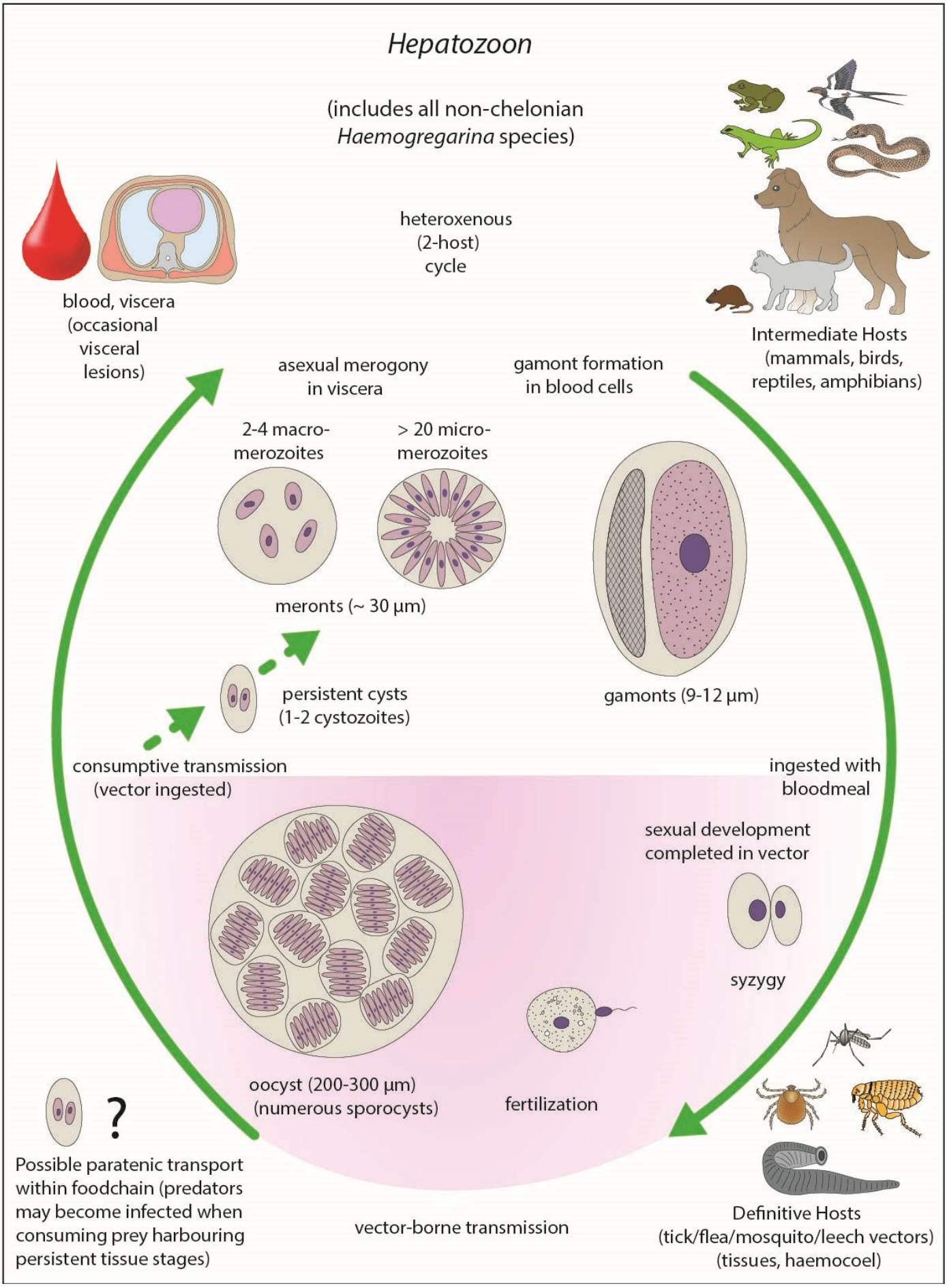
Pathogenesis: Most infections in vertebrates are asymptomatic and have not been associated with any clinical disease in wildlife or domesticated animals. Heavy infections by several species, however, may cause disease (hepatozoonosis) when proliferating

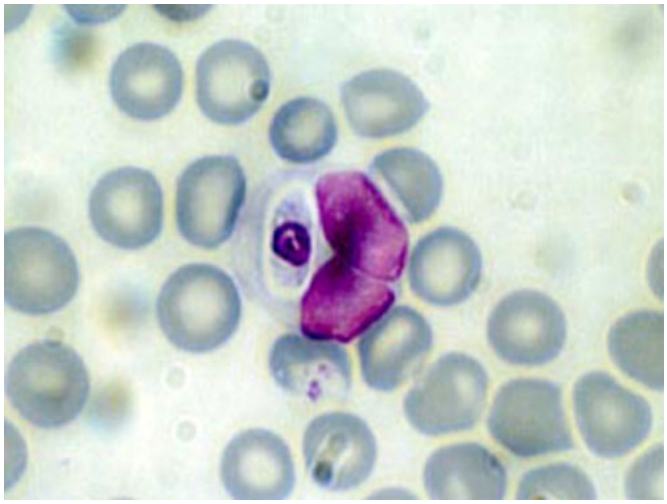
merogonous (schizogonous) stages damage host tissues, particularly in canids and felids. Developing schizonts may be disseminated throughout many host tissues, including haemolymphatic organs (bone marrow, spleen, lymph nodes) and internal visceral organs (liver, kidney, lungs). Upon maturation, schizonts lyse their host cells thus causing structural deficits, with cumulative losses leading to functional deficits and disease expression. Small lesions may develop in host tissues with necrotic foci and diffuse inflammation contributing to splenomegaly, hepatomegaly, hepatitis with Kupffer cell hyperplasia, pneumonitis, interstitial pneumonia, lymphadenopathy, glomerulonephritis and interstitial nephritis, and blood cell losses leading to progressive non-responsive anaemia (usually normocytic, normochromic, regenerative, sometimes with thrombocytopenia). There may be elevated monocyte counts with increasing numbers of monoblasts detected in peripheral blood (sometimes mistaken for monocytic leukaemia). Clinical signs are generally nonspecific and include fever, diarrhoea, icterus, ulcerative glossitis with hypersalivation, serous nasal-ocular discharge, intermittent anorexia, weight loss, emaciation, and death. Serum chemistry abnormalities include hyperproteinaemia (hyperglobulinaemia but hypoalbuminaemia) with increased creatine kinase (CK) and alkaline phosphatase (ALP) activities. Following schizogony, the parasites form gamonts in blood cells (especially neutrophils) and while many consider these to be latent stages, high parasitaemias (sometimes up to 50-100% of circulating neutrophils) have been associated with severe disease in dogs, characterized by lethargy, fever, severe weight loss and cachexia. Clinical infections are more abundant and severe in young or immuno-compromised animals, as they appear to be more susceptible to new infection or the reactivation of existing infections from persistent cystic stages in tissues. Various immunological studies have suggested that even in the absence of clinical signs, *Hepatozoon* infections of leucocytes may act to compromise and even suppress host immune responses, allowing infections to persist and predisposing animals to secondary infections.

Developmental cycle and mode of transmission: Hepatozoids have obligative heteroxenous (2-host) life cycles involving merogony and gamont formation in vertebrates (intermediate hosts), and gametogony, oocyst formation and sporogony in invertebrate hosts (definitive hosts or vectors). When vertebrates ingest vectors infected with mature oocysts, the oocysts excyst in their intestines releasing the containing infective sporozoites which penetrate the gut wall. The sporozoites invade mononuclear cells and are disseminated haematogenously or via the lymph to various host tissues and organs. They develop into meronts (schizonts) that undergo asexual internal (endogenous) division to form numerous merozoites; either 2-4 macro-merozoites or 20-30 micro-merozoites (depending on the parasite species). When mature, the meronts rupture releasing the merozoites which invade circulating neutrophils (or nucleated erythrocytes in non-mammalian hosts) and develop into gamonts in the peripheral circulation. In some instances, several *Hepatozoon* spp. also form small monozoic or dizoic cysts which persist in host organs resulting in long-term (chronic) infections. It has been suggested that these cystic stages may also facilitate paratenic transport between intermediate hosts by predation within the food chain (i.e. when carnivorous predators eat smaller infected prey). In one exceptional instance, vertical transmission has been reported for one species (*H. canis*) when proliferative stages cross the placenta in pregnant dogs. The life-cycles have been determined for over 60 *Hepatozoon* spp. and they all involve haematophagous invertebrate vectors (including leeches, ticks, mites, lice, fleas, mosquitoes, and tsetse flies). Infections are acquired by the vectors when they feed on vertebrate blood and ingest blood cells containing gamonts. The blood cells are digested in the vector gut releasing the gamonts which initiate extracellular gametogenesis by pairing up and developing into sexually dimorphic gametes. Macrogametocytes (female) form single 'egg-like' macrogametes while microgametocytes (male) form several 'sperm-like' flagellated microgametes. Fertilization occurs producing non-motile zygotes that develop into oocysts which undergo endogenous sporulation to form numerous sporocysts, each containing numerous sporozoites. Mature oocysts occur within various vector tissues, and they tend to accumulate in the haemocoel after moulting. In arthropod vectors, parasites may be transferred trans-stadially from larvae to nymphs to adults, but not trans-ovarially from females to their eggs (as occurs for some piroplasms). Infections are transmitted to vertebrate hosts when infected vectors are eaten and not via vector bite (i.e. transmission is consumptive rather than inoculative). Vectors are often consumed during grooming processes (self or communal grooming) and many vectors move between vertebrate hosts as larvae, nymphs and adults may feed on different individuals. The biogeographic distribution of many parasite species therefore closely follows that of their vectors. Transmission is often greatest during warm-hot seasons when vectors are more active, but infections in vertebrates may still be found throughout the year presumably due to persistent tissue stages replenishing gamont populations, particularly in immunosuppressed hosts.

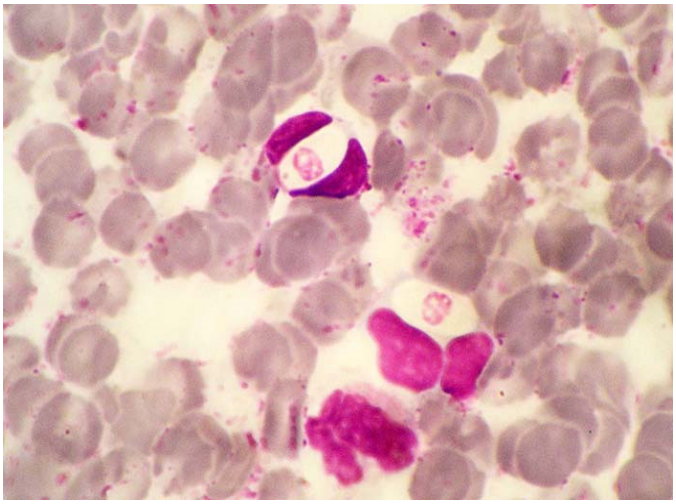
Differential diagnosis: Infections may be indicated in certain hosts (esp. dogs and cats) by a history of tick infestation with compatible clinical signs, including leucocytosis, non-regenerative anaemia, hypoalbuminaemia and increased serum alkaline phosphatase activity. However, other infectious, immune-mediated or metabolic diseases and several neoplasias may cause similar signs. Infections are conventionally diagnosed by the direct microscopic detection of gamonts in blood smears stained with Giemsa or Wright's stains. Several studies have found the examination of buffy coat smears from centrifuged samples to be more sensitive than examining routine blood smears. Schizonts are usually detected by the histological examination of autopsy (sometimes biopsy) material, and radiological studies have been used to reveal periosteal reactions in the long bones of dogs infected with *H. americanum*. Infections in leech or arthropod vectors may be detected by the microscopy of wet smear/squash preparations of tissues looking for the presence of large polysporocystic oocysts. Several serological tests (fluorescent-antibody tests, enzyme immunoassays) have been developed to detect specific host antibodies against gamont antigens, but little is known about test sensitivity or specificity, and they have mainly been used for research and several epidemiological studies. More recently, molecular biological techniques have been used to detect and characterize parasites in both vertebrates and vectors following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (predominantly small subunit (18S) ribosomal DNA).

Treatment and control: Asymptomatic or subclinical infections are usually not treated, but those infections producing clinical disease (particularly in dogs and cats) often require chemotherapeutic intervention to prevent their persistence, escalation or potentially fatal outcome. A range of antiprotozoal (antimalarial and coccidiostatic) drugs have been used with variable efficacy to treat animals, including sulphonamides (sulfamethoxazole, sulfadimethoxine, sulfadoxine/pyrimethamine), diaminopyrimidines (trimethoprim), aminoquinolines (primaquine), hydroxyquinolones (decoquinate), diamidines (diminazene aceturate) and imidazolines (imidocarb), with or without antibiotics (oxytetracycline, doxycycline, clindamycin, chloramphenicol). Some treatments produced adverse side-effects in the hosts, including cholinergic conditions requiring atropine. They varied considerably in their efficacy against schizonts and/or gamonts, with none eliminating infections and none effective against persistent cystic stages. Relapses in treated animals were common but could be forestalled by prolonged treatment (sometimes extending to years). Preventive measures are based around vector control to limit transmission to susceptible hosts. Topical or systemic insecticides and acaricides may be used to reduce infestations by ectoparasitic arthropods, together with the regular cleaning and grooming of individual animals to prevent them from ingesting vectors. As some parasite species may also be transmitted horizontally via predation on infected prey or vertically via transplacental transfer, carnivores in endemic areas should be restricted from hunting or consuming raw meat, and infected dams should be treated before mating.

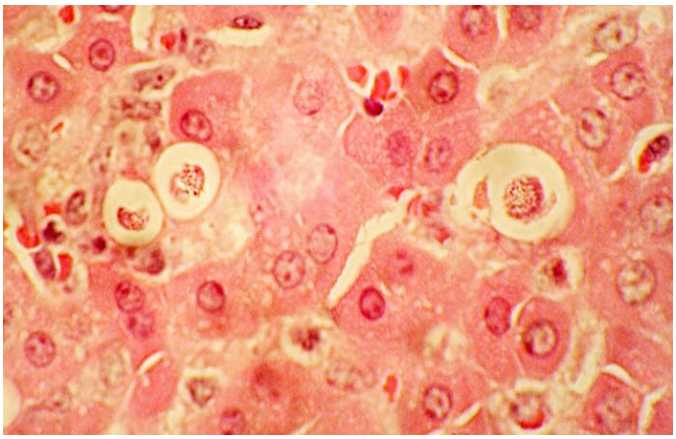

Hepatozoon
(includes all non-chelonian
Haemogregarina species)
heteroxenous
(2-host)
cycle
blood, viscera
(occasional
visceral
lesions)
Intermediate Hosts
(mammals, birds,
reptiles, amphibians)
asexual merogony
in viscera
gamont formation
in blood cells
2-4 macro-
merozoites
> 20 micro-
merozoites
meronts (~ 30 µm)
gamonts (9-12 µm)
persistent cysts
(1-2 cystozoites)
consumptive transmission
(vector ingested)
ingested with
bloodmeal
sexual development
completed in vector
syzygy
oocyst (200-300 µm)
(numerous sporocysts)
fertilization
?
Possible paratenic transport
within foodchain (predators
may become infected when
consuming prey harbouring
persistent tissue stages)
vector-borne transmission
Definitive Hosts
(tick/flea/mosquito/leech vectors)
(tissues, haemocoel)



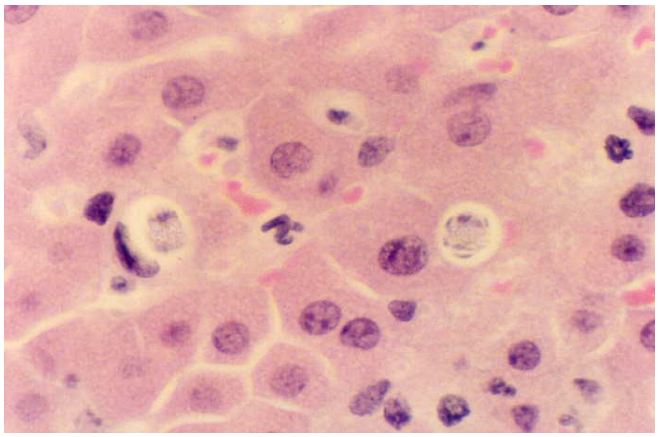
Hepatozoon gamont in dog blood



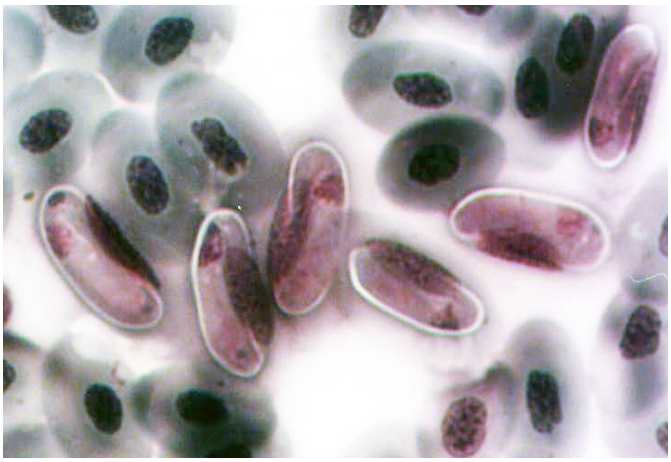
Hepatozoon gamont in dog blood



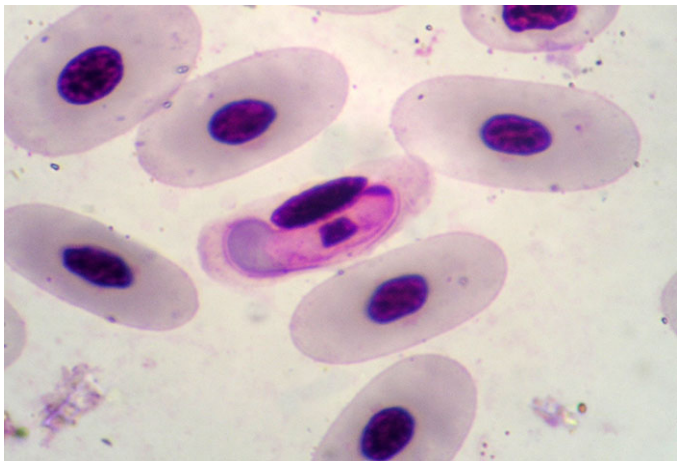
Hepatozoon schizonts in dog liver



Hepatozoon sachizonts in dog liver



Hepatozoon (*Haemogregarina s.l.*) gamonts in snake blood



Hepatozoon (*Haemogregarina s.l.*) gamont in snake blood

Klossiella
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). Klossiellids are adeleorine coccidia which have monoxenous (1-host) life cycles and are commonly found in equids, rodents and marsupials. Parasites undergo merogony (= schizogony), gamogony and sporogony in the kidneys of vertebrate hosts culminating in the formation of numerous sporocysts which are passed with host urine. Most infections appear to asymptomatic, although several species have been associated with renal lesions in horses and dasyurids.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Adeleina (syzygy, 1-4 microgametes)
Family:	Klossiellidae (zygote inactive, sporocysts formed (rather than oocysts))
Genus:	*Klossiella* (parasitic in kidneys of mammals)
Species:	various species cause renal infections in rodents and horses

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, Apicomplexa possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic ‘haemococcidia’ in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Klossiellid parasites are adeleid coccidia with monoxenous (1-host) life cycles. They do not infect erythrocytes but undergo the typical adeleorine developmental cycle of merogony, gamogony and sporogony in the kidneys of vertebrate hosts. Unlike the eimeriid coccidia, klossiellid gametocytes occur in pairs (syzygy) and few microgametes are produced. The resultant zygote is nonmotile and sporulates producing numerous sporocysts which are passed with host urine. Infections have been recorded in various hosts in several tropical and subtropical countries (mainly in mice, rats, guinea pigs, horses, donkeys, burro, zebra, bats). A single species, *K. equi,* occurs in horses and infections have been detected in many countries. In Australia, infections have been detected in native water rats, bandicoots, gliders, wallabies, hare-wallabies, pademelons, bettongs and kangaroos.

***Klossiella* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
K. bettongiae	Diprotodontia: potoroid (eastern bettong)	kidneys		Australia
K. beveridgei	Diprotodontia: macropodid (spectacled hare-wallaby)	kidneys		Australia

K. boae	Serpentes: boid (boa constrictor)	kidneys	enteritis, anorexia	America
K. callitris	Diprotodontia: macropodid (western grey kangaroo)	kidneys		Australia
K. cobayae	Rodentia: caviid (guinea pig)	kidneys		Africa, Europe, North America
K. convolutor	Diprotodontia: pseudocheirid (ringtail possum)	kidneys		Australia
K. dulcis	Diprotodontia: petaurid (sugar glider)	kidneys		Australia
K. equi	Perissodactyla: equid (horse, donkey, burro, zebra)	kidneys		cosmopolitan
K. hydromys	Rodentia: murid (water rat)	kidneys		Australia
K. killicki	Chiroptera: hipposiderid (roundleaf bat), rhinolophid (horseshoe bat)	kidneys		Africa, North America
K. mabokensis	Rodentia: murid (soft-furred mouse, house mouse)	kidneys		Africa
K. muris	Rodentia: murid (house mouse), caviid (guinea pig)	kidneys	tubule necrosis, death	worldwide
K. quimrensis	Peramelemorphia: peramelid (southern brown bandicoot, eastern barred bandicoot, western barred bandicoot)	kidneys	renal coccidiosis	Australia
K. rufi	Diprotodontia: macropodid (red kangaroo)	kidneys		Australia
K. rufogrisei	Diprotodontia: macropodid (Bennett's wallaby)	kidneys		Australia
K. schoinobatis	Diprotodontia: pseudocheirid (greater glider)	kidneys		Australia
K. serendipensis	Diprotodontia: macropodid (swamp wallaby)	kidneys		Australia
K. tejerai	Didelphimorphia: didelphid (opossum, big-eared opossum, Linnaeus's mouse opossum)	kidneys	'ballooning necrosis' of tubular epithelia	South America
K. thylogale	Diprotodontia: macropodid (Tasmanian pademelon)	kidneys		Australia

Parasite morphology: *Klossiella* spp. form 3 different types of morphological stages during their developmental cycles: namely, meronts (or schizonts), gamonts (male and female), and sporonts (producing sporocysts and sporozoites). Meronts appear as small basophilic bodies (8-20 µm) in kidney cells where they undergo internal (endogenous) division to form numerous slender merozoites (3-7 x 0.5-2.0 µm). Most species form 2 meront generations in the kidneys, although one (*K. muris*) only forms one generation, and another (*K. mabokensis*) apparently forms meronts in intestinal villi before invading the kidneys. The first meront generation usually produces 8-12 merozoites, while the second generation meronts usually form 40-60 merozoites, sometimes up to 100. Gamonts appear as sexually dimorphic stages that develop (often in pairs) into macrogametocytes (female) and microgametocytes (male). Macrogametocytes are rounded stages (4-14 µm in diameter) that produce single macrogametes with a central nucleus and a pale-staining vacuolated cytoplasm. Microgametocytes are also rounded stages (8-12 µm in diameter) that produce variable numbers (1-13) of small (6 x 2 µm) slender peripherally-located microgametes that are non-flagellated (*K. muris* produces 1-2 microgametes, *K. cobayae* 2-4, and *K. equi* 8-10). Gamete fertilization produces a non-motile zygote that undergoes a unique sporulation process. Typical oocysts are not formed, but membrane-bound sporonts produce sporoblasts that form sporocysts, which in turn form sporozoites. Early sporonts appear as ovoid (10-18 µm) cytoplasmic masses containing 8 or more peripheral nuclei (each surrounded by a clear halo) and 10-20 small plastin granules. Developing sporonts are irregular in size and shape (40-100 x 30-60 µm) as the enclosed sporoblasts produce numerous (8-40) subspherical-ellipsoidal sporocysts (ranging in size from 18-24 x 12-22 µm). *K. killicki* forms 8 sporocysts, *K. hydromyos* and *K. mabokensis* form 12, *K. tejerai* forms 18, *K. cobayae* forms 20-24, and *K. equi* forms 30-40. Each sporocyst contains numerous (12-35) falciform- to banana-shaped sporozoites (7 x 3 µm) lying side-by-side with a small residual body.

Site of infection: All developmental stages occur in the kidneys of vertebrate hosts, mostly in marsupials (diprotodonts, peramelemorphids, didelphimorphids) but also including equids, bats, rodents, and snakes. Meronts are typically found in glomeruli (Bowman's capsules) and convoluted tubules, but have occasionally been detected in other organs (intestines, liver, lung, spleen, thyroid, lymph nodes, brain, pituitary, thyroid or adrenal glands). Gamonts, sporonts and sporocysts are found within proximal convoluted tubules; and mature sporocysts are shed in the urine.

Pathogenesis: Most *Klossiella* infections are asymptomatic or subclinical and do not cause overt clinical signs, even though parasite development occurs intracellularly within renal cells resulting in their eventual lysis to release parasite progeny. A few species, however, have been associated with mild-severe clinical disease (klossiellosis) characterized by impaired renal function with tubular

nephrosis and interstitial nephritis, including *K. muris* in rodents, *K. tekerai* in opossums, and *K. quimrensis* in bandicoots. Heavily-parasitized kidneys developed grossly visible lesions, evident as small grey foci scattered over the cortical surface, often in the region of the cortico-medullary junction. The grey foci were found microscopically to be areas of cellular necrosis and proliferation. Infections did not cause inflammatory responses in the immediate vicinity of the parasites, but lymphocytes, histiocytes and sometimes fibroblasts did infiltrate the interstitium, notably surrounding blood vessels. Developing schizonts caused significant enlargement of host endothelial cells with compression of surrounding structures, and developing sporonts sometimes occluded the lumina of convoluted tubules. Infections by *K. equi* in horses have occasionally been associated with multifocal tubular necrosis and, in the case of tubular rupture, with interstitial infiltrates of lymphocytes and plasma cells, but renal function essentially remained normal (although a few sporadic cases of granulomatous nephritis and haematuria were observed in immunosuppressed horses with acute kidney injury secondary to nonsteroidal anti-inflammatory (NSAID) administration). Infections by *K. boae* in the kidneys and intestines of constrictor have been associated with haemorrhagic enteritis, intussusception, anorexia and restlessness.

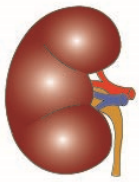
Developmental cycle and mode of transmission: *Klossiella* spp. have homoxenous or monoxenous (one-host) life-cycles involving asexual proliferation (merogony), sexual reproduction (gamogony) and asexual spore formation (sporogony) all occurring within the same host. Infections are transmitted between hosts when mature sporocysts are voided in urine into the external environment where they contaminate food and water supplies to be ingested by new hosts. Transmission does not involve vectors or other alternate intermediate or paratenic hosts. Sporocysts ingested by susceptible hosts excyst in the gut releasing sporozoites that penetrate the gut wall into the circulation. They invade glomerular endothelial cells and form meronts (schizonts) which multiply asexually by internal (endogenous) division forming numerous merozoites. Meronts of some species are occasionally found in capillary endothelia in other organs, either as part of their proliferative cycle (e.g. *K. mabokensis* in intestinal villi) or as ectopic sites of infection. There are often 2 meront generations in the kidneys, with the second generation producing more merozoites than the first (40-100 cf. 8-12). Last generation merozoites invade epithelial cells lining the proximal convoluted tubules and undergo sexual differentiation and reproduction. Female macrogametocytes and male microgametocytes are often found in pairs in tubular epithelial cells and they mature to form single macrogametes and multiple (1-10) nonflagellated microgametes. Fertilization occurs by gamete fusion producing a zygote (sporont) that undergoes multiple fission to form 8-40 sporoblasts and a residual body (it has been argued that these are not true oocyst stages as the surrounding sac appears to be formed by the parasitized host cell rather than laid down by the parasites themselves). Each sporoblast matures into a sporocyst which contains 12-35 sporozoites. These stages greatly distend the host cell until it ruptures releasing sporocysts into the tubule lumen and passing to the bladder to be voided with urine. The prepatent period (time from infection to first sporocyst excretion) was found to vary considerably with reports ranging from 4-5 days, 7-11 days, 30 days and even 6-7 weeks in different hosts. The patent period (duration of sporocyst excretion) was reported to be as long as 8-10 months in some horses. Shed sporocysts are infective to new susceptible hosts when they are ingested via grooming, contact with contaminated fomites, or in contaminated food or water. The sporocysts are not thought to survive for long in the external environment as the thin sporocyst wall would provide little protection against desiccation, heat and solar radiation.

Differential diagnosis: Infections are diagnosed ante-mortem by the microscopic detection of sporocysts in urinary concentrates (sediments, floats), or post-mortem by the detection of developmental stages of histological sections of host tissues. Molecular biological techniques have also been used to characterize isolates following the polymerase chain reaction (PCR) amplification of nuclear (small subunit (18S) ribosomal DNA) and mitochondrial (cytochrome c oxidase I and III, cytochrome b) gene sequences.

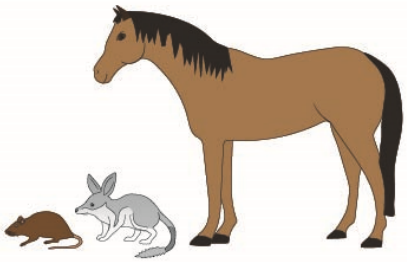
Treatment and control: A small number of drugs have been used in attempts to treat infections in horses, donkeys, marsupials and mice, including sulphonamides alone (sulfadimethoxine) or in combination (sulfadiazine/trimethoprim, co-trimoxazole (trimethoprim/sulfamethoxazole)), coccidiostats (amprolium) and cephalosporin antibiotics (ceftiofur). Few treatments were effective and none appeared to eliminate infections. Animals responded well to supportive care with intravenous fluid therapy, whilst awaiting the restoration of kidney function. Various preventive measures have been implemented in intensive husbandry situations to reduce the risks of urine contamination and parasite transmission, including the regular cleaning and disinfection of animal enclosures, proper waste drainage and elimination, the provision of clean water and food, periodic health screening, isolating and even culling infected individuals.

Klossiella

monoxenous
(1-host)
cycle

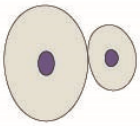


kidney
(tubular nephrosis,
interstitial nephritis,
renal lesions)

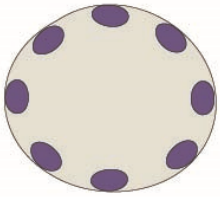


Definitive Hosts
(mammals, esp.
equids, rodents,
marsupials)

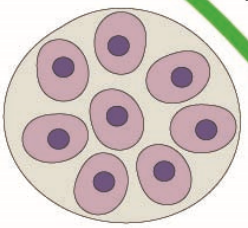
sexual
gamogony



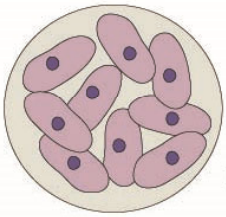
gamonts
(syzygy)
(4-14 µm)



sporont
(10-18 µm)

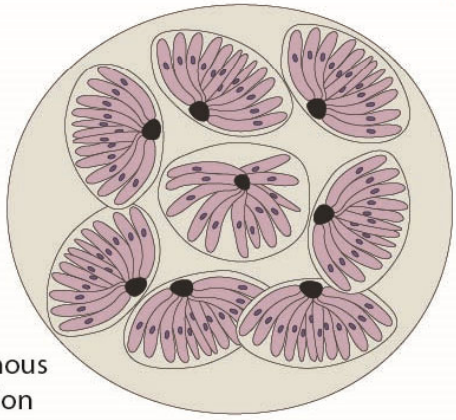


sporoblasts



asexual
merogony

meront
(8-20 µm)



endogenous
sporulation

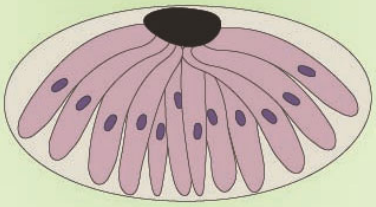
oocyst
(40-100 µm)



excystation
(sporozoites
released)

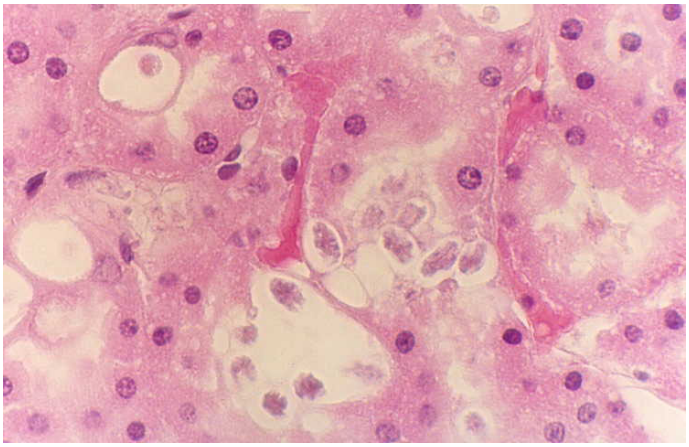
ingested

sporocysts
voided in
urine

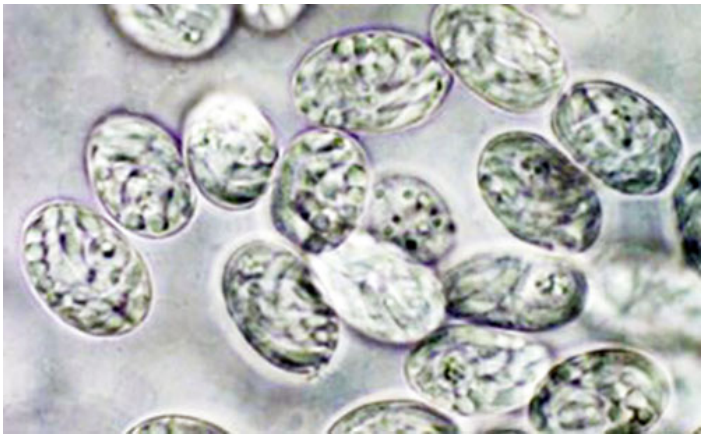


sporocyst
(18-24 µm)

direct transmission via ingestion of sporocysts
contaminating environment (soil, water, food)



Klossiella development in kidney tubules



Klossiella sporocysts in urine

Caryospora
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). *Caryospora* are eimeriid coccidia that were initially thought to be monoxenous (1-host) parasites where merogony (= schizogony), gamogony and sporogony occurred in the digestive tracts of raptorial birds or snakes (definitive hosts). However, recent studies have shown that parasites may undergo complete development in rodent secondary hosts with thin-walled oocysts excysting *in situ* releasing sporozoites which become dormant in monozoic cysts (caryocysts) being infective to new secondary or primary hosts. Mature *Caryospora* oocysts contain a single sporocyst with 8 sporozoites (1:1:8 configuration). Most infections are asymptomatic.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Eimeriorina (no syzygy, many microgametes)
Family:	Eimeriidae (monoxenous, endogenous intracellular merogony and gamogony, exogenous sporogony)
Genus:	*Caryospora* (parasitic in gut/tissues of birds/reptiles/mammals)
Species:	various species cause enteritis in animals

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic ‘haemococcidia’ in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Numerous species of eimeriid coccidia have been described from a wide range of vertebrate and invertebrate hosts. Some 50 genera have been classified in 11 families in the suborder Eimeriorina, including 21 genera in the family Eimeriidae. Most genera are characterized by the formation of oocysts with unique configurations in terms of the numbers of contained sporocysts and sporozoites. The genus *Caryospora* forms oocysts with a 1:1:8 configuration; that is, oocysts are monosporocystic (contain 1 sporocyst) and each sporocyst is octosporozoic (contains 8 sporozoites).

Parasite genera	No. spp.	Life-cycle	Hosts	Oocyst configuration
Family: EIMERIIDAE				
Diaspora	1	monoxenous	invertebrates (arthropods)	0:1:1

Tyzzeria	12	monoxenous	vertebrates (birds, reptiles)	1:0:8
Pfeifferinella	6	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Alveocystis	4	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Mantonella	5	monoxenous	invertebrates (panarthropods), vertebrates (turtles, rodents, birds, some possibly pseudoparasites)	1:1:4
Caryospora	70	monoxenous	vertebrates (birds, reptiles)	1:1:8
Cyclospora	19	monoxenous	vertebrates (mammals)	1:2:2
Dorisa	13	monoxenous	vertebrates (reptiles, mammals)	1:2:8
Isospora	360	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (molluscs)	1:2:4
Sivatoshella	1	monoxenous	vertebrates (birds)	1:2:16
Eimeria	1,700	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (arthropods, annelids, hemichordates, protochordates)	1:4:2
Epieimeria	3	monoxenous	vertebrates (fish)	1:4:2
Choleoeimeria	16	monoxenous	vertebrates (reptiles)	1:4:2
Wenyonella	18	monoxenous	vertebrates (mammals, birds, reptiles)	1:4:4
Margolisiella	6	monoxenous	invertebrates (molluscs)	1:n:2-4
Octosporella	6	monoxenous	vertebrates (fish, reptiles, echidnas, some possibly pseudoparasites)	1:8:2
Gousseffia	1	monoxenous	vertebrates (hedgehogs, possibly pseudoparasites)	1:8:n
Polysporella	1	monoxenous	vertebrates (birds, possibly pseudoparasites)	1:9-15:2
Skrjabinella	1	monoxenous	vertebrates (rodents, possibly pseudoparasites)	1:16:1
Hoarella	1	monoxenous	vertebrates (lizards)	1:16:2
Pythonella	3	monoxenous	vertebrates (reptiles, birds)	1:16:4

Over 70 *Caryospora* spp. have been described from reptiles (predominantly snakes) and birds (predominantly raptors). The parasites undergo asexual and sexual reproduction in intestinal epithelial cells, culminating in the excretion of oocysts into the external environment. The life-cycle is therefore deemed to be monoxenous (one-host) with transmission to new susceptible hosts occurring when they ingest oocysts. However, several *Caryospora* spp. have also been found to have heteroxenous (2-host) life-cycles involving caryocyst formation in secondary hosts, particularly rodent prey for predatory reptiles and birds. Oocysts ingested by rodents excyst releasing sporozoites which migrate to extra-intestinal tissues (usually skin) where they lead to the formation of dormant caryocysts until ingested by new hosts. Extraintestinal development involving merogony, gamogony and sporogony has also occasionally been observed in companion animals (dogs and cats) in association with disfiguring nodular dermatitis.

***Caryospora* species**	**Oocyst size (µm)**	**Hosts**	**Distribution**
Species in snakes (Serpentes)			
C. ahaetullae	25	colubrid (long-nosed whip snake, Oriental whip snake	South Asia
C. barnardae	14	colubrid (Malagasy colubrid)	Madagascar
C. bengalensis	22	colubrid (rainbow water snake)	India
C. bigenetica	13	viperid (timber rattlesnake, eastern diamondback rattlesnake, western diamondback rattlesnake, pygmy rattlesnake, massasauga, copperhead); plus heteroxenous cycle involving Carnivora: canid (dog), felid (cat); Artiodactyla: bovid (goat), suid (pig); Rodentia: murid (house mouse, Mongolian gerbil), cricetid (common vole, hispid cotton rat)	North America, Europe
C. bothriechis		viperid (yellow-blotched palm pit viper)	Central America
C. brasiliensis	22 x 21	colubrid (Brazilian green racer, Mboi-obi, Nuazo, culebra)	South America
C. brygooi	20	colubrid (Madagascar cat-eye snake)	Madagascar
C. carajasensis	23 x 22	colubrid (false coral snake)	South America
C. choctawensis		colubrid (flathead snake)	North America
C. cobrae	19 x 17	elapid (Indian cobra)	India
C. colubris	24	colubrid (dwarf colubrid, horseshoe snake, large whip snake, western whip snake)	Europe
C. coniophanis	19 x 18	colubrid (black striped snake)	Central America
C. conophae	20	colubrid (road guarder snake)	Central America
C. constancieae	21 x 19	elapid (Amazonian coral snake)	South America
C. corallae	22	boid (emerald tree boa)	South America

C. demansiae	20	elapid (yellow-faced whip snake)	Australia
C. dendrelaphis	21 x 20	colubrid (common tree snake)	Australia
C. durrelli	19 x 18	boid (Round Island boa)	Mauritius
C. duszynskii	26 x 24	colubrid (corn snake, red corn snake, Texas rat snake, black rat snake, prairie kingsnake	North America
C. epicratesi	23 x 21	boid (Brazilian rainbow boa)	South America
C. gracilis	24 x 23	colubrid (flat headed snake)	North America
C. guatemalensis	24 x 23	colubrid (scarlet kingsnake)	Central America
C. hermae	22 x 21	colubrid (western striped sand snake)	Africa
C. heterodermus	20	colubrid (variable green snake)	Africa
C. japonicum	19	colubrid (tiger keelback)	Asia
C. jararacae	14	viperid (coffee palm viper, fer-de-lance, jararaca)	South America
C. kalimantanensis	15 x 11	colubrid (mangrove snake)	Malaysia
C. lampropeltis	23	colubrid (prairie kingsnake, desert kingsnake, red milk snake)	North America
C. legeri	30 x 26	colubrid (striped sand snake)	Africa
C. maculatus	12	viperid (spotted night adder)	Africa
C. madagascariensis	26 x 24	colubrid (Madagascar cat-eye snake, Malagasy colubrid)	Madagascar
C. masticophis	14 x 13	colubrid (eastern coachwhip, southern black racer)	North America
C. matatu	20	viperid (horned bush viper)	Africa
C. maxima	43 x 42	colubrid (Forskal's sand snake)	Middle-East
C. mayorum	26 x 24	colubrid (road guarder snake)	Central America
C. micruri	16	elapid (Amazonian coral snake)	South America
C. minuta	12	colubrid (Madagascar hognose snake)	Madagascar
C. najadae	21 x 15	colubrid (Dahl's whip snake)	Middle-East
C. najae	15	elapid (red spitting cobra)	Africa
C. paraensis	17	colubrid (false coral snake)	South America
C. peruensis	29 x 26	colubrid (Argentine vine snake)	South America
C. psammophi	29 x 27	colubrid (western striped sand snake)	Africa
C. pseustesi	26 x 25	colubrid (yellow bellied puffing snake)	South America
C. regentensis	17 x 16	elapid (eastern green mamba, western green mamba)	Africa
C. relictae	19 x 18	colubrid (Florida crowned snake)	North America
C. saudiarabiensis	43 x 41	viperid (African carpet viper)	Africa
C. serpentis	17	colubrid (Madagascar hognose snake, Madagascar cat-eye snake, Madagascar colubrid)	Madagascar
C. simplex	15	viperid (European asp viper, Russell's viper, nose-horned viper, northern viper, Kaznakov's viper, Palestine viper, Ottoman viper); plus heteroxenous cycle involving Artiodactyla: bovid (goat); Rodentia: murid (house mouse), cricetid (hispid cotton rat)	Europe, North America
C. tantillae	20 x 19	colubrid (Florida crowned snake)	North America
C. telescopus	15 x 11	colubrid (European cat snake)	Europe
C. veselyi	19	colubrid (long nosed whip snake)	India
C. weyerae	16 x 15	colubrid (western striped sand snake)	Africa
C. zuckermanae	17	colubrid (spotted whip snake)	Eurasia
C. zacapensis	23 x 22	colubrid (neotropical whip snake)	Central America
Species in lizards (Sauria)			
C. ernsti		dactyloid (Carolina anole)	North America
C. gekkonis	20	gekkonid (Tokay gecko)	India
C. varani nomen dubium		varanid (ornate monitor)	Africa
Species in turtles (Testudines)			
C. cheloniae	33.8-40.1 x 11-14.6	chelonid (green sea turtle)	Australia, Caribbean
Species in birds (Aves)			
C. aquilae		Accipitriformes: accipitrid (golden eagle)	Holarctic
C. arcayae		Accipitriformes: accipitrid (roadside hawk, broad winged hawk)	Americas
C. argentati	20 x 17	Charadriiformes: larid (European herring gull)	Europe
C. biarmicusis		Falconiformes: falconid (lanner falcon)	Africa, Eurasia
C. boeri		Falconiformes: falconid (Eurasian kestrel)	Europe
C. bubonis		Strigiformes: strigid (great horned owl) plus heteroxenous cycle involving Rodentia: murid (mouse)	Americas
C. circi		Accipitriformes: accipitrid (western marsh harrier)	Eurasia

C. falconis	33	Falconiformes: falconid (peregrine falcon, Eurasian hobby, European kestrel)	Eurasia
C. gloriae	32 x 28	Passeriformes: icterid (Cuban blackbird)	Cuba
C. henryae	39 x 32	Strigiformes: strigid (Eurasian eagle-owl); Accipitriformes: cathartid (turkey buzzard), accipitrid (black kite), Falconiformes: falconid (kestrel, hobby)	cosmopolitan
C. jiroveci		Passeriformes: muscicapid (European robin)	Palearctic
C. kansasensis		Accipitriformes: accipitrid (Swainson's hawk)	North America
C. kutzeri (syn. *C. falconis p.p., henryi p.p.*)		Falconiformes: falconid (lanner falcon, Saker falcon, Laggar falcon, prairie falcon, peregrine falcon, gyrfalcon, Eurasian hobby, European kestrel)	Eurasia, Americas
C. lindsayi		Accipitriformes: accipitrid (red tailed hawk)	North America
C. megafalconis		Falconiformes: falconid (Saker falcon, gyrfalcon, Eurasian falcon)	Europe
C. neofalconis		Falconiformes: falconid (lanner falcon, prairie falcon, peregrine falcon, Eurasian hobby, European kestrel)	Eurasia, Americas
C. strigis		Strigiformes: tytonid (barn owl)	cosmopolitan
C. tremula		Accipitriformes: cathartid (turkey vulture)	Americas
C. undata	33 x 29	Charadriiformes: larid (European herring gull), alcid (tufted puffin, common murre)	Holarctic
C. uptoni		Accipitriformes: accipitrid (red tailed hawk)	North America
Species in mammals (Mammalia)			
C. microti nomen dubium	10 x 9	Rodentia: cricetid (meadow mouse)	North America

Parasite morphology: *Caryospora* spp. form 3 different types of sequential developmental stages (meronts, gamonts, and oocysts) in host cells, but some species may occasionally form a fourth stage (caryocysts) in certain hosts. Meronts (schizonts) appear as basophilic bodies located within parasitophorous vacuoles in host cells. They range in size (5-20 x 4-10 µm) and divide internally to form up to 25 merozoites. The merozoites are tightly packed in some meronts or loosely packed in other, occasionally being radially arranged in a wheel-spoke configuration around a central eosinophilic body. The merozoites were larger in some meronts than others (4 x 1.6 cf. 2.4 x 1.2 µm), suggesting the occurrence of 2 meront generations or asynchronous development or overlapping infections (most natural infections contained mixtures of the different types of meronts). Gamonts were also located in parasitophorous vacuoles in host cells, and they exhibited sexual differentiation into macrogametocytes (female) and microgametocytes (male), the former being more plentiful than the latter. Macrogametocytes were elongate ellipsoidal stages (10-37 x 9-14 µm) aligned along the long axis of the host cell. They were bound by a thin wall and contained fine eosinophilic granular cytoplasmic reticulum, a small round central eosinophilic nucleus with a basophilic nucleolus, and they become heavily vacuolated as they matured to uninucleate macrogametes. Microgametocytes were oval-round stages (10-43 x 9-27 µm) that often displaced the host cell nucleus laterally. They were bound by a thin wall and became multinucleated as they developed numerous (> 20) basophilic rod-like microgametes (1-4 µm long) that were biflagellated. Gamete fertilization produced non-motile zygotes that commenced oocyst formation by producing thick membranous oocyst walls. Developing oocysts contained a central sporoblast that produced a single sporocyst enclosed by membranous sporocyst walls. Each sporocyst formed 8 vermiform sporozoites with central nuclei and posterior refractile bodies. The resultant oocyst:sporocyst:sporozoite configuration was 1:1:8, which is considered to be characteristic for the genus *Caryopsora*. Mature oocysts were spherical-ovoid in shape, lacked micropyles and residual bodies, and ranged in diameter from 10-43 µm depending on the parasite species. The sporocysts were subspherical-ovoid in shape, ranged in diameter from 8-35 µm, possessed a residual body, and those of most species contained a Stieda body evident as a prominent anterior dome. The sporozoites varied considerably in size (4-20 x 1-12 µm) and shape, with those of some species being short and stubby, and those of other species being long and slender, sometimes crescentic. Merogony, gamogony and oocyst formation have also been reported in some mammalian hosts, but the oocysts were thin-walled and only produced a few sporozoites which became encysted in host tissues. These so-called caryocysts appeared as small rounded stages (10-18 x 10-16 µm) within parasitophorous vacuoles in macrophages and connective tissue cells, and they usually contained one (sometimes 2 or 3) robust sporozoites (4-6 x 2-3 µm).

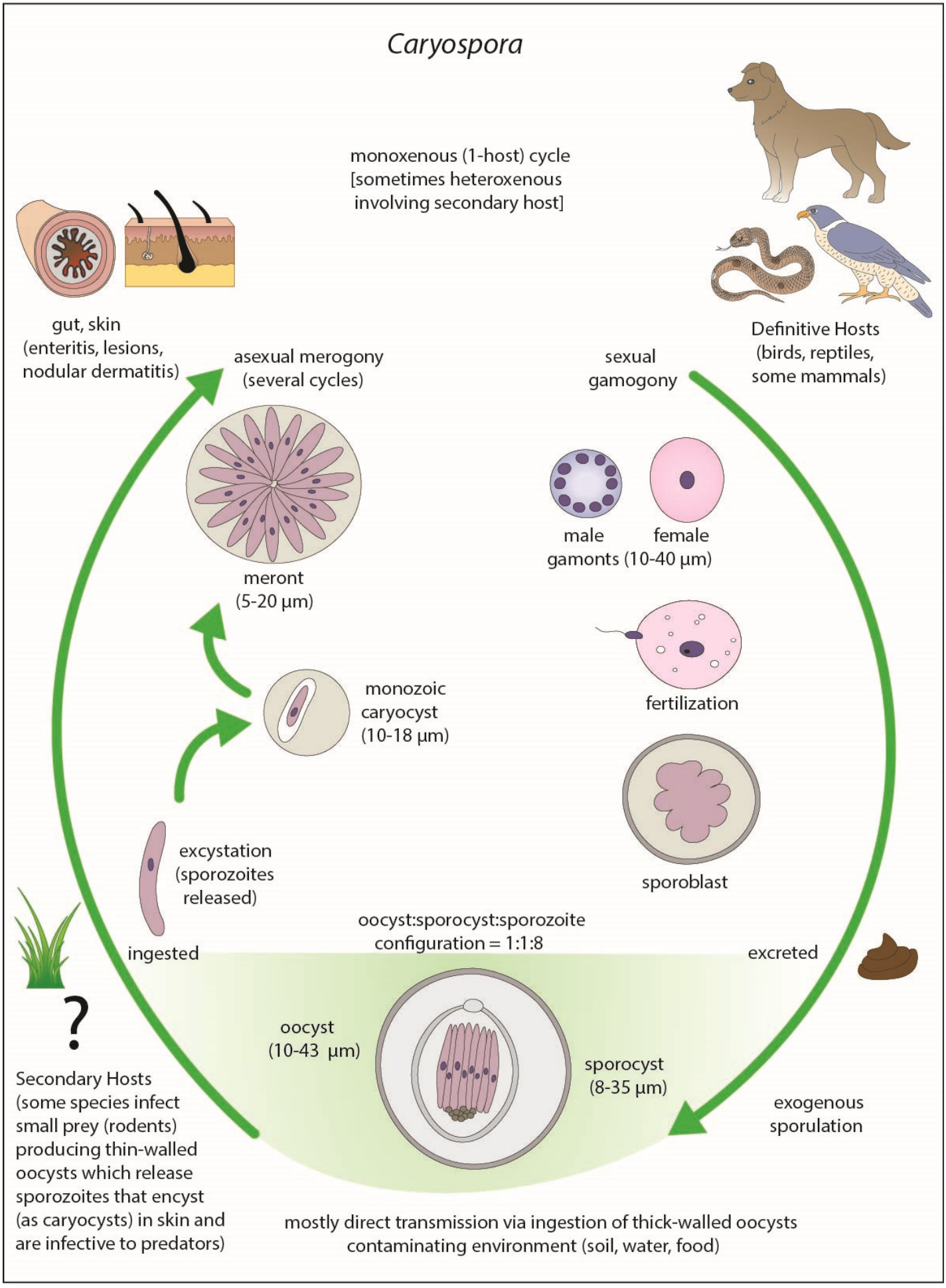
Site of infection: Infections are commonly found in the digestive tracts of reptiles and birds, with 54 parasite species reported in snakes (colubrids, elapids, viperids, boids), 2-3 species in lizards, one in turtles, and 20 species in birds, mostly birds of prey (Accipitriformes, Falconiformes and Strigiformes) but also some Charadriiformes (gulls, puffins) and Passeriformes (robins). These hosts are considered to be primary (predatory) hosts in which parasites completed asexual proliferation and sexual reproduction culminating in the excretion of oocysts. Natural and experimental infections have also been detected in extraintestinal tissues (usually dermal tissues) in various mammals, usually small rodents which are normally prey for predatory reptiles or birds, but sometimes in carnivores (dogs, cats) and experimentally in ungulates (pigs, goats). These hosts are considered to be secondary (prey) hosts (and not intermediate or paratenic hosts) as the parasites complete both asexual and sexual development, culminating in the formation of dormant sporozoites (caryocysts) in host tissues.

Pathogenesis: Even though parasite developmental stages infect and lyse host enterocytes in primary hosts, most infections are asymptomatic as the cumulative damage was not severe enough to cause disease. Heavy infections by some species, however, may cause enough damage to manifest in disease (coccidiosis), with focal haemorrhagic lesions, epithelial hyperplasia and inflammation (enteritis) producing clinical signs, including diarrhoea, regurgitation, reduced appetite, weight loss, depression, and even acute death. Clinical infections have been reported primarily in birds, and occasionally in reptiles (especially green turtles). Natural infections have also been reported in secondary hosts, including rodents (rats, mice) and carnivores (dogs, cats), and experimental infections in ungulates (pigs, goats). Some of the infections in dogs and cats have been associated with an unusual clinical disease involving progressive pyogranulomatous dermatitis, panniculitis (inflammation of subcutaneous fat), oedema, and perivascular to interstitial infiltrates of neutrophils and macrophages that coalesce into papules and nodules. Parasite developmental stages found within lesions included meronts, gamonts, unsporulated and sporulated thin-walled oocysts and caryocysts.

Developmental cycle and mode of transmission: *Caryospora* spp. are eimeriid coccidia that were initially thought to only have monoxenous (one-host) life-cycles where merogony, gamogony and sporogony occurred in the digestive tracts of primary hosts (raptorial birds, snakes). Over 1-2 weeks, parasites underwent asexual proliferation followed by sexual reproduction in host enterocytes, leading to the formation of thick-walled oocysts that were excreted in host faeces. Sporulation was often (but not always) completed exogenously when sporocysts formed numerous infective sporozoites. The prepatent period (time from infection to first oocyst excretion) ranged from 8-13 days, and the patent period (duration of oocyst excretion) ranged from 9-18 days, sometimes longer. Transfer between hosts was direct and accomplished by the faecal-oral transmission of oocysts shed in faeces contaminating food and water supplies to be ingested by new hosts. Some *Caryospora* species, however, were also found to have facultatively or obligatory heteroxenous (2-host) life-cycles involving mammalian prey animals (usually rodents) as alternate hosts. By definition, these hosts were not paratenic (transport) hosts as parasites developed further in their tissues, and they were not intermediate hosts as the parasites completed both asexual and sexual development. They have therefore frequently been referred to as secondary (prey) hosts. Parasite development typically took place in extraintestinal sites (usually the skin) resulting in the production of thin-walled oocysts which underwent endogenous sporulation forming small numbers of sporozoites. Oocyst excystation occurred *in situ* releasing small robust sporozoites which became dormant in host tissues as caryocysts. The caryocysts were found to be infective to new secondary or primary hosts, with transmission occurring via predation.

Differential diagnosis: Infections are usually detected by the coprological examination of faecal concentrates (sediments, floats) for the presence of distinctive oocysts. Endogenous developmental stages are usually detected at post-mortem by the microscopic examination of histological sections, sometimes aided by immunolabelling with antiserum conjugated to fluorochrome or enzyme tags. Molecular biological techniques have been used to detect and characterize parasite isolates following the polymerase chain reaction (PCR) amplification of nuclear (small subunit (18S) ribosomal DNA) or mitochondrial (cytochrome c oxidase subunit 1) gene sequences.

Treatment and control: There have been several attempts to treat natural infections in birds and reptiles, with the application of sulphonamides (sulfadimidine), thiamine analogues (amprolium), nitroimidazoles (metronidazole) and triazinones (toltrazuril, ponazuril) producing reasonable results, although some treatments produced adverse side-effects requiring supportive therapy or dietary supplementation. Dogs and cats with disfiguring nodular dermatitis have been successfully treated with combinations of trimethoprim-sulfamethoxazole or pyrimethamine and clindamycin with the resolution of lesions within 6 weeks (although some animals relapsed following the discontinuation of treatment). Various preventive strategies have been recommended to break both faecal-oral and predator-prey transmission cycles, including regular health surveillance to detect infected individuals for treatment, quarantine or culling, better sanitation to reduce faecal oocyst contamination, improved hygiene to disinfect holding facilities, rodent control to prevent the ingress of wildlife into colonies, and curbing the hunting/scavenging behaviours of pets and captive predators.


Caryospora
monoxenous (1-host) cycle
[sometimes heteroxenous
involving secondary host]
gut, skin
(enteritis, lesions,
nodular dermatitis)
Definitive Hosts
(birds, reptiles,
some mammals)
asexual merogony
(several cycles)
sexual
gamogony
meront
(5-20 µm)
male
gamonts (10-40 µm)
female
monozoic
caryocyst
(10-18 µm)
fertilization
excystation
(sporozoites
released)
sporoblast
ingested
oocyst:sporocyst:sporozoite
configuration = 1:1:8
excreted
oocyst
(10-43 µm)
sporocyst
(8-35 µm)
exogenous
sporulation
?
Secondary Hosts
(some species infect
small prey (rodents)
producing thin-walled
oocysts which release
sporozoites that encyst
(as caryocysts) in skin and
are infective to predators)
mostly direct transmission via ingestion of thick-walled oocysts
contaminating environment (soil, water, food)



Caryospora oocysts in snake faeces

Cyclospora
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). Enteric coccidia are monoxenous (1-host) parasites in the digestive tracts of vertebrates. They undergo three sequential developmental stages: endogenous multiplication by asexual merogony (= schizogony) followed by sexual gamogony (male microgametes fertilize female macrogametes) producing oocysts which undergo asexual sporogony (sporozoite formation). *Cyclospora* oocysts contain two sporocysts each with two sporozoites (1:2:2 configuration). Infections have been reported in various animals, with one species infecting humans and causing acute diarrhoeal disease.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Eimeriorina (no syzygy, many microgametes)
Family:	Eimeriidae (monoxenous, endogenous intracellular merogony and gamogony, exogenous sporogony)
Genus:	*Cyclospora* (parasitic in gut of mammals and reptiles)
Species:	*C. cayetanensis* (causes diarrhoea in humans)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic ‘haemococcidia’ in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Numerous species of eimeriid coccidia have been described from a wide range of vertebrate and invertebrate hosts. Some 50 genera have been classified in 11 families in the suborder Eimeriorina, including 21 genera in the family Eimeriidae. Most genera are characterized by the formation of oocysts with unique configurations in terms of the numbers of contained sporocysts and sporozoites. The genus *Cyclospora* forms oocysts with a 1:2:2 configuration; that is, oocysts are disporocystic (contain 2 sporocysts) and each sporocyst is disporozoic (contains 2 sporozoites).

Parasite genera	No. spp.	Life-cycle	Hosts	Oocyst configuration
Family: EIMERIIDAE				
Diaspora	1	monoxenous	invertebrates (arthropods)	0:1:1
Tyzzeria	12	monoxenous	vertebrates (birds, reptiles)	1:0:8

Pfeifferinella	6	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Alveocystis	4	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Mantonella	5	monoxenous	invertebrates (panarthropods), vertebrates (turtles, rodents, birds, some possibly pseudoparasites)	1:1:4
Caryospora	70	monoxenous	vertebrates (birds, reptiles)	1:1:8
Cyclospora	19	monoxenous	vertebrates (mammals)	1:2:2
Dorisa	13	monoxenous	vertebrates (reptiles, mammals)	1:2:8
Isospora	360	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (molluscs)	1:2:4
Sivatoshella	1	monoxenous	vertebrates (birds)	1:2:16
Eimeria	1,700	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (arthropods, annelids, hemichordates, protochordates)	1:4:2
Epieimeria	3	monoxenous	vertebrates (fish)	1:4:2
Choleoeimeria	16	monoxenous	vertebrates (reptiles)	1:4:2
Wenyonella	18	monoxenous	vertebrates (mammals, birds, reptiles)	1:4:4
Margolisiella	6	monoxenous	invertebrates (molluscs)	1:n:2-4
Octosporella	6	monoxenous	vertebrates (fish, reptiles, echidnas, some possibly pseudoparasites)	1:8:2
Gousseffia	1	monoxenous	vertebrates (hedgehogs, possibly pseudoparasites)	1:8:n
Polysporella	1	monoxenous	vertebrates (birds, possibly pseudoparasites)	1:9-15:2
Skrjabinella	1	monoxenous	vertebrates (rodents, possibly pseudoparasites)	1:16:1
Hoarella	1	monoxenous	vertebrates (lizards)	1:16:2
Pythonella	3	monoxenous	vertebrates (reptiles, birds)	1:16:4

Around 19 *Cyclospora* spp. have been described in millipedes, insectivores, moles, rodents, reptiles (mostly snakes) and primates, including humans. *C. cayentanensis* is the only species found in humans. Its identity was unclear for many years and infections were reported as CLBs: an acronym for coccidia-like bodies (sometimes mistaken for large *Cryptosporidium*) or cyanobacterium-like bodies (once called blue-green algae). The coccidial nature of CLBs was subsequently demonstrated by ultrastructural and molecular characterization studies. *C. cayentanensis* differs from most other *Cyclospora* species in that its oocysts are smaller and spherical rather than oblong. The detection of similar species in non-human primates (*C. cercopitheci* in green monkeys, *C. colobi* in colobus monkeys, and *C. papionis* in baboons) suggested that two species groups may exist: those that infect primates and produce small spherical oocysts; and those that infect insectivores and rodents and form large oblong oocysts. All species described to date are thought to be highly host specific and experimental studies attempting to cross-transmit isolates between a variety of animals and humans have proven unsuccessful. Epidemiological studies have not implicated any animal species as reservoirs of human infection, despite the occasional detection of *Cyclospora* oocysts in the faeces of asymptomatic domestic animals (ducks, chickens and dogs) in endemic areas (their occurrence is thought to be due to high environmental contamination). While *C. cayetanesis* has been found worldwide in developed and developing countries and in urban and rural areas, it is most common in tropical and subtropical areas, particularly Latin America, the Indian subcontinent, and Southeast Asia.

Cyclospora* species	**Oocyst size (µm)**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
C. angimurinensis	22 x 19	Rodentia: heteromyid (hispid pocket mouse)	jejunum		North America
C. ashtabulensis	18 x 14	Eulipotyphla: talpid (hairy-tailed mole)	jejunum		North America
C. caryolytica	18 x 12	Eulipotyphla: talpid (European mole, eastern mole, hairy-tailed mole)	small and large intestines (intranuclear)		Europe
C. cayetanensis	10 x 8	Primates: hominid (human, chimpanzee, baboon)	small intestines	watery diarrhoea	cosmopolitan
C. cercopitheci	8-10	Primates: cercopithecid (African green monkey)	duodenum/jejunum		Africa
C. colobi	8-9	Primates: cercopithecid (colobus monkey)	duodenum/jejunum		Africa
C. duszynskii	11 x 10	Eulipotyphla: talpid (eastern mole)	intestines		North America
C. glomericola (type species)	30 x 9	Diplopoda: glomerid (pill millipede)	intestines		Europe

C. macacae	8-9	Primates: cercopithecid (rhesus macaque, crab-eating macaque)	intestines		China
C. megacephali	19 x 16	Eulipotyphla: talpid (eastern mole)	jejunum		North America
C. niniae	15 x 13	Serpentes: colubrid (redback coffee snake)	small intestines	gut destruction	Central America
C. papionis	8-10	Primates: cercopithecid (olive baboon)	duodenum/jejunum		Africa
C. parascalopi	17 x 14	Eulipotyphla: talpid (hairy-tailed mole)	jejunum		North America
C. schneideri	20 x 17	Serpentes: aniliid (coral cylinder snake)	small intestines	nonpathogenic	South America
C. scinci	10 x 7	Sauria: scincid (sandfish skink)	small intestine		Egypt
C. talpae	14 x 10	Eulipotyphla: talpid (European mole)	liver, bile ducts		Europe
C. viperae (syn. *C. babaulti*)	17 x 10	Serpentes: viperid (European asp viper, northern viper, smooth snake)	small intestines		Europe
C. yatesi	17 x 15	Eulipotyphla: talpid (eastern mole)	intestines		North America
C. zamenis (syn. *C. tropidonoti*)	17 x 10	Serpentes: colubrid (green whip snake, common grass snake, Indian grass snake)	small intestines		Eurasia

*Un-named species of *Cyclospora* have also been reported from various hosts: including non-human primates (macaques, drills, vervets, howlers, baboons), carnivores (dogs), artiodactyls (bovids), rodents (rats, mice), birds (chickens, crows), insects (cockroaches) and molluscs (shellfish).

Parasite morphology: *Cyclospora* spp. form 3 different developmental stages: meronts (forming merozoites), gamonts (forming male and female gametes); and oocysts (forming sporocysts containing sporozoites). Meronts (sometimes called schizonts) appear as pleomorphic basophilic stages measuring ~15-20 µm in diameter. As they mature, they divide internally to form multiple slender merozoites. Two types of meronts are formed: type I meronts (first generation) producing 8-12 small merozoites ranging in size from 3-4 x 0.5 µm; and type II meronts (second generation) producing 4 larger merozoites ranging in size from 12-15 x 0.7-0.8 µm. Gamonts appear as round-ovoid cells (10-33 µm in diameter) which exhibit sexual dimorphism as they develop into pale uninucleate macrogametocytes (female) and darker multinucleate microgametocytes (male). Macrogametocytes mature to produce single macrogametes which are highly vacuolated due to the presence of numerous small and large wall-forming bodies often located peripherally. Microgametocytes appear multinucleated as they mature to produce numerous slender flagellated microgametes (5 x 1 µm). Fertilization produces non-motile zygotes which form ovoid oocysts ranging in size from 7-10 µm in diameter. Oocysts are surrounded by bilayered membranous walls and are initially unsporulated containing an undifferentiated sporoblast. As they sporulate, each oocyst produces 2 sporocysts bound by membranous sporocyst walls and containing a small polar body and an oocyst residuum. The sporocysts are ovoid measuring 6 x 4 µm and have Stieda and sub-Stieda bodies located at one pole. Each sporocyst contains a granular residuum and 2 elongate folded sporozoites (9 x 1 µm) lacking crystalloid and refractile bodies. The resultant oocyst:sporocyst:sporozoite configuration of 1:2:2 is characteristic for the genus *Cyclospora*.

Site of infection: Some 19 parasite species have been described and named from 22 host species, including 12 mammalian species (cercopithecid and hominid primates, talpid moles, heteromyid rodents), 8 snake species (colubrids, viperids, aniliids), one lizard species (scincid) and one invertebrate (glomerid millipede). For those species where the sites of endogenous development have been determined, the parasites were located within parasitophorous vacuoles in small intestinal epithelial cells, particularly at tips of villi in the jejunum and duodenum. A few species have also been found to infect the large intestines, one species in moles infects the liver, and another in moles develops in the nuclei of epithelial cells. Mature oocysts are exogenous stages that are voided into the external environment with host faeces.

Pathogenesis: These coccidial parasites undergo obligatory endogenous development within intestinal epithelia leading to host cell destruction in order to liberate parasite progeny. The gut lining therefore suffers structural losses which lead to functional abnormalities. The extent of damage depends on the intensity of infection, parasite pathogenicity (virulence) and host susceptibility. Many infections in animals were detected incidentally in asymptomatic individuals, but infections have been associated with clinical disease (cyclosporiasis) in humans. Endogenous developmental stages may cause surface epithelial injury, moderate to marked erythema and inflammation in the intestines. Mucosal architecture becomes disorganised with villous atrophy, crypt hyperplasia and alterations in enterocyte shapes from columnar to cuboidal to pleomorphic with loss of the microvillous brush border. Infections are characterized initially by mild-severe small bowel diarrhoea, often explosive with soft to watery stools, and acute with abrupt onset

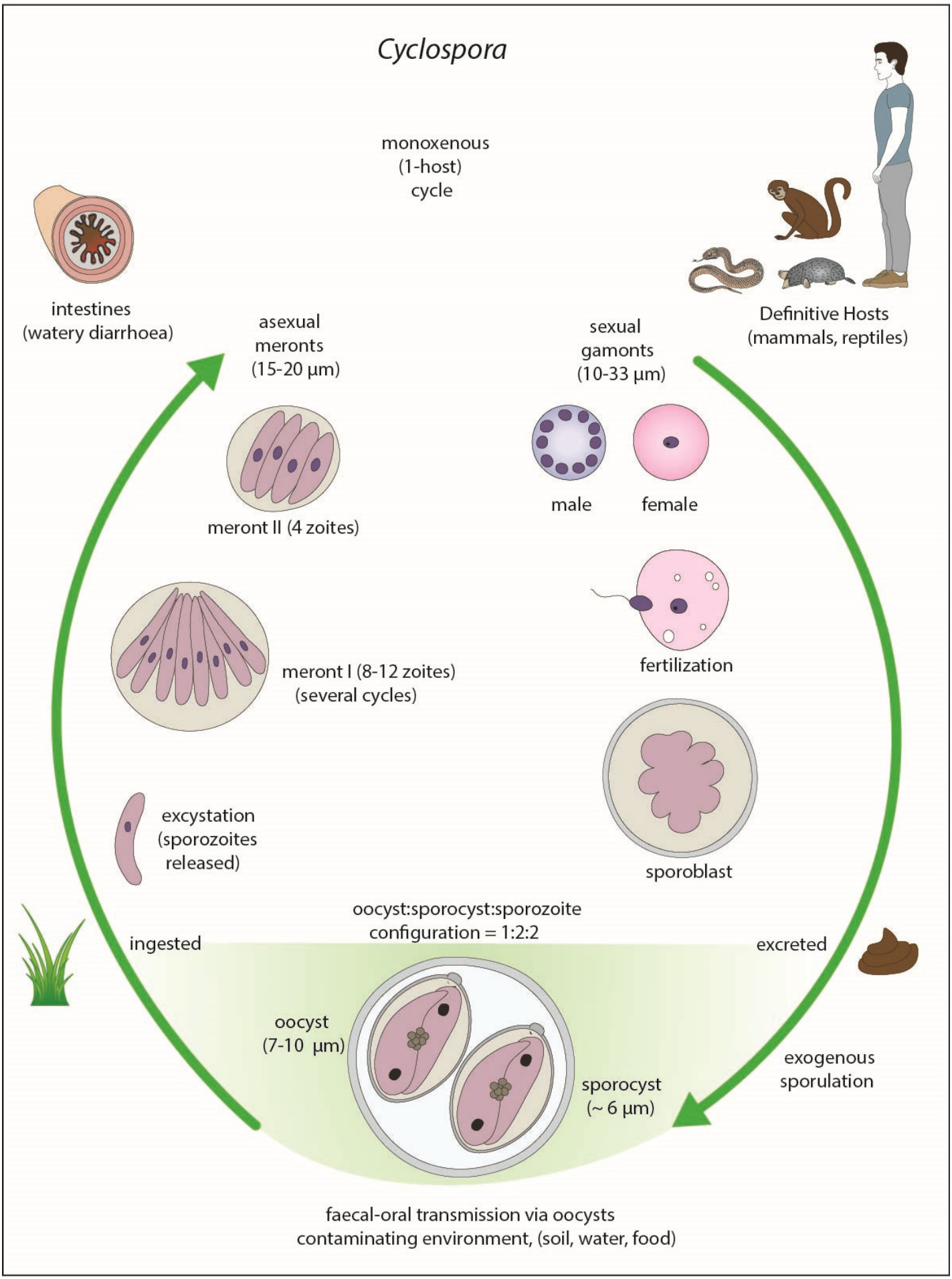
but varying in duration from transient to protracted. Most infections are self-limiting but prolonged or relapsing infections may occur leading to a chronic illness with prominent fatigue and anorexia, along with intermittent nausea and diarrhoea. Other associated clinical signs have included flu-like symptoms, nausea, vomiting, dyspepsia, malabsorption, impaired D-xylose absorption, dehydration, abdominal cramping, bloating, flatulence, myalgia, weight loss, and sometimes low-grade fever and tachycardia. The severity of disease depends on the age, nutritional and immune state of the host. Infections occur in people of all age groups, but young children have more severe clinical symptoms and increased duration of infection. The incubation period ranges from 7-14 days, but onset may be delayed by several weeks in some instances. The course of disease usually ranges from 1-7 weeks, but symptoms can persist for several months especially in immunocompromised patients.

Developmental cycle and mode of transmission: *Cyclospora* spp. are enteric coccidia with monoxenous (one-host) life-cycles involving the faecal-oral transmission of resistant oocysts excreted into the external environment to infect new hosts via contaminated food or water. Ingested oocysts excyst in the gut following exposure to gastric acids, bile salts and pancreatic enzymes. The released sporozoites invade epithelial cells and form meronts (schizonts) which undergo asexual proliferation by internal (endogenous) division to form numerous merozoites which invade neighbouring cells. It is thought that at least 2 cycles of merogony occur, with first generation (type I) meronts producing 8-12 merozoites, and second generation (type II) meronts producing 4 merozoites. However, it has occasionally been observed that several cycles of each meront type may be completed before type II merozoites begin to form gamonts. Sexual development (gamogony) involves the formation of male and female gametocytes which produce gametes, robust female macrogametes and small 'sperm-like' male microgametes. Fertilization occurs by gamete fusion resulting in the production of a non-motile zygote which develops into an oocyst with a thick wall. Oocysts are excreted with host faeces into the external environment as unsporulated non-infectious stages. They become infectious by exogenous sporulation over 7-15 days to produce infective sporozoites contained within sporocysts (1:2:2 oocyst:sporocyst:sporozoite configuration). The prepatent period (time from infection to first oocyst excretion) ranged from 2-11 days, and the patent period (duration of oocyst excretion) ranged varied considerably from weeks to months in chronic infections. The environmentally-resistant oocysts contaminate food, water and soil, where they can be inadvertently ingested by new susceptible hosts. Infections have been associated with the consumption of a range of foods, mostly fresh salad greens and vegetables (lettuce, snow peas, spinach, mustard), herbs (basil, coriander, mint, marjoram) and fruits (raspberries) contaminated by human waste during production (indiscriminate defaecation by workers or organic fertilizers containing untreated faeces) or processing (washing produce with contaminated water). Oocysts have also been found in association with numerous water sources, mostly raw untreated waters but also potable and treated waters. The oocysts are small enough to be discharged with final effluents from waste stabilization ponds and sewage treatment works, and they are highly resistant to many disinfectants, including chlorination procedures used for water treatment. Recreational water venues (water parks, sprinkler fountains, lakes, rivers and oceans) have also been implicated in episodic transmission events, and oocysts have also been found in filter-feeding shellfish in several markets. Contaminated soil also poses a risk, particularly in children playing in muddy soils or indulging in geophagia (pica). Many outbreaks of disease appear to be seasonal, particularly in summer rainy seasons in tropical countries, and they have also been linked to unexplained traveler's diarrhoeal disease following international travel to tropical areas.

Differential diagnosis: Infections are usually diagnosed by the microscopic detection of oocysts in faecal samples, and sometimes in duodenal or jejunal biopsy samples. It is also recommended that multiple stool samples be collected on alternate days as oocyst excretion can be intermittent. Oocysts may be concentrated from samples by various sedimentation-floatation techniques, including ethyl acetate-formalin sedimentation, and floatation in saturated heavy metal salt solutions or discontinuous sucrose, caesium chloride or Percoll gradients. Wet mounts are best observed by high contrast microscopy (bright-field, phase-contrast or differential interference-contrast) or epifluorescence microscopy (oocysts autofluoresce white-blue using 330-380 nm excitation filters or fluorescent-green with 450-490 nm filters). Alternatively, fixed faecal smears may be examined following acid-fast or safranin staining. Definitive oocyst identification is made difficult by the extended period required for sporulation (1-2 weeks in dilute potassium dichromate). Several immunological techniques (fluorescent-antibody tests, enzyme immunoassays, Western blotting) have been used experimentally to examine host antibody responses to specific parasite antigens, but no commercial tests are available. Molecular biological techniques have been used to detect and characterize parasite isolates by the polymerase chain reaction (PCR) amplification of nuclear gene sequences (18S and 5.8S ribosomal DNA, and internal transcribed spacer region 1), by restriction fragment length polymorphism (RFLP) analyses, and multilocus sequence typing (MLST) based on 5 microsatellite markers.

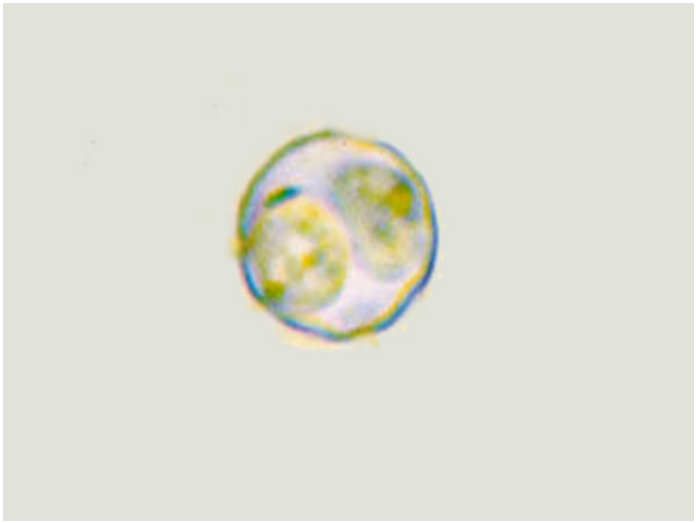
Treatment and control: Clinical infections in both immuno-competent and immuno-compromised patients have responded well to daily treatment for 4-7 days with the combination antibiotic medication trimethoprim-sulfamethoxazole (co-trimoxazole), usually resulting in the resolution of symptoms and the cessation of oocyst excretion. For patients allergic to sulfa components, treatment with ciprofloxacin or nitazoxanide helped but were not as effective. All patients benefited from supportive rehydration therapy (oral or intravenous) to replenish fluid losses from profuse and/or prolonged diarrhoea. Various preventive control measures have been instituted to reduce the risks of oocyst transmission through improvements in sanitation, food hygiene, water treatment and personal hygiene. The source of infections are oocysts in human excreta, so proper sanitation processes should be used to collect, treat and dispose of human waste. Nightsoil (fresh faeces) and partially-treated sewage must not be used as organic fertilizers for food crops, and farm workers should be provided with facilities to prevent indiscriminate defaecation around plant crops. Food industries should

endeavour to properly process and package foods. Studies have shown that washing produce in clean water does not remove all contaminating oocysts, but that oocysts may be killed by cooking (temperatures > 70°C or microwave heating), freeze-drying (desiccation), freezing (temperatures < -40°C) or some disinfectants (sodium dichloroisocyanurate (NaDCC), or magnesium oxide nanoparticles). Water treatment facilities should be checked, and upgraded as required, to provide safe drinking water. Oocysts have proven to be more resistant to chlorination treatments than to ozonation, and membrane filtration appeared to be more effective in removing oocysts than conventional sand filtration. Small volumes of water may be disinfected by boiling, and surrogate studies (using other coccidian oocysts) have suggested that gamma irradiation may be effective. Recreational water providers should periodically check for oocyst contamination and provide toilet facilities to prevent contamination. Public health education programs may be used to promote personal hygiene practices and raise awareness of the disease in populations at risk, including international travellers to tropical holiday destinations.


Cyclospora
monoxenous
(1-host)
cycle
intestines
(watery diarrhoea)
asexual
meronts
(15-20 µm)
meront II (4 zoites)
meront I (8-12 zoites)
(several cycles)
excystation
(sporozoites
released)
ingested
oocyst:sporocyst:sporozoite
configuration = 1:2:2
oocyst
(7-10 µm)
sporocyst
(~ 6 µm)
sexual
gamonts
(10-33 µm)
male
female
fertilization
sporoblast
excreted
exogenous
sporulation
Definitive Hosts
(mammals, reptiles)
faecal-oral transmission via oocysts
contaminating environment, (soil, water, food)



Cyclospora oocysts in human faecal smear



Cyclospora oocyst from faeces

Isospora* and *Cystoisospora
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). Most isosporid species are monoxenous (1-host) parasites in the digestive tracts of vertebrates, although some have recently been found to form encysted (monozoic) stages in the tissues of intermediate hosts. There are three sequential stages in the parasite life-cycle: endogenous multiplication by asexual merogony (= schizogony) followed by sexual gamogony (male microgametes fertilize female macrogametes) producing oocysts which are excreted and undergo asexual sporogony (sporozoite formation). Isosporid oocysts typically contain two sporocysts, each with four sporozoites (1:2:4 configuration). Contemporary phylogenetic studies indicate isosporid coccidia have polyphyletic origins: one group forming sporocysts with Stieda bodies in birds and reptiles being similar to other monoxenous eimeriid coccidia (species retained in the genus *Isospora*), and one group forming sporocysts without Stieda bodies in carnivorous mammals, as well as small encysted stages in the tissues of paratenic hosts, being more closely related to the heteroxenous sarcocystid coccidia (species transferred to genus *Cystoisospora*). Many isosporid species have been associated with clinical disease (coccidiosis) characterized by gastrointestinal perturbations and sometimes extraintestinal lesions.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Eimeriorina (no syzygy, many microgametes)
Family:	Eimeriidae (monoxenous, endogenous intracellular merogony and gamogony, exogenous sporogony)
Genus:	*Isospora* (= *Atoxoplasma*) (parasitic in intestines of birds and lizards)
Species:	various species cause clinical coccidiosis (mostly in neonates)
Family:	Sarcocystidae (heteroxenous, disporocystic oocysts, tissue cyst formation in intermediate/paratenic hosts)
Subfamily:	Cystoisosporinae (monozoic cysts in paratenic transport hosts, sporocysts without Stieda bodies)
	Cystoisospora (formerly mammalian *Isospora*) (parasitic in intestines, sometimes tissues, of mammals)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the

gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as 'haemogregarines' in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	**Family**	**Genera**	**Hosts**	**Site**	**Trans-mission***
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Numerous species of eimeriid coccidia have been described from a wide range of vertebrate and invertebrate hosts. Some 50 genera have been classified in 11 families in the suborder Eimeriorina, including 21 genera in the family Eimeriidae. Most genera are characterized by the formation of oocysts with unique configurations in terms of the numbers of contained sporocysts and

sporozoites. The genera *Isospora* and *Cystoisospora* form oocysts with a 1:2:4 configuration; that is, oocysts are disporocystic (contain 2 sporocysts) and each sporocyst is tetrasporozoic (contains 4 sporozoites).

Parasite genera	No. spp.	Life-cycle	Hosts	Oocyst configuration
Family: EIMERIIDAE				
Diaspora	1	monoxenous	invertebrates (arthropods)	0:1:1
Tyzzeria	12	monoxenous	vertebrates (birds, reptiles)	1:0:8
Pfeifferinella	6	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Alveocystis	4	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Mantonella	5	monoxenous	invertebrates (panarthropods), vertebrates (turtles, rodents, birds, some possibly pseudoparasites)	1:1:4
Caryospora	70	monoxenous	vertebrates (birds, reptiles)	1:1:8
Cyclospora	19	monoxenous	vertebrates (mammals)	1:2:2
Dorisa	13	monoxenous	vertebrates (reptiles, mammals)	1:2:8
Isospora	360	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (molluscs)	1:2:4
Sivatoshella	1	monoxenous	vertebrates (birds)	1:2:16
Eimeria	1,700	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (arthropods, annelids, hemichordates, protochordates)	1:4:2
Epieimeria	3	monoxenous	vertebrates (fish)	1:4:2
Choleoeimeria	16	monoxenous	vertebrates (reptiles)	1:4:2
Wenyonella	18	monoxenous	vertebrates (mammals, birds, reptiles)	1:4:4
Margolisiella	6	monoxenous	invertebrates (molluscs)	1:n:2-4
Octosporella	6	monoxenous	vertebrates (fish, reptiles, echidnas, some possibly pseudoparasites)	1:8:2
Gousseffia	1	monoxenous	vertebrates (hedgehogs, possibly pseudoparasites)	1:8:n
Polysporella	1	monoxenous	vertebrates (birds, possibly pseudoparasites)	1:9-15:2
Skrjabinella	1	monoxenous	vertebrates (rodents, possibly pseudoparasites)	1:16:1
Hoarella	1	monoxenous	vertebrates (lizards)	1:16:2
Pythonella	3	monoxenous	vertebrates (reptiles, birds)	1:16:4

Isosporan infections have been detected throughout the world, mainly in carnivores (particularly canids and felids) as well as in some omnivores (humans, pigs), lizards and birds. Some 250 species have been described, mostly on the basis of host occurrence and oocyst morphometrics. Most species are considered to be highly host-specific and only parasitize single host species (oioxenous), although some species in birds and reptiles may parasitize closely-related hosts (stenoxenous) or even unrelated hosts (euryxenous). Many hosts also harbour multiple species of coccidia which may vary considerably in morphology, developmental cycle, site of infection and pathogenicity. Historically, there has been considerable confusion in the identification of coccidian genera, particularly since the discovery of species with heteroxenous (two-host) life-cycles alternating between enteric stages in predators and tissue cysts in prey animals. It has recently been demonstrated that some *Isospora* spp. in mammals form encysted monozoic stages (cystozoites) in the tissues of paratenic (transport) hosts (esp. rodents), prompting their classification with the tissue cyst-forming coccidia (*Sarcocystis*, *Frenkelia*, *Hammondia*, *Besnoitia* and *Toxoplasma*) under the name *Cystoisospora.* Many phylogenetic studies have now indicated that *Isospora* spp. from vertebrates may be divided into two major groups: those species that have sporocysts with a Stieda body are closely related to the monoxenous Eimeriidae and occur mainly in birds; while those species that have sporocysts without a Stieda body are most closely associated with the tissue cyst-forming Sarcocystidae and occur in mammals. The latter may also be divided into two types: larger forms with distinct oocyst walls that maintain their integrity within the gastrointestinal tract and sporulate exogenously (species transferred to the genus *Cystoisospora*); and smaller forms with thin membranous oocyst walls that sporulate endogenously and often release their sporocysts within the gastrointestinal tract (species transferred to the genus *Sarcocystis*). Infections by *Cystoisospora* spp. are common in mammals (particularly carnivores), while infections by *Isospora* spp. are common in birds (especially passerines) and lizards (skinks, geckoes and dragons). *Atoxoplasma* infections in birds are currently considered to be *Isospora* infections which have disseminated into extra-intestinal tissues and blood cells.

In the family Eimeriidae, some 360 *Isospora* spp. have been described from a range of wild and captive animals: with 88 species identified in mammals, 162 in birds, 92 in reptiles, 14 in amphibia, 2 in fish, and one in an invertebrate (limacid slug). The website “Coccidia of the World” attempts to catalogue parasite biodiversity (= species richness) together with taxonomic authorities, including numerous host records for un-named species. The following table lists named taxa for which parasite descriptions are consistent with taxonomic guidelines (as stipulated by the International Code of Zoological Nomenclature).

Isospora spp.	Oocyst size (µm)	Definitive hosts
Mammalian hosts		
I. agrarii	23	Rodentia: murid (striped field mouse)
I. aksaica	26	Artiodactyla: bovid (cattle)
I. almaataensis (*almataensis*)	28 x 26	Artiodactyla: suid (pig)
I. anatolicum	12 x 10	Rodentia: spalacid (lesser mole-rat)
I. aprutina (syn. *I. vulpina* var. *aprutina*)	25 x 21	Carnivora: canid (red fox)
I. aquatici	21 x 18	Eulipotyphla: talpid (eastern mole)
I. araneae (*aranei*)	17	Eulipotyphla: soricid (Eurasian shrew)
I. arvalis		Rodentia: cricetid (common vole)
I. ashtabulensis	20 x 14	Eulipotyphla: talpid (hairy-tailed mole)
I. assensis		Rodentia: sciurid (yellow ground squirrel)
I. aurangabadensis		Rodentia: murid (black rat)
I. batabatica	24 x 21	Rodentia: cricetid (northern water vole)
I. bigemina (large oocyst morphotype = var. *canis*; small oocyst morphotype = var. *cati* = *Toxoplasma?*)	large 19 x 15 small 12 x 8	Carnivora: canid (dog, red fox), felid (cat), mustelid (American mink, polecat)
I. bisoni	29 x 22	Artiodactyla: bovid (gaur)
I. boughtoni	18 x 17	Didelphimorpha: didelphid (North American opossum)
I. brevicauda	17 x 16	Eulipotyphla: soricid (northern short-tailed shrew)
I. californica	24 x 23	Rodentia: cricetid (California mouse, brush mouse, Pinyon mouse, North American deermouse)
I. calomyscus	22 x 18	Rodentia: calomyscid (Zagros Mountains mouse-like hamster)
I. capreoli	43 x 31	Artiodactyla: cervid (roe deer)
I. cebi	21 x 20	Primates: cebid (white-fronted capuchin)
I. chilensis [probably *Sarcocystis* sp.]		Primates: hominid (human)
I. citelli	22 x 21	Rodentia: sciurid (rock squirrel, yellow ground squirrel)
I. clethrionomydis	25	Rodentia: cricetid (bank vole, grey red-backed vole, northern red-backed vole)
I. clethrionomysis	10 x 9	Rodentia: cricetid (bank vole, northern red-backed vole)
I. condylurae	19 x 9	Eulipotyphla: talpid (star-nosed mole)
I. cristatae	16 x 10	Eulipotyphla: talpid (star-nosed mole)
I. dawadimiensis	24 x 21	Rodentia: dipodid (lesser Egyptian jerboa)
I. dymecodi	16 x 13	Eulipotyphla: talpid (True's shrew mole)
I. dyromidis		Rodentia: glirid (forest dormouse)
I. egypti	21 x 18	Rodentia: murid (Shaw's jird)
I. erinacei	30 x 26	Eulipotyphla: erinaceid (European hedgehog)
I. erythrourica	21 x 18	Rodentia: murid (Libyan jird)
I. fennechi	28 x 17	Carnivora: canid (fennec fox)
I. fonsecai	25 x 23	Carnivora: ursid (brown bear)
I. freundi	20	Rodentia: cricetid (European hamster)
I. golemanskii		Rodentia: murid (yellow-necked mouse, wood mouse)
I. hammondi	27 x 19	Rodentia: cricetid (marsh rice rat)
I. hastingsi	31 x 23	Rodentia: cricetid (pinyon mouse)
I. hominis [probably *Sarcocystis* sp.]		Primates: hominid (human)
I. hylomysis	12 x 11	Eulipotyphla: erinaceid (short-tailed gymnure)
I. ichneumonis species inquirenda	22 x 19	Carnivora: herpestid (Egyptian mongoose)
I. jakimovi		Carnivora: mustelid (sable)
I. krishnamurthyi		Rodentia: murid (black rat)
I. laguri	28 x 19	Rodentia: cricetid (steppe lemming)
I. lamoillensis	22 x 13	Eulipotyphla: talpid (star-nosed mole)
I. lutreolinae	21 x 18	Didelphimorphia: didelphid (latrine opossum)

I. lyncis (*species inquirenda*)	44 x 32	Carnivora: felid (lynx)
I. marquardti		Lagomorpha: ochotonid (American pika)
I. masoni		Rodentia: cricetid (hispid cotton rat)
I. mcdowelli	10 x 9	Rodentia: cricetid (meadow vole)
I. merionis	24 x 20	Rodentia: murid (midday jird, Vinogradov's jird, Mongolian jird)
I. mexicanasubsimi	24 x 23	Rodentia: cricetid (Mexican vole)
I. motleiensis	14 x 12	Eulipotyphla: talpid (eastern mole)
I. mustelae (*nomen nudum*)	7 x 2	Carnivora: mustelid (European pine marten)
I. neomyi	14	Eulipotyphla: soricid (Mediterranean water shrew, Eurasian water shrew)
I. neurotrichi	14 x 12	Eulipotyphla: talpid (American shrew mole)
I. neyrai	13 x 9	Artiodactyla: suid (pig)
I. ordubadica	20 x 17	Rodentia: murid (Persian jird)
I. orlovi	31 x 18	Artiodactyla: camelid (camel)
I. palustris	18 x 17	Eulipotyphla: soricid (Pacific shrew, northern water shrew, montane shrew, Trowbridge shrew, long-clawed shrew)
I. papionis [probably *Sarcocystis*]	17 x 11	Primates: cercopithecid (chacma baboon)
I. parascalopi	15 x 13	Eulipotyphla: talpid (hairy-tailed mole)
I. peromysci	35 x 21	Rodentia: cricetid (California mouse, North American deermouse, pinyon mouse)
I. putorii	ns	Carnivora: mustelid (stoat)
I. rangiferis	29 x 25	Artiodactyla: cervid (reindeer)
I. rastegaievae	19 x 17	Eulipotyphla: erinaceid (European hedgehog)
I. ratti	23 x 21	Rodentia: murid (brown rat)
I. riccii	23 x 15	Eulipotyphla: talpid (northern mole)
I. saimirae	25 x 22	Primates: cebid (squirrel monkey)
I. samsenis		Rodentia: sciurid (yellow ground squirrel)
I. schmaltzi	26	Eulipotyphla: erinaceid (European hedgehog)
I. sofiae	12 x 11	Eulipotyphla: talpid (European mole)
I. soricis	24 x 17	Eulipotyphla: soricid (Eurasian shrew)
I. spalacensis	15 x 11	Rodentia: spalacid (Middle East blind mole-rat)
I. spermophili		Rodentia: sciurid (suslik)
I. sporopointaea	17 x 11	Eulipotyphla: talpid (European mole)
I. sundarbanensis		Artiodactyla: suid (pig)
I. talpae	18 x 12	Eulipotyphla: talpid (European mole)
I. tamariscini		Rodentia: murid (tamarisk jird)
I. teres	30	Rodentia: cricetid (steppe lemming)
I. tropicalis [= *Sarcocystis* sp.]	16	Carnivora: canid (golden jackal)
I. uralicae	26 x 23	Rodentia: murid (wood mouse)
I. urotrichi	13 x 12	Eulipotyphla: talpid (Japanese shrew mole)
I. vanadica	24 x 19	Rodentia: murid (Persian jird)
I. vinogradovi	27 x 22	Rodentia: murid (Vinogradov's jird)
I. vizcacha		Rodentia: chinchillid (plains viscacha)
I. vulpis	25 x 24	Carnivora: canid (red fox, silver fox, Indian fox)
I. yukonensis		Lagomorpha: ochotonid (collared pika)
Avian hosts		
I. alaudae		Passeriformes: alaudid (Eurasian skylark)
I. albicollis	25 x 20	Passeriformes: turdid (white-necked thrush)
I. ampullacea	27	Passeriformes: sylviid (garden warbler)
I. anseris		Anseriformes: anatid (Canada goose, emperor goose) plus experimental infections in greylag goose, snow goose)
I. anthi		Passeriformes: motacillid (meadow pipit)
I. arrui		Passeriformes: fringillid (common linnet)
I. ashmoonmensis		Passeriformes: sylviid (Eurasian blackcap)
I. atrata		Passeriformes: fringillid (black siskin)
I. automoli		Passeriformes: furnariid (olive-backed foliage-gleaner, buff-throated foliage-gleaner)
I. aycardii		Passeriformes: cisticolid (zitting cisticola)

I. balaericae		Gruiformes: gruid (grey crowned crane)
I. bellericae	22 x 20	Gruiformes: gruid (grey crowned crane)
I. bellicosa		Passeriformes: icterid (Peruvian meadowlark)
I. bengalensis	21	Passeriformes: corvid (house crow)
I. bioccai		Passeriformes: fringillid (grey-capped greenfinch)
I. blagburni		Passeriformes: pycnonotid (white-spectacled bulbul)
I. boxae		Passeriformes: passerid (house sparrow)
I. brachyrhynchi		Passeriformes: corvid (American crow)
I. brayi		Passeriformes: zosteropid (Japanese white-eye)
I. buteonis	18 x 15	Accipitriformes: accipitrid (Cooper's hawk, red-tailed hawk, Swainson's hawk, Eurasian sparrowhawk, golden eagle, common buzzard, long-legged buzzard); Falconiformes: falconid (lesser kestrel, common kestrel, American kestrel, peregrine falcon); Strigiformes: tytonid (barn owl), strigid (little owl, long-eared owl, tawny owl),
I. cacici		Passeriformes: icterid (yellow-rumped cacique)
I. cadimi	24 x 23	Passeriformes: thraupid (Brazilian tanager)
I. caerulei		Passeriformes: parid (Eurasian blue tit)
I. calocitta		Passeriformes: corvid (white-throated magpie-jay)
I. canaria		Passeriformes: fringillid (canary)
I. cannabinae		Passeriformes: fringillid (common linnet)
I. capistrata		Passeriformes: leiothrichid (rufous sibia)
I. cardellinae		Passeriformes: parulid (red warbler)
I. cardinalis		Passeriformes: emberizid (black-crested finch)
I. carduelis	28 x 24	Passeriformes: fringillid (goldfinch)
I. certhiae		Passeriformes: certhiid (short-toed treecreeper)
I. ceylonensis		Passeriformes: muscicapid (grey-headed flycatcher)
I. cheeli	14 x 11	Falconiformes: accipitrid (black kite)
I. chloridis	25 x 22	Passeriformes: fringillid (greenfinch, chaffinch)
I. choudari		Galliformes: phasianid (grey junglefowl)
I. cincli		Passeriformes: cinclid (white-throated dipper)
I. concentrica		Passeriformes: dendrocolapid (Amazonian barred woodcreeper)
I. concinnus		Passeriformes: aegithalid (black-throated bushtit)
I. corvi (corviae)	20 x 18	Passeriformes: corvid (large-billed crow)
I. couderti		Passeriformes: sylviid (zitting cisticola)
I. cyanocoracis		Passeriformes: corvid (plush-crested jay)
I. daphnensis		Passeriformes: emberizid (medium ground finch)
I. dilatata	24	Passeriformes: sylviid (Eurasian blackcap, garden warbler, common whitethroat), motacillid (meadow pipit), sturnid (common starling, pied starling)
I. divitis	26 x 23	Passeriformes: icterid (Cuban blackbird)
I. elmahalensis		Passeriformes: pycnonotid (Himalayan bulbul)
I. emberizae	23 x 20	Passeriformes: emberizid (red-headed bunting)
I. erithaci		Passeriformes: turdid (European robin)
I. ernsti		Passeriformes: pycnonotid (white-spectacled bulbul)
I. exigua		Passeriformes: emberizid (small tree finch)
I. fatiguei		Passeriformes: passerid (house sparrow)
I. ficedulae	20	Passeriformes: muscicapid (European pied flycatcher)
I. formarum		Passeriformes: emberizid (slate-coloured grosbeak)
I. fragmentata		Passeriformes: emberizid (small tree finch)
I. fringillae	21	Passeriformes: fringillid (chaffinch)
I. gallicolumbae		Columbiformes: columbid (bronze ground dove)
I. gallinae	24 x 20	Galliformes: phasianid (chicken)
I. gallinarum	29 x 26	Galliformes: phasianid (chicken)
I. garrulae (garrulacis)	21 x 20	Passeriformes: leiothrichid (streaked laughing thrush)
I. garrulusae (garruli)	25 x 21	Passeriformes: corvid (Himalayan jay)
I. geospizae		Passeriformes: emberizid (medium ground finch)
I. ginginiana	23	Passeriformes: sturnid (bank myna)
I. gonnetae		Passeriformes: passerid (house sparrow)
I. graculae		Passeriformes: sturnid (hill myna)
I. gryphoni		Passeriformes: fringillid (American goldfinch)
I. gypsi	20 x 18	Falconiformes: accipitrid (white-rumped vulture)

I. heissini	29	Galliformes: phasianid (turkey)
I. hirundinis	30 x 25	Passeriformes: hirundinid (barn swallow), muscicapid (black redstart, common redstart)
I. hyloctistum		Passeriformes: furnariid (striped woodhaunter)
I. iansmithi		Passeriformes: passerid (house sparrow)
I. indonesianensis		Passeriformes: estrildid (tricoloured munia)
I. ivensae		Passeriformes: estrildid (scaly-breasted munia)
I. jacobfrenkeli		Passeriformes: passerid (house sparrow)
I. koreani		Galliformes: phasianid (common pheasant, green pheasant)
I. kouyatei		Passeriformes: passerid (house sparrow)
I. lacazei	21	Passeriformes: fringillid (goldfinch)
I. landauae		Passeriformes: muscicapid (European pied flycatcher)
I. leiothrixi		Passeriformes: sylviid (red-billed leiothrix)
I. leucogastroides		Passeriformes: estrildid (Javan munia)
I. lickfeldi	24	Passeriformes: sylviid (Eurasian blackcap, garden warbler, common whitethroat)
I. loaei		Passeriformes: estrildid (Javan munia)
I. lonchurae	25 x 22	Passeriformes: estrildid (scaly-breasted munia), sturnid (pied myna)
I. loxopis		Passeriformes: drepanidid (amakihi)
I. lusciniae		Passeriformes: turdid (common nightingale)
I. lyonensis		Passeriformes: estrildid (scaly-breasted munia)
I. lyruri	15	Galliformes: phasianid (black grouse, western capercaillie)
I. magna		Passeriformes: dendrocolapid (Amazonian barred woodcreeper)
I. malabaricae		Passeriformes: sturnid (chestnut-tailed starling)
I. malayaensis		Passeriformes: estrildid (Javan munia)
I. mandari		Anseriformes: anatid (mandarin duck)
I. manoaensis		Passeriformes: zosteropid (Japanese white-eye)
I. mayuri	23 x 21	Galliformes: phasianid (blue peafowl, green peafowl)
I. mcquistioni		Passeriformes: fringillid (grey-capped greenfinch)
I. megalaimae	24	Piciformes: capitonid (coppersmith barbet)
I. mejiro		Passeriformes: zosteropid (Japanese white-eye)
I. melopsittaci		Psittaciformes: psittacid (budgerigar)
I. michaelbakeri		Passeriformes: passerid (house sparrow)
I. mikei		Passeriformes: passerid (house sparrow)
I. miltgeni		Passeriformes: passerid (house sparrow)
I. monedulae	18	Passeriformes: corvid (western jackdaw)
I. muniae	28 x 16	Passeriformes: estrildid (tricoloured munia)
I. nancyae		Passeriformes: passerid (house sparrow)
I. nankinovi	33 x 26	Passeriformes: corvid (Eurasian jay)
I. navarroi	21	Passeriformes: thraupid (Brazilian tanager)
I. nortoni		Passeriformes: fringillid (serin)
I. nucifragae	24 x 21	Passeriformes: corvid (spotted nutcracker)
I. ocellati		Passeriformes: dendrocolapid (ocellated woodcreeper)
I. pari		Passeriformes: parid (grey-crested tit)
I. paroariae		Passeriformes: emberizid (red-crested cardinal)
I. parusae	24 x 21	Passeriformes: parid (grey crested tit)
I. parvae		Passeriformes: muscicapid (red-breasted flycatcher)
I. passeris		Passeriformes: passerid (house sparrow)
I. passerum		Passeriformes: laniid (red-backed shrike)
I. perroncitoi	20	Passeriformes: fringillid (bullfinch)
I. petrochelidon		Passeriformes: hirundinid (American cliff swallow)
I. phaeornis		Passeriformes: muscicapid (Hawaiian thrush)
I. phoenicuri	31 x 20	Passeriformes: turdid (common redstart)
I. pityli		Passeriformes: emberizid (slate-coloured grosbeak)
I. plectrophenaxia		Passeriformes: calcariid (snow bunting)
I. psittaculae	31 x 26	Psittaciformes: psittacid (Alexandrine parakeet)
I. puella		Passeriformes: irenid (Asian fairy-bluebird)
I. pycnonotus (pycnonoti, pycnonotae)	24 x 20	Passeriformes: pycnonotid (red-whiskered bulbul), leiothrichid (jungle babbler)
I. raggianae		Passeriformes: paradisaeid (Raggiana bird-of-paradise)
I. rajulii		Passeriformes: sturnid (common myna)

I. robini		Passeriformes: turdid (American robin)
I. rochalimai	24 x 20	Passeriformes: corvid (Eurasian magpie)
I. rodhaini	25 x 23	Passeriformes: corvid (carrion crow)
I. rothschildi		Passeriformes: sturnid (Bali myna)
I. rotunda		Passeriformes: emberizid (small tree finch)
I. sagittulae		Passeriformes: formicariid (spotted antbird)
I. scholtysecki		Accipitriformes: accipitrid (Eurasian sparrowhawk); Falconiformes: falconid (saker falcon, lesser kestrel)
I. schwetzi	25 x 23	Passeriformes: corvid (carrion crow)
I. sclerurii		Passeriformes: furnariid (black-tailed leaftosser)
I. seicerci (seicercusae)	25 x 23	Passeriformes: sylviid (grey-hooded warbler)
I. serini		Passeriformes: fringillid (bullfinch)
I. sittae		Passeriformes: sittid (Eurasian nuthatch)
I. solimanae		Coraciiformes: upupid (Eurasian hoopoe)
I. spratti		Passeriformes: passerid (house sparrow)
I. striata		Passeriformes: dendrocolapid (ocellated woodcreeper)
I. strigis	23 x 21	Strigiformes: strigid (short-eared owl)
I. struthionis	31	Struthioniformes: struthionid (ostrich)
I. sturniae	25	Passeriformes: sturnid (chestnut-tailed starling)
I. sylviae	30 x 27	Passeriformes: sylviid (Eurasian blackcap, green warbler, common whitethroat)
I. sylvianthina	27 x 24	Passeriformes: sylviid (Eurasian blackcap, green warbler, common whitethroat), motacillid (meadow pipit)
I. temenuchi	23 x 21	Passeriformes: sturnid (Brahminy starling)
I. temeraria		Passeriformes: emberizid (medium ground finch)
I. tenuis		Passeriformes: estrildid (Javan munia)
I. thibetana		Passeriformes: fringillid (Tibetan serin)
I. thraupis		Passeriformes: thraupid (palm tanager)
I. tiaris		Passeriformes: emberizid (sooty grassquit)
I. tristis	26 x 22	Passeriformes: sturnid (common myna)
I. tucuruiensis	17	Passeriformes: turdid (white-necked thrush)
I. turdi	19 x 16	Passeriformes: turdid (common blackbird, fieldfare)
I. ubique		Passeriformes: dendrocolapid (wedge-billed woodcreeper)
I. upupae	26	Coraciiformes: upupid (Eurasian hoopoe)
I. vagoi		Passeriformes: estrildid (zebra finch)
I. vanriperorum		Passeriformes: emberizid (northern cardinal)
I. volki	18 x 16	Passeriformes: paradisaeid (Lawe's parotia, brown sicklebill, superb bird-of-paradise, green manucode, greater bird-of-paradise, red-plumed bird-of-paradise, white-plumed bird-of-paradise, lesser bird-of-paradise, blue bird-of-paradise, twelve-wired bird-of-paradise, red bird-of-paradise)
I. wurmbachi	22	Passeriformes: sylviid (Eurasian blackcap, green warbler, common whitethroat), phylloscopid (willow warbler), muscicapid (whinchat, African stonechat, European pied flycatcher), motacillid (meadow pipit)
I. xerophila		Passeriformes: ploceid (yellow-crowned bishop, southern red bishop, speckle-fronted weaver, village weaver, black-headed weaver, red-billed quelea)
I. yesi		Passeriformes: passerid (house sparrow)
I. zosteropis	20 x 16	Passeriformes: zosteropid (Oriental white-eye)
Reptilian hosts		
I. abdallahi		Sauria: lacertid (Bosc's fringe-toed lizard)
I. ablephari	26 x 25	Sauria: scincid (snake-eyed skink)
I. acanthodactyli		Sauria: lacertid (Bosc's fringe-toed lizard)
I. albogularis		Sauria: sphaerodactylid (yellow-headed gecko)
I. altiatlantis		Sauria: sphaerodactylid (atlas day gecko)
I. ameivae	19 x 16	Sauria: teiid (ameiva, rainbow whiptail)
I. amphiboluri	25 x 24	Sauria: agamid (eastern bearded dragon, inland bearded dragon)
I. ashkhabadensis [possibly *Sarcocystis*]	17 x 11	Serpentes: viperid (Levantine viper)
I. basilisci	27 x 21	Sauria: corytophanid (brown basilisk)
I. bronchocelae		Sauria: agamid (green crested lizard)
I. calotesi	28	Sauria: agamid (Oriental garden lizard)

I. camillerii	22	Sauria: scincid (ocellated skink)
I. canariensis		Sauria: phyllodactylid (Tenerife wall gecko)
I. cannoni		Sauria: agamid (Tommy roundhead dragon)
I. caryophila		Sauria: agamid (great anglehead lizard)
I. cenchoae	22 x 15	Serpentes: colubrid (blunt-headed vine snake)
I. chalchidis		Sauria: scincid (ocellated skink)
I. chamaeleolidis		Sauria: dactyloid (western bearded anole)
I. chelydrae	10 x 7	Testudines: chelydrid (common snapping turtle)
I. choochotei		Sauria: agamid (Indo-Chinese forest lizard)
I. cnemidophori	28 x 19	Sauria: teiid (rainbow ameiva, green ameiva, rainbow whiptail)
I. colubris	11 x 8	Serpentes: colubrid (western whip snake)
I. cryptoblephari		Sauria: scincid (snake-eyed skink)
I. crotali [probably *Sarcocystis*]	19 x 12	Serpentes: viperid (Gaboon viper, prairie rattlesnake), colubrid (California banded king snake)
I. decipiens		Serpentes: colubrid (South American green racer)
I. deserti		Sauria: agamid (desert agama, Afghan ground agama)
I. dipasi	15	Serpentes: colubrid (slug-eating snake)
I. diplometopon		Sauria: trogonophid (Zarudny's worm lizard)
I. dirumpens [= *Sarcocystis dirumpens*]	16 x 10	Serpentes: viperid (western rattlesnake, long-nosed viper, puff adder), colubrid (Himalayan keelback, eastern racer, western rat snake, eastern fox snake, western gopher snake, grass snake)
I. egerniae	15 x 11	Sauria: scincid (White's skink)
I. eimanae		Sauria: scincid (ocellated skink)
I. fragilis [possibly *Sarcocystis*]	21 x 15	Serpentes: viperid (European asp viper)
I. frenatus		Sauria: gekkonid (common house gecko)
I. gallotiae	17	Sauria: lacertid (Tenerife lizard)
I. gardneri		Sauria: gekkonid (stripeless day gecko)
I. gekkonis		Sauria: gekkonid (gold dust day gecko, Madagascar giant day gecko)
I. goncephali		Sauria: agamid (great anglehead lizard)
I. guarocuyai		Sauria: dactyloid (bark anole)
I. guersae	32 x 30	Serpentes: viperid (Levantine viper)
I. guzarica	18 x 13	Serpentes: colubrid (spotted desert racer)
I. gymnodactyli		Sauria: gekkonid (Turkestan thin-toed gecko)
I. hemidactyli	23	Sauria: gekkonid (tropical house gecko)
I. hendersoni		Sauria: dactyloid (Armour's anole, large-headed anole)
I. insularius		Sauria: tropidurid (Hood lava lizard)
I. jacarei	15 x 13	Crocodilia: alligatorid (broad-snouted caiman)
I. jaracimrmani		Sauria: chamaeleonid (veiled chameleon)
I. jedlickai		Sauria: teiid (common ameiva)
I. kaschcadarinica		Sauria: lacertid (Lalezhar racerunner)
I. kiamichiensis		Serpentes: colubrid (eastern coachwhip)
I. knowlesi	22	Sauria: gekkonid (yellow-belly gecko)
I. lacertae		Sauria: agamid (oriental garden lizard)
I. ladiguensis		Sauria: gekkonid (Seychelles giant day gecko)
I. laverani	12 x 10	Serpentes: colubrid (Montpellier snake)
I. lenti	13 x 10	Serpentes: viperid (jacaraca)
I. leptodeirae	23 x 19	Serpentes: colubrid (southern cat-eyed snake)
I. manchacensis		Sauria: scincid (little brown skink)
I. mesnili	30	Sauria: chamaeleonid (common chameleon)
I. minuta [possibly *Sarcocystis*]	15 x 8	Serpentes: elapid (Asian cobra)
I. muriyu		Sauria: chamaeleonid (Jackson's chameleon)
I. nagasakiensis		Sauria: lacertid (Japanese grass lizard)
I. naiae [possibly *Sarcocystis*]	17 x 9	Serpentes: elapid (Cape cobra); viperid (timber rattlesnake)
I. natricis	14	Serpentes: colubrid (common grass snake)
I. necasi		Sauria: chamaeleonid (giant one-horned chameleon)
I. neivai [*species inquirenda*]	20 x 12	Serpentes: viperid (jararaca)
I. oudrii		Sauria: phyllodactylid (Oudri's fan-footed gecko)

I. pachydactyli		Sauria: gekkonid (Bibron's sand gecko)
I. phisalixae	31 x 14	Serpentes: colubrid (four-lined snake)
I. phrynocephali	26	Sauria: agamid (sun-watcher toad-head agama)
I. platyurusi		Sauria: gekkonid (frilled house gecko)
I. ptyodactyli		Sauria: phyllodactylid (Levante fan-fingered gecko)
I. rayi	26	Sauria: agamid (green fan-throated lizard)
I. reui		Sauria: dactyloid (long-snouted anole)
I. rodriguesae	25 x 21	Testudines: testudinid (yellow-footed tortoise)
I. roudabushi [= *Sarcocystis* sp.]	20 x 12	Serpentes: colubrid (western gopher snake, eastern racer, black rat snake)
I. rustamovi		Sauria: agamid (reticulated toad-headed agama)
I. schlegeli		Sauria: gekkonid (common house gecko)
I. scinci		Sauria: scincid (five-lined skink, broadhead skink)
I. seychellensis		Sauria: scincid (Seychelles skink)
I. spilogaster		Sauria: scincid (Kalahari tree skink)
I. stenodactyli		Sauria: gekkonid (short-fingered gecko)
I. tahuayoensis		Sauria: dactyloid (slender anole)
I. testudae	26	Testudines: testudinid (Horsfield's tortoise)
I. thavari		Sauria: gekkonid (stump-toed gecko)
I. tigris		Sauria: chamaeleonid (Seychelles tiger chameleon)
I. turkmenica	*nomen nudum*	Serpentes: boid (dwarf sand boa)
I. uptoni		Sauria: gekkonid (common house gecko)
I. varani	nd	Sauria: varanid (desert monitor)
I. viridanae		Sauria: scincid (West canary skink)
I. wildi		Sauria: chamaeleonid (flap-necked chameleon)
I. wilkiei	33 x 29	Crocodilia: crocodylid (American crocodile)
I. wilsoni	17	Serpentes: colubrid (flathead snake)
I. xantusiae	26	Sauria: xantusiid (granite night lizard, desert night lizard)
Amphibian hosts		
I. brumpti	24 x 16	Anura: bufonid (European green toad)
I. cogginsi	19 x 15	Anura: hylid (western chorus frog)
I. cruzi	21 x 17	Anura: hylid (dwarf tree frog, neotropical nasal tree frog, red-snouted tree frog, Venezuela snouted tree frog)
I. delicatus	14 x 8	Anura: hylid (Strecker's chorus frog, Illinois chorus frog)
I. fragosum	19	Anura: microhylid (western narrow-mouthed toad)
I. hightoni	23	Lissamphibia: plethodontid (western slimy salamander)
I. hylae	33 x 23	Anura: hylid (European tree frog)
I. jeffersonianum	20	Urodela: ambystomatid (Jefferson salamander)
I. lieberkuehni (*species inquirenda*)	nr	Anura: ranid (edible frog, northern leopard frog, marsh frog, European grass frog)
I. neos	26 x 22	Anura: ranid (moor frog)
I. ranae (*nomen nudum*)	nr	Anura: ranid (green frog)
I. stomaticae	26 x 18	Anura: bufonid (Indian marbled toad)
I. wenyoni	18 x 12	Anura: bufonid (Asian black-spined toad, Indian cricket frog, Asian bullfrog)
I. wladimirovi	21 x 18	Anura: hylid (European tree frog)
Piscine hosts		
I. sinensis	32 x 22	freshwater Cypriniformes: cyprinid (sharpbelly)
I. lotae	26	freshwater Gadiformes: lotid (burbot)
Invertebrate hosts		
I. rara [type species]	ns	Gastropoda: limacid (land slugs)

Another 47 species have been transferred to the genus *Cystoisospora* classified in the subfamily Cystoisosporinae in the family Sarcocystidae.

***Cystoisospora* species**	**Oocyst size**	**Definitive hosts**	**Distribution**

	(µm)	[and transport hosts]	
Species in mammals (Mammalia)			
C. africana (syn. *Isospora africana*)	26	Carnivora: mustelid (Saharan striped polecat)	Africa
C. altaica (syn. *Isospora altaica*)	33 x 28	Carnivora: mustelid (mountain weasel)	Asia
C. arctopitheci (syn. *Isospora arctopitheci, I. scorzai, I. callimico, I. endocallimici, I. natalensis*)	28 x 24	Primates: callithrichid (black-tufted marmoset, Geoffroy's tamarin, red-crested tamarin, Goeldi's marmoset), cebid (white-headed capuchin, squirrel monkey), pithecid (red bald-headed uakari); hominid (human), plus experimental infections in Primates: aotid (three-striped night monkey), atelid (black-headed spider monkey, black howler monkey), cebid (squirrel monkey), galagid (Senegal bushbaby); Carnivora: canid (dog), procyonid (ring-tailed coati, kinkajou), mustelid (tayra), felid (cat); Didelphimorphia: didelphid (southern opossum) [plus tissues of experimental transport hosts Rodentia: murid (house mouse); Galliformes: phasianid (chicken)]	worldwide
C. belli (syn. *Isospora hominis p.p.*)	32 x 14	Primates: hominid (human), plus experimental infection in hylobatid (gibbon)	worldwide
C. buriatica (syn. *Isospora buriatica*)	25 x 19	Carnivora: canid (corsac fox, Bengal fox, red fox, Arctic fox)	Asia, India
C. burrowsi (syn. *Isospora burrowsi*)	20 x 17	Carnivora: canid (dog) [plus tissues of experimental transport hosts Rodentia: murid (house mouse, brown rat)]	Europe, North America
C. canis (syn. *Isospora canis*)	38 x 30	Carnivora: canid (dog, coyote, red fox, golden jackal) [plus tissues of experimental transport hosts Rodentia: murid (house mouse), Artiodactyla: camelid (one-humped camel), bovid (sheep); Carnivora: felid (cat)]	worldwide
C. canivelocis (syn. *Isospora canivelocis*)	33 x 28	Carnivora: canid (swift fox, red fox, Artic fox)	Eurasia, North America
C. chobotari (syn. *Isospora chobotari*)	17 x 14	Carnivora: procyonid (raccoon)	North America
C. dasguptai (syn. *Isospora dasguptai*)	21 x 17	Carnivora: herpestid (Indian gray mongoose, small Asian mongoose)	India
C. dutoiti (syn. *I. dutoiti*) [possibly *Hammondia* or *Neospora*]	12 x 10	Carnivora: canid (golden jackal)	Russia
C. eversmanni (syn. *Isospora eversmanni*)	20	Carnivora: mustelid (steppe polecat, European polecat)	Asia
C. felis (syn. *Isospora felis, I. bengalensi, I. cati, I. leopardi, I. nandankani, I. pantheri, I. pardusi*)	40 x 30	Carnivora: felid (cat, jungle cat, wildcat, ocelot, serval, tiger, Bengal tiger, lion, clouded leopard, leopard, leopard cat, jaguar, lynx) [plus tissues of experimental transport hosts Rodentia: murid (house mouse, brown rat), cricetid (golden hamster), Artiodactyla: bovid (cattle); Carnivora: canid (dog), felid (cat); Galliformes: phasianid (chicken)]	worldwide
C. frenkeli (syn. *Isospora frenkeli*)	28 x 22	Carnivora: felid (cat) [plus tissues of experimental transport hosts Rodentia: murid (house mouse, brown rat)]	South America
C. garnhami (syn. *Isospora garnhami*)	29 x 25	Carnivora: herpestid (dwarf mongoose, long-nosed kusimanse, Indian gray mongoose)	Africa
C. gottschalki (syn. *Isospora lutrae p.p.*)	33 x 26	Carnivora: mustelid (European otter)	Europe
C. goussevi (syn. *Isospora goussevi*)	22 x 17	Carnivora: mustelid (least weasel)	
C. herpestei (syn. *Isospora herpestei*)	20 x 15	Carnivora: herpestid (small Asian mongoose, Indian gray mongoose)	India
C. hoarei	17 x 15	Carnivora: herpestid (dwarf mongoose, Indian gray	Africa

(syn. *Isospora hoarei*)		mongoose)	
C. hoogstraali (syn. *Isospora hoogstraali*)	38 x 33	Carnivora: mustelid (Saharan striped polecat)	Africa
C. israeli	29 x 21	Carnivora: otariid (brown fur seal)	Israel
C. laidlawi (syn. *Isospora laidlawi*)	34 x 29	Carnivora: mustelid (European polecat, American mink); canid (red fox) [plus tissues of transport host Rodentia: murid (house mouse)]	Eurasia, North America
C. leonina (syn. *Isospora leonina*)	32 x 28	Carnivora: felid (lion)	India
C. levinei (syn. *Isospora levinei*)	27 x 25	Carnivora: hyaenid (striped hyena)	India
C. lutrae (syn. *Isospora lutrae*)	32 x 30	Carnivora: mustelid (European otter)	Europe
C. martessii (syn. *Isospora martessii*)	27 x 19	Carnivora: mustelid (sable)	Siberia
C. melis (syn. *Isospora melis*)	30 x 24	Carnivora: mustelid (Eurasian badger)	Europe
C. mirungae (syn. *Isospora mirungae*)	20 x 12	Carnivora: phocid (southern elephant seal)	Europe
C. mungoi (syn. *Isospora mungoi*)	34 x 27	Carnivora: herpestid (Indian gray mongoose)	India
C. neorivolta (syn. *Isospora neorivolta*)	13 x 11	Carnivora: canid (dog, coyote)	North America
C. nivalis (syn. *Isospora nivalis*)	21 x 18	Carnivora: mustelid (least weasel)	Asia
C. ohioensis (syn. *Isospora ohioensis*)	24 x 21	Carnivora: canid (dog, coyote, wolf, dingo, red fox, raccoon dog) [plus tissues of experimental transport hosts Rodentia: murid (house mouse); Carnivora: felid (cat); Lagomorpha: leporid (rabbit); Artiodactyla: bovid (sheep)]	worldwide
C. pavlodarica (syn. *Isospora pavlodarica*)	24 x 21	Carnivora: canid (red fox, Arctic fox)	Asia
C. pavlovskyi (syn. *Isospora pavlovskyi*)	39 x 30	Carnivora: mustelid (steppe polecat)	Asia
C. pellerdyi (syn. *Isospora pellerdyi, I. knowlesi, I. dubeyi*)	28 x 23	Carnivora: herpestid (grey mongoose)	India
C. rivolta [syn. *Isospora rivolta, I. felina, I. mohini, I. novocati*]	25 x 20	Carnivora: felid (cat, wildcat, jungle cat, tiger, Bengal tiger, serval, clouded leopard, leopard, leopard cat, lion, cheetah) [plus tissues of experimental transport hosts Rodentia: murid (house mouse, brown rat), cricetid (golden hamster), Artiodactyla: bovid (cattle), Carnivora: canid (dog), Galliformes: phasianid (chicken)]	worldwide
C. sengeri (syn. *Isospora sengeri*)	20 x 15	Carnivora: mustelid (eastern spotted skunk)	North America
C. spilogales (syn. *Isospora spilogales*)	34 x 26	Carnivora: mustelid (eastern spotted skunk)	North America
C. suis (syn. *Isospora suis*)	23 x 18	Artiodactyla: suid (pig)	worldwide
C. theileri (syn. *Isospora theileri*) [possibly *Sarcocystis*]	21 x 18	Carnivora: canid (golden jackal)	Russia
C. timoni	26 x 25	Carnivora: herpestid (slender-tailed meerkat)	Africa
C. triffitti (syn. *Isospora triffitti*) [possibly *Hammondia* or *Neospora*?]	12 x 11	Carnivora: canid (Arctic fox, red fox)	Asia
C. ursi (syn. *Isospora ursi*)	37 x 25	Carnivora: ursid (sloth bear)	India

C. viverrae (syn. *Isospora viverrae*)	23 x 19	Carnivora: viverrid (African civet)	Africa
C. viverrina (syn. *Isospora viverrina*)	32 x 27	Carnivora: felid (fishing cat)	India
C. vulpina (syn. *Isospora vulpina*)	25 x 21	Carnivora: canid (red fox, Bengal fox, Arctic fox, dog), plus experimental infection in tissues of Rodentia: murid (house mouse)	Europe, North America
C. zorillae (syn. *Isospora zorillae*)	12 x 10	Carnivora: mustelid (Saharan striped polecat)	Africa

Parasite morphology: Coccidian parasites form three developmental stages: schizonts (meronts), gamonts and oocysts. Schizonts first appear as small basophilic rounded cells (mother meronts) located intracellularly within host cells. The meronts form numerous daughter merozoites by endogenous division of the nucleus followed by cytokinesis. Mature schizonts range in diameter from 10-50 µm and appear as membrane-bound clusters of small basophilic bodies (similar to bunches of grapes). Gamonts exhibit sexual differentiation, with microgamonts (male) apparent as multinucleate basophilic stages ultimately shedding small biflagellated microgametes; and macrogamonts (female) evident as uninucleate eosinophilic cells with a single ovoid nucleus. Developing oocysts contain numerous eosinophilic wall-forming bodies which give rise to the tough outer oocyst walls. Unsporulated oocysts contain a developing sporoblast which eventually undergoes sporulation forming sporocysts which contain the infective sporozoites. Isosporid oocysts exhibit a characteristic 1:2:4 configuration, that is, each oocyst contains 2 sporocysts each containing 4 sporozoites. Oocysts are generally ovoid to ellipsoid in shape, range from 10-40 µm in length by 10-30 µm in width, and vary in their possession of specialized structures, such as oocyst spines, projections, micropyles, micropyle caps, residua, polar granules, sporocyst sporopodia, ridges, sutures, residua, Stieda bodies, sub-Stieda or para-Stieda bodies, sporozoite nuclei, refractile bodies and striations.

Site of infection: Parasites undergo merogony and gamogony in the small intestinal mucosa, located intracellularly within the cytoplasm of epithelial cells (although some reptilian species exhibit intranuclear development). They undergo several cycles of schizogony, each culminating in host cell lysis releasing merozoites. Ultimately, gamonts are formed which mature to produce micro- and macro-gametes that undergo fertilization forming a non-motile zygote (oocyst) which is excreted with host faeces. The monozoic cysts of *Cystoisospora* spp. are thought to be encysted sporozoites (cystozoites) located within host cells (mainly in lymphoid tissue of rodent hosts). These zoites do not undergo further development or multiplication, so their rodent hosts are considered to be paratenic (transport) hosts rather than intermediate hosts. The zoites are infective to definitive carnivorous hosts when they feed on rodent host tissues. *Atoxoplasma* infections in birds may also involve extraintestinal stages in various host tissues and in mononuclear cells.

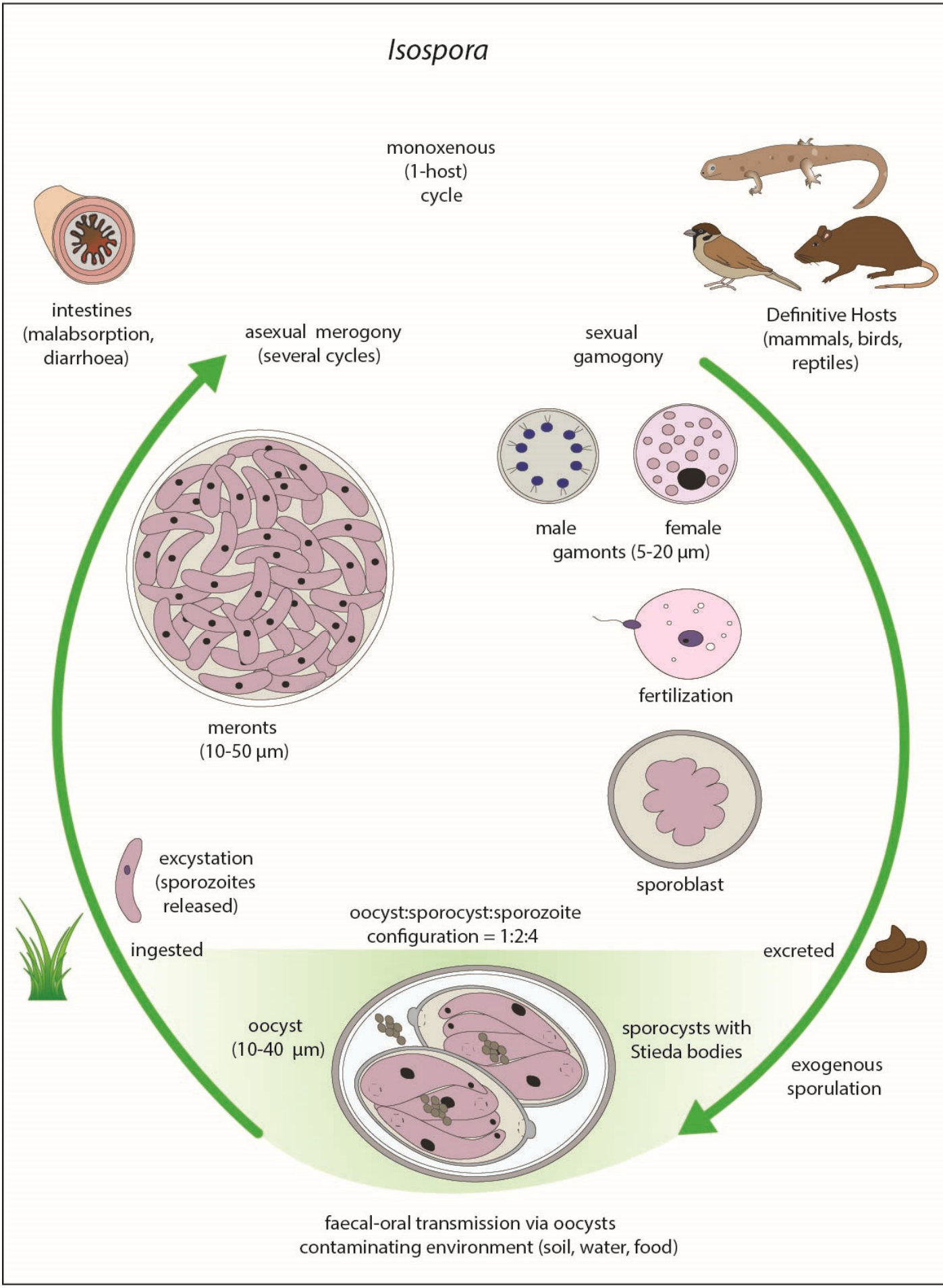
Pathogenesis: Most enteric species are only mildly pathogenic but can cause transient diarrhoea, colic, weight loss and fever. When mature, endogenous developmental stages of the parasite lyse their host epithelial cells lining small intestinal villi, producing villous atrophy, crypt hypertrophy, inflammation, malabsorption and sometimes petechial haemorrhages. There is substantial epidemiological evidence that the severity of infections may be exacerbated by concomitant viral disease or other immunosuppressive agents. Young animals (puppies, kittens, piglets, etc.) are most susceptible to disease but develop a strong specific protective immunity thereafter. Some species in birds may cause disseminated infections which have been associated with severe disease and death. Atoxoplasmosis is a chronic wasting disease of passerine birds, especially captive canaries and finches, and is unusual in that extra-intestinal stages (merozoites) may disseminate within the host in blood cells (mostly lymphocytes).

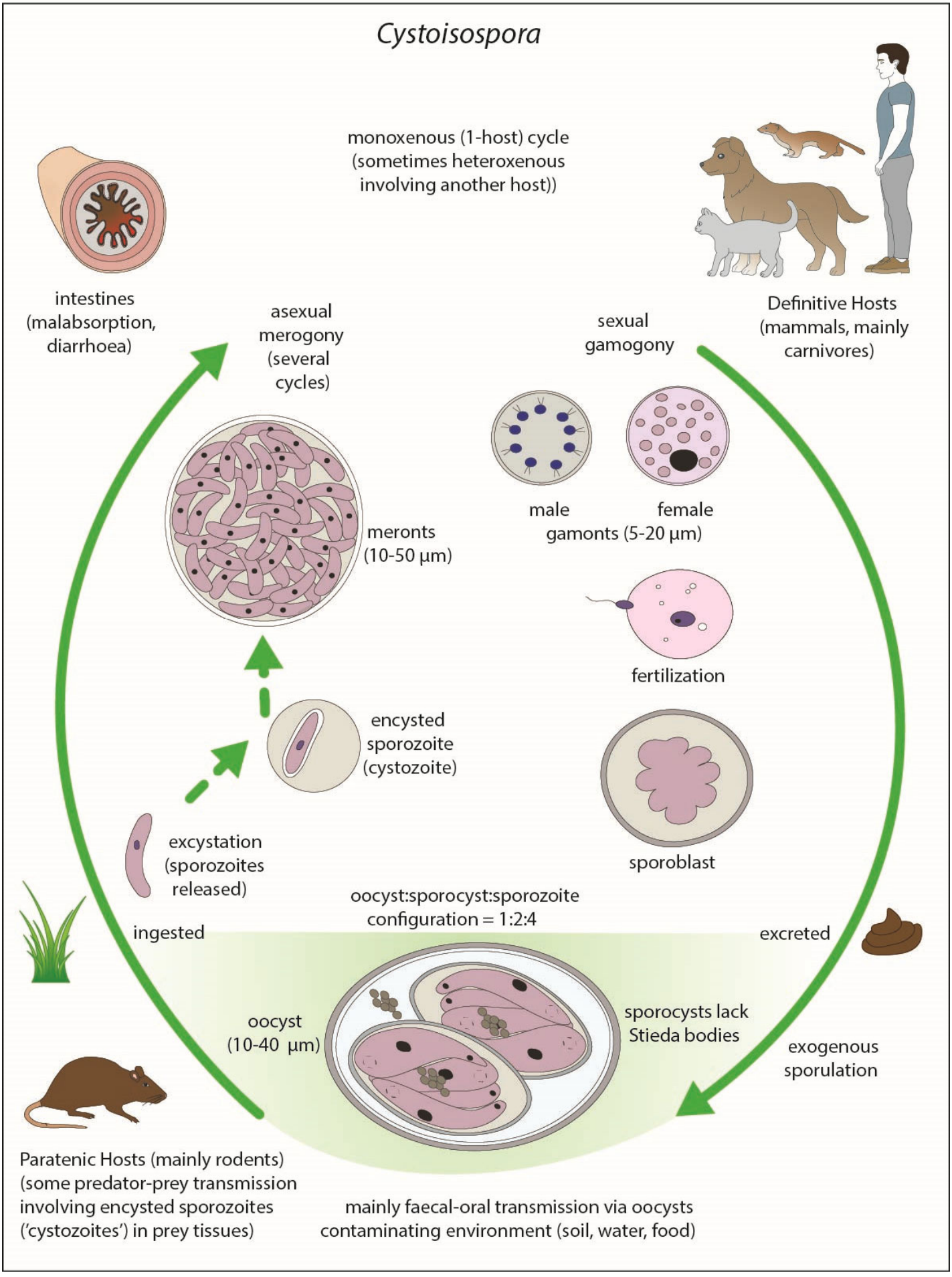
Developmental cycle and mode of transmission: Infections are passed between hosts by the faecal-oral transmission of infective oocysts contaminating the external environment, including food and water supplies. Oocysts are excreted unsporulated from definitive hosts and undergo exogenous sporulation over several days in the external environment. Following ingestion by susceptible hosts, the oocysts and sporocysts excyst in the intestines releasing their contained sporozoites which invade host cells and undergo merogony and gamogony. *Cystoisospora* spp. are also thought to also utilize predator-prey transmission when dormant stages (cystozoites) in paratenic hosts (e.g. rodents) are ingested by carnivorous definitive hosts.

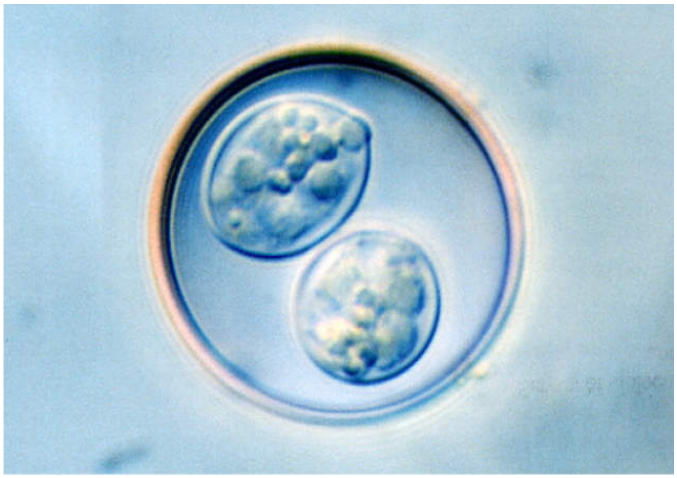
Differential diagnosis: Although clinical signs generally coincide with parasite patency (period during which oocysts are produced), longitudinal samples should be examined whenever possible as asexual developmental stages of virulent species may cause gut damage before oocyst formation. Infections are usually diagnosed by the coprological examination of host faeces for coccidial oocysts (concentrated using various sedimentation-flotation techniques). *Cystoisospora* and *Isospora* species form medium-sized oocysts (20-50 µm) whereas *Sarcocystis, Toxoplasma, Hammondia* and *Neospora* species form smaller oocysts (10-15 µm). Faeces from carnivores can also be pretreated with ether/chloroform to remove fatty material. Unstained oocysts are best observed by light microscopy using suboptimal transmitted illumination (condenser wound down to introduce diffraction), phase-contrast or interference-contrast optics. Alternatively, oocysts can be stained with Giemsa or acid-fast stains of dried smears or with

fluorescence dyes (auramine-rhodamine) in wet preparations. Fresh faecal samples may only contain unsporulated oocysts so differential specific diagnosis may sometime require short-term storage to facilitate sporulation (2% potassium dichromate is often used to suppress microflora during storage, and refrigeration can slow the process down if required for field samples).

Treatment and control: Coccidiostatic drugs, particularly toltrazuril and sulfonamides (trimethoprim-sulfamethoxazole), are effective for therapeutic use, acting against endogenous developmental stages to limit infections. However, commencement of treatment when oocysts are being voided is not often followed by rapid resolution of clinical signs as the damage has already been done and the drug has been used too late in the course of infection. Control measures include good sanitation, proper effluent disposal, isolation of infected individuals and avoiding crowding, particularly in intensive husbandry situations, breeding establishments, kennels and rescue centres. Oocysts passed in faeces take several days to sporulate and become infectious, so the judicious daily removal of waste from animal containment facilities has great effect in reducing contamination. Conventional disinfectants (bleaches and detergents) are ineffective against coccidian oocysts, although some ammonia-based products and steam-cleaning have been shown to kill infective oocysts. Nevertheless, the process of cleaning aids decontamination by removing oocysts from holding facilities. Vermin should be excluded from kennels, and carnivores should be discouraged from hunting and scavenging.


Isospora
monoxenous
(1-host)
cycle
intestines
(malabsorption,
diarrhoea)
asexual merogony
(several cycles)
sexual
gamogony
Definitive Hosts
(mammals, birds,
reptiles)
male
female
gamonts (5-20 µm)
meronts
(10-50 µm)
fertilization
sporoblast
excystation
(sporozoites
released)
ingested
oocyst:sporocyst:sporozoite
configuration = 1:2:4
excreted
oocyst
(10-40 µm)
sporocysts with
Stieda bodies
exogenous
sporulation
faecal-oral transmission via oocysts
contaminating environment (soil, water, food)

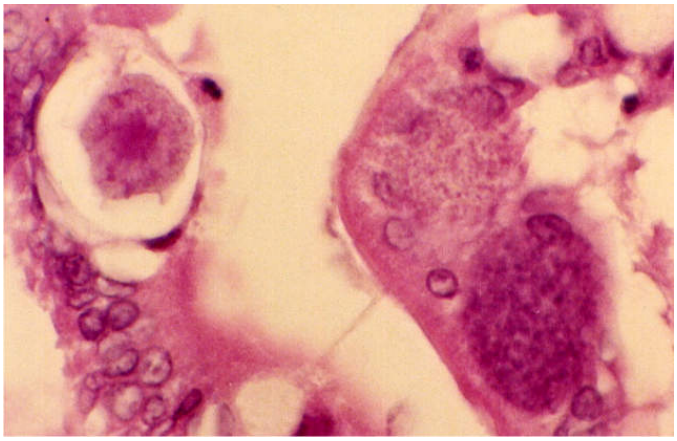

Cystoisospora
monoxenous (1-host) cycle
(sometimes heteroxenous
involving another host))
intestines
(malabsorption,
diarrhoea)
Definitive Hosts
(mammals, mainly
carnivores)
asexual
merogony
(several
cycles)
sexual
gamogony
meronts
(10-50 µm)
male
female
gamonts (5-20 µm)
fertilization
encysted
sporozoite
(cystozoite)
excystation
(sporozoites
released)
sporoblast
oocyst:sporocyst:sporozoite
configuration = 1:2:4
ingested
excreted
oocyst
(10-40 µm)
sporocysts lack
Stieda bodies
exogenous
sporulation
Paratenic Hosts (mainly rodents)
(some predator-prey transmission
involving encysted sporozoites
('cystozoites') in prey tissues)
mainly faecal-oral transmission via oocysts
contaminating environment (soil, water, food)



Isospora oocyst from lizard faeces



Isospora oocyst from bird faeces



Cystoisospora gamonts in dog gut

Eimeria
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile environmentally-resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). The enteric coccidia are monoxenous (1-host) parasites in the digestive tracts of vertebrates. They undergo three sequential developmental stages: endogenous multiplication by asexual merogony (= schizogony) followed by sexual gamogony (male microgametes fertilize female macrogametes) producing oocysts which are excreted and undergo asexual sporogony (sporozoite formation). *Eimeria* oocysts typically contain four sporocysts each with two sporozoites (1:4:2 configuration). Infections are prevalent in birds (esp. fowl), reptiles (snakes and lizards), mammals (esp. ruminants) and fish. Many species have been associated with clinical disease (coccidiosis) characterized by gastrointestinal disturbances and sometimes extraintestinal tissue lesions.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Eimeriorina (no syzygy, many microgametes)
Family:	Eimeriidae (monoxenous, endogenous intracellular merogony and gamogony, exogenous sporogony)
Genus:	*Eimeria* (parasitic in vertebrates, esp. herbivores)
Species:	various species cause coccidiosis in their hosts

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are

heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Numerous species of eimeriid coccidia have been described from a wide range of vertebrate and invertebrate hosts. Some 50 genera have been classified in 11 families in the suborder Eimeriorina, including 21 genera in the family Eimeriidae. Most genera are characterized by the formation of oocysts with unique configurations in terms of the numbers of contained sporocysts and sporozoites. The genus *Eimeria* forms oocysts with a 1:4:2 configuration; that is, oocysts are tetrasporocystic (contain 4 sporocysts) and each sporocyst is disporozoic (contains 2 sporozoites).

Parasite genera	No. spp.	Life-cycle	Hosts	Oocyst configuration

Family: EIMERIIDAE				
Diaspora	1	monoxenous	invertebrates (arthropods)	0:1:1
Tyzzeria	12	monoxenous	vertebrates (birds, reptiles)	1:0:8
Pfeifferinella	6	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Alveocystis	4	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Mantonella	5	monoxenous	invertebrates (panarthropods), vertebrates (turtles, rodents, birds, some possibly pseudoparasites)	1:1:4
Caryospora	70	monoxenous	vertebrates (birds, reptiles)	1:1:8
Cyclospora	19	monoxenous	vertebrates (mammals)	1:2:2
Dorisa	13	monoxenous	vertebrates (reptiles, mammals)	1:2:8
Isospora	360	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (molluscs)	1:2:4
Sivatoshella	1	monoxenous	vertebrates (birds)	1:2:16
Eimeria	1,700	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (arthropods, annelids, hemichordates, protochordates)	1:4:2
Epieimeria	3	monoxenous	vertebrates (fish)	1:4:2
Choleoeimeria	16	monoxenous	vertebrates (reptiles)	1:4:2
Wenyonella	18	monoxenous	vertebrates (mammals, birds, reptiles)	1:4:4
Margolisiella	6	monoxenous	invertebrates (molluscs)	1:n:2-4
Octosporella	6	monoxenous	vertebrates (fish, reptiles, echidnas, some possibly pseudoparasites)	1:8:2
Gousseffia	1	monoxenous	vertebrates (hedgehogs, possibly pseudoparasites)	1:8:n
Polysporella	1	monoxenous	vertebrates (birds, possibly pseudoparasites)	1:9-15:2
Skrjabinella	1	monoxenous	vertebrates (rodents, possibly pseudoparasites)	1:16:1
Hoarella	1	monoxenous	vertebrates (lizards)	1:16:2
Pythonella	3	monoxenous	vertebrates (reptiles, birds)	1:16:4

Infections by *Eimeria* spp. have been recorded throughout the world in most vertebrate species, including eutherian and metatherian mammals, birds, reptiles and fish. Most coccidian species are considered to be highly host-specific and only parasitize single host species (oioxenous), although some species in birds and reptiles may parasitize closely-related hosts (stenoxenous) and a few species in fish may parasitize unrelated hosts (euryxenous). Many hosts also harbour multiple species of coccidia which may vary considerably in morphology, developmental cycle, site of infection and pathogenicity. Twelve *Eimeria* spp. have been described from cattle, 12 from sheep, 12 from goats, and seven from chickens. In general, the small rapidly-developing species are generally the most pathogenic. The following table lists representative *Eimeria* taxa from domestic animals together with morphometric data, tissue tropism and pathogenic potential, while the following tables provide comprehensive host-parasite lists.

***Eimeria* species**	**Oocyst size (µm)**	**Hosts**	**Site of infection**	**Pathogenicity**
Ruminants				
E. alabamensis	19 x 13	Artiodactyla; bovid (cattle, zebu, water buffalo)	small and large intestines	moderate
E. auburnensis	38 x 23	Artiodactyla; bovid (cattle, zebu, water buffalo, bison)	small intestine	low
E. bovis (syn. *E. smithi, aareyi*)	28 x 21	Artiodactyla; bovid (cattle, zebu, gaur, banteng, water buffalo, wisent, bison)	small and large intestines	high
E. brasiliensis (syn. *E. boehmi, orlovi, helenae*)	38 x 27	Artiodactyla; bovid (cattle, zebu, water buffalo, bison)	intestines?*	low
E. bukidnonensis	49 x 35	Artiodactyla; bovid (cattle, zebu, banteng, water buffalo)	intestines?	low
E. wyomingensis	40 x 28	Artiodactyla; bovid (cattle, zebu, water buffalo)	intestines?	low
E. canadensis (syn. *E. zurnabadensis*)	32 x 23	Artiodactyla; bovid (cattle, zebu, banteng, water buffalo, wisent, bison)	intestines?	low
E. cylindrica	24 x 14	Artiodactyla; bovid (cattle, zebu, water buffalo)	intestines?	low
E. ellipsoidalis	23 x 16	Artiodactyla; bovid (cattle, zebu, wisent)	small intestine	low

E. pellita	40 x 28	Artiodactyla; bovid (cattle, zebu)	intestines?	low
E. subspherica	11 x 10	Artiodactyla; bovid (cattle, zebu, water buffalo)	intestines?	low
E. zuernii	18 x 16	Artiodactyla; bovid (cattle, zebu, water buffalo, wisent)	small and large intestines	high
E. ahsata	33 x 24	Artiodactyla: bovid (sheep, bighorn, mouflon)(early reports include goat, Siberian ibex)	small intestine	low
E. bakuensis	29 x 19	Artiodactyla: bovid (sheep, bighorn, argali, mouflon)	small intestine	low
E. crandallis	22 x 19	Artiodactyla: bovid (sheep, bighorn, mouflon, argali)(early reports include goat, Siberian ibex)	small and large intestines	high
E. faurei	35 x 22	Artiodactyla: bovid (sheep, bighorn, argali, mouflon, urial, Barbary sheep) (early reports include goat, chamois, ibex, Siberian ibex)	small and large intestines	low
E. granulosa	29 x 21	Artiodactyla: bovid (sheep, bighorn) (early reports include goat)	intestines?	low
E. intricata	46 x 33	Artiodactyla: bovid (sheep, bighorn, mouflon) (early reports include goat)	small and large intestines	low
E. marsica	19 x 13	Artiodactyla: bovid (sheep)	intestines?	low
E. ovinoidalis	24 x 20	Artiodactyla: bovid (sheep, bighorn, mouflon)	small and large intestines	moderate
E. pallida	16 x 12	Artiodactyla: bovid (sheep, goat, ibex)	intestines?	low
E. parva (syn. *E. galouzoi*)	17 x 13	Artiodactyla: bovid (sheep, bighorn, mouflon, argali, urial))(early reports in goat, ibex, Siberian ibex)	small and large intestines	low
E. weybridgensis	24 x 17	Artiodactyla: bovid (sheep)	small intestine	low
E. punctata	26 x 20	Artiodactyla: bovid (sheep, goat)	small intestine	low
E. alijevi	18 x 16	Artiodactyla: bovid (goat, ibex, Siberian ibex)	small and large intestines	low
E. arloingi	28 x 20	Artiodactyla: bovid (goat, wild goat, ibex, Siberian ibex, markhor, chamois, Himalayan tahr) [plus early reports in sheep, mouflon, argali]	small and large intestines	high
E. aspheronica	31 x 23	Artiodactyla: bovid (goat)	intestines?	low
E. capralis	29 x 20	Artiodactyla: bovid (goat)	intestines?	low
E. caprina	32 x 23	Artiodactyla: bovid (goat)	small and large intestines	moderate
E. caprovina	30 x 24	Artiodactyla: bovid (goat, plus experimental infection in sheep)	intestines?	low
E. charlestoni	23 x 17	Artiodactyla: bovid (goat)	intestines?	low
E. christenseni	38 x 25	Artiodactyla: bovid (goat)	small intestine	high
E. hirci	22 x 18	Artiodactyla: bovid (goat, wild goat, Siberian ibex, alpine ibex)	intestines?	moderate
E. jolchijevi	31 x 22	Artiodactyla: bovid (goat)	intestines?	low
E. masseyensis	22 x 17	Artiodactyla: bovid (goat)	intestines?	low
E. ninakohlyakimovae	24 x 19	Artiodactyla: bovid (goat, wild goat, ibex, Siberian ibex)(early reports include black-tailed gazelle, sheep, bighorn sheep, mouflon, snow sheep, Barbary sheep, urial)	small and large intestines	moderate
Pigs				
E. debliecki	25 x 17	Artiodactyla: suid (pig)	small intestine	moderate
E. neodebliecki	21 x 16	Artiodactyla: suid (pig)	intestines?	low
E. perminuta	14 x 12	Artiodactyla: suid (pig)	intestines?	low
E. polita	26 x 18	Artiodactyla: suid (pig)	small intestine	moderate
E. porci	22 x 16	Artiodactyla: suid (pig)	small intestine	low
E. scabra	32 x 22	Artiodactyla: suid (pig)	small and large intestines	low
E. spinosa	21 x 15	Artiodactyla: suid (pig)	small intestine	low
E. suis	18 x 14	Artiodactyla: suid (pig)	intestines?	low
Horses				
E. leuckarti	80 x 60	Perissodactyla: equid (horse, ass)	small intestines	low

E. solipedum	22 x 10	Perissodactyla: equid (horse, ass)	small intestines	low
E. uniungulata	20 x 15	Perissodactyla: equid (horse, ass)	small intestines	low
Rabbits				
E. coecicola	34 x 20	Lagomorpha: leporid (rabbit)	small intestines	low
E. exigua	15 x 13	Lagomorpha: leporid (rabbit)	small intestines	low
E. flavescens	30 x 21	Lagomorpha: leporid (rabbit)	small and large intestines	low
E. intestinalis	27 x 19	Lagomorpha: leporid (rabbit)	small intestines	moderate
E. irresidua	38 x 26	Lagomorpha: leporid (rabbit, eastern cottontail)	small intestines	low
E. magna	35 x 24	Lagomorpha: leporid (rabbit, black-tailed jackrabbit, eastern cottontail, European hare, Arctic hare)	small intestines	low
E. media	31 x 19	Lagomorpha: leporid (rabbit, black-tailed jackrabbit, eastern cottontail, mountain cottontail)	small intestines	low
E. perforans	25 x 15	Lagomorpha: leporid (rabbit, snowshoe hare, black-tailed jackrabbit, eastern cottontail, European hare, Arctic hare)	small intestines	low
E. piriformis	29 x 18	Lagomorpha: leporid (rabbit)	large intestines	low
E. stiedai (syn. *E. cuniculi, E. oviformis*)	37 x 21	Lagomorpha: leporid (rabbit, cottontails, hares)	liver, bile ducts	high
E. vejdovsyi	32 x 19	Lagomorpha: leporid (rabbit)	small intestines	low
Rodents				
E. caviae	19 x 17	Rodentia: caviid (guinea pig, Brazilian guinea pig)	large intestines	moderate
E. hasei	18 x 14	Rodentia: murid (black rat)	intestines?	low
E. nieschulzi	23 x 18	Rodentia: murid (black rat, brown rat, pygmy rice rat, red spiny rat, Hawaiian rat, Sunda rat)	small intestines	low
E. nochti	17 x 14	Rodentia: murid (black rat, brown rat)	intestines?	low
E. ratti	23 x 15	Rodentia: murid (black rat)	intestines?	low
E. falciformis [type species]	21 x 18	Rodentia: murid (house mouse)	small and large intestines	low
E. hindlei	23 x 19	Rodentia: murid (house mouse)	intestines?	low
E. keilini	29 x 19	Rodentia: murid (house mouse)	intestines?	low
E. krijgsmanni	22 x 15	Rodentia: murid (house mouse)	intestines?	low
E. musculi	24	Rodentia: murid (house mouse)	intestines?	low
E. schueffneri	21 x 15	Rodentia: murid (house mouse)	intestines?	low
Poultry				
E. acervulina	20 x 14	Galliformes: phasianid (chicken, Sri Lanka junglefowl)	anterior small intestine	high
E. brunetti	27 x 22	Galliformes: phasianid (chicken))	small and large intestines	high
E. maxima	29 x 23	Galliformes: phasianid (chicken), odontophorid (California quail)	mid small intestine	moderate
E. mitis	16 x 14	Galliformes: phasianid (chicken), odontophorid (California quail, mountain quail)	small and large intestines	low
E. necatrix	17 x 14	Galliformes: phasianid (chicken))	small intestine, caecum	high
E. praecox	21 x 17	Galliformes: phasianid (chicken))	small intestine	low
E. tenella (syn. *E. avium, bracheti, globosa*)	23 x 19	Galliformes: phasianid (chicken, rock partridge, grey partridge, red grouse, common pheasant), odontophorid (bobwhite quail, California quail, mountain quail)	caecum	high
E. grenieri	26 x 24	Galliformes: phasianid (helmeted guinea fowl)	intestines, caecum	moderate
E. numidae	19 x 15	Galliformes: phasianid (helmeted guinea fowl)	intestines, caecum	high
E. adenoides	25 x 16	Galliformes: phasianid (turkey)	small and large intestines	high
E. dispersa	23 x 19	Galliformes: phasianid (turkey, Gould's turkey, common pheasant, chicken),	anterior small intestine	moderate

		odontophorid (bobwhite quail)		
E. gallopavonis	26 x 21	Galliformes: phasianid (turkey)	small and large intestines	moderate
E. innocua	22 x 21	Galliformes: phasianid (turkey)	small intestine	low
E. meleagridis	24 x 17	Galliformes: phasianid (turkey)	caecum	moderate
E. meleagrimitis	19 x 16	Galliformes: phasianid (turkey)	anterior small intestine	high
E. subrotunda	22 x 20	Galliformes: phasianid (turkey)	small intestine	low
E. anseris (syn. *E. parvula*)	22 x 17	Anseriformes: anatid (goose, snow goose, Canada goose)	small and large intestines	moderate
E. nocens	29 x 20	Anseriformes: anatid (greylag goose, lesser white-fronted goose, snow goose)	small intestines	moderate
E. truncata	21 x 16	Anseriformes: anatid (greylag goose, Ross's goose, snow goose, Canada goose)	kidney	moderate
E. anatis	17 x 14	Anseriformes: anatid (ducks)	small intestines	low
E. stigmosa	23 x 17	Anseriformes: anatid (ducks)	intestines	low
E. duodenalis	21 x 19	Galliformes: phasianid (common pheasant)	small intestines	moderate
E. colchici	27 x 17	Galliformes: phasianid (common pheasant)	caecum	high
E. phasiani	23 x 16	Galliformes: phasianid (common pheasant, golden pheasant, Reeve's pheasant, white-eared pheasant, silver pheasant)	caecum	moderate
E. legionensis	21 x 15	Galliformes: phasianid (red-legged partridge, rock partridge)	caecum	moderate
E. bateri	23 x 18	Galliformes: phasianid (common quail, gray quail)	intestines	low
E. azura	24 x 19	Galliformes: phasianid (Japanese quail)	intestines	moderate
E. tsunodai	18 x 14	Galliformes: phasianid (Japanese quail)	caecum	high
Fish				
E. variabilis	13.3	marine Scorpaeniformes: cottid (lonspined bullhead); Anguilliformes: anguillid (European eel); Perciformes: labrid (corkwing wrasse); Gobiiformes: gobiid (rock goby)	pyloric caeca, rectum	low
E. nucleocola	12-14	marine Scorpaeniformes: cottid (shorthorn sculpin)	pyloric caeca	low
E. cotti	9-11	freshwater Scorpaeniformes: cottid (European bullhead, slimy sculpin)	intestines	low
E. catalana	11	marine Perciformes: labrid (axillary wrasse)	intestines	low
E. hexagona	12	marine Gadiformes: lotid (shore rockling)	intestines, pyloric caeca	moderate
E. dykovae	7.8	marine Perciformes: latrid (red morwong)	intestines, pyloric caeca	low
E. osmeri	10.7	freshwater Osmeriformes: osmerid (rainbow smelt)	intestines	low
E. truttae	12	anadromous and freshwater Salmoniformes: salmonid (masu, rainbow trout, brown trout, grayling)	intestines, pyloric caeca	low
E. brevoortiana	26 x 22	marine Clupeiformes: clupeid (menhaden)	pyloric caeca, testes	low
E. rutili	22 x 10	freshwater Cypriniformes: cyprinid (roach)	kidneys	moderate
E. branchyphila	23 x 9	freshwater Cypriniformes: cyprinid (roach)	kidneys, gills, spleen, muscles, brain	moderate
E. sardinae	50	marine Clupeiformes: clupeid (herring, pilchard, anchovy, shad, sprat)	seminiferous tubules	high
E. quentini	37.8 x 12.6	marine Myliobatiformes: myliobatid (spotted eagle ray)	peritoneal cells	low
E. halleri	?	marine Myliobatiformes: urotrygonid (round stingray)	spiral valve	low

*site of endogenous development not known, but presumed to be intestines because oocysts detected in faeces

Collectively, over 1,620 *Eimeria* spp. have been described from a wide range of wild and captive animals; with around 935 species recorded from mammals; 218 from birds; 250 from reptiles; 41 from amphibia; 167 from fish; and 9 from invertebrates. The website "Coccidia of the World" attempts to catalogue parasite biodiversity (= species richness) together with taxonomic authorities, including numerous host records for un-named species. The following tables list named taxa for which parasite descriptions are consistent with taxonomic guidelines (as stipulated by the International Code of Zoological Nomenclature).

Eimeria spp.	Oocyst size (µm)	Hosts
Mammals		
E. abdildaevi		Rodentia: glirid (forest dormouse)
E. abenovi	32 x 23	Artiodactyla: bovid (goitered gazelle)
E. abidzhanovi		Rodentia: murid (great gerbil)
E. absheronae	30 x 23	Artiodactyla: bovid (goat, Alpine ibex, Siberian ibex)
E. abusalimovi	30 x 22	Rodentia: glirid (forest dormouse)
E. abuschevi	26 x 23	Rodentia: murid (Major's pine vole)
E. achburunica	20 x 17	Rodentia: murid (Libyan jird)
E. adiyamanensis		Rodentia: spalacid (Middle East blind mole rat)
E. adleri	22	Carnivora: canid (red fox)
E. aepyprymni	37 x 22	Diprotodontia: potoroid (rufous rat-kangaroo)
E. aeromysis	35 x 22	Rodentia: sciurid (black flying squirrel)
E. aethiospora	19 x 13	Eulipotyphla: talpid (hairy-tailed mole)
E. africana	17 x 14	Rodentia: murid (rusty-bellied brush-furred rat)
E. africiensis	25 x 20	Artiodactyla: bovid (goat)
E. agouti		Rodentia: agoutid (spotted paca)
E. agrarii	25	Rodentia: murid (striped field mouse)
E. aguti	17	Rodentia: dasyproctid (red-rumped agouti)
E. ahsata	33 x 24	Artiodactyla: bovid (sheep, bighorn, mouflon) (early reports include goat, Siberian ibex)
E. ailuri	24 x 13	Carnivora: ailurid (red panda)
E. airculensis	13	Rodentia: sciurid (yellow ground squirrel)
E. akeriana		Rodentia: murid (Tristram's jird)
E. akodoni		Rodentia: cricetid (Venezuelan vole mouse)
E. alabamensis	19 x 13	Artiodactyla: bovid (cattle, zebu, water buffalo)
E. alactagae	24	Rodentia: dipodid (great jerboa)
E. albertensis	42 x 22	Carnivora: ursid (American black bear)
E. albigulae	22 x 20	Rodentia: cricetid (white-throated wood rat)
E. alces	37 x 25	Artiodactyla: cervid (moose)
E. alijevi	18 x 16	Artiodactyla: bovid (goat, ibex, Siberian ibex)
E. alischerica	34 x 23	Rodentia: murid (brown rat)
E. allactagae	24	Rodentia: dipodid (great jerboa, small five-toed jerboa, Egyptian jerboa)
E. almaataensis (syn. *E. almataensis*)	30 x 24	Artiodactyla: suid (pig)
E. alpacae	24 x 20	Artiodactyla: camelid (alpaca)
E. alpina	12	Artiodactyla: bovid (chamois)
E. amburdariana	21	Rodentia: murid (golden hamster)
E. americana	38 x 21	Lagomorpha: leporid (white-tailed jackrabbit)
E. ammonis	25 x 21	Artiodactyla: bovid (argali)
E. amorphospora	21 x 18	Eulipotyphla: talpid (Japanese shrew mole)
E. andamanensis	14	Chiroptera: emballonurid (black-bearded tomb bat)
E. andrewsi	21 x 15	Rodentia: sciurid (red squirrel)
E. anekalensis	27 x 20	Carnivora: felid (leopard)
E. ankarensis	39 x 26	Artiodactyla: bovid (water buffalo)
E. antilocaprae	31 x 26	Artiodactyla: antilocaprid (pronghorn)
E. antilocervi	31 x 14	Artiodactyla: bovid (blackbuck)
E. antonellii		Rodentia: murid (eastern woodrat)
E. antrozoi	25 x 22	Chiroptera: vespertilionid (pallid bat)
E. anzanensis	18 x 13	Rodentia: spalacid (Middle East blind mole-rat)
E. aoluguyaensis		Artiodactyla: cervid (reindeer)
E. apionodes	20 x 17	Rodentia: murid (yellow-necked mouse)
E. apodemi	24 x 20	Rodentia: murid (yellow-necked mouse, wood mouse, striped field mouse)
E. aquatici	17 x 11	Eulipotyphla: talpid (eastern mole)
E. arabiana	25 x 20	Rodentia: murid (Vinogradov's jird)
E. arasinaensis	19 x 16	Rodentia: murid (house mouse)
E. araxena	23 x 19	Rodentia: murid (Shaw's jird)
E. arctica	36 x 28	Artiodactyla: cervid (reindeer)

E. arctomysi	24 x 20	Rodentia: sciurid (alpine marmot)
E. arctowski	46 x 28	Pinnipeda: phocid (Weddell seal)
E. argenteus		Rodentia: murid (small Japanese field mouse, large Japanese field mouse, Korean field mouse)
E. arizonensis	22 x 19	Rodentia: murid (pinyon mouse, North American deer mouse, cactus mouse, white-footed mouse)
E. arkhari	22 x 17	Artiodactyla: bovid (argali, urial)
E. arkutinae		Rodentia: murid (wood mouse, yellow-necked mouse, striped field mouse)
E. arloingi	28 x 20	Artiodactyla: bovid (goat, wild goat, ibex, Siberian ibex, markhor, chamois, Himalayan tahr) [plus early reports in sheep, mouflon, argali]
E. arundeli	64 x 43	Diprotodontia: vombatid (common wombat)
E. arusica	23	Rodentia: murid (grey dwarf hamster)
E. arvicanthis	24 x 12	Rodentia: murid (Ethiopian grass mouse)
E. arvicolae (*arvalis*)	20 x 16	Rodentia: murid (snow vole, common vole, Strelzov's vole)
E. asadovi	25 x 22	Rodentia: glirid (forest dormouse)
E. ascotensis	24 x 15	Rodentia: sciurid (grey squirrel, fox squirrel)
E. ashata		Artiodactyla: bovid (sheep)
E. aspheronica		Artiodactyla: bovid (goat)
E. assaensis	28 x 25	Rodentia: murid (tamarisk jird)
E. astrachanbazarica	22 x 19	Rodentia: murid (Shaw's jird)
E. asymmetrica	29 x 17	Artiodactyla: cervid (red deer)
E. athabascensis		Lagomorpha: leporid (snowshoe hare)
E. auburnensis	38 x 23	Artiodactyla; bovid (cattle, zebu, water buffalo, bison)
E. audubonii	21 x 17	Lagomorpha: leporid (desert cottontail, eastern cottontail)
E. aurata	16	Rodentia: cricetid (golden hamster)
E. auritanensis	34 x 30	Didelphimorphia: didelphid (big-eared opossum)
E. aurei	16 x 15	Carnivora: canid (Sri Lankan jackal)
E. auriti	20 x 19	Eulipotyphla: erinaceid (long-eared hedgehog)
E. austriaca	21 x 17	Artiodactyla: cervid (red deer)
E. avonensis	15 x 10	Eulipotyphla: talpid (European mole)
E. azerbaidschanica	45 x 22	Artiodactyla: bovid (cattle, water buffalo)
E. azul		Lagomorpha: leporid (eastern cottontail)
E. babaevi	23 x 21	Artiodactyla: bovid (Siberian ibex)
E. babatica		Lagomorpha: leporid (European hare)
E. bactriani	32 x 26	Artiodactyla: camel (Bactrian camel, dromedary)
E. badamlinica	16	Rodentia: murid (wood mouse)
E. badchisica		Rodentia: murid (great gerbil)
E. baghdadensis		Rodentia: murid (house mouse)
E. bailwardi		Rodentia: murid (Zagros Mountains mouse-like hamster)
E. baiomysis	23 x 19	Rodentia: murid (northern pygmy mouse, southern pygmy mouse)
E. bakanensis	14 x 11	Carnivora: canid (red fox), mustelid (ermine)
E. bakuensis	29 x 19	Artiodactyla: bovid (sheep, bighorn, argali, mouflon)
E. balchanica		Lagomorpha: ochotonid (Afghan pika)
E. balphae	17 x 14	Rodentia: heteromyid (Ord's kangaroo rat, agile kangaroo rat, Merriam's kangaroo rat, banner-tailed kangaroo rat)
E. bandicota		Rodentia: murid (lesser bandicoot rat)
E. bandipurensis	18 x 16	Rodentia: sciurid (Indian palm squirrel, jungle palm squirrel)
E. banffensis	28 x 23	Lagomorpha: ochotonid (American pika, collared pika, northern pika)
E. bareillyi	29 x 20	Artiodactyla: bovid (water buffalo)
E. barleyi		Rodentia: murid (eastern woodrat)
E. barretti	33 x 24	Lagomorpha: ochotonid (American pika)
E. baskanica (*species inquirenda*)	12 x 9	Carnivora: mustelid (stoat)
E. bassagensis		Rodentia: murid (flat-headed vole)
E. batabatensis	19 x 15	Rodentia: murid (European water vole)
E. beckeri (syn. *E. ussuriensis*)	21 x 18	Rodentia: sciurid (Belding's ground squirrel, yellow ground squirrel, little souslik, relict ground squirrel, long-tailed ground squirrel)
E. beecheyi (syn. *E. cochisensis, E. asiatici*)	19 x 16	Rodentia: sciurid (Gunnison's prairie dog, white-tailed prairie dog, black-tailed prairie dog, yellow-bellied marmot, California ground squirrel, Wyoming ground squirrel, relict ground squirrel, Richardson's

		ground squirrel, Townsend's ground squirrel, thirteen-lined ground squirrel, long-tailed ground squirrel, rock squirrel, yellow ground squirrel, red-cheeked ground squirrel, common chipmunk, gray-footed chipmunk, cliff chipmunk, California chipmunk, Townsend's chipmunk)
E. belorussica	27 x 15	Lagomorpha: leporid (European hare, varying hare)
E. bentongi	17 x 15	Eulipotyphla: erinaceid (short-tailed gymnure)
E. berea	12 x 11	Eulipotyphla: talpid (European mole)
E. bereillyi		Artiodactyla: bovid (water buffalo)
E. berkinbaevi	33 x 27	Rodentia: sciurid (yellow ground squirrel, red-cheeked ground squirrel)
E. betica	23 x 13	Artiodactyla: suid (pig)
E. betongi	17 x 15	Eulipotyphla: soricid (short-tailed gymnure)
E. bicolor	23 x 13	Diprotodontia: macropodid (swamp wallaby)
E. bicrustae	21 x 15	Rodentia: sciurid (Gunnison's prairie dog)
E. bijlikuli	32 x 26	Eulipotyphla: erinaceid (long-eared hedgehog)
E. bilamellata	32 x 26	Rodentia: sciurid (golden-mantled ground squirrel, Uinta ground squirrel, California ground squirrel, European souslik, Franklin's ground squirrel, thirteen-lined ground squirrel, Columbian ground squirrel, Richardson's ground squirrel, rock squirrel)
E. bistratum	20 x 19	Rodentia: murid (Vinogradov's jird)
E. biswapatti		Rodentia: murid (short-tailed bandicoot rat)
E. blarinae	21 x 18	Eulipotyphla: soricid (northern short-tailed shrew)
E. bohemica	20 x 12	Rodentia: murid (European water vole)
E. boliviensis		Rodentia: hydrochoerid (capybara)
E. bombayansis	37 x 22	Artiodactyla: bovid (zebu)
E. boonderooensis	27 x 16	Diprotodontia: macropodid (allied rock wallaby, unadorned rock wallaby)
E. borealis	30 x 15	Carnivora: ursid (American black bear)
E. botelhoi	36 x 28	Rodentia: sciurid (Ingram's squirrel)
E. bovis (syn. *E. smithi, E. aareyi*)	28 x 21	Artiodactyla; bovid (cattle, zebu, gaur, banteng, water buffalo, wisent, bison)
E. braganaensis	16 x 15	Chiroptera: emballonurid (lesser dog-like bat)
E. brasiliensis (syn. *E. boehmi, E. orlovi, E. helenae*)	38 x 27	Artiodactyla: bovid (cattle, zebu, water buffalo, bison)
E. brevicauda	20 x 19	Eulipotyphla: soricid (northern short-tailed shrew)
E. briansmithi	21 x 20	Rodentia: murid (Mongolian jird)
E. bukidnonensis	49 x 35	Artiodactyla; bovid (cattle, zebu, banteng, water buffalo)
E. burdai		Rodentia: bathyergid (silvery mole-rat)
E. bychowskyi	25 x 18	Rodentia: murid (brown rat)
E. cabassusi	27	Cingulata: chlamyphorid (southern naked-tailed armadillo)
E. cagandzeeri		Artiodactyla: bovid (Mongolian gazelle)
E. cahirinensis		Rodentia: murid (Cairo spiny mouse)
E. calentinei	29 x 20	Lagomorpha: ochotonid (American pika, collared pika, northern pika)
E. californicensis	21 x 18	Chiroptera: vespertilionid (California myotis)
E. callosciuri	28 x 22	Rodentia: sciurid (Asian tricoloured squirrel, plaintain squirrel, grey-bellied squirrel, black-striped squirrel)
E. callospermophili	19 x 16	Rodentia: sciurid (Gunnison's prairie dog, white-tailed prairie dog, black-tailed prairie dog, grey marmot, bobak marmot, yellow-bellied marmot, groundhog, Tarbagan marmot, Uinta ground squirrel, California ground squirrel, Belding's ground squirrel, Columbian ground squirrel, European ground squirrel, Wyoming ground squirrel, red-cheeked ground squirrel, Franklin's ground squirrel, yellow ground squirrel, golden-mantled ground squirrel, Mexican ground squirrel, relict ground squirrel, Richardson's ground squirrel, spotted ground squirrel, Townsend's ground squirrel, thirteen-lined ground squirrel, long-tailed ground squirrel, rock squirrel)
E. calomyscus		Rodentia: murid (Zagros Mountains mouse-like hamster)
E. caluromydis	32 x 31	Didelphimorphia: didelphid (bare-tailed woolly opossum)
E. cameli	87 x 64	Artiodactyla: camelid (Bactrian camel, Arabian camel, llama)
E. campania		Lagomorpha: leporid (white-tailed jackrabbit, European hare, Indian hare)

E. canadensis (syn. *E. zurnabadensis*)	32 x 23	Artiodactyla; bovid (cattle, zebu, banteng, water buffalo, wisent, bison)
E. canis	31 x 19	Carnivora: canid (dog, coyote, dingo)
E. canivelocis	19 x 16	Carnivora: canid (silver fox)
E. canna	24 x 18	Artiodactyla: bovid (common eland)
E. capibarae	30 x 26	Rodentia: hydrochaerid (capybara)
E. capra	27 x 22	Artiodactyla: bovid (Siberian ibex)
E. capralis	29 x 20	Artiodactyla: bovid (goat)
E. capreoli	30 x 21	Artiodactyla: cervid (European roe deer, chamois)
E. capricornis	48 x 34	Artiodactyla: bovid (Japanese serow)
E. caprina	32 x 23	Artiodactyla: bovid (goat)
E. capromydis	24 x 20	Rodentia: capromyid (Desmarest's hutia)
E. caprovina	30 x 24	Artiodactyla: bovid (goat, plus experimental infection in sheep)
E. caripensis	20	Rodentia: echimyid (Guyenne spiny rat)
E. carmelensis	19 x 17	Rodentia: spalacid (Middle-East blind mole-rat)
E. carolinensis	18 x 11	Rodentia: murid (white-footed mouse)
E. cati	21 x 17	Carnivora: felid (cat, jungle cat, wildcat)
E. catronensis	22 x 15	Chiroptera: vespertilionid (little brown bat, Yuma myotis)
E. catubrina	31 x 25	Artiodactyla: cervid (European roe deer)
E. causeyi	26 x 16	Rodentia: castorid (Nort American beaver)
E. caviae	19 x 17	Rodentia: caviid (guinea pig, Brazilian guinea pig)
E. celebii	14 x 11	Rodentia: spalacid (Middle-East blind mole-rat)
E. cephalophi	22 x 16	Artiodactyla: bovid (blue duiker)
E. cernae	20 x 16	Rodentia: cricetid (bank vole, northern red-backed vole, grey red-backed vole)
E. cervi	33 x 21	Artiodactyla: cervid (red deer, European roe deer)
E. cervis	14 x 11	Artiodactyla: cervid (chital)
E. chaetodipi		Rodentia: heteromyid (agile kangaroo rat, Texas kangaroo rat, Merriam's kangaroo rat, Ord's kangaroo rat, banner-tailed kangaroo rat)
E. chagasi	14	Eulipotyphla: soricid (common shrew)
E. chaparralensis		Artiodactyla: tayassuid (collared peccary)
E. charlestoni		Artiodactyla: bovid (goat)
E. chatangae		Rodentia: murid (Siberian brown lemming)
E. chaus	20 x 18	Carnivora: felid (jungle cat)
E. chausinghi	25 x 18	Artiodactyla: bovid (four-horned antelope)
E. cheetali	26 x 15	Artiodactyla: cervid (chital)
E. chetae		Rodentia: cricetid (Middendorf's vole)
E. chihuahuaensis		Rodentia: heteromyid (Merriam's kangaroo rat)
E. chinchillae	18 x 16	Rodentia: chinchillid (long-tailed chinchilla); murid (four-striped grass mouse)
E. chinkari	25 x 22	Artiodactyla: bovid (mountain gazelle)
E. chiropteri	24 x 21	Chiroptera: vespertilionid (Kuhl's pipistrelle)
E. chobotari	48 x 35	Rodentia: heteromyid (Merriam's kangaroo rat, chisel-toothed kangaroo rat, agile kangaroo rat, Ord's kangaroo rat)
E. choloepi		Pilosa: megalonychid (Linnaeus's two-toed sloth)
E. christenseni	38 x 25	Artiodactyla: bovid (goat)
E. chudatica	21 x 17	Rodentia: cricetid (social vole)
E. circumborealis		Lagomorpha: ochotonid (collared pika, American pika, northern pika)
E. citelli	19 x 16	Rodentia: sciurid (Belding's ground squirrel, European ground squirrel, red-cheeked ground squirrel, yellow ground squirrel, little souslik, speckled ground squirrel, thirteen-lined ground squirrel, long-tailed ground squirrel)
E. clethrionomyis	19 x 15	Rodentia: cricetid (southern red-backed vole)
E. coahuiliensis	30 x 20	Rodentia: cricetid (Mexican vole)
E. cochabambensis	22 x 20	Didelphimorphia: didelphid (Dorothy's slender opossum, gray short-tailed opossum, elegant fat-tailed mouse opossum)
E. coecicola		Lagomorpha: leporid (rabbit)
E. comminispora		Rodentia: sciurid (Hodgson's giant flying squirrel)
E. condylurae	18 x 16	Eulipotyphla: talpid (star-nosed mole)
E. conevi		Rodentia: murid (great gerbil)

E. confusa	36 x 28	Rodentia: sciurid (eastern grey squirrel, fox squirrel)
E. congolensis	30 x 22	Artiodactyla: bovid (waterbuck)
E. connochaetei	22 x 14	Artiodactyla: bovid (blue wildebeest)
E. contorta	21 x 17	Rodentia: murid (brown rat), plus experimental infection in murid (house mouse, Natal multimammate mouse)
E. correptionis	22 x 17	Rodentia: cricetid (Major's pine vole)
E. corticulata		Pilosa: myrmecophagid (collared anteater)
E. cotiae	29 x 18	Rodentia: dasyproctid (red-rumped agouti)
E. coucangi	21 x 17	Primates: lorisid (greater slow loris)
E. couesii	21 x 18	Rodentia: cricetid (Coues' rice rat)
E. coypi	23 x 15	Rodentia: echimyid (coypu)
E. crandallis	22 x 19	Artiodactyla: bovid (sheep, bighorn, mouflon, argali) (early reports include goat, Siberian ibex)
E. criceti	18	Rodentia: cricetid (European hamster)
E. cricetomysi	19 x 16	Rodentia: nesomyid (Gambian pouched rat)
E. cricetuli	40 x 28	Rodentia: cricetid (grey dwarf hamster)
E. crocidurae (*species inquirenda*)	16 x 13	Eulipotyphla: soricid (greater white-toothed shrew)
E. cryptobarretti	30 x 21	Lagomorpha: ochotonid (American pika)
E. cryptotis	16 x 15	Eulipotyphla: soricid (North American least shrew)
E. cubinica	20 x 16	Rodentia: murid (social vole)
E. cusarica	27 x 22	Rodentia: murid (social vole)
E. cyclopis		Pilosa: cyclopedid (silky anteater)
E. cylindrica	24 x 14	Artiodactyla; bovid (cattle, zebu, water buffalo)
E. cynomysis	35 x 30	Rodentia: sciurid (Gunnison's prairie dog, white-tailed prairie dog, black-tailed prairie dog, Uinta ground squirrel, California ground squirrel, European ground squirrel, Columbian ground squirrel, Wyoming ground squirrel, Franklin's ground squirrel, golden-mantled ground squirrel, Richardson's ground squirrel, Townsend's ground squirrel, thirteen-lined ground squirrel, rock squirrel)
E. dacunhai		Cingulata: chlamyphorid (naked-tailed armadillo)
E. dalli	44 x 37	Artiodactyla: bovid (thin horn sheep)
E. damirchinica	19 x 16	Rodentia: dipodid (small five-toed jerboa)
E. danielle (*species inquirenda*)	.	Artiodactyla: bovid (sheep)
E. darjeelingensis	17 x 15	Eulipotyphla: soricid (Asian house shrew)
E. dasymysis	20 x 17	Rodentia: murid (West African shaggy rat)
E. dathei	55 x 37	Artiodactyla: bovid (waterbuck)
E. daurica	21 x 14	Lagomorpha: ochotonid (Daurian pika)
E. davisi	28 x 23	Rodentia: cricetid (white-throated woodrat)
E. dawari	22 x 20	Artiodactyla: cervid (red muntjac)
E. debliecki	25 x 17	Artiodactyla: suid (pig)
E. delicata	14 x 11	Rodentia: cricetid (North American deermouse)
E. dendrohyracis	26 x 18	Hyracoidea: procaviid (southern tree hyrax)
E. dendrolagi	34 x 18	Diprotodontia: macropodid (Lumholtz's tree-kangaroo)
E. derenica	29 x 21	Rodentia: cricetid (common vole)
E. deserticola	20 x 17	Rodentia: sciurid (yellow ground squirrel)
E. desmaresti	17 x 10	Diprotodontia: macropodid (red-necked wallaby)
E. dicotylensis		Artiodactyla: tayassuid (collared peccary)
E. dicrostonicis	29 x 25	Rodentia: cricetid (Nearctic collared lemming, Arctic lemming, Siberian brown lemming)
E. didelphidis	16	Didelphimorphia: didelphid (big-eared opossum)
E. dipodomysis	54 x 40	Rodentia: heteromyid (Merriam's kangaroo rat, Phillip's kangaroo rat, Ord's kangaroo rat)
E. disaensis	23 x 18	Rodentia: murid (Persian jird)
E. dissimilis	28 x 19	Eulipotyphla: soricid (Eurasian shrew)
E. divichinica	24 x 19	Rodentia: murid (wood mouse)
E. dogeli		Rodentia: murid (Persian jird)
E. dolichotis	24 x 19	Rodentia: caviid (Patagonian mara)
E. domashnevae (*species inquirenda*)	14 x 13	Eulipotyphla: soricid (Tien Shan shrew)

E. dorcadis	29 x 18	Artiodactyla: bovid (dorcas gazelle)
E. dorneyi	26 x 15	Rodentia: sciurid (northern flying squirrel)
E. dorsalisi		Hyracoidea: procaviid (western tree hyrax)
E. dromedarii	28 x 23	Artiodactyla: camelid (Bactrian camel, Arabian camel)
E. dukei	24 x 20	Chiroptera: molossid (little free-tailed bat)
E. dusii		Rodentia: cricetid (eastern woodrat)
E. dyromidis	22 x 19	Rodentia: glirid (forest dormouse)
E. dzhahriana	21 x 19	Rodentia: murid (Shaw's jird, Tristam's jird)
E. dzhulfaensis	24 x 21	Rodentia: cricetid (social vole)
E. echidnae		Monotremata: tachyglossid (short-beaked echidna)
E. edwardsi	29 x 22	Rodentia: murid (Edward's long-tailed rat)
E. egypti	28 x 16	Rodentia: murid (Shaw's jird)
E. elaphi	13 x 12	Artiodactyla: cervid (red deer)
E. elater	26 x 21	Rodentia: dipodid (small five-toed jerboa)
E. elegans	34 x 20	Artiodactyla: bovid (black-tailed gazelle)
E. elerybeckeri		Rodentia: murid (black rat)
E. ellipsoidalis	23 x 16	Artiodactyla: bovid (cattle, zebu, wisent)
E. elliptica		Rodentia: spalacid (lesser mole-rat)
E. ellobii	30 x 24	Rodentia: cricetid (northern mole vole)
E. elongata		Lagomorpha: leporid (rabbit)
E. environ	26 x 19	Lagomorpha: leporid (mountain cottontail, eastern cottontail, desert cottontail)
E. eremici	25 x 21	Rodentia: cricetid (cactus mouse)
E. ernsti	33 x 23	Artiodactyla: bovid (mountain goat)
E. erschovi	21 x 19	Lagomorpha: ochotonid (Daurian pika, Pallas's pika)
E. erythrourica	21 x 18	Rodentia: murid (Libyan jird)
E. escomeli	21 x 17	Pilosa: myrmecophagid (giant anteater)
E. eubeckeri	34 x 24	Rodentia: sciurid (Franklin's ground squirrel, red squirrel)
E. eumopos	29 x 26	Chiroptera: molossid (western mastiff bat)
E. europaea	32 x 18	Lagomorpha: leporid (European hare)
E. eutamiae	27 x 21	Rodentia: sciurid (cliff chipmunk)
E. evoti	21 x 19	Chiroptera: vespertilionid (gleaning myotis)
E. exigua	15 x 13	Lagomorpha: leporid (rabbit, Arctic hare, eastern cottontail)
E. falciformis [type species]	21 x 18	Rodentia: murid (house mouse)
E. faurei	35 x 22	Artiodactyla: bovid (sheep, bighorn, argali, mouflon, urial, Barbary sheep) (early reports in goat, chamois, ibex, Siberian ibex)
E. fedoseevi (*species inquirenda*)	28 x 19	Eulipotyphla: soricid (Tien Shan shrew)
E. felina	24 x 15	Carnivora: felid (cat, jungle cat, wildcat, lion)
E. ferrisi	18 x 15	Rodentia: murid (house mouse)
E. ferruginea	34 x 28	Scandentia: tupaiid (Sumatran treeshrew)
E. firestonei	19 x 16	Eulipotyphla: soricid (Fraser's musk shrew)
E. fitzgeraldi	28 x 22	Rodentia: geomyid (northern pocket gopher)
E. flavescens		Lagomorpha: leporid (rabbit)
E. flexilis	22	Eulipotyphla: talpid (European mole)
E. flindersi	44 x 29	Diprotodontia: macropodid (tammar wallaby, antilopine wallaroo, red-necked wallaby)
E. fluviatilis	19 x 17	Rodentia: echimyid (coypu)
E. franchinii	24 x 15	Rodentia: sciurid (red squirrel)
E. franklinii	21 x 15	Rodentia: sciurid (Franklin's ground squirrel, red squirrel)
E. fumeus	28 x 22	Eulipotyphla: soricid (smoky shrew, montane shrew, Pacific shrew, long-clawed shrew)
E. furonis	13 x 12	Carnivora: mustelid (European polecat, American mink, black-footed ferret, ermine)
E. gaimardi	35 x 24	Diprotodontia: potoroid (eastern bettong)
E. galago	22 x 21	Primates: galagid (Senegal bushbaby)
E. gallatii	28 x 19	Rodentia: cricetid (southern red-backed vole, grey red-backed vole, northern red-backed vole)
E. gallivalerioi	20 x 12	Artiodactyla: cervid (red deer, fallow deer)
E. gambai	26 x 20	Didelphimorpha: didelphid (big-eared opossum)

E. gandobica	19 x 17	Rodentia: murid (striped field mouse)
E. garnhami	16 x 15	Rodentia: sciurid (striped ground squirrel)
E. garridoi	17 x 15	Rodentia: capromyid (Desmarest's hutia)
E. garumarana	18	Rodentia: murid (common field rat)
E. gazella	24 x 20	Artiodactyla: bovid (black-tailed gazelle)
E. genettae (*species inquirenda*)	25 x 19	Carnivora: viverrid (common genet)
E. genitali		Rodentia: cricetid (golden hamster)
E. geomydis	13 x 12	Rodentia: geomyid (plains pocket gopher)
E. gerbilli	21 x 16	Rodentia: murid (greater Egyptian gerbil)
E. giganteos	33 x 28	Rodentia: sciurid (black-tailed prairie dog; gray marmot, bobak marmot, groundhog)
E. gilruthi	nd	Artiodactyla: bovid (sheep, goat, Siberian ibex)
E. glauceae		Rodentia: cricetid (eastern woodrat)
E. glaucomydis	16 x 12	Rodentia: sciurid (southern flying squirrel)
E. gliris	21 x 16	Rodentia: glirid (fat dormouse)
E. globula	21 x 20	Eulipotyphla: talpid (European mole)
E. godmani	30 x 17	Diprotodontia: macropodid (Godman's rock wallaby, allied rock wallaby, black-flanked rock wallaby)
E. gokaki	27 x 21	Artiodactyla: bovid (water buffalo)
E. golemanskii		Rodentia: murid (wood mouse, yellow-necked mouse)
E. gomurchaica	29 x 24	Rodentia: cricetid (common vole)
E. gomurica	27 x 21	Rodentia: murid (wood mouse)
E. gonocilia	29 x 24	Eulipotyphla: talpid (Japanese shrew mole)
E. gonzalezi	32 x 22	Artiodactyla: bovid (sheep)
E. gorgonis	23 x 17	Artiodactyla: bovid (blue wildebeest)
E. gousseffi		Rodentia: murid (short-tailed bandicoot rat)
E. goussevi	22 x 16	Eulipotyphla: talpid (European mole)
E. gozaishoensis	29 x 21	Artiodactyla: bovid (Taiwan serow)
E. granifera		Rodentia: ctenomyid (highland tuco-tuco)
E. granulosa	29 x 21	Artiodactyla: bovid (sheep, bighorn) (early reports include goat)
E. groenlandica		Lagomorpha: leporid (Arctic hare)
E. gubleri (species inquirenda)	20	Primates: hominid (human) liver?
E. guentherii		Rodentia: cricetid (Gunther's vole)
E. guevarai	28 x 16	Artiodactyla: suid (pig)
E. gumbaschica	17	Rodentia: murid (wood mouse)
E. gundii		Rodentia: ctenodactylid (common gundi)
E. gungahlinensis	17 x 15	Diprotodontia: macropodid (western grey kangaroo, western grey kangaroo)
E. haberfeldi	30 x 20	Didelphimorpha: didelphid (bare-tailed woolly opossum)
E. hadrutica	21 x 17	Rodentia: cricetid (social vole)
E. halli	24 x 17	Rodentia: murid (brown rat)
E. hammondi	27 x 21	Carnivora: felid (jungle cat)
E. hansonorum	18 x 16	Rodentia: murid (house mouse)
E. haranica		Rodentia: spalacid (Middle East blind mole-rat)
E. harbelensis	32 x 23	Rodentia: murid (rusty-bellied brush-furred rat)
E. hartmanni	23 x 14	Carnivora: felid (tiger, leopard, panther)
E. hasei	18 x 14	Rodentia: murid (black rat)
E. hegneri	17 x 12	Artiodactyla: cervid (red deer, elk)
E. heissini	20	Carnivora: canid (corsac fox)
E. hessei	18	Chiroptera: rhinolophid (lesser horseshoe bat)
E. hestermani	66 x 47	Diprotodontia: macropodid (eastern grey kangaroo, western grey kangaroo, red-necked wallaby, black-striped wallaby, tammar wallaby)
E. heterocapita	26 x 21	Eulipotyphla: talpid (American shrew mole)
E. heterocephali (*species inquirenda*)	ns	Rodentia: heterocephalid (naked mole-rat)
E. hiepei	17 x 13	Carnivora: mustelid (European mink, American mink)
E. hindlei	23 x 19	Rodentia: murid (house mouse)
E. hippuri	35 x 22	Rodentia: sciurid (horse-tailed squirrel)
E. hirci	23 x 18	Artiodactyla: bovid (goat, wild goat, Siberian ibex, alpine ibex)

E. hispidensis		Rodentia: heteromyid (hispid pocket mouse)
E. hoffmeisteri	18 x 16	Rodentia: sciurid (spotted ground squirrel)
E. holmesi		Lagomorpha: leporid (snowshoe hare)
E. honessi	28 x 20	Lagomorpha: leporid (eastern cottontail, desert cottontail, mountain cottontail)
E. honshuensis	16 x 11	Eulipotyphla: talpid (True's shrew mole, Japanese shrew mole)
E. hudsonii		Rodentia: dipodid (meadow jumping mouse)
E. humboldtensis	23 x 21	Chiroptera: vespertilionid (California myotis)
E. hungarica	14 x 13	Lagomorpha: leporid (European hare, Indian hare)
E. hungaryensis	20 x 18	Rodentia: murid (yellow-necked mouse, wood mouse, striped field mouse)
E. hydrochoeri	21 x 19	Rodentia: caviid (capybara)
E. hylopetis	35 x 24	Rodentia: sciurid (red-cheeked flying squirrel)
E. hypsiprymnodontis	29 x 23	Diprotodontia: hypsiprymodontid (musky rat-kangaroo)
E. ibicis	27 x 18	Artiodactyla: bovid (ibex)
E. ibrahimovae	25 x 22	Artiodactyla: suid (pig)
E. ichiloensis		Rodentia: hydrochaerid (capybara)
E. ictidea	24 x 18	Carnivora: mustelid (European polecat, black-footed ferret, steppe polecat, American mink)
E. idmii	42 x 30	Artiodactyla: bovid (Arabian mountain gazelle)
E. ildefonsoi	42 x 28	Artiodactyla: bovid (cattle)
E. illinoisensis	27 x 21	Artiodactyla: bovid (cattle)
E. imantauica (*species inqirenda*)	14 x 10	Carnivora: canid (Arctic fox)
E. immodulata	24 x 17	Rodentia: cricetid (grey dwarf hamster)
E. impalae	33 x 22	Artiodactyla: bovid (impala)
E. indianensis	18 x 16	Didelphimorphia: didelphid (North American opossum)
E. inornata	35 x 20	Diprotodontia: macropodid (unadorned rock wallaby, black-flanked rock wallaby, brush-tailed rock wallaby)
E. intestinalis	27 x 18	Lagomorpha: leporid (rabbit)
E. intricata	46 x 33	Artiodactyla: bovid (sheep, bighorn, mouflon) (early reports include goat)
E. inundatus	22 x 15	Rodentia: murid (striped field mouse)
E. inuyamensis		Rodentia: murid (small Japanese field mouse, large Japanese field mouse)
E. inyoni	22 x 19	Eulipotyphla: soricid (Inyo shrew)
E. iradiensis	25 x 21	Rodentia: murid (common vole)
E. iraqiensis		Artiodactyla: camelid (Arabian camel)
E. irara	23 x 19	Carnivora: mustelid (tayra)
E. irresidua	38 x 26	Lagomorpha: leporid (rabbit, eastern cottontail)
E. ismailovi	28 x 24	Artiodactyla: bovid (saiga antelope)
E. iturina	23 x 18	Artiodactyla: bovid (blue duiker)
E. ivensae	33 x 21	Artiodactyla: cervid (mule deer)
E. ivgeeltensis	28 x 23	Rodentia: murid (Mongolian jird)
E. iwanoffi	22 x 18	Rodentia: cricetid (common vole)
E. jacksonensis	23 x 18	Chiroptera: vespertilionid (evening bat)
E. jakunini		Rodentia: dipodid (Tien Shan birch mouse)
E. jalpaiguriensis	22 x 19	Carnivora: herpestid (Indian gray mongoose)
E. jardimlinica	25 x 19	Rodentia: cricetid (grey dwarf hamster)
E. jemezi		Rodentia: geomyid (northern pocket gopher)
E. jerfinica	26 x 22	Rodentia: murid (wood mouse)
E. jersenica		Rodentia: murid (Libyan jird)
E. jiroveci	28 x 26	Rodentia: capromyid (Desmarest's hutia)
E. jolchijevi	31 x 22	Artiodactyla: bovid (goat)
E. joyeuxi	26 x 21	Rodentia: dipodid (great jerboa)
E. jurschuaensis	34 x 27	Rodentia: murid (Vinogradov's jird)
E. kairiensis	13 x 12	Diprotodontia: hypsiprymnodontid (musky rat-kangaroo)
E. kamoshika	30 x 15	Artiodactyla: bovid (Japanese serow)
E. kanchili	11	Artiodactyla: tragulid (Java mouse-deer)
E. kanyana	19 x 18	Peramelemorphia: peramelid (western barred bandicoot)
E. karschinica		Rodentia: murid (midday jird)

E. katangensis	41 x 25	Artiodactyla: bovid (Defassa waterbuck)
E. kaunensis		Rodentia: murid (striped field mouse)
E. kazakhstanensis	28 x 24	Rodentia: cricetid (northern mole vole)
E. keilini	29 x 19	Rodentia: murid (house mouse)
E. keithi		Lagomorpha: leporid (snowshoe hare)
E. khurodensis	42 x 29	Artiodactyla: bovid (cattle)
E. kinsellai	27 x 17	Rodentia: cricetid (marsh rice rat)
E. klondikensis		Lagomorpha: ochotonid (collared pika, northern pika, American pika)
E. kniplingi	24 x 14	Rodentia: sciurid (fox squirrel)
E. knoxjonesi	17 x 12	Rodentia: cricetid (white-ankled mouse)
E. kobi	38 x 28	Artiodactyla: bovid (defassa waterbuck)
E. kocharii	45 x 37	Artiodactyla: bovid (goat, ibex, Siberian ibex)
E. kogoni	37 x 21	Diprotodontia: macropodid (eastern grey kangaroo)
E. kolabski	29 x 24	Rodentia: cricetid (social vole)
E. kolanica	21 x 19	Rodentia: cricetid (common vole)
E. komareki	16 x 14	Eulipotyphla: soricid (common shrew)
E. kostencovi	33 x 28	Rodentia: murid (midday jird, Mongolian jird)
E. kosti	15 x 14	Artiodactyla: bovid (cattle)
E. kotuji		Rodentia: cricetid (Middendorf's vole)
E. krijgsmanni	22 x 15	Rodentia: murid (house mouse)
E. krilovi	35 x 29	Rodentia: murid (Persian jird)
E. kruidenieri	29 x 19	Rodentia: murid (rusty-bellied brush-furred rat)
E. kuhliensis	28 x 26	Chiroptera: vespertilionid (Kuhl's pipistrelle)
E. kunmingensis	18 x 16	Chiroptera: vespertilionid (Rickett's big-footed bat)
E. kvienae	41 x 35	Rodentia: murid (midday jird)
E. lachrymalis		Rodentia: murid (cactus mouse)
E. ladronensis		Rodentia: cricetid (white-throated woodrat)
E. lagorchestis	48 x 27	Diprotodontia: macropodid (spectacled hare-wallaby)
E. lagostomi		Rodentia: chinchillid (plains viscacha)
E. lalahanensis		Rodentia: spalacid (lesser mole-rat)
E. lamae	36 x 25	Artiodactyla: camelid (llama)
E. lancasterensis	25 x 17	Rodentia: sciurid (red squirrel, fox squirrel)
E. landersi	25 x 24	Rodentia: hystricid (long-tailed porcupine)
E. langebarteli	21 x 14	Rodentia: cricetid (brush mouse, white-footed mouse, pinyon mouse)
E. lateralis (syn. *E. beldingii, E. sarseni, E. tuscarorensis, E. wisconsinensis, E. larimerensis*)	35 x 27	Rodentia: sciurid (Gunnison's prairie dog, white-tailed prairie dog, black-tailed prairie dog, gray marmot, bobak marmot, groundhog, Uinta ground squirrel, California ground squirrel, Belding's ground squirrel, Columbian ground squirrel, Wyoming ground squirrel, golden-mantled ground squirrel, Richardson's ground squirrel, spotted ground squirrel, Townsend's ground squirrel, thirteen-lined ground squirrel, rock squirrel, California chipmunk, eastern chipmunk)
E. lavieri	17	Rodentia: dipodid (great jerboa)
E. lemniscomysis	28 x 19	Rodentia: murid (typical striped grass mouse)
E. lemuris	51 x 41	Primates: galagid (Senegal bushbaby)
E. leporis	32 x 16	Lagomorpha: leporid (European hare, Tolai hare, Cape hare, mountain hare, snowshoe hare, Indian hare, eastern cottontail)
E. lerikaensis	19 x 16	Rodentia: murid (Persian jird)
E. leuckarti	80 x 60	Perissodactyla: equid (horse, ass)
E. leucodonica		Rodentia: spalacid (lesser mole-rat)
E. leucodontis	21	Eulipotyphla: soricid (bicoloured white-toothed shrew)
E. leucopi	19 x 17	Rodentia: cricetid (white-footed mouse)
E. levinei	22 x 18	Chiroptera: molossid (gland-tailed free-tailed bat)
E. li	31 x 23	Carnivora: canid (red fox)
E. liberiensis	24 x 17	Rodentia: murid (rusty-bellied brush-furred rat)
E. liomysis	20 x 17	Rodentia: heteromyid (painted spiny pocket mouse, Mexican spiny pocket mouse)
E. lipura	33 x 24	Rodentia: hystricid (long-tailed porcupine)
E. lobatoi	31 x 23	Artiodactyla: cervid (Mazama deer coprolites)
E. lomarii	27 x 21	Carnivora: canid (Bengal fox)
E. longirostris	17 x 16	Eulipotyphla: soricid (masked shrew, Inyo shrew, Maryland shrew, smoky shrew, Hayden's shrew, southeastern shrew, montane shrew,

		ornate shrew, Pacific shrew, northern water shrew, Trowbridge shrew)
E. lophuromysis	21 x 14	Rodentia: murid ((rusty-bellied brush-furred rat)
E. ludoviciani	21 x 18	Rodentia: sciurid (white-tailed prairie dog, black-tailed prairie dog)
E. luisieri	33 x 24	Rodentia: sciurid (red squirrel)
E. lumholtzi	22 x 11	Diprotodontia: macropodid (Lumholtz's tree-kangaroo)
E. lupi		Carnivora: canid (common wolf)
E. luteola		Rodentia: cricetid (Middenorf's vole)
E. lutescensis (lutescenae)		Rodentia: cricetid (Transcaucasian mole vole)
E. lyncis		Carnivora: felid (Eurasian lynx)
E. maarmosopos		Didelphimorphia: didelphid (Dorothy's slender opossum)
E. macarthuri	18 x 17	Rodentia: murid (Cordillera striped shrew-rat)
E. macieli	30 x 21	Artiodactyla: bovid (waterbuck)
E. macropodis (syn. *E. fausti, E. cunnamullensis, E. purchasei*)	26 x 13	Diprotodontia: macropodid (red-necked wallaby, eastern grey kangaroo, western grey kangaroo, red kangaroo, western brush wallaby, whiptail wallaby, black-striped wallaby, tammar wallaby, parma wallaby)
E. macrosculpta		Lagomorpha: leporid (European hare)
E. macrotis	32 x 19	Carnivora: canid (kit fox)
E. macusaniensis	94 x 67	Artiodactyla: camelid (alpaca)
E. macyi	19 x 18	Chiroptera: vespertilionid (tricoloured bat)
E. madagascariensis	16 x 15	Eulipotyphla: tenrecid (greater hedgehog tenrec)
E. madisonensis	16 x 15	Artiodactyla: cervid (mule deer)
E. magna	35 x 24	Lagomorpha: leporid (rabbit, black-tailed jackrabbit, eastern cottontail, European hare, Arctic hare)
E. magnirostrumi	24 x 21	Chiroptera: phyllostomid (brown tent-making bat)
E. maior	48 x 30	Lagomorpha: leporid (mountain cottontail, eastern cottontail, desert cottontail)
E. majorici	23 x 17	Rodentia: cricetid (Major's pine vole, common vole)
E. malabaricas		Rodentia: sciurid (jungle palm squirrel)
E. malayensis	38 x 20	Rodentia: sciurid (spotted giant flying squirrel, red giant flying squirrel)
E. manafovae	37 x 21	Artiodactyla: bovid (saiga antelope)
E. manatus		Sirenia: trichechid (West Indian manatee)
E. mansonbahri (species inquirenda)	46 x 34	Primates: hominid (human)
E. marajoensis		Xenarthra: myrmecophagid (collared anteater)
E. maralikiensis		Rodentia: spalacid (lesser mole-rat)
E. marasensis		Rodentia: spalacid (Middle East blind mole-rat)
E. marconii	13 x 11	Rodentia: cricetid (southern red-backed vole, northern red-backed vole)
E. markovi	32 x 26	Rodentia: murid (tamarisk jird)
E. marmotae	51 x 42	Rodentia: sciurid (alpine marmot)
E. marmosopos	22 x 20	Didelphimorphia: didelphid (Dorothy's slender opossum, common opossum)
E. marsica	19 x 13	Artiodactyla: bovid (sheep)
E. marsupialium	22 x 18	Diprotodontia: macropodid (western grey kangaroo, eastern grey kangaroo)
E. martunica	26 x 22	Rodentia: murid (Libyan jird)
E. masseyensis		Artiodactyla: bovid (goat)
E. mastomyis	27 x 21	Rodentia: murid (Natal multimammate mouse)
E. mathurai	22 x 19	Carnivora: felid (jungle cat)
E. matschoulskyi	24 x 17	Rodentia: cricetid (Chinese striped hamster)
E. matsubayashii	25 x 18	Lagomorpha: leporid (rabbit)
E. mayeri	17 x 15	Artiodactyla: cervid (reindeer)
E. mccordocki	35 x 27	Artiodactyla: cervid (mule deer, white-tailed deer)
E. media	31 x 19	Lagomorpha: leporid (rabbit, black-tailed jackrabbit, eastern cottontail, mountain cottontail)
E. mehelyi	41 x 35	Chiroptera: rhinolophid (Mehely's horseshoe bat)
E. mehlhorni		Rodentia: murid (African grass rat)
E. melanuri	*sp. inquir.*	Rodentia: myoxid (garden dormouse, Asian garden dormouse)
E. melis	20 x 16	Carnivora: mustelid (European badger, American mink)
E. menzbieri	24 x 21	Rodentia: sciurid (Menzbier's marmot)
E. mephitidis	21 x 19	Carnivora: mustelid (striped skunk, eastern spotted skunk, ferret?)

(*species inquirenda*)		
E. meridiana	25 x 20	Rodentia: murid (midday jird)
E. merionis	19 x 15	Rodentia: murid (Mongolian gerbil, tamarisk jird)
E. merriami		Rodentia: heteromyid (Merriam's kangaroo rat)
E. mesnili (*species inquirenda*)	18 x 14	Carnivora: canid (Arctic fox)
E. metelkini	24 x 19	Lagomorpha: ochotonid (Daurian pika)
E. micouri	25 x 18	Didelphimorphia: didelphid (white-bellied woolly mouse opossum)
E. micromydis		Rodentia: murid (harvest mouse)
E. micropiliana	23 x 19	Rodentia: cricetid (social vole)
E. micropylifera		Rodentia: sciurid (Hodgson's giant flying squirrel)
E. microspalacis	9 x 6	Rodentia: spalacid (Middle-East blind mole-rat)
E. microtina	17 x 15	Rodentia: cricetid (social vole)
E. middendorfi		Rodentia: cricetid (Middendorf's vole)
E. migratoria	19	Rodentia: cricetid (grey dwarf hamster)
E. milleri	15 x 14	Eulipotyphla: soricid (Fraser's musk shrew)
E. minasensis	35 x 26	Artiodactyla: bovid (goat)
E. minima	13 x 11	Lagomorpha: leporid (eastern cottontail)
E. mira	36 x 24	Rodentia: sciurid (red squirrel)
E. mirgai	49 x 30	Artiodactyla: bovid (blackbuck)
E. miyairii (syn. *E. carinii*)	22 x 17	Rodentia: murid (black rat, brown rat, Whitehead's spiny rat, Malayan field rat)
E. modesta	21 x 20	Scandentia: tupaiid (common treeshrew)
E. moelleri	25 x 16	Rodentia: sciurid (eastern gray squirrel)
E. mohavensis	24 x 16	Rodentia: heteromyid (Panamint kangaroo rat, plus experimental infections in Merriam's kangaroo rat, Fresno kangaroo rat, Heermann's kangaroo rat, desert kangaroo rat, agile kangaroo rat)
E. molossi	24 x 18	Chiroptera: molossid (black mastiff bat)
E. monacis (syn. *E. dura*)	20 x 18	Rodentia: sciurid (grey marmot, bobak marmot, alpine marmot, Menzbier's marmot, groundhog, Tarbagan marmot)
E. monocrustae	27 x 24	Rodentia: cricetid (common vole)
E. montanaensis	19 x 15	Artiodactyla: bovid (Rocky Mountain goat)
E. montgomeryae		Rodentia: murid (wood mouse, small Japanese field mouse, large Japanese field mouse, Korean field mouse, Japanese wood mouse)
E. montuosi		Rodentia: ctenomyid (highland tuco-tuco)
E. morainensis	20 x 20	Rodentia: sciurid (Gunnison's prairie dog, white-tailed prairie dog, black-tailed prairie dog, yellow-bellied marmot, Wyoming ground squirrel, golden-mantled ground squirrel, Richardson's ground squirrel, Townsend's ground squirrel, thirteen-lined ground squirrel, rock squirrel)
E. moreli	29 x 22	Rodentia: nesomyid (Gambian pouched rat)
E. moschati	21 x 17	Artiodactyla: bovid (muskox)
E. moschus		Rodentia: sciurid (Eurasian red squirrel)
E. motleiensis	17 x 15	Eulipotyphla: talpid (eastern mole)
E. mrigai	49 x 30	Artiodactyla: bovid (blackbuck)
E. mucosa		Diprotodontia: macropodid (brush-tailed rock-wallaby)
E. muehlensi	36 x 27	Artiodactyla: cervid (reindeer)
E. muhlensi	36 x 27	Artiodactyla: cervid (reindeer)
E. mundaragi	37 x 27	Artiodactyla: bovid (zebu)
E. mundayi	17 x 16	Diprotodontia: potoroid (long-nosed potoroo)
E. murinus	19 x 16	Eulipotyphla: soricid (Asian house shrew)
E. muris	21 x 15	Rodentia: murid (wood mouse)
E. musajevi	28 x 25	Rodentia: murid (Vinogradov's jird)
E. musculi	24	Rodentia: murid (house mouse)
E. musculoidei	20 x 17	Rodentia: murid (Temminck's mouse)
E. mustelae	22 x 19	Carnivora: mustelid (least weasel, American mink)
E. muuli		Rodentia: murid (pencil-tailed tree mouse)
E. mykytowyczi	31 x 18	Diprotodontia: macropodid (agile wallaby, antilopine wallaroo, whiptail wallaby)
E. myocastori	14 x 12	Rodentia: echimyid (coypu)
E. myopotami	23 x 22	Rodentia: echimyid (coypu)

E. myotis (*species inquirenda*)	15 x 14	Chiroptera: vespertilionid (greater mouse-eared bat)
E. myoxi	18 x 15	Rodentia: glirid (garden dormouse, Asian garden dormouse)
E. nachitschevanica	24 x 19	Rodentia: glirid (forest dormouse)
E. naganoensis	20 x 16	Artiodactyla: bovid (Japanese serow)
E. nagpurensis	23 x 13	Lagomorpha: leporid (rabbit)
E. nana	17 x 15	Artiodactyla: bovid (Siberian ibex, mouflon)
E. nasuae	18 x 16	Carnivora: procyonid (white-nosed coati)
E. nasuta		Rodentia: sciurid (Hodgson's giant flying squirrel)
E. nativa		Rodentia: cricetid (Siberian brown lemming)
E. naye	20 x 13	Rodentia: murid (wood mouse)
E. nazijrovi		Artiodactyla: bovid (Siberian ibex)
E. nehramaensis	20 x 18	Rodentia: murid (Shaw's jird, Tristam's jird)
E. neitzi	32 x 30	Artiodactyla: bovid (impala)
E. neodebliecki	21 x 16	Artiodactyla: suid (pig)
E. neoirresidua	26 x 18	Lagomorpha: leporid (desert cottontail)
E. neoleporis	39 x 20	Lagomorpha: leporid (eastern cottontail, rabbit)
E. neomyi	18 x 17	Eulipotyphla: soricid (southern water shrew, northern water shrew)
E. neosciuri	25 x 16	Rodentia: sciurid (eastern grey squirrel, red squirrel)
E. neotomae	22 x 16	Rodentia: murid (dusky-footed woodrat)
E. nereensis		Rodentia: murid (wood mouse)
E. nesokiae		Rodentia: murid (short-tailed bandicoot rat)
E. neurotrichi	18 x 14	Eulipotyphla: talpid (American shrew mole)
E. newalai	19 x 15	Carnivora: herpestid (Indian gray mongoose)
E. nieschulzi	23 x 18	Rodentia: murid (black rat, brown rat, pygmy rice rat, red spiny rat, Hawaiian rat, Sunda rat)
E. nigricani	19 x 17	Chiroptera: vespertilionid (black myotis)
E. nihonis	30 x 21	Artiodactyla: bovid (Japanese serow)
E. nilgai	21 x 18	Artiodactyla: bovid (nilgai)
E. ninakohlyakimovae	24 x 19	Artiodactyla: bovid (goat, wild goat, ibex, Siberian ibex)(early reports include black-tailed gazelle, sheep, bighorn sheep, mouflon, snow sheep, Barbary sheep, urial)
E. nitedulae	27 x 24	Rodentia: glirid (forest dormouse)
E. nochti	17 x 14	Rodentia: murid (black rat, brown rat)
E. nodulosa		Sirenia: trichechid (West Indian manatee)
E. noelleri	19	Rodentia: cuniculid (lowland paca)
E. noraschenica	23 x 21	Rodentia: murid (Persian jird)
E. nordensheldi	17 x 14	Rodentia: cricetid (Arctic lemming)
E. normanlevinei	35 x 28	Rodentia: capromyid (Desmarest's hutia)
E. notati	39 x 33	Rodentia: sciurid (plaintain squirrel)
E. novowenyoni (*species inquirenda*)	15	Carnivora: felid (tiger, leopard, panther)
E. nutriae	20 x 16	Rodentia: echimyid (coypu)
E. nuttalli	20 x 14	Carnivora: procyonid (raccoon, pygmy raccoon)
E. nyctali	20 x 18	Chiroptera: vespertilionid (common noctule)
E. nycticebi	17	Primates: lorisid (Sundra slow loris)
E. obendorfi	30 x 16	Diprotodontia: macropodid (Tasmanian pademelon)
E. obitzwadowski		Rodentia: echimyid (coypu)
E. occidentalis	23 x 18	Diprotodontia: macropodid (black-flanked rock wallaby, short-eared rock wallaby, Rothschild's rock wallaby)
E. ochotona	20 x 14	Lagomorpha: ochotonid (Daurian pika)
E. ochrogasteri	29 x 23	Rodentia: cricetid (prairie vole, Mexican vole, tundra vole, singing vole, meadow vole)
E. odocoilei	27 x 24	Artiodactyla: cervid (mule deer, white-tailed deer)
E. ojastii	17 x 13	Rodentia: cricetid (Tome's rice rat)
E. ondatrazibethicae	22 x 18	Rodentia: cricetid (muskrat)
E. ontarioensis	37 x 24	Rodentia: sciurid (eastern grey squirrel, fox squirrel, Abert's squirrel)
E. onychomysis	20 x 19	Rodentia: murid (northern grasshopper mouse)
E. oomingmakensis	48 x 34	Artiodactyla: bovid (muskox)
E. operculata	32 x 20	Rodentia: cricetid (Stephen's woodrat)
E. opimi		Rodentia: ctenomyid (highland tuco-tuco)

E. ordubadica	26 x 23	Rodentia: murid (Persian jird)
E. oreamni	29 x 19	Artiodactyla: bovid (mountain goat)
E. orthogeomydos	13 x 11	Rodentia: geomyid (giant pocket gopher)
E. oruroensis		Rodentia: ctenomyid (highland tuco-tuco)
E. oryctolagi	37 x 19	Lagomorpha: leporid (rabbit)
E. oryzomysi	24 x 17	Rodentia: cricetid (rice rat?)
E. os	24 x 20	Rodentia: sciurid (bobak marmot, grey marmot, long-tailed marmot, Menzbier's marmot, Tarbagan marmot, groundhog)
E. ostertagi	33 x 27	Eulipotyphla: erinaceid (European hedgehog)
E. otolicni	26 x 25	Primates: galagid (Senegal bushbaby)
E. otomyis	20 x 15	Rodentia: murid (Southern African vlei rat)
E. ovata	26 x 17	Rodentia: sciurid (golden-mantled ground squirrel, eastern chipmunk, gray-collared chipmunk)
E. ovibovis	23 x 19	Artiodactyla: bovid (muskox)
E. ovina	27 x 20	Artiodactyla: bovid (sheep, bighorn sheep, argali, mouflon)
E. ovinoidalis	24 x 20	Artiodactyla: bovid (sheep, bighorn, mouflon)
E. ovoidalis	36 x 24	Artiodactyla: bovid (water buffalo)
E. oytuni	25 x 19	Rodentia: spalacid (Middle East blind mole-rat)
E. pachydactyli		Primates: lorisid (greater slow loris)
E. pachylepyron	35 x 32	Primates: lorisid (greater slow loris)
E. pahangi	35 x 31	Rodentia: sciurid (plaintain squirrel)
E. pallasi	26 x 21	Lagomorpha: ochotonid (Pallas's pika)
E. pallida	16 x 12	Artiodactyla: bovid (sheep, goat, ibex)
E. palustris	24 x 18	Rodentia: cricetid (marsh rice rat)
E. panda	30 x 17	Artiodactyla: cervid (European roe deer)
E. pandei	23 x 19	Carnivora: herpestid (Indian gray mongoose)
E. panguii	48 x 32	Artiodactyla: bovid (African dwarf goat)
E. papillata	22 x 19	Rodentia: murid (house mouse)
E. paraensis	37 x 33	Rodentia: dasyproctid (red-rumped agouti)
E. paragachaica	28 x 22	Rodentia: murid (house mouse)
E. parahi	18 x 14	Artiodactyla: cervid (Indian hog deer)
E. parasciurorum	29 x 16	Rodentia: sciurid (southern flying squirrel)
E. parastiedica	27 x 26	Eulipotyphla: talpid (American shrew mole)
E. parma	21 x 12	Diprotodontia: macropodid (parma wallaby)
E. parryi	29 x 13	Diprotodontia: macropodid (whiptail wallaby)
E. parva (syn. *E. galouzoi*)	17 x 13	Artiodactyla: bovid (sheep, bighorn, mouflon, argali, urial) (early reports in goat, ibex, Siberian ibex)
E. patavina	24 x 16	Artiodactyla: cervid (European roe deer)
E. paulistana	43 x 24	Lagomorpha: leporid (Brazilian cottontail, eastern cottontail)
E. pavlovskyi	23 x 19	Rodentia: dipodid (Mongolian five-toed jerboa)
E. pecari		Artiodactyla: tayassuid (collared peccary)
E. pelandoki	18 x 17	Artiodactyla: tragulid (Java mouse-deer)
E. pellerdyi	23 x 13	Artiodactyla: camelid (Bactrian camel)
E. pellita	40 x 28	Artiodactyla; bovid (cattle, zebu)
E. pellucida	35 x 21	Rodentia: echimyid (coypu)
E. penicillati	18 x 15	Rodentia: heteromyid (desert pocket mouse, silky pocket mouse)
E. perardi	20 x 15	Eulipotyphla: erinaceid (European hedgehog)
E. perforans	25 x 15	Lagomorpha: leporid (rabbit, snowshoe hare, black-tailed jackrabbit, eastern cottontail, European hare, Arctic hare)
E. perforoides	23 x 18	Rodentia: sciurid (groundhog)
E. perminuta	14 x 12	Artiodactyla: suid (pig)
E. perognathi	20 x 15	Rodentia: heteromyid (rock pocket mouse)
E. peromysci	29 x 24	Rodentia: cricetid (pinyon mouse, North American deermouse)
E. peruviana	32 x 19	Artiodactyla: camelid (llama)
E. peschankae	22 x 21	Rodentia: murid (tamarisk jird)
E. petauristae	50 x 38	Rodentia: sciurid (red giant flying squirrel)
E. petrogale	23 x 14	Diprotodontia: macropodid (allied rock wallaby, Godman's rock wallaby, unadorned rock wallaby, black-flanked rock wallaby, brush-tailed rock wallaby, Proserpine rock wallaby)
E. philanderi	24 x 22	Didelphimorphia: didelphid (gray four-eyed opossum)
E. phocae	44 x 27	Pinnipedia: phocid (harbour seal, gray seal)

E. phyllotis	26 x 14	Rodentia: murid (friendly leaf-eared mouse)
E. picti	26 x 23	Rodentia: heteromyid (painted spiny pocket mouse)
E. pilarensis	15 x 14	Chiroptera: vespertilionid (western small-footed bat)
E. pileata	25 x 23	Rodentia: cricetid (southern red-backed vole)
E. pintoensis	24 x 16	Lagomorpha: leporid (Brazilian cottontail)
E. pipistrellus	25 x 23	Chiroptera: vespertilionid (Kuhl's pipistrelle)
E. piriformis	29 x 18	Lagomorpha: leporid (rabbit)
E. pitymydis		Rodentia: cricetid (European pine vole)
E. plecoti (*species inquirenda*)	16 x 14	Chiroptera: vespertilionid (brown long-eared bat)
E. polaris	30 x 18	Artiodactyla: cervid (reindeer)
E. polessica (syn. *E. musaevi*)	25 x 18	Rodentia: murid (striped field mouse)
E. polita	26 x 18	Artiodactyla: suid (pig)
E. poljanskii	33 x 32	Rodentia: murid (Vinogradov's jird)
E. ponderosa	42 x 29	Artiodactyla: cervid (European roe deer)
E. popovi	23 x 19	Rodentia: murid (Mongolian five-toed jerboa)
E. porci	22 x 16	Artiodactyla: suid (pig)
E. poti	30 x 18	Carnivora: procyonid (kinkajou)
E. potoroi	26 x 19	Diprotodontia: potoroid (long-nosed potoroo)
E. poudrei	26 x 18	Lagomorpha: leporid (desert cottontail)
E. pragensis	25 x 20	Rodentia: murid (house mouse)
E. praomysis	21 x 19	Rodentia: murid (Tullberg's soft-furred mouse)
E. prasadi	26 x 20	Rodentia: murid (wood mouse, yellow-necked mouse)
E. pretoriensis	24 x 19	Rodentia: murid (four-striped grass mouse)
E. primbelica	27 x 23	Rodentia: cricetid (common vole)
E. princepsis	22 x 17	Lagomorpha: ochotonid (American pika)
E. prionotemni	37 x 22	Diprotodontia: macropodid (tammar wallaby, whiptail wallaby, red-necked wallaby, agile wallaby, black-striped wallaby)
E. procyonis	23 x 18	Carnivora: procyonid (raccoon)
E. proechimyi	23 x 17	Rodentia: echimyid (Guyenne spiny rat)
E. pseudospermophili	29 x 25	Rodentia: sciurid (Townsend's ground squirrel, black-tailed prairie dog)
E. ptilocerci	23 x 20	Scandentia: ptilocercid (pen-tailed treeshrew)
E. pumilioi	18 x 12	Rodentia: murid (four-striped grass mouse)
E. punctata	26 x 20	Artiodactyla: bovid (sheep, goat)
E. punjabensis	23 x 22	Lagomorpha: leporid (Indian hare)
E. punoensis	20 x 16	Artiodactyla: camelid (alpaca)
E. putevelata	27 x 20	Rodentia: murid (typical striped grass mouse)
E. pyramidi	20 x 17	Rodentia: murid (greater Egyptian gerbil)
E. quenda	25 x 24	Peramelemorphia: peramelid (southern brown bandicoot)
E. quiyarum		Rodentia: echimyid (coypu)
E. quokka	18 x 11	Diprotodontia: macropodid (quokka)
E. rachmatullinae	28 x 20	Artiodactyla: bovid (argali)
E. rajasthani	36 x 25	Artiodactyla: camelid (dromedary)
E. ramgai	20 x 17	Artiodactyla: tragulid (Sri Lankan spotted chevrotain)
E. ratti	23 x 15	Rodentia: murid (black rat)
E. rayii (*species inquirenda*)	27 x 20	Carnivora: canid (dog)
E. razgovica	21 x 17	Rodentia: murid (golden hamster)
E. redukeri	20 x 18	Chiroptera: vespertilionid (Java pipistrelle)
E. reedi	23 x 21	Rodentia: heteromyid (long-tailed pocket mouse)
E. residua	26 x 22	Rodentia: cricetid (dusky-footed woodrat)
E. residualis	32 x 20	Artiodactyla: suid (pig)
E. rhabdomyis	13 x 12	Rodentia: murid (four-striped grass mouse)
E. rheemi	25 x 21	Artiodactyla: bovid (Arabian sand gazelle)
E. rhynchonycteridis	26	Chiroptera: emballonurid (proboscis bat)
E. riedmulleri	20 x 17	Artiodactyla: bovid (chamois)
E. ringaroomaensis	28 x 18	Diprotodontia: macropodid (Tasmanian pademelon)
E. rioarribaensis	25 x 20	Chiroptera: vespertilionid (western small-footed myotis)
E. robertsoni	42 x 26	Lagomorpha: leporid (Arctic hare, white-tailed jackrabbit, European

		hare, snowshoe hare, Indian hare)
E. robusta	37 x 27	Artiodactyla: cervid (red deer)
E. rochesterensis		Lagomorpha: leporid (snowshoe hare)
E. romaniae	32 x 25	Artiodactyla: suid (pig)
E. roperi		Rodentia: cricetid (hispid cotton rat)
E. ropotamae	24 x 21	Eulipotyphla: soricid (bicoloured white-toothed shrew)
E. rotunda	15 x 12	Artiodactyla: cervid (European roe deer)
E. roudabushi	22 x 19	Rodentia: cricetid (white-footed mouse)
E. rowani		Lagomorpha: leporid (snowshoe hare)
E. ruficaudati	32 x 14	Lagomorpha: leporid (Indian hare, snowshoe hare)
E. rufusi (rufi)	25	Diprotodontia: macropodid (red kangaroo)
E. rugosa	24 x 16	Rodentia: murid (yellow-necked mouse)
E. rupicaprae	21 x 17	Artiodactyla: bovid (chamois)
E. russiensis	22	Rodentia: murid (wood mouse)
E. rutilus	31 x 21	Rodentia: cricetid (northern red-backed vole, grey red-backed vole)
E. rysavyensis		Rodentia: cricetid (bank vole)
E. rysavyi	25 x 20	Rodentia: cricetid (bank vole)
E. sabani	29 x 22	Rodentia: murid (long-tailed giant rat, Whitehead's spiny rat)
E. sablii	13 x 11	Carnivora: mustelid (sable)
E. sadaraktica	23 x 19	Rodentia: murid (Vinogradov's jird)
E. saiga	31 x 30	Artiodactyla: bovid (saiga antelope)
E. sajanica	21 x 18	Artiodactyla: bovid (saiga antelope)
E. salasuzica	24 x 21	Rodentia: murid (Persian jird, Mongolian jird, midday jird)
E. sardari	29 x 14	Artiodactyla: cervid (Indian muntjac)
E. saudiensis	31 x 25	Artiodactyla: bovid (Arabian oryx)
E. saxei	13 x 10	Rodentia: cricetid (meadow vole, California vole, Mexican vole, creeping vole, long-tailed vole, singing vole, tundra vole)
E. scabra	32 x 22	Artiodactyla: suid (pig)
E. scalopi	14 x 13	Eulipotyphla: talpid (eastern mole)
E. scapani	19 x 16	Eulipotyphla: talpid (broad-footed mole, Temminck's mole)
E. schachtachtiana	24 x 20	Rodentia: murid (Tristam's jird, Mongolian jird)
E. schamchorica	24 x 21	Rodentia: murid (Libyan jird)
E. schelkovnikovi	20 x 17	Rodentia: cricetid (Schelkovnikov's pine vole)
E. schiwicki		Rodentia: cricetid (northern red-backed vole)
E. schoenbuchi	59	Artiodactyla: cervid (red deer)
E. scholtysecki	25 x 20	Rodentia: heteromyid (agile kangaroo rat, San Quintin kangaroo rat, Panamint kangaroo rat, banner-tailed kangaroo rat)
E. schoutedeni	15 x 12	Rodentia: murid (giant rat)
E. schueffneri	21 x 15	Rodentia: murid (house mouse)
E. sciurorum	24 x 15	Rodentia: sciurid (red squirrel, red-bellied squirrel, southern flying squirrel, grey squirrel, fox squirrel)
E. scrofae	24 x 15	Artiodactyla: suid (pig)
E. sculpta	37 x 29	Lagomorpha: leporid (Arctic hare, white-tailed jackrabbit)
E. seideli	46 x 40	Rodentia: echimyid (coypu)
E. sejnijevi		Artiodactyla: bovid (argali)
E. semisculpta	38 x 25	Lagomorpha: leporid (European hare, white-tailed jackrabbit)
E. semispinosi	19 x 14	Eulipotyphla: tenrecid (lowland streaked tenrec)
E. separata	16 x 14	Rodentia: murid (black rat, brown rat, dark-tailed tree rat, Defau rat, chestnut white-bellied rat, Hawaiian rat, Muller's giant Sunda rat, Malayan field rat)
E. septentrionalis	24 x 21	Lagomorpha: leporid (mountain hare, white-tailed jackrabbit)
E. serbica	28 x 18	Rodentia: sciurid (red squirrel)
E. setonicis	30 x 18	Diprotodontia: macropodid (quokka)
E. setosi	25 x 22	Eulipotyphla: tenrecid (greater hedgehog tenrec)
E. sevilletensis	17 x 16	Rodentia: cricetid (Mearn's grasshopper mouse, northern grasshopper mouse, scorpion mouse)
E. sharmani	28 x 17	Diprotodontia: macropodid (allied rock wallaby, Godman's rock wallaby, unadorned rock wallaby, black-flanked rock wallaby, brush-tailed rock wallaby, Proserpine rock wallaby, Rothschild's rock wallaby)
E. shubini	22	Lagomorpha: ochotonid (Pallas's pika, American pika)

E. sibirica	25 x 19	Carnivora: mustelid (sable)
E. sicistae		Rodentia: dipodid (Tien Shan birch mouse)
E. sigmodontis		Rodentia: cricetid (hispid cotton rat)
E. sikapusii	21 x 17	Rodentia: murid (rusty-bellied brush-furred rat)
E. silvana	17 x 14	Rodentia: sciurid (red squirrel)
E. siniffi	28 x 18	Rodentia: cricetid (North American deermouse)
E. skrjabini	*sp. inquir.*	Artiodactyla: bovid (goat)
E. solipedum	22 x 10	Perissodactyla: equid (horse, ass)
E. sordida	32 x 23	Artiodactyla: cervid (red deer)
E. soricinae (*species inquirenda*)	50 x 30	Eulipotyphla: soricid (common shrew)
E. soricis	20 x 14	Eulipotyphla: soricid (common shrew, Eurasian pygmy shrew, ornate shrew)
E. spalacensis	9 x 7	Rodentia: spalacid (Middle East blind mole-rat)
E. spalacis	19 x 12	Rodentia: spalacid (Middle East blind mole-rat)
E. spearei	17 x 16	Diprotodontia: potoroid (musky rat-kangaroo)
E. spermophili	25 x 21	Rodentia: sciurid (Gunnison's prairie dog, white-tailed prairie dog, black-tailed prairie dog, yellow-bellied marmot, Wyoming ground squirrel, Franklin's ground squirrel, Richardson's ground squirrel)
E. spinosa	21 x 15	Artiodactyla: suid (pig)
E. spratti	21 x 19	Diprotodontia: potoroid (musky rat-kangaroo)
E. sprehni	18 x 12	Rodentia: castorid (North American beaver, Eurasian beaver)
E. stefanskii	64 x 36	Lagomorpha: leporid (European hare)
E. stiedai (syn. *E. cuniculi, E. oviformis*)	37 x 21	Lagomorpha: leporid (rabbit, European hare, snowshoe hare, black-tailed jackrabbit, mountain hare, blue hare, eastern cottontail, mountain cottontail, plus experimental infections in desert cottontail)
E. stiedae (*species inquirenda*)	12 x 7	Carnivora: canid (dog)
E. strakonicensis	28 x 25	Rodentia: cricetid (common vole)
E. strangfordensis		Rodentia: cricetid (eastern woodrat)
E. subsimi	25 x 19	Rodentia: cricetid (Mexican vole)
E. subspherica	11 x 10	Artiodactyla: bovid (cattle, zebu, water buffalo)
E. suis	18 x 14	Artiodactyla: suid (pig)
E. sultanovi		Rodentia: murid (great gerbil)
E. sumgaitica	22 x 19	Rodentia: murid (Libyan jird)
E. suncus	20 x 16	Eulipotyphla: soricid (Asian house shrew)
E. sundarbanensis	28 x 21	Artiodactyla: bovid (goat)
E. sundermannae		Artiodactyla: cervid (white-tailed deer)
E. superba	50 x 31	Artiodactyla: cervid (roe deer)
E. suppereri	45 x 34	Artiodactyla: bovid (chamois)
E. surifer	35 x 25	Rodentia: murid (red spiny rat)
E. surki	22 x 14	Rodentia: sciurid (grey marmot, bobak marmot)
E. surkovae	25 x 22	Artiodactyla: bovid (argali)
E. susliki	32 x 25	Rodentia: sciurid (yellow ground squirrel)
E. svanbaevi	25 x 21	Rodentia: murid (wood mouse)
E. sylvatica	19 x 14	Rodentia: murid (wood mouse)
E. sylvilagi	29 x 18	Lagomorpha: leporid (Brazilian cottontail, eastern cottontail)
E. synaptomys	27 x 22	Rodentia: cricetid (southern bog lemming, northern bog lemming)
E. tachyglossi		Monotremata: tachyglossid (short-beaked echidna)
E. tachyoryctis	23 x 17	Rodentia: spalacid (Rwanda African mole-rat)
E. tadarida	25 x 19	Chiroptera: molossid (pocketed free-tailed bat)
E. tadshikistanica	22	Rodentia: cricetid (Transcaucasian mole vole)
E. tadzhikistanica		Carnivora: felid (Eurasian lynx)
E. taimyrica		Rodentia: cricetid (Middendorf's vole)
E. talboti	36 x 25	Artiodactyla: bovid (Coke's hartebeest)
E. talikiensis		Rodentia: spalacid (lesser mole-rat)
E. talischaensis	21	Rodentia: cricetid (European water vole)
E. talpini	24	Rodentia: cricetid (northern mole vole)
E. talpoidei	21 x 13	Eulipotyphla: talpid (Japanese shrew mole)
E. tamanduae	25 x 22	pilosa: myrmecophagid (southern tamandua)
E. tamariscini	19 x 18	Rodentia: murid (tamarisk jird)

E. tamiasciuri	33 x 19	Rodentia: sciurid (red squirrel, Abert's squirrel, American red squirrel, Mearn's squirrel, cliff chipmunk, Merriam's chipmunk, California chipmunk), cricetid (montane vole)
E. tamiensis		Rodentia: sciurid (eastern chipmunk)
E. tanabei	12 x 7	Eulipotyphla: talpid (large Asian mole)
E. tarandina	20 x 18	Artiodactyla: cervid (reindeer)
E. tarsii	17 x 12	Primates: tarsiid (Philippine tarsier)
E. tasakendica	23 x 21	Rodentia: murid (Vinogradov's jird)
E. tasmaniae	83	Diprotodontia: vombatid (southern hairy-nosed wombat)
E. tatarica	30 x 24	Artiodactyla: bovid (saiga antelope)
E. taterae		Rodentia: murid (Indian gerbil)
E. tatusi	32	Xenarthra: dasypodid (nine-banded armadillo, southern naked-tailed armadillo, big hairy armadillo)
E. taylori	20 x 15	Rodentia: cricetid (northern pygmy mouse)
E. tekenovi	29 x 22	Artiodactyla: bovid (saiga antelope)
E. telekii	20 x 16	Rodentia: murid (typical striped grass mouse)
E. tenggilingi		Pholidota: manid (Sunda pangolin)
E. terrestris	21 x 16	Rodentia: cricetid (European water vole)
E. theileri	20 x 17	Rodentia: murid (Natal multimammate mouse)
E. thianethi	43 x 29	Artiodactyla: bovid (water buffalo, cattle, zebu)
E. thomomysis	14	Rodentia: geomyid (Botta's pocket gopher)
E. thylogale	32 x 21	Diprotodontia: macropodid (Tasmanian pademelon)
E. tianschanica		Rodentia: dipodid (Tien Shan birch mouse)
E. tikusi	30 x 24	Rodentia: murid (Edward's swamp rat)
E. tinaroonensis	26 x 24	Diprotodontia: potoroid (musky rat-kangaroo)
E. tirupatiensis	40 x 28	Artiodactyla: bovid (goat)
E. titthus	16 x 14	Eulipotyphla: talpid (hairy-tailed mole)
E. toddi	40 x 32	Rodentia: sciurid (American red squirrel)
E. toganmainensis	39 x 25	Diprotodontia: macropodid (red kangaroo, eastern grey kangaroo, western grey kangaroo, red-necked wallaby, tammar wallaby)
E. tolucadensis	25 x 20	Rodentia: cricetid (Mexican vole)
E. tomopea	31 x 25	Chiroptera: vespertilionid (blunt-eared bat)
E. torosicum		Rodentia: spalacid (Middle East blind mole-rat)
E. townsendi	40 x 28	Lagomorpha: leporid (European hare, mountain hare, white-tailed jackrabbit)
E. tragocamelis	24 x 19	Artiodactyla: bovid (nilgai)
E. traguli		Artiodactyla: tragulid (Java mouse-deer)
E. travassosi	51 x 40	Cingulata: dasypodid (southern long-nosed armadillo), chlamyphorid (six-banded armadillo)
E. trichechi		Sirenia: trichechid (Amazonian manatee)
E. trichosuri	41 x 23	Diprotodontia: phalangerid (mountain brushtail possum, common brushtail possum, short-eared possum)
E. triffittae	21 x 18	Artiodactyla: bovid (common eland)
E. tristrami	26 x 22	Rodentia: murid (Tristram's jird)
E. tschernobyli	13 x 11	Rodentia: murid (striped field mouse)
E. tsogoi	25 x 20	Rodentia: murid (midday jird)
E. tuberculata		Rodentia: murid (black rat)
E. tunisiensis		Artiodactyla: bovid (goat)
E. tupaiae	20 x 19	Scandentia: tupaiid (common treeshrew, lesser treeshrew, large treeshrew)
E. turkestanica	26 x 19	Rodentia: murid (Turkestan rat)
E. turkmenica		Rodentia: spalacid (lesser mole-rat)
E. turnbulli	32 x 23	Artiodactyla: bovid (bay duiker)
E. tuskegeensis		Rodentia: cricetid (hispid cotton rat)
E. tuzdili		Rodentia: spalacid (lesser mole-rat)
E. tyanchanensis	24 x 19	Rodentia: sciurid (Menzbier's marmot)
E. uilenbergi (*species inquirenda*)	17 x 16	Eulipotyphla: tenrecid (tailless tenrec)
E. uniungulata	20 x 15	Perissodactyla: equid (horse, ass)
E. uptoni		Rodentia: murid (wood mouse, small Japanese field mouse, large Japanese field mouse, Korean field mouse)

E. urfensis		Rodentia: spalacid (Middle East blind mole-rat)
E. ursi	14 x 12	Carnivora: ursid (brown bear)
E. ursini	24 x 20	Diprotodontia: vombatid (southern hairy-nosed wombat)
E. utahensis	42 x 40	Rodentia: heteromyid (agile kangaroo rat, San Quintin kangaroo rat, Merriam's kangaroo rat, chisel-toothed kangaroo rat)
E. utinensis [probably *Klossiella equi*]	nr	Perissodactyla: equid (horse)
E. uzbekistanica		Rodentia: murid (midday jird)
E. vagrantis	27 x 22	Eulipotyphla: soricid (smoky shrew, montane shrew, Trowbridge shrew)
E. vahidovi	22 x 17	Rodentia: murid (Vinogradov's jird)
E. vejdovsyi		Lagomorpha: leporid (rabbit)
E. vejsovi	21 x 18	Chiroptera: vespertilionid (common noctule)
E. vermiformis	23 x 18	Rodentia: murid (house mouse)
E. vespertilii	25 x 22	Chiroptera: vespertilionid (part-coloured bat)
E. vilasi (syn. *E. adaensis, E. dorsalis*)	18 x 14	Rodentia: sciurid (white-tailed prairie dog, black-tailed prairie dog, groundhog, Mexican ground squirrel, Townsend's ground squirrel, gray-footed chipmunk, cliff chipmunk, Merriam's chipmunk, California chipmunk, eastern chipmunk, Townsend's chipmunk)
E. vinckei	22 x 13	Rodentia: murid (tree rat)
E. vinogradovi	22 x 19	Rodentia: murid (Vinogradov's jird)
E. virginianus	49 x 33	Artiodactyla: cervid (white-tailed deer)
E. viridis (*species inquirenda*)	20 x 14	Chiroptera: molossid (greater horseshoe bat)
E. vison	20 x 15	Carnivora: mustelid (European polecat, American mink)
E. visonlevinei	23 x 15	Carnivora: mustelid (American mink)
E. voinjamensis	20 x 18	Primates: galagid (Prince Demidoff's bushbaby)
E. volckertzooni	22 x 13	Diprotodontia: macropodid (quokka)
E. volgensis	27 x 22	Rodentia: sciurid (red-cheeked ground squirrel, little ground squirrel, relict ground squirrel, long-tailed ground squirrel)
E. voronezhensis	23 x 21	Carnivora: mustelid (striped skunk)
E. vulpis (*species inquirenda*)	17 x 14	Carnivora: canid (Bengal fox, red fox)
E. wallabiae	33 x 20	Diprotodontia: macropodid (swamp wallaby)
E. walleri	29 x 24	Artiodactyla: bovid (giraffe gazelle)
E. wapiti	38 x 26	Artiodactyla: cervid (red deer)
E. wassilewskyi	18 x 14	Artiodactyla: cervid (chital, red deer, sika)
E. webbae		Rodentia: cricetid (hispid cotton rat)
E. weddelli	48 x 30	Pinnipedia: phocid (Weddell seal)
E. weissi	24 x 19	Rodentia: cricetid (friendly leaf-eared mouse)
E. wenrichi	19 x 14	Rodentia: cricetid (meadow vole, beach vole, Mexican vole, montane vole, creeping vole, tundra vole, long-tailed vole, singing vole, taiga vole)
E. weybridgensis	24 x 17	Artiodactyla: bovid (sheep)
E. whitakeri	17 x 16	Eulipotyphla: soricid (North American least shrew)
E. wilcanniensis	32 x 20	Diprotodontia: macropodid (red kangaroo, eastern grey kangaroo, western grey kangaroo, common wallaroo, red-necked wallaby)
E. williamsi	18 x 14	Rodentia: dipodid (Euphrates jerboa)
E. wombati	75 x 57	Diprotodontia: vombatid (southern hairy-nosed wombat)
E. worleyi	14 x 13	Lagomorpha: ochotonid (American pika)
E. wyomingensis	40 x 28	Artiodactyla: bovid (cattle, zebu, water buffalo)
E. xanthopus	25 x 17	Diprotodontia: macropodid (yellow-footed rock wallaby)
E. xeri	21 x 17	Rodentia: sciurid (striped ground squirrel)
E. yakimoffmatschoulskyi	28 x 21	Artiodactyla: bovid (chamois)
E. yakimovi	37 x 24	Artiodactyla: bovid (nilgai)
E. yathongensis	21 x 14	Diprotodontia: macropodid (western grey kangaroo, eastern grey kangaroo)
E. yukonensis	25 x 13	Rodentia: sciurid (long-tailed ground squirrel)
E. yunnanensis		Artiodactyla: bovid (cattle)
E. zajacae		Artiodactyla: cervid (white-tailed deer)
E. zakirica	25 x 23	Chiroptera: vespertilionid (parti-coloured bat)

E. zapi		Rodentia: dipodid (meadow jumping mouse, western jumping mouse, Pacific jumping mouse)
E. zaurica	23 x 21	Rodentia: murid (wood mouse)
E. zejnijevi	46 x 38	Artiodactyla: bovid (argali)
E. zemphirica	25 x 21	Rodentia: murid (Persian jird)
E. zuernii	18 x 16	Artiodactyla; bovid (cattle, zebu, water buffalo, wisent)
E. zulfiaensis	25 x 20	Rodentia: murid (Vinogradov's jird)
E. zuvandica	22 x 17	Rodentia: cricetid (common vole)
E. zygodontomyis		Rodentia: cricetid (spotted bolo mouse)
Birds		
E. abramovi	22 x 17	Anseriformes: anatid (mallard duck)
E. accipitris	13	Accipitriformes: accipitrid (Eurasian sparrowhawk)
E. acervulina	20 x 14	Galliformes: phasianid (chicken, guineafowl, Sri Lanka junglefowl), odontophorid (California quail, northern bobwhite quail, plumed quail)
E. adenoeides	26 x 16	Galliformes: phasianid (turkey)
E. aestivae	37 x 24	Psittaciformes: psittacid (turquoise-fronted amazon)
E. ahmadi		Charadriiformes: charadriid (white-tailed lapwing)
E. alakuli		Gruiformes: rallid (Eurasian coot)
E. alectorae	24 x 15	Galliformes: phasianid (rock partridge)
E. anatis	17 x 14	Anseriformes: anatid (mallard duck)
E. angusta	30 x 17	Galliformes: phasianid (hazel grouse, spruce grouse, ruffed grouse, greater sage-grouse, sharp-tailed grouse)
E. anili		Passeriformes: sturnid (pied myna)
E. anseris (syn. *E. parvula*)	22 x 17	Anseriformes: anatid (goose, snow goose, Canada goose)
E. anthi	26 x 22	Passeriformes: motacillid (meadow pipit)
E. arabica		Galliformes: phasianid (peacock)
E. aratinga		Psittaciformes: psittacid (orange-fronted parakeet)
E. ardeae		Ciconiiformes: ardeid (grey heron, purple heron)
E. asturi	10 x 6	Accipitriformes: accipitrid (northern goshawk)
E. atheni		Strigiformes: strigid (spotted owlet)
E. aythyae	20 x 16	Anseriformes: anatid (lesser scaup)
E. azura		Galliformes: phasianid (Japanese quail)
E. balozeti	25 x 21	Passeriformes: sturnid (common starling)
E. baltica		Gruiformes: gruid (common crane)
E. barbeta	23 x 10	Piciformes: capitonid (blue-throated barbet)
E. bateri	23 x 18	Galliformes: phasianid (common quail, gray quail)
E. battakhi	21 x 18	Anseriformes: anatid (mallard duck)
E. bazi	24 x 17	Pelecaniformes: threskiornithid (red-naped ibis)
E. bemricki		Strigiformes: strigid (great grey owl)
E. bhutanensis	16	Galliformes: phasianid (peacock-pheasant)
E. bonasae	21	Galliformes: phasianid (hazel grouse, ruffed grouse, willow ptarmigan, spruce grouse, sharp-tailed grouse)
E. boschadis	24 x 13	Anseriformes: anatid (mallard duck)
E. bosquei		Gruiformes: gruid (sandhill crane)
E. bragini		Gruiformes: rallid (Eurasian coot)
E. brantae	23 x 18	Anseriformes: anatid (Canada goose, Hutchin's goose)
E. brinkmanni	29 x 19	Galliformes: phasianid (Canadian rock ptarmigan)
E. brunetti	27 x 22	Galliformes: phasianid (chicken)
E. bubonis		Strigiformes: strigid (great horned owl)
E. bucephalae	30 x 16	Anseriformes: anatid (common goldeneye)
E. burhinici		Charadriiformes: burhinid (Eurasian stone-curlew)
E. caucasica	33 x 19	Galliformes: phasianid (Chukar partridge, red-legged partridge)
E. centrocerci	23 x 17	Galliformes: phasianid (greater sage-grouse)
E. certhiidarum		Passeriformes: certhiid (short-toed treecreeper)
E. charadrii	16 x 12	Charadriiformes: charadriid (Caspian plover)
E. choudari		Columbiformes: columbid (Eurasian collared dove)
E. christianseni	17 x 11	Anseriformes: anatid (mute swan)
E. clarkei	27 x 19	Anseriformes: anatid (snow goose, Canada goose)
E. colchici	27 x 17	Galliformes: phasianid (common pheasant)
E. colini		Galliformes: odontophorid (northern bobwhite quail)

E. columbae	16 x 14	Columbiformes: columbid (rock dove)
E. columbarum	20 x 19	Columbiformes: columbid (rock dove)
E. coracias		Coraciiformes: coraciid (European roller)
E. cotornicis		Galliformes: phasianid (rock partridge)
E. coturnicis	33 x 23	Galliformes: phasianid (common quail)
E. crassa	26 x 21	Anseriformes: anatid (Canada goose)
E. creutzi	13 x 12	Charadriiformes: larid (black-headed gull)
E. crusti		Galliformes: phasianid (mountain quail)
E. crypturelli		Tinamiformes: tinamid (little tinamou)
E. curvata		Columbiformes: columbid (ruddy ground dove, scaled dove)
E. danailovi	19 x 12	Anseriformes: anatid (mallard duck, plus experimental infection in greylag goose)
E. dauki	18 x 12	Gruiformes: rallid (white-breasted waterhen)
E. dendrocopi	29 x 17	Piciformes: picid (great spotted woodpecker)
E. depuytoraci		Passeriformes: sylviid (garden warbler)
E. dispersa	23 x 19	Galliformes: phasianid (turkey, Gould's turkey, common European quail, common pheasant, chicken, ruffed grouse, sharp-tailed grouse), odontophorid (bobwhite quail)
E. dissanaikei	21 x 14	Galliformes: phasianid (Ceylon junglefowl)
E. dubeyi	31 x 22	Galliformes: phasianid (red junglefowl)
E. duculai		Columbiformes: columbid (Torresian imperial pigeon)
E. duncani		Coraciiformes: alcedinid (sacred kingfisher)
E. dunsingi	35 x 25	Psittaciformes: psittacid (budgerigar)
E. duodenalis	21 x 19	Galliformes: phasianid (common pheasant)
E. fanthami	28 x 19	Galliformes: phasianid (Canadian rock ptarmigan)
E. farrae	23 x 18	Anseriformes: anatid (greater white-fronted goose)
E. forresteri		Piciformes: ramphastid (Toco toucan)
E. francolini		Galliformes: phasianid (black francolin)
E. fraterculae		Charadriiformes: alcid (Atlantic puffin)
E. fulica	16 x 13	Gruiformes: rallid (water rail, spotted crake)
E. fulva	30 x 22	Anseriformes: anatid (greylag goose, snow goose, Canada goose)
E. galateai		Coraciiformes: alcedinid (common paradise kingfisher)
E. gallinagoi	21 x 14	Charadriiformes: scolopacid (common snipe)
E. gallopavonis	27 x 17	Galliformes: phasianid (turkey)
E. garzettae		Ciconiiformes: ardeid (little egret)
E. gaviae		Gaviiformes: gaviid (common loon)
E. gennaeuscus	21 x 18	Galliformes: phasianid (kalij pheasant)
E. globulosa		Gruiformes: gruid (common crane)
E. goelandi		Charadriiformes: larid (European herring gull)
E. gonzalezcastroi		Galliformes: phasianid (red-legged partridge)
E. gorakhpuri	20 x 14	Galliformes: phasianid (helmeted guineafowl)
E. gouriae		Columbiformes: columbid (Victoria crowned pigeon)
E. grallinida		Passeriformes: monarchid (magpie-lark)
E. grenieri	24 x 16	Galliformes: phasianid (helmeted guinea fowl)
E. gruis (syn. *E. kazanskii*)	19 x 12	Gruiformes: gruid (Demoiselle crane)
E. grusi	22 x 17	Gruiformes: gruid (sarus crane)
E. haematodi		Psittaciformes: lorid (coconut lorikeet)
E. hagani	19 x 18	Galliformes: phasianid (red junglefowl)
E. hermani	26 x 19	Anseriformes: anatid (greylag goose, snow goose, Canada goose, cackling goose)
E. hydrobatidis	19 x 18	Procellariformes: hydrobatid (European storm petrel)
E. indentata	30 x 21	Galliformes: phasianid (Ceylon junglefowl)
E. innocua	22 x 21	Galliformes: phasianid (turkey)
E. johnsoni [*species inquirenda*]	22 x 18	Galliformes: phasianid (chicken)
E. kapotei	26 x 24	Columbiformes: columbid (rock dove)
E. karatauica		Galliformes: phasianid (chukar partridge)
E. kofoidi	20 x 18	Galliformes: phasianid (rock partridge, red-legged partridge, gray partridge, chukar)
E. koganae	22 x 16	Anseriformes: anatid (northern pintail, teal, mallard, garganey, gadwall,

		pochard)
E. kotlani	31 x 24	Anseriformes: anatid (greylag goose)
E. kustanaica (syn. *E. krylovi*)	18 x 15	Anseriformes: anatid (northern shoveler, Eurasian teal, Eurasian wigeon, garganey, gadwall, pochard)
E. labbeana	18 x 15	Columbiformes: columbid (rock dove, domestic pigeon, stock dove, common wood pigeon, Oriental turtle dove, Eurasian collared dove, common ground dove)
E. lafayettei	20 x 14	Galliformes: phasianid (Ceylon junglefowl)
E. lagopodi	24 x 15	Galliformes: phasianid (alpine rock ptarmigan)
E. langeroni	33 x 18	Galliformes: phasianid (common pheasant, white-winged pheasant)
E. lari	24 x 17	Charadriiformes: larid (European herring gull, black-headed gull)
E. legionensis	21 x 15	Galliformes: phasianid (red-legged partridge, rock partridge)
E. leninogorica		Galliformes: phasianid (hazel grouse)
E. lettyae		Galliformes: odontophorid (northern bobwhite quail)
E. leucuri		Galliformes: phasianid (white-tailed ptarmigan)
E. longa		Gruiformes: gruid (common crane)
E. lophortygis	23 x 19	Galliformes: odontophorid (California quail, mountain quail)
E. lophurae		Galliformes: phasianid (kalij pheasant)
E. lucknowensis	23 x 18	Passeriformes: motacillid (white wagtail)
E. lyruri	26 x 15	Galliformes: phasianid (western capercaillie, black grouse, grey partridge)
E. magnalabia	22 x 16	Anseriformes: anatid (greater white-fronted goose, domestic goose, snow goose, Canada goose, cackling goose)
E. malaccae	29 x 17	Passeriformes: estrildid (tricoloured munia)
E. mandali	18 x 17	Galliformes: phasianid (Indian peafowl)
E. maxima	29 x 23	Galliformes: phasianid (chicken), odontophorid (California quail)
E. mayurai	23 x 14	Galliformes: phasianid (Indian peafowl, green peafowl)
E. megabubonis		Strigiformes: strigid (great horned owl)
E. megalostomata	24 x 19	Galliformes: phasianid (common pheasant)
E. meleagridis	24 x 17	Galliformes: phasianid (turkey)
E. meleagrimitis	18 x 15	Galliformes: phasianid (turkey)
E. mellumi	17 x 13	Charadriiformes: larid (European herring gull)
E. meservei	18 x 17	Charadriiformes: larid (Forster's tern)
E. mitis	16 x 14	Galliformes: phasianid (chicken), odontophorid (California quail, mountain quail)
E. mivati	16 x 13	Galliformes: phasianid (chicken)
E. mongolica	14 x 13	Gruiformes: rallid (Eurasian coot)
E. mulardi		Anseriformes: anatid (mallard duck)
E. musophagi	23 x 19	Musophagiformes: musophagid (purple-crested turaco)
E. muta	25 x 17	Galliformes: phasianid (Icelandic rock ptarmigan)
E. mutum	25 x 22	Galliformes: cracid (bare-faced curassow)
E. nadsoni	25 x 21	Galliformes: phasianid (black grouse)
E. necatrix	17 x 14	Galliformes: phasianid (chicken)
E. nocens	29 x 20	Anseriformes: anatid (greylag goose, lesser white-fronted goose, snow goose)
E. nonbrumpti	22	Piciformes: picid (great spotted woodpecker)
E. nottion		Anseriformes: anatid (mallard duck
E. numenii	22	Charadriiformes: scolopacid (Eurasian curlew)
E. numidae	19 x 15	Galliformes: phasianid (helmeted guinea fowl)
E. nycteae		Strigiformes: strigid (snowy owl)
E. nyroca	25 x 18	Anseriformes: anatid (ferruginous duck)
E. okanaganensis	26 x 20	Galliformes: odontophorid (California quail, mountain quail)
E. oreoecetes		Galliformes: phasianid (white-tailed ptarmigan, dusky grouse)
E. oreortygis		Galliformes: odontophorid (California quail, mountain quail)
E. pacifica	22 x 18	Galliformes: phasianid (common pheasant, golden pheasant, Reeve's pheasant, Tibetan eared pheasant, silver pheasant)
E. padulensis		Galliformes: phasianid (red-legged partridge)
E. paludosa	15 x 11	Gruiformes: rallid (white-breasted waterhen, American coot, Eurasian coot, common moorhen)
E. palumbi		Columbiformes: columbid (Galapagos dove)
E. paradisaeai		Passeriformes: paradisaeid (Raggiana bird-of-paradise)

E. patnaiki	19 x 16	Galliformes: phasianid (Indian peafowl)
E. pattersoni	20 x 14	Galliformes: phasianid (greater sage-grouse, black grouse)
E. pavonina	24 x 18	Galliformes: phasianid (Indian peafowl)
E. pavonis	23 x 18	Galliformes: phasianid (Indian peafowl)
E. pelecani		Pelecaniformes: pelecanid (brown pelican)
E. phasiani	23 x 16	Galliformes: phasianid (common pheasant, golden pheasant, Reeve's pheasant, white-eared pheasant, silver pheasant)
E. philomachusi		Charadriiformes: scolopacid (wood sandpiper)
E. picta (pictus)	19 x 15	Galliformes: phasianid (golden pheasant, silver pheasant)
E. pluvialina	19 x 14	Charadriiformes: charadriid (Caspian plover)
E. polycephali	17 x 14	Gruiformes: rallid (western swamphen)
E. porphyrulae		Gruiformes: rallid (American purple gallinule)
E. praecox	21 x 17	Galliformes: phasianid (chicken)
E. procera	30 x 17	Galliformes: phasianid (grey partridge, western capercaillie)
E. psittacina		Psittaciformes: psittacid (budgerigar)
E. pternistis		Galliformes: phasianid (yellow-necked francolin)
E. pulchella	24 x 15	Anseriformes: anatid (Canada goose)
E. pusilla		Gruiformes: gruid (common crane)
E. raichoi	21 x 18	Galliformes: phasianid (Japanese rock ptarmigan)
E. reichenowi	19 x 14	Gruiformes: gruid (Demoiselle crane, sandhill crane, sarus crane, whooping crane)
E. renicola	25 x 24	Charadriiformes: larid (black-headed gull)
E. rhynchoti	25 x 22	Tinamiformes: tinamid (red-winged tinamou)
E. ridjakovi	27 x 18	Galliformes: phasianid (grey partridge)
E. rissae	19 x 14	Charadriiformes: larid (black-legged kittiwake)
E. riyadhae		Galliformes: phasianid (peacock)
E. rjupa	25 x 22	Galliformes: phasianid (Icelandic rock ptarmigan)
E. roscoviensis	17 x 15	Charadriiformes: charadriid (Kentish plover, little ringed plover, golden plover); scolopacid (turnstone, dunlin, common sandpiper, whimbrel, redshank); Passeriformes: motacillid (white wagtail); Pelecaniformes: phalacrocoracid (European shag)
E. saitamae	19 x 13	Anseriformes: anatid (mallard duck)
E. saubenovae		Gruiformes: rallid (Eurasian coot)
E. schachdagica	24 x 18	Anseriformes: anatid (mallard duck)
E. schokpaki		Coraciiformes: coracid (European roller)
E. serventyi	28 x 26	Procellariiformes: procellariid (short-tailed shearwater)
E. somateriae	32 x 14	Anseriformes: anatid (long-tailed duck, common eider, greater scaup)
E. speotytoi	33 x 25	Strigiformes: strigid (burrowing owl)
E. sphenocercae	19 x 13	Columbiformes: columbid (wedge-tailed green pigeon)
E. sporadica		Galliformes: phasianid (chicken)
E. stercorariae	12 x 9	Charadriiformes: stercorariid (Arctic skua)
E. stigmosa	23 x 17	Anseriformes: anatid (ducks)
E. striata		Anseriformes: anatid (greylag goose, snow goose, Canada goose)
E. strigis	35 x 30	Strigiformes: strigid (tawny owl)
E. subrotunda	22	Galliformes: phasianid (turkey)
E. symmetrica	35 x 29	Galliformes: phasianid (Ceylon junglefowl)
E. tahamensis		Galliformes: phasianid (Arabian quail)
E. taldykurganica		Galliformes: phasianid (common quail)
E. teetari	24 x 20	Galliformes: phasianid (black francolin, grey francolin)
E. tenella (syn. *E. avium, E. bracheti, E. globosa*)	23 x 19	Galliformes: phasianid (chicken, rock partridge, grey partridge, red grouse, common pheasant), odontophorid (bobwhite quail, California quail, mountain quail)
E. tetartooimia		Galliformes: phasianid (common pheasant)
E. tetricis	31 x 15	Galliformes: phasianid (black grouse)
E. tropicalis	20	Columbiformes: columbid (rock dove)
E. truncata	21 x 16	Anseriformes: anatid (greylag goose, Ross's goose, snow goose, Canada goose)
E. tsunodai		Galliformes (Japanese quail)
E. turaco	28 x 20	Musophagiformes: musophagid (purple-crested turaco)
E. turturi	26 x 22	Columbiformes: columbid (European turtle dove)
E. tyzzeri	32 x 23	Galliformes: phasianid (chicken)

E. uekii	24 x 15	Galliformes: phasianid (Japanese rock ptarmigan)
E. urnula (syn. *E. cernula*)	20 x 13	Pelecaniformes: phalacrocoracid (great cormorant)
E. ustkamenogorica		Galliformes: phasianid (hazel grouse)
E. uzura	24 x 19	Galliformes: phasianid (Japanese quail)
E. vanelli	29 x 14	Charadriiformes: charadriid (yellow-wattled lapwing)
E. vanmurghavi	16 x 12	Galliformes: phasianid (red junglefowl, grey junglefowl)
E. varia		Strigiformes: strigid (tawny owl)
E. ventriosa	32 x 21	Galliformes: phasianid (western capercaillie)
E. vitellini		Piciformes: ramphastid (channel-billed toucan)
E. waiganiensis		Columbiformes: columbid (common emerald dove, pheasant pigeon)
E. wobeseri		Charadriiformes: larid (European herring gull)
E. yakisevi (syn. *E. brumpti*)	24 x 20	Galliformes: phasianid (western capercaillie)
Reptiles		
E. ablephari	23 x 18	Sauria: scincid (snake-eyed skink)
E. acanthodactyli	31 x 21	Sauria: lacertid (Nidua fringe-fingered lizard)
E. aesculapi	15 x 13	Serpentes: colubrid (false coral snake)
E. agamae	23 x 12	Sauria: agamid (common agama)
E. ahtanumensis	34 x 20	Sauria: phrynosomatid (western fence lizard)
E. albemarlensis		Sauria: tropidurid (Galapagos lava lizard)
E. alligatori		Crocodilia: alligatorid (American alligator)
E. amarili	30 x 18	Serpentes: viperid (Neuwied's lancehead)
E. amazonensis	12 x 9	Testudines: testudinid (red-footed tortoise)
E. ameivae	22 x 20	Sauria: teiid (rainbow ameiva)
E. amphisbaeniarum		Sauria: amphisbaenid (Mann's worm lizard)
E. amphorae	25 x 22	Serpentes: colubrid (Florida crowned snake)
E. amreini	*nomen nudum*	Sauria: phrynosomatid (common side-blotched lizard)
E. amydae	20 x 15	Testudines: trionychid (northern spiny softshell turtle, pallid spiny softshell turtle)
E. annea		Serpentes: colubrid (smooth green snake, ribbon snake, common garter snake)
E. anolidis		Sauria: dactyloid (Carolina anole)
E. apalone	17 x 13	Testudines: trionychid (pallid spiny softshell turtle, western spiny softshell turtle)
E. arabukoskokensis	27 x 15	Serpentes: colubrid (tiger cat snake)
E. arakanensis	28 x 24	Testudines: geoemydid (Akaran forest turtle)
E. arnaldoi	30 x 15	Serpentes: colubrid (coastal house snake)
E. arnyi	17 x 15	Serpentes: colubrid (prairie ringneck snake)
E. atheridis	23	Serpentes: viperid (western bush viper)
E. attenuata	22 x 13	Serpentes: colubrid (red-sided garter snake, yellow-belly water snake, blotched water snake, broad-banded water snake, northern water snake, western ribbon snake, redstripe ribbon snake)
E. avilae		Sauria: dactyloid (desert grass anole)
E. baltrocki		Sauria: scincid (Berber skink)
E. barnardi		Sauria: gekkonid (common Namib day gecko)
E. basilisci	33 x 18	Sauria: corytophanid (common basalisk)
E. bautistae		Sauria: teiid (common ameiva)
E. beccari		Sauria: varanid (emerald tree monitor)
E. becki		Sauria: helodermatid (Gila monster)
E. beyerae		Sauria: scincid (desert lidless skink)
E. bitis	35 x 20	Serpentes: viperid (puff adder); colubrid (smooth green snake, common garter snake, ribbon snake)
E. boae	26 x 21	Serpentes: boid (emerald tree boa)
E. bohemii		Sauria: chamaeleonid (Meller's chameleon)
E. bongaonensis		Sauria: gekkonid (Tokay gecko)
E. bothropis	24 x 19	Serpentes: viperid (common lancehead)
E. boveroi	18	Sauria: gekkonid (Moreau's tropical house gecko)
E. brodeni	30 x 19	Testudines: testudinid (spur-thighed tortoise)
E. brygooi		Sauria: gekkonid (gold dust day gecko)
E. caesicia	27 x 24	Sauria: tropidurid (Amazon lava lizard)

E. caimani		Crocodilia: alligatorid (Yacare caiman)
E. cameronensis		Sauria: agamid (great anglehead lizard)
E. carajasensis	22 x 19	Testudines: testudinid (red-footed tortoise)
E. carbonaria	19 x 18	Testudines: testudinid (red-footed tortoise)
E. caretta	25 x 22	Testudines: cheloniid (loggerhead sea turtle)
E. carri	16 x 15	Testudines: emydid (common box turtle, eastern box turtle, three-toed box turtle, ornate box turtle)
E. cascabeli	37 x 17	Serpentes: viperid (prairie rattlesnake, Southern Pacific rattlesnake)
E. cenchoae	23 x 16	Serpentes: colubrid (common blunt-headed tree snake)
E. cerastis	40 x 20	Serpentes: viperid (horned desert viper, Sahara sand viper)
E. cerberi	18 x 17	Serpentes: colubrid (dog-faced water snake)
E. chalcides		Sauria: scincid (ocellated skink)
E. chamaeleolidisbatbati		Sauria: dactyloid (western bearded anole)
E. chelydrae	15 x 14	Testudines: chelydrid (common snapping turtle)
E. chrysemydis	23 x 15	Testudines: emydid (western painted turtle, Cagle's map turtle, common map turtle, Big Bend slider, red-eared slider)
E. cicaki		Sauria: gekkonid (common four-clawed gecko, common house gecko)
E. cnemidophori	18 x 17	Sauria: teiid (rainbow whiptail)
E. coelopeltis	11 x 6	Serpentes: colubrid (Montpellier snake)
E. collanuli	33 x 18	Serpentes: colubrid (prairie ringneck snake)
E. colonorum		Sauria: agamid (red0headed rock agama)
E. conanti	18 x 13	Serpentes: colubrid (green water snake, redbelly water snake, copperbelly water snake, Harter's water snake, Concho water snake)
E. coniophanes	29 x 15	Serpentes: colubrid (yellowbelly snake)
E. coniophis	32 x 17	Serpentes: colubrid (road guarder snake)
E. cooteri	26 x 11	Testudines: emydid (Texas River cooter)
E. crocodyli	16 x 14	Crocodilia: crocodylid (American crocodile)
E. crotalae	32 x 22	Serpentes: viperid (Gaboon viper, Cascabel rattlesnake)
E. crotalviridis	26 x 22	Serpentes: viperid (prairie rattlesnake)
E. cyclopion	19 x 13	Serpentes: colubrid (green water snake, yellow-belly water snake, broad-banded water snake, diamondback water snake)
E. cystisfelleae	33 x 21	Serpentes: colubrid (common grass snake)
E. delagei	20 x 17	Testudines: emydid (European pond turtle, eastern painted turtle)
E. delalandii		Sauria: phyllodactylid (Teneriffe wall gecko)
E. dericksoni	15 x 13	Testudines: trionychid (eastern spiny softshell turtle, western spiny softshell turtle, pallid spiny softshell turtle)
E. desotoensis	18 x 17	Serpentes: colubrid (rough earth snake, smooth earth snake)
E. dhamini	29 x 16	Serpentes: colubrid (oriental ratsnake)
E. dipasi	17	Serpentes: colubrid (slug-eating snake)
E. dixoni		Sauria: gekkonid (common house gecko)
E. drymarchoni	32 x 18	Serpentes: colubrid (indigo snake)
E. egerniae	30 x 16	Sauria: scincid (White's skink)
E. egregia		Sauria: scincid (mole skink)
E. emydis	23 x 17	Testudines: emydid (European pond turtle)
E. eremiasica		Sauria: lacertid (rapid fringe-toed lizard)
E. fasciatus		Sauria: scincid (five-lined skink)
E. fibrilosa	26 x 18	Serpentes: colubrid (rainbow water snake)
E. filamentifera	23 x 19	Testudines: chelydrid (common snapping turtle)
E. frenatus		Sauria: gekkonid (common house gecko)
E. furmani		Sauria: gekkonid (common house gecko)
E. galapagoensis		Sauria: tropidurid (hood lava lizard)
E. gallaeciaensis	19 x 16	Testudines: emydid (European pond turtle)
E. gallotiae (possibly *Choleoeimeria*)	31 x 16	Sauria: lacertid (Gallot's lizard)
E. gastrosauris		Sauria: gekkonid (northern dtella)
E. gehyrae	33 x 21	Sauria: gekkonid (variegated dtella)
E. gekkonis	19 x 14	Sauria: gekkonid (Schlegel's Japanese gecko)
E. gelasina	35 x 23	Serpentes: colubrid (dog-faced water snake)
E. geochelona	22 x 18	Testudines: testudinid (Charles Island giant tortoise)
E. ghaffari		Sauria: lacertid (Bosc's fringe-toed lizard)
E. graptemydos	13 x 11	Testudines: emydid (common map turtle, western painted turtle,

		southern painted turtle, Cagle's map turtle, Mississippi map turtle, Texas map turtle, Big Bend slider, red-eared slider); kinosternid (yellow mud turtle, Mississippi mud turtle)
E. gupti (syn. *E. cylindrical*)	36 x 18	Serpentes: colubrid (Asiatic water snake)
E. guyuanensis		Sauria: teiid (giant ameiva)
E. harlani	13 x 12	Testudines: chelydrid (alligator snapping turtle)
E. hatcheri		Crocodilia: alligatorid (American alligator)
E. helenlevineae		Sauria: gekkonid (spotted Indian house gecko)
E. helmisophis	14 x 11	Serpentes: colubrid (western worm snake, Midwest worm snake, blotched water snake, Brazo's water snake, diamondback water snake)
E. hemidactyli	18 x 15	Sauria: gekkonid (yellow-belly gecko)
E. hispidi		Sauria: tropidurid (Peters' lava lizard)
E. hobartsmithi	18 x 16	Serpentes: colubrid (rough earth snake, western earth snake)
E. hydrophis	15 x 11	Serpentes: colubrid (northern water snake, yellow-belly water snake, blotched water snake, Brazo's water snake, midland water snake, diamondback water snake)
E. hynekprokopi	16 x 9	Testudines: geoemydid (Indochinese box turtle)
E. infirmus	12	Serpentes: colubrid (diamondback water snake)
E. innominata	18 x 14	Testudines: trionychid (Indian flapshell turtle)
E. intermedia	20 x 15	Sauria: polychrotid (white anole)
E. iowaensis	18 x 16	Serpentes: colubrid (red-sided gartersnake, broad-banded water snake, wandering garter snake, northern water snake)
E. irregularis	15	Testudines: trionychid (Indian flapshell turtle)
E. iversoni	14 x 10	Testudines: testudinid (Galapagos tortoise)
E. jaboti	18 x 16	Testudines: testudinid (yellow-footed tortoise)
E. jaegeri	17	Serpentes: colubrid (Jaeger's ground snake)
E. japaluris		Sauria: agamid (Ryukyu japalura)
E. japonicus		Sauria: gekkonid (Schlegel's Japanese gecko)
E. jirkamoraveci	11 x 9	Testudines: chelid (Amazon toadhead turtle)
E. juniataensis	14 x 13	Testudines: emydid (northern map turtle)
E. kachua	15 x 14	Testudines: geoemydid (Indian tent turtle)
E. kennicotti	27 x 21	Serpentes: colubrid (prairie ringneck snake)
E. kermorganti (syn. *Coccidium*)	21	Crocodilia: gavialid (gharial)
E. knowlesi	18 x 16	Sauria: gekkonid (yellow-belly gecko)
E. koidzumii	30 x 14	Sauria: gekkonid (Schlegel's Japanese gecko)
E. koormae (syn. *E. boormae*)	15	Testudines: trionychid (Indian flapshell turtle)
E. korros	24 x 17	Serpentes: colubrid (Indo-Chinese ratsnake)
E. lacertae		Sauria: scincid (Far Eastern skink)
E. lainsoni	19 x 18	Testudines: testudinid (yellow-footed tortoise)
E. lampropeltis	30 x 16	Serpentes: colubrid (prairie kingsnake)
E. lampropeltisgetuli	38 x 21	Serpentes: colubrid (California banded kingsnake)
E. lampropholidus	20 x 15	Sauria: scincid (common garden skink)
E. lagunculata	19 x 13	Testudines: podocnemidid (Arrau turtle)
E. largeni		Sauria: chamaeleonid (graceful chameleon)
E. lecontei	28 x 16	Testudines: emydid (wood turtle)
E. legeri	17	Testudines: trionychid (Indian flapshell turtle)
E. leimadophi	17	Serpentes: colubrid (Rainha snake)
E. leiocephali		Sauria: leiocephalid (orange-bellied curly-tailed lizard, green-legged curly-tailed lizard)
E. leiolopismatis	19 x 16	Sauria: scincid (orange-tailed shadeskink)
E. leptophis	30 x 17	Serpentes: colubrid (Mexican parrot snake)
E. lineri		Sauria: gekkonid (rough-tailed gecko, tropical house gecko, Mediterranean house gecko)
E. liolaemi	21 x 20	Sauria: liolaemid (striped tree iguana)
E. liophi	13 x 12	Serpentes: colubrid (banded tricoloured snake)
E. lokuma	14 x 13	Testudines: pelomedusid (African helmeted turtle)
E. lutotestudinis	12 x 11	Testudines: kinosternid (yellow mud turtle, Mississippi mud turtle), emydid (Cagle's map turtle, common map turtle, Texas river cooter,

		red-eared slider)
E. maboia	20 x 17	Sauria: scincid (tropical house gecko)
E. mammiformis	30 x 19	Testudines: pedocnemidid (Arrau turtle)
E. marginata	22 x 18	Testudines: emydid (western painted turtle, common map turtle, eastern river cooter, Big Bend slider, red-eared slider)
E. mascoutini	14 x 12	Testudines: trionychid (spiny softshell turtle, pallid spiny softshell turtle)
E. megalostiedai	14 x 13	Testudines: emydid (wood turtle)
E. michikoa		Sauria: gekkonid (Schlegel's Japanese gecko)
E. micruri	20 x 15	Serpentes: elapid (slender coral snake)
E. mikanii	28 x 19	Serpentes: colubrid (slug-eater snake)
E. minetti	20 x 13	Sauria: scincid (long-tailed skink)
E. mirabilis	33 x 19	Sauria: anguid (European legless lizard)
E. mitraria	15 x 10	Testudines: geoemydid (Reeve's turtle, Arakan forest turtle), chelydrid (common snapping turtle), emydid (western painted turtle, Blanding's turtle, European pond turtle, northern map turtle, false map turtle, Texas map turtle, Texas River cooter, three-toed box turtle, red-eared slider), kinosternid (yellow mud turtle, Illinois mud turtle), chelid (Amazon toadhead turtle)
E. molochis	34 x 23	Sauria: agamid (thorny devil)
E. motelo	17 x 9	Testudines: testudinid (yellow-footed tortoise)
E. murphyi		Sauria: cordylid (armadillo girdled lizard)
E. najae	25 x 17	Serpentes: elapid (Indian cobra)
E. natricis	32 x 18	Serpentes: colubrid (northern water snake, yellow-belly water snake, broad-banded water snake, midland water snake, western ribbon snake)
E. navillei		Serpentes: colubrid (viperine water snake)
E. nebulosi		Sauria: varanid (clouded monitor)
E. noctisauris	35 x 23	Sauria: xantusiid (Island night lizard)
E. nyschanica		Sauria: agamid (Turkestan rock agama)
E. ondinae	21	Serpentes: colubrid (Rio tropical racer)
E. ornata	18 x 16	Testudines: emydid (ornate box turtle)
E. oxybelis	32 x 17	Serpentes: colubrid (Mexican vine snake)
E. pachybibroni		Sauria: gekkonid (Bibron's tick-toed gecko)
E. palawanensis	16	Testudines: geoemydid (Asian leaf turtle)
E. pallidus	23 x 22	Testudines: trionychid (pallid spiny softshell turtle)
E. pangshurae	17 x 13	Testudines: geoemydid (Assam roofed turtle)
E. papillosum	32 x 18	Serpentes: colubrid (Texas patch-nosed snake)
E. paraguayensis		Crocodilia: alligatorid (Yacare caiman)
E. patta	13 x 9	Testudines: geoemydid (Indian black turtle)
E. paynei	23 x 19	Testudines: testudinid (gopher tortoise)
E. pellopleuris		Sauria: scincid (Ryukyu short-legged skink)
E. peltocephali	54 x 19	Testudines: podocnemidid (big-headed Amazon River turtle)
E. perazae		Sauria: teiid (rainbow whiptail)
E. persica	29 x 16	Serpentes: colubrid (Balkan grass snake)
E. petrasi	23 x 19	Testudines: geoemydid (Asian leaf turtle)
E. phelsumae		Sauria: gekkonid (Madagascar day gecko)
E. phisalixae	40 x 20	Serpentes: viperid (horned desert viper)
E. pintoi	32 x 21	Crocodilia: alligatorid (alligator)
E. piscatori	30 x 23	Serpentes: colubrid (checkered keelback)
E. pleistocenensis	28 x 19	Serpentes: colubrid (Florida crowned snake)
E. podocnemis	17 x 13	Testudines: podocnemidid (Arrau turtle)
E. poecilogyri	15	Serpentes: colubrid (Rainha snake)
E. polydaedali		Sauria: varanid (Nile monitor)
E. pseudemydis	19 x 18	Testudines: emydid (ornate slider, red-eared slider, western chicken turtle, wood turtle, Texas River cooter, Big Bend slider)
E. pseudogeographica	20 x 14	Testudines: emydid (false map turtle, western painted turtle, Cagle's map turtle, Ouachita map turtle, Big Bend slider, red-eared slider)
E. ptyas	35 x 25	Serpentes: colubrid (oriental rat snake)
E. pythonis	28 x 17	Serpentes: boid (Indian rock python, African rock python)
E. rabiti		Sauria: gekkonid (leopard gecko?)
E. raillieti	18 x 15	Sauria: anguid (slowworm)

E. rangei		Sauria: gekkonid (Namib sand gecko)
E. rhombifera	13	Serpentes: colubrid (green water snake, diamondback water snake)
E. rimahensis		Sauria: varanid (desert monitor)
E. rochalimai	31 x 17	Sauria: gekkonid (Moreau's tropical house gecko)
E. rountreei		Sauria: lacertid (Japanese grass lizard)
E. sami		Sauria: scincid (Ousima skink)
E. samyadeli (syn. *E. samiae nomen preoccupied*)	45	Serpentes: boid (reticulated python)
E. sanctaluciae	17	Sauria: dactyloid (St Lucia anole)
E. scaphiodontophis	30 x 15	Serpentes: colubrid (Guatemala neckband snake)
E. sceloporis	27 x 22	Sauria: phrynosomatid (Clark's spiny lizard, desert spiny lizard, western fence lizard)
E. schmidti		Sauria: lacertid (Schmidt's fringe-fingered lizard)
E. schwartzi		Sauria: dactyloid (armoured anole)
E. scincellae		Sauria: scincid (little brown skink)
E. scinci	33 x 19	Sauria: scincid (sandfish skink)
E. scriptae	24 x 14	Testudines: emydid (red-eared slider)
E. septemvittata	15 x 14	Serpentes: colubrid (queen snake)
E. serpenticola	20 x 18	Serpentes: colubrid (redstripe ribbon snake, broad-banded water snake, midland water snake, western ribbon snake, checkered garter snake)
E. serpentina	13 x 8	Testudines: chelydrid (common snapping turtle)
E. sexlineatus		Sauria: teiid (six-lined racerunner)
E. sibon	24 x 14	Serpentes: colubrid (cloudy snail-eating snake)
E. simonkingi		Saura: gekkonid (Smith's green-eyed gecko, lined gecko, lined day gecko)
E. sinaitae		Sauria: agamid (Sinai agama)
E. sipedon	18 x 16	Serpentes: colubrid (northern water snake, blotched water snake, yellow-belly water snake, broad-banded water snake, midland water snake)
E. somervellensis	21 x 16	Testudines: emydid (Texas River cooter, Missouri River cooter)
E. spinfera	16 x 14	Testudines: trionychid (pallid spiny softshell turtle)
E. stenocerci (syn. *E. tropidura*)	26 x 20	Sauria: tropidurid (Amazon lava lizard)
E. stenodactyli		Sauria: gekkonid (elegant gecko)
E. sternfeldi		Sauria: scincid (Centralian blue-tongued skink)
E. stolatae	20	Serpentes: colubrid (buff striped keelback)
E. striatula	13	Serpentes: colubrid (rough earth snake)
E. stylosa	17 x 13	Testudines: emydid (red-eared slider, Big Bend slider)
E. subcylindrica		Sauria: teiid (giant ameiva)
E. surinensis	23 x 21	Testudines: geoemydid (Mekong snail-eating turtle)
E. takydromi	28 x 16	Sauria: lacertid (six-striped long-tailed lizard, green grass lizard, Japanese grass lizard)
E. tarentolae		Sauria: gekkonid (Moorish wall gecko)
E. telfordi		Sauria: gekkonid (common four-clawed gecko)
E. tenuis	17 x 11	Serpentes: colubrid (redbelly water snake, diamond-backed water snake, common water snake)
E. tetradacrutata	20 x 19	Testudines: emydid (western painted turtle, common map turtle, red-eared slider)
E. texana	21 x 8	Testudines: emydid (Texas River cooter)
E. tilburyi		Sauria: chamaeleonid (Jackson's chameleon)
E. tokayae		Sauria: gekkonid (Tokay gecko)
E. trachemydis	25 x 14	Testudines: emydid (red-eared slider, western painted turtle, Cagle's map turtle, Big Bend slider)
E. triangularis	13	Testudines: trionychid (Ganges softshell turtle)
E. trionyxae	17	Testudines: trionychid (Ganges softshell turtle)
E. tropidonoti	23 x 14	Serpentes: colubrid (common grass snake)
E. turcicus		Sauria: gekkonid (Mediterranean house gecko)
E. typhlopisi	29 x 20	Serpentes: typhlophid (European blind snake)
E. umis	33 x 19	Sauria: phrynosomatid (Colorado desert fringe-toed lizard)
E. urosauris	32 x 20	Sauria: phrynosomatid (long-tailed brush lizard)

E. varani	19 x 13	Sauria: varanid (monitor)
E. vesicostieda	23 x 19	Testudines: trionychid (eastern spiny softshell turtle, western spiny softshell turtle)
E. vittati		Sauria: gekkonid (lined gecko)
E. welcomei	30 x 16	Testudines: testudinid (red-footed tortoise)
E. witcheri		Sauria: amphisbaenid (Mann's worm lizard)
E. zbatagura	7 x 6	Testudines: geoemydid (northern river terrapin)
E. zamenis	29 x 17	Serpentes: colubrid (eastern blue racer, prairie king snake, speckled king snake, eastern milk snake, eastern coachwhip)
E. zulphinensis		Sauria: varanid (desert monitor)
Amphibia		
E. algonquini	16	Anura: ranid (American bullfrog, green frog, mink frog, wood frog)
E. ambystomae	31 x 18	Urodela: ambystomatid (tiger salamander, seal salamander, blackbelly salamander)
E. belawini	12	Anura: hylid (European tree frog)
E. bufomarini	9	Anura: bufonid (cane toad)
E. canaliculata	39 x 23	Urodela: salamandrid (alpine newt, northern crested newt, palmate newt, smooth newt)
E. cyanophlyctis	18 x 16	Anura: dicroglossid (skittering frog)
E. dermophis	20 x 18	Gymnophiona: dermophiid (Mexican burrowing caecilian)
E. distorta	30 x 16	Urodela: ambystomatid (tiger salamander)
E. fitchi	22 x 14	Anura: ranid (wood frog)
E. flexuosa	17	Anura: hylid (Strecker's chorus frog)
E. fragilis	19 x 15	Anura: rhacophorid (central foam-nest tree frog)
E. grobbeni	11 x 10	Urodela: salamandrid (alpine salamander)
E. himalayana	9	Anura: bufonid (Himalayan toad)
E. kermiti	25 x 20	Anura: ranid (American bullfrog, green frog, mink frog, wood frog)
E. kingi	20 x 18	Urodela: ambystomatid (tiger salamander)
E. labbei	nd	Urodela: salamandrid (great crested newt)
E. laminata	10	Anura: bufonid (black-spined toad)
E. leptodactyli	23 x 17	Anura: leptodactylid (criolla frog)
E. longaspora	28	Urodela: salamandrid (eastern newt)
E. mazzai (syn. *E. transcaucasica*)	17	Anura: bufonid (common toad)
E. megaresidua	43 x 33	Urodela: salamandrid (eastern newt)
E. microcapi	38 x 25	Urodela: ambystomatid (barred tiger salamander)
E. neglecta	10	Anura: ranid (edible frog, common frog)
E. nipponensis	50 x 35	Urodela: salamandrid (Japanese firebelly newt)
E. opacum	17 x 12	Urodela: ambystomatid (marbled salamander)
E. prevoti	21 x 14	Anura: ranid (edible frog)
E. propria	40 x 24	Urodela: salamandrid (alpine salamander, alpine newt, warty newt, palmate newt, marbled newt, smooth newt)
E. pyrrogaster	43 x 40	Urodela: salamandrid (Japanese firebelly newt)
E. ranae	20	Anura: ranid (edible frog, common frog)
E. ranarum	19 x 14	Anura: ranid (edible frog, common frog)
E. saitamaensis	25	Urodela: salamandrid (Japanese firebelly newt)
E. salamandrae	24	Urodela: salamandrid (fire salamander)
E. salamandraeatrae (*species inquirenda*)	27 x 23	Urodela: salamandrid (alpine salamander)
E. spherica	35	Urodela: salamandrid (alpine newt, northern crested newt, palmate newt, smooth newt, sword-tail newt)
E. streckeri	19	Anura: hylid (Strecker's chorus frog, western chorus frog)
E. tarichae	12 x 11	Urodela: salamandrid (orange-bellied newt)
E. terraepokotorum	20 x 16	Anura: dicroglossid (African tigrine frog)
E. tertia	26 x 21	Urodela: salamandrid (alpine newt, northern crested newt)
E. urodela	22	Urodela: ambystomatid (tiger salamander, barred tiger salamander)
E. waltoni	22 x 19	Urodela: ambystomatid (tiger salamander)
E. wambaensis	17 x 13	Anura: hyperoliid (common reed frog)
Bony fish		
E. acerinae	11	freshwater Perciformes: percid (Eurasian ruffe)
E. adioryxi	9.7	marine Beryciformes: holocentrid (red soldierfish)

E. ambassi		freshwater Cypriniformes: cyprinid (barb)
E. amudarinica	26	freshwater Cypriniformes: cyprinid (topmouth gudgeon, Chinese lake gudgeon)
E. amurensis	24	freshwater Cypriniformes: cyprinid (topmouth gudgeon, common rudd)
E. aristichthysi	12	freshwater Cypriniformes: cyprinid (bighead carp, silver carp)
E. ashburneri	7.7-9.2	freshwater Perciformes: percichthyid (golden perch); marine Spariformes: sparid (red pandora, blue-spotted seabream)
E. atherinae	11.5-13.5	euryhaline amphidromous Atheriniformes: atherinid (big-scale sand smelt)
E. banyulensis	6.5-8.5	marine Labriformes: labrid (axillary wrasse, grey wrasse)
E. barbi	24 x 21	freshwater Cypriniformes: cyprinid (Bulatmai barbel)
E. baueri	19 x 16	freshwater Cypriniformes: cyprinid (Crucian carp)
E. bouixi	6.0-7.6	marine Perciformes: moronid (European sea bass)
E. branchyphila	23 x 9	freshwater Cypriniformes: cyprinid (roach)
E. brevoortiana	17-30 x 15-22	marine Clupeiformes: clupeid (menhaden)
E. capoetobramae		freshwater Cypriniformes: cyprinid (sharpray)
E. carassii	22	freshwater Cypriniformes: cyprinid (Crucian carp)
E. carassiusaurati	14	freshwater Cypriniformes: cyprinid (goldfish)
E. catalana		marine Labriformes: labrid (axillary wrasse, grey wrasse, blackbar hogfish), scarid (Guinean parrotfish))
E. catostomi	7	freshwater Cypriniformes: catostomid (white sucker)
E. cheilodactyli	10.5-11.5	marine Perciformes: latrid (red morwong)
E. cheissini	20	freshwater Cypriniformes: cyprinid (gudgeon, sharpbelly, barbel steed)
E. chenchingensis	23 x 13	freshwater Cypriniformes: cyprinid (goldfish)
E. ciliatae	13.4-14.2	marine Perciformes: sillaginid (sand whiting)
E. citriformis	15	marine Scorpaeniformes: agonid (poacher)
E. clini	16 x 13	marine Perciformes: clinid (highfin klipfish)
E. cobitis	20	freshwater Cypriniformes: cobitidid (spined loach)
E. coreia	11	freshwater Cypriniformes: cyprinid (bronze gudgeon)
E. cotti	11	freshwater Scorpaeniformes: cottid (European bullhead, slimy sculpin)
E. credintsi	13	freshwater Gobiiformes: gobiid (tubenose goby)
E. ctenopharyngodoni	25	freshwater Cypriniformes: cyprinid (grass carp)
E. culteri	10	freshwater Cypriniformes: cyprinid (predatory carp)
E. cylindrospora	11	freshwater Cypriniformes: cyprinid (common bleak)
E. cyprini	9	freshwater Cypriniformes: cyprinid (Crucian carp, European carp, tench)
E. cyprinorum	13	freshwater Cypriniformes: cyprinid (common bream, common barbel, roach, Eurasian minnow, common minnow, common rudd)
E. dakarensis	11.4	marine Perciformes: serranid (blue-spotted seabass, blacktip grouper)
E. daviesae	13	freshwater Gobiiformes: gobiid (bighead goby, monkey goby)
E. degiustii	21	freshwater Cypriniformes: cyprinid (common shiner, bluntnose minnow, fathead minnow)
E. dicentrarchi	10.6-12.2	marine Perciformes: moronid (European bass)
E. dingleyi	16.1-20 x 13.9-19.2	marine Perciformes: blenniid (shanny)
E. dogieli (syn. *E. sphaerica*)	5	marine Perciformes: stichaeid (ocellated blenny)
E. duszynskii	12	freshwater Scorpaeniformes: cottid (mottled sculpin)
E. dykovae	7.2-8.4	marine Perciformes: latrid (red morwong)
E. eiminens (eminens)	15	catadromous Anguilliformes: anguillid (Japanese eel)
E. esoci	13 x 11	freshwater Esociformes: esocid (northern pike), Perciformes: centrarchid (pumpkinseed)
E. etheostomae		freshwater Perciformes: percid (Iowa darter, Johnny darter)
E. ethmalosae	22-53	freshwater Clupeiformes: clupeid (bonga shad)
E. etrumei	33-36	marine Clupeiformes: dussumierid (round-herring)
E. evaginata	10-12	marine Scorpaeniformes: sebastid (white-edged rockfish), cottid (Steller's sculpin)
E. fernandoae	8 x 7	freshwater Cypriniformes: catostomid (white sucker, northern hogsucker)
E. fluviatili	20-22.5	freshwater Perciformes: percid (European perch)
E. gabonensis	9.6	marine Scorpaeniformes: triglid (Gabon gurnard)

E. glenorensis	11	freshwater Perciformes: moronid (white perch)
E. glossogobii	11 x 10	freshwater Perciformes: gobiid (tank goby)
E. gobii	18 x 14	marine Perciformes: gobiid (barehead goby)
E. haichengensis	8	freshwater Cypriniformes: cyprinid (European carp)
E. haneki	7	freshwater Gasterosteiformes: gasterosteid (brook stickleback)
E. harpodoni	12-16	freshwater Aulopiformes: synodontid (bummalo)
E. hemibarba	10	freshwater Cypriniformes: cyprinid (spotted steed)
E. hemiculterii	11	freshwater Cypriniformes: cyprinid (sharpbelly)
E. hexagona	12	marine Gadiformes: lotid (shore rockling)
E. hoffmani	12 x 9	freshwater Esociformes: umbrid (central mudminnow)
E. huizhouensis	12	freshwater Siluriformes: clariid (Hong Kong catfish)
E. hunggangensis	38	freshwater Cypriniformes: cobitidid (pond loach)
E. hupehensis	10	freshwater Cypriniformes: cyprinid (goldfish)
E. hybognathi	14	freshwater Cypriniformes: cyprinid (brassy minnow)
E. hypophthalmichthys	24 x 21	freshwater Cypriniformes: cyprinid (silver carp)
E. ictaluri	10	freshwater Siluriformes: ictalurid (brown bullhead)
E. insignis	10-13	marine Scorpaeniformes: scorpaenid (small red scorpionfish)
E. iroquoina	10	freshwater Cypriniformes: cyprinid (common shiner), plus experimental infections in cyprinid (fathead minnow)
E. ivanae	10-11.5	marine Perciformes: serranid (comber, painted comber)
E. jadvigae		marine Gadiformes: macrourid (whiptail, bigeye grenadier)
E. kassaii	12	freshwater Esociformes: umbrid (European mudminnow)
E. kotorensis	13-14.5	marine Perciformes: centracanthid (blotched picarel)
E. kwangtungensis	10	freshwater Perciformes: channid (northern snakehead, blotched snakehead)
E. lairdi	10-15	marine Scorpaeniformes: cottid (shorthorn sculpin)
E. laureleus (syn. *Goussia*)	12	freshwater Perciformes: percid (yellow perch), centrarchid (pumpkinseed)
E. liaohoensis	27	freshwater Cypriniformes: cyprinid (goldfish)
E. liaoningensis	8	freshwater Cypriniformes: cyprinid (Chinese false gudgeon, goldfish)
E. liuhaoensis	25 x 22	freshwater Cypriniformes: cyprinid (bighead carp, silver carp)
E. lydiae	12	freshwater Salmoniformes: salmonid (brown trout)
E. macoresidualis	14	freshwater Cypriniformes: cyprinid (white-finned gudgeon)
E. macropoda	10	freshwater Anabantiformes: osphronemid (paradise fish)
E. maggieae	12	marine Perciformes: sparid (common pandora)
E. marmorata	10	marine Perciformes: gobiid (tubenose goby)
E. matskasii	11	freshwater Esociformes: umbrid (European mudminnow)
E. merlangi		marine Gadiformes: gadid (whiting)
E. meszarosi	11	freshwater Esociformes: umbrid (European mudminnow)
E. micropteri	12	freshwater Perciformes: centrarchid (smallmouth bass, largemouth bass)
E. misgurni	15	freshwater Cypriniformes: cobitidid (European weather loach, spined loach)
E. molnari	19 x 12	freshwater Cypriniformes: cyprinid (gudgeon)
E. moronei	8	freshwater Perciformes: moronid (white perch)
E. muraiae	47 x 36	freshwater Cypriniformes: cobitidid (European weather loach)
E. myoxocephali	34-40	marine Scorpaeniformes: cottid (great sculpin)
E. nemethi	18 x 13	freshwater Cypriniformes: cyprinid (common bleak)
E. nesowai	12-14	marine Perciformes: gerreid (common silver belly)
E. newchongensis	18	freshwater Cypriniformes: cyprinid (goldfish, predatory carp)
E. nicollei	26 x 16	freshwater Cypriniformes: cyprinid (crucian carp)
E. nishin	48	marine Clupeiformes: clupeid (Atlantic herring, Pacific herring)
E. notopteri	24 x 22	freshwater Osteoglossiformes: notopterid (bronze featherback, Indian featherback)
E. nucleocola	12-14	marine Scorpaeniformes: cottid (shorthorn sculpin)
E. ochetobiusi	8	freshwater Cypriniformes: cyprinid (sale niglask)
E. odontobutis	14	freshwater Gobiiformes: odontobutid (dark sleeper)
E. ojibwana	11	freshwater Scorpaeniformes: cottid (mottled sculpin)
E. ophiocephali	9	freshwater Anabantiformes: channid (snakehead, blotched snakehead)
E. orientalis	30	freshwater Cypriniformes: cobitid (Amur weatherfish)
E. osmeri	11	freshwater Osmeriformes: osmerid (rainbow smelt)

E. parasiluri	10	freshwater Siluriformes: silurid (Amur catfish)
E. pastuszkoi	14 x 12	freshwater Cypriniformes: nemacheilid (stone loach)
E. patagonensis	43-44.1	marine Clupeiformes: engraulid (Argentine anchovy)
E. patersoni	12 x 11	freshwater Perciformes: centrarchid (pumpkinseed)
E. percae	13	freshwater Perciformes: percid (redfin perch)
E. perciformis	9.7	marine Perciformes: haemulid (bastard grunt), serranid (Dungat grouper)
E. petrovici	11-12.5	marine Perciformes: labrid (ocellated wrasse)
E. philypnodoni	8.4-9.2	freshwater Gobiiformes: eleotrid (bighead gudgeon)
E. phyllopterycis (syn. *E. phyllopteryx*)	28-34.4	marine Syngnathiformes: syngnathid (common seadragon)
E. piraudi	12	freshwater Scorpaeniformes: cottid (European bullhead)
E. pleurostici	9.1-9.6	marine Tetraodontiformes: tetraodontid (toadfish)
E. pneumatophori	12.5-13	marine Scombriformes: scombrid (chub mackerel)
E. pseudorasbori	26	freshwater Cypriniformes: cyprinid (stone moroko)
E. pungitii	13 x 10	freshwater Gasterosteiformes: gasterosteid (ninespine stickleback)
E. quadricornis	16	marine Scorpaeniformes: cottid (fourhorn sculpin)
E. quentini		marine Myliobatiformes: myliobatid (spotted eagle ray)
E. radae	27 x 24	freshwater Cypriniformes: cyprinid (spined loach)
E. raibauti	30-40 x 29-35	marine Gadiformes: gadid (poor cod, Norway pout)
E. rivieri	14 x 9	freshwater Perciformes: percid (redfin perch)
E. rohdei	7-8.5	marine Tetraodontiformes: monacanthid (fan-bellied leatherjacket)
E. roussillona	10-12	marine Perciformes: labrid (brown wrasse)
E. rouxi	10	freshwater Cypriniformes: cyprinid (tench)
E. rutili	29 x 11	freshwater Cypriniformes: cyprinid (roach)
E. ryptici	8.1	marine Perciformes: serranid (spotted soapfish)
E. salvelini	12	freshwater Salmoniformes: salmonid (brown trout)
E. sardinae (syn. *E. oxyphila, oxyspora, snijdersi, Coccidium*)	33-65	marine Clupeiformes: clupeid (Atlantic herring, European pilchard, South American pilchard, round sardinella, Madeiran sardinella, European anchovy, European sprat)
E. saurogobii	9	freshwater Cypriniformes: cyprinid (grass carp)
E. schizothoraci		freshwater Cypriniformes: cyprinid (Sattar snowtrout)
E. schulmani	20	freshwater Cypriniformes: cyprinid (common chub)
E. scorpaenae	11	marine Scorpaeniformes: scorpaenid (black scorpionfish)
E. sericei (syn. *E. rhodei*)	19	freshwater Cypriniformes: cyprinid (Amur bitterling)
E. siliculiformis (syn. *Goussia*)	27 x 14	freshwater Cypriniformes: cyprinid (common bream, common bleak, common roach, common rudd, gudgeon, long-snouted Amur gudgeon)
E. stankovitchi (syn. *Goussia*)	10	freshwater Cypriniformes: cyprinid (common bream, common bleak, asp, Pacific redfin, common rudd)
E. sillaginis	8-9.5	marine Perciformes: sillaginid (sand whiting)
E. siluri	26 x 22	freshwater Siluriformes: silurid (wels catfish)
E. smaris (syn. *E. maenae*)	8-9.5	marine Perciformes: sparid (picarel)
E. soufiae (syn. *E. sontlae*)	18	freshwater Cypriniformes: cyprinid (western vairone)
E. sourogobii		freshwater Cypriniformes: cyprinid (Chinese lizard gudgeon)
E. stizostedioni	11 x 8	freshwater Perciformes: percid (zander)
E. strelkovi	16	freshwater Cypriniformes: cyprinid (stone moroko)
E. syacii	10.7	marine Pleuronectiformes: paralichthyid (Channel flounder)
E. symphodi	16-19	marine Perciformes: labrid (pointed-snout wrasse)
E. syngnathi	24.5-32 x 16.7-24.5	marine Syngnathiformes: syngnathid (black-striped pipefish)
E. syrdarinica	25	freshwater Cypriniformes: cyprinid (grass carp)
E. tedlai	10	freshwater Perciformes: percid (yellow perch)
E. triglae	9.8-19.5	marine Scorpaeniformes: triglid (tub gurnard, piper gurnard)
E. variabilis (syn. *Goussia, Coccidium*)	11.9-14.6 x 9.2-11.9	marine Scorpaeniformes: cottid (lonspined bullhead); Anguilliformes: anguillid (European eel); Perciformes: labrid (corkwing wrasse); Gobiiformes: gobiid (rock goby)
E. varicorhini		freshwater Cypriniformes: cyprinid (Caucasian scraper)
E. wierzejski	12	freshwater Cypriniformes: cyprinid (European carp)

Cartilaginous fish		
E. chollaensis	11.2-16 x 8-10.8	marine Myliobatiformes: urotrygonid (round stingray)
E. euzeti	12.5-14	marine Myliobatiformes: myliobatid (common eagle ray)
E. gigantea (syn. *Pfeifferia, Pfeifferella, Coccidium*)	70 x 40	marine Carcharhiniformes: scyliorhinid (porbeagle)
E. halleri	15-18	marine Myliobatiformes: urotrygonid (round stingray)
E. kayarensis	16.7 x 13.9	marine Rajiformes: rajid (brown ray)
E. ottojiroveci	12-13	marine Rajiformes: rajid (thornback skate, brown ray)
E. palavensis	12-14.4	marine Carcharhiniformes: pentanchid (blackmouth catshark)
E. raiarum (syn. *E. rajarum*)	17.5-28	marine Rajiformes: rajid (blue skate)
E. scylii	*nomen nudum*	marine Carcharhiniformes: scyliorhinid (catshark)
E. southwelli (syn. *E. quentini*)	15-63 x 10-15	marine Rajiformes: aetobatid (white-spotted eagle ray), rhinopterid (cownose ray)
E. zygaenae	12.1-14.3	marine Carcharhiniformes: sphyrnid (winghead shark)
Invertebrates		
E. beauchampi	*nomen nudum*	Hemichordata: ptychoderid (acorn worm)
E. ekdysios	30 x 18	Diplopoda: julid (black millipede)
E. epidermica	*nomen nudum*	Hemichordata: ptychoderid (acorn worm)
E. hagenmuelleri	17 x 14	Chilopoda: himantariid (centipede)
E. hirsuta	25	Coleoptera: gyrinid (whirligig beetle)
E. hyalinum	16	Coleoptera (unspecified beetle)
E. lacazei	38 x 32	Chilopoda: lithobiid (centipedes)
E. mecistophori	nr	Chilopoda: mecistocephalid (centipede)
E. perichaetae	*nomen nudum*	Oligochaeta: megascolecid (earthworms)
E. pfeifferi	nr	Chilopoda: geophilid (centipede)
E. schaudinniana (syn. *E. schubergi*)	19	Chilopoda: lithobiid (centipede)
E. simondi	24	Chilopoda: himantariid (centipede), lithobiid (centipedes)

Parasite morphology: Coccidian parasites form three developmental stages: meronts (schizonts), gamonts and oocysts. Meronts range in size depending on parasite species, location in the host and stage of maturity. They begin as small basophilic rounded cells (mother meronts) located intracellularly within host cells. The meronts form numerous daughter merozoites by endogenous division of the nucleus followed by cytokinesis. Mature meronts appear as membrane-bound clusters of small basophilic bodies (similar to bunches of grapes). Individual meronts usually range in diameter from 10-100 µm but some species form enormous megalo-schizonts (up to 1 mm in diameter). Gamonts exhibit sexual differentiation, with microgamonts (male) apparent as multinucleate basophilic stages ultimately shedding small biflagellated microgametes; and macrogamonts (female) evident as uninucleate eosinophilic cells with a single ovoid nucleus. Developing oocysts contain numerous eosinophilic wall-forming bodies which give rise to the tough outer oocyst walls. Unsporulated oocysts contain a developing sporoblast which eventually undergoes sporulation forming sporocysts which contain the infective sporozoites. *Eimeria* oocysts exhibit a characteristic 1:4:2 configuration, that is, each oocyst contains 4 sporocysts each containing 2 sporozoites. Oocysts are generally ovoid to ellipsoid in shape, range from 10-40 µm in length by 10-30 µm in width, and vary in their possession of specialized structures, such as oocyst spines, projections, micropyles, micropyle caps, residua, polar granules, sporocyst sporopodia, ridges, sutures, residua, Stieda bodies, sub-Stieda or para-Stieda bodies, sporozoite refractile bodies and striations.

Site of infection: Most species undergo endogenous development in the intestinal mucosa (small and/or large intestines) whereas some species develop in the liver, gall bladder or kidneys. They generally exhibit rigid tissue tropism, infecting host cells in particular locations. The parasites undergo several cycles of schizogony culminating in the lysis of host cells to release numerous merozoites (often 30 or more per generation). Ultimately, gamonts are formed which mature to produce micro- and macro-gametes that undergo fertilization forming a non-motile zygote (oocyst) which is excreted with host faeces.

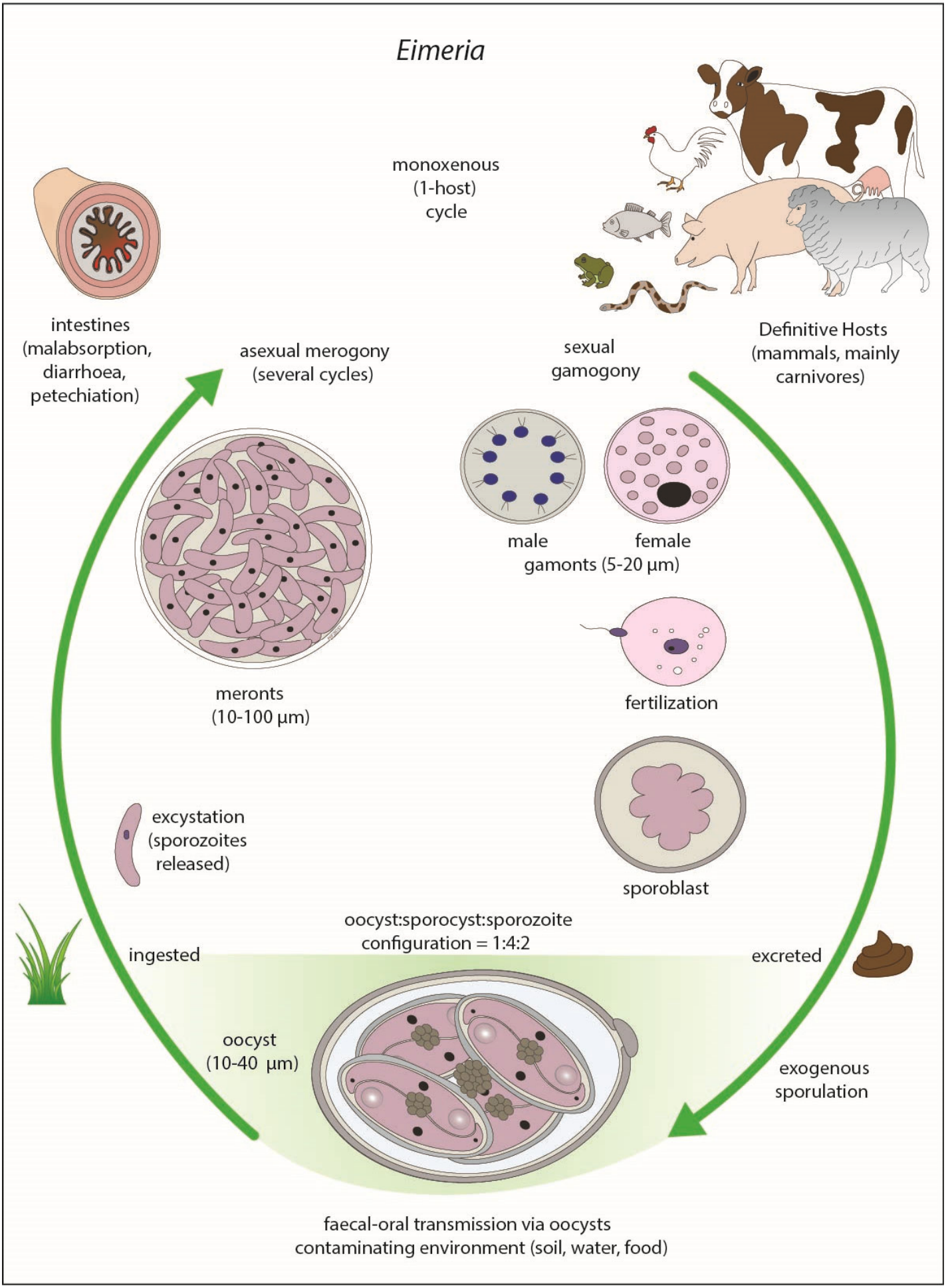
Pathogenesis: Most species are not significant pathogens and cause little or no disease. Certain species, however, are highly pathogenic and cause catarrhal or haemorrhagic enteritis by severe erosion of the mucosal membranes through cell lysis resulting in profuse watery-to-bloody diarrhoea. Clinical disease is not usually manifest until cumulative tissue damage occurs; often associated with second or third generation merogony (parasite pathogenicity is often directly related to the species proliferative potential). Moderately-affected animals may show progressive signs such as poor weight gain or weight loss, weakness and emaciation, while severely-affected individuals may die soon after the appearance of disease. Pathogenicity depends on many factors; such as parasite species, viability, infectivity, virulence, tropism, host age, nutritional status, immunological competence, as well as prevailing

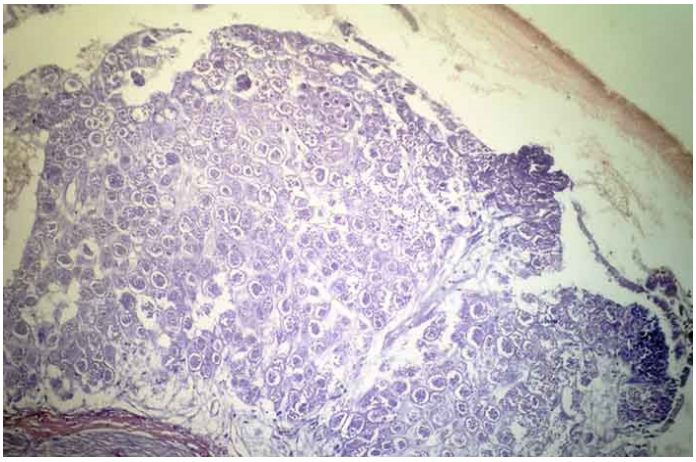
environmental conditions (temperature, moisture) and management practices. Young animals are most susceptible to clinical disease, although survivors develop strong specific protective immunity against subsequent infection and disease.

Developmental cycle and mode of transmission: Oocysts excreted with host faeces contaminate the external environment, but they must undergo internal sporulation (sporozoite formation) before they become infective (usually takes several days). New hosts are infected when they ingest sporulated oocysts contaminating food or water supplies (faecal-oral transmission). Following ingestion, oocysts and sporocysts excyst in the intestines releasing their contained sporozoites which invade host cells to begin merogony. Excystation stimuli include appropriate post-gastric physico-chemical conditions, such as oxygen levels, pH, bile salts, pancreatic enzymes, etc. The parasites undergo 2-3 successive generations of merogony before forming male and female gametes which fertilize to form oocysts subsequently voided with host faeces.

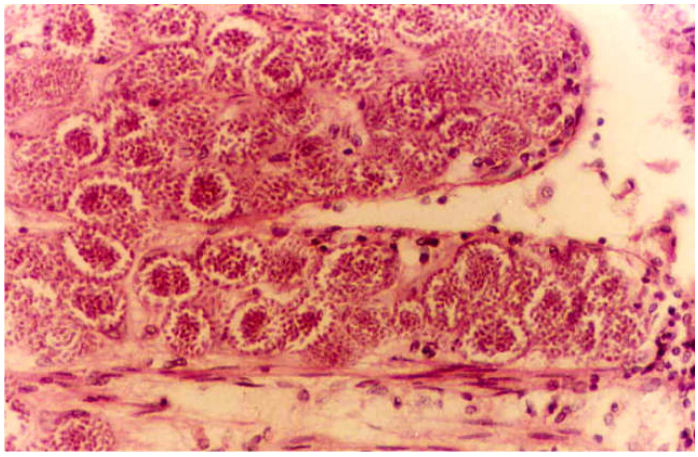
Differential diagnosis: Clinical signs usually coincide with parasite patency (patent period = period during which oocysts are produced). Infections are usually diagnosed by the coprological examination of host faeces for coccidial oocysts (concentrated using various sedimentation-flotation techniques). Unstained oocysts are best observed by light microscopy using suboptimal transmitted illumination (condenser wound down to introduce diffraction), phase-contrast or interference-contrast optics. Fresh faecal samples may only contain unsporulated oocysts so differential specific diagnosis may sometime require short-term storage to facilitate sporulation (2% potassium dichromate is often used to suppress microflora during storage, but not for piscine species, and refrigeration can slow the process down if required for field samples). In the event of fatalities, autopsy may reveal blood in the lumen of the intestines, small white foci in inflamed gut tissues and numerous endogenous developmental stages in mucosal scrapings. Researchers have recently used a range of molecular techniques to characterize genetic variation between and within parasite species, but few techniques are suitable for routine diagnostic use.

Treatment and control: Disease progression is usually so rapid that any therapeutic (curative) treatment may simply be too late. For this reason, continuous in-food or in-water medication is often used for prophylactic (preventative) treatment in many intensive animal industries. A wide range of drugs are available, including those with coccidio-static (reversible suppressive) activity or coccidio-cidal (irreversible lethal) activity. The main drug groups include sulfonamides (sulfanilamide, trimethoprim, ethopabate), pyridinoles (clopidol, decoquinate), nitrobenzamides (zoalene), organic arsenicals (roxarsone), nitrofurans (furazolidone, amprolium), quinazolinones (halofuginone), polyether ionophorous antibiotics (monensin, laslocid, salinomycin, narasin), asymmetric (diclazuril) and symmetric (toltrazuril) triazines. Regrettably, there are mounting problems being encountered with drug resistance amongst many coccidian species, especially that against synthetic drugs which tends to persist within parasite populations. Many industries recommend periodic rotation between different drug groups and the use of combination (cocktail) drugs to minimize the occurrence of resistance. Most coccidial infections stimulate the development of strong protective immune responses, albeit transient unless premunitive (short-lived unless parasites persist). There has been considerable success with control through immunoprophylaxis using attenuated or precocious strains of parasites, particularly in the poultry industry. Researchers are now attempting to develop recombinant subcellular vaccines. Outbreaks can generally be controlled by management practices based around improving hygiene, proper sanitation, reducing crowding, removing contaminated litter, isolating infected individuals, pasture rotation, cleaning water and feed troughs and preventing their contamination with faecal material. Chemical disinfection is usually impractical as the oocysts are resistant to many conventional disinfectants.

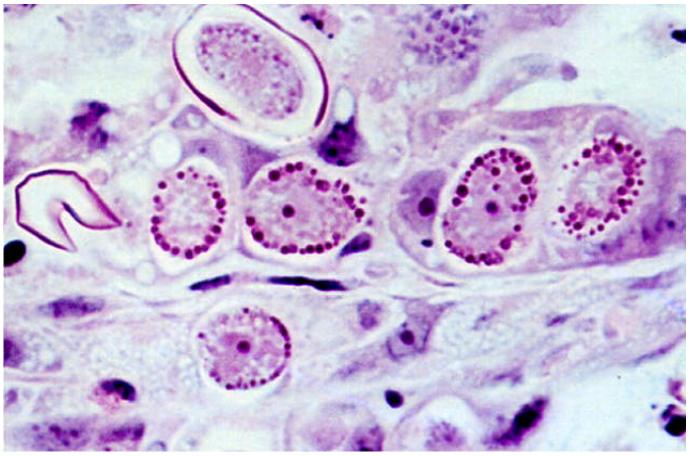

Eimeria
monoxenous
(1-host)
cycle
intestines
(malabsorption,
diarrhoea,
petechiation)
Definitive Hosts
(mammals, mainly
carnivores)
asexual merogony
(several cycles)
sexual
gamogony
male
female
gamonts (5-20 µm)
meronts
(10-100 µm)
fertilization
sporoblast
excystation
(sporozoites
released)
oocyst:sporocyst:sporozoite
configuration = 1:4:2
ingested
excreted
oocyst
(10-40 µm)
exogenous
sporulation
faecal-oral transmission via oocysts
contaminating environment (soil, water, food)



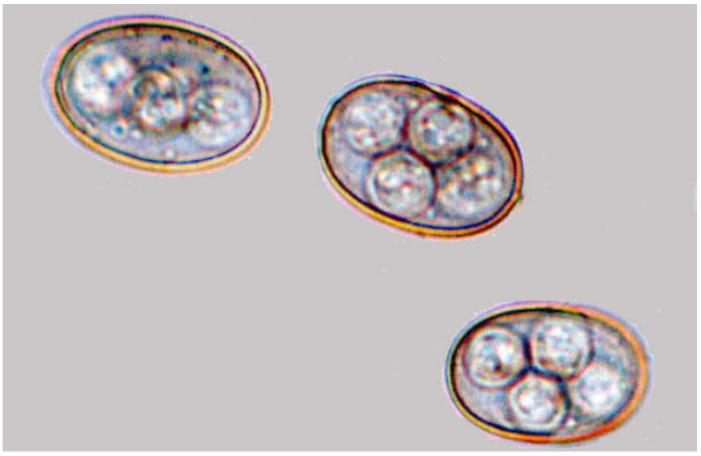
Eimeria endogenous development in kangaroo gut



Eimeria schizonts in kangaroo gut



Eimeria gamonts in sheep gut



Eimeria oocysts from faeces



Eimeria oocyst from bird faeces



Eimeria oocyst from gecko faeces

Goussia (fish coccidia)
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile environmentally-resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). The enteric coccidia are monoxenous (one-host) parasites in the digestive tracts of vertebrates. They undergo three sequential developmental stages: endogenous multiplication by asexual merogony (alternatively known as schizogony) followed by sexual gamogony (male microgametes fertilize female macrogametes) producing oocysts which are excreted and undergo asexual sporogony (forming sporocysts containing infective sporozoites). Many genera are recognized on the basis of oocyst configuration (the number of sporocysts per oocyst, and the number of sporozoites per sporocyst). Eimeriid oocysts typically contain four sporocysts each with two sporozoites (1:4:2 configuration). Infections are prevalent in birds (esp. fowl), reptiles (snakes and lizards), mammals (esp. ruminants) and fish. Many species in several genera (esp. *Goussia*) have been associated with clinical disease (coccidiosis) in fish characterized by gastrointestinal disturbances and extraintestinal tissue lesions.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Eimeriorina (no syzygy, many microgametes)
Family:	Eimeriidae (monoxenous, endogenous intracellular merogony and gamogony, exogenous sporogony)
Genus:	*Goussia* (parasitic in the intestinal mucosa of fish)
Species:	various species cause coccidiosis in fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors);

and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Numerous species of coccidia have been described from a wide range of vertebrate and invertebrate hosts. Some 50 genera have been classified in 11 families in the suborder Eimeriorina, including 21 genera in the family Eimeriidae and 3 genera in the family Barrouxiidae. Most genera are characterized by the formation of oocysts with unique configurations in terms of the numbers of contained sporocysts and sporozoites. The genera *Epieimeria* and *Goussia* form oocysts with a 1:4:2 configuration; that is, oocysts are tetrasporocystic (contain 4 sporocysts) and each sporocyst is disporozoic (contains 2 sporozoites).

Parasite	No.	Life-cycle	Hosts	Oocyst

genera	spp.			configuration
Family: EIMERIIDAE				
Diaspora	1	monoxenous	invertebrates (arthropods)	0:1:1
Tyzzeria	12	monoxenous	vertebrates (birds, reptiles)	1:0:8
Pfeifferinella	6	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Alveocystis	4	monoxenous	invertebrates (molluscs, priapulids)	1:0:8-14
Caryospora	70	monoxenous	vertebrates (birds, reptiles)	1:1:8 (SB-)
Cyclospora	19	monoxenous	vertebrates (mammals)	1:2:2 (SB+)
Dorisa	13	monoxenous	vertebrates (reptiles, mammals)	1:2:8
Isospora	360	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (molluscs)	1:2:4 (SB+)
Sivatoshella	1	monoxenous	vertebrates (birds)	1:2:16
Eimeria	1,700	monoxenous	vertebrates (mammals, birds, reptiles, fish), invertebrates (arthropods, annelids, hemichordates, protochordates)	1:4:2 (SB+)
Epieimeria	5	monoxenous	vertebrates (fish)	1:4:2 (SB+)
Choleoeimeria	16	monoxenous	vertebrates (reptiles)	1:4:2
Wenyonella	18	monoxenous	vertebrates (mammals, birds, reptiles)	1:4:4
Margolisiella	6	monoxenous	invertebrates (molluscs)	1:n:2-4
Mantonella	5	monoxenous	invertebrates (panarthropods), vertebrates (turtles, rodents, birds, some possibly pseudoparasites)	1:1:4
Octosporella	6	monoxenous	vertebrates (fish, reptiles, echidnas, some possibly pseudoparasites)	1:8:2
Gousseffia	1	monoxenous	vertebrates (hedgehogs, possibly pseudoparasites)	1:8:n
Skrjabinella	1	monoxenous	vertebrates (rodents, possibly pseudoparasites)	1:16:1
Polysporella	1	monoxenous	vertebrates (birds, possibly pseudoparasites)	1:9-15:2
Hoarella	1	monoxenous	vertebrates (lizards)	1:16:2
Pythonella	3	monoxenous	vertebrates (reptiles, birds)	1:16:4
Family: Barrouxiidae				
Barrouxia	10	monoxenous	invertebrates (arthropods, molluscs)	1:n:1
Crystallospora	1	monoxenous	vertebrates (fish)	1:4:2 (SB-)
Goussia	94	monoxenous	vertebrates (fish, amphibians, reptiles)	1:4:2 (SB-)
Family: Calyptosporiidae				
Calyptospora	5	heteroxenous	vertebrates (fish), invertebrate IH (shrimp)	1:4:2 (SB-)

Some 190 species of fish coccidia have been described in freshwater and marine fish throughout the world but little experimental information is available on their actual host or tissue specificity other than that accompanying clinical records. Numerous *Eimeria* species have been described from fish, with merogony, gamogony and sporogony occurring within host epithelial cells mainly in the intestines but sometimes in the gall bladder, swim bladder, liver or kidney. The genus *Goussia* was erected for unique enteric coccidian species in fish and amphibians which form oocysts with 4 sporocysts whose walls are composed of 2 valves joined by a longitudinal suture. In some species, the suture is associated with a membranous structure but it is delicate and often difficult to observe. Developmental stages are located intracellularly in parasitophorous vacuoles (sometimes deemed extracytoplasmic) which initially have monopodial points of contact with the host cell membrane and later having polypodial (spider-like) points of contact. The genus currently contains some 94 species which occur mainly in fish (freshwater and marine species) as well as a few non-piscine hosts (amphibians, geckos and insects). Most species have monoxenous/homoxenous (one-host) life-cycles, although a few apparently have heteroxenous (2-host) cycles involving tubificid worms as secondary (intermediate or paratenic) hosts.

Goussia species	Oocyst size (µm)	Hosts	Location	Distribution
Species in piscine hosts				
G. acipenseris	10 x 8	freshwater Acipenseriformes: acipenserid (starlet)	intestines, pyloric caeca	Hungary
G. aculeati (syn. *Eimeria*)	14.5 x 11	marine Gasterosteiformes: gasterosteid (three-spined (stickleback)	intestines	Europe
G. alburni (syn. *Eimeria*)	20	freshwater Cypriniformes: cyprinid (gudgeon, roach, rudd)	intestines	Europe
G. anopli	8-9	freshwater Cypriniformes: cyprinid (chubbyhead barb)	foregut	Africa
G. arinae	17.5 x 12.5	freshwater Cypriniformes: cyprinid	faeces	Russia

		(sabre carp)		
G. arrawarra	14.3-15.1 x 10.1-10.9	marine Perciformes: sillaginid (sand whiting)	intestines	Australia
G. aurati (syn. *Eimeria*)	20 x 16	freshwater Cypriniformes: cyprinid (goldfish)	intestines	USA
G. auxidis (syn. *Eimeria*)	17-37	marine Scombriformes: scombrid (bullet tuna, albacore, slender tuna, skipjack tuna, yellowfin tuna, blue mackerel); Beloniformes: scomberesocid (Pacific saury)	kidney, liver, spleen	Pacific
G. balatonica	22 x 14	freshwater Cypriniformes: cyprinid (white bream)	intestines	Europe
G. bayae	22-30 x 18-25	freshwater Moroniformes: moronid (white perch)	liver, gallbladder	Atlantic
G. bettae	7.5-8.5	freshwater Anabantiformes: osphronemid (Siamese fighting fish)	foregut	Asia
G. bigemina (syn. *Eimeria*)	28	marine Trachiniformes: ammodytid (lesser sand eel)	intestines	Atlantic
G. biwaensis	8-9	freshwater Cypriniformes: cyprinid (pike gudgeon)	foregut	Japan
G. bohemica	15 x 13	freshwater Cypriniformes: cyprinid (gudgeon)	intestines	Europe
G. callinani (syn. *Eimeria*)	8.4-9.2	freshwater Gobiiformes: eleotrid (empire gudgeon)	intestines	Australia
G. carassici (syn. *Eimeria*)	18	freshwater Cypriniformes: cyprinid (goldfish)	intestines	Asia
G. carpelli (syn. *Eimeria cyprini*)	10	freshwater Cypriniformes: cyprinid (common bleak, bighead carp, European carp, Crucian carp, silver carp, common barbel, goldfish, gudgeon, sunbleak, Marmara chub, common dace, Eurasian minnow, stone moroko, common roach, tench); Scorpaeniformes: abyssocottid (Herzenstein's rough sculpin, Vitim sculpin), cottocomephorid (bighead sculpin, Kessler's sculpin) [plus indirect transmission via sporozoites in Oligochaeta: naidid (sludge worm *Tubifex tubifex*, red worm *Limnodrilus hoffmeisteri*)]	intestinal epithelia (enteritis)	Europe
G. caseosa	40-47	marine Gadiformes: macrourid (roughhead grenadier)	intestines, swim bladder, gall bladder (granulomas)	Atlantic
G. centropomi	19.1 x 17.6	marine Perciformes: centropomid (common snook)	intestines	North America
G. cernui	15-22.5	freshwater Perciformes: percid (Eurasian ruffe)	faeces	Russia
G. chalupskyi (syn. *Eimeria*)	10.5-11.5	freshwater Cypriniformes: cyprinid (Marmara chub)	faeces	Europe
G. cheni	9	freshwater Cypriniformes: cyprinid (bighead carp, silver carp, black carp)	intestinal epithelia	Far East, China
G. cichlidarum (syn. *Eimeria*)	31 x 27	freshwater Cichliformes: cichlid (redbelly tilapia, blue tilapia, mango tilapia, Nile tilapia)	swim bladder	Middle-East, Africa
G. clupearum (syn. *Coccidium, Eimeria, E. wenyoni*)	14-30	marine Beloniformes: belonid (garfish); Clupeiformes: clupeid (European pilchard, Atlantic herring, Pacific herring, European pilchard, European sprat, Japanese sardine, Pontic shad, round sardinella, Madeiran sardinella), engraulid (European anchovy); Carangiformes: carangid (false scad, lookdown, Atlantic horse mackerel);	liver, gonads, stomach, intestines (inflammation, necrosis)	cosmopolitan

		Gadiformes: gadid (blue whiting, pouting); Mulliformes: mullid (West African goatfish); Scombriformes: scombrid (Atlantic mackerel, Atlantic chub mackerel, bullet tuna, little tunny); Spariformes: sparid (two-banded seabream, red porgy, blackspot picarel)		
G. cruciata (syn. *Coccidium, Eimeria*)	17-26	marine Carangiformes: carangid (Atlantic horse mackerel, Mediterranean horse mackerel, Cape horse mackerel, Cunene horse mackerel, Chilean jack mackerel, blue jack mackerel, rough scad, white trevally)	liver, pancreas, pyloric caeca (hepatic lesions)	Atlantic, Mediterranean, Pacific, Adriatic
G. cultrati	22.5-30	freshwater Cypriniformes: cyprinid (sabre carp)	faeces	Russia
G. dakarensis	13-17	marine Perciformes: haemulid (parrot grunt, bigeye grunt), polynemid (lesser African threadfin))	liver	Atlantic
G. decapteri	13-18.5	marine Carangiformes: carangid (false scad)	liver	Africa
G. degiustii	24 x 19	freshwater Cypriniformes: cyprinid (shiners, minnows)	spleen, swim bladder, kidney, intestines (splenic lesions)	Canada
G. desseri	13-20	freshwater Perciformes: percid (zander, Volga pikeperch)	intestines (nodules)	Eurasia
G. echinata	18-19.3 x 9.4-11.7	marine Clupeiformes: clupeid (Atlantic herring)	intestines, caeca	Atlantic
G. emissolei	16-22 x 11.5-18	marine Carcharhiniformes: leptochariid (barbeled houndshark)	intestines	Africa
G. erythroculteri (syn. *Eimeria*)	37 x 26	freshwater Cypriniformes: cyprinid (redfin culter)	kidney	China
G. ethmalotis	30-37	marine Clupeiformes: clupeid (Bonga shad)	liver	Africa
G. exoceti	23-30 x 22-25	marine Beloniformes: exocoetid (fourwing flyingfish)	liver	Africa
G. floridana	19-21 x 14-18	marine Perciformes: sciaenid (red drum)	intestines, caeca	North America
G. gadi (syn. *Eimeria, E. jadviagae*)	20-33	marine Gadiformes: gadid (haddock, Atlantic cod, saithe, pollock), lotid (fourbeard rockling), macrourid (bigeye grenadier, blue grenadier)	swim bladder (eventually filled with viscoid exudates)	North Sea, Atlantic, Baltic
G. gasterostei (syn. *Eimeria, Coccidium*)	17	freshwater Gasterosteiformes: gasterosteid (three-spined stickleback, ninespine stickleback)	liver	Europe
G. girellae (syn. *Eimeria*)	20.1-28.8 x 12.5-16.3	marine Perciformes: kyphosid (rudderfish)	intestines, liver, spleen, gills (moribund)	North America
G. grygieri	10-11	freshwater Cypriniformes: cyprinid (pike gudgeon)	foregut	Asia
G. gymnocephali	25	freshwater Perciformes: percid (Eurasian ruffe)	intestines	Russia
G. iroquoina	10	freshwater Cypriniformes: cyprinid (common shiner, hornyhead chub, blacknose shiner, rosyface shiner, bluntnose minnow, fathead minnow, eastern blacknose dace, creek chub)	intestinal epithelia	Canada
G. janae (syn. *Eimeria*)	18 x 13	freshwater Cypriniformes: cyprinid (Eurasian dace, Marmara chub)	intestines	Eurasia
G. kessleri	11 x 8	freshwater Gobiiformes: gobiid (round goby, bighead goby, monkey goby)	intestines	Eurasia
G. koertingi	15.8-16.5 x 12.8-13.5	freshwater Cypriniformes: cyprinid (common barbel)	intestines (nodular coccidiosis)	Europe

G. kuehae	37-40 x 28-30	estuarine Perciformes: latid (barramundi)	intestines	Australasia
G. langdoni (syn. *Eimeria*)	10.5-12	freshwater Perciformes: percichthyid (golden perch)	intestines, caeca	Australia
G. leucisci (syn. *G. scardinii, freemani Eimeria leucisci*)	25 x 22	freshwater Cypriniformes: cyprinid (Siberian dace, carp bream, common bleak, common roach, common rudd, white bream, common shiner)	kidney interstitium, renal tubules	Europe, North America
G. lomi (syn. *Eimeria*)	14.3-16.8	freshwater Perciformes: percichthyid (Murray cod)	intestines	Australia
G. luciae (syn. *Eimeria*)	9.5-10.8	marine Perciformes: mullid (red mullet)	intestines	Europe
G. lucida (syn. *Eimeria, E. scylli, Coccidium*)	10.5-11.5	marine Carcharhiniformes: triakid (smooth-hound, dusky smooth-hound), scyliorhinid (lesser spotted dogfish, nursehound), squalid (spiny dogfish, longnose spurdog)	intestines	Europe
G. luciopercae	30-35 x 30	freshwater Perciformes: percid (zander)	intestines	Russia
G. lusca	28.8-35.4	marine Gadiformes: gadid (pouting)	liver	Europe
G. malayensis	33-38	freshwater Cyprinodontiformes: aplocheilid (blue panchax)	foregut	Asia
G. metchnikovi (syn. *Eimeria, E. macroresidualis*)	25	freshwater Cypriniformes: cyprinid (white-finned gudgeon, gudgeon, Kessler's gudgeon, Amur whitefin gudgeon)	spleen, kidney, liver (splenic lesions)	Europe
G. microcanthi	11.7-13.5 x 10.1-11.7	marine Perciformes: kyphosid (stripey)	intestines	Australia
G. minuta (syn. *Eimeria*)	10	freshwater Cypriniformes: cyprinid (tench), percid (redfin perch)	kidney, liver	Europe
G. molnarica	14-16 x 9-10	freshwater Siluriformes: clariid (African sharptooth catfish)	intestines	Africa
G. motellae	14	marine Gadiformes: lotid (three-bearded rockling)	intestines, caeca	Europe
G. mylopharyngodoni (syn. *Eimeria*)	13	freshwater Cypriniformes: cyprinid (black carp)	intestines, liver, kidney	Eurasia
G. nipponica	10-12	marine Cypriniformes: cyprinid (big-scaled redfin)	foregut	Asia
G. notemigonica	21	freshwater Cypriniformes: cyprinid (golden shiner)	kidney, spleen swim bladder	Canada
G. notropicum	9	freshwater Cypriniformes: cyprinid (common shiner)	intestines	Canada
G. pannonica	11 x 9	freshwater Cypriniformes: cyprinid (white bream)	intestines	Eurasia
G. peleci	37.5-45 x 35-42.5	freshwater Cypriniformes: cyprinid (sabre carp)	intestines	Russia
G. pigra (syn. *Eimeria*)	18 x 14	freshwater Cypriniformes: cyprinid (common rudd)	intestinal epithelia	France
G. platichthyus	30-35 x 27.5-30	marine Pleuronectiformes: pleuronectid (European flounder)	faeces	Europe
G. pogonognathi	10-13	freshwater Beloniformes: zenarchopterid (forest halfbeak)	foregut	Asia
G. polylepidis	15-23 x 14-20	freshwater Cypriniformes: cyprinid (Iberian nase)	swim bladder, kidney	Europe
G. sasyki	7.5-11.3	freshwater Clupeiformes: clupeid (Black Sea sprat)	intestines, gall bladder	Europe
G. senegalensis	15.5-19	marine Perciformes: lutjanid (African forktail snapper)	liver	Africa
G. sinensis (syn. *Eimeria*)	12	freshwater Cypriniformes: cyprinid (bighead carp, silver carp)	intestines (enteritis)	Asia, Europe
G. soumbediounensis	10-14.5	marine Carcharhiniformes: leptochariid (barbeled houndshark)	intestines	Africa
G. subepithelialis (syn.	16-21 x 13-18	freshwater Cypriniformes: cyprinid	intestines	Europe

Eimeria)		(common carp, tench) [plus indirect transmission via oocysts/sporozoites in Oligochaeta: naidid (sludge worm *Tubifex*)]	(nodular coccidiosis)	
G. sparis (syn. *Eimeria*)	9.4-14.6	marine Perciformes: sparid (redbanded seabream, gilthead bream, bluespotted seabream)	intestines	Eurasia
G. spraguei	16.2-16.8	marine Gadiformes: gadid (Atlantic cod, haddock)	kidney tubules	Canada
G. squali (syn. *Eimeria*)	24-36 x 20-29	marine Squaliformes: squalid (spiny dogfish)	spiral valve	North America
G. suliculiformis	22	freshwater Cypriniformes: cyprinid (gudgeons)	serosa of swim bladder, intestines, liver, kidney	Eurasia
G. szekelyi	14-15.5	freshwater Gobiiformes: gobiid (round goby, monkey goby)	intestines	Europe
G. thelohani (syn. *Eimeria*, *Coccidium*)	16-23	marine Perciformes: labrid (East Atlantic peacock wrasse), sparid (yellowfin bream, goldlined seabream)	liver	Europe, Australia
G. trachinoti	9.5-12	marine Carangiformes: carangid (pompani)	liver	Africa
G. trichogasteri (syn. *Eimeria*)	12.5-22.5	freshwater Anabantiformes: osphronemid (snakeskin gourami)	foregut	Asia
G. truttae (syn. *Eimeria*)	12.3-13	anadromous and freshwater Salmoniformes: salmonid (masu, rainbow trout, brown trout, brook trout, grayling)	caeca	North America
G. vanasi (syn. *Eimeria*)	15-17 x 11-13	freshwater Cichliformes: cichlid (blue tilapia, Nile tilapia, mango tilapia, Mozambique tilapia, banded tilapia, southern mouthbrooder)	foregut	Africa
G. vargai (syn. *Eimeria*)	12.6-20	freshwater Acipenseriformes: acipenserid (sterlet)	intestines	Europe
G. vimbae	15-22.5	marine Cypriniformes: cyprinid (vimba bream)	intestines	Russia
G. wakabayashii	8-9	freshwater Gobiiformes: gobiid (numa-chichibu)	foregut	Japan
G. zarnowskii (syn. *Eimeria*)	19 x 9	freshwater Gasterosteiformes: gasterosteid (three-spined stickleback)	intestines	Europe
Species in non-piscine hosts				
G. flaviviridis (syn. *Eimeria*)	18-35 x 10-16	terrestrial Sauria: gekkonid (yellow-belly gecko)	gall bladder	Asia
G. hyalina (syn. *Coccidium, Eimeria*)	10-17	freshwater Coleoptera (unspecified beetle)	Malpighian tubules	Europe
G. hyperolisi	7-9.8	freshwater Anura: hyperoliid (tadpoles of common reed frog)	gut mucosa	Africa
G. lacazei (syn. *Bananella*, *Eimeria*, *Coccidium schneideri*)	30-40	terrestrial Chilopoda: lithobiid (*Lithobius forficatus, martini* centipedes)	intestines	Holarctic
G. neglecta	8.5-12.5	freshwater Anura: ranid (tadpoles of edible frog, marsh frog, little water frog, grass frog)	intestines	Europe
G. noelleri	10.5-11.5 x 8-11	freshwater Anura: ranid (common frog, agile frog)	intestines	Eurasia

The genus *Epieimeria* was erected for *Eimeria*-like coccidian species whose developmental stages are attached to the surface of intestinal epithelial cells protruding into the lumen (considered to be an epi-cellular location). Oocysts form 4 sporocysts, each with an apical pore and a Stieda body. Sporogony may exogenously after oocysts are excreted from the host, or intercellularly when oocysts infiltrate the mucosa and accumulate in the viscera or body cavities where they sporulate and are liberated only after death of the host. The genus contains 5 species which have been recorded in marine fish and anadromous eels.

Epieimeria species	Oocyst/sporocyst sizes (µm)	Hosts	Location (Disease)	Distribution
E. anguillae (syn. *Eimeria*) (type species)	oo: 8.0-12.8 sp: 5.6-8.8 x 2.4-5.6	freshwater Anguilliformes: anguillid (New Zealand longfin eel, long-finned eel, short-finned eel, European eel, American eel), congrid (European conger)	intestines, caeca (mucosal degeneration, emaciation)	Holarctic, Australia, New Zealand
E. isabellae	oo: 12-14 sp: 7.6-8.4 x 5-6	marine Anguilliformes: congrid (conger eel)	intestines	Mediterranean
E. lomae	oo: 10-12 sp: 6.5-7.5 x 4-5	marine Scorpaeniformes: scorpaenid (black scorpionfish)	pyloric caeca	Adriatic
E. ocellata	oo: 8.8-11 x 8-11 sp: 6-8 x 4-5	marine Perciformes: sciaenid (red drum)	intestines	North America
E. puytoraci	oo: 13-14.5 sp: 8.5-10 x 4.5-5.5	marine Labriformes: labrid (East Atlantic peacock wrasse)	intestines	Adriatic

The genus *Calyptospora* was originally created for the species *Eimeria funduli* when it was found that the sporocysts were radically different from those of typical Eimeria spp. in that they lacked Stieda and sub-Stieda bodies and were covered by a thin veil supported by tentacle-like sporopodia. The sporocysts possessed an anterior apical opening sometimes associated with an incomplete longitudinal fissure (which does not divide the sporocyst into 2 valves like *Goussia* spp.). The parasites usually develop in the livers of fish hosts and they are thought to have monoxenous (one-host) cycles where transmission occurs via the excretion and subsequent ingestion of oocysts. However, some species may have heteroxenous (2-host) life-cycles where oocysts ingested by shrimp (paratenic or intermediate) hosts have been found to excyst releasing sporozoites which invade the gut wall ready to be ingested by predatory fish.

*Calyptospora** species	Oocyst/sporocyst size (µm)	Hosts	Location	Transmission	Distribution
C. empristica	19.6-24.5	freshwater Cyprinodontiformes: fundulid (starhead topminnow)	liver, pancreas	possibly indirect (sporozoites in Decapoda: palaemonid (*Palaemon kadiakensis*)	North America
C. funduli (syn. *Eimeria*) (type species)	oo: 19-31 sp: 9-11 x 5-7	marine; Cyprinodontiformes: fundulid (Gulf killifish, saltmarsh topminnow, Bayou killifish, longnose killifish, mummichog, inland silverside); Batrachoidiformes: batrachoidid (Gulf toadfish)	liver, pancreas, intestines, ovary, dermis (hepatic and pancreatic lesions)	direct (oocyst ingestion) and indirect (sporozoites in Decapoda: palaemonid (*Palaemonetes pugio, vulgaris, paludosus, kadiakensis, Macrobrachium ohione*)	North America
C. gonzaguensis	19.6	freshwater Characiformes: triportheid (dusky narrow hatchetfish)	liver, gall bladder, adipose tissue		South America
C. paranaidji	22.1	freshwater Cichliformes: cichlid (blue peacock wrasse)	liver		South America
C. serrasalmi	23.5-25.5	freshwater Characiformes: serrasalmid (black piranha, redeye piranha, peppered piranha)	liver		South America
C. spinosa	21.1-23.4	freshwater Cichliformes: cichlid (pike cichlid)	liver, gonads		South America
C. tucunarensis	23-26	freshwater Cichliformes: cichlid (butterfly peacock bass)	liver		South America

*Note that the genus *Calyptospora* may also refer to pucciniomycete fungi (Basidomycota)

The genus *Crystallospora* was created for a single species (originally *Coccidium crystalloides*) which produced highly unusual crystal-like sporocysts that were dodecahedral in shape and composed of 2 hexagonal pyramidal valves joined at their bases by a suture. Infections have only been detected in marine fish (rockling) around coastal Europe.

***Crystallopsora* species**	**Oocyst size (µm)**	**Hosts**	**Location**	**Transmission**	**Distribution**
C. crystalloides (syn. *C. thelohani, Coccidium, Eimeria*)	oo: 20-24 sp: 15 x 9.5	marine, Gadiformes: lotid (shore rockling, three-bearded rockling)	intestines	direct	Atlantic, Mediterranean

Parasite morphology: Piscine coccidia belonging to the genera *Goussia*, *Epieimeria*, *Calyptospora* and *Crystallospora* undergo merogony (asexual multiplication), gamogony (formation of gamonts then gametes) and sporogony (formation of oocysts, sporocysts and sporozoites) in their developmental cycles, somewhat similar to *Eimeria* spp. However, the locations of the developmental stages in host tissues and the structure of the oocysts and sporocysts differ markedly from that of typical *Eimeria* spp. Meronts, gamonts and oocysts of *Goussia, Epieimeria, Calyptospora* and *Crystallospora* are generally small, appearing as rounded colourless-basophilic bodies ranging in diameter from 5-25 µm. They are located within membrane-bound parasitophorous vacuoles within host cells (intracellular, but extracytoplasmic) and many species are located epicellularly; that is, attached to the luminal surface of epithelial cells by finger-like attachment organelles (monopodial or polypodial). Meronts are rounded basophilic stages that divide asexually to form numerous merozoites. Gamonts are also rounded stages, but female gamonts (macrogamonts) are lightly stained uninucleate vacuolated stages, while male gamonts (micro-gamonts) are basophilic and become multinucleate as they form several microgametes. Fertilization produces a zygote, evident as an immature oocyst with a thin fragile oocyst envelope lacking a micropyle. Oocysts mature (sporulate) to produce 4 sporocysts, each with 2 sporozoites (typical eimeriid 1:4:2 configuration). Members of the genus *Epieimeria* form ovoid to ellipsoidal sporocysts with polar plugs and/or Stieda bodies (like *Eimeria* spp.), while members of the genus *Goussia* form sporocysts without Stieda bodies but with walls consisting of 2 cup-like valves joined along a longitudinal suture (sometimes associated with a delicate membranous structure). The sporocysts of *Calyptospora* spp. lack Stieda and sub-Stieda bodies but are surrounded by amorphous material covered by a thin veil supported by tentacle-like sporopodia. The sporocysts have an apical opening often associated with a short longitudinal fissure. The single *Crystallospora* sp. forms unusual crystal-like sporocysts consisting of 2 hexagonal pyramidal valves joined along a transverse suture line.

Site of infection: Most piscine coccidia infect the intestinal mucosa (epithelium and/or submucosa), but developmental stages may sometimes be found in extra-intestinal tissues and organs (stomach, caeca, gall bladder, liver, spleen, pancreas, kidneys, swim bladder, spleen, gills, and gonads). A total of 88 *Goussia* spp. have been described from the intestines, and sometimes extra-intestinal tissues, in 156 fish species: with 32 species recorded in 79 marine fish species belonging to 29 families in 14 orders, and 56 parasite species in 77 freshwater fish species belonging to 19 families in 14 orders. Another 6 *Goussia* spp. have also been found in the guts of several amphibians, a few insects (centipedes, beetle) and a lizard (gecko). Sporozoite developmental stages of several species have also been detected in freshwater oligochaetes (tubificids) which may act as secondary hosts (paratenic or intermediate hosts). Seven *Calyptospora* spp. have been found in the livers, and sometimes other organs, in 15 fish species (8 freshwater, 7 marine) belonging to 5 families in 4 orders. Sporozoites have also been detected in the guts of 5 species of palaemonid shrimp which act as secondary hosts. Five *Epieimeria* spp. have been described attached to the surface of intestinal epithelial cells (epicellular location) in 10 fish species (6 freshwater, 4 marine) belonging to 5 families in 4 orders. Oocysts are usually voided into the external environment, although those of some species accumulate in the viscera or body cavities and are only liberated after the death of the host. Only one *Crystallospora* sp. has been reported in the intestines of 2 species of marine rockling.

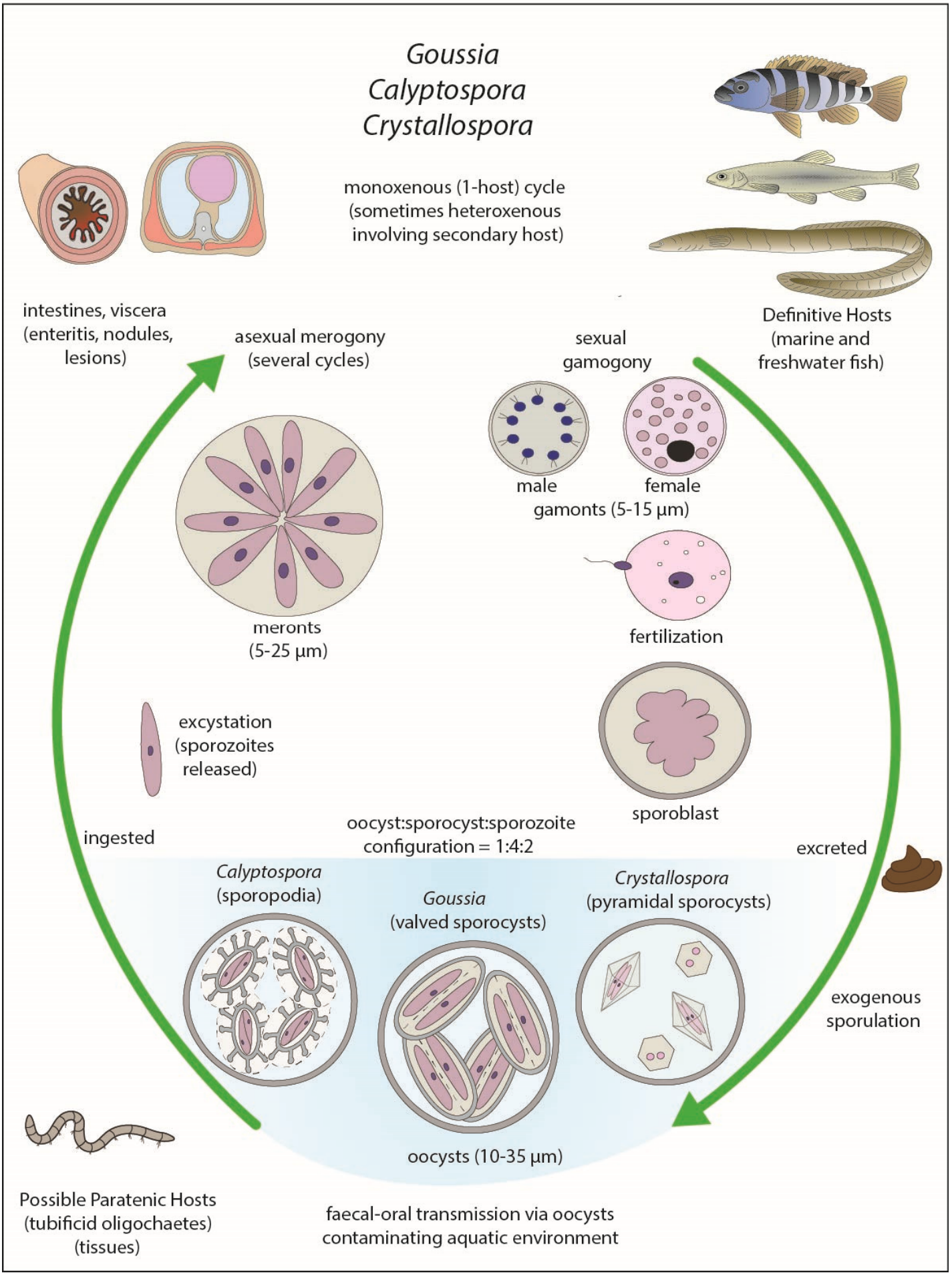
Pathogenesis: Infections in fish ranged from asymptomatic-subclinical to causing mild-severe disease, sometimes with mortalities. The parasites formed both asexual and sexual developmental stages intracellularly within host cells which ultimately led to host cell lysis to liberate parasite progeny. The resultant structural losses to host tissues was sometimes severe enough to result in functional abnormalities and disease expression. Many parasite species exhibit strong tissue tropism (site specificity), with development occurring in or on intestinal epithelial cells (intracytoplasmic or epicytoplasmic) or in visceral (extra-intestinal) organs, although several species may develop in multiple locations, sometimes apparently in sequence (e.g. *Goussia girellae* in rudderfish). Infections in the gastro-intestinal tract usually cause regressive epithelial changes (dystrophy, necrosis, desquamation) and mild-severe inflammatory responses, with affected fish sometimes showing inappetence, darkened bodies and protracted low grade mortalities. Examples of enteric disease include diffuse enteritis caused by *Goussia carpelli* and *G. sinensis* in carp and *G. clupearum* in pilchards, and nodular coccidiosis caused by *G. subepithelialis* in carp, *G. desseri* in perch, and *G. koertingi* in barbels. Extra-intestinal infections may result in necrotic lesions sometimes with granuloma formation: e.g. hepatic lesions caused by *Calyptospora funduli* in killifish and *G. cruciata* in mackerel, splenic lesions by *G. degiustii* in minnows and *G. metchnikovi* in gudgeon, kidney lesions by *G. leucisci* in cyprinids and *G. spraguei* in haddock, and swim bladder lesions by *G. gadi* in cod and *G. caseosa* in grenadier. Clinical infections and disease are more prevalent and severe in young fish (fry to fingerling stages) and some

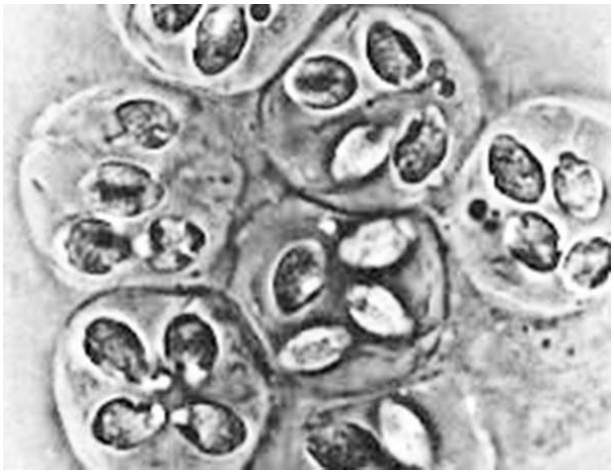
infections appear to be seasonal with peaks occurring in spring (thought to be associated with host reproductive cycles, and possibly with the seasonal abundance of putative secondary hosts (such as oligochaetes and shrimp).

Developmental cycle and mode of transmission: The life-cycles of most coccidian species infecting fishes remain to be definitively determined, but most are assumed to have monoxenous (one-host) life-cycles involving the faecal-oral transmission of oocysts voided by infected hosts being ingested by new susceptible hosts. Ingested oocysts excyst in the fish gut releasing the infective sporozoites which invade host tissues. They form meronts (schizonts) which undergo asexual proliferation by internal (endogenous) division to form numerous merozoites. Depending on the parasite species, there may be several cycles of merogony before sexual development begins. Sexually-dimorphic gamonts form macrogametocytes (female) that mature into single macrogametes while microgametocytes (male) produce several flagellated ('sperm-like') microgametes. Fertilization occurs by gamete fusion producing zygotes which begin oocyst formation by producing membranous oocyst walls. The oocysts undergo an asexual sporulation process to produce 4 sporocysts, each of which contains 2 sporozoites. Sporulation often occurs exogenously after oocysts are excreted from the host. However, some species undergo endogenous (intercellular) sporulation when oocysts infiltrate the mucosa and accumulate in the viscera or body cavities where they sporulate and are liberated only after the death of the host. The whole life-cycle may be completed as quickly as 15 days or may take up to 7 months. In addition, some parasite species also exhibit heteroxenous (2-host) transmission involving secondary hosts which act either as paratenic hosts (transporting parasite stages without development) or as true intermediate hosts (supporting parasite asexual development). Several *Goussia* spp. (e.g. *G. carpelli, G. subepithelialis*) may be transmitted directly between carp by oocyst ingestion, but they may also be transmitted indirectly to fish by the ingestion of infected tubificid oligochaetes living in pond sediments. It is not yet known whether the oligochaetes support parasite development or not, although it has been shown that some ingested oocysts excyst in the oligochaete gut releasing sporozoites into the lumen with some also invading intestinal epithelial cells. Infections are readily transmitted to fry feeding on infected worms. Several *Calyptospora* spp. (e.g. *C. funduli, C. empristica*) in minnows have been shown to be transmitted indirectly between fish by the ingestion of infected palaemonid shrimp which harbour sporozoites in their gut walls. Following the ingestion of shrimp by the predatory fish, the sporozoites penetrated the fish gut wall and were carried to the liver where they underwent asexual and sexual development.

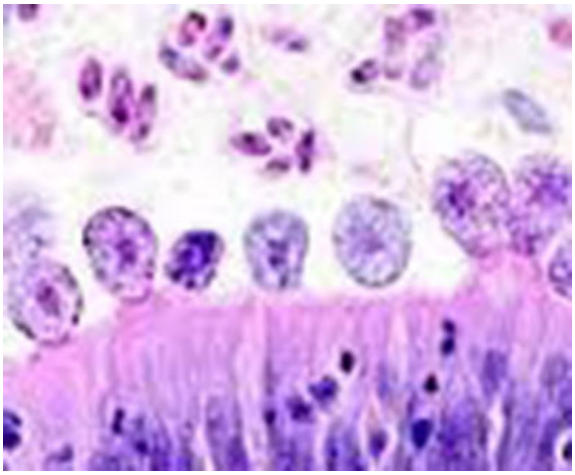
Differential diagnosis: Infections are diagnosed by the direct microscopic detection of parasites in tissue or faecal samples. Wet mounts of gut content, mucosal smears or tissue squashes may be examined by high-contrast microscopy (bright-field, phase- or interference-contrast) for endogenous stages and developing oocysts. Thin sections of fixed tissues may also be examined after staining with routine histological stains. Fresh faecal samples may be examined as wet mounts or following concentration by sedimentation-floatation techniques. Molecular biological techniques have been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (usually small subunit (18S) ribosomal DNA). While *in vivo* parasite culture has not been used for diagnostic purposes, experimental studies have successfully infected carp fry by feeding them tubificid oligochaetes exposed to Goussia carpelli oocysts.

Treatment and control: Various coccidiostatic and coccidiocidal drugs have been developed for the treatment of avian and mammalian coccidiosis, and some are used off-label for the treatment of piscine coccidiosis. Aquarium fish may be treated by topical or systemic applications either individually or in small batches, whereas aquaculture and mariculture facilities with larger fish populations rely on in-feed medications. Clinical infections in fish by several *Goussia* spp. have responded to treatment with some anticoccidial drugs (diclazuril, lasalocid, robenidine, maduramicin, orazole, furazolidone, furanace) but not with others (amprolium, toltrazuril, monensin, narasin, salinomycin), while fish infected with *Calyptospora* sp. were responsive to monensin. Various treatments produced some side-effects and several drugs required lengthy with-holding periods when used in food animals. Various strategies have been suggested to prevent infections by reducing oocyst contamination in culture facilities. Fish should be screened for infections before their introduction into culture, with positive fish held in isolation for treatment or culling. Dead or dying fish should be removed from ponds promptly and disposed of by incineration or burial. Water flow and quality should be managed to reduce the accumulation of sediments and organic wastes in ponds and prevent their colonization by oligochaetes which may act as paratenic hosts for some coccidian species. Infected ponds should be drained, dried and disinfected (with lime) to kill any contaminating oocysts. Fish may become more susceptible to infection and disease when stressed (and immuno-compromised), so husbandry procedures should endeavour to avoid stressful situations (such as overcrowding, over-handling, poor diets, and poor water quality).


Goussia
Calyptospora
Crystallospora
monoxenous (1-host) cycle
(sometimes heteroxenous
involving secondary host)
intestines, viscera
(enteritis, nodules,
lesions)
asexual merogony
(several cycles)
sexual
gamogony
Definitive Hosts
(marine and
freshwater fish)
male
female
gamonts (5-15 µm)
meronts
(5-25 µm)
fertilization
excystation
(sporozoites
released)
sporoblast
ingested
oocyst:sporocyst:sporozoite
configuration = 1:4:2
excreted
Calyptospora
(sporopodia)
Goussia
(valved sporocysts)
Crystallospora
(pyramidal sporocysts)
exogenous
sporulation
oocysts (10-35 µm)
Possible Paratenic Hosts
(tubificid oligochaetes)
(tissues)
faecal-oral transmission via oocysts
contaminating aquatic environment



Goussia oocysts from fish gut



Goussia development on fish gut

***Sarcocystis* (incl. *Frenkelia*)**
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). Tissue cyst-forming coccidia have heteroxenous (two-host) life-cycles alternating between enteric stages in predators (definitive hosts) and encysted stages in prey (intermediate) hosts. *Sarcocystis* spp. (including former *Frenkelia* spp.) form elongate cysts containing metrocytes then bradyzoites (= cystozoites) predominantly in the striated muscles of numerous omnivores/herbivores (mammals, birds, reptiles). The cysts have elaborate cyst walls and some may become macroscopic in size causing unsightly lesions in the flesh. Precyst merogonous (= schizogonous) stages in vascular endothelia have occasionally been associated with haemorrhagic clinical diseases in domestic ruminants. Gamogony (male microgametes fertilize female macrogametes) and oocyst formation occurs directly (without merogony) in subepithelial intestinal tissues in a range of carnivores (mammals, birds and reptiles). Sporogony occurs endogenously resulting in the shedding of free sporocysts each with 4 sporozoites. Different species exhibit relative strict host specificity, with particular predator-prey combinations hosting individual species e.g. two species having a dog-sheep cycle.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Eimeriorina (no syzygy, many microgametes)
Family:	Sarcocystidae (heteroxenous, oocysts with two sporocysts, tissue cyst formation in intermediate host)
Subfamily:	Sarcocystinae (metrocytes present in cysts, simple/elaborate cyst walls)
Genus:	*Sarcocystis* (syn. *Frenkelia*) (tissue cyst-forming coccidian parasites of mammals/birds/reptiles)
Species:	various species cause acute sarcocystosis and/or chronic sarcosporidiosis in animals

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia

are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as 'haemogregarines' in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoitia*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Numerous species of coccidia have been described from a wide range of vertebrate and invertebrate hosts. Some 50 genera have been classified in 11 families in the suborder Eimeriorina, including nine genera in the family Sarcocystidae. These apicomplexans are often referred to as cyst-forming coccidia, as they undergo gamogony and sporogony producing oocysts (1:2:4 oocyst:sporocyst:sporozoite configuration) in the intestines of carnivorous definitive hosts (DHs) as well as merogony and tissue cyst formation in the tissues of omnivorous or herbivorous intermediate hosts (IHs). They have heteroxenous (two-host) life-cycles with cyclic transmission between predatory animals and their prey. Two main subfamilies are recognized mainly on the basis of

differences in cyst development (metrocytes present or absent) and site of oocyst sporulation (endogenous or exogenous). Members of the subfamily Sarcocystinae form cysts with metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate endogenously before being voided from the definitive host. Members of the subfamily Toxoplasmatinae form cysts without metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate exogenously after being voided from the definitive host. A third subfamily has recently been added with the discovery that some *Isospora* spp. in mammals form encysted monozoic stages (cystozoites) in the tissues of paratenic (transport) hosts (esp. rodents), prompting their classification with the tissue cyst-forming coccidia under the name *Cystoisospora* in the new subfamily Cystoisosporinae.

Parasite genera	**No. spp.**	**Life-cycle**	**Definitive Hosts (DH) Intermediate Hosts (IH) Paratenic Hosts (PH)**	**Oocyst configuration***
Family: Sarcocystidae (3 subfamilies)				
Subfamily: Cystoisosporinae (monozoic cysts in PH, sporocysts without Stieda bodies)				
Cystoisospora	50	heteroxenous	vertebrate DH (carnivores, primates), vertebrate PH (mammals, birds)	1:2:4
Subfamily: Sarcocystinae (metrocytes, endogenous sporulation)				
Sarcocystis (incl. *Frenkelia*)	135	heteroxenous	vertebrate DH (predatory mammals, birds, reptiles), vertebrate IH (mammals, birds, reptiles)	1:2:4
Subfamily: Toxoplasmatinae (no metrocytes, exogenous sporulation)				
Toxoplasma	1	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals), invertebrate PH (annelids, insects)	1:2:4
Hammondia	3	heteroxenous	vertebrate DH (canids, felids), vertebrate IH (mammals)	1:2:4
Neospora	2	heteroxenous	vertebrate DH (canids), vertebrate IH (mammals)	1:2:4
Besnoitia	7	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals, reptiles), possibly invertebrate PH (insects)	1:2:4
Hyaloklossia	1	monoxenous	vertebrates (amphibians)	1:2:4
Nephroisospora	1	monoxenous	vertebrates (bats)	1:2:4

*1:2:4 = one oocyst contains 2 sporocysts, each sporocyst contains 4 sporozoites

The genera *Sarcocystis* and *Frenkelia* are classified within the subfamily Sarcocystinae as they form 2 generations of zoites within tissue cysts (metrocytes then bradyzoites (sometimes called cystozoites)), the bradyzoites develop directly into gametes, and the isosporid-type oocysts sporulate endogenously before being voided. Recent molecular phylogenetic studies have indicated that these genera may be conspecific and many authorities have transferred all *Frenkelia* spp. into the genus *Sarcocystis*. The parasites are obligatory heteroxenous with cyclic predator-prey transmission usually occurring between carnivorous DHs and herbivorous IHs. Transmission from IH to DH occurs via carnivory (predator consuming cysts in tissues of prey) and transmission from DH to IH occurs via faecal-oral contamination (excretion of oocysts/sporocysts in faeces of predators to contaminate foodstuffs of prey). Recent studies have also shown some species may exhibit diheteroxenous cycles where the IH and DH are the same host (supporting both tissue cyst and sporocyst formation) or where IH-IH transmission may occur via cannibalism or transplacental infection (or via ingestion of a paratenic host).

Over 220 *Sarcocystis* spp. have been described worldwide, predominantly by the detection of macroscopic and/or microscopic cysts in striated muscles (hence the name sarcocysts) in numerous mammalian, avian and reptilian hosts. Members of the former genus *Frenkelia* have similar cycles to *Sarcocystis* except that they use birds of prey as definitive hosts and they form cysts in nervous tissues of their rodent intermediate hosts. The cysts of most species had unique cyst wall architecture when examined by transmission electron microscopy, and over 80 ultrastructural types/subtypes have been described. Infections by tissue cysts are prevalent in domestic animals in many countries (e.g. 90% of sheep, 60% of cattle), particularly those kept under intensive husbandry in tropical and temperate regions. However, the complete life-cycles have only been determined for around 100 species by the demonstration of sporocyst formation in carnivores fed tissues cysts. Canids and felids were found to be definitive hosts for many species in domestic animals, particularly those species forming micro-cysts being infective for dogs and those forming macro-cysts being infective for cats. Host specificity was relatively strict for both definitive and intermediate hosts, and multiple parasite species have been found in individual host species (e.g. at least 4 species in sheep, and 3 in cattle). Infections in humans are uncommon, but they may serve either as intermediate hosts (in which tissue cysts develop) or definitive hosts (in which sporocysts are formed). [Historically, it should be noted that some parasite species have inadvertently been given 2 names, one under the genus *Sarcocystis* for the tissue cysts found in herbivorous (intermediate) hosts, and another under the genus *Isospora* for the oocysts/sporocysts found in carnivorous (definitive) hosts. While some attempts have been made to establish nomenclatural priority, it should be noted that few transmission studies have ever been conducted to ascertain that both stages belong to the same species,

apart from some experimental studies on several well-known species in domestic animals. Even then, little variation is evident in the morphology of the oocysts and sporocysts, and because some carnivores host multiple parasite species, it is often unclear as to which species the original descriptions referred to. Future molecular characterization studies may help match different life-cycle stages for individual species, but regrettably no type material of oocysts/sporocysts exists for earlier descriptions. I have therefore listed all *Sarcocystis* spp. according to the morphological (ultrastructural) characteristics of the tissue cysts detected in their different intermediate hosts].

***Sarcocystis* species**	**Intermediate hosts (IH)**		**Definitive hosts (DH)**	**Distribution**
	Species	**Cyst wall**		
Species with mammalian intermediate hosts				
S. africana	Artiodactyla: hippopotamid (hippopotamus)	type 15b	unknown	Africa
S. alces	Artiodactyla: cervid (moose)	smooth	Carnivora: canid (Arctic fox, red fox)	Europe
S. alceslatrans	Artiodactyla: bovid (Eurasian elk, moose)	type 7b	Carnivora: canid (dog, coyote)	North America, Europe
S. americana	Artiodactyla: cervid (mule deer)	hair-like villar protrusions	unknown	North America
S. arctica	Carnivora: canid (arctic fox, Alaskan wolf)	type 9c	unknown	Norway, Alaska
S. arctosi	Carnivora: ursid (brown bear)	type 1a	unknown	North America, Asia
S. arieticanis	Artiodactyla: bovid (sheep, wild sheep, mouflon, Alpine ibex)	type 7b	Carnivora: canid (dog)	cosmopolitan
S. atheridis	Experimental infection in Rodentia: murid (house mouse, Barbary striped mouse)	macrocysts type 1b	Serpentes: viperid (Nitsche's bush viper)	Africa
S. aucheniae (syn. *S. guanicoecanis, S. tilopodi*)	Artiodactyla: camelid (llama, guanaco, alpaca)	macrocysts type 21b	Carnivora: canid (dog)	South America, Australia
S. azevedoi	Rodentia: cricetid (large-headed rice rat)	striated wall	unknown	South America
S. baibacinacanis (syn. *S. baibacina*)	Rodentia: sciurid (grey marmot, steppe marmot, golden marmot)	nr	Carnivora: canid (dog, wolf, red fox)	Central Asia
S. balaenopteralis	Cetacea: balaenopterid (sei whale)	type 1a	unknown	Pacific
S. bertrami (syn. *S. equicanis, S. asinus*)	Perissodactyla: equid (horse, kiang, Burchell's zebra, ass/donkey)	macrocysts type 11c	Carnivora: canid (dog)	cosmopolitan
S. bettongiae sp. inq.	Diprotodontia: potoroid (burrowing bettong)	nr	unknown	Australia
S. booliati	Eulipotyphla: erinaceid (moonrat)	type 1b	unknown	South-East Asia
S. bovifelis	Artiodactyla: bovid (cattle, gaur, banteng, European bison, American bison)	macrocysts	Carnivora: felid (cat)	Europe
S. bovini	Artiodactyla: bovid (cattle)	finger-like protrusions	unknown	Argentina, New Zealand, China
S. bozemanensis	Rodentia: sciurid (Richardson's ground squirrel)	type 1a	unknown	North America
S. bubalis sp. inq.	Artiodactyla: bovid (Coke's hartebeest)	macrocysts striated wall	unknown	Africa
S. buffalonis	Artiodactyla: bovid (water buffalo)	type 28	Carnivora: felid (cat)	South-East Asia
S. cafferi	Artiodactyla: bovid (African buffalo)	type 23b	unknown	Africa
S. cameli	Artiodactyla: camelid (Arabian camel, Bactrian camel)	type 9j	Carnivora: canid (dog)	Eurasia, Africa
S. camelopardalis	Artiodactyla: giraffid (giraffe)	type 36	unknown	Africa
S. campestris	Rodentia: sciurid (Richardson's ground squirrel, thirteen-lined	macrocysts type 9a	Carnivora: mustelid (American badger)	North America

	ground squirrel)			
S. caninum	Carnivora: canid (dog)	type 9c	unknown	North America
S. canis	Carnivora: canid (dog), ursid (American black bear, polar bear), otariid (California sea lion, Steller sea lion), phocid (Hawaiian monk seal), Rodentia: chinchillid (long-tailed chinchilla), Artiodactyla: delphinid (striped dolphin), Perissodactyla: equid (horse)	only schizonts known (pre-cyst stages)	unknown	North America
S. capracanis	Artiodactyla: bovid (goat), plus molecular detection in sheep	type 14	Carnivora: canid (dog, wolf, coyote, red fox, corsac fox, wood fox, crab-eating dog, raccoon dog)	cosmopolitan
S. capreolicanis (syn. *capreoli*)	Artiodactyla: cervid (European roe deer)	type 6	Carnivora: canid (dog, swift fox, red fox, raccoon dog)	Europe
S. capricornis	Artiodactyla: bovid (Japanese serow)	type 27	unknown	Japan
S. caviae sp. inq.	Rodentia: caviid (guinea pig)	nr	unknown	South America
S. cernae	Rodentia: cricetid (common European vole)	type 1	Falconiformes: falconid (Eurasian kestrel)	Europe
S. cervicanis	Artiodactyla: cervid (red deer)	type 8a	Carnivora: canid (dog, coyote)	Europe
S. citellibuteonis	Rodentia: sciurid (yellow ground squirrel)	type 1	Accipitriformes: accipitrid (Eurasian buzzard)	Europe
S. citellivulpes	Rodentia: sciurid (yellow ground squirrel)	macrocysts type 9	Carnivora: canid (red fox, corsac fox), mustelid (steppe polecat)	Central Asia
S. clethrionomyelaphis	Experimental infections in Rodentia: cricetid (bank vole, common vole, Gunther's vole, tundra vole)	type 9	Serpentes: colubrid (striped Aesculapian rat snake), plus experimental infection in colubrid (steppe rat snake, corn snake, western rat snake, four-lined snake, ladder snake)	Europe, Middle-East, North America
S. clethrionomysi	Rodentia: cricetid (grey-sided vole)	thick	unknown	Japan
S. cornagliai	Artiodactyla: bovid (Alpine ibex, chamois)	type 24	unknown	Europe
S. corsaci sp. inq.	Carnivora: canid (corsac fox), diheteroxenous	nr	Carnivora: canid (corsac fox)	Central Asia
S. cricetuli	Rodentia: cricetid (Chinese hamster)	nr	unknown	Asia
S. crotali	Rodentia: murid (house mouse)	type 1a	Serpentes: viperid (Mojave rattlesnake)	North America
S. cruzi (syn. *bovicanis*)	Artiodactyla: bovid (cattle, bison, wisent, gaur, banteng, water buffalo) [causes Dalmeny disease in cattle]	type 7a	Carnivora: canid (dog, coyote, red fox, crab-eating fox, wolf, raccoon dog, crab-eating dog), procyonid (raccoon)	cosmopolitan
S. cuniculorum (syn. *S. cuniculi*)	Lagomorpha: leporid (rabbit, European hare, mountain hare)	type 10b	Carnivora: felid (cat)	Europe, Australia, New Zealand
S. cymruensis (syn. *S. rodentifelis*)	Rodentia: murid (house mouse, brown rat, black rat, greater	type 1c	Carnivora: felid (cat)	Asia, Europe

	bandicoot rat, Oriental house rat), cricetid (bank vole), also diheteroxenous (rodent-rodent transmission via cannibalism, paratenic hosts, transplacental)			
S. danzani	Artiodactyla: bovid (Mongolian gazelle)	type 29a	unknown	Asia
S. dasypi	Cingulata: dasypodid (nine-banded armadillo)	type 11	unknown	Americas
S. didelphidis	Didelphimorpha: didelphid (black-eared opossum)	macrocysts	unknown	South America
S. diminuta	Cingulata: dasypodid (nine-banded armadillo)	type 11	unknown	Americas
S. dirumpens	Rodentia: murid (house mouse, Natal multimammate mouse, Mongolian gerbil, pale gerbil, Barbary striped grass mouse, brown rat, grey-headed thicket rat), cricetid (golden hamster, Djungarian hamster)	type 1b	Serpentes: viperid (puff adder, rhinoceros viper, horned viper, Gaboon viper)	Africa
S. dispersa	Rodentia: murid (house mouse)	type 18a	Strigiformes: tytonid (barn owl, masked owl), strigid (long-eared owl)	Europe
S. dogeli	Lagomorpha: ochotonid (Daurian pika)	macrocysts	unknown	Asia
S. dubeyella	Artiodactyla: suid (desert warthog)	type 30	unknown	South Africa
S. elongata	Artiodactyla: cervid (red deer)	thin finger-like protrusions	unknown	Europe
S. entzerothi	Artiodactyla: cervid (European roe deer)	macrocysts type 10a	unknown	Europe
S. eothenomysi	Rodentia: cricetid (Yunnan red-backed vole)	type 18a	unknown	China
S. erdmanae	Carnivora: mephitid (striped skunk)	nr	Carnivora: canid (dog)	North America
S. espinosai	Rodentia: cricetid (North American deer mouse)	type 1h	Strigiformes: strigid (Northern saw-whet owl)	North America
S. eutamias	Rodentia: sciurid (chipmunk)	nr	unknown	Asia
S. eversmanni	Carnivora: mustelid (steppe polecat)	nr	unknown	Central Asia
S. fayeri	Perissodactyla: equid (horse, donkey, onager, plains zebra)	type 11a	Carnivora: canid (dog)	cosmopolitan
S. fedoseenkoi	Rodentia: cricetid (great gerbil)	type 9	unknown	Central Asia
S. felis	Carnivora: felid (cat, bobcat, Florida panther, Florida cougar, cheetah, Geoffroy's cat, oncilla, margay, colocolo, lion, jaguarundi)	type 9c	unknown	North America
S. ferovis	Artiodactyla: bovid (bighorn sheep)	type 3a	Carnivora: canid (coyote)	North America
S. fusiformis (syn. *S. blanchardi, S. siamensis, S. bubali*)	Artiodactyla: bovid (water buffalo)	macrocysts type 21b	Carnivora: felid (cat)	Eurasia, Africa, South America
S. galuzoi	Lagomorpha: ochotonid (alpine pika)	macrocysts	unknown	Central Asia
S. garnhami	Didelphimorphia: didelphid (black-eared opossum, gray four-eyed opossum)	macrocysts type 9m	unknown	Americas
S. gazellae	Artiodactyla: bovid (red-fronted gazelle, Grant's gazelle,	macrocysts type 14	unknown	Africa

	Thomson's gazelle, springbok)			
S. gerbillechis	Rodentia: cricetid (lesser Egyptian gerbil, pale gerbil), murid (Shaw's jird, fat sand rat, fat-tailed gerbil)	macrocysts type 1b	Serpentes: viperid (Arabian saw-scaled viper)	Egypt
S. gigantea (syn. *S. ovifelis*)	Artiodactyla: bovid (sheep, bighorn, goat)	macrocysts type 21a	Carnivora: felid (cat), canid (red fox)	cosmopolitan
S. giraffae	Artiodactyla: giraffid (giraffe)	macrocysts type 34	unknown	South Africa
S. glareoli (syn. *Toxoplasma glareoli, Isospora buteonis, Frenkelia buteonis, F. clethrionomyobuteonis, F. glareoli*) [recently transferred from genus *Frenkelia* to *Sarcocystis* on the basis of genotypic studies]	Rodentia: cricetid (common vole, bank vole, northern red-backed vole, grey-sided vole, field vole, European water vole), murid (Eurasian field mouse)	non-lobate cysts type 1a	Accipitriformes: accipitrid (common buzzard, rough legged buzzard)	Europe, Japan
S. gracilis	Artiodactyla: cervid (European roe deer, Siberian roe deer); bovid (cattle)	type 1g	Carnivora: canid (red fox, Arctic fox, raccoon dog)	Europe
S. greineri	Didelphimorphia: didelphid (Virginia opossum)	type 9b	unknown	North America
S. grueneri (*gruneri*, *grüneri*)	Artiodactyla: cervid (reindeer, red deer, reindeer, sika deer, fallow deer)	type 8a	Carnivora: canid (dog, Arctic fox, red fox, raccoon dog)	Eurasia
S. gusevi sp. inq.	Artiodactyla: bovid (Marco Polo sheep)	nr	unknown	Central Asia
S. hardangeri	Artiodactyla: cervid (reindeer, red deer)	macrocysts type 26	unknown	Europe
S. hemioni	Artiodactyla: cervid (mule deer)	type 10d	unknown	North America
S. hemionilatrantis	Artiodactyla: cervid (mule deer, European roe deer)	type 17	Carnivora: canid (dog, coyote)	North America
S. hippopotami	Artiodactyla: hippopotamid (hippopotamus)	type 33	unknown	South Africa
S. hircicanis	Artiodactyla: bovid (goat), cervid (mule deer)	type 7a	Carnivora: canid (dog)	cosmopolitan
S. hirsuta (syn. *S. bovifelis*)	Artiodactyla: bovid (cattle, gayal, banteng, bison, wisent)	macrocysts type 28	Carnivora: felid (cat, wildcat)	cosmopolitan
S. hjorti	Artiodactyla: cervid (red deer, moose)	thin hair-like protrusions	Carnivora: canid (red fox, Arctic fox)	Europe
S. hoarensis	Experimental infections in Rodentia: murid (house mouse, Natal multimammate mouse, pale gerbil, Mongolian gerbil), cricetid (golden hamster, Djungarian hamster)	macrocysts type 42	Serpentes: viperid (puff adder, rhinoceros viper), plus experimental infection in viperid (horned adder, Gaboon viper)	Mediterranean
S. hofmanni	Carnivora: mustelid (European badger), procyonid (raccoon)	macrocysts type 10b	unknown	Europe
S. hominis (syn. *bovihominis*)	Artiodactyla: bovid (cattle, gayal, banteng, bison, wisent, water buffalo)	type 10b	Primates: hominid (human, chimpanzee), cercopithecid (rhesus macaque, long-tailed macaque, yellow baboon)	Americas, Europe, Asia
S. hueti	Carnivora: otariid (California sea lion)	type 1e	unknown	North America
S. hydrurgae	Carnivora: phocid (leopard seal)	type 1e	unknown	Antarctic
S. inghami	Didelphimorpha: didelphid (Virginia opossum)	type 9n	unknown	North America

S. ippeni	Artiodactyla: camelid (Arabian camel)	type 32	unknown	Africa
S. jaypeedubeyi (syn. for original *S. microti*) [name replaced to overcome homonym caused by transfer of *Frenkelia microti* to genus *Sarcocystis*]	Rodentia: cricetid (meadow vole, long-tailed vole)	type 9o	unknown	North America
S. jorrini	Artiodactyla: cervid (fallow deer)	macrocysts type 15	unknown	Spain
S. kalvikus	Carnivora: mustelid (wolverine)	macrocysts type 1a	unknown	North America, Eurasia
S. kirkpatricki	Carnivora: procyonid (raccoon)	type 11b	unknown	North America
S. kitikmeotensis	Carnivora: mustelid (wolverine)	type 9h	unknown	North America, Eurasia
S. klaseriensis	Artiodactyla: giraffid (giraffe)	type 35	unknown	South Africa
S. kortei	Primates: cercopithecid (rhesus macaque, bonnet macaque, patas monkey, diademed monkey, sooty mangabey, Angolan talapoin)	type 10	unknown	Asia, Africa
S. lamacanis sp. inq. (syn. *S. lamacenis*)	Artiodactyla: camelid (llama, alpaca)	nr	Carnivora: canid (dog)	South America
S. lampropeltii	Rodentia: cricetid (prairie vole)	type 1a	Serpentes: colubrid (speckled kingsnake)	North America
S. leporum	Lagomorpha: leporid (eastern cottontail, mountain cottontail, marsh rabbit)	macrocysts type 10b	Carnivora: procyonid (raccoon), felid (cat)	North America
S. levinei	Artiodactyla: bovid (water buffalo)	macrocysts type 7a	Carnivora: canid (dog)	Asia, South America
S. lindemanni	Primates: hominid (humans)	nr	unknown	equatorial
S. lutrae	Carnivora: mustelid (American mink, beech marten, Eurasian badger, Eurasian otter, European polecat), canid (Arctic fox)	type 1a	unknown	Europe
S. markusi	Primates: cercopithecid (vervet monkey)	type 9i	unknown	Africa
S. marmosae	Didelphimorpha: didelphid (Linnaeus's mouse opossum)	finger-like villi	unknown	South America
S. medusiformis	Artiodactyla: bovid (sheep, argali)	macrocysts type 20	Carnivora: felid (cat)	Australia, New Zealand, Europe
S. melampi	Artiodactyla: bovid (common impala)	type 40	unknown	Africa
S. melis	Carnivora: mustelid (European badger, least weasel)	type 1f	unknown	Europe
S. menglaensis	Artiodactyla: tragulid (Williamson's mouse deer)	type 10f	unknown	China
S. mephitisi	Carnivora: mephitid (striped skunk)	type 9m	unknown	North America
S. micros	Artiodactyla: bovid (sheep)	type 27	Carnivora: canid (dog)	China
S. microti (syn. *Frenkelia microti*) [recently transferred to genus *Sarcocystis* on the basis of genotypic studies] [homonym overcome by renaming original *S.*	Rodentia: cricetid (short-tailed vole, common vole, American vole, prairie vole, Syrian hamster, European hamster), murid (wood mouse, yellow-necked mouse, striped field mouse, house mouse, Natal multimammate mouse, brown rat), chinchillid (long-tailed	lobulated cysts type 1a	Accipitriformes: accipitrid (common buzzard, red tailed hawk)	Northern Hemisphere

microti as *S. jaypeedubeyi*]	chinchilla); Lagomorpha: leporid (rabbit)			
S. miescheriana [type species] (syn. *suicanis*)	Artiodactyla: suid (pig)	type 10b	Carnivora: canid (dog, wolf, red fox, golden jackal, raccoon dog), procyonid (raccoon)	cosmopolitan
S. mihoensis	Artiodactyla: bovid (sheep)	macrocysts type 39	Carnivora: canid (dog)	Japan
S. mongolica	Artiodactyla: bovid (Mongolian gazelle)	macrocysts type 1c	unknown	Mongolia
S. montanaensis	Rodentia: cricetid (prairie vole, meadow vole, long-tailed vole)	type 1a	Serpentes: viperid (southern copperhead)	North America
S. moulei (syn. *S. caprifelis*)	Artiodactyla: bovid (goat)	macrocysts type 21	Carnivora: felid (cat)	Eurasia, Africa
S. mucosa	Diprotodontia: macropodid (allied rock wallaby, brush-tailed rock wallaby, Bennett's wallaby, Tasmanian pademelon)	macrocysts type 13	unknown	Australia
S. murinotechis	Rodentia: murid (black rat, bush rat, eastern swamp rat, long-tailed mouse, broad-toothed mouse), plus experimental infection in murid (house mouse, brown rat)	type 9b	Serpentes: elapid (black tiger snake)	Australasia
S. muris (syn. *S. musculi*)	Rodentia: murid (house mouse), plus diheteroxenous (rodent-rodent via cannibalism)	macrocysts type 1a	Carnivora: felid (cat), mustelid (ferret), plus sporocyst production in experimentally infected Rodentia: murid (mice)	cosmopolitan
S. muriviperae	Experimental infection in Rodentia: murid (house mouse)	type 18b	Serpentes: viperid (Palestinian viper), colubrid (black whipsnake)	Middle-East
S. nelsoni sp. inq.	Artiodactyla: bovid (waterbuck, kob, puku)	macrocysts	unknown	Africa
S. neotomafelis	Rodentia: cricetid (Southern Plains woodrat)	macrocysts type 1c	Carnivora: felid (cat)	Mexico
S. nesbitti	Primates: cercopithecid (rhesus macaque, long-tailed macaque, sooty mangabey, baboon), possibly hominid (human)	type 1	unknown	Africa, Indo-Asia
S. neurona	Perissodactyla: equid (horse, causes equine protozoal myeloencephalitis (EPM), zebra); Carnivora: procyonid (raccoon), mustelid (ferret, sea otter, mink, fisher), mephitid (striped skunk), felid (cat, bobcat), canid (dog), ailurid (red panda), phocid (Pacific Harbor seal), otariid (California sea lion), Artiodactyla: phocoenid (Pacific Harbor porpoise), Cingulata: dasypodid (nine-banded armadillo), Passeriformes: icterid (brown-headed cowbird), Pelecaniformes: threskiornithid (straw-necked ibis); experimental infections in Rodentia: murid (KO mice); DNA detection by PCR in other	type 11	Didelphimorphia: didelphid (Virginia opossum, white-eared opossum, common opossum)	Americas

	marine mammals (seals, dolphins, whales)			
S. novaki sp. inq.	Artiodactyla: bovid (cattle)	type 24	unknown	Central Asia
S. ochotonae	Lagomorpha: ochotonid (Daurian pika, plateau pika)	type 1a	unknown	China
S. odocoileocanis	Artiodactyla: cervid (whitetail, sika deer), bovid (cattle, sheep)	type 17	Carnivora: canid (dog, wolf, coyote, red fox, grey fox)	North America
S. odoi	Artiodactyla: cervid (white-tailed deer)	type 10a	Carnivora: felid (cat)	North America
S. oreamni	Artiodactyla: bovid (Rocky Mountain goat)	type 29	unknown	North America
S. orientalis sp. inq.	Artiodactyla: bovid (Siberian ibex)	macrocysts	unknown	Siberia
S. oryzomyos	Rodentia: cricetid (large-headed rice rat)	striated wall	unknown	South America
S. ovalis	Artiodactyla: cervid (moose, red deer)	macrocysts type 26	Passeriformes: corvid (hooded crow, magpie)	Europe
S. oviformis	Artiodactyla: cervid (European roe deer)	macrocysts	unknown	Europe
S. peromysci	Rodentia: cricetid (North American deermouse)	hairy protrusions	unknown	North America
S. phacochoeri	Artiodactyla: suid (warthog)	type 29b	unknown	South Africa
S. pilosa	Artiodactyla: cervid (sika deer)	type 7a	unknown	Europe
S. pitymysi sp. inq.	Rodentia: cricetid (Savi's pine vole)	nr	unknown	Europe
S. poephagi	Artiodactyla: bovid (yak)	macrocysts type 28	Carnivora: felid (cat)unknown	China
S. poephagicanis	Artiodactyla: bovid (yak)	macrocysts type 6/7	Carnivora: canid (dog)	China
S. porcifelis sp. inq.	Artiodactyla: suid (pig)	macrocysts thin striated wall	Carnivora: felid (cat)	Russia, Romania, Japan, India
S. proechimyos	Rodentia: echimyid (Guyenne spiny rat)	striated wall	unknown	South America
S. pseudois	Artiodactyla: bovid (naur)	type 14	unknown	China
S. putorii	Rodentia: cricetid (common European vole, field vole)	macrocysts type 9b	Carnivora: mustelid (common ferret, least weasel, stoat, mink)	Europe
S. rangi	Artiodactyla: cervid (reindeer)	type 7a	Carnivora: canid (Arctic fox, red fox)	Europe
S. rangiferi	Artiodactyla: cervid (reindeer, red deer)	macrocysts type 15a	unknown	Europe
S. rauschorum	Rodentia: cricetid (Richardson's collared lemming)	type 1h	Strigiformes: strigid (snowy owl)	North America
S. rhombomys	Rodentia: cricetid (great gerbil)	type 1	Carnivora: canid (red fox)	Central Asia
S. richardii	Carnivora: phocid (harbour seal)	macrocysts	unknown	Bering Sea
S. rommeli	Artiodactyla: bovid (cattle)	slender villar protrusions	Carnivora: felid (cat)	Asia
S. idahoensis	Rodentia: murid (North American deermouse)	thin wall	Serpentes: colubrid (Great Basin gopher snake)	North America
S. roudabushi	unknown		Serpentes: colubrid (gopher snake, black rat snake, fox snake)	North America
S. rzepcyzkii	Rodentia: murid (bush rat)	nr	Serpentes: boid (carpet python)	Australia
S. russuli sp. inq.	Eulipotyphla: soricid (greater white-toothed shrew)	nr	unknown	Central Asia
S. saiga sp. inq.	Artiodactyla: bovid (saiga	nr	unknown	Central Asia

	antelope)			
S. scandinavica	Artiodactyla: cervid (moose)	nr	unknown	Europe
S. scotti	Rodentia: murid (house mouse)	type 1	Strigiformes: strigid (tawny owl)	Eurasia
S. sebeki	Rodentia: muris (house mouse, wood mouse)	type 1b	Strigiformes: strigid (tawny owl)	Eurasia
S. sehi	Rodentia: erethizontid (North American porcupine)	type 1e	unknown	North America
S. sibirica	Artiodactyla: cervid (Siberian roe deer)	type 27	unknown	Asia
S. sigmodontis	Rodentia: cricetid (cotton rat)	macrocysts type 4	unknown	North America
S. silva	Artiodactyla: cervid (European roe deer, moose)	macrocysts type 10a	unknown	Europe
S. sinensis (syn. *S. dubeyi* or *vice versa*)	Artiodactyla: bovid (water buffalo)	type 10c	Carnivora: felid (cat)	Asia
S. singaporensis (replacement name for *S. orientalis* Zaman & Colley, 1975)	Rodentia: murid (brown rat, black rat, dusky rat, long-haired rat, Malaysian field rat, Polynesian rat, ricefield rats, bandicoot rats, yellow-haired hill rat, fraternal hill rat, Sulawesi giant rat, Musschenbroek's spiny rat, Bartel's spiny rat, yellow-tailed rat)	type 19	Serpentes: pythonid (reticulated python, rock python, Timor python, black-headed python)	Australasia
S. speeri	experimental infection in Rodentia: murid (immunodeficient mice)	macrocysts type 38	Didelphimorphia: didelphid (Virginia opossum, white-eared opossum, common opossum)	North America
S. suihominis (syn. *porcihominis*)	Artiodactyla: suid (pig)	macrocysts type 31	Primates: hominid (human, chimpanzee), cercopithecid (rhesus monkey, long-tailed macaque, yellow baboon)	Europe, India, Japan
S. sulawesiensis	Rodentia: murid (yellow-haired hill rat, fraternal hill rat, Sulawesi giant rat)	type 5	unknown	Indonesia
S. svanai	Carnivora: canid (dog, Pampas fox)	type 1a	unknown	North America
S. sybillensis (syn. *S. cervi*)	Artiodactyla: cervid (elk, red deer)	type 12	Carnivora: canid (dog, coyote)	Europe, North America
S. taeniata	Artiodactyla: cervid (Canadian moose, red deer, sika deer)	type 7a	unknown	Americas, Europe
S. talpini sp. inq.	Rodentia: cricetid (northern mole vole)	nr	unknown	Central Asia
S. tamanduae sp. inq.	Pilosa: myrmecophagid (collared anteater)	nr	unknown	South America
S. tarandi	Artiodactyla: cervid (reindeer, red deer)	type 10e	unknown	Europe
S. tarandivulpes	Artiodactyla: cervid (reindeer)	type 17	Carnivora: canid (Arctic fox, red fox, dog, raccoon dog)	Europe
S. taugulusi	Artiodactyla: tragulid (Williamson's mouse deer)	type 24	unknown	China
S. tenella (syn. *ovicanis*)	Artiodactyla: bovid (sheep, wild sheep, mouflon, chamois)	type 14	Carnivora: canid (dog, wolf, dingo, coyote, red fox, jackal, raccoon dog)	cosmopolitan

S. terrestri sp. inq.	Rodentia: cricetid (northern water vole)	hirsute protrusions	unknown	Central Asia
S. tupaia	Scandentia: tupaiid (northern treeshrew)	type 1a	unknown	China
S. tropicalis sp. inq.	unknown	nr	Carnivora: canid (golden jackal)	India
S. truncata	Artiodactyla: cervid (red deer)	thick finger-like protrusions	unknown	Europe
S. undulati	Rodentia: sciurid (long-tailed ground squirrel)	macrocysts	Carnivora: canid (red fox, corsac fox), mustelid (steppe polecat)	Central Asia
S. ursusi	Carnivora: ursid (American black bear)	type 9g	unknown	North America
S. villivillosi	Rodentia: murid (brown rat, black rat, ricefield rats, Malayan field rat, Polynesian rat, long-haired rat, dusky rat, bandicoot rats)	type 22	Serpentes: pythonid (reticulated python, Timor python, rock python, black-headed python)	Asia
S. vulpis sp. inq.	Carnivora: canid (red fox)	nr	unknown	Central Asia
S. wapiti	Artiodactyla: cervid (wapiti)	type 2	Carnivora: canid (dog, coyote)	Europe
S. wetzeli (syn. *Isospora wetzeli*)	unknown		Carnivora: canid (red fox)	Europe
S. woodhousei	Artiodactyla: bovid (Grant's gazelle, Thomson's gazelle, springbok, Kirk's dik-dik, eland, kewel)	type 29a	unknown	Africa
S. youngi	Artiodactyla: cervid (mule deer)	type 16	unknown	North America
S. zamani	Rodentia: murid (brown rat, black rat, Polynesian rat, Annandale's rat, bandicoot rat)	type 18c	Serpentes: pythonid (reticulated python)	Asia
S. zuoi	Rodentia: murid (brown rat)	type 17	Serpentes: colubrid (king rat snake)	China
Species with avian intermediate hosts				
S. accipitris sp. inq.	Experimental infection in Passeriformes: fringillid (canary)	nr	Accipitriformes: accipitrid (northern goshawk)	Europe
S. alectoributeonis	Galliformes: phasianid (chukar)	macrocysts	Accipitriformes: accipitrid (common buzzard)	Europe
S. alectorivulpes	Galliformes: phasianid (chukar)	type 9/10	Carnivora: canid (red fox, corsac fox)	Europe
S. albifronsi	Anseriformes: anatid (white-fronted goose)	type 9a	Carnivora: canid (Arctic fox)	Europe
S. ammodrami sp. inq.	Passeriformes: passerellid (grassland sparrow)	nr	unknown	South America
S. anasi	Anseriformes: anatid (mallard)	type 9a	unknown	Europe
S. aramidis sp. inq.	Gruiformes: rallid (slaty-breasted wood rail)	nr	unknown	South America
S. calchasi	Columbiformes: columbid (pigeon); plus captive Psittaciformes: psittaculid (princess parrot), cacatuid (long-billed corella, galah), plus experimental infections in Columbiformes: columbid (pigeon), Passeriformes: parid (great tit), Psittaciformes: cacatuid (cockateil)	type 1a	Accipitriformes: accipitrid (Eurasian sparrowhawk, northern goshawk)	Europe, North America
S. cheeli sp. inq.	unknown	nr	Accipitriformes: accipitrid (black kite)	India

S. chloropusae	Gruiformes: rallid (common moorhen)	type 10	unknown	Egypt
S. colii sp. inq.	Coliiformes: coliid (red-faced mouse bird)	macrocysts	unknown	nr
S. columbae	Columbiformes: columbid (wood pigeon)	type 1a	Accipitriformes: accipitrid (Eurasian sparrowhawk, northern goshawk)	Europe
S. cornixi	Passeriformes: corvid (hooded crow)	type 1g	Accipitriformes: accipitrid (Eurasian sparrowhawk, northern goshawk)	Europe
S. corvusi	Passeriformes: corvid (jackdaw)	type 1d	unknown	Central Asia
S. debonei sp. inq.	Passeriformes: icterid (cowbird)	nr	unknown	North America
S. falcatula	Passeriformes: cardinalid (rose-breasted grosbeak), icterid (cowbirds, grackles), meropid (carmine bee-eater); Cuculiformes: cuculid (guira cuckoo), Strigiformes: strigid (great horned owl), Accipitriformes: accipitrid (bald eagle, golden eagle); Columbiformes: columbid (Luzon bleeding-heart pigeon, Pinon's imperial pigeon, nutmeg imperial pigeon, Victoria crowned pigeon); Psittaciformes: psittacid (African grey parrot, burrowing parrot, Cuban amazon, vinaceous amazon, eclectus parrot, Meyer's parrot, Alexandrine parrot, ring-necked parakeet, thick-billed parrot), psittaculid (Weber's lorikeet, green naped lorikeet, ornate lorikeet, rainbow lorikeet, red lory, Duivenbode's lory, yellow-streaked lory, cardinal lory, violet-necked lory, yellow-bibbed lory, chattering lory, black-capped lory, Derbyan parakeet), cacatuid (Moluccan cockatoo, bare-eyed cockatoo, white cockatoo), and experimentally Columbiformes: columbid (pigeon), Passeriformes: fringillid (finch, canary), passerid (sparrow); Psittaciformes: psittaculid (budgerigar); Galliformes: numidid (guineafowl)	macrocysts type 11b	Didelphimorphia: didelphid (Virginia opossum, white-eared opossum, big-eared opossum, common opossum)	Americas
S. garzettae	Pelecaniformes: ardeid (little egret)	type 5	unknown	South Africa
S. halieti	unknown	nr	Accipitriformes: accipitrid (white-tailed sea eagle)	Norway
S. horvathi (syn. *S. gallinarum*)	Galliformes: phasianid (chicken)	macrocysts, striated wall	Carnivora: canid (dog), felid (cat)	Europe, Australasia, North America
S. jacarinae sp. inq.	Passeriformes: thraupid (blue-black grassquit)	nr	unknown	South America

S. kaiserae	Columbiformes: columbid (laughing dove)	type 9j	unknown	South Africa
S. kirmsei	Galliformes: phasianid (Siamese fireback)	type 9	unknown	Asia
S. lari	Charadriiformes: larid (great black-backed gull)	type 1d	Accipitriformes: accipitrid (white-tailed eagle)	Europe
S. lindsayi	experimental infection in Psittaciformes: psittaculid (budgerigar)	type 11d	Didelphimorphia: didelphid (white-eared opossum, big-eared opossum)	South America
S. nontenella sp. inq.	Accipitriformes: accipitrid (common buzzard)	nr	unknown	Eurasia
S. oliverioi sp. inq.	Psittaciformes: psittacid (green-rumped parrotlet)	nr	unknown	South America
S. otus	Accipitriformes: accipitrid (Eurasian buzzard), Strigiformes: strigid (long-eared owl)	hirsute protrusions	unknown	Germany
S. peckai	Galliformes: phasianid (common pheasant)	finger-like protrusions	Carnivora: canid (dog), felid (cat)	Europe
S. phoeniconaii	Phoenicopteriformes: phoenicopterid (lesser flamingo)	macrocysts type 9l	unknown	Africa
S. ramphastosi	Piciformes: ramphastid (keel-billed toucan)	macrocysts type 9e	unknown	ex: Central America
S. rileyi	Anseriformes: anatid (mallard, northern pintail, American wigeon, green-winged teal, northern shoveler, blue-winged teal, mottled duck, American black duck, wood duck, gadwall, lesser scaup, redhead, greater scaup, canvasback, Eurasian teal, Sunda teal, bufflehead, goldeneye, Eurasian wigeon, white-winged scooter, common eider)	macrocysts type 23	Carnivora: mephitid (striped skunk); canid (red fox, raccoon dog): Didelphimorpha: didelphid (North American opossum)	North America, Europe
S. setophagae	Passeriformes: parulid (American redstart)	macrocysts	unknown	North America
S. spaldingae	Pelecaniformes: ardeid (great blue heron, striated heron, great egret, little blue heron, white ibis, yellow-crowned night-heron)	macrocysts type 9	unknown	North America
S. sulfuratusi	Piciformes: ramphastid (keel-billed toucan)	type 9f	unknown	Central America
S. turdusi (incl. *turdi nomen nudum*)	Passeriformes: turdid (common blackbird)	type 18b	Accipitriformes: accipitrid (Eurasian sparrowhawk, northern goshawk)	Europe
S. wenzeli	Galliformes: phasianid (chicken)	type 9k	Carnivora: canid (dog), felid (cat)	Europe, China, Australasia
S. wobeseri	Anseriformes: anatid (barnacle goose, mallard)	type 1d		Europe
Species with reptilian intermediate hosts				
S. acanthocolubri	Sauria: lacertid (fringe-toed lizard, Bosc's fringe-toed lizard, leopard fringe-toed lizard)	macrocysts type 9d	Serpentes: colubrid (diadem snake)	Egypt
S. ameivamastigodryasi	Sauria: teiid (giant ameiva)	type 1b	Serpentes: colubrid (Rio tropical racer, Boddaert's tropical racer)	Brazil

S. atlanticae	Sauria: lacertid (Atlantic lizard), diheteroxenous	type 37	Sauria: lacertid (Atlantic lizard)	Canary Islands
S. atractaspidis sp. inq.	Serpentes: lamprophiid (Ogaden burrowing asp)	nr	unknown	Africa
S. bunopusi	Sauria: gekkonid (rock gecko)	type 1a	unknown	Saudi Arabia
S. chalcidicolubris	Sauria: scincid (ocellated skink, Gran Canarian skink, Canarian cylindrical skink)	type 1e	Serpentes: colubrid (spotted whip snake, Balkan racer, green whip snake, Dahl's whip snake)	Mediterranean
S. chamaeleonis	Sauria: chamaeleonid (Fischer's chameleon)	nr	unknown	Africa
S. ctenosauris sp. inq.	unknown	nr	Sauria: iguanid (black iguana)	Central America
S. dugesii	Sauria: lacertid (Madeiran wall lizard), diheteroxenous	type 17	Sauria: lacertid (Madeiran wall lizard)	Mediterranean
S. gallotiae	Sauria: lacertid (Tenerife lizard), diheteroxenous	type 37a	Sauria: lacertid (Tenerife lizard)	Canary Islands
S. gongyli	Sauria: lacertid (ocellated lizard)	type 9d	Serpentes: colubrid (diadem snake)	Sicily
S. kinosterni	Testudines: kinosternid (scorpion mud turtle)	thin wall	unknown	South America
S. lacertae	Sauria: lacertid (European wall lizard)	macrocysts type 37a	Serpentes: colubrid (smooth snake)	Europe
S. lacertaeutae (syn. *S. utae*)	Sauria: lacertid (common side-blotched lizard)	smooth	unknown	North America
S. mitrani	Sauria: scincid (Arabian sand skink)	macrocysts type 9d	unknown	Saudi Arabia
S. platydactyli	Sauria: phyllodactylid (Moorish gecko)	macrocysts striated wall	unknown	Mediterranean
S. platydactyliscleropori	Sauria: iguanid (western fence lizard)	thick wall	unknown	North America
S. podarcicolubris	Sauria: lacertid (ruin lizard, Tyrrhenian wall lizard, Erhard's wall lizard, Iberian wall lizard, Lilford's wall lizard, Dalmatian wall lizard, Milos wall lizard, Peloponnese wall lizard, Ibiza wall lizard, common wall lizard, sand lizard, Brown's rock lizard, Carpetane rock lizard, Anatolian rock lizard, Italian wall lizard, jewelled lacerta, sharp-snouted rock lizard, Balkan green lizard, Caucasus emerald lizard, meadow lizard, Armenian lizard, viviparous lizard, blue-throated keeled lizard)	type 9m	Serpentes: colubrid (green whip snake, Balkan racer, large whip snake, Dahl's whip snake, spotted whip snake, false smooth snake)	Europe
S. pythonis	Serpentes: pythonid (carpet python)	thin	unknown	Australia
S. schneideri	Sauria: scincid (barber skink)	type 1b	unknown	Egypt
S. scelopori	Sauria: iguanid (western fence lizard)	striated wall	unknown	North America
S. simonyi	Sauria: lacertid (El Hierro giant lizard), diheteroxenous	type 37a	Sauria: lacertid (El Hierro giant lizard)	Canary Islands
S. stehlinii	Sauria: lacertid (Gran Canaria giant lizard), diheteroxenous	type 7c	Sauria: lacertid (Gran Canaria giant lizard)	Spain
S. stenodactylicolubris	Experimental infections in Sauria: phyllodactylid (Sinai fan-fingered gecko), gekkonid (Jordan short-fingered gecko)	type 4	Serpentes: colubrid (Dahl's whip snake), plus experimental infection in colubrid (Roger's racer)	Middle-East

S. turcicii	Sauria: gekkonid (Mediterranean house gecko)	type 9d	unknown	Saudi Arabia
Species with piscine intermediate hosts				
S. salvelini sp. inq.	Salmoniformes: salmonid (brook trout)		unknown	North America

Parasite morphology: *Sarcocystis* spp. undergo 3 different developmental cycles in their hosts: typically involving 2 generations of asexual merogony (sometimes called schizogony) followed by tissue cyst formation in intermediate hosts; and then one generation of sexual gamogony (gamete formation) with fertilization producing zygotes (oocysts) that undergo sporogony (sporozoite formation) in definitive hosts. Meronts appear as pleomorphic basophilic bodies located within host endothelial cells: first-generation meronts (M1) in arterioles and second-generation meronts (M2) in capillaries. The meronts undergo internal (endogenous) division to form multiple merozoites (sometimes called tachyzoites). Undifferentiated M1 meronts appear as ovoid-ellipsoidal bodies (10-20 x 5-10 μm) which form elongate differentiated bodies (10-35 x 5-20 μm) containing numerous (10-40) uninucleate merozoites (1-8 x 0.5-3.0 μm). Undifferentiated M2 meronts appear as ovoid bodies (11-16 x 5-10 μm) which form elliptical thin-walled differentiated bodies (12-35 x 3-16 μm) containing numerous (3-50) uninucleate merozoites (1.5-5 x 0.5-2 μm). Tissue cyst (sarcocyst) formation occurs in striated muscles with the appearance of small elongate basophilic bodies (14-33 x 3-6 μm) that begin internal divisions. Cysts are initially thin-walled and microscopic in size (38-110 x 7-15 μm) containing numerous (14-85) undifferentiated spherical (3-5 x 1-3 μm) cells (metrocytes) around the periphery. Maturing cysts become larger (28-184 x 15-36 μm) and may cause host cell distention (the cysts of several species may grow to become macroscopically visible, up to 1 cm in diameter). The cysts are oval-elongate and cylindrical in shape (originally called Meischer's tubules) and are often white-cream in colour. Most cysts are septate and divided into compartments by an internal network of fibrils. Cysts contain several (0-40) spherical (2-5 x 2-4 μm) metrocytes as well as numerous (8-140) crescent-shaped bradyzoites (sometimes called cystozoites) initially being elongate (4-11 x 1.5 μm) but maturing to become banana-shaped (8-15 x 1-4 μm). Ultrastructural studies reveal the bradyzoites to possess an anterior conoid associated with electron-dense organelles (rhoptries and micronemes), lateral micropores, and rigid pellicles with 22 subpellicular microtubules. The cysts are bound by a thin primary cyst wall, comprising a thickened unit membrane with vesicle-like invaginations and species-specific protrusions. The primary cyst walls of some species appear thick (1.5-2.5 μm) and striated due to the presence of prominent radial protrusions. A few species (e.g. *S. gigantea*) also possess a secondary cyst wall consisting of amorphous granular and fibrillar material apparently deposited around the cyst by the host. Ultrastructural studies have, so far, identified 77 different cyst wall types for over 180 *Sarcocystis* spp. Sexual stages (both microgamonts (male) and macrogamonts (female)) develop directly in intestinal cells of definitive hosts, without any preceding asexual multiplication (merogony/schizogony). Macrogamonts form macrogametocytes that appear as ovoid (10-20 μm) lightly-basophilic cells that mature into single macrogametes with prominent lipid bodies and amylopectin granules. Microgamonts form microgametocytes that appear as ovoid-elongate (7 x 5 μm) darkly-basophilic cells which undergo internal division to form multiple (3-11) slender uninucleate microgametes (4 x 0.5 μm) which often appear as rosettes around the periphery. Microgametes are biflagellated and contained a compact nucleus, mitochondrion and 8-10 microtubules. Fertilization involves fusion of a macrogamete and a microgamete creating a zygote that develops into an oocyst. Developing oocysts form thick refractile membranous walls from eosinophilic wall-forming bodies and then begin sporogonous division. The inner mass (sporont) divides into 2 sporoblasts that each form a membrane-bound sporocyst, within which 4 sporozoites are formed (resulting in a typical 1:2:4 oocyst:sporocyst:sporozoite configuration, usually referred to as *Isospora*-like). *Sarcocystis* oocysts, however, are unusual in that endogenous sporulation occurs within the lamina propria of the gut (rather than exogenously outside the host)) and the resultant oocysts are thin-walled and often break apart so that free sporocysts are passed into the gut lumen. The sporocysts are small and oval (13-19 x 8-11 μm), lack Stieda bodies and contain 4 crescent-shaped sporozoites and a granular residual body.

Site of infection: In intermediate hosts, parasites first undergo several cycles of asexual proliferation in the endothelial cells of the host vasculature (arterioles then capillaries) followed by tissue cyst formation usually within striated (skeletal and cardiac) musculature. Some species also show an affinity for neural tissue, including peripheral nerve fibres and ganglia, cardiac Purkinje fibres, and white and grey matter in the spinal cord, cerebellum and cerebrum (notably *S. neurona* in horses). In definitive hosts, gamogony and sporogony occurs in subepithelial locations in the small intestines culminating in the excretion of free sporocysts. The genus *Sarcocystis* is biodiverse with many species occurring in many hosts (mammals, birds and reptiles), but the host specificity of individual species is often narrow, being confined to a small number of intermediate hosts and fewer definitive hosts. Some 88 *Sarcocystis* spp. have been found to form sarcocysts in around 227 mammalian hosts, comprising 62 artiodactylan species (bovid, camelid, cervid, delphinid, giraffid, hippopotamid, phocoenid, suid, tragulid), 7 perissodactyls (equids), 1 cetacean (balaenopterid), 1 cingulate (dasypodid), 9 lagomorphs (leporid, ochotonid), 1 pilosan (myrmecophagid), 1 scandentian (tupaiid), 4 didelphimorphs (didelphids), 5 diprotodonts (macropodid, potoroid), 2 eulipotyphlans (erinaceid, soricid), 82 rodents (caviid, chinchillid, cricetid, echimyid, erethizontid, murid, sciurid), 42 carnivores (ailurid, canid, felid, mephitid, mustelid, otariid, phocid, procyonid, ursid), and 10 primates (cercopithecid, hominid). Definitive hosts are known for only 85 of these parasite species, with sporocyst production found in 22 carnivore species (canid, felid, mustelid, procyonid), 3 didelphimorphs (didelphid), 5 primates (hominid, cercopithecid), 1 rodent (murid), 26 snake species (boid, colubrid, elapid, pythonid, viperid), and 13 bird species (accipitrid, falconid, corvid, strigid, tytonid). Another 37 parasite species have been found to form sarcocysts within some 100 avian hosts belonging to 28 families from 14 orders; including 4 Accipitriformes (accipitrid); 23 Anseriformes (anatid); 1 Charadriiformes

(larid); 1 Coliiformes (coliid); 7 Columbiformes (columbid); 1 Cuculiformes (cuculid); 4 Galliformes (numidid, phasianid); 2 Gruiformes (rallids); 7 Pelecaniformes (ardeids); 1 Phoenicopteriformes (phoenicopterid); 1 Piciformes (ramphastid); 31 Psittaciformes (cacatuid, psittacid, psittaculid); 2 Strigiformes (strigid); and 11 Passeriformes (cardinalid, corvid, fringillid, icterid, meropid, parid, parulid, passerellid, passerid, thraupid, turdid). Definitive hosts have been identified for only 17 parasite species of birds, with sporocyst formation reported in 7 mammalian carnivore species (canid, felid, mephitid), 5 didelphimorphs (didelphid), and 6 birds of prey (accipitrids). Around 25 *Sarcocystis* spp. have been reported to form sarcocysts in around 50 reptilian hosts, including 47 lizard species belonging to 7 families (mostly lacertids but also chamaeleonids, gekkonids, iguanids, phyllodactylids, scincids and teiids), 2 snakes species belonging to 2 families (lamprophiid and pythonid), and one tortoise species from one family (kinosternid). Definitive hosts are known only for 15 of these parasite species, all involving reptiles with sporocyst production found in 6 lizard species belonging to 2 families (iguanids and lacertids) and 13 snake species belonging to 2 families (mostly colubrids and one viperid).

Pathogenesis: Many *Sarcocystis* spp. have not been associated with any clinical disease, with infections in both intermediate hosts (herbivores) and definitive hosts (carnivores) remaining asymptomatic or subclinical. Some species, however, have been linked to disease (initially called sarcosporidosis, but now sarcocystosis): either systemic due to merogony and tissue cyst formation in intermediate hosts, or enteric due to gamogony in definitive hosts. Infections by tissue cysts (sarcocysts) are often latent without any overt pathology, even though they may elicit mild inflammation with cyst destruction (sometimes calcification) and host cell repair (e.g. muscular myophagia). Sarcocysts are often detected incidentally in wildlife, but some heavy infections by macroscopic cysts cause unsightly streaks in skeletal muscle bundles (notably in waterfowl and rodents). Infections by cysts are quite prevalent in domestic animals (especially ungulates), but occasionally chronic infections may cause muscle atrophy and myositis/myocarditis resulting in weakness, lameness, muscle pain, swelling and rarely paralysis. In some countries, infections by macroscopic cysts are classified as carcase lesions by meat inspection services, resulting in enforced carcase trimming or meat condemnation from human consumption, with attendant economic losses. Humans have occasionally been found infected with sarcocysts (around 100 cases worldwide), with some infections associated with malaise, nausea, muscle cramps, pain, swelling, weakness and fatigue. It is only relatively recently that experimental studies have shown that asexual stages preceding cyst formation may cause acute systemic disease in intermediate hosts due to vascular endothelial damage. First and second generation meronts lyse host endothelial cells (arterioles then capillaries) causing petechial haemorrhages throughout most organs and tissues. Heavy experimental infections in domestic livestock may cause acute transient disease around 4 weeks after infection with severe acute vasculitis, massive perivascular infiltration of mononuclear cells and multi-organ haemorrhages resulting in profound anaemia, fever, weakness, recumbency, sudden mortality, and reproductive losses through abortion and stillbirth in pregnant animals (but the parasites do not cross the placenta). Surviving animals sometimes developed subacute disease, exhibiting inappetence, weight loss, loss of hair or wool breakage, poor or stunted growth, muscle atrophy, lethargy, and weakness. Subclinical infections have also been associated with weaner illthrift, reduced weight gain, poor wool growth and reduced milk production. Experimental studies demonstrated that animals developed strong protective immune responses, with animals surviving acute disease becoming resistant to lethal challenge and disease. Acute disease is rarely seen in field conditions, presumably due to early low-dose exposures (e.g. trickle infections) protecting animals while allowing some parasites to develop and persist in host musculature (a state known as premunitive immunity). Nonetheless, natural infections have been linked to several instances of acute sarcocystosis in cattle (colloquially called Dalmeny disease) and an unusual aggressive form of disease in horses causing equine protozoal myeloencephalitis (EPM) with parasites occurring behind the blood-brain barrier in the spinal cord and brain resulting in neurologic disorders, encephalitis, seizures, paralysis and depression. Infections by sexual developmental stages (gamonts) and oocyst formation generally do not cause clinical signs in definitive hosts (primates, carnivores, snakes, birds), but some may cause enteric disease due to intestinal lesions, inflammation, epithelial flattening, villus atrophy and crypt hyperplasia resulting in abnormal function. Clinical signs include malabsorption, watery diarrhea, abdominal pain and distension, stomach ache, nausea, vomiting, fever and sometimes eosinophilia, rapid pulse and difficulty in breathing. Disease is usually mild and self-limiting with spontaneous recovery, but may occasionally be severe, particularly in immunocompromised patients, with protracted diarrhoea leading to dehydration and complications such as jaundice, cholestatic hepatitis, pruritic rashes and weakness.

Developmental cycle and mode of transmission: *Sarcocystis* spp. have heteroxenous (2-host) life-cycles involving predator-prey transmission between carnivorous definitive hosts (in which sexual development of the parasite occurs) and herbivorous/omnivorous intermediate hosts (in which asexual development occurs). Definitive hosts become infected by consuming meat containing tissue cysts whereas intermediate hosts become infected by ingesting sporocysts excreted by the definitive hosts. Once ingested, sporocysts are triggered to excyst by biochemical cues (low oxygen, pH and bile enzymes) facilitating the release of the contained sporozoites. Parasites then undergo asexual (merogonous) multiplication within host tissues: the site of development, number of generations, and number of progeny varying for each parasite species. Typically, motile sporozoites move through the gut wall into the circulation where they infect the endothelial cells of small arteries and arterioles throughout the body. They form first-generation meronts (M1) within 6-19 days of infection which produce numerous merozoites that are released by host cell lysis. These merozoites are swept downstream where they infect endothelial cells in capillaries in numerous sites (lymphatic, respiratory, urinary, digestive, nervous, muscular, reproductive, endocrine and dermal tissues and organs). They form second-generation meronts (M2) from 21-36 days after infection which produce numerous merozoites that are also released by host cell lysis. Merozoites then enter striated muscle cells, rounding up to form metrocytes and initiating cyst formation. Developing cysts are evident within 40-45 days of infection and they exhibit rapid metrocyte division over 5-10 days with cystozoite and cyst wall

formation occurring thereafter. The cyst maturation process takes around 2 months or so until the contained bradyzoites become infectious. The cysts may persist for months, even years, within host muscles where they are walled off from the immune system. When mature cysts are ingested by carnivores consuming infected flesh, the cyst wall is digested in the gut facilitating the release of the contained bradyzoites. The motile bradyzoites invade the lamina propria of the small intestines within 3-6 hours and commence sexual reproduction by gamogony (without any preceding asexual multiplication like other coccidia). Male and female gamonts develop into gametocytes which produce gametes in 1-2 days. Female gametocytes produce one uninucleate macrogamete, while male gametocytes produce several biflagellated microgametes which are released to find and fertilize receptive macrogametes. The resultant zygote develops into an oocyst within the gut wall, which then undergoes endogenous sporulation forming sporocysts and sporozoites while resident within the lamina propria of the gut wall. The *Isospora*-like oocysts (with 1:2:4 configuration) are thin-walled and break open so that free sporocysts are released into the gut lumen and excreted with host faeces. These sporocysts are immediately infectious for intermediate hosts via contaminated food and water (and do not require an exogenous maturation phase like some other coccidia). The prepatent period (time from infection to sporocyst excretion) ranges from 7-14 days, and the patent period (duration of sporocyst excretion) ranges from days to weeks depending on both host and parasite species. Humans may act as definitive or definitive hosts for several *Sarcocystis* spp.: developing enteric infections after eating raw or undercooked beef or pork containing mature sarcocysts of *S. hominis* (syn. *S. bovihominis*) or *S. suihominis* and shedding sporocysts 11-18 days later; or developing muscle cysts after consuming sporocysts voided by definitive hosts with predator-primate cycles (e.g. pythons with monkey prey). It is hoped that modern molecular genotypic characterization studies will help to identify these heteroxenous parasites.

Differential diagnosis: Infections are conventionally diagnosed by the detection of parasite developmental stages in host samples by microscopy. Enteric infections are diagnosed by the demonstration of characteristic sporocysts in faecal smears or concentrates (following floatation in high specific gravity salt or sugar solutions), in post-mortem gut scrapings (following enzymatic digestion to liberate parasites from subepithelial locations) or in gut tissues (stained histological sections). Different *Sarcocystis* spp. cannot be identified on the basis of sporocyst morphology as they are all very similar in size, shape and appearance. Muscle infections are diagnosed either by the detection of sarcocysts in biopsy or autopsy material (by macroscopic examination of fresh tissues or by microscopic examination of fresh squash (trichinoscopic) preparations or fixed stained histological sections) or the detection of bradyzoites in muscle digest sediments (following pepsin-acid digestion of ground meat samples). Medical imaging techniques (including computed tomography (CT) and magnetic resonance imaging (MRI)) have occasionally been used to demonstrate sarcocysts in host muscles (especially calcified cysts). A range of immunoserological techniques have also been developed to detect specific host antibodies against parasite antigens (including complement fixation, haemagglutination, immunofluorescence and enzyme imunoassays), with the detection of specific IgM or IgG antibodies indicating acute or chronic infections respectively. Polyclonal and monoclonal antibodies have been produced and used in immuno-histochemical studies to locate parasites in tissues. Immunoblotting techniques have also been used to detect parasite antigens in the cerebrospinal fluid from horses suffering from equine protozoal myeloencephalitis (EPM). Modern molecular biological techniques have recently been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear (18S and 23S ribosomal DNA) and mitochondrial (cytochrome c oxidase subunit 1) gene sequences.

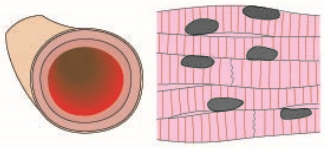
Treatment and control: A variety of chemicals have been used in attempts to treat infections in livestock, companion animals and miscellaneous wildlife. Treatment of enteric infections in carnivores is often not required as they are usually asymptomatic, transient and self-limiting. In exceptional cases, animals with clinical signs have responded well to treatment with anti-coccidial drugs, including ionophores (maduramicin), triazinones (toltrazuril, diclazuril), sulfonamides (sulfadiazine, co-trimoxazole), quinazolinones (halofuginone) and even some nitroimidazoles (tinidazole). Animals also benefited from supportive rehydration therapy, as well as concurrent antibiotic treatment for secondary bacterial infections. The treatment of livestock with chronic infections by tissue cysts is also not warranted as they do not cause clinical signs and the parasites are locked away in membrane-bound intracellular cysts. However, livestock experiencing acute clinical disease due to pre-cyst parasite proliferation within the vasculature have responded reasonably well to treatment with several anticoccidial drugs, including thiamine analogues (amprolium), ionophores (salinomycin), triazinones (toltrazuril, diclazuril), folic acid antagonists (pyrimethamine), diaminopyrimidines (trimethoprim), sulfonamides (sulfadiazine) and sulfanilamides (sulfamethoxazole). While treatment did not eliminate parasites, it significantly reduced their numbers thus curtailing overt pathology and providing sufficient time for the development of protective host immune responses. A variety of preventive control measures may be adopted to reduce the risk of parasite transmission between livestock and companion animals, mostly based around good hygiene and sanitation. Domestic carnivores should not have access to animal carcases and they should be prevented from hunting and from defaecating on pastures or fodder stores (outbreaks of Dalmeny disease have been attributed to the contamination of supplementary fodder by cats used to control rodent populations in haysheds). Meat infected with sarcocysts should not be fed to farm dogs and cats, but could be thoroughly cooked or deep-frozen to kill infectious bradyzoites. Livestock should have access to clean water that has not been contaminated by carnivore faeces, with conventional water treatment by chlorination and/or filtration effectively killing sporocysts. Despite common-sense interventions, parasite control may prove difficult due to the apparent ubiquitous nature of the organisms. In many instances, eradication and control may not be appropriate because lightly infected hosts are protected against acute disease, afforded by the development of premunitive immunity (where parasites are not eradicated but small numbers persist in tissues providing protection against superinfection). Hosts and parasites are said to have achieved enzootic stability which, paradoxically,

could be upset by control programs if parasite numbers are reduced to the point that hosts no longer develop protective immunity and become susceptible to acute disease.

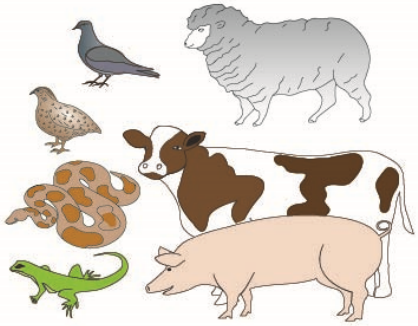
Sarcocystis

heteroxenous (2-host) cycle

predator-prey transmission
(predator ingests tissue cysts in prey)
(prey ingests sporocysts shed by predator)

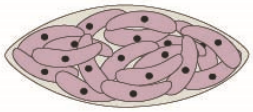


blood vessels, muscles
(petechial haemorrhages,
space-occupying lesions)

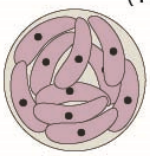


Intermediate Hosts
(mammals, esp. herbivores,
birds, reptiles)

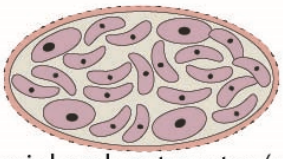
asexual merogony in
vascular endothelia
(arterioles then capillaries)



meronts
(10-35 µm)

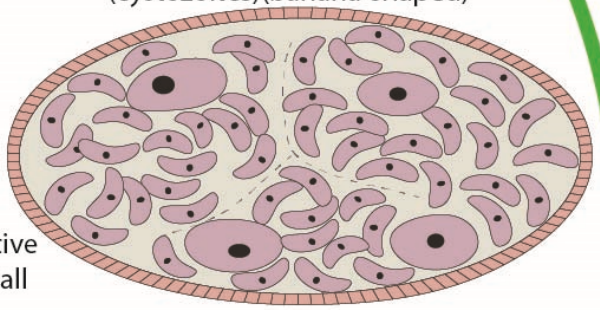


tissue cyst formation
in striated musculature



peripheral metrocytes (rounded)

numerous bradyzoites
(cystozoites)(banana-shaped)



distinctive
cyst wall

tissue cysts ('sarcocysts')
(30 µm - 1 cm)



excystation



sporocysts
ingested

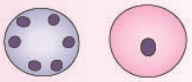


sporocyst
(13-19 µm)

sporocysts
excreted



tissue cysts
ingested



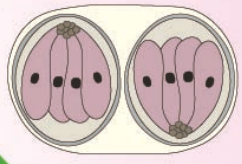
male
gamonts

female
(10-20 µm)

sexual
gamogony

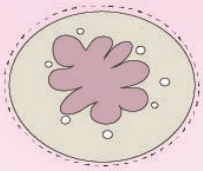


fertilization



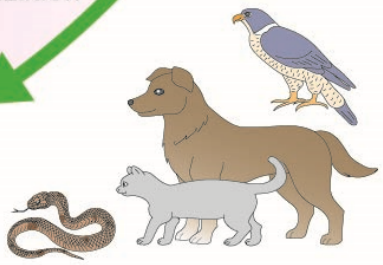
endogenous
sporogony &
sporulation

oocyst

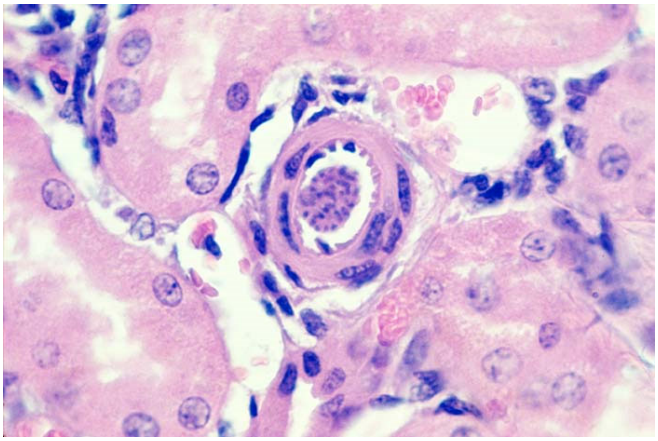


sporoblast

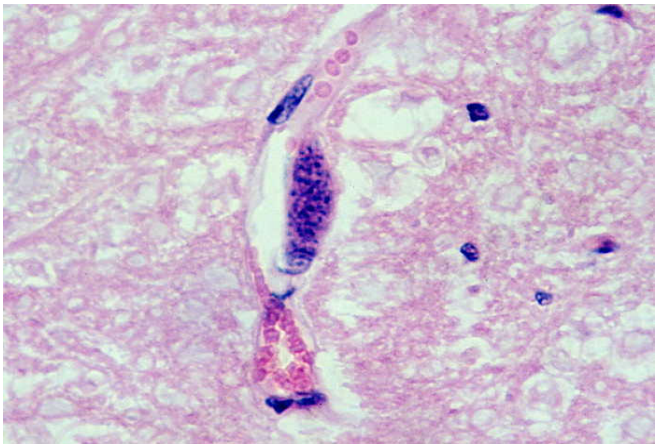
oocyst:sporocyst:sporozoite
configuration = 1:2:4



Definitive Hosts
(carnivores)
(intestines)



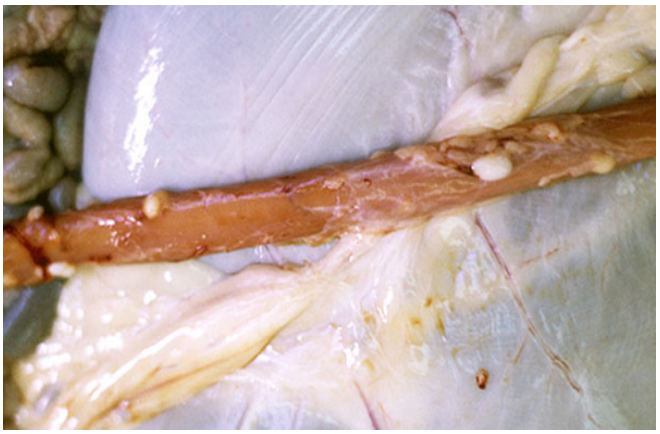
Sarcocystis schizont in sheep kidney arteriole



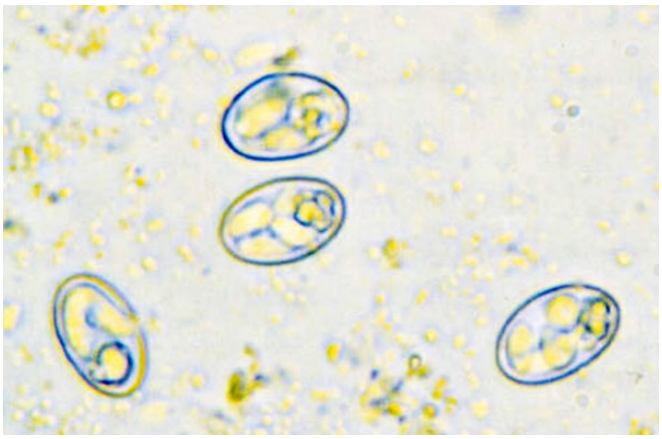
Sarcocystis schizont in sheep brain capillary



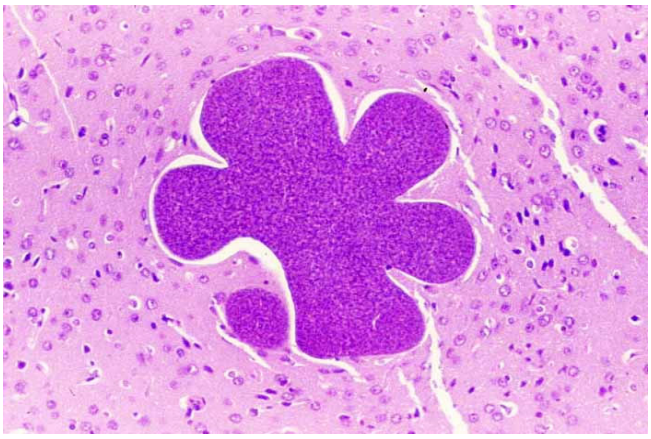
Sarcocystis thick-walled cyst in sheep muscle



Sarcocystis macrocysts on sheep oesophagus



Sarcocystis sporocysts from dog faeces



Sarcocystis (*Frenkelia*) cyst in rodent brain

Besnoitia
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). Tissue cyst-forming coccidia have heteroxenous (two-host) life-cycles alternating between enteric stages in predators (definitive hosts) and encysted stages in prey (intermediate) hosts. *Besnoitia* spp. form large globular cysts containing numerous bradyzoites (= cystozoites) predominantly in fibroblasts of domestic and wild ruminants and some marsupials. The cysts have exceptionally thick cyst walls and the host cell nucleus is enclosed within the cyst wall. Merogony (= schizogony), gamogony (male microgametes fertilize female macrogametes) and oocyst formation occurs in the intestinal epithelia of cats. Sporogony occurs exogenously and mature oocysts contain 2 sporocysts each with 4 sporozoites (1:2:4 configuration). Different species exhibit relative strict host specificity, with particular predator-prey combinations hosting individual species.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Eimeriorina (no syzygy, many microgametes)
Family:	Sarcocystidae (heteroxenous, oocysts with two sporocysts, tissue cyst formation in intermediate host)
Subfamily:	Toxoplasmatinae (metrocytes not present, thin cyst walls)
Genus:	*Besnoita* (tissue cyst-forming coccidian parasites of mammals/reptiles)
Species:	various species cause lesions/cysts in animals

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are

heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Numerous species of coccidia have been described from a wide range of vertebrate and invertebrate hosts. Some 50 genera have been classified in 11 families in the suborder Eimeriorina, including nine genera in the family Sarcocystidae. These apicomplexans are often referred to as cyst-forming coccidia, as they undergo gamogony and sporogony producing oocysts (1:2:4 oocyst:sporocyst:sporozoite configuration) in the intestines of carnivorous definitive hosts (DHs) as well as merogony and tissue cyst formation in the tissues of omnivorous or herbivorous intermediate hosts (IHs). They have heteroxenous (two-host) life-cycles with cyclic transmission between predatory animals and their prey. Two main subfamilies are recognized mainly on the basis of differences in cyst development (metrocytes present or absent) and site of oocyst sporulation (endogenous or exogenous). Members of the subfamily Sarcocystinae form cysts with metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate endogenously before being voided from the definitive host. Members of the subfamily Toxoplasmatinae form cysts without

metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate exogenously after being voided from the definitive host. A third subfamily has recently been added with the discovery that some *Isospora* spp. in mammals form encysted monozoic stages (cystozoites) in the tissues of paratenic (transport) hosts (esp. rodents), prompting their classification with the tissue cyst-forming coccidia under the name *Cystoisospora* in the new subfamily Cystoisosporinae.

Parasite genera	**No. spp.**	**Life-cycle**	**Definitive Hosts (DH) Intermediate Hosts (IH) Paratenic Hosts (PH)**	**Oocyst configuration***
Family: Sarcocystidae (3 subfamilies)				
Subfamily: Cystoisosporinae (monozoic cysts in PH, sporocysts without Stieda bodies)				
Cystoisospora	50	heteroxenous	vertebrate DH (carnivores, primates), vertebrate PH (mammals, birds)	1:2:4
Subfamily: Sarcocystinae (metrocytes, endogenous sporulation)				
Sarcocystis (incl. *Frenkelia*)	135	heteroxenous	vertebrate DH (predatory mammals, birds, reptiles), vertebrate IH (mammals, birds, reptiles)	1:2:4
Subfamily: Toxoplasmatinae (no metrocytes, exogenous sporulation)				
Toxoplasma	1	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals), invertebrate PH (annelids, insects)	1:2:4
Hammondia	3	heteroxenous	vertebrate DH (canids, felids), vertebrate IH (mammals)	1:2:4
Neospora	2	heteroxenous	vertebrate DH (canids), vertebrate IH (mammals)	1:2:4
Besnoitia	7	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals, reptiles), possibly invertebrate PH (insects)	1:2:4
Hyaloklossia	1	monoxenous	vertebrates (amphibians)	1:2:4
Nephroisospora	1	monoxenous	vertebrates (bats)	1:2:4

*1:2:4 = one oocyst contains 2 sporocysts, each sporocyst contains 4 sporozoites

The genera *Toxoplasma*, *Hammondia*, *Neospora* and *Besnoitia* are obligatory or facultatively heteroxenous with cyclic predator-prey transmission usually between carnivorous definitive hosts (DH) and herbivorous intermediate hosts (IH). Transmission from IH to DH occurs carnivorism (predator consuming cysts in tissues of prey) and transmission from DH to IH occurs via faecal-oral contamination (excretion of oocysts/sporocysts in faeces of predators to contaminate foodstuffs of prey). Several species are also di-heteroxenous (less common term di-homoxenous), meaning that infections can be passed horizontally between intermediate hosts by carnivorism (ingestion of tissue cysts in IH or PH) or vertically from mother to offspring (via transplacental or transmammary infection). These heteroxenous genera within the subfamily Toxoplasmatinae form tissue cysts without metrocytes, the bradyzoites undergo asexual division before gamete formation and the oocysts sporulate exogenously after being voided. More recently, encysted stages of two monoxenous genera (*Hyaloklossia* and *Nephroisospora*) have been found in the tissues of amphibians and bats, prompting their placement in the subfamily Toxoplasmatinae.

The genus *Besnoitia* comprises some 13 species which form large cysts (sometimes grossly visible) in the connective tissues (primarily fibroblasts) of a range of intermediate hosts (ruminants, horses, opossums, rodents and lizards). The intracellular cysts (sometimes called pseudocysts) lack subdivisions and are surrounded by thick laminated nucleated cyst walls. Several species have been associated with high morbidity and low mortality in ruminants and horses, with disease endemic in some tropical and subtropical areas, and sporadic in other areas. Experimental studies have revealed the definitive hosts for 5 *Besnoitia* spp. to be cats, which excrete small unsporulated isosporid oocysts in their faeces (oocyst:sporocyst:sporozoite configuration of 1:2:4 resembling those of *Toxoplasma*). Transmission between hosts has been demonstrated following oocyst ingestion (faecal-oral transmission from DH to IH), tissue cyst ingestion (predator-prey transmission from IH to DH) as well as mechanically by blood-sucking arthropods (vector-borne transmission between IHs).

***Besnoitia* species**	**Intermediate hosts (IH)**		**Definitive hosts (DH)**	**Distribution**
	Species	**Location**		
B. akodoni	Rodentia: cricetid (montane grass mouse), experimental infection in murid (house mouse, gerbil)	abdominal muscles	unknown	Brazil
B. bennetti	Perissodactyla: equid (horse, mule, burro, donkey)	eyes, mouth, testes, cutis,	unknown	Africa, Europe, North America

		subcutis		
B. besnoiti (type species)	Artiodactyla: bovid (cattle, zebu, water buffalo, sheep, goat, wild goat, blue wildebeest, impala, kudu, duiker), cervid (deer); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig), murid (house mouse, jird), sciurid (yellow ground squirrel, marmot), cricetid (golden hamster)	cutis, subcutis connective tissue, fascia, serosae, mucosae	Carnivora: felid (cat, African wild cat)	South America, Southern Europe, Africa, Asia
B. caprae	Artiodactyla: bovid (goat, sometimes sheep)		unknown	Africa, southern Europe, New Zealand
B. darlingi (syn. *B. panamensis, Sarcocystis darlingi*)	Didelphimorphia: didelphid (black-eared opossum, Virginia opossum, big-eared opossum, Derby's woolly opossum, grey four-eyed opossum); Primates: callitrichid (Geoffroy's tamarin); Chiroptera: phyllostomid (Seba's short-tailed bat); Rodentia: sciurid (red-tailed squirrel, variegated squirrel), murid (house mouse), cricetid (golden hamster); Sauria: corytophanid (common basilisk, brown basilisk), teiid (giant ameiva, tiger ameiva, delicate ameiva)	striated muscles, connective tissue	Carnivora: felid (cat)	Americas
B. jellisoni	Rodentia: murid (house mouse, brown rat), cricetid (North American deer mouse, cloud forest grass mouse, golden hamster, voles), heteromyid (kangaroo-rats), sciurid (ground squirrels), caviid (guinea pig); Didelphimorphia: didelphid (Virginia opossum)	connective tissue, serosae	unknown	North America
B. neotomofelis	Rodentia: cricetid (Southern Plains woodrat), plus experimental infection in murid (house mouse, brown rat); di-heteroxenous (IH-IH) transmission via carnivorism	muscles, subcutis	Carnivora: felid (cat)	North America
B. oryctofelis	Lagomorpha: leporid (rabbit), plus experimental infection in Rodentia: murid (mice, gerbil); Lagomorpha: leporid (rabbit); Carnivora: felid (cat)	tissues	Carnivora: felid (cat)	South America
B. panamensis	Sauria: corytophanid (brown basilisk), teiid (giant ameiva), plus experimental infection in Rodentia: murid (mouse)		unknown	Panama
B. paraguayensis	Cingulata: dasypodid (nine-banded armadillo)		unknown	South America
B. sauriana	Sauria: corytophanid (brown basilisk)		unknown	Belize
B. tarandi	Artiodactyla: cervid (reindeer, caribou, mule deer), bovid (musk ox)	fibrous connective tissue, skin (head, legs, scrotum) [alopecia, thickening, ulceration, 'cornmeal' disease]	unknown	Finland, Canada
B. wallacei (syn. *Isospora wallacei*)	Rodentia: murid (house mouse, brown rat, black rat, Polynesian rat, Mongolian gerbil), cricetid (Japanese grass vole); Lagomorpha: leporid (rabbit)	connective tissue	Carnivora: felid (cat)	Australasia, Hawaii

Parasite morphology: *Besnoitia* spp. form 5 different types of developmental stages: meronts and tissue cysts in intermediate hosts (IH); and meronts, gamonts and oocysts in definitive hosts (DH). Meronts (often called schizonts) in IH are small asexual multiplicative forms found in host cells (fibroblasts, macrophages, endothelial cells) as small basophilic rounded bodies (10-25 μm) that undergo internal division (endogeny) to produce numerous (4-20) daughter merozoites (often called tachyzoites) that are characteristically crescent- or banana-shaped (5-8 x 1-2 μm). Tissue cysts are larger encapsulated round-elongate stages formed within host cells (often fibroblasts). They may range in size from microscopic (~200 μm diameter) to macroscopic (up to several mm in diameter). Cysts have thick collagenous walls (10-100 μm thick) that also contain numerous hypertrophic host cell nuclei, and *Besnoitia* cysts have thick secondary cyst walls (unlike most other cyst-forming sporozoa). The cysts undergo repeated internal division to contain thousands of bradyzoites (cyst merozoites, cystozoites) which are elongate crescent-shaped cells (9 x 1.5 μm). Ultrastructural studies reveal bradyzoites to possess a conoid, rhoptries, micronemes and to be bound by pellicular membranes with 22 subpellicular microtubules. Meronts in DH are asexual stages found in subepithelial locations in the intestines, sometimes in extraintestinal tissues. They appear as round basophilic bodies (10-45 μm) that divide asexually to produce numerous (4-30) merozoites. Sexual development (gamogony) occurs in goblet cells in the small intestinal epithelium, with sexually-dimorphic gamonts producing gametes. Macrogamonts (female) develop into rounded macrogametocytes (12-18 μm) which mature to form single macrogametes that are uninucleate egg-like cells with many cytoplasmic vacuoles. Microgamonts (male) form basophilic microgametocytes (10-15 μm) that divide internally to produce multiple (4-8) microgametes that are small slender biflagellated sperm-like stages (4 x 1 μm). Fertilization occurs by fusion of macro- and micro-gametes producing zygotes that form oocysts which are excreted unsporulated. Developing oocysts are surrounded by thin membranous walls and they undergo internal sporulation (sporogony) to produce 2 sporocysts, each of which produces 4 sporozoites (resulting in *Isospora*-like oocysts with 1:2:4 oocyst:sporocyst:sporozoite configuration). The oocysts are ovoid (11-17 x 11-12 μm) and lack micropyles and polar granules. The sporocysts are elliptical (8-11 x 6-8 μm) and lack Stieda bodies. The sporozoites are slender crescent-shaped cells (4-6 x 2 μm) which often have refractile bodies.

Site of infection: Asexual development of the parasite takes place in intermediate hosts (usually herbivores), with meronts forming in vascular endothelial cells or connective tissues cells (fibroblasts, macrophages) in various host tissues and organs, followed by cyst formation in connective tissues (mainly fibroblasts), particularly in the skin, mucous and serous membranes (e.g. conjunctiva, mesentery) and scrotum. Infections by tissue cysts have been recorded in small but diverse array of vertebrates, including 15 artiodactylan species (mainly bovids, some cervids), 4 perissodactylans (equids), 20 rodents (caviids, cricetids, heteromyids, murids, sciurids), 5 opossums (didelphids), one lagomorph (leporid), one bat (phyllostomid), one cingulate (dasypodid), one primate (callitrichid) and 5 lizard species (corytophanids, teiids). Both asexual and sexual reproduction of the parasite occurs in definitive hosts (some carnivores), with one merogonous generation developing in the lamina propria of the small intestines; followed by gamete formation, fertilization and oocyst formation in epithelial cells (usually goblet cells). In those *Besnoitia* spp. for which life-cycles have been determined (namely, *B. besnoiti, darlingi, neotomofelis, oryctofelis, wallacei*), sexual development apparently occurs exclusively in felids (cats).

Pathogenesis: Many infections are asymptomatic and often go unnoticed, but some may cause acute or chronic clinical disease known as besnoitiosis (originally called globidiosis) which varies in severity from mild to fatal. In cattle, disease (also known as bovine elephantiasis, bovine anasarque, or elephant skin disease) occurs in 2 stages: an acute 'anasarca' stage associated with painful swellings; and a chronic 'scleroderma' stage associated with thickening and hardening of the skin. Acute disease is caused by meronts proliferating in vascular endothelial cells causing focal lesions, necrosis of venules and arterioles, thrombosis and vasculitis. Small white elevated macules may be observed on the scleral conjunctiva and nasal, pharyngeal and laryngeal mucosa. Animals may develop transient hyperthermia or fever (40-41.6°C) for 3-10 days with warm painful swellings (anasarca) occurring mainly in ventral parts of the body, but oedema contributing to respiratory disorders, orchitis and limps. Other signs include congestive mucosa, lacrimation, rhinitis with increased nasal discharge (initially serous, but may become mucopurulent and contain blood), tachycardia, swollen lymph nodes, diarrhoea, anorexia, weight loss, depression and photophobia. Acute signs may last for 1-3 weeks and then subside as the parasites begin cyst formation exhibiting a special tropism for connective tissues throughout the body. Chronic infection then develops as cysts grow, fill with bradyzoites and become encapsulated by thick collagenous cyst walls. Cysts occur in the dermis, subcutis, fascia, mucosa of the upper respiratory tract, pharynx, conjunctiva, lower reproductive tract in females and testes and epididymis in males and become fully developed within 4-7 weeks of infection. Their presence may cause debilitating disease characterized by cellular destruction, inflammation (including granulomatous reactions against ruptured cysts) and gross disfigurement of the skin with alopecia, dermatitis, eczema, hyperpigmentation, hyperkeratosis and scleroderma (hardened thickened skin). Heavy infections may result in wrinkled corrugated skin thrown into folds around the neck, shoulders, rump and carpal/tarsal areas, with nodules, scars and cracks allowing secondary bacterial infections and myiasis. Other signs include focal disseminated myositis, periostitis, endostitis, lymphadenitis, arteritis, perineuritis, pneumonia, periorchitis, orchitis, epididymitis, anorexia, emaciation, lethargy, and death (reports of up to 10% mortalities). Males may also become sterile due to aspermatogenesis caused by necrotizing orchitis with testicular atrophy and induration. Chronic infections have been associated with production losses in livestock, through unsightly lesions, disfigurement, damaged hides, reduced milk production, infertility/sterility in males, and sometimes abortion due to persistent fever in dams (but parasites do not cross the placenta). Infections in goats mostly involve chronic disease with dermatitis of the ventral abdomen and legs varying from mild thickening with superficial scaling to marked scleroderma with hyperpigmentation and sometimes serous discharges. Infections in equids may cause small white nodules on the sclera, nares, soft palate, pharynx, larynx causing nasal discharges and inspiratory dynspoea as well as skin lesions on the ventral

abdomen and legs often associated with exercise intolerance. Unusual cases have been reported in kangaroos suffering, and occasionally dying, from nose-bleeds (epistaxis), with parasites detected in nasal flushes.

Developmental cycle and mode of transmission: Studies have shown that some *Besnoitia* spp. have heteroxenous life cycles where cysts in herbivorous intermediate hosts are infective to carnivorous definitive hosts resulting in oocyst production. Cats have been found to act as definitive hosts for several species (*B. besnoiti, darlingi, neotomofelis, oryctofelis, wallacei*) but the life-cycles for the remaining species have yet to be determined. When cats consume infected flesh, the tissue cysts are digested in the gut facilitating the release of the contained bradyzoites which invade the lamina propria in the small intestines. The parasites undergo one asexual generation forming meronts over 4-13 days which produce and release numerous tachyzoites. These cells invade goblet cells in the mucosal epithelium and undergo sexual reproduction ultimately producing macrogametes (female) and microgametes (male) which fuse to form zygotes that differentiate into oocysts. Unsporulated oocysts are excreted with host faeces and undergo exogenous sporulation in 2-3 days, each oocyst forming 2 sporocysts, and each sporocyst forming 4 sporozoites (1:2:4 configuration). The prepatent period (time interval from infection to oocyst production) ranges from 9-14 days, and the patent period (duration of oocyst excretion) ranges from 3-13 days. The oocysts are highly resistant to external environmental conditions and contaminate food and water supplies. When susceptible intermediate hosts ingest infective oocysts, they excyst in the small intestines releasing the contained sporozoites. The sporozoites invade vascular endothelial cells and connective tissue cells (fibroblasts and macrophages) where they undergo asexual proliferation forming meronts that produce numerous tachyzoites. The tachyzoites the invade connective tissue cells (mainly fibroblasts) where they initiate cyst formation around 30-36 days after infection. The cysts mature over several weeks to months, some growing to macroscopic size and containing thousands of bradyzoites. The parasite life-cycle is completed when cysts are consumed by carnivorous definitive hosts. In addition to heteroxenous predator-prey transmission, experimental studies have shown that some *Besnoitia* spp. can be transmitted horizontally between hosts by needle inoculation of tachyzoites or bradyzoites. Because many outbreaks of disease in cattle or goats occur in fly seasons, it has been postulated that biting insects may be important vectors or paratenic hosts. Mechanical transmission by biting arthropods has been mooted for *B. tarandi* and *B. caprae* and demonstrated for *B. besnoiti* via tsetse flies (*Glossina*), stable flies (*Stomoxys*) and horse flies (*Tabanus, Atylotus*). There is no evidence to support transplacental or venereal transmission, despite occasional abortions in pregnant animals (thought to be due to persistent fever) and the high prevalence of scrotal infections in males.

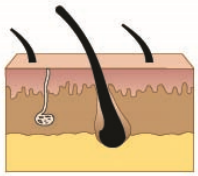
Differential diagnosis: Infections may be diagnosed in intermediate hosts by the direct detection or cultivation of parasites in clinical samples, by the immunological detection of specific host antibodies against parasites, or by the molecular detection of parasite DNA in host materials. Animals may be subject to antemortem clinical examination looking for tissue cysts in subcutaneous tissues, scleral conjunctiva or nasal mucosa. Biopsy material may be collected, including scrapings (skin, scleral conjunctiva, vestibulum vaginae), punch or incisional biopsies, needle aspirates, and blood), and smears or trichinoscopic squash preparations examined for characteristic crescent-shaped bradyzoites. More frequently, tissue cysts are detected at autopsy by gross or microscopic examination. Tissues may be fixed and histological sections examined for parasites following staining with haematoxylin and eosin or Giemsa. Polyclonal and monoclonal antibodies have also been produced against tachyzoites and bradyzoites and used for the immuno-localization of parasites in tissue preparations by fluorochrome or chromogenic labelling. Parasites may be readily cultured *in vitro* one various tissue culture cell lines, including primary bovine umbilical vein endothelial cells (BUVEC), African green monkey kidney cells (CV-1, MARC-145) and bovine macrophages (M617), as well as *in vivo* by needle passage in laboratory mice (including interferon-gamma gene knockout mice) or Mongolian gerbils. Experimental studies have examined changes in haematological and biochemical parameters during infection, noting reduced leukocyte and erythrocyte concentrations, haematocrit, serum albumin, urea, magnesium and calcium concentrations, elevated serum total protein, globulin, total bilirubin, creatinine, creatine kinase, and aspartate transaminase, but most findings could be attributed to inflammation and muscle necrosis. Several immunological techniques (indirect fluorescent-antibody tests, microagglutination tests, enzyme immunoassays) have been developed to detect host antibodies against parasite antigens, with considerable variability observed in their sensitivity and specificity depending on antigen types (tachyzoites/bradyzoites, cultured/harvested cells, whole/subcellular fractions), reagent fidelity (antiserum specificity, immunoglobulin classes, contaminants (e.g. foetal bovine or horse serum used in culture medium) and possible concomitant infections by related cyst-forming sporozoa (notably *Neospora caninum* and *Toxoplasma gondii*). Immunoblot techniques have also been used to detect parasite antigens in host sera, with some variability observed under reducing or non-reducing run conditions. More recently, molecular biological techniques have been applied to the detection and characterization of parasites in blood, biopsy and necropsy samples following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (18S and 5.8S ribosomal DNA, internal transcribed spacer region 1, protein disulphide isomerase) or by genotyping at 6 microsatellite loci (Bt-5,6,7,9,20,21).

Treatment and control: A wide range of chemotherapeutic agents have been used in attempts to treat or prevent *Besnoitia* infections in animals, but few have been effective. Treatments with semimetallic compounds (antimony) and sulphonamide antibiotics (sulfanilamide) were found to suppress cyst development in rabbits, and treatments with tetracycline antibiotics (oxytetracycline) were moderately effective if given early enough in the course of disease. However, the use of more regular antiprotozoal drugs, including thiazolides (nitazoxanide, tizoxanide), sulphonamides (sulfadiazine), bumped kinase inhibitors, triazinones (diclazuril, toltrazuril, ponazuril), quinolones (decoquinate) and naphthoquinones (buparvaquone), were ineffective.

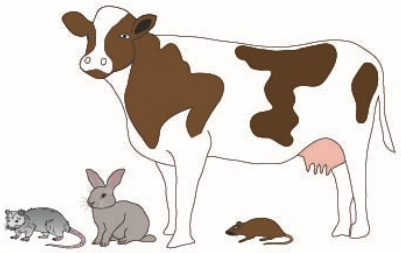
Experimental *in vitro* studies found that polyphenolic compounds (curcumin) were effective against *Besnoitia* tachyzoites in tissue culture, but in vivo studies are outstanding. Some enteric infections in cats responded well to treatment with lincosamide antibiotics (clindamycin), but the effect of conventional anti-coccidial drugs on oocyst production remains to be determined. Preventive measures focus on reducing the risks of transmission through health surveillance, biosecurity and herd management. Animals should be regularly tested with screening carried out in intensive systems prior to moving livestock indoors. Infected animals should be isolated and/or culled from herds, and all new replacement stock screened for infections, in quarantine if necessary. It is advisable to maintain closed herds and to avoid co-mingling and sharing pastures. This includes not sharing bulls, but rather to using artificial insemination programs involving seronegative bulls. Farms should endeavour to keep cats away from supplementary food storage areas and to adopt alternative rodent control measures if required. Despite supporting evidence, cattle isolated and protected from arthropod ectoparasites would be less at risk from any horizontal mechanical transmission involving biting insects. The use of indoor traps, repellents (diethyl-meta-toluamide (DEET), pyrethroids), insecticides (novaluron) and insect growth regulators (cyromazine) in pens and feeding sites have helped reduce muscid and tabanid fly numbers and their activity during peak fly season. Several experimental vaccines have been developed using live attenuated cultures of parasites, and they are used in several countries to prevent infections in cattle, especially in imported bulls.

Besnoitia

heteroxenous (2-host) cycle
predator-prey transmission
(predator ingests tissue cysts in prey)
(prey ingests sporocysts shed by predator)



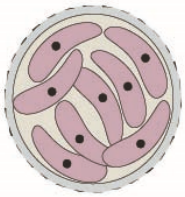
connective tissues, skin
(space-occupying lesions,
dermatitis, scleroderma)



Intermediate Hosts (IH)
(mammals, esp. ungulates,
rodents, lagomorphs)

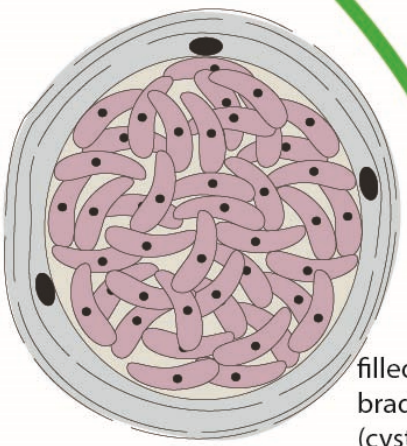
asexual merogony in
reticuloendothelial cells

tissue cyst formation
in fibroblasts





meronts
(10-25 µm)



thick collagenous
cyst wall with
hypertrophic
host cell nuclei

filled with
bradyzoites
(cystozoites)

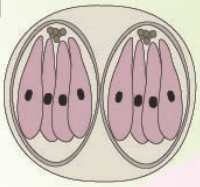
tissue cysts
(200 µm - 5 mm)



excystation



oocysts
ingested



oocyst
(11-17 µm)
sporocysts
(8-11 µm,)

tissue cysts
ingested



meronts (10-45 µm)

oocysts
excreted





male
gamonts (10-20 µm)

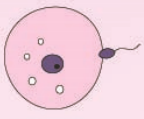
female



exogenous
sporulation



sporoblast



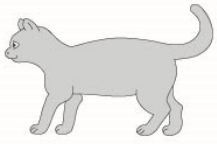
fertilization

sexual
gamogony

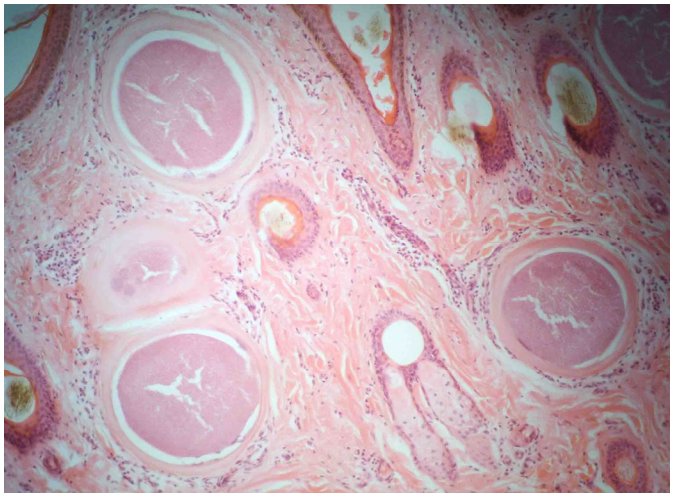


Possible Paratenic Hosts
(IHs may sometimes be infected
by mechanical transport of
zoites by biting flies)

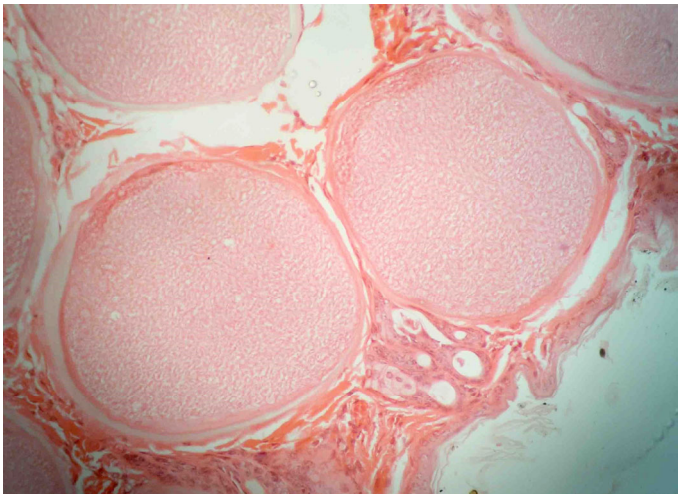
oocyst:sporocyst:sporozoite
configuration = 1:2:4



Definitive Hosts
(felids, intestines)
(mild enteritis)



Besnoitia cysts in cow skin



Besnoitia cysts in cow skin



Besnoitia oocyst from cat faeces

Neospora
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). Tissue cyst-forming coccidia have heteroxenous (two-host) life-cycles alternating between enteric stages in predators (definitive hosts) and encysted stages in prey (intermediate) hosts. *Neospora* spp. only form oocysts in dogs – merogony (= schizogony), gamogony (male microgametes fertilize female macrogametes) and oocyst formation occur in the intestinal epithelia. Sporogony occurs exogenously and mature oocysts contain 2 sporocysts each with 4 sporozoites (1:2:4 configuration). Thick-walled tissue cysts filled with bradyzoites (= cystozoites) are formed in the central nervous systems of domestic ruminants, horses and dogs following merogonous division of tachyzoites in macrophages. Enteric infections in dogs appear to be asymptomatic but systemic infections may produce neurological lesions in dogs as well as abortion and neonatal mortalities in ruminants, especially cattle.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Eimeriorina (no syzygy, many microgametes)
Family:	Sarcocystidae (heteroxenous, oocysts with two sporocysts, tissue cyst formation in intermediate host)
Subfamily:	Toxoplasmatinae (metrocytes not present, thin cyst walls)
Genus:	*Neospora* (tissue cyst-forming coccidian parasites of mammals)
Species:	several species cause neosporosis in ruminants, equids and canids

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid

coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Numerous species of coccidia have been described from a wide range of vertebrate and invertebrate hosts. Some 50 genera have been classified in 11 families in the suborder Eimeriorina, including nine genera in the family Sarcocystidae. These apicomplexans are often referred to as cyst-forming coccidia, as they undergo gamogony and sporogony producing oocysts (1:2:4 oocyst:sporocyst:sporozoite configuration) in the intestines of carnivorous definitive hosts (DHs) as well as merogony and tissue cyst formation in the tissues of omnivorous or herbivorous intermediate hosts (IHs). They have heteroxenous (two-host) life-cycles with cyclic transmission between predatory animals and their prey. Two main subfamilies are recognized mainly on the basis of differences in cyst development (metrocytes present or absent) and site of oocyst sporulation (endogenous or exogenous). Members of the subfamily Sarcocystinae form cysts with metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate

endogenously before being voided from the definitive host. Members of the subfamily Toxoplasmatinae form cysts without metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate exogenously after being voided from the definitive host. A third subfamily has recently been added with the discovery that some *Isospora* spp. in mammals form encysted monozoic stages (cystozoites) in the tissues of paratenic (transport) hosts (esp. rodents), prompting their classification with the tissue cyst-forming coccidia under the name *Cystoisospora* in the new subfamily Cystoisosporinae.

Parasite genera	**No. spp.**	**Life-cycle**	**Definitive Hosts (DH) Intermediate Hosts (IH) Paratenic Hosts (PH)**	**Oocyst configuration***
Family: Sarcocystidae (3 subfamilies)				
Subfamily: Cystoisosporinae (monozoic cysts in PH, sporocysts without Stieda bodies)				
Cystoisospora	50	heteroxenous	vertebrate DH (carnivores, primates), vertebrate PH (mammals, birds)	1:2:4
Subfamily: Sarcocystinae (metrocytes, endogenous sporulation)				
Sarcocystis (incl. *Frenkelia*)	135	heteroxenous	vertebrate DH (predatory mammals, birds, reptiles), vertebrate IH (mammals, birds, reptiles)	1:2:4
Subfamily: Toxoplasmatinae (no metrocytes, exogenous sporulation)				
Toxoplasma	1	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals), invertebrate PH (annelids, insects)	1:2:4
Hammondia	3	heteroxenous	vertebrate DH (canids, felids), vertebrate IH (mammals)	1:2:4
Neospora	2	heteroxenous	vertebrate DH (canids), vertebrate IH (mammals)	1:2:4
Besnoitia	7	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals, reptiles), possibly invertebrate PH (insects)	1:2:4
Hyaloklossia	1	monoxenous	vertebrates (amphibians)	1:2:4
Nephroisospora	1	monoxenous	vertebrates (bats)	1:2:4

*1:2:4 = one oocyst contains 2 sporocysts, each sporocyst contains 4 sporozoites

The genera *Toxoplasma*, *Hammondia*, *Neospora* and *Besnoitia* are obligatory or facultatively heteroxenous with cyclic predator-prey transmission usually between carnivorous definitive hosts (DH) and herbivorous intermediate hosts (IH). Transmission from IH to DH occurs carnivorism (predator consuming cysts in tissues of prey) and transmission from DH to IH occurs via faecal-oral contamination (excretion of oocysts/sporocysts in faeces of predators to contaminate foodstuffs of prey). Several species are also di-heteroxenous (less common term di-homoxenous), meaning that infections can be passed horizontally between intermediate hosts by carnivorism (ingestion of tissue cysts in IH or PH) or vertically from mother to offspring (via transplacental or transmammary infection). These heteroxenous genera within the subfamily Toxoplasmatinae form tissue cysts without metrocytes, the bradyzoites undergo asexual division before gamete formation and the oocysts sporulate exogenously after being voided. More recently, encysted stages of two monoxenous genera (*Hyaloklossia* and *Nephroisospora*) have been found in the tissues of amphibians and bats, prompting their placement in the subfamily Toxoplasmatinae.

The genus *Neospora* was described in the 1980s as the aetiological agent of a unique neurological disease involving hindlimb paralysis in dogs, while subsequent studies found it to be a major cause of abortion in both beef and dairy cattle around the world. The parasite was similar to *Toxoplasma*, but *Neospora* tissue cysts had thicker walls (1–4 cf. 0.5 µm), were more restricted to neural tissue (cf. many tissues for *Toxoplasma*), and were antigenically distinct (exhibiting little cross-reactivity with *Toxoplasma*). Infections have been reported in a wide range of intermediate hosts, especially carnivores (12 families), several ungulates (bovids, cervids and equids), a few birds (passerids, corvids and accipitrids), and experimentally to rodents. Experimental transmission studies found the definitive hosts for *Neospora* to be canids (dogs, wolves, foxes) rather than felids (as occurs for *Toxoplasma*). It appears that all life-cycle stages; namely, tachyzoites (in meronts), bradyzoites (in tissue cysts), and sporozoites (in oocysts) are infectious for both intermediate and definitive hosts, and transmission has been confirmed by oocyst ingestion (faecal-oral transmission), tissue cyst ingestion (predator-prey transmission) and transplacental passage (vertical transmission). Molecular characterization studies using multiple gene sequences have identified 2 *Neospora* spp.; *N. caninum* in dogs, cattle, sheep, goats, horses and deer in North America, Europe and Australia; and *N. hughesi* in horses with neurological disease in North America.

***Neospora* species**	**Intermediate hosts (IH)**	**Definitive hosts**	**Distribution**
N. caninum	Carnivora: canid (dog), ursid (brown bear), hyaenid (spotted hyena), mustelid (fisher, Eurasian badger, pine martin, European polecat,	Carnivora: canid (dog, dingo, bush dog, coyote, culpeo, red fox, gray fox,	worldwide

	ferret, ermine, beech marten, American mink, Eurasian otter, North American river otter, sea otter), herpestid (Egyptian mongoose), viverrid (common genet), ailurid (red panda), procyonid (raccoon), felid (cat, wildcat, cheetah, caracal, colocolo, Geoffroy's cat, ocelot, little spotted cat, serval, lynx, fishing cat, puma, jaguar, jaguarundi, leopard, clouded leopard, snow leopard, tiger, lion), otariid (sea lion), phocid (bearded seal, harbor seal, ribbon seal, ringed seal, spotted seal), odobenid (walrus); Artiodactyla: bovid (cattle, buffalo, sheep, goat), cervid (deer, whitetail), Perissodactyla: equid (horse), Galliformes: phasianid (chicken), Passeriformes: corvid (magpie), passerid (house sparrow): Accipitriformes: accipitrid (buzzards); plus experimental infection in Rodentia: murid (rat, mouse, gerbil), Lagomorpha: leporid (rabbit), Artiodactyla: suid (pig), Carnivora: canid (dingo, fox); also diheteroxenous (IH-IH) vertical (transplacental) transmission.	crab-eating fox, fennec fox, Pampas fox, hoary fox, blue fox, Chiloe fox, maned wolf, Eurasian wolf, gray wolf, golden jackal, raccoon dog)	
N. hughesi	Perissodactyla: equid (horse) [cause of equine protozoal myeloencephalitis (EPM)]	unknown	North America

Parasite morphology: *Neospora* spp. form 4 different types of developmental stages: meronts producing tachyzoites, cysts producing bradyzoites, gamonts producing gametes, and oocysts producing sporocysts and sporozoites. Meronts (sometimes called schizonts) are asexual proliferative forms located within parasitophorous vacuoles in a range of cells in intermediate hosts. The appear as rounded basophilic bodies (10-20 µm) that undergo rapid internal division (repeated endodyogeny) to form numerous (4-20) merozoites (usually called tachyzoites – 'tachy' meaning 'fast'). Tachyzoites may be ovoid/globular, rod-like, lunate/crescentic or banana-shaped ranging from 4.3-8.4 x 1.0-2.5 (often 6 x 2) µm depending on their state of maturation. They may be located within a parasitophorous vacuole or lie free in the host cell cytoplasm. Ultrastructurally, each tachyzoite possessed an anterior conoid, 4-24 rhoptries, micronemes, dense granules, a single nucleus and was bound by a pellicular membrane with 22 subpellicular microtubules. Tissue cysts are encapsulated stages found within host cells throughout the body. Cysts are microscopic but vary in size (6-107 µm long) depending on their age, tissue tropism and host specificity. They are aseptate and bound by a PAS-positive (periodic acid-Schiffs reagent) primary cyst wall (0.5-4.0 µm thick) consisting of a thickened unit membrane that may have a wavy contour but lacks protrusions and a secondary cyst wall. *Neospora* cysts are morphologically similar to those of *Toxoplasma* (although the cyst wall of the latter is thinner at 0.5 µm), but they are serologically distinct and do not cross-react with *Toxoplasma* immune sera or antisera. Internally, the cysts form cystozoites (usually called bradyzoites – 'brady' meaning 'slow) that multiply by internal division (endodyogeny) such that larger cysts may contain 200 or more. Bradyzoites are elongate cells (4-8 x 1-3 µm) that contain a conoid, 6-12 rhoptries, micronemes, dense granules, a subterminal nucleus and pellicular membranes with 22 subpellicular microtubules (some studies suggest that bradyzoites can be differentiated from tachyzoites by certain subcellular features, but several reviews have revealed considerable pleomorphy between isolates). Parasite development in the intestines of definitive hosts is known to culminate in the production of characteristic oocysts, but the preceding asexual and/or sexual developmental stages have yet to be demonstrated. One study tentatively identified schizont-like structures (basophilic bodies 8-12 µm) that labelled strongly with *Neospora* antisera, as well as weakly-labelled microgamont-like bodies ('small spots with flagella-like structures'). Developing oocysts have been found in mucosal and crypt epithelial cells as round-oval stages (around 10 µm in diameter) that are bound by smooth membranous oocyst walls (0.6–0.8 µm thick). Mature oocysts (9.4-13.4 µm) are shed unsporulated in host faeces and then undergo internal division (sporulation) to form 2 sporocysts (7.0-9.0 x 5.6-6.4 µm), each of which forms 4 elongate sporozoites (6.0-7.0 x 1.8-2.2 µm) and a residual body. The oocysts therefore have an isosporid configuration (1:2:4 oocyst:sporocyst:sporozoite) and are morphologically similar to those of *Toxoplasma* and *Hammondia.*

Site of infection: Most *Neospora* infections have involved the detection of tissue cysts in intermediate host tissues, particularly in the brain, spinal cord and skeletal muscles, but sometimes in hepatic, uterine, placental and foetal tissues (often in vascular endothelial cells and macrophages). Developing meronts (schizonts) have also been found in many cell types, including nerve and muscle cells, hepatocytes, macrophages, renal tubular epithelial cells, skin cells, fibroblasts, vascular endothelial cells, and even retinal cells. Infections by *N. caninum* have been recorded in around 60 vertebrate species: mostly mammals, including 7 artiodactylans (bovid, cervid, suid), one perissodactylan (equid), 44 carnivores (ailurid, canid, felid, herpestid, hyaenid, mustelid, odobenid, otariid, phocid, procyonid, ursid, viverrid), 3 rodents (murid), and one lagomorph (leporid); and 4 bird species (phasianid, corvid, passerid, and accipitrid). In contrast, infections by *N. hughesi* have only been detected in the neural tissues of horses.

Following the discovery that *N. caninum* was able to undergo sexual reproduction in carnivorous (definitive) hosts, oocyst production has been documented in some 18 canid species (dogs, wolves, foxes, jackals), but the detection of earlier schizont and gamont developmental stages has remained elusive. One study reported the occurrence of schizont-like and microgamont-like stages in intestinal epithelial cells, while several studies have demonstrated developing oocysts in jejunal and ileal epithelia.

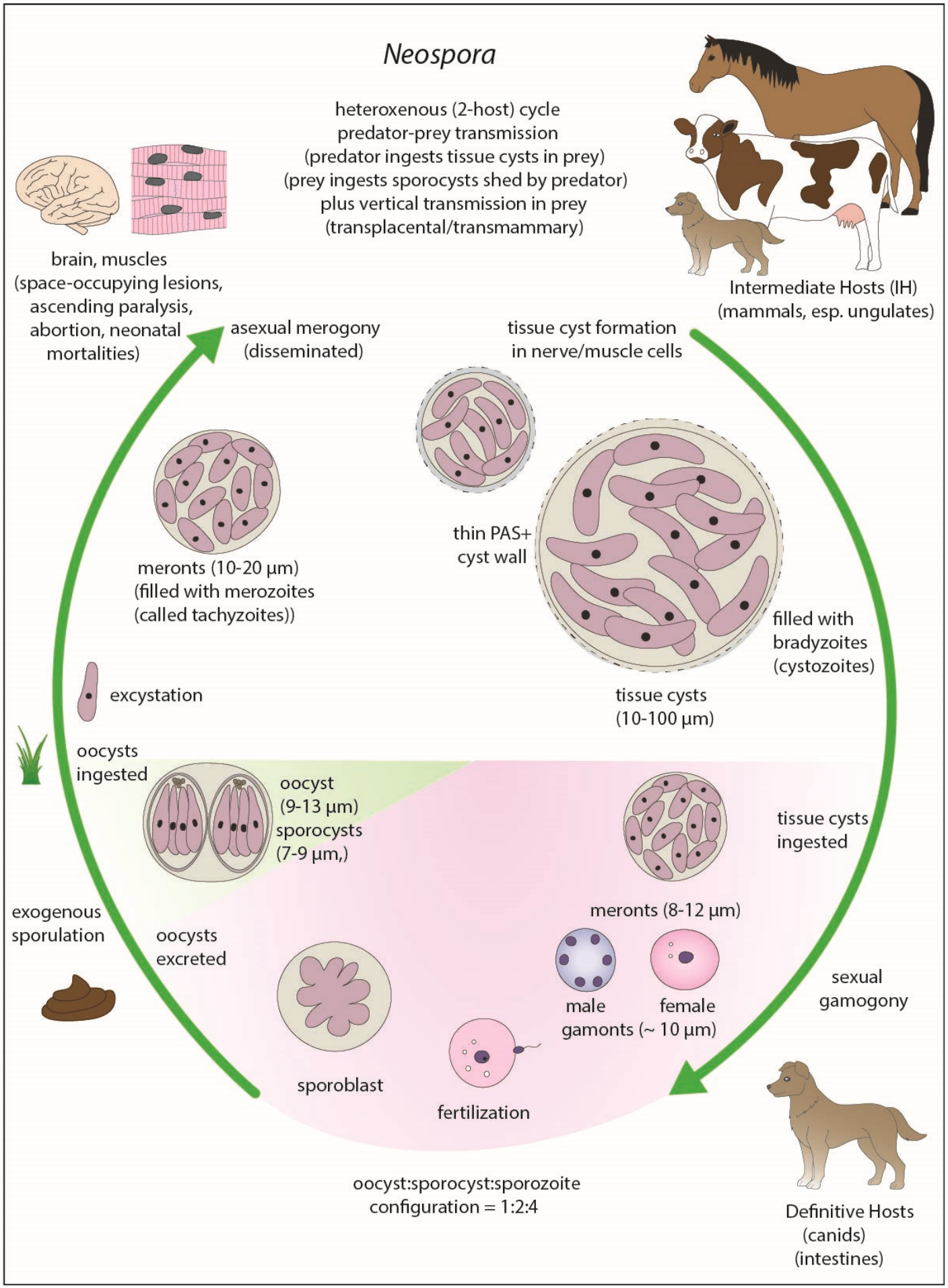
Pathogenesis: The intracellular (schizogonous) proliferation of parasites ultimately leads to host cell lysis releasing tachyzoites to invade other cells. Their subsequent encystment in host tissues and the formation of cysts containing numerous bradyzoites results in small space-occupying lesions often associated with inflammation, necrosis and fibrosis. Light infections may remain asymptomatic or subclinical, but heavier disseminated infections may cause mild-severe clinical disease (neosporosis). Infections in dogs may take 2 forms depending on whether they act as definitive or intermediate hosts: enteric infections by developing oocysts have not been associated with disease; while systemic infections by schizonts and cysts may cause neuromuscular degeneration leading to ascending paralysis of the limbs. Hyperextension is common due to myositis and upper motor neuron paralysis leading to fibrous contracture of muscles and fixation of joints (arthrogryposis). Infected animals may die at any age, but most mortalities occur in young dogs (< 6 months old). Infections may also cause abortion in pregnant dogs, but more commonly they give birth to infected pups which may exhibit muscle atrophy and ascending paralysis. Infections in cattle are generally latent and asymptomatic in non-pregnant animals, but primary, secondary or recrudescent infections in pregnant cows can result in mid-gestation abortions, foetal reabsorption, mummification, autolysis, stillbirth, or the birth of weak underweight calves which may have symptomatic disease (ataxia, paralysis, exophthalmus (pop-eye)) or harbour chronic infections. Infections commonly involve neural tissues (brain, spinal cord, nerve roots, retina) where they cause inflammation (encephalomyelitis) and necrotic areas (focal malacia) with subsequent fibrosis, resulting in a range of neurological signs. Infections in cardiac tissues may cause focal or diffuse myocarditis, infections in skeletal muscles cause necrosis and myositis, and infections in the liver cause multifocal hepatocellular necrosis and periportal hepatitis. Chronically-infected calves are more likely to go on to produce infected calves or to experience abortion themselves. In aborted foetuses, parasites and inflammatory infiltrates are usually found in the brain, spinal cord and heart, or in the liver when abortion storms occur. Infections have been associated with both epidemic and endemic bovine abortions, conditions associated with horizontal and vertical transmission, respectively. Epidemic abortions follow postnatal exposure to infective oocysts, with parasites causing acute disease and typically being found in the hearts and livers of aborted foetuses with multifocal hepatocellular necrosis. Endemic abortions occur in chronically infected cattle when latent encysted parasites are reactivated during pregnancy and cross the placenta where they may be found in the brains of aborted foetuses. Infections by *N. hughesi* in horses are often subclinical but some may cause equine protozoal myeloencephalitis (EPM) resulting in generalized neurological symptoms such as ataxia, weakness, seizures, paralysis, vision problems, or behavioural changes.

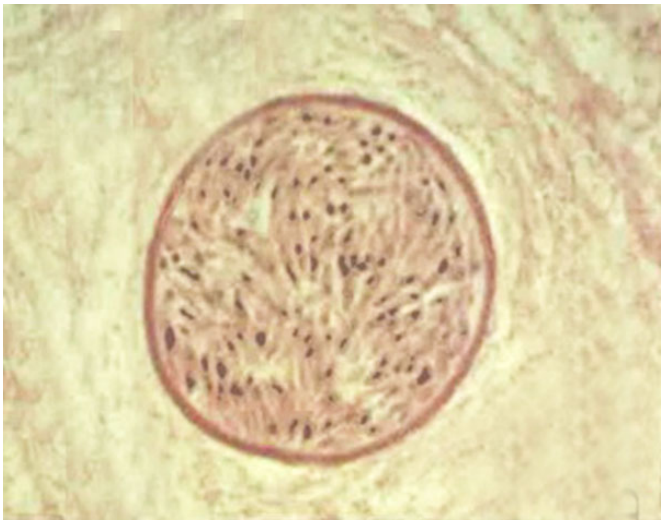
Developmental cycle and mode of transmission: Experimental cross-transmission studies demonstrated that *N. caninum* had a heteroxenous (2-host) life-cycle involving cattle as intermediate hosts (IH) in which asexual proliferation occurred, and dogs as definitive hosts (DH) in which sexual reproduction took place. Case studies have now confirmed infections by tissue cysts in a range of herbivorous and omnivorous animals, as well as infections resulting in oocyst formation in a range of canids. Curiously, dogs may act as either DH producing oocysts or as IH with schizonts and cysts infecting tissues and sometimes causing systemic disease resulting in paralysis or abortion (similar to that occurring in ungulates). Transmission from IH to DH occurs horizontally (laterally, post-natally) via predator-prey interactions when infected flesh is eaten by canids, either by direct predation (eating infected IH), scavenging (eating infected remains, including carcases, aborted foetal tissues or placental tissues) or being fed flesh from farm ration animals (eating raw meat or carcase offcuts). It has been shown experimentally that both tachyzoites from schizonts and bradyzoites from tissue cysts may initiate infections in dogs. While transmission studies have not yet demonstrated all the stages involved in the enteric cycle in dogs (other than oocyst formation), they are thought to first involve an asexual schizont cycle then the formation of sexually-dimorphic gametocytes producing macrogametes (female) and flagellated microgametes (male) that undergo fertilization by fusion to form zygotes. Oocyst formation has been observed in intestinal epithelial cells resulting in the excretion of unsporulated oocysts in canid faeces. Sporulation occurs exogenously with the formation of sporocysts and sporozoites taking several days. The prepatent period (time interval from infection to first oocyst excretion) varies from 2-13 days, and the patent period (duration of oocyst excretion ranges from 8-27 days, but some reports suggest intermittent oocyst excretion may still occur after several months. The intensity of oocyst shedding depends on the age of the dogs (more in puppies) and the type of flesh they have consumed (more in dogs fed skeletal muscles from cattle, sheep or goats than those fed other tissues or infected mouse cadavers). Transmission from DH to IH occurs horizontally via faecal-oral interactions where oocysts contaminating food and water sources are consumed by omnivores/herbivores (mostly mammals but including some birds). Ingested oocysts excyst in the gut releasing sporozoites which invade host cells forming schizonts which produce numerous tachyzoites by asexual internal division (endodyogeny) over several days. Mature schizonts ultimately lyse their host cells releasing the contained tachyzoites to invade further cells. Several cycles of schizogony may occur facilitating the rapid increase in parasite numbers and their dissemination throughout host tissues. Eventually, the tachyzoites are transformed to begin bradyzoite production within intracellular membrane-bound cysts (transformation linked to strong gamma-interferon dominated cell-mediated host immune responses). Tissue cysts typically occur in neural or skeletal muscle cells where they may persist for several months or years. The life cycle is completed when mature cysts containing infective bradyzoites are eaten by canids. In addition to the heteroxenous (IH-DH) life-cycle, infections may also exhibit diheteroxenous (IH-IH) vertical transmission when tachyzoites cross the placenta in pregnant animals and invade foetal tissues. Transplacental infections may lead to the termination of pregnancy with abortion or stillbirth, but they may also lead to the birth of live offspring harbouring congenital infections. Such infections may occasionally cause systemic

disease in young animals, but they often remain latent for long periods and become reactivated during gestation for several pregnancies (thought to be due to the transient immunosuppression developing in the host to avoid foetal rejection). Congenital infections therefore facilitate the transmission of infections between multiple generations of animals. Transplacental and congenital infections are considered to be the major routes of infection in domestic cattle (both beef and dairy herds). Epidemiological studies have indicated that infected cows have a 50-90% chance of congenital infection, with only some infections resulting in endemic abortion, although some herds occasionally experience abortion 'storms' around 4-7 months of gestation. In horses infected with *N. hughesi*, vertical transmission has been found between latently-infected mares and foals via endogenous transplacental transmission.

Differential diagnosis: *Neospora* infections may be indicated in animals on the basis of history and clinical signs (paralysis and/or abortion), but they must be confirmed (and differentiated from *Toxoplasma*) by the detection of parasites in clinical samples by microscopic examination or culture, the molecular detection of parasite DNA, or the demonstration of specific host antibodies against defined parasite antigens. Infections are usually provisionally diagnosed by the microscopic detection of schizonts and/or cysts in histological sections of tissues collected from deceased animals or freshly-aborted foetuses, notably neural tissues, striated muscles (heart, skeletal musculature) and sometimes the liver and lungs. The generic identity of the parasites is confirmed by staining with specific antiserum (which does not cross-react with *Toxoplasma* stages) tagged to fluorochrome or chromogenic labels. *Neospora* spp. in horses can sometimes be differentiated on the basis of cyst morphology, with *N. caninum* cysts usually being larger than those of *N. hughesi* and being bound by thicker cyst walls. Infections in canid definitive hosts are diagnosed by the coprological examination of faecal samples for the presence of characteristic oocysts (isosporid-like with 1:2:4 configuration) following concentration by sedimentation-floatation techniques. Regrettably, differential diagnosis is confounded by other parasite genera having similar oocysts. *Neospora* oocysts (from canids) are identical to those of *Toxoplasma gondii* (found in felids) and *Hammondia* spp. (found in canids and felids). Several bioassays have been developed to study parasites cultured *in vitro* in cell cultures (e.g. Vero cells in RPMI-1640 media, bovine aorta endothelial cells, murine epidermal keratinocytes, and organotypic slice explants of rat brain cortex) or *in vivo* in laboratory mice (Swiss white mice, BALB/c, CBA/ca, ICR, interferon-gamma gene knockout strains) or gerbils. A range of serological tests (agglutination tests, indirect fluorescent-antibody tests (IFAT), enzyme immunoassays) have been developed to detect specific host antibodies (in serum or cerebrospinal fluid) against parasite antigens using either whole zoites, sonicate extracts or defined recombinant antigens (notably P37 and P29/30 immunodominant antigens). The different tests varied in their sensitivity and specificity depending on the host species and samples tested, but the IFAT was found to provide the most reliable results (and has been adopted by some authorities as the diagnostic standard). More recently, molecular biological techniques have been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (18S ribosomal DNA, internal transcribed spacer region 1, alpha-tubulin, beta-tubulin, heat shock protein 70, repetitive DNA (Nc5 repeat sequence), by random amplified polymorphic DNA (RAPD) analyses, or by mini- and micro-satellite analyses.

Treatment and control: Once clinical disease has become apparent, there is currently no effective treatment for neosporosis. The prognosis in dogs with hindlimb paralysis is poor, although some early cases have responded to treatments with various combinations of lincosamide antibiotics (clindamycin) and antiprotozoals including diaminopyrimidines (trimethoprim), sulfonamides (sulfadiazine) and diaminopyrimidines (pyrimethamine). Cattle have been treated with clindamycin and triazine-based coccidiostats (toltrazuril, ponazuril) with variable effects but treatments were costly and there were mandated withholding periods for meat and milk. Various preventive measures have been implemented to interrupt transmission cycles on farms through improved hygiene and sanitation as well as to manage herd health through husbandry practices. To prevent oocyst production, it is important to deny dogs access to raw meat, carcases, aborted foetuses and placentas by restricting their roaming and scavenging behaviours and maintaining them on diets involving cooked/processed meats. Programs could also be instituted to control wild or feral animals (dogs, dingoes and foxes) using barriers, baits or by hunting. Domestic dogs should be prevented from defaecating on or near fodder storage facilities, animal enclosures and water sources and efforts should be made to keep livestock feeding and drinking areas clean by regular washing/flushing. Health surveillance programs should be established to monitor for clinical cases and all new or replacement livestock should be screened for infections. Serological testing of whole herds may also be used to select sero-negative animals for breeding and possibly to cull sero-positive animals (impractical in herds with high levels of infection – most often only aborting animals are culled). Several vaccines have been developed for use in cattle, but they are relatively expensive and while they reduce the rate of abortion, they do not prevent vertical transmission. The treatment of *N. hughesi* in horses is difficult as diagnosis is often made post-mortem, and there may be latent infections in other horses without clinical symptoms. Some successes have been reported treating horses with triazine-based coccidiostats (toltrazuril, ponazuril). Serological screening horse populations may identify infected individuals which could be selectively culled but often little is done due to the rarity of symptomatic disease.


Neospora
heteroxenous (2-host) cycle
predator-prey transmission
(predator ingests tissue cysts in prey)
(prey ingests sporocysts shed by predator)
plus vertical transmission in prey
(transplacental/transmammary)
Intermediate Hosts (IH)
(mammals, esp. ungulates)
brain, muscles
(space-occupying lesions,
ascending paralysis,
abortion, neonatal
mortalities)
asexual merogony
(disseminated)
tissue cyst formation
in nerve/muscle cells
thin PAS+
cyst wall
meronts (10-20 µm)
(filled with merozoites
(called tachyzoites))
filled with
bradyzoites
(cystozoites)
tissue cysts
(10-100 µm)
excystation
oocysts
ingested
oocyst
(9-13 µm)
sporocysts
(7-9 µm,)
tissue cysts
ingested
meronts (8-12 µm)
exogenous
sporulation
oocysts
excreted
male
female
gamonts (~ 10 µm)
sexual
gamogony
sporoblast
fertilization
oocyst:sporocyst:sporozoite
configuration = 1:2:4
Definitive Hosts
(canids)
(intestines)



Neospora cyst in cow brain



Neospora oocyst from dog faeces

Toxoplasma
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). Tissue cyst-forming coccidia have heteroxenous (2-host) life-cycles alternating between enteric stages in predators (definitive hosts) and encysted stages in prey (intermediate) hosts. *Toxoplasma gondii* will only form oocysts in cats – merogony (= schizogony), gamogony (male microgametes fertilize female macrogametes) and oocyst formation occur in the intestinal epithelia. Sporogony occurs exogenously and mature oocysts contain 2 sporocysts each with 4 sporozoites (1:2:4 configuration). Thin-walled tissue cysts filled with bradyzoites (= cystozoites) are formed in the striated muscles and neurons of many different vertebrate hosts (mammals and birds) following merogonous division of tachyzoites in macrophages. Infections in cats are asymptomatic while infections in intermediate hosts (including humans) have been associated with mild to severe clinical disease (systemic, neurological or reproductive toxoplasmosis).

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Eimeriorina (no syzygy, many microgametes)
Family:	Sarcocystidae (heteroxenous, oocysts with two sporocysts, tissue cyst formation in intermediate host)
Subfamily:	Toxoplasmatinae (metrocytes not present, thin cyst walls)
Genus:	*Toxoplasma* (tissue cyst-forming coccidian parasite of mammals)
Species:	*T. gondii* (causes toxoplasmosis in humans and animals)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid

coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Numerous species of coccidia have been described from a wide range of vertebrate and invertebrate hosts. Some 50 genera have been classified in 11 families in the suborder Eimeriorina, including nine genera in the family Sarcocystidae. These apicomplexans are often referred to as cyst-forming coccidia, as they undergo gamogony and sporogony producing oocysts (1:2:4 oocyst:sporocyst:sporozoite configuration) in the intestines of carnivorous definitive hosts (DHs) as well as merogony and tissue cyst formation in the tissues of omnivorous or herbivorous intermediate hosts (IHs). They have heteroxenous (two-host) life-cycles with cyclic transmission between predatory animals and their prey. Two main subfamilies are recognized mainly on the basis of differences in cyst development (metrocytes present or absent) and site of oocyst sporulation (endogenous or exogenous). Members of the subfamily Sarcocystinae form cysts with metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate

endogenously before being voided from the definitive host. Members of the subfamily Toxoplasmatinae form cysts without metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate exogenously after being voided from the definitive host. A third subfamily has recently been added with the discovery that some *Isospora* spp. in mammals form encysted monozoic stages (cystozoites) in the tissues of paratenic (transport) hosts (esp. rodents), prompting their classification with the tissue cyst-forming coccidia under the name *Cystoisospora* in the new subfamily Cystoisosporinae.

Parasite genera	**No. spp.**	**Life-cycle**	**Definitive Hosts (DH) Intermediate Hosts (IH) Paratenic Hosts (PH)**	**Oocyst configuration***
Family: Sarcocystidae (3 subfamilies)				
Subfamily: Cystoisosporinae (monozoic cysts in PH, sporocysts without Stieda bodies)				
Cystoisospora	50	heteroxenous	vertebrate DH (carnivores, primates), vertebrate PH (mammals, birds)	1:2:4
Subfamily: Sarcocystinae (metrocytes, endogenous sporulation)				
Sarcocystis (incl. *Frenkelia*)	135	heteroxenous	vertebrate DH (predatory mammals, birds, reptiles), vertebrate IH (mammals, birds, reptiles)	1:2:4
Subfamily: Toxoplasmatinae (no metrocytes, exogenous sporulation)				
Toxoplasma	1	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals), invertebrate PH (annelids, insects)	1:2:4
Hammondia	3	heteroxenous	vertebrate DH (canids, felids), vertebrate IH (mammals)	1:2:4
Neospora	2	heteroxenous	vertebrate DH (canids), vertebrate IH (mammals)	1:2:4
Besnoitia	7	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals, reptiles), possibly invertebrate PH (insects)	1:2:4
Hyaloklossia	1	monoxenous	vertebrates (amphibians)	1:2:4
Nephroisospora	1	monoxenous	vertebrates (bats)	1:2:4

*1:2:4 = one oocyst contains 2 sporocysts, each sporocyst contains 4 sporozoites

The genera *Toxoplasma*, *Hammondia*, *Neospora* and *Besnoitia* are obligatory or facultatively heteroxenous with cyclic predator-prey transmission usually between carnivorous definitive hosts (DH) and herbivorous intermediate hosts (IH). Transmission from IH to DH occurs carnivorism (predator consuming cysts in tissues of prey) and transmission from DH to IH occurs via faecal-oral contamination (excretion of oocysts/sporocysts in faeces of predators to contaminate foodstuffs of prey). Several species are also di-heteroxenous (less common term di-homoxenous), meaning that infections can be passed horizontally between intermediate hosts by carnivorism (ingestion of tissue cysts in IH or PH) or vertically from mother to offspring (via transplacental or transmammary infection). These heteroxenous genera within the subfamily Toxoplasmatinae form tissue cysts without metrocytes, the bradyzoites undergo asexual division before gamete formation and the oocysts sporulate exogenously after being voided. More recently, encysted stages of two monoxenous genera (*Hyaloklossia* and *Nephroisospora*) have been found in the tissues of amphibians and bats, prompting their placement in the subfamily Toxoplasmatinae.

Toxoplasma infections have been detected worldwide in a diverse range of warm-blooded vertebrate hosts; mostly mammals (carnivores, omnivores, herbivores, insectivores, rodents, primates including humans) and occasionally birds. Sexual development and oocyst formation only occurs, however, in feline hosts. One species is currently considered valid: *T. gondii* which is facultatively heteroxenous (and diheteroxenous) using a wide range of mammals and birds as intermediate hosts and felids as definitive hosts. *Hammondia hammondi* exhibits many similarities to *T. gondii,* but is obligatorily heteroxenous cycling between some rodents and cats. Other *Toxoplasma* species have been reported but they are considered as *species inquirenda* or *nomen dubium* due to a lack of descriptive or biologic information. Laboratory studies have recognized various strains of *T. gondii* on the basis of their variable infectivity, growth, virulence and gene expression. Recent genetic studies indicate that *T. gondii* propagates primarily by clonal, asexual or uniparental clonal reproduction, and various strains have been allocated to three clonal lineages (Types I, II and III) on the basis of analyses of multiple independent single-copy loci as well as microsatellite markers. Type I strains are most often associated with disease in immunocompetent adults and in congenital infections, type II strains with immunocompromised individuals, and type III strains with patients with ocular toxoplasmosis. The prevalence of infections varies according to host populations and geographic location but seroprevalence estimates range from 5-75% in many countries.

***Toxoplasma* species**	**Intermediate hosts (IH)**	**Definitive hosts (DH)**	**Distribution**
T. gondii	Warm-blooded vertebrates, including Primates (humans, apes,	Carnivora:	worldwide

(type species)	monkeys, lemurs, lorises, tarsiers), Chiroptera (megabats, microbats), Cetacea (whales, dolphins, porpoises), Carnivora (canids, mephitids, mustelids, procyonids, ursids, pinnipeds, felids, herpestids, hyaenids, viverrids), Artiodactyla (camelids, suids, cetaceans, hippopotamids, tragulids, antilocaprids, giraffids, cervids, bovids), Perissodactyla (equids, rhinocerotids, tapirids), Proboscidea (elephants), Rodentia (mice, rats, squirrels, prairie dogs, chipmunks, porcupines, beavers, guinea pigs, hamsters, gerbils, capybaras), Lagomorpha (rabbits, hares, pikas), Monotremata (echidnas, platypus), Diprotodontia (macropodids, phalangerids, vombatids), Dasyuromorphia (dasyurids, myrmecobiids), Peramelemorphia (bandicoots, bilbies), Didelphimorphia (opossums), Cingulata (dasypodids, chlamyphorids), Pilosa (anteaters, sloths), Scandentia (treeshrews), Soricomorpha (shrews, moles), Afrosoricida (tenrecs, golden moles), Erinaceomorpha (hedgehogs, gymnures); Aves: Anseriformes (ducks), Accipitriformes (hawks), Casuariiformes (cassowaries), Charadriiformes (gulls, terns), Ciconiiformes (egrets), Columbiformes (pigeons, doves), Falconiformes (vultures), Galliformes (chickens, bowerbirds, partridges, pheasant), Gruiformes (coots), Strigiformes (owls), Passeriformes (crows, ravens, bulbuls, canaries, sparrows, finches, shrikes, jays, starlings, thrushes, tits, robins, tanagers, grackles, blackbirds, mynahs), Pelecaniformes (boobies). Psittaciformes (parrots, budgerigars, lories), and Sphenisciformes (penguins). Facultatively heteroxenous (involving diheteroxenous (IH-IH) horizontal transmission (via carnivorism or ingestion of paratenic hosts) and vertical transmission (via transplacental or transmammary infection). Paratenic hosts include Insecta: diptera (filth flies), blattodea (cockroaches) and Annelida: oligochaeta (earthworms).	felid (domestic cat, African wild cat, European wild cat, bobcat, Geoffroy's cat, iriomote cat, leopard cat, Amur leopard cat, Pampas cat, Pallas cat, cheetah, cougar, jaguar, jaguarundi, leopard, lion, ocelot, tiger)	

Some workers have proposed as many as 6 named *Toxoplasma* species in poikilotherms, but most remain convinced that there is only one species in mammals (*T. gondii*) with a worldwide distribution.

***Toxoplasma* species inquirenda, nomen dubium**	**Intermediate hosts (IH)**	**Distribution**
T. alencari (maybe *Lankesterella*)	pseudocysts in brain of Anura: leptodactylid (butter frog)	South America
T. brumpti	zoites in circulating white blood cells in Sauria: iguanid (common green iguana)	Americas
T. colubri (syn. *T. plimmeri*)	zoites in circulating white blood cells in Serpentes: colubrid (pine snake, green whip snake)	Europe
T. ranae	pseudocysts in tissues of Anura: ranid (northern leopard frog)	North America
T. serpai (maybe *Dactylosoma*)	zoites in blood cells and tissues of Anura: bufonid (cane toad)	Americas
T. wassilewsky (maybe *Eimeria*)	zoites in tissues of Cypriniformes: cyprinid (bream)	Eurasia

Parasite morphology: Four developmental stages are formed; schizonts, tissue cysts, gamonts and oocysts. Schizonts (sometimes called meronts) appear as small basophilic intracellular bodies which divide rapidly to form small collections of merozoites (usually called tachyzoites – 'tachy' meaning 'fast') measuring 4-5 x 1-2 µm. Tissue cysts (measuring 10-100 µm in diameter) are surrounded by a thin primary cyst wall (< 0.5 µm thick) and contain hundreds of basophilic cystozoites (usually called bradyzoites – 'brady' meaning 'slow') measuring 3-4 by 1-2 µm. Gamonts exhibit sexual differentiation, with microgamonts (male) apparent as multinucleate basophilic stages ultimately shedding small biflagellated microgametes; and macrogamonts (female) evident as uninucleate eosinophilic cells with a single ovoid nucleus. Oocysts are small ovoid stages (10-13 x 9-11 µm) and contain two round sporocysts (without Stieda bodies), each sporocyst containing four elongate sporozoites (isosporid-like 1:2:4 configuration).

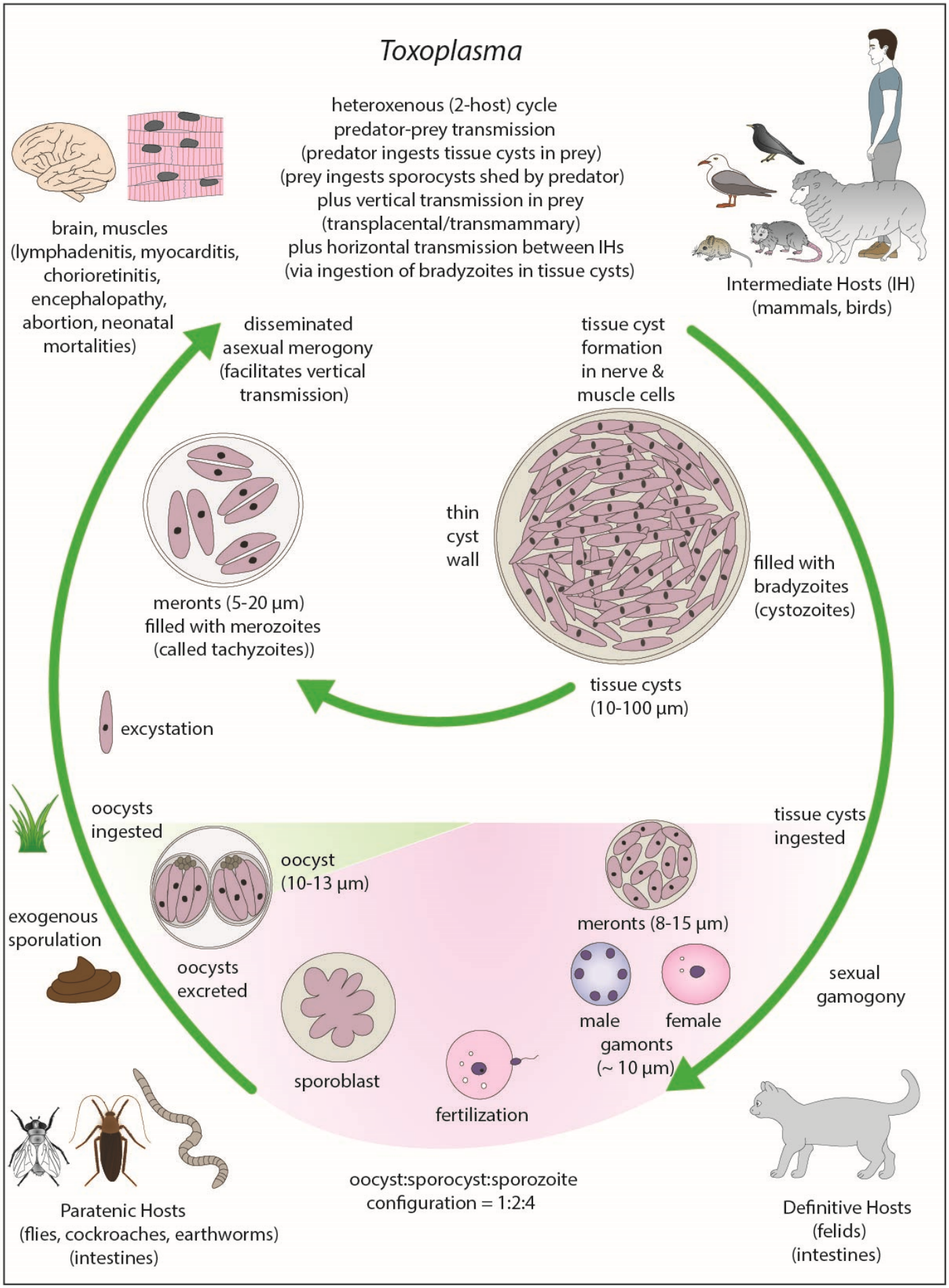
Site of infection: In cats, parasites undergo asexual and then sexual multiplication in intestinal epithelial cells culminating in the formation of oocysts 3-5 days after infection. The parasite patent period (during which oocysts are shed) lasts several days to weeks and then cats become immune to infection. In all other vertebrate hosts, parasites undergo asexual multiplication in a wide range of extra-intestinal locations (cells of the lymphatic and circulatory systems, nervous tissue, skeletal musculature, etc.). During the acute phase of infection, the parasites divide rapidly forming small groups of 8-32 tachyzoites which lyse the host cells. As infections become chronic, the parasites divide more slowly forming large accumulations of bradyzoites particularly within the brain, heart and skeletal muscle. These tissue cysts are surrounded by a thin cyst wall and they persist for months or even years after infection. Cyst formation (change from tachyzoite to bradyzoite stages) coincides with the development of host protective immunity (not a sterile immunity where the infection is eliminated, but a state of premunition or concomitant immunity where some parasites persist within hosts that are resistant to super-infection). In cats, both the sexual (enteroepithelial) and asexual (extraintestinal) phases of infection may occur simultaneously.

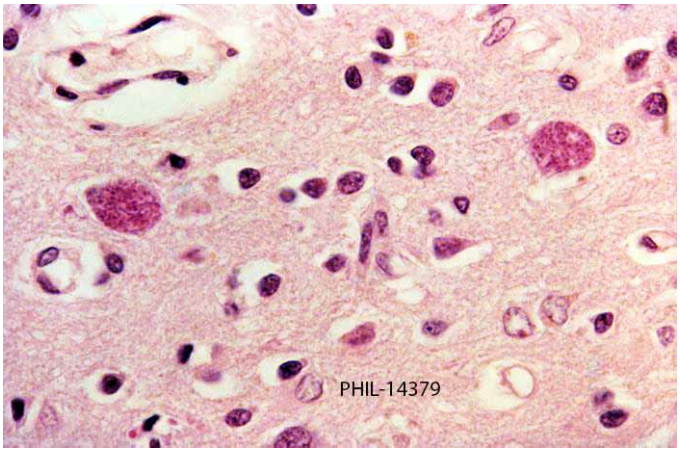
Pathogenesis: Many host species exhibit an age-related resistance to disease therefore most infections in adults and weaned individuals are asymptomatic. In susceptible hosts, symptomatic infections may be acute, subacute or chronic. Acute infections by proliferating tachyzoites cause flu-like symptoms, including lymphadenitis, fever, headache, muscle pain, malaise and anaemia. Symptoms generally subside with the development of immunity, but may sometimes persist producing subacute disease, characterized by extensive lesions in the lung, liver, heart, brain or eyes. Postnatal infections often involve lymphadenitis, myocarditis, central nervous system involvement and retinochoroiditis. Chronic infections by encysted bradyzoites usually cause few clinical signs, although degenerating cysts have been associated with hypersensitive inflammatory reactions, resulting in, for example, encephalitis, myocarditis and/or chorioretinitis. The tissue cysts lay quiescent (dormant) in the tissues for some time, occupying little space and apparently causing few functional deficits, although there is contradictory evidence that infections may be associated with some learning disabilities, slower reflexes and altered behaviour in intermediate hosts (such as increased movement and diminished fear in rodents possibly leading to their enhanced predation by felines). In immunocompetent hosts, concomitant immunity provides protection against clinical toxoplasmosis and appears to be mediated primarily through cellular responses involving both CD4+ and CD8+ T lymphocytes and gamma-interferon. Latent cyst infections may be reactivated in immunocompromised patients (i.e. those undergoing immunosuppressive therapy or with acquired immunodeficiencies) resulting in cell lysis, expanding focal lesions, rapid dissemination, encephalopathy and meningoencephalitis. Infections may also be transmitted transplacentally, but only if the mother/dam contracts infection during pregnancy. In these situations, the invading parasites may cross the placenta and infect the foetus with dire consequences depending on the trimester of pregnancy. Infections in the first trimester may lead to foetal death and spontaneous abortion, infections in the second trimester may also lead to foetal death resulting in stillbirth or foetal retention and mummification, while infections acquired in the third trimester may not kill the developing foetus but the newborn may exhibit profound congenital abnormalities, such as hydrocephalus, brain calcification, chorioretinitis and mental retardation. If the mother/dam is infected prior to pregnancy, her immunity is transferred to her foetus which is consequently protected. Nevertheless, the parasite is considered to be a major abortifacient in domestic livestock, with the exception of cattle (where *Neospora* causes reproductive losses). Infections in cats by enteric sexual developmental stages are generally subclinical, transient and leave the cat with a strong protective immunity against subsequent oocyst production. The duration of protection has not been demonstrated unequivocally, although laboratory studies indicate it may last several years but not be life-long.

Developmental cycle and mode of transmission: Infections are transmitted horizontally between hosts by the ingestion of oocysts excreted by cats, and vertically between mother and offspring by transplacental or even transmammary transmission of proliferative tachyzoites. Infections may also be transferred between intermediate hosts through the food chain via carnivorism (the ingestion of fresh or undercooked meat containing viable cysts). Bradyzoites released during digestive processes are resistant to enzymatic digestion and revert back to tachyzoite stages which infect the host, multiply, spread and lead to new cyst formation. Infections are more prevalent in human populations which have traditional cultural practices involving the consumption of raw or partially cooked meat (e.g. steak tartare, partly cured smallgoods). When intermediate hosts ingest sporulated oocysts, excystation occurs in the small intestines resulting in the release of the infective sporozoites. These stages penetrate the gut wall and may establish infections within a variety of host cells, notably macrophages, where they undergo asexual multiplication via endodyogeny (internal formation of two daughter cells) within parasitophorous vacuoles. Mature schizonts eventually lyse the host cell releasing tachyzoite stages which invade neighbouring cells or disseminate via the circulatory system to infect other organs. After several cycles of tachyzoite proliferation, the host mounts an immune response which suppresses tachyzoite growth. This coincides with their transformation to bradyzoite stages which sequester and multiply slowly within host cells to produce tissue cysts, particularly within nervous tissue and striated musculature. In immunocompetent intermediate hosts, these cysts persist as quiescent or dormant stages for years. When felid definitive hosts consume infected flesh, the parasites are released from cysts by enzymatic digestive processes and invade small intestinal cells. Here they undergo asexual multiplication followed by sexual reproduction involving the formation of female (macro-) and male (micro-) gametes which undergo fertilization to produce zygotes (immature oocysts). Oocysts excreted by cats take 1-5 days to sporulate before they become infective and they are resistant to external environmental conditions and may remain viable in contaminated soil and water for some time. They can survive periods of freezing at -20°C and temperatures as high as 50°C, and may even remain viable in seawater for several months. Infective oocysts have also been shown to be transmitted via paratenic (transport) hosts, including insects (filth flies, cockroaches) and oligochaetes (earthworms).

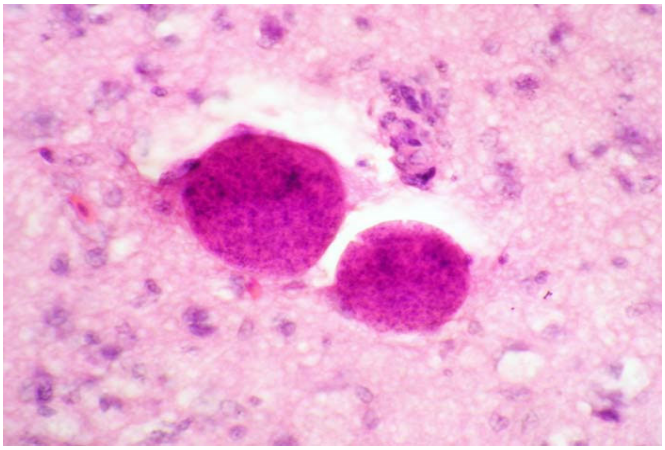
Differential diagnosis: Parasites may be detected in autopsy or biopsy material by histology, immunolabelling, *in vitro* tissue culture (e.g. in HeLa cells) or *in vivo* following inoculation into laboratory rodents. Zoites in smears stain well with Giemsa and other Romanowsky stains while cysts in sections have silver-positive walls and the bradyzoites are strongly PAS (periodic acid-Schiff) positive. Monoclonal and polyclonal antibody labels have also been used to detect parasites in tissue sections, and molecular studies using polymerase chain reaction (PCR) amplification techniques have detected parasite DNA (targeting the B1 repetitive sequence, P30 (SAG1) surface antigen or 18S ribosomal RNA genes). Given the low sensitivity of microscopic techniques, the long duration of culture techniques, the technical difficulty of molecular techniques and the invasive nature of specimen collection, most ante-mortem infections are diagnosed serologically using a range of immunoassays (dye tests; fluorescent-antibody tests; enzyme-linked immunosorbent assays; direct, indirect and modified agglutination tests; and Western immunoblotting techniques). It is important that sequential (longitudinal) samples be examined to establish the time course of infection. Recent/acute infections are indicated by a 4-16 fold increase in specific antibody titre over a two-week period, or by the detection of specific IgM antibody titres.

Treatment and control: Chemotherapy is successful when diaminopyrimidines (pyrimethamine) and sulfonamides (sulfadiazine) are given together as they act synergistically. The toxic side-effects of bone marrow depression can be relieved by the administration of folinic acid. Clindamycin, spiramycin and azithromycin have also been reported to be effective. The risk of transmission can be reduced by maintaining high standards of hygiene (particularly where cats are involved), by thoroughly cooking or deep-freezing meat prior to consumption, treating potable water (filtration and chlorination) and washing foodstuffs potentially contaminated by oocysts (e.g. vegetables from the garden). Many health agencies publish recommended hygiene/safety guidelines for patient groups considered to be most at risk (e.g. pregnant women and HIV-infected individuals). Molecular vaccines are currently being developed for high-risk patient groups, and a live vaccine using a low-virulent non-persistent strain has been marketed to protect sheep against toxoplasmosis.

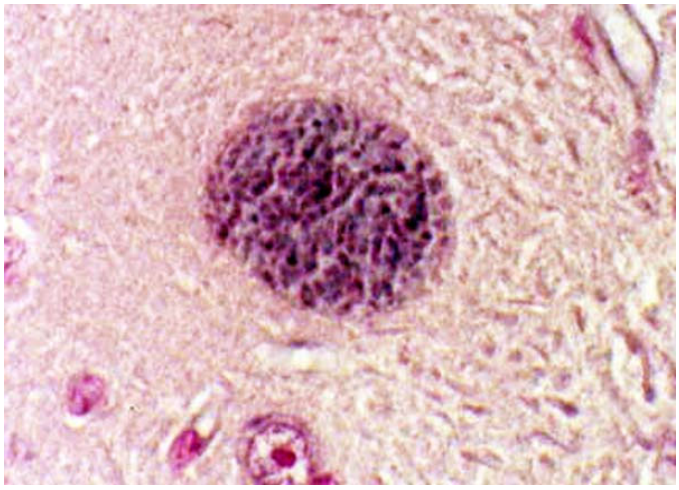

Toxoplasma
heteroxenous (2-host) cycle
predator-prey transmission
(predator ingests tissue cysts in prey)
(prey ingests sporocysts shed by predator)
plus vertical transmission in prey
(transplacental/transmammary)
plus horizontal transmission between IHs
(via ingestion of bradyzoites in tissue cysts)
brain, muscles
(lymphadenitis, myocarditis, chorioretinitis, encephalopathy, abortion, neonatal mortalities)
Intermediate Hosts (IH)
(mammals, birds)
disseminated asexual merogony (facilitates vertical transmission)
tissue cyst formation in nerve & muscle cells
thin cyst wall
filled with bradyzoites (cystozoites)
meronts (5-20 µm) filled with merozoites (called tachyzoites))
tissue cysts (10-100 µm)
excystation
oocysts ingested
oocyst (10-13 µm)
tissue cysts ingested
meronts (8-15 µm)
exogenous sporulation
oocysts excreted
sporoblast
male
female
gamonts (~ 10 µm)
sexual gamogony
fertilization
oocyst:sporocyst:sporozoite configuration = 1:2:4
Paratenic Hosts
(flies, cockroaches, earthworms)
(intestines)
Definitive Hosts
(felids)
(intestines)



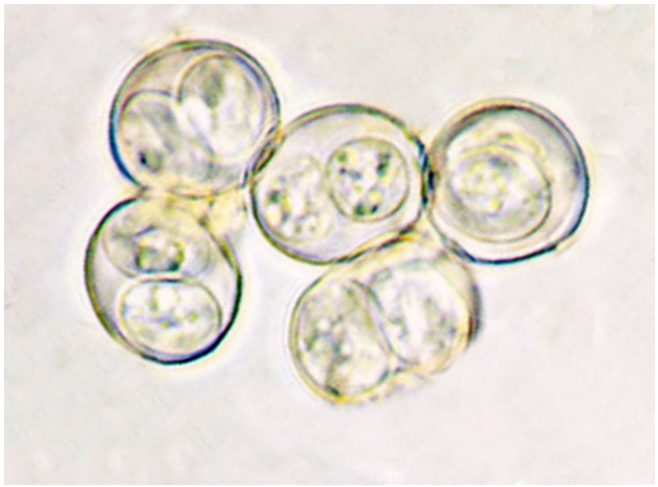
Toxoplasma cysts in brain



Toxoplasma cysts in owl brain



Toxoplasma cyst in mouse brain



Toxoplasma oocysts from cat faeces

Hammondia
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Coccidia form non-motile resistant oocysts that contain infective sporozoites usually confined within secondary spores (sporocysts). Tissue cyst-forming coccidia have heteroxenous (two-host) life-cycles alternating between enteric stages in predators (definitive hosts) and encysted stages in prey (intermediate) hosts. *Hammondia* spp. form ellipsoidal cysts containing bradyzoites (= cystozoites) predominantly in the striated muscles of rodents. The cysts have thin cyst walls and may persist in the tissues for years. Merogony (= schizogony), gamogony (male microgametes fertilize female macrogametes) and oocyst formation occurs in the intestinal epithelia of cats or dogs. Sporogony occurs exogenously and mature oocysts contain 2 sporocysts each with 4 sporozoites (1:2:4 configuration). Different species exhibit relative strict host specificity, with particular predator-prey combinations hosting individual species.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Coccidiomorphea [Conoidasida] (with conoid)
Subclass:	Coccidia [Coccidiasina] (small intracellular gamonts)
Order:	Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)
Suborder:	Eimeriorina (no syzygy, many microgametes)
Family:	Sarcocystidae (heteroxenous, oocysts with two sporocysts, tissue cyst formation in intermediate host)
Subfamily:	Toxoplasmatinae (metrocytes not present, thin cyst walls)
Genus:	*Hammondia* (tissue cyst-forming coccidian parasites of mammals)
Species:	various species cause lesions/cysts in dogs, cats, cattle and rodents]

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are

heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic 'haemococcidia' in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmorida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Numerous species of coccidia have been described from a wide range of vertebrate and invertebrate hosts. Some 50 genera have been classified in 11 families in the suborder Eimeriorina, including nine genera in the family Sarcocystidae. These apicomplexans are often referred to as cyst-forming coccidia, as they undergo gamogony and sporogony producing oocysts (1:2:4 oocyst:sporocyst:sporozoite configuration) in the intestines of carnivorous definitive hosts (DHs) as well as merogony and tissue cyst formation in the tissues of omnivorous or herbivorous intermediate hosts (IHs). They have heteroxenous (two-host) life-cycles with cyclic transmission between predatory animals and their prey. Two main subfamilies are recognized mainly on the basis of differences in cyst development (metrocytes present or absent) and site of oocyst sporulation (endogenous or exogenous). Members of the subfamily Sarcocystinae form cysts with metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate endogenously before being voided from the definitive host. Members of the subfamily Toxoplasmatinae form cysts without

metrocytes within the tissues of their intermediate hosts, and their oocysts sporulate exogenously after being voided from the definitive host. A third subfamily has recently been added with the discovery that some *Isospora* spp. in mammals form encysted monozoic stages (cystozoites) in the tissues of paratenic (transport) hosts (esp. rodents), prompting their classification with the tissue cyst-forming coccidia under the name *Cystoisospora* in the new subfamily Cystoisosporinae.

Parasite genera	**No. spp.**	**Life-cycle**	**Definitive Hosts (DH) Intermediate Hosts (IH) Paratenic Hosts (PH)**	**Oocyst configuration***
Family: Sarcocystidae (3 subfamilies)				
Subfamily: Cystoisosporinae (monozoic cysts in PH, sporocysts without Stieda bodies)				
Cystoisospora	50	heteroxenous	vertebrate DH (carnivores, primates), vertebrate PH (mammals, birds)	1:2:4
Subfamily: Sarcocystinae (metrocytes, endogenous sporulation)				
Sarcocystis (incl. *Frenkelia*)	135	heteroxenous	vertebrate DH (predatory mammals, birds, reptiles), vertebrate IH (mammals, birds, reptiles)	1:2:4
Subfamily: Toxoplasmatinae (no metrocytes, exogenous sporulation)				
Toxoplasma	1	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals), invertebrate PH (annelids, insects)	1:2:4
Hammondia	3	heteroxenous	vertebrate DH (canids, felids), vertebrate IH (mammals)	1:2:4
Neospora	2	heteroxenous	vertebrate DH (canids), vertebrate IH (mammals)	1:2:4
Besnoitia	7	heteroxenous	vertebrate DH (felids), vertebrate IH (mammals, reptiles), possibly invertebrate PH (insects)	1:2:4
Hyaloklossia	1	monoxenous	vertebrates (amphibians)	1:2:4
Nephroisospora	1	monoxenous	vertebrates (bats)	1:2:4

*1:2:4 = one oocyst contains 2 sporocysts, each sporocyst contains 4 sporozoites

The genera *Toxoplasma*, *Hammondia*, *Neospora* and *Besnoitia* are obligatory or facultatively heteroxenous with cyclic predator-prey transmission usually between carnivorous definitive hosts (DH) and herbivorous intermediate hosts (IH). Transmission from IH to DH occurs carnivorism (predator consuming cysts in tissues of prey) and transmission from DH to IH occurs via faecal-oral contamination (excretion of oocysts/sporocysts in faeces of predators to contaminate foodstuffs of prey). Several species are also di-heteroxenous (less common term di-homoxenous), meaning that infections can be passed horizontally between intermediate hosts by carnivorism (ingestion of tissue cysts in IH or PH) or vertically from mother to offspring (via transplacental or transmammary infection). These heteroxenous genera within the subfamily Toxoplasmatinae form tissue cysts without metrocytes, the bradyzoites undergo asexual division before gamete formation and the oocysts sporulate exogenously after being voided. More recently, encysted stages of two monoxenous genera (*Hyaloklossia* and *Nephroisospora*) have been found in the tissues of amphibians and bats, prompting their placement in the subfamily Toxoplasmatinae.

The genus *Hammondia* is characterized by the formation of small intracellular cysts in intermediate hosts – the cysts usually conforming to the shape of their host cells (most being elongate ellipsoidal in tubular skeletal muscle cells, and some being ovoidal-subspheroidal in brain cells). The cysts are thin-walled and do not bear radial striations nor septae. The cysts are remarkably similar to those of *Toxoplasma,* and the 2 genera do exhibit some degree of immunological cross-reactivity. Experimental studies have shown *Hammondia* spp. to have either canid or felid definitive hosts, where enteroepithelial multiplication (merogony) occurs, followed by gamogony, fertilization and oocyst formation with unsporulated oocysts shed in their faeces. Contemporary molecular characterization studies involving multiple gene sequences have indicated the genus *Hammondia* is paraphyletic with *Neospora* and *Toxoplasma*.

***Hammondia* species**	**Intermediate hosts (IH)**	**Definitive hosts (DH)**	**Distribution**
H. hammondi (syn. *Isospora, Toxoplasma*)	Rodentia: murid (house mouse, brown rat, multimammate mouse), caviid (guinea pig), cricetid (golden hamster, deer mice); Lagomorpha: leporid (rabbit); Artiodactyla: bovid (goat), cervid (roe deer), suid (pig); Carnivora: canid (dog); Primates: callitrichid (black-and-red tamarin)	Carnivora: felid (cat, wildcat)	cosmopolitan

H. heydorni (syn. *Isospora heydorni, I. wallacei, I. bahiensis, I. babiensis, Toxoplasma bahiensis*)	Artiodactyla: bovid (cattle, water buffalo, sheep, goats, gazelle), camelid (camels), cervid (moose, wapiti, whitetail); Lagomorpha: leporid (rabbit), Rodentia: murid (gerbil), caviid (guinea pig)	Carnivora: canid (dog, dingo, coyote, red fox, crab-eating fox, Arctic fox), mustelid (mink)	cosmopolitan
H. pardalis	Experimental infection in Rodentia: murid (house mouse)	Carnivora: felid (ocelot, cat, jaguarundi, cougar, jaguar)	Central America
H. triffittae	Artiodactyla: bovid (sheep, goat), cervid (reindeer, moose); Lagomorpha: leporid (rabbit); Carnivora: canid (arctic fox)	Carnivora: canid (red fox, arctic fox)	Europe

Parasite morphology: *Hammondia* spp. form 5 different types of developmental stages: meronts and tissue cysts in intermediate hosts; and meronts, gamonts and oocysts in definitive hosts. Meronts (also called schizonts) are asexual proliferative stages that appear as intracellular rounded basophilic bodies (5-20 µm in diameter) in host cells. They undergo internal division (endodyogeny) to produce numerous (up to 20) merozoites (usually called tachyzoites) which are slender elongate cells (4-9 x 2-3 µm). Ultrastructural studies have shown that *Hammondia* tachyzoites contain a central nucleus, an anterior conoid and typical apicomplexan organelles, including several (up to 8) rhoptries that are electron-dense (electron-lucent in *Toxoplasma* tachyzoites) as well as micronemes and dense granules. Tissue cysts are located in striated muscle cells, and they range in size from 100-340 x 40-95 µm, depending on their maturity. They are bound by a thin smooth primary cyst wall (< 0.5 µm) consisting of a thickened unit membrane (cyst wall similar to that of *Toxoplasma* but thinner than that of *Neospora*). The cysts are aseptate (lacking internal compartments) and mature cysts contain numerous (hundreds) of cystozoites (usually called bradyzoites) which have formed by endogenous division. Bradyzoites are elongate slender cells ranging in size from 6-8 x 2-3 µm. Ultrastructural studies have shown them to contain a posterior nucleus, an anterior conoid, few (< 8) rhoptries but numerous micronemes and dense granules, and pellicular membranes with 22 subpellicular microtubules. In definitive hosts, parasites form both asexual and sexual developmental stages prior to oocyst formation. Meronts (schizonts) appear as rounded basophilic bodies (5-12 µm) located intracellularly within host enterocytes. They undergo asexual division by endodyogeny to form numerous (up to 16) merozoites that are slender elongate stages (4-5 x 1-3 µm). Gamonts then appear as rounded basophilic bodies (8-10 µm) in host cells, developing into macrogametocytes (female) with single nuclei and multiple cytoplasmic vacuoles, and microgametocytes (male) with multiple (up to 8) uninucleated microgametes (1-2 µm) evident around the periphery. Following gamete fertilization, the resultant zygote begins oocyst formation by developing external membranous walls from internal cytoplasmic wall-forming bodies. Unsporulated oocysts are excreted in host faeces as spherical stages (10-14 x 10-13 µm) containing a central granulated sporoblast but lacking a micropyle, polar granules or an oocyst residuum. Sporulation occurred in the external environment with oocysts forming 2 sporocysts (6-8 x 4-6 µm), each containing 4 sporozoites (4-7 x 1-2 µm) and a sporocyst residuum but lacking Stieda and sub-Stieda bodies The resultant oocyst:sporocyst:sporozoite configuration was 1:2:4 (usually referred to as isosporid-type). Morphological studies have shown *Hammondia* sporozoites to possess a crystalloid body (like other coccidia but absent in *Toxoplasma*).

Site of infection: *Hammondia* spp. first form schizonts in the intestinal lamina propria, muscles, Peyer's patches, and mesenteric lymph nodes mainly of herbivorous/omnivorous intermediate hosts, followed by cyst formation in their striated muscles, mainly skeletal but sometimes cardiac. Infections have been recorded in some 23 mammalian species, including artiodactylans (bovids, camelids, cervids, suids), rodents (caviids, cricetids, murids), lagomorphs (leporids), carnivores (canids) and primates (callitrichids). Schizonts, gametocytes, and developing oocysts are found in enterocytes in the intestinal mucosa of carnivorous definitive hosts (canids, felids and mustelids). *Hammondia* spp. exhibit many similarities to the closely-related species *Toxoplasma gondii*, but detailed comparative studies have conclusively proven that they are structurally, biologically, antigenically, and genetically distinct. *Hammondia* spp. have a much smaller intermediate host range, and they can utilize either canids or felids as definitive hosts.

Pathogenesis: Infections by *Hammondia* spp. are not considered to be pathogenic and they have not been associated with clinical disease in either intermediate or definitive hosts. Nonetheless, intracellular parasite proliferation ultimately causes lysis of the host cell and cyst formation in skeletal muscles may result in small space-occupying lesions. The resultant damage, however, appears to be insufficient to cause enough structural and/or functional deficits in their hosts to induce clinical disease. The only exceptions have been several cases where enteric infections by *H. heydorni* are thought to have caused anorexia and diarrhoea in immunosuppressed dogs.

Developmental cycle and mode of transmission: Experimental cross-transmission studies have demonstrated that *Hammondia* spp. have an obligatory heteroxenous (2-host) life-cycle involving predator-prey transmission of tissue cysts from intermediate hosts (herbivores/omnivores) to definitive hosts (carnivores), and faecal-oral transmission of oocysts from definitive hosts to intermediate hosts. Following ingestion, oocysts excyst in the small intestines of herbivores/omnivores releasing infective sporozoites which penetrate the gut wall. They infect cells in or near the intestines and undergo asexual proliferation forming schizonts which produce

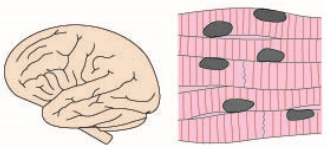
numerous tachyzoites over 7-10 days. The host cells break down releasing the tachyzoites which then infect striated muscle fibres around 14 days after infection. Here they form encapsulated tissue cysts which undergo internal division to produce hundreds of bradyzoites over several weeks. When infected flesh is consumed by cats or dogs, the tissue cysts are digested in the gut releasing the infective bradyzoites which invade intestinal enterocytes within 1-3 days. They form intracellular schizonts which divide asexually to produce numerous merozoites that are released to invade neighbouring cells. The parasites then form female and male gamonts which produce gametes from 4-7 days after infection: female macrogametocytes forming single egg-like macrogametes; and male microgametocytes forming several sperm-like flagellated microgametes. Fertilization occurs by gamete fusion resulting in zygotes that begin oocyst formation. Developing oocysts produce membranous oocyst walls from endogenous wall-forming bodies before they are excreted unsporulated in host faeces. The prepatent period (time from infection to first oocyst excretion) ranges from 5-17 days, while the patent period (duration of oocyst excretion) ranges from 10-28 days. The oocysts undergo sporulation in the external environment over 2-3 days whereby each oocyst forms 2 sporocysts, each of which produces 4 sporozoites (resulting in a 1:2:4 isosporid-type configuration). Sporulated oocysts contaminate food and water sources and are infective to suitable intermediate hosts when inadvertently consumed. Unlike *Toxoplasma*, *Hammondia* spp. do not infect extraintestinal organs in their definitive hosts, and they do not exhibit transplacental or congenital infections in either intermediate or definitive hosts.

Differential diagnosis: Infections by *Hammondia* spp. are asymptomatic and are generally detected in hosts incidentally by the detection of tissue cysts in histological sections of post-mortem material. *Hammondia* cysts are morphologically similar to those of *Toxoplasma* and *Neospora,* but the different genera can sometimes be distinguished by careful examination of the cyst wall (thicker in *Neospora*), bradyzoite ultrastucture (electron-dense rhoptries in *Hammondia*, electron-lucent in *Toxoplasma*) and by differential staining with antisera tagged with fluorochrome or chromogenic labels (little cross-reactivity between genera). Infections in definitive hosts are diagnosed by the microscopic detection of oocysts in faecal samples following concentration by sedimentation/floatation techniques. Several serological tests (fluorescent and enzyme immunoassays) have been developed to detect specific host antibodies against parasite antigens, but many *Hammondia* infections only stimulate low levels of antibodies in their hosts and they sometimes cross-react with *Toxoplasma* antigens. Attempts to cultivate parasites *in vitro* in tissue culture (e.g. feline kidney cells) met with partial success but continuous culture of tachyzoites was not achieved as the parasites began cyst formation and were 'outgrown' by host cells. Several *in vivo* bioassays were developed in rodent models, but infections ensued only after feeding oocysts rather than tachyzoites or bradyzoites (in contrast to *Toxoplasma* where all 3 stages triggered infections). *Hammondia* cysts are more frequently found in striated muscles of experimentally-infected mice (while *Toxoplasma* cysts occur more frequently in the brain). Contemporary molecular biological techniques have been used to detect and characterize parasites following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (large subunit ribosomal DNA, internal transcribed spacer region 1). Comparative phylogenetic studies have clearly differentiated between *Hammondia, Neospora* and *Toxoplasma* species, and shown the 3 genera to be very closely-related (paraphyletic).

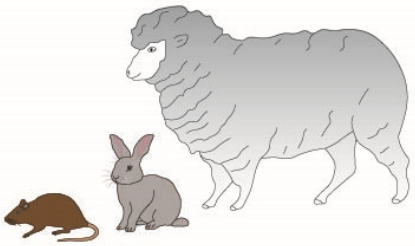
Treatment and control: Natural infections by parasitic cysts are generally detected incidentally in the course of histological studies on naturally-infected intermediate hosts, where parasite development has not been associated with any clinical disease requiring treatment. Several attempts have been made to treat experimental infections in rodents using antiprotozoal and antibiotic drugs, but none have been effective. In contrast, experimental infections in definitive hosts have been reported to respond to treatment with coccidiostats, such as sulfonamides (sulfadiazine) or triazinones (ponazuril, toltrazuril, diclazuril), with the apparent suppression of oocyst development. While natural infections are unlikely to occur in modern laboratory rodent colonies, care should be taken not to introduce infected rodents (by serological screening, culling and wild rodent control), excluding carnivores (using barriers), providing clean food (heat-processed pellets) and water (filtered/chlorinated), and regularly cleaning cages and equipment.

Hammondia

heteroxenous (2-host) cycle
predator-prey transmission
(predator ingests tissue cysts in prey)
(prey ingests sporocysts shed by predator)



brain, muscles
(subclinical space-occupying lesions)

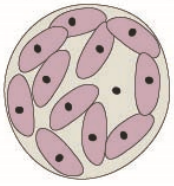


Intermediate Hosts
(mammals)

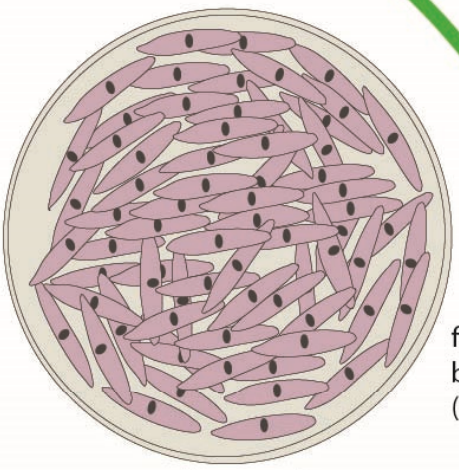
asexual merogony
in gut wall

tissue cyst formation
in musculature

filled with
merozoites
(tachyzoites)



meronts
(5-20 µm)



thin
cyst
wall

filled with
bradyzoites
(cystozoites)

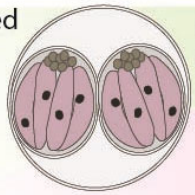
tissue cysts
(100-340 µm)



excystation



oocysts
ingested



oocyst (10-14 µm)
sporocysts (6-8 µm)

tissue cysts
ingested



meronts (5-12 µm)

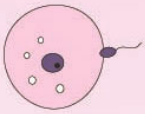


oocysts
excreted

exogenous
sporulation



sporoblast



fertilization

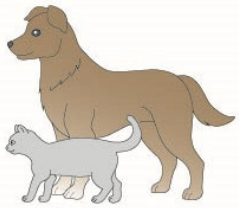


male gamonts
(8-10 µm)



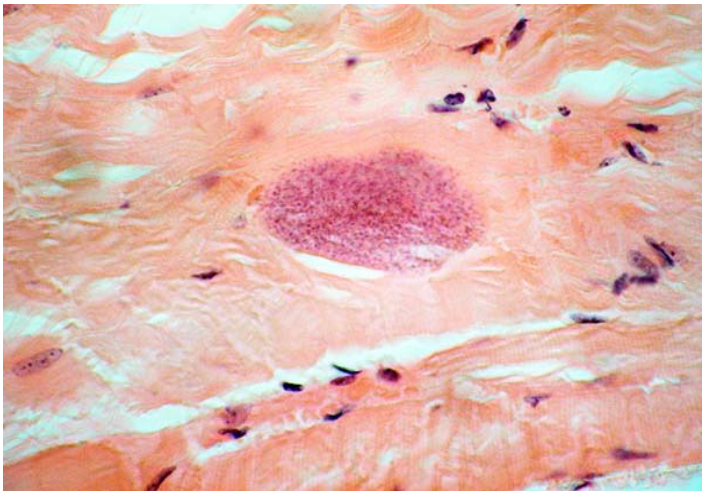
female

sexual
gamogony

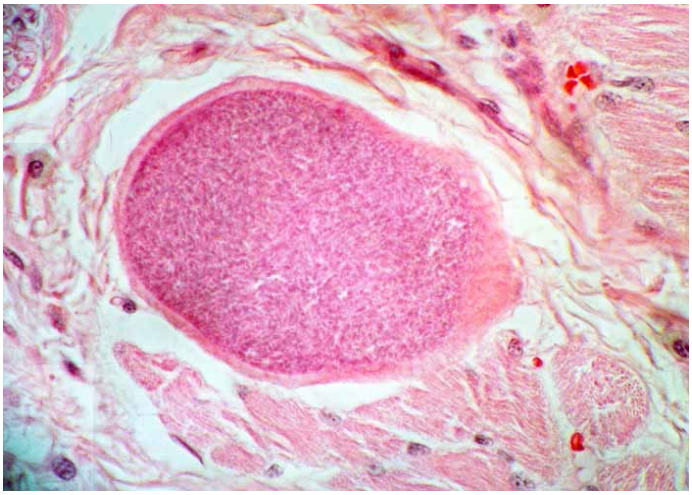


Definitive Hosts
(felids, canids)
(intestines)

oocyst:sporocyst:sporozoite
configuration = 1:2:4



Hammondia cyst in mouse muscle



Hammondia cyst in mouse muscle

***Plasmodium* (mammalian species)**
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Haematozoa are small blood-borne parasites which undergo merogony (= schizogony) and gamogony (gamete formation) in vertebrates and sporogony (sporozoite formation) in blood-sucking invertebrate vectors. Two main groups are recognised in terrestrial vertebrates: haemosporidia with insect vectors; and piroplasms with arachnid vectors. Haemosporidian parasites multiply in the tissues of vertebrates before forming gamonts in blood cells (*Plasmodium* spp. also undergo cyclic merogony in erythrocytes). Most species produce haemozoin pigment granules as a byproduct of haemoglobin metabolism. Gametes ingested by insect vectors undergo fertilization in the gut forming motile zygotes (ookinetes) which form oocysts and then thousands of sporozoites which invade the salivary glands. Infections by *Plasmodium* spp. are transmitted by mosquitoes and numerous species have been described in mammals, birds and reptiles; most causing no apparent harm, except those infecting humans causing one of the worst fever scourges of mankind, the disease malaria.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Aconoidasida (asexual stages without conoid)
Order:	Haemosporida (pleomorphic stages in blood of vertebrates, insect vectors. motile zygote (ookinete))
Family:	Plasmodiidae (schizogony in tissues then blood cells, gamonts in blood cells, haemozoin pigment)
Genus:	*Plasmodium* (vector-borne haemosporidian parasites of vertebrates)
Species:	various species cause malaria in humans, and infections in mammals/birds/reptiles

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic ‘haemococcidia’ in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Haemosporida are spore-forming apicomplexan parasites with heteroxenous life-cycles, with merogony in cells of fixed tissues and in the blood of vertebrate (intermediate) hosts and sporogony in haematophagous invertebrate vectors (definitive hosts). In vertebrate blood cells, haemosporidia develop intracellularly forming sexually dimorphic gametocytes: macrogametocytes (female) with compact nuclei and dark-stained cytoplasm (plentiful ribosomes for protein synthesis), and microgametocytes (male) with larger diffuse nuclei (ready for microgamete production) and pale-staining cytoplasm [a simple pneumonic often used is “blue for girls, pink for boys”]. Gametocytes develop independently (without syzygy) and each microgamont produces about eight flagellated microgametes. Haemozoin granules (residual pigment formed due to incomplete haemoglobin digestion) may or may not be produced in infected erythrocytes. In the vector, the zygote is motile (ookinete) and ultimately forms numerous naked sporozoites (without sporocysts). Around 590 species belonging to some 19 haemosporidian genera have been described from a wide range of mammalian, avian and reptilian hosts around the world.

Four haemosporidian families are recognized mainly on the basis of their developmental cycles and whether haemozoin pigment is produced: namely, Plasmodiidae (merogony in tissues then cyclic in erythrocytes, pigment present); Haemoproteidae (merogony in tissues only, pigment present); Leucocytozoidae (merogony in tissues, pigment absent) and Garniidae (merogony in leucocytes, pigment absent). Vertebrates act as intermediate hosts in which the parasites undergo asexual multiplication within tissues and/or blood cells. Even though parasites begin gamete formation in vertebrates, sexual multiplication is not completed until after they are transmitted to their haematophagous invertebrate vectors, which therefore act as definitive hosts. Some 11 genera are recognized in the family Plasmodiidae on the basis of multiple biological characters (including morphology, development, host specificity and range): *Plasmodium* in mammals, birds and reptiles; *Hepatocystis, Polychromophilus, Nycteria, Biguetiella, Bioccala* and *Dionisia* in bats, *Rayella* in flying squirrels, *Billbraya* and *Haemocystidium* (including *Simondia*) in reptiles, and *Mesnilium* in fish.

Haemosporidian genera	**No. spp.**	**Site* of development in vertebrate**		**Vertebrate hosts**	**Invertebrate vector**
		meronts	**gamonts**		
Family: Plasmodiidae (merogony in tissues and erythrocytes, haemozoin pigment present)					
Plasmodium	225	liver, rbc	rbc	mammals, birds, reptiles	diptera
Hepatocystis	25	liver	rbc	primates/bats	midges
Polychromophilus	5	viscera	rbc	bats	nycterids
Nycteria	7	liver	rbc	bats	
Biguetiella	1	liver	rbc	bats	
Bioccala	2	RE cells	rbc	bats	
Dionisia	1	liver	rbc	bats	
Rayella	3	liver	rbc	flying squirrels	
Billbraya	1	rbc	rbc	lizards	
Mesnilium	1	RE cells, rbc	rbc	fish	leeches/insects
Haemocystidium (*Simondia*)	33	RE cells	rbc	lizards/tortoises	arthropods
Family: Haemoproteidae (merogony in tissues (not in blood cells), haemozoin pigment present in gametocytes)					
Haemoproteus (*Halteridium*)	6	RE cells	rbc	birds	louse flies
Haemoproteus (*Parahaemoproteus*)	150	RE cells	rbc	birds	midges
Johnsprentia	1	RE cells	rbc	flying foxes	
Sprattiella	1	RE cells	rbc	bats	
Family: Leucocytozoidae (merogony in tissues (not in blood cells), haemozoin pigment absent)					
Leucocytozoon (*Akiba*)	100	RE cells	blood cells	birds	black flies
Saurocytozoon	3	viscera	leucocytes	lizards	mosquitoes
Family: Garniidae (merogony in leucocytes, haemozoin pigment absent)					
Fallisia	12	leucocytes	leucocytes	lizards	arthropods
Garnia	10	leucocytes	leucocytes	lizards	arthropods
Progarnia	1	leucocytes	blood cells	crocodiles	

*rbc = red blood cells (erythrocytes); RE = reticuloendothelial cells

Many molecular phylogenetic studies using nuclear, mitochondrial and apicoplast gene sequences have demonstrated a clear relationship between haemosporidian genera not only with their vertebrate hosts but also their invertebrate vectors. There were clear groupings of *Leucocytozoon* from birds, *Haemoproteus* (*Haemoproteus*) from birds, *Haemoproteus* (*Parahaemoproteus*) from birds, *Plasmodium* from birds and reptiles, *Plasmodium* from rodents and primates, and *Hepatocystis* from bats. These groups were clearly associated with different vectors; namely, simuliids (black-flies), hippoboscids (louse-flies), ceratopogonids (midges), culicine mosquitoes, anopheline mosquitoes, and midges, respectively. There appears to have been a transition from haemosporidia which do not form haemozoin pigment (*Leucocytozoon* in white blood cells) to genera that do form pigment indicating haemoglobin digestion by parasites in red blood cells (*Haemoproteus*, *Plasmodium* and *Hepatocystis*). This was followed by a transition from haemosporidia which undergo schizogony exclusively in host tissues (*Leucocytozoon* and *Haemoproteus*) to those that undergo schizogony in blood cells (*Plasmodium*). While there appears to be a general shift in haemosporidian genera from birds and reptiles to mammals (from nucleated to non-nucleated blood cells), each genus is associated with a particular vector group: black-flies transmitting *Leucocytozoon* to birds; louse-flies transmitting *Haemoproteus* (*Haemoproteus*) to birds; midges transmitting *Haemoproteus* (*Parahaemoproteus*) to birds; culicine mosquitoes transmitting *Plasmodium* to birds and lizards; and anopheline mosquitoes transmitting *Plasmodium* to mammals. The exception to this general trend was *Hepatocystis* which does not undergo blood schizogony and is transmitted to bats by midges.

Over 225 *Plasmodium* species have been classified in 14 subgenera on the basis of parasite morphology, development and host occurrence. Three subgenera contain species in mammals, five subgenera contain those in birds, and six contain those in reptiles:

- *P.* (*Plasmodium*), with large erythrocytic schizonts and round gametocytes, in primates;
- *P.* (*Lavernia*), with large erythrocytic schizonts and crescentic gametocytes, in primates;
- *P.* (*Vinckeia*), with small erythrocytic schizonts and round gametocytes, in antelopes, rodents and other mammals (except primates);

- *P.* (*Haemamoeba*), with large erythrocytic schizonts and round gametocytes, in birds;
- *P.* (*Bennettinia*), with small erythrocytic schizonts and round gametocytes, in birds;
- *P.* (*Huffia*), with large schizonts and elongate gametocytes mostly in immature erythrocytes, in birds;
- *P.* (*Giovannolaia*), with large erythrocytic schizonts and elongate gametocytes, in birds;
- *P.* (*Novyella*), with small erythrocytic schizonts and elongate-oval gametocytes, in birds;

- *P.* (*Sauramoeba*), with large erythrocytic schizonts and large gametocytes, in lizards;
- *P.* (*Lacertamoeba*), with medium erythrocytic schizonts and medium gametocytes, in lizards;
- *P.* (*Paraplasmodium*), with medium erythrocytic schizonts and large gametocytes, in lizards;
- *P.* (*Carinamoeba*), with small erythrocytic schizonts and small gametocytes, in lizards;
- *P.* (*Asiamoeba*), with small erythrocytic schizonts and large gametocytes, in lizards; and
- *P.* (*Ophidiella*), with large erythrocytic meronts and small elongate gametocytes, in snakes.

Humans are hosts for four main *Plasmodium* species, although they can occasionally be infected by other species from nonhuman primates. Most species are confined to tropical and subtropical areas depending on the distribution of their insect vectors. On a global basis, ~40% of human infections are due to *P. falciparum*, ~10% are due to *P. malariae*, ~50% to *P. vivax* and <1% to *P. ovale.* It is estimated by global healthcare agencies that some 300 million people become infected each year, with around 1.5 million deaths.

***Plasmodium* species**	**Mammalian intermediate hosts (IH)**	**Periodicity* (erythrocytic cycle)**	**Patho-genicity**	**Definitive hosts (DH) (vectors)**	**Geographic distribution**
Subgenus: *Lavernia* (large erythrocytic schizonts, crescentic gametocytes, in primates)					
P. (*L.*) *falciparum* [type species]	Primates: hominid (human, gorilla, chimpanzee, bonobo); aotid (night monkey)	tertian (48 hrs)	high	Diptera: culicid (*Anopheles* spp.)	worldwide in tropics, subtropics & temperate regions
Subgenus: *Plasmodium* (large erythrocytic schizonts, round gametocytes, in primates)					
P. (*P.*) *malariae* [type species]	Primates: hominid (human, chimpanzee), atelid (howler monkey)	quartan (72 hrs)	low	Diptera: culicid (*Anopheles* spp.)	scattered in tropics and subtropics
P. (*P.*) *ovale* [incl. subspp. *curtisi, wallikeri*]	Primates: hominid (human, chimpanzee)	tertian (49-50 hrs)	moderate	Diptera: culicid (*Anopheles* spp.)	mainly tropical Africa
P. (*P.*) *vivax* [incl. subspp. *vivax, hibernans*, *chesson, multinucleatum*]	Primates: hominid (human, orangutan, chimpanzee), atelid (howler monkey), callitrichid (tamarin)	tertian (48 hrs)	variable	Diptera: culicid (*Anopheles* spp.)	worldwide in tropics and subtropics

*cycles first classified by ancient Romans who did not recognize zero, thus 'tertian' enigmatically refers to a 2-day cycle and 'quartan' to a 3-day cycle.

Another 60 *Plasmodium* spp. have previously been described in mammals, mostly primates and rodents, predominantly on the basis of host occurrence and parasite morphology. Contemporary molecular phylogenetic studies are helping to unlock their taxonomic affinities and resolve their evolutionary origins.

***Plasmodium* species**	**Mammalian intermediate hosts (IH)**	**Periodicity (erythrocytic cycle)**	**Patho-genicity**	**Definitive hosts (DH) (vectors)**	**Geographic distribution**
Subgenus: *Lavernia* (large erythrocytic schizonts, crescentic gametocytes, in primates)					
P. (*L.*) *"adleri"* (= *P.* GorA)	Primates: hominid (gorilla)				West Africa
P. (*L.*) *billbrayi*	Primates: hominid				Central Africa

	(chimpanzee)				
P. (*L.*) *billcollinsi*	Primates: hominid (chimpanzee)				Central Africa
P. (*L.*) *"blacklocki"* (= *P.* GorB)	Primates: hominid (gorilla)				West Africa
P. (*L.*) *"gaboni"*	Primates: hominid (chimpanzee)				West Africa
P. (*L.*) *lomamiensis*	Primates: hominid (bonobo)				West Africa
P. (*L.*) *praefalciparum*	Primates: hominid (gorilla)				West Africa
P. (*L.*) *reichenowi*	Primates: hominid (chimpanzee, gorilla)	tertian (48 hrs)	low	Diptera: culicid (*Anopheles* spp.)	West Africa
Subgenus: *Plasmodium* (large erythrocytic schizonts, round gametocytes, in primates)					
P. (*P.*) *brasilianum*	Primates: cercopithecid (spider monkey), aotid (night monkey), pitheciid (uakari), cebid (capuchin, squirrel monkey), atelid (woolly monkey, howler monkey)	quartan (72 hrs)	moderate	Diptera: culicid (*Anopheles cruzi, freeborni, maculatus, stephensi, gambiae*)	South America
P. (*P.*) *coatneyi*	Primates: cercopithecid (macaque, leaf monkey)	tertian (48 hrs)	low	Diptera: culicid (*Anopheles hackeri, dirus*)	South-East Asia
P. (*P.*) *cynomolgi* [incl. subspp. *bastianellii*, *ceylonensis, cyclopis, cynomolgi*]	Primates: cercopithecid (macaque, leaf monkey, langur), rarely hominid (human)	tertian (48 hrs)	low	Diptera: culicid (*Anopheles balabacensis, atroparvus, freeborni, maculatus, quadrimaculatus, stephensi, dirus, hackeri, elegans, introlatus, dirus*)	South-East Asia
P. (*P.*) *eylesi*	Primates: hylobatid (gibbon)	tertian (48 hrs)	nil		South-East Asia
P. (*P.*) *fieldi*	Primates: cercopithecid (macaque)	tertian (48 hrs)	nil	Diptera: culicid (*Anopheles balabacensis, maculatus, stephensi, hackeri, introlatus, dirus*)	South-East Asia
P. (*P.*) *fragile*	Primates: cercopithecid (macaque)	tertian (48 hrs)	high	Diptera: culicid (*Anopheles balabacensis, elegans, dirus*)	India, Sri Lamka
P. (*P.*) *georgesi*	Primates: cercopithecid (mangabey)				Central Africa
P. (*P.*) *gonderi*	Primates: cercopithecid (mangabey, drill)	tertian (48 hrs)	low	Diptera: culicid (*Anopheles balabacensis, freeborni, maculatus, stephensi, dirus*)	West Africa
P. (*P.*) *hylobati*	Primates: hylobatid (gibbon)	tertian (48 hrs)			South-East Asia
P. (*P.*) *inui* [incl. subspp. *inui, shortii*]	Primates: cercopithecid (macaque, leaf monkey, bonnet monkey, toque monkey)	quartan (72 hrs)	low	Diptera: culicid (*Anopheles balabacensis, maculatus, stephensi, elegans,*	South-East Asia

				leucosphyrus, introlatus, dirus)	
P. (*P.*) *jeffreyi*	Primates: hylobatid (gibbon)	tertian (48 hrs)	nil		South-East Asia
P. (*P.*) *knowlesi* [incl. subspp. *edesoni, knowlesi*]	Primates: cercopithecid (long-tailed macaque, pig-tailed macaque, Old World macaques, banded leaf monkey, olive baboon), callitrichid (New World marmoset), occasionally hominid (human)	quotidian (24 hrs)	moderate	Diptera: culicid (*Anopheles balabacensis, hackeri, dirus*)	Asia
P. (*P.*) *petersi*	Primates: cercopithecid (mangabey)				Central Africa
P. (*P.*) *pitheci*	Primates: hominid (orangutan)	tertian (48 hrs)	nil		Indonesia
P. (*P.*) *rhodaini*	Primates: hominid (chimpanzee, gorilla)	quartan (72 hrs)	?		Africa
P. (*P.*) *schwetzi*	Primates: hominid (chimpanzee, gorilla)	tertian (48 hrs)	nil	Diptera: culicid (*Anopheles* spp.)	Africa
P. (*P.*) *simium*	Primates: atelid (howler monkey, spider monkey), cebid (squirrel monkey)	tertian (48 hrs)	low	Diptera: culicid (*Anopheles cruzi, stephensi*)	Brazil
P. (*P.*) *simiovale*	Primates: cercopithecid (macaque)	tertian (48 hrs)	moderate	Diptera: culicid (*Anopheles balabacensis, maculatus, dirus*)	Sri Lanka
P. (*P.*) *silvaticum*	Primates: hominid (orangutan)	tertian (48 hrs)			Indonesia
P. (*P.*) *youngi*	Primates: hylobatid (gibbon, siamang)	tertian (48 hrs)	low	Diptera: culicid (*Anopheles* spp.)	South-East Asia
Subgenus: *Vinckeia* (small erythrocytic schizonts, round gametocytes, in antelopes, rodents and other mammals (except primates other than lemurs))					
P. (*V.*) *aegyptensis*	Rodentia: murid (grass rats)				North Africa
P. (*V.*) *anomaluri*	Rodentia: anomalurid (scaly-tailed squirrel)		nil	Diptera: culicid (*Anopheles machardyi*)?	East Africa
P. (*V.*) *atheruri*	Rodentia: hystricid (porcupine)	quotidian (24 hrs)	nil	Diptera: culicid (*Anopheles smithii*)	West Africa
P. (*V.*) *berghei*	Rodentia: murid (rat, mouse, jerboa, hamster), myoxid (dormouse), heteromyid (kangaroo rat), sciurid (squirrel); Chiroptera: pteropid (fruit bat)	quotidian (22-25 hrs)	moderate	Diptera: culicid (*Anopheles* spp.)	originally from West Africa
P. (*V.*) *booliati*	Rodentia: sciurid (flying squirrel)		nil		Malaysia
P. (*V.*) *brodeni*	Macroscelidea: macroscelidid (elephant shrew)	tertian (50 hrs)	nil		East Africa
P. (*V.*) *brucei*	Artiodactyla: bovid (duiker)		low	Diptera: culicid (*Anopheles* spp.)	East Africa
P. (*V.*) *bubalis* *[type species]*	Artiodactyla: bovid (water buffalo)	quartan (72 hrs)	low	Diptera: culicid (*Anopheles* spp.)	India
P. (*V.*) *bucki*	Primates: lemurid (lemur)				Madagascar
P. (*V.*) *cephalophi*	Artiodactyla: bovid (duiker)	quartan (72 hrs)	low		Africa
P. (*V.*) *chabaudi* [incl. subspp. *chabaudi,*	Rodentia: murids (rat, mouse)	quotidian (24 hrs)	low	Diptera: culicid (*Anopheles* spp.)	originally from West

adami]					Africa
P. (*V.*) *coulangesi*	Primates: lemurid (lemur)				Madagascar
P. (*V.*) *cyclopsi*	Chiroptera: hipposiderid (leaf-nosed bat)				West Africa
P. (*V.*) *foleyi*	Primates: lemurid (lemur)				Madagascar
P. (*V.*) *girardi*	Primates: lemurid (lemur)		low		Madagascar
P. (*V.*) *inopinatum*	Rodentia: murid (rat)				Europe
P. (*V.*?) *joyeuxi* [maybe *Hepatocystis kochi*]	Primates: cercopithecid (guenon)				West Africa
P. (*V.*) *landauae*	Rodentia: anomalurid (scaly-tailed squirrel)				West Africa
P. (*V.*) *lemuris*	Primates: lemurid (lemur)		low		Madagascar
P. (*V.*) *malagasi*	Primates: lemurid (lemur)				Madagascar
P. (*V.*) *odocoilei*	Artiodactylia: cervid (white tailed deer)			Diptera: culicid (*Anopheles punctipennis*)	North America
P. (*V.*) *percygarnhami*	Primates: lemurid (lemur)				Madagascar
P. (*V.*) *pulmophilum*	Rodentia: anomalurid (scaly-tailed squirrel)				West Africa
P. (*V.*) *roussetti*	Chiroptera: pteropodid (fruit bat)		nil		West Africa
P. (*V.*) *sandoshami*	Dermoptera: cyanocephalid (colugo)	quartan (72 hrs)	low	Diptera: culicid (*Anopheles* spp.)	Malaya
P. (*V.*) *traguli*	Artiodactyla: tragulid (mouse deer)		low	Diptera: culicid (*Anopheles* spp.)	Malayasia, Indonesia
P. (*V.*) *uilenbergi*	Primates: lemurid (lemur)				Madagascar
P. (*V.*) *vinckei* [incl. subspp. *vinckei, petteri, lentum, brucechwatti*]	Rodentia: murids (rat, mouse)	quotidian (24 hrs)	low	Diptera: culicid (*Anopheles* spp.)	originally from West Africa
P. (*V.*) *voltaicum*	Chiroptera: pteropodid (fruit bat)		nil	Diptera: culicid (*Anopheles* spp.)	West Africa
P. (*V.*) *watteni*	Rodentia: sciurid (flying squirrel)				Taiwan
P. (*V.*) *yoelii* [incl. subspp. *killicki, nigeriensis, yoelii*]	Rodentia: murids (rat, mouse)	quotidian (22-25 hrs)	high	Diptera: culicid (*Anopheles* spp.)	originally from West Africa
Unplaced or uncertain reports (*species inquirenda, nomen dubium*)					
P. tyrio	Pholidota: manid (pangolin)	?	-		Asia
P. roubaudi	Carnivora: mustelid (zorilla)		-		Africa
P. narayani	Carnivora: mustelid (otter)		-		India
P. equi	Perissodactyla: equid (horse)	now thought to be a piroplasm			
P. canis	Carnivora: canid (dog)	now thought to be *Babesia canis*			

All mammalian *Plasmodium* species complete their developmental cycles in anopheline mosquitoes where gamogony and sporogony is completed, however, not all *Anopheles* species are able to support and transmit infections. Observations and experiments on vector specificity and competence are by no means comprehensive for individual parasite species, and a range of species have been implicated in their transmission. It is worth noting that individual mosquito species may transmit multiple parasite species, thus facilitating concurrent/concomitant infections. It is also worth remembering that once a mosquito is infected, it is infected for the remainder of its life and may transmit infections with every subsequent meal.

Invertebrate vectors for human malaria	***Plasmodium* species**				
	P. falciparum	***P. malariae***	***P. ovale***	***P. vivax***	***P. knowlesi***
Anopheles aconitus	+	+	-	-	-
A. albimanus	+	-	+	+	-
A. albitarsis	+	-	-	+	-

A. algeriensis	+	-	-	+	-
A. annularis	+	-	-	+	+
A. annulipes	-	+	-	-	-
A. aquasalis	+	-	-	+	-
A. argyritarsis	+	-	-	-	-
A. atropos	-	-	-	+	-
A. aztecus	-	+	-	-	+
A. bachmani	-	-	-	+	-
A. balabacensis	+	-	-	-	-
A. bancrofti	+	-	-	-	-
A. barbirostris	+	-	-	+	-
A. bellator	-	-	-	+	-
A. claviger	+	+	-	+	-
A. crucians	+	-	-	+	-
A. cruzi	+	-	-	-	-
A. culicifacies	+	+	-	+	-
A. darlingi	+	+	-	+	-
A. dirus	-	-	-	+	-
A. dthali	+	-	-	-	-
A. farauti	+	-	-	+	-
A. fluviatilis	+	+	-	+	-
A. freeborni	+	+	-	+	-
A. fuliginosus	-	+	-	-	-
A. funestus	+	+	+	-	-
A. gambiae	+	+	+	-	-
A. hackeri	-	-	-	-	+
A. hancocki	+	-	-	-	-
A. hargreavesi	+	-	-	-	-
A. hyrcanus	-	+	-	+	-
A. jeyporiensis	+	+	-	+	-
A. karwari	+	-	-	-	-
A. kochi	+	-	-	+	+
A. koliensis	+	-	-	-	-
A. kweiyangensis	+	-	-	-	-
A. labranchiae	+	+	+	+	+
A. lesteri	+	-	-	-	-
A. letifer	+	-	-	-	+
A. leucosphyrus	+	-	-	-	-
A. lindsayi	-	+	-	-	-
A. ludlowi	+	+	-	+	-
A. maculatus	+	+	-	+	+
A. maculipennis	+	-	-	+	-
A. mangyanus	+	-	-	-	-
A. melas	+	+	-	-	-
A. messeae	-	+	-	-	-
A. minimus	+	+	-	+	-
A. moucheti	+	+	-	-	-
A. multicolor	+	-	-	-	-
A. nigerrimus	+	-	-	-	-
A. nili	+	-	-	-	-
A. nuneztovari	+	-	-	-	-
A. oswaldi	+	-	-	-	-
A. pattoni	+	-	-	-	-
A. pharoensis	+	-	-	+	-
A. philippinensis	+	-	-	+	+
A. plumbeus	+	+	-	+	-
A. pseudopunctipennis	+	-	-	+	-
A. pulcherrimus	+	-	-	-	-
A. punctimacula	+	-	-	+	-
A. punctipennis	+	+	-	+	-
A. punctulatus	+	+	-	+	-

A. pujutensis	-	-	-	-	+
A. quadrimaculatus	+	+	+	+	-
A. sacharovi	+	+	-	-	-
A. sergenti	+	-	-	-	-
A. sinensis	+	-	-	-	-
A. splendidus	-	+	-	-	-
A. stephensi	+	+	-	+	+
A. strodei	-	-	-	+	-
A. subpictus	+	-	-	+	-
A. sundaicus	+	+	-	+	+
A. superpictus	+	-	+	-	-
A. tesselatus	+	+	-	-	-
A. umbrosus	+	-	-	+	-
A. vagus	+	-	-	+	+
A. varuna	+	+	-	+	-
A. walkeri	+	-	-	-	-
A. wilmorei	-	-	-	+	-

Parasite morphology: Malarial parasites form four developmental stages in humans (hepatic meronts (schizonts) and then intraerythrocytic trophozoites, meronts (schizonts) and gamonts) and three developmental stages in mosquitoes (ookinetes, oocysts and sporozoites). Liver meronts appear as clusters of small basophilic bodies (merozoite nuclei) located within host hepatocytes, measuring 40-80 µm in diameter when mature. Intraerythrocytic stages consist of small rounded trophozoites (ring forms) measuring 1-2 µm in diameter, amorphous multinucleate meronts measuring up to 7-8 µm in length, and microgametocytes (male) and macrogametocytes (female) ranging in length from 7-14 µm. The morphological characteristics (size, shape and appearance) of the blood stages are characteristic for each *Plasmodium* spp. Infected erythrocytes may also exhibit unique inclusions: Maurer's clefts associated with protein trafficking in cells infected with *P. falciparum*; and Schuffner's dots associated with caveola-vesicle complexes in cells infected with *P. ovale* or *P. malariae*. In the mosquito, long slender microgametes (15-25 µm in length) produced by exflagellation fertilize the rounded macrogametes to form motile ookinetes (15-20 x 2-5 µm) which migrate through the gut wall to form ovoid oocysts (up to 50 µm in diameter) on the exterior surface. The oocysts produce thousands of thin elongate sporozoites (12-15 x 1 µm) which ultimately infect the salivary glands.

Site of infection: Sporozoites injected by mosquitos into the hosts bloodstream move rapidly to the liver where they first undergo massive amplification by asexual exoerythrocytic merogony (schizogony) in liver cells. Some sporozoites of *P. vivax* and *P. ovale* may also exhibit arrested development in the liver forming hypnozoites (dormozoites) which are quiescent stages responsible for malaria relapses. Merozoites released from the liver then invade erythrocytes and transform into trophozoites which undergo merogonous (schizogonous) division. This cycle of asexual multiplication in the red blood cells occurs with regular periodicity. Ultimately, intraerythrocytic gametocytes are formed which do not divide further in the human host. When ingested by mosquitoes during feeding, mature gametocytes undergo fertilization in the mosquito gut forming motile ookinetes which migrate through the gut wall to form oocysts. The oocyst then produces hundreds of sporozoites which migrate into the salivary glands where they remain a source of infection for the remainder of the mosquito's life.

Pathogenesis: There are five *Plasmodium* spp. which infect humans: *P. falciparum, P. vivax, P. ovale, P. malariae* and *P. knowlesi*. Infection with these parasites results in an acute febrile illness known as malaria. Disease occurs through several pathways, some of which are species specific. One common feature is the pathology caused by parasites multiplying within host erythrocytes resulting in their rupture and the release of parasite material causing periodic fever/chill cycles. The disease malaria is characterized by its long persistence in infected individuals in endemic areas, with characteristic recrudescences (*P. falciparum, P. malariae, P. knowlesi*) or relapses (*P. vivax, P. ovale*), sometimes after years of subclinical infection. Infection with *P. falciparum* causes the most severe clinical disease in humans frequently resulting in the death of susceptible individuals such as children, pregnant women and travellers. Clinical expression is characterized by cyclic paroxysms of fever/chills (produced by host inflammatory responses), haemolysis and erythrophagocytosis (resulting in anaemia), and organ hypoperfusion due to ischaemia (in the case of *P. falciparum* this arises through cytoadherence of infected cells to vascular endothelia), disseminated intravascular coagulation, erythrocyte rosetting, and haemozoin pigment accumulation. Vague prodromal signs may first develop prior to parasitaemia, including headache, anorexia and mild fever. Thereafter, characteristic febrile paroxysms and haemolytic anaemia develop and become progressively worse. Depending on the parasite species involved, severe complications may arise, including splenic rupture, cerebral signs, haemolytic anaemia, cardiac, pulmonary and renal failure. Paroxysms coincide with intraerythrocytic parasite developmental cycles (tertian = 2-day cycle, quartan = 3-day cycle) and may be accompanied by dizziness, nausea, vomiting, delirium, hepatosplenomegaly, leucopenia and thrombocytopenia. Infected cells are removed from the circulation by erythrophagocytosis during passage through the spleen. Some uninfected cells may also be removed if damaged or coated with debris or parasite antigens, thus exacerbating anaemic conditions. As the parasites grow within erythrocytes, they ingest and digest haemoglobin

leaving behind characteristic dark pigment deposits, termed haemozoin (metabolic byproducts containing the indigestible iron-containing part of the haemoglobin molecule). Haemozoin may accumulate in organs and tissues resulting in impaired function. In the case of *P. falciparum*, infected erythrocytes develop sticky protrusions by which they adhere to vascular endothelial cells (cytoadherence), or clump together (rosetting), resulting in restricted blood flow (ischaemia) and end-organ anoxia. Molecular studies are slowly unravelling the complex host-parasite interactions involved in infection and disease. A range of molecules associated with parasite membranes or secreted from parasites (mostly from apical complex organelles) have been implicated in host cell attachment, invasion via tight junctions, parasitophorous vacuole formation and erythrocyte membrane alteration (including merozoite surface proteins (MSP), apical membrane antigens (AMA), subtilisin-like proteases, erythrocyte-binding antigens, Duffy-binding proteins, thrombospondin-related adhesive proteins (TRAP), knob-associated histidine-rich proteins, erythrocyte membrane-associated proteins (EMP), and various cytoadherence ligands). Several host receptor molecules have also been associated with parasite interactions (including CD36 on monocytes and endothelial cells, intracellular adhesion molecules (ICAM) in the brain, and chondroitin sulfate A (CSA) in the placenta).

Characteristics	***P. falciparum***	***P. malariae***	***P. ovale***	***P. vivax***
Type of malaria:	malignant tertian	benign quartan	benign tertian	benign tertian
Erythrocytic cycle:	48 hours	72 hours	48 hours	48 hours
Exoerythrocytic cycle:	9 days	14-15 days	9 days	8 days
Gametocytes:	crescent	ovoid	ovoid	ovoid
Disease:	recrudescent malaria		relapsing malaria	
Persistence:	continuance of infection by persistent erythrocytic forms		persistent exoerythrocytic schizogony and occurrence of hypnozoites	

P. falciparum causes malignant tertian malaria (sometimes known as malaria tropica), a severe disease with high parasitaemia because the parasites infect both young and mature erythrocytes. Unlike other human malaria species, however, erythrocytes infected with *P. falciparum* do not remain in the circulation for their entire developmental cycle as those containing mature trophozoites adhere to endothelial cells - this sequestration contributing to the severity of disease caused by *P. falciparum*. Symptoms appear 8-12 days after infection, being vague for 3-4 days (aches, pains, headache, fatigue, anorexia) then becoming acute in onset (fever, severe headache, nausea, vomiting, epigastric pain) with paroxysms exhibiting a periodicity of <48 hours. Schizogony often occurs in vessels in organs so disease severity may not correlate with parasitaemia. Various complications may arise due to ischaemic changes, including cerebral malaria (comatose), bilious remittent fever (hepatomegaly), dysentery (malabsorption diarrhoea), algid malaria (circulatory collapse) and blackwater fever (haemoglobinuria). Cerebral malaria occurs when capillaries are blocked by infected erythrocytes causing small haemorrhages which rapidly increase in size (conspicuous in retina). Symptoms include abnormal behaviour, fits, change in level of consciousness, coma, elevated cerebrospinal fluid (CSF) pressure, and classic decerebrate rigidity associated with hypoglycaemia. There are often neurological sequelae, such as hemiparesis, cerebral ataxia, cortical blindness, hypotonia, mental retardation, generalized spasticity, or aphasia.

P. malariae causes benign quartan malaria, a moderately severe disease with reduced parasitaemia because parasites only infect mature erythrocytes. The incubation period ranges from 27-40 days, with vague symptoms developing for 3-4 days (headache, photophobia, muscle aches, anorexia) followed by severe paroxysms of chills and fevers every 72 hours (long chill stage, more severe symptoms during fever stage). Proteinuria is common in infected individuals and a nephrotic syndrome may develop in children.

P. vivax and *P. ovale* cause benign tertian malaria, a moderately severe disease with high parasitaemia as both species preferentially infect reticulocytes (young erythrocytes). *P. vivax* infections are clinically similar to those of *P. ovale*, but they are more severe and relapses occur more frequently. Symptoms appear 7-10 days after infection and are vague for 3-4 days (headache, photophobia, muscle aches, anorexia), developing to steady or irregular low-grade fever then paroxysms with a regular 2-day cycle. Many patients exhibit slow irregular recovery over 3-8 weeks but relapses may occur after weeks/months/years when dormant zoites (hypnozoites) in the liver are reactivated. Splenomegaly is evident during the first few weeks of infection and leukopenia is usually present. Severe complications are rare but *P. vivax* infections can sometimes include cerebral malaria with neurological signs, haemolytic anaemia, renal failure and pulmonary failure.

Many other *Plasmodium* spp. infect a wide range of animal hosts (mammals, birds and reptiles) but comparatively few cause severe clinical disease (sometimes even when parasitaemias are very high). Many theories have been postulated as to why non-primate hosts are more refractory to disease, if not infection. Conventional dogma considered animals to be more tolerant of haemosporidian parasites by virtue of their longer co-evolutionary histories (with human hosts being late arrivals). However, there is little evidence to suggest that parasitism evolves from virulence upon initial contact to avirulence in long-established relationships. Studies on the capacity of parasites to cause disease (virulence) and the ability of hosts to ameliorate disease (resistance) have been attributed changes to habituation, adaptation, immuno-regulation, immuno-evasion, proliferation, reproduction, population density, infection kinetics and dynamics, transmission biology and vector competence. A negative correlation has been observed between parasite virulence and transmission (increasing one decreases the other) suggesting a trade-off between these two linked traits. Further

studies on host-parasite molecular interactions may help unravel the many complexities involved in parasite virulence and host resistance.

Developmental cycle and mode of transmission: Malaria has long been recognized as one of the great fevers afflicting human populations throughout history. Infections were initially thought to be associated with exposure to bad air (*mal-aria*) or swamp gases (miasmas), but we now know infections are vector-borne, being transmitted by *Anopheles* mosquitoes which breed profusely in standing waters and swamps. Some 460 species of *Anopheles* are found worldwide, but malaria has only been shown to be transmitted by around 100 species, with 30 species considered to be the most important vectors. Infections are only transmitted by female mosquitoes - only females feed on blood as they require high protein diets in order to produce eggs. The mosquito is not simply a vector, it acts as the definitive host in which sexual reproduction of the parasite occurs. Gametocytes ingested during feeding undergo fertilization forming an ookinete which moves through the gut wall to form an oocyst on the outer wall. The oocyst undergoes sporogony to form numerous sporozoites which are liberated into the haemocoel and penetrate the adjacent salivary glands. Once a mosquito is infected, it is infected for life and may continue to transmit infections. Sporozoites are injected with saliva into vertebrate hosts during the process of feeding, as mosquito saliva has anticoagulant properties and prevents vertebrate blood from clotting in the mouthparts. Sporozoites are swept away in the host circulation and invade hepatocytes in the liver where they undergo exo-erythrocytic schizogony, producing hundreds to thousands of merozoites. In several *Plasmodium* spp., some sporozoites in the liver form hypnozoites (dormozoites) which can undergo arrested development for long periods, ultimately resuming development leading to relapses of infection. Merozoites released from the liver invade host red blood cells in the circulation and undergo erythrocytic schizogony, first forming ring-stage trophozoites and then meronts (schizonts) which divide to form several merozoites which are released by erythrolysis. Most species undergo several cycles of erythrocytic schizogony before merozoites invade red blood cells to form gametocytes (macro = female, micro = male). These stages are infectious to mosquitoes when ingested during feeding.

Differential diagnosis: Diagnosis is conventionally made by a combination of clinical symptomatology and the detection of parasites in thick or thin peripheral blood smears stained with one of the Romanowsky's stains, usually Giemsa's, Leishman's or Field's stains. Fluorochrome stains have also been used to detect parasites in blood samples, but the morphological features of the stages detected are often obscure. It is important that infections by individual parasite species be differentiated as it impacts on treatment and prognosis. All infections should be considered to be immediately life-threatening, and a complete clinical history should be taken (symptoms/signs), including history of travel, transfusions, recreational drug use, and previous medications (especially anti-malarials). A variety of immunological tests have been developed to detect host antibodies (fluorescent-antibody tests, haemagglutination tests, enzyme immunoassays) or parasite antigens (immunochromatography) in blood samples. While these tests have proven useful for preliminary screening, they have exhibited several problems in sensitivity and specificity. Molecular biological techniques using polymerase chain reaction (PCR) amplification of gene fragments are now under development and they have shown great potential not only for differential diagnosis but also for the detection of drug resistance. PCR targets have included nuclear genes [18S (small subunit) ribosomal DNA, 28S (large subunit) ribosomal DNA, adenylosuccinate lyase, nuclear elongation factor 2, lactate dehydrogenase, dihydrofolate reductase-thymidylate synthase], mitochondrial genes [cytochrome b, cytochrome oxidase 1] and plastid genes [caseinolytic protease C, protein synthesis elongation factor A].

Treatment and control: A variety of drugs have been developed for therapeutic (treatment) and prophylactic (preventive) use. While most enjoyed years of efficacy, there are now widespread problems with drug resistance amongst the parasites. Early explorers noticed that Peruvian Indians used brews from 'fever bark' (*Cinchona*) trees to stave off fevers. The active drug quinine was isolated from the bark around 1820 and this become the mainstay for malaria treatment throughout the world, essentially based on *Cinchona* tree plantations in tropical colonies. Supply shortages due to the World Wars prompted research on synthetic drugs. Pamaquine, mepacrine and chloroquine were developed in the 1930s, proguanil in the 1940s, and pyrimethamine in the 1950s. Chloroquine, in particular, was found to be highly effective, cheap to produce and had low toxicity. However, resistance to chloroquine emerged in the 1960s and soon spread around the world. Sulphonamides were developed in the 1960s, mefloquine and a series of related drugs in the 1970s, and artemisinin was discovered in a Chinese herbal remedy in the 1980s. A holistic and strategic approach to the treatment of infected individuals is required based on whether suppressive, radical or preventive treatment is required, and the level of drug resistance present. Antimalarial drugs of choice are primaquine, chloroquine (despite the emergence of chloroquine-resistant strains), sulfadoxine, pyrimethamine, mefloquine, quinine, artemisinin and tetracycline. Preventive measures based on vector control programmes had many early successes (including those using DDT), but the rapid emergence of insecticide resistance (and the recognition of the toxicity of DDT and its prohibition) have led to the resurgence of malaria in many countries. At present, the best protection is the avoidance of mosquito bites, using screens, bed nets, insect repellents, and residual insecticide sprays.

Drug	**TISSUE STAGES**		**BLOOD STAGES**	
	primary	**latent**	**schizonts**	**gametocytes**
Quinine	-	-	+++	++ (early stage I-III)
Chloroquine	-	-	+++	++ (early stage I-III)

Proguanil	++	-	++	++
Pyrimethamine	++	+	++	+++ (reduces transmission)
Primaquine	++	+++	++	+++
Doxycycline	+	?	++	-
Mefloquine	-	-	+++	+ (early stage I-II)
Halofantrine	-	-	+++	-
Artemisinin	-	-	+++	++ (early stage I_III)
	causal prophylaxis	antirelapse radical cure	suppression clinical cure	prevent spread

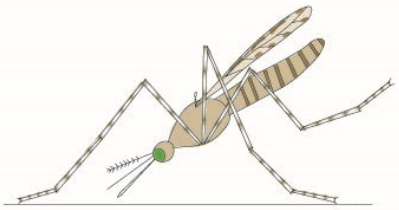
Clinical target		**Drug**	**Main effect**
Non-resistant malaria	Attack	chloroquine	blood schizonts
	Recrudescence (*P.f./P.m.*)	chloroquine	blood schizonts
	Recurrence (*P.v./P.o.*)	primaquine	tissue zoites
	Prophylaxis	pyrimethamine	tissue/blood schizonts
		combinations	tissue/blood schizonts
Drug-resistant malaria	Attack	quinine	blood schizonts
		combinations	blood schizonts
	Prophylaxis	mefloquine	febrile reaction

Plasmodium
(mammalian species)

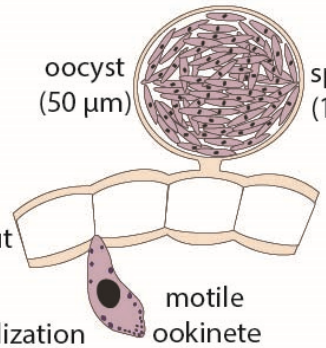
3 subgenera in mammals:
P. (*Plasmodium*)
P. (*Lavernia*)
P. (*Vinckeia*)

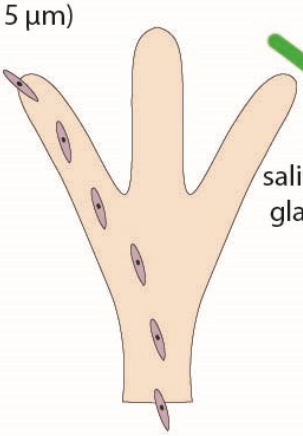
all transmitted by female mosquitoes (once infected, they remain infected for life & may transmit parasites with every meal)

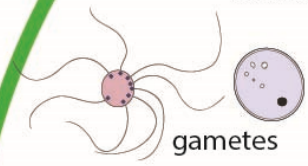
heteroxenous (2-host) cycle
vector-borne transmission
(sexual development in invertebrate host)
(asexual development in vertebrate host)



Definitive Hosts (vectors)
(anopheline mosquitoes)

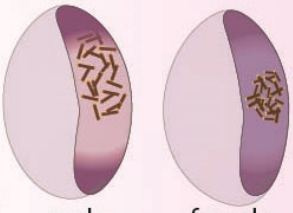




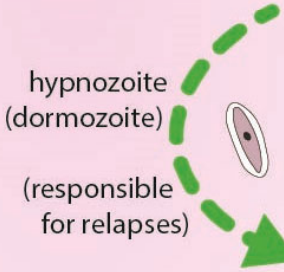


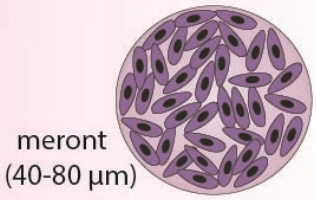
gamonts ingested

sporozoites injected



gamonts
(7-14 µm)



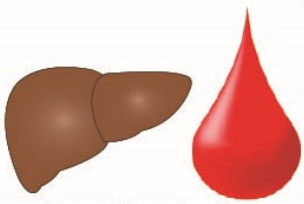


exo-erythrocytic
merogony (liver)



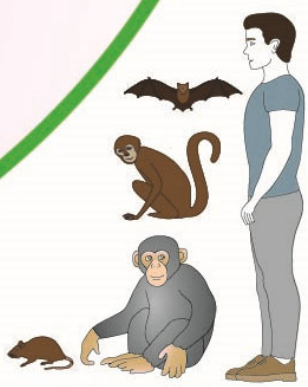
meront
(schizont)
(7-8 µm)

trophozoite
(ring stage)
(1-2 µm)

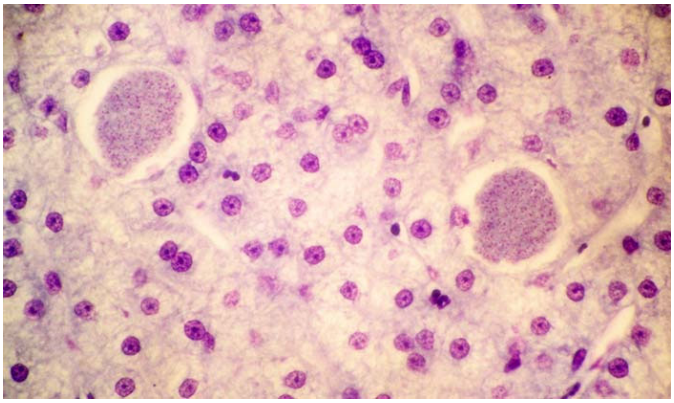


liver, blood cells
(cyclic fevers, haemolytic anaemia, ischaemia)

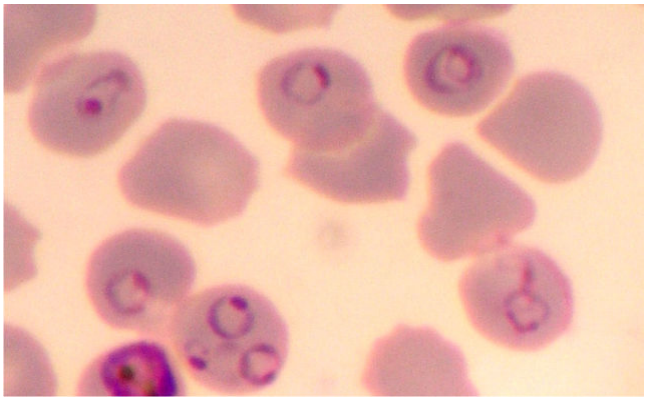
Four species cause severe disease in humans
(*P. falciparum* causes malignant tertian malaria,
P. malariae causes benign quartan malaria,
P. ovale and *P. vivax* cause benign tertian malaria)



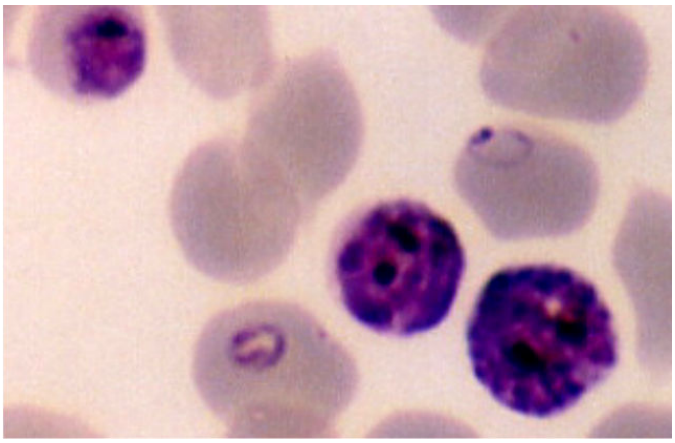
Intermediate Hosts
(mammals, esp. primates)



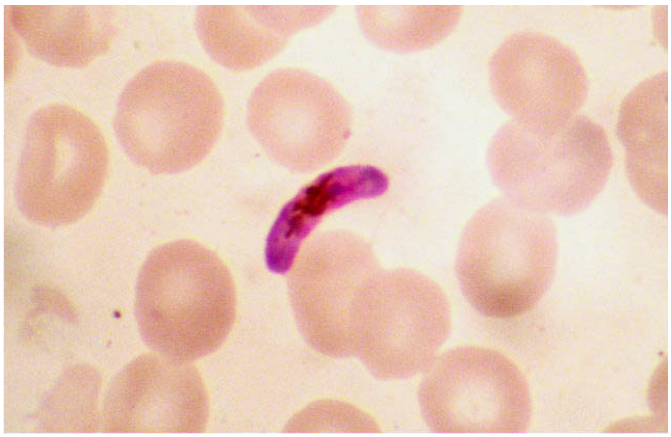
Plasmodium schizonts in human liver



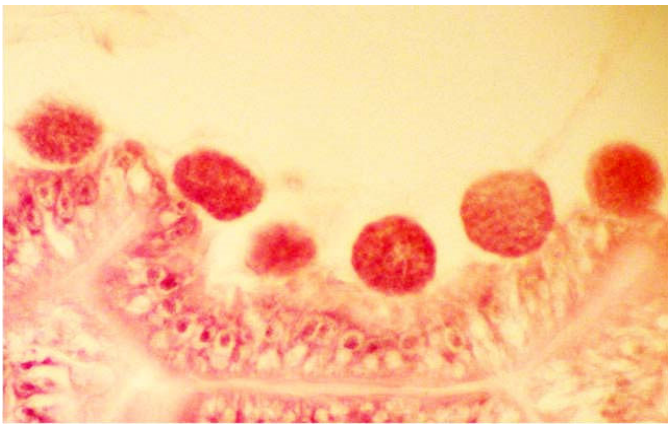
Plasmodium ring-stage trophozoites in human blood



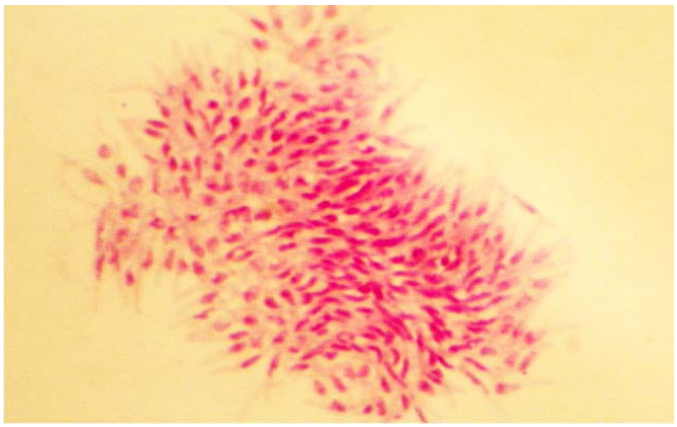
Plasmodium intraerythrocytic schizonts in human blood



Plasmodium gamont in human blood



Plasmodium oocysts on mosquito gut wall



Plasmodium sporozoites from mosquito salivary gland

***Plasmodium* spp. (avian species)**
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Haematozoa are small blood-borne parasites which undergo merogony (= schizogony) and gamogony (gamete formation) in vertebrates and sporogony (sporozoite formation) in blood-sucking invertebrate vectors. Two main groups are recognised in terrestrial vertebrates: haemosporidia with insect vectors; and piroplasms with arachnid vectors. Haemosporidian parasites multiply in the tissues of vertebrates before forming gamonts in blood cells (*Plasmodium* spp. also undergo cyclic merogony in erythrocytes). Most species produce haemozoin pigment granules as a byproduct of haemoglobin metabolism. Gametes ingested by insect vectors undergo fertilization in the gut forming motile zygotes (ookinetes) which form oocysts and then thousands of sporozoites which invade the salivary glands. Infections by *Plasmodium* spp. are transmitted by mosquitoes and numerous species have been described in mammals, birds and reptiles; most causing no apparent harm, except those infecting humans causing one of the worst fever scourges of mankind, the disease malaria.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Aconoidasida (asexual stages without conoid)
Order:	Haemosporida (pleomorphic stages in blood of vertebrates, insect vectors. motile zygote (ookinete))
Family:	Plasmodiidae (schizogony in tissues then blood cells, gamonts in blood cells, haemozoin pigment)
Genus:	*Plasmodium* (vector-borne haemosporidian parasites of vertebrates)
Species:	various species cause infections in mammals/birds/reptiles

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic ‘haemococcidia’ in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Haemosporida are spore-forming apicomplexan parasites with heteroxenous life-cycles, with merogony in cells of fixed tissues and in the blood of vertebrate (intermediate) hosts and sporogony in haematophagous invertebrate vectors (definitive hosts). In vertebrate blood cells, haemosporidia develop intracellularly forming sexually dimorphic gametocytes: macrogametocytes (female) with compact nuclei and dark-stained cytoplasm (plentiful ribosomes for protein synthesis), and microgametocytes (male) with larger diffuse nuclei (ready for microgamete production) and pale-staining cytoplasm [a simple pneumonic often used is “blue for girls, pink for boys”]. Gametocytes develop independently (without syzygy) and each microgamont produces about eight flagellated microgametes. Haemozoin granules (residual pigment formed due to incomplete haemoglobin digestion) may or may not be produced in infected erythrocytes. In the vector, the zygote is motile (ookinete) and ultimately forms numerous naked sporozoites (without sporocysts). Around 590 species belonging to some 19 haemosporidian genera have been described from a wide range of mammalian, avian and reptilian hosts around the world.

Four haemosporidian families are recognized mainly on the basis of their developmental cycles and whether haemozoin pigment is produced: namely, Plasmodiidae (merogony in tissues then cyclic in erythrocytes, pigment present); Haemoproteidae (merogony in tissues only, pigment present); Leucocytozoidae (merogony in tissues, pigment absent) and Garniidae (merogony in leucocytes, pigment absent). Vertebrates act as intermediate hosts in which the parasites undergo asexual multiplication within tissues and/or blood cells. Even though parasites begin gamete formation in vertebrates, sexual multiplication is not completed until after they are transmitted to their haematophagous invertebrate vectors, which therefore act as definitive hosts. Some 11 genera are recognized in the family Plasmodiidae on the basis of multiple biological characters (including morphology, development, host specificity and range): *Plasmodium* in mammals, birds and reptiles; *Hepatocystis, Polychromophilus, Nycteria, Biguetiella, Bioccala* and *Dionisia* in bats, *Rayella* in flying squirrels, *Billbraya* and *Haemocystidium* (including *Simondia*) in reptiles, and *Mesnilium* in fish.

Haemosporidian genera	**No. spp.**	**Site* of development in vertebrate**		**Vertebrate hosts**	**Invertebrate vector**
		meronts	**gamonts**		
Family: Plasmodiidae (merogony in tissues and erythrocytes, haemozoin pigment present)					
Plasmodium	225	liver, rbc	rbc	mammals, birds, reptiles	diptera
Hepatocystis	25	liver	rbc	primates/bats	midges
Polychromophilus	5	viscera	rbc	bats	nycterids
Nycteria	7	liver	rbc	bats	
Biguetiella	1	liver	rbc	bats	
Bioccala	2	RE cells	rbc	bats	
Dionisia	1	liver	rbc	bats	
Rayella	3	liver	rbc	flying squirrels	
Billbraya	1	rbc	rbc	lizards	
Mesnilium	1	RE cells, rbc	rbc	fish	leeches/insects
Haemocystidium (*Simondia*)	33	RE cells	rbc	lizards/tortoises	arthropods
Family: Haemoproteidae (merogony in tissues (not in blood cells), haemozoin pigment present in gametocytes)					
Haemoproteus (*Halteridium*)	6	RE cells	rbc	birds	louse flies
Haemoproteus (*Parahaemoproteus*)	150	RE cells	rbc	birds	midges
Johnsprentia	1	RE cells	rbc	flying foxes	
Sprattiella	1	RE cells	rbc	bats	
Family: Leucocytozoidae (merogony in tissues (not in blood cells), haemozoin pigment absent)					
Leucocytozoon (*Akiba*)	100	RE cells	blood cells	birds	black flies
Saurocytozoon	3	viscera	leucocytes	lizards	mosquitoes
Family: Garniidae (merogony in leucocytes, haemozoin pigment absent)					
Fallisia	12	leucocytes	leucocytes	lizards	arthropods
Garnia	10	leucocytes	leucocytes	lizards	arthropods
Progarnia	1	leucocytes	blood cells	crocodiles	

*rbc = red blood cells (erythrocytes); RE = reticuloendothelial cells

Many molecular phylogenetic studies using nuclear, mitochondrial and apicoplast gene sequences have demonstrated a clear relationship between haemosporidian genera not only with their vertebrate hosts but also their invertebrate vectors. There were clear groupings of *Leucocytozoon* from birds, *Haemoproteus* (*Haemoproteus*) from birds, *Haemoproteus* (*Parahaemoproteus*) from birds, *Plasmodium* from birds and reptiles, *Plasmodium* from rodents and primates, and *Hepatocystis* from bats. These groups were clearly associated with different vectors; namely, simuliids (black-flies), hippoboscids (louse-flies), ceratopogonids (midges), culicine mosquitoes, anopheline mosquitoes, and midges, respectively. There appears to have been a transition from haemosporidia which do not form haemozoin pigment (*Leucocytozoon* in white blood cells) to genera that do form pigment indicating haemoglobin digestion by parasites in red blood cells (*Haemoproteus*, *Plasmodium* and *Hepatocystis*). This was followed by a transition from haemosporidia which undergo schizogony exclusively in host tissues (*Leucocytozoon* and *Haemoproteus*) to those that undergo schizogony in blood cells (*Plasmodium*). While there appears to be a general shift in haemosporidian genera from birds and reptiles to mammals (from nucleated to non-nucleated blood cells), each genus is associated with a particular vector group: black-flies transmitting *Leucocytozoon* to birds; louse-flies transmitting *Haemoproteus* (*Haemoproteus*) to birds; midges transmitting *Haemoproteus* (*Parahaemoproteus*) to birds; culicine mosquitoes transmitting *Plasmodium* to birds and lizards; and anopheline mosquitoes transmitting *Plasmodium* to mammals. The exception to this general trend was *Hepatocystis* which does not undergo blood schizogony and is transmitted to bats by midges.

Over 225 *Plasmodium* species have been classified in 14 subgenera on the basis of parasite morphology, development and host occurrence. Three subgenera contain species in mammals, five subgenera contain those in birds, and six contain those in reptiles:

- *P.* (*Plasmodium*), with large erythrocytic schizonts and round gametocytes, in primates;
- *P.* (*Lavernia*), with large erythrocytic schizonts and crescentic gametocytes, in primates;
- *P.* (*Vinckeia*), with small erythrocytic schizonts and round gametocytes, in antelopes, rodents and other mammals (except primates);

- *P.* (*Haemamoeba*), with large erythrocytic schizonts and round gametocytes, in birds;
- *P.* (*Bennettinia*), with small erythrocytic schizonts and round gametocytes, in birds;
- *P.* (*Huffia*), with large schizonts and elongate gametocytes mostly in immature erythrocytes, in birds;
- *P.* (*Giovannolaia*), with large erythrocytic schizonts and elongate gametocytes, in birds;
- *P.* (*Novyella**), with small erythrocytic schizonts and elongate-oval gametocytes, in birds;

- *P.* (*Sauramoeba*), with large erythrocytic schizonts and large gametocytes, in lizards;
- *P.* (*Lacertamoeba*), with medium erythrocytic schizonts and medium gametocytes, in lizards;
- *P.* (*Paraplasmodium*), with medium erythrocytic schizonts and large gametocytes, in lizards;
- *P.* (*Carinamoeba*), with small erythrocytic schizonts and small gametocytes, in lizards;
- *P.* (*Asiamoeba*), with small erythrocytic schizonts and large gametocytes, in lizards; and
- *P.* (*Ophidiella*), with large erythrocytic meronts and small elongate gametocytes, in snakes.

*A novel subgenus, *P.* (*Papernaia*), was proposed for species in the subgenus *P.* (*Novyella*) which did not possess refractory 'vitreous' globules in erythrocytic developmental stages. However, morphological and molecular studies have shown that the presence/absence of these globules varied for the species *P. ashfordi* when passaged between different hosts, thereby not providing support for this character to be used to split the subgenus *P.* (*Novyella*).

In contrast to the narrow host specificities of most mammalian *Plasmodium* spp., avian species often demonstrate broader host specificities, capable of infecting many bird species belonging to different families, and even orders, and being transmitted by multiple genera of Culicidae (*Aedes, Anopheles, Coquillettidia*, *Culisetta, Culex, Mansonia, Psorophora, Theobaldia* and *Wyeomyia* mosquitoes). The developmental cycles of avian *Plasmodium* spp. are similar to those of mammalian species, yet subtle differences may be involved. Exo-erythrocytic merogony occurs mostly in cells of the reticulo-endothelial system (haemopoietic system for the subgenus *Huffia*) rather than in hepatocytes, erythrocytic merozoites (of many species) may induce secondary tissue merogony in birds contributing to ischaemic pathology, and oocysts may be pedunculated (subgenus *Bennettinia*) with leg-like outgrowths attaching them to the mosquito midgut wall. Development in their vectors appears to occur faster and at lower temperatures, which may accommodate rapid transmission to birds undertaking annual seasonal migrations between continents. These features may explain the wide geographic distribution of avian malaria species in all landscape regions (from mountains to shores), often spanning multiple zoogeographic regions: species richness (biodiversity) being greatest in Nearctic (North America), Palearctic (Europe and Asia = Eurasia), Ethiopian/African (sub-Saharan Africa) and Oriental (India, South-East Asia, Western Indonesia) regions, and poorest in Australasian (Australia, Eastern Indonesia, New Guinea, New Zealand) and Neotropical (South America) regions. Survey records indicate species richness to be greatest in Passeriformes, Galliformes, Columbiformes, Coraciiformes and Piciformes, medium in Ciconiiformes, Anseriformes, Falconiformes, Gruiformes, Charadriiformes and Strigiformes, and poorest in relatively old groups such as Sphenisciformes, Struthioniformes, Tinamiformes, Pelecaniformes, Turniciformes, Musophagiformes, Coliiformes and Trogoniformes. While the vast majority of avian *Plasmodium* spp. have been recorded in birds in tropical or subtropical countries or in Holarctic migrants overwintering in warmer regions, several species have become widespread in many bird species throughout the world (notably, *P. (Ha.) cathemerium, P. (Ha.) relictum, P. (Hu.) elongatum, P. (G.) circumflexum, P (N.) nucleophilum* and *P. (N.) vaughani*).

***Plasmodium* species**	**Avian intermediate hosts (IH)**	**Periodicity (pathogenicity)**	**Definitive hosts (DH) (vectors)**	**Zoogeographic distribution**
Subgenus: *Haemamoeba* (large erythrocytic schizonts, round gametocytes, in birds)				
P. (*Ha.*) *caloti*	Passeriformes: alaudid (skylarks)			Palearctic
P. (*Ha.*) *cathemerium* (syn. *centropi p.p.*)	Passeriformes: cardinalid (cardinals, grosbeaks), corvid (crows, jays, magpies), emberizid (buntings), fringillid (canaries, finches, redpolls), hirudinid (swallows), icterid (cowbirds, grackles, meadowlarks), laniid (shrikes), mimid (mockingbirds, thrashers), monarchid (monarchs), motacillid (pipits, wagtails), muscicapid (redstarts, robins), parid (tits),	24 hrs (pathogenic, anaemia, ischaemia)	Diptera: culicid (*Aedes aegypti, cantator, geniculatus, sollicitans, Anopheles norestensis, quadrimaculatus, strodei, Culex bitaeniorhynchus, fuscanus, pipiens, quinquefasciatus, salinarius, stigmatostoma, tarsalis, territans, tritaeniorhynchus, Culiseta*	Holarctic, Neotropical, Ethiopian, Oriental

	parulid (warblers), passerid (sparrows), passerellid (juncos), ploceid (weavers), sturnid (starlings), thraupid (grassquit, tanagers), timaliid (babbler), troglodytid (wrens), turdid (blackbirds, chats, thrushes), tyrannid (flycatchers); Apodiformes: apodid (swifts); Caprimulgiformes: capramulgid (nightjars); Columbiformes: columbid (pigeons, doves); Gruiformes: rallid (rails); Piciformes: ramphistid (toucans); Sphenisciformes: spheniscid (penguins): Strigiformes: strigid (fish owls)		*melaneum, morsitans, Psorophora ferox*)	
P. (*Ha.*) *coturnixi*	Galliformes: phasianid (quail)	24 hrs		Oriental (Pakistan)
P. (*Ha.*) *gallinaceum* (syn. *metastaticum*)	Galliformes: phasianid (chickens, junglefowl, grey partridge); Passeriformes: corvid (house crow)	36 hrs (pathogenic, anaemia, ischaemia)	Diptera: culicid (*Aedes aegypti, albolateralis, albipictus, atropalpus, campestris, canadensis, cantator, chrysolineatus, geniculatus, jamesi, japonicus, lepidus, pallirostris, pseudoalbopictus, pseudotaeniatus, scutellaris, stimulans, stokesi, togoi, triseriatus, trivittatus, unilineatus, vexans, vittatus, Anopheles freeborni, pulcherrimus, quadrimaculatus, sacharovi, Armigeres annulipalpis, aureolineatus, kuchingensis, magnus, obturbans, subalbatus, Culex mimulloides, pipiens, salinarius, tarsalis, Culiseta inornata, Mansonia albimanus, crassipes, erturbans*)	Oriental
P. (*Ha.*) *giovannolai*	Passeriformes: fringillid (canaries), turdid (thrushes)	24 hrs (death in canaries)	Diptera: culicid (*Culex pipiens*)	Palearctic (Italy)
P. (*Ha.*) *griffithsi*	Galliformes: phasianid (turkeys)			Oriental (Burma)
P. (*Ha.*) *lutzi*	Gruiformes: rallid (rails)	asynchronous		Neotropical
P. (*Ha.*) *maior*	Passeriformes: passerid (sparrows)			Palearctic
P. (*Ha.*) *matutinum*	Passeriformes: passerid (sparrows), turdid (thrushes); Columbiformes: columbid (doves, pigeons)	24 hrs (organ congestion)	Diptera: culicid (*Culex pipiens, stigmatosoma, tarsalis*)	Holarctic, Oriental
P. (*Ha.*) *parvulum*	Passeriformes: vangid (vangas)			Madagascar
P. (*Ha.*) *relictum* [type species] [incl. subspp. *relictum, matutinum*] (syn. *paddae, alaudae p.p., biziurae, passeris,*	Passeriformes: alaudid (larks, skylarks), callaeid (saddlebacks), campephagid (minivets), cardinalid (cardinals), cisticolid (tailorbirds), corvid (choughs, crows, ravens, jays, magpies), dicaeid (flowerpeckers), dicrurid (drongos), emberizid (buntings), estrildid (mannikins,	30-36 hrs (pathogenic, lesions in tissues)	Diptera: culicid (*Aedes aegypti, communis, concolor, dorsalis, mariae, vexans, Anopheles albimanus, crucians, freeborni, quadrimaculatus, subpictus, Culex apicalis,*	cosmopolitan (except Antarctic)

major, bioccai, grassii, muniae, majoris p.p., inconstans, pericrocati, capistrani, placeii, spheniscidae, chloropsidis, ginsburgi, dorsti, coluzzii, and *Haemoproteus mcleani*?)	pytilias), eulacestomatid (ploughbills), fringillid (crossbills, euphonias, finches, grosbeaks, honeycreepers, siskins), hirudinid (swallows), icterid (caciques, grackles, marshbirds, meadowlarks), laniid (shrikes), locustellid (grassbirds), mimid (thrashers), monarchid (monarchs, flycatchers), motacillid (pipits, wagtails), muscicapid (batis, chats, nightingales, robins, shamas, wheatears), oriolid (orioles), nectariniid (sunbird), paradoxornithid (parrotbills), parulid (tits, warblers), passerellid (snowbird), passerid (sparrows), ploceid (weavers), polioptilid (gnatcatchers), ptilonorhynchid (catbirds), pycnonotid (bulbuls), rhipidurid (fantails), sturnid (starlings, mynas), thamnophilid (antbirds), thraupid (grassquits, saltators, tanagers), timaliid (babblers), troglodytid (wrens), turdid (blackbirds, thrushes), tyrannid (tyrannulets), vireonid (vireos), zosteropid (white-eyes); Accipitriformes: accipitrid (buzzards); Anseriformes: anatid (ducks, eiders, geese); Apodiformes: apodid (swifts); Charadriiformes: alcid (auks, puffins), charadriid (plovers), larid (gulls), scolopacid (snipes); Coraciiformes: coraciid (rollers), meropid (bee-eaters); Cuculiformes: cuculid (cuckoos, koels); Columbiformes: columbid (doves, pigeons); Falconiformes: falconid (falcons, hawks); Galliformes: phasianid (chickens, grouse, partridges, pheasant, quail), numidid (guineafowl); Gruiformes: rallid (bush-hens, coots, rails): Otidiformes: otidid (bustards); Suliformes: sulid (gannets); Piciformes: bucconid (puffbirds), picid (woodpeckers); Procellariiformes: diomedeid (albatross); Psittaciformes: psittaculid (parrots); Sphenisciformes: spheniscid (penguins); Strigiformes: strigid (owls)		*bitaeniorhynchus, fatigans, fuscanus, gelidus, hortensis, pipiens, quinquefasciatus, salinarius, stigmatasoma, tarsalis, territans, theileri, whitmorei, Culiseta annulata, longiareolata*)	
P. (*Ha.*) *subpraecox* (syn. *wasielewskii*)	Strigiformes: strigid (little owl, red-chested owlet, snowy owl, screech owl); Passeriformes: alaudid (skylark), passerid (sparrow)	24 hrs	Diptera: culicid (*Culex pipiens*)	Holarctic
P. (*Ha.*) *tejerai*	Galliformes: phasianid (turkeys. quail), numidid (guineafowl); Anseriformes: anatid (ducks, geese)	? (death in exptl infections)		Neotropical
Subgenus: *Bennettinia* (small erythrocytic schizonts, round gametocytes, in birds)				
P. (*B.*)	Galliformes: phasianid (chickens,	24 hrs	Diptera: culicid (*Culex*	Neotropical,

juxtanucleare (syn. *japonicum*) [type species]	partridges, peafowl, turkeys); Sphenisciformes: spheniscid (penguins)	(mildly pathogenic, tissue lesions)	*annulus, gelidus, pipiens, pseudovishnui, sitiens, tritaeniorhynchus*)	Ethiopian, Oriental
Subgenus: *Huffia* (large erythrocytic schizonts, elongate gametocytes mostly in immature erythrocytes, in birds)				
P. (*Hu.*) *elongatum* (incl. *alloelongatum*) [type species]	Passeriformes: fringillid (canaries), meliphagid (bellbirds), sylviid (warblers), thraupid (honeycreepers); Anseriformes: anatid (ducks); Falconiformes: falconid (eagles, hawks); Accipitriformes: accipitrid (sparrowhawks); Galliformes: phasianid (quail); Sphenisciformes: spheniscid (penguins); Strigiformes: strigid (owls)	24 hrs (pathogenic in captive penguins due to tissue lesions)	Diptera: culicid (*Culex pipiens, restuans, nigripalpus, salinarius, tarsalis, territans*)	Holarctic, Neotropical, Ethiopian, Oriental
P. (Hu.) hermani	Galliformes: phasianid (turkeys, quail); Charadriiformes: scolopacid (knots)		Diptera: culicid (*Culex nigripalpus, restuans, salinarius, Wyeomyia vanduzeei*)	Nearctic
P. (Hu.) huffi	Piciformes: ramphastid (toucans)	48 hrs (moderately pathogenic)		Neotropical
P. (Hu.) polymorphum	Passeriformes: alaudid (skylark)			Palearctic
Subgenus: *Giovannolaia* (large erythrocytic schizonts, elongate gametocytes, in birds)				
P. (*G.*) *anasum*	Anseriformes: anatid (ducks)			Oriental
P. (*G.*) *bigueti* (*species inquirenda*)	Passeriformes: passerid (sparrows)			Palearctic
P. (G.) buteonis (*species inquirenda*)	Accipitriformes: accipitrid (buzzards)			Palearctic
P. (*G.*) *circumflexum* (incl. *homocircumflexum*) (syn. *heroni*) [type species]	Passeriformes: cardinalid (cardinals), corvid (jays), fringillid (canaries), mimid (thrashers), parulid (warblers), passerid (sparrows), ptilonorhynchid (catbirds), sturnid (starlings), turdid (blackbirds, robins, thrushes); Anseriformes: anatid (ducks, swans); Columbiformes: columbid (pigeons); Coraciiformes: alcedinid (kingfishers); Charadriiformes: glareolid (waders); Falconiformes: falconid (hawks); Galliformes: phasianid (chickens, partridges, pheasant, quail, turkeys), numidid (guineafowl); Strigiformes: strigid (owls)	24 or 48 hrs (anaemia and ischaemia)	Diptera: culicid (*Culiseta longiareolata, melaneura, morsitans, Mansonia crassipes, Theobaldia annulata*)	cosmopolitan (except Antarctic)
P. (*G.*) *durae*	Galliformes: phasianid (francolins, turkeys, peafowl), numidid (guineafowl)	24 hrs (convulsions and anemia in turkeys)	Diptera: culicid (*Culex antennatus, pipiens, univittatus*)	Ethiopian
P. (*G.*) *fallax*	Strigiformes: strigid (eagles, hawks, owls); Accipitriformes: accipitrid (vultures); Galliformes: phasianid (guineafowl); Passeriformes: emberizid (buntings) parulid (warblers)	asynchronous (ischaemia in exptl. infections)	Diptera: culicid (*Aedes aegypti, albopictus, atropalpus, triseriatus, Anopheles quadrimaculatus, Culex quinquefasciatus, tarsalis*)	Ethiopian, Oriental, Palearctic
P. (*G.*) *formosanum*	Galliformes: phasianid (partridges); Gruiformes: rallid (rails)	48 hrs		Oriental
P. (*G.*) *gabaldoni*	Columbiformes: columbid (pigeons); Anseriformes: anatid	24 hrs (pathogenic in	Diptera: culicid (*Aedes aegypti, Culex pipiens*)	Neotropical

	(ducks)	young birds)		
P. (*G.*) *garnhami*	Bucerotiformes: bucerotid (hoopoes); Coraciiformes: coraciid (rollers); Passeriformes: laniid (shrikes)	48 hrs (severe in young birds)	Diptera: culicid (*Culex pipiens*)	Ethiopian, Southern Palearctic
P. (G.) ghadiriani (*species inquirenda*)	Passeriformes: alaudid (skylarks), corvid (magpies)			Palearctic
P. (*G.*) *gundersi*	Strigiformes: strigid (owl); Galliformes: phasianid (partridges); Passeriformes: fringillid (canaries)	24 hrs (severe in canaries)		Oriental
P. (*G.*) *hegneri*	Anseriformes: anatid (teals)	asynchronous		Oriental
P. (*G.*) *leanucleus*	Passeriformes: passerid (sparrows), pycnonotid (bulbuls)	24 hrs ()	Diptera: culicid (*Culex pipiens, Anopheles dirus*)	Oriental
P. (*G.*) *lophurae*	Galliformes: phasianid (chickens, pheasant, turkeys); Columbiformes: columbid (doves); Anseriformes: anatid (ducks)	24-36 hrs (organ congestion and anemia, esp. in ducks)	Diptera: culicid (*Aedes albopictus, aegypti, atropalpus, Anopheles quadrimaculatus, Culex restuans*)	Oriental
P. (*G.*) *octamerium*	Passeriformes: estrildid (waxbills), fringillid (canaries, finches), passerid (sparrows), ploceid (weavers), sturnid (starlings), viduid (whydahs); Anseriformes: anatid (ducks); Columbiformes: columbid (doves, pigeons); Galliformes: phasianid (chickens, partridges, quail)	24 hrs (cerebral signs in exptl. infections in partridges)		Ethiopian
P. (*G.*) *pedioecetae*	Galliformes: phasianid (grouse, partridges, quail); Tinamiformes: tinamid (nothuras); Passeriformes: fringillid (canaries)			Nearctic, Neotropical
P. (*G.*) *pinottii*	Piciformes: ramphastid (toucans); Passeriformes: thraupid (bananaquits, grassquits, thrushes); fringillid (canaries), passerid (sparrows), parulid (warblers); Anseriformes: anatid (ducks); Columbiformes: columbid (doves, pigeons); Galliformes: phasianid (chickens); Gruiformes: rallid (rails)	24 hrs		Neotropical
P. (*G.*) *polare*	Passeriformes: cardinalid (cardinals), emberizid (buntings), hirundinid (swallows), muscicapid (chats), parid (tits), passerid (sparrows), pycnonotid (bulbuls), thamnophilid (antshrikes), turdid (blackbirds, thrushes); Anseriformes: anatid (ducks); Caprimulgiformes: caprimulgid (nighthawks); Columbiformes: columbid (doves); Falconiformes: falconid (eagles, falcons); Galliformes: phasianid (francolins, grouse): Gruiformes: gruid (cranes), Tinamiformes: tinamid (nothuras)	24 hrs	Diptera: culicid (*Culiseta longiareolata, morsitans*)	Holarctic, Neotropical, Ethiopian, Oriental
P. (G.) tranieri (*species inquirenda*)	Passeriformes: corvid (magpies)			Palearctic
Subgenus: *Novyella* (small erythrocytic schizonts and elongate-oval gametocytes, in birds)				
P. (*N.*) *accipiteris*	Accipitriformes: accipitrid (sparrowhawks)			Palearctic

P. (*N.*) *ashfordi*	Passeriformes: fringillid (crossbills, siskins), parulid (warblers)			Palearctic
P. (*N.*) *beaucournui* (*species inquirenda*)	Passeriformes: corvid (magpies)			Palearctic
P. (*N.*) *bertii*	Gruiformes: rallid (rails)	asynchronous		Neotropical
P. (*N.*) *columbae*	Columbiformes: columbid (pigeons); Anseriformes: anatid (ducks)	little periodicity (pathogenic in ducklings)		Neotropical
P. (*N.*) *delichoni*	Passeriformes: hirudinid (house martin)	asynchronous		Palearctic
P. (N.) dherteae (*species inquirenda*)	Passeriformes: alaudid (skylarks), corvid (magpies)			Palearctic
P. (*N.*) *dissanaikei*	Psittaciformes: psittaculid (parakeets); Anseriformes: anatid (ducks); Passeriformes: fringillid (canaries)	(anaemia in ducklings)		Oriental
P. (*N.*) *forresteri*	Strigiformes: strigid (owls); Falconiformes: falconid (hawks, eagles); Galliformes: phasianid (quail): Anseriformes: anatid (ducks)		Diptera: culicid (*Culex restuans*)	Nearctic
P. (*N.) globularis*	Passeriformes: pycnonotid (greenbuls)			African
P. (*N.*) *hexamerium* (syn. *oti*)	Passeriformes: alaudid (skylarks), cardinalid (cardinals), corvid (crows, magpies, jays), emberizid (buntings), fringillid (canaries, finches, grosbeaks), icterid (cowbirds, grackles, troupials, meadowlarks), mimid (catbirds, thrashers), motacillid (pipits, wagtails), parulid (warblers), passerellid (juncos, towhees), passerid (sparrows), sturnid (starlings), turdid (blackbirds, bluebirds, thrushes), tyrannid (kingbirds); Anseriformes: anatid (ducks); Galliformes: phasianid (turkeys); Ciconiiformes: ciconiid (storks); Columbiformes: columbid (doves, pigeons); Accipitriformes: accipitrid (plumbeous kites); Coraciiformes: meropid (bee-eaters); Strigiformes: strigid (scops owls, wood owls)	little periodicity		Nearctic, Neotropical
P. (*N.*) *hoionucleophilum*	Passeriformes: parulid (warblers)			Palearctic
P. (*N.*) *homopolare*	Passeriformes: fringillid (finches), icterid (cowbirds), parulid (warblers), passerellid (towhees), passerid (sparrows), sittid (nuthatches), thraupid (tanagers), troglodytid (wrens)		Diptera: culicid (*Culex tarsalis, restuans, Culiseta particeps*)	Nearctic, Neotropical
P. (N.) jeanriouxi (*species inquirenda*)	Passeriformes: alaudid (skylarks)			Palearctic
P. (*N.*) *kempi*	Galliformes: phasianid (turkeys, partridges, peafowl, quail), numidid (guineafowl); Anseriformes: anatid (ducks, geese); Passeriformes: fringillid (canaries)		Diptera: culicid (*Culex pipiens, restuans, tarsalis*)	Nearctic

P. (N.) lenoblei (*species inquirenda*)	Passeriformes: corvid (crows, magpies)			Palearctic
P. (*N.*) *lucens*	Passeriformes: nectariniid (olive sunbirds)			African
P. (*N.*) *megaglobularis*	Passeriformes: nectariniid (sunbirds)			African
P. (*N.*) *multivacuolaris*	Passeriformes: icterid (greenbuls)			African
P. (*N.*) *nucleophilum* subsp. *nucleophilum*	Passeriformes: cardinalid (ant tanager), corvid (magpies), emberizid (buntings), fringillid (canaries, finches), furnariid (woodcreepers), grallariid (antpittas), hirudinid (martins, swallows), mimid (catbirds, mockingbirds), monarchid (flycatchers), oriolid (orioles), parid (tits), parulid (warblers), passerid (sparrows), piprid (manakin), ploceid (weavers), sturnid (starlings, mynas), thraupid (grassquits, tanagers), tityrid (becards), turdid (blackbirds, thrushes), tyrannid (kingbirds, tyrannulets), vireonid (vireos, greenlets); Anseriformes: anatid (ducks, geese); Piciformes: ramphastid (toucans); Pelecaniformes: threskiornithid (ibises); Caprimulgiformes: caprimulgid (nightjars); Psittaciformes: psittaculid (parrots); Columbiformes: columbid (doves)	24 hrs		Holarctic, Neotropical, Ethiopian, Oriental
P. (*N.*) *nucleophilum* subsp. *toucani* (syn. *P. toucani*)	Piciformes: ramphastid (toucans)	24 hrs		Neotropical
P. (N.) pachysomum (*species inquirenda*)	Passeriformes: motacillid (pipits)			Palearctic
P. (*N.*) *parahexamerium*	Passeriformes: muscicapid (white-tailed alethes)			African
P. (*N.*) *paranucleophilum*	Passeriformes: thraupid (tanagers), fringillid (canaries)			Neotropical
P. (N.) pfefferi (*species inquirenda*)	Passeriformes: corvid (magpies)			Palearctic
P. (N.) reniai (*species inquirenda*)	Passeriformes: alaudid (skylarks)			Palearctic
P. (*N.*) *rouxi* (syn. *mohammedi*)	Passeriformes: alaudid (skylarks), chloropseid (leafbirds), cisticolid (prinias), estrildid (mannikins), fringillid (canaries, finches, grosbeaks), malaconotid (bushshrikes), monarchid (flycatchers), motacillid (pipits, wagtails), muscicapid (robins, wheatears), nectariniid (sunbirds), parulid (warblers), passerid (sparrows), pittid (pittas), platysteirid (batis), ploceid	24 hrs (anaemia, splenomegaly)	Diptera: culicid (*Culex pipiens, tarsalis, territans*)	Holarctic, Ethiopian, Oriental, African

	(weavers), pycnonotid (bulbuls, finchbills), thraupid (grassquits, saltators), timaliid (babblers), turdid (blackbirds, thrushes), zosteropid (yuhinas); Apodiformes: apodid (swifts); Gruiformes: rallid (wood rails); Galliformes: phasianid (francolins, partridges, pheasant), numidid (guineafowl); Piciformes: ramphastid (toucans)			
P. (N.) sergentorum (*species inquirenda*)	Passeriformes: alaudid (skylarks), corvid (magpies)			Palearctic
P. (N.) snounoui (*species inquirenda*)	Passeriformes: corvid (magpies)			Palearctic
P. (N.) stellatum (*species inquirenda*)	Passeriformes: monarchid (flycatchers)			Palearctic
P. (*N.) unalis*	Passeriformes: turdid (thrushes)			Neotropical
P. (*N.) valkiunasi*	Passeriformes: corvid (magpies)			Palearctic
P. (*N.*) *vaughani* (type species) [incl. subspp. *vaughani*, *tenuis*, *merulae, tumbayaensis*]	Passeriformes: alaudid (larks), cardinalid (cardinals), cisticolid (camaroptera), conophagid (gnateaters), corvid (crows, jays, magpies), dicaeid (flowerpeckers), dicrurid (drongos), estrildid (waxbills), fringillid (canaries, finches, grosbeaks), furnariid (woodcreepers), icterid (bobolink, cowbirds, grackles, marshbirds, meadowlarks), laniid (shrikes), leiothrichid (leiothrix), malaconotid (boubous, bushshrikes), mimid (catbirds, mockingbirds), monarchid (flycatchers), motacillid (pipits, wagtails), muscicapid (chats, robins, shamas), nectariniid (sunbirds), parid (tits), parulid (ovenbirds, warblers), passerellid (juncos), passerid (sparrows), pittid (pittas), ploceid (weavers, widowbirds), oriolid (orioles), piprid (manakins), pycnonotid (bulbuls), sturnid (mynas, starlings), sylviid (blackcaps), thamnophilid (antbirds, antshrikes), thraupid (bananaquits, grassquits, seedeaters, tanagers), timaliid (babblers), troglodytid (wrens), turdid (blackbirds, solitaires, thrushes), vireonid (vireos), zosteropid (white-eyes, yuhinas); Anseriformes: anatid (dabbling ducks, geese, wood duck); Charadriiformes: turnicid (buttonquail), glareolid (waders); Columbiformes: columbid (doves, pigeons); Coraciiformes: meropid (bee-eaters), alcedinid (kingfishers); Cuculiformes: cuculid (koels, malkohas); Gruiformes: rallid (bush-hens, rails); Piciformes: capitonid (barbets), ramphastid (toucans);	24-26 hrs, but often asynchronous (nonpathogenic)	Diptera: culicid (*Culiseta morsitans, Culex pipiens*)	cosmopolitan (except Antarctic)

	Psittaciformes: psittaculid (racket-tails); Musophagiformes: musophagid (turacos)			

Parasite morphology: The developmental cycles of avian *Plasmodium* spp. are similar to those of mammalian species, but subtle differences are involved. In birds, the parasites may undergo 3 forms of exo-erythrocytic merogony (forming cryptozoic, metacryptozoic and phanerozoic meronts, sometimes enigmatically referred to as cryptozoites, metacryptozoites and phanerozoites even though all of them produce merozoites) and then cyclic erythrocytic merogony that leads to gametocyte formation. In mosquito vectors, the parasites complete sexual development (gamogony) culminating in oocyst formation and sporozoite production (sporogony). There are initially 2 exo-erythrocytic generations of merogony (known as 'primary' pre-erythrocytic merogony): the first involving rounded (10-45 µm diameter) basophilic cryptozoic meronts that become multinucleate as they undergo internal division (endogeny) usually forming < 100 ovoid to spindle-shaped merozoites (1-3 µm); and the second generation involving larger ellipsoidal (20-80 µm long) metacryptozoic meronts that become multinucleate as they divide internally usually forming > 100 ovoid-rhomboid merozoites (1-2 µm). A third exo-erythrocytic generation of merogony (known as 'secondary' post-erythrocytic merogony) may occur later, involving ellipsoidal-vermiform (up to 120 µm long) basophilic phanerozoic meronts that form up to 180 small ovoid-rhomboid merozoites (1-2 µm). Erythrocytic merogony involves a cyclic process where small rounded (1-3 µm) irregular trophozoites form pleomorphic (plasmodial) stages (rather than ring stages formed by mammalian species), followed by round-irregular (5-10 µm) meronts that divide internally to form 4-36 (frequently 10-24) small round merozoites (1-2 µm). The meronts may occupy up to half the volume of the host erythrocyte and they contain plentiful eosinophilic cytoplasm with brown-black refringent pigment (haemozoin) granules (0.2-1.0 µm). Eventually, merozoites invade erythrocytes and form round-oval (5-10 µm) gametocytes which exhibit sexual dimorphism (accentuated by Giemsa staining giving rise to the paradoxical adage 'blue for girls, pink for boys'): where macrogametocytes (female) have a basophilic cytoplasm (due to the presence of numerous ribosomes and plentiful endoplasmic reticulum) with a Golgi apparatus, an unusual 'spherical body', a compact nucleus with a nucleolus, and usually less than 30 pigment granules; while microgametocytes (male) have a pale eosinophilic cytoplasm (fewer ribosomes and endoplasmic reticulum) with a large pale nucleus (without a nucleolus) and up to 30 pigment granules but no Golgi apparatus or 'spherical body'. In mosquitoes, male gametocytes undergo exflagellation releasing motile microgametes (8-16 x 0.5-1.0 µm) that fertilize robust macrogametes (5-8 µm) producing a motile zygote (known as an ookinete). The ookinete is an elongate worm-like stage (12-20 x 2-5 µm) containing scattered vacuoles, pigment granules, and eventually a residual body. It matures to form a membrane-bound oocyst containing pigment granules in loose aggregated clumps. The oocysts of most species are rounded (30-50 µm) although those in the subgenus *Bennettinia* may be pedunculated with stalk-like projections used for attachment. The oocysts undergo sporogony and divide internally to form large numbers (hundreds) of elongate to spindle-shaped sporozoites (10-16 x 1-2 µm) with prominent central nuclei.

Site of infection: In birds, the parasites do not undergo exo-erythrocytic multiplication in hepatocytes (like mammalian species) but rather in cells of the reticulo-endothelial system (and the haemopoietic system for the subgenus *Huffia*). Primary meronts (cryptozoic and metacryptozoic) often develop in macrophages and fibroblasts in the skin, but they may occur in numerous organs. Secondary meronts (phanerozoic) develop in endothelial cells of capillaries in various tissues, especially in the brain for some species. Erythrocytic merogony occurs in cells in the circulatory system, with dividing meronts lysing host cells while gametocytes are longer-lasting persistent stages. In mosquito vectors, fertilization of exflagellated microgametes and robust macrogametes occurs in the gut lumen. The resultant ookinete is motile and penetrates the gut to form an oocyst on the outer wall. Mature oocysts release sporozoites into the haemocoel where they invade the salivary glands. Infections have been recorded in numerous bird species belonging to many different families and orders. In general, host specificity has not usually been observed for individual host species, but is often considered to be operational at the level of host family and even order. Parasite species in birds demonstrate broad host specificities, with some species considered to be regionally specific infecting many sympatric bird species. Parasite species richness is greatest in Passeriformes, Galliformes, Columbiformes, Coraciiformes and Piciformes, medium in Ciconiiformes, Anseriformes, Falconiformes, Gruiformes, Charadriiformes and Strigiformes, and poorest in relatively old groups such as Sphenisciformes, Struthioniformes, Tinamiformes, Pelecaniformes, Turniciformes, Musophagiformes, Coliiformes and Trogoniformes. Infections have been found in birds from all landscape regions (from mountains to shores), often spanning multiple zoogeographic regions: being most prevalent in Nearctic (North America), Palearctic (Europe and Asia = Eurasia), Ethiopian/African (sub-Saharan Africa) and Oriental (India, South-East Asia, Western Indonesia) regions, and poorest in Australasian (Australia, Eastern Indonesia, New Guinea, New Zealand) and Neotropical (South America) regions. The vast majority of parasite species have been recorded in birds in tropical or subtropical countries or in Holarctic migrants overwintering in warmer regions, but several species have become widespread cosmopolitan parasites in many bird species throughout the world. The parasites exhibit greater host specificity for their invertebrate vectors (which act as definitive hosts), being found only in mosquitoes of the family Culicidae (genera *Aedes, Anopheles, Coquillettidia*, *Culisetta, Culex, Mansonia, Psorophora, Theobaldia* and *Wyeomyia*). Some avian *Plasmodium* spp. may develop in up to 26 culicid species, while others only develop in 1-2 culicid species.

Pathogenesis: Many *Plasmodium* infections in birds are asymptomatic and have not been associated with any clinical signs, but several species may cause mild-severe episodic disease, with outbreaks involving mortalities recorded in domestic poultry and waterfowl, captive and aviary birds and wild bird populations. The parasites may cause disease either by merogony within tissues

causing lesions or by merogony within erythrocytes causing haemolytic anaemia, both possibly contributing to ischaemia. Infections proceed through 3 phases of infection corresponding to pre-erythrocytic, erythrocytic and post-erythrocytic merogony. Initial pre-erythrocytic generations usually cause little damage as the parasites are sparse and develop rapidly eliciting few inflammatory reactions. Subsequent erythrocytic generations occur more frequently over protracted periods sometimes resulting in chronic conditions but often only resulting in low chronic parasitaemias. However, merozoites from earlier phases may undergo secondary post-erythrocytic merogony in host tissues which cause greater damage due to their larger size and persistence. All developmental stages may contribute to clinical disease characterized by circulatory perturbations. Blood stages have been associated with haemolytic anaemia, exacerbated by erythrophagocytosis by reticuloendothelial cells with enlargement and whitening of the spleen and liver and the accumulation of haemozoin pigment in organs. Persistent intra-erythrocytic gametocytes vary in their effect on host cells, and only some species cause hypertrophy, vacuolation and/or nuclear displacement. Tissue stages cause the most serious pathology by blocking capillaries in various organs (including the brain for some species) with downstream ischaemia due to the disrupted blood supply resulting in anoxia, cell death, necrosis, oedema, cellular infiltrates, and sometimes cerebral paralysis (e.g. *P. gallinaceum, P. cathemerium, P. durae, P. lophorae, P. elongatum, P. octamerium*). Post-mortem findings include anaemia, splenomegaly (occasionally with infarcts), hepatomegaly, and pigment deposits in many visceral organs. It has often been speculated that subclinical infections may impact on host fitness by reducing competitiveness, feeding efficiency, nutrition, reproduction, immunology and behaviour (such as migration or irruption). Infections in birds are often marked by their recrudescence due to the resumption of erythrocytic merogony, or by relapses due to the activation of exo-erythrocytic merogony (rather than the reactivation of dormant sporozoites (hypnozoites) as occurs in mammals). Relapses of avian malaria may be seasonal (especially in spring) or nonseasonal (usually in countries with warm climates). Infections occur in birds of all ages, with young birds being more susceptible but adult birds having greater exposure. Chronic infections may last for the lifespan of the bird species, generally 2-10 years depending on size (smallest birds with shortest lifespans). Outbreaks have also been associated with birds kept in stressful situations (captivity, intensive husbandry, poor nutrition) presumably due to their reduced immunocompetence. Immunological studies have shown birds to vary considerably in their natural innate immunity (resistance/susceptibility to infection) and in their acquired immunity (humoral and cellular responses) following infection. It is thought that birds may develop premunitive immunity whereby small numbers of parasites persist but elicit strong protection against disease from challenge or super-infections.

Developmental cycle and mode of transmission: Avian *Plasmodium* spp. have indirect heteroxenous (2-host) life-cycles involving serial transmission between birds (acting as intermediate hosts in which parasites undergo asexual proliferation) and mosquito vectors (acting as definitive hosts in which parasites undergo sexual reproduction). Infective sporozoites injected into birds by feeding mosquitoes invade reticulo-endothelial cells and form exo-erythrocytic cryptozoic meronts that produce numerous merozoites. The merozoites are not infective to erythrocytes but infect macrophages forming exo-erythrocytic metacryptozoic meronts that produce numerous merozoites. These merozoites are highly infective for various host cells and may lead to several different outcomes. Some infect other macrophages leading to a new cycle of metacryptozoic merogony. Some infect red blood cells leading either directly to gametocyte formation but more usually leading to erythrocytic merogony. Some infect capillary endothelial cells in host tissues forming secondary exo-erythrocytic phanerozoic meronts that produce numerous merozoites. Erythrocytic merogony is cyclic (periodicity of 24-36 hours) with invading merozoites transforming into pleomorphic trophozoites that mature into meronts (sometimes called schizonts) to produce numerous merozoites. These merozoites may infect additional red blood cells to undergo further merogony or to begin gamogony forming sexually dimorphic gametocytes, or they may infect endothelial cells and form post-erythrocytic phanerozoic meronts whose progeny may initiate new cycles of erythrocytic merogony and gamogony. The prepatent period (from the time of infection to the first formation of gametocytes) is usually < 120 hours. Infections are transmitted to mosquitoes when they feed on bird blood and ingest gametocytes in red blood cells. Only female mosquitoes feed on blood as they require high protein diets in order to produce eggs. Male microgametocytes undergo exflagellation in the gut to release motile microgametes which fertilize female macrogametes. The resultant zygote (ookinete) moves through the gut wall to form an encapsulated oocyst on the outer wall. The oocyst forms several germinative centres that divide asexually (sporogony) to form many hundreds of sporozoites that are liberated into the haemocoel and penetrate the adjacent salivary glands. Infections are transmitted to birds when sporozoites and saliva (with anticoagulant properties) are injected during feeding (inoculative transmission). Avian *Plasmodium* spp. usually have a faster rate of sexual development in mosquitoes than mammalian *Plasmodium* spp. (7 days cf. 10-12 days) and once a mosquito is infected, it is infected for life and continues to transmit infections over its remaining lifespan. Predisposing factors for infections in birds include species with large body sizes, long nestling periods, open or ground nests, sedentary activities, and gregarious colony-forming behaviours. Many bird species undertake seasonal migrations to feed and/or breed, but infections are usually not associated with breeding seasons, but rather with 'over-wintering' sites (often near lakes where vectors abound) or in tropical/subtropical regions (where vectors are active all year round).

Differential diagnosis: Infections are conventionally diagnosed by the direct microscopic detection of intra-erythrocytic parasites in thick or thin peripheral blood smears stained with Romanowsky's stains (Giemsa, Leishman's or Field's stains). Test sensitivity may be poor due to very low parasitaemias or diurnal changes in parasitaemias. Host tissues may be collected at autopsy and examined as impression smears or histological sections for exo-erythrocytic meronts. Several experimental studies have used fluorochrome labels and *in situ* DNA hybridization techniques to help reveal parasites, but they have not been developed for routine use. Infections in vectors may be detected by trapping mosquitoes and examining squash or gut preparations for developing oocysts or salivary gland extracts for sporozoites. There are also occasional reports of infections being detected by in vivo culture following

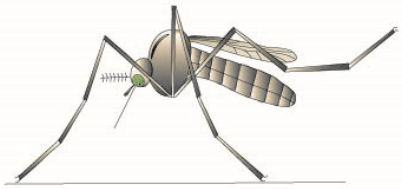
the subinoculation of samples into susceptible bird species. Several immunoserological tests have been developed to detect host antibodies (fluorescent-antibody tests, haemagglutination tests, enzyme immunoassays) or parasite antigens (immunochromatography), but they have varied in their sensitivity and specificity. Molecular biological techniques have been used to detect and characterize parasites and infer phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear genes (notably small subunit (18S) ribosomal DNA) and mitochondrial genes (particularly cytochrome b).

Treatment and control: Various antimalarial drugs have been used to treat infections in birds, including primaquine, chloroquine, proguanil and pyrimethamine, despite some indications that drug-resistance may become problematic. It is recommended that combinations of drugs be used to target both tissue and blood stages, particularly since the former is responsible for much of the pathology associated with bird malaria as well as the persistence of infections. For example, treatment with both primaquine and chloroquine is recommended as primaquine is active against tissue stages while chloroquine is active against blood stages. Medications are usually administered to birds via medicated water supplies or by oral intubation. It is important that birds be isolated and screened for infections, particularly when restocking poultry houses, and translocating exotic species for zoos and aviaries. At present, the best preventive measures involve isolating birds from vectors using physical barriers (screens) and/or chemical barriers (residual insecticides) and undertaking local vector control programmes targeting standing water sources for mosquito larvae, resting sites for adult mosquitoes, and even releasing sterile males to reduce reproduction rates.

Plasmodium
(avian species)

5 subgenera in birds:
- *P.* (*Haemamoeba*)
- *P.* (*Bennettinia*)
- *P.* (*Hoffia*)
- *P.* (*Giovannolaia*)
- *P.* (*Novyella*)

heteroxenous (2-host) cycle
vector-borne transmission
(sexual development in invertebrate host)
(asexual development in vertebrate host)



Definitive Hosts (vectors)
(culicid mosquitoes)

oocyst
(30-50 µm)

sporozoites
(10-16 µm)

gut

motile
ookinete
(12-20 µm)

fertilization

salivary
gland

gametes

gamonts ingested

sporozoites injected

gamonts
(5-10 µm)

male

female

cryptozoic merogony

meront
(10-45 µm)

exo-erythrocytic
cycle (reticulo-
endothelial
(RE) cells)

metacryptozoic merogony
(macrophages)

trophozoite
(1-2 µm)

meront
(20-80 µm)

erythrocytic merogony
(red blood cells)

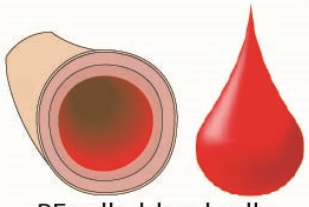
meront
(5-10 µm)

trophozoite
(1-3 µm)

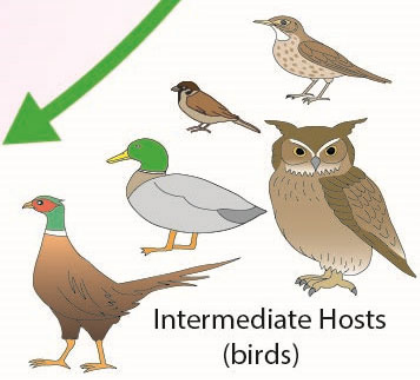
phanerozoic merogony
(endothelial cells)

meront
(< 120 µm)

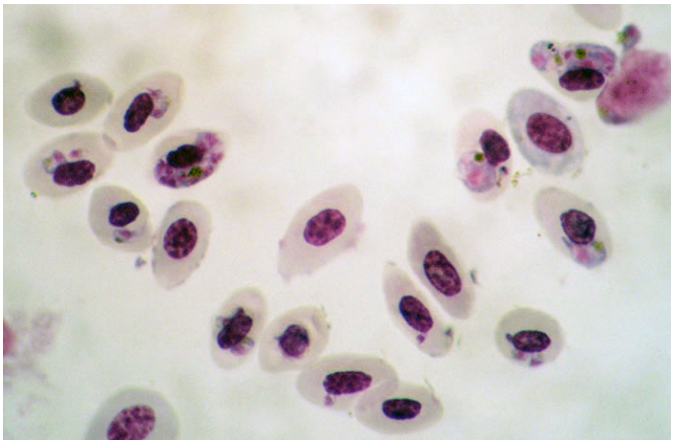
trophozoite
(1-2 µm)



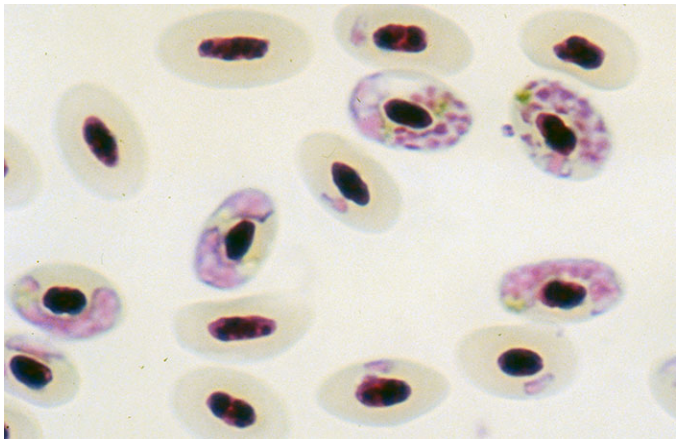
RE cells, blood cells
(occasionally anaemia,
ischaemia)



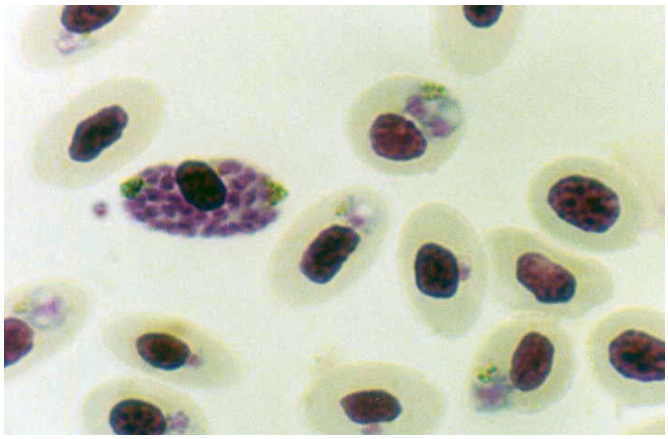
Intermediate Hosts
(birds)



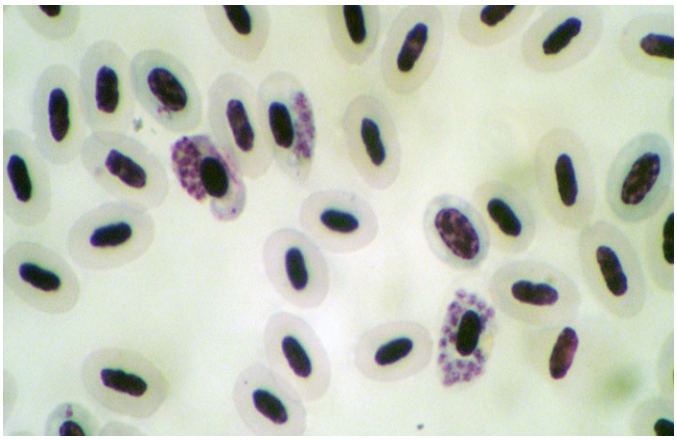
Plasmodium stages in bird blood



Plasmodium stages in bird blood



Plasmodium stages in bird blood



Plasmodium stages in bird blood

***Plasmodium* spp. (reptilian species)**
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Haematozoa are small blood-borne parasites which undergo merogony (= schizogony) and gamogony (gamete formation) in vertebrates and sporogony (sporozoite formation) in blood-sucking invertebrate vectors. Two main groups are recognised in terrestrial vertebrates: haemosporidia with insect vectors; and piroplasms with arachnid vectors. Haemosporidian parasites multiply in the tissues of vertebrates before forming gamonts in blood cells (*Plasmodium* spp. also undergo cyclic merogony in erythrocytes). Most species produce haemozoin pigment granules as a byproduct of haemoglobin metabolism. Gametes ingested by insect vectors undergo fertilization in the gut forming motile zygotes (ookinetes) which form oocysts and then thousands of sporozoites which invade the salivary glands. Infections by *Plasmodium* spp. are transmitted by mosquitoes and numerous species have been described in mammals, birds and reptiles; most causing no apparent harm, except those infecting humans causing one of the worst fever scourges of mankind, the disease malaria.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Aconoidasida (asexual stages without conoid)
Order:	Haemosporida (pleomorphic stages in blood of vertebrates, insect vectors. motile zygote (ookinete))
Family:	Plasmodiidae (schizogony in tissues then blood cells, gamonts in blood cells, haemozoin pigment)
Genus:	*Plasmodium* (vector-borne haemosporidian parasites of vertebrates)
Species:	various species cause infections in mammals/birds/reptiles

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic ‘haemococcidia’ in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Haemosporida are spore-forming apicomplexan parasites with heteroxenous life-cycles, with merogony in cells of fixed tissues and in the blood of vertebrate (intermediate) hosts and sporogony in haematophagous invertebrate vectors (definitive hosts). In vertebrate blood cells, haemosporidia develop intracellularly forming sexually dimorphic gametocytes: macrogametocytes (female) with compact nuclei and dark-stained cytoplasm (plentiful ribosomes for protein synthesis), and microgametocytes (male) with larger diffuse nuclei (ready for microgamete production) and pale-staining cytoplasm [a simple pneumonic often used is “blue for girls, pink for boys”]. Gametocytes develop independently (without syzygy) and each microgamont produces about eight flagellated microgametes. Haemozoin granules (residual pigment formed due to incomplete haemoglobin digestion) may or may not be produced in infected erythrocytes. In the vector, the zygote is motile (ookinete) and ultimately forms numerous naked sporozoites (without sporocysts). Around 590 species belonging to some 19 haemosporidian genera have been described from a wide range of mammalian, avian and reptilian hosts around the world.

Four haemosporidian families are recognized mainly on the basis of their developmental cycles and whether haemozoin pigment is produced: namely, Plasmodiidae (merogony in tissues then cyclic in erythrocytes, pigment present); Haemoproteidae (merogony in tissues only, pigment present); Leucocytozoidae (merogony in tissues, pigment absent) and Garniidae (merogony in leucocytes, pigment absent). Vertebrates act as intermediate hosts in which the parasites undergo asexual multiplication within tissues and/or blood cells. Even though parasites begin gamete formation in vertebrates, sexual multiplication is not completed until after they are transmitted to their haematophagous invertebrate vectors, which therefore act as definitive hosts. Some 11 genera are recognized in the family Plasmodiidae on the basis of multiple biological characters (including morphology, development, host specificity and range): *Plasmodium* in mammals, birds and reptiles; *Hepatocystis, Polychromophilus, Nycteria, Biguetiella, Bioccala* and *Dionisia* in bats, *Rayella* in flying squirrels, *Billbraya* and *Haemocystidium* (including *Simondia*) in reptiles, and *Mesnilium* in fish.

Haemosporidian genera	**No. spp.**	**Site* of development in vertebrate**		**Vertebrate hosts**	**Invertebrate vector**
		meronts	**gamonts**		
Family: Plasmodiidae (merogony in tissues and erythrocytes, haemozoin pigment present)					
Plasmodium	225	liver, rbc	rbc	mammals, birds, reptiles	diptera
Hepatocystis	25	liver	rbc	primates/bats	midges
Polychromophilus	5	viscera	rbc	bats	nycterids
Nycteria	7	liver	rbc	bats	
Biguetiella	1	liver	rbc	bats	
Bioccala	2	RE cells	rbc	bats	
Dionisia	1	liver	rbc	bats	
Rayella	3	liver	rbc	flying squirrels	
Billbraya	1	rbc	rbc	lizards	
Mesnilium	1	RE cells, rbc	rbc	fish	leeches/insects
Haemocystidium (*Simondia*)	33	RE cells	rbc	lizards/tortoises	arthropods
Family: Haemoproteidae (merogony in tissues (not in blood cells), haemozoin pigment present in gametocytes)					
Haemoproteus (*Halteridium*)	6	RE cells	rbc	birds	louse flies
Haemoproteus (*Parahaemoproteus*)	150	RE cells	rbc	birds	midges
Johnsprentia	1	RE cells	rbc	flying foxes	
Sprattiella	1	RE cells	rbc	bats	
Family: Leucocytozoidae (merogony in tissues (not in blood cells), haemozoin pigment absent)					
Leucocytozoon (*Akiba*)	100	RE cells	blood cells	birds	black flies
Saurocytozoon	3	viscera	leucocytes	lizards	mosquitoes
Family: Garniidae (merogony in leucocytes, haemozoin pigment absent)					
Fallisia	12	leucocytes	leucocytes	lizards	arthropods
Garnia	10	leucocytes	leucocytes	lizards	arthropods
Progarnia	1	leucocytes	blood cells	crocodiles	

*rbc = red blood cells (erythrocytes); RE = reticuloendothelial cells

Many molecular phylogenetic studies using nuclear, mitochondrial and apicoplast gene sequences have demonstrated a clear relationship between haemosporidian genera not only with their vertebrate hosts but also their invertebrate vectors. There were clear groupings of *Leucocytozoon* from birds, *Haemoproteus* (*Haemoproteus*) from birds, *Haemoproteus* (*Parahaemoproteus*) from birds, *Plasmodium* from birds and reptiles, *Plasmodium* from rodents and primates, and *Hepatocystis* from bats. These groups were clearly associated with different vectors; namely, simuliids (black-flies), hippoboscids (louse-flies), ceratopogonids (midges), culicine mosquitoes, anopheline mosquitoes, and midges, respectively. There appears to have been a transition from haemosporidia which do not form haemozoin pigment (*Leucocytozoon* in white blood cells) to genera that do form pigment indicating haemoglobin digestion by parasites in red blood cells (*Haemoproteus*, *Plasmodium* and *Hepatocystis*). This was followed by a transition from haemosporidia which undergo schizogony exclusively in host tissues (*Leucocytozoon* and *Haemoproteus*) to those that undergo schizogony in blood cells (*Plasmodium*). While there appears to be a general shift in haemosporidian genera from birds and reptiles to mammals (from nucleated to non-nucleated blood cells), each genus is associated with a particular vector group: black-flies transmitting *Leucocytozoon* to birds; louse-flies transmitting *Haemoproteus* (*Haemoproteus*) to birds; midges transmitting *Haemoproteus* (*Parahaemoproteus*) to birds; culicine mosquitoes transmitting *Plasmodium* to birds and lizards; and anopheline mosquitoes transmitting *Plasmodium* to mammals. The exception to this general trend was *Hepatocystis* which does not undergo blood schizogony and is transmitted to bats by midges.

Over 225 *Plasmodium* species have been classified in 14 subgenera on the basis of parasite morphology, development and host occurrence. Three subgenera contain species in mammals, five subgenera contain those in birds, and six contain those in reptiles:

- *P.* (*Plasmodium*), with large erythrocytic schizonts and round gametocytes, in primates;
- *P.* (*Lavernia*), with large erythrocytic schizonts and crescentic gametocytes, in primates;
- *P.* (*Vinckeia*), with small erythrocytic schizonts and round gametocytes, in antelopes, rodents and other mammals (except primates);

- *P.* (*Haemamoeba*), with large erythrocytic schizonts and round gametocytes, in birds;
- *P.* (*Bennettinia*), with small erythrocytic schizonts and round gametocytes, in birds;
- *P.* (*Huffia*), with large schizonts and elongate gametocytes mostly in immature erythrocytes, in birds;
- *P.* (*Giovannolaia*), with large erythrocytic schizonts and elongate gametocytes, in birds;
- *P.* (*Novyella*), with small erythrocytic schizonts and elongate-oval gametocytes, in birds;

- *P.* (*Sauramoeba*), with large erythrocytic schizonts and large gametocytes, in lizards*;
- *P.* (*Lacertamoeba*), with medium erythrocytic schizonts and medium gametocytes, in lizards;
- *P.* (*Paraplasmodium*), with medium erythrocytic schizonts and large gametocytes, in lizards;
- *P.* (*Carinamoeba*), with small erythrocytic schizonts and small gametocytes, in lizards;
- *P.* (*Asiamoeba*), with small erythrocytic schizonts and large gametocytes, in lizards; and
- *P.* (*Ophidiella*), with large erythrocytic meronts and small elongate gametocytes, in snakes.

*Another 2 subgenera from lizards, *P.* (*Garnia*) and *P.* (*Fallisia*), have been afforded generic status and allocated to the genera *Garnia* and *Fallisia* in the family Garniidae because their developmental stages do not produce haemozoin pigment in host erythrocytes (*Garnia*) or leucocytes (*Fallisia*). Confoundingly, recent molecular studies have shown that several *Plasmodium* spp. from lizards comprised co-infections with cryptic species whose development was confined to white blood cells rather than red blood cells. Further studies are required to determine the validity of the family Garniidae and its constituent genera.

Around 90 *Plasmodium* spp. have been described in reptiles, mostly in semiaquatic and terrestrial lizards, and occasionally in snakes. The parasites varied in their host specificity and geographic range, with most species being found in one or a few closely-related hosts predominantly in tropical and subtropical regions (only a few had broad ranges). In contrast, sexual development and transmission is accomplished in a greater range of blood-sucking dipteran insects, including Culicidae (mosquitoes), Ceratopogonidae (midges) and Phlebotomidae (sand flies). A total of 6 *Plasmodium* subgenera have been identified from reptiles: with 17 *P.* (*Sauramoeba*) spp. found in 10 lizard families mainly from the Southern hemisphere; 39 *P.* (*Lacertamoeba*) spp. from 12 lizard families around the world; 3 *P.* (*Paraplasmodium*) spp. from 2 lizard families in the Americas; 10 *P.* (*Carinamoeba*) spp. in 8 lizard families mainly from the Southern hemisphere; 6 *P.* (*Asiamoeba*) spp. from 4 lizard families from Asia; and 7 *P.* (*Ophidiella*) spp. from 4 snake families from South America and Africa. Reptilian *Plasmodium* spp. are morphologically and biologically (hence taxonomically) diverse, possibly due to the more restricted or isolated habitats of their vertebrate hosts, their lower vagility (dispersal), and their broader vector specificity. Most *Plasmodium* spp. in reptiles undergo hepatic merogony followed by erythrocytic merogony culminating in the formation of gametocytes. During the course of infection, asexual meronts may be found in circulating cells as well as fixed cells in various organs, including erythrocytes, lymphocytes, monocytes, thrombocytes, granulocytes, endothelial and connective tissue cells. Infections in reptiles are generally not associated with clinical disease, with most being chronic or latent as the parasites seem to persist in the larger erythrocytes found in reptiles.

***Plasmodium* species**	**Intermediate hosts**	**Gametocyte shape (pathogenicity)**	**Definitive hosts (vectors)**	**Geographic distribution**
Subgenus: *Sauramoeba* (large erythrocytic schizonts, large gametocytes, in lizards (Sauria))				
P. (*S.*) *achiotense*	corytophanid (common basilisk)	ovoid		Central America
P. (*S.*) *acuminatum*	chamaeleonid (Fischer's chameleon)	elongate and acuminate		East African
P. (*S.*) *agamae*	agamid (common agama, Atlas agama)	ovoid-elongate (mildly pathogenic)	Diptera: ceratopogonid (*Culicoides nubeculosus*)	East, Central and West African
P. (*S.*) *australis*	agamid (bearded dragon)	ovoid		Australia
P. (*S.*) *balli*	dactyloid (lion anole, slender anole, dappled anole)	elongate		Central and South America
P. (*S.*) *beltrani*	phrynosomatid (teapen rosebelly lizard)	elongate, or bulky		North America
P. (*S.*) *caucasica*	agamid (rock agama)	ovoid-elongate		southern

				Asia
P. (*S.*) *cnemidophori*	teiid (rainbow whiptail, giant whiptail)	elongate, or bulky		South America
P. (*S.*) *diploglossi* (type species)	diploglossid (banded galliwasp), scincid (greater Martinique skink)	ovoid-lentiform		South America
P. (*S.*) *egerniae*	scincid (land mullet)	ovoid		Australia
P. (*S.*) *giganteum*	agamid (common agama, blue-bellied ridgeback agama)	round-elongate, or bulky	Diptera: culicid (*Aedes aegypti*)	West African
P. (*S.*) *guyannense*	trophidurid (collared tree runner)	ovoid		South America
P. (*S.*) *heischi*	scincid (African striped skink)	spindle		East African
P. (*S.*) *kentropyxi*	teiid (striped forest whiptail)	elongate		South America
P. (*S.*) *lacertiliae*	scincid (Indonesian brown skink)	ovoid		New Guinea
P. (*S.*) *michikoa*	chamaeleonid (Matschie's dwarf chameleon)	elongate		East African
P. (*S.*) *robinsoni*	chamaeleonid (short-horned chameleon)	oval-elongate, or bulky		Madagascar
Subgenus: *Lacertamoeba* (medium erythrocytic schizonts, medium gametocytes, in lizards (Sauria))				
P. (*L.*) *arachniformis*	chamaeleonid (Werner's three-horned chameleon)	elongate		East African
P. (*L.*) *aurulentum*	dactyloid (slender anole), phyllodactylid (turniptail gecko)	ovoid-lentiform		Central America
P. (*L.*) *basilisci*	corytophanid (common basilisk)	ovoid		North, Central and South America
P. (*L.*) *beebei*	sphaerodactylid (Estado Aragua gecko)	ovoid		South America
P. (*L.*) *billbraya*	gekkonid (marbled gecko)	ovoid (pronounced anaemia)		Australia
P. (*L.*) *brumpti*	phrynosomatid (horrible spiny lizard)	ovoid-elongate		North America
P. (*L.*) *brygooi*	chamaeleonid (short-horned chameleon)	oval-elongate		Madagascar
P. (*L.*) *circularis*	scincid (Gidgee spiny-tailed skink)	ovoid		Australia
P. (*L.*) *cnemaspi*	gekkonid (African gecko)	elongate		East African
P. (*L.*) *colombiense*	dactyloid (grass anole)	ovoid-elongate		South America
P. (*L.*) *draconis*	agamid (common flying dragon)	ovoid		Philippines, Malaysia
P. (*L.*) *fairchildi* (incl. subspp. *fairchildi, hispaniolae*)	dactyloid (slender anole, bark anole)	ovoid-elongate		Central and South America
P. (*L.*) *fischeri*	chamaeleonid (Fischer's chameleon)	oblong-elongate		East African
P. (*L.*) *floridense*	dactyloid (yellow-chinned anole, slender anole, giant green anole, lichen anole, bridled anole, brown anole, humble anole, lion anole, great scaly anole, ghost anole, large-headed anole, bark anole, Jeremie anole, snake anole, Jamaican anole, stripefoot anole, Graham's anole, Bluefield's anole, Grand Cayman anole, Isla San Andres anole, Anguilla anole, Saban anole, panther anole, Plymouth anole, Dominican anole, green anole), phrynosomatid (fence lizard, rosebelly lizard), iguanid (emerald swift); plus exptl infection in iguanid (common collared lizard), crotaphytid (longnose leopard lizard), phrynosomatid (Texas spiny lizard, Florida scrub lizard)	ovoid-elongate	Diptera: culicid (*Aedes aegypti, Culex erraticus, quinquefasciatus, territans*)	North and Central America, Caribbean

P. (*L.*) *gologoloense*	chamaeleonid (Matschie's dwarf chameleon)	ovoid		East African
P. (*L.*) *holaspi*	lacertid (sawtail lizard)	elongate		East African
P. (*L.*) *iguanae*	iguanid (green iguana)	ovoid		South America
P. (*L.*) *intabazwe*	cordylid (highveld crag lizard)	reniform		South African
P. (*L.*) *josephinae*	teiid (rainbow ameiva)	ellipsoidal		North America
P. (*L.*) *lepidoptiformis*	teiid (striped forest whiptail)	elongate		South America
P. (*L.*) *loveridgei*	gekkonid (painted dwarf gecko)	elongate		East African
P. (*L.*) *mackerrasae*	scincid (Cunningham's skink)	elongate		Australia
P. (*L.*) *maculilabre*	skink (speckle-lipped mabuya)	ovoid-elongate		West African
P. (*L.*) *mossambica*	agamid (Mozambique agama)	elongate		East African
P. (*L.*) *pelaezi*	phrynosomatid (tropical tree lizard)	ovoid-elongate		North America
P. (*L.*) *pitmani*	scincid (speckle-lipped mabuya, African striped mabuya)	ovoid		Central and West African
P. (*L.*) *rhacodactyli*	diplodactylid (New Caledonian giant gecko)	ovoid		New Caledonia
P. (*L.*) *sasai*	lacertid (oriental racers)	ovoid-elongate		Japan, Thailand
P. (*L.*) *tanzaniae*	chamaeleonid (Werner's three-horned chameleon)	elongate		East African
P. (*L.*) *telfordi*	teiid (giant whiptail)	ovoid-elongate		South America
P. (*L.*) *torrealbai*	dactyloid (anole)	ovoid-elongate		South America
P. (*L.*) *tropiduri* (incl. subspp. *aquaticum, caribbense, panamense, tropiduri*)	tropidurid (Amazon lava lizard, Peter's lava lizard, calango), dactyloid (large-headed anole, stripefoot anole, Neotropical green anole, lichen anole, lion anole, dappled anole), scincid (Greater Martinique skink), gekkonid (tropical house gecko)	ovoid		Central and South America, Caribbean
P. (*L.*) *tribolonoti*	scincid (red-eyed crocodile skink)	ovoid		Indonesia
P. (*L.*) *uluguruense*	gekkonid (boabab gecko)	ovoid		East African
P. (*L.*) *uncinatum*	tropidurid (collared tree runner)	elongate		South America
P. (*L.*) *uzungwiense*	chamaeleonid (Werner's three-horned chameleon)	elongate		East African
P. (*L.*) *vacuolatum*	tropidurid (blue-lipped tree lizard)	ovoid		South America
P. (*L.*) *vautieri*	leiosaurid (Brazilian Steppe iguana)	ovoid		South America
P. (*L.*) *zonuriae*	cordylid (common girdled lizard), gerrhosaurid (giant plated lizard)	elongate		South African
Subgenus: *Paraplasmodium* (medium erythrocytic schizonts, large gametocytes, in lizards (Sauria))				
P. (*P.*) *chiricahuae*	phrynosomatid (Clark's spiny lizard, Yarrow's spiny lizard, desert spiny lizard)	ovoid-elongate		North America
P. (*P.*) *mexicanum*	phrynosomatid (crevice swift, fence lizards, sagebrush lizard, mesquite lizard), iguanid (spiny-tailed iguana), anguid (alligator lizard), plus exptl. infection in phrynosomatid (spiny lizards, horned lizards), iguanid (eastern collared lizard)	ovoid-elongate (mildly pathogenic)	Diptera: psychodid (*Lutzomyia vexator, stewarti*)	North America
P. (*P.*) *pifanoi*	teiid (giant ameiva)	elongate		South

				America
Subgenus: *Carinamoeba* (small erythrocytic schizonts, small gametocytes, in lizards (Sauria))				
P. (*C.*) *attenuatum*	teiid (giant ameiva)	elongate		South America
P. (*C.*) *auffenbergi*	varanid (peacock monitor)	ovoid		Philippines
P. (*C.*) *cordyli*	cordylid (dwarf sungazer, girdled lizard)	ovoid		East and South African
P. (*C.*) *gracilis*	scincid (red-eyed crocodile skink)	ovoid		Indonesia
P. (*C.*) *mabuiae*	scincid (African five-lined skink)	elongate		East African
P. (*C.*) *marginatum*	dactyloid (bridled anole)	ovoid		Central America
P. (*C.*) *minasense* (type species) (incl. subspp. *anolisi, calcaratae, capitoi, carinii, diminutivum, minasense, plicae, tegui*)	scincid (Greater Martinique skink), iguanid (green iguana), polychrotid (Brazilian bush anole), dactyloid (slender anole, large-headed anole, bark anole, Jeremie anole, bighead anole), tropidurid (harlequin racerunners), teiid (gold tegu, giant ameiva, striped forest whiptail)	ovoid-elongate		South and Central America, Caribbean, Malaysia
P. (*C.*) *rhadinurum*	iguanid (green iguana, black iguana, prairie lizard)	ovoid		North America
P. (*C.*) *scelopori*	phrynosomatid (rosebelly lizards)	ovoid		Central America
P. (*C.*) *volans*	agamid (flying lizard)	ovoid-elongate		Philippines, Malaysia
Subgenus: *Asiamoeba* (small erythrocytic schizonts, large gametocytes, in lizards (Sauria))				
P. (*A.*) *clelandi*	varanid (Indian monitor)	encircle host nucleus		Sri Lamka
P. (*A.*) *lionatum*	gekkonid (smooth-backed gliding gecko)	elongate		Thailand
P. (*A.*) *lygosomae*	scincid (Moco skink, Chatham Islands skink)	ovoid-reniform		New Zealand
P. (*A.*) *nucleoversans*	scincid (copper-tailed skink, green-blooded skink)	elongate		Solomon Islands
P. (*A.*) *saurocaudatum*	scincid (common sun skink)	ovoid		Singapore, Thailand
P. (*A.*) *vastator*	agamid (common flying dragon)	reniform-elongate, or bulky		Malaysia, Philippines
Subgenus: *Ophidiella* (large erythrocytic meronts, small elongate gametocytes, in snakes (Serpentes))				
P. (*O.*) *bitis*	viperid (puff adders)	ovoid-elongate		South African
P. (*O.*) *causi* (*species inquirenda,* possibly stages of *Dactylosoma*)	viperid (African night adder)			African
P. (*O.*) *melanoleuca*	elapid (forest cobra)	ovoid		East African
P. (*O.*) *pessoai*	colubrid (caninana), viperid (Atlantic forest bush master)	elongate		Central America
P. (*O.*) *pythonis*	pythonid (African rock python)	elongate		South African
P. (*O.*) *tomodoni*	colubrid (pampas snake)	ovoid		South America
P. (*O.*) *wenyoni* [type species]	colubrid (Amazon coastal house snake)	ovoid		South America
Unplaced				
P. ouropretensis (separated from *P.* (*L.*) *tropiduri* by occurrence in white blood cells and molecular studies)	tropidurid (Amazon lava lizard, Peter's lava lizard)	ovoid		South America

Parasite morphology: Reptilian *Plasmodium* spp. form similar developmental stages to avian species, except that various stages may become dormant allowing parasites to survive for long periods and cause relapses. In reptiles, the parasites may undergo 3

types of asexual exo-erythrocytic merogony (forming cryptozoic, metacryptozoic and phanerozoic meronts, sometimes enigmatically referred to simply as cryptozoites, metacryptozoites and phanerozoites, even though all produce merozoites) as well as erythrocytic merogony (trophozoites forming meronts, merozoites and gametocytes). Some sporozoites invading the liver may become inactive inside host cells forming uninucleate dormant hypnozoites (2-5 μm) located within membrane-bound parasitophorous vacuoles. First-generation cryptozoic meronts appear as round-oval basophilic bodies (6-15 x 4-8 μm) that become multinucleate as they divide internally to produce numerous (12-45, sometimes more) merozoites containing golden pigment granules. Some of these cryptozoic merozoites may also become inactive inside host cells. Second-generation metacryptozoic meronts appear as similar rounded basophilic bodies (19-27 μm) that produce numerous merozoites. Erythrocytic merogony involves a cyclic process where pleomorphic (plasmodial) trophozoites (1-4 μm) evident as signet-ring structures or focal packets form meronts (3-6 x 2-5 μm) that are usually fan-shaped (sometimes rosette, cruciform, oval or morulum (spherical mass)) with scattered or clumped dark pigment granules. The meronts produce variable numbers (4-28, rarely more) of merozoites that may be round, oval, elongate or lentiform in shape. Eventually gametocytes appear in erythrocytes as ovoid-elongate (6-18 x 4-10 μm) stages that exhibit sexual dimorphism: with female macrogametocytes being more elongate with a basophilic cytoplasm (due to abundant ribosomes) and compact nucleus; and male microgametocytes being shorter with a pale eosinophilic cytoplasm and a large pale nucleus (giving rise to the paradoxical adage 'blue for girls, pink for boys' when stained with Giemsa). Gametocytes vary in their location within the erythrocyte cytoplasm, being polar, lateral, lateropolar, dumbbell-shaped or halteridial (halter-shaped). Merozoites produced in erythrocytes may also infect white blood cells where they undergo para-erythrocytic merogony, or endothelia and connective tissues in various organs where they undergo a third type of exo-erythrocytic development (phanerozoic merogony), possibly for several generations. Phanerozoic meronts appear as larger ovoid-elongate basophilic bodies (7-28 x 4-16 μm) that become multinucleate as they produce variable numbers (16-210) of merozoites. These merozoites may infect red or white blood cells in the circulation or fixed cells in organs, with some becoming encysted in tissues as dormant stages (termed chronozoites) responsible for relapses. In dipteran vectors, the parasites complete sexual development (gamete formation and fertilization) producing zygotes that mature to oocysts producing numerous sporozoites (sporogony). Male microgametocytes undergo exflagellation producing thin slender microgametes (15 μm long) which fertilize rounded female macrogametes (10 x 7 μm) to produce ookinetes (motile zygotes). Ookinetes are elongate stages (14-20 x 2-5 μm) that mature to form rounded membrane-bound oocysts (22-54 μm) that undergo internal sporulation to form numerous slender sporozoites (7-22 x 1-2 μm).

Site of infection: Exo-erythrocytic proliferation occurs in different sites within reptilian hosts: first-generation cryptozoic meronts developing in hepatic parenchymal cells; second-generation metacryptozoic meronts in macrophages (prominent in hepatic sinuses); and third-generation phanerozoic meronts forming in endothelial and connective tissue cells in various organs (including the heart, lungs, muscles, brain, and testes). Erythrocytic merogony occurs in nucleated red blood cells (especially immature cells), and para-erythrocytic merogony occurs in other circulating cells (lymphocytes, monocytes, thrombocytes and sometimes granulocytes). A total of 83 parasite species have been described in reptiles: including 76 parasite species in 117 lizard species (belonging to 22 families); and another 7 parasite species in 8 snake species (from 4 families). Gamete formation and fertilization occurs in the gut lumen of dipteran vectors, while the motile ookinete penetrates the gut wall to form an encapsulated oocyst. Mature oocysts release sporozoites into the haemocoel where they invade the salivary glands. A small number of vectors have been found for reptilian *Plasmodium* spp.: including 4 species of culicid mosquitoes, 2 species of psychodid sandflies and one species of ceratopogonid biting midges.

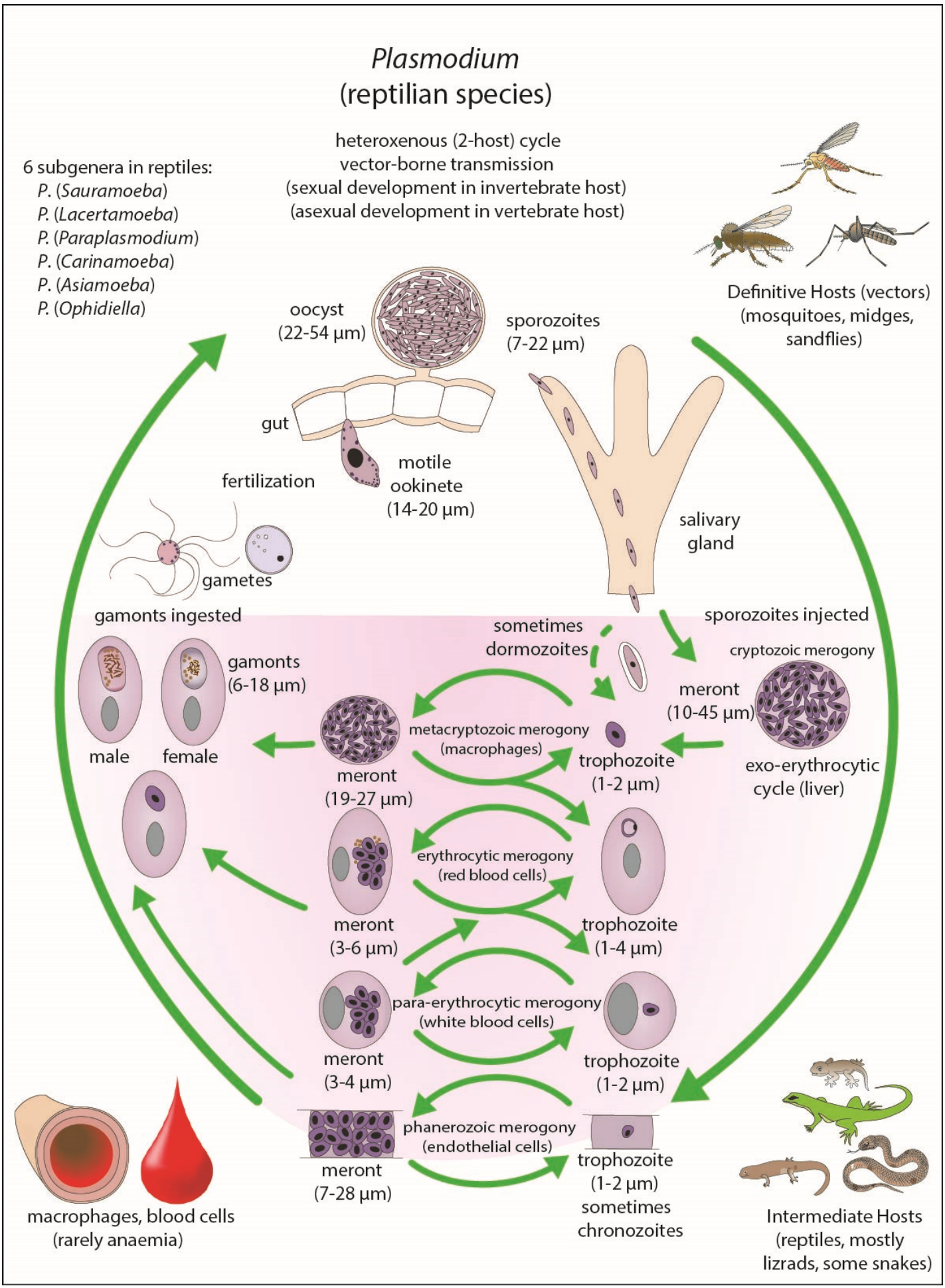
Pathogenesis: Infections in most reptiles are asymptomatic during the acute and chronic phases of infection, with intra-erythrocytic gametocytes often the only stages detected. Some natural infections have been associated with mild anaemia, lethargy, anorexia, dehydration and stomatitis in several lizard species, and an un-named species has been associated with fatal haemolytic anaemia in star tortoises. Several parasite species are thought to cause seasonal mortalities due to progressive damage caused by pernicious tissue meronts. Experimental infections have sometimes caused severe anaemia and thrombosis in capillary beds, with occasional mortalities. Post-mortem pathological observations have included anaemia, hepatomegaly and splenomegaly with pigment deposits found throughout visceral organs. Haematological perturbations have included erythrocytic distortions in size, shape and nuclear position with reductions in haematocrit, haemoglobin levels and increased numbers of immature red cells (polychromatophils). Several physiological studies have also linked infections to impaired oxygen consumption by lizards (exercise physiology), reduced running activity, slower tail repair (after loss due to predation), alterations in coloration, reduced fat storage, decreased clutch sizes, and reduced competitiveness in males with decreased testis size and testosterone levels. Chronic infections in reptiles are thought to persist for years and possibly for the lifespan of the host.

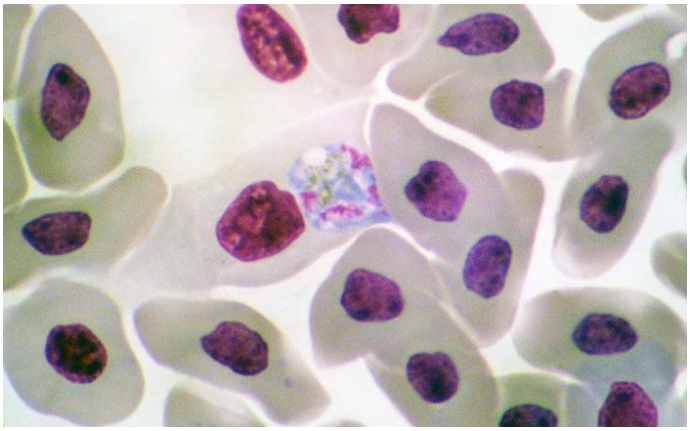
Developmental cycle and mode of transmission: Reptilian *Plasmodium* spp. have obligatory heteroxenous (2-host) life-cycles involving parasite asexual development in lizards and some snakes (acting as intermediate hosts) and sexual development in dipteran vectors (by definition, acting as definitive hosts). Transmission occurs by vector bite, with gametocytes taken up by vectors when feeding on blood and sporozoites injected during feeding (inoculative transmission). In reptiles, sporozoites invade the liver and undergo at least 2 generations of pre-erythrocytic merogony, first forming cryptozoic meronts and then metacryptozoic meronts. After a relatively long prepatent period (5-45 days), merozoites invade red and white blood cells where they undergo erythrocytic or para-erythrocytic merogony respectively. Merogony involves the transformation of invading trophozoites into meronts which produce numerous merozoites. Eventually, merozoites invading erythrocytes form sexually-dimorphic gametocytes, which may be

transitory or persistent stages which vary in morphology according to the phase of infection (more rounded in chronic infections). Merozoites may also infect capillary endothelia and connective tissues in various organs and undergo cyclic exo-erythrocytic phanerozoic merogony. Parasitaemias may reach peaks as high as 20% over 35-96 days. The acute phase of infection may last for 15-183 days before becoming chronic and persisting for months to years. Several developmental stages have been observed to become inactive in host tissues forming dormant encysted stages, including sporozoites forming hypnozoites, cryptozoic merozoites and phanerozoic merozoites forming relapsing stages called chronozoites. Dormant stages facilitate chronic infections of long duration, frequent relapses and allow parasites to overwinter in hibernating hosts. While most life-cycles are not known, transmission studies on a few parasite species have found vectors to include members of several diverse and ancient groups of blood-sucking dipteran insects, including Culicidae (mosquitoes), Ceratopogonidae (midges) and Phlebotomidae (sand flies). Ingested gametocytes complete gamete formation in the vector gut with fertilization occurring through gamete fusion. The resultant motile ookinete migrates into the gut wall and forms an oocyst extracellularly between intestinal epithelial cells near the outer wall. The oocysts undergo internal sporulation producing hundreds of sporozoites which are released into the haemocoel to invade the salivary glands. Sporozoites are inoculated into new reptilian hosts when the vector next feeds. Once infected, vectors are thought to remain infected for their entire lives.

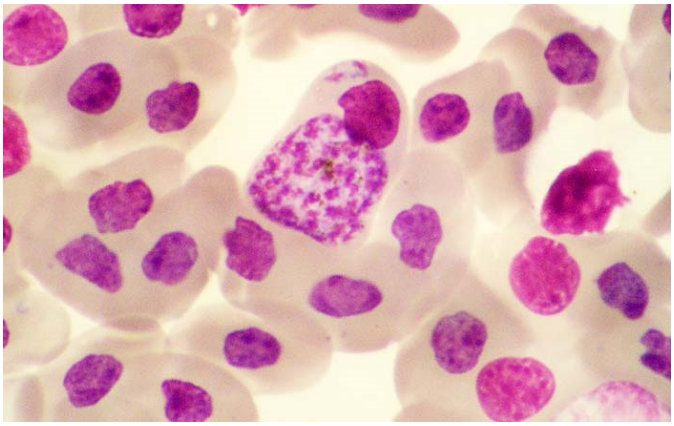
Differential diagnosis: Infections are usually diagnosed by the direct microscopic detection of parasite stages in fixed blood smears following staining with Giemsa. Multiple sequential samples may need to be examined to detect low or intermittent parasitaemias. Observations can be made on parasite morphology (size, shape, appearance, pigmentation) and any effects on host cells (hypertrophy, distortions, nuclear displacement). Histological sections of host tissues and organs collected at post-mortem may be examined for merogonous developmental stages. Dipteran vectors may also be examined for endogenous stages by examining squash preparations (especially of the salivary glands) or histological sections. Molecular biological techniques have been used to detect and characterize parasites by the polymerase chain reaction (PCR) amplification of nuclear (small subunit (18S) ribosomal DNA) or mitochondrial (cytochrome b) gene sequences.

Treatment and control: Several attempts to treat clinical infections in reptiles have yielded encouraging results, with several antimalarial drugs (quinine, mepacrine, sulphamethoxazole-trimethoprim, chloroquine-primaquine) leading to the resolution of clinical signs and/or the elimination of parasitaemia in lizards and tortoises. Preventive measures adopted by professional herpetaria or hobbyists have revolved around vector control by installing screens around holding facilities, applying chemical insecticides either to animals or fomites, and eliminating local breeding grounds for dipteran vectors (water disinfection and/or vegetation clearance).


Plasmodium
(reptilian species)
heteroxenous (2-host) cycle
vector-borne transmission
(sexual development in invertebrate host)
(asexual development in vertebrate host)
6 subgenera in reptiles:
P. (*Sauramoeba*)
P. (*Lacertamoeba*)
P. (*Paraplasmodium*)
P. (*Carinamoeba*)
P. (*Asiamoeba*)
P. (*Ophidiella*)
Definitive Hosts (vectors)
(mosquitoes, midges,
sandflies)
oocyst
(22-54 µm)
sporozoites
(7-22 µm)
gut
motile
ookinete
(14-20 µm)
fertilization
gametes
salivary
gland
gamonts ingested
sporozoites injected
sometimes
dormozoites
cryptozoic merogony
gamonts
(6-18 µm)
male
female
meront
(10-45 µm)
metacryptozoic merogony
(macrophages)
meront
(19-27 µm)
trophozoite
(1-2 µm)
exo-erythrocytic
cycle (liver)
erythrocytic merogony
(red blood cells)
meront
(3-6 µm)
trophozoite
(1-4 µm)
para-erythrocytic merogony
(white blood cells)
meront
(3-4 µm)
trophozoite
(1-2 µm)
phanerozoic merogony
(endothelial cells)
meront
(7-28 µm)
trophozoite
(1-2 µm)
sometimes
chronozoites
macrophages, blood cells
(rarely anaemia)
Intermediate Hosts
(reptiles, mostly
lizrads, some snakes)



Plasmodium intraerythrocytic stage in lizard blood



Plasmodium developmental stage in lizard blood

OTHER PLASMODIIDAE GENERA

A range of haemosporidian genera have been described primarily on the basis of differences in parasite morphology and development. Contemporary molecular characterization studies on representative species have tended to confirm their taxonomy, but have indicated their polyphyletic origins and revealed the presence of hitherto cryptic species with intermediary characteristics.

Family Plasmodiidae (merogony in tissues and erythrocytes, haemozoin pigment present)

Haemosporidian genera	No. spp.	Site* of development in vertebrate		Vertebrate hosts	Invertebrate vector
		meronts	gamonts		
Family: Plasmodiidae (merogony in tissues and erythrocytes, haemozoin pigment present)					
Plasmodium	225	liver, rbc	rbc	mammals, birds, reptiles	diptera
Hepatocystis	25	liver	rbc	primates/bats	midges
Polychromophilus	5	viscera	rbc	bats	nycterids
Nycteria	7	liver	rbc	bats	
Biguetiella	1	liver	rbc	bats	
Bioccala	2	RE cells	rbc	bats	
Dionisia	1	liver	rbc	bats	
Rayella	3	liver	rbc	flying squirrels	
Billbraya	1	rbc	rbc	lizards	
Mesnilium	1	RE cells, rbc	rbc	fish	leeches/insects
Haemocystidium (*Simondia*)	33	RE cells	rbc	lizards/tortoises	arthropods

*rbc = red blood cells (erythrocytes); RE = reticuloendothelial cells

Genus *Hepatocystis*: Some 25 species have been described in various mammals (primates, rodents, bats, artiodactyls), especially arboreal species in the tropics in the Old World (lower monkeys, fruit bats, squirrels). Sporozoites first invade liver parenchyma cells and develop into large schizonts (meronts) called megaloschizonts or merocysts (4-6 mm in diameter) which become vacuolated and filled with colloid. Merozoites then invade erythrocytes and develop into dimorphic ('*vivax*-type') gametocytes. Haemozoin pigment is produced in infected blood cells. Parasites are transmitted between vertebrate hosts by invertebrate vectors (biting midges) which act as definitive hosts in which gamogony is completed and sporogony occurs (oocysts formed in the head and thorax).

***Hepatocystis* species**	**Intermediate hosts**	**Gametocyte shape (pathogenicity)**	**Definitive hosts (vectors)**	**Geographic distribution**
H. bainae	Chiroptera: hipposiderid (leaf-nosed bats)			Malaysia
H. bouillezi	Primates: cercopithecid (mona monkey)	spherical		West African
H. brayi	Rodentia: sciurid (tricoloured squirrel, three-striped ground squirrels)			Malaysia
H. brosetti	Chiroptera: pteropodid (Franquet's epauletted fruit bat)	round		Gabon
H. carpenteri	Chiroptera: pteropodid (hammer-headed bat)	round		Gabon
H. cercopitheci	Primates: cercopithecid (white-nosed monkeys, red-tail monkeys)	spherical		West and East African
H. epomophori	Chiroptera: pteropodid (Franquet's epauletted fruit bat, hammer-headed bats, epauletted fruit bats)	spherical		tropical African
H. fieldi	Artiodactyla: tragulid (mouse deer)	spherical		Malaya, Sri Lanka
H. foleyi [syn. *Plasmodium foleyi*]	Primates: lemurid (lemurs)	spherical		Madagascar
H. garnhami	Chiroptera: pteropodid (greater short-nosed fruit bat)	round		Thailand
H. hippopotami	Artiodactyla: hippopotamid (hippopotamus)	spherical		Zimbabwe
H. hipposideri	Chiroptera: hipposiderid (roundleaf bats)			Taiwan
H. kochi	Primates: cercopithecid (vervets, mangabeys, colobi)	spherical	Diptera: ceratopogonid (*Culicoides adersi, fulvithorax*)	African
H. levinei	Chiroptera: pteropid (flying foxes)		Diptera: ceratopogonid (*Culicoides nubeculosus*)	Australia
H. limnotragi (syn. *Plasmodium limnotragi*)	Artiodactyla: bovid (sitatungas, bushbucks)	spherical		East African
H. muuli	Rodentia: sciurid (Berdmore's ground squirrel)			Thailand
H. oriheli	Primates: cercopithecid (talapoins)			Central African
H. peronnae	Chiroptera: pteropodid (little collared fruit bat, Angolan fruit bat)			Central African
H. pteropi	Chiroptera: pteropodid (fruit bats, spotted-winged fruit bat, naked-backed fruit bats)	spherical		Australasian, Malaya

H. rayi	Rodentia: sciurid (flying squirrels)	spherical		Indo-China
H. rodhaini [may be syn. of *P. malariae*]	Chiroptera: hipposiderid (roundleaf bats)			Malaysia
H. semnopitheci	Primates: cercopithecid (langurs, macaques)	spherical		southern Asia
H. simiae [type species]	Primates: cercopithecid (baboons)	spherical		West and East African
H. taiwanensis	Primates: cercopithecid (macaques)	spherical		Taiwan
H. vassali [incl. subsp. *malayensis, ratufae, yokogawai*]	Rodentia: sciurid (squirrels, tricoloured squirrel, slender squirrel)	oval		Indo-China

Genus *Polychromophilus*: Five species have been reported from insectivorous bats in Europe and West Asia. The parasites undergo merogony first in mesodermal cells of various organs (lungs, kidney, spleen, liver, adrenal glands), often forming macromeronts, and then in reticulo-endothelial cells, forming micromeronts, particularly in hepatic Kupfer cells. Meronts are ellipsoidal and surrounded by a thick brightly-pink capsule. Merozoites invade erythrocytes where they form rounded gametocytes ('*malariae*-type') containing haemozoin pigment. The parasites are transmitted by nycteribiid bat flies, in which oocysts develop in the midgut wall.

***Polychromophilus* species**	**Intermediate hosts**	**Gametocyte shape (pathogenicity)**	**Definitive hosts (vectors)**	**Geographic distribution**
P. adami	Chiroptera: miniopterid (least long-fingered bat)	round		Congo
P. corradetti	Chiroptera: miniopterid (common bentwing bat)	round		Gabon
P. mackiei (syn. Plasmodium mackiei)	Chiroptera: vespertilionid (Nepalese whiskered bat)	round		India
P. melanipherus [type species]	Chiroptera: miniopterid (common bentwing bat), vespertilionid (vesper bats, mouse-eared bats), hipposiderid (roundleaf bats), rhinolophid (horseshoe bats)	round	Diptera: nycteribiid (*Nycteribia, Penicillidia fulvida*)	African, Middle-East, Europe, Australia
P. monosoma	Chiroptera: vespertilionid (pipistrelle)			Vietnam

Genus *Bioccala*: This genus was formerly a subgenus of *Polychromophilus* but was elevated to genus status because the parasites formed small unpigmented meronts in macrophages (mostly in the liver) before forming elongate pigmented gametocytes ('*falciparum*-type') in host erythrocytes. Two species have been reported in microbats from the New and Old Worlds and they are transmitted by nycteribiid bat flies.

***Bioccala* species**	**Intermediate hosts**	**Gametocyte shape (pathogenicity)**	**Definitive hosts (vectors)**	**Geographic distribution**
B. deanei (syn. *Polychromophilus*)	Chiroptera: vespertilionid (big brown bat, black myotis, mouse-eared bats), phyllostomatid (leaf-nosed bats), hipposiderid (roundleaf bats)	ellipsoidal	Diptera: nycteribiid (*Basilia* sp.)	Americas, Asia
B. murinus (syn. *Polychromophilus*)	Chiroptera: vespertilionid (parti-coloured bat, greater mouse-eared bat, Natterer's bat, Daubenton's bat), miniopterid (common bent-winged bat, least long-fingered bat, pipistrelles), rhinolophid (horseshoe bats)	ellipsoidal	Diptera: nycteribiid (*Penicillidia*, *Nycteribia kolenatii*)	Europe, Middle-East, African

Genus *Nycteria*: Seven species have been described in insectivorous micro-bats from Africa and Asia. The parasites form large hepatic meronts (rounded or lobulated) but they do not form large merocysts. Rounded pigmented gametocytes ('*malariae*-type') develop in host erythrocytes. The vectors are unknown.

***Nycteria* species**	**Intermediate hosts**	**Gametocyte shape**	**Definitive hosts (vectors)**	**Geographic distribution**
N. brucechwalti	Chiroptera: hipposiderid (leaf-nosed bats)	round		Thailand
N. congolensis	Chiroptera: rhinolophid (horseshoe bats)	round		tropical African
N. erardi	Chiroptera: nycterid (Bate's slit-faced bat)	round		Congo, Gabon
N. gabonensis	Chiroptera: rhinolophid (horseshoe bats)			Congo, Gabon, Sudan
N. houini	Chiroptera: nycterid (dwarf slit-faced bat)	round		Congo, Gabon
N. krampitzi	Chiroptera: rhinolophid (horseshoe bats)			Congo, Gabon
N. medusiformis [type species]	Chiroptera: nycterid (Egyptian slit-faced bat, common slit-faced bat)	round		African

Genus *Biguetiella*: This genus is monotypic and contains a single species reported from hipposiderid bats in Asia. The parasite forms small intra-hepatocytic schizonts (< 15 µm) in the liver and then elongate pigmented gametocytes ('*falciparum*-type') in erythrocytes. The vectors are unknown.

***Biguetiella* species**	**Intermediate hosts**	**Gametocyte shape**	**Definitive hosts (vectors)**	**Geographic distribution**
B. minuta (type species)	Chiroptera: hipposiderid (leaf-nosed bats)	ellipsoidal		Thailand

Genus *Dionisia*: This monotypic genus contains one species recorded from hipposiderid bats from Africa. The parasites form small rounded schizonts in hypertrophied reticulo-endothelial cells in the liver before forming dimorphic gametocytes in host erythrocytes; macrogametocytes being elongate ('*falciparum*-type') and microgametocytes being rounded ('*malariae*-type'). The vectors are unknown.

***Dionisia* species**	**Intermediate hosts**	**Gametocyte shape (pathogenicity)**	**Definitive hosts (vectors)**	**Geographic distribution**
D. bunoi (type species)	Chiroptera: hipposiderid (roundleaf bats)	ovoid		Gabon

Genus *Rayella*: Three species have been described from flying squirrels in India. Their development appears similar to that of *Hepatocystis* spp., with hepatic meronts developing as clusters of cystic bodies (merocysts) in blood vessels, and pigmented gametocytes (‘*vivax*-type’) forming in erythrocytes.

***Rayella* species**	**Intermediate hosts**	**Gametocyte shape (pathogenicity)**	**Definitive hosts (vectors)**	**Geographic distribution**
R. gigantica	Rodentia: sciurid (spotted giant flying squirrels)			India
R. hylopetei	Rodentia: sciurid (particoloured flying squirrels)	amoeboid		India
R. rayi [type species]	Rodentia: sciurid (Himalayan flying squirrels)			India, Taiwan

Genus *Haemocystidium*: This genus was originally created to accommodate pigmented haemosporidial gametocytes in geckos and then tortoises. These species were subsequently reclassified together in the genus *Haemoproteus,* and then later split between the haemoproteid genus *Simondia* (for those species in tortoises) and the resurrected plasmodiid genus *Haemocystidium* (for those species in lizards). More recently, it was proposed on both morphological and molecular grounds that all *Haemoproteus* spp. of reptiles be transferred to the genus *Haemocystidium,* and that those species in chelonians be assigned to the subgenus *Simondia* and those in squamates to the subgenus *Haemocystidium*. Species in the genus *Haemocystidium* are distinguished from those of *Plasmodium* by the absence of an asexual cycle in circulating blood cells, and from those of *Haemoproteus* by the development of meronts that do not form pseudocytomeres.

***Haemocystidium* species**	**Intermediate hosts**	**Gametocyte shape**	**Definitive hosts (vectors)**	**Geographic distribution**
Subgenus *Haemocystidium*: species in squamates; lizards (Sauria) and snakes (Serpentes)				
H. (*H.*) *apigmentada*	Sauria: agamid (spiny-tailed lizard)	elongate		Middle-East
H. (*H.*) *balli*	Serpentes: elapid (Egyptian cobra)	ovoid		Africa
H. (*H.*) *edomensis*	Sauria: agamid (roughtail rock agama)	ovoid-elongate		Middle-East
H. (*H.*) *gehyrae*	Sauria: gekkonid (house gecko)	ovoid		Australia
H. (*H.*) *gonzalezi*	Sauria: dactyloid (giant green anole)	ovoid		South America
H. (*H.*) *grahami*	Sauria: agamid (rock agama)	ovoid		Iran
H. (*H.*) *kopki*	Sauria: gekkonid (Brooke's house gecko)	ovoid		India
H. (*H.*) *lacertae*	Sauria: lacertid (Italian wall lizard)			Europe
H. (*H.*) *lygodactyli*	Sauria: gekkonid (Cape dwarf gecko)	ovoid-elongate		East Africa
H. (*H.*) *mackerrasae*	Sauria: gekkonid (Bynoe's gecko)	elongate		Australia
H. (*H.*) *mesnili*	Serpentes: elapid (spitting cobras)	halteridial		West Africa
H. (*H.*) *oedurae*	Sauria: gekkonid (velvet gecko)	elongate		Australia
H. (*H.*) *opluri*	Sauria: oplurid (collared iguana)	ovoid-elongate		Madagascar
H. (*H.*) *papernai*	Sauria: agamid (rock agama)	elongate		Pakistan
H. (*H.*) *phyllodactyli*	Sauria: phyllodactylid (leaf-toed gecko)	elongate		Iran
H. (*H.*) *ptyodactyli*	phyllodactylid (fan-footed gecko)	elongate		Middle-East
H. (*H.*) *quettaensis*	Sauria: agamid (rock agama)	ovoid		Pakistan
H. (*H.*) *simondi*	Sauria: gekkonid (leaf-toed gecko)	round-lentiform		Sri Lanka
H. (*H.*) *sudani*	Sauria: phyllodactylid (white-spotted wall gecko)			North Africa
H. (*H.*) *tarentolae*	Sauria: phyllodactylid (crocodile gecko)	elongate		North Africa
H. (*H.*) *underwoodsauri*	Sauria: gekkonid (barking gecko)	elongate		Australia
Subgenus *Simondia*: species in tortoises/turtles (Testudines)				
H. (*S.*) *anatolicum*	testudinid (common tortoise)			Turkey
H. (*S.*) *caucasica* (possibly including *species inquirenda Plasmodium smirnovi*)	testudinid (common tortoise)	ovoid-halteridial		Georgia
H. (*S.*) *chelodinae*	chelid (eastern long-necked turtle)	ovoid-reniform		Australia
H. (*S.*) *metchnikowi* (syn. *Haemamoeba, Simondia*)	trionychid (Indian softshell tortoise), emydid (painted turtle, cooter, sawback turtle, Blanding's turtle)	ovoid	Diptera: tabanid (*Chrysops callidus*)	India, North America
H. (*S.*) *geochelonis*	testudinid (yellow-footed tortoise)	ovoid-reniform		South America
H. (*S.*) *natalensis*	testudinid (Natal hingeback tortoise)	halteridial and circumnuclear		South Africa
H. (*S.*) *pacayae*	podocnemidid (Arrau turtle)	elongate		South America

H. (*S.*) *peltocephali*	podocnemidid (Arrau turtle)	ovoid		South America
H. (*S.*) *roumei*	testudinid (Bell's hingeback tortoise)	ovoid-halteridial		West Africa
H. (*S.*) *testudinalis* (syn. *balazuci*)	testudinid (leopard tortoise, Lobatse hingeback tortoise, Bell's hingeback tortoise)	microhalteridial to halteridial		Africa
H. (*S.*) *testudinis*	testudinid (leopard tortoise)	ovoid-reniform		South Africa
H. (*S.*) *trionyxii*	trionychid (Indian softshell turtle)	round		India
Uncertain reports (*species inquirenda, nomen dubium, incertae sedis*)				
Species in lizards (Sauria)				
H. catenatus (possibly gametocyte stages of *Plasmodium*)	Sauria: leiosaurid (Wied's fathead anole)			South America
Species in frogs/toads (Anura)				
H. lanoraiea (syn. *Haemoproteus*)	bufonid (American toad)			North America
H. laurentiae (syn. *Haemoproteus*)	bufonid (American toad)			North America
H. lavalia (syn. *Haemoproteus*)	bufonid (American toad)			North America
H. ovalis (syn. *Haemoproteus*)	dicroglossid (Asian grass frog)			Asia

Genus *Billbraya*: This genus was erected for haemosporidians in lizards which exhibited merogony in erythrocytes (often two per cell) and monocytes, then formed gametocytes in erythrocytes. It is considered monotypic with a single species.

***Billbraya* species**	**Intermediate hosts**	**Gametocyte shape (pathogenicity)**	**Definitive hosts (vectors)**	**Geographic distribution**
B. australis	Sauria: gekkonid (marbled gecko)			Australia

Genus *Mesnilium*: This genus was erected for haemosporidians in fish that underwent merogony in erythrocytes and reticulo-endothelial cells, and then gamogony in erythrocytes. Pigment was only observed in gametocytes, and the probable vectors were thought to be leeches. It has only been detected once.

***Mesnilium* species**	**Intermediate hosts**	**Gametocyte shape**	**Definitive hosts (vector)**	**Distribution**
M. malariae [type species]	freshwater Anabantiformes: channid (snakeheads)	round	Hirudinea: cylicobdellid (*Hirundinaria*)	India

ALLIED GENERA

Family: Garniidae (merogony in leucocytes, haemozoin pigment absent)

This family contains haemosporidians that undergo merogony in cells of fixed tissues in reptiles (rarely birds), and then merogony in blood cells (esp. leucocytes) followed by gametocyte formation. Haemozoin pigment is absent in all stages and the vectors are largely unknown. Three genera are recognized: *Garnia* forming schizonts and non-pigmented gametocytes in red blood cells in lizards; *Fallisia* forming schizonts and gametocytes in white blood cells in lizards and birds; and *Progarnia* forming schizonts and gametocytes in white blood cells in crocodiles. The genera *Garnia* and *Fallisia* were previously thought to be subgenera of reptilian *Plasmodium*, but have now been accorded generic status on the basis of molecular studies.

Haemosporidian genera	**No. spp.**	**Site* of development in vertebrate**		**Vertebrate hosts**	**Invertebrate vector**
		meronts	**gamonts**		
Family: Garniidae (merogony in leucocytes, haemozoin pigment absent)					
Fallisia	12	leucocytes	leucocytes	lizards	arthropods
Garnia	10	leucocytes	leucocytes	lizards	arthropods
Progarnia	1	leucocytes	blood cells	crocodiles	

Genus *Garnia*: This genus was once considered a subgenus of *Plasmodium* but some authorities consider it to be a separate genus as the cognate species do not produce haemozoin pigment. They differ from non-pigmented Leucocytozoidae by undergoing schizogony in peripheral blood cells (red or white cells) and they parasitize lizards. Recently, molecular studies on the species originally called *Plasmodium* (*Garnia*) *azurophilum* revealed co-infections with a cryptic species that infected leucocytes instead of erythrocytes, and it was subsequently named *P. (G.) leucocytica* (despite conforming to the revised definition of the genus *Fallisia*). Further studies are required to determine the status of both the erythrocytic and non-erythrocytic species of plasmodiid species infecting lizards and thus the validity of the genera in the family Garniidae.

***Garnia* species**	**Intermediate hosts**	**Gametocyte shape (pathogenicity)**	**Definitive hosts (vectors)**	**Geographic distribution**
Species in lizards (Sauria)				
G. azurophilum (syn. *Plasmodium*)	Sauria: dactyloid (Graham's anole, large-headed anole, olive bush anole, stripefoot anole, yellow-chinned anole, savannah anole)	ovoid		Caribbean
G. gonatodi (type species)	Sauria: sphaerodactylid (Trinidad gecko, Wiegmann's striped gecko, yellow-headed gecko)	elongate		Central and South America
G. karyolytica	Sauria: phyllodactylid (turniptail gecko)	ovoid-elongate		South America
G. lainsoni	Sauria: phyllodactylid (Margarita leaf-toed gecko)	ovoid		South America
G. leucocytica (syn. *Plasmodium*)	Sauria: dactyloid (large-headed anole)	ovoid (in white blood cells)		Caribbean
G. morulum	Sauria: scincid (Greater Martinique skink)	ovoid	Diptera: culicid (*Culex pipiens*)	Central America
G. multiformis	Sauria: tropidurid (harlequin racerunner)	ovoid-elongate		South America
G. scorzai	Sauria: phyllodactylid (Margarita leaf-toed gecko)	elongate		South America
G. uranoscodoni	Sauria: tropidurid (diving lizard)	ovoid		South America
G. utingensis	Sauria: dactyloid (spotted anole)	ovoid		South America

Genus *Fallisia*: This genus was once considered to be a subgenus of *Plasmodium*, but recent revision led to its elevation to generic rank. Merogony and gametogony occur in peripheral blood cells (leucocytes and thrombocytes) and haemozoin pigment is not produced. Two subgenera are recognized: *F.* (*Fallisia*) containing 12 species infecting lizards, and *F.* (*Plasmodioides*) being monotypic with a single species infecting birds. Recent molecular studies found that lizards infected with the species *Plasmodium tropiduri* were also co-infected with a cryptic species that only infected host thrombocytes and lymphocyte-like cells, which was subsequently named *P. ouropretensis* (despite conforming to the revised definition of the genus *Fallisia*). Further studies are required to determine the status of both the erythrocytic and non-erythrocytic species of plasmodiid species infecting lizards and thus the validity of the genera in the family Garniidae.

***Fallisia* species**	**Intermediate hosts**	**Gametocyte shape (pathogenicity)**	**Definitive hosts (vectors)**	**Geographic distribution**
Subgenus: *Fallisia* (in lizards)				
F. (*F.*) *audaciosa*	tropidurid (harlequin racerunner)	ovoid		South America
F. (*F.*) *biporcati*	dactyloid (giant green anole, lion anole)	ovoid		Central America
F. (*F.*) *copemani*	scincid (blue-throated rainbow skink)	ovoid		Australia
F. (*F.*) *dominicensis*	dactyloid (large-headed anole)	ovoid		Caribbean
F. (*F.*) *effusa*	gymnophthalmid (two-faced neusticurus)	elongate		South America
F. (*F.*) *kantoensis*	scincid (Japanese five-lined skink)	ovoid		Japan
F. (*F.*) *modesta*	tropidurid (Peter's lava lizard)	ovoid		South America
F. (*F.*) *poecilopi*	dactyloid (dappled anole)	ovoid-elongate		Central America
F. (*F.*) *siamense*	agamid (spotted flying dragon)	ovoid-elongate		Thailand
F. (*F.*) *simplex*	tropidurid (harlequin racerunner)	ovoid		South America
F. (*F.*) *thecadactyli*	phyllodactylid (turniptail gecko)	ovoid-elongate		Central America
Subgenus: *Plasmodioides* (in birds)				
F. (*P.*) *neotropicalis*	Columbiformes: columbid (pigeons), Ciconiiformes: ciconiid (storks), Pelecaniformes: ardeid (bitterns, egrets, herons), threskiornithid (ibis, spoonbills)	ovoid (moderately pathogenic in pigeon squabs)	Diptera: cuclicid (*Aedeomyia squamipennis, Anopheles albimanus*)	South America

Genus *Progarnia*: This genus is represented by a single species found in caimans. Merogony and gametogony occur principally in leucocytes and thrombocytes but may also involve erythrocytes. The vectors are unknown.

***Progarnia* species**	**Intermediate hosts**	**Gametocyte shape**	**Definitive hosts (vectors)**	**Geographic distribution**
P. archosauriae	Crocodilia: alligatorid (spectacled caiman)	spherical		South America

Haemoproteus
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Haematozoa are small blood-borne parasites which undergo merogony (= schizogony) and gamogony (gamete formation) in vertebrates and sporogony (sporozoite formation) in blood-sucking invertebrate vectors. Two main groups are recognised in terrestrial vertebrates: haemosporidia with insect vectors; and piroplasms with arachnid vectors. Haemosporidian parasites multiply in the tissues of vertebrates before forming gamonts in blood cells. Most species produce haemozoin pigment granules as a byproduct of haemoglobin metabolism. Gametes ingested by insect vectors undergo fertilization in the gut forming motile zygotes (ookinetes) which form oocysts and then thousands of sporozoites which invade the salivary glands. Haemoproteid infections are transmitted by biting midges, hippoboscid and tabanid flies and are frequently detected in birds and some reptiles. most apparently causing no harm.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Aconoidasida (asexual stages without conoid)
Order:	Haemosporida (pleomorphic stages in blood of vertebrates, insect vectors. motile zygote (ookinete))
Family:	Haemoproteidae (schizogony in tissues, gamonts in blood cells, haemozoin pigment)
Genus:	*Haemoproteus* (parasitic in endothelia/erythrocytes of birds/lizards/turtles)
Species:	various species cause infections mainly in birds

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic ‘haemococcidia’ in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Haemosporida are spore-forming apicomplexan parasites with heteroxenous life-cycles, with merogony in cells of fixed tissues and in the blood of vertebrate (intermediate) hosts and sporogony in haematophagous invertebrate vectors (definitive hosts). In vertebrate blood cells, haemosporidia develop intracellularly forming sexually dimorphic gametocytes: macrogametocytes (female) with compact nuclei and dark-stained cytoplasm (plentiful ribosomes for protein synthesis), and microgametocytes (male) with larger diffuse nuclei (ready for microgamete production) and pale-staining cytoplasm [a simple pneumonic often used is “blue for girls, pink for boys”]. Gametocytes develop independently (without syzygy) and each microgamont produces about eight flagellated microgametes. Haemozoin granules (residual pigment formed due to incomplete haemoglobin digestion) may or may not be produced in infected erythrocytes. In the vector, the zygote is motile (ookinete) and ultimately forms numerous naked sporozoites (without sporocysts). Around 590 species belonging to some 19 haemosporidian genera have been described from a wide range of mammalian, avian and reptilian hosts around the world.

Four haemosporidian families are recognized mainly on the basis of their developmental cycles and whether haemozoin pigment is produced: namely, Plasmodiidae (merogony in tissues then cyclic in erythrocytes, pigment present); Haemoproteidae (merogony in tissues only, pigment present); Leucocytozoidae (merogony in tissues, pigment absent) and Garniidae (merogony in leucocytes, pigment absent). Vertebrates act as intermediate hosts in which the parasites undergo asexual multiplication within tissues and/or blood cells. Even though parasites begin gamete formation in vertebrates, sexual multiplication is not completed until after they are transmitted to their haematophagous invertebrate vectors, which therefore act as definitive hosts. Three genera are recognized in the family Haemoproteidae on the basis of multiple biological characters (including morphology, development, host specificity and range): *Haemoproteus* (syn. *Halteridium*) in birds; and *Johnsprentia* and *Sprattiella* in bats. Two subgenera are recognized in the genus *Haemoproteus*: *H.* (*Haemoproteus*) in columbiform birds with hippoboscid (louse fly) vectors; and *H.* (*Parahaemoproteus*) in non-columbiform birds with ceratopogonid (biting midge) vectors. Species in another genus *Simondia* (in tortoises) and all reptilian *Haemoproteus* species have recently been transferred to the plasmodiid genus *Haemocystidium* on the basis of contemporary morphological, biological and molecular studies.

Haemosporidian genera	**No. spp.**	**Site* of development in vertebrate**		**Vertebrate hosts**	**Invertebrate vector**
		meronts	**gamonts**		
Family: Plasmodiidae (merogony in tissues and erythrocytes, haemozoin pigment present)					
Plasmodium	225	liver, rbc	rbc	mammals, birds, reptiles	diptera
Hepatocystis	25	liver	rbc	primates/bats	midges
Polychromophilus	5	viscera	rbc	bats	nycterids
Nycteria	7	liver	rbc	bats	
Biguetiella	1	liver	rbc	bats	
Bioccala	2	RE cells	rbc	bats	
Dionisia	1	liver	rbc	bats	
Rayella	3	liver	rbc	flying squirrels	
Billbraya	1	rbc	rbc	lizards	
Mesnilium	1	RE cells, rbc	rbc	fish	leeches/insects
Haemocystidium (*Simondia*)	33	RE cells	rbc	lizards/tortoises	arthropods
Family: Haemoproteidae (merogony in tissues (not in blood cells), haemozoin pigment present in gametocytes)					
Haemoproteus (*Halteridium*)	6	RE cells	rbc	birds	louse flies
Haemoproteus (*Parahaemoproteus*)	150	RE cells	rbc	birds	midges
Johnsprentia	1	RE cells	rbc	flying foxes	
Sprattiella	1	RE cells	rbc	bats	
Family: Leucocytozoidae (merogony in tissues (not in blood cells), haemozoin pigment absent)					
Leucocytozoon (*Akiba*)	100	RE cells	blood cells	birds	black flies
Saurocytozoon	3	viscera	leucocytes	lizards	mosquitoes
Family: Garniidae (merogony in leucocytes, haemozoin pigment absent)					
Fallisia	12	leucocytes	leucocytes	lizards	arthropods
Garnia	10	leucocytes	leucocytes	lizards	arthropods
Progarnia	1	leucocytes	blood cells	crocodiles	

*rbc = red blood cells (erythrocytes); RE = reticuloendothelial cells

Many molecular phylogenetic studies using nuclear, mitochondrial and apicoplast gene sequences have demonstrated a clear relationship between haemosporidian genera not only with their vertebrate hosts but also their invertebrate vectors. There were clear groupings of *Leucocytozoon* from birds, *Haemoproteus* (*Haemoproteus*) from birds, *Haemoproteus* (*Parahaemoproteus*) from birds, *Plasmodium* from birds and reptiles, *Plasmodium* from rodents and primates, and *Hepatocystis* from bats. These groups were clearly associated with different vectors; namely, simuliids (black-flies), hippoboscids (louse-flies), ceratopogonids (midges), culicine mosquitoes, anopheline mosquitoes, and midges, respectively. There appears to have been a transition from haemosporidia which do not form haemozoin pigment (*Leucocytozoon* in white blood cells) to genera that do form pigment indicating haemoglobin digestion by parasites in red blood cells (*Haemoproteus*, *Plasmodium* and *Hepatocystis*). This was followed by a transition from haemosporidia which undergo schizogony exclusively in host tissues (*Leucocytozoon* and *Haemoproteus*) to those that undergo schizogony in blood cells (*Plasmodium*). While there appears to be a general shift in haemosporidian genera from birds and reptiles to mammals (from nucleated to non-nucleated blood cells), each genus is associated with a particular vector group: black-flies transmitting *Leucocytozoon* to birds; louse-flies transmitting *Haemoproteus* (*Haemoproteus*) to birds; midges transmitting *Haemoproteus* (*Parahaemoproteus*) to birds; culicine mosquitoes transmitting *Plasmodium* to birds and lizards; and anopheline mosquitoes transmitting *Plasmodium* to mammals. The exception to this general trend was *Hepatocystis* which does not undergo blood schizogony and is transmitted to bats by midges.

Haemoproteids are malaria-like parasites found mainly in birds, but a few species in bata. They are characterized by exoerythrocytic schizogony occurring in fixed tissues followed by intraerythrocytic gametogony (no erythrocytic merogony). Most species form haemozoin pigment and they are transmitted by insect vectors other than mosquitoes, including biting midges, hippoboscid and tabanid flies. Six species assigned to the subgenus *Haemoproteus* (*Haemoproteus*) occur mainly in columbiform birds and have hippoboscid vectors, while over 180 species placed in the subgenus *Haemoproteus* (*Parahaemoproteus*) occur in many non-columbiform bird families and have ceratopogonid vectors. Haemoproteids have a widespread distribution, species richness (biodiversity) being richest in Holarctic, Ethiopian and Oriental regions, and poorest in Neotropical and Australasian regions, with infections recorded in 18 bird orders, particularly Passeriformes, Coraciiformes, Galliformes, Piciformes, Falconiformes and Columbiformes. The zoogeographic boundaries of individual species are unclear as most studies have consisted of patchy surveys and the life-cycles and vectors for most species are unknown. Nevertheless, observations suggest that the dispersal of several species has been assisted by anthropogenic activities (aviary trade) and annual bird migrations (where overwintering sites appear to be more important for transmission than breeding sites).

Haemoproteus* species	**Intermediate hosts [pathology]**	**Gamont shape**	**Definitive hosts (vectors)**	**Geographic distribution**
Subgenus: *Haemoproteus* (definitive hosts: hippoboscid flies; intermediate hosts: columbiform birds)				
H. (*H.*) *columbae* (syn. *maccallumi*, *melopeliae*) [type species]	Columbiformes: columbid (pigeons, doves), Cuculiformes: cuculid (coucals, cuckoos), Passeriformes: emberizid (buntings), estrildid (mannikins), fringillid (finches), laniid (shrikes), nectariniid (sunbirds), passerid (sparrows), ploceid (bishops, weavers); Strigiformes: strigid (pygmy owls, wood owls);Accipitriformes: accipitrid (goshawks) [megalomeront lesions in tissues]	halteridial	Diptera: hippoboscid (*Microlynchia pusilla, Pseudolynchia brunnea, canariensis* (= *Lynchia capensis, lividicolor, maura*))	cosmopolitan (except Antarctica)
H. (*H.*) *krylovi*	Columbiformes: pteroclid (sandgrouse)	halteridial		Palearctic
H. (*H.*) *palumbis*	Columbiformes: columbid (wood-pigeons)	halteridial	Diptera: hippoboscid (*Ornithomyia avicularia, Pseudolynchia canariensis*)	Palearctic
H. (*H.*) *pteroclis*	Columbiformes: pteroclid (sandgrouse)	halteridial		Palearctic
H. (*H.*) *sacharovi*	Columbiformes: columbid (pigeons, doves)	pleomorphic	Diptera: hippoboscid (*Ornithomyia avicularia, Pseudolynchia canariensis* (= *maura*)*, brunne, capensis, Microlynchia pusilla*)	Holarctic, Neotropical, Ethiopian, Oriental
H. (*H.*) *turtur*	Columbiformes: columbid (pigeons, doves)	halteridial	Diptera: hippoboscid (*Pseudolynchia canariensis*)	Palearctic
Subgenus: *Parahaemoproteus* (definitive hosts: biting midges; intermediate hosts: non-columbiform birds)				
H. (*P.*) *abdusalomovi*	Charadriiformes: glareolid (pratincoles)	halteridial		Palearctic
H. (*P.*) *aegithinae*	Passeriformes: aegithinid (ioras), chloropseid (leafbirds)	halteridial		Oriental
H. (*P.*) *aegyptius*	Strigiformes: strigid (eagle-owls)			Palearctic
H. (*P.*) *africanus*	Passeriformes: fringillid (finches), ploceid (weavers)	halteridial		Ethiopian
H. (*P.*) *alaudae*	Passeriformes: alaudid (larks)	halteridial-circum-nuclear		Holarctic, Ethiopian, Oriental
H. aluci	Strigiformes: strigid (barn			Holarctic,

nomen dubium	owls, eagle-owls, marsh owls, wood owls)			African, Oriental
H. americaniae *nomen nudum*	Coraciiformes: coraciid (Indian rollers)			Oriental
H. (*P.*) *ammoperdix*	Galliformes: phasianid (partridges)	halteridial		Palearctic
H. (*P.*) *anthi*	Passeriformes: motacillid (pipits, wagtails)	halteridial		Oriental, Ethiopian, Palearctic
H. (*P.*) *antigonis*	Gruiformes: gruid (cranes); Otidiformes: otidid (bustards)	halteridial		Oriental, Ethiopian, Holarctic
H. (*P.*) *apodus*	Apodiformes: apodid (swifts)	micro-halteridial		Neotropical
H. (*P.*) *archilochus*	Apodiformes: trochilid (hummingbirds)	circum-nuclear		Nearctic, Neotropical
H. (*P.*) *asturisdussumieri* (*incertae sedis*)	Accipitriformes: accipitrid (goshawks)			Oriental, African
H. (*P.*) *attenuatus*	Passeriformes: muscicapid (robins)	halteridial		Palearctic
H. (*P.*) *balearicae*	Gruiformes: gruid (cranes)	micro-halteridial		Holarctic, Ethiopian
H. balfouri *nomen nudum*	Galliformes: numidid (helmeted guineafowl)			African
H. (*P.*) *balmorali*	Passeriformes: muscicapid (flycatchers), turdid (thrushes)	halteridial	Diptera: ceratopogonid (*Culicoides impunctatus*)	Palearctic, Ethiopian, Oriental
H. (*P.*) *bambusicolae*	Galliformes: phasianid (bamboo partridge)			Oriental
H. (*P.*) *beckeri*	Passeriformes: mimid (thrashers, catbirds, mockingbirds)	halteridial		Nearctic
H. (*P.*) *belopolskyi* (syn. *sylvae*)	Passeriformes: sylviid (warblers)	halteridial-circum-nuclear	Diptera: ceratopogonid (*Culicoides impunctatus*)	Oriental, Ethiopian, Palearctic
H. (*P.*) *bennetti*	Piciformes: picid (yellownapes)	rhabdosomal		Oriental
H. (*P.*) *bilobata*	Piciformes: capitonid (barbets)	micro-halteridial		Oriental
H. (*P.*) *borgesi*	Piciformes: picid (woodpeckers, wrynecks)	halteridial		Oriental, Ethiopian, Neotropical
H. (*P.*) *brachiatus*	Falconiformes: falconid (kestrels)	halteridial-circum-nuclear		Holarctic
H. (*P.*) *bramae* (*species inquirenda*)	Strigiformes: strigid (little owl)			Palearctic
H. (*P.*) *bubalornis*	Passeriformes: ploceid (weavers)	halteridial		Ethiopian
H. bubonis *nomen dubium*	Strigiformes: strigid (barn owl, short-eared owl)			Holarctic, Oriental African
H. (*P.*) *bucconis*	Piciformes: bucconid (puffbirds)	rhabdosomal		Neotropical
H. (*P.*) *bucerotis*	Bucerotiformes: bucerotid (hornbills)	halteridial		Ethiopian
H. (*P.*) *burhini*	Charadriiformes: scolopacid (curlews)	halteridial		Ethiopian
H. (*P.*) *buteonis*	Falconiformes: falconid (buzzards, hawks, harriers)	halteridial		Holarctic
H. (*P.*) *calandrellae*	Passeriformes: alaudid (larks)	halteridial		Palearctic
H. (*P.*) *caprimulgi*	Caprimulgiformes: caprimulgid (nightjars, nighthawks)	halteridial-circum-nuclear		Holarctic, Oriental

H. (*P.*) *cellii* (syn. *noctuae* var. *celli*)	Strigiformes: strigid (bay owls, boobooks, eagle-owl, owlets, pygmy owls, scops owls, screech owls, wood owls)			cosmopolitan
H. (*P.*) *centropi* (syn. *froilanoi*)	Cuculiformes: cuculid (cuckoos, anis)	halteridial		Oriental
H. (*P.*) *cerchneisi* (*species inquirenda*)	Falconiformes: falconid (Eurasian kestrel)			Palearctic
H. (*P.*) *chapini* (*species inquirenda*)	Galliformes: phasianid (Congolese peafowl)			African
H. (*P.*) *chelidonis* (*incertae sedis*)	Passeriformes: hirundinid (martins, swallows)			Holarctic, Oriental
H. (*P.*) *circumnuclearis*	Passeriformes: muscicapid (flycatchers)	circum-nuclear		Neotropical
H. (*P.*) *circus* (*incertae sedis*)	Accipitriformes: accipitrid (harriers)			Palearctic
H. (*P.*) *clamatori*	Cuculiformes: cuculid (pied cuckoo)	halteridial		African
H. (*P.*) *clelandi*	Passeriformes: meliphagid (honeyeater)			Australasian
H. (*P.*) *coatneyi* (syn. *coereba, paruli, thraupi*)	Passeriformes: emberizid (buntings), fringillid (finches), passerid (sparrows), sylviid (warblers), thraupid (tanagers)	halteridial	Diptera: culicid (*Anopheles balabacensis*)	Holarctic, Neotropical
H. (*P.*) *contortus*	Charadriiformes: glareolid (waders), scolopacid (whimbrels)	circum-nuclear		Oriental (Philippines)
H. (*P.*) *coraciae* (syn. *coraciae* var. *benghalensis, cruzferreirae, fontesi, fontessi* var. *cyanogaster, velascoi*)	Coraciiformes: coraciid (rollers)	halteridial-circum-nuclear		Oriental, Ethiopian
H. (*P.*) *cornuata*	Piciformes: capitonid (barbets)	halteridial		Oriental, Ethiopian
H. corvi *nomen dubium*	Passeriformes: corvid (corvids)			Europe
H. (*P.*) *cracidarum*	Galliformes: cracid (chachalacas, guans)	halteridial		Neotropical
H. (*P.*) *crumenium* (syn. *brodkorbi*)	Ciconiiformes: ciconiid (storks)	halteridial		Ethiopian, Nearctic
H. (*P.*) *cublae*	Passeriformes: laniid (shrikes), malaconotid (boubous)	micro-halteridial		Ethiopian
H. (*P.*) *cuculis*	Cuculiformes: cuculid (Asian koel)	halteridial		Australasian
H. (*P.*) *danilewskii* [type species]	Passeriformes: corvid (crows, jays, nutcrackers)	circum-nuclear-halteridial	Diptera: ceratopogonid (*Culicoides arboricola, crepuscularis, downesi, edeni, sphagnumensis, stilobezzioides*)	Nearctic (North America)
H. (*P.*) *dicaeus*	Passeriformes: dicaeid (flowerpeckers)	halteridial		Oriental
H. (*P.*) *dicruri*	Passeriformes: dicrurid (drongos)	halteridial		Oriental, Ethiopian
H. (*P.*) *dolniki*	Passeriformes: fringillid (finches)	halteridial	Diptera: ceratopogonid (*Culicoides impunctatus*)	Palearctic
H. (*P.*) *elani*	Falconiformes: falconid (kites, hawks, vultures, eagles)	halteridial		Oriental, Ethiopian, Holarctic
H. (*P.*) *enucleator*	Coraciiformes: alcedinid (kingfisher)	rhabdosomal		Ethiopian
H. (*P.*) *eurylaimus*	Passeriformes: eurylaimid	halteridial		Oriental

	(broadbills)			
H. (*P.*) *eurystomae*	Coraciiformes: coraciid (rollers)	halteridial		Ethiopian, Oriental
H. (*P.*) *fallisi* (syn. *rhipiduris*)	Passeriformes: muscicapid (forktails, nightingales, redstarts, robins, robinchats), passerid (sparrows), parulid (warblers), ploceid (weavers), timaliid (babblers), turdid (chats, thrushes)	micro-halteridial		Holarctic, Neotropical, Ethiopian, Oriental
H. (*P.*) *figueiredoi*	Accipitriformes: accipitrid (eagles, sparrowhawks)			Eurasia, Nearctic
H. (*P.*) *formicarius*	Passeriformes: thamnophiliid (antbirds)	halteridial		Neotropical
H. (*P.*) *forresteri*	Coraciiformes: brachypteraciid (ground rollers)	halteridial-circum-nuclear		African
H. (*P.*) *fringillae* (syn. *chloriis*)	Passeriformes: corvid (jays), emberizid (buntings), estrildid (pytilias), fringillid (canaries, crossbills, finches, grosbeaks, redpolls), laniid (shrikes), muscicapid (robins, shamas), parid (tits), parulid (warblers), passerid (sparrows), prunellid (accentors), ploceid (weavers), sittid (nuthatches), sturnid (starlings), thraupid (bananaquits, grassquits, orangequits, tanagers), turdid (thrushes)	halteridial	Diptera: ceratopogonid (*Culicoides crepuscularis, impunctatus, sphagnumensis, stilobezzioides*)	cosmopolitan (except Australia, Antarctic)
H. (*P.*) *furnarius*	Passeriformes: parulid (ovenbirds)	halteridial		Neotropical
H. (*P.*) *fusca*	Coraciiformes: alcedinid (kingfishers)	circum-nuclear		Oriental, Ethiopian, Palearctic
H. (*P.*) *gallinulae*	Gruiformes: rallid (crakes, rails, coots, waterhens)	halteridial		Oriental, Ethiopian, Holarctic
H. (*P.*) *gavrilovi*	Coraciiformes: meropid (bee-eaters)	rhabdosomal		Palearctic
H. (*P.*) *geocichlae* (*species inquirenda*)	Passeriformes: turdid (ground-thrush)			Palearctic
H. glaucidii *nomen dubium*	Strigiformes: strigid (owlets)			Oriental, Neotropical
H. (*P.*) *glaucidiumi* (*species inquirenda*)	Strigiformes: strigid (pygmy owls)			Neotropical
H. (*P.*) *globulosus* (*species inquirenda*)	Passeriformes: fringillid (finches)	circum-nuclear		Palearctic (Spain)
H. (*P.*) *goodmani*	Coraciiformes: brachypteraciid (ground rollers)	halteridial		African
H. (*P.*) *greineri*	Anseriformes: anatid (ducks, geese, swans)	circum-nuclear		Holarctic
H. (*P.*) *halcyonis*	Coraciiformes: alcedinid (kingfishers)	halteridial		Oriental, Ethiopian, Palearctic
H. (*P.*) *handai* (syn. *desseri*)	Psittaciformes: cacatuid (cockatoos), psittaculid (parakeets, budgerigars, lorikeets, parrots) [megalomeront lesions in tissues]	circum-nuclear	Diptera: ceratopogonid (*Culicoides nubeculosus*)	Australasian, Oriental, Ethiopian, Neotropical
H. (*P.*) *hartmanni* (*species inquirenda*)	Pelecaniformes: ardeid (night herons)			Holarctic

H. (*P.*) *hedymelis*	Passeriformes: fringillid (grosbeaks, rosefinches)			Holarctic
H. (*P.*) *herodiadis* (*incertae sedis*)	Pelecaniformes: ardeid (herons, bitteren)	halteridial		Oriental, Holarctic
H. (*P.*) *hirundinis*	Passeriformes: hirudinid (swallows, martins)	halteridial		Holarctic, Ethiopian, Oriental
H. (*P.*) *indicator*	Piciformes: indicatorid (honeyguides)	halteridial		Ethiopian
H. (*P.*) *iwa*	Suliformes: fregatid (frigatebirds)	halteridial		Hawaii
H. (*P.*) *janovyi*	Falconiformes: falconid (hawks), cathartid (vultures)	circum-nuclear		Ethiopian
H. (*P.*) *kairullaevi*	Passeriformes: sturnid (starlings)	micro-halteridial		Palearctic
H. (*P.*) *khani*	Passeriformes: dicurid (drongos)	circum-nuclear		African
H. (*P.*) *killangoi*	Passeriformes: zosteropid (white-eyes)	halteridial		Oriental, Ethiopian
H. (*P.*) *lairdi*	Coraciiformes: meropid (bee-eaters)	rhabdosomal		Ethiopian
H. (*P.*) *lanii*	Passeriformes: laniid (shrikes)	halteridial-circum-nuclear	Diptera: ceratopogonid (*Culicoides impunctatus*)	Oriental, Ethiopian, Palearctic
H. (*P.*) *larae* (syn. *lari*)	Charadriiformes: larid (gulls, terns)	circum-nuclear		Palearctic, Ethiopian
H. (*P.*) *lophortyx*	Galliformes: phasianid (quail)	circum-nuclear	disputed (initially proposed to be hippoboscids *Stilbometopa impressa, Lynchia* (*Icosta*) *hirsuta*)	Holarctic, Ethiopian
H. (*P.*) *macropigmentatus*	Passeriformes: fringillid (finches, canaries)	halteridial		Holarctic, Ethiopian
H. (*P.*) *madagascariensis*	Passeriformes: vangid (vangas)	halteridial		African
H. (*P.*) *magnus*	Passeriformes: fringillid (finches)	halteridial-circum-nuclear		Palearctic
H. (*P.*) *majoris* (syn. *machlolophi*)	Passeriformes: parid (tits), parulid (warblers)	halteridial		Holarctic, Ethiopian, Oriental
H. (*P.*) *mansoni* (syn. *canachites, meleagridis*)	Galliformes: phasianid (grouse, partridges, turkeys, pheasant) [megalomeront lesions in tissues, acute disease in turkeys]	halteridial-circum-nuclear	Diptera: ceratopogonid (*Culicoides arboricola, edeni, haematopotus, hinmani, knowltoni, sphagnumemsis*)	Holarctic
H. (*P.*) *manwelli*	Coraciiformes: meropid (bee-eaters)	halteridial		Oriental
H. (*P.*) *mathislegeri* (syn. *herodiadis* var. *mathislegeri*)	Pelecaniformes: ardeid (little bitterns)	micro-halteridial		African, Palearctic
H. (*P.*) *mazzai*	Passeriformes: fringillid (golden grosbeaks)	halteridial		Neotropical
H. (*P.*) *megapodius*	Galliformes: megapodid (scrubfowl)	micro-halteridial		Oriental
H. (*P.*) *meliornis* (*species inquirenda*)	Passeriformes: meliphagid (honey-eater)			Australasian
H. (*P.*) *meropis*	Coraciiformes: meropid (bee-eaters)	halteridial		Oriental, Ethiopian, Palearctic
H. (*P.*) *minutus*	Passeriformes: turdid (blackbirds)	micro-halteridial		Palearctic
H. (*P.*) *monarchus*	Passeriformes: monarchid	halteridial		Oriental,

	(monarchs)			Ethiopian
H. (*P.*) *montezi*	Musophagiformes: musophagid (turacos)	halteridial		Ethiopian
H. (*P.*) *morneti*	Passeriformes: sturnid (glossy starlings, wattled starlings)			African
H. moruony *nomen dubium*	Passeriformes: muscicapid (shamas)			African, Oriental
H. (*P.*) *motacillae*	Passeriformes: motacillid (wagtails, pipits)	halteridial		Ethiopian, Oriental, Palearctic
H. (*P.*) *multiparasitans* (*species inquirenda*)	Strigiformes: strigid (little owls)			Palearctic
H. (*P.*) *nascimentoi* (*incertae sedis*)	Charadriiformes: charadriid (lapwings)	micro-halteridial		African
H. (*P.*) *nebraskensis* (syn. *noctuae* var. *nebraskensis*)	Strigiformes: strigid (horned owl)			Nearctic
H. (*P.*) *neseri*	Passeriformes: turdid (robin-chats)	halteridial		Ethiopian
H. (*P.*) *nettionis* (syn. *anatis, anseris, eulabeiae, gabaldoni, hermani*)	Anseriformes: anatid (ducks) [anaemia with heavy parasitaemia]	halteridial	Diptera: ceratopogonid (*Culicoides downesi*)	cosmopolitan (except Antarctica)
H. (*P.*) *nipponensis*	Passeriformes: tyrannid (flycatchers)	halteridial-circum-nuclear		Oriental, Ethiopian
H. (*P.*) *nisi*	Falconiformes: falconid (hawks, eagles, buzzards, harriers, kites)	halteridial-circum-nuclear		Holarctic, Ethiopian, Oriental
H. (*P.*) *noctuae* (syn. *tytoni*)	Strigiformes: strigid (boobooks, eared owls, horned owls, little owls, owlets, pygmy owls, scops owls, true owls, wood owls), tytonid (barn owls): Falconiformes: falconid (falcons)	circum-nuclear		cosmopolitan (except Antarctica)
H. (*P.*) *nucleophilus*	Passeriformes: dicaeid (flowerpeckers), melanocharitid (berrypeckers)	micro-halteridial		Australasian
H. (*P.*) *orioli* (syn. *pintoi*)	Passeriformes: oriolid (orioles)	halteridial		Oriental, Ethiopian, Palearctic
H. (*P.*) *orizivorae* (syn. *paddae*)	Passeriformes: estrildid (seedcrackers, bluebills, waxbills), fringillid (finches)	halteridial		Oriental, Ethiopian, southern Palearctic
H. (*P.*) *ortalidum* (syn. *rotundus ortalidium*)	Galliformes: cracid (chachalacas, guans)	discosomal		Neotropical
H. (*P.*) *otocompsae*	Passeriformes: pycnonotid (bulbuls)	halteridial		Oriental, Ethiopian, South Palearctic
H. (*P.*) *pachycephalus*	Passeriformes: pachycephalid (whistlers)	micro-halteridial		Australasian, Oriental
H. (*P.*) *pallidus*	Passeriformes: tyrannid (flycatchers)	halteridial-circum-nuclear		Palearctic, Ethiopian
H. (*P.*) *parus*	Passeriformes: parid (tits)	discosomal		Nearctic
H. (*P.*) *passeris* (syn. *danilewskii* var. *urbanensis, garnhami, granulosum, gymnorhidis, wenyoni, zasukhini*)	Passeriformes: alaudid (crested larks, skylarks), cisticolid (tailorbirds), parulid (warblers), passerid (petronias, sparrows), ploceid (weavers) [megalomeront lesions in tissues]	halteridial		cosmopolitan (except Antarctica)

H. (*P.*) *pastoris*	Passeriformes: sturnid (starlings, mynas)	halteridial		Oriental, Ethiopian, Palearctic
H. (*P.*) *payevskyi*	Passeriformes: parulid (warblers)	micro-halteridial		Palearctic, Ethiopian
H. (*P.*) *peircei*	Ciconiiformes: ciconiid (saddle-billed stork, yellow-billed stork)	circum-nuclear		African, Oriental
H. (*P.*) *pelouroi*	Ciconiiformes: threskiornithid (ibis)	micro-halteridial		Ethiopian
H. (*P.*) *philemon* (*species inquirenda*)	Passeriformes: meliphagid (honey-sucker)			Australasian
H. (*P.*) *philippinensis*	Passeriformes: pycnonotid (bulbuls)	micro-halteridial		Oriental, Ethiopian, South Palearctic
H. (*P.*) *picae*	Passeriformes: corvid (magpies, crows, jays)	halteridial		Holarctic
H. piresi *nomen dubium*	Columbiformes: columbid (pigeons)			Holarctic
H. (*P.*) *pittae*	Passeriformes: pittid (pittas)	halteridial-circum-nuclear		Oriental
H. (*P.*) *plataleae* (syn. *galatheae*)	Ciconiiformes: ciconiid (storks), threskiornithid (spoonbills, ibis)	halteridial-circum-nuclear		cosmopolitan (except Antarctica)
H. (*P.*) *porzanae*	Gruiformes: rallid (crakes, rails, marsh hens)	micro-halteridial		Palearctic, New Guinea
H. (*P.*) *pratasi*	Galliformes: numidid (guineafowl)	halteridial		Ethiopian
H. (*P.*) *prognei*	Passeriformes: hirudinid (martins, swallows)	halteridial		Holarctic, Neotropical
H. (*P.*) *psittaci*	Psittaciformes: psittaculid (parrots)	micro-halteridial		Ethiopian
H. (*P.*) *ptilotis* (*species inquirenda*)	Passeriformes: meliphagid (honeyeaters, friarbirds)	halteridial-circum-nuclear		Australasian
H. (*P.*) *quelea* (*species inquirenda*)	Passeriformes: fringillid (finches), ploceid (weavers)	halteridial		Ethiopian, Oriental
H. (*P.*) *quiscalus*	Passeriformes: icterid (grackles, cowbirds), turdid (blackbirds)	halteridial		Nearctic, Neotropical
H. raymundi *nomen dubium*	Passeriformes: nectariniid (sunbirds)			Oriental
H. (*P.*) *rileyi* (*species inquirenda*)	Galliformes: phasianid (peafowl, pheasant, partridges, quail, junglefowl)	halteridial		Oriental, Ethiopian, South Palearctic
H. (*P.*) *rotator*	Charadriiformes: glareolid (waders)	halteridial-circum-nuclear		Oriental (Philippines)
H. rotundus *nomen nudum*	Galliformes: phasianid (chachalacas, grouse): Charadriiformes: scolopacid (woodcock)			Palearctic, Neotropical
H. (*P.*) *sanguinis*	Passeriformes: pycnonotid (bulbuls)	micro-halteridial		Oriental, Ethiopian
H. (*P.*) *santosdiasi* (*species inquirenda*)	Galliformes: phasianid (chickens, partridges)			Oriental
H. (*P.*) *savianae* (*incertae sedis*)	Accipitriformes: accipitrid (lizard hawks, bald eagle)			African, Nearctic
H. (*P.*) *scolopaci*	Charadriiformes: glareolid (waders), scolopacid (woodcocks, phalaropes, sandpipers)	halteridial-circum-nuclear		Palearctic, Oriental
H. (*P.*) *sequeirae*	Passeriformes: nectariniid (sunbirds)	halteridial		Oriental, Ethiopian

H. (*P.*) *serini* (*species inquirenda*)	Passeriformes: fringillid (canary)			Nearctic
H. (*P.*) *silvai* (*species inquirenda*)	Galliformes: numidid (guineafowl)			Oriental
H. (*P.*) *sittae*	Passeriformes: sittid (nuthatches)	halteridial		Oriental, Holarctic
H. (*P.*) *souzalopesi*	Passeriformes: muscicapid (flycatchers)	discosomal		Neotropical
H. (*P.*) *stableri*	Galliformes: phasianid (grouse)	circum-nuclear		Nearctic
H. (*P.*) *stellaris*	Passeriformes: hirudinid (swallows)	halteridial		Ethiopian
H. (*P.*) *sturni*	Passeriformes: sturnid (mynas, starlings)			cosmopolitan
H. (*P.*) *syrnii* (syn. *phodili*)	Strigiformes: strigid (owls)	halteridial		Holarctic, Neotropical, Ethiopian, Oriental
H. (*P.*) *tartakovskyi*	Passeriformes: fringillid (crossbills, grosbeaks, siskins)	rhabdosomal	Diptera: ceratopogonid (*Culicoides impunctatus*)	Palearctic
H. (*P.*) *telfordi*	Otidiformes: otidid (bustards)	circum-nuclear		Ethiopian
H. (*P.*) *tendeiroi*	Otidiformes: otidid (bustards)	halteridial		African
H. (*P.*) *tephrodornis* (*species inquirenda*)	Passeriformes: campephagid (cuckoo-shrikes)	halteridial		African, Oriental
H. (*P.*) *thereicerycis*	Piciformes: capitonid (barbets)	halteridial		Oriental, Ethiopian
H. (*P.*) *timalus*	Passeriformes: leiothrichid (sibas), timaliid (babblers), turdid (thrushes)	halteridial		Oriental, Ethiopian
H. (*P.*) *tinnunculi*	Falconiformes: falconid (falcons, kestrel); Accipitriformes: accipitrid (buzzards, eagles, harriers, kites, sparrowhawks)	halteridial-circum-nuclear		Holarctic, Ethiopian, Oriental
H. (*P.*) *trochili*	Apodiformes: apodid(hummingbirds)	halteridial		Neotropical
H. (*P.*) *trogonis*	Trogoniformes: trogonid (trogons)	halteridial		Oriental, Neotropical
H. (*P.*) *tyranni*	Passeriformes: tyrannid (flycatchers)	halteridial		Neotropical, Nearctic
H. (*P.*) *undulatus*	Coliiformes: coliid (mousebirds)	halteridial to circum-nuclear		Ethiopian
H. (*P.*) *upupae*	Bucerotiformes: upupid (hoopoes)	halteridial		Oriental, South Palearctic
H. (*P.*) *uraeginthus*	Passeriformes: estrildid (cordonbleus)	rhabdosomal		Oriental
H. (*P.*) *vangii*	Passeriformes: vangid (vangas)	halteridial		African
H. (*P.*) *velans*	Piciformes: picid (woodpeckers, wrynecks)	circum-nuclear	Diptera: ceratopogonid (*Culicoides sphagnumensis, stilobezzioides*)	Nearctic, Oriental
H. vilhenai *nomen dubium*	Anseriformes: anatid (spur-winged goose)			African
H. (*P.*) *vireonis*	Passeriformes: vireonid (vireos)	halteridial		Neotropical, Nearctic
H. (*P.*) *witti*	Apodiformes: apodid (hummingbirds)	halteridial		Neotropical (Jamaica)
H. (*P.*) *xantholaemae*	Piciformes: capitonid (barbets)	halteridial		Oriental, Ethiopian
H. (*P.*) *zosteropis* (syn. *johnstoni*)	Passeriformes: parulid (warblers), rhipidurid (fantails), zosteropid (white-	halteridial		Oriental, Ethiopian, Australasian,

	eyes)			Palearctic

**incertae sedis* (uncertain placement), *species inquirenda* (doubtful identity requiring further investigation), *nomen dubium* (doubtful name), *nomen nudum* (name unavailable due to lack of description, reference or indication)

Parasite morphology: *Haemoproteus* spp. form 6 different types of developmental stages: meronts and gametocytes in avian hosts; and gametes, ookinetes, oocysts and sporozoites in insect vectors. In birds, there are at least 2 generations of exo-erythrocytic merogony in host tissues before the appearance of gametocytes in blood cells (there is no erythrocytic merogony). Invading sporozoites form primary (first-generation) meronts which appear as basophilic bodies (10-100 µm) which become multinucleated as they divide internally to form numerous elongate merozoites (5-6 µm). Most meronts are rounded, but some may be elongate, vermiform, branched or even split into separate parts (cytomeres) containing several nuclei. Secondary meronts are similar in appearance and location, and further generations may persist contributing to relapses and chronic infections. Some parasite species also produce large ellipsoidal megalomeronts (200-500 µm) surrounded by thick hyaline walls and producing hundreds of small rounded merozoites (~1 µm). Merozoites from second and subsequent meront generations invade erythrocytes and transform directly into gametocytes (10-24 x 2-4 µm) which are often crescentic and curved around the host cell nucleus, although 5 morphogroups have been recognized: halteridial, microhalteridial (bilobulated), circum-nuclear, rhabdosomal (elongate) and discosomal (discoidal). Gametocytes are uninucleated and contain granular cytoplasm with brown-black pigment granules (haemozoin) as well as some violet volutin granules. They exhibit sexual dimorphism: with female macrogametocytes having more intensive cytoplasmic staining (due to abundant ribosomes), a compact nucleus with a nucleolus, and numerous scattered pigment granules; and male microgametocytes having a paler cytoplasm, a diffuse nucleus without a nucleolus, and pigment granules usually gather at either end. In insect vectors, microgametocytes produce and release 5-20 slender (10-18 µm) microgametes (process known as exflagellation) while macrogametocytes mature to form single robust (6-7 µm) macrogametes. Fertilization produces a motile zygote (ookinete) and becomes elongated (8-18 µm), develops a distal residual body containing most of the pigment granules, and those of some species may form short blunt or long digitiform outgrowths of the wall to aid attachment. The ookinete transforms into a rounded oocyst which undergoes sporogony to produce numerous sporozoites from germinative centres. In midge vectors, *Haemoproteus* (*Parahaemoproteus*) spp. form smaller oocysts (< 20 µm) that have one germinative centre producing < 100 long (> 10 µm) sporozoites. In hippoboscid vectors, *Haemoproteus* (*Haemoproteus*) spp. form larger oocysts (> 20 µm) with multiple germinative centres producing > 100 shorter (< 10 µm) sporozoites.

Site of infection: In birds, the parasites undergo several cycles of exoerythrocytic merogony in vascular endothelial cells and then fixed macrophages in various organs (mainly the lungs, liver and spleen, sometimes the kidneys, heart, skeletal muscles and skin). Some species also form large megalomeronts, usually within capillary endothelial cells and myofibroblasts in striated musculature (skeletal and cardiac muscles). Merozoites released into the circulation invade erythrocytes and develop into gametocytes. Around 180 haemoproteid species have been found in birds belonging to 90 families in 23 orders: including 6 *Haemoproteus* (*Haemoproteus*) spp. described in birds belonging to 12 families in 5 orders (mainly Columbiformes); and 170 *Haemoproteus* (*Parahaemoproteus*) spp. in birds belonging to 82 families in 22 orders (mainly Passeriformes (45 families)). It has been estimated from discordant data-base records that haemoproteid infections have so far been found in around 2,200 bird species (around 20% of the global avifauna). The host specificities of the different parasite species remain to be established. Epidemiological observations and some experimental transmission studies suggest specificity may operate at level of bird family (or even order), but there are numerous contradictory findings suggesting it may wider than expected. In dipteran vectors, gametes and fertilization occur in the gut while the motile ookinete penetrates the peritrophic membrane and develops into an oocyst under the basal lamina, ultimately producing sporozoites and releasing them into the haemocoel where they invade the salivary glands. Little is known about the extent of vector specificity for most parasite species, but it is an important distinguishing character for differentiating subgenera, with *Haemoproteus* (*Haemoproteus*) spp. utilizing hippoboscid louse flies**,** and *Haemoproteus* (*Parahaemoproteus*) spp. using ceratopogonid biting midges, sometimes culicid mosquitoes, as vectors.

Pathogenesis: Birds are hosts for both tissue and blood stages of haemoproteid parasites. The proliferative tissue stages (meronts) ultimately result in host cell lysis to liberate parasite progeny, but infections by most species are benign because few meronts are involved and they are small fast transient stages causing little inflammation. The exceptions are those species that form numerous meronts or large megalomeronts which can damage tissue integrity resulting in structural and functional abnormalities. Heavy infections in pigeons have been associated with capillary blockages leading to airsac congestion, pneumonia-like symptoms, hepatosplenomegaly with pigment deposits, anaemia, anorexia, restlessness and occasional deaths, particularly in young squabs. Megalomeronts in ducklings and chickens have caused cardiomyopathies, and infections in turkeys and currawongs have caused seasonal lethal myopathies in several countries. Megalomeronts in other birds, especially parrots, have caused intense inflammation in various tissues and their rupture has been associated with the formation of necrotic nidi, calcificates and myopathies. In contrast, the blood stages (gametocytes) do not proliferate in host cells but reside as persistent transmissive stages. Parasitaemias are usually low (< 0.1%) although higher parasitaemias (up to 30%) may occasionally be found in individual birds but apparently with little effect on host. In some instances, mild anaemia may develop in the course of infection, due not to overt haemolysis but to erythrophagocytosis when infected cells are removed from the circulation by reticuloendothelial cells of the spleen, liver, bone marrow and some other organs. Hepatosplenomegaly may result due to hyperplasia of lymphoid-macrophage cells, and organ rupture may occasionally occur due to accumulations of insoluble pigments. Infections in birds often become chronic, with parasitaemia maintained for weeks-months by successive cycles of merogony. Relapses of infection have also been recorded, often

coincident with the onset of bird reproduction. There is also growing evidence suggesting that subclinical but persistent haemoproteid infections may reduce host fitness by decreasing growth rates (especially around peak parasitaemias), change food acquisition behaviours (birds become more sedentary), altering fright behaviours (hide rather than flight), and affecting migration success (poorer accumulation of migratory fat reserves).

Developmental cycle and mode of transmission: *Haemoproteus* spp. have obligative heteroxenous (2-host) life-cycles involving asexual proliferation in birds (acting as intermediate hosts) and sexual development in dipteran vectors (acting as definitive hosts). Vector-borne transmission occurs when haematophagous dipteran insects feed on bird blood. Sporozoites injected into birds invade endothelial cells in various tissues and undergo asexual multiplication (merogony) by internal division (endogeny) producing numerous merozoites usually within 5 days. The merozoites invade new host cells (often fixed macrophages) and undergo another round of merogony, although some species may also form large megalomeronts in host muscles producing hundreds of merozoites over several weeks. Further merogonous generations may occur in host tissues which facilitates relapses and chronic infections. After at least 2 merogonous cycles, merozoites may then invade host erythrocytes where they do not divide further but transform over 2-6 days into gametocytes (male and female). The prepatent period (time from infection to first appearance of gametocytes) ranges from 11-21 days. The longevity of gametocytes in host erythrocytes is not known, but parasitaemias may persist for long periods (being replenished by merozoites from tissue meronts). Dipteran vectors become infected when they ingest erythrocytes containing gametocytes with their bloodmeals. Although the life-cycles for many parasite species have yet to be determined, studies have implicated different vectors for members of each subgenus. Infections by species in the subgenus *Haemoproteus* are transmitted by hippoboscid louse flies, while those in the subgenus *Parahaemoproteus* are transmitted by ceratopogonid biting midges (one species, *H.* (*P.*) *coatneyi,* has also been reported to develop in culicid mosquitoes). Within the vectors, the ingested gametocytes complete gamete development within the gut, with male microgametocytes exflagellating to produce microgametes which fertilize female macrogametes. The resultant zygote (ookinete) is motile and invades the gut wall to form an oocyst under the basal lamina in the external wall. The oocysts undergo asexual division from germinative centres to produce numerous sporozoites which are released into the haemocoel and invade the salivary glands. In hippoboscid vectors, oocysts are larger and take more than 10 days to produce hundreds of small sporozoites. In midge vectors, oocysts are smaller and take less than 10 days to produce less than 100 long sporozoites (the quicker development and release of sporozoites accommodates the shorter gonadotrophic cycles of these vectors allowing parasites to be ready for transmission the next time the vector feeds). Birds become infected when vectors feed on their blood injecting saliva containing sporozoites into feeding sites (inoculative transmission). Birds vary enormously in their susceptibility/resistance to infection, with younger birds being more susceptible and infections accumulating in birds with higher exposure to vectors. The abundance, distribution and activity of vectors is often a function of climate, with summer rises in populations recorded in warmer regions. In birds that migrate long distances in order to feed and/or breed, studies have shown infections to be more prevalent in feeding sites where birds overwinter rather than breeding sites. Risk factors for infections include bird species that have open nests or ground nests, produce offspring that stay longer in nests, and those that congregate together in large colonies.

Differential diagnosis: Infections may be diagnosed by the direct microscopic detection of intra-erythrocytic gametocytes in fixed thin blood smears stained with Giemsa or Leishman's stains. Multiple serial samples may need to be examined as parasitaemias may be low or intermittent. Merogonous stages may be detected in tissues by the microscopic examination of impression smears or histological sections of tissues/organs collected at autopsy. Several experimental studies have reported some success in maintaining blood samples *in vitro* in moist chambers to induce gametocyte exflagellation, fertilization and ookinete development. Infections may be detected in insect vectors by dissection and examining squash preparations or salivary gland extracts. More recently, great success has been achieved using molecular biological techniques to detect and characterize parasites in birds and vectors following the polymerase chain reaction (PCR) amplification of nuclear (small subunit (18S) ribosomal DNA) and mitochondrial (cytochrome b, cytochrome c oxidase subunits 1 and 3) gene sequences.

Treatment and control: Because most infections in birds are asymptomatic, treatment is usually not required. When clinical disease is apparent, parasites are often present as proliferative meronts within host tissues. Treatment with conventional antimalarial drugs may not be effective as many are not active against exo-erythrocytic tissue stages. However, good success has been reported treating infections in poultry, pigeons and raptors using quinacrine, chloroquine and bupavaquone, and moderate success using atebrine and plasmochine (despite some toxicity issues). Preventive control measures applicable to farmed and aviary birds basically involve screening new stock for infections and isolating birds from vectors by protecting holding facilities using screen barriers, insect traps, topical or environmental insecticides, and eliminating potential breeding sites (clearing moist organic wastes and vegetation).

Haemoproteus

2 subgenera:
H. (*Parahaemoproteus*)
mainly in passeriform birds
with ceratopogonid vectors
H. (*Haemoproteus*) in
columbiform birds with
hippoboscid vectors

heteroxenous (2-host) cycle
vector-borne transmission
(sexual development in invertebrate host)
(asexual development in vertebrate host)



Definitive Hosts (vectors)
(biting midges,
louse flies)

oocyst
(16-50 µm)

sporozoites
(~ 10 µm)

gut

ookinete
(8-18 µm)

fertilization

salivary
gland

gametes

gamonts ingested

sporozoites injected

gametocytes
(10-24 µm)

male

female

meront
(10-100 µm)

exo-erythrocytic
merogony
(endothelia)

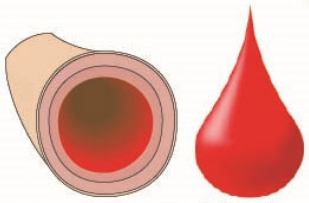
secondary
merogony
(macrophages)

meront
(10-100 µm)

trophozoite
(5-6 µm)

trophozoite
(5-6 µm)

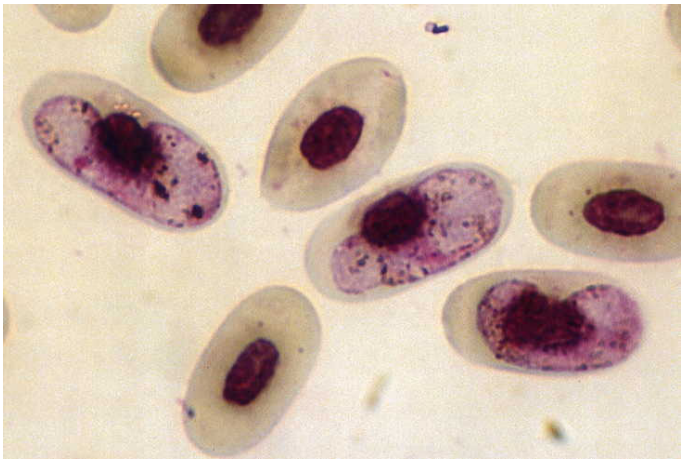
megalomeront
(200-500 µm)
(musculature)



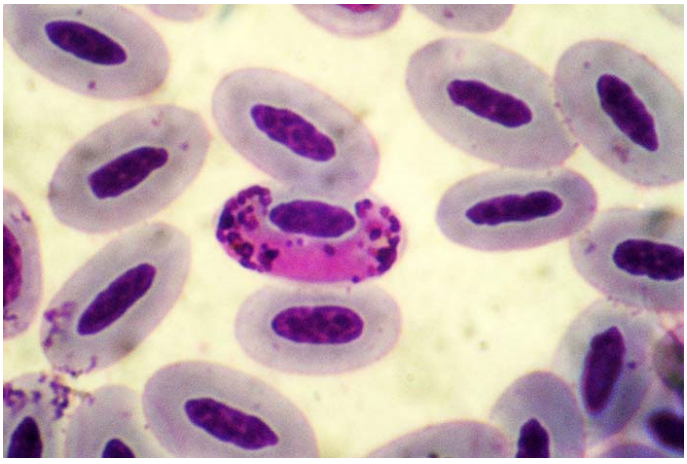
macrophages, blood cells
(rarely anaemia)



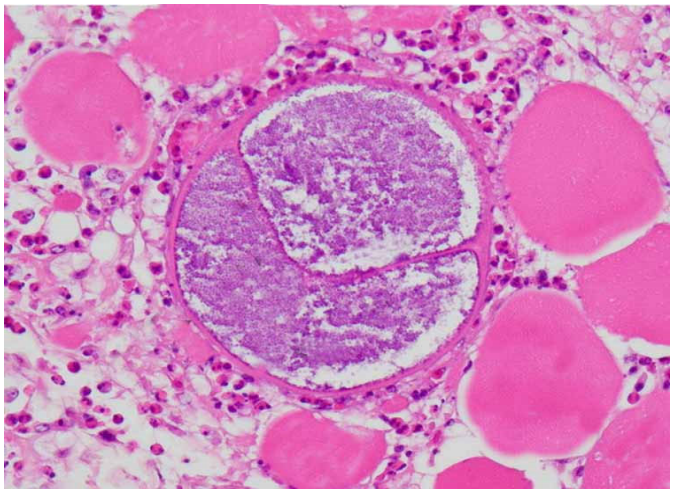
Intermediate Hosts
(birds)



Haemoproteus gametocytes in bird blood



Haemoproteus gametocyte in bird blood



Haemoproteus megalomeront in bird muscle

OTHER HAEMOPROTEID GENERA

Family: Haemoproteidae (merogony in tissues (not in blood cells), haemozoin pigment present in gametocytes)

Haemosporidian genera	No. spp.	Site* of development in vertebrate		Vertebrate hosts	Invertebrate vector
		meronts	gamonts		
Family: Haemoproteidae (merogony in tissues (not in blood cells), haemozoin pigment present in gametocytes)					
Haemoproteus (*Halteridium*)	6	RE cells	rbc	birds	louse flies
Haemoproteus (*Parahaemoproteus*)	150	RE cells	rbc	birds	midges
Johnsprentia	1	RE cells	rbc	flying foxes	
Sprattiella	1	RE cells	rbc	bats	

*rbc = red blood cells (erythrocytes); RE = reticuloendothelial cells

Genus *Johnsprentia*: This monotypic genus was created for an unusual species found in flying foxes in Australia. Large elongate meronts were found in reticuloendothelial cells in the lungs but they did not produce colloid. Rounded pigmented gametocytes ('*vivax*-type') were produced in host erythrocytes and were characterized by the possession of peripheral crescentic nuclei and dense chromophilic cytoplasmic bands. The vectors are unknown.

***Johnsprentia* species**	**Intermediate hosts**	**Gametocyte shape**	**Definitive hosts (vectors)**	**Geographic distribution**
J. copemani	Chiroptera: pteropid (flying fox)	ovoid		Australia

Genus *Sprattiella*: This monotypic genus was also erected for an unusual species found in flying foxes in Australia. This parasite formed small elongate schizonts (without colloid) in reticuloendothelial cells in renal veins, inside hypertrophied cells surrounded by fibrous bright pink substance (up to 2 µm thick). They then formed rounded intra-erythrocytic gametocytes ('*vivax*-type') containing diffuse nuclei and fine pigment granules. The vectors are unknown.

***Sprattiella* species**	**Intermediate hosts**	**Gametocyte shape**	**Definitive hosts (vectors)**	**Geographic distribution**
S. alecto	Chiroptera: pteropid (flying foxes)	ovoid		Australia

Leucocytozoon
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Haematozoa are small blood-borne parasites which undergo merogony (= schizogony) and gamogony (gamete formation) in vertebrates and sporogony (sporozoite formation) in blood-sucking invertebrate vectors. Two main groups are recognised in terrestrial vertebrates: haemosporidia with insect vectors; and piroplasms with arachnid vectors. Haemosporidian parasites multiply in the tissues of vertebrates before forming gamonts in blood cells. Leucocytozoid gamonts occur in leucocytes (sometimes immature erythrocytes) and they do not produce haemozoin pigment. Gametes ingested by insect vectors undergo fertilization in the gut forming motile zygotes (ookinetes) which form oocysts and then thousands of sporozoites which invade the salivary glands. Leucocytozoid infections are transmitted by simuliid black flies and biting midges and are detected in birds, sometimes in association with disease caused by large tissue meronts.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Aconoidasida (asexual stages without conoid)
Order:	Haemosporida (pleomorphic stages in blood of vertebrates, insect vectors. motile zygote (ookinete))
Family:	Leucocytozoidae (schizogony in tissues, gamonts in blood cells, no haemozoin pigment)
Genus:	*Leucocytozoon* (parasitic in tissues/leucocytes of birds)
Species:	various species cause infections in birds
	[*Akiba* effectively *Leucocytozoon caulleryi*]

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic ‘haemococcidia’ in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Haemosporida are spore-forming apicomplexan parasites with heteroxenous life-cycles, with merogony in cells of fixed tissues and in the blood of vertebrate (intermediate) hosts and sporogony in haematophagous invertebrate vectors (definitive hosts). In vertebrate blood cells, haemosporidia develop intracellularly forming sexually dimorphic gametocytes: macrogametocytes (female) with compact nuclei and dark-stained cytoplasm (plentiful ribosomes for protein synthesis), and microgametocytes (male) with larger diffuse nuclei (ready for microgamete production) and pale-staining cytoplasm [a simple pneumonic often used is “blue for girls, pink for boys”]. Gametocytes develop independently (without syzygy) and each microgamont produces about eight flagellated microgametes. Haemozoin granules (residual pigment formed due to incomplete haemoglobin digestion) may or may not be produced in infected erythrocytes. In the vector, the zygote is motile (ookinete) and ultimately forms numerous naked sporozoites (without sporocysts). Around 590 species belonging to some 19 haemosporidian genera have been described from a wide range of mammalian, avian and reptilian hosts around the world.

Four haemosporidian families are recognized mainly on the basis of their developmental cycles and whether haemozoin pigment is produced: namely, Plasmodiidae (merogony in tissues then cyclic in erythrocytes, pigment present); Haemoproteidae (merogony in tissues only, pigment present); Leucocytozoidae (merogony in tissues, pigment absent) and Garniidae (merogony in leucocytes, pigment absent). Vertebrates act as intermediate hosts in which the parasites undergo asexual multiplication within tissues and/or blood cells. Even though parasites begin gamete formation in vertebrates, sexual multiplication is not completed until after they are transmitted to their haematophagous invertebrate vectors, which therefore act as definitive hosts. Two genera are recognized in the family Leucocytozoidae on the basis of multiple biological characters (including morphology, development, host specificity and range): *Leucocytozoon* in birds with simuliid and ceratopogonid vectors; and *Saurocytozoon* in lizards with culicid vectors.

Haemosporidian genera	**No. spp.**	**Site* of development in vertebrate**		**Vertebrate hosts**	**Invertebrate vector**
		meronts	**gamonts**		
Family: Plasmodiidae (merogony in tissues and erythrocytes, haemozoin pigment present)					
Plasmodium	225	liver, rbc	rbc	mammals, birds, reptiles	diptera
Hepatocystis	25	liver	rbc	primates/bats	midges
Polychromophilus	5	viscera	rbc	bats	nycterids
Nycteria	7	liver	rbc	bats	
Biguetiella	1	liver	rbc	bats	
Bioccala	2	RE cells	rbc	bats	
Dionisia	1	liver	rbc	bats	
Rayella	3	liver	rbc	flying squirrels	
Billbraya	1	rbc	rbc	lizards	
Mesnilium	1	RE cells, rbc	rbc	fish	leeches/insects
Haemocystidium (*Simondia*)	33	RE cells	rbc	lizards/tortoises	arthropods
Family: Haemoproteidae (merogony in tissues (not in blood cells), haemozoin pigment present in gametocytes)					
Haemoproteus (*Halteridium*)	6	RE cells	rbc	birds	louse flies
Haemoproteus (*Parahaemoproteus*)	150	RE cells	rbc	birds	midges
Johnsprentia	1	RE cells	rbc	flying foxes	
Sprattiella	1	RE cells	rbc	bats	
Family: Leucocytozoidae (merogony in tissues (not in blood cells), haemozoin pigment absent)					
Leucocytozoon (*Akiba*)	100	RE cells	blood cells	birds	black flies
Saurocytozoon	3	viscera	leucocytes	lizards	mosquitoes
Family: Garniidae (merogony in leucocytes, haemozoin pigment absent)					
Fallisia	12	leucocytes	leucocytes	lizards	arthropods
Garnia	10	leucocytes	leucocytes	lizards	arthropods
Progarnia	1	leucocytes	blood cells	crocodiles	

*rbc = red blood cells (erythrocytes); RE = reticuloendothelial cells

Many molecular phylogenetic studies using nuclear, mitochondrial and apicoplast gene sequences have demonstrated a clear relationship between haemosporidian genera not only with their vertebrate hosts but also their invertebrate vectors. There were clear groupings of *Leucocytozoon* from birds, *Haemoproteus* (*Haemoproteus*) from birds, *Haemoproteus* (*Parahaemoproteus*) from birds, *Plasmodium* from birds and reptiles, *Plasmodium* from rodents and primates, and *Hepatocystis* from bats. These groups were clearly associated with different vectors; namely, simuliids (black-flies), hippoboscids (louse-flies), ceratopogonids (midges), culicine mosquitoes, anopheline mosquitoes, and midges, respectively. There appears to have been a transition from haemosporidia which do not form haemozoin pigment (*Leucocytozoon* in white blood cells) to genera that do form pigment indicating haemoglobin digestion by parasites in red blood cells (*Haemoproteus*, *Plasmodium* and *Hepatocystis*). This was followed by a transition from haemosporidia which undergo schizogony exclusively in host tissues (*Leucocytozoon* and *Haemoproteus*) to those that undergo schizogony in blood cells (*Plasmodium*). While there appears to be a general shift in haemosporidian genera from birds and reptiles to mammals (from nucleated to non-nucleated blood cells), each genus is associated with a particular vector group: black-flies transmitting *Leucocytozoon* to birds; louse-flies transmitting *Haemoproteus* (*Haemoproteus*) to birds; midges transmitting *Haemoproteus* (*Parahaemoproteus*) to birds; culicine mosquitoes transmitting *Plasmodium* to birds and lizards; and anopheline mosquitoes transmitting *Plasmodium* to mammals. The exception to this general trend was *Hepatocystis* which does not undergo blood schizogony and is transmitted to bats by midges.

Around 95 *Leucocytozoon* species have been described in a wide range of bird families and species. They all undergo merogony in internal organs (often forming large meronts divided into cytomeres) before forming gametocytes (lacking pigment) in blood cells (leucocytes and/or erythrocytes). They are transmitted by insect vectors in which they rapidly (3-5 days) form small

nonexpanding oocysts producing < 100 short thick sporozoites. Two *Leucocytozoon* subgenera are recognized: *L.* (*Akiba*) being monotypic with a single species (*L.* (*A.*) *caulleryi*) in galliform birds with biting midge (ceratopogonid) vectors; and *L.* (*Leucocytozoon*) with many species in many bird families with blackfly (simuliid) vectors. Many species appear to have a global distribution, with species richness (biodiversity) being greatest in the Holarctic, Ethiopian and Oriental zoogeographic regions, and poorest in the Australasian and Neotropical regions. Indeed, many infections have been detected in Nearctic migrating birds in their wintering grounds. Host specificity varies from narrow (oioxenous) to broad (stenoxenous), with a few species being host specific (e.g. *L.* (*A.*) *caulleryi* in chickens); some apparently specific for individual bird families or subfamilies (e.g. meleagridids and phasianids in Galliformes, emberizids, icterids and estrildids in Passeriformes) but many thought to be specific for bird orders (esp. Anseriformes, Galliformes, Columbiformes, Charadriiformes, Strigiformes and Passeriformes). Pathogenic *Leucocytozoon* infections have been detected throughout the world, particularly in domestic (ducks, geese, turkeys, chickens) and aviary birds (pigeons, canaries) and occasionally in wild birds (swans, owls, magpies, frogmouths, kestrels).

***Leucocytozoon* species**	**Intermediate hosts (IH)**	**Gametocyte shape (pathogenicity)**	**Definitive hosts (DH) (vectors)**	**Zoogeographic distribution**
Subgenus: *Akiba* (IH: galliform birds, merogony not in hepatocytes; DH: biting midges)				
L. (*A.*) *caulleryi*	Galliformes: phasianid (chicken), numidid (crested guineafowl, helmeted guineafowl)	round (pathogenic, megalomeronts in tissues)	Diptera: ceratopogonid (*Culicoides arakawae, circumscriptus, guttifer, odibilis, schultzei*)	Oriental
Subgenus: *Leucocytozoon* (IH: birds, merogony in hepatocytes; DH: simuliid flies)				
L. (*L.*) *andrewsi*	Galliformes: phasianid (chicken)			cosmopolitan
L. (*L.*) *anellobiae*	Passeriformes: meliphagid (honeyeaters, wattlebirds)	round		Australasian
L. (*L.*) *artamidis*	Passeriformes: artamid (pied butcherbird)	round		Australasian
L. (*L.*) *ardeae*	Pelecaniformes: ardeid (egrets, herons)	round		cosmopolitan
L. (*L.*) *artamidis*	Passeriformes: artamid (pied butcherbird, grey butcherbird, Australian magpie, pied currawong)	round		Australia
L. (*L.*) *audieri*	Accipitriformes: accipitrid (African sea eagle)			African
L. (*L.*) *bacelari*	Accipitriformes: accipitrid (lizard buzzard)			African
L. (*L.*) *balmorali*	Passeriformes: malaconotid (bushshrikes, puffbacks, tchagras), sylviid (warblers)	round, fusiform		Ethiopian
L. (*L.*) *beaurepairei*	Accipitriformes: sagittariid (secretarybird)	fusiform		African
L. (*L.*) *bennetti*	Coraciiformes: coraciid (rollers)	round		Palearctic, African
L. (*L.*) *berestneffi*	Passeriformes: corvid (magpies, jays)	round	Diptera: simuliid (*Simulium aureum, Prosimulium decemarticulatum*)	Holarctic
L. (*L.*) *bonasae*	Galliformes: phasianid (ptarmigans, prairie chicken, prairie grouse, grouse, ruffled grouse, sage grouse, sooty grouse, spruce grouse)			Nearctic
L. (*L.*) *brimonti*	Passeriformes: pyconotid (bulbuls)	round		Oriental, African
L. (*L.*) *bubonis*	Accipitriformes: accipitrid (buzzards, harriers, kites, sparrowhawks); Falconiformes: falconid (falcons)			Holarctic, African
L. (*L.*) *buteonis*	Accipitriformes: accipitrid (common buzzard)	fusiform		Eurasia
L. (*L.*) *californicus*	Falconiformes: falconid (American kestrel)	round		North America

L. (*L.*) *caprimulgi*	Caprimulgiformes: caprimulgid (frogmouths, nightjars)	round, fusiform		Palearctic, Ethiopian, Australasian
L. (*L.*) *centropi*	Cuculiformes: cuculid (coucals, cuckoos)	round		Nearctic, Ethiopian, Oriental
L. (*L.*) *cheissini*	Galliformes: phasianid (snowcocks)	fusiform		Oriental
L. (*L.*) *chloropsidis*	Passeriformes: chloropseid (leafbird)	round		Oriental
L. (*L.*) *circaeti*	Accipitriformes: accipitrid (snake eagle)			Palearctic
L. (*L.*) *coccyzi*	Cuculiformes: cuculid (didric cuckoo, pied cuckoo, yellow-billed cuckoo)			Nearctic
L. (*L.*) *colius*	Coliiformes: coliid (mousebirds)	round		South African
L. (*L.*) *communis* (syn. *bucerotis, dacelo*)	Bucerotiformes: bucerotid (hornbills), upupid (hoopoes, hornbills); Coraciiformes: alcedinid (kingfishers)	round		Ethiopian, Oriental, Australasian, Palearctic
L. (*L.*) *coraciae*	Coraciiformes: coraciid (rollers)			Oriental
L. (*L.*) *costae*	Galliformes: numidid (grey-breasted helmet guineafowl)			African
L. (*L.*) *danilewskyi* (syn. *L. ziemanni*)	Strigiformes: strigid (boobooks, eagle-owls, eared owls, hawk owls, little owls, pygmy owls, scops owls, wood owls), tytonid (barn owls); Accipitriformes: accipitrid (buzzards, eagles, harriers, kites, sparrowhawks); Falconiformes: falconid (falcons); Passeriformes: fringillid (grosbeaks), motacillid (pipits), oriolid (orioles), parid (tits), turdid (blackbirds); Pelecaniformes: ardeid (herons); Bucerotiformes: bucerotid (hornbills); Piciformes: picid (wrynecks); Columbiformes: columbid (doves); Charadriiformes: glareolid (waders)	round, fusiform (megalomeronts in organs)	Diptera: simuliid (*Prosimulium decemarticulatus, Simulium aureum, latipes, vernum*)	cosmopolitan (except Antarctic)
L. (*L.*) *dinizi*	Musophagiformes: musophagid (plaintain-eaters, turacos)	round		Ethiopian
L. (*L.*) *dubreuili* (syn. *francai, nectariniae, seabrae*)	Passeriformes: bombycillid (waxwings), fringillid (finches, grosbeaks), icterid (cowbirds), mimid (catbirds), muscicapid (chats, flycatchers, redstarts, warblers), parid (tits), parulid (ovenbirds), passerid (sparrows), pycnonotid (bulbuls), sturnid (starlings), turdid (bluebirds, robins, robin-chats, thrushes)	round	Diptera: simuliid (*Prosimulium decemarticulatum, Cnephia ornithophila, Simulium aureum, latipes, quebecense, vernum*)	cosmopolitan (except Antarctic)
L. (*L.*) *enriquesi*	Passeriformes: chloropseid (blue-winged leafbird)			Oriental
L. (*L.*) *eurystomi* (syn. *huchzermeyeri*)	Coraciiformes: coraciid (kingfishers, rollers), meropid (bee-eaters)	round, fusiform		Palearctic, Ethiopian, Oriental
L. (*L.*) *francai*	Coraciiformes: coraciid (broad-billed roller)			African
L. (*L.*) *franchini*	Passeriformes: corvid (blue jays, Eurasian jays); Galliformes: phasianid (Barbary partridge)			Holarctic, African
L. (*L.*) *frasci*	Coraciiformes: coraciid (ground rollers)	round		African
L. (*L.*) *fringillinarum* (syn. *bouffardi, cambournaci, deswardti, dutoiti, gentili, icteris, monardi,*	Passeriformes: alaudid (larks), bombycillid (waxwings), cardinalid (cardinals), certhiid (treecreepers), cisticolid (cisticolas, prinias), corvid (jays), emberizid (buntings), estrildid (mannikins, munias, pytilias), fringillid (finches, crossbills, grosbeaks, redpolls),	round	Diptera: simuliid (*Cnephia ornithophilia, Prosimulium (Helodon) decemarticulatus, Simulium*	cosmopolitan (except Antarctic)

muscicapa, parulis, pittae p.p., prionopis, roubaudi, sturni, thraupis, timallae, whitworthi)	glareolid (warblers), hirudinid (swallows), icterid (cowbirds, grackles), laniid (shrikes), malaconotid (boubous), melanocharitid (longbills), meliphagid (friarbirds, honeyeaters, miners, wattlebirds), mimid (catbirds), motacillid (pipits, wagtails), muscicapid (flycatchers, nightingales), nectariniid (sunbirds), oriolid (orioles), paradisaeid (birds-of-paradise), parid (tits), parulid (ovenbirds), passerellid (juncos, towhees), passerid (sparrows), ploceid (weavers, fodies), pycnonotid (bulbuls), sturnid (starlings), thraupid (tanagers), turdid (blackbirds, robins, thrushes), viduid (indigobirds), vireonid (vireos); Musophagiformes: musophagid (turacos); Piciformes: capitonid (barbets)		*anatinum, annulus, aureum, latipes, quebecense*, *vernum, venustum*)	
L. (*L.*) *giovannolai*	Passeriformes: turdid (redwings)			Palearctic
L. (*L.*) *grallariae*	Passeriformes: grallariid (undulated antpitta)	fusiform		South America
L. (*L.*) *greineri*	Passeriformes: nectariniid (sunbirds), philepittid (velvet asity)	round		African
L. (*L.*) *grusi*	Gruiformes: gruid (cranes)	round, fusiform		Nearctic
L. (*L.*) *hamiltoni*	Passeriformes: parid (tits)	symmetrical fusiform		Palearctic
L. (*L.*) *hirundinis*	Passeriformes: hirudinid (swallows)			Holarctic
L. (*L.*) *ibisi*	Pelecaniformes: threskiornithid (white ibis)	round		Australasian
L. (*L.*) *irenis*	Passeriformes: irenid (fairy bluebirds)	round		Oriental
L. (*L.*) *kerandeli*	Galliformes: phasianid (francolins)			African
L. (*L.*) *lairdi*	Passeriformes: vangid (vangas)	round		African
L. (*L.*) *leboeufi* (syn. *ardeolae, iowense*)	Pelecaniformes: ardeid (bitterns, herons, ibis), Ciconiiformes: ciconiid (storks)	round		Holarctic, Ethiopian, Oriental
L. (*L.*) *legeri*	Charadriiformes: scolopacid (snipes, stints, waders, woodcocks)	round		Palearctic
L. (*L.*) *liothricis*	Passeriformes: leiothricid (red-billed leiothrix)	round		Oriental
L. (*L.*) *lovati*	Galliformes: phasianid (grouse)	round, fusiform	Diptera: simuliid (*Simulium aureum, croxtoni, latipes, quebecense, vernum*)	Holarctic
L. (*L.*) *lutzi*	Strigiformes: strigid (pygmy owls)			Neotropical
L. (*L.*) *maccluri*	Passeriformes: turdid (darksided thrush)	round, fusiform		Oriental
L. (*L.*) *macleani* (syn. *francolini*)	Galliformes: phasianid (partridges, peafowl, pheasant, quail, chickens)	round, fusiform (pathogenic in chickens)	Diptera: simuliid (*Simulium metatarsale*)	Palearctic, Ethiopian, Oriental
L. (*L.*) *majoris* [type species] (syn. *bishopi, oriolis, pitae p.p., pycnonoti*)	Passeriformes: corvid (jays), fringillid (finches), glareolid (warblers), laniid (shrikes), mimid (catbirds), nectariniid (sunbirds), parid (tits), parulid (ovenbirds, yellowthroats), passerid (sparrows), pycnonotid (bulbuls), sturnid (starlings), thraupid (tanagers), turdid (blackbirds, thrushes)	round		cosmopolitan (except Neotropical, Antarctic)
L. (*L.*) *mansoni*	Galliformes: phasianid (wood grouse)			Palearctic
L. (*L.*) *marchouxi*	Columbiformes: columbid (doves, pigeons)	round		Holarctic, Ethiopian, Oriental, Neotropical

L. (*L.*) *martini*	Galliformes: phasianid (Oriental peafowl)			Oriental
L. (*L.*) *martyi*	Accipitriformes: accipitrid (Indian goshawk)			Oriental
L. (*L.*) *mathisi*	Accipitriformes: accipitrid (buzzards, sparrowhawks)	fusiform		cosmopolitan
L. (*L.*) *melloi*	Coraciiformes: coraciid (Indian roller)			Oriental
L. (*L.*) *mesnili*	Galliformes: phasianid (francolins, partridges, pheasant, quail); Pterocliformes: pteroclid (sandgrouse); Otidiformes: otidid (bustards); Columbiformes: columbid (doves)			Palearctic, African, Oriental
L. (*L.*) *mirandae*	Passeriformes: corvid (jays), turdid (thrushes); Galliformes: phasianid (grouse)			Palearctic, African, Oriental
L. (*L.*) *molpastis*	Passeriformes: pycnonotid (bulbuls)			Oriental
L. (*L.*) *muratovi*	Accipitriformes: accipitrid (marsh harrier)			African
L. (*L.*) *neavei*	Galliformes: phasianid (francolins, pheasant), numidid (guineafowl); Strigiformes: strigid (eagle-owls, owlets); Accipitriformes: accipitrid (kites)	round, fusiform	Diptera: simuliid (*Simulium adersi, nyasalandicum*)	Ethiopian
L. (*L.*) *neophrontis*	Accipitriformes: accipitrid (vultures)			African
L. (*L.*) *neotropicalis*	Passeriformes: cotingid (green-and-black fruiteater)	fusiform		South America
L. (*L.*) *nycticoraxi*	Pelecaniformes: ardeid (herons)	round, fusiform		Palearctic
L. (*L.*) *nyctyornis* (syn. *alcedinis*)	Coraciiformes: alcedinid (kingfishers), meropid (bee-eaters)	round		Palearctic, Ethiopian, Oriental
L. (*L.*) *otidis*	Otidiformes: otidid (Kori bustard)	round		African
L. (*L.*) *peaolopesi*	Galliformes: phasianid (red-necked spurfowl)	round-fusiform		African
L. (*L.*) *peircei*	Passeriformes: glareolid (warblers)	fusiform		African
L. (*L.*) *phylloscopus*	Passeriformes: phylloscopid (greenish warbler)	round		Palearctic
L. (*L.*) *podargii*	Caprimulgiformes: caprimulgid (tawny frogmouth)	round		Australasian
L. (*L.*) *polynuclearis*	Piciformes: picid (northern flicker, white-headed woodpecker)	round		North America
L. (*L.*) *pogoniuli*	Piciformes: capitonid (barbets)	round		African
L. (*L.*) *pterotenuis*	Passeriformes: grallariid (chestnut-crowned antpitta)	fusiform		South America
L. (*L.*) *quynzae*	Apodiformes: trochilid (amethyst-throated sunangel, mountain avocetbill, Tyrian metaltail, blue-throated starfrontlet)	round		South America
L. (*L.*) *ralli species inquirenda*	Gruiformes: rallid (water rails)	round		Palearctic, African
L. (*L.*) *sabrazesi*	Galliformes: phasianid (chickens, francolins, pheasant)			Oriental, African
L. (*L.*) *sakharoffi* (syn. *laverni*)	Passeriformes: corvid (ravens, treepies, jays, nutcrackers)	round (megalomeronts in tissues)	Diptera: simuliid (*Simulium angustitarse, aureum, latipes, Prosimulium decemarticulatum*)	Holarctic
L. (*L.*) *sanarelli*	Pelecaniformes: ardeid (night herons)	round		Australasian
L. (*L.*) *schoutedeni*	Galliformes: phasianid (chickens)	round (low pathogenicity)	Diptera: simuliid (*Simulium adersi, impukane, nyasalandicum,*	Ethiopian, Nearctic, Oriental

			vorax)	
L. (*L.*) *shaartusicum*	Passeriformes: muscicapid (African stonechats)	round		African
L. (*L.*) *simondi*	Anseriformes: anatid (ducks, eiders, geese, mergansers, swans)	round, fusiform (pathogenic, esp. in young birds, due to anaemia and organ damage)	Diptera: simuliid (*Cnephia ornithophila, Simulium anatinum, fallisi, innocens, parnassum, rendalense, rugglesi, usovae, venustum, vittatum*)	Holarctic
L. (*L.*) *smithi*	Galliformes: phasianid (turkeys, partridges)	round, fusiform (pathogenic in turkeys due to organ congestion	Diptera: simuliid (*Prosimulium hirtipes, Simulium aureum, congareenarum, jenningsi, meridionale, pictipes, slossonae, vittatum*)	Holarctic, Ethiopian
L. (*L.*) *sousadiasi*	Charadriiformes: charadriid (waders)	fusiform		Ethiopian
L. (*L.*) *squamatus* (syn. *capitonis*)	Piciformes: megalaimid (barbets), picid (woodpeckers, wrynecks)	round		Holarctic, Ethiopian, Oriental
L. (*L.*) *struthionis*	Struthioniformes: struthionid (ostriches)	round (pathogenic in chicks)		Ethiopian
L. (*L.*) *tawaki*	Sphenisciformes: spheniscid (penguins)	round	Diptera: simuliid (*Austrosimulium australense, dumbletoni, ungulatum*)	New Zealand, South African
L. (*L.*) *toddi*	Accipitriformes: accipitrid (black eagle, buzzards, harriers, kites, sparrowhawks, vultures); Falconiformes: falconid (eagles, falcons, hawks)	round, fusiform (pathogenic in chicks)	Diptera: simuliid (*Simulium aureum, quebecense, vernum, Prosimulium decemarticulatum*)	Holarctic, Neotropical, Ethiopian, Oriental
L. (*L.*) *trachyphoni*	Piciformes: megalaimid (barbets)	round		African
L. (*L.*) *underhilli*	Passeriformes: sturnid (starlings)	round		African
L. (*L.*) *vandenbrandeni*	Suliformes: sulid (darters); Pelecaniformes: phalacrocoracid (cormorants)	round		Ethiopian, Australasian
L. (*L.*) *vangis*	Passeriformes: vangid (hook-billed vanga)	round		African
L. (*L.*) *zosteropis*	Passeriformes: zosteropid (white-eyes)	round		African, Oriental

A small number of *Saurocytozoon* spp. infect reptiles (lizards) forming meronts in tissues (in lymphocytes?) before forming large gametocytes (without pigment) in peripheral blood (leucocytes) causing gross host cell distortion. They are transmitted by culicine mosquitoes in which large expanding oocysts develop slowly (over 16 days) producing several hundred long thin sporozoites.

***Saurocytozoon* species**	**Intermediate hosts**	**Gametocyte shape**	**Definitive hosts (vectors)**	**Geographic distribution**
S. agamidorum	Sauria: agamid (rock agama)	ovoid		southern Asia
S. mabuyi	Sauria: scincid (sun skinks)	ovoid		South America

S. tupinambi [type species]	Sauria: teiid (gold tegu)	ovoid	Diptera: culicid (*Culex pipiens*)	South America

Parasite morphology: *Leucocytozoon* spp. form 2 main developmental stages in birds (tissue meronts and blood gametocytes) and 4 stages in insect vectors (gametes fusing to form ookinetes that mature to oocysts producing sporozoites). First generation exo-erythrocytic meronts appear as rounded basophilic bodies (10-45 μm) that often invaginate and break into separate parts (cytomeres, or spawning syncytia) containing numerous uninuclear merozoites (1-2 μm). These merozoites may invade blood cells where they transform into small rounded gametocytes (2-5 μm) with cup-like peripheral nuclei (the parasites do not undergo erythrocytic merogony). Merozoites or syncytia (meront fragments with 2 or more nuclei) are also spread via the blood to various organs where they are phagocytosed by macrophages and other reticuloendothelial cells. They may then give rise to large megalomeronts (50-400 μm) which are host cell-parasite complexes with a central body (markedly hypertrophied host cell nucleus) and numerous cytomeres that produce thousands of small merozoites (1 μm). Merozoites from megalomeronts may invade other reticuloendothelial cells and repeat the process (thus contributing to chronic infections and sometimes spring relapses) or they may invade blood cells where they transform into round-fusiform gametocytes (12-22 μm) that displace the host cell nuclei laterally and often cause the host cells to become elongate and spindle-shaped. Some parasite species form round gametocytes, others form fusiform gametocytes, and several form both. None contain haemozoin pigment, but some may have volutin (pseudo-pigment) granules. Gametocytes exhibit sexual dimorphism, with macrogametocytes (female) having a dark-staining cytoplasm (due to abundant ribosomes) and a compact nucleus, while microgametocytes (male) have a pale-staining cytoplasm and a larger diffuse nucleus. In vectors, microgamonts exflagellate producing several (up to 8) long thin (20-23 μm) microgametes that fertilize more robust uninucleate macrogametes. The resultant zygote (known as an ookinete) is motile and is elongate and saccular (30 x 4 μm) with a central nucleus and numerous clear cytoplasmic vacuoles. The ookinete develops into a spherical oocyst (9-14 μm) surrounded by capsule-like wall. The oocyst produces numerous (< 100) elongate sporozoites (8 x 1 μm) with one pointed end and the other rounded.

Site of infection: In birds, sporozoites invade hepatocytes in the liver and undergo merogonous proliferation. The parasites then invade immature blood cells (erythrocytes or leucocytes) and develop into gametocytes, or they invade macrophages in host tissues (spleen, lymph nodes, brain, heart, liver, kidney) to form large megaloschizonts. Almost 95 parasite species have been recorded in birds belonging to 23 orders (from 42 passerine families and 33 non-passerine families). Many parasite species appear to have a global distribution, with species richness (biodiversity) being greatest in the Holarctic, Ethiopian and Oriental zoogeographic regions, and poorest in the Australasian and Neotropical regions. The parasite species vary in their host specificity from narrow (oioxenous) to broad (stenoxenous), with a few species being specific for individual host species, some being specific for individual bird families or subfamilies, but many apparently being specific for bird orders. In insect vectors, gametes are formed in the gut, ookinete zygotes move through the gut wall to form oocysts near the basal lamina, and sporozoites are liberated into the haemocoel where they invade the salivary glands. Vectors are known only for some 14 *Leucocytozoon* spp., all using with simuliid blackflies (totaling 34 species in 4 genera, mostly *Simulium* but also some *Austrosimulium, Cnephia* and *Prosimulium* spp.) and the sole exception being *L.* (*Akiba*) *caulleryi* which uses ceratopogonid biting midges (5 species in the genus *Culicoides*).

Pathogenesis: Infections in birds are characterized by the merogonous proliferation of parasites in host tissues leading to the carriage of gametocytes in blood cells. Tissue stages are transient but ultimately lyse host cells sometimes causing disruptive lesions with variable inflammation, while blood stages persist as transmissive stages until infected cells are removed or degenerate. The development of tissue meronts is often asynchronous, with different stages linked to variable rates of tissue penetration and multiplication. Most infections are asymptomatic or subclinical and have not been associated with clinical disease. However, the occurrence of multiple meronts (especially megalomeronts) may cause mild-severe disease (leucocytozoonosis) characterized by small necrotic or large space-occupying lesions, impedance of blood flow, ischaemia, focal haemorrhages due to burst capillaries (disease sometimes called haemorrhagic fever), inflammation with cellular infiltrates (macrophages, plasma cells, heterophils) and eventual fibrosis and calcification. Clinical signs exhibited by birds vary depending on the tissues/organs involved, but have included anaemia, leucocytosis, hepatosplenomegaly (but no pigment accumulation), haemorrhages, anaemia, respiratory difficulties, diarrhoea, myositis, listlessness, lethargy, anorexia, emaciation, debilitation, convulsions, paralysis, and death. In contrast, blood stages have rarely been associated with pathogenic changes although they may contribute to anaemic conditions, less due to haemolysis but more due to the erythrophagocytosis of infected cells by reticuloendothelial cells in the haemopoetic system. Anaemia may also be exacerbated by the phagocytosis of uninfected cells due to the appearance of an anti-erythrocyte factor in plasma which increases their osmotic fragility with subsequent haemolysis. Several parasite species are highly pathogenic in domestic poultry and waterfowl with outbreaks of disease causing significant economic losses in chicken, turkey, goose and duck production. Occasional epizootics have been reported in free-range wild birds, including illness and deaths in swans, geese, ducks and weaver finches. There are few outbreaks in zoo or aviary birds possibly due to the lower abundance of natural vectors, but some clinical cases have been associated with translocations of exotic bird species. In general, infections may occur in birds of all ages: young birds are more susceptible but older birds have more sustained exposure to vectors. Studies have suggested that even subclinical infections in young birds may affect their productivity (reduced growth rates, fewer eggs) and fitness (reduced mating intensity, and delayed migration). Several studies have also indicated that infections in simuliid blackflies may reduce vector fitness and competence as evidenced by shorter lifespans. Bird species at greatest risk of infection are those with long nesting periods, open or ground nests, close proximity to aquatic breeding sites for blackfly vectors, and gregarious or flocking behaviours. While

infections may last months following single challenge, persistent exo-erythrocytic tissue stages may lead to intermittent relapses of parasitaemia and the development of chronic infections, but at the same time may provide some protection from disease through the development of premunitive immunity. In countries with temperate climates, relapses tend to occur in the spring and have tentatively been associated host sex hormone changes at the onset of breeding.

Developmental cycle and mode of transmission: *Leucocytozoon* spp. have obligate heteroxenous (2-host) life-cycles with transmission occurring between vertebrate intermediate hosts (birds) and invertebrate definitive hosts (haematophagous dipteran insects). Transmission occurs via vector bite during blood feeding. Most species utilize blackflies (simuliids) as vectors, while one species uses biting midges (ceratopogonids). Sporozoites injected into birds by blood-feeding vectors invade hepatocytes and form first-generation exo-erythrocytic meronts over 4-5 days. The meronts undergo asexual internal division forming separate cytomeres (spawning syncytia) that produce numerous merozoites which are released into the circulation when the mature meronts bursts the host cell. The merozoites may invade other hepatocytes and undergo further merogonous division, or they may invade red blood cells (erythroblasts and erythrocytes) and form small rounded gametocytes over 5 days (no merogony in blood cells). In some parasite species, merozoites or syncytia (meront fragments with 2 or more nuclei) may infect macrophages and reticuloendothelial cells in host tissues forming large exo-erythrocytic megalomeronts which develop slowly to produce thousands of merozoites. These merozoites may periodically lead to the development of more megalomeronts (contributing to spring relapses and chronic infections) or they may invade white blood cells (lymphocytes and other mononuclear leucocytes) and form large fusiform gametocytes. Several parasite species have been observed to exhibit diurnal cycles of parasitaemia (peaking during the daytime). Infections are transmitted to simuliid black flies when they ingest blood cells containing gametocytes when feeding on bird blood. Gametocytes complete gamete formation in the gut with microgametes fertilizing macrogametes over 5 days to produce motile zygotes. These ookinetes penetrate the gut peritrophic membrane and form oocysts near the basal lamina without bulging into the haemocoel. The oocysts mature over 7-18 days and produce numerous sporozoites (< 100) that are released into the haemocoel where they invade the salivary glands or enter the proboscis directly. Sporozoites are injected into birds when the vector feeds on blood (inoculative transmission). Studies have noted differences in vector competence and specificity depending on their feeding specializations (mammals or birds as preferred hosts), vertical distribution (ground-dwelling or tree canopy), temporal abundance (seasonal or year-round) and prevailing climatic conditions (warm weather in high latitudes, or humid periods following rains). It is noteworthy that many infections have been detected in Nearctic migrating birds in their wintering grounds.

Differential diagnosis: Infections are diagnosed by the direct microscopic detection of gametocytes in blood cells in thin blood smears stained with any of the Romanowsky's stains, notably Giemsa. It is recommended that multiple serial blood samples be examined to detect low or intermittent parasitaemias. Tissue meronts or megalomeronts may be detected following autopsy by the microscopic examination of tissue impression smears or histological sections. The identification of individual parasite species is difficult due to the pleomorphy demonstrated by many stages and their ready deformation during processing, the high over-lapping inter-specific variability in many characters, and differences in their developmental cycles (only some form megalomeronts, and they may form fusiform or rounded gametocytes, or both). Vectors may also be trapped and examined for infections by oocysts and sporozoites by dissection and microscopic examination of gut or salivary gland preparations. Several immunoserological tests (latex agglutination, enzyme immunoassays) have been used experimentally to monitor specific antibody responses in birds, but little is known about their sensitivity or specificity. Molecular biological techniques have been used to detect and characterize parasites by the polymerase chain reaction (PCR) amplification of nuclear (small subunit (18S) ribosomal DNA) and mitochondrial (cytochrome b) gene sequences.

Treatment and control: Most clinical infections are detected after considerable damage has been wrought by parasite proliferative stages in vital organs of the host, so chemotherapeutic (curative) treatments have not been very successful. Several antiprotozoal (antimalarial and coccidiostatic) drugs have been found to be effective in reducing rates of infection, parasitaemia and disease when used for chemoprophylactic (preventive) purposes in poultry houses or aviaries as food or water additives, including sulphonamides, pyrimethamine, trimethoprim-sulfamethoxazole, sulphadimethoxine, furazolidone, quinacrine and clopidol. Other preventive measures have centred around vector control by protecting birds using insect screens and topical or environmental insecticides. Experimental vaccination studies have reported good protection in chickens immunized with recombinant R7 protein from *L.* (*Akiba*) *caulleryi* which elicited strong humoral antibody responses.

Leucocytozoon

2 subgenera:
L. (*Akiba*) in galliform birds with ceratopogonid vectors
L. (*Leucocytozoon*) in many bird families with simuliid blackfly vectors

heteroxenous (2-host) cycle
vector-borne transmission
(sexual development in invertebrate host)
(asexual development in vertebrate host)



Definitive Hosts (vectors)
(blackflies, biting midges)

oocyst
(9-14 µm)

sporozoites
(~ 8 µm)

gut

ookinete
(30 µm)

fertilization

gametes

salivary gland

gametocytes ingested

sporozoites injected

male female

erythrocytes

round gametocytes
(2-5 µm)

meront
(10-45 µm)

liver merogony
(hepatocytes)

trophozoite
(1-2 µm)

male female

leucocytes

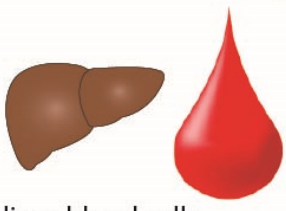
fusiform gametocytes
(10-22 µm)

megalomeront
(50-400 µm)
(internal tissues)

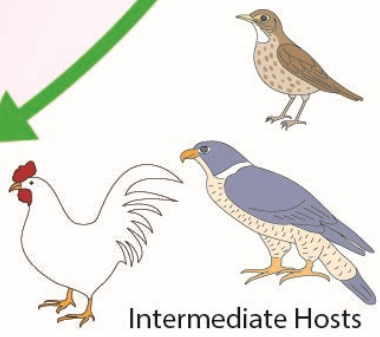
tissue merogony
(macrophages)

syncytia
(1-5 µm)

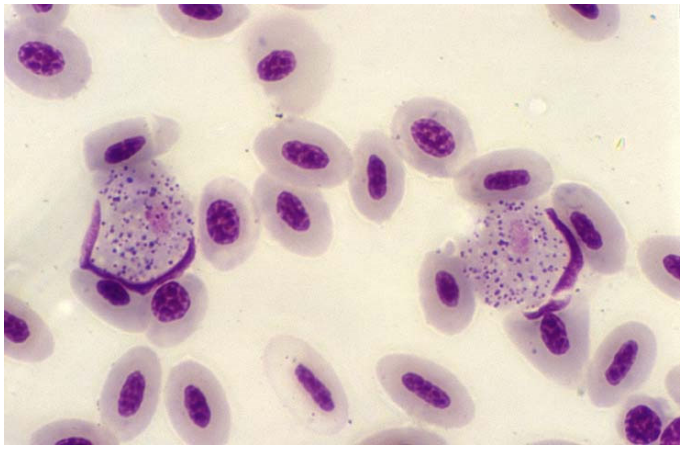
meronts often divided internally into cytomeres



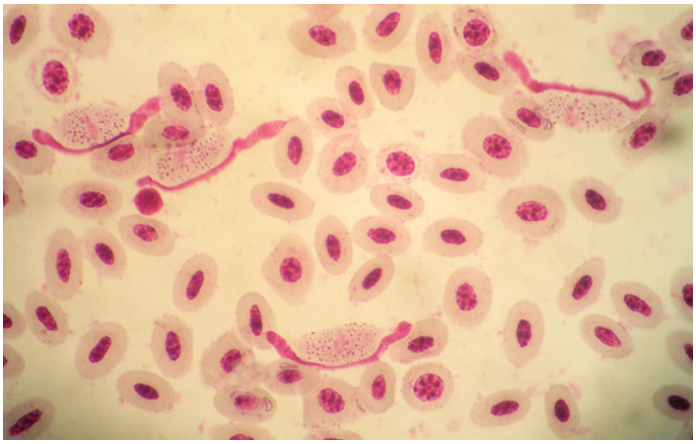
liver, blood cells
(sometimes necrotic lesions, ischaemia)



Intermediate Hosts
(birds)



Leucocytozoon round gametocytes in bird blood



Leucocytozoon fusiform gametocytes in bird blood



Leucocytozoon megalomeront in bird tissues

Babesia
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Haematozoa are small blood-borne parasites which undergo merogony (= schizogony) and gamogony (gamete formation) in vertebrates and sporogony (sporozoite formation) in blood-sucking invertebrate vectors. Two main groups are recognised in terrestrial vertebrates: haemosporidia with insect vectors; and piroplasms with arachnid vectors. In mammals, piroplasm parasites multiply in blood cells by a form of merogony forming small characteristic pear-shaped merozoites. When ingested by ixodid ticks, the parasites form unique paired bodies (strahlenkorper) which give rise to numerous schizonts leading to the production of numerous sporozoites in the salivary glands. Infections persist in ticks during metamorphosis (trans-stadial transmission) and are passed by female ticks to their progeny (trans-ovarian transmission). Many *Babesia* spp. have been detected in mammalian hosts and have been associated with severe disease syndromes (tick fevers).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria)
Group: Alveolata (with cortical alveoli)
Phylum: Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class: Aconoidasida (asexual stages without conoid)
Order: Piroplasmida (pear-shaped stages in blood cells of vertebrates, tick vectors)
Family: Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission in ticks)
Genus: *Babesia* (mammals, erythrocytes, indirect (ixodid tick vectors))
Species: various species cause tick fever (babesiosis) in mammals

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic ‘haemococcidia’ in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Piroplasms undergo unique 'sexual' reproduction involving pairing of ray-bodies (Strahlenkorper) in tick 'vectors' (making them definitive hosts) and then asexual developmental (merogony) in erythrocytes, and sometimes other circulating and fixed cells, in vertebrates (making them intermediate hosts). They differ from other blood-borne Apicomplexa (haemosporidia and haemococcidia) in that they do not form conoids, oocysts, spores or pseudocysts. Infections by piroplasms have been detected in over 130 species in mammals and in some birds and reptiles. Three families are recognized essentially on the basis of their site of development in their vertebrate hosts: Babesiidae (in erythrocytes of mammals and some birds); Theileridae (in lymphocytes then erythrocytes of mammals); and Haemohormidiidae (in nucleated erythrocytes of reptiles). The parasites undergo trans-stadial transmission in their tick vectors (parasites persist when ticks metamorphose from larvae to nymphs to adults) while some babesiids also undergo trans-ovarian (vertical) transmission (eggs become infected in gravid female ticks).

Piroplasms	No.	Site of development in	Vertebrate	Invertebrate

	spp.	vertebrates		hosts	vectors
		meronts	'gamonts'		
Family: Babesiidae (erythrocytes of mammals and birds)					
Babesia	100	erythrocytes	erythrocytes	mammals, birds	ticks
Family: Theileridae (lymphocytes then erythrocytes of mammals)					
Theileria	15	lymphocytes	erythrocytes	ruminants	ticks
Cytauxzoon	4	vascular endothelia	erythrocytes	carnivores	ticks
Family: Haemohormidiidae (nucleated erythrocytes of reptiles and fish)					
Sauroplasma (*Serpentoplasma*)	3	erythrocytes	erythrocytes	lizards, snakes	ticks?
Haemohormidium (*Haematractidium*)	12	erythrocytes	erythrocytes	tortoises, frogs, fish	leeches

Two broad *Babesia* spp. morphotypes occur in host erythrocytes; some species forming small (1-2 µm) merozoites shorter than the erythrocyte radius (e.g. *B. bovis, B. divergens, B. gibsoni, B.ovis*); and others forming large (2-5 µm) merozoites longer than the erythrocyte radius (e.g. *B. bigemina, B. canis, B. major, B. motasi*). Molecular biological studies on comparative gene sequences have shown that the Babesiidae may be divided into two major clades: *Babesia s.s.* (*sensu stricto,* in the narrowest sense) comprising those species forming two merozoites in the erythrocytes of carnivores and rodents and undergoing trans-stadial and trans-ovarian transmission in ticks (e.g. *B. bovis, B. canis*); and *Babesia s.l.* (*sensu lato,* in the broadest sense) comprising those species forming four merozoites in the erythrocytes of rodents, carnivores and deer and only undergoing trans-stadial transmission in ticks (e.g. *B. microti, B. conradae*). These clades are apparently split by an intermediary *Theileria/Cytauxzoon* clade comprising species which exhibit pre-erythrocytic schizogony before forming four merozoites in erythrocytes in ungulates and felids and undergoing trans-stadial transmission in ticks (e.g. *T. parva, C. felis*).

Babesia infections have been detected in most domestic animals (cattle, sheep, goats, horses, pigs, dogs, cats) and numerous wild animals (over 70 species) and humans. Five species cause tick fever in cattle: two small piroplasms *B. bovis* (syn. *B. argentina, B. berbera*) and *B. divergens*; and three large piroplasms *B. bigemina, B. major* and *B. ovata.* Two species were originally thought to infect horses, large *B. caballi* and small *B. equi*, but the latter was recently re-classified as *Theileria equi* due to the discovery of exo-erythrocytic (intra-lymphocytic) merogony. A similar discovery resulted in *B. microti* from rodents being re-classified as *Theileria microti* (both re-classifications supported by contemporary molecular biological studies). The host specificities of *Babesia* spp. for both vertebrate and invertebrate hosts is variable, but most are stenoxenous with parasite species only infecting closely-related hosts, although zoonotic infections in humans have been attributed to *B. divergens* and *B. venatorum* from ruminants in Europe and *T. microti* from rodents in North America. All parasite species are limited in their distribution in accordance with that of their tick vectors.

Parasite species	Vertebrate hosts	Merozoite size (µm)	Vectors	Distribution
Species in mammals				
B. alberti	Carnivora: hyaenid (spotted hyena)			Africa
B. avicularis	Rodentia: murid (striped zebra mouse, Abyssinian grass rat)			Africa
B. bandicootia	Rodentia: murid (greater bandicoot rat), plus experimentally murid (brown rats, gerbils), cricetid (hamsters)			Asia
B. beliceri	Artiodactyla: bovid (cattle)			Russia
B. bigemina	Artiodactyla: bovid (cattle, buffalo, zebu, yak, bison, sheep, Soemmerring's gazelle), cervid (brocket deer, white-tailed deer)	large (1.5-5.0)	one-host ticks (*Rhipicephalus annulatus, R. australis, R. decoloratus, R. geigyi, R. microplus*), two-host ticks (*R. evertsi*)	Europe, Africa, Asia, Australia, Americas
B. bovis (syn. *B. argentina, B. berbera*) [type species]	Artiodactyla: bovid (cattle, zebu, buffalo), cervid (red deer?, European roe deer, Panama white-tailed deer?)	small (1.0-2.4)	one-host ticks (*Rhipicephalus annulatus, R. australis, R. calcaratus, R. geigyi, R. microplus*), 2-host ticks (*R. bursa*), 3-host ticks (*Ixodes ricinus, I. persulcatus*)	Europe, Africa, Asia, Australia, South & Central America

B. brachyceri	Artiodactyla: bovid (dwarf buffalo)			Africa
B. brasiliensis	Didelphimorphia: didelphid (four-eyed opossums, white-eared opossum, black-eared opossum)			Central and South America
B. brygooi	Afrosoricida: tenrecid (hedgehog tenrecs)			Madagascar
B. caballi	Perissodactyla: equid (horse, donkey, mule, plains zebra)	large (2.0-5.0)	one-host ticks (*Dermacentor albipictus, D. nitens, Hyalomma scupense*), two-host ticks (*Hy. excavatum, Hy. truncatum, Rhipicephalus bursa, R. evertsi*), three-host ticks (*D. marginatus, D. reticulatus, D. silvarum, D. variabilis, R. sanguineus*)	Europe, Asia, Africa, Americas, Australia
B. campana	Rodentia: murid (field mice)			Africa
B. canis canis	Carnivora: canid (dog, raccoon dog, red fox, coyote), plus molecular detection in felid (cat) [haemolytic disease in dogs)	large (2.0-5.0)	three-host ticks (*Dermacentor marginatus, D. reticulatus, D. variabilis, Rhipicephalus sanguineus*)	Europe, now cosmopolitan
B. canis presentii	Carnivora: felid (cat)	large (2.0-5.0)	?	Israel
B. canis rossi (syn. *B. rossi*)	Carnivora: canid (dog, African wild dog) [haemolytic disease]	large (2.0-5.0)	three-host ticks (*Haemaphysalis elliptica* syn. *leachi*)	Southern Africa
B. canis vogeli (syn. *B. vogeli*)	Carnivora: canid (dog) [mild disease]	large (2.0-5.0)	three-host ticks (*Rhipicephalus sanguineus*)	cosmopolitan
B. capreoli	Artiodactyla: cervid (European roe deer, red deer)			Europe
B. cati	Carnivora: felid (cat)	3.0	unknown	South Africa, India
B. cheirogalei	Primates: cheirogaleid (greater dwarf lemur)			Madagascar
B. citelli	Rodentia: sciurid (leopard ground squirrel)			North America
B. civettae	Carnivora: viverrid (African civet)			Africa
B. colesi	Rodentia: murid (wood mouse)			Europe, Africa
B. conradae	Carnivora: canid (dog)	small (1.0-3.0)	three-host ticks (*Dermacentor variabilis, Rhipicephalus sanguineus*)	North America
B. crassa	Artiodactyla: bovid (sheep, and experimentally goats); Primates: hominid (human)		three-host ticks (*Ixodes persulcatus*, *Haemaphysalis concinna*)	Asia
B. cricetuli	Rodentia: cricetid (Daurian hamster)			Eurasia
B. crocidurae	Eulipotyphla: soricid (bicolored shrew, Eurasian shrew)			Africa, Eurasia
B. cynicti	Carnivora: herpestid (yellow mongoose)			Africa
B. decumani	Rodentia: murid (brown rat, and experimentally house mouse)			Africa, Asia
B. divergens	Artiodactyla: bovid (cattle, mouflon), cervid (fallow deer, red deer, reindeer, European roe deer); and splenectomized Rodentia: murid (gerbil); Primates:	small (1.5-2.0)	three-host ticks (*Dermacentor marginatus, Ixodes ricinus, I. persulcatus*)	Western & Central Europe, North Africa

	cercopithecid (rhesus macaque), hominid (chimpanzee, human)			
B. duncani (WA1)	Primates: hominid (human); Artiodactyla: cervid (mule deer), bovid (bighorn sheep); Perissodactyla: equid (horse); Rodentia: cricetid (hamster)	variable (0.5-4.0)	one-host tick (*Dermacentor albipictus*)	North America
B. eliomysi	Rodentia: glirid (garden dormouse)			Europe
B. epsteini	Rodentia: sciurid (little souslik)			Asia
B. equi [now *Theileria equi*]	Perissodactyla: equid (horse, donkey, mule, zebra)	small (2.0-3.0)	one-host ticks (*Dermacentor albipictus, D. nitens, Hyalomma scupense*), two-host ticks (*Hy. anatolicum, Hy. dromedarii, Hy. marginatum, Rhipicephalus bursa, R. evertsi*), three-host ticks (*D. reticulatus, D. variabilis, R. sanguineus*)	Europe, Africa, Asia, Americas
B. ernestoi	Didelphimorpha: didelphid (black-eared opossum, white-eared opossum)			Central and South America
B. felis (syn. *Babesiella felis, Nuttallia felis, Nicollia felis*)	Carnivora: felid (cat, lion, leopard, Sudanese wild cat, puma, American lynx)	small (1.5-3.0)	three-host ticks (*Haemaphysalis elliptica* syn. *leachi*)	Africa, now cosmopolitan
B. foliata	Artiodactyla: bovid (sheep)			India
B. galagolata	Primates: galagid (brown greater galago), and experimentally Primates: cercopithecid (rhesus monkey), Rodentia: murid (brown rat, house mouse, gerbil), cricetid (golden hamster), caviid (guinea pig)			Africa
B. garnhami	Carnivora: viverrid (common genet, Cape genet)			Africa
B. genettae	Carnivora: viverrid (common genet)			Africa
B. gerbilli	Rodentia: murid (great gerbil)			Asia
B. gibsoni	Carnivora: canid (dog, wolf, jackal, dhole, fennec fox), herpestid (mongoose), mustelid (Burmese ferret-badger)	small (1.0-3.0)	three-host ticks (*Haemaphysalis bispinosa, Ha. longicornis, Rhipicephalus sanguineus*), also transmitted transplacentally and via dog bites	India, Asia, North Africa, North America
B. golundae	Rodentia: murid (striped grass mouse)			Africa
B. graingeri	Rodentia: sciurid (striped ground squirrel)			Africa
B. heischi	Carnivora: herpestid (African dwarf mongoose)			Africa
B. herpailuri	Carnivora: felid (jaguarundi, ocelot, cat)	2.3-3.0		Americas
B. herpestedis	Carnivora: herpestid (Egyptian mongoose)			Africa
B. hoarei	Carnivora: herpestid (dwarf mongoose)			Africa
B. hylomysci	Rodentia: murid (Stella wood mouse), plus experimentally Rodentia: murid (Cairo spiny mouse, European wood mouse, Natal multimammate mouse, Mongolian gerbil, Shaw's jird, house mouse, brown rat), cricetid (bank vole, Syrian hamster, Chinese hamster, steppe			Eurasia, Africa

	lemming, deer mouse, hispid cotton rat), sciurid (chipmunk); Primates: cercopithecid (rhesus macaque)			
B. kolzovi	Rodentia: sciurid (little ground squirrel)			Asia
B. legeri	Carnivora: herpestid (water mongoose)			Africa
B. lemniscomysi	Rodentia: murid (striped grass mouse)			Africa
B. leo	Carnivora: felid (lion)			Africa
B. leporis	Lagomorpha: leporid (hare)			Europe
B. lotori	Carnivora: procyonid (raccoon); Rodentia: cricetid (hamster)	small		North America
B. loxodontis	Proboscidea: elephantid (African bush elephant)			Africa
B. macaci	Primates: cercopithecid (long-tailed macaque, rhesus macaque, vervet monkey)			Asia, Africa
B. macropus	Diprotodontia: macropodid (eastern grey kangaroos, agile wallabies)	1-5		Australia
B. major	Artiodactyla: bovid (cattle)	large (1.8-3.0)	three-host ticks (*Haemaphysalis longicornis, Ha. punctata*)	Europe, North Africa, Asia, Americas
B. meles	Carnivora: mustelid (European badger)			Europe
B. mephitis	Carnivora: mephitid (striped skunk)	large		North America
B. meri	Rodentia: murid (fat sand rat), and experimentally murid (spiny mouse, unstriped grass mouse, multimammate mouse, house mouse, rats, gerbil), cricetid (hamster)			
B. merionis	Rodentia: cricetid (gerbils, jirds)			Eurasia
B. microti [now *Theileria microti*]	Rodentia: murid (mice, field mice, white-footed mice, thicket rats), cricetid (deer mice, pack rats, voles, red-backed voles); sciurid (ground squirrels); Eulipotyphla: soricid (shrews, water shrews); Lagomorpha: leporid (cottontail rabbits), occasionally Primates: hominid (human), plus experimentally Rodentia: murid (gerbils, mice, multimammate mice), cricetid (cotton rats, hamsters, lemmings), Primates: cebid (capuchins, squirrel monkeys), cercopithecid (baboons, guenons, macaques), hominid (chimpanzees)	small (1.5-2.0)	three-host ticks (*Ixodes muris, I. ricinus, I. scapularis* syn. *dammini, I. persulcatus, I. ovatus*)	Northern Hemisphere (+ lab model worldwide)
B. missirolii	Carnivora: mustelid (European badger)			Europe
B. motasi	Artiodactyla: bovid (sheep, goat)	large (2.5-4.0)	three-host ticks (*Dermacentor silvarum, Haemaphysalis otophila, Ha. punctata*), two-host ticks (*Rhipicephalus bursa*)	Europe, Middle-East, North Africa, Asia
B. mungo	Carnivora: herpestid (Indian grey mongoose)			India
B. muratovi	Rodentia: murid (house mouse, brown rat), sciurid (long-clawed ground squirrel)			Eurasia
B. muris	Rodentia: murid (brown rat, long-tailed field mouse)			Europe
B. musculi	Rodentia: murid (house mouse)			Europe
B. mustelae	Carnivora: mustelid (European polecat)			Eurasia
B. myoxi	Rodentia: glirid (fat dormouse)			Europe
B.	Carnivora: canid (grey wolf)			Europe

ninakohlyakimovae				
B. ninensis	Eulipotyphla: erinaceid (European hedgehog, Algerian hedgehog, long-eared hedgehog), soricid (Eurasian shrew)			Eurasia
B. occultans	Artiodactyla: bovid (cattle)		two-host ticks (*Hyalomma marginatum*)	Africa
B. odocoilei	Artiodactyla: cervid (white-tailed deer)		three-host ticks (*Ixodes scapularis*)	North America
B. ovata	Artiodactyla: bovid (cattle)	large (3)	three-host ticks (*Haemaphysalis longicornis, Ha. punctata*)	Asia
B. ovis	Artiodactyla: bovid (sheep, goat)	small (1.0-2.5)	three-host ticks (*Dermacentor marginatus, D. reticulatus, Haemaphysalis punctata, Ixodes ricinus, I. persulcatus, Rhipicephalus turanicus*), two-host ticks (*Hyalomma anatolicum, Hy. excavatum, R. bursa, R. evertsi*)	Southern and Eastern Europe, North Africa, Middle-East, Asia
B. pantherae	Carnivora: felid (leopard),and experimentally felid (cat)	small (1.5-2.5)		Africa
B. pattoni	Artiodactyla: cervid (spotted deer, sambar)			Asia
B. perodictici	Primates: lorisid (potto)			Africa
B. perroncitoi	Artiodactyla: suid (pig, boar)	small (0.7-3.0)	three-host ticks (*Dermacentor reticulatus, Rhipicephalus appendiculatus, R. sanguineus*)	Southern Europe, West and Central Africa, Vietnam
B. pitheci	Primates: cercopithecid (guenons, mangabeys, baboons)			Africa
B. procyoni	Carnivora: canid (raccoon dog)			Asia
B. propitheci	Primates: indriid (white sifaka)			Madagascar
B. quadrigernina	Rodentia: ctenodactylid (common gundi)			North Africa
B. ratti	Rodentia: murid (Natal multimammate mouse)			Africa
B. rhombomys	Rodentia: murid (great gerbil)			Central Asia
B. rigolleti	Rodentia: glirid (Huet's dormouse)			Africa
B. rodhaini	Rodentia: murid (rats, mice)	small (1.0-2.5)		Europe, Africa (+ lab model worldwide)
B. roubaudi	Carnivora: mustelid (striped polecat)			Africa
B. tachyglossi	Monotremata: tachyglossid (echidna)			Australia
B. talpae	Eulipotyphla: talpid (European mole)			Europe
B. taterae	Rodentia: murid (Indian gerbil)			India
B. taterillae	Rodentia: murid (Emin's gerbil)			Africa
B. taylori	Artiodactyla: bovid (goat)	small (1.5-2.0)	?	Eurasia
B. thomasi	Hyracoidea: procaviid (rock hyrax, bush hyrax)			Africa
B. thylacis	Peramelemorphia: peramelid (southern brown bandicoot), Dasyuromorphia: dasyurid (quolls)			Australia

B. trautmanni	Artiodactyla: suid (pig)	large (2.5-4.0)	one-host ticks (*Rhipicephalus decloratus*), three-host ticks (*Dermacentor reticulatus, R. appendiculatus, R. sanguineus*)	Southern Europe, Africa, Asia
B. tucotucoi	Rodentia: Ctenomyid (tuco-tuco)			South America
B. vanhoofi	Carnivora: herpestid (common dwarf mongoose)			Africa
B. venatorum	Artiodactyla: cervid (European roe deer), occasionally Primates: hominid (human)	small (1.0-3.0)	three-host ticks (*Ixodes ricinus, I. persulcatus*)	Eurasia
B. vespertilionis	Chiroptera: vespertilionid (common noctule)			Eurasia, Africa
B. vesperugina	Chiroptera: vespertilionid (noctule bats, mouse-eared bats, long-eared bats, pipistrelles)			Eurasia, Africa
B. volgensis	Rodentia: sciurid (yellow ground squirrel)			Central Asia
B. vulpes (syn. *B. microti*-like, *Theileria annae*)	Carnivora: canid (dogs, fox)	small (< 2)	three-host ticks (*Dermacentor reticulatus, Ixodes canisuga, I. hexagonus*, *I. ricinus, Rhipicephalus sanguineus*)	North America, Europe
B. wrighti	Rodentia: sciurid (rock squirrel)			North America
B. yakimovi	Rodentia: sciurid (Siberian chipmunk, Chinese rock squirrel)			Asia
B. zolotarevi	Artiodactyla: bovid (bison)			North America
Species in birds				
B. avium (*incertae sedis*)	Galliformes: phasianid (rock partridges)	2		Iran
B. ardea	Pelecaniformes: ardeid (grey heron)	cruciform		Eurasia
B. balearica	Gruiformes: gruid (black-crowned crane)			Africa
B. bennetti	Charadriiformes: larid (yellow-legged gull)	2.9-4.6		Mediterranean
B. emberizica	Passeriformes: emberizid (buntings)			Asia
B. frugilegica	Passeriformes: corvid (rook, house crow, treepie, chough)			Europe, Asia
B. henryi (*nomem nudum* – possibly rickettsias)	Anseriformes: anatid (swan goose, ducks)	< 1.2		Asia
B. kazachstanica	Passeriformes: alaudid (crested lark)			Eurasia
B. kiwiensis	Apterygiformes: apterygid (kiwis)			Australasian
B. krylovi	Bucerotiformes: upupid (hoopoe)			Afro-Eurasia
B. moshkovskii (*species inquirenda* – other records referable to *B. shortti*)	Accipitriformes: accipitrid (bearded vulture)	rings, tetrads, cruciforms (plus schizonts? in leucocytes and RE cells)		Africa, Eurasia
B. mujunkumica (syn. *socius*)	Passeriformes: passerid (Indian sparrow), ploceid (sociable weavers)	1-2.1 x 0.4-0.5		India, Africa
B. necrophorum (*nomen nudum* – tabulation and mis-translation errors)	Passeriformes: corvid (crows, rooks, jays, magpies, nutcracker), Galliformes: phasianid (grouse), Charadriiformes: scolopacid (woodcock, snipe)	-	-	Russia
B. peircei	Sphenisciformes: spheniscid (jackass penguin)	1.5-4.0		Africa
B. poelea	Suliformes: sulid (boobies)	nr		Melanesia

B. rustica	Passeriformes: passerid (barn swallow, red-rumped swallow)			Afro-Eurasia, Americas
B. shortti	Falconiformes: falconid (kestrels, prairie falcon, saker falcon) [pathogenic]	1.6-2.4 x 0.7-1.0		Europe, North America
B. tropicus (*nomem nudum* – confused description)	Galliformes: phasianid (chickens)			India
Species in reptiles				
B. passeritae	Serpentes: colubrid (Malayan green whipsnake)			Malaya

Parasite morphology: The parasites form pyriform (pear-shaped) bodies in the erythrocytes of vertebrates and vermiform (worm-like) bodies in tissues of their tick vectors. In vertebrates, intraerythrocytic stages appear singly as small round, ovoid or elongate trophozoites (1-4 µm), in pairs as pyriform merozoites (hence the common name piroplasm), or in tetrads as cruciform merozoites (sometimes called Maltese cross forms). Babesial stages do not form haemozoin pigment and they do undergo erythrocytic merogony. Erythrocytic stages are usually basophilic with dense chromatin granules, and some stages form large central vacuoles that gives the piroplasm a ring-shape. Blood stages do not cause alterations in red cell morphology nor produce Maurer's clefts, Schuffner's dots or James's dots (as observed for *Plasmodium* spp.). Individual species are often grouped into 'small *Babesia'* (merozoites 1.0-2.5 µm long) or 'large *Babesia'* (merozoites > 2.5 µm long. In very high parasitaemias, merozoites may also be found occasionally as extracellular forms, either singly or as syncytial structures. Merozoites typically lack a conoid, micropores and mitochondria but possess other apical complex organelles (rhoptries, micronemes, polar rings and subpellicular microtubules). In ticks, some ingested parasites (presumably gametocytes) develop unique anterior arrowhead-shaped organelles (called Strahlenkorper or ray-bodies). These parasites pair up and fuse to form motile kinetes which invade tick body tissues before undergoing division to produce vermiform sporozoites (2-3 µm long) in the salivary glands.

Site of infection: In vertebrates, parasites infect host erythrocytes and undergo transformation to form trophozoites which divide by binary merogony (schizogony) and undergo differentiation to form merozoites. The host cell is ultimately lysed and the merozoites infect new cells, repeating the cycle of development. A total of 126 parasite species have been described: 107 parasite species in over 160 mammalian species (belonging to 39 families in 16 orders); 18 parasite species in over 30 bird species (belonging to 12 orders); and one species in a reptile (colubrid snake). In vectors, parasites form ray-bodies in the gut, ookinetes and sporokinetes in tick tissues, and finally sporonts and sporozoites in the salivary glands. A total of 42 species of ixodid ticks have been identified as vectors, including 24 species of 3-host ticks (belonging to 4 genera), 8 species of 2-host ticks (2 genera) and even 10 species of 1-host ticks (3 genera).

Pathogenesis: Many infections remain asymptomatic or subclinical in healthy individuals, but heavy infections by various species may cause mild-severe disease (called babesiosis or piroplasmosis). Infected animals develop a high persistent fever (commonly known as tick fever) becoming dull, listless and anorexic. Piroplasms affect erythrocyte membrane fragility which can lead to extensive intravascular haemolysis (erythrocyte rupture) producing progressive signs of anaemia. Erythrocyte destruction may be as high as 75% in fatal cases and even milder infections produce severe anaemia (macrocytic, hypochromic). Haemoglobin clearance mechanisms become overloaded, resulting in jaundice, hyperbilirubinuria and haemoglobinuria (red discolouration of the urine, 'red-water' in bovine babesiosis). Haemolysis involves the release of many pharmacologically active agents (e.g. proteolytic enzymes) which affect microcirculation (vasodilatation, increased permeability) leading to hypotension and oedema, and affect blood (viscosity, coagulation, cytoadherence) leading to ischaemia (congestion and degenerative changes in tissues/organs). Infected animals may exhibit diarrhoea, nausea, vomiting, pyrexia, tachycardia, tachypnoea (perhaps dyspnoea), abortion if pregnant, myalgia, muscle tremors, cerebral signs (due to sequestration of infected erythrocytes in cerebral capillaries), ataxia, anorexia, lethargy, fatigue, weakness, wasting, coma and death. Chronically infected animals remain weak, thin and out of condition for several weeks before recovery. Animals that recover are usually immune for life, sometimes thought to be due to complete cure (sterile immunity) but more often associated with the persistence of small numbers of parasites (premunitive immunity). There is an inverse age-resistance to infection and disease, with young cattle being less susceptible than older cattle. There is also a genetic component to resistance, with *Bos taurus* cattle being more susceptible than *Bos indicus* (zebu) cattle. Infections in humans have proven severe and fatal in asplenic or otherwise immuno-compromised individuals, with symptoms appearing 10-20 days after tick bite and presenting as a fulminant febrile haemolytic disease over 9 weeks (with subsequent relapses), characterized by general malaise, then fever, shaking chills, sweating, arthralgias, myalgias, fatigue, weakness, occasional hepatosplenomegaly, jaundice and occasionally retinal infarctions, ecchymoses and petechiae, acute respiratory failure, congestive heart failure, disseminated intravascular coagulation, liver and renal failure and splenic rupture.

Developmental cycle and mode of transmission: Infections are transmitted by ixodid (hard-bodied) ticks which may be one-, two- or three-host ticks. After ticks have fed on infected host blood, some parasites are liberated from ingested erythrocytes in the tick gut and form elongate stages (gametocytes?) with unique arrowhead-shaped organelles (ray-bodies or Strahlenkorper). These bodies pair up (syzygy) and fuse (syngamous fertilization?) to produce a nonmotile zygote which uses its spike-like arrowhead organelle upon contact to invade an epithelial cell and transform into a motile ookinete stage. Ookinetes penetrate the gut wall into the body cavity and invade tick tissues where they form more kinetes (sporokinetes). Sporokinetes undergo trans-stadial transmission, thus infections persist during metamorphosis from larvae to nymphs to adults. Kinetes of some *Babesia* species may also invade the tick ovary and penetrate developing eggs where they divide to form small round organisms. These stages facilitate trans-ovarian transmission, so that nearly all the progeny are born already infected (particularly important process for one-host ticks whose developmental stages do not move between different individual hosts). To complete the cycle, some kinetes eventually invade the salivary glands and form polymorphic multinucleate sporonts (or sporoblasts) which produce hundreds of vermiform sporozoites through a budding process. When the tick next feeds, the sporozoites are injected with tick saliva into the vertebrate host. In this host, *Babesia* parasites do not undergo exo-erythrocytic division in host tissues but directly invade host erythrocytes where they undergo cyclic merogony dividing by binary fission to produce 2-4 characteristic piroplasm merozoites. It has been reported that some merozoites grow slowly and fold to form accordion-like structures which may be pre-gametocytes destined to undergo further development in tick vectors. Infections by a few species have occasionally been transmitted between vertebrate hosts by blood transfusions and infrequently by transplacental or perinatal infection.

Differential diagnosis: A history of tick infestation and clinical signs of fever, anaemia and haemoglobinuria are suggestive of babesiosis (tick fever). Congested abdominal organs, watery blood, haemoglobinaemia, jaundice and dark red urine may be observed at necropsy. Confirmation of diagnosis is conventionally afforded by the detection of intraerythrocytic stages in smears of peripheral blood stained with any of the Romanowsky's stains, notably Giemsa. However, once the acute febrile phase has passed, parasites may be difficult to find as they are rapidly removed from the circulation. Some parasites may be cultured *in vivo* by inoculation into susceptible laboratory animals (golden hamsters, jirds, mice) or *in vitro* by inoculation into autologous blood preparations, but considerable variation has been observed in host susceptibility and culture success. Diagnostic recourse is therefore often made to immunoserological tests to detect specific host antibodies against the parasites (fluorescent-antibody tests, enzyme immunoassays and immunoblotting). Molecular biological techniques have also been developed to detect parasite DNA following the polymerase chain reaction (PCR) amplification of specific gene sequences (18S (small subunit) ribosomal RNA (SSU rRNA), internal transcribed spacers (ITS), beta-tubulin).

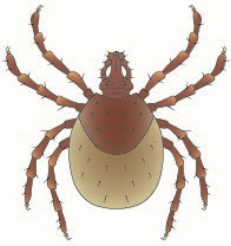
Treatment and control: Timely chemotherapy is generally effective, although the small virulent species (such as *B. bovis*) are usually more difficult to treat than other less aggressive species. One of the first successful treatments for bovine babesiosis was the azonaphthalene dye, trypan blue, but it was not very effective against *B. bovis*. The most commonly used compounds are the diamidines (diminazene diaceturate, imidocarb, amicarbalide), and quinuronium and acridine derivatives. Naphthoquinones (atovaquone), macrolide antibiotics (clindamycin, azithromycin), tetracyclines (oxytetracycline, chlortetracycline) and cinchona alkaloids (quinine) have shown variable effects against human infections, with other interventions including blood exchange transfusion for life-threatening infections, and dialysis in case of renal failure. Cats have been treated with long courses of primaquine, with blood transfusion supplementation if required. Treatment can facilitate recovery, leaving latent infections or complete cure. However, elimination of all parasites may also eliminate premunitive immunity. Because young animals in endemic areas develop infection-immunity (premunition), this has been exploited for immunological control through premunization or chemoimmunization (infect animals then treat them) or vaccination using whole parasites (attenuated strains) or subcellular (subunit) fractions. Several commercially available preparations have proven effective in regional areas, but a universal vaccine is not yet available. Prevention strategies involving tick control programmes (barriers, quarantine, tick treatment, tick-resistant hosts) have been relatively effective in several countries in controlling or eliminating infections in domestic stock. If possible, wild or feral animals acting as reservoir populations for parasites and/or ticks (especially deer populations) should be excluded from farms or treated using medicated foods or acaricidal rubbing posts. Humans at high risk of tick bite (farm workers and hikers) may use long clothing to cover exposed skin and apply repellents to skin or clothing (permethrin, DEET).

Babesia

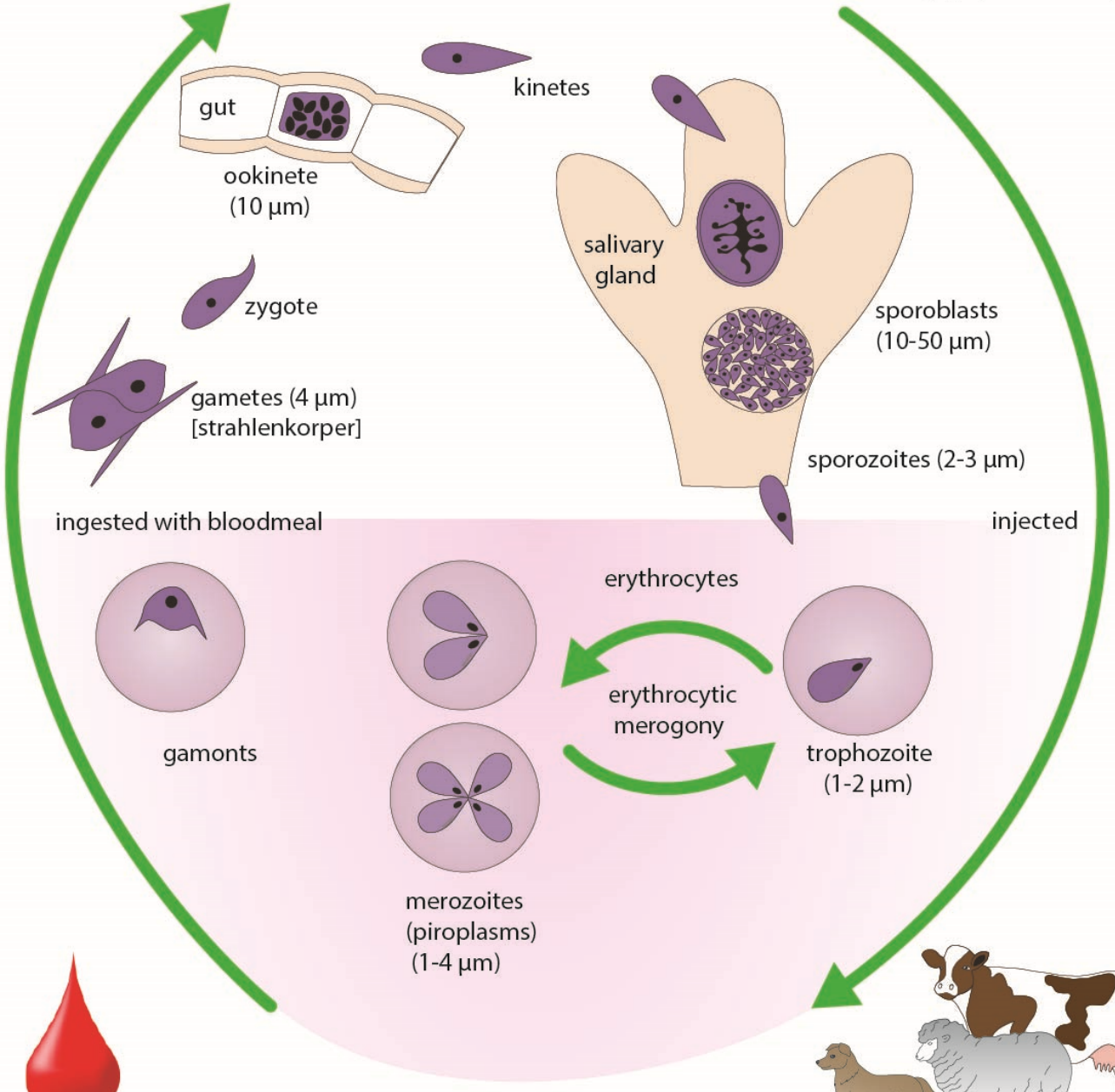
2 major clades:
Babesia s.s.
(forming 2 piroplasms, undergo trans-stadial and trans-ovarian transmission in ticks)
Babesia s.l.
(forming 4 piroplasms, only undergo trans-stadial transmission in ticks)

heteroxenous (2-host) cycle
vector-borne transmission
(sexual development in invertebrate host)
(asexual development in vertebrate host)

trans-stadial and trans-ovarian transmission may occur within tick developmental stages

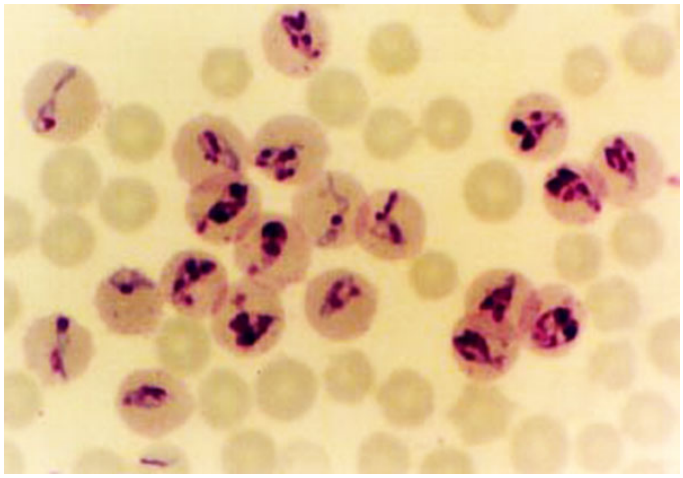


Definitive Hosts (vectors)
(1-, 2-, 3-host ticks)

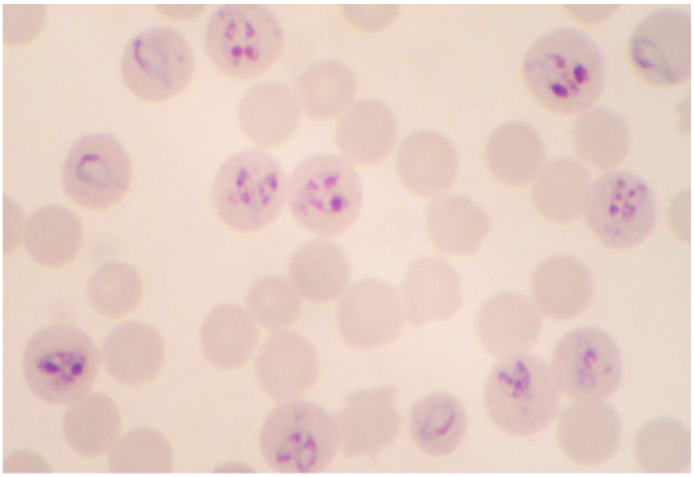


blood cells
(fever, anaemia,
jaundice, ischaemia)

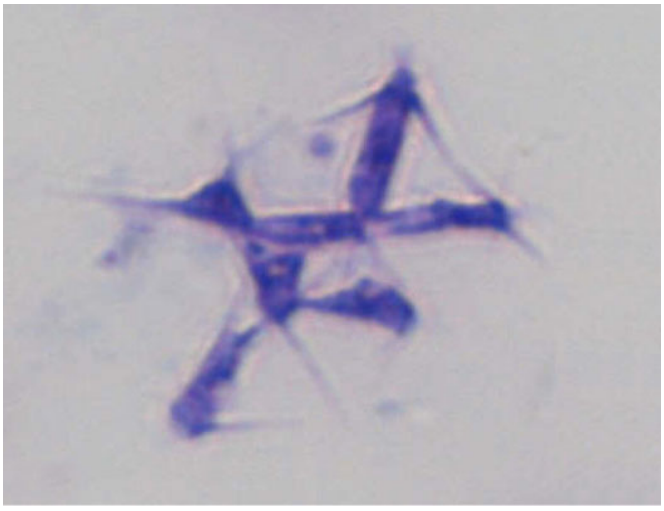
Intermediate Hosts
(mammals, esp. ungulates,
carnivores, rodents)



Babesia piroplasms in cow blood



Babesia piroplasms in cow blood



Babesia ray bodies in tick gut



Tick vector for *Babesia*

Theileria
(protist: apicomplexan)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Apicomplexan cells possess a distinctive apical complex of organelles, comprising a conoid, polar ring, rhoptries, micronemes and subpellicular microtubules, which facilitate entry into host cells as they are obligate intracellular parasites for most of their life-cycles. There are three main apicomplexan groups: gregarines, coccidia and haematozoa. Haematozoa are small blood-borne parasites which undergo merogony (= schizogony) and gamogony (gamete formation) in vertebrates and sporogony (sporozoite formation) in blood-sucking invertebrate vectors. Two main groups are recognised in terrestrial vertebrates: haemosporidia with insect vectors; and piroplasms with arachnid vectors. In mammals, piroplasm parasites multiply in blood cells by a form of merogony forming small characteristic pear-shaped merozoites. Theileriid species develop firstly in lymphocytes (which can undergo clonal expansion) and then in erythrocytes. When ingested by ixodid ticks, the parasites form unique paired bodies (strahlenkorper) which give rise to numerous schizonts leading to the production of numerous sporozoites in the salivary glands. *Theileria* infections persist in ticks during metamorphosis (trans-stadial transmission) but do not undergo vertical (trans-ovarian) transmission. Many *Theileria* spp. have been detected in mammalian hosts and some have been associated with severe disease syndromes (tick fevers).

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Apicomplexa (with apical complex, all parasitic, sexual development (gamogony))
Class:	Aconoidasida (asexual stages without conoid)
Order:	Piroplasmida (pear-shaped stages in blood cells of vertebrates, tick vectors)
Family:	Theileriidae (merogony in leucocytes then erythrocytes, transstadial transmission in ticks)
Genus:	*Theileria* (parasitic in ruminants, leucocytes/erythrocytes, indirect (ixodid tick vectors))
Species:	various species cause tick fever (theileriosis) in mammals

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Over 4,000 species of Apicomplexa have been described as obligate parasites from vertebrate and invertebrate hosts. At some stage in their development, these possess unique cytoskeletal and membrane-bound organelles (conoid, rhoptries, micronemes, subpellicular microtubules) forming an apical complex that facilitates host cell invasion. Apicomplexans undergo cyclic development involving up to three different divisional processes: asexual merogony (schizogony) either by fission (splitting of maternal cell) or endogeny (internal formation of daughter cells); gamogony involving formation of gametes (macrogametes = female, microgametes = male) which undergo fertilization to recombine by fusion (syngamy) with or without paired alignment (syzygy); and sporogony (formation of infective sporozoites).

Three main apicomplexan groups are recognized: haematozoa, gregarines, and coccidia. Haematozoa are small blood-borne parasites in vertebrates which complete their development in blood-sucking invertebrate vectors; with pleomorphic haemosporidia being transmitted by insects and pear-shaped piroplasms being transmitted by ticks. Gregarines are lumen-dwelling parasites that form large extracellular (sometimes septate) gamonts with an anterior holdfast organelle (mucron or epimerite) used to attach to the gut or body cavity of invertebrates. Coccidia are tissue-invading parasites that form small intracellular gamonts (lacking a mucron or epimerite) and most species undergo sexual reproduction by anisogamous fusion without syzygy forming non-motile resistant spores (oocysts) containing infective sporozoites usually confined within secondary spores (sporocysts). Three groups of coccidia are recognized: coelotrophiid coccidia in marine annelids; adeleid coccidia in marine and terrestrial animals (including blood parasites paradoxically known as ‘haemogregarines’ in reptiles and amphibians with leech or arthropod vectors); and eimeriid coccidia in vertebrates. Many eimeriid coccidia are monoxenous gut parasites undergoing faecal-oral transmission, but some are heteroxenous alternating between enteric stages in predators and encysted stages in prey (there are also a few enigmatic ‘haemococcidia’ in the blood of reptiles and birds).

Higher taxonomy	Family	Genera	Hosts	Site	Trans-mission*
Class: Aconoidasida (asexual stages without conoid)					
Subclass: Haematozoa (clade of vector-borne spore-forming haemo-protozoa)					
Order: Haemosporida (pleomorphic blood stages, insect vectors, motile ookinete)	Plasmodiidae (schizogony in tissues then blood cells, haemozoin pigment)	*Plasmodium*	mammals, birds, reptiles	liver, erythrocytes	indirect (v-b)
	Haemoproteidae (schizogony in tissues, haemozoin pigment)	*Haemoproteus*	birds	endothelia, erythrocytes	indirect (v-b)
	Leucocytozoidae (schizogony in tissues, no haemozoin pigment)	*Leucocytozoon* (*Akiba*)	birds	tissues, leucocytes	indirect (v-b)
Order: Piroplasmida (pear-shaped blood stages, tick vectors)	Babesiidae (merogony in erythrocytes, trans-stadial + trans-ovarian transmission)	*Babesia*	mammals	erythrocytes	indirect (v-b)
	Theileriidae (merogony in leucocytes, trans-stadial transmission in ticks)	*Theileria*	ruminants	leucocytes, erythrocytes	indirect (v-b)
Class: Coccidiomorphea [Conoidasida] (with conoid)					
Subclass: Coccidia [Coccidiasina] (small intracellular gamonts)					
Order: Eucoccidiorida (cyclic merogony (schizogony), gamogony, sporogony)					
Suborder: Adeleina (syzygy, 1-4 microgametes)	Haemogregarinidae (ookinete, gamonts in blood cells, invertebrate vectors)	*Haemogregarina*	reptiles, amphibia, fish	tissues, blood	indirect (v-b)
		Hepatozoon	mammals, reptiles	tissues, blood	indirect (v-b)
	Klossiellidae (sporocysts)	*Klossiella*	mammals	kidney	direct (f-o)
Suborder: Eimeriorina (no syzygy, >4 microgametes)	Eimeriidae (monoxenous, endogenous merogony and gamogony, exogenous sporogony)	*Caryospora*	birds, reptiles	gut	direct (f-o)
		Cyclospora	mammals, reptiles	gut	direct (f-o)
		Isospora	birds, reptiles	gut	direct (f-o)
		Eimeria	vertebrates	gut, tissues	direct (f-o)
		Epieimeria	fish	gut	direct (f-o)
		Goussia	fish	gut	direct (f-o)
	Sarcocystidae (heteroxenous, 1:2:4 oocyst:sporocyst:sporozoite configuration)				
	subfamily Cystoisosporinae (monozoic cysts)	*Cystoisospora* (no Stieda bodies)	carnivores, omnivores	gut, tissues	direct (f-o), indirect (p-p)
	subfamily: Sarcocystinae (thick-walls, metrocytes)	*Sarcocystis* (*Frenkelia*)	mammals, birds, reptiles	gut, muscles	indirect (p-p)
	subfamily: Toxoplasmatinae (thin-walled cysts without metrocytes)	*Besnoita*	mammals, reptiles	gut, tissues	indirect (p-p)
		Hammondia	mammals	gut, tissues	indirect (p-p)
		Neospora	herbivores, dogs	gut, tissues	indirect (p-p)
		Toxoplasma	vertebrates, cats	gut, tissues	indirect (p-p)
Class: Gregarinomorphea (gregarines, trophonts with specialized attachment epimerite or mucron, syzygy)					
Subclass: Cryptogregaria (epicellular parasites of vertebrates with feeder organelle but lacking apicoplast)					
	Cryptosporidiidae (naked sporozoites)	*Cryptosporidium*	vertebrates	gut, lungs	direct (f-o)

* f-o = faecal-oral transmission; p-p = predator-prey transmission; v-b = vector-borne transmission.

Piroplasms undergo unique ‘sexual’ reproduction involving pairing of ray-bodies (Strahlenkorper) in tick ‘vectors’ (making them definitive hosts) and then asexual developmental (merogony) in erythrocytes, and sometimes other circulating and fixed cells, in vertebrates (making them intermediate hosts). They differ from other blood-borne Apicomplexa (haemosporidia and haemococcidia) in that they do not form conoids, oocysts, spores or pseudocysts. Infections by piroplasms have been detected in over 130 species in mammals and in some birds and reptiles. Three families are recognized essentially on the basis of their site of development in their vertebrate hosts: Babesiidae (in erythrocytes of mammals and some birds); Theileridae (in lymphocytes then erythrocytes of mammals); and Haemohormidiidae (in nucleated erythrocytes of reptiles). The parasites undergo trans-stadial transmission in their tick vectors (parasites persist when ticks metamorphose from larvae to nymphs to adults) while some babesiids also undergo trans-ovarian (vertical) transmission (eggs become infected in gravid female ticks).

Piroplasms	No. spp.	Site of development in vertebrates		Vertebrate hosts	Invertebrate vectors
		meronts	'gamonts'		
Family: Babesiidae (erythrocytes of mammals and birds)					
Babesia	100	erythrocytes	erythrocytes	mammals, birds	ticks
Family: Theileridae (lymphocytes then erythrocytes of mammals)					
Theileria	15	lymphocytes	erythrocytes	ruminants	ticks
Cytauxzoon	4	vascular endothelia	erythrocytes	carnivores	ticks
Family: Haemohormidiidae (nucleated erythrocytes of reptiles and fish)					
Sauroplasma (*Serpentoplasma*)	3	erythrocytes	erythrocytes	lizards, snakes	ticks?
Haemohormidium (*Haematractidium*)	12	erythrocytes	erythrocytes	tortoises, frogs, fish	leeches

Molecular phylogenetic studies clearly distinguished between theileriid and babesiid piroplasms, babesiids split into two major lineages (*Babesia sensu stricto* and *Babesia sensu lato*) separated by an intermediary *Theileria/Cytauxzoon* lineage. The *Babesia sensu stricto* clade comprised those species which formed two merozoites in the erythrocytes of ruminants, carnivores and rodents, while the *Babesia sensu lato* clade consisted of those species which formed four merozoites in the erythrocytes of rodents, carnivores and deer. Species belonging to the intermediary *Theileria/Cytauxzoon* clade (family Theileridae) formed four merozoites in the erythrocytes of ungulates and felids, but they also exhibited pre-erythrocytic merogony (schizogony) which does not occur for any *Babesia* species. Traditionally, *Theileria* spp. were regarded to form meronts first in lymphocytes then erythrocytes; while *Cytauxzoon* spp. formed meronts in histiocytes (macrophages) then erythrocytes. However, recent studies using molecular characterization techniques have revealed wide variations in the host cell phenotypes infected by developing parasites, with schizonts found in leucocytes (B and T lymphocytes and lymphoblasts), monocyte-macrophage lineages, and fixed histiocytes (macrophages, and reticulo-endothelial cells). Further studies are required to resolve the host cell specificity exhibited by the different species. In general, the most pathogenic *Theileria* spp. are considered to be 'transforming' species as their schizonts initiate a pseudo-neoplastic transformation of the infected lymphocytes leading to hyperproliferation (clonal expansion) with parasites infecting all progeny (parasite replication linked to host cell replication). This allows tremendous amplification of the parasites, often leading to inflammatory intravascular and perivascular lesions with fibrin thrombi, necrosis, haemorrhage and oedema. Benign or mildly pathogenic *Theileria* spp. are usually 'non-transforming' species as their schizonts do not induce leucocyte clonal expansion. All species then form small intra-erythrocytic stages which may be round, oval, rod-like, bacilliform, comma-shaped or pyriform, with highly reduced apical complexes (with rhoptries and micropores but lacking conoids, polar rings, micronemes and usually subpellicular microtubules). *Theileria* spp. are transmitted by ixodid tick vectors in which the parasites complete gamogony in the gut before multiplying in tick tissues to form infective sporozoites in the salivary glands. Over 40 *Theileria* spp. have been reported from a wide range of mammals, particularly in domestic and wild ungulates in Africa, Asia and southern Europe as well as in wild and domestic felids in North America. The distribution of infections often mirrors that of their tick vectors. In particular, 2 species (*T. parva* and *T. annulata*) are responsible for substantial economic losses to the cattle industry in Africa and Eurasia by causing East Coast fever and Mediterranean Coast fever, respectively.

***Theileria* species**	**Vertebrate hosts**	**Disease**	**Vectors**	**Distribution**
T. annae (syn. *B. microti*-like) [now *B. vulpes*]	Carnivora: canid (dog, fox)	anaemia, thrombo-cytopenia	three-host ticks (*Dermacentor reticulatus, Rhipicephalus sanguineus, Ixodes canisuga, I. hexagonus*, *I. ricinus*)	North America, Europe
T. annulata (syn. *T. dispar, turkestanica*)	Artiodactyla: bovid (cattle, Asiatic buffalo)	Mediterranean coast fever, tropical theileriosis	two-host ticks (*Hyalomma marginatum, Hy. truncatum, Hy. turanicum, Hy. anatolicum*), three-host ticks (*Hy. detritum, Hy. dromedarii, Hy. excavatum, Hy. asiaticum, Rhipicephalus turanicus*)	North Africa, Southern Europe, India, China
T. aristotelis	Artiodactyla: cervid (sambar)			Indo-Asia
T. barnetti	Artiodactyla: bovid (Cape buffalo)			Africa
T. brasiliensis	Didelphimorphia: didelphid (quica, black-eared opossum)			Americas
T. brimonti	Pilosa: bradypodid (pale-throated sloth)			South America
T. camelensis	Artiodactyla: camelid (camels)		three-host ticks (*Hyalomma dromedarii*)	?

T. capreoli	Artiodactyla: cervid (European roe deer)			Europe
T. caviae	Rodentia: caviid (guinea pig)			South America
T. cellii	Primates: cercopithecid (toque macaque)			Sri Lanka
T. cervi	Artiodactyla: cervid (fallow deer, wapiti, white-tailed deer, mule deer, sika deer, barking deer, red deer, reindeer)	-	three-host ticks (*Amblyomma americanum*)	Europe, North America, Japan
T. equi	Perissodactyla: equid (horses, donkeys, zebra)	biliary fever, piroplasmosis	one-host ticks (*Dermacentor albipictus, D. nitens, Hyalomma scupense, Rhipicephalus microplus*), two-host ticks (*Hy. anatolicum, Hy. marginatum, Rhipicephalus bursa, R. evertsi*), three-host ticks (*Amblyomma cajennense, D.nuttalli, D. reticulatus, D. variabilis, Hy. detritum, Hy. dromedarii, Hy. lusitanicum, R. sanguineus*)	Southern Europe, Africa, Asia, Americas, Australia
T. felis	Carnivora: felid (cat, bobcat), and experimentally Artiodactyla: bovid (sheep), Lagomorpha: leporid (rabbit)	'cytauxzoonosis'	three-host ticks (*Dermacentor variabilis*)	United States
T. gorgonis	Artiodactyla: bovid (blue wildebeest)			Africa
T. grunnei	Artiodactyla: bovid (yak)			Central Asia
T. haneyi	Perissodactyla: equid (horse)			North America
T. herpestis	Carnivora: herpestid (Egyptian mongoose)			Africa
T. hippotragi	Artiodactyla: bovid (roan antelope)			Africa
T. hirci (syn. *T. lestoquardi*)	Artiodactyla: bovid (sheep, goats)	malignant ovine/caprine theileriosis	two-host ticks (*Hyalomma anatolicum, Rhipicephalus bursa*), three-host ticks (*R. turanicus*)	Mediterranean, Asia Minor
T. jakimovi	Rodentia: sciurid (Siberian chipmunk)			Asia
T. leporis	Lagomorpha: leporid (European hare, Tolai hare)			Eurasia
T. lotozkyi	Artiodactyla: cervid (red deer)			Europe
T. luwenshuni	Artiodactyla: bovid (sheep, goats), cervid (red deer)		three-host ticks (*Haemaphysalis qinghaiensis, longicornis*)	China, Europe
T. marti	Carnivora: mustelid (beech marten)			Eurasia
T. melis	Carnivora: mustelid (European badger)			Europe
T. microti [formerly *Babesia microti*]	Rodentia: murid (mice, field mice, thicket rats), cricetid (deer mice, pack rats, voles, red-backed voles); sciurid (ground squirrels); Eulipotyphla: soricid (shrews, water shrews); Lagomorpha: leporid (cottontail	small (1.5-2.0 μm)	three-host ticks (*Ixodes muris, I. ricinus, I. scapularis* syn. *dammini*)	Northern Hemisphere (+ lab model worldwide)

	rabbits), occasionally Primates: hominid (human), plus experimentally Rodentia: murid (gerbils, mice, multimammate mice), cricetid (cotton rats, hamsters, lemmings), Primates: cebid (capuchins, squirrel monkeys), cercopithecid (baboons, guenons, macaques), hominid (chimpanzees)			
T. mutans	Artiodactyla: bovid (cattle, buffalo, sheep)	benign African theileriosis I	three-host ticks (*Amblyomma hebraeum, A. cohaerens, A. gemma, A. lepidum, A. variegatum*)	Africa, Caribbean
T. ninakohlyakimovae	Carnivora: canid (fox)			Eurasia
T. orientalis (syn. *T. sergenti, T. buffeli*)	Artiodactyla: bovid (cattle, buffalo)	bovine anaemia, oriental theileriosis	three-host ticks (*Amblyomma cohaerens, A. hebraeum, A. moreliae, A. variegatum, Haemaphysalis bispinosa, Ha. douglasi, Ha. longicornis, Ha. megaspinosa, Ixodes ovatus, I. persulcatus*)	Africa, Asia, Japan, India, Australia, North America
T. ornithorhynchi	Monotremata: ornithorhynchid (platypus)		three-host ticks (*Haemaphysalis bancrofti, Ha. longicornis*)	Australia
T. ovis (syn. *T. recondita, T. separata*)	Artiodactyla: bovid (sheep, goats), cervid (deer)	benign ovine theileriosis	one-host ticks (*Ornithodorus lahorensis, O. moubati*), two-host ticks (*Hyalomma marginatum* syn. *plumbeum, Rhipicephalus evertsi, R. bursa*), three-host ticks (*Dermacentor marginatus, Haemaphysalis punctata, Ha. sulcata, Ixodes persulcatus, R. sanguineus, R. turanicus*)	Africa, Europe, India
T. parva [type species] (incl. subspp. *parva*, *bovis*, *lawrencei*) (syn. *T. bovis, lawrencei*)	Artiodactyla: bovid (cattle, Cape buffalo, Asiatic buffalo, waterbuck)	East Coast fever, Corridor disease, January disease	two-host ticks (*Hyalomma anatolicum*), three-host ticks (*Hy. dromedarii, Hy. impressum, Rhipicephalus appendiculatus, R. duttoni, R. zambeziensis, R. simus, R. evertsi*)	East, Central and Southern Africa
T. peramelis	Peramelemorphia: peramelid (bandicoots), Diprotodontia: potoroid (potoroo)		three-host ticks (*Haemaphysalis bancrofti, Ha. longicornis*)	Australia
T. rossica	Rodentia: murid (striped field mouse)			Eurasia
T. stordyi	Artiodactyla: bovid (Grant's gazelle)			Africa
T. strepsicerosi	Artiodactyla: bovid (Cape kudu)			Africa
T. sylvicaprae	Artiodactyla: bovid (common duiker)			Africa
T. tachyglossi	Monotremata: tachyglossid (short-beaked echidna)		three-host ticks (*Haemaphysalis bancrofti, Ha. longicornis*)	Australia
T. talpae	Eulipotyphla: talpid (European mole), soricid (Eurasian shrew),			Eurasia

	Rodentia: cricetid (short-tailed vole)			
T. tarandi	Artiodactyla: cervid (reindeer)			Eurasia, North America
T. taurotragi	Artiodactyla: bovid (common eland, cattle, zebu, sheep, goats)	Turning sickness, benign African theileriosis II	three-host ticks (*Rhipicephalus appendiculatus, R. pulchellus, R. zambeziensis*)	Eastern, Southern and Central Africa
T. tragelaphi	Artiodactyla: bovid (harnessed bushbuck)			Africa
T. uilenbergi	Artiodactyla: bovid (sheep), cervid (red deer, sika deer)		three-host ticks (*Haemaphysalis qinghaiensis*)	China
T. velifera	Artiodactyla: bovid (cattle, buffalo)		three-host ticks (*Amblyomma hebraeum, A. lepidum, A. variegatum*)	South and Central Africa, Caribbean

Parasite morphology: *Theileria* spp. form 2 different types of developmental stages in vertebrates (meronts forming merozoites in lymphocytes, piroplasms in erythrocytes) and 6 types in tick vectors (gamonts, gametes, zygotes, kinetes, sporoblasts and sporozoites). In vertebrates, sporozoites invade host leucocytes and develop into intracytoplasmic trophozoites which form meronts (previously called schizonts, an interchangeable name that persists in much of the literature, but the term meront is used here to denote an asexual divisional process known as merogony). Meronts appear as rounded basophilic syncytial stages that become multinucleate as they divide internally to produce numerous merozoites with irregular eosinophilic nuclei. The meronts may occur singly or in small aggregations in lymphocytes (while those of *Cytauxzoon* are multiple and form large aggregations). Two types of meronts may be formed: macro-meronts (sometimes called Koch's blue bodies) ranging in size from 5-25 μm and producing 5-18 merozoites (0.4-2.0 μm); and micro-meronts ranging in size from 4-10 μm and forming 8-12 merozoites (2 x 1 μm). Merozoites from micro-meronts invade host red blood cells to form pleomorphic intraerythrocytic piroplasms initially within parasitophorous vacuoles but then free in the cytoplasm. Piroplasms are small (1.5-2.0 x 0.5-1.0 μm) and vary in size and shape during infection and between species, being pear-shaped (pyriform), comma-shaped, rod-shaped, oval or round. They have a highly reduced apical complex (but always including rhoptries) and an eccentric nucleus, and they do not contain haemozoin pigment, although some may possess a rectangular veil-like body (crystalline substance) and a bar-like structure connecting them to the host cell membrane. Piroplasms in erythrocytes may or may not divide depending on the species. For example, those of *T. parva* do not divide, while those of *T. orientalis, T. mutans* and *T. equi* do divide into 2 or 4 daughter cells, with those of *T. equi* often forming tetrads (Maltese crosses). In vectors, piroplasms develop into elongate (5-10 μm) stages (gamonts) with small anterior arrowhead-shaped organelles. Gametogenesis is completed to form male and female gametes which pair up (syzygy) and fuse (syngamous fertilization) to produce a transitory nonmotile zygote which invades an epithelial cell. Zygotes are round-elongate stages (4-12 μm) that produce motile pyriform kinetes which penetrate the gut wall and move through the haemolymph to the salivary glands. The kinetes invade specific acinar cells and undergo sporogony to form polymorphic multinucleated sporoblasts (10-40 μm). Kinetes do not invade other tick tissues and do not undergo trans-ovarian transmission. The sporoblasts produce hundreds of small ovoid-pyriform sporozoites (1-1.5 μm) which are released into the saliva of feeding ticks.

Site of infection: In vertebrate (intermediate) hosts, *Theileria* spp. first infect lymphocytes (sometimes macrophages and dendritic cells) in various host organs (esp. spleen, lymph nodes, liver) where they form asexual multiplicative forms (meronts or schizonts producing merozoites). They undergo at least 2 cycles of merogony with macro- and micro-meronts producing numerous merozoites. Merozoites from micro-meronts then invade erythrocytes in the circulation and form piroplasms. Some species exhibit intraerythrocytic merogony yielding uninucleate merozoites which are released by erythrolysis to infect other cells. All species ultimately form gamonts which persist in erythrocytes and are infective to ticks. In tick vectors (definitive hosts), ingested gamonts form gametes in the gut which fuse (fertilization) to produce zygotes that move into the gut wall. These stages transform to kinetes which migrate to the body cavity and haemolymph to invade the salivary glands (specific acinar cells) where they produce numerous sporozoites (infective to vertebrates). Some 44 *Theileria* spp. have been recorded in over 75 mammalian host species, including ungulates (bovids, cervids, camelids, equids), carnivores (canids, felids, mustelids, herpestids), marsupials (didelphids, peramelid, potorid), monotremes (tachyglossid, ornithorhynchid), lagomorphs (leporids), shrews (soricids, talpids), rodents (cricetids, murids, sciurids, caviid), sloths (brachypodid) and primates (cebids, cercopithecids and hominid (including humans)). Infections are particularly common in domestic and wild ungulates in Africa, Asia and southern Europe as well as in wild and domestic felids in North America. All *Theileria* spp. have ixodid tick vectors, mostly three-host ticks (*Amblyomma, Dermacentor, Hyalomma, Rhipicephalus, Haemaphysalis, Ixodes*) but also some two-host ticks (*Hyalomma, Rhipicephalus*) and a few one-host ticks (*Dermacentor, Hyalomma, Rhipicephalus, Ornithodorus*). The distribution of infections by *Theileria* spp. infections often mirrors that of their tick vectors.

Pathogenesis: *Theileria* infections vary significantly in their pathogenicity depending on the parasite species (and strains), the phase of infection (pre-erythrocytic and/or erythrocytic), the duration of infection (acute-chronic), innate host resistance (varies with host

species/breed, age, genetic susceptibility and stress conditions), immune status (acquired immunity), the intensity of infection, and various environmental factors (especially regional and seasonal variations in climate impacting tick burdens). These parasites are unique in that pre-erythrocytic merogony occurs in leucocytes (mostly lymphocytes) and that some species induce host cells to undergo blastogenesis and clonal expansion (pseudo-neoplastic (cancer-like) transformation and immortalization) but in synchrony with parasite proliferation so that all daughter cells are infected. This leads to the rapid multiplication of parasites within the host (up to 10-fold increases approximately every 3 days). The 'transformed' leucocytes become disseminated in peripheral blood and a variety of lymphoid and nonlymphoid organs and may cause overwhelming systemic inflammation and acute fatal theileriosis. *Theileria* spp. are often classified as pathogenic or benign on the basis of whether their meronts induce lymphocyte transformation and proliferation or not (i.e. meront 'transforming' or 'non-transforming'). Pathogenic species typically cause disease by inducing uncontrolled lymphocyte blastogenesis, proliferation and dissemination resulting in widespread lesions, leucocytolysis, acute disease and death (e.g. *T. annulata* causing tropical theileriosis in Africa and Eurasia, *T. parva* causing East Coast fever in Africa). Benign species usually do not induce lymphocyte transformation and have not been associated with disease (e.g. *T. sinensis* and *T. velifera* in cattle, *T. ovis* and *T. separata* in sheep and goats). However, this classification is an oversimplification as some species (and strains) are not consistently pathogenic or benign in mammalian hosts (e.g. non-transforming *T. mutans, T. orientalis* and *T. taurotragi* are occasionally pathogenic in cattle, but disease is due to piroplasm-induced haemolysis and not pre-erythrocytic merogony). *T. taurotragi* may also cause cerebral theileriosis (turning sickness) in some African ungulates due to meronts developing in neural and other tissues. Disease may therefore be caused by the asexual proliferation of meronts in lymphocytes in tissues (e.g. *T. parva*) or the proliferation of piroplasms within erythrocytes in the circulation (e.g. *T. equi, T. orientalis*), or both (e.g. *T. annulata, T. felis, T. lestoquardi*). Acute disease due to meront proliferation is a generalized leucosis-like or lymphoproliferative condition with hyperplasia, oedema and hyperaemia of lymph nodes and lymphoid tissues leading to necrosis, often inducing immunosuppression in the host. The incubation period varies from 7-24 days and the disease may last for 4 days to several weeks. Clinical signs include lymphadenopathy, pyrexia (fevers up to 42°C), petechial and ecchymotic haemorrhages on mucous membranes of the conjunctiva and buccal cavity, haemorrhagic diarrhoea, anorexia, loss of condition, depression, lethargy, weakness, wasting, emaciation and exercise intolerance (some animals may collapse and die if forced to run). Other signs are occasionally observed, including haematuria, anaemia, icterus (jaundice), tachycardia (rapid heartbeat), respiratory difficulties (due to interlobular emphysema and pulmonary oedema), frothy nasal discharges, faint cough, lacrimation (runny eyes), swollen eyelids, corneal opacities and progressive leucopenia. Surviving animals develop acquired protective immunity to disease, but often remain carriers. Persistent chronic infections may lead to decreased growth rates in calves and limit production in adults by reducing weight gain and milk production as well as causing prenatal and postnatal mortalities (abortions and stillbirths are common in pregnant cows). Infections by 'non-transforming' species cause milder disease as piroplasms proliferate in erythrocytes resulting in haemolytic anaemia, jaundice, lethargy, tachycardia and late-term abortion in pregnant animals. The anaemia can be variable depending upon piroplasm multiplication rates, being low in some species (e.g. *T. annulata, T. lestoquardi, T. felis*) but high in others (e.g. *T. mutans, T. orientalis, T. equi*). The incubation period ranges from 10-15 days and the disease may persist for weeks. Common clinical signs include pale mucous membranes, mild fever and progressive loss of condition, but some cases have been reported involving acute septicaemia, laboured breathing with pulmonary oedema and cerebral signs sometimes occasioning death. Many infections may remain subclinical, but stress conditions (due to malnutrition, translocations and concomitant infections) may cause recrudescence of disease. Calves are more susceptible to disease than adult cattle which apparently acquire some protective immunity through prior exposure. However, chronic infections may persist in animals, sometimes for life. Taurine breeds of cattle are more susceptible to infection than zebu or sanga breeds, while wildlife (indigenous ruminants) are often refractory to disease, but may act as reservoirs or long-term carriers of infection.

Developmental cycle and mode of transmission: *Theileria* spp. have obligate heteroxenous (2-host) life-cycles involving asexual proliferation in vertebrates (acting as intermediate hosts) and sexual development in invertebrate vectors (acting as definitive hosts). Transmission occurs via vector bite when haematophagous ixodid ticks feed on vertebrate blood. In mammals, the parasites proliferate in lymphocytes in at least 2 pre-erythrocytic phases of merogony before invading erythrocytes and forming piroplasms. Sporozoites injected with the saliva of feeding ticks first invade select host leucocytes (lymphocytes) within the localized inflammatory reaction of the tick bite or in local lymph nodes. The form macro-meronts within 5-8 days which divide internally to produce numerous merozoites. The intracellular meronts are closely associated with the mitotic spindle apparatus of the lymphocytes, and some species induce host cells to acquire a pseudo-neoplastic phenotype characterized by reversible blast transformation and clonal expansion. The parasites divide at the same time as the host cells thereby perpetuating infections in all daughter cells which become disseminated throughout host tissues. Mature merozoites are released by host cell lysis (leukocytolysis) at which time leucoproliferation decreases significantly. The merozoites then infect new lymphocytes and form micro-meronts which produce merozoites that are able to infect red blood cells transforming into pleomorphic piroplasms within 10-25 days of infection. The piroplasms of some species do not multiply within erythrocytes (e.g. *T. parva*), those of several species do so sporadically (e.g. *T. annulata, T. lestoquardi*, *T. felis*), while those of other species do so prolifically (e.g. *T. orientalis, T. mutans, T. equi*). Eventually, some merozoites invading erythrocytes form spherical-ovoid stages (gamonts) that are infective to tick vectors. In ticks, the gamonts undergo further development within masses of blood cells in the tick gut and are released into the lumen where they complete gametogenesis. Macrogamonts (female) mature to form uninucleate macrogametes, while quadri-nucleate microgamonts (male) divide to form uninucleate microgametes. Gametes pair up and fuse to produce a nonmotile ovoid zygote which stretches and increases in length using an anterior spike upon contact to invade a gut epithelial cell. The zygote undergoes meiotic division and grows in size producing motile pyriform kinetes (often in synchrony with the process of tick moulting). The kinetes have distinct anterior arrowhead-like structures used to penetrate the gut wall into haemocoel and invade the salivary glands.

Parasites undergo trans-stadial transmission in ticks (from larvae to nymphs to adults), but not transovarian transmission. The kinetes infect specialized acinar epithelial cells in the salivary glands and form giant multinucleated sporonts divided into numerous small sporoblasts. When ticks feed and engorge on new hosts, sporoblasts are triggered to complete sporogony and they bud hundreds of small sporozoites into the saliva to be injected into new vertebrate hosts (inoculative transmission). *Theileria* sporozoites only mature and enter the saliva after ticks attach to a host usually for 48–72 hours, but if environmental temperatures are high, sporozoites may develop before attachment and be infective within hours of attachment. Infected ticks may survive on pastures for up to 2 years depending on climatic conditions. Most transmission cycles involve 3-host ticks, but some 2-host and even a few 1-host ticks may act as vectors. Adult ticks transmit more sporozoites than nymphs, so disease often depends on adult tick abundance and activity (more active in warm wet summer months). The distribution of ticks also varies according to climate (temperature and humidity), land management (suitable vegetation types), farming practices (animal husbandry) and the spatial and temporal availability of suitable vertebrate hosts. Other forms of transmission have occasionally been implicated, with some species (e.g. *T. orientalis*) occasionally being mechanically transmitted between vertebrates by routine husbandry practices involving contaminated equipment, and lice and tabanid flies (March flies) also acting as mechanical vectors under experimental conditions.

Differential diagnosis: The clinical diagnosis of theileriosis on the basis of symptomatology, history and vector distribution is difficult due to other confounding vector-borne diseases, such as heartwater, trypanosomiasis, babesiosis, anaplasmosis, malignant catarrhal fever, and contagious bovine pleuropneumonia. Diagnosis is conventionally made by the microscopic detection of parasites in blood cells in fixed thin blood smears or buffy coat preparations stained with Romanowsky stains, usually Giemsa. Test sensitivity is often poor and may fail to detect low parasitaemias such as occur in chronic infections or asymptomatic carriers. Lymph node biopsies may also be collected and smears or sections examined for developing stages, both meronts (including Koch's blue bodies) and piroplasms. Similarly, various tissues and organs (notably spleen, lungs, kidneys) collected at autopsy may be examined for developing stages. Differential diagnosis to species level is difficult as most piroplasms are morphologically similar and meronts are not always present in superficial lymph nodes. Various haematological and biochemical tests may be conducted but their findings are nonspecific but serve to quantify anaemia and organ damage. Various experimental studies have cultured parasites *in vitro* by passaging bovine lymphoid cells in various media (Leibovitz L-15, McCoy and Leibovitz L-15, Dulbecco DMEM, RPMI 1640 or Eagles's minimum essential medium) usually supplemented foetal calf serum. Early workers cultured parasites *in vivo* for xenodiagnosis by feeding laboratory-reared ticks on test animals. Various immunoserological techniques (especially indirect fluorescent antibody tests and enzyme immunoassays) were then developed to detect specific host antibodies against crude, purified or recombinant antigens, with considerable success despite variable sensitivities and some cross-reactivity. More recently, a range of molecular biological techniques have been used to detect and characterize parasites, such as polymerase chain reaction (PCR) amplification, real-time PCR, loop-mediated isothermal (LAMP) amplification, and restriction fragment length polymorphism (RFLP) analyses of a spectacular range of parasite genes, including mitochondrial cytochrome c oxidase 1, nuclear 18S ribosomal DNA and genes encoding specific proteins (*T. parva* repeat gene family (TpR), *T. parva* macromeront GPI-anchored surface protein (p104), *T. parva* sporozoite surface protein (p67), *T. parva* polymorphic immunodominant molecule (PIM), *T. annulata* merozoite surface 1 antigen (Tams1), *T. annulata* macromeront stage protein (TaSP), *T. orientalis* p33/34 antigens, *T. uilenbergi* immunodominant protein (TuIP), and *T. lestoquardi* 30 kDa mero-zoite surface gene (Tlms)). Genotypic studies have revealed considerable variation both between and within species and strains and now provide a vital tool for molecular epidemiological studies tracing infections and characterizing outbreaks.

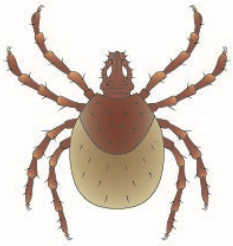
Treatment and control: Few treatments are effective once clinical signs of theileriosis have become apparent, and even then, chemotherapy may not eradicate infections leading to the development of carrier hosts. Treating bovines with naphthoquinones (parvaquone and it derivative buparvaquone) is often successful during the early stages of disease prior to the destruction of lymphoid and haematopoietic tissues. Clinicians have reported some successes using antibiotics (oxytetracycline), urea derivatives (imidocarb), antimalarials (pamaquine, primaquine) or coccidiostats (halofuginone) to treat various infections if applied during the incubation period. Disease control often depends on rigorous health surveillance and vector control. Livestock should be screened for infections before translocations or during quarantine isolation. Tick populations may be managed by various chemical, physical and/or biological control programmes, although the long-term use of acaricides is costly and may lead to the development of drug-resistance in tick populations. Immunological studies have led to the development of several vaccines for *T. parva* and *T. annulata*, using live attenuated parasites (low virulence strains or cultured lines), recombinant subunit antigens (surface proteins) or sporozoite challenge followed by tetracycline treatment (chemo-immunization). Immunized animals developed strong protective immunity against disease, but they sometimes remained carriers of chronic infections. Epidemiological studies have consistently shown indigenous ungulates to be highly resistant to disease while introduced ruminants remain highly susceptible. This suggests native animals have developed a state of enzootic or endemic stability whereby low levels of infection lead to premunitive protective immunity. Care should therefore be taken with treatment and control interventions as they may reduce the force of infection leading to endemic instability and sporadic outbreaks of clinical disease in hitherto resistant host populations.

Theileria

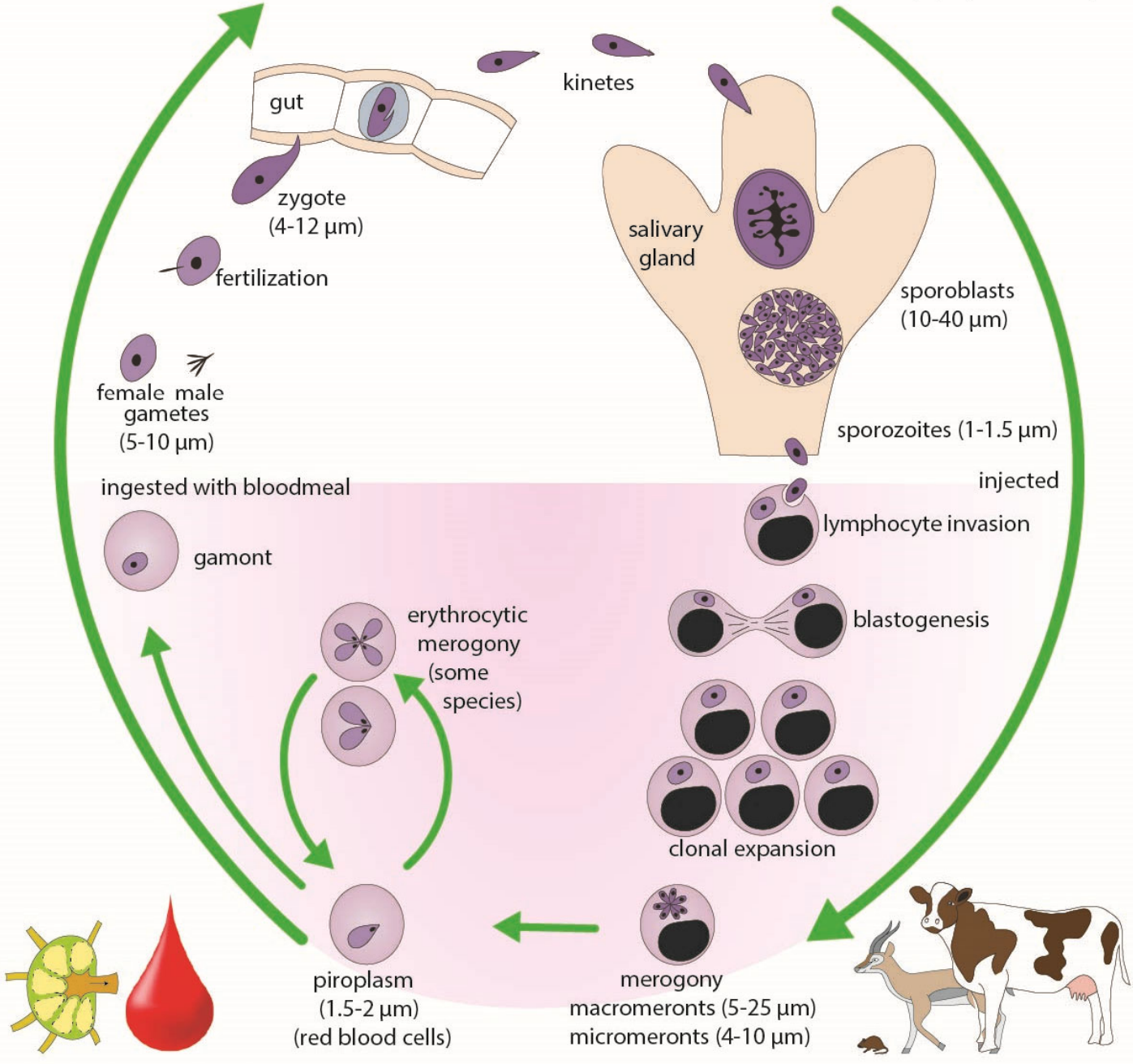
most pathogenic are 'transforming' species as meronts initiate pseudo-neoplastic transformation of infected lymphocytes leading to proliferation (parasites infect all progeny cells)

heteroxenous (2-host) cycle
vector-borne transmission
(sexual development in invertebrate host)
(asexual development in vertebrate host)

trans-stadial transmission occurs within ticks
(but not trans-ovarian transmission)

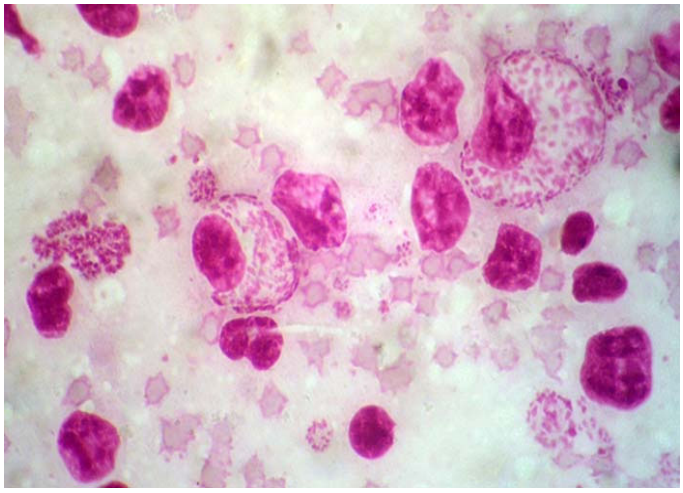


Definitive Hosts (vectors)
(1-, 2-, 3-host ticks)

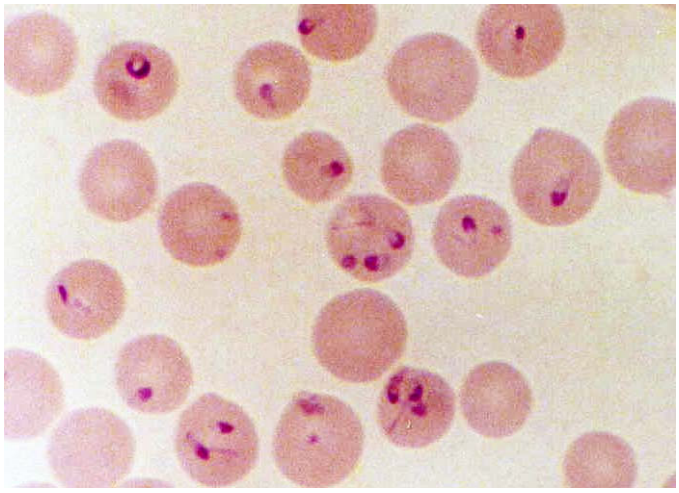


lymphoid tissue, blood
(fever, odema, inflammatory intra- & peri-vascular lesions)

Intermediate Hosts
(mammals, esp. ungulates, rodents)



Theileria schizonts in bovine white blood cells



Theileria piroplasms in bovine red blood cells

OTHER GENERA

Family: Theileridae (lymphocytes then erythrocytes of mammals)

Genus *Cytauxzoon*: This genus was created to accommodate the *Theileria*-like parasites with pre-erythrocytic merogony (schizogony) in macrophages rather than in lymphocytes. However, subsequent studies have shown that the presumed specificity of meronts (schizonts) for various *Theileria* and *Cytauxzoon* spp. is not as strict as previously thought, with meronts reported from a range of cell phenotypes, including leucocytes (B and T lymphocytes) and histiocytes (monocytes, macrophages, vascular endothelial cells). This has led to many species revisions, particularly for those found in African wildlife, but further studies are required to unravel their classification, including not only the molecular characterization of parasite species but also the immuno-phenotypic characterization of the host cells parasitized by meronts. Macrophages engorged by meronts often line the lumina of blood vessels and may obstruct blood flow causing tissue lesions and inflammation. The disease cytauxzoonosis may develop rapidly in felids with haemolysis, regenerative anaemia, jaundice, fever, dehydration, and hepatosplenomegaly occurring in 14-20 days.

***Cytauxzoon* species**	**Vertebrate hosts**	**Disease**	**Pathogenicity**	**Vectors**	**Distribution**
C. felis (syn. *Theileria felis*)	Carnivora: felid (cat, bobcat, Florida panther, Texas cougar, captive white tiger, captive cheetahs), plus experimentally to Artiodactyla: bovid (sheep)]	cytauxzoonosis	high [haemolytic anaemia, thrombo-cytopenia]	three-host ticks (*Amblyomma americanum, Dermacentor variabilis*)	North America
Cytauxzoon spp.	Artiodactyla: bovid (eland, gray duiker, greater kudu, sable antelope, roan antelope, tsessebe)	disease	medium		Africa

Family HAEMOHORMIDIIDAE (nucleated erythrocytes of reptiles and fish)

Genus *Sauroplasma* (syn. *Serpentoplasma*): This genus was erected for piroplasms that appeared to only undergo asexual multiplication by binary fission or budding in the nucleated erythrocytes of lizards (exo-erythrocytic merogony absent). Host cells contained up to 4 piroplasms with distinct nuclei but lacking endosomes or nucleoli. The vectors involved in transmission are not known but are thought to be ticks.

***Sauroplasma* species**	**size**	**Vertebrate hosts**	**Location (disease)**	**Vectors**	**Distribution**
Species in lizards					
S. boreale		Sauria: lacertid (sand lizard)			Europe
S. thomasi (type species)		Sauria: cordylid (giant girdled lizard); gerrhosaurid (Madagascar girdled lizard)			Africa, Madagascar
S. zonorum		Sauria: cordylid (Transvaal girdled lizard)			South Africa

Genus *Haemohormidium* (syn. *Haematractidium*): This genus was erected for piroplasms that multiplied in nucleated blood cells of aquatic vertebrates (fish and tortoises). The parasites underwent merogony mainly in red blood cells forming up to 4 merozoites with distinct nuclei lacking endosomes and nucleoli. There has been great confusion with developmental stages of several *Haemogregarina* and *Babesiosoma* spp. with authorities recommending various revisions. Molecular characterization studies are required to establish the validity of these species and to determine their vectors (currently thought to be leeches).

***Haemohormidium* species**	**size**	**Vertebrate hosts**	**Location (disease)**	**Vectors**	**Distribution**
Species in fish					
H. beckeri		marine Scorpaeniformes: anarhichadid (Atlantic wolffish), cottid (longhorn sculpin), zoarcid (Newfoundland eelpout, Vahl's eelpout)	red blood cells		North Sea
H. clariae		freshwater Siluriformes: clariid (sharptooth catfish)			Africa
H. cotti [type species]	4.5 µm	marine Scorpaeniformes: cottid (longspined bullhead, shorthorn sculpin)	red blood cells		Isle of Man
H. esoci (syn. *Haemogregarina esoci*)	µm	freshwater Esociformes: esocid (pike)	red blood cells		Asia
H. scombri (syn. *Haematractidium, Babesiosoma*)	rings 2-6 µm binucleate form up to 9 µm	marine Scombriformes: scombrid (mackerel)	red and white blood cells		Atlantic
H. terranovae		marine Acanthuriformes: sciaenid (Norfolk spot); Gadiformes: gadid (haddock), merlucciid (silver hake), phycid (white hake, red hake), Pleuronectiformes: pleuronectid (yellowtail flounder, winter flounder, witch flounder, American plaice): Scorpaeniformes: agonid (sea raven); Trachiniformes: ammodytid (American sandlance)			Atlantic
Species in reptiles					
H. guglielmi		Testudines: testudinid (marginated tortoise)			Europe

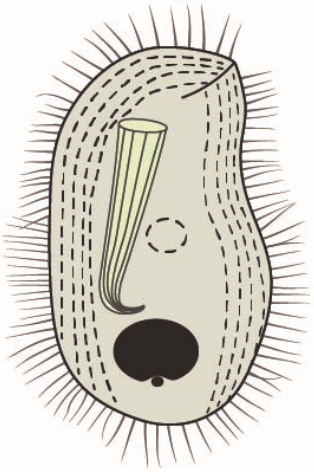
Protista
(ciliates)

Ciliates

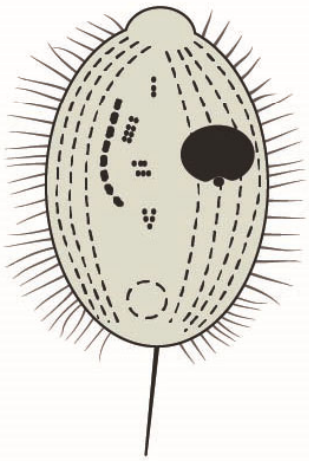
Balantidium
(30-150 µm)



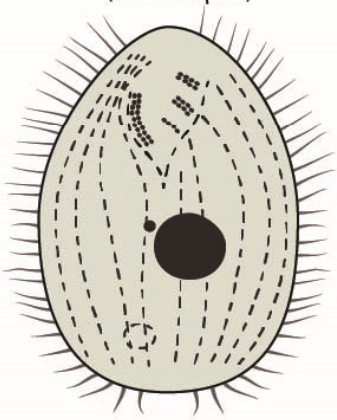
Chilodonella
(27-85 µm)



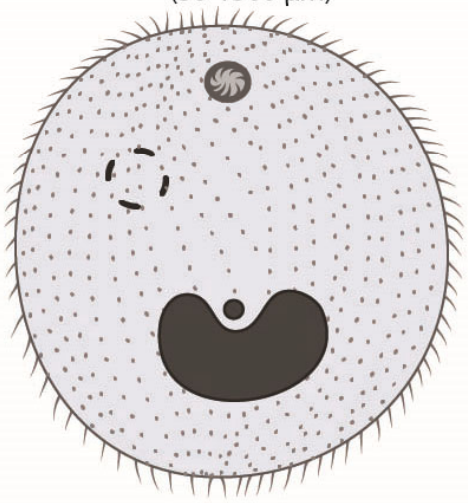
Uronema
(20-50 µm)



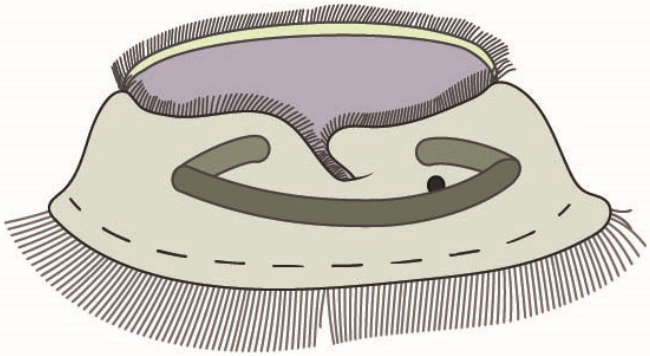
Tetrahymena
(10-100 µm)



Ichthyophthirius
(30-1500 µm)



Trichodina
(10-150 µm)



peritrichs
(10-80 µm)



Balantidium
(protist: ciliate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Ciliated protozoa are unique eukaryotes as they exhibit nuclear dualism (vegetative macronucleus and reproductive micronucleus), the process of conjugation (exchange of micronuclei between pairs), have membrane-bound sacs (subpellicular alveoli) supporting the plasma membrane, and move using cilia (2+9 undulipodia with compound subpellicular infraciliature). Most ciliates are free-living in aquatic and terrestrial habitats, but some are symbiotic in vertebrate and invertebrate hosts. Ten major monophyletic lineages are recognized on the basis of their infraciliature, i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). Members of the subphylum Intramacronucleata are united by the presence of microtubules inside the macronuclear envelope during division; including the litostomes ('simple mouthed') with a noncurved tubular cytopharyngeal apparatus (rhabdos). Vestibuliferid ciliates have a pronounced vestibulum and the balantidids are monoxenous (one-host) endocommensals in vertebrates, sometimes becoming histophagous parasites. Infections by *Balantidium* may cause diarrhoeal disease in mammals, notably in pigs and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Ciliophora (with cilia, nuclear dualism, pellicular alveoli, reproductive conjugation)
Subphylum:	Intramacronucleata (microtubules occur inside macronuclear envelope during division))
Class:	Litostomatea (simple mouths, special somatic kineties)
Subclass:	Trichostomatia (endosymbionts, holotrichous ciliation)
Order:	Vestibuliferida (distinct oral depression (= vestibulum))
Family:	Balantidiidae (monoxenous symbiotes, in vertebrates, sometimes histophagous)
Genus:	*Balantidium* (parasitic in pigs/primates, large intestine, direct (faecal-oral))
Species:	*B. coli* (causes balantidiasis in vertebrates, esp. pigs and humans)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Ciliated protozoa are unique amongst the unicellular eukaryotes because they are the only group to exhibit nuclear dualism. Individual cells possess two different types of nuclei; vegetative macronuclei and reproductive micronuclei. Asexual reproduction occurs by transverse binary fission across rows of cilia (homothetogenic fission) whereas some species exhibit sexual reproduction by the phenomenon of conjugation (temporary fusion of two conjugates which exchange micronuclei). As their common name implies, ciliates are also characterized by the possession of simple cilia, or compound ciliary organelles, in at least one stage of their life cycles (compound subpellicular infraciliature is universally present even when cilia are absent). Cilia are elongate hair-like extensions of the cell membrane with an internal microtubular core (universal 2+9 configuration = 2 single central microtubules surrounded by 9 peripheral doublets). They are organelles of motility used for locomotion and/or feeding. Cilia (singular, cilium) are similar in ultrastructure to flagella (singular, flagellum), and they are collectively often called undulipodia (singular, undulipodium) because both use cross-linked proteins (dynein-walking mechanism) to undulate about their basal kinetosome (unlike the rotary motion unique to flagella in bacteria). Ciliates, together with dinoflagellates and apicomplexans, possess subpellicular alveoli which are membrane-bound sacs beneath the plasma membrane. Alveoli are thought to serve many varied functions: ranging from support (helping maintain body shape, act as fulcrum for undulipodia); metabolism (storage); osmoregulation (mucocysts); excretion (extrusomes); protection (toxicysts, trichocysts); and even hunting (haptocysts).

Most ciliate species are free-living in aquatic or terrestrial habitats but many are commensals in vertebrate or invertebrate hosts and some are parasitic. Early classification systems recognized three main classes of ciliates mainly on the basis of their patterns of somatic (body) and buccal (oral) ciliation. The 'lower holotrichs' have simple body and oral ciliature; most are free-living species but some are highly specialized symbionts aiding cellulose digestion in herbivores. The 'higher holotrichs' have

simple body ciliature but more specialized oral ciliature forming membranelles; most occur as free-living organisms but some live as commensals or parasites in a range of animals. The 'spirotrichs' have reduced body ciliation but well-developed oral ciliature forming an adoral zone of membranelles; most are bactivores living in aquatic and terrestrial habitats. More recently, ten major monophyletic lineages have been recognized on the basis of their infraciliature; i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). These lineages (ranked as classes) have been well supported by modern molecular biological studies using several gene sequences.

Class	Etymology	Defining characters	Lifestyles*	Genera covered
Subphylum: **Postciliodesmatophora** [somatic dikinetids with postciliodesmata (overlapping microtubular ribbons)]				
Karyorelictea	'primitive-nucleus'	macronuclei not dividing but replaced by division of micronuclei	free-living (aquatic benthic/planktonic)	
Heterotrichea	'different-hair'	compound ciliary organelles around mouth, macronuclei divided by external microtubules	free-living (aquatic planktonic/benthic)	
Subphylum: **Intramacronucleata** [macronuclei divided by internal microtubules]				
Spirotrichea	'coiled-hair'	conspicuous right and left oral ciliature, left polykinetids leading into oral cavity	free-living (aquatic, terrestrial)	
Litostomatea	'simple-mouths'	cytostome with noncurved tubular cytopharyngeal apparatus (rhabdos)	free-living (often predatory), symbiotic	*Balantidium*
Phyllopharyngea	'leaf-throated'	mouth with radial microtubular ribbons (phyllae), some with sticky feeding tentacles	free-living (aquatic), epizoic, symbiotic	*Chilodonella*
Colpodea	'breast-shaped'	reniform bodies, somatic cilia with transversodesmata (overlapping ribbons)	terrestrial, some aquatic (bactivores)	
Nassophorea	'pot-bearer'	oral nematodesmata well-developed (basket-like nasse or cyrtos supporting cytopharynx)	free-living (aquatic, terrestrial)	
Prostomatea	'before-mouth'	simple apical mouths, some with oral microtubular band, some with oral brush	free-living (often predatory)	
Plagiopylea	'misshapen-marker'	with twisted oral tubes, most with hydrogenosomes	free-living (anoxic habitats)	
Oligo-hymenophorea	'few membrane-bearer'	typically with ventral groove containing mouth and compound ciliary organelles (usually adoral zone of three membranelles)	free-living, epizoic, symbiotic (micro-phagous)	*Uronema, Ichthyophthirus, Tetrahymena, Trichodina, Vorticella*

*Symbiosis *sensu latu* ranges from commensalism, mutualism and parasitism (depending on the benefit/detriment to the host)

The class Litostomatea contains ciliates with a unique infraciliature consisting of 2 transverse microtubular ribbons (tangential and radial), a convergent postciliary ribbon, and a laterally directed kinetodesmal fibril not overlapping adjacent kineties. Litostome ciliates are 'lower' holotrichs as there is little distinction between the oral and somatic ciliature. Most possess an apical cytostome (sometimes subapical or midventral) and a conspicuous cytopharyngeal apparatus. They are found in many diverse habitats ranging from free-living to endoparasitic, and are often carnivorous in feeding habit. Three litostome subclasses are recognized, each containing 2-3 orders: namely, Haptoria (containing free-living Haptorida, Pleurostomatida and Spathidiida); Rhynchostomatia (containing free-living Dileptida and Tracheliida); and Trichostomatia (containing endosymbiotic Vestibulifera and Entodiniomorphida). Trichostomes have mouths lined with cilia derived from the anterior somatic kineties and leading through a noncurved rhabdos to the cytostome. Most species occur in the gastro-intestinal tracts of vertebrates, either as endocommensals, some as mutualists (e.g. 'rumen protozoa' in ruminants), and a few as parasites. The order Entodiniomorphida contains some 33 genera classified in 6 families in 3 suborders, most characterized by the possession of rigid bodies with posterior rudder-like projections and somatic ciliature present as specialized tufts or bands. The order Vestibuliferida contains 13 genera grouped into 5 families (Amylovoracidae, Balantidiidae, Isotrichidae, Paraisotrichidae, and Pycnotrichidae), all characterized by the possession of ovoid bodies with distinct oral depressions (= vestibula) and holotrichous somatic ciliation. Balantidiids are monoxenous endocommensals in vertebrates, but some can become histophagous parasites. More than 80 species of the genus *Balantidium* (syn. *Balantidiopsis, Balantioides, Parabursaria, Paranyctotherus*) have been recorded throughout the world in various species of crustaceans, insects, fish, amphibians, reptiles, birds and mammals (including humans). Infections by *B. coli* are particularly prevalent in pigs, monkeys and humans, especially in the tropics, with zoonotic transmission from pigs to humans frequently implicated by epidemiological studies. While few morphotypic differences have been observed between trophozoites and/or cysts of most *Balantidium* spp., recent molecular characterization studies have revealed distinct genotypic differences between isolates from mammals and amphibians (with a new genus *Neobalantidium* being proposed for the latter) as well as genotypic similarities between some isolates from primates and another ciliate (*Buxtonella sulcata*) from cattle. Several genotypes have been detected in *B. coli* isolates from mammals: including genotypes A and B in pigs and genotype C in gorillas. *B. struthionis* isolates from ostriches were also found to be similar to *B. coli* genotypes A and B prompting their amalgamation. Further studies are required to determine the extent and significance of such genetic variation, particularly with respect to host occurrence and specificity.

Balantidium spp.	Vertebrate* hosts	Location	Clinical signs	Distribution
Species in mammals				
B. coli (syn. *B. aragaoi, cunhamunizi, philippinensis, rhesum, simile, struthionis, suis*, *wenrichi*)	Primates: hominid (human, chimpanzee, gorilla, Sumatran orangutan), cercopithecid (chacma baboon, macaques); Artiodactyla: suid (pig), bovid (cattle, buffalo), camelid (camel); Carnivora: canid (dog); Rodentia: murid (rats, mice); Aves: Struthioniformes (ostrich)	colon	inflammation, diarrhoea, ulceration	cosmopolitan (esp. tropics)
B. caviae	Rodentia: caviid (guinea pig)	colon		cosmopolitan (pet and lab animals)
Species in amphibians				
B. amblystomatis	Urodela: ambystomatid (tiger salamander)			North America
B. amygdalli	Anura: bufonid (big-eared toad)	intestines		India
B. andianusis	Urodela: cryptobranchid (Chinese giant salamander)	intestines		China
B. aurangabadensis	Anura: dicroglossid (Asian bullfrog)	rectum		India
B. bicavata	Anura: bufonid (Asian toad)	intestines		India
B. claperedei	Anura: ranid (marsh frog)	intestines		Turkey
B. corlissi	Anura: dicroglossid (skittering frog)	rectum		India
B. cyanophlycti	Anura: dicroglossid (skittering frog)	rectum		India
B. duodeni (syn. *B. hyalinum, rotundum*)	Anura: ranid (common frog, edible frog, marsh frog), ptychadenid (grass frog), micrixalid (black torrent frog)	intestines		Europe, Asia
B. elongatum	Anura: ranid (common frog, edible frog, marsh frog), pelobatid (common spadefoot), ptychadenid (grass frog), bombinatorid (yellow-bellied toad); Urodela: salamandrid (common newt, northern crested newt, smooth newt, alpine newt)	intestines		Europe, Asia
B. entozoon [type species]	Anura: ranid (edible frog), ptychadenid (grass frog), bombinatorid (yellow-bellied toad, European fire-bellied toad), bufonid (European green toad, nutterjack toad); Urodela: salamandrid (common newt, crested newt)	intestines, rectum		Europe
B. falciformis	Anura: ranis (pickerel frog)	intestines		North America
B. ganapatii	Anura: dicroglossid (skittering frog)	rectum		India
B. giganteum	Anura: ranid (edible frog, marsh frog)			Asia, Europe
B. gracile	Anura: dicroglossid (Asian bullfrog, Indian green frog, marbled sand frog, verrucose frog), micrixalid (torrent frog)	intestines		India
B. grimi	Anura: dicroglossid (Chinese spiny frog)	rectum		China
B. helenae (syn. *B. ovale*)	Anura: ranid (edible frog, European common frog, bicolored frog, marsh frog), dicroglossid (marble sand frog, verrucose frog, Asian bullfrog), micrixalid (torrent frog)	intestines		Asia, Europe
B. honghuensis	Anura: ranid (black-spotted pond frog), dicroglossid (Asian grass frog)	rectum		China
B. kirbyi	Anura: pipid (African clawed frog)	large intestines		South Africa
B. megastomae	Anura: dicroglossid (skittering frog)	rectum		India
B. mininucleatum	Anura: dicroglossid (skittering frog)	rectum		India
B. nucleus	Anura: ranid (edible frog, European common frog)			Europe
B. ranae/ranarum	Anura: dicroglossid (Asian bullfrog)	rectum		India
B. rayi	Urodela: salamandrid (Himalayan newt)	intestines		Indochina
B. sinensis	Anura: ranid (black-spotted pond frog, eastern golden frog); Urodela: cryptobranchid (Chinese giant salamander)	intestines		China
B. singaporensis	Anura: bufonid (Asian toad)	rectum		Singapore

B. sushilii	Anura: dicroglossid (Asian bullfrog)	intestines		India
B. tigrinae	Anura: dicroglossid (Asian bullfrog)	rectum		India
B. tylototritonis	Urodela: salamandrid (Himalayan newt)	intestines		Indochina
B. vanensis	Anura: ranid (marsh frog)	intestines		Turkey
B. xenopi	Anura: pipid (Fraser's clawed frog)	intestines		Africa
Species in tortoises				
B. testudinis	Testudines: testudinid (tortoises, incl. Galapagos tortoise)	intestines		Asia, Africa, South America
B. bacteriophorus	Testudines: cheloniid (green sea turtle)	intestines		Caribbean
B. dogieli	Testudines: trionychid (Indian flapshell turtle)	intestines		India
Species in freshwater fish				
B. barbi	Cypriniformes: cyprinid (carp)	intestines		Central Asia
B. ctenopharyngodoni	Cypriniformes: cyprinid (grass carp)	intestines	enteritis	China, Europe
B. fulinensis	Cypriniformes: cyprinid (carp)	intestines	ulceration	China
B. granulosum	Salmoniformes: salmonid (brook trout)	stomach		America
B. grevolosum	Salmoniformes: salmonid (brook trout)	gut		Americas, Europe
B. mrigalae	Cypriniformes: cyprinid (mrigal carp)	intestines		Asia
B. pangasi	Siluriformes: pangasid (Pangas catfish)	intestines		Asia
B. piscicola	Characiformes: serrasalmid (pirapitinga)	intestines		South America
B. polyvacuolum	Cypriniformes: cyprinid (blackbelly, yellowtail, David's yellowfin, smallscale yellowfin, common carp)	rectum	ulceration	China, Middle-East
B. procyprini	Cypriniformes: cyprinid (carp)	intestines		China
B. semilabeai	Cypriniformes: cyprinid (carp)	intestines		China
B. senilabeai	Cypriniformes: cyprinid (carp)	intestines		China
B. spinibarbichthys	Cypriniformes: cyprinid (Chinese phoenix barb)	intestines		China
B. steinae	Cypriniformes: cyprinid (Chinese phoenix barb)	intestines		China
B. strelkovi	Cypriniformes: cyprinid (mud carp)	intestines		Asia
B. yangtzensis	Cypriniformes: cyprinid (carp)	rectum		China
B. yinjiangensis	Cypriniformes: cyprinid (carp)	rectum		China
Species in marine fish				
B. acanthuri	Acanthuriformes: acanthurid (powder blue tang)	intestines		Indian Ocean
B. jocularum	Acanthuriformes: acanthurid (bulbnose unicornfish)	intestines		Pacific
B. macrodextroral	Acanthuriformes: acanthurid (black tang, whitespotted surgeonfish, Achilles surgeonfish)	intestines		Pacific
B. prionurium	Acanthuriformes: acanthurid (yellowtail surgeonfish)	intestine		Pacific
B. sigani	Perciformes: siganid (streamlined spinefoot)	rectum		Red Sea
B. zebrascopi	Acanthuriformes: acanthurid (brown tang)	intestines		Oceania

*Other *Balantidium* species have been described from invertebrate hosts (but are not listed here)

Parasite morphology: Two developmental stages are formed: trophozoites and cysts. Trophozoites are variable in size ranging from 30-150 μm in length and 25-120 μm in width. They are oblong-spherical in shape and are covered by longitudinal kineties (rows of cilia). At the anterior end there is a depression (vestibulum) leading to the cytostome (mouth) and cytopharyngeal complex (tubular rhabdos). Internally, they contain a single large reniform macronucleus (vegetative), a small spherical micronucleus (reproductive), several contractile vacuoles (water regulation) and hydrogenosomes (instead of mitochondria). The cysts appear as membrane-bound ovoid bodies ranging from 40-60 μm in diameter.

Site of infection: *B. coli* is found in the large intestine, caecum and terminal ileum of their hosts. They are actively swimming organisms and they reproduce asexually (by transverse binary fission) and sexually (by conjugation involving the exchange of micronuclei between paired trophozoites).

Pathogenesis: Infections are usually not associated with any changes in the colonic mucosa. Healthy individuals often exhibit spontaneous recovery or become symptomless carriers. However, under certain conditions, the organisms produce proteolytic enzymes which digest away the epithelium producing flask-shaped ulcers. This stimulates inflammatory changes with lymphocytic

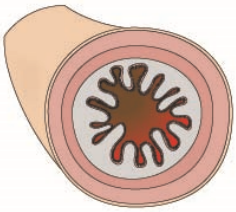
infiltration and haemorrhage and secondary bacterial invasion may follow. Infections may cause a dysentery-like syndrome, involving diarrhoea, tenesmus, nausea, vomiting, anorexia, headache, insomnia and weakness. Diarrhoea may persist for long periods resulting in acute fluid loss. Colonic ulceration involves mucosal sloughing, necrosis, fluid loss, haemorrhage, occasional abscess formation but rarely perforation of the bowel. Factors predisposing to ciliate multiplication and clinical infections have usually involved changes to the microbial gut flora associated with dietary changes, antibiotic use and stressful conditions.

Developmental cycle and mode of transmission: Infections are passed horizontally between hosts by faecal-oral transmission. Cysts passed in the faeces of infected hosts contaminate the environment. When ingested with contaminated food or water, the cysts excyst releasing trophozoites in the digestive tract. Trophozoites multiply primarily by asexual transverse binary fission across rows of cilia (homothetogenic fission), although they may occasionally pair-up in a unique sexual process of conjugation where micronuclei are exchanged via a temporary cytoplasmic bridge. Infections in humans are more prevalent in communities which farm pigs (under intensive or extensive husbandry) and in individuals working with pigs or in slaughterhouses.

Differential diagnosis: Infections are diagnosed by coprological examination and the detection of characteristic cysts in faecal material or trophozoites in colonic biopsy material. Multiple stool samples should be examined as the cysts may be excreted intermittently. Molecular techniques have been developed in several research laboratories to characterize isolates using polymerase chain reactions (PCR) to amplify specific sequences (small subunit ribosomal RNA (SSU rRNA) and internal transcribed spacer (ITS) genes].

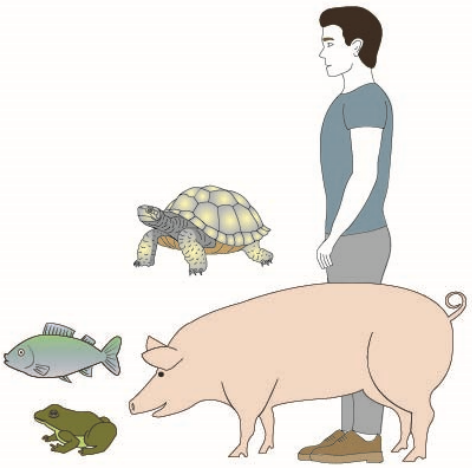
Treatment and control: Clinical infections may be treated with metronidazole, di-iodohydroxyquin, tetracycline or carbarsone. Prevention and control depend on strict hygiene to prevent the contamination of food and water supplies, particularly by faeces from humans and pigs. Sewage should be collected and treated and drinking water supplies should be purified by filtration and/or chlorination. Effluent from intensive piggeries should not be used to fertilize vegetable gardens or edible crops. In developing countries, pigs should not be left to roam free in rural villages, but are best confined to pens and sties where proper waste disposal can be practiced.

Balantidium

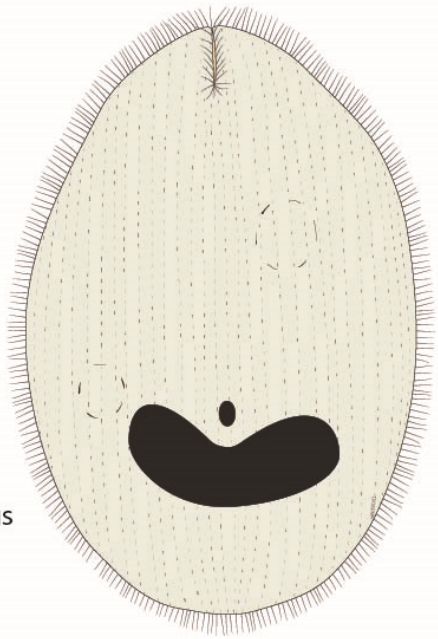


large intestines
(mucosal ulceration,
haemorrhages,
diarrhoea)

may reproduce asexually
(by transverse binary fission)
or sexually (by conjugation)



Vertebrate Hosts
(mammals, frogs,
tortoises, fish)

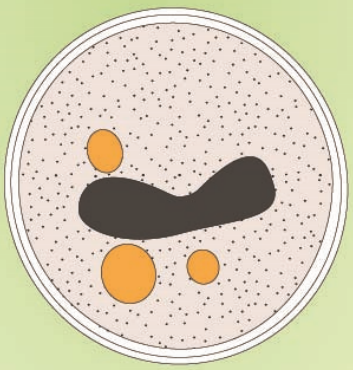


trophozoite
(30-150 µm)



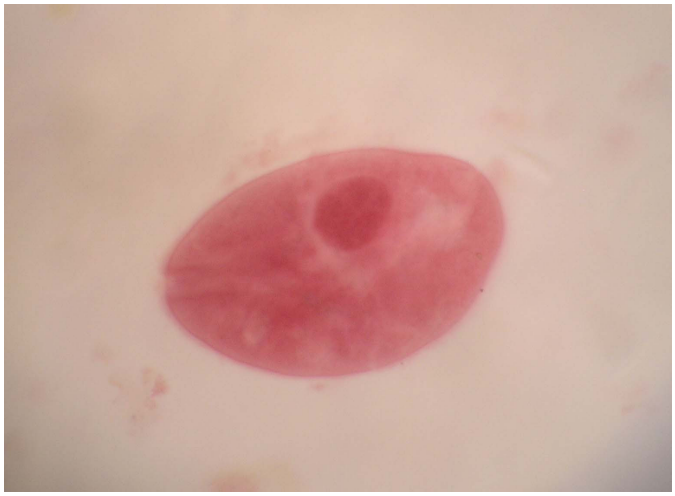
cysts
ingested

cysts excreted
in faeces



cyst
(40-60 µm)

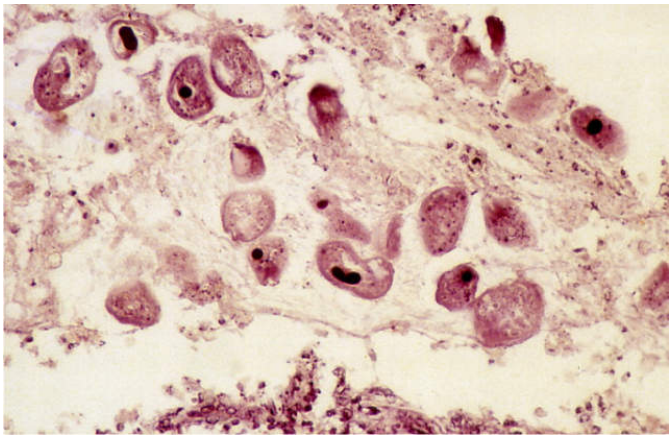
direct faecal-oral transmission
via contaminated environment (soil, water, food)



Balantidium trophozoite in human bowel



Balantidium cyst from human faeces



Balantidium lesion in pig bowel

Chilodonella
(protist: ciliate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Ciliated protozoa are unique eukaryotes as they exhibit nuclear dualism (vegetative macronucleus and reproductive micronucleus), the process of conjugation (exchange of micronuclei between pairs), have membrane-bound sacs (subpellicular alveoli) supporting the plasma membrane, and move using cilia (2+9 undulipodia with compound subpellicular infraciliature). Most ciliates are free-living in aquatic and terrestrial habitats, but some are symbiotic in vertebrate and invertebrate hosts. Ten major monophyletic lineages are recognized on the basis of their infraciliature, i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). Members of the subphylum Intramacronucleata are united by the presence of microtubules inside the macronuclear envelope during division; including the phyllopharyngids ('leaf throated') with cytopharyngeal phyllae. Chlamydodontid ciliates have dorsoventrally flattened bodies, with only the ventral surface being ciliated. In chilodonellids, the ventral ciliature is reduced to two longitudinal belts close to the body margins. Many *Chilodonella* spp. are free-living aquatic organisms, but some are ectoparasitic on the gills and skin of freshwater fishes, sometimes causing respiratory difficulties and mortalities.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Ciliophora (with cilia, nuclear dualism, pellicular alveoli, reproductive conjugation)
Subphylum:	Intramacronucleata (microtubules occur inside macronuclear envelope during division))
Class:	Phyllopharyngea (cytopharynx with leaf-like phyllae)
Subclass:	Phyllopharyngia (cyrtos, ventral cilia, free-living/symbiotic)
Order:	Chlamydodontida (body dorsoventrally flattened, ventral cilia thigmotactic)
Family:	Chilodonellidae (reniform body dorsoventrally flattened, two fields of dorsal ciliary rows)
Genus:	*Chilodonella* (parasitic in fish on gills/skin)
Species:	various species cause hypoxic gill diseases in fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Ciliated protozoa are unique amongst the unicellular eukaryotes because they are the only group to exhibit nuclear dualism. Individual cells possess two different types of nuclei; vegetative macronuclei and reproductive micronuclei. Asexual reproduction occurs by transverse binary fission across rows of cilia (homothetogenic fission) whereas some species exhibit sexual reproduction by the phenomenon of conjugation (temporary fusion of two conjugates which exchange micronuclei). As their common name implies, ciliates are also characterized by the possession of simple cilia, or compound ciliary organelles, in at least one stage of their life cycles (compound subpellicular infraciliature is universally present even when cilia are absent). Cilia are elongate hair-like extensions of the cell membrane with an internal microtubular core (universal 2+9 configuration = 2 single central microtubules surrounded by 9 peripheral doublets). They are organelles of motility used for locomotion and/or feeding. Cilia (singular, cilium) are similar in ultrastructure to flagella (singular, flagellum), and they are collectively often called undulipodia (singular, undulipodium) because both use cross-linked proteins (dynein-walking mechanism) to undulate about their basal kinetosome (unlike the rotary motion unique to flagella in bacteria). Ciliates, together with dinoflagellates and apicomplexans, possess subpellicular alveoli which are membrane-bound sacs beneath the plasma membrane. Alveoli are thought to serve many varied functions: ranging from support (helping maintain body shape, act as fulcrum for undulipodia); metabolism (storage); osmoregulation (mucocysts); excretion (extrusomes); protection (toxicysts, trichocysts); and even hunting (haptocysts).

Most ciliate species are free-living in aquatic or terrestrial habitats but many are commensals in vertebrate or invertebrate hosts and some are parasitic. Early classification systems recognized three main classes of ciliates mainly on the basis of their patterns of somatic (body) and buccal (oral) ciliation. The 'lower holotrichs' have simple body and oral ciliature; most are free-living species but some are highly specialized symbionts aiding cellulose digestion in herbivores. The 'higher holotrichs' have

simple body ciliature but more specialized oral ciliature forming membranelles; most occur as free-living organisms but some live as commensals or parasites in a range of animals. The 'spirotrichs' have reduced body ciliation but well-developed oral ciliature forming an adoral zone of membranelles; most are bactivores living in aquatic and terrestrial habitats. More recently, ten major monophyletic lineages have been recognized on the basis of their infraciliature; i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). These lineages (ranked as classes) have been well supported by modern molecular biological studies using several gene sequences.

Class	Etymology	Defining characters	Lifestyles*	Genera covered
Subphylum: **Postciliodesmatophora** [somatic dikinetids with postciliodesmata (overlapping microtubular ribbons)]				
Karyorelictea	'primitive-nucleus'	macronuclei not dividing but replaced by division of micronuclei	free-living (aquatic benthic/planktonic)	
Heterotrichea	'different-hair'	compound ciliary organelles around mouth, macronuclei divided by external microtubules	free-living (aquatic planktonic/benthic)	
Subphylum: **Intramacronucleata** [macronuclei divided by internal microtubules]				
Spirotrichea	'coiled-hair'	conspicuous right and left oral ciliature, left polykinetids leading into oral cavity	free-living (aquatic, terrestrial)	
Litostomatea	'simple-mouths'	cytostome with noncurved tubular cytopharyngeal apparatus (rhabdos)	free-living (often predatory), symbiotic	*Balantidium*
Phyllopharyngea	'leaf-throated'	mouth with radial microtubular ribbons (phyllae), some with sticky feeding tentacles	free-living (aquatic), epizoic, symbiotic	*Chilodonella*
Colpodea	'breast-shaped'	reniform bodies, somatic cilia with transverso-desmata (overlapping ribbons)	terrestrial, some aquatic (bactivores)	
Nassophorea	'pot-bearer'	oral nematodesmata well-developed (basket-like nasse or cyrtos supporting cytopharynx)	free-living (aquatic, terrestrial)	
Prostomatea	'before-mouth'	simple apical mouths, some with oral microtubular band, some with oral brush	free-living (often predatory)	
Plagiopylea	'misshapen-marker'	with twisted oral tubes, most with hydrogenosomes	free-living (anoxic habitats)	
Oligo-hymenophorea	'few membrane-bearer'	typically with ventral groove containing mouth and compound ciliary organelles (usually adoral zone of three membranelles)	free-living, epizoic, symbiotic (micro-phagous)	*Uronema, Ichthyophthirus, Tetrahymena, Trichodina, Vorticella*

*Symbiosis *sensu latu* ranges from commensalism, mutualism and parasitism (depending on the benefit/detriment to the host)

The class Phyllopharyngea contains ciliates with an infraciliature consisting of unique ultrastructural elements supporting their kinetosomes (lateral kinetodesmal fibril, reduced transverse microtubular ribbon accompanied by a left-directed transverse fibre, and convergent postciliary ribbon extending posteriorly to accompany those of adjacent kineties). While the class has been named after the possession of prominent cytopharyngeal phyllae (radial microtubular ribbons), some representatives (Suctoria) actually lack mouths and phyllae and possess unique sticky feeding tentacles. Depending on the classification system used, the class contains 2-4 subclasses, nominally identified as Chonotrichia, Phyllopharyngia, Rhynchodia, and Suctoria. The subclass Phyllopharyngia (also known as Cyrtophoria) is characterized by ciliates with mouths whose oral ciliature consists of one preoral and 2 circumoral kineties, with phyllae and rod-shaped nematodesmata forming a distinct cyrtos (cytopharyngeal basket). Two orders are recognized: Dysteriida containing 17 genera of free-living ciliates with laterally compressed bodies; and Chlamydodontida containing 17 genera of free-living or symbiotic ciliates with dorsoventrally-flattened bodies. Chlamydodontids include free-living (aquatic, terrestrial) and symbiotic (epizoic, parasitic) species, but they are essentially free-swimming ciliates that may attach to substrates by thigmotactic ventral cilia. They are classified into 6 families (Chilodonellidae, Chitonelidae, Chlamydodontidae, Gastronautidae, Kryoprorodontidae, Lynchellidae) on the basis of their structural features. Members of the family Chilodonellidae have reniform dorsoventrally-flattened bodies with somatic cilia arranged into 2 longitudinal fields on the ventral aspect only. Five genera are recognized (*Chilodonatella, Chilodonella* (syn. *Chilodon*)*, Phascolodon, Pseudochilodonopsis,* and *Thigmogaster*) with members of the genus *Chilodonella* characteristically having an arched right ventral ciliary belt and long phyllae leading to the cytostome located around the mid-body. The genus includes free living species as well as some that are facultative, and even obligate, parasites on the gills and/or skin of freshwater fishes, including farmed, ornamental and wild fish species in warm and cold waters.

***Chilodonella* species**	**Trophont size (µm)**	**Life-style (Hosts) [Clinical signs]**	**Distribution**

C. acuta	30-49	terrestrial and freshwater, free-living on bladderwort (*Utricularia*) (recently reported as epizoic on skin/gills of freshwater fish Perciformes: latid (barramundi))	Saudi Arabia (Australia)
C. aplanata	40-60	terrestrial and freshwater, free-living on mosses and bladderwort (*Utricularia*)	Europe, America
C. calkinsi (syn. *C. pediculatus*)	40-60	brackish water (salt lake), free-living	Europe
C. capucina	40-70	freshwater, epizoic on carapace of Amphipoda: gammarid (*Gammarus*); Isopoda: asellid (*Asellus*)	Eurasia
C. caudata	42	freshwater, free-living on duckweed (*Azolla*)	Europe
C. crebricostata	57-76	brackish water, free-living	?
C. cucullulus (syn. *Trithigmostoma, Kolpoda, C. steini*)	130-300	fresh and brackish water, free-living	cosmopolitan
C. elongata (syn. *Phascolodon*)	130	freshwater, free-living	New Zealand
C. fluviatilis	50	freshwater, free-living	Europe
C. gouraudi (syn. *Odontochlamys, Chilodon geographicus*)	30-50	freshwater and terrestrial, free-living and on mosses	Europe, America
C. granulata	30-35	freshwater, epizoic on carapace of Amphipoda: gammarid (*Gammarus*); Isopoda: asellid (*Asellus*)	Eurasia
C. helgolandica	55-90	marine, free-living (benthic)	Europe
C. hexasticha	30-65	freshwater, epizoic on skin and gills of fish (Anabantiformes: nandid (Gangetic leaf-fish); Atheriniformes: melanotaeniid (eastern rainbowfish); Cichliformes: cichlid (redbelly tilapia, redbreast tilapia, mango tilapia, banded tilapia, red discus, southern mouthbrooder, Mozambique tilapia, Nile tilapia); Clupeiformes: dorosomatid (bony bream); Cypriniformes: cyprinid (goldfish, Eurasian carp, crucian carp, grass carp, bighead carp, straightfin barb, rohu); Gymnotiformes: gymnotid (naked-backed knifefish); Perciformes: latid (barramundi), percid (European perch), sinipercid (mandarin fish), terapontid (silver perch, spangled grunter, barred grunter); Salmoniformes: salmonid (rainbow trout, brown trout, Atlantic salmon); Siluriformes: bagrid (yellowhead catfish), clariid (African sharptooth catfish), ictalurid (channel catfish), plotosid (eeltail catfish) [skin lesions, epithelial hyperplasia, infiltrates, petechia, oedema, necrosis]	worldwide
C. labiata	40-50	freshwater, free-living	Europe
C. longipharynx		freshwater, epizoic on carapace of Amphipoda: talitrid (*Orchestia palustris, Talorchestia longicornis*)	Eurasia
C. megalotrochae	45-60	freshwater, epizoic on carapace of Rotifera: floscullariid (*Megalotrocha*)	Europe
C. nana	15-20	marine, free-living	
C. parauncinata		freshwater, free-living	China
C. piscatoris [now *Pseudochilodonopsis*]	65-80	freshwater, free-living on plants (*Lemna, Hottonia*)	Europe
C. piscicola (syn. *C. cyprini, Chilodon*)	30-80	freshwater (occasionally estuarine and brackish waters), epizoic on skin and gills of fish (Characiformes: characid (neon tetra); Cichliformes: cichlid (redbreast tilapia, banded tilapia, redbelly tilapia, mango tilapia, blue tilapia, Mozambique tilapia, Nile tilapia, southern mouthbrooder); Cypriniformes: catastomid (longnose sucker), cyprinid (goldfish, grass carp, rock carp, naked schizothoracin, yarlungi marinka, karestikumarinka); Perciformes: perichthyid (Murray cod), percid (European perch); Salmoniformes: salmonid (brown trout, masu salmon, Atlantic salmon, rainbow trout); Siluriformes: ictalurid (channel catfish) [skin lesions, epithelial hyperplasia, infiltrates, petechia, oedema, necrosis]	worldwide
C. porcellionis	30	terrestrial, endozoic in genital spaces of Isopoda: porcellionid	Europe

		(*Porcellio* woodlice)	
C. propellens	~50	freshwater, free-living (planktonic?)	Europe
C. psammophila		euryhaline, free-living	Europe
C. rotunda		freshwater, epizoic on carapace of Amphipoda: talitrid (*Orchestia agilis*)	Eurasia
C. schewiakoffi	250	free-living, freshwater	Europe
C. subtilis		freshwater, free-living	Europe
C. turgidula	50-55	freshwater, free-living (benthic)	Europe
C. uncinata [type species] (syn. *C. algivora, curvidens, dentata, dorsisuprema, rigida, Chilodon uncinatus*)	50-90	freshwater, free-living (recently reported as epizoic on skin/gills of fish (Perciformes: latid (barramundi), Cypriniformes: cyprinid (carp, goldfish))	cosmopolitan (Australia, Mexico)
C. wisconsinensis	50	terrestrial, free-living on mosses	America

A small range of other *Chilodonella* spp. have been re-examined and re-assigned to other sister genera: with *C. bavariensis, C. chattoni, C. hyalina, C. marginata, C. schedoeublepharis* and *C. steini* (syn. *Chilodontopsis bengalensis*) transferred to the genus *Thigmogaster; C. convexa* to the genus *Odontochlamys, C. minuta* to the genus *Chilodonatella*, and *C. plurivacuolata* to the genus *Alinostoma.*

Parasite morphology: *Chilodonella* spp. form motile trophic stages (trophozoites) that use cilia to swim with a distinctive gliding movement in fluid media or to browse over inert or living substrates. Trophozoites have oval, heart- or kidney-shaped bodies (many with an anterior notch) and they are dorsoventrally flattened. The cells vary in size depending on the species and their state of nutrition, most ranging from 27-85 x 13-62 µm (*C. piscicola* 30-80 x 20-62 µm, *C. hexasticha* 30-65 x 20-50 µm, *C. acuta* 30-49 x 16-30 µm, *C. uncinata* 27-42 x 13-29 µm). The dorsum is slightly convex and non-ciliated (although sometimes appearing to have a short anterior ciliary row, which is usually apical or subventral). The ventrum is flat or slightly concave and has a distinctive subapical buccal opening (mouth) consisting of a circular depressed cytostome with a tube- or funnel-like cytopharyngeal apparatus formed by a circlet of long rod-like nematodesmata (phyllae) surrounding the cytopharyngeal tube (consistent with other 'leaf-throated' phyllopharyngid ciliates). The ventral surface is ciliated with 3 short oral rows located anterior to the cytostome, and with 2 large conspicuous ciliary belts running longitudinally down the left and right sides close to the body margins (straight left belt, arched right belt). The number of kineties (ciliary rows) in each belt varies according to species, with most ranging from 3-14 rows in the left belt and 4-15 rows in the right belt (*C. piscicola* (7-15 right, 8-14 left; *C. hexasticha* 5-7 right, 5-9 left; *C. acuta* 4 right, 5 left; *C. uncinata* 4 right, 3 left). Trophozoites have a single large ovoid macronucleus with a small adjacent micronucleus, both often located midbody or in the posterior half of the cell. Trophozoites usually possess 2 contractile vacuoles located diagonally across the midbody. Some early studies conducted in Russia observed cyst formation in '*Chilodon cyprini'* (now a junior synonym of *C. piscicola*). An attached figure illustrated the cysts as rounded uninucleate stages (30-40 µm in diameter) with no cilia or kineties, but with a central mass not quite extending to the peripheral membranous wall. There have since been few observations of cysts.

Site of infection: Most *Chilodonella* spp. are free-living, with some 27 species found in aquatic or moist terrestrial habitats (most freshwater, some brackish and saltwater) where they are free-swimming or may browse on plants (e.g. bladderworts, duckweed, mosses) or occur as ectocommensals on invertebrates (e.g. amphipods, isopods, rotifers). Two free-living species (*C. acuta* and *C. uncinata*) may also become facultatively or opportunistically parasitic and invade the gills or skin of freshwater fish. Another 2 species (*C. hexasticha* and *C. piscicola*) are obligate parasites on the gills, skin and fins of fish (mostly freshwater species but also some estuarine species). Infections have been recorded on over 40 fish species belonging to 18 families in 10 orders (mainly Cypriniformes and Perciformes, but also Cichliformes, Siluriformes, Salmoniformes, and occasionally Anabantiformes, Atheriniformes, Characiformes, Clupeiformes, and Gymnotiformes).

Pathogenesis: Infections in fish may be asymptomatic or subclinical when parasite numbers are low, but under favourable condition, parasite populations can build in number and cause mild-severe clinical disease (chilodonellosis). Infections generally cause disease and mortalities when fish are physiologically stressed (and thus immunocompromised) due to environmental changes in water quality (rapid temperature fluctuations and extremes, low sunlight, reduced oxygen levels, high/low pH, organic overloads), age (young), diet (inadequate nutrition) and poor husbandry (overcrowded unhygienic conditions). Clinical disease has been recorded globally in many freshwater fish species, particularly in food or ornamental fish culture. *C. hexasticha* and *C. piscicola* may cause significant epidemics in wild and farmed freshwater fish when they attach to external surfaces (skin, fins and gills) using their cytopharyngeal apparatus and ventral cilia. Feeding trophozoites disintegrate surface epithelial tissues and take up the resultant cellular debris, mucus and organic material, as well as any attached bacteria, diatoms and filamentous algae. The presence of feeding organisms causes epithelial irritation, hyperplasia, inflammation with cellular infiltrates, excessive mucus production and dystrophic changes. Skin lesions may develop with pigment and scale loss, lymphocytic dermatitis or necrosis, pale mottled gray appearance, ulcerations, petechiae and abrasions. Gill filaments may become clubbed, fused, clogged with mucus, or even

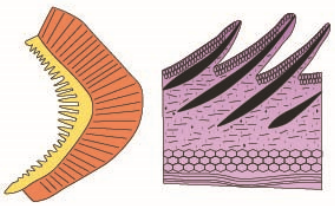
completely destroyed. Fish become lethargic, cease feeding, lose condition and show signs of hypoxia with breathing difficulties such as gaping, gasping and slow swimming at the water surface. They often exhibit uncoordinated swimming and flashing behaviours (attempting to dislodge parasites). Heavy infections can be fatal with many epidemics occurring in culture facilities resulting in high mortalities. Opportunistic infections by *C. acuta* and *C. uncinata* are usually not as severe and cause inflammatory foci on the skin or in the gills, but some have been associated with mortalities in goldfish.

Developmental cycle and mode of transmission: Trophozoites reproduce asexually by transverse binary fission, and repeated division may occur within several hours under favourable conditions, particularly in waters with low dissolved oxygen (often associated with high stocking densities), accumulated organic material (associated with overfeeding) and abundant anaerobic bacteria (considered to be a favoured food). Under adverse conditions, particularly when food is limited, the ciliates may undergo sexual reproduction by conjugation (pairing and exchanging genetic material (micronuclei)). Direct transmission typically occurs with free-swimming ciliates moving between hosts and attaching to gills and body surfaces. Trophozoites may infect fish of all ages, especially when they are stressed (immunocompromised) due to sudden changes in environment (e.g. temperature transitions from summer to autumn) or improper culture conditions (poor diet, low oxygen, overstocking). The involvement of possible cyst formation in transmission cycles is unclear due to their infrequent occurrence, but the source report stated that “in the presence of adverse conditions, chiefly during separation from the host, large specimens were able to form resting cysts that were able to survive for a long period on the bed of the pond and in open water”. Further studies are required to determine the significance of any cyst formation with respect to parasite survival, viability and infectivity.

Differential diagnosis: Infections are diagnosed by the direct microscopic detection of ciliates in wet mounts or scrapings taken from the gills, skin or fins. Motile ciliates exhibit a gliding and circular rotating motion over substrates and they have a distinctive dorsoventrally-flattened ovoid body with an anterior notch. Ciliates may be enrobed on albuminized slides, fixed and stained with a variety of silver stains (silver nitrate, silver carbonate or silver proteinate (protargol) to highlight their nuclei and kineties (argentophilic basal bodies (kinetosomes)). Ciliates may also be cultured in the dark in liquid media, including filtered water with added rice grains or cereal (wheat) infusions with feeder bacteria (e.g. *Klebsiella*). Molecular biological techniques have been used to characterize ciliates following the polymerase chain reaction (PCR) amplification of nuclear (small subunit ribosomal DNA, 5.8S rDNA, internal transcribed spacer regions 1 and 2, beta-tubulin P3 (protein coding locus)) and mitochondrial (cytochrome c oxidase subunit 1) gene sequences.

Treatment and control: Clinical infections in fish have responded well to bath treatments with salt, formalin, hydrogen peroxide, potassium permanganate or copper sulphate solutions, but the fish become rapidly re-infected when returned to their source ponds or tanks. Where possible, aquaculture systems should be regularly flushed with clean water to remove planktonic ciliates as well as accumulated organic wastes, debris, and bacteria. Producers have sometimes resorted to draining and drying ponds to curb persistent infections. Parasites can multiply rapidly in favourable conditions and they infect fish more readily when hosts are stressed by suboptimal culture (e.g. crowded ponds, poor water quality, organic enrichment and bacterial blooms usually due to overfeeding). It is essential that fish be kept healthy in clean ponds so they are less susceptible to infection, and that any infected individuals be quickly identified and removed for treatment or culling.

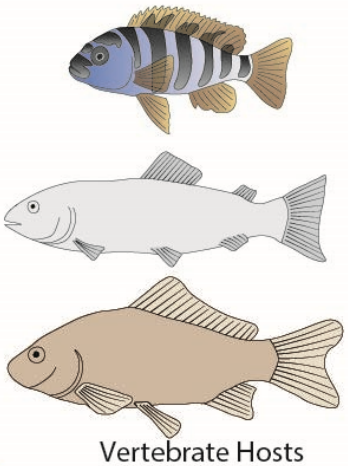
Chilodonella



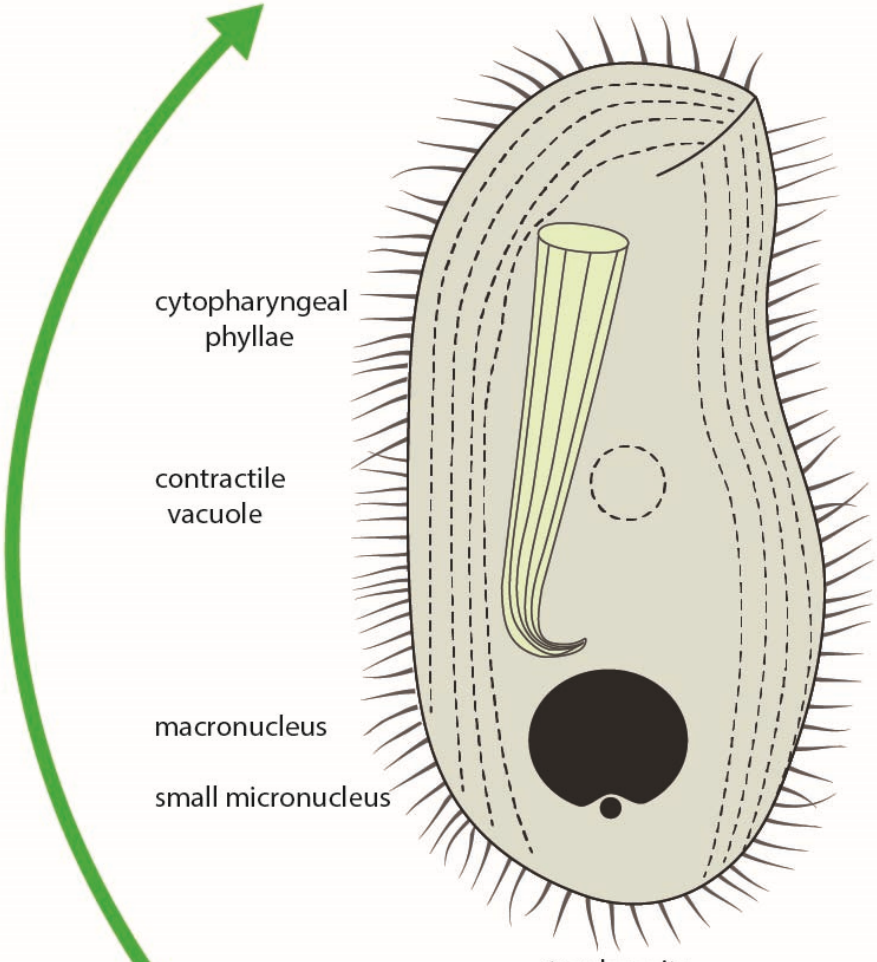
gills, skin
(irritation, inflammation,
congestion, lesions)

may reproduce asexually
(by transverse binary fission)
or sexually (by conjugation)

many free-living aquatic species
some facultatively/opportunistically parasitic
a few obligate parasites



Vertebrate Hosts
(freshwater fish)



trophozoite
(27-85 µm)

no cyst formation

direct transmission between hosts
via free-swimming trophozoites in water column



Chilodonella trophozoites on fish gill

Uronema
(protist: ciliate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Ciliated protozoa are unique eukaryotes as they exhibit nuclear dualism (vegetative macronucleus and reproductive micronucleus), the process of conjugation (exchange of micronuclei between pairs), have membrane-bound sacs (subpellicular alveoli) supporting the plasma membrane, and move using cilia (2+9 undulipodia with compound subpellicular infraciliature). Most ciliates are free-living in aquatic and terrestrial habitats, but some are symbiotic in vertebrate and invertebrate hosts. Ten major monophyletic lineages are recognized on the basis of their infraciliature, i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). Members of the subphylum Intramacronucleata are united by the presence of microtubules inside the macronuclear envelope during division; including the oligohymenophoreans ('few membrane-bearer') with an adoral zone of buccal (oral) ciliature. Scuticociliates have a small paroral membrane located on the right side of the buccal cavity and three membranelles on the left side, plus a characteristic postoral scuticum usually composed of barren kinetosomes. Philasterids have a short paroral dikinetid membrane and uronematids have small ovoid sparsely-ciliated bodies. *Uronema* spp. are mostly free-living aquatic organisms, but several species are facultative histophagous parasites of marine fishes, sometimes causing significant mortalities in farmed tuna.

Uronema
clickable life-cycle
one-page PDF: overview and life-cycle

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Ciliophora (with cilia, nuclear dualism, pellicular alveoli, reproductive conjugation)
Subphylum:	Intramacronucleata (microtubules occur inside macronuclear envelope during division))
Class:	Oligohymenophorea (distinct oral ciliature, comprising right paroral membrane and 3 left membranelles)
Subclass:	Scuticociliatia (with scuticum or scuticovestige)
Order:	Philasterida (short paroral dikinetid membrane)
Family:	Uronematidae (membranelles aligned with long axis, anterior pole non-ciliated)
Genus:	*Uronema* (opportunistic parasites in fish)
Species:	various species cause encephalitis in fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Ciliated protozoa are unique amongst the unicellular eukaryotes because they are the only group to exhibit nuclear dualism. Individual cells possess two different types of nuclei; vegetative macronuclei and reproductive micronuclei. Asexual reproduction occurs by transverse binary fission across rows of cilia (homothetogenic fission) whereas some species exhibit sexual reproduction by the phenomenon of conjugation (temporary fusion of two conjugates which exchange micronuclei). As their common name implies, ciliates are also characterized by the possession of simple cilia, or compound ciliary organelles, in at least one stage of their life cycles (compound subpellicular infraciliature is universally present even when cilia are absent). Cilia are elongate hair-like extensions of the cell membrane with an internal microtubular core (universal 2+9 configuration = 2 single central microtubules surrounded by 9 peripheral doublets). They are organelles of motility used for locomotion and/or feeding. Cilia (singular, cilium) are similar in ultrastructure to flagella (singular, flagellum), and they are collectively often called undulipodia (singular, undulipodium) because both use cross-linked proteins (dynein-walking mechanism) to undulate about their basal kinetosome (unlike the rotary motion unique to flagella in bacteria). Ciliates, together with dinoflagellates and apicomplexans, possess subpellicular alveoli which are membrane-bound sacs beneath the plasma membrane. Alveoli are thought to serve many varied functions: ranging from support (helping maintain body shape, act as fulcrum for undulipodia); metabolism (storage); osmoregulation (mucocysts); excretion (extrusomes); protection (toxicysts, trichocysts); and even hunting (haptocysts).

Most ciliate species are free-living in aquatic or terrestrial habitats but many are commensals in vertebrate or invertebrate hosts and some are parasitic. Early classification systems recognized three main classes of ciliates mainly on the basis of their patterns of somatic (body) and buccal (oral) ciliation. The 'lower holotrichs' have simple body and oral ciliature; most are free-living species but some are highly specialized symbionts aiding cellulose digestion in herbivores. The 'higher holotrichs' have simple body ciliature but more specialized oral ciliature forming membranelles; most occur as free-living organisms but some live as commensals or parasites in a range of animals. The 'spirotrichs' have reduced body ciliation but well-developed oral ciliature forming an adoral zone of membranelles; most are bactivores living in aquatic and terrestrial habitats. More recently, ten major monophyletic lineages have been recognized on the basis of their infraciliature; i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). These lineages (ranked as classes) have been well supported by modern molecular biological studies using several gene sequences.

Class	Etymology	Defining characters	Lifestyles*	Genera covered
Subphylum: **Postciliodesmatophora** [somatic dikinetids with postciliodesmata (overlapping microtubular ribbons)]				
Karyorelictea	'primitive-nucleus'	macronuclei not dividing but replaced by division of micronuclei	free-living (aquatic benthic/planktonic)	
Heterotrichea	'different-hair'	compound ciliary organelles around mouth, macronuclei divided by external microtubules	free-living (aquatic planktonic/benthic)	
Subphylum: **Intramacronucleata** [macronuclei divided by internal microtubules]				
Spirotrichea	'coiled-hair'	conspicuous right and left oral ciliature, left polykinetids leading into oral cavity	free-living (aquatic, terrestrial)	
Litostomatea	'simple-mouths'	cytostome with noncurved tubular cytopharyngeal apparatus (rhabdos)	free-living (often predatory), symbiotic	*Balantidium*
Phyllopharyngea	'leaf-throated'	mouth with radial microtubular ribbons (phyllae), some with sticky feeding tentacles	free-living (aquatic), epizoic, symbiotic	*Chilodonella*
Colpodea	'breast-shaped'	reniform bodies, somatic cilia with transverso-desmata (overlapping ribbons)	terrestrial, some aquatic (bactivores)	
Nassophorea	'pot-bearer'	oral nematodesmata well-developed (basket-like nasse or cyrtos supporting cytopharynx)	free-living (aquatic, terrestrial)	
Prostomatea	'before-mouth'	simple apical mouths, some with oral microtubular band, some with oral brush	free-living (often predatory)	
Plagiopylea	'misshapen-marker'	with twisted oral tubes, most with hydrogenosomes	free-living (anoxic habitats)	
Oligo-hymenophorea	'few membrane-bearer'	typically with ventral groove containing mouth and compound ciliary organelles (usually adoral zone of three membranelles)	free-living, epizoic, symbiotic (micro-phagous)	*Uronema, Ichthyophthirus, Tetrahymena, Trichodina, Vorticella*

*Symbiosis *sensu latu* ranges from commensalism, mutualism and parasitism (depending on the benefit/detriment to the host)

The class Oligohymenophorea contains ciliates whose somatic (body) kinetosomes (basal bodies) are associated with unique ultrastructural elements (collectively referred to as infraciliature) comprising anteriorly-directed overlapping kinetodesmal fibrils, divergent postciliary microtubular ribbons and radial transverse ribbons. Members are considered to be 'higher' holotrichs as there is clear distinction between the oral and somatic ciliature. They possess distinctive oral kineties consisting of a right paroral kinety (membrane) and typically 3 left oral polykinetids (membranelles) located in a buccal or infundibular cavity with an inconspicuous cytopharyngeal apparatus. They are widely distributed as free-living or symbiotic forms, although a few are parasitic mainly in fish. The class contains 6 subclasses (Apostomatia, Astomatia, Hymenostomatia, Peniculia, Peritrichia, Scuticociliatia) differentiated predominantly on the basis of their patterns of somatic and oral ciliation. Scuticociliates have a small paroral membrane located on the right side of the buccal cavity and three membranelles on the left side (paroral files (membranoids) of dikinetids with a, b and c segments), plus a characteristic postoral scuticum (or scutico-vestige) usually composed of barren kinetosomes. Three scuticociliate orders are recognized: Philasterida; Pleuronematida; and Thigmotrichida. Philasterids have elongate bodies with uniform somatic ciliation and a long caudal cilium as well as oral ciliature with a short paroral dikinetid membrane (typically by reduction of a and c segments). A total of 15 philasterid families are recognized, including the Uronematidae comprising 7 genera (*Homalogastra, Pseudouronema, Urocyclon, Uronema* (syn. *Uronemita*)*, Uronemella, Uronemopsis,* and *Uropedalium*) whose members have small ovoid sparsely-ciliated bodies with a long caudal cilium, a flat non-ciliated anterior pole with a long buccal area and oral membranelles aligned longitudinally. The genus *Uronema* contains both freshwater and marine species which are mostly free-living filter-feeding scavengers, but several species may become histophagous and opportunistically infect fish causing skin and/or gill lesions, sometimes invading internal organs (viscera and brain) with fatal consequences.

Uronema* **species**	**Length (µm) [no. somatic kineties]**	**Life-style (Hosts) [Clinical signs]**	**Distribution**
U. acutum	24-70 [9-14]	marine, free-living	North Sea
U. apomarinum	25-35 [12-13]	brackish water, free-living	China
U. castellonesis	28-38 [13]	freshwater, free-living	Europe
U. elegans (syn. *Cryptochilum*)	33-90 [21-27]	marine, free-living	Mediterranean
U. gallicum	20-30 [13-15]	marine, free-living	Europe
U. granulatum	25	freshwater, free-living	Europe
U. heteromarinum	25-50 [15-16]	marine, free-living	China
U. marinum [type species] (syn. *U. marina, schewiakoffi, Cohnilembus pusillus, Loxocephalus putrinus*)	19-60 x 7-27 [10-16]	marine, free-living (esp. amongst algae) and parasitic in skin, gills and viscera of fish (Acanthuriformes: acanthurid (yellow tang); Labriformes: labrid (California sheephead wrasse, red-lined wrasse, cunner); Moroniformes: moronid (European seabass); Perciformes: chaetodontid (pennant coralfish, teardrop butterflyfish, diagonal butterflyfish, threadfin butterflyfish, bluecheek butterflyfish, vagabond butterflyfish, copperband butterflyfish, longnose butterflyfish), opistognathid (yellowhead jawfish), pomacanthid (threespot angelfish, goldspotted angelfish, pygmy angelfish), pomacentrid (garibaldi, Vanderbilt's chromis, bluegreen damselfish, maroon clownfish, tomato clownfish), pseudochromid (orchid dottyback), serranid (sea goldie); Pleuronectiformes: paralichthyid (olive flounder), scophthalmid (turbot); Salmoniformes: salmonid (Atlantic salmon); Scombriformes: stromateid (silver pomfret); Scorpaeniformes: scorpaenid (lionfish); Syngnathiformes: syngnathid (lined seahorse, yellow seahorse); Tetraodontiformes: tetraodontid (Japanese puffer)] [lesions, respiratory distress, death]	worldwide (patchy)
U. nigricans (syn. *Cyclidium, U. parduczi*)	21-29 [11-16]	freshwater/marine, free-living and parasitic in gills and brain of fish (Cyprinodontiformes: poeciliid (guppy); Carangiformes: carangid (yellowtail amberjack); Scombriformes: scombrid (southern bluefin tuna)) [lesions, respiratory distress, swimmer syndrome, death]	worldwide (patchy)
U. orientalis	25-58 [15-20]	marine, free-living	China
U. pluricaudatum		marine, free-living	Europe
U. rabaudi	40	marine, epizoic on carapace of invertebrates (Copepoda: acartid (*Acartia clausi*), clausiid (*Clausia elongata*))	Europe
U. tortum (syn. *Cryptochilum*)	36-58 [6-8]	marine, free-living	Mediterranean

Several free-living species previously assigned to the genus *Chilodonella* have since been reassigned to other genera: including *U. biceps* [= *Balanonema*]; *U. digitiformis* [= *Philasterides*]; *U. filificum* [= *Uronemella*]; *U. microcrepis* [= *Dexiotrichides*]; and *U. sociale* [= *Platynematum*]. *Confusingly, the genus name *Uronema* (and some species names, e.g. *U. marinum*) are shared in the botanical nomenclature with some epiphytic microfilamentous green algae (Chlorophyceae: Chaetophorales: Uronemataceae) living in freshwater and marine environments (viz: *U. acuminatum, africanum, belkae, brasiliense, confervicola, curvatum, elongatum, falcatum, indicum, intermedium, marinum, minutum, simplicissimum, subelongatum, terrestre* and *trentonense*).

Parasite morphology: *Uronema* spp. form motile trophic stages (trophozoites) that swim continuously in the water column using holotrichous (whole body) ciliation. Cyst formation has not been reported. Trophozoites are typically ovoid-ellipsoid (sometimes pyriform) in shape with a rounded posterior and a truncated anterior end (flattened and nonciliated). Free-swimming ciliates are more slender and transparent than those recovered from fish which are robust and opaque. Trophozoites vary in size from 20-50 µm in length depending on their nutritional state (well fed individuals being more rotund) and species (*U. marinum* 30-50 x 10-20 µm;

U. nigricans 20-34 x 12-20 µm). The ciliates are clearly hymenostomes with well-defined oral and somatic ciliature. Members of the genus *Uronema* have a large shallow buccal cavity located in the upper half of the body, surrounded by distinctive rows of cilia forming a paroral undulating membrane and 3 membranelles aligned with the long axis of the body. Like other members of the suborder Philasterina, the undulating membranes were shorter than the other oral structures and they were not reinforced by ribbed walls. The first membranelle consisted of one row of basal bodies (kinetosomes), the second and third membranelles had 2 or more longitudinal rows, and the paroral membrane extended forward to the anterior end of the second membranelle. A distinctive scuticum (consisting of several basal body pairs) was located immediately below the oral structures (characteristic for all scuticociliates). The cell body was uniformly covered with longitudinal rows (kineties) of short somatic cilia, except for the nonciliated anterior pole. The number of kineties ranged from 6-27 depending on the species, with *U. marinum* and *U. nigricans* typically having 10-16. Each row of cilia had 12-32 kinetids, with the anterior half being dikinetids (paired basal bodies) and the posterior half being monokinetids (single basal bodies). Trophozoites also possessed a long prominent caudal cilium, being 1-2 times the length of the body. Cells contained a single large ovoid macronucleus and a small round adjacent micronucleus, both located just anterior to the midbody. Trophozoites contained a single translucent contractile vacuole located near the posterior pole, and their cytoplasm appeared granular due to the presence of food vacuoles in the posterior half of the body. While cyst formation has not been observed, experimental studies on *U. marinum* cultures have shown that starved trophozoites undergo 2-3 successive cell divisions forming 4-8 small slender 'swarmer' cells to aid dispersion.

Site of infection: All *Uronema* spp. are free-living filter-feeding scavengers in aquatic environments, 9 species occurring in marine waters (including *U. marinum*), 2 in freshwater, one in brackish water, and one (*U. nigricans*) in marine and freshwater. Both *U. marinum* and *U. nigricans* may also occur as opportunistic histophagous parasites in the tissues of fish, particularly ornamental and farmed species. Infections have been recorded in some 35 fish species belonging to 19 families in 12 families (mainly in Perciformes, but also in Acanthuriformes, Carangiformes, Cyprinodontiformes, Labriformes, Moroniformes, Pleuronectiformes, Salmoniformes, Scombriformes, Scorpaeniformes, Syngnathiformes and Tetraodontiformes). Parasitic ciliates may be found in fish in the gills, skin, musculature and internal organs (viscera and brain).

Pathogenesis: Scuticociliates may cause clinical disease (known generally as scuticociliatosis or scutica infection) in a range of fish, crustaceans and molluscs. Two *Uronema* spp. opportunistically infect fish causing superficial and/or systemic disease (generically known as uronemosis, with specific regional variants such as red band disease in ornamental fish, red sores in damselfish, or blue swimmer syndrome in tuna). When free-living bactivorous trophozoites come into contact with fish, they may attach to superficial surfaces (skin and gills) but may sometimes invade to deeper tissues (muscles, viscera, brain) causing significant disease and mortality. Trophozoites break down host tissues using proteolytic enzymes and they feed on the resultant cellular debris as well as on host erythrocytes. Ciliate secretions also appear to impair host cellular responses by inhibiting or neutralizing the respiratory burst activity used by phagocytes to kill pathogens. Feeding trophozoites may cause white slimy necrotic skin patches which progress to areas of depigmentation, scale loss, haemorrhagic lesions, or open ulcerated wounds (red sores). Infections in ornamental aquarium fish may also involve behavioural abnormalities (rubbing skin on substrates, hiding, listlessness, disorientation) and breathing difficulties (gasping, gaping, gulping) resulting in some mortalities. Parasite may also enter the bloodstream through lesions and invade the musculature, stomach, intestines, liver, spleen, brain, spinal canal, kidneys or urinary bladder, with infections often becoming systemic and causing extensive degeneration, necrosis, haemorrhages, cellular vacuolization, inflammation, granuloma formation, epithelial hyperplasia, abdominal swelling, reddened ascites, muscular oedema, necrotizing myositis, meningitis, olfactory neuritis, perineuritis and brain liquefaction. Trophozoites are thought to first invade olfactory rosettes and then track along branches of the olfactory nerve to enter brain. Intraocular infections can lead to exophthalmos (bulging) with the eyes becoming cloudy and possibly leading to blindness. Infected fish may exhibit locomotory dysfunction, respiratory distress, compulsive vigorous or erratic swimming, discolouration (blue swimmer syndrome in tuna), rapid loss of condition and death may occur within days of infection (due to cumulative respiratory, excretory and neural dysfunction). Risk factors for disease include stressed and immunocompromised fish (due to captivity, poor nutrition, poor water quality), particularly cultured or aquarium fish which are crowded in unhygienic conditions (often due to bacterial blooms due to overfeeding).

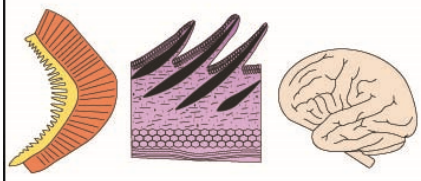
Developmental cycle and mode of transmission: *Uronema* spp. are free-living ciliates aquatic environments where they filter feed on bacterial flora, being commonly found among decaying algae. Trophozoites are able to survive in water over a wide range of temperatures (6-30°C) and salinities (10-35 ppt), with optimal growth occurring when bacteria are plentiful in waters ranging from 10-25°C. When food is abundant, they are able to multiply rapidly (within several hours) by asexual transverse binary fission. When food becomes limited, they may initiate sexual reproduction by conjugation involving pairs fusing anteriorly and exchanging genetic material (micronuclei). Some *Uronema* spp. also exhibit a starvation response whereby they rapidly divide to form small slender cells that begin rapid erratic 'swarming' behaviour and may survive starvation for 100-170 hours (i.e. the equivalent of ~ 45 generations of well-fed cells). It is thought swarming increases the likelihood of ciliates encountering hosts with higher body temperatures more suitable for growth and development. Only 2 species (*U. marinum* and *U. nigricans*) have been found to opportunistically infect fish, especially stressed and immunocompromised fish due to recent capture, transport, poor diet, crowded culture, or concomitant infections. Transmission between fish is direct via free-swimming stages in the water column. Ciliates are released from live and dead fish back into aquatic environments where they can survive for long periods as free-living individuals or they can opportunistically infect new susceptible fish. Some infected fish may act as asymptomatic carriers, with disease only

developing in highly susceptible species or compromised individuals (especially in ornamental aquarium fish). Many infections in cultured fish species (particularly southern bluefin tuna) occur during the winter when water temperatures drop below 15-18°C.

Differential diagnosis: Infections may be indicated by the presence of suspicious lesions on fish surfaces with behavioural changes suggesting breathing difficulties. Diagnosis is reliant, however, on the direct microscopic detection of parasitic ciliates in host tissues, including skin scrapings, lesion biopsies, gill clippings, blood, cerebrospinal fluid, diced organs and tissue fragments. Samples may be examined as wet mounts, impression smears, squash preparations, or histological sections of fixed tissues. Live ciliates may be counter-stained with methyl-green pyronin to reveal nuclei, but they are best enrobed on albuminized slides and subject to silver staining (usually silver proteinate (protargol), but also silver carbonate and silver nitrate) to reveal oral and somatic ciliary patterns (basal bodies are strongly argentophilic). Clinical biochemical studies conducted on infected tuna revealed nonspecific elevations in serum protein, magnesium, sodium, chloride, cortisol and glucose, with reduced levels of potassium. Trophozoites readily adapt to cultivation in the laboratory in filtered water or tissue broth infusions so long as bacteria are added as a food source (usually *Vibrio* strains in marine systems, *Enterobacter* in freshwater systems). Several attempts have been made to develop specific antibody labels to help identify ciliates in clinical samples, but most exhibited problems with reagent cross-reactivity. Molecular biological techniques have been used to detect and characterize ciliates following the polymerase chain reaction (PCR) amplification of nuclear (small subunit ribosomal DNA) and mitochondrial (cytochrome c oxidase subunit 1) gene sequences.

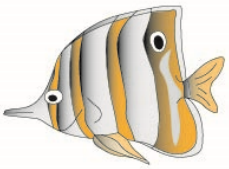
Treatment and control: Infections in fish may be superficial and/or systemic, the former responding in some cases to chemotherapy, while treatment of the latter is ineffective due to the speed and severity of disease. Fish with topical infections have been treated by bathing in various chemicals (formalin, malachite green, methylene blue, copper, acriflavine, hydrogen peroxide), fed foods medicated with nitroimidazoles (metronidazole) or dosed internally (stomach tube or injections) with metronidazole, and even some anti-malarial drugs (chloroquine, quinacrine). Concurrent antibiotic therapy (e.g. nitrofurazone) was often used as secondary bacterial infections were common in skin and gill lesions. Many of the chemicals used, however, exhibited some toxicity to fish with the development of adverse side-effects, and treated fish often became rapidly re-infected when returned to their source waters. There is no fallow (fishless) period that can be used to combat *Uronema* infections, as the parasites can survive in tanks almost indefinitely once present. Control measures must therefore be adopted to decontaminate culture facilities and aquaria, prevent the introduction and growth of parasites in holdings, and help fish resist infections by avoiding stressful situations. Clean water (filtered and chlorinated where possible) should be used to rear and hold fish, with good flow and regular exchange. Ozonation and ultraviolet illumination have been used in aquaria to kill ciliates, although best results are obtained by draining and drying tanks before restocking. Sea cages should be regularly moved to avoid the accumulation of organic wastes, and they should be periodically treated for biofouling. Fish should be subject to regular health screening and new stock should be held in quarantine. In the event of disease outbreaks, sick fish should be promptly removed and/or culled and carcases removed for land disposal (burn or bury). Immunocompromised fish are more susceptible to infection and disease, so every effort should be made to minimize stressful events (capture, handling, sudden changes in environment) and eliminating predisposing factors (over-stocking, poor water quality, poor nutrition, organic enrichment through over-feeding leading to bacterial blooms). Experiments have also shown that some dietary immunostimulants (such as plants extracts from *Punica granatum*, *Chrysanthemum cinerariaefolium* or *Zanthoxylum shinifolium*) enhanced the innate immunity of olive flounder and improved their survival to challenge with *U. marinum*. Experimental vaccination studies have yielded some promising results when variable surface proteins on trophozoites known as immobilization antigens (i-antigens) were bound to PLGA nanoparticles (poly d,l-lactide-co-glycolic acid) and inoculated into kelp groupers where they significantly reduced mortalities when challenged with *U. marinum.*

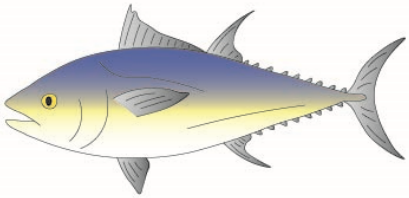
Uronema



gills, skin, brain, viscera
(necrosis, haemorrhages,
lesions, encephalitis)

may reproduce asexually
(by transverse binary fission)
or sexually (by conjugation)





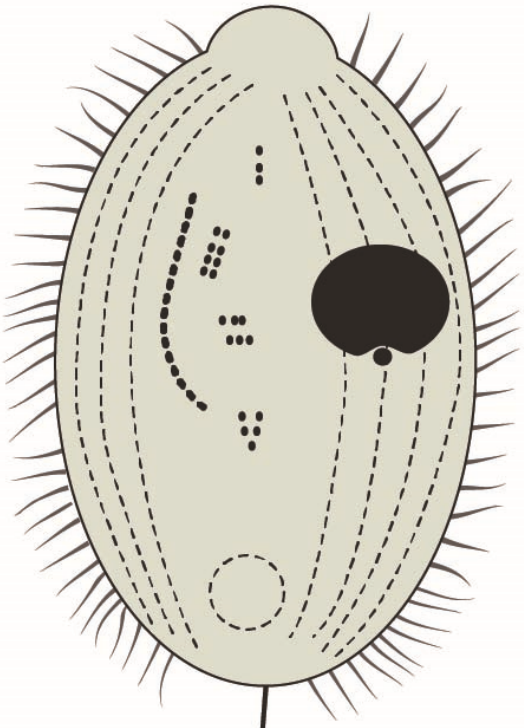
Vertebrate Hosts
(freshwater and
marine fish)

mostly free-living aquatic species,
some facultative histophagous parasites

oral ciliature:
paroral membrane
and 3 membranelles

post-oral scuticum

somatic ciliature:
10-16 longitudinal
kineties



macronucleus

micronucleus

contractile vacuole

long caudal
cilium

trophozoite
(20-50 µm)

no cyst formation

direct transmission between hosts
via free-swimming trophozoites in water column



Uronema trophozoite from salmon sea-cage



Uronema trophozoite from salmon skin (silver stain)

Ichthyophthirius
(protist: ciliate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Ciliated protozoa are unique eukaryotes as they exhibit nuclear dualism (vegetative macronucleus and reproductive micronucleus), the process of conjugation (exchange of micronuclei between pairs), have membrane-bound sacs (subpellicular alveoli) supporting the plasma membrane, and move using cilia (2+9 undulipodia with compound subpellicular infraciliature). Most ciliates are free-living in aquatic and terrestrial habitats, but some are symbiotic in vertebrate and invertebrate hosts. Ten major monophyletic lineages are recognized on the basis of their infraciliature, i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). Members of the subphylum Intramacronucleata are united by the presence of microtubules inside the macronuclear envelope during division; including the oligohymenophoreans ('few membrane-bearer') with an adoral zone of buccal (oral) ciliature. Hymenostomes have a paroral membrane located on the right side of the buccal cavity and three membranelles on the left side, while their bodies are mostly covered by uniform somatic ciliature. Ophryoglenines have a buccal cavity opening at the bottom of a deep depression and they possess a lens-like (watchglass) organelle. Ichthyophthiriids are monoxenous (one-host) ectoparasites of fishes. Trophonts infect epithelial tissues, often causing visible lesions evident as white spots (disease known as freshwater whitespot, ichthyophthiriosis or simply 'ich'). When replete, they leave the host and form encysted stages (tomonts) in the external environment. These cysts produce hundreds of infective stages (tomites) which are released as swarmers (theronts) which actively seek new hosts.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Ciliophora (with cilia, nuclear dualism, pellicular alveoli, reproductive conjugation)
Subphylum:	Intramacronucleata (microtubules occur inside macronuclear envelope during division))
Class:	Oligohymenophorea (distinct oral ciliature, comprising right paroral membrane and 3 left membranelles)
Subclass:	Hymenostomatida (right paroral dikinetid plus 1-3 left polykinetids)
Order:	Hymenostomatida (preoral suture, somatic monokinetids)
Suborder:	Ophryoglenina (with organelle of Lieberkuhn (watchglass organelle))
Family:	Ichthyophthiriidae (monoxenous ectoparasites, form encysted tomonts which release swarmers/theronts)
Genus:	*Ichthyophthirius* (ectoparasitic on skin/gills of fish)
Species:	*I. multifiliis* (causes whitespot disease ('ich') in freshwater fishes)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Ciliated protozoa are unique amongst the unicellular eukaryotes because they are the only group to exhibit nuclear dualism. Individual cells possess two different types of nuclei; vegetative macronuclei and reproductive micronuclei. Asexual reproduction occurs by transverse binary fission across rows of cilia (homothetogenic fission) whereas some species exhibit sexual reproduction by the phenomenon of conjugation (temporary fusion of two conjugates which exchange micronuclei). As their common name implies, ciliates are also characterized by the possession of simple cilia, or compound ciliary organelles, in at least one stage of their life cycles (compound subpellicular infraciliature is universally present even when cilia are absent). Cilia are elongate hair-like extensions of the cell membrane with an internal microtubular core (universal 2+9 configuration = 2 single central microtubules surrounded by 9 peripheral doublets). They are organelles of motility used for locomotion and/or feeding. Cilia (singular, cilium) are similar in ultrastructure to flagella (singular, flagellum), and they are collectively often called undulipodia (singular, undulipodium) because both use cross-linked proteins (dynein-walking mechanism) to undulate about their basal kinetosome (unlike the rotary motion unique to flagella in bacteria). Ciliates, together with dinoflagellates and apicomplexans, possess subpellicular alveoli which are membrane-bound sacs beneath the plasma membrane. Alveoli are thought to serve many varied functions: ranging from support (helping maintain body shape, act as fulcrum for undulipodia); metabolism (storage); osmoregulation (mucocysts); excretion (extrusomes); protection (toxicysts, trichocysts); and even hunting (haptocysts).

Most ciliate species are free-living in aquatic or terrestrial habitats but many are commensals in vertebrate or invertebrate hosts and some are parasitic. Early classification systems recognized three main classes of ciliates mainly on the basis of their patterns of somatic (body) and buccal (oral) ciliation. The 'lower holotrichs' have simple body and oral ciliature; most are free-living species but some are highly specialized symbionts aiding cellulose digestion in herbivores. The 'higher holotrichs' have simple body ciliature but more specialized oral ciliature forming membranelles; most occur as free-living organisms but some live as commensals or parasites in a range of animals. The 'spirotrichs' have reduced body ciliation but well-developed oral ciliature forming an adoral zone of membranelles; most are bactivores living in aquatic and terrestrial habitats. More recently, ten major monophyletic lineages have been recognized on the basis of their infraciliature; i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). These lineages (ranked as classes) have been well supported by modern molecular biological studies using several gene sequences.

Class	Etymology	Defining characters	Lifestyles*	Genera covered
Subphylum: **Postciliodesmatophora** [somatic dikinetids with postciliodesmata (overlapping microtubular ribbons)]				
Karyorelictea	'primitive-nucleus'	macronuclei not dividing but replaced by division of micronuclei	free-living (aquatic benthic/planktonic)	
Heterotrichea	'different-hair'	compound ciliary organelles around mouth, macronuclei divided by external microtubules	free-living (aquatic planktonic/benthic)	
Subphylum: **Intramacronucleata** [macronuclei divided by internal microtubules]				
Spirotrichea	'coiled-hair'	conspicuous right and left oral ciliature, left polykinetids leading into oral cavity	free-living (aquatic, terrestrial)	
Litostomatea	'simple-mouths'	cytostome with noncurved tubular cytopharyngeal apparatus (rhabdos)	free-living (often predatory), symbiotic	*Balantidium*
Phyllopharyngea	'leaf-throated'	mouth with radial microtubular ribbons (phyllae), some with sticky feeding tentacles	free-living (aquatic), epizoic, symbiotic	*Chilodonella*
Colpodea	'breast-shaped'	reniform bodies, somatic cilia with transverso-desmata (overlapping ribbons)	terrestrial, some aquatic (bactivores)	
Nassophorea	'pot-bearer'	oral nematodesmata well-developed (basket-like nasse or cyrtos supporting cytopharynx)	free-living (aquatic, terrestrial)	
Prostomatea	'before-mouth'	simple apical mouths, some with oral microtubular band, some with oral brush	free-living (often predatory)	
Plagiopylea	'misshapen-marker'	with twisted oral tubes, most with hydrogenosomes	free-living (anoxic habitats)	
Oligo-hymenophorea	'few membrane-bearer'	typically with ventral groove containing mouth and compound ciliary organelles (usually adoral zone of three membranelles)	free-living, epizoic, symbiotic (micro-phagous)	*Uronema, Ichthyophthirus, Tetrahymena, Trichodina, Vorticella*

*Symbiosis *sensu latu* ranges from commensalism, mutualism and parasitism (depending on the benefit/detriment to the host)

The class Oligohymenophorea contains ciliates whose somatic (body) kinetosomes (basal bodies) are associated with unique ultrastructural elements (collectively referred to as infraciliature) comprising anteriorly-directed overlapping kinetodesmal fibrils, divergent postciliary microtubular ribbons and radial transverse ribbons. Members are considered to be 'higher' holotrichs as there is clear distinction between the oral and somatic ciliature. They possess distinctive oral kineties consisting of a right paroral kinety (membrane) and typically 3 left oral polykinetids (membranelles) located in a buccal or infundibular cavity with an inconspicuous cytopharyngeal apparatus. They are widely distributed as free-living or symbiotic forms, although a few are parasitic mainly in fish. The class contains 6 subclasses (Apostomatia, Astomatia, Hymenostomatia, Peniculia, Peritrichia, Scuticociliatia) differentiated predominantly on the basis of their patterns of somatic and oral ciliation. The hymenostomes have a well-defined buccal cavity and conspicuous oral ciliature evident as a paroral membrane of dikinetids on the right side and 1-3 left polykinetids (membranelles) on the left side, while their bodies are mostly covered by somatic ciliature. The single order Hymenostomatida contains 2 suborders: Ophryoglenina (cells with dense somatic ciliature, preoral sutures, buccal cavity opening at the bottom of a deep depression, presence of a unique lens-like organelle of Lieberkuhn (watchglass organelle), and teloparakinetal stomatogenesis); and Tetrahymenina (cells with uniform somatic ciliature, inconspicuous oral cavity (except in species that undergo macrostome transformation), absence of organelle of Lieberkuhn, and monoparakinetal stomatogenesis). Ophryoglenines also exhibit division whilst free-swimming or by palintomy within cysts. The ciliates may also develop into histophagous forms which feed on other aquatic organisms (invertebrates and vertebrates). Two families are recognized: Ichthyophthiriidae (monoxenous (one-host) ectoparasites of fishes)); and Ophryoglenidae (monoxenous parasites on the tissues of molluscs and other invertebrates). Both families form feeding trophonts which drop off their hosts to form encysted tomonts that divide internally into tomites which are then released as swarmers (theronts). The genus *Ichthyophthirius* (syn. *Chromatophagus, Ichthyophthirioides*) in monotypic with the single species *I. multifiliis* causing skin lesions (freshwater white spot disease) on ornamental, farmed and wild freshwater

fishes. It is thought to have originated in Asia on carp but now has a global distribution on a wide range of fish species. It has extremely low host specificity (euryxenous) and can infect virtually any freshwater fish species. It is an important pathogen in temperate and tropical regions and causes significant economic losses in many aquaculture industries, including the ornamental fish trade, and epizootics in wild fish populations resulting in mass mortalities. There is some conjecture about the existence of different parasite races, which may have different temperature tolerances, being adapted to hosts with specific temperature preferences, or they may be geographic races varying in virulence in introduced and/or endemic fish species. Several reports have been made of 'ich'-like parasites (*Ichthyophthiriodes browni* and *Neoichthyophthirius scholtfeldti*) from tropical freshwater fish, and a similar parasite, *Cryptocaryon irritans* (originally classified as *I. marinus*) found on marine fish and associated with marine white spot disease. Despite many similarities in ciliate biology, molecular phylogenetic studies have found that *Cryptocaryon* is more closely related to protostome ciliates than to the hymenostomes like *Ichthyophthirius*.

***Ichthyophthirius* species**	**Hosts**	**Location (Clinical signs)**	**Distribution**
I. multifiliis (syn. *I. cryptostomus, Chromatophagus parasiticus*) [type species]	freshwater fish (Anguilliformes: anguillid (short-finned eel, African longfin eel); Atheriniformes: melanotaeniid (eastern rainbowfish, Lake Eacham rainbowfish); Characiformes: acestrorhynchid (red-tailed freshwater barracuda, big-eyed cachorro), characid (banded tetra, black tetra, feather tetra, cardinal tetra), erythrinid (wolf fish, gold wolf fish), gasteropelecid (black-winged hatchetfish, marbled hatchetfish), lebiasinid (diptail pencilfish, one-lined pencilfish), serrasalmid (tambaqui, pirapitinga, small-scaled pacu), triportheid (dusky narrow hatchetfish, curtus hatchetfish); Cichliformes: cichlid (oscar, blue tilapia, Nile tilapia, Mossambique tilapia, saddle cichlid, convict cichlid, royal acara cichlid, dwarf cichlid, flag cichlid, perunsukkula-ahven, angelfish, blue discus, red discus); Clupeiformes: dorosomatid (threadfin shad, American gizzard shad); Cypriniformes: cyprinid (goldfish, common carp, grass carp, mrigal carp, silver carp, bighead carp, common barbel, shabout, common chub, roundtail chub, barbel chub, Papaloapan chub, tench, redtail barb, straightfin barb, smallmouth yellowfish, Caucasian scraper, Levantine scraper, bhakura, zebrafish, rohu, Levantine barbel, common snowtrout); Cyprinodontiformes: cyprinodontid (Soffia toothcarp, leukakilli), fundulid (blackstripe topminnow), goodeid (splitfin, relict splitfin), poeciliid (twospot livebearer, porthole livebearer, sailfin molly, short-finned molly, guppy, green swordtail, moonfish); Esociformes: esocid (northern pike); Galaxiiformes: galaxiid (common galaxias, climbing galaxias); Gobiiformes: eleotrid (giant bully), gobiid (round goby, monkey goby, bighead goby); Moroniformes: moronid (white bass, striped bass); Mugiliformes: mugilid (greenback mullet, flathead grey mullet); Osmeriformes: retropinnid (Australian smelt); Osteoglossifoirmes: osteoglossid (arapaima, silver arowana); Perciformes: chaetodontid (butterflyfish), latid (barramundi), percichthyid (Murray cod, trout cod. golden perch, Macquarie perch, river blackfish), percid (yellow perch), terapontid (silver perch); Salmoniformes: salmonid (rainbow trout, brown trout, brook trout); Scorpaeniformes: gasterosteid (three-spined stickleback); Siluriformes: clariid (African sharptooth catfish, vundu), claroteid (golden Nile catfish), heptapterid (South American catfish), ictalurid (channel catfish), loricariid (common pleco, tiger pleco, starlight bristlenose pleco), pangasiid (Pangas catfish), pimelodid (sailfin pim, spotted sorubim, barred sorubim), plotosid (eel-tailed catfish), sisorid (south sisorid catfish); Synbranchiformes: mastacembelid (Euphrates spiny eel); Anura: limnodynastid (striped marsh frog, tadpoles)	skin, fins, gills, eyes ('ich' = whitespot disease, death)	worldwide (esp. aquaria, culture ponds)

Parasite morphology: The parasite *I. multifiliis* forms three developmental stages: trophonts, tomonts containing tomites, and theronts. Trophonts on fish are variable in size (from 30 µm up to 1-1.5 mm in diameter) and possess a horseshoe-shaped

macronucleus encircling a single micronucleus (although up to four micronuclei have been observed). Depending on their size, the trophonts have may up to 2,000 meridional (longitudinal) rows of somatic (body) cilia (kineties) interrupted only by a subapical vestibulum (mouth) with up to 15 buccal (oral) kineties lining the cylindrical prebuccal space. The trophonts possess many peripheral mucocysts (crystalline and secretory), several contractile vacuoles (water regulation organelles) and a unique anterior discoid body known as Lieberkuhn's (or watchglass) organelle (complex photo-receptive structure absent in the marine species *Cryptocaryon irritans*). As trophonts feed and grow, Lieberkuhn's organelle disappears and the cell fills with vacuoles (food, lipid, glycogen, protein). When replete, trophonts leave the host and form free tomonts which become encysted on available substrates. The tomonts begin internal division and repeatedly divide to form 250-2,000 smaller tomites. The tomites are mouthless but have active somatic cilia which keeps them spinning within the cyst. The tomites eventually break through the cyst wall to become free-swimming cylindrical theronts (swarmers) that actively seek hosts. Theronts range in size from 25-70 x 15-22 µm and are covered with 36-48 meridional kineties converging anteriorly around the pre- and post-oral sutures. The pre-oral suture forms an elevated pellicular crest raised apically into a pointed elevation (perforatorium) used to penetrate host tissues. Theronts possess an ellipsoidal macronucleus with an adjacent spherical micronucleus, one contractile vacuole with several excretory pores, a single anterior Lieberkuhn's organelle and a long caudal cilium.

Site of infection: Trophonts may infect the epidermis, gill filaments, cornea, mouth and tongue of their fish hosts. They generally occur in surface epithelia adjacent to the basal lamina, but invasions into subepidermal tissues may occur in advanced stages of disease.

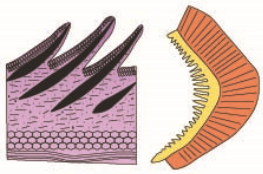
Pathogenesis: *I. multifiliis* causes freshwater white spot disease known as ichthyophthiriosis (or 'ich') in freshwater fishes. Theronts use the elevated pointed ridge (perforatorium) to penetrate host tissues and they discharge mucocysts to form a sticky envelope glued to the host's epithelium. Within minutes, the parasites penetrate deeper into epithelial or epidermal tissues where they feed (exhibiting intense phagocytic activity) and grow (increasing their volume up to 3,000 times). The trophonts cause significant tissue damage as a result of histolysis and trauma and usually form grey-white pustules in the skin of their hosts. Infected fish produce excess mucus to combat the irritation but many epidermal cells are destroyed and are sloughed. In some tropical fishes, pustules are not formed and the ciliates remain free on the surface or burrow into the epithelium. In other fishes, the parasites may form nonpurulent 'pustules' characterized by epithelial hyperplasia. Irrespective of lesion type, skin damage often predisposes to secondary bacterial infections. Heavy infections of the gill filaments may also interfere with gas exchange and may prove fatal. Lesions containing engorging trophonts appear as visible white spots up to 1-1.5 mm in diameter. Affected fish are anorexic and lethargic and may exhibit respiratory difficulties (gulping air, increased opercular flaring, crowding inlets) and 'flashing' (rapid turning to expose belly, often involving contact with substrates). Fish surviving infection exhibit some protective immunity against subsequent infections, with many disease outbreaks (epizootics) appearing cyclic (seasonal) due to the waxing and waning of protective immunity in fish populations and age-cohorts. While parasite densities are generally low in wild fish populations, heavy infections may develop in closed systems with reticulated water supplies (aquaria, tanks, ponds) leading to mass mortalities and significant economic losses. Disease risk factors include host susceptibility (some host species are more resistant than others), physiological condition (suboptimal due to poor nutrition, over-crowding, spawning, chemical pollutants, and other stressors), immunological status (varies with age and previous exposure) and environmental conditions (particularly poor water quality and warming waters over spring).

Developmental cycle and mode of transmission: Parasites are not transmitted directly from fish to fish, but rather via contamination of the water by dividing stages which release free-swimming stages that actively seek new hosts. Engorged trophonts of *I. multifiliis* are liberated from ruptured pustules on fish into the water column where they settle on convenient substrates or on the bottom. Within hours, they form a gelatinous cyst (tomont) which undergoes a series of 10-12 divisions (repeated binary fission) without intervening growth thus producing numerous equally-sized tomites (250-2,000 per cyst). [*C. irritans* produces fewer tomites per cyst (< 200) and they are smaller cells cleaved from the larger tomont]. Tomonts complete division within 24 hours at 15-25°C but up to 6 days at 5°C. Tomites are then released to become free-swimming theronts which actively search for new hosts. Theronts generally survive for up to 24 hours but their infectivity decreases after 12 hours. When theronts infect suitable hosts, they transform to trophonts which usually feed for around 7 days at 20ºC, although they can persist for several weeks or even months at lower temperatures. The number, size and duration of the life-cycle stages for either species depends upon prevailing environmental conditions, particularly temperature (no development occurs below 2°C or above 30°C). The whole life-cycle may be completed in as little as 3-8 days at 23-24°C, but it progressively takes longer at lower temperatures (up to 3 months at 4-5°C).

Differential diagnosis: Infections are diagnosed by the detection of characteristic pustules on the external surfaces of fish and then confirmed microscopically by observing trophonts in fresh wet tissue preparations. Pustules are generally white to grey in colour and variable in size and shape. In heavy infections, the skin may become thickened, ulcerative and/or necrotic with flaking scales. Trophonts appear heavily ciliated and contain a distinctive large horseshoe-shaped macronucleus. Various molecular techniques have been utilized to characterize ciliate isolates; including immunoblot analyses of immobilization antigens, and polymerase chain reaction (PCR) amplification of partial DNA sequences (18S small subunit (SSU) ribosomal DNA); but such tests are restricted in use to molecular epidemiology or immunology research rather than diagnostics.

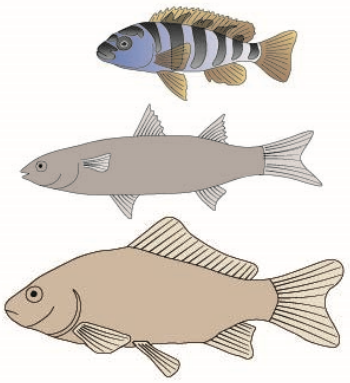
Treatment and control: Seasonal variations observed in the prevalence of *Ichthyophthirius* infections have been attributed to seasonal differences in water quality and the abundance of susceptible hosts. The prevalence and severity of infections is often exacerbated by poor water quality and/or overstocking which stresses fish and affects their susceptibility. While ciliates do not multiply on their hosts, their numbers amplify greatly in water sources through tomont/tomite division and theront release. Many outbreaks have been associated with the introduction of new stock and closed culture systems are particularly at risk of sustained contamination. Quarantining new stock, destocking and resting ponds and periodic flushing of tanks and ponds with clean fresh water have all been shown to reduce contamination levels. Water treatment strategies used to prevent infections by reducing theront production and survival have included raising water temperature (usually possible only in aquaria or small tanks) or adding salt (to increase salinity), quicklime (to increase pH) or toxic chemicals (chlorine, chloramine, formalin, potassium permanganate, copper sulphate, silver nitrate, sodium percarbonate, methylene blue, ronidizole, bronopol). There is currently no acceptable curative drug for inclusion in fish food, although preliminary studies with antiprotozoals (quinine, toltrazuril, salinomycin, secnidazole, amprolium, metronidazole) and immune enhancers (ascorbic acid) have shown promise. Diseased fish infected with trophonts have been treated by bathing in dilute concentrations of toxic chemicals (formalin, malachite green, methylene blue, copper sulphate, hydrogen peroxide, peracetic acid). However, most of these chemicals are not appropriate for fish destined for human consumption and others are contraindicated for aquaria fish due to toxicity issues. Repeat treatments are often required, the frequency depending on their efficacy as well as the multiplicative potential of the parasites (kinetics and dynamics dependent on water temperature). Previous infections have been shown to impart some protective immunity to fish against subsequent re-infection and experimental studies have been relatively successful in protecting fish vaccinated with various ciliate extracts, especially those containing immobilization (i-) antigens. However, the logistics and mechanics of vaccine production and delivery in aquatic systems remain problematic.

Ichthyophthirius



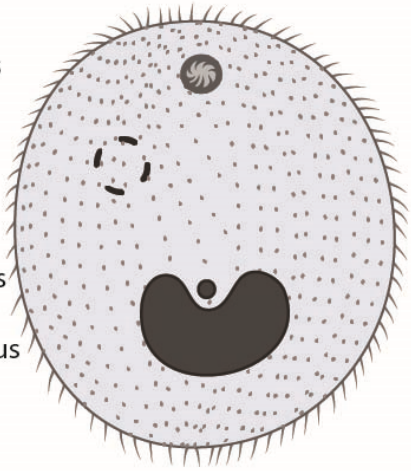
skin, gills
(irritation, cystic lesions
'whitespot/ich')

may reproduce asexually
(by transverse binary fission)
or sexually (by conjugation)

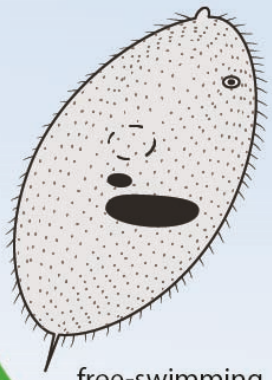


Vertebrate Hosts
(freshwater fish)

obligate monoxenous ectoparasites



trophonts
(30-1500 µm)



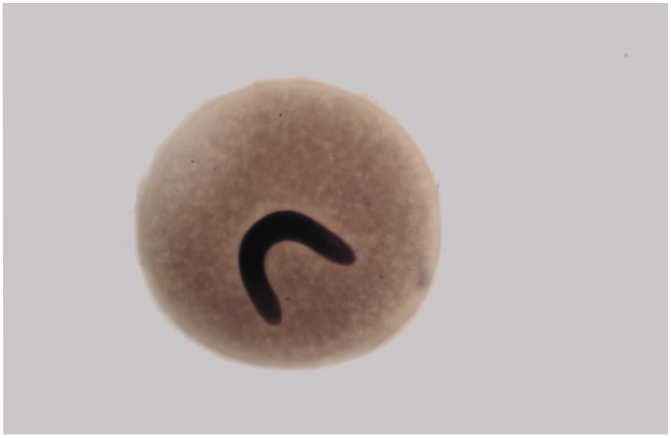
36-48
meridional
kineties

free-swimming
theronts
(25-70 µm)

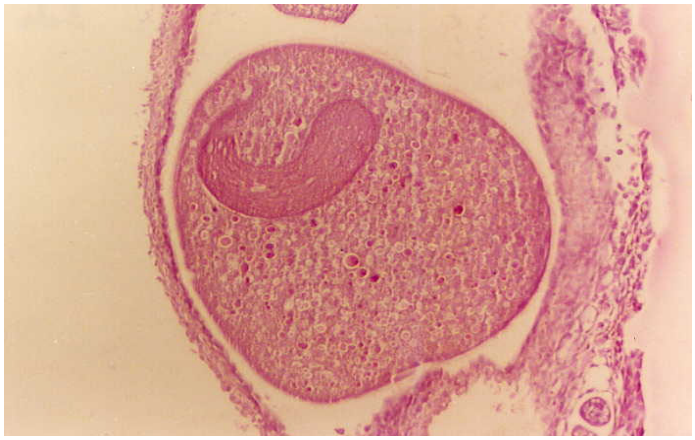


reproductive cysts
(tomonts) with
tomites

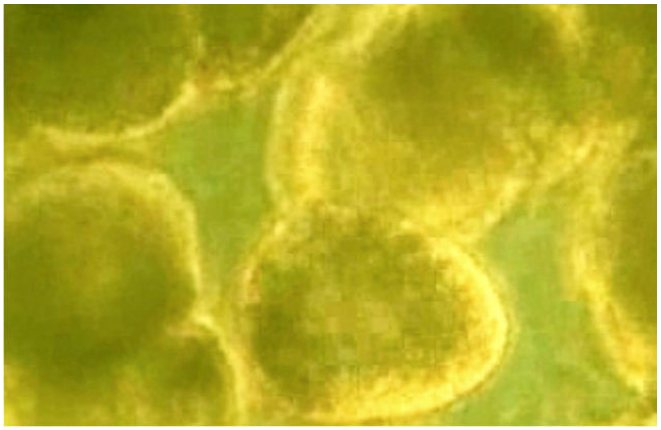
transmission via water contaminated by
dividing stages which release host-seeking 'swarmers'



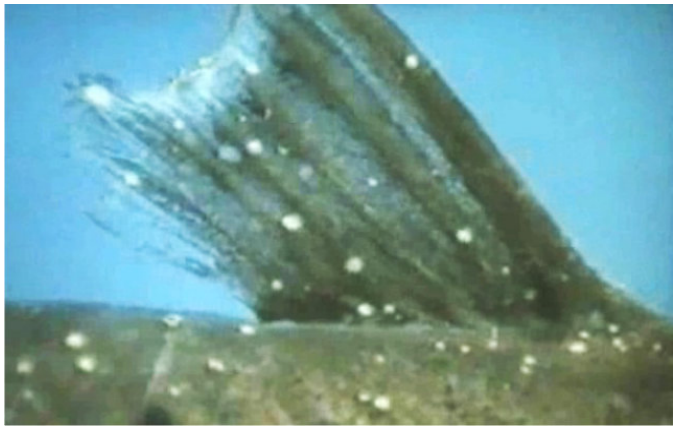
Ichthyophthirius trophont from fish skin



Ichthyophthirius trophont on fish gill



Ichthyophthirius tomites from aquarium



Ichthyophthirius white-spot lesions on fish

Tetrahymena
(protist: ciliate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Ciliated protozoa are unique eukaryotes as they exhibit nuclear dualism (vegetative macronucleus and reproductive micronucleus), the process of conjugation (exchange of micronuclei between pairs), have membrane-bound sacs (subpellicular alveoli) supporting the plasma membrane, and move using cilia (2+9 undulipodia with compound subpellicular infraciliature). Most ciliates are free-living in aquatic and terrestrial habitats, but some are symbiotic in vertebrate and invertebrate hosts. Ten major monophyletic lineages are recognized on the basis of their infraciliature, i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). Members of the subphylum Intramacronucleata are united by the presence of microtubules inside the macronuclear envelope during division; including the oligohymenophoreans ('few membrane-bearer') with an adoral zone of buccal (oral) ciliature. Hymenostomes have a paroral membrane located on the right side of the buccal cavity and three membranelles on the left side, while their bodies are mostly covered by uniform somatic ciliature. Tetrahymenids have longitudinal rows of somatic cilia with several rows interrupted by the buccal cavity. Most *Tetrahymena* spp. are free-living aquatic organisms, although some are facultative parasites that may invade the skin and tissues of aquatic animals, sometimes causing lesions and mortalities in fishes.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Ciliophora (with cilia, nuclear dualism, pellicular alveoli, reproductive conjugation)
Subphylum:	Intramacronucleata (microtubules occur inside macronuclear envelope during division))
Class:	Oligohymenophorea (distinct oral ciliature, comprising right paroral membrane and 3 left membranelles)
Subclass:	Hymenostomatida (right paroral dikinetid plus 1-3 left polykinetids)
Order:	Hymenostomatida (preoral suture, somatic monokinetids)
Suborder:	Tetrahymenina (organelle of Lieberkuhn absent)
Family:	Tetrahymenidae (pyriform body, longitudinal ciliary rows)
Genus:	*Tetrahymena* (most free-living aquatic species, some opportunistic parasites in skin/gills/organs of fish)
Species:	several species cause invasive disease ('tet') in fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Ciliated protozoa are unique amongst the unicellular eukaryotes because they are the only group to exhibit nuclear dualism. Individual cells possess two different types of nuclei; vegetative macronuclei and reproductive micronuclei. Asexual reproduction occurs by transverse binary fission across rows of cilia (homothetogenic fission) whereas some species exhibit sexual reproduction by the phenomenon of conjugation (temporary fusion of two conjugates which exchange micronuclei). As their common name implies, ciliates are also characterized by the possession of simple cilia, or compound ciliary organelles, in at least one stage of their life cycles (compound subpellicular infraciliature is universally present even when cilia are absent). Cilia are elongate hair-like extensions of the cell membrane with an internal microtubular core (universal 2+9 configuration = 2 single central microtubules surrounded by 9 peripheral doublets). They are organelles of motility used for locomotion and/or feeding. Cilia (singular, cilium) are similar in ultrastructure to flagella (singular, flagellum), and they are collectively often called undulipodia (singular, undulipodium) because both use cross-linked proteins (dynein-walking mechanism) to undulate about their basal kinetosome (unlike the rotary motion unique to flagella in bacteria). Ciliates, together with dinoflagellates and apicomplexans, possess subpellicular alveoli which are membrane-bound sacs beneath the plasma membrane. Alveoli are thought to serve many varied functions: ranging from support (helping maintain body shape, act as fulcrum for undulipodia); metabolism (storage); osmoregulation (mucocysts); excretion (extrusomes); protection (toxicysts, trichocysts); and even hunting (haptocysts).

Most ciliate species are free-living in aquatic or terrestrial habitats but many are commensals in vertebrate or invertebrate hosts and some are parasitic. Early classification systems recognized three main classes of ciliates mainly on the basis of their

patterns of somatic (body) and buccal (oral) ciliation. The 'lower holotrichs' have simple body and oral ciliature; most are free-living species but some are highly specialized symbionts aiding cellulose digestion in herbivores. The 'higher holotrichs' have simple body ciliature but more specialized oral ciliature forming membranelles; most occur as free-living organisms but some live as commensals or parasites in a range of animals. The 'spirotrichs' have reduced body ciliation but well-developed oral ciliature forming an adoral zone of membranelles; most are bactivores living in aquatic and terrestrial habitats. More recently, ten major monophyletic lineages have been recognized on the basis of their infraciliature; i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). These lineages (ranked as classes) have been well supported by modern molecular biological studies using several gene sequences.

Class	Etymology	Defining characters	Lifestyles*	Genera covered
Subphylum: **Postciliodesmatophora** [somatic dikinetids with postciliodesmata (overlapping microtubular ribbons)]				
Karyorelictea	'primitive-nucleus'	macronuclei not dividing but replaced by division of micronuclei	free-living (aquatic benthic/planktonic)	
Heterotrichea	'different-hair'	compound ciliary organelles around mouth, macronuclei divided by external microtubules	free-living (aquatic planktonic/benthic)	
Subphylum: **Intramacronucleata** [macronuclei divided by internal microtubules]				
Spirotrichea	'coiled-hair'	conspicuous right and left oral ciliature, left polykinetids leading into oral cavity	free-living (aquatic, terrestrial)	
Litostomatea	'simple-mouths'	cytostome with noncurved tubular cytopharyngeal apparatus (rhabdos)	free-living (often predatory), symbiotic	*Balantidium*
Phyllopharyngea	'leaf-throated'	mouth with radial microtubular ribbons (phyllae), some with sticky feeding tentacles	free-living (aquatic), epizoic, symbiotic	*Chilodonella*
Colpodea	'breast-shaped'	reniform bodies, somatic cilia with transverso-desmata (overlapping ribbons)	terrestrial, some aquatic (bactivores)	
Nassophorea	'pot-bearer'	oral nematodesmata well-developed (basket-like nasse or cyrtos supporting cytopharynx)	free-living (aquatic, terrestrial)	
Prostomatea	'before-mouth'	simple apical mouths, some with oral microtubular band, some with oral brush	free-living (often predatory)	
Plagiopylea	'misshapen-marker'	with twisted oral tubes, most with hydrogenosomes	free-living (anoxic habitats)	
Oligo-hymenophorea	'few membrane-bearer'	typically with ventral groove containing mouth and compound ciliary organelles (usually adoral zone of three membranelles)	free-living, epizoic, symbiotic (micro-phagous)	*Uronema, Ichthyophthirus, Tetrahymena, Trichodina, Vorticella*

*Symbiosis *sensu latu* ranges from commensalism, mutualism and parasitism (depending on the benefit/detriment to the host)

The class Oligohymenophorea contains ciliates whose somatic (body) kinetosomes (basal bodies) are associated with unique ultrastructural elements (collectively referred to as infraciliature) comprising anteriorly-directed overlapping kinetodesmal fibrils, divergent postciliary microtubular ribbons and radial transverse ribbons. Members are considered to be 'higher' holotrichs as there is clear distinction between the oral and somatic ciliature. They possess distinctive oral kineties consisting of a right paroral kinety (membrane) and typically 3 left oral polykinetids (membranelles) located in a buccal or infundibular cavity with an inconspicuous cytopharyngeal apparatus. They are widely distributed as free-living or symbiotic forms, although a few are parasitic mainly in fish. The class contains 6 subclasses (Apostomatia, Astomatia, Hymenostomatia, Peniculia, Peritrichia, Scuticociliatia) differentiated predominantly on the basis of their patterns of somatic and oral ciliation. The hymenostomes have a well-defined buccal cavity and conspicuous oral ciliature evident as a paroral membrane of dikinetids on the right side and 1-3 left polykinetids (membranelles) on the left side, while their bodies are mostly covered by somatic ciliature. The single order Hymenostomatida contains 2 suborders: Ophryoglenina (cells with dense somatic ciliature, preoral sutures, buccal cavity opening at the bottom of a deep depression, presence of a unique lens-like organelle of Lieberkuhn (watchglass organelle), and teloparakinetal stomatogenesis); and Tetrahymenina (cells with somatic meridional kineties, inconspicuous anteroventral buccal cavities, preoral sutures, absence of organelle of Lieberkuhn, and monoparakinetal stomatogenesis). Tetrahymenines occur mostly as freshwater microphagous forms filter-feeding on bacteria, particulates and solutes, but a few species exhibit polymorphic variation when they transform to macrostome histophagous forms that feed on aquatic hosts (insects, gastropods and fish). Five families are recognized (Curimostomatidae, Glaucomidae, Spirozonidae, Tetrahymenidae, and Turaniellidae) principally on the basis of differences in their somatic and oral ciliature. Tetrahymenids have pyriform bodies, long ciliary rows, oral membranelles that are uniform in width, and 1-3 postoral kineties ending at the posterior margin of the buccal cavity. The family Tetrahymenidae contains 5 genera (*Blepharostoma, Deltopylum, Lambornella, Melacophrya*, and *Tetrahymena*) with the genus *Tetrahymena* (syn. *Cystidium, Leptoglena, Leucophrydium, Leucophrys, Paraglaucoma, Protobalantidium, Roquea, Tetrahymen, Tetrahymenia, Turchiniella*) being characterized by the possession of 20-30 meridional kineties, 2 being postoral while the rest converge anteriorly around an argentophilic pellicular structure (forming an apical loop and preoral suture). The genus contains almost 50 species which are

mostly saprozoic in freshwater habitats, although a few species may be facultative parasites on the body surfaces of freshwater fishes, and occasionally invade the skin, muscles and internal organs causing a disease known as 'Tet' in ornamental and farmed fishes.

While tetrahymenids have been known for at least 200 years, they became popular in research laboratories from the 1950's due to their ease of culture and their genetic manipulability. Many publications arose on their biochemistry and physiology, but most research was inadvertently conducted on amicronucleate (asexual) strains which were subsequently characterized by isoenzyme electrophoresis and allocated to phenosets A-E. Following the discovery of conjugation in sexual strains (with micronuclei), many studies described up to 7 different mating types, particularly in what was called the *Tetrahymena pyriformis*-complex, with the identification of numerous strains and varieties (subsequently called syngens). Early workers grouped various *Tetrahymena* spp. into three complexes based on their morphological and life history traits: the *T. pyriformis*-complex with microstomal mouthparts, simple life-cycles alternating between feeding trophonts and dispersal theronts, with occasional resting cyst formation (e.g. *T. pyriformis, setifera, chironomi, americanis, canadensis, malaccensis, asiatica, nanneyi, elliotti, tropicalis*); the *T. patula*-complex comprising the microstome-macrostome transformers, with cycles involving trophonts, theronts and division cysts producing > 2 tomites (e.g. *T. patula, paravorax, vorax, caudata, silvana*); and the *T. rostrata*-complex with larger bodied microstomal forms that are strongly histophagous and/or parasitic, and have cycles involving trophonts, theronts, resting cysts and division cysts producing 2 tomites (e.g. *T. rostrata, limacis, corlissi, stegomyiae*). However, recent molecular (multi-gene) phylogenetic studies have indicated that these complexes are paraphyletic. Instead, two major clades were detected, an 'australis' clade of closely-related species (involving *T. australis, asiatica, capricornis, cosmopolitanis, hegewischi, hyperangularis, nanneyi, patula, pigmentosa, shanghaiensis, sonneborni*); and a 'borealis' clade with less closely-related species (comprising *T. borealis, canadensis, farleyi, malaccensis, pyriformis, thermophila, tropicalis*). Members of both clades show convergence for histophagy, macrostome formation and cyst formation. Comparative genetic studies have shown that some members of these clades exhibit different patterns of conjugation (involving micronuclear meiosis, reciprocal fertilization, and macronucleus assembly) which impacts on their subsequent mating-type determination: with most of the 'australis' clade being synclonal (mating-type determined at fertilization); and several of the 'borealis' clade being karyonidal (mating-type determined during macronuclear development). The following table lists species in groups recognized by contemporary molecular studies, but further studies are required to identify cryptic species and resolve several inconsistencies (esp. synonyms) as well as to determine conjugation types.

***Tetrahymena* species[1,2]**	**Trophont[3] size (µm) [no. kineties]**	**Life-styles (Hosts)**	**Distribution**
***T. pyriformis* group**			
T. leucophrys	microstome 60-94 x 27-54 macrostome 66-99 x 36-71 [19-23]	free-living (freshwater)	North America
T. pyriformis [= amicronucleate phenoset A] [type species] (syn. *T. geleii, Saprophilus oviformis, Leucophrys, Glaucoma*)	10-90 x 10-70 [15-25]	free-living (water, soil) and facultatively parasitic (histophagous) in viscera of terrestrial slugs (Gastropoda: agriolimacid (*Deroceras reticulatum*)), freshwater crayfish (Decapoda: parastacid (*Cherax quadricarinatus*) and fish (Cypriniformes: cyprinid (carp, goldfish, tiger barb, cherry barb, straightfin barb); Cyprinodontiformes: poecilid (guppy, molly); Cichliformes: cichlid (redbelly tilapia, blue-spotted tilapia, angelfish); Characiformes: characid (neon tetra, X-ray tetra); Salmoniformes: salmonid (rainbow trout); Siluriformes: ictalurid (catfish)	North America, Eurasia, Australia
T. setosa (syn. *Glaucoma, T. setifera*)	33-49 x 22-29 [21-26] [caudal cilium]	free-living (freshwater) and facultatively histophagous	North America, Eurasia
T. silvana	not stated[4] macrostome [resting cyst]	free-living (freshwater)	Asia
T. vorax	microstome 30-80 [18-23] macrostome 100-250 [19-28] [reproductive cysts]	free-living (freshwater)	North America
***T. thermophila* group**			
T. elliotti	not stated	free-living (freshwater)	Americas,

[= amicronucleate phenoset B]	[selfing]		Eurasia
T. malaccensis	not stated [karyonidal]	free-living (freshwater)	Malaysia
T. thermophila (syn. *T. pyriformis* syngen 1)	50 [karyonidal]	free-living (freshwater and briny pond)	North America
***T. tropicalis* group**			
T. aquasubterranea	37-53 x 18-27 [17-19]	free-living (well groundwater)	Africa
T. furgasoni (syn. *T. pyriformis* strain W [= amicronucleate phenoset C], *T. lwoffi* [= amicronucleate phenoset E])	not stated	free-living (freshwater)	North America
T. tropicalis (syn. *T. pyriformis* syngen 9)	not stated	free-living (freshwater)	North America, Pacific
***T. borealis* group**			
T. borealis (syn. *T. pyriformis* syngen 3)	not stated [karyonidal]	free-living (freshwater)	North America, Europe
T. canadensis (syn. *T. pyriformis* syngen 7)	not stated [karyonidal]	free-living (freshwater)	North America, Malaysia
T. mimbres	35-48 x 17-26 [16-18]	free-living (hot springs)	North America, China
T. rostrata (syn. *Paraglaucoma*]	35-90 x 24-56 free-living [26-39], parasitic [35-58] [caudal cilium] [resting cysts] [reproductive cysts]	free-living (edaphic in soil, litter, moss) and facultatively parasitic (histophagous) in viscera of terrestrial slugs/snails (Gastropoda: agriolimacid (*Deroceras reticulatum, laeve*, *panormitanum*), arionid (*Arion circumscriptus*, *intermedius*), clausiliid (*Macrogastra latestriata*), cochlicopid (*Cochlicopa lubrica*), discid (*Discus rotundatus*), helicid (*Helix aspersa*), milacid (*Milax gagates*, *Tandonia sowerbyi*), oleacinid (*Poiretia algira*), valloniid (*Vallonia pulchella*), vitrinid (*Vitrina pellucida*), zonitid (*Zonitoides nitidus*), and possibly the skin of cultured fish (Salmoniformes: salmonid (Atlantic salmon)	North America, Europe, Australia
***T. americanis* group**			
T. americanis (syn. *T. pyriformis* syngen 2)	not stated [resting cysts] [synclonal]	free-living (freshwater)	Americas, Asia
T. asiatica	not stated [synclonal]	free-living (freshwater)	Asia
T. australis (syn. *T. pyriformis* syngen 11)	20-50 x 10-30 [19-22] [synclonal]	free-living (freshwater)	Australia, Americas, Eurasia
T. capricornis (syn. *T. pyriformis* syngen 12)	not stated [synclonal]	free-living (freshwater)	Australia
T. cosmopolitanis (syn. *T. pyriformis* syngen 4)	not stated	free-living (freshwater)	North America, Eurasia
T. empidokyrea	32-52 x 18-32 [16-19]	parasitic (histophagous) in insects (Diptera: culicid (*Aedes* adult mosquitoes))	North America
T. hegewischi (syn. *T. pyriformis* syngen 5)	not stated [synclonal]	free-living (freshwater)	North America
T. hyperangularis (syn. *T. pyriformis* syngen 10)	not stated [synclonal]	free-living (freshwater)	North America,

			Europe
T. nanneyi	not stated [synclonal]	free-living (freshwater)	North America
T. nipissingi (syn. *T. pyriformis* syngen 14)	not stated [synclonal]	free-living (freshwater)	North America
T. patula (syn. *Leucophrys*)	microstome 45 x 28 [32-41] macrostome 80-160 [35-45] [reproductive cysts]	free-living (freshwater)	North America
T. shanghaiensis	33-60 x 21-30 [16-20]	free-living (freshwater)	Asia
T. sonneborni (syn. *T. pyriformis* syngen 13)	not stated [synclonal]	free-living (freshwater)	North America, Europe
Miscellaneous group			
T. caudata	microstome 54-61 x 26-37 macrostome 81-101 x 58-81 [17-26] [caudal cilium] [resting cyst]	free-living (freshwater)	Asia
T. chironomi	40 x 23 [23-28] [selfing]	parasitic in haemolymph of insects (Diptera: chironomid (*Chironomus plumosus* larvae)	Europe, North America
T. corlissi	30-70 x 20-45 [23-31] [caudal cilium] [resting cysts] [reproductive cysts]	free-living (freshwater), facultatively parasitic (histophagous) in skin, muscles and body cavity of fish (Anabantiformes: osphronemid (dwarf gourami, kissing gourami); Cyprinodontiformes: poecilid (guppy, molly, platyfish); Cichliformes: cichlid (mango tilapia); Characiformes: characid (tetras); Perciformes: percichthyid (golden perch); Siluriformes: ictalurid (bullhead catfish) and amphibians (Urodela: plethodontid (*Pseudotriton* larvae)	North America, Europe, Australia
T. dimorpha	microstome 33-49 x 25-38 [19-24] macrostome 56-89 x 41-70 [30-66]	parasitic in haemolymph of insects (Diptera: simuliid (*Simulium equinum* larvae, pupae, adults, *S. ornatum* larva)	Europe
T. farahensis	26-43 x 21-36	free-living (wastewater)	Pakistan
T. farleyi	42-56 x 14-26 [15-17]	parasitic in urinary tract of vertebrate (Carnivora: canid (dog))	North America
T. limacis (syn. *Paraglaucoma*)	28-68 x 17-42 free-living [24-32] parasitic [26-46] [selfing]	terrestrial, parasitic (histophage) in viscera of slugs/snail (Gastropoda: agriolimacid (*Deroceras reticulatum, laeve*), arionid (*Arion hortensis*, *Prophysaon andersoni*, *Monadenia fidelis*), daudebardiid (*Daudebardia rufa*), helicid (*Helix pomatia*), hygromiid (*Trichia lubomirskii*, *Perforatella dibothrion*), limacid (*Lehmannia marginatus*, *valentiana*, *Limacus flavus*, *maximus*), milacid (*Milax gagates*, *Tandonia budapestensis*), succineid (*Oxyloma pfeifferi*, *Succinea oblonga*), vitrinid (*Vitrina pellucida*), zonatid (*Nesovitrea hammonis*, *Oxychilus depressus*)	Europe, North America, Africa
T. paravorax	microstome 80 x 40 [22-30] macrostome 100-200 [24-28] [caudal cilium] [selfing]	free-living (freshwater)	Europe
T. rotunda	41-89 x 40-80	parasitic in haemolymph of insects	North

	[50-66]	(Diptera: simuliid (*Simulium venustum* larvae, pupae, adults, *S. tuberosum* larvae))	America
T. sialidos	32-51 x 18-33 [22-27] [selfing]	parasitic in haemolymph of insects (Megaloptera: sialid (*Sialis lutaria* larvae))	Europe
Uncharacterized species			
T. bergeri	50-70 x 25-30 [26-33] [reproductive cysts]	free-living (freshwater) and facultatively histophagous	Europe
T. edaphoni	40-50 x 20 [18-20] [resting cysts]	free-living (terrestrial, spruce forest)	Europe
T. glochidiophila	bactivore 30-49 x 19-27 histophage 41-59 x 19-31 [23-26] [caudal cilium?]	freshwater, parasitic (histophagous) in mantle cavity of mollusc larvae (Bivalvia: unionid (*Lampsilis siliquoidea* glochidia larvae))	North America
T. mobilis (syn. *Saprophilus*)	30-40 [22]	free-living (activated sludge) and facultatively histophagous (experimentally on fragmented mealworms *Tenebrio molitor*)	Europe
T. pigmentosa (syn. *T. pyriformis* syngen 6, 8)	not stated [synclonal]	free-living (freshwater)	North America, Europe, Africa
T. stegomyiae (syn. *Lambornella*)	60 [25-30] [resting cysts]	parasitic in haemolymph of insects (Diptera: culicid (*Aedes* larvae))	Africa

[[1]Environmental and clinical isolates of tetrahymenids not identified to species have not been included in this table]
[[2]Three species (*T. faurei, T. glaucomaeformis* and *T. parasitica*) are considered *nomen dubium* due to incomplete/inadequate descriptions, and are excluded from most species lists]
[[3]Selfing = intraclonal conjugation; synclonal = exconjugant mating-type determined at fertilization; karyonidal = exconjugant mating-type determined during macronuclear development]
[[4]Not stated = no morphometrics given in species description]

Parasite morphology: All *Tetrahymena* spp. form at least 2 developmental stages (feeding trophonts and dispersal theronts), while some species may also form resting cysts and/or reproductive (division) cysts ('tomonts'). The trophonts are broad ovoid to pyriform stages, bluntly pointed anteriorly and rounded posteriorly. They swim slowly, feed constantly and become darkened in colour by the growing abundance of food vacuoles. They vary considerably in size depending on species and nutritional status, becoming larger as they feed to repletion (particularly in favourable culture conditions). Trophonts of most species range from 10-100 µm in length, but some may enlarge and grow up to 250 µm long. Cells have both specialized oral (buccal) and somatic (body) ciliation. The oral apparatus is located subapically in the anterior body and consists of a buccal cavity leading to the cytostome, both being surrounded by a paroral undulating membrane on the right side and by 3 serially-arranged membranelles on the left side. Most species have small (ca. 10 x 6 µm) mouthparts (microstome forms) facilitating saprozoic filter-feeding (on solutes and particulates, including bacteria). Some species, however, are able to transform into larger cells (100-250 µm) with enlarged (ca. 30 x 20 µm) mouthparts (macrostome forms), sometimes with deep cytopharyngeal pouches that grossly distort their anterior ends. These enlarged mouthparts allow the ciliates to prey on other ciliates as carnivores (even cannibals) and/or to become histophagous (facultative or obligate parasites of invertebrates (insects, gastropods) and vertebrates (fish)). Transformation from microstome to macrostome forms is generally reversible depending on environmental conditions and food availability. The trophont body is covered in longitudinal (meridional) rows (kineties) of ciliary basal bodies (kinetosomes) giving rise to short eukaryotic cilia (microtubular core with 2 single central microtubules and 9 peripheral doublets). The number of somatic kineties varies from 15-66 (most with 20-30) depending on the ciliate species, trophont maturity and the occurrence of macrostome forms. Trophonts have a straight pre-oral suture with 1-3 postoral kineties beginning at the posterior margin of the buccal cavity, and some species may possess a single caudal cilium. Cells possess a large spherical-ovoid central macronucleus with an adjacent small dense micronucleus, and a single terminal contractile vacuole with 2-6 pores (2-3 in microstomal forms, 3-6 in macrostomes). Theronts act as dispersal stages and they are generally smaller than trophonts and have narrow elongate bodies with rounded posterior ends and pointed anterior ends often curved slightly to the right. These cells are highly active and they swim rapidly spirally up and down in the water column frequently changing direction. In the absence of food, the theronts of some species (e.g. *T. americanis, T. caudata, T. corlissi, T. rostrata, T. silvana,* and *T. stegomyiae*) form small inactive resting cysts (18-20 µm in diameter) encapsulated by cyst walls formed by secretions of mucocysts. Several species may also form larger (35-40 µm) division (reproductive) cysts known as tomonts which divide internally to form 2-8 (rarely 16) tomites (often observed rotating within cysts), with *T. bergeri* and *T. corlissi* forming 2 tomites, and *T. patula* and *T. vorax* forming > 2 tomites. When food becomes available, both types of cysts undergo

excystment, with resting cysts releasing stages that develop into trophonts while division cysts release tomites that may form trophonts or theronts.

Site of infection: Most *Tetrahymena* spp. are free-living filter-feeding ciliates usually found in freshwater bodies. The trophonts of a few species, however, have been found to infect the haemolymph of insects, the mantle cavities and viscera of slugs and snails, or the external surfaces (skin and gills) of fish and sometimes their internal tissues (muscles and viscera). Infections have been commonly reported in cultured freshwater fish and tropical ornamental species. However, many reports only identified the parasites as belonging to the genus *Tetrahymena,* so little is known about the identity, host range or specificity of the species that actually infect fish. Four species (*T. corlissi, T. pyriformis, T. rostrata,* and *T. faurei*) have been reported as being histophagous in fish, but even their identification to species level has often been presumptive. *T. corlissi* is probably the most common and pathogenic species in fish, while the remaining 3 species have usually been associated with terrestrial gastropods (snails and slugs) and only occasionally with fish. *T. pyriformis* is widespread but has many congeners with similar morphological characteristics (e.g. species included in the classical (biologic) *T. pyriformis*-complex and the contemporary (molecular) *T. pyriformis* group). *T. rostrata* has been tentatively linked to rare cranial lesions in some cultured salmonids, while *T faurei* reported as parasitic in carp, catfish and trout is generally considered *nomen dubium* due to the lack of sufficient descriptive data. Theronts are free-swimming planktonic stages; while resting and division cysts are inactive stages that usually sink onto benthic substrates.

Pathogenesis: Free-swimming tetrahymenids occur as filter-feeders in freshwater lakes, ponds and streams, but the trophonts of some species are attracted to hosts by chemokinesis (involving host peptides) and can switch from free-living to epizoic (attaching to host) ranging from commensalistic (no harm to host) to parasitic (harms host). The ciliates feed on fish surfaces using their microstome mouthparts or transform to histophagous forms with macrostome mouthparts and invade tissues. They may ingest solutes, cellular debris, particulate material and even host cells (including erythrocytes). Light infections in fish may be asymptomatic or subclinical, but parasites may proliferate rapidly resulting in heavy infections causing superficial and/or systemic disease (colloquially called 'Tet'). Infections of the skin initially produce small white patches with masses of ciliates in copious mucus, but often progress to deeper invasion with tissue necrosis, epidermal sloughing, lifting of scales, haemorrhage, oedema, granular lesions and open wounds. Infections of the gills may result in extensive necrosis, epithelial hyperplasia and sloughing, congestion with excessive mucus production and respiratory distress. Ciliates that develop macrostome mouthparts become histophagous and invade internal tissues, including somatic musculature, body cavity organs and sometimes central nervous tissues. This may produce considerable necrosis and degeneration resulting in focal expanding lesions contributing to dysfunctional changes (loss of equilibrium, fin clamping, lethargy) and mortalities. Infections are rarely associated with inflammatory reactions and while some fibroblast responses have been recorded, they have not led to any significant fibrosis. Occasionally, masses of ciliates accumulating around the rim of the eye socket may cause a condition known as 'spectacled eye', and intraocular infections may lead to exophthalmos ('pop-eye'). Systemic infections may cause death in 1-3 weeks, with female fish succumbing before male fish. Fry are particularly susceptible to clinical disease, particularly those with injured integuments.

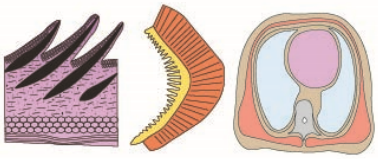
Developmental cycle and mode of transmission: Tetrahymenids are essentially free-living ciliates, with microstomal species feeding mainly on bacteria, but some able to reversibly transform to macrostomal carnivorous forms and/or histophagous parasites (most facultative, but some obligate) with direct transmission to aquatic/terrestrial invertebrates (insects, gastropods) or vertebrates (fish). Different species have different life-cycles, involving cyclic transformation between feeding trophonts (which may divide asexually by binary fission when food is available) and active free-swimming theronts (which do not feed or divide, but disperse seeking food). When food is scarce, theronts may sometimes forming resting cysts (containing immotile stages), division (reproductive) cysts (tomonts) which divide asexually to produce tomites (that mature to theronts or trophonts when released), or mate sexually by the process of conjugation (involving micronuclear meiosis, reciprocal fertilization, and new macronucleus assembly). Studies have shown that up to 7 different sexes (mating types) may be produced; with a few able to undergo intraclonal conjugation ('selfing') but most committed to cross-breeding with exconjugant mating-types determined at fertilization (synclonal) or during macronuclear assembly (karyonidal). Members of the *T. pyriformis*-complex generally exhibit simple cycles, with small microstomal trophonts from both amicronucleate and micronucleate species growing and dividing by binary fission when food is available. Under starvation conditions, the trophonts form theronts for dispersion (some also form resting cysts) and micronucleate species may also undergo conjugation. Members of the *T. patula*-complex include larger species which may reversibly form macrostome mouthparts and prey on other ciliates (as carnivores, and even cannibals); some even developing huge cytopharyngeal pouches. When food is depleted, several of these species form reproductive cysts in which multiple (2-16) tomites are formed. Members of the *T. rostrata*-complex are also larger bodied species, which are strongly histophagous and/or parasitic. In unfavourable conditions, some produce both resting and reproductive cysts (usually only yielding 2 tomites). The transmission of parasitic species between piscine hosts occurs directly via free-swimming stages, both dispersal theronts and sometimes feeding trophonts (particularly in crowded conditions).

Differential diagnosis: Infections are diagnosed by the microscopic detection of motile ciliates in wet mounts of skin or other tissues. Trophonts are best observed using high-contrast microscopy or they can be counter-stained with methyl green-pyronin. Generic and specific identification involves enrobing ciliates onto albuminized slides and subjecting them to silver staining (silver

proteinate (protargol), silver nitrate, silver carbonate) to reveal their distinctive patterns of oral and somatic ciliation (ciliary basal bodies are strongly argentophilic). Ciliates can be readily cultivated *in vitro* in a variety of media, including plant infusions (hay, rye, lettuce), axenic cultures (proteose-peptone, skim-milk, chemically-defined) and monoxenic cultures (with feeder bacteria). This has facilitated numerous studies on ciliate physiology, reproduction, and genetics, including the determination of mating compatibilities to discriminate species (often impractical as living stocks of multiple mating types are required but many isolates are either asexual or sexually immature). Molecular studies have examined isoenzyme electrophoretic profiles for many isolates, but consistent differences between species were only found occasionally. More recently, molecular biological techniques have been used to characterize isolates following the polymerase chain reaction (PCR) amplification of specific gene sequences, with low interspecific variation noted for nuclear genes (small and large subunit ribosomal DNA, internal transcribed spacer regions) and greater variability found for faster-evolving mitochondrial genes (cytochrome c oxidase subunit 1).

Treatment and control: Ectozoic infections on the superficial aspects of fish have responded to treatments with various chemical baths (e.g. formalin, potassium permanganate, methylene blue), but there are no effective treatments for endozoic systemic infections. Several anthelmintics (e.g. niclosamide, albendazole) and anti-malarials (e.g. chloroquine) have shown some efficacy in killing parasites in aquaria. Preventive measures have focussed on reducing contamination by ciliates in culture systems and avoiding conditions predisposing to infections and disease. Animals should be screened prior to their introduction into facilities, with suspect fish quarantined or culled. Fish should be reared in clean water sources (filtered and chlorinated if possible) with regular flushing and water exchange. Care should be taken to avoid over-feeding as accumulated organic wastes increases the likelihood of biofouling and bacterial blooms that are conducive to ciliate growth. Dead and dying fish should be promptly removed and carcases disposed of by burying on land or incineration. Contaminated tanks should be drained, disinfected, and dried before restocking. Management practices should endeavour to avoid stressful (immunocompromising) situations that affect host susceptibility, such as poor water quality, poor nutrition, excessive handling, overcrowding, concomitant infections and injuries. Experimental vaccination studies using live attenuated ciliates or lysates, with or without adjuvants and/or boosters, have given variable results with some protection linked to increased lysozyme activity in challenged fish.

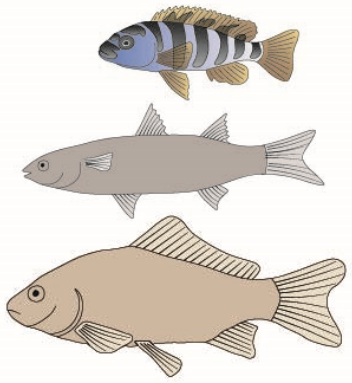
Tetrahymena



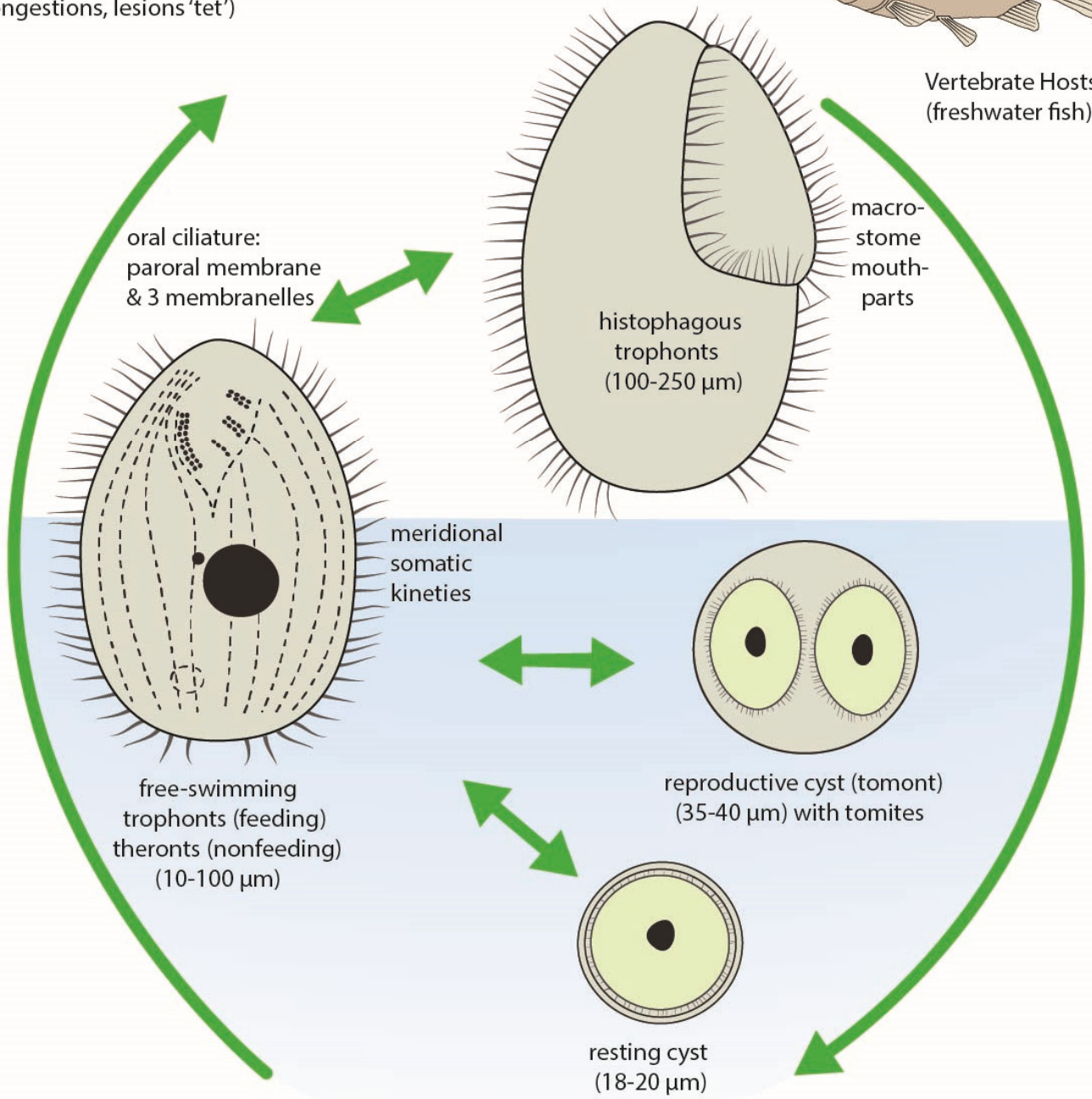
skin, gills, viscera
(necrosis, haemorrhages,
congestions, lesions 'tet')

may reproduce asexually
(by transverse binary fission)
or sexually (by conjugation)

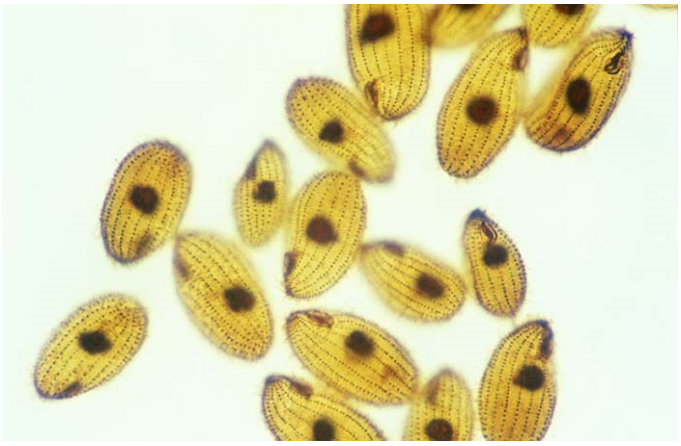
mostly free-living saprozoic species,
some facultative histophagous parasites



Vertebrate Hosts
(freshwater fish)



transmission via free-swimming stages
(theronts and sometimes trophonts) in water column



Tetrahymena trophonts from aquarium



Tetrahymena trophont from fish skin (silver stain)



Tetrahymena trophonts from fish skin (silver stain)

Trichodina
(protist: ciliate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Ciliated protozoa are unique eukaryotes as they exhibit nuclear dualism (vegetative macronucleus and reproductive micronucleus), the process of conjugation (exchange of micronuclei between pairs), have membrane-bound sacs (subpellicular alveoli) supporting the plasma membrane, and move using cilia (2+9 undulipodia with compound subpellicular infraciliature). Most ciliates are free-living in aquatic and terrestrial habitats, but some are symbiotic in vertebrate and invertebrate hosts. Ten major monophyletic lineages are recognized on the basis of their infraciliature, i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). Members of the subphylum Intramacronucleata are united by the presence of microtubules inside the macronuclear envelope during division; including the oligohymenophoreans ('few membrane-bearer') with an adoral zone of three membranelles. Peritrichous ciliates are filter-feeders with a left-hand spiral of oral cilia leading to cytostome. They live attached permanently (sessilines) or temporarily (mobilines) to substrates, which may include other aquatic animals. Trichodinids form mobile discoid trophonts with an aboral holdfast organelle comprising an elaborate concave disc with proteinaceous denticles (thorns and blades) subtended by radial pins. Several genera are recognized on the basis of differences in their oral ciliary wreaths and adhesive discs. Most species are ectoparasitic on fish and many cause skin lesions, although a few species have been found as endozoic organisms in the digestive tracts of elasmobranchs and some fishes where they apparently do no harm.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Ciliophora (with cilia, nuclear dualism, pellicular alveoli, reproductive conjugation)
Subphylum:	Intramacronucleata (microtubules occur inside macronuclear envelope during division))
Class:	Oligohymenophorea (distinct oral ciliature, comprising right paroral membrane and 3 left membranelles)
Subclass:	Peritrichia (lacking somatic kineties, oral cilia extend from infundibulum, predominantly bactivores, often stalked)
Order:	Mobilida (mature trophont mobile, aboral holdfast organelle)
Family:	Trichodinidae (stout cylindrical body, posterior adhesive disc with denticular ring)
Genus:	*Trichodina* (ectoparasitic on skin/gills of fish)
Species:	many species cause skin lesions on freshwater and marine fish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Ciliated protozoa are unique amongst the unicellular eukaryotes because they are the only group to exhibit nuclear dualism. Individual cells possess two different types of nuclei; vegetative macronuclei and reproductive micronuclei. Asexual reproduction occurs by transverse binary fission across rows of cilia (homothetogenic fission) whereas some species exhibit sexual reproduction by the phenomenon of conjugation (temporary fusion of two conjugates which exchange micronuclei). As their common name implies, ciliates are also characterized by the possession of simple cilia, or compound ciliary organelles, in at least one stage of their life cycles (compound subpellicular infraciliature is universally present even when cilia are absent). Cilia are elongate hair-like extensions of the cell membrane with an internal microtubular core (universal 2+9 configuration = 2 single central microtubules surrounded by 9 peripheral doublets). They are organelles of motility used for locomotion and/or feeding. Cilia (singular, cilium) are similar in ultrastructure to flagella (singular, flagellum), and they are collectively often called undulipodia (singular, undulipodium) because both use cross-linked proteins (dynein-walking mechanism) to undulate about their basal kinetosome (unlike the rotary motion unique to flagella in bacteria). Ciliates, together with dinoflagellates and apicomplexans, possess subpellicular alveoli which are membrane-bound sacs beneath the plasma membrane. Alveoli are thought to serve many varied functions: ranging from support (helping maintain body shape, act as fulcrum for undulipodia); metabolism (storage); osmoregulation (mucocysts); excretion (extrusomes); protection (toxicysts, trichocysts); and even hunting (haptocysts).

Most ciliate species are free-living in aquatic or terrestrial habitats but many are commensals in vertebrate or invertebrate hosts and some are parasitic. Early classification systems recognized three main classes of ciliates mainly on the basis of their patterns of somatic (body) and buccal (oral) ciliation. The 'lower holotrichs' have simple body and oral ciliature; most are free-living species but some are highly specialized symbionts aiding cellulose digestion in herbivores. The 'higher holotrichs' have simple body ciliature but more specialized oral ciliature forming membranelles; most occur as free-living organisms but some live as commensals or parasites in a range of animals. The 'spirotrichs' have reduced body ciliation but well-developed oral ciliature forming an adoral zone of membranelles; most are bactivores living in aquatic and terrestrial habitats. More recently, ten major monophyletic lineages have been recognized on the basis of their infraciliature; i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). These lineages (ranked as classes) have been well supported by modern molecular biological studies using several gene sequences.

Class	Etymology	Defining characters	Lifestyles*	Genera covered
Subphylum: **Postciliodesmatophora** [somatic dikinetids with postciliodesmata (overlapping microtubular ribbons)]				
Karyorelictea	'primitive-nucleus'	macronuclei not dividing but replaced by division of micronuclei	free-living (aquatic benthic/planktonic)	
Heterotrichea	'different-hair'	compound ciliary organelles around mouth, macronuclei divided by external microtubules	free-living (aquatic planktonic/benthic)	
Subphylum: **Intramacronucleata** [macronuclei divided by internal microtubules]				
Spirotrichea	'coiled-hair'	conspicuous right and left oral ciliature, left polykinetids leading into oral cavity	free-living (aquatic, terrestrial)	
Litostomatea	'simple-mouths'	cytostome with noncurved tubular cytopharyngeal apparatus (rhabdos)	free-living (often predatory), symbiotic	*Balantidium*
Phyllopharyngea	'leaf-throated'	mouth with radial microtubular ribbons (phyllae), some with sticky feeding tentacles	free-living (aquatic), epizoic, symbiotic	*Chilodonella*
Colpodea	'breast-shaped'	reniform bodies, somatic cilia with transverso-desmata (overlapping ribbons)	terrestrial, some aquatic (bactivores)	
Nassophorea	'pot-bearer'	oral nematodesmata well-developed (basket-like nasse or cyrtos supporting cytopharynx)	free-living (aquatic, terrestrial)	
Prostomatea	'before-mouth'	simple apical mouths, some with oral microtubular band, some with oral brush	free-living (often predatory)	
Plagiopylea	'misshapen-marker'	with twisted oral tubes, most with hydrogenosomes	free-living (anoxic habitats)	
Oligo-hymenophorea	'few membrane-bearer'	typically with ventral groove containing mouth and compound ciliary organelles (usually adoral zone of three membranelles)	free-living, epizoic, symbiotic (micro-phagous)	*Uronema, Ichthyophthirus, Tetrahymena, Trichodina, Vorticella*

*Symbiosis *sensu latu* ranges from commensalism, mutualism and parasitism (depending on the benefit/detriment to the host)

The class Oligohymenophorea contains ciliates whose somatic (body) kinetosomes (basal bodies) are associated with unique ultrastructural elements (collectively referred to as infraciliature) comprising anteriorly-directed overlapping kinetodesmal fibrils, divergent postciliary microtubular ribbons and radial transverse ribbons. Members are considered to be 'higher' holotrichs as there is clear distinction between the oral and somatic ciliature. They possess distinctive oral kineties consisting of a right paroral kinety (membrane) and typically 3 left oral polykinetids (membranelles) located in a buccal or infundibular cavity with an inconspicuous cytopharyngeal apparatus. They are widely distributed in aquatic habitats (fresh, brackish and marine waters) where they occur as free-living stages (free-swimming or attached to substrates), some being epizoic (rarely endozoic) on aquatic animals (mainly crustacea and fish). Free-living aquatic species are highly sensitive to environmental changes and a range of species are used as bioindicators for the assessment of water quality (saprobic classifications) and even sludge activity in wastewater treatment. The class contains 6 subclasses (Apostomatia, Astomatia, Hymenostomatia, Peniculia, Peritrichia, Scuticociliatia) differentiated predominantly on the basis of their patterns of somatic and oral ciliation. Peritrichous ciliates are filter-feeders with inverted bell-shaped bodies having prominent buccal ciliature encircling the apical pole (forming a peristomial field) and winding counterclockwise (left hand spiral) to plunge into the oral cavity (infundibulum) to the cytostome (mouth). The peristomal border consists of a dikinetid file (considered homologous to the paroral membrane) surrounding a triple row of cilia (considered homologous to the polykinetid membranelles). The narrow antapical pole of the cells possess barren kinetosomes as part of a holdfast apparatus (scopula or adhesive disc). Mature trophonts (often called zooids) lack somatic kineties but the transient dispersal telotroch (swarmer) stages may develop temporary ciliary rings for locomotion. Two peritrich orders are recognized depending on whether mature trophonts live attached permanently (Sessilida) or temporarily (Mobilida) to substrates, which in many cases may include other aquatic animals and plants.

Higher taxonomy	Family	Exemplar genera	Hosts	Site	Trans-mission
Subclass: Peritrichia (lacking somatic kineties, oral cilia extend from infundibulum)					
Order: Mobilida (mature trophont mobile, aboral holdfast organelle)	Trichodinidae (stout cylindrical body, posterior adhesive disc with denticular ring)	*Trichodina*	fish	skin, gills	direct
Order: Sessilida (mature trophont sessile, attached to substrate by scopula (special flat thigmotactic area) with or without stalk)	Epistylididae (scopula produces noncontractile stalk, retractile lip encircles elevated peristomial disc)	*Apiosoma*	fish	skin, gills	direct
		Epistylis	fish, crustacea	exoskeleton	direct
	Scyphidiidae (solitary ciliates, attached by scopula)	*Scyphidia*	fish, crustacea	exoskeleton	direct
		Ambiphrya	fish, crustacea	exoskeleton	direct
	Vorticellidae (solitary, gregarious or colonial, retractile stalks with central myoneme)	*Vorticella*	fish, crustacea	exoskeleton	direct
		Carchesium	fish, crustacea	exoskeleton	direct
	Zoothamniidae (solitary or colonial, retractile stalks with shared myonemes)	*Zoothamnium*	fish, crustacea	exoskeleton	direct
	Vaginicolidae (upright lorica)	*Cothurnia*	crustacea	exoskeleton	direct
		Vaginicola	crustacea	exoskeleton	direct
	Lagenophryidae (discoid lorica)	*Lagenophrys*	crustacea	gills	direct

The order Mobilida contains species whose mobile trophonts have conical-cylindrical discoid bodies with an aboral holdfast organelle. The holdfast functions as a slightly contractile adhesive disc with complex ring-like skeletal armature of denticles and fibres surrounding a vestigal scopula. The oral region is not contractile and contains a permanently-ciliated trochal band typically comprising 3 ciliary wreaths (2 locomotory oral polykinetids and a third short perpendicular polykinetid with immobile tactile cilia). The ciliates are usually ectosymbiotic, often on the skin or gills of aquatic invertebrates and some vertebrates. They are essentially bactivorous, obtaining prey from the water column and sometimes being microphagous on cellular debris from their hosts. A total of 5 families have been recognized on the basis of various biologic and morphologic differences: with members of the Leiotrochidae (genus *Leiotrocha*), Polycyclidae (genus *Polycycla*), Trichodinopsidae (genus *Trichodinopsis*) and Urceolariidae (genus *Urceolaria*,) comprising ciliates with smooth denticles in their adhesive discs; and only members of the Trichodinidae having complex denticles in their adhesive discs. Trichodinids have stout cylindrical-discoidal bodies, adoral (peristomial) ciliary wreaths spiraling from half a turn to 3 turns, and an aboral concave adhesive disc consisting of a ring of hollow conical elements with flat lateral projections (denticles) with centrifugal processes (blades) and centripedal rays (thorns). The denticles are inserted into each other and subtended by a ring of fine skeletal rods (radial pins). Over 20 trichodinid genera have been proposed, with recent revisions combining them into 9 genera primarily on the basis of differences in oral ciliary wreaths and adhesive disc morphology: namely, *Hemitrichodina*, *Heterobladetrichodina*, *Pallitrichodina*, *Paratrichodina*, *Semitrichodina* (syn. *Trichodoxa*)*, Trichodina* (syn. *Acyclochaeta, Anhymenia, Cyclochaeta, Cyclocyrrha, Nummulella, Paravauchomia, Poljanskina, Torquatina*)*, Trichodinella* (syn. *Brachyspira, Dipartiella, Dogielina, Foliella*), *Tripartiella* and *Vauchomia.*

Genus	Turns to adoral spiral	Denticle composition	No. spp.	Hosts*	Site
Vauchomia	2-3	well-developed blades and thorns	2	fw fish	urinary tract
Hemitrichodina	1-2	blades stunted, well developed thorns	1	fw fish	skin, fins
Trichodina	1-1½	well-developed blades and thorns	170	fw & mar fish	gills, skin
Pallitrichodina	¾	well-developed blades, short thorns	2	terrestrial snails	mantle cavity
Semitrichodina	½-¾	well-developed blades and thorns	3	terrestrial snails	mantle cavity, genitals
Paratrichodina	½-¾	perpendicular blades, prominent thorns	15	fw & mar fish	gills, bladder
Tripartiella	½-¾	oblique blades, prominent thorns	19	fw & mar fish	gills
Trichodinella	½-¾	prominent blades, vestigial thorns	11	fw & mar fish	gills
Heteroblade-trichodina	<½	rays with thin perpendicular projections	2	fw fish	gills

*fw = freshwater; mar = marine

Most species are epizoic on aquatic organisms, including the skin, fins and gills of a range of ornamental, farmed and wild fishes, both freshwater and marine. Some species are thought to be host specific while others occur over a wide range of hosts, but information on their actual host specificity is often lacking. Some infections persist in euryhaline habitats (over a wide range of salinities such as encountered by estuarine fish), while others apparently survive catadromous or anadromous migrations (fish

moving from freshwater to seawater to spawn, or vice versa). A growing number of species have been associated with eruptive or ulcerative skin lesions, particularly in cultured fishes in crowded conditions. A few species have also been found as endozoic organisms in the urogenital tracts of elasmobranchs and some fish but they apparently live as endocommensals and do no harm.

Ciliate species	Adhesive disc (AD) diameter (µm), number of denticles (ND)	Habitat (Hosts)	Location	Distribution
Genus ***Hemitrichodina*** (adoral ciliary spiral makes between 1-2 turns, denticles with reduced blades but well-developed central parts and thorns)				
H. robusta [type species]	AD 43-70 ND 18-24	freshwater, epizoic on fish (Characiformes: alestid (sharptooth tetra), hepsetid (African pike, African pike characin); Osteoglossiformes: mormyrid (bulldog))	skin, fins	Africa
Genus ***Heterobladetrichodina*** (adoral ciliary spiral less than one turn, denticles with thorns ending in thin projections folded underneath at right angles)				
H. punctatus [type species]		freshwater, epizoic on fish (Siluriformes: ictalurid (channel catfish))		China
H. kazubski (syn. *Dipartiella*)	AD 14-19 ND 23-33	freshwater, epizoic on fish (Siluriformes: bagrid (tengra), silurid (helicopter catfish))	gills	India
Genus ***Pallitrichodina*** (adoral ciliary spiral makes ¾ turn, denticles with well-developed blades, short thorns, body with distinct indentations due to microfibrillar attachments)				
P. rogenae [type species]	AD 27-44 ND 18-22	terrestrial, endozoic in snails (Gastropoda: achatinid (*Achatina fulica, panthera*))	mantle cavity	Mauritius, Taiwan
P. stephani	AD 30-53 ND 18-30	terrestrial, endozoic in snails (Gastropoda: achatinid (*Achatina fulica, panthera*))	mantle cavity	Mauritius
Genus ***Paratrichodina*** (adoral ciliary spiral makes ½-¾ turns, denticles wedged together only by central parts, well-developed thorns, blades attached perpendicularly)				
P. africana	AD 12-25 ND 17-27	freshwater, epizoic on fish (Cichliformes: cichlid (Nile tilapia, mango tilapia); Perciformes: latid (Nile perch))	gills, skin	Africa, South America
P. alburni (syn. *Trichodina*)	AD 25-44 ND 23-29	freshwater, endozoic in fish (Cypriniformes: cyprinid (common bleak), leuciscid (common minnow))	urinary tract	Europe
P. bassonae	AD 11-15 ND 18-21	freshwater, epizoic on fish (Siluriformes: bagrid (Gangetic mystus))	gills	India
P. corlissi	AD 19-25 ND 18-24	freshwater, epizoic on fish (Cypriniformes: cyprinid (gudgeon, Kessler's gudgeon); Gobiiformes: gobiid (marbled goby))	gills	Eurasia
P. degiustii	AD 31-36 ND 27-32	freshwater, endozoic in fish (Cypriniformes: cyprinid (blackchin shiner))	urinary tract	North America
P. erectispina	AD 20-31 ND 23-27	freshwater, epizoic on fish (Cypriniformes: cyprinid (bullhead minnow))	gills	North America
P. globonucleata [type species as subgenus of *Tripartiella*]	AD 12-30 ND 15-28	marine, epizoic on fish (Gadiformes: lotid (shore rockling); Ophidiiformes: ophidiid (snake blenny); Scorpaeniformes: agonid (spinycheek starsnout), cottid (slim sculpin), psychrolutid (spinyhead sculpin scorpaenid (Korean rockfish); Syngnathiformes: syngnathid (long-snouted seahorse))	gills	Atlantic, Pacific, Mediterranean
P. incissa (*incisa*) (syn. *Tripartiella*, *Paratrichodina*)	AD 11-36 ND 15-31	freshwater, epizoic on fish (Cypriniformes: cyprinid (common carp, roach, rudd, dace, ide, zope), leuciscid (Eurasian minnow, lake minnow, Pacific redfin), nemacheilid (stone loach); Salmoniformes: salmonid (Arctic grayling); and amphibians (Anura: ranid (edible frog, tadpoles))	gills	Eurasia
P. lizae	AD 13-20 ND 18-21	estuarine, epizoic on fish (Mugiliformes: mugilid (goldspot mullet))	gills	Brazil

P. obliqua	AD 17-19 ND 19-21	marine, epizoic on fish (Perciformes: mullid (red mullet); Pleuronectiformes: paralichthyid (olive flounder))	gills	Europe
P. phoxini (syn. *Trichodina*)	AD 25-44 ND 23-39	freshwater, endozoic in fish (Cypriniformes: leuciscid (common minnow))	urinary tract	Eurasia
P. uralensis	AD 20-26 ND 18-25	freshwater, epizoic on fish (Acipenseriformes: acipenserid (sterlet))	gills	Russia
P. tasmaniensis	AD 24-32 ND 26-29	marine, epizoic on fish (Atheriniformes: atherinid (small-mouth hardyhead, small-scale hardyhead, short-snout hardyhead, pikehead hardyhead, silver fish))	gills	Australia
P. voikarensis	AD 18-26 ND 22-25	freshwater, epizoic on fish (Salmoniformes: salmonid (broad whitefish, peled))	gills	Russia
P. yangtzeus	AD 20-26 ND 20-22	freshwater, epizoic on fish (Siluriformes: silurid (Amur catfish))	gills	China
Genus ***Semitrichodina*** (syn. *Trichodoxa*) (adoral ciliary spiral makes ½ to ¾ turn, denticles with well-developed blades and thorns, interlocked by central parts, body with oblique grooves or circumferential spines)				
S. sphaeronuclea [type species as subgenus of *Trichodinella*]	AD 28-54 ND 26-38	terrestrial, endozoic in slugs (Gastropoda: limacid (*Limax maximus, cineroniger, Lehmannia marginata, Bielzia coerulans*), vitrinid (*Semilimax semilimax*), zonitid (*Aegopinella epipedostoma, Oxychilus* (*Schistophallus*) *orientalis*)	pallial cavity	Eurasia
S. convexa	AD 32-47 ND 22-25	terrestrial, endozoic in snails (Gastropoda: clausiliid (*Cochlodina laminata*))	pallial cavity	Europe
S. genitalis (syn. *Trichodoxa, Trichodina*)	AD 33-72 ND 12-39	terrestrial, endozoic in snails (Gastropoda: charopid (*Trachycystis leucocarina, contrasta*))	genital system	Africa
S. phalli (syn. *Trichodoxa*)	AD 39-67 ND 23-31	terrestrial, endozoic in snails (Gastropoda: charopid (*Trachycystis menkeana*))	genital system	Africa
Genus ***Trichodina*** (adoral ciliary spiral makes 1-1½ turns, denticles with well-developed blades and thorns, some species with aboral cirri, most species epizoic on skin, fins, gills, nasal pits of aquatic animals; some endozoic in gut, urinary or reproductive tracts)				
T. achatinae *nomen nudum*		terrestrial, endozoic in snails (Gastropoda: achatinid (*Achatina zebra*))	receptaculum seminis	Europe (ex Africa)
T. acuta	AD 30-66 ND 17-33	freshwater, epizoic on fish (Cichliformes: cichlid (redbelly tilapia, redbreast tilapia, banded tilapia, Mozambique tilapia, southern mouthbrooder); Cypriniformes: acheilognathid (Amur bitterling), cyprinid (goldfish, grass carp, European carp, silver carp, sunbleak, bitterling, threespot barb, tench), leuciscid (Eurasian minnow); Cyprinodontiformes: fundulid (seminole killifish), poeciliid (barred killifish); Gadiformes: lotid (burbot); Perciformes: centrarchid (pumpkinseed, largemouth bass), percid (European perch, redfin perch, yellow perch, zander); Salmoniformes: salmonid (rainbow trout, brown trout); Siluriformes: bagrid (Day's mystus), ictalurid (brown bullhead, speckled madtom))	skin, fins, gills	North America, Eurasia
T. algonquinensis	AD 43-57 ND 35-42	freshwater, endozoic in fish (Cypriniformes: cyprinid (common shiner); Perciformes: percid (yellow perch))	urinary tract	Canada
T. amblypharyngodoni	AD 60-65 ND 31-33	freshwater, epizoic on fish (Cypriniformes: cyprinid (mola carplet))	gills	Bangladesh
T. anabantidarum	AD 39-54 ND 21-28	freshwater, epizoic on fish (Anabantiformes: anabantid (blackspot climbing perch, manyspined climbing perch)	gills, skin, fins	Africa
T. anguilli	AD 23-28 ND 20-22	estuarine, epizoic on fish (Anguilliformes: anguillid (European eel))	gills	Europe
T. arctica		marine, epizoic on fish (Scorpaeniformes: agonid (butterfly sculpin))	surface	Atlantic
T. asterisci		marine, epizoic on starfish (Echinodermata:	dorsal papules	Europe

(syn. *Cyclochaeta*)		asterinid (*Asterina gibbosa*))		
T. astericola (syn. *Cyclochaeta*)	cell 40-50	marine, epizoic on starfish (Echinodermata: asterinid (*Asterias rubens*))	tube feet	Europe
T. astropectinis		marine, epizoic on starfish (Echinodermata: astropectinid (*Astropecten bispinosus*))	surface	Eurasia
T. australis	AD 32-44 ND 20-24	marine, epizoic in fish (Atheriniformes: atherinid (small-mouth hardyhead, small-scale hardyhead, short-snout hardyhead, pikehead hardyhead, silver fish))	gills	Australia
T. bassonae	AD 30-38 ND 23-26	freshwater, epizoic on fish (Perciformes: scatophagid (spotbanded scat))	skin	Australia
T. bellottii	AD 50-64 ND 21-26	freshwater: epizoic on fish (Cyprinodontiformes: rivulid (Argentine pearl fish))	skin, fins	South America
T. bidentata	cell 60	marine, epizoic on fish (Scorpaeniformes: scorpaenid (unspecified scorpionfish))	skin	Europe
T. blennii	AD 24-27 ND 24-32	marine, epizoic on fish (Blenniiformes: blenniid (tentacled blenny))	gills	Europe
T. borealis	AD 33-40 ND 24-30	marine, epizoic on fish (Pleuronectiformes: pleuronectid (European plaice); Blenniiformes: blenniid (zebra blenny))	gills	Scotland, Hawaii
T. borokensis	AD 43-67 ND 24-31	freshwater, epizoic in fish (Cypriniformes: cyprinid (goldfish, sabrefish))	gills	Eurasia
T. branchicola	AD 19-33 ND 20-26	marine, epizoic on fish (Blenniiformes: blenniid (shanny, tompot blenny); Gadiformes: lotid (fivebeard rockling, shore rockling); Perciformes: cottid (longspined bullhead); Pleuronectiformes: pleuronectid (European plaice); Scorpaeniformes: gasterosteid (sea stickleback), triglid (tub gurnard))	gills	North America
T. caecellae	AD 25-32 ND 20-24	marine, epizoic on invertebrates (Bivalvia: mesodesmatid (*Coecella chinensis*))	gills	China
T. californica (syn *Tripartiella*)	AD 35-50 ND 25-32	freshwater, epizoic on fish (Salmoniformes: salmonid (chinook salmon, Siberian salmon, cherry salmon, pink salmon, chum salmon, king salmon, dolly varden, Far East char))	skin, gills	Pacific
T. cancilae	AD 42-60 ND 28-32	freshwater, epizoic on fish (Beloniformes: belonid (freshwater gar))	gills	Asia
T. canton	AD 43-57 ND 25-31	freshwater, epizoic on fish (Cichliformes: cichlid (Mozambique tilapia))	skin, gills	China
T. cardii (syn. *Cyclochaeta*)		marine, epizoic on cockle (Bivalvia: cardiid (*Cardium edule*))	pallial cavity	Europe
T. caspilosae		marine, epizoic on fish (Clupeiformes: alosid (Caspian shad), clupeid ('dolgina' herring))	gills	Caspian Sea
T. centrostrigeata	AD 30-48 ND 23-30	freshwater, epizoic on fish (Cichliformes: cichlid (southern mouthbrooder, Nile tilapia, Mozambique tilapia, redbreast tilapia, redbelly tilapia, banded tilapia, threespot tilapia, banded jewel cichlid, thinface cichlid, redeye labeo); Characiformes: alestid (striped robber); Cypriniformes: cyprinid (common carp, common barb); Perciformes: latid (Nile perch); Siluriformes: mochokid (leopard squeaker))	gills, skin, fins	Africa, Asia
T. chelidonichthys	AD 19-32 ND 30	marine, epizoic on fish (Scorpaeniformes: triglid (Cape gurnard))	gills	Africa
T. chlamydis	AD 29-33 ND 22-25	marine, epizoic on shellfish (Bivalvia: pectinid (*Azumapecten farreri*))	gills	China
T. claviformis	AD 47-67 ND 25-29	marine, epizoic on fish (Gadiformes: gadid (Atlantic cod, merling); Pleuronectiformes: pleuronectid (European flounder))	gills, skin	Baltic Sea
T. clini	AD 20 ND 24	marine, epizoic on fish (Blenniiformes: clinid (snaky klipfish)	gills	Africa
T. cobitis	AD 32-52	freshwater, epizoic on fish (Cypriniformes: cobitid	gills	Eurasia

	ND 22-30	(spined loach))		
T. colisae	AD 24-40 ND 17-25	freshwater, epizoic on fish (Characiformes: characid (Mexican tetra), serrasalmid (small-scaled pacu, pirapatinga))	mucus from skin, gills	Americas
T. compacta	AD 29-49 ND 15-21	freshwater, epizoic on fish (Characiformes: distichodontid (multibar citharine); Cichliformes: cichlid (redbreast tilapia, three-spotted tilapia, mango tilapia, Mozambique tilapia, banded tilapia, Zambezi happy, canary kurper, southern mouthbrooder, thinface cichlid); Cypriniformes: cyprinid (Eurasian carp, redeye barb, orangefin barb, threespot barb, redeye labeo, largemouth yellowfish, largescale yellowfish, river sardine); Cyprinodontiformes: poeciliid (barred killifish, lowland livebearer, Sinaloa livebearer), procatopodid (Johnston's topminnow); Osteoglossiformes: mormyrid (bulldog, churchill); Perciformes: latid (Nile perch); Siluriformes: mochokid (shortspine suckermouth))	skin, fins	Africa, Middle-East, Asia
T. cooperi	AD 81-107 ND 24-29	marine, epizoic on fish (Gadiformes: gadid (Atlantic cod); Siluriformes: callichthyid (mottled corydoras))	skin	Americas
T. corydori	AD 28-37 ND 23-27	freshwater, epizoic on fish (Siluriformes: callichthyid (pepper cory))	gills	South America
T. cottidarum	AD 25-44 ND 19-30	marine, epizoic on fish (Gadiformes: lotid (fourbeard rockling); Gobiiformes: gobiid (ashishirohaze); Pleuronectiformes: pleuronectid (marbled flounder); Scorpaeniformes: agonid (saburo); cottid (antlered sculpin, belligerent sculpin, long-spined bullhead, longhorn sculpin, fourhorn sculpin, shorthorn sculpin, tidepool sculpin), pholid (rock gunnel))	gills	Holarctic
T. cribbi	AD 40-60 ND 25-37	freshwater, epizoic on fish (Cyprinodontiformes: anablepid (one-sided livebearer); Gobiiformes: eleotrid (firetail gudgeon))	skin, gills	Australia, South America
T. cubanensis	AD 29-43 ND 22-26	freshwater, epizoic on fish (Cichliformes: cichlid (Cuban cichlid))	skin	Cuba
T. cyprinocola	AD 45-55 ND 22-24	freshwater, epizoic on fish (Cypriniformes: cyprinid (common carp))	gills	China
T. dampanula	AD 38-48 ND 28-35	freshwater, endozoic in amphibians (Anura: bufonid (guttural toad))	urinary bladder	Africa
T. davisi	AD 41-67 ND 21-25	freshwater, epizoic on fish (Moroniformes: moronid (striped bass))	skin, gills	North America
T. decipiens	AD 18-27 ND 23-34	marine, epizoic on fish (Scorpaeniformes: agonid (tubenose poacher, saburo, tilesiin, silver-spotted sculpin), cottid (padded sculpin, snowy sculpin), hexagrammid (masked greenling), liparid (suna-bikunin), stichaeid (nagazuka, scaly prickleback))	gills	Pacific
T. diaptomi	AD 31 ND 18-20	marine, epizoic on invertebrates (Branchiopoda: bosminid (*Bosmina huaroensis*), daphniid (*Daphnia laevis*); Copepoda: diaptomid (*Arctodiaptomus dorsalis*, *Diaptomus*, *Leptodiaptomus siciloides*, *Mastigodiaptomus albuquerquensis*, *montezumae*, *Notodiaptomus deitersi*))	carapace	Eurasia, Africa, Australia, Americas
T. digitodiscus	ND 12-14	freshwater, epizoic on invertebrates (Hydrozoa: hydrid (*Hydra vulgaris*))	surface	Europe
T. discoidea	AD 35-51 ND 18-30	freshwater, epizoic on fish (Perciformes: centrarchid (bluegill, black crappie, rock bass); Siluriformes: ictalurid (channel catfish))	gills	North America
T. domerguei (syn. *Cyclochaeta*)	AD 33-68 ND 18-31	freshwater and marine, epizoic on invertebrates (Copepoda: diaptomid (*Diaptomus, Eudiaptomus*);	skin, fins, gills	Holarctic

		fish (Cypriniformes: cyprinid (goldfish, Eurasian carp, crucian carp, grass carp, sunbleak, Amur bitterling), Cyprinodontiformes: cyprinodontid (Kizilirmak toothcarp), poeciliid (eastern mosquitofish, twospot livebearer); Esociformes: esocid (northern pike); Gadiformes: gadid (merling); Gobiiformes: gobiid (round goby, monkey goby, marbled goby); Labriformes: labrid (five-spotted wrasse, pointed-snout wrasse); Moroniformes: moronid (European seabass); Perciformes: lateopercid (Japanese sea bass), mullid (red mullet), percid (European perch, Eurasian ruffe, zander); Pleuronectiformes: pleuronectid (European flounder), soleid (common sole); Salmoniformes: salmonid (Arctic grayling); Scorpaeniformes: cottid (shorthorn sculpin, moustache sculpin, buffalo sculpin, European bullhead), cyclopterid (lumpfish), gasterosteid (three-spined stickleback, ninespine stickleback, Sakhalin stickleback), pholid (rock gunnel); Spariformes: sparid (gilt-head bream) and amphibians (Anura: bufonid (common toad), bombinatorid (European fire-bellied toad), hylid (European tree frog), ranid (common frog, edible frog, marsh frog))		
T. elegans	AD 15-21 ND 21-25	freshwater, epizoic on fish (Scorpaeniformes: gasterosteid (Sakhalin stickleback))	surface	Asia
T. elegini	AD 25-40 ND 22-27	marine, epizoic on fish (Gadiformes: gadid (saffron cod, Alaska pollock); Scorpaeniformes: cottid (antlered sculpin, belligerent sculpin), zoarcid (viviparous eelpout))		Pacific
T. elizabethae	AD 25-37 ND 19-24	marine, epizoic on fish (Scorpaeniformes: stichaeid (radiated shanny))	gills	North Atlantic
T. entzii		freshwater, endozoic in amphibians (Anura: ranid (marsh frog, edible frog, pool frog))	urinary bladder	Europe
T. equitoralis		freshwater, epizoic on fish (Cichliformes: cichlid (tilapia))	gills	Africa
T. erbilensis	AD 22-27 ND 23-27	freshwater, epizoic on fish (Siluriformes: silurid (Tigris catfish))	surface	Iraq
T. esocis	AD 38-69 ND 20-28	freshwater, epizoic on fish (Esociformes: esocid (northern pike), Perciformes: percid (European perch, zander))	skin, gills	North America
T. fahaka	AD 26-28 ND 24-27	freshwater, epizoic on fish (Tetraodontiformes: tetraodontid (Fahaka pufferfish))	gills	Africa
T. fariai	AD 20-42 ND 24-28	marine, endozoic in fish (Tetraodontiformes: tetraodontid (checkered puffer))	intestines	Caribbean
T. faurefremieti	AD 49-54 ND 30-34	freshwater, endozoic in amphibians (Urodela: salamandrid (northern crested newt))	urinary bladder	Europe
T. frenata	AD 25-32 ND 19-23	freshwater, epizoic on fish (Cichliformes: cichlid (mango tilapia); Perciformes: latid (Nile perch); Synbranchiformes: mastacembelid (long-tailed spiny eel))	gills	Africa
T. frequentis	AD 25-35 ND 27-36	marine, epizoic on fish (Gadiformes: gadid (saffron cod); Pleuronectiformes: pleuronectid (yellow striped flounder); Scorpaeniformes: cottid (plain sculpin), hexagrammid (masked greenling, fat greenling, whitespotted greenling, Arabesque greenling), stichaeid (scaly prickleback), zoarctid (viviparous eelpout); Tetraodontiformes: tetraodontid (Japanese puffer, panther puffer))	surface	Pacific
T. fultoni	AD 62-90 ND 25-31	freshwater, epizoic on fish (Anguilliformes: anguillid (European eel); Cichliformes: cichlid (Nile tilapia); Cypriniformes: cyprinid (tench,	skin, gills (pathogenic to eels)	North Atlantic, Eurasia

		white sucker, cutlips minnow, gudgeon, common shiner, rosyface shiner, mirror shiner, blacknose dace, pearl dace, creek chub), nemacheilid (stone loach); Perciformes: centrarchid (rock bass, smallmouth bass, largemouth bass, speckled bass, green sunfish, pumpkinseed, bluegill); Salmoniformes: salmonid (rainbow trout, brook trout); Siluriformes: clariid (African sharptooth catfish), ictalurid (channel catfish))		
T. funduli	AD 54-65 ND 23-27	freshwater, epizoic on fish (Cyprinodontiformes: fundulid (starhead topminnow))	skin	North America
T. galyae	AD 48-65 ND 25-28	marine, epizoic on fish (Scorpaeniformes: cyclopterid (lumpfish))	gills	North Atlantic
T. gasterostei	AD ND	freshwater, epizoic on fish (Scorpaeniformes: gasterosteid (three-spined stickleback))	skin	North America
T. globosa	AD 25-34 ND 20-23	freshwater, epizoic on fish (Perciformes: percid (orangebelly darter))	skin	North America
T. glossogobae	AD 31-47 ND 22-24	freshwater, epizoic on fish (Gobiiformes: gobiid (tank goby))	gills	India
T. gobii	AD 20-41 ND 18-27	marine, epizoic on fish (Anguilliformes: anguillid (European eel); Callionymiformes: callionymid (common dragonet); Gadiformes: gadid (merling); Gobiiformes: gobiid (round goby, sand goby); Labriformes: labrid (grey wrasse, ocellated wrasse); Ophidiiformes: ophidiid (snake blenny); Pleuronectiformes: soleid (Egyptian sole))	gills	Eurasia, Americas, Australia
T. guberleti	AD 50-100 ND 28-32	freshwater, epizoic on fish (Cypriniformes: cyprinid (redside shiner, speckled dace))	gills, skin	North America
T. gulshae	AD 44-71 ND 21-28	estuarine, epizoic on fish (Siluriformes: bagrid (Gangetic mystus))	gills	India
T. haldari	AD 34-45 ND 20-22	freshwater, epizoic on fish (Gobiiformes: gobiid (tank goby))	gills	India
T. halli	AD 30-54 ND 26-34	marine, epizoic on fish (Tetraodontiformes: tetraodontid (northern puffer))	gills, skin	North America
T. heterodentata	AD 38-82 ND 20-30	freshwater, epizoic on fish (Anabantiformes: anabantid (three-spot gourami), osphronemid (three spot gourami); Atheriniformes: melanotaeniid (Pacific blue-eye); Characiformes: alestid (elongate tigerfish, sharptooth tetra), serrasalmid (small-scaled pacu); Cichliformes: cichlid (redbreast tilapia, redbelly tilapia, Mozambique tilapia, Nile tilapia, redbelly tilapia, banded tilapia, Canary kurper, southern mouthbrooder, electric blue hap); Cypriniformes: cobitid (pond loach), cyprinid (goldfish, common carp, European carp, bighead carp, grass carp, silver carp, straightfin barb, orangefin barb, threespot barb, Mexican stoneroller, Taiwan horsemouth, Conchos chub, redeye labeo, largescale yellowfish, river sardine, rainbow gudgeon), gastromyzontid (tassel-mouthed loach); Cyprinodontiformes: cyprinodontid (Kizilirmak toothcarp), poeciliid (eastern mosquitofish, western mosquitofish, guppy, green swordtail, southern platyfish, molly), procatopodid (Johnston's topminnow); Galaxiiformes: galaxiid (mountain galaxias, inanga); Gobiiformes: eleotrid (empire gudgeon, firetail gudgeon, western carp gudgeon, flathead gudgeon), gobiid (tank goby, monkey goby, marbled goby, tubenose goby), oxudercid (Amur goby); Kurtiformes: apogonid (mouth almighty); Osteoglossiformes: mormyrid (bulldog, churchill); Perciformes: ambassid	skin, fins, gills	Australasia, Middle-East, South America, Africa

		(Agassiz's perchlet), centrarchid (largemouth bass), percichthyid (golden perch), percid (zander); Siluriformes: mochokid (brown squeaker))		
T. hexagrammi	AD 19-26 ND 20-25	marine, epizoic on fish (Pleuronectiformes: pleuronectid (barfin flounder); Scorpaeniformes: agonid (tubenose poacher), hexagrammid (whitespotted greenling, fat greenling, masked greenling), zoarctid (viviparous eelpout))	surface	Pacific
T. histiocotti	AD 20-26 ND 21-27	marine, epizoic on fish (Scorpaeniformes: agonid (crested sculpin))	surface	Pacific
T. hoffmani	AD 28-41 ND 17-25	freshwater, epizoic on fish (Perciformes: percid (brown darter, blackside darter); Siluriformes: bagrid (Tengara catfish))	skin	North America, Bangladesh
T. hypsilepsis	AD 40-57 ND 20-24	freshwater, epizoic on fish (Cypriniformes: cyprinid (highscale shiner) and amphibians (Anura: unidentified tadpoles))	skin	North America
T. indica	AD 45-50 ND 14-32	freshwater, epizoic on fish (Anabantiformes: channid (spotted snakehead, dwarf snakehead); Cypriniformes: cyprinid (mrigal carp, reba carp, mola carplet, catla, large razorbelly minnow, rohu, orangefin labeo); Perciformes: ambassid (elongate glassy perchlet, Indian glassy fish))	gills, skin	India
T. intermedia	AD 25-46 ND 22-37	freshwater, epizoic on fish (Cypriniformes: cyprinid (Eurasian minnow))	gills, skin	Eurasia
T. izyumovae	AD 52-69 ND 29-32	freshwater, epizoic on fish (Cypriniformes: cyprinid (ide))	gills	Eurasia
T. jadranica	AD 17-35 ND 15-27	freshwater and marine, epizoic on fish (Blenniiformes: blenniid (zebra blenny), tripterygiid (network triplefin); Callionymiformes: callionymid (common dragonet); Cypriniformes: cobitid (spiny loach); Gadiformes: gadid (Atlantic cod); Gobiiformes: eleotrid (Sandwich Island sleeper), gobiid (sand goby, monkey goby); Labriformes: labrid (grey wrasse); Perciformes: mullid (red mullet); Pleuronectiformes: paralichthyid (bay whiff, olive flounder), pleuronectid (European flounder, stone flounder, marbled flounder, barfin flounder, rock sole), scophthalmid (Black Sea turbot), soleid (common sole, blackhand sole); Scorpaeniformes: agonid (saburo), cottid (threaded sculpin, aikajika), hexagrammid (masked greenling), liparid (suna-bikunin))	gills, skin	Atlantic, Pacific, Mediterranean, Black Sea
T. japonica	AD 17-28 ND 18-23	catadromous, epizoic on fish (Anguilliformes: anguillid (Japanese eel); Perciformes: lateolabracid (Japanese sea bass); Spariformes: sparid (red seabream))	gills	Asia
T. jarmilae	AD 23-30 ND 19-23	marine, epizoic on fish (Gobiiformes: gobiid (ashishirohaze); Scorpaeniformes: agonid (sea raven, silver-spotted sculpin, tubenose poacher, saburo, tilesiin), cottid (plain sculpin, snowy sculpin, Steller's sculpin, elegant bero), liparid (unspecified snailfish), pholid (nishikiginpo), stichaeid (scaly prickleback))	gills	Pacific
T. jenynsii	AD 55-67 ND 23-26	freshwater, epizoic on fish (Cyprinodontiformes: anablepid (one-sided livebearer))	skin	South America
T. jiroveci	AD 29-35 ND 24-27	freshwater, epizoic on fish (Gobiiformes: gobiid (monkey goby))	gills	Europe
T. kalimbeza	AD 21-30 ND 16-19	freshwater, epizoic on fish (Characiformes: distichodontid (multibar citharine); Cichliformes: cichlid (redbreast tilapia); Cypriniformes: cyprinid (African banded barb))	skin, fins	Africa
T. kazubski	AD 27-45	freshwater, epizoic on fish (Cypriniformes:	skin, fins, gills	China,

	ND 19-26	cyprinid (goldfish, bighead carp, straightfin barb, threespot barb))		Africa
T. korschelti (syn. *Cyclochaeta*)	cell 30-35	marine, epizoic on chitons (Polyplacophora: chitonid (*Chiton marginatus*)	mantle	Europe
T. kuleminae (syn. *T. rectangli*, *meridionalis*)	AD 35-40 ND 18-21	freshwater, epizoic on fish (Cypriniformes: cyprinid (goldfish, crucian carp, European carp, white bream, vimba bream, common shiner, golden shiner, blacknose shiner, common roach); Perciformes: percid (yellow perch))	nasal cavity, skin	Eurasia, North America
T. kupermanni	AD 29-44 ND 20-28	freshwater, epizoic on fish (Cypriniformes: cyprinid (blue bream, grass carp))	gills	Eurasia
T. kwando	AD 32-39 ND 25-27	freshwater, epizoic on fish (Characiformes: alestid (striped robber, sharptooth tetra))	gills, skin, fins	Africa
T. labrorum	AD 30-34 ND 21	marine, epizoic on fish (Labriformes: labrid (corkwing wrasse, East Atlantic peacock wrasse))	gills	Atlantic
T. labyrinthipicis	AD 31-48 ND 20-26	freshwater; epizoic on fish (Anabantiformes: anabantid (blackspot climbing perch, manyspined climbing perch)	gills, skin	Africa
T. lairdi	AD 59-81 ND 30-35	marine, epizoic on fish (Scorpaeniformes: cottid (tidepool sculpin))	gills	Pacific
T. lepsi	AD 19-27 ND 18-25	marine, epizoic on fish (Mugiliformes: mugilid (flathead grey mullet, golden grey mullet); Perciformes: percid (European perch))	gills, skin	Atlantic
T. liana	AD 31-41 ND 21-25	marine, epizoic on shellfish (Bivalvia: solenid (*Solena gracilis*))	gills	China
T. lieni	AD 31-43 ND 20-24	estuarine, epizoic on fish (Cypriniformes: cyprinid (crucian carp, grass carp, Changchun bream, variegated carp, silver carp); Anabantiformes: channid (snakehead); Perciformes: sinipercid (mandarin fish); Clupeiformes: engraulid (long-tailed anchovy))	skin, gills	China
T. linyanta	AD 30-50 ND 24-28	freshwater, epizoic on fish (Cichliformes: cichlid (banded jewel cichlid, three-spotted tilapia))	skin, gills	Africa
T. liparisi		marine, epizoic on fish (Scorpaeniformes: liparid (striped seasnail))	gills	Barents Sea
T. lishuiensis	AD 29-38 ND 26-31	freshwater, endozoic in amphibians (Anura: ranid (piebald odorous frog))	urinary bladder	China
T. luba	AD 30-40 ND 26-37	marine, endozoic in fish (Acanthuriformes: acanthurid (yellowfin surgeonfish))	colon	Africa, Pacific
T. luciopercae		freshwater, epizoic on fish (Perciformes: percid (zander))	gills	Eurasia
T. macomarum	AD 39-47 ND 22-25	marine, epizoic on clams (Bivalvia: mactrid (*Mactra veneriformis*))	gills	China
T. mactrae	AD 33-40 ND 22-24	marine, epizoic on clams (Bivalvia: mactrid (*Mactra veneriformis*))	gills	China
T. magna	AD 46-95 ND 24-30	freshwater, epizoic on fish (Characiformes: hepsetid (African pike, African pike characin); Cichliformes: cichlid (redbreast tilapia, redbelly tilapia, banded tilapia, three-spotted tilapia, mango tilapia, thinface cichlid, Mozambique tilapia, Nile tilapia, southern mouthbrooder); Cypriniformes: cyprinid (river sardine); Cyprinodontiformes: procatopodid (Johnston's topminnow); Osteoglossiformes: mormyrid (bulldog, churchill); Perciformes: centrarchid (largemouth bass), latid (Nile perch); Siluriformes: clariid (African sharptooth catfish), schilbeid (African butter catfish))	skin, fins, gills	Africa
T. major		freshwater, epizoic on fish (Gadiformes: lotid (burbot))	gills	Holarctic
T. mandarin	AD 45-55 ND 24-30	freshwater, epizoic on fish (Cypriniformes: cobitid (pond loach), cyprinid (rainbow gudgeon, Taiwan	skin, fins, gills	China

		horsemouth), gastromyzontid (tassel-mouthed loach); Siluriformes: clariid (Hong Kong catfish))		
T. maritinkae	AD 31-50 ND 20-32	freshwater, epizoic on fish (Characiformes: characid (blind cave fish); Siluriformes: clariid (blotched catfish, Hong Kong catfish, African sharptooth catfish, snake catfish, vundu))	gills	Africa, Asia
T. matsu	AD 15-40 ND 20-27	freshwater, epizoic on fish (Cypriniformes: gastromyzontid (tassel-mouthed loach); Siluriformes: bagrid (adiposalis catfish), clariid (African sharptooth catfish))	gills, skin, fins	Africa, China
T. meretricis	AD 44-52 ND 23-27	marine, epizoic on clams (Bivalvia: venerid (*Meretrix meretrix*))	gills	China
T. microbis		marine, epizoic on fish (Labriformes: labrid (peacock wrasse))	gills	Pacific
T. microdenticulata	AD 12-16 ND 15-18	freshwater, epizoic on fish (Clupeiformes: dorosomatid (threadfin shad))	skin, gills	North America
T. micromaculata	AD 28-42 ND 20-27	marine, epizoic on fish (Mugiliformes: mugilid (flathead grey mullet); Scorpaeniformes: opisthocentrid (muroranginpo), pholid (nishikiginpo))	surface	Pacific
T. microspina	AD 19-33 ND 18-23	freshwater, epizoic on fish (Anabantiformes: anabantid (blackspot climbing perch, manyspined climbing perch)	skin, fins, gills	Africa
T. minima	AD 16-17 ND 17-19	marine, epizoic on fish (Scorpaeniformes: stichaeid (tauegaji))	surface	Pacific
T. mira		freshwater, epizoic on fish (Cypriniformes: leuciscid (lake minnow))	gills	Russia
T. miranda	AD 38-54 ND 27-31	freshwater, epizoic on fish (Scorpaeniformes: gasterosteid (three-spined stickleback))	surface	Pacific
T. modesta (syn. *T. spathulata*)	AD 18-43 ND 20-26	freshwater, epizoic on fish (Characiformes: characid (Mexican tetra); Cypriniformes: cobitid (pond loach), cyprinid (common bream, bronze bream, silver bream, vimba bream), gastromyzontid (tassel-mouthed loach); Cyprinodontiformes: cyprinodontid (Kizilirmak toothcarp), poeciliid (twospot livebearer); Gobiiformes: oxudercid (Amur goby))	gills, skin	Eurasia
T. mugilis	AD 23-28 ND 32	marine, epizoic on fish (Mugiliformes: mugilid (thinlip grey mullet))	gills	Europe
T. murmanica	AD 35-70 ND 21-31	marine, epizoic on fish (Gadiformes: gadid (Atlantic cod); Spariformes: sparid (blackhead seabream))	gills, skin	Pacific, Atlantic
T. mutabilis	AD 30-74 ND 21-36	freshwater, epizoic on fish (Characiformes: characid (Mexican tetra); Cichliformes: cichlid (Nile tilapia); Cypriniformes: cyprinid (common carp, goldfish, grass carp, European carp, silver carp, bighead carp, sunbleak, sabrefish, bitterling, roach, rudd, straightfin barb, threespot barb); Cyprinodontiformes: poeciliid (eastern mosquitofish); Salmoniformes: salmonid (rainbow trout))	gills, skin	Eurasia, Americas, Africa, Australia
T. multidentis	AD 12-45 ND 30-37	marine, epizoic on fish (Blenniformes: blenniid (blenny), clinid (orange clinid), tripterygiid (New Zealand topknot))	gills	New Zealand
T. myicola	AD 29-46 ND 26-36	marine, epizoic on clams (Bivalvia: myid (*Mya arenaria*))	oral epithelia	North America
T. nemachili		freshwater, epizoic on fish (Cypriniformes: nemacheilid (stone loach))	skin, gills	Europe
T. nesogobii	AD 30-33 ND 19-23	marine, epizoic on fish (Gobiiformes: gobiid (unspecified sandgoby))	gills	Australia
T. ngoma	AD 29-50 ND 21-27	marine, epizoic on fish (Characiformes: distichodontid (multibar citharine))	skin, fins, gills	Africa
T. nigra	AD 20-70	freshwater, epizoic on fish (Cichliformes: cichlid	skin, gills	Eurasia,

	ND 16-29	(banded tilapia, Mozambique tilapia, Nile tilapia, southern mouthbrooder); Cypriniformes: cyprinid (common bream, blue bream, common bleak, goldfish, grass carp, European carp, crucian carp, silver carp, gudgeon, Amur ide, Marmara chub, European chub, sabrefish, roach, rudd, tench, straightfin barb), leuciscid (lake minnow); Perciformes: centrarchid (bluegill), nandid (mottled nandus), nandid (Gangetic leaffish), percid (common zingel, redfin perch, zander); Salmoniformes: salmonid (Arctic char, brown trout, rainbow trout, sea trout, peled); Siluriformes: silurid (wels catfish), and amphibians (Anura: bombinatorid (European fire-bellied toad, tadpoles), bufonid (common toad, tadpoles), hylid (European tree frog, tadpoles), ranid (edible frog, common frog, tadpoles))		Africa
T. nkasa	AD 24-35 ND 19-22	freshwater, epizoic on fish (Siluriformes: mochokid (leopard squeaker, largespot squeaker))	gills	Africa
T. nobilis (syn. *T. nobillis*)	AD 50-77 ND 21-28	freshwater, epizoic on fish (Cichliformes: cichlid (unspecified tilapia); Cypriniformes: cyprinid (grass carp, European carp, bighead carp, goldfish, gold barb, silver carp); Cyprinodontiformes: poeciliid (giant sailfin molly, guppy))	skin, gills	Eurasia
T. noturi	AD 35-45 ND 23-27	freshwater, epizoic on fish (Siluriformes: ictalurid (speckled madtom))	skin, gills	North America
T. okajimae	AD 20-40 ND 34-38	freshwater, epizoic on amphibians (Urodela: hynobiid (Tokyo salamander))	surface	Asia
T. oligocotti	AD 23-34 ND 19-26	marine, epizoic on fish (Pleuronectiformes: pleuronectid (barfin flounder))	surface	Pacific
T. opeongoensis	AD 35-51 ND 24-34	freshwater, endozoic on fish (Cypriniformes: cyprinid (golden shiner, creek chub))	urinary tract	North America
T. ophiocephalus	AD 43 ND 55	freshwater, epizoic on fish (Anabantiformes: channid (northern snakehead); Cypriniformes: cyprinid (blue bream))	gills	Eurasia
T. ophiotricis (syn. *Cyclochaeta*)	cell 47	marine, epizoic on brittle star (Echinodermata: ophiothricid (*Ophiotrix fragilis*))	surface	Europe
T. orientalis	AD 46-63 ND 24-27	freshwater, epizoic on fish (Cypriniformes: cyprinid (crucian carp, black carp, grass carp, triangular bream, variegated carp, silver carp))	skin, gills	China
T. oviducti	AD 83-271 ND 40-60	marine, endozoic on fish (Rajiformes: rajid (thornback skate, winter skate, thorny skate, Magellan skate, blonde ray, raspthorn sand skate))	oviducts [mucoid exudates]	Atlantic, Barents, Pacific
T. oviformis	AD 22-38 ND 24-29	freshwater, epizoic on fish (Cypriniformes: cyprinid (goldfish, common carp, crucian carp, black carp, grass carp, variegated carp, silver carp, common shiner, false salmon, Changchun bream, triangular bream, silvery chub, large-spined bitterling, scanty-scaled bitterling, stone moroko), cobitid (loach, spined loach); Anabantiformes: channid (snakehead); Perciformes: percid (yellow perch), sinipercid (mandarin fish))	gills	Asia, North America
T. ovonucleata	AD 17-29 ND 18-26	marine, epizoic on fish (Blenniiformes: blenniid (tentacled blenny, rusty blenny); Gadiformes: lotid (shire rockling); Labriformes: labrid (grey wrasse, five-spotted wrasse); Ophidiiformes: ophidiid (Roche's snake blenny); Perciformes: mullid (red mullet), percid (perch), Pleuronectiformes: scophthalmid (kalkan); Syngnathiformes: syngnathid (seadragons), Scombriformes: scombrid (Atlantic mackerel); Scorpaeniformes: agonid (saburo), cottid (plain sculpin),	gills	Mediterranean, Pacific, Black Sea

		hexagrammid (masked greenling))		
T. oxystelis	AD 32-44 ND 21-29	marine, epizoic on sea snails (Gastropoda: trochid (*Oxystele sinensis, tabularis, tigrina, variegata, impervia*))	mantle cavity, shell	Africa
T. pagoda	AD 19-43 ND 19-24	freshwater, epizoic on fish (Anabantiformes: channid (small snakehead))	skin, gills	China
T. pala	AD 24-37 ND 21-26	marine, epizoic on fish (Scorpaeniformes: zoarctid (viviparous eelpout))	surface	Pacific
T. parabranchicola	AD 10-30 ND 16-26	marine, epizoic on fish (Blenniiformes: clinid (orange clinid), tripterygiid (New Zealand topknot, variable triplefin, blackhead triplefin), plesiopid (New Zealand rockfish, three-lined rockfish); Gobiesociformes: gobiesocid (striped clingfish, orange clingfish))	gills	New Zealand
T. paraheterodentata	AD 37-55 ND 20-22	freshwater, epizoic on fish (Perciformes: sinipercid (mandarin fish))	skin	China
T. parasiluri	AD 32-58 ND 20-25	freshwater, epizoic on fish (Cypriniformes: cyprinid (black carp, grass carp, variegated carp, silver carp); Anabantiformes: channid (snakehead), osphronemid (Chinese paradise fish); Perciformes: sinipercid (mandarin fish))	gills, skin	China
T. parvula	AD 23-30 ND 20-23	marine, epizoic on fish (Scorpaeniformes: psychrolutid (spinyhead sculpin))	gills	Pacific
T. patellae	AD 40-50	marine, epizoic on limpet (Gastropoda: patellid (*Patella vulgata*))	gills	Europe
T. pectenis	AD 27-38 ND 22-31	marine, epizoic on scallops (Bivalvia: pectinid (*Mizuhopecten yessoensis*) and sand dollars (Echinodermata: echinarachniid (*Echinarachnius parma*)))	gills	China, Russia
T. pediculus [type species as *Cyclidium*]	AD 27-85 ND 16-36	freshwater, epiphytic on moss (Bryozoa: cristatellid (*Cristatella mucedo*), plumatellid (*Plumatella repens*) and epizoic on invertebrates (Hydrozoa: hydrid (*Hydra attenuata, fusca, vulgaris, viridis, Pelmatohydra oligactis*); jellyfish (Cnidaria: olindiid (*Limnocnida indica*); mussels (Bivalvia: unionid (*Margaritifera margaritifera*)), fish (Cichliformes: cichlid (redbreast tilapia, banded tilapia, Mozambique tilapia, Nile tilapia, electric yellow cichlid, pindani); Cypriniformes: cyprinid (goldfish, crucian carp, Eurasian carp, grass carp, black carp, bighead carp, silver carp, common bream, common bleak, sunbleak, rudd, swamp barb, olive barb, stigma barb, common chub, common roach); Cyprinodontiformes: poeciliid (giant sailfin molly, short-finned molly); Esociformes: esocid (northern pike); Perciformes: centrarchid (largemouth bass), percid (European perch, ruffe, zander); Salmoniformes: salmonid (vendace); Scorpaeniformes: gasterosteid (three-spined stickleback); and amphibians (Anura: bufonid (common toad, tadpoles), ranid (common frog, tadpoles): Urodela: salamandrid (smooth newt, larvae)	gills, skin, fins	cosmopolitan
T. percae	AD 42-64 ND 22-25	freshwater, epizoic on fish (Perciformes: percid (redfin perch))	skin	Russia
T. perforata	AD 37-55 ND 22-26	freshwater, epizoic on fish (Cypriniformes: cyprinid (crucian carp, common carp, common bleak, European carp, white-finned gudgeon, Kessler's gudgeon))	gills	Eurasia
T. platyformis	AD 53-76 ND 26-35	freshwater, epizoic on fish (Cypriniformes: leuciscid (pearl dace, blacknose dace))	gills	North America, Europe
T. ploveri		marine, epizoic on fish (Clupeiformes: clupeid	surface	Pacific

		(Atlantic herring))		
T. polaridiae		marine, epizoic on mussels (Bivalvia: cardiid (*Cardium namarcki*))	gills	Europe
T. polycirra	AD 48-58 ND 38-55	freshwater, endozoic in fish (Cypriniformes: cyprinid (bream, common roach, carp bream, common carp))	urinary tract	Eurasia
T. polystriata		freshwater, epizoic on fish (Perciformes: centrarchid (pumpkinseed))	gills	North America
T. porocephalusi	AD 27-42 ND 20-27	freshwater, epizoic on fish (Gobiiformes: eleotrid (orange-bellied sleeper))	gills	India
T. prowazeki	AD 39-55 ND 22-26	freshwater, epizoic on fish (Cypriniformes: cobitid (loach))	gills	Europe
T. pseudoheterodentata	AD 61-74 ND 23-25	freshwater, epizoic on fish (Siluriformes: ictalurid (channel catfish))	gills	China
T. puytoraci	AD 42-52 ND 25-28	euryhaline, epizoic on fish (Gadiformes: gadid (merling); Mugiliformes: mugilid (golden grey mullet, flathead grey mullet, leaping mullet))	gills	Europe
T. raabei	AD 22-32 ND 23-29	marine, epizoic on fish (Gadiformes: gadid (saffron cod); Pleuronectiformes: pleuronectid (European flounder, common dab, marbled flounder); Scorpaeniformes: agonid (saburo), cottid (plain sculpin), hexagrammid (masked greenling, Arabesque greenling))	gills, skin	Baltic Sea, White Sea
T. rajae	AD 69-90 ND 34-41	marine, endozoic on fish (Rajiformes: arhynchobatid (raspthorn sandskate))	oviducts	Pacific
T. ranae	AD 38-52 ND 28-33	freshwater, endozoic in amphibians (Anura: ranid (marsh frog, edible frog, pool frog))	urinary bladder	Europe
T. rectuncinata	AD 19-42 ND 20-35	marine, epizoic on fish (Blenniiformes: blenniid ((butterfly blenny, tentacled blenny, peacock blenny, rusty blenny, combtooth blenny, shanny), tripterygid (network triplefin, grass goby, Molly Miller); Gadiformes: gadid (merling), lotid (shore rockling); Gobiesociformes: gobiesocid (blackstripe clingfish); Gobiiformes: gobiid (grass goby, island frillfin); Labriformes: labrid (grey wrasse, five-spotted wrasse, East Atlantic peacock wrasse, goldsinny wrasse); Perciformes: lateolabracid (Japanese seabass); Scorpaeniformes: cottid (padded sculpin), hexagrammid (spotty-bellied greenling); Syngnathiformes: syngnathid (long-snout seahorse) [possibly erroneously reported from freshwater fish (Cichliformes: cichlid (Nile tilapia); Perciformes: latid (Nile perch); Siluriformes: clariid (African sharptooth catfish)]	gills	Atlantic, Pacific, Adriatic
T. reticulata	AD 31-66 ND 21-34	freshwater, epizoic on fish (Acipenseriformes: acipenserid (Siberian sturgeon); Cichliformes: cichlid (Nile tilapia); Cypriniformes: cyprinid (goldfish, common carp, crucian carp))	skin, gills [mortalities]	Europe, North America, Africa
T. rhinobatae	AD 29-42 ND 27-34	marine, endozoic in fish (Rhinopristiformes: rhinobatid (lesser guitarfish))	urogenital tract	Africa
T. rostrata	AD 44-55 ND 26-28	freshwater, epizoic on fish (Cypriniformes: cyprinid (common roach, bronze bream, European carp, bitterling); Cyprinodontiformes: goodeid (dark-edged splitfin))	skin	Europe, Mexico
T. ruditapicis	AD 33-52 ND 21-29	marine, epizoic in shellfish (Bivalvia: venerid (*Saxidomus purpurata*, *Ruditapes philippinarum*), solenid (*Solen grandis*))	gills	China
T. salmincola	AD 40-59 ND 21-26	freshwater, epizoic on fish (Salmoniformes: salmonid (rainbow trout, brook trout)	skin	North America
T. sangwala	AD 39-59 ND 23-31	freshwater, epizoic on fish (Siluriformes: clariid (African sharptooth catfish), schilbeid (African butter catfish))	gills	Africa

T. scapharcae	AD 23-30 ND 20-24	marine, epizoic on clams (Bivalvia: arcid (*Scapharca subcrenata*))	gills	China
T. schizothoraci		freshwater, endozoic in fish (Cypriniformes: cyprinid (Sattar snowtrout))	urinary tract	Asia
T. scorpaenae (syn. *Cyclochaeta*)	cell 40-50	marine, epizoic on fish (Scorpaeniformes: triglid (unspecified))	surface	Europe
T. serpularum (syn. *Cyclochaeta*)	cell 25-40	marine, epizoic on tubeworm (Polychaeta: serpulid (*Serpula*)	surface	Europe
T. shitalakshyae	AD 30-37 ND 18-21	estuarine, epizoic on fish (Gobiiformes: gobiid (tank goby))	gills	India
T. siluri	AD 22-46 ND 23-27	freshwater, epizoic on fish (Siluriformes: silurid (wels catfish))	gills	Eurasia
T. sinonovaculae	AD 48-67 ND 24-27	marine, epizoic on clam (Bivalvia: pharid (*Sinonovacula constricta*))	gills	China
T. spheroidesi	AD 14-54 ND21-31	marine, epizoic on fish (Tetraodontiformes: tetraodontid (northern puffer))	gills, skin	North America
T. spongillae	AD 60 ND 37	freshwater, planktonic and endozoic on sponge (Porifera: spongillid (*Spongilla fluviatilis*))	inside body	Europe
T. steini	AD 40-50 ND 21-26	aquatic, epizoic on flatworms (Tricladida: dugesiid (*Dugesia lugubris*), planariid (*Polycelis nigra, cornuata*))	surface	Europe
T. strelkovi	AD 33-58 ND 25-28	freshwater, epizoic on fish (Cypriniformes: cyprinid (false osman), nemacheilid (Tibetan stone loach); Mugiliformes: mugilid (Abu mullet)) [and on parasitic trematodes (Monogenea: dactylogyrid (*Dactylogyrus auriculatus, falcatus*)]	skin, gills [carapace]	Eurasia
T. subtilihamata	AD 38-48 ND 26-29	freshwater, epizoic on fish (Cypriniformes: cyprinid (goldfish))	gills	China
T. sylhetensis	AD 25-38 ND 23-24	freshwater, epizoic on fish (Perciformes: nandid (mud perch))	gills	India
T. synaptae (syn. *Cyclochaeta*)	cell 56-95	marine, epizoic on sea cucumber (Echinodermata: synatid (*Synapta*))	surface	Europe
T. tegula	AD 30-50 ND 22-31	marine, epizoic on sea snails (Gastropoda: tegulid (*Tegula funebralis, ligulata*))	mantle cavity	North America
T. tenuidens	AD 40-79 ND 25-38	anadromous/euryhaline, epizoic on fish (Cyprinodontiformes: fundulid (mummichog); Scorpaeniformes: gasterosteid (three-spined stickleback, ninespine stickleback))	gills, skin	North America
T. tisae	AD 40-58 ND 23-29	freshwater, epizoic on fish (Perciformes: percid (zander))	gills	Eurasia
T. trichiuri		marine, epizoic on fish (Scombriformes: trichiurid (largehead hairtail))	surface	Pacific
T. trigonofibulae		marine, epizoic on fish (Scorpaeniformes: agonid (butterfly sculpin))	surface	Pacific
T. truttae	AD 76-142 ND 27-34	freshwater, epizoic on fish (Cichliformes: cichlid (Nile tilapia); Salmoniformes: salmonid (humpback salmon, chum salmon, masu salmon, yellowfin cutthroat trout))	skin, gills	North America, Russia
T. tumefaciens	AD 27-38 ND 19-27	freshwater, epizoic on fish (Scorpaeniformes: cottid (mottled sculpin); Cypriniformes: cyprinid (golden shiner, creek chub); Perciformes: centrarchid (pumpkinseed), percid (yellow perch))	gills, skin	North America
T. tunnae	AD 26-35 ND 19-22	freshwater, epizoic on fish (Perciformes: percid (European perch))	skin, gills	Australia
T. uniforma	AD 50-57 ND28-30	freshwater, epizoic on fish (Cypriniformes: cyprinid (goldfish))	skin, fins, gills	China, Africa
T. unionis	AD 41-53 ND 22-28	freshwater, epizoic on snails (Gastropoda: lymnaeid (*Stagnicola*), physid (*Physella acuta*), planorbid (*Gyraulus siamensis*))	surface	Canada, Asia
T. urechi	cell 25-50 ND 18-25	marine, endozoic in worm (Polychaeta: urechid (*Urechis caupo*))	midgut	North America
T. uretra	AD 42-65	freshwater, endozoic in fish (Cypriniformes:	urinary bladder,	Africa

	ND 47-54	cyprinid (threespot barb))	ureters	
T. urinaria	AD 36-60 ND 14-41	freshwater, endozoic in fish (Cypriniformes: cyprinid (common shiner, golden shiner); Perciformes: percid (zander, yellow perch, redfin perch))	urinary tract	Holarctic
T. urinicola	AD 34-35 ND 26-36	freshwater, endozoic in amphibians (Anura: bufonid (common toad, tadpoles); Urodela: salamandrid (northern crested newt, smooth newt, larvae))	urinary tract	Europe
T. valkanovi	AD 38-53 ND 26-29	freshwater, epizoic on fish (Cypriniformes: cyprinid (bitterling))	gills	Europe
T. vallata	AD 31-49 ND 18-23	freshwater, epizoic on fish (Siluriformes: ictalurid (channel catfish))	skin, gills	North America
T. vancouverense	AD 8-23 ND 16-25	marine, epizoic on fish (Scorpaeniformes: cottid (padded sculpin))	gills	Pacific
T. vesicola		freshwater, endozoic in amphibians (Anura: ranid (Japanese wrinkled frog))	urinary bladder	Asia
T. vesicularum	AD 19-47 ND 21-33	freshwater, endozoic in amphibians (Urodela: salamandrid (smooth newt, Carpathian newt, palmate newt))	urinary bladder	Europe
T. wellborni	AD 36-46 ND 21-26	freshwater, epizoic on fish (Cypriniformes: cyprinid (Eurasian carp, Amur carp); Perciformes: centrarchid (largemouth bass))	gills	North America
T. wulai	AD 47-62 ND 24-26	freshwater, epizoic on fish (Siluriformes: silurid (Amur catfish))	gills	Asia
T. xenopodos	AD 68-94 ND 46-55	freshwater, endozoic in amphibians (Anura: pipid (African clawed frog))	urinary bladder	Africa
T. zambeziensis	AD 20-28 ND 16-20	freshwater, epizoic on jellyfish (Cnidaria: olindiid (*Limnocnida tanganjicae*))	surface of medusae	Africa
Genus ***Trichodinella*** (adoral ciliary spiral makes ½-¾ turns, denticles wedged together by central parts and blades, thorns absent or stunted to form short hooks)				
T. baltica (syn. *Trichodina*, *Brachyspira*)	cell 16-43	estuarine, epizoic on snails (Gastropoda: neritid (*Neritina* (*Theodoxus*) *fluviatilis*), and fish (Gobiiformes: gobiid (black goby))	mantle cavity, gills	Baltic Sea
T. carpi	AD 14-19 ND 15-20	freshwater, epizoic on fish (Cypriniformes: cyprinid (Eurasian carp))	gills	Philippines
T. crennulata	AD 17-23 ND 21-26	freshwater, epizoic on fish (Characiformes: characid (sharptooth tetra))	gills	Africa
T. epizootica (syn. *Tripartiella, T. carassii p.p., maior, percarum, lotae*) [type species as *Brachyspira*]	AD 13-47 ND 16-30	freshwater, epizoic on fish (Anguilliformes: anguillid (European eel); Cichliformes: cichlid (redbreast tilapia, Mozambique tilapia, southern mouthbrooder); Cypriniformes: cyprinid (riffle minnow, roundnose minnow, goldfish, common carp, crucian carp, European carp, bighead carp, grass carp, silver carp, common barbel, tench, straightfin barb, threespot barb, bluebream, common roach, common rudd, white bream, ziege, Amur bitterling), cobitid (weatherfish), danionid (river sardine), leuciscid (lake minnow); Esociformes: esocid (northern pike); Gadiformes: lotid (burbot); Perciformes: percid (Eurasian ruffe, redfin perch, zander, zingel); Osteoglossiformes: mormyrid (elephant-snout fish); Perciformes: percid (European perch, zander); Salmoniformes: salmonid (sockeye salmon, brown trout, rainbow trout)	gills	cosmopolitan
T. lawleri	AD 12-17 ND 15-19	marine, epizoic on fish (Spariformes: sparid (pinfish))	gills	North America
T. longispira		freshwater, epizoic on fish (Esociformes: esocid (northern pike, Amur pike))	gills	Asia
T. lomi	AD 15-24 ND 20-29	marine, epizoic on fish (Perciformes: lateolabracid (Japanese seabass); Spariformes: sparid (red seabream))	gills	Asia

T. minuta (syn. *Trichodina*) [possible synonym of *T. epizootica*]	AD 11-36 ND 15-24	freshwater, epizoic on fish (Cichliformes: cichlid (banded jewel cichlid, banded tilapia, Mozambique tilapia, southern mouthbrooder); Cypriniformes: cyprinid (grass carp, bighead carp, silver carp, threespot barb))	gills, skin, fins	Eurasia
T. myakkae (syn. *Trichodina*)	AD 11-25 ND 17-24	freshwater, epizoic on fish (Cypriniformes: catostomid (smallmouth buffalo, river carpsucker), cyprinid (silver carp, bighead carp, grass carp, stone moroko); Perciformes: centrarchid (largemouth bass); Salmoniformes: salmonid (brook trout))	gills	Asia, North America
T. simplex (syn. *Dipartiella, Dogielina*)	AD 10-30 ND 17-28	marine, epizoic on fish (Gobiiformes: gobiid (black goby); Perciformes: lateolabracid (Japanese sea bass))	gills	Baltic Sea, Yellow Sea
T. subtilis (syn. *T. carassii p.p., Trichodina*)	AD 14-32 ND 16-36	freshwater, epizoic on fish (Cypriniformes: cyprinid (Eurasian carp, goldfish, crucian carp, white bream, tench, ziege, Amur bitterling); Salmoniformes: salmonid (rainbow trout))	gills	Eurasia
T. symmetrica (syn. *Trichodina*) [possible mixture of species, thus regarded as *nomen nudum*]	AD 24-35 ND 21-28	freshwater, epizoic on fish (Cypriniformes: cyprinid (goldfish, Eurasian carp, common shiner, golden shiner, creek chub), leuciscid (pearl minnow, eastern blacknose dace); Perciformes: percid (yellow perch); Siluriformes: ictalurid (channel catfish))	skin, gills	North America
T. tilapae	AD 14-20 ND 22-25	freshwater, epizoic on fish (Cichliformes: cichlid (redbelly tilapia))	gills	Philippines
Genus ***Tripartiella*** (adoral ciliary spiral makes ½-¾ turns, denticles with well-developed thorns, blades extend obliquely backwards, denticles interlocked by central parts and by anterior projections)				
T. bulbosa (syn. *Trichodina, T. ovaliformis, Tripartiella leucisci)*)	AD 13-26 ND 19-28	freshwater, epizoic on fish (Anabantiformes: osphronemid (round-tailed paradisefish, giant gourami); Cypriniformes (grass carp, silver carp, bighead carp, black carp, mrigal carp, catla, rohu, bata, dace, Allegheny pearl dace, Java barb); Gobiiformes: butid (marble goby); Perciformes: ambassid (elongate glassy perchlet); Siluriformes: bagrid (Day's mystus), clariid (broadhead catfish), pangasiid (sutchi catfish, (spot pangasius) and amphibians (Anura: bufonid (common toad, tadpoles), ranid (Japanese wrinkled frog, tadpoles))	gills	Eurasia, North America
T. bursiforms (syn. *Trichodina*)	AD 25-36 ND 23-32	freshwater, epizoic on fish (Perciformes: centrarchid (mud sunfish, rock bass))	gills	North America
T. cichlidarum	AD 22-30 ND 30-32	freshwater, epizoic on fish (Cichliformes: cichlid (blue tilapia))	gills	Israel
T. clavodonta	AD 15-20 ND 18-24	freshwater, epizoic on fish (Cichliformes: cichlid (Mozambique tilapia, southern mouthbrooder); Cypriniformes: cyprinid (river sardine))	gills	Africa, Asia
T. copiosa [type species]	AD 13-45 ND 17-33	freshwater, epizoic on fish (Cypriniformes: cobitid (spined loach), cyprinid (common carp, mrigal carp, common roach, common bleak, sunbleak, common dace, common chub, rohu, bata, catla, Amur bitterling, bronze bream, silver bream, ide); Siluriformes: bagrid (striped dwarf catfish))	gills	Eurasia
T. ctenopomae	AD 18-32 ND 26-34	freshwater, epizoic on fish (Anabantiformes: anabantid (manyspined climbing perch))	gills	Africa
T. dactylodentata	AD 22-27 ND 27-32	freshwater, epizoic on fish (Osteoglossiformes: mormyrid (elephant-snout fish), Siluriformes: schilbeid (African butter catfish))	gills	Africa
T. kashkovskyi	AD 20-27 ND 23-29	freshwater, epizoic on fish (Cyprinodontiformes: fundulid (starhead topminnow))	gills	North America
T. lata	AD 17-25 ND 20-24	freshwater, epizoic on fish (Cypriniformes: cyprinid (bullhead minnow), leuciscid (Eurasian minnow); Salmoniformes: salmonid (sockeye	gills	Eurasia

		salmon, rainbow trout))		
T. lechridens	AD 15-20 ND 20-26	freshwater, epizoic on fish (Characiformes: alestid (sharptooth tetra); Cichliformes: cichlid (Mozambique tilapia); Cypriniformes: cyprinid (Eurasian carp, straightfin barb, threespot barb, redeye labeo), danionid (river sardine))	gills	Africa
T. leptospina	AD 14-22 ND 16-21	freshwater, epizoic on fish (Cichliformes: cichlid (Mozambique tilapia))	gills	Africa
T. macrosoma	AD 14-20 ND 22-25	freshwater, epizoic on fish (Cypriniformes: cyprinid (orangefin barb); Cyprinodontiformes: cyprinodontid (Kizilirmak toothcarp))	gills	Africa, Europe
T. melanogrammi	AD 37-69 ND 28-32	marine, epizoic on fish (Gadiformes: gadid (haddock)	gills, fins	Eurasia
T. microctenopomae	AD 13-23 ND 21-31	freshwater, epizoic on fish (Anabantiformes: anabantid (blackspot climbing perch)	gills	Africa
T. nana	AD 13-22 ND 16-19	freshwater, epizoic on fish (Cichliformes: cichlid (Mozambique tilapia))	gills	Africa
T. obliqua (syn. *T. inversa*)	AD 14-19 ND 18-26	marine, epizoic on fish (Labriformes: labrid (grey wrasse); Mugiliformes: mugilid (flathead grey mullet); Pleuronectiformes: paralichthyid (olive flounder); Scombriformes: scombrid (Atlantic mackerel), trichiurid (largehead hairtail); Scorpaeniformes: triglid (tub gurnard))	gills	Atlantic, Black Sea
T. obtusa	AD 10-23 ND 17-27	freshwater, epizoic on fish (Cypriniformes: cyprinid (gudgeon, rohu); Osteoglossiformes: notopterid (bronze featherback))	gills	Eurasia
T. orthodens	AD 14-32 ND 19-28	freshwater, epizoic on fish (Cichliformes: cichlid (redbreast tilapia, mango tilapia); Siluriformes: bagrid (rita, shining catfish))	gills	Africa, Asia
T. pseudoplatystomae	AD 23-37 ND 27-31	freshwater, epizoic on fish (Siluriformes: pimelodid (spotted sorubim))	gills	South America
T. pungitii		freshwater, epizoic on fish (Scorpaeniformes: gasterosteid (ninespine stickleback); Cichliformes: cichlid (redbelly tilapia); Salmoniformes: salmonid (chum salmon))	gills	Pacific, Iraq
T. rhombi	AD 18-30 ND 20-28	estuarine, epizoic on fish (Pleuronectiformes: scophthalmid (turbot); Cypriniformes: cyprinid (common carp))	gills	Eurasia
T. tetramerii	AD 27-38 ND 23-25	freshwater, epizoic on fish (Cichliformes: cichlid (saddle cichlid))	gills	South America
T. tilapiae	AD 16-25 ND 21-27	freshwater, epizoic on fish (Cypriniformes: cyprinid (grass carp))	gills	Asia
Genus ***Vauchomia*** (adoral ciliary spiral makes 2-3 turns, denticles with well-developed blades and thorns, striated border membrane with fused rings of rays and myonemes)				
V. nephritica (syn. *Trichodina*) [type species]	AD 53-75 ND 33-42	freshwater, endozoic in fish (Esociformes: esocid (muskellunge))	urinary tract	North America
V. renicola (syn. *Trichodina*)	AD 75-97 ND 44-65	freshwater, endozoic in fish (Esociformes: esocid (chain pickerel, pike))	urinary tract	North America

Parasite morphology: *Trichodina* spp. form trophic stages (trophonts) that have 3 distinctive features: an oral ciliary spiral for feeding; a ring of somatic cilia for motility; and a complex adhesive disc for temporary attachment to hosts. Trophonts are discoidal to hemispherical in shape, appearing circular when viewed from above, and flattened or convex when viewed from the side. They vary considerably in size depending on species, ranging from 10-150 µm in diameter. They are covered by a thin pellicular membrane and contain a large macronucleus (usually horseshoe-shaped, rarely ellipsoidal) with a small dense adjacent micronucleus. Trophonts have specialized 'peritrichous' mouthparts located on the surface facing away from the host (termed the upper or oral surface) with a prominent paroral membrane formed by ciliary rows spiralling through 1-1½ counter-clockwise turns down to the central cytostome (mouth), accompanied by a smaller series of lateral membranelles. Other trichodinid genera may be partly distinguished by the number of spiral turns made by their paroral membranes (*Paratrichodina*, *Semitrichodina*, *Tripartiella* and *Trichodinella* making ½-¾ turns, *Pallitrichodina* ¾ turns, *Heterobladetrichodina* < 1 turn, *Hemitrichodina* 1-2 turns, and *Vauchomia* 2-3 turns). The body of the trophont bears several rings of peripheral cilia which are used for locomotion, including a compound wreath of oblique ciliary rows (6-10 cilia per row), a basal row of single cilia (separated from the compound wreath by a

septum), sometimes a third ring of marginal cilia (located adoral to the basal cilia), and rarely several aboral cirri (compound ciliary organelles). The aboral surface of the trophonts contains an elaborate adhesive disc used for temporary attachment to substrates. The adhesive disc is formed by a distinctive ring of radial interlocking cytoskeletal denticles, each with a distal blade, hook-like centrum, and proximal ray (or thorn). The denticular ring is surrounded by a ring of fine skeletal rods (radial pins). The structure of the adhesive disc varies depending on the trichodinid genus and species, with *Trichodina* spp. possessing discs ranging from 10-150 µm in diameter (mostly 30-40 µm) and containing 12-55 denticles (mostly 20-30) with well-developed flat straight-semicircular blades, central parts lacking anteriorly-directed projections, and spine- or needle-shaped rays.

Site of infection: *Trichodina* spp. are essentially commensals, most being epizoic on superficial aspects of aquatic hosts (skin, fins, gills, nasal pits) but some being endozoic in the lumina of tubular organs (mostly the urinary tract, sometimes the intestinal or reproductive tracts). Over 125 *Trichodina* spp. have been reported as epizoic commensals/parasites on almost 290 species of freshwater fish belonging to 74 families in 29 orders (especially Cypriniformes, Cichliformes, Perciformes, Salmoniformes and Siluriformes, but also including Acipenseriformes, Anabantiformes, Anguilliformes, Atheriniformes, Beloniformes, Blenniiformes, Callionymiformes, Characiformes, Clupeiformes, Cyprinodontiformes, Esociformes, Gadiformes, Galaxiiformes, Gobiiformes, Kurtiformes, Labriformes, Moroniformes, Mugiliformes, Osteoglossiformes, Pleuronectiformes, Scorpaeniformes, Spariformes, Synbranchiformes, and Tetraodontiformes). Several freshwater species have also been reported attached to larval stages of amphibians (toads, frogs, newts and salamanders) and there have been occasional reports in association with freshwater mussels, snails, copepods, bryozoans, hydrozoans, jellyfish, sponges and flatworms. An additional 86 *Trichodina* spp. have been recorded as epizoic commensals/parasites on 165 species of marine fish belonging to 56 families in 26 orders (particularly Scorpaeniformes, but also including Anabantiformes, Anguilliformes, Atheriniformes, Blenniformes, Callionymiformes, Characiformes, Clupeiformes, Cypriniformes, Cyprinodontiformes, Esociformes, Gadiformes, Gobiesociformes, Gobiiformes, Labriformes, Moroniformes, Mugiliformes, Ophidiiformes, Perciformes, Pleuronectiformes, Salmoniformes, Scombriformes, Siluriformes, Spariformes, Syngnathiformes, and Tetraodontiformes). Another 6 marine species have been found as endozoic organisms within the urogenital tracts of marine fish (surgeonfish, guitarfish, puffers and skates) and there have been occasional reports of infestations in association with bivalves (clams, cockles, scallops, limpets, mussels), chitons, star fish, brittle stars, sea snails, sea cucumbers, branchiopods, copepods, polychaetes and tubeworms. Other trichodinid genera are found mainly on the gills of freshwater and marine fish (including 23 *Tripartiella* spp., 15 *Paratrichodina* spp., 13 *Trichodinella* spp.), some exclusively on surfaces of freshwater fish (2 *Heterobladetrichodina* spp., one *Hemitrichodina* sp.) or in the urinary tracts of freshwater fish (2 *Vauchomia* spp.) and a few in the mantle cavities of terrestrial snails (4 *Semitrichodina* spp., 2 *Pallitrichodina* spp.).

Pathogenesis: Trophonts use their aboral adhesive discs to attach to hosts where they filter-feed on waterborne solutes and particles, including bacteria. Most species attach to the superficial surfaces of fish, but some reside in the cavities of tubular organs. During attachment, the adhesive disc acts as a sucking cup drawing up epithelial cells and sometimes resulting in attachment-related pathologies. The discs play no part in feeding as the mouthparts and feeding ciliary spirals are located on the opposite oral surface. The presence of a few trophonts usually has little effect on healthy hosts, but in young fish or those debilitated by stress (poor water quality, inadequate nutrition, concomitant infections), skin barriers and their protective chemicals may be impaired allowing trichodinids to proliferate. The trophonts are highly mobile constantly attaching and detaching on epidermal and epithelial surfaces (sometimes colloquially referred to as ‘scrubbing bubbles’). Attachment may cause irritation, cellular damage and inflammation, but does not result in distinctive lesions. Fish may develop focal patches of blotchy blue-grey skin with epithelial hyperplasia, peeling and excessive mucus production. Heavily infected fins may appear tattered and frayed. Infected gills can become congested with mucus and gill filaments can become clubbed or fused. Clinical signs may include breathing difficulties, sluggish swimming just beneath the surface or near the water’s edge, sometimes flashing behaviour (abrupt movements exposing the silvery undersides of fish), lethargy, loss of appetite, cessation of feeding, rapid loss of condition, and occasionally mortalities in both wild and cultured fishes. Affected fish also become prone to secondary fungal and bacterial infections in areas of damaged tissue. Several trichodinid species are endozoic and occur in the urinary tracts of fish, sometimes the genital or intestinal tracts, where their attachment may cause extensive epithelial desquamation and occasionally yellowish mucoid exudates, but not overt disease. Trichodinids become problematic in aquaculture systems when water quality is poor resulting in eutrophication with bacterial blooms providing abundant food for trichodinid growth and proliferation. Clinical infections are found more frequently in young fish fry, particularly during the spring in fish stressed by harsh winter conditions.

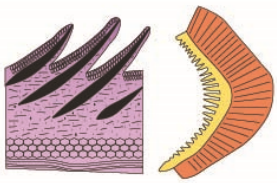
Developmental cycle and mode of transmission: Trichodinids are mobiline peritrichous ciliates in aquatic habitats, attaching to hosts using their aboral holdfast organelles but also able to swim freely. They do not form cysts so all transmission between hosts is direct via free-swimming stages, particularly when incidental contact is made between fish, but also through contact with ciliates in the water column. The discoidal trophonts swim with the aboral surface facing forwards, but upon making contact with a suitable substrate, they move laterally with the aboral surface facing the substrate. Attached trophonts reproduce asexually by binary fission, with nuclear division, replication of the adhesive disc, oral and somatic ciliature followed by transverse splitting into 2 cells. Daughter cells become free-swimming and are ready to attach to hosts within 24 hours. Under ideal growth conditions (usually when food is abundant), trophonts may divide every several days. When conditions are not ideal, ciliates may initiate sexual reproduction by conjugation which involves 2 cells coming together to form a mating pair with fusion of their cell membranes producing a cytoplasmic bridge through which genetic material is exchanged (gametic pronuclei derived from micronuclear meiotic

divisions). Reproduction by conjugation enhances genetic diversity and is thought to help promote the survival of at least some offspring in adverse conditions. There has also been speculation that the transmission of some endozoic species in the urogenital tracts of fish may occur venereally, but conclusive studies are outstanding.

Differential diagnosis: Infections are diagnosed by the direct microscopic detection of trophonts in wet mounts of skin scrapings, mucus, fin snips, gill filaments, or the contents of tubular organs (mainly the urinary bladder). Live trophonts are best observed by high-contrast microscopy and may be seen as small motile rotating ciliated discs in fluids or as sedentary cells attached to host tissues. Differential diagnosis is afforded by enrobing specimens onto albuminized slides and subjecting them to silver staining (silver nitrate, silver proteinate (protargol) or silver carbonate) to reveal details of their adhesive discs, ciliature and nuclei. In particular, staining with silver nitrate accentuates the adhesive disc by staining the cell cytoplasm black but leaving the denticles white. Molecular biological techniques have been used to characterize trichodinid species and determine phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit (18S) ribosomal DNA).

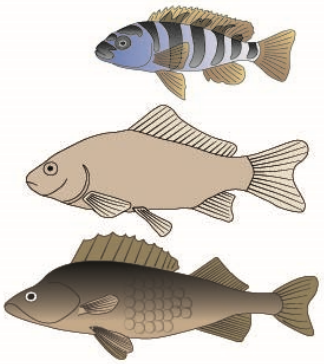
Treatment and control: Infected fish may be treated using a range of chemical baths, including formalin, copper sulphate, potassium permanganate, malachite green and dilute acetic acid, but some treatments may produce adverse side-effects or pose toxicity problems (many chemicals are prohibited for use in food animals). Other treatments have included freshwater baths for marine fish or saltwater baths for freshwater fish. A range of preventive measures have been suggested to control infections in aquaculture through improved hygiene, sanitation and husbandry. Regular health surveillance should be conducted to screen new stock, identify infected animals for treatment, quarantine or culling. Ponds and tanks should be decontaminated by chemical disinfection or draining and drying. Fish should be reared in clean water, with good flow or regular flushing, and any dead or dying fish should be promptly removed. Every effort should be made to avoid over-feeding and organic enrichment (eutrophication) in holding facilities as they lead to bacterial blooms that enhance ciliate growth. Fish should also be kept in good health by avoiding stressful (immunocompromising) situations (over-handling, over-crowding, inadequate nutrition, poor water quality) and any injuries or concomitant infections should be treated.

Trichodina

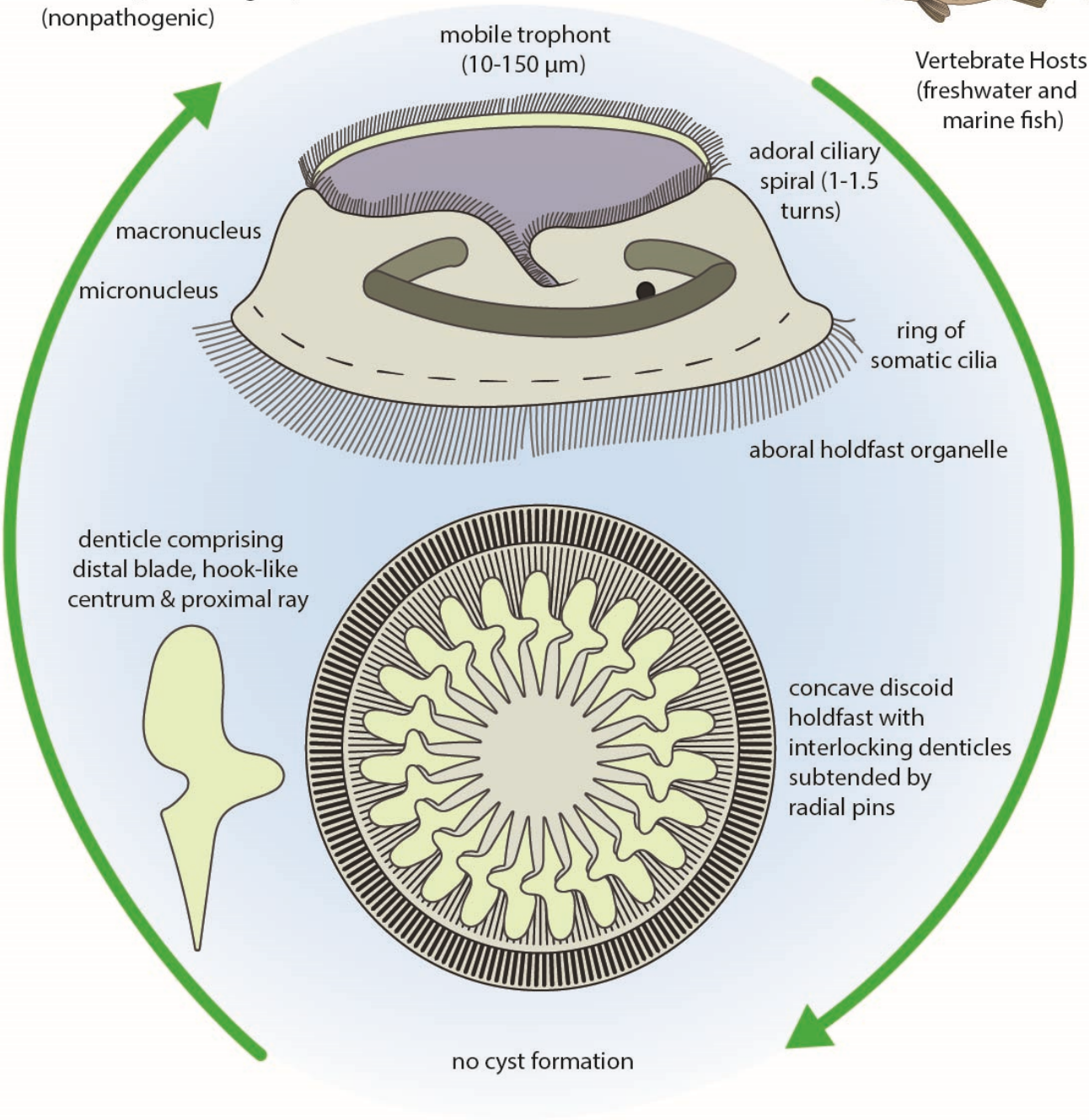


most epizoic (skin, gills)
(irritation, lesions, ulkcers)
some endozoic (tubular organs)
(nonpathogenic)

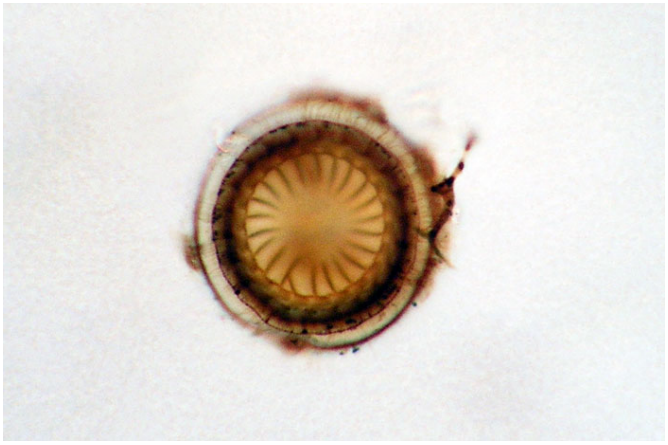
may reproduce asexually
(by transverse binary fission)
or sexually (by conjugation)



Vertebrate Hosts
(freshwater and
marine fish)



transmission via free-swimming
trophonts in water column



Trichodina trophont adhesive disc from fish skin



Trichodina trophont adhesive disc from fish skin



Trichodina trophont adhesive disc from fish skin

Epistylis, Apiosoma, Scyphidia, Ambiphrya, Vorticella, Carchesium, Zoothamnium, Cothurnia, Vaginicola, Lagenophrys
(protist: ciliate)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three major alveolate groups are recognized: ciliates, apicomplexans and dinoflagellates. Ciliated protozoa are unique eukaryotes as they exhibit nuclear dualism (vegetative macronucleus and reproductive micronucleus), the process of conjugation (exchange of micronuclei between pairs), have membrane-bound sacs (subpellicular alveoli) supporting the plasma membrane, and move using cilia (2+9 undulipodia with compound subpellicular infraciliature). Most ciliates are free-living in aquatic and terrestrial habitats, but some are symbiotic in vertebrate and invertebrate hosts. Ten major monophyletic lineages are recognized on the basis of their infraciliature, i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). Members of the subphylum Intramacronucleata are united by the presence of microtubules inside the macronuclear envelope during division; including the oligohymenophoreans ('few membrane-bearer') with an adoral zone of three membranelles. Peritrichous ciliates are filter-feeders with a left-hand spiral of oral cilia leading to cytostome. They live attached permanently (sessilines) or temporarily (mobilines) to substrates, which may include other aquatic animals. Many species cause significant fouling of the external surfaces and/or gills of fish and shellfish, some tentatively associated with diminished respiratory and feeding functions, and severe fouling leading to consumer aversion.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Alveolata (with cortical alveoli)
Phylum:	Ciliophora (with cilia, nuclear dualism, pellicular alveoli, reproductive conjugation)
Subphylum:	Intramacronucleata (microtubules occur inside macronuclear envelope during division))
Class:	Oligohymenophorea (distinct oral ciliature, comprising right paroral membrane and 3 left membranelles)
Subclass:	Peritrichia (body inverted bell-shaped, conspicuous buccal ciliature encircles apical pole (peristomial field) winding counterclockwise plunging to buccal infundibulum, antapical pole with holdfast (scopula or adhesive disc), predominantly bactivores, often stalked)
Order:	Sessilina (attached to substrate with scopula (specialized flattened thigmotactic area) with or without stalk
Family:	Epistylididae (scopula produces noncontractile stalk, retractile lip encircles elevated peristomial disc)
Genus:	*Apiosoma* (circular scopula, sometimes lobed/split into ramiform projections, epizoic on skin/gills of fish)
Genus:	*Epistylis* (colonial ciliates, stalk, noncontractile, branched, epizoic on fish and crustacea)
Family:	Scyphidiidae (solitary ciliates, attached by scopula)
Genus:	*Scyphidia* (large scopula, cell usually cylindrical, epizoic on fish and crustacea)
Genus:	*Ambiphrya* (scopula, locomotory fringe of cilia, motile in swarmers, epizoic on fish and crustacea)
Family:	Vorticellidae (solitary, gregarious or colonial, retractile stalks with central myoneme)
Genus:	*Vorticella* (stalk, contractile, unbranched, solitary or gregarious, epizoic on fish and crustacea)
Genus:	*Carchesium* (stalk, basal part contractile, branched, colonial, epizoic on fish and crustacea)
Family:	Zoothamniidae (solitary or colonial, retractile stalks with shared myonemes, epizoic on fish and crustacea)
Genus:	*Zoothamnium* (stalk, contractile, branched, colonial)
Family:	Vaginicolidae (upright lorica)
Genus:	*Cothurnia* (vase-shaped, short stalk, epizoic on crustacea)
Genus:	*Vaginicola* (urn-shaped, stalkless, epizoic on crustacea)
Family:	Lagenophryidae (flat discoid lorica)
Genus:	*Lagenophrys* (lateral aperture, epizoic on crustacea)

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Three diverse alveolate groups are recognized: Ciliophora (with cilia), Dinoflagellata (with flagella) and Apicomplexa (with gliding motion, some also with flagellated microgametes). Ciliated protozoa are unique amongst the unicellular eukaryotes because they are the only group to exhibit nuclear dualism. Individual cells possess two different types of nuclei; vegetative macronuclei and reproductive micronuclei. Asexual reproduction occurs by transverse binary fission across rows of cilia (homothetogenic fission) whereas some species exhibit sexual reproduction by the phenomenon of conjugation (temporary fusion of two conjugates which exchange micronuclei). As their common name implies, ciliates are also

characterized by the possession of simple cilia, or compound ciliary organelles, in at least one stage of their life cycles (compound subpellicular infraciliature is universally present even when cilia are absent). Cilia are elongate hair-like extensions of the cell membrane with an internal microtubular core (universal 2+9 configuration = 2 single central microtubules surrounded by 9 peripheral doublets). They are organelles of motility used for locomotion and/or feeding. Cilia (singular, cilium) are similar in ultrastructure to flagella (singular, flagellum), and they are collectively often called undulipodia (singular, undulipodium) because both use cross-linked proteins (dynein-walking mechanism) to undulate about their basal kinetosome (unlike the rotary motion unique to flagella in bacteria). Ciliates, together with dinoflagellates and apicomplexans, possess subpellicular alveoli which are membrane-bound sacs beneath the plasma membrane. Alveoli are thought to serve many varied functions: ranging from support (helping maintain body shape, act as fulcrum for undulipodia); metabolism (storage); osmoregulation (mucocysts); excretion (extrusomes); protection (toxicysts, trichocysts); and even hunting (haptocysts).

Most ciliate species are free-living in aquatic or terrestrial habitats but many are commensals in vertebrate or invertebrate hosts and some are parasitic. Early classification systems recognized three main classes of ciliates mainly on the basis of their patterns of somatic (body) and buccal (oral) ciliation. The 'lower holotrichs' have simple body and oral ciliature; most are free-living species but some are highly specialized symbionts aiding cellulose digestion in herbivores. The 'higher holotrichs' have simple body ciliature but more specialized oral ciliature forming membranelles; most occur as free-living organisms but some live as commensals or parasites in a range of animals. The 'spirotrichs' have reduced body ciliation but well-developed oral ciliature forming an adoral zone of membranelles; most are bactivores living in aquatic and terrestrial habitats. More recently, ten major monophyletic lineages have been recognized on the basis of their infraciliature; i.e. the ultrastructural organization of their kinetids (comprising basal bodies (= kinetosomes) and associated microtubular ribbons and fibrils). These lineages (ranked as classes) have been well supported by modern molecular biological studies using several gene sequences.

Class	Etymology	Defining characters	Lifestyles*	Genera covered
Subphylum: **Postciliodesmatophora** [somatic dikinetids with postciliodesmata (overlapping microtubular ribbons)]				
Karyorelictea	'primitive-nucleus'	macronuclei not dividing but replaced by division of micronuclei	free-living (aquatic benthic/planktonic)	
Heterotrichea	'different-hair'	compound ciliary organelles around mouth, macronuclei divided by external microtubules	free-living (aquatic planktonic/benthic)	
Subphylum: **Intramacronucleata** [macronuclei divided by internal microtubules]				
Spirotrichea	'coiled-hair'	conspicuous right and left oral ciliature, left polykinetids leading into oral cavity	free-living (aquatic, terrestrial)	
Litostomatea	'simple-mouths'	cytostome with noncurved tubular cytopharyngeal apparatus (rhabdos)	free-living (often predatory), symbiotic	*Balantidium*
Phyllopharyngea	'leaf-throated'	mouth with radial microtubular ribbons (phyllae), some with sticky feeding tentacles	free-living (aquatic), epizoic, symbiotic	*Chilodonella*
Colpodea	'breast-shaped'	reniform bodies, somatic cilia with transverso-desmata (overlapping ribbons)	terrestrial, some aquatic (bactivores)	
Nassophorea	'pot-bearer'	oral nematodesmata well-developed (basket-like nasse or cyrtos supporting cytopharynx)	free-living (aquatic, terrestrial)	
Prostomatea	'before-mouth'	simple apical mouths, some with oral microtubular band, some with oral brush	free-living (often predatory)	
Plagiopylea	'misshapen-marker'	with twisted oral tubes, most with hydrogenosomes	free-living (anoxic habitats)	
Oligo-hymenophorea	'few membrane-bearer'	typically with ventral groove containing mouth and compound ciliary organelles (usually adoral zone of three membranelles)	free-living, epizoic, symbiotic (micro-phagous)	*Uronema, Ichthyophthirus, Tetrahymena, Trichodina, Vorticella*

*Symbiosis *sensu latu* ranges from commensalism, mutualism and parasitism (depending on the benefit/detriment to the host)

The class Oligohymenophorea contains ciliates whose somatic (body) kinetosomes (basal bodies) are associated with unique ultrastructural elements (collectively referred to as infraciliature) comprising anteriorly-directed overlapping kinetodesmal fibrils, divergent postciliary microtubular ribbons and radial transverse ribbons. Members are considered to be 'higher' holotrichs as there is clear distinction between the oral and somatic ciliature. They possess distinctive oral kineties consisting of a right paroral kinety (membrane) and typically 3 left oral polykinetids (membranelles) located in a buccal or infundibular cavity with an inconspicuous cytopharyngeal apparatus. They are widely distributed in aquatic habitats (fresh, brackish and marine waters) where they occur as free-living stages (free-swimming or attached to substrates), some being epizoic (rarely endozoic) on aquatic animals (mainly crustacea and fish). Free-living aquatic species are highly sensitive to environmental changes and a range of species are used as bioindicators for the assessment of water quality (saprobic classifications) and even sludge activity in wastewater treatment. The

class contains 6 subclasses (Apostomatia, Astomatia, Hymenostomatia, Peniculia, Peritrichia, Scuticociliatia) differentiated predominantly on the basis of their patterns of somatic and oral ciliation. Peritrichous ciliates are filter-feeders with inverted bell-shaped bodies having prominent buccal ciliature encircling the apical pole (forming a peristomial field) and winding counterclockwise (left hand spiral) to plunge into the oral cavity (infundibulum) to the cytostome (mouth). The peristomal border consists of a dikinetid file (considered homologous to the paroral membrane) surrounding a triple row of cilia (considered homologous to the polykinetid membranelles). The narrow antapical pole of the cells possess barren kinetosomes as part of a holdfast apparatus (scopula or adhesive disc). Mature trophonts (often called zooids) lack somatic kineties but the transient dispersal telotroch (swarmer) stages may develop temporary ciliary rings for locomotion. Two peritrich orders are recognized depending on whether mature trophonts live attached permanently (Sessilida) or temporarily (Mobilida) to substrates, which in many cases may include other aquatic animals and plants.

Higher taxonomy	**Family**	**Exemplar genera**	**Hosts**	**Site**	**Trans-mission**
Subclass: Peritrichia (lacking somatic kineties, oral cilia extend from infundibulum)					
Order: Mobilida (mature trophont mobile, aboral holdfast organelle)	Trichodinidae (stout cylindrical body, posterior adhesive disc with denticular ring)	*Trichodina*	fish	skin, gills	direct
Order: Sessilida (mature trophont sessile, attached to substrate by scopula (special flat thigmotactic area) with or without stalk)	stalkless				
	Scyphidiidae (solitary ciliates, attached by scopula)	*Scyphidia*	fish, crustacea	exoskeleton	direct
		Ambiphrya	fish, crustacea	exoskeleton	direct
	stalked				
	Epistylididae (scopula produces noncontractile stalk, retractile lip encircles elevated peristomial disc)	*Apiosoma*	fish	skin, gills	direct
		Epistylis	fish, crustacea	exoskeleton	direct
	Vorticellidae (solitary, gregarious or colonial, retractile stalks with central myoneme)	*Vorticella*	fish, crustacea	exoskeleton	direct
		Carchesium	fish, crustacea	exoskeleton	direct
	Zoothamniidae (solitary or colonial, retractile stalks with shared myonemes)	*Zoothamnium*	fish, crustacea	exoskeleton	direct
	loricate				
	Vaginicolidae (upright lorica)	*Cothurnia*	crustacea	exoskeleton	direct
		Vaginicola	crustacea	exoskeleton	direct
	Lagenophryidae (discoid lorica)	*Lagenophrys*	crustacea	gills	direct

The order Sessilida is characterized by ciliates with inverted bell-shaped or conical-cylindrical bodies that are attached to substrates by an aboral scopula (specialized flattened thigmotactic area) with or without a stalk. They have prominent oral ciliature, organized around a peristome (expanded oral region for suspension-feeding), comprising a prominent paroral membrane (outer haplokinety) accompanied by a smaller series of membranelles (inner polykinety, often triple) circling counter-clockwise around the apical funnel-shaped oral cavity. The apical surface inside the peristomial spiral is often vaulted (forming an epistomial disc) and raised above the borders (peristomial lips) when the zooid is relaxed and feeding, but can be retracted when the zooid is disturbed and contracts. The ciliates are dimorphic with mature trophonts (zooids) being the sedentary (sessile) attached stages, and telotrochs being unattached mobile migratory (dispersal) stages. The zooids of some species may also exhibit significant size variation, forming 'ordinary' zooids, large macro-zooids and sometimes smaller micro-zooids. Cyst formation has also been described for some species experiencing adverse environmental conditions. Trophonts may exhibit isotomic or anisotomic division, and many species are gregarious forming small colonies (many species with long stalks form arboroid (tree-like) colonies). Sessiline peritrichs are often free-living attaching to inert substrates (e.g. periphytic, epiphytic) but some also attach to the surfaces of aquatic animals as ectosymbiotes (epizoic, rarely endozoic). The trophonts are stationary suspension/filter-feeders, using their oral ciliature to sweep bacteria, phytoplankton and particulate material into their mouths. However, heavy infestations of animals (especially crustaceans such as crayfish and shrimp) may cause significant fouling imparting an unsightly appearance, obstructing oral structures interfering with feeding leading to poor growth and development with loss of condition, or obstructing the gills compromising respiratory function leading to anoxia and respiratory distress and sometimes death. Blooms of fouling organisms may cause serious economic losses in aquaculture due to loss of product through morbidity and mortality.

Numerous peritrichous ciliate species have been described, with many subsequently being revised and reassigned to different genera as new characters were incorporated into taxonomic classifications. Some early descriptions were deemed inadequate or incomplete, leading to *species inquirenda* ('doubtful identity'), *nomina dubia* ('doubtful names') or *nomina nuda* ('invalid names'). Some studies have also misidentified other small aquatic organisms with distinct ciliary wreaths and/or stalks or peduncles,

especially small rotifers, other ciliates (folliculinds, stentorids), and occasionally dinoflagellates, hydrozoans and bryozoans. This has led to many species being synonymized, disputed or disregarded. Molecular characterization studies are slowly bringing some clarity to peritrich phylogeny, but studies are in their infancy and workers are generally stuck with having to provide multiple names to ensure historical and contemporary relevance. At present, over 130 genera of sessile peritrichs are recognized within 14 families which may be allocated to 3 broad groups: those without stalks; those with prominent stalks; and those with loricae.

Stalkless sessiline peritrichs have been classified into 6 families:

- The family Scyphidiidae contains species with solitary zooids attached to substrates by scopulary organelles forming flattened discs distinct from the rest of the body. They are generally found as epibionts on aquatic organisms and have been grouped into 9 genera: *Ambiphrya, Corlissetta, Gonzeella, Mantoscyphidia, Pachystomos, Ophrydiopsis* (syn. *Scyphidiella*), *Paravorticella, Riboscyphidia,* and *Scyphidia.* [A proposal to recognize genera based on hosts/substrates has only been partly adopted; with *Mantoscyphidia* and *Riboscyphida* containing species on gastropods and fish respectively, *Scyphidiella* containing species on waterborne Coleoptera synonymized with *Ophrydiopsis*, and free-living and epiphytic species retained in the genus *Scyphidia* (rather than divided into *Speleoscyphidia* and *Myoscyphidia*)].
- The family Astylozoidae contains species with elongate to vase-shaped bodies lacking aboral rings of cilia but with posterior spines and sometimes long recurved cortical spines. The family contains 2 genera: *Astylozoon* (syn. *Geleiella*) and *Hastatella.*
- The family Ellobiophryidae contains species whose scopulae form cylindrical projections that encircle gill filaments of marine molluscan and piscine hosts. The family contains 2 genera: *Caliperia* and *Ellobiophrya* (syn. *Clausophrya*).
- The family Ophrydiidae contains species with bulbous bodies housed in gelatinous cases or embedded in solid jelly-like masses, often supported by posterior spines. They have peristomial ciliary wreaths with 1-3 turns and have been allocated to 2 genera: *Gerda* (syn. *Ophionella p.p.*) and *Ophyrdium* (syn. *Ophionella p.p., Echinella, Raphanella*).
- The family Opisthonectidae contains species with conical-cylindrical bodies with or without epistomial membranes but with an aboral ring of cilia with strongly argentophilic granules. The family contains 2 genera: *Opisthonecta* and *Telotrochidium.*
- The family Termitophryidae contains one or more species that form unique pad-like attachment discs within the hindguts of termites, all allocated to the single genus *Termitophrya.*

STALKLESS PERITICHS				
Species	**Trophont size (µm)**	**Habitat/Hosts**	**Life-style [disease]**	**Distribution**
Family: **Astylozoidae**				
Genus: ***Astylozoon*** (lanceolate bodies, aboral ring of cilia absent but with several short stiff cilia)				
A. enriquesi	40-65	freshwater (planktonic)	free-living	Europe
A. fallax [type species]	36-100	freshwater (planktonic)	free-living	Eurasia
A. faurei	35-65 x 30-55	freshwater (planktonic)	free-living	Eurasia
A. pyriforme (syn. *A. amphoriforme*)	35-65 x 37-40	freshwater (planktonic)	free-living	Europe
Ax. vagans (syn. *Geleiella*)	43-75 x 50-60	freshwater (planktonic)	free-living	Europe
Genus: ***Hastatella*** (vase-shaped bodies, aboral ring of cilia absent but with spine, body with 2-4 rings of long conical ectoplasmic processes (spines))				
H. aesculacantha	30-52 x 24-41	freshwater (planktonic)	free-living	Europe
H. radians (syn. *H. microradians*) [type species]	30-75 x 25-70	freshwater (planktonic)	free-living	Eurasia, America
Family: **Ellobiophryidae** (solitary, stalkless, scopula with cylindrical projections (limbs) that form a ring-like holdfast (cinctum) encircle gill filaments or feeding tentacles of marine hosts (fish and molluscs))				
Genus*:* ***Caliperia*** (cinctum noncontractile with non-joined limbs, internal rod-like organelle present)				
C. brevipes (syn. *Ellobiophrya*)	29-73 x 21-38	marine, attached to fish (Rajiformes: rajid (little skate)	epizoic (gills)	North America
C. longipes [type species]	31-68 x 24-53	marine, attached to fish (Blenniiformes: clinid (orange clinid); Gobiesociformes: gobiesocid (striped clingfish))	epizoic (gills)	New Zealand
Genus: ***Ellobiophrya*** (cinctum contractile with joined limbs, lacking internal rod-like organelle)				
E. branchialis (syn. *Clausophrya*)	57-120 x 28-55	marine, attached to fish (Atheriniformes: atherinid (short snout hardyhead, small mouth hardyhead, pikehead hardyhead, silver fish)	epizoic (gills)	Australia

E. brevipes	54-60 x 35	marine, attached to fish (Rajiformes: rajid (little skate)	epizoic (gills)	North America
E. conviva	46 x 27	marine, attached to bryozoa (Gymnolaemata: bugulid (*Bugula neritina, turrita)*	epizoic (tentacles)	North America
E. donacis [type species]	40-100 x 30-40	marine, attached to shellfish (Bivalvia: donacid (*Donax vittatus*))	epizoic (gills)	Europe
E. maliculiformis	50-125 x 15-30	marine, attached to ciliates (Peritricha: scyphidiid (*Mantoscyphidia spadiceae, midae, branchi*) attached to gills of abalone (Gastropoda: haliotid (*Haliotis spadicea*, *midae*) and limpets (Gastropoda: patellid (*Scutellastra barbara*))	epizoic (near scopula)	South Africa
E. oblida (syn. *Clausophrya*)	180 x 36	marine, attached to fish (Gobiiformes: gobiid (tubenose goby))	epizoic (skin)	Black Sea
Family **Scyphidiidae**				
Genus ***Ambiphrya*** (permanent equatorial ciliary fringe, motile in swarmers but motionless in attached zooids, cilia often shielded by thin pellicular fold (median membrane))				
A. ameiuri (syn. *Scyphidia*)	34-95 x 20-61	freshwater, attached to fish (Cichliformes: cichlid (mango tilapia); Cypriniformes: cyprinid (common carp, grass carp); Cyprinodontiformes: anablepid (onesided livebearer); Perciformes: latid (Nile perch); Siluriformes: ictalurid (channel catfish, black bullhead catfish))	epizoic (gills, skin) [respiratory problems]	Eurasia, Americas
A. macropodia (syn. *Scyphidia*)	35-46 x 20-25	freshwater, attached to fish (Perciformes: centrarchid (bluegill); Siluriformes: ictalurid (brown bullhead, channel catfish))	epizoic (skin, gills)	North America
A. miri [type species]	45 x 25	brackish water, attached to fish (Syngnathiformes: syngnathid (straightnose pipefish))	epizoic (gills)	Europe
A. neobolae	44-84 x 24-45	freshwater, attached to fish (Cypriniformes: danionid (river sardine))	epizoic (skin)	Africa
A. tholiformis (syn. *Scyphidia*)	59 x 35	freshwater, attached to fish (Perciformes: centrarchid (smallmouth bass, largemouth bass)	epizoic (gills, skin)	North America
Genus ***Corlissetta*** (solitary, elongate zooids, transversely striated, short basal pointed scopula)				
C. anivica	71-74 x 17-19	marine, attached to invertebrates (Polychaeta: nephtyid (*Nephtys californiensis*))	epizoic	Atlantic
Genus ***Gonzeella*** (colonial, zooids in gelatinous mass, colony hollow and ball-like, zooids without zoochlorellae)				
G. coloniaris [type species]	60-95 x 24-32	freshwater	free-living	Africa
Genus: ***Mantoscyphidia*** (solitary, cylindrical bodies, broad scopula, peristomial ciliary wreath with 1½ turns, associated with aquatic gastropods)				
M. acanthophora (syn. *Scyphidia*)	20-40	marine, associated with sea snails (Gastropoda: trochid (*Gibbula umbilicalis, Monodonta lineata*)	epizoic (mantle cavity)	Europe
M. australorbicola (syn. *Glossatella*)		freshwater, associated with snails (Gastropoda: planorbid (*Australorbis*))	epizoic (gills)	South America
M. bengalensis		estuarine, associated with mud snails (Gastropoda: potamidid (*Cerithidea cingulata*))	epizoic (mantle cavity)	India
M. branchi	44-78 x 17-32	marine, associated with sea snails (Gastropoda: patellid (*Patella aphanes, argenvillei, barbara, cochlear, compressa, concolor, granatina, granularis, longicosta, miniata, obteca, oculus, pica, tabularis, Helcion dunkeri,*	epizoic (gills)	Africa

		pectunculus, pruinosus), nacellid (*Cellana capensis*))		
M. capitis		freshwater, associated with snails (Gastropoda (unspecified))	epizoic	Asia
M. fanthami	80-130 x 25-35	marine, associated with sea snails (Gastropoda: trochid (*Oxystele sinensis, tabularis, tigrina, variegata, impervia*))	epizoic (gills)	Africa
M. fischeri (syn. *Scyphidia, Scyphidiella*)	60	marine, associated with sea snails (Gastropoda: truncatellid (*Truncatella truncatula*))	epizoic (mantle and genital cavities)	Europe
M. hydrobiae (syn. *Scyphidia*)	70	brackish water, associated with sea snails (Gastropoda: hydrobiid (*Hydrobia ventrosa*), littorinid (*Littorina rudis*))	epizoic (tentacles, mouth)	Europe
M. inclinata		freshwater, associated with snails (Gastropoda: hydrobiid (*Cincinnatia*))	epizoic	North America
M. limacina (syn. *Scyphidia, Vorticella*)	70-100	freshwater, associated with snails (Gastropoda: planorbid (*Planorbis*))	epizoic (mantle cavity)	Europe
M. littorinae [type species as *Scyphidia*]		marine, associated with sea snails (Gastropoda: littorinid (*Littorina*))	epizoic	Adriatic Sea
M. lusitana		marine, associated with sea snails (Gastropoda: patellid (*Patella vulgata*))	epizoic	Europe
M. midae	65-150 x 18-45	marine, associated with abalone (Gastropoda: haliotid (*Haliotis midae*))	epizoic (gills)	Africa
M. patellae (syn. *Cothurnia, Scyphidia*)	30-45	marine, associated with sea snails (Gastropoda: patellid (*Patella argentea, vulgata*))	epizoic (mantle cavity)	Europe
M. physarum (syn. *Scyphidia, Scyphidiella*)	80-110	freshwater, associated with snails (Gastropoda: physid (*Physa*), neritid (*Neritina*))	epizoic (mantle cavity)	Europe
M. spadiceae	70-140 x 20-40	marine, associated with abalone (Gastropoda: haliotid (*Haliotis spadicea*))	epizoic (gills)	Africa
M. ubiquita (syn. *Scyphidia, Gerda*)	30-117 x 25-52	marine, associated with limpets (Gastropoda: acmaeid (*Acmaea pelta*, *digitalis*, *limatula*, *scabra*, *insessa*, *fenestrata*), fissurellid (*Fissurella volcano*), littorinid (*Littorina*), lottid (*Lottia gigantea*, *pelta*, *digitalis*, *Tectura persona*, *scutum*), tegulid (*Tegula funebralis*, *ligulata*), trochid (*Gibbula*)	epizoic (mantle cavity)	North America
Genus: ***Ophrydiopsis*** (solitary in gelatinous/mucilaginous case, elongate trumpet-shaped body, truncated diagonally anteriorly, without peristomial lip (opercullariform), tube-like posterior extension to disc-like scopula)				
O. concava [type species] (syn. *Scyphidiella*)	70-80	freshwater	free-living	Europe
Genus ***Pachystomos*** (solitary, globular zooid with apical peristome, 2 posterior pseudopodial-like projections enable zooid to slide along filamentous substrates)				
P. olisthus [type species]	200	freshwater	free-living	North America
Genus: ***Paravorticella*** (solitary, elongate trumpet-shaped bodies, stalkless (but often appearing to have a very short stalk), narrow scopula, highly contractile, peristomial disc not stalked)				
P. clymenellae	100	marine, attached to worm (Polychaeta: maldanid (*Clymenella torquata*))	epizoic	Europe
P. lycastis		freshwater, attached to worm (Polychaeta: nereidid (*Lycastis indica*))	epizoic (parapodia)	India
P. nerillae	60-70 x 15-25	marine, attached to worm (Polychaeta: nerillid (*Nerilla antennata*))	epizoic	Europe
P. terebellae	120	marine, attached to worm (Polychaeta:	epizoic (surface)	Europe

[type species as *Scyphidia*]		terebellid (*Terebella lapidaria*))		
Genus: ***Riboscyphidia*** (solitary, cylindrical barrel-shape, sometimes with collar, broad disc-like basal scopula, flat epistomial disc, peristomial lips (epistyliform), telotrochs disc-shaped)				
S. adunconucleata (syn. *Scyphidia*)	75	marine, attached to fish (Pleuronectiformes: pleuronectid (European plaice))	epizoic (surface)	Scotland
R. arctica (syn. *Scyphidia*)	62-84 x 36-42	marine, attached to fish (Scorpaeniformes: cottid (butterfly sculpin, longhorn sculpin), liparid (snailfish); Salmoniformes: salmonid (Atlantic salmon, brown trout))	epizoic (gills)	North Atlantic, Pacific
R. salmonis	24-62 x 14-46	marine, attached to fish (Salmoniformes: salmonid (brown trout, brook trout))	epizoic	Europe
R. scorpenae [type species as *Scyphidia*]	53	marine, attached to fish (Scorpaeniformes: scorpaenid (scorpionfish))	epizoic (gills)	Europe
R. siluri (syn. *Scyphidia*)		marine, attached to fish (Siluriformes: silurid (unspecified catfish))	epizoic	Ukraine
Genus: ***Scyphidia*** (solitary, cylindrical bodies, broad disc-like basal scopula, adoral spiral making one turn around epistomial disc with peristomial lip (epistyliform), aboral locomotory fringe only in telotroch swarmers)				
S. acanthoclini	32-60 x 24-46	freshwater, attached to fish (Ovalentaria: plesiopid (New Zealand rockfish))	epizoic	New Zealand
S. ambigua	65	freshwater, attached to moss (*Sphagnum*)	epiphytic	Europe
S. amphibiarum	76 x 33	freshwater, attached to green algae (*Pediastrum*) and amphibians (Anura: ranid (common frog, tadpoles))	epiphytic, epizoic	Eurasia
S. annulata	80	freshwater, attached to algae	epiphytic	Europe
S. baninae	38-58 x 27-46	brackish water, attached to fish (Clupeiformes: alosid (Caspian shad))	epizoic (skin)	Russia
S. beebei		freshwater	free-living	Europe
S. constricta (syn. *Scopulata*)	33-80 x 20-34	freshwater, attached to fish (Cichliformes: cichlid (Mozambique tilapia) and worms (Annelida: naidid (*Nais*))	epizoic (skin)	Africa, Europe
S. coronalis		freshwater	free-living	Europe
S. craterellus	6	freshwater, attached to algae	epiphytic	Europe
S. cyclopiscola		freshwater	free-living	Europe
S. cypris		freshwater	free-living	Europe
S. delphinicola		freshwater	free-living	Europe
S. dentata (syn. *Scyphidiella*)		freshwater, attached to beetles (Coleoptera: hydrophilid (*Helochares*))	epizoic	Eurasia
S. dermata (syn. *Scopulata*)	46-61 x 25-38	marine, attached to fish (Characiformes: alestid (sharptooth tetra); Cichliformes: cichlid (Mozambique tilapia, redbreast tilapia, banded tilapia, southern mouthbrooder); Cypriniformes: cyprinid (threespot barb); Osteoglossiformes: mormyrid (bulldog))	epizoic (skin)	Africa
S. discostyla	90	freshwater, attached to worm (Annelida: naidid (*Nais*))	epizoic	Europe
S. dixoecola		freshwater	free-living	Europe
S. doliaris	31-42 x 55-60	freshwater, attached to fish (Cypriniformes: cyprinid (Eurasian carp))	epizoic (skin)	Russia
S. epibranchialis (syn. *Scopulata*)	27-40 x 20-27	freshwater, Cichliformes: cichlid (Mozambique tilapia, southern mouthbrooder); Perciformes: centrarchid (smallmouth bass))	epizoic (skin, gills)	Africa

S. fasticens		freshwater	free-living	Europe
S. fromentellii		freshwater, attached to plants (*Sida*) and invertebrates (Branchiopoda: daphniid (*Daphina pulex*); Amphipoda: gammarid (*Gammarus pulex*); Copepoda: cyclopid (*Cyclops*)	epiphytic, epizoic	North America
S. gammaricola	25	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*)	epizoic	Europe
S. haemopis		freshwater, attached to leech (Hirudinea: haemopid (*Haemopis sanuisuga*))	epizoic	Eurasia
S. helobdellae (syn. *Scyphidiella*)		freshwater, attached to leech (Hirudinea: glossiphoniid (*Helobdella stagnalis*))	epizoic	Europe
S. hirudineorum		freshwater, attached to leeches (unspecified)	epizoic	Europe
S. inclinans	50-56	freshwater, attached to oligochaetes (Clitellata: tubificid (*Nais*))	epizoic	North America
S. indica	52 x 25	freshwater, attached to water fleas (Branchiopoda: daphniid (*Daphnia*))	epizoic	Eurasia
S. inquilina		freshwater	free-living	Europe
S. limacina		freshwater, attached to snails (Gastropoda: planorbid (*Planorbis*))	epizoic	North America
S. lumbriculi (syn. *Rhabdostyla*)	70	freshwater, planktonic and attached to oligochaete (Clitellata: lumbriculid (*Lumbriculus*))	free-living, epizoic	Europe
S. marioni (syn. *Mantoscyphidia*)	63-128 x 26-69	marine, attached to limpet (Gastropoda: nacellid (*Nacella delesserti*))	gills	Southern Ocean
S. odontides		freshwater	free-living	Europe
S. ophidonais		freshwater	free-living	Europe
S. ostracodarum		freshwater, attached to invertebrates (Ostracoda: notodromadid (*Notodromas monachi*))	epizoic	North America
S. ovata	34-42	freshwater, planktonic and attached to worm (Annelida: unspecified))	free-living, epizoic	Europe
S. perezuzae	50-60 x 50-70	marine, attached to fish (Scorpaeniformes: scorpaenid (black-banded rockfish))	epizoic (skin)	China
S. periscelis	19	freshwater	free-living	Europe
S. planorbicola		freshwater	free-living	Europe
S. podurae		freshwater	free-living	Europe
S. polyphonicola		freshwater	free-living	Europe
S. prosternans	15	freshwater	free-living	Europe
S. ranae		freshwater, attached to amphibians (Anura: ranid (common frog))	epizoic	Eurasia
S. rhizopoda (syn. *Epistylis*)	33-51	freshwater	free-living	Europe
S. rugosa [type species]	90-100 x 45	freshwater, attached to inanimate substrates, detritus, and moss (*Sphagnum*)	free-living, epiphytic	Eurasia
S. scorpaenae	53	marine, attached to fish (Scorpaeniformes: scorpaenid (unspecified *Scorpaena* sp.))	epizoic	Russia
S. slavinicola		freshwater	free-living	Europe
S. spionicola	45-65	marine, attached to worm (Annelida: spionid (*Pygospio*))	epizoic	Atlantic
S. temporaria		freshwater, attached to amphibians (Anura: ranid (common frog))	epizoic	Eurasia
S. terebellidis	45-55	marine, attached to worm (Annelida: unspecified))	epizoic	Eurasia
S. trituri		freshwater, attached to amphibian	epizoic	Eurasia

		(Urodela: salamandrid (smooth newt))		
S. turbinata		freshwater, attached to inanimate substrates and plants (*Lemna*))	free-living, epiphytic	Europe
S. urnulea		freshwater	free-living	Europe
S. variabilis (syn. *Rhabdostyla*)	60-90	marine, attached to worm (Annelida: terebellid (*Terebella*))	epizoic	Europe
S. vascelloides		freshwater	free-living	Europe
S. vorticelloides		freshwater	free-living	Europe
Family: **Termitophryidae**				
Genus: ***Termitophrya*** (body inverted cone-shaped, scopula forms unique pad-like disc, endocommensals of termites)				
T. africana [type species]	110-200	terrestrial, in termites (Isoptera: termitid (*Jugositermes tuberculatus,* and possibly *Astalotermes, Phoxotermes*)	endozoic (hindgut)	Africa
Family: **Ophrydiidae**				
Genus: ***Gerda*** (solitary, elongate bulbous body in gelatinous/mucilaginous case, no basal scopula, sausage-shaped macronucleus)				
G. annulata (syn. *Scyphidia*)	80	freshwater, attached to algae and plants (*Ruppia*)	free-living, epiphytic	Europe, North America
G. fixa	100	freshwater, attached to plants (*Myriophyllum*)	free-living, epiphytic	Europe
G. glans (syn. *G. sigmoides, vernalis, Ophrydium, O. boreale, lemnae*) [type species]	60-200	terrestrial and freshwater, attached to detritus, filamentous algae, mosses (*Sphagnum*) and plants (*Lemna*)	free-living, epiphytic	Europe, North America
G. inclinans		freshwater	free-living	Europe
G. picta (syn. *Ophionella*)		freshwater, attached to plants (*Myriophyllum spicatum, Anacharis*)	free-living	Europe
Genus: ***Ophrydium*** (colonies in jelly-like mass, colony solid, zooids often with green zoochlorellae, zooids with long posterior spines, peristomial ciliary wreath with 1½-2½ turns)				
O. adae	225-400 x 35-50	freshwater	free-living	Eurasia
O. caudata (syn. *Astylozoon*, *Gerda*)		freshwater (planktonic)	free-living	Europe
O. crassicaule	115-280 x 18-45	freshwater, planktonic and attached to inanimate substrates, filamentous algae, and submerged plants (*Ceratophyllum*)	free-living, epiphytic	Eurasia
O. ectatum	225-400	freshwater	free-living	Europe
O. eichornii (syn. *O. problematicum, versatile* var. *hyalinum*)	160-300 x 25-50	freshwater	free-living	Asia
O. eutrophicum	250-350 x 25-40	freshwater, planktonic and attached to inanimate substrates, and plants (stoneworts and *Phragmites*)	free-living, epiphytic	Europe
O. fixa (syn. *Gerda*)	135-150	freshwater, attached to plants (*Myriophyllum*)	free-living, epiphytic	Eurasia
O. flexile	90-160	freshwater	free-living	Asia
O. hyalinum	180-300 x 25-30	freshwater	free-living	Eurasia
O. insolitum	130 x 20	freshwater	free-living	Europe
O. naumanni	40-50 x 10	freshwater (euplanktonic)	free-living	Europe, South America?
O. ophrydiiformis	220-260 x 36-40	freshwater	free-living	Eurasia
O. pictum (syn. *Ophionella*)	160	freshwater, attached to plants (*Myriophyllum*)	epiphytic	Europe
O. sessile	280-320 x 55-80	freshwater, attached to inanimate substrates and submerged plants (*Elodea*, *Myriophyllum*)	free-living, epiphytic	Europe, Americas
O. sigmoides (syn. *Gerda*)	135-150	freshwater	free-living	Europe
O. vernale (syn. *Gerda*)	250	freshwater	free-living	Europe
O. versatile [type species as	300-600 x 20-40	freshwater, planktonic and attached to submerged algae (*Chara*), plants	free-living, epiphytic, epizoic	Europe, America

Vorticella]		(*Myriophyllum, Potamogeton, Phragmites, Chara, Anacharis*) and mussels (Bivalvia: unspecified)		
Family: **Opisthonectidae**				
Genus: ***Opisthonecta*** (free-swimming, with strongly developed epistomial membrane, truncated conical-shape, broad base, aboral ciliary wreath with strongly argentophilic granules on one side, trochal band ciliated)				
O. bivacuolata	140-180	freshwater	free-living	Europe
O. dubia	80-100	freshwater (planktonic)	free-living	Europe
O. henneguyi (syn. *Telotrochidium*) [type species]	90-170 x 80-130	freshwater (planktonic)	free-living	Eurasia, America
O. patula (possible syn. of *O. henneguyi*)	120-150	freshwater (planktonic)	free-living	Europe
O. minima	90-120	freshwater (planktonic)	free-living	Europe
Genus: ***Telotrochidium*** (lacking epistomial membrane, very small scopula, aboral ciliary wreath in zooids and telotrochs, with strong argentophilic granules on both sides of ciliary girdle, trochal band ciliated)				
T. crateriformis [type species] (syn. *Vorticella vaga*)	100	freshwater (planktonic)	free-living	Europe
T. cylindricum	130-170	freshwater	free-living	Europe
T. elongatum	80-145	freshwater (planktonic)	free-living	Europe
T. johanninae	60-70	freshwater (planktonic)	free-living	Europe
T. matiense (syn. *Opisthonecta*)	45-73 x 25-40	freshwater and wastewater	free-living	Europe
T. matthaii	145 x 108	freshwater (planktonic)	free-living	Europe
T. nathei	100	freshwater, planktonic	free-living	India

Stalked sessiline peritrichs have been allocated to 7 main families:

- The family Epistylididae contains numerous species whose zooids form noncontractile stalks that are often branched to form colonies. They often contain a retractile peristomial lip encircling a wide elevated peristomial disc, and are found attached to many diverse aquatic substrates, both inanimate and living (plants and animals). The family contains 8 genera: *Apiosoma* (syn. *Cordylosoma, Glossatella, Scopulata*)*, Campanella, Epistylis* (syn. *Allomeron, Digitalina, Indosphaera, Mespilina, Myrtilina, Nidula, Orthochona*)*, Foissnerella, Heteropolaria, Orborhabdostyla, Pseudepistylis,* and *Rhabdostyla* (syn. *Opisthostyla*). [Recent molecular studies on several *Campanella* and *Rhabdostyla* spp. have suggested the erection of 2 new families (Campanellidae and Rhabdostylidae), but more inclusive studies are required].
- The family Operculariidae also contains species with zooids forming noncontractile stalks, but they have well developed thecae and unique epistomial discs with anterior opercula. They are usually found as epibionts on aquatic insects and arthropods and have been allocated to 7 genera: *Ballodora, Opercularia* (syn. *Cochlearia p.p., Discotheca, Kindella, Operculina, Valvularia*), *Opercullariella, Orbopercularia* (syn. *Serioscyphus p.p., Syncyathella*)*, Orbopyxidiella* (syn. *Ampullaster*)*, Propyxidium* (syn. *Pyxidiella, Pyxidium*), and *Triadopercularia.*
- The family Vorticellidae contains species with zooids mounted on prominent stalks as solitary individuals or as branched colonies. The stalks have central myonemes which contracts in a zigzag or spiral fashion when disturbed. They are prevalent in aquatic habitats where they attach to inanimate objects, plants or animals. The family contains over 20 genera: *Apocarchesium, Baikalaster, Baikalonis, Carchesium, Cotensita, Entziella, Epicarchesium, Grainis, Intranstylum, Parazoothamnium, Pelagovorticella, Piesika, Planeticovorticella, Pseudocarchesium, Pseudovorticella, Ruthiella, Spinivorticella, Systylis, Tucolesca, Vorticella* (syn. *Convallarina, Craterina p.p., Diceratella p.p., Ecclissa p.p., Erythropsis, Kerobalana, Ophyidia p.p., Rinella, Spastosatyla, Vorticellopsis*) and *Vorticellides*.
- The family Zoothamniidae contains solitary and colonial species with branched stalks that contract in a zigzag fashion, the shared myoneme (spasmoneme) being continuous making the entire colony contractile. Some 8 genera are recognized: *Haplocaulus* (syn. *Monintranstylum*)*, Craspedomyoschiston, Mesothamnium, Myoschiston, Pseudohaplocaulus, Zoothamnioides, Zoothamnium,* and *Zoothamnopsis.*
- The family Bezedniellidae contains a few species whose zooids have noncontractile stalks and laterally displaced peristomes forming curved cylindrical trunks. They are found attached to ostracods and 2 genera are recognized: *Bezedniella* (colonial zooids on long branched stalks) and *Nuchterleinella* (solitary zooids on short stalks)**.**
- The family Usconophryidae contains 2 unusual genera (*Cyclodonta, Usconophrys*) whose zooids occur in flexible loricae with simple apertures lacking closure structures.
- The family Rovinjellidae contains a single *Rovinjella* sp. whose colonial zooids occur in groups within unique loricae with wide apertures and bipartite stalks.

STALKED PERITRICHS				
Species	**Trophont size (µm)**	**Habitat/Hosts**	**Life-style [disease]**	**Distribution**
Family **Epistylididae**				
Genus ***Apiosoma*** (solitary, elongate conical body, circular scopula sometimes with very short stalk, often lobed/split into ramiform projections, compact posterior macronucleus, adoral spiral about one turn, infundibular fringe with more than half a turn, epizoic on fish or amphibia)				
A. alburni	42 x 29	freshwater, attached to fish (Cypriniformes: cyprinid (common bleak))	epizoic (gills)	Europe
A. amoebae (syn. *A. cryptonucleata, Glossatella, G. conica, Scyphidia*)	21-80 x 12-44	freshwater, attached to fish (Cypriniformes: cyprinid (grass carp, Eurasian carp, silver carp); Perciformes: latid (Nile perch); Scorpaeniformes: gasterosteid (three-spined stickleback))	epizoic (gills, skin)	Africa, Europe
A. amurensis		freshwater: attached to fish (Cypriniformes: leuciscid (*Phoxinus*))	epizoic	Russia
A. baikalensis	65 x 40	freshwater, attached to fish (unspecified)	epizoic (skin, gills)	Russia
A. baninae	40-60 x 25-35	freshwater, attached to fish (Cypriniformes: cyprinid (common dace, ide))	epizoic (skin)	Europe
A. baueri (syn. *Glossatella*)	29-58 x 20-40	freshwater, attached to fish (Esociformes: esocid (northern pike); Perciformes: percid (European perch))	epizoic (skin)	Russia
A. basiramosa (syn. *Glossatella*)	20-41 x 11-20	freshwater, attached to fish (Cypriniformes: xenocyprinid (Amur threelips))	epizoic (gills)	Russia
A. campanulatum (syn. *Glossatella*)	22-68 x 15-32	freshwater, attached to fish (Cypriniformes: cyprinid (common roach); Perciformes: percid (European perch, Eurasian ruffe, zander))	epizoic (skin)	Russia
A. carpelli	21-54 x 9-22	freshwater, attached to fish (Cypriniformes: cyprinid (crucian carp, Eurasian carp))	epizoic (skin, gills)	Russia
A. caulata	46-74 x 31-61	freshwater, attached to fish (Cypriniformes: cyprinid (river sardine))	epizoic (skin, gills)	Africa
A. compacta	80-85 x 30-35	freshwater, attached to fish (Cypriniformes: leuciscid (common minnow))	epizoic (gills)	Europe
A. conica (syn. *Glossatella*)	22-79 x 14-38	freshwater, attached to fish (Cichliformes: cichlid (redbelly tilapia); Scorpaeniformes: gasterosteid (unspecified sticklebacks))	epizoic (gills)	Africa, Russia
A. constricta	36-60 x 28-46	freshwater, attached to fish (Characiformes: alestid (sharptooth tetra); Cichliformes: cichlid (redbreast tilapia, banded tilapia, Mozambique tilapia, southern mouthbrooder); Cypriniformes: cyprinid (threespot barb); Osteoglossiformes: mormyrid (bulldog); Perciformes: percid (European perch)	epizoic (skin)	Africa, Eurasia
A. cotti (syn. *Glossatella, G. tintinnabulum* var. *cotti*)	40-75 x 20-34	freshwater, attached to fish (Cypriniformes: cyprinid (gudgeon); Scorpaeniformes: cottid (common bullhead)	epizoic (gills)	Europe
A. curvinucleata	114-172 x 31-51	freshwater, attached to fish (Cichliformes: cichlid (Mozambique tilapia))	epizoic (skin)	Africa
A. dalli (syn. *Glossatella*)	37-51 x 27-33	freshwater, attached to fish (Esociformes: esocid (Alaska blackfish))	epizoic (skin)	Russia
A. dermatum	40-61 x 25-38	freshwater, attached to fish	epizoic (skin)	South Africa

		(Characiformes: alestid (sharptooth tetra); Cichliformes: cichlid (redbreast tilapia, banded tilapia, Mozambique tilapia, southern mouthbrooder); Cypriniformes: cyprinid (threespot barb); Osteoglossiformes: mormyrid (bulldog))		
A. doliaris (syn. *Glossatella*)	27-52 x 17-36	freshwater, attached to fish (Cypriniformes: cyprinid (common rudd); Perciformes: latid (Nile perch))	epizoic (gills)	Russia, Africa
A. epibranchialis (syn. *Scopulata*)	34-50 x 23-37	freshwater, attached to fish (Cichliformes: cichlid (mango tilapia, Mozambique tilapia, southern mouthbrooder); Perciformes: centrarchid (smallmouth bass), latid (Nile perch))	epizoic (skin)	Africa
A. esconium		freshwater, attached to fish (unspecified)	epizoic	Russia
A. extensa	80-85 x 30-35	freshwater, attached to fish (Cypriniformes: leuciscid (common minnow))	epizoic (gills)	Europe
A. filiformis	50 x 25	freshwater, attached to fish (Cypriniformes: leuciscid (common minnow))	epizoic (gills)	Europe
A. fungiformis	25-54 x 22-36	freshwater, attached to fish (Cypriniformes: cyprinid (asp))	epizoic	Eurasia
A. gasterostei (syn. *Epistylis, Scyphidia*)	40-70 x 22-34	freshwater, attached to fish (Scorpaeniformes: gasterosteid (three-spined stickleback))	epizoic (gills)	Europe
A. gigantica (syn. *Glossatella*)	86-93 x 41-45	freshwater, attached to fish (unspecified)	epizoic	Europe
A. glabra (syn. *Glossatella, Cordylosoma*)	70-80	freshwater, attached to fish (unspecified) and amphibians (Urodela: salamandrid (crested newt))	epizoic (skin)	Europe
A. gobionis	32-55 x 18-28	freshwater, attached to fish (Cypriniformes: cyprinid (gudgeon, common roach))	epizoic (skin, gills)	Europe
A. guhli	50-55 x 28-30	freshwater, attached to fish (Scorpaeniformes: gasterosteid (ninespine stickleback))	epizoic (gills)	Europe
A. kesselri	30 x 26	freshwater, attached to fish (unspecified)	epizoic (gills)	Russia
A. leuciscus	34-45 x 25-40	freshwater, attached to fish (Cypriniformes: cyprinid (common rudd, common roach))	epizoic (skin, gills)	Europe
A. lomi	56 x 33	freshwater, attached to fish (Cypriniformes: cyprinid (dace))	epizoic (gills)	Europe
A. longiciliaris	33-50 x 11-20	freshwater, attached to fish (Esociformes: esocid (northern pike))	epizoic (gills)	Russia
A. lopuchinae	37-39 x 15-17	freshwater, attached to fish (Cypriniformes: cyprinid (common roach))	epizoic	Russia
A. lotae	16 x 5	freshwater, attached to fish (unspecified)	epizoic (gills)	Russia
A. matthesi	65-106 x 34-50	freshwater, attached to fish (Cypriniformes: cyprinid (chub))	epizoic (skin)	Europe
A. maxima	70-100 x 24-60	freshwater, attached to fish (Cypriniformes: cyprinid (dace, chub))	epizoic (gills)	Europe
A. megamicronucleata (syn. *Glossatella*)	30-42 x 18-30	freshwater, attached to fish (Esociformes: esocid (northern pike); Gadiformes: lotid (burbot); Siluriformes: silurid (wels catfish))	epizoic (skin)	Russia
A. micralesti	31-54 x 19-37	freshwater, attached to fish (Characiformes: alestid (sharptooth tetra))	epizoic (skin)	Africa
A. micropteri (syn. *Scyphidia*)	59 x 22	freshwater, attached to fish (Perciformes: centrarchid (largemouth bass, smallmouth bass); Esociformes: esocid (American	epizoic (skin, gills) [suffocation]	North America

		pickerel))		
A. microstyla	50 x 30	freshwater, attached to fish (Cypriniformes: cyprinid (common dace))	epizoic (gills)	Europe
A. miniciliata	36-40 x 16-20	freshwater, attached to fish (Perciformes: percid (Eurasian ruffe))	epizoic (gills)	Europe
A. minimicronucleata	16-43 x 16-32	freshwater, attached to fish (Esociformes: esocid (northern pike); Perciformes: percid (European perch))	epizoic (skin)	Russia
A. minuta (syn. *Glossatella*)	14-26 x 10-13	freshwater, attached to fish (Cypriniformes: cyprinid (Eurasian carp, barbel chub, sharpbelly, white Amur bream, common bleak), cobitid (pond loach); Siluriformes: bagrid (yellowhead catfish))	epizoic (skin)	Asia
A. mothlapitsis	20-38 x 11-26	freshwater, attached to fish (Cypriniformes: cyprinid (largescale yellowfish))	epizoic (skin)	Africa
A. mucusani	38 x 18	freshwater, attached to fish (unspecified)	epizoic (gills)	Russia
A. nasalis (syn. *Glossatella*)	28-60 x 14-24	freshwater, attached to fish (Cichliformes: cichlid (southern mouthbrooder); Cypriniformes: acheilognathid (Khanka spiny bitterling), cyprinid (goldfish, Chinese lake gudgeon, Amur ide), gobionid (Cherskii's thicklip gudgeon))	epizoic (skin, gills)	Russia, Africa
A. obliqua	29-54 x 17-34	freshwater, attached to fish Cypriniformes: cyprinid (redeye labeo))	epizoic (skin)	Africa
A. olae	37-69 x 19-24	freshwater, attached to fish (Cypriniformes: cyprinid (common roach, common bleak, ide))	epizoic	Russia
A. paracotti	50 x 33	freshwater, attached to fish (unspecified)	epizoic (gills)	Russia
A. peculiformis (syn. *Glossatella*)	31-44 x 15-18	freshwater, attached to fish (Scorpaeniformes: cottid (slimy sculpin))	epizoic	Russia
A. phiala	22-50 x 15-34	freshwater, attached to fish (Cichliformes: cichlid (Mozambique tilapia, southern mouthbrooder); Cypriniformes: cyprinid (slender barb, threespot barb, straightfin barb, matemba, redeye labeo, Orange River mudfish, river sardine))	epizoic (skin, gills)	Africa
A. phoxini	36-55 x 19-25	freshwater, attached to fish (Cypriniformes: leuciscid (common minnow))	epizoic (skin, gills)	Europe
A. piscicola (syn. *A. magna, Glossatella, G. cyprini, cylindriformis*) [type species]	32-110 x 13-50	freshwater, attached to fish (Cichliformes: cichlid (redbreast tilapia, redbelly tilapia, Mozambique tilapia, southern mouthbrooder); Cypriniformes: cyprinid (grass carp, black carp, silver carp, redfin, straightfin barb, threespot barb, redeye labeo); Esociformes: esocid (northern pike); Osteoglossiformes: mormyrid (bulldog); Perciformes: centrarchid (smallmouth bass), latid (Nile perch), percid (European perch); Salmoniformes: salmonid (Atlantic salmon, brown trout, brook trout))	epizoic (gills, skin) [white spots]	Eurasia, North America, South Africa
A. poteriformis (syn. *Glossatella*)	33-57 x 14-27	freshwater, attached to fish (Cypriniformes: nemacheilid (stone loach); Perciformes: latid (Nile perch))	epizoic (gills, skin)	Russia, Africa
A. pseudopiscicola	60 x 20	freshwater, attached to fish (Cypriniformes: cyprinid (crucian carp))	epizoic (mouth cavity)	Europe
A. pyriformis (syn. *Glossatella*)	38-47 x 18-21	freshwater, attached to fish (Cypriniformes: cyprinid (roho labeo, catla, mrigal carp, reba carp))	epizoic (skin)	India

A. robusta (syn. *Glossatella*)	42-45 x 22-37	freshwater, attached to fish (Esociformes: esocid (Alaska blackfish))	epizoic (gills)	Russia
A. schulmani	23-62 x 14-36	freshwater, attached to fish (Gadiformes: lotid (burbot))	epizoic	Russia
A. siewingi	40 x 20	freshwater, attached to fish (Cypriniformes: leuciscid (common minnow))	epizoic (gills)	Europe
A. tenera	34-57 x 20-32	freshwater, attached to fish (Cypriniformes: cyprinid (Eurasian carp))	epizoic	Russia
A. tintinnabulum (syn. *Glossatella, Spirochona*)	30-43	freshwater, attached to amphibian (Urodela: salamandrid (unspecified salamander))	epizoic	Europe
A. tretzli	35-38 x 22-24	freshwater, attached to fish (Cypriniformes: cyprinid (sunbleak, common chub))	epizoic (gills)	Europe
A. triangularis (syn. *Glossatella*)	52-71	freshwater, attached to fish (Cypriniformes: cyprinid (golden shiner, common shiner, creek chub); Perciformes: percid (yellow perch))	epizoic (gills, nares, fins)	Canada
A. usckani	54 x 18	freshwater, attached to fish (unspecified)	epizoic (gills)	Russia
A. viridis	33-91 x 14-45	freshwater, attached to fish (Cichliformes: cichlid (redbreast tilapia, banded tilapia, Mozambique tilapia, canary kurper, southern mouthbrooder))	epizoic (skin)	Africa
Genus: ***Campanella*** (prominent tubular stalks, branched, colonial, but branches terminate in single zooids, noncontractile without myonemes, adoral spiral with 4-6 turns, infundibular fringe with 2 turns, peristome with lip) (genus considered valid by some workers, while others regard it as a synonym of *Epistylis, Carchesium, Opercularia*, or a subgenus of *Epistylis*)				
C. hanchuanensis	140-165 x 100-131	freshwater, attached to plants (*Jussiea repens*)	free-living, epiphytic	China
C. ovata (syn. *C. purneri* f. *ovata*)		freshwater	free-living	Europe
C. purneri		freshwater	free-living	Europe
C. sinica	125-240 x 80-120	freshwater, attached to plants	epiphytic	China
C. umbellaria (syn. *Hydra, Epistylis flavicans, grandis, liebmanni, liebermanni, tincta*)	105-305 x 86-135	freshwater, attached to inanimate substrates, detritus, plants and invertebrate animals (Gastropoda: lymnaeid (*Lymnaea*); Bivalvia: dreissenid (*Dreissenia polymorpha*); Isopoda: asellid (*Asellus aquaticus*)	free-living, epiphytic, epizoic	cosmopolitan
Genus ***Epistylis*** (prominent stalk, dichotomously branched bearing many zooids in colony, stalk noncontractile without myoneme, adoral spiral with 1-2 turns, infundibular fringe with about one turn, wide epistomial disc, zooid contractile with retractile peristomial lip, transverse silverline system, aboral ring of cilia on telotroch encircles apparent width of body)				
E. acinosa (syn. *Vorticella*)		freshwater	free-living	Europe
E. acuminata	bimorphic: microzooids 30-55 x 21-44; macrozooids 68-84 x 49-58	marine, attached to invertebrates (Decapoda: penaeid (*Penaeus orientalis*)	epizoic	China
E. agrionis	43	freshwater	free-living	Europe
E. alpestris	100-140	freshwater	free-living	Europe
E. amphitae		marine, attached to unknown crustaceans (‘*Amphitae vallenti’*)	epizoic (pleopods)	Black Sea
E. anaestica		freshwater	free-living	Europe
E. anastatica (syn. *E. lacustris, nympharum p.p., stilleri, Vorticella, V. doliolum*)	44-130 x 20-62	freshwater, attached to aquatic plants (incl. hornwort *Ceratophyllum*) and invertebrates (Copepoda: cyclopid (*Cyclops agilis, Mesocyclops albidus, isabellae*); Branchiopoda: cercopagidid (*Bythotrephes longimanus*), daphniid (*Daphnia pulex*), triopsid (*Lepidurus apus, hyalina*); Amphipoda: gammarid	free-living, epiphytic, epizoic	Eurasia, Africa, North America

		(*Gammarus roeselii*); Arachnida: unionicolid (*Unionicola crassipes*); and Decapoda: cambarid (*Cambarellus patzcuarensis*))		
E. anilocrae (syn. *Orthochona*)	50	marine, attached to invertebrate (Isopoda: cymothoid (*Anilocra*))	epizoic	Europe
E. anodontae		freshwater, attached to mussel (Bivalvia: unionid (*Sinanodonta lauta*))	epizoic (gills, muscle)	Asia
E. anophelis		freshwater, attached to mosquito larvae (Diptera: culicid (*Anopheles*))	epizoic	Europe
E. apiosomae		freshwater, attached to fish (Scorpaeniformes: cottid (unspecified sculpins) and also to their peritrichous ectocommensals (Ciliophora: epistylidid (*Apiosoma*)	epizoic (surface)	Europe
E. arabica (syn. *Vorticella*)		freshwater	free-living	Europe
E. arcuata	45	freshwater	free-living	Europe
E. arenicolae		marine	free-living	Europe
E. articulata	75	freshwater	free-living	Europe
E. aselli	25-40	freshwater, attached to invertebrates	epizoic	Asia
E. astaci		freshwater, attached to invertebrates (Decapoda: astacid (*Astacus astacus, fluviatilis, leptodactylus, Austropotamobius torrentium*))	epizoic (gills)	Europe
E. autumnalis	80	freshwater, attached to plants (*Lemna*)	epiphytic	Europe
E. axile		estuarine, attached to crabs (Decapoda: macrophthalmid (*Macrophthalmus japonicus*), sesarmid (*Chiromantes haematocheir*))	epizoic (setae, pleopods)	Asia
E. azelicola		freshwater, attached to inanimate substrates and invertebrates (Isopoda: asellid (*Asellus aquaticus*)	free-living, epizoic	Europe
E. bagoi		freshwater, attached to beetle (Coleoptera: curculionid (*Bagous cylindrus*))	epizoic	Europe
E. balatonica	90-100	freshwater, attached to mussel (Bivalvia: unionid (*Unio pictorum*)	epizoic	Europe
E. barbata	70-90	marine, attached to detritus	free-living	Europe
E. bellis (syn. *Vorticella*)		freshwater	free-living	Europe
E. bimarginata	36-93 x 15-39	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Carinogammarus roeselii, Gammarus*); crayfish (Decapoda: astacid (*Astacus astacus, fluviatilis*), cambarid (*Cambarellus patzcuarensis*)	epizoic (appendages, exoskeleton, gills)	Europe, North America
E. branchiophila (syn. *E. formosa*)	18-90 x 15-48	freshwater, attached to algae, caddisfly larvae (Trichoptera: phryganeid (unspecified); crayfish (Decapoda: cambarid (*Cambarellus patzcuarensis*), and parasitic copepods (Copepoda: lernaeid (*Lernaea cyprinacea*))	epizoic	Africa, North America
E. breviramosa	40-60 x 25-30	freshwater, attached to invertebrates (Branchiopoda: bosminid (*Bosmina longirostris*), chydorid (*Alona affinis*), daphniid (*Daphnia*); Copepoda: cyclopid (*Cyclops*)	epizoic	Europe
E. cactistyla		marine, attached to crabs (Decapoda: macrophthalmid (*Macrophthalmus japonicus*), sesarmid (*Parasesarma pictum*), varunid (*Gaetice depressus, Hemigraspus penicillatus*) and shrimp	epizoic (gills)	Asia

		(Decapoda: upogebiid (*Upogebia major*))		
E. caliciformis	70-100	freshwater, attached to filamentous algae	free-living	?
E. callinectes	40-57 x 17-33	marine, attached to crabs (Decapoda: portunid (*Callinectes sapidus*)	epizoic	North America
E. cambari	50	freshwater, attached to crayfish (Decapoda: astacid (*Astacus leptodactylus*), cambarid (*Cambarus*)	epizoic (gills)	North America
E. campanella	35	freshwater	free-living	Europe
E. carinogammari	44-88 x 30-66	freshwater, attached to invertebrates (Amphipoda: gammarid (*Carcinogammarus*); Decapoda: cambarid (*Cambarellus patzcuarensis*))	epizoic	North America
E. cauliculus	10	freshwater, attached to invertebrates (Rotifera: collothecid (*Stephanoceros*), flosculariid (*Floscularia*))	epizoic	Europe
E. cerviciformis	70	freshwater	free-living	Europe
E. chlorelligerum	160-260 x 45-95	freshwater	free-living	Asia
E. chrysemydis (syn. *E. balatonica, polenici, Opercularia bimarginata, moldavica*)	120-220 x 55-110	freshwater (and activated sludge), attached to inanimate substrates, detritus, filamentous algae, submerged plants, invertebrate animals (*Trichoptera* caddisfly larvae) and vertebrate animals (Testudines: unspecified tortoises)	free-living, epiphytic, epizoic	Europe, America
E. clampi	35-70 x 20-35	marine, attached to inanimate substrates and crabs (Decapoda: portunid (*Callinectes sapidus*)	free-living, epizoic	North America, China
E. collariata		freshwater marshes	free-living	Europe
E. complanata		freshwater	free-living	Europe
E. constricta (syn. *Opercularia*)	130	freshwater, attached to butterfly pupae (Lepidoptera, unspecified)	epizoic	America
E. coronata	70-120	freshwater, attached to filamentous bacteria (*Sphaerotilus*)	free-living, epiphytic	Europe
E. corymbosus		freshwater	free-living	Europe
E. crassicollis	100	freshwater, attached to unspecified Entomostraca, and crayfish (Decapoda: astacid (*Astacus astacus, leptodactylus*)	epizoic	Europe
E. crataegaria (syn. *Vorticella*)		freshwater, attached to invertebrates (Hydrozoa: hydrid (*Hydra*))	epizoic	Europe
E. culexi		freshwater, attached to mosquito larvae (Diptera: culicid (*Culex pipiens*))	epizoic (surface)	Asia
E. cyprinaceae		freshwater, attached to parasitic copepod (Copepoda: lernaeid (*Lernaea cyprinacea*) of fish)	epizoic	Africa
E. daphniae	31-45 x 25-35	freshwater, attached to invertebrates (Branchiopoda: daphniid (*Daphnia magna*), moinid (*Moina macrocopa*); Copepoda: centropagid (*Boeckella triarticulata*)	epizoic	New Zealand
E. diaptomi		freshwater, attached to invertebrates (Copepoda: diaptomid (*Diaptomus*))	epizoic	
E. digitalis (syn. *Vorticella*)	60-120 x 20-40	freshwater, attached to invertebrates (Copepoda: cyclopid (*Cyclops agilis*, *Eucyclops serratulus*), canthocamptid (*Canthocampus*); Arachnida (unspecified mites))	free-living, epizoic	Eurasia, America
E. dudekemi	360	freshwater	free-living	?
E. dupla		freshwater	free-living	Europe
E. elongata	100	freshwater, attached to plants (*Lemna*) and clams (Bivalvia: mactrid (*Mactra quadrangularis*), venerid (*Ruditapes philippinarum*, *Meretrix meretrix*))	epiphytic, epizoic (gills)	Eurasia
E. entzii	107-190 x 80	freshwater (and activated sludge),	free-living,	Europe, America

		attached to inanimate substrates, detritus, mosses (*Fontinalis*), submerged plants, invertebrates (Gastropoda: planorbid (*Planorbis*); Bivalvia: unionid (*Unio pictorum*); Trichoptera (caddisfly larvae); and vertebrates (Testudines: unspecified tortoises)	epiphytic, epizoic	
E. epibarnimiana		freshwater, attached to parasitic copepods (Copepoda: lernaeid (*Lernaea barnimiana*) of fish)	epizoic	Africa
E. epibioticum	45-53	freshwater, attached to stalks of other colonial peritrichs (*Epistylis, Carchesium*)	epizoic	Eurasia
E. epistyliformis (syn. *Opercularia*)		freshwater, attached to woodlice (Isopoda: ligiid (*Ligidium agile*, *hypnorum*) and crabs (Decapoda: carcinid (*Carcinus maenas*))	epizoic	Europe
E. exilipes		freshwater	free-living	Europe
E. fastigata	30	freshwater	free-living	Europe
E. fastibilis	50	freshwater	free-living	Europe
E. fluitans	160	freshwater (swamp)	free-living	?
E. foissneri	110-190 x 20-30	freshwater (lake)	free-living	China
E. flabelliformis	43	freshwater	free-living	Europe
E. flectens		freshwater	free-living	Europe
E. flexistyla		marine, attached to crabs (Decapoda: varunid (*Gaetice depressus*))	epizoic (pleopods)	Asia
E. fugitans	50-60	freshwater, attached to invertebrates (Branchiopoda: sidid (*Sida crystallina*))	epizoic	North America
E. galea (syn. *Vorticella, E. umbellata*)	160-225 x 50-70, plus macro- & micro-zooids	freshwater, attached to inanimate substrates, submerged plants (*Ceratophyllum, Utricularia, Typha, Iris*)	free-living, epiphytic	Europe
E. gammari	26-74 x 11-52	freshwater and marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus oceanicus, salinus, tigrinus*); Decapoda: cambarid (*Cambarellus patzcuarensis*))	epizoic (antennae)	Europe, North America
E. geleii	45-50	freshwater, attached to mayfly larvae (Ephemeroptera: heptageniid (*Epeorus*))	epizoic	Europe
E. halophila	40	freshwater, attached to invertebrates (Branchiopoda: daphniid (*Daphnia pulex, longispina*))	epizoic	Europe
E. harpacticola	28-40	marine, attached to invertebrates (Copepoda: harpacticid (unspecified))	epizoic	Europe
E. helenae		freshwater, attached to invertebrates (Branchiopoda: chydorid (*Chydorus sphaericus*), daphniid (*Daphnia pulex*, *magna*, *obtusa*, *longispina*, *curvirostris*, *Ceriodaphnia pulchella*, *reticulata*, *laticauda*, *Simocephalus serratula*, *vetulus*), moinid (*Moina macropa*, *micrura*), sidid (*Diaphanosoma leuchtenbergianum*))	epizoic	North America
E. helicostylum		freshwater, attached to invertebrates (Ostracoda: cypridid (*Eucypris virens*))	epizoic (extremities)	Europe
E. hentscheli	100-235 x 35-80	freshwater, attached to inanimate substrates, and submerged plants	free-living, epiphytic	Eurasia
E. hollandei		freshwater, attached to moth larvae (Lepidoptera: crambid (*Nymphula nymphaeata*))	epizoic	Eurasia
E. hospes	125	freshwater	free-living	?
E. humilis (syn. *Opercularia*)	40-50	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus*); Ostracoda (unspecified))	epizoic	Europe

E. inclinans		freshwater	free-living	Europe
E. invaginata	60	freshwater, attached to beetle (Coleoptera: hydrophilid (*Hydrophilus*)	epizoic	Europe
E. jaerae		marine, attached to invertebrates (Isopoda: janirid (*Jaera marina*))	epizoic	Europe
E. jaworowskii	67	freshwater, attached to plants	epiphytic	Europe
E. kolbi	43-62 x 23-32	freshwater, attached to invertebrates (Amphipoda: gammarid (*Carinogammarus roeseli*))	epizoic	Europe
E. lacustris		freshwater, attached to inanimate substrates and aquatic insects (unspecified)	free-living, epizoic (surface)	Eurasia
E. laxipes (syn. *Vorticella*)	17-20	freshwater, attached to inanimate substrates and algae	free-living, epiphytic	Europe
E. leucoa	200	freshwater, attached to plants (*Carex*)	epiphytic	Europe
E. longicaudatum	35-61	freshwater	free-living	Europe
E. longicorpora	280-429 x 50-96	freshwater, attached to inanimate substrates, mussels (Bivalvia: unionid (*Sinanodonta lauta*) and fish (Cypriniformes: cyprinid (goldfish, Eurasian carp))	free-living, epizoic (mollusc shell, fish skin)	Eurasia
E. longifila		freshwater, attached to invertebrates (Copepoda: diaptomid (*Eudiaptomus zachariasi*))	epizoic	Europe
E. longipes	13	freshwater	free-living	Europe
E. longistyla		marine, attached to crabs (Decapoda: macrophthalmid (*Macrophthalmus japonicus*), sesarmid (*Parasesarma pictum*), varunid (*Gaetice depressus*))	epizoic (mouth, pleopods)	Asia
E. magna		freshwater, attached to parasitic copepod (Copepoda: lernaeid (*Lernaea cyprinacea*) on fish)	epizoic	Africa
E. major (*nomen nudum*, named but not described)		marine, attached to crabs (Decapoda: sesarmid (*Chiromantes haematocheir*))	epizoic (setae)	Asia
E. microdiscum	45-55 x 30-35	freshwater, attached to plants (Lemna minor) and invertebrates (Copepoda: cyclopid (*Cyclops strenuus*))	epiphytic, epizoic (antennae)	Eurasia
E. mirandella	35	freshwater, attached to inanimate substrates and plants (*Lemna*)	free-living, epiphytic	Europe
E. multicapitata (syn. *Nidula*)		freshwater	free-living	Lake Baikal
E. naisidicola	7-10	freshwater, attached to worms (Tubificida: naidid (*Dero*))	epizoic	Europe
E. niagarae	48-196 x 30-131	freshwater, attached to invertebrates (Copepoda: cyclopid (*Eucyclops serratulus*); Amphipoda: gammarid (*Gammarus roeselii*); Branchiopoda: daphniid (*Daphnia pulex*, *rosea*, *Ceriodaphnia reticulata*, *Scapholeberis mucronata*); Isopoda: asellid (*Asellus*); Decapoda: astacid (*Astacus leptodactylus*, *Austropotamobius torrentium*), cambarid (*Cambarellus patzcuarensis*, *Orconectes limosus*) and turtle shells (Testudines: chelydrid (unspecified snapping turtle), emydid (unspecified painted turtle)	epizoic (body surface)	North America
E. nigrelli	35-50 x 33	marine, attached to barnacles (Cirripedia: balanid (*Balanus eburneus*))	epizoic (mantle cavity)	North America
E. nitocrae		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus tigrinus*))	epizoic	North America

E. nympharum	60-150 x 20-25	freshwater, attached to plants (*Lemna*) and invertebrate animals (Diptera: chironomid (midge larvae); Ephemeroptera: ephemerid (mayfly larvae); Trichoptera (caddisfly larvae); Coleoptera: dytiscid (*Agabus nitidus*); Copepoda: argulid (*Dolops ranarum*), cyclopid (*Cyclops*, *Macrocyclops fuscus*), diaptomid (*Diaptomus gracilis*); Gastropoda: lymnaeid (*Lymnaea stagnalis*): Acari (unspecified mites)	epizoic	Eurasia, Africa
E. ophidioidea	dimorphic, 280-400	freshwater	free-living	Europe
E. ovalis		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus tigrinus*, *pulex*); Decapoda: astacid (*Astacus fluviatilis*)	epizoic	Europe, North America
E. ovum	30-38	freshwater, attached to plants and invertebrates (Copepoda: cyclopid (*Cyclops strenuus*); Rotifera (unspecified); Branchiopoda: bosminid (*Bosmina*), daphniid (*Daphnia pulex*), leptodorid (*Leptodora kindtii*))	epiphytic, epizoic	Europe
E. parvannulata		freshwater	free-living	Europe
E. perrieri		freshwater	free-living	Europe
E. phoxini		freshwater, attached to fish (Cypriniformes: leuciscid (common minnow))	epizoic	Europe
E. plicatilior		freshwater	free-living	Europe
E. plicatilis [type species]	70-162 x 25-50	freshwater, attached to inanimate substrates, detritus, submerged plants (*Lemna*), invertebrates (Amphipoda: gammarid (*Gammarus*); Copepoda: cyclopid (*Cyclops vernalis, bicuspidatus, Eucyclops agilis*); Isopoda: asellid (*Asellus*); Gastropoda (*Physa acuta, Radix japonica, Lymnaea*), Coleoptera (*Dytiscus* beetles), and amphibians (Anura (unspecified tadpoles))	free-living, epiphytic, epizoic	Eurasia, New Zealand, Americas
E. podurae		freshwater, attached to springtails (Poduromorpha: podurid (*Podura aquatica*))	epizoic	Europe
E. polenici	97-145	freshwater, attached to inanimate substrates and mollusc shells	free-living, epizoic	Eurasia
E. procumbens (syn. *E. rotans*)	60-140 x 30-70	freshwater (euplanktonic)	free-living	Eurasia, America
E. pseudovum		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus*))	epizoic	Europe
E. pygmaeum	22-50 x 17-45	freshwater, attached to plants (*Bosmina*), diatoms (*Fragilaria*), and invertebrates (Copepoda: cyclopid (*Cyclops*); Ostracoda (unspecified); rotifers (Rotifera: brachionid (*Brachionus angularis*); Amphipoda: gammarid (unspecified); Branchiopoda: daphniid (*Daphnia hyalina*, *Ceriodaphnia*) and mayfly larvae (Ephemeroptera (unspecified))	epizoic	Eurasia, North America
E. pyriformis	100	freshwater, attached to cranefly larvae (Diptera: tipulid (unspecified))	epizoic (surface)	Europe
E. racemosa	40-51	freshwater, attached to invertebrates (Copepoda: diaptomid (*Diaptomus*))	epizoic	Europe
E. raikowi	45-60 x 20-35	marine	free-living	China

E. regularis (syn. *Vorticella*)		freshwater, attached to inanimate substrates, Plants (*Myrophyllum*, *Lemna*) and invertebrates (Gastropoda: planorbid (*Planorbis contortus*))	free-living, epiphytic, epizoic	Europe
E. rotans		marine, attached to invertebrates (Isopoda: ligiid (*Ligia exotica*); Copepoda: cyclopid (unspecified))	epizoic (gills, carapace)	Asia
E. rotatorium	35	freshwater, attached to rotifers (Rotifera; brachionid (*Brachionus*))	epizoic	Europe
E. salina		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*))	epizoic	North America
E. scaralistyla		marine, attached to shrimp (Decapoda: upogebiid (*Upogebia major*))	epizoic (setae)	Asia
E. semiciculus	79-172 x 32-88	freshwater, attached to crayfish (Decapoda: cambarid (*Procambarus clark*ii))	epizoic (pereopods, gills)	China
E. sesarmae		marine, attached to crabs (Decapoda: sesarmid (*Parasesarma pictum*)	epizoic (mouth, pleopods)	Asia
E. sevastopoli		marine, attached to crabs (Decapoda: grapsid (*Pachygrapsus marmoratus*))	epizoic (mouthparts)	Black Sea
E. sommerae	48-57 x 29-38	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*))	epizoic (legs)	Europe
E. sphaerostyla		aquatic, attached to invertebrates (Isopoda: sphaeromatid (*Gnorimosphaeroma*))	epizoic (gills)	Asia
E. stammeri	44-74 x 22-47	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Decapoda: cambarid (*Cambarellus patzcuarensis*))	epizoic	North America, Europe
E. subcylindrica	50-80	freshwater	free-living	Europe
E. tenuistyla (syn. *E. etenuistyla*)		freshwater, attached to crayfish (Decapoda: cambarid (*Procambarus clarkii*))	epizoic (pleopods)	Asia
E. thienemanni		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex, tigrinus*))	epizoic (gills)	North America
E. tornatilis		freshwater	free-living	Europe
E. transvaalensis	27-45 x 20-38	freshwater, attached to fish (Cichliformes: cichlid (Mozambique tilapia, southern mouthbrooder))	epizoic (skin)	South Africa
E. tubificis (syn. *Rhabdostyla*)	100	freshwater, attached to oligochaetes (Clitellata: tubificid (*Tubifex rivulorum*))	epizoic	Europe
E. umbilicata	40-60 x 21-33	freshwater, attached to invertebrates (Isopoda: asellid (Asellus); Copepoda: cyclopid (*Cyclops*), worms (unspecified) and mosquito larvae (Diptera: culicid (unspecified))	epizoic	Europe
E. urceolata	120-190	freshwater, attached to mussels (Bivalvia: unionid (*Unio*), snails (Gastropoda: planorbid (*Planorbis*) and caddisfly larvae (Trichoptera (unspecified))	epizoic	Europe
E. uyemurai		marine	free-living	China
E. vaginata	60	freshwater	free-living	Europe
E. vaginula	60-125 x 20-55	freshwater, attached to inert substrates and plants (*Ceratophyllum*)	free-living, epiphytic	Eurasia
E. variabilis	40-96 x 22-47	freshwater, attached to inanimate substrates and crayfish (Decapoda: cambarid (*Cambarellus patzcuarensis*))	free-living, epizoic	Europe, North America
E. vermicola	50-60	freshwater (benthic), attached to worms (Oligochaeta (unspecified))	epizoic	Europe

E. verticillata	150	freshwater	free-living	Europe
E. vestita (syn. *Opercularia*)	80	freshwater, attached to plants	epiphytic	Europe
E. violacea	60-90	freshwater, attached to midge larvae (Diptera: chironomid (unspecified))	epizoic	North America
E. vittata	200	freshwater, attached to snails (Gastropoda: physid (*Physa*))	epizoic	Europe
E. wenrichi		freshwater, attached to mussels (Bivalvia: unionid (*Sinanodonta lauta*))	epizoic (shell)	Asia
E. wuhanensis	90-220	freshwater, attached to fish (Siluriformes: bagrid (yellowhead catfish) and parasitic copepods (Copepoda: lernaeid (*Lernaea cyprinacea*) parasitizing fish (Gobiiformes: oxudercid (Amur goby); Perciformes: centrarchid (bluegill))	epizoic (fish fins, copepod body surface)	Asia
E. zschokkei (syn. *Opercularia*)	50	freshwater, attached to invertebrates (Copepoda: cyclopid (*Cyclops*), canthocamptid (*Canthocamptus*); Amphipoda: gammarid (*Gammarus tigrinus*); Branchiopoda: macrothricid (*Acantholebris curvirostris*))	epizoic (appendages)	Europe
Genus: ***Foissnerella*** (colonial, stalked, bulbous stalks, branched, noncontractile, small colonies)				
F. physonica	42-51 x 34-38	freshwater, attached to invertebrates (Isopoda: sphaeromatid (*Gnorimosphaeroma noblei*)	epizoic	Eurasia
Genus: ***Heteropolaria*** (prominent stalk, branched, colonial, noncontractile without myoneme, adoral spiral with 1-1½ turns, peristome with lip, telotrochs flattened with aboral ring of cilia encircling apparent length of body)				
H. horizontalis [type species as *Eipstylis*]	46-50 x 25-29	marine, attached to barnacles (Cirripedia: balanid (*Balanus balanoides, balanus, crenatus, eburneus, amphitrite*))	epizoic (mantle cavity)	North America, Russia
H. colisarum (syn. *Epistylis*)	150-300 x 40-60	freshwater, attached to fish (Anabantiformes (unspecified gouramis); Perciformes: centrarchid (green sunfish); Siluriformes: ictalurid (channel catfish))	epizoic (skin) [red-sore disease]	East Asia, North America
H. lwoffi (syn. *Epistylis, Rhabdostyla cyprini*)	40-80 x 20-30 [4 stalk ecoforms]	freshwater, attached to fish (Cypriniformes: cyprinid (Eurasian carp, crucian carp, common bream, white bream, common roach, common rudd, gudgeon), nemacheilid (stone loach); Perciformes: percid (European perch, Eurasian ruffe, zander); Scorpaeniformes: cottid (European bullhead), gasterosteid (three-spined stickleback); Salmoniformes: salmonid (Atlantic salmon, brown trout))	epizoic (gills, skin)	Eurasia, North America
Genus ***Orborhabdostyla*** (solitary, short stalk, sometimes bent at base, noncontractile without myoneme, peristome with lip, discoidal-ellipsoidal macronucleus, transverse silverline system)				
O. bromelicola	50-75 x 13-18	freshwater, attached within tanks of bromeliads (*Guzmania musaica*)	free-living, epiphytic	Jamaica
O. brevipes (syn. *Epistylis, Rhabdostyla*)	80-90	freshwater, attached to fly larvae (Diptera (unspecified))	epizoic	Europe
O. kahli (syn. *Rhabdostyla*)	60	freshwater, attached to worms (Annelida: lumbriculid (*Lumbriculus*))	epizoic	Europe
Genus: ***Pseudepistylis*** (prominent stalk, branched, colonial, noncontractile, peristomial disc not on stalk, peristomial ciliary wreath makes < 2 turns, reticulate silverline system, telotrochs cylindrical)				
P. paramphora	170-285 x 110-190	freshwater	free-living	China
Genus: ***Rhabdostyla*** (solitary, short stalk, sometimes bent at base, noncontractile without myoneme, peristome with lip, adoral spiral with about one turn, infundibular ring with almost half a turn, horseshoe-shaped macronucleus, transverse silverline system)				
R. annularis (syn. *Vorticella*)		freshwater	free-living	Europe

R. annulata (syn. *Opisthostyla*)	22-23	freshwater, attached to filamentous algae	epiphytic	Europe
R. arenicolae	45-60	marine, attached to worms (Polychaeta: arenicolid (*Arenicola piscatorum*))	epizoic	Europe
R. arenaria	50-65	marine, attached to sea cucumber (Echinodermata: synaptid (*Synapta inhaerens*))	epizoic	Europe
R. bosminae	38-44 x 18-20	freshwater, attached to water fleas (Branchiopoda: bosminid (*Bosmina*))	epizoic	Europe
R. chironomi	60	brackish water, attached to midge larvae (Diptera: chironomid (unspecified))	epizoic	Europe
R. commensalis	35-70 x 20-30	intertidal, attached to invertebrates (Polychaeta: capitellid (*Capitella capitata*), syllid (*Salvatoria*), trichobranchid (*Terebellides stromii*); Amphipoda: gammarid (*Gammarus*)	epizoic	China
R. congregata	38-40	freshwater, attached to rotifers (Rotifera: brachionid (*Brachionus*))	epizoic	Europe
R. conipes	40-46	fresh and brackish water, attached to invertebrates (Branchipoda: daphniid (*Daphnia magna, longispina, Scapholeberis mucronata*))	epizoic	Europe
R. cyclopis	30	freshwater, attached to invertebrates (Copepoda: cyclopid (*Cyclops*); Ostracoda (unspecified))	epizoic	Europe
R. cylindrica	28	freshwater, attached to water fleas (Branchiopoda: leptorid (*Leptodora kindtii*))	epizoic	Eurasia
R. dubia	30-35	freshwater	free-living	Europe
R. ephemerae	75	freshwater, attached to mayfly larvae (Ephemeroptera: ephemerid (unspecified))	epizoic	Europe
R. fromenteli (syn. *Scyphidia*) [type species]	80	freshwater	free-living	Europe
R. globularis (syn. *Opisthostyla*)	25-34 x 17-20	freshwater, attached to algae and water fleas (Branchipoda: bosminid (*Bosmina longirostris*), sidid (*Diaphanosoma brachyurum)*)	epiphytic, epizoic	Europe
R. hungarica	35-40	freshwater, attached to water fleas (Branchiopoda: leptorid (*Leptodora kindtii*))	epizoic	Eurasia
R. inclinans (syn. *R. chaeticola, lumbriculi, Vorticella, Opercularia, Gerda*)	45-80 x 35-42	freshwater, attached to invertebrate animals (Annelida: lumbriculid (*Lumbriculus*), naidid (*Nais, Stylaria*, *Tubifex*, *Pristina*), esp. amongst filamentous bacteria (*Sphaerotilus*)	epizoic	Eurasia, America
R. invaginata	35	marine, attached to barnacles (Cirripedia: balanomorphid (*Cypris*))	epizoic	Europe
R. libera	60	marine, attached to algae	epiphytic	Europe
R. limnophili	55	freshwater, attached to 'kettle-fly' larvae (Diptera (unspecified))	epizoic	Europe
R. longipes (syn. *Opisthostyla*)	70	freshwater, attached to algae	epiphytic	Europe
R. mapuche	23-31 x 16-19	marine, attached to worms (Polychaeta: syllid (*Syllis*, *Salvatoria*))	epizoic	Europe
R. muscorum	40	freshwater, attached to mosses	epiphytic	Europe
R. nebulifera (syn. *Epistylis*)	125	freshwater, attached to watercress	free-living, epiphytic	Europe
R. nereicola	45 x 55-62	marine, attached to worms (Polychaeta: nereidid (*Nereis dumerili*))	epizoic	Europe
R. patula		freshwater	free-living	Eurasia

(syn. *Scyphidia*)				
R. porculus	135-155	freshwater, attached to detritus	free-living	Europe
R. pristinis	37 x 48	freshwater	free-living	Europe
R. pusilla (syn. *Opisthostyla*)	25	freshwater, attached to algae	epiphytic	Europe
R. putrina (syn. *Vorticella*)	60-90	freshwater and marine (polysaprobic)	free-living	Europe
R. pyriformis (syn. *Scyphidia, R. ovum*)	25-40	freshwater, attached to invertebrates (Branchiopoda: chydorid (*Alona rectangula*, *Leydigia acanthocercoides*), daphniid (*Daphnia longispina, hyalina, pulex, magna, cucullata, atkinsoni, curvirostris, obtusa, Ceriodaphnia reticulata, laticaudata, pulchella, megalops, Scapholebris mucronata, Simocephalus vetulus*), leptodorid (*Leptodora kindtii*), moinid (*Moina micrura*); Copepoda (unspecified) and Rotifera (unspecified))	epizoic	Eurasia
R. ringens (syn. *Epistylis, Vorticella*)	80	freshwater, attached to oligochaetes (Clitellata: tubificid (*Nais*))	free-living, epizoic	Europe
R. scyphidiformis		freshwater, attached to amphibians (Anura: bombinatorid (European fire-bellied toad), bufonid (European green toad), hylid (European tree frog), pelobatid (European spadefoot toad), ranid (edible frog))	epizoic	Eurasia
R. scyphoides	35-44 x 24-27	marine, attached to prawns (Decapoda: penaeid (*Penaeus orientalis*))	epizoic	China
R. sertularium (syn. *Opisthostyla*)	40	marine, attached to invertebrates (Hydrozoa: aglaopheniid (*Aglaophenia pluma*); Ophiurida: amphiurid (*Amphirua squamata* brittlestar))	epizoic	Eurasia
R. sessilis	43-45	freshwater, attached to invertebrates (Copepoda: cyclopid (*Cyclops*))	epizoic	Europe
R. similis (syn. *Opisthostyla*)	22	freshwater	free-living	Europe
R. sphaeroides (syn. *Epistylis*)	60	freshwater, attached to watercress	free-living, epiphytic	Europe
R. thienemanni (syn. *Opisthostyla*)		marine	free-living	North America
R. tuboadui	30-45 x 15-23	marine, attached to worms (Polychaeta: syllid (*Syllis prolifera*))	epizoic	Eurasia
R. variabilis	60-90	marine, attached to worms (Polychaeta: terebellid (unspecified))	epizoic	Eurasia
R. vernalis	50	marine, attached to invertebrates (Cirripedia: balanomorphid (*Cypris*); Copepoda: cyclopid (*Cyclops*, *Eucyclops agilis*))	epizoic	Europe
R. volvocis		freshwater, attached to colonial flagellates (Chlorophyceae: volvocaceae (*Volvox globator*))	epiphytic	Europe
Family **Bezedniellidae** (stalk, noncontractile, solitary or colonial, laterally displaced peristome, often into curved cylindrical trunk, epizoic on ostracods)				
Genus: ***Bezedniella*** (colonial, long branched stalk)				
B. bambergensis	50-68 x 38-48	freshwater, attached to invertebrates (Ostracoda: cypridid (*Cypria ophthalmica*))	epizoic (inner surface)	Europe
B. prima [type species]		freshwater, attached to invertebrates (Ostracoda: cypridid (*Cypria*))	epizoic	Europe
Genus ***Nuchterleinella*** (solitary, short stalk)				

N. corneliae	57-122 x 34-83	freshwater, attached to invertebrates (Ostracoda: cypridid (*Cypria ophthalmica*), cyclocyprinid (*Cyclocypris ovum*))	epizoic (furca, penis)	Europe
Family: **Operculariidae** (noncontractile stalks, well-developed thecae, unique epistomial discs with anterior opercula, usually epibiotic on aquatic insects and arthropods)				
Genus: ***Ballodora*** (globular flexible body with short lateral stalk, on terrestrial isopods)				
B. dimorpha (syn. *Opercularia*)		terrestrial, attached to wood lice (Isopoda: agnarid (*Protracheoniscus politus*), cylisticid (*Cylisticus convexus*), porcellionid (*Porcellio scaber*, *Porcelliens, Porcellium conspersum*), oniscid (*Oniscus asellus*), trachelipodid (*Tracheoniscus rathkei, Trachelipus ratzburgii*)	epizoic	Europe
B. marceli (syn. *Opercularia*)	50 x 40	terrestrial, attached to wood lice (Isopoda: trichoniscid (*Trichoniscus* (*Spiloniscus*) *provisorius*, *dentiger*, *Hyloniscus riparius, Titanethes*))	epizoic (appendages)	Europe
Genus: ***Opercularia*** (prominent stalk, branched, colonial, noncontractile without myoneme, horseshoe-shaped macronucleus, peristome without lip, rim often scalloped, peristomial ciliary wreath with < 2 turns)				
O. archiorbopercularia		freshwater	free-living	Europe
O. arenicola	80	freshwater; attached to fly larvae (Diptera (unspecified))	epizoic	Europe
O. articulata (syn. *O. phryganeae, confusa*) [type species]	80-260 x 30-70	freshwater, attached to inanimate substrates, detritus, filamentous algae, mosses, submerged plants, and invertebrate animals (Isopoda: asellid (*Asellus*); Amphipoda: gammarid (*Carinogrammus*); Coleoptera: dytiscid (*Dytiscus* water beetles)	free-living, epiphytic, epizoic	Europe
O. assellicola	120	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus*))	epizoic	Europe
O. cema	27-39 x 18-25	marine, attached to invertebrates (Amphipoda: talitrid (*Orchestia montagui*, *bottae*))	epizoic (appendages)	Black Sea
O. clepsinis	100-130	marine, attached to leeches (Hirudinea: glossiphoniid (*Clepsine bioculata* = *Helobdella stagnalis*))	epizoic	Europe
O. coarctata (syn. *Epistylis*)	40-65 x 25-30	freshwater (and activated sludge), attached to inanimate substrates, detritus, filamentous bacteria (*Sphaerotilus*), plants and invertebrates (Copepoda (unspecified); Bivalvia: sphaeriid (*Sphaerium*)	free-living, epiphytic, epizoic	cosmopolitan
O. collegata		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Helochares*))	epizoic	Europe
O. confervarum		marine, attached to filamentous algae	epiphytic	Europe
O. corethrae	75-78	freshwater, attached to mosquito larvae (Diptera: culicid (*Corethra*))	epizoic	Europe
O. coronata		freshwater, attached to water boatman (Hemiptera: corixid (*Corixa punctata*))	epizoic	Europe
O. crustaceorum		freshwater, attached to crayfish (Decapoda: astacid (*Astacus astacus, Austropotamobius torrentium*))	epizoic	North America
O. cupulata		marine, attached to invertebrates (Isopoda: sphaeromatid (*Cymodoce truncata*))	epizoic	Europe
O. cylindrata	50	freshwater, attached to invertebrates (Copepoda: cyclopid (*Cyclops*))	epizoic	Europe
O. dytiscidarum		freshwater, attached to diving beetles (Coleoptera: dytiscid (unspecified))	epizoic	Europe

O. elongata	125-150	freshwater, attached to plants	epiphytic	Europe
O. eumelita		freshwater, attached to ciliates (Ciliophora: operculariid (*Orbopercularia catillicola*) attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus coarctatus*))	epizoic	Europe
O. faurei	800	freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Hydrophilus aterrimus, piceus*))	epizoic	Europe
O. franconia		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Hydrophilus aterrimus, piceus*))	epizoic	Europe
O. gammari		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus*))	epizoic	Europe
O. glomerata	450	freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Hydrophilus piceus*))	epizoic	Europe
O. gracilis	80	freshwater, attached to snails (Gastropoda: lymnaeid (*Lymnea*))	epizoic	Europe
O. halipli		freshwater, attached to water beetle (Coleoptera: haliplid (*Haliplus flavicollis*))	epizoic	Europe
O. hydrachinidarum		freshwater, attached to mites (Acari: hydrachnid (*Hydrachna*))	epizoic	Europe
O. hydroi		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Hydrophilus aterrimus, piceus*))	epizoic	Europe
O. improbata		freshwater, attached to ciliates (Ciliophora: opercularid (*Orbopercularia enochri, matthesi*) attached to water scavenger beetles (Coleopteria: hydrophilid (*Enochrus testaceus*))	epizoic	Europe
O. irritabilis		freshwater, attached to tortoises (Testudines (unspecified))	epizoic	North America
O. lichtensteini	130	marine, attached to crabs (Decapoda (unspecified) and molluscs (Bivalvia (unspecified))	epizoic	Europe
O. ligiae		marine, attached to sea slaters (Isopoda: ligiid (*Ligia italica*))	epizoic	Europe
O. longigula		marine	free-living	North America
O. medians	470	freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Hydrophilus, Hydrous aterrinus*))	epizoic	Europe
O. microdiscum	70-90	freshwater, attached to hoverfly larvae (Diptera: syrphid (unspecified))	epizoic	Europe
O. minima	40	freshwater, attached to mites (Acari (unspecified)	epizoic	Europe
O. naucoris		freshwater, attached to creeping water bug (Hemiptera: naucorid (*Naucoris cimicoides*))	epizoic	Europe
O. nautonectae		freshwater, attached to water boatman (Hemiptera: corixid (*Corixa geoffroyi*))	epizoic	Europe
O. nutans (syn. *O. allensi, microstoma, ramosa, Epistylis ramosa, Pyxidium ramosa*)	50-141 x 25-40	freshwater/marine, attached to inanimate substrates, detritus, filamentous algae (*Enteromorpha, Cladophora*), submerged plants (*Ceratophyllum, Hottonia, Lemna, Myriophyllum*) and invertebrate animals (Diptera: chironomid (midge larvae), Ephemeroptera: ephemerid (*Caenis* mayfly larvae); Branchiopoda: chydorid (*Alona affinis*); Megaolptera: sialid (*Sialis* alderfly larvae); Amphipoda: gammarid (scuds); Decapoda: astacid (*Astacus*	free-living, epiphytic, epizoic	cosmopolitan

		leptodactylus)		
O. parallela	70	freshwater	free-living	Europe
O. penardi	90-110	freshwater, attached to plants (*Lemna polyrrhiza*)	epiphytic	Europe
O. phryganeae	120	freshwater, attached to caddisfly larvae (Trichoptera (unspecified))	epizoic	Europe
O. plicatilis	250	freshwater, attached to plants	epiphytic	Europe
O. prossi		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Hydrophilus aterrimus, piceus*))	epizoic	Europe
O. protecta	80-112 x 35-40	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*))	epizoic (appendages)	Europe
O. reichelei		freshwater, attached to crayfish (Decapoda: astacid (*Astacus leptodactylus*))	epizoic (appendages)	Europe
O. reichenowi		freshwater, attached to water boatman (Hemiptera: corixid (*Sigara striata*))	epizoic	Europe
O. rugosa	150-200	freshwater, attached to plants	epiphytic	Europe
O. sommerae	38-52 x 18-22	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus*))	epizoic (body)	Europe
O. stammeri		terrestrial, attached to wood lice (Isopoda: oniscid (*Oniscus asellus*))	epizoic	Europe
O. stenostoma	110	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic	Europe
O. venusta		freshwater	free-living	Europe
Genus: ***Opercullariella*** (colonial, barrel-shaped body on short rigid stalk, branched, endozoic in oesophagus of beetle)				
O. parasitica [type species]	100-110	terrestrial, located in diving beetle (Coleoptera: dytiscid (unspecified); [also possibly in stag beetle Coleoptera: lucanid (*Aegus currani*)]	endozoic (oesophagus) [hindgut]	Europe [Philippines]
Genus: ***Orbopercularia*** (prominent stalk, branched, colonial, noncontractile without myoneme, discoidal-spherical macronucleus, peristome without lip, < 2 adoral spirals, striated silverline system)				
O. acilii (syn. *Opercularia*)	51 x 27	freshwater, attached to water beetles (Coleoptera: dytiscid (unspecified)	epizoic	Europe
O. agabi		freshwater, attached to water beetles (Coleoptera: dytiscid (unspecified)	epizoic	Europe
O. assimilis (syn. *Syncyathella*)	50-60 x 30-35	freshwater, attached to water scavenger beetle (Coleoptera: dytiscid (*Hydaticus*), hydrophilid (*Helochares*))	epizoic (appendages)	Asia
O. astacicola (syn. *Opercularia*)		freshwater, attached to crayfish (Decapoda: astacid (*Austropotamobius torrentium*))	epizoic (appendages)	North America
O. berberina [type species as *Vorticella*]	62-130 x 28-33	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus roeselii*) and water bugs (Hemiptera: naucorid (*Naucoris cimicoides*))	epizoic	Europe
O. calix		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus testaceus*))	epizoic	Europe
O. carlae		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Laccobius*))	epizoic	Europe
O. catillicola (syn. *Syncyathella*)		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus coarctatus*))	epizoic	Europe
O. corlissi	72-80 x 24	freshwater, attached to moss beetles (Coleoptera: hydraenid (*Hydraena*))	epizoic (legs)	Europe
O. cylindrica	48-68 x 20-24	freshwater, attached to backswimmer bug (Hemiptera: pleid (*Plea*))	epizoic (appendages)	China
O. discostyla		freshwater, attached to water beetles (Coleoptera: dytiscid (unspecified)	epizoic	Europe

O. dominiki	38-54 x 20-38	freshwater, attached to invertebrates (Ostracoda: cypridid (*Cypria ophthalmica*), cyclocyprinid (*Cyclocypris ovum*)	epizoic (legs, antennae)	Europe
O. dreyeri		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus testaceus*))	epizoic	Europe
O. enochri		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus testaceus*))	epizoic (legs)	Europe
O. erlangensis (syn. *Serioscyphus*)		freshwater	free-living	Europe
O. exigata		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Laccobius*))	epizoic	Europe
O. femoralis		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus testaceus*))	epizoic	Europe
O. finki		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus testaceus*))	epizoic	Europe
O. finleyi	60-66 x 36	freshwater, attached to water beetles (Coleoptera: hydrophilid (*Berosus luridus*))	epizoic	Europe
O. fusiformis (syn. *Syncyathella*)	100-110 x 32-36	freshwater, attached to water beetle (Coleoptera: dytiscid (*Hydaticus*))	epizoic (appendages)	China
O. gnathophila		freshwater, attached to whirligig beetles (Coleoptera: gyrinid (unspecified)	epizoic (preoral cavity)	Europe
O. haliplorum		freshwater, attached to water beetles (Coleoptera: dytiscid (unspecified)	epizoic	Europe
O. hasenfussi		freshwater	free-living	Europe
O. hebetata		freshwater, attached to water beetles (Coleoptera: dytiscid (unspecified)	epizoic	Europe
O. helocharidis		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Helochares*))	epizoic	Europe
O. hydropori		freshwater, attached to water beetles (Coleoptera: dytiscid (unspecified)	epizoic	Europe
O. hyphidri		freshwater, attached to diving beetles (Coleoptera: dytiscid (*Hyphydrus ferrungineus*))	epizoic	Europe
O. illustris		freshwater, attached to diving beetles (Coleoptera: dytiscid (*Hydroporus tristis*))	epizoic	Europe
O. ilybii		freshwater, attached to water beetles (Coleoptera: dytiscid (unspecified)	epizoic	Europe
O. inclinata		freshwater, attached to water beetles (Coleoptera: dytiscid (unspecified)	epizoic	Europe
O. krauteri		freshwater	free-living	Europe
O. laccobii (syn. *Opercularia*)		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Laccobius*))	epizoic	Europe
O. lichtensteini	56-84 x 30-40	freshwater, attached to water boatman (Hemiptera: corixid (*Corisella edulis*) and beetles (Coleoptera: noterid (*Noterus clavicornis, crassicornis*), dytiscid (*Agabus congener, didymus, sturnii, Colymbetes fuscus, Hydroporus ferrugineus, Ilybus aenescens, angustior, ater, fenestratus, fuliginosus, subaenus, Laccophilus virescens, Rhantus exoletus, punctatus, suturellus*))	epizoic (appendages, body, eyes)	Eurasia, North America

O. liebmanni		freshwater, attached to water beetles (Coleoptera: dytiscid (unspecified)	epizoic	Europe
O. loricata		freshwater	free-living	Europe
O. lusti (syn. *Syncyathella*)		freshwater, attached to moss beetles (Coleoptera: hydraenid (*Hydraena britteni*))	epizoic	Europe
O. macronucleata		freshwater	free-living	Europe
O. matthesi		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Enochrus coarctatus*))	epizoic	Europe
O. micronectae	45-50 x 20	freshwater, attached to water bugs (Hemiptera: micronectid (*Micronecta*))	epizoic (legs)	Eurasia
O. nenningerae		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus testaceus, Helochares lividus*))	epizoic	Europe
O. nodosa		freshwater	free-living	Europe
O. oligochaetae		freshwater, attached to inert substrates and worms (Oligochaeta (unspecified))	free-living, epizoic	Russia
O. ominosa		freshwater, attached to whirligig beetles (Coleoptera: gyrinid (unspecified)	epizoic (preoral cavity)	Europe
O. oschei		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Helochares*))	epizoic	Europe
O. ovalis (syn. *Syncyathella*)	69-82 x 35-41	freshwater, attached to water beetle (Coleoptera: dytiscid (*Hydaticus*))	epizoic (appendages)	China
O. philydri		freshwater, attached to water scavenger beetles (Coleoptera: dytiscid (unspecified), hydrophilid (*Enochrus ochropterus*))	epizoic	Europe
O. plachteri		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Helochares lividus*))	epizoic (antennae)	Europe
O. pleae		freshwater, attached to backswimmer bug (Hemiptera: pleid (*Plea leachi, minutissima*))	epizoic	Europe
O. pulchra	70 x 25-28	freshwater, attached to backswimmer bugs (Hemiptera: notonectid (*Notonecta marmorea*))	epizoic (legs)	Eurasia
O. quasiinvoluta		freshwater, attached to diving beetle (Coleoptera: dytiscid (*Dystiscus marginalis*))	epizoic	Europe
O. quinquaginta		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus testaceus*))	epizoic	Europe
O. rara		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Enochrus testaceus, melanocephalus*))	epizoic	Europe
O. rhanti		freshwater, attached to water beetles (Coleoptera: dytiscid (unspecified)	epizoic	Europe
O. robusta		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Laccobius, Enochrus testaceus*))	epizoic	Europe
O. scheloskei		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Laccobius*))	epizoic	Europe
O. scheubeli		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus testaceus*))	epizoic	Europe
O. schremmeri		freshwater	free-living	Europe
O. scyphostyla	80	freshwater, attached to beetle (Coleoptera: noterid (*Noterus clavicornis*))	free-living, epizoic (legs)	Europe
O. serrata		freshwater, attached to water beetles	epizoic	Europe

		(Coleoptera: dytiscid (unspecified)		
O. siewingi		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus testaceus*))	epizoic	Europe
O. sitiens	63-71 x 25-27	freshwater, attached to water beetles (Coleoptera: dytiscid (unspecified)	epizoic	Europe
O. steffani		freshwater, attached to water scavenger beetles (Coleoptera: hydrophilid (*Enochrus coarctatus*))	epizoic	Europe
O. tobsinella		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Laccobius*))	epizoic	Europe
O. turgida		freshwater, attached to water boatman (Hemiptera: corixid (*Sigara falleni*) and water beetle (Coleoptera: dytiscid (*Agabus*))	epizoic (rostrum bristle)	Europe
O. triangulata	53 x 30	freshwater, attached to diving beetle (Coleoptera: dytiscid (*Rhantus punctatus*))	epizoic	Europe
O. valvata		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Laccobius*))	epizoic	Europe
O. wetzeli		freshwater, attached to water beetle (Coleoptera: dytiscid (*Acilius sulcatus*))	epizoic	Europe
O. xinjiangensis	48-52 x 15-18	freshwater, attached to water beetle (Coleoptera: dytiscid (*Hydaticus*))	epizoic (antennae, appendages)	China
genus: ***Orbopyxidiella*** (solitary, short stalk with small basal plate, fastened obliquely to substrate, no peristomial lip, striated silverline system				
O. helophori (syn. *Propyxidium*, *Pyxidiella*)	88-100	freshwater, attached to water scavenger beetles (Coleoptera: helophorid (*Helophorus*), hydrophilid (unspecified))	epizoic	Eurasia
O. matthesi	21-30	freshwater, attached to worms (Oligochaeta (unspecified))	epizoic	Europe
O. minuta		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (unspecified))	epizoic	Europe
O. stammeri (syn. *Ampullaster*) [type species]		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (unspecified))	epizoic	Europe
O. susannae	33-45 x 15-25	freshwater, attached to invertebrates (Ostracoda: cypridid (*Cypria ophthalmica*), cyclocypridid (*Cyclocypris ovum*))	epizoic (carapace)	Europe
O. tretzeli (syn. *Opercularia*)	43-67	freshwater, attached to invertebrates (Ostracoda (unspecified)	epizoic	Europe
Genus: ***Propyxidium*** (solitary, short stalk, noncontractile without myoneme, peristome without lip)				
P. acaule (syn. *Pyxidiella, Pyxidium*)	100	freshwater, attached to mosquito larvae (Diptera: culicid (*Corethra*))	epizoic	Europe
P. aselli (syn. *Pyxidium*)	80-125	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus*))	epizoic	Europe
P. asymmetricum (syn. *Pyxidium*)		freshwater, attached to crayfish (Decapoda: astacid (*Astacus astacus*))	epizoic	Europe
P. bosminae (syn. *Pyxidium*)	40-50	freshwater, attached to water fleas (Branchiopoda: bosminid (*Bosmina*))	epizoic	Europe
P. canthocampti (syn. *Pyxidium*)	25-32	freshwater, attached to invertebrates (Copepoda: canthocamptid (*Canthocamptus*))	epizoic	Europe
P. collare (syn. *Pyxidium*)	90	freshwater, attached to plants (*Lemna*) and water mites (Trombidiiformes (unspecified))	epiphytic, epizoic	Europe

P. cothurnoides (syn. *Pachytrocha*) [type species]	50	freshwater, attached to plants and invertebrates (Ostracoda: cypridid (*Cypris*))	epiphytic, epizoic	Europe
P. curvicaule (syn. *Pyxidium*)	40-80	freshwater/terrestrial, attached to moss	epiphytic	Europe
P. fabrei (syn. *Pyxidium, Opercularia*)	120	freshwater, attached to hoverfly larvae (Diptera: syrphid (*Eristalis*)	epizoic	Europe
P. grelli (syn. *Pyxidiella, Orbopyxidiella)*)		freshwater, attached to beetle (Coleoptera: dytiscid (*Platambus maculeatus*))	epizoic	Europe
P. hebes (syn. *Pyxidium, Opercularia*)	73-150 x 39-59	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic (body, appendages)	Europe
P. henneguyi (syn. *Opercularia, Orbopercularia*)	50-85	freshwater, attached to invertebrates (Copepoda: cyclopid (*Cyclops*))	epizoic	Europe
P. inclinans (syn. *Pyxidium, Opercularia*)	80	freshwater, attached to algae and oligochaetes (Clitellata: tubificid (*Nais*))	epiphytic, epizoic	Europe
P. invaginatum (syn. *Pyxidium*)	80	freshwater, attached to moss and plants (*Lemna*)	epiphytic	Europe
P. kahli (syn. *Pyxidium, Orbopyxidiella*)		freshwater	free-living	Europe
P. longicollum (syn. *Pyxidium*)	Biegel 1954	terrestrial (soil), attached to inert substrates and the shells of testate amoebae	free-living, epizoic?	Europe
P. nutans (syn. *Pyxidium*)	60	freshwater, attached to plants	epiphytic	Europe
P. piscicolae (syn. *Pyxidiella, Pyxidium*)		freshwater, attached to leeches (Hirudinea: piscicolid (*Piscicola geometra*))	epizoic	Europe
P. singulare		freshwater, attached to water beetles (Coleoptera (unspecified))	epizoic	Europe
P. sinuosa (syn. *Pyxidiella*)		freshwater, attached to water scavenger beetle (Coleoptera: hydrophilid (*Helochares*))	epizoic	Europe
P. tardigradum (syn. *Pyxidium*)	35-78	limno-terrestrial (freshwater, soil, moss, lichen (e.g. *Xanthoria parientina*)), attached to water bears (Tardigrada: milnesiid (*Milnesium* cf. *tardigradum*, *variefidum*), hypsibiid (*Hypsibius* cf. *scabropygus*, *Isohypsibius undulatus*), macrobiotid (*Macrobiotus* cf. *hufelandi*, *scoticus*, *Minibiotus* cf. *intermedius*), ramazzottiid (*Ramazzottius* cf. *oberhausei*))	epizoic (body)	Europe
P. tectiformis	52 x 19	freshwater, attached to fish (Cypriniformes: leuciscid (common minnow))	epizoic (gills)	Africa
P. urceolatum (syn. *Pyxidium*)	90	freshwater, attached to plants (*Lemna*)	epiphytic	Europe
P. ventriosa (syn. *Pyxidiella, Pyxidium*)		freshwater, attached to mosquito larvae (Diptera: cuculid (*Corethra*))	epizoic	Europe
P. vernale (syn. *Pyxidium*)	70	freshwater, attached to algae	epiphytic	Europe
genus: ***Triadopercularia*** (fossil taxon, cup-like pseudochitinous lorica fossilized, triangular stems with short basal stalk for attachment to fossilized ostracod host)				
T. spitzbergensis [type species]	167-200 x 88-117	fossilized ostracods		Europe

Family: **Rovinjellidae**				
Genus: ***Rovinjella*** (1-4 zooids in shared cup-like lorica with wide aperture and short basal stalk, zooids attached internally by short stalk (branched in colonies) with central continuous myoneme)				
R. spheromae [type species]	100 x 98	marine (beach), associated with Isopoda: sphaeromatid (*Sphaeroma serratum*)	epizoic	Europe
Family: **Usconophryidae** (lorica, lack of closure apparatus operated by peristomial sphincter, opercullariform peristome (without lip))				
Genus: ***Cyclodonta*** (upright lorica, vase-shaped with broad aperture, with short stalk, often bent, open aperture, zooid attached to base of lorica by a series of membranes)				
C. bipartita (syn. *Lagenophrys, Cothurnia affinis, bipartita, longipes, rheotypica*, *trilobata, voigti*) [type species as *Cothurnia*]	50-165 x 40-70	freshwater or marine, attached to seaweeds and invertebrates (Bryozoa (unspecified); Copepoda: harpacticoid (unspecified), canthocamptid (*Canthocamptus minutus, staphylinus, veidovskyi*); Branchiopoda: daphniid (*Daphnia*); Decapoda: astacid (*Astacus leptodactylus*), cambarid (*Cambarus affinis*, *Orconectes limosus*))	epiphytic, epizoic (carapace)	Eurasia, North America
Genus: ***Usconophrys*** (lorica hemispheroidal, distorted laterally and flattened, open aperture at anterior dorsal surface surrounded by projecting rim)				
U. aperta [type species as *Lagenophrys*] (syn. *U. dauricus*)	49-85 x 44-74 x 14-24	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus, hilgendorfi, Caecidotea*))	epizoic (gills)	Europe, North America
U. rotunda (syn. *Lagenophrys*)		freshwater, attached to invertebrates (Ostracoda (unspecified))	epizoic	Europe
Family: **Vorticellidae**				
Genus: ***Apocarchesium*** (stalked, unbranched, colonial whereby zooids cluster in rosette at expanded tip of primary stalk, sinusoidal myoneme contracts in helical fashion, vegetative zooids and macrozooids not connected to myoneme of colony stalk, occasional microzoids connected to microneme, transverse silverline system)				
A. arndti	150-210 x 25-35	freshwater	free-living	Europe
A. rosettum	80-100 x 30-40	freshwater	free-living	Asia
Genus: ***Baikalonis*** (solitary, short stalk, unbranched, straight continuous spasmoneme, stalk contracts by shortening longitudinally and becomes partly enveloped by zooid)				
B. foissneri [type species]	50-60 x 20	freshwater, attached to caddisfly larvae (Trichoptera: apataniid (*Baicalina bellicosa*))	epizoic	Russia
B. gammari (syn. *Halpocaulus*)	75 x 45	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*))	epizoic	Europe
B. microdiscus	20-30 x 15-20	intertidal, attached to invertebrates (Copepoda: harpacticoid (unspecified species))	epizoic	China
B. undulata (syn. *Vorticella, Vorticellopsis*)	110 x 72	marine, attached to algae (*Desmaresita viridis*)	epiphytic	Eurasia
Genus: ***Baikalaster*** (solitary, Zooids with lateral pseudopodial extensions, stalk, unbranched, central myoneme contracts in spiral fashion)				
B. pelagicus [type species]	46-57 x 78-109	freshwater, attached to filamentous cyanobacteria (*Anabaena*) and desmidiacid algae (*Micrasterias*)	epiphytic	Eurasia
Genus ***Carchesium*** (prominent stalk, either unbranched bearing single zooids or branched bearing small colonies, with discontinuous sinusoidal myonemes, contracts in spiral fashion)				
C. amphibiarum		freshwater, attached to amphibians (Anura (unspecified tadpoles))	epizoic	Europe
C. batorligetiense		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus roeselii, Rivulogammarus triacanthus*)	epizoic	Europe
C. bipartitum	18	freshwater	free-living	Europe
C. brevistylum		freshwater, attached to invertebrates (Branchiopoda: leptodorid (*Leptodora kindtii*)	epizoic	Europe

C. cyclopidarum	50 x 30-35	freshwater, attached to invertebrates (Copepoda: cyclopid (*Cyclops viridis*)	epizoic	Europe
C. dipneumon	43-81 x 35-58	freshwater, attached to invertebrates (Amphipoda: gammarid (*Dikerogammarus vilosus, Gammarus fossarum, pulex, roeselii*)	epizoic	Europe
C. duplex	13	freshwater	free-living	Europe
C. duplicatum		marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus locusta, oceanicus, pulex*)	epizoic	Europe
C. epistylidis		freshwater, attached to algae and invertebrates (Copepoda: cyclopid (*Cyclops viridis*)	epizoic	Europe, North America
C. epistylis (syn. *C. septatum*)	50	freshwater, free-swimming and attached to caddisfly larvae (Trichoptera: phryganid (unspecified))	free-living, epizoic	Europe
C. gammari		freshwater and marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus locusta, insensibilis*))	epizoic (appendages)	Europe
C. gemellum		marine	free-living	Europe
C. gracilis		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum*)	epizoic	Europe
C. granulatum	100	freshwater, attached to plants (‘*Buffalo’*) and crayfish (Decapoda: cambarid (*Cambarus*))	epizoic	North America
C. jaerae		marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus tigrinus*); Isopoda: janarid (*Jaera albifrons, marina*))	epizoic	Europe
C. limbatum		freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic	Europe
C. longipes		freshwater, attached to plants (watercress)	epiphytic	Europe
C. margaritatum		freshwater, attached to plants (watercress)	epiphytic	Europe
C. marginatum		freshwater	free-living	Europe
C. palnigeniae	20-39	freshwater, attached to fairy shrimp (Branchiopoda: branchipodid (*Branchipus*))	epizoic	Europe
C. prechti		marine	free-living	Eurasia
C. racemosa (syn. *Vorticella*)		marine	free-living	Europe
C. ramosissima (syn. *Vorticella*)		marine	free-living	Europe
C. spectabile (syn. *C. lachmanni*)		freshwater (stagnant)	free-living	Europe
C. steueri		freshwater	free-living	Europe
C. trichopterarum		freshwater	free-living	Europe
C. valentinae		freshwater	free-living	Eurasia
C. voigti		marine, attached to invertebrates (Isopoda: ligiid (*Ligia oceanica*))	epizoic	Europe
C. wassenum	229-280 x 55-71	freshwater, attached to prawns (Decapoda: atyid (*Caridina nilotica*))	epizoic	Africa
Genus: ***Cotensita*** (solitary, stalk with folded sheath below zooid, unbranched, straight discontinuous spasmoneme, upon contraction zooid bends to one side)				
C. commensalis [type species]	46 x 36	freshwater, attached to caddisfly larvae (Trichoptera: apataniid (*Baicalina bellicosa*))	epizoic	Russia
Genus ***Entziella*** (prominent stalk, branched supporting colonies, continuous straight myoneme permeating entire colony, contracts in zig-zag fashion, peristome without lip)				
E. aselli		freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic (carapace)	Europe
E. asellicola		freshwater, attached to invertebrates	epizoic	Europe

[type species] (syn. *Zoothamnium mirus*)		(Isopoda: asellid (*Asellus aquaticus*))	(carapace)	
E. orchestis	32-45 x 17-31	freshwater, attached to invertebrates (Amphipoda: talitrid (*Orchestia bottae, montagui*))	epizoic	Black Sea
Genus: ***Epicarchesium*** (stalk, branched, colonial, interrupted myoneme, contractile, reticulate silverline system)				
E. abrae (syn. *Carchesium*)	45-85 x 35-55	marine	free-living	China
E. corlissi	60-70 x 25-35	marine	free-living	China
E. granulatum (syn. *Carchesium*) [type species]	65-105 x 30-60	freshwater, attached to crayfish (Decapoda: cambarid (*Cambarus*))	epizoic	America
E. pectinatum (syn. *Carchesium*, *Zoothamnium, Z. limneticum*)	40-70 x 60	freshwater (potamoplankton)	free-living	Eurasia, Americas
E. sinense	45-60 x 30-40	freshwater	free-living	China
E. variable (syn. *Carchesium*)	100-120 x 50-65	marine	free-living	China
Genus: ***Grainis*** (flexible thick-walled shell (lorica) housing 1-2 vasiform zooids, attached by short thick stalks (basostyles) with short discontinuous myonemes, contraction independent)				
G. dizoon [type species]	60-73x21-28	freshwater, attached to invertebrates (Amphipoda: gammarid (*Poekilogammarus*)	epizoic (pleopods)	Russia
Genus ***Intranstylum*** (prominent stalks, branched, colonial, discontinuous straight myonemes short and not progressing beyond forks in stalk, contracts in zig-zag fashion)				
I. antarcticum	100 x 60	marine	free-living	Antarctica
I. barendrechti		estuarine, attached to invertebrates (Amphipoda: gammarid (*Gammarus tigrinus*))	epizoic	Europe
I. brachymyon		marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus locusta*))	epizoic	Europe
I. coniferum		marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus locusta*))	epizoic	Europe
I. contrahens (basionym *Epistylis steini* var. *contrahens*) [type species]		freshwater	free-living	Europe
I. duplicatum		estuarine, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus duebeni, locusta*)	epizoic	Europe
I. eismondi		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*))	epizoic	Europe
I. intermedium	80-92 x 42-56	marine, attached to invertebrates (Decapoda: penaeid (*Penaeus orientalis*)	epizoic	China
I. invaginatum (syn. *Rhabdostyla*)		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*); Branchiopoda: bosmid (*Bosmina*), chydorid (*Chydorus sphaericus*), daphniid (*Daphnia atkinsoni*, *longispina*, *magna*, *obtusa*, *pulex*, *Scapholeberis mucronata*); Copepoda: cyclopid (*Cyclops viridis*); Ostracoda: candonid (*Candona*), cypridid (unspecified)	epizoic	Europe
I. longum		marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus locusta*))	epizoic	Europe

I. macrostylum (syn. *Zoothamnium*)		freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic	Europe
I. ovulum	44-60 x 24-32	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus*))	epizoic	Eurasia
I. palaemoni		freshwater, attached to invertebrates (Decapoda: palaeminid (*Macrobrachium nipponense*)	epizoic	Asia
I. rhabdostyla (syn. *Epistylis*)	27-43 x 15-25	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*))	epizoic	Europe
I. simulans (syn. *Epistylis*)		freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*)	epizoic	Europe
I. steinii (syn. *Epistylis*)	40-55	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus fossarum*, *pulex*, *triacanthus*, *Carinogrammus roeselii*, *Chaetogrammus*, *Dikerogrammus*), niphargid (*Niphargus costozzae*)	epizoic	Europe
I. triformum	48-62 x 30-36	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*, *roeselii*)	epizoic	Europe
I. variabilis		marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus tigrinus*))	epizoic	Europe
Genus ***Parazoothamnium*** (solitary, prominent stalk, unbranched, straight continuous spasmoneme, contracts in 2 stage process, shortens in concertina-like fashion, then bends and loops, transverse silverline system)				
P. claparedei (syn. *Vorticella*)	85 x 60	marine, attached to filamentous algae	epiphytic	Russia
P. stenotica [type species]	70 x 50	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum, pulex*))	epizoic	Europe
Genus: ***Pelagovorticella*** (solitary, stalk, nonbranched, contractile, usually found as pelagic/planktonic zooids)				
P. mayeri [type species] (syn. *Vorticella*)	30-55 x 25-45	estuarine (euplanktonic)	free-living	Eurasia, America
P. natans (syn. *Vorticella, V. convallaria* var. *natans*)	70-100 x 50-70	estuarine, euplanktonic, and attached to invertebrates (Decapoda: cambarid (*Cambarellus patzcuarensis*)	free-living, epizoic	Eurasia, America
Genus ***Piesika*** (solitary, stalk, unbranched, straight continuous spasmoneme, contracts in 2 stage process, shortens longitudinally in concertina-like fashion, then loops and folds, reticulate silverline system)				
P. gammari [type species as *Parazoothamnium*]	70 x 50	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*))	epizoic	Europe
Genus: ***Planeticovorticella*** (unique life-stages comprising free trophonts swimming with peristomial cilia and sessile trophonts attaching to each other in small clusters (doublets, tetrads) with short noncontractile stalks or occasionally as individuals to substrates with scopula or short stalks)				
P. finleyi [type species]	38-59 x 21-30	estuarine (planktonic)	free-living	North America
P. paradoxa (syn. *Carchesium, Epistylis*)	48-85 x 32-45	marine, free-swimming and attached to clams (Bivalvia: venerid (*Meretrix meretrix*))	free-living, epizoic (gills)	China
Genus ***Pseudocarchesium*** (prominent stalks, branched, colonial, discontinuous straight myonemes variable in length, some progressing beyond forks in stalk, contracts in zig-zag fashion)				
P. amstelodamensis		estuarine, attached to invertebrates (Amphipoda: gammarid (*Gammarus tigrinus*))	epizoic	Europe
P. aselli (syn. *Carchesium*)	50-100	freshwater/marine, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus fossarum*, *pulex*); Decapoda:	epizoic	Eurasia, America

		penaeid (*Penaeus chinensis/orientalis*))		
P. asellicola (syn. *Intranstylum*)	35-55	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic	Eurasia
P. branchialis	48-82 x 27-44	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*)	epizoic (gills)	Europe
P. brevistyla (syn. *Vorticella*)	80	freshwater, attached to invertebrates (Branchiopoda: leptodorid (*Leptodora kindtii*))	epizoic	Europe
P. erlangensis (syn. *Carchesium*)		freshwater, attached to invertebrates (Copepoda: cyclopid (*Cyclops*, *Diacyclops bicuspidatus*, *Macrocyclops fuscus*); Amphipoda: gammarid (*Gammarus pulex*); Branchiopoda: chirocephalid (*Eubranchipus grubii*), daphniid (*Daphnia*, *Simocephalus*), ilyocryptid (*Ilyocryptus sordidus*))	epizoic	Europe
P. gammari		estuarine, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum, locusta, pulex*)	epizoic	Europe
P. inconjunctum (syn. *Carchesium*)		freshwater	free-living	Europe
P. limbatum	78-94 x 46-53	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic	Europe
P. ovatum	32-45 x 26-30	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum, pulex, Dikeogrammus vilosus*))	epizoic	Europe
P. polypina (syn. *Sertularia, Carchesium polypinum, C. corymbosum, Epistylis corymbosum, Vorticella spectabilis*) [type species]	bimorphic: microzooids 35-100 x 30-56; macrozooids 95-140 x 47-85	freshwater, attached to inanimate substrates, detritus, plants (algae, mosses) and invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Carinogammarus*, *Gammarus fossarum*, *pulex*); Branchiopoda: bosminid (*Bosmina*), daphniid (*Daphnia magna*); Decapoda: cambarid (*Cambarellus patzouarensis*, *zempoalensis*))	free-living, epiphytic, epizoic	cosmopolitan
P. rhyacophilae		aquatic	free-living	Eurasia
P. simulans	35-45 x 18-28	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic	Europe
P. steinii (syn. *Carchesium*)	33-53 x 22-30	estuarine, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum, locusta, pulex, roeselii, Dikerogrammus villosus*)	epizoic	cosmopolitan
P. umbilicatum (syn. *Carchesium*)		aquatic	free-living	Caspian Sea
Genus: ***Pseudovorticella*** (solitary, hyaline shell, prominent stalk, unbranched, often gregarious with stalks attached to form small pseudo-colonies, stalk with sinusoidal myoneme, contracts in spiral/helical fashion, reticulate silverline system, often with pellicular blisters)				
P. alani	70-90 x 50-65	brackish water	free-living	Asia
P. annulata (syn. *Vorticella*)	35-40 x 25-30	marine	free-living	Eurasia
P. anomala (syn. *Vorticella*)	30-40 x 35-40	marine	free-living	Eurasia
P. apogracilis	60-70 x 30-40	marine	free-living	Asia
P. banatica (syn. *Vorticella*)	60-80 x 50-70	marine	free-living	China
P. bidulphiae (syn. *Vorticella*)	30-40 x 20-40	marine, attached to inanimate substrates and invertebrates (Bacillariophyta (diatom): biddulphiaceae (*Biddulphia sinensis*)	free-living, epiphytic	Asia
P. bromelicola	60-75 x 30-50	freshwater, attached to tanks of bromeliads (*Guzmania scherzeriana*)	free-living, epiphytic	Costa Rica

P. chlamydophora (syn. *Vorticella, V. vestita*)	40-80 x 35-65	freshwater, attached to inanimate substrates, detritus, filamentous algae, plants (*Utricularia*) and invertebrates (Amphipoda: gammarid (*Gammarus roeselii*); Isopoda: asellid (*Asellus aquaticus*), and mollusc shells)	free-living, epiphytic, epizoic	Europe
P. chlorelligera (syn. *Vorticella*)	78-95 x 50	freshwater	free-living	Europe
P. clampi	70-110 x 50-75	marine	free-living	China
P. cylindrica (syn. *Vorticella*)	40-50 x 45-50	marine, free-living and attached to invertebrates (Hydrozoa: sertulariid (*Diphasia*)	free-living, epizoic	Eurasia
P. dalianensis	50-60 x 30-35	marine (coastal waters)	free-living	China
P. difficilis (incl. var. *magnistriata*) (syn. *Vorticella*)	50-140 x 35-70	marine/estuarine, free-living and attached to invertebrates (Amphipoda: gammarid (*Gammarus locusta*); Isopoda: idoteid (*Idotea chelipes*), sphaeromatid (*Lekanesphaera rugicauda*)	free-living, epizoic	Eurasia
P. elongata (syn. *Vorticella, V. conica, multangula, plicata p.p., subcylindrica*)	48-150 x 32-44	freshwater or marine, attached to inanimate substrates, algae, plants (*Hydrocharis*) and invertebrates (Copepoda: cyclopid (*Cyclops*)	free-living, epiphytic, epizoic	America, Eurasia
P. fasciculata (syn. *P. margaritata* f. *chlorigera* (*chlorelligera*))		freshwater, attached to filamentous bacteria (*Anabaena*, *Microcystis*, *Tabellaria*)	free-living, epiphytic?	Europe
P. faurefremieti	85-95 x 45-50	marine	free-living	China
P. foissneri	20-30 x 40-50	marine	free-living	China
P. haiboensis	65-75x25-35	marine		China
P. jaerae (syn. *Vorticella*)	40-55 x 25-45	marine/estuarine, attached to inanimate substrates and invertebrates (Isopoda: janirid (*Jaera albifrons, marina*)	free-living, epizoic	Eurasia
P. jankowskii	40-50 x 40-45	marine	free-living	Asia
P. jiangi	75-90 x 55-65	marine (prawn culture tank)	free-living	China
P. liangae	75-85x70-80	marine		China
P. lima (syn. *Vorticella*)	60-70 x 30	marine, attached to inanimate substrates and to invertebrates (Isopoda: sphaeromatid (*Sphaeroma serratum, Nassa bidentata*))	free-living, epizoic (legs)	Eurasia
P. longa	30-45 x 15-25	marine (mollusc-breeding pond)	saprozoic	China
P. margaritata (syn. *Vorticella*)	59-70 x 50	freshwater, attached to plants (*Utricularia, Ceratophyllum, Lemna, Potamol? (Potamogeton) crispus*)	epiphytic	Europe
P. marina (syn. *Vorticella, V. minuta*)	35-70 x 35-50	marine, attached to inanimate substrates, algae, and invertebrates (Decapoda: penaeid (*Penaeus chinensis/orientalis*)	free-living, epiphytic, epizoic	Eurasia
P. micata (syn. *Vorticella*)	60-70 x 40-50	marine	free-living	Eurasia
P. mollis (syn. *Vorticella*)	40-45 x 25	freshwater, attached to plants (*Lemna*)	free-living, epiphytic	Europe
P. monilata [type species] (syn. *Vorticella, V. lockwoodi*)	40-80 x 35-60	freshwater, attached to inanimate substrates, detritus, seston, filamentous cyanobacteria (*Anabaena flos-aquae*), plants (*Lemna*, *Utricularia*) and invertebrate animals (Copepoda: cyclopid (*Cyclops viridis*))	free-living, epiphytic, epizoic	Eurasia, Americas
P. mutans (syn. *Vorticella*)	65-95 x 18-25	freshwater	free-living	Europe
P. nebulifera (syn. *Vorticella, V. similis, cavolini*)	38-90 x 20-50	freshwater and marine, attached to inanimate substrates, detritus, plants (including planktonic algae) and	free-living, epiphytic, epizoic	Eurasia, America

		invertebrate animals (Isopoda: asellid (*Asellus aquaticus*), idotheid (*Idothea baltica*); Copepoda: cyclopid (*Cyclops strenuus*, viridis); Decapoda: carcinid (*Carcinus mediterraneus*), penaeid (*Penaeus chinensis*/*orientalis*), insect larvae and mollusc shells)		
P. papillata	35-80 x 22-50	freshwater		
P. paracratera	40-90 x 60-145	marine	free-living	China
P. parafornicata	20-30 x 20-30	marine	free-living	China
P. parakenti	50-60 x 40-45	marine	free-living	China
P. paramarina	50-60 x 30-40	marine	free-living	China
P. parannulata	45-55 x 30-35	marine	free-living	China
P. patellina (syn. *Vorticella*)	55-110 x 50-100	marine, attached to inanimate substrates and crabs (Decapoda: carcinid (*Carcinus mediterraneus*), polybiid (*Macropipus holsatus*))	free-living, epizoic (body, legs)	Europe
P. pattersoni	40-50 x 30-40	marine	free-living	China
P. pseudocampanula	32-50 x 20	freshwater	free-living	Europe
P. pseudokenti		marine	free-living	China
P. punctata (syn. *Vorticella, V. perlata, subconica*)	40-57 x 45-67	marine, attached to inanimate substrates and invertebrates (Decapoda: carcinid (*Carcinus maenas*), crangonid (*Crangon crangon*), palaemonid (*Palaemon adspersus*); Amphipoda: gammarid (*Gammarus locusta*); Isopoda: janirid (*Jaera albifrons*); Hydrozoa: sertulariid (*Diphasia abictina*); Echinodermata: asteriid (*Asterias rubens*))	free-living, epizoic	Europe
P. quadrata	65-80 x 55	freshwater, attached to inert substrates and invertebrates (Decapoda: cambarid (*Cambarellus patzcuarensis*)	epizoic	Europe, Mexico
P. sauwaldensis	35-45 x 20	freshwater	free-living	Europe
P. shii	45-55 x 20-30	marine	free-living	China
P. sinensis	50-60 x 35-45	marine	free-living	China
P. sphagni	40-50 x 30	freshwater (and *Sphagnum* bogs)	free-living	Europe
P. stilleri	85 x 80	freshwater, attached to plants (*Lemna*)	epiphytic	Europe
P. verrucosa (syn. *Vorticella, V. singularis*)	30-60 x 30-65	estuarine, attached to inert substrates and invertebrates (Decapoda: laomediid (*Laomedea*)	free-living, epizoic	Eurasia
P. zhengae	40-80 x 60-100	marine	free-living	China
P. zhejiangensis	50-70 x 45-70	brackish (coastal pond)	free-living	China
P. zooanthelligera (syn. *Vorticella*)	40-42 x 40	freshwater	free-living	Eurasia
Genus: ***Ruthiella*** (stalk, branched, forms small colonies with several zooids sharing asymmetric cup-like loricae, discontinuous straight myonemes short and not progressing beyond forks in stalk, contracts in zig-zag fashion)				
R. gammari [type species]	120 x 30-50	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex, Carinogammarus roeselii*)	epizoic (labium)	Europe
Genus: ***Spinivorticella*** (*Vorticella*-like, but zooids with distinct radial spines)				
S. echini (*echina*) (syn. *Vorticella, Spinivorticellides, Echinovorticella*)	30-45 x 20-40	freshwater (benthic)	free-living	Africa, North America
S. voeltzkowi (syn. *Vorticella, Pseudovorticella, Spinivorticellides*)		freshwater	free-living	Europe
Genus: ***Systylis*** (prominent stalk, branched, colonial, noncontractile without myoneme, branches of stalk terminate in rosettes of many (40-160) zooids, peristome with lip)				
S. hoffi [type species]	200-265	freshwater (vernal pools, some alkaline)	free-living	Europe, North America

Genus: ***Tucolesca*** (stalked, zooid with long prominent cilia, without peristomial lip, when zooid contracts the peristome remains open with cilia extended while stalk folds in loose coils)				
T. mirabilis [type species as *Leptodiscus*]	27-30 x 19	hypersaline lake	free-living	Romania
Genus ***Vorticella*** (prominent stalk, unbranched bearing single zooids, often gregarious with stalks attached to form small pseudo-colonies, stalk with sinusoidal myoneme, contracts in spiral/helical fashion, oral ciliature making 1-1½ turns, one epistomial membrane, transverse silverline system)				
V. convallaria-complex				
V. convallaria (incl. var. *compacta, similis,* f. *citrina*) (syn. *V. brevipes, chinensis, citrina, cothurnata, cyathina, cyclopis, limosa*) [type species as *Hydra*]	30-120 x 22-70	freshwater/marine, attached to inanimate substrates, detritus, algae, moss, plants (*Lemna minor*) and invertebrate animals (Amphipoda: gammarid (*Gammarus pulex*, *tigrinus*), corophiid (*Corophium curvispinum*); Branchiopoda: daphniid (*Scapholeberis mucronata*, *Simocephalus vetulus*), sidid (*Sida crystallina*), triopsid (*Lepidurus apus*); Copepoda: cyclopid (*Cyclops strenuus*, *viridis*, *Macrocyclops albidus*, *fuscus*), lernaeid (*Lernaea cyprinacea*); Isopoda: asellid (*Asellus aquaticus*); Ostracoda: cyclocyprinid (*Cyclocypris ovum*); Decapoda: cambarid (*Cambarellus zempoalensis*), carcinid (*Carcinus mediterraneus*), potamid (*Potamon*); insect larvae and mollusc shells)	free-living, epiphytic, epizoic	cosmopolitan
V. microstoma-complex (comprising *V. microstoma, aequilata, alpestris*)				
V. microstoma (incl. var. *defluviatilis*, *typica*, f. *elongata*, *hians*, *turgescens*, *typica*) (syn. *V. chydoricola, cupifera, cyclopicola, fluvialis, longimacronucleata, magna, mammillata, partita, pileolata, submicrostoma*)	30-120 x 22-50	freshwater (esp. stagnant and activated sludge), attached to inanimate substrates, detritus, cyanobacterial colonies (*Microcystis*), plants (*Utricularia*) and invertebrate animals (Amphipoda: gammarid (*Gammarus tigrinus, roeselii*); Branchiopoda: chydorid (*Rhynchotalona rostrata*, *Disparalona rostrata*), daphniid (*Scapholeberis kingi*), eurycercid (*Eurycercus lamellatus*), lernaeid (*Lernaea cyprinacea*), macrothricid (*Macrothrix laticornis*); Copepoda: cyclopid (*Cyclops strenuus*, *viridis*, *Megacyclops viridis*); Isopoda: asellid (*Asellus aquaticus*), idotheid (*Idothea baltica*); Decapoda: cambarid (*Camberellus patzcuarensis*), carcinid (*Carcinus mediterraneus*), penaeid (*Penaeus chinensis*/*orientalis*))	free-living, epiphytic, epizoic	cosmopolitan
V. aequilata	40-50 x 20	freshwater/marine, attached to inanimate substrates and invertebrates (Amphipoda: gammarid (*Gammarus tigrinus*))	free-living, epizoic	Europe
V. alpestris	35-45 x 20	freshwater	free-living	Europe
V. octava-complex (comprising *V. octava, hamata, limnetis, striata*)				
V. octava	23-60	freshwater, attached to inanimate substrates, detritus, algae, plants (*Utricularia*) and invertebrate animals (Copepoda: cyclopid (*Cyclops*); Amphipoda: gammarid (*Gammarus tigrinus*); Branchiopoda: chydorid (*Chydorus sphaericus*), daphniid (*Daphnia magna*, *longispina*, *obtusa*, *Simocephalus vetulus*, *serratulus*, *Scapholeberis mucronata*, *kingi*, *Ceriodaphnia quadrangula*), eurycercid	free-living, epiphytic, epizoic	Eurasia, America

		(*Eurycercus lamellatus*), macrothricid (*Macrothrix laticornis*), polyphemid (*Polyphemus pediculus*), sidid (*Diaphanosoma brachyurum*); Decapoda: penaeid (*Penaeus chinensis*/*orientalis*))		
V. hamata (syn. *Vorticella delicatulata*)	40 x 15	freshwater or marine	free-living	Europe, North America
V. limnetis	50 x 35	freshwater	free-living	Europe
V. striata (syn. *V. conochili, latestriata, lemnae, minima, oceanica, pusilla, pyrum, pyumcollaris, rhabdostyloides, striatula, suboctava*)	20-60 x 15-40	freshwater/marine (rarely terrestrial), attached to inanimate substrates, detritus, plants (*Lemna, Potamogeton crispus*), diatoms (*Stephanodiscus*), algae and invertebrate animals (Amphipoda: gammarid (*Gammarus fasciatus, tigrinus*); Branchiopoda: chydorid (*Chydorus sphaericus*), daphniid (*Ceriodaphnia quadrangula*, *Daphnia longispina*, *magna*, *obtusa*, *pulex*, *Scapholeberis kingi, mucronata, Simocephalus serratulus, vetulus*), eurycercid (*Eurycercus lamellatus*), macrothricid (*Macrothrix laticornis*), polyphemid (*Polyphemus pediculus*), sidid (*Diaphanosoma brachyurum*); Isopoda: asellid (*Asellus aquaticus*), idoteid (*Idotea chelipes*), janirid (*Jaera albifrons*), sphaeromatid (*Lekanesphaera rugicauda, Sphaeroma serratum*); Mysida: mysid (*Neomysis integer*); Gastropoda: planorbid (*Planorbis spirorbis*); Hydrozoa: sertulariid (*Sertularia pumila*); Rotifera: conochilid (*Conochilus unicornis*); Decapoda: cambarid (*Camberellus patzcuarensis*), crangonid (*Crangon crangon*), penaeid (*Penaeus chinensis*/*orientalis*); Ostracoda: cytherdeid (*Cyprideis litoralis*) and insect larvae)	free-living, epiphytic, epizoic	Eurasia, America
Other *Vorticella* species				
V. aerotenci	90-140 x 32-60	freshwater (activated sludge)	free-living	Russia
V. alba (syn. *Haplocaulus*)	60-80 x 25	freshwater, attached to inanimate substrates and invertebrates (Amphipoda: gammarid (*Gammarus pulex*); Copepoda: cyclopid (*Cyclops viridis, Macrocyclops albidus*)	free-living, epizoic	Europe
V. annulata (syn. *V. brevistyla* var. *annulata*)	55 x 35	estuarine	free-living	Eurasia
V. apunctata		freshwater	free-living	Europe
V. ascoideum		freshwater	free-living	Europe
V. biddulphae		marine	free-living	Europe
V. bipartita		freshwater	free-living	Europe
V. bivacuolata	95-120 x 55-68	freshwater (and activated sludge)	free-living	Asia
V. bosminae	25-40 x 20-30	freshwater/brackish, attached to inanimate substrates and invertebrates (Branchiopoda: bosminid (*Bosmina longirostris*); Copepoda: cyclopid (*Mesocyclops leuckarti, viridis, Thermocyclopsis hyalinus*)	free-living, epizoic	Europe
V. brachionicola		freshwater, attached to invertebrates (Rotifera: brachionid (*Brachionus*))	epizoic	Europe
V. brevistyla		marine	free-living	North America

V. cacabuoides		freshwater	free-living	Europe
V. calciformis	90 x 65	marine	free-living	Europe
V. campanula (syn. *V. aperta, cylindrica p.p., dilatata, lunaris, macrostoma, margaritifera*)	50-160 x 35-100	freshwater/marine, attached to inanimate substrates, detritus, plants (*Ceratophyllum, Lemna minor, Myriophyllum*) and invertebrate animals (Amphipoda: gammarid (*Gammarus pulex, locusta*, *Carinogrammus*); Branchiopoda: daphniid (*Ceriodaphnia reticulata*, *Daphnia magna*, *obtusa*, *pulex*, *rosea*, *Scapholeberis mucronata*, *Simocephalus vetulus*), polyphemid (*Polyphemus pediculus*), sidid (*Sida crystallina*, *Diaphanosoma*); Copepoda: cyclopid (*Cyclops viridis*, *Eucyclops serratulus*); Decapoda: cambarid (*Cambarellus patzcuarensis*), carcinid (*Carcinus maenas, mediterraneus*), penaeid (*Penaeus chinensis*/*orientalis*); Isopoda: asellid (*Asellus aquaticus*), idotheid (*Idothea baltica*), sphaeromatid (*Sphaeroma terebrans*); mollusc shells and insect larvae)	free-living, epiphytic, epizoic	cosmopolitan
V. campanulata	45 x 50	freshwater or marine	free-living	Europe
V. chamaeleontina		freshwater	free-living	Europe
V. chiangi	35-50x35-50	marine (aquaculture ponds)		China
V. chlorostigma (syn. *V. chlorellata, Carchesium*)	75-110 x 58-85 (44-64 x 25-48)	freshwater, planktonic and attached to colonial bacteria (*Gloeotricha*) and plants (bladderwort *Utricularia*)	free-living, epiphytic	Europe, Americas
V. cinctula		freshwater	free-living	Europe
V. claparedi		marine, attached to crabs (Decapoda: carcinid (*Carcinus mediterraneus*))	epizoic (carapace)	Black Sea
V. communis (syn. *V. subsphaerica*)	30-36 x 25	freshwater or marine, attached to invertebrates (Decapoda: cambarid (*Cambarellus patzcuarensis*); Hydrozoa: sertulariid (*Sertularia pumila*))	epizoic	Europe, North America
V. confluens		freshwater	free-living	Europe
V. corrugis	12	freshwater, attached to algae	epiphytic	Europe
V. cratera (syn. *V. dudekemi*)	120-130 x 100	freshwater or marine	free-living	Eurasia
V. craterella		freshwater	free-living	Europe
V. cupularis		freshwater	free-living	Europe
V. cupulifera		freshwater	free-living	Europe
V. curvifrons	20	freshwater, attached to algae	epiphytic	Europe
V. curvipes		freshwater, attached to inanimate substrates and plants (watercress)	free-living, epiphytic	Europe
V. cyatiformis		freshwater	free-living	Europe
V. cyclopis	55	marine, attached to invertebrates (Copepoda: cyclopid (unspecified))	epizoic	Europe
V. dejecta		freshwater	free-living	Europe
V. dimorpha	32-35 x 15-20	freshwater, attached to inanimate substrates and invertebrates (Rotifera: conochilid (*Conochilus unicornis*))	epizoic	Europe
V. dubia	40	freshwater	free-living	Europe
V. exilis	48-60 x 15-20	freshwater, attached to snails (Gastropoda: lymnaeid (*Lymnaea stagnalis*)) and damselfly larvae (Zygoptera: lestid (*Lestes virens*))	free-living, epizoic	Europe
V. extinctoria		freshwater	free-living	Europe
V. extuberrans		freshwater	free-living	Europe
V. filopes		freshwater	free-living	Europe
V. flexipes		freshwater	free-living	Europe

V. flexuosa	126-144 x 70	freshwater, attached to liverworts (*Ricciocarpos natans*) and invertebrates (Isopoda: asellid (*Asellus aquaticus*)	epiphytic, epizoic	Europe
V. fluviatilis		freshwater	free-living	Europe
V. fornicata	24-42	marine, attached to algae (*Laminaria*)	epiphytic	Europe, North America
V. fragilariae		freshwater, attached to diatoms	epiphytic	Europe
V. fromenteli (syn. *V. cucullus*)	70-90 x 30-50	freshwater, attached to inanimate substrates, detritus, and invertebrates (Decapoda: cambarid (*Cambarellus patzcuarensis*))	free-living	Eurasia
V. geispicae	68-122 x 24-48	freshwater (activated sludge)	free-living	Russia
V. geminata		freshwater	free-living	Europe
V. globosa (syn. *V. urnula*)	25-65 x 20-45	freshwater, attached to inanimate substrates and invertebrates (Copepoda: cyclopid (*Macrocyclops fuscus*); Decapoda: atyid (*Caridina lanceolata*))	free-living, epizoic	Eurasia
V. globularia (syn. *V. salina, sphaerica*)	160 x 150	freshwater, attached to inanimate substrates and invertebrates (Copepoda: cyclopid (*Cyclops*))	free-living, epizoic	Europe
V. gracilis	50-85 x 25-45	freshwater, attached to inanimate substrates and plants (tanks of bromeliads)	free-living, saprobic	Europe, Costa Rica
V. granulata	50-60 x 30-35	marine	free-living	Europe
V. gyrans		freshwater	free-living	Europe
V. halophila	40-50 x 30-35	freshwater, attached to detritus	free-living	Europe
V. hirsuta		freshwater	free-living	Europe
V. idiothea		marine, attached to invertebrate (Isopoda: idoteid (*Idothea baltica*))	epizoic (body)	Black Sea
V. incisa	65-80 x 50-55	freshwater, attached to plants (*Myriophyllum*)	epiphytic	Europe
V. inclinata		freshwater, attached to inanimate substrates and plants (*Lemna*)	free-living, epiphytic	Europe
V. inconstans	20-26	freshwater, attached to invertebrates (Branchiopoda: macrothricid (*Macrothrix hirsuticornis*))	epizoic	Europe
V. incurva		freshwater	free-living	Europe
V. inflata		freshwater	free-living	Europe
V. inflexa		freshwater	free-living	Europe
V. invaginata		freshwater	free-living	Europe
V. kenti (syn. *V. floridensis, spectabilis*)	85-170 x 60	freshwater, attached to plants (*Lemna*, *Cypress* swamps)	epiphytic	North America
V. latifunda	60 x 30	freshwater, attached to crayfish (Decapoda: cambarid (*Cambarellus patzcuarensis*) and damselfly larvae (Zygoptera: lestid (*Lestes sponsa, virens*)))	epizoic	Mexico
V. lichenicola (syn. *V. inconstantans*)	50-65 x 25-30	freshwater, attached to inanimate substrates, lichen, mosses and invertebrates (Branchiopoda: daphniid (*Daphnia pulex*), macrothricid (*Macrothrix hirsuticornis*))	free-living, epiphytic, epizoic	Greenland
V. longifilum (syn. *V. macrocaulis, simplex*)	45-90 x 30-35	freshwater, attached to plants (*Myriophyllym, Lemna*) and invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Dikerogrammus haemobaphes*, *Gammarus tigrinus*); Ostracoda (unspecified))	epiphytic, epizoic	Europe
V. longiseta	82 x 50	marine	free-living	Europe
V. longitricha	30 x 25	marine, attached to invertebrates (Amphipoda: gammarid (unspecified))	epizoic	Europe

V. lutea	140 x 75-80	freshwater, attached to plants (*Myriophyllum, Lemna*)	epiphytic	Europe
V. lymnaearum	26-30 x 25-35	freshwater, attached to snails (Gastropoda: lymnaeid (*Lymnaea natalensis*))	epizoic	Africa
V. macrophya	38-50 x 15-20	freshwater, attached to plants (*Lemna*)	epiphytic	North America
V. macrostyla	50 x 30	freshwater	free-living	Egypt
V. mamillata		freshwater marshes	free-living	Europe
margaritata				
V. marginata	70-90 x 32-45	freshwater, attached to inanimate substrates, detritus, filamentous algae (*Cladophora, Enteromorpha intestinalis*), plants and invertebrates (Isopoda sowbug)	free-living, epiphytic, epizoic	Eurasia
V. micra		marine, attached to crabs (Decapoda: carcinid (*Carcinus maenas*))	epizoic (body)	Black Sea
V. microscopica	12-15 x 8	freshwater	free-living	Europe
V. molesta		freshwater	free-living	Europe
V. muralis	90-125 x 35-45	freshwater and *Sphagnum* bogs	epiphytic	Europe
V. nebulifera		freshwater, attached to plants (*Lemna*)	epiphytic	Europe
V. nigra	15-16	freshwater	free-living	Europe
V. nutans (syn. *V. gemella, procumbens, Epistylis gemella*)	60-85 x 25-30	freshwater or marine, attached to moss, plants (*Stratiotes*) and snails (Gastropoda: planorbid (*Planorbis*))	epiphytic, epizoic	Eurasia
V. obconica (syn. *V. conica*)	55-100 x 45	estuarine, attached to invertebrates (Copepoda: cyclopid (*Cyclops*); Polychaeta: serpulid (*Spirorbis*)	epizoic	North America, Europe
V. oblonga		marine	free-living	Europe
V. ondulata		freshwater	free-living	Europe
V. opercullariformis	45-55 x 30-50	freshwater	free-living	Europe
V. operculata		freshwater	free-living	India
V. ophiocomae		marine, attached to brittle star (Echinodermata: ophiocomid (*Ophiocoma neglecta*))	epizoic	Europe
V. ovum (syn. *V. incerta, Carchesium incerta*)	90-105 x 50-60	freshwater or marine, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus*))	epizoic	Europe
V. parachiangi	50-65 x 55-70	marine (mangrove)	free-living	China
V. paralima	35-50 x 20-30	brackish water (mangrove)	free-living	Europe
V. parapulchella	25-30 x 20-25	marine, attached to inanimate substrates	free-living	China
V. parasita (syn. *V. ephemerae*)	40 x 10	freshwater, attached to mayfly larvae (Ephemeroptera: ephemerid (unspecified))	epizoic	North America
V. parvula		freshwater	free-living	Europe
V. peterhoffi	62-80 x 35-46	freshwater (activated sludge)	free-living	Russia
V. picta (syn. *Carchesium*, *V. appunctata*)	35-90 x 20-50	freshwater, attached to inanimate substrates, detritus, algae, plants and invertebrates (Isopoda: asellid (*Asellus aquaticus*); Rotifera: collothecid (*Stephanoceros*))	free-living, epiphytic, epizoic	Eurasia, Americas
V. plicatula		freshwater	free-living	Europe
V. plicosa	12	freshwater, attached to plants (*Nenuphar*)	epiphytic	Europe
V. poznaniensis	68-85 x 62-68	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Copepoda: cyclopid (*Cyclops*))	epizoic	Europe
V. pulchella	46 x 30	marine, attached to invertebrates (Copepoda: cyclopid (*Cyclops*); Decapoda: penaeid (*Penaeus chinensis/orientalis*))	epizoic	Asia
V. pulchra	40-50 x 20	estuarine, attached to invertebrates (Decapoda: cambarid (*Cambarellus*	epizoic	Mexico

		zempoalensis))		
V. pyriforme (syn. *V. intermissa*)	45-70 x 30-40	freshwater or marine	free-living	Europe
V. pyxidata		freshwater	free-living	Europe
V. quadrangularis (syn. *V. sinuata, zealandica*)	125-200 x 60	freshwater, attached to plants (*Myriophyllum*)	epiphytic	Europe, New Zealand
V. regularis				
V. repanda		freshwater	free-living	Europe
V. rhabdophora	80 x 30	fresh and brackish water	free-living	Europe
V. rotunda	49 x 30	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Branchiopoda: daphniid (*Daphnia magna*); Amphipoda: gammarid (*Gammarus tigrinus*) and damselfly larvae (Zygoptera: lestid (*Lestes*))	epizoic	Europe
V. rotundata		freshwater	free-living	Europe
V. rubristigma	30-35 x 20	freshwater	free-living	North America
V. rugata		freshwater, attached to inanimate substrates and plants (*Rannunculus aquatilis*)	free-living, epiphytic	Europe
V. sagittaricola	13	freshwater, attached to plants (*Sagittaria sagittifolia*)	epiphytic	Europe
V. scapiformis	40-50 x 40-55	freshwater (sewage outlet)	free-living	China
V. sepulcreti	45-55 x 25-30	freshwater	free-living	Eurasia
V. sinica	20-30 x 10-20	marine	free-living	China
V. sphaeroidalis	20-30 x 15-25	freshwater (ditch)	free-living	China
V. sphaeroides		freshwater	free-living	Europe
V. sphaeroma		marine, attached to invertebrates (Isopoda: sphaeromatid (*Sphaeroma serratum*))	epizoic (body)	Black Sea
V. spuripicta		freshwater (sewage outlet)	free-living	China
V. subcylindrica	15	freshwater	free-living	Europe
V. subprocumbens (syn. *V. nana, solitaria, Epistylis solitaria*)	27-50 x 20-30	freshwater or marine, attached to plants (*Lemna trisulca*) and invertebrates (Branchiopoda (unspecified cladocerans); Gastropoda: planorbid (*Planorbis*))	epiphytic, epizoic	Europe
V. subsinuata (syn. *V. longipharyngea*)	40-50 x 35-40	freshwater	free-living	Europe
V. sucreta		freshwater	free-living	Europe
V. supina	12	freshwater, attached to plants (*Potamol?* (*Potamogeton*) *crispus*)	epiphytic	Europe
V. sureta	11	freshwater	free-living	Europe
V. szczepanowskii (syn. *V. plicata p.p.)*	43 x 25	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic	Europe
V. telescopoides (syn *V. telescopica, telescopiformis*)	55-70 x 15-25	freshwater or marine	free-living	Europe
V. tenuis		freshwater, attached to inanimate substrates and plants (*Lemna*, *Myrophyllum*)	free-living, epiphytic	Europe
V. tornatilis		freshwater	free-living	Europe
V. tripartita		freshwater	free-living	Europe
V. turbinata		freshwater	free-living	Europe
V. turgicula	60-70 x 52-64	freshwater, attached to mosses	epiphytic	Asia
V. umbilicola	8-10	freshwater, attached to invertebrates (Gastropoda: planorbid (*Planorbis*))	epizoic	Europe
V. vaginata		freshwater swamp	free-lining	Europe
V. ventosa	10-14	freshwater, attached to plants (*Callitriche*)	epiphytic	Europe
V. venusta	35-44 x 23-30	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic	Europe

V. vernalis	40-56 x 20-44	freshwater, attached to inanimate substrates, diatoms (*Fragilaria*) and rotifers (Rotifera: collothecid (*Stephanoceros*)	free-living, epiphytic, epizoic	Europe, North America
Genus ***Vorticellides*** (prominent stalk, unbranched bearing single zooids, often gregarious with stalks attached to form small colonies, with sinusoidal myoneme, contracts in spiral/helical fashion, oral ciliature making 1-1½ turns, small barrel-shaped bodies with 2 epistomial membranes (ciliated only in swarmers), transverse silverline system)				
V. aquadulcis-complex (comprising *Vorticella aquadulcis, astyliformis, costata, platysoma*)				
V. aquadulcis (syn. *Vorticella, V. striata p.p.*)	15-55 x 10-35	freshwater (and activated sludge), attached to inanimate substrates, detritus, filamentous algae (*Enteromorpha, Cladophora*), diatoms (*Asterionella formosa, Fragilaria crotonensis*), mosses, plants (*Lemna*, bromeliads) and invertebrates (Branchiopoda: daphniid (*Daphnia galeata, longispina*), leptodorid (*Leptodora kindtii*); Ephemeroptera: baetid (*Baetis* mayfly larvae), Rotifera (unspecified))	free-living, epiphytic, epizoic	cosmopolitan
V. astyliformis	28-50 x 12-45	freshwater and terrestrial (alpine soil)	free-living	Europe
V. costata (syn. *V. octava* f. *costata*)	20-28 x 15-20	freshwater	free-living	Europe
V. platysoma	22-25 x 15	freshwater, attached to inanimate substrates, algae and invertebrates (Branchiopoda: daphniid (*Scapholeberis mucronata*))	free-living, epizoic	Europe
V. infusionum-complex (comprising *Vorticella infusionum, hians, utriculus*)				
V. infusionum (syn. *Vorticella, V. abbreviata, microstoma p.p., striata p.p.*)	30-90 x 18-40	freshwater/marine (rarely terrestrial), attached to inanimate substrates, detritus, plants (*Lemna*) and invertebrates (Copepoda: cyclopid (*Cyclops viridis*); Branchiopoda: daphniid (*Daphnia pulex*) and unspecified cladocerans; Amphipoda: gammarid (*Gammarus roeselii*); Isopoda: asellid (*Asellus aquaticus*); Diptera: culicid (*Culex pipiens* larvae); Decapoda: cambarid (*Cambarellus patzcuarensis*))	free-living, epiphytic, epizoic	cosmopolitan
V. hians	60	freshwater (microaerophilic)	free-living	Europe
V. utriculus (syn. *Vorticella striata* f. *utriculus*)	35-60 x 18-30	marine, attached to invertebrates (Decapoda: penaeid (*Penaeus chinensis/orientalis*))	epizoic	China
Family: **Zoothamniidae**				
Genus: ***Craspedomyoschiston*** (prominent stalk, colonial, continuous straight myoneme does not continue down main trunk of colony, only upper colony contractile in zig-zag fashion, stalk with flattened lorica-like extensions)				
C. duplicatum		marine, attached to opossum shrimp (Mysida: mysid (*Neomysis integer*))	epizoic	Europe
C. sphaeromae (syn. *Myoschiston*) [type species]		estuarine, attached to invertebrates (Isopoda: sphaeromatid (*Lekanesphaera* (*Sphaeroma*) *rugicauda*))	epizoic	Europe
Genus: ***Haplocaulus*** (solitary zooids, prominent stalks, unbranched, contractile, straight myonemes, contract in zig-zag fashion, peristomial disc, striated pellicles, attached to plant, animal and inanimate substrates)				
H. amphibiarum	134-155 x 52-65	freshwater, attached to amphibians (Anura: ranid (European common frog))	epizoic	Russia
H. amphiurae (syn. *Vorticella*)	25-40	marine, attached to brittle star (Echinodermata: amphiurid (*Amphiura squamata*))	epizoic	Eurasia
H. brehmi	80 x 70	freshwater, attached to caddisfly larvae (Trichoptera: glossosomatid (*Agapetus*)	epizoic (gills)	Europe?
H. carinogammari (syn. *Vorticella*)	45-75 x 38-46	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus fossarum*, *roeselii*, *Carcinogammarus,*	epizoic	Europe

		Rivulogammarus)		
H. ceriodaphniae		freshwater, attached to invertebrates (Branchiopoda: daphniid (*Daphnia pulex*, *Ceriodaphnia reticulata*, *rotunda*); Copepoda: cyclopid (*Cyclops*)	epizoic	Russia
H. chydoridae		freshwater, attached to invertebrates (Branchiopoda: chydorid (*Chydorus sphaericus*)	epizoic	Russia
H. claudicans (syn. *Vorticella*)	40-55 x 30	freshwater, attached to mosses	epiphytic	Europe?
H. conosomus (syn. *Vorticella conosoma, Pyxidium, Propyxidium*)	75 x 30	freshwater, attached inert substrates and invertebrates (Rotifera: conochilid (*Conochilus unicornis, volvox*))	free-living, epizoic	North America
H. contrahens		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum*, *pulex, roeselii*)	epizoic	Europe
H. crassicaulis (syn. *Vorticella, Paravorticella*)	45-90 x 16-25	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*)	epizoic	Eurasia
H. dipneumon (syn. *Vorticella*)	50-56 x 25	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*)	epizoic	Europe
H. distinguendus (syn. *H. hengsti*)	60-79 x 34-49	freshwater, attached to inanimate substrates, river weed (*Enteromorpha intestinalis*) and invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus pulex, tigrinus*)	free-living, epiphytic, epizoic	Europe
H. eforianus (syn. *Vorticella*)	55-60 x 20	marine	free-living	Europe?
H. elegans (syn. *Intranstylum, Vorticella*)	42-84 x 35-40	freshwater or marine, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Copepoda: cyclopid (*Cyclops*); Amphipoda: gammarid (*Gammarus tigrinus*); Polychaeta: serpulid (*Spirorbis*)	epizoic	Eurasia
H. epizoicus (syn. *Vorticella*)	25-46 x 18-37	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum*); Copepoda: cyclopid (*Cyclops, Megacyclops viridis*); Branchiopoda: bosminid (*Bosmina longirostris*), daphniid (*Scapholeberis*)	epizoic	Europe
H. extensa (syn. *Vorticella*)	50-100 x 15-27	freshwater, attached to inert substrates, and river weed (*Enteromorpha intestinalis*)	free-living, epiphytic	Europe
H. fluviatilis	28-48 x 14-30	freshwater, attached to invertebrates (Ostracoda: cypridid (*Heterocypris*)	epizoic	Europe?
H. furcellariae [type species]	98x40	marine, attached to seaweed (*Furcellaria*)	epiphytic	Europe?
H. fusca (syn. *Vorticella*)	88-110 x 55-75	marine, attached to inanimate substrates and algae (*Enteromorpha* sea lettuce)	free-living, epiphytic	Eurasia
H. fusiformis (syn. *Vorticella*)	140-162 x 60	freshwater, attached to amphibians (Anura (unspecified tadpoles))	epizoic (tails)	Europe?
H. kahlii (syn. *Vorticella*)	32-44 x 24-36	freshwater, attached to invertebrates (Branchiopoda: daphniid (*Daphnia galeata, longispina, hyalina*), leptodorid (*Leptodora kindtii*, *hyalina*), sidid (*Sida crystallina*; Amphipoda: gammarid (*Gammarus tigrinus*); Copepoda: cyclopid (*Macrocyclops albidus, Megacyclops viridis*)	epizoic	Europe
H. leanderi	30-32 x 22-24	marine, attached to invertebrates (Decapoda: palaemonid (*Leander*))	epizoic	Europe

H. lentus		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex*))	epizoic	Russia
H. longinuclei	43-61 x 41-49	freshwater, attached to amphibians (Anura: ranid (European common frog, tadpoles))	epizoic (tails)	Europe
H. macronucleatus (syn. *Vorticella*)	92 x 35	freshwater, attached to mayfly larvae (Ephemeroptera: ephemerid (*Ephemera vulgata*))	epizoic	Europe
H. pelagicus (syn. *Vorticella, Peudovorticella*)	30-40 x 50	marine	free-living	Europe
H. procerus (syn. *Vorticella*)	78-103 x 37-41	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus roeselii*), and amphibians (Anura (unspecified tadpoles))	epizoic	Europe
H. ranae (syn. *Intranstylum, Monintranstylum*)	65-90 x 35-50	freshwater, attached to amphibians (Anura (unspecified tadpoles))	tail fins	Europe
H. rhabdostyloides (syn. *Vorticella*)		freshwater, attached to invertebrates (Copepoda: cyclopid (*Acanthocyclops*))	epizoic	Russia
H. rotundus (syn. *Monintranstylum*)		freshwater, attached to invertebrates (Branchiopoda: daphniid (*Daphnia longispina*)0	epizoic	Europe
H. sertulariarum (syn. *Spastostyla, Vorticella*)	60-109 x 34-48	marine and freshwater, attached to invertebrates (Echinozoa (unspecified sea urchins), Cnidaria (unspecified polyps); Decapoda: cambarid (*Cambarellus zempoalensis*); Copepoda: cyclopid (*Eucyclops serrulatus*); Hydrozoa: aglaopheniid (*Aglaophenia*)) and amphibians (Anura: ranid (European common frog, tadpoles))	epizoic	Mexico, Russia
H. sommeri (syn. *Monintranstylum*)		freshwater, attached to invertebrates (Copepoda: cyclopid (*Eucyclops serrulatus*); Ostracoda: cypridid (*Cypris*))	epizoic	Europe
H. stammeri (syn. *Monintranstylum*)		freshwater, attached to invertebrates (Branchiopoda: daphniid (*Daphnia pulex*, *Ceriodaphnia quadrangulata*), polyphemid (*Polyphemus pediculus*); Copepoda: cyclopid (*Cyclops, Eucyclops serratulus*); Ostracoda: cypridid (*Cypris*))	epizoic	Europe
H. stilleri	60 x 27	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum, pulex*))	epizoic	Europe
H. terrenus	40-60 x 20-26	terrestrial (alpine soils)	free-living	Europe
H. walteri	55-75 x 40-60	freshwater (activated sludge)	free-living	Europe?
Genus ***Mesothamnium*** (zooids without dimorphism (form microzooids only), symbionts of crustaceans)				
M. hiketes (syn. *Zoothamnium*) [type species as *Zoothamnium*]	60-85 x 30-40	estuarine, attached to inanimate substrates and invertebrates (Amphipoda: gammarid (*Gammarus duebeni, locusta, oceanicus, salinus, zaddachi*); Isopoda: janirid (*Jaera albifrons*))	free-living, epizoic	Baltic Sea, China Sea
Genus: ***Myoschiston*** (prominent stalk, colonial, continuous straight myoneme does not continue down main trunk of colony, only upper colony contractile in zig-zag fashion, stalk without lorica-like extension)				
M. balanorum (syn. *Epistylis*)	100	marine, attached to barnacles (Cirripedia: balanid (*Amphibalanus improvisus, Balanus balanoides*))	epizoic	Atlantic, Baltic Sea
M. carcini (syn. *Epistylis*)		marine, attached to crabs (Decapoda: carcinid (*Carcinus maenas*))	epizoic	Europe, Baltic Sea
M. centropagidarum		marine, attached to invertebrates (Copepoda: acartiid (*Acartia tonsa*), centropagid (*Centropages hamatus*),	epizoic	Baltic Sea

		temorid (*Eurytemora affinis*))		
M. cypridicola (syn. *Epistylis*)	50-60 x 20-25	marine and brackish water, attached to invertebrates (Ostracoda: cyprid (*Cyprideis littoralis*); Gastropoda: hydrobiid (*Hydrobia ulvae*, *jenkinsi*))	epizoic	Europe, Baltic Sea
M. duplicatum [type species]	42-79 x 34-52	marine, attached to invertebrates (Decapoda: carcinid (*Carcinus maenas*), varunid (*Hemigrapsus*); Isopoda: odoteid (*Idotea balthica*, *tricuspidata*, *chelipes*, *viridis*))	epizoic	Baltic Sea, Black Sea, Korea
M. neomysidis		marine, attached to invertebrates (Mysida: mysid (*Neomysis integer*, *vulgaris*))	epizoic	Baltic Sea
M. simile	30-67 x 17-33	marine, attached to invertebrates (Decapoda: penaeid (*Penaeus orientalis*))	epizoic	Yellow Sea
Genus ***Pseudohaplocaulus*** (solitary zooids, prominent stalks, unbranched, straight myonemes, contracts in zig-zag fashion, reticulate silverline system)				
P. anabaenae (syn. *Vorticella, Haplocaulus*)	40-45 x 40	freshwater, attached to cyanobacterium (*Anabaena*)	epiphytic	North America
P. infravacuolatus	47-67 x 32-42	free-living (epiplanktonic), attached to cyanobacterium (*Anabaena*)		Europe
P. nicoleae [type species as *Haplocaulus*]	35-40 x 25	marine, attached to worm (Polychaeta: terebellid (*Nicolea zostericola*))	epizoic	Europe?
Genus ***Zoothamnioides*** (prominent stalk, branched, colonial, continuous myonemes, zooids with double peristomial lip, telotrochs with eccentric scopula)				
Z. femoralis	59-83 x 29-45	freshwater, attached to invertebrates (Amphipoda: gammarid (*Dikerogammarus villosus*))	epizoic	Europe
Genus ***Zoothamnium*** (prominent stalk, unbranched bearing single zooids or branched bearing small colonies, continuous straight myoneme permeating entire colony, contracts in zig-zag fashion, dimorphic zooids (micro- and macro-zooids), peristome with lip, transverse silverline system)				
Z. adamsi	60	freshwater and marine, attached to plants (*Cladophora*)	epiphytic	North America, Europe
Z. affine	30-100 x 24-45	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Dikerogrammarus villosus*, *Echinogrammarus trichiatus*, *Gammarus fossarum*, *pulex*, *roeselii*, *tigrinus*); Decapoda: penaeid (*Penaeus chinensis/orientalis*) and insect larvae)	epizoic	Eurasia
Z. alrasheidi	dimorphic, 80-120 x 50-60, micro-zooids 60-70 x 30-40	marine	free-living	China
Z. alternans (sometimes misspelt as *alterans*) (syn. *Z. chlamydis*)	dimorphic, micro-zooids 40-56 x 25-35; macro-zooids 70-90 x 45-55	marine, attached to inanimate substrates, algae, plants (*Ruppia*) and invertebrates (Copepoda: acartiid (*Acartia tonsa*); Isopoda: sphaeromatid (*Spaheroma serratum*), and scallops (Bivalvia: pectinid (*Chlamys farreri*))	free-living, epiphytic, epizoic	Eurasia, North America
Z. apoarbuscula	25-50 x 20-30	marine	free-living	China
Z. apohentscheli	40-65 x 25-40	marine	free-living	China
Z. arbuscula (syn. *Vorticella, Z. geniculatum*)	dimorphic 225 x 180, micro-zooids 40-80 x 30-65	freshwater attached to inanimate substrates, detritus, plants (*Elodea*, *Nymphaea*) and invertebrates (Decapoda: cambarid (*Cambarellus montezumae*, *zempoalensis*); Copepoda: cyclopid (*Cyclops*), diaptomid (*Diaptomus*); Isopoda: janirid (*Jaera sarsi*))	free-living, epiphytic, epizoic	cosmopolitan
Z. arcuatum	63-95 x 32-56	brackish water, attached to algae	epiphytic	China
Z. aselli	65-125 x 35-50	freshwater, attached to invertebrates	epizoic	Eurasia

		(Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus fossarum*, *pulex*), niphargid (*Niphargus puteanus*))		
Z. asellicola		freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic	Europe
Z. astacicolae		freshwater, attached to invertebrates (Decapoda: astacid (*Pontastacus leptodactylus*))	epizoic	Europe
Z. balticum		marine	free-living	Baltic Sea
Z. belliformum		freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus roeselii*))	epizoic	Europe
Z. bucciniiformum	40-55 x 40-50	marine, attached to inert substrates	free-living	China
Z. candelabrum	60	marine	free-living	Pacific
Z. carcini		marine and freshwater, attached to invertebrates (Decapoda: carcinid (*Carcinus maenas*))	epizoic	Europe
Z. carinogammari	29-54 x 20-25	freshwater, attached to invertebrates (Amphipoda: gammarid (*Dikerogrammarus haemobaphes, villosus, Gammarus fossarum, pulex, roeselii, tigrinus*))	epizoic	Europe
Z. caulodes		freshwater	free-living	Europe
Z. charae		freshwater, attached to plants (*Chara*)	epiphytic	Europe
Z. cienkowskii	35-50	marine	free-living	Europe
Z. commune	60-104 x 48-56	marine	free-living	China
Z. conchulaecola		freshwater, attached to inanimate substrates and invertebrates (Gastropoda: planorbid (*Planorbis rotundatus*))	free-living, epizoic	Europe
Z. congermanum		freshwater	free-living	Europe
Z. congerminale		freshwater	free-living	Europe
Z. constrictum		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum, roeselii, Carinogammarus triacanthus*))	epizoic	Europe
Z. corymbiformis	20-25	freshwater	free-living	Europe
Z. cupiferum (syn. *Z. cupiforum*)	82-105 x 44-63	marine, attached to invertebrates (Decapoda: penaeid (*Penaeus orientalis*))	epizoic	Yellow Sea
Z. dichotomum	50-65 x 20-35	freshwater, attached to inanimate substrates and invertebrates (Decapoda: cambarid (*Cambarellus patzcuarensis*))	free-living, epizoic	Europe, Mexico
Z. dudekemi (syn. *Z. parasitica*)	61-90	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus fossarum*, *pulex, roeselii, Carinogrammus*))	epizoic	Europe
Z. duplicatum	60-85 x 35-45	marine, attached to inanimate substrates, invertebrates (Decapoda: carcinid (*Carcinus maenas*), majid (*Maja squinado*), penaeid (*Penaeus chinensis*/*orientalis*); Amphipoda: gammarid (*Gammarus locusta*, *oceanicus*, *pulex*); Isopoda: idoteid (*Idotea chelipes*/*viridis*), janirid (*Jaera albifrons*/*marina*), sphaeromarid (*Lekanesphaera rugicauda*) and fish (Scorpaeniformes: cottid (shorthorn sculpin); Syngnathiformes: syngnathid (straightnose pipefish))	free-living, epizoic	cosmopolitan
Z. elegans	80	fresh and brackish water	free-living	Europe

Z. elegantissimum	35-37	freshwater, attached to inanimate substrates and invertebrates (Gastropoda: planorbid (*Planorbis rotundatus*)	free-living, epizoic	Europe
Z. fasciculare		freshwater	free-living	Europe
Z. florens	85-110 x 45-60	marine (mangrove)	free-living	China
Z. foissneri	70-110 x 30-42	marine	free-living	China
Z. gajewskajum (syn. *Vorticella constricta*)	11	freshwater	free-living	Europe
Z. gammari	60-100 x 30-50	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum*, *pulex, roeselii, Dikerogrammus villosus*))	epizoic	Eurasia
Z. gemmans		freshwater	free-living	Europe
Z. glesnicum	100	marine	free-living	Europe
Z. grossi	45-60 x 35-40	brackish water, attached to algae	epiphytic	China
Z. haplocaulis	38-50	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus roeselii*))	epizoic	Europe
Z. hartwigi	75-90 x 40-50	marine	free-living	China
Z. helicaecola		freshwater	free-living	Europe
Z. hiketes	60-80 x 30-40	marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus locusta, oceanicus, zaddachi, salinus, tigrinus*))	epizoic	Eurasia
Z. hyalinum (syn. *Vorticella*)	45-70 x 25-40	estuarine, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum, pulex, roeselii*))	epizoic	Europe
Z. hydrobiae	70	brackish water, attached to invertebrates (Gastropoda: hydrobiid (*Hydrobia*))	epizoic	Europe
Z. ignavum	trimorphic: microzooids 39 x 29; terminal zooids 52 x 23; macrozooids 35-86	marine	free-living	Mediterranean
Z. infundubulum		freshwater	free-living	Europe
Z. intermedium	35-52 x 27-37	marine, attached to inert substrates and invertebrates (Copepoda: acartiid (*Acartia clausi*, *tonsa*, *Paracartia latisetosa*), pseudodiaptomid (*Calanipeda aquadulcis*); Decapoda: atyid (*Caridina lanceolata*), crangonid (*Crangon crangon*), hippolytid (*Hippolyte leptocerus*/*longirostris*), palaemonid (*Palaemon adspersus*), penaeid (*Penaeus chinensis*/*orientalis*), temorid (*Eurytemora affinis*); Amphipoda: aorid (*Microdeutopus gryllotalpa*))	free-living, epizoic	Eurasia, North America
Z. kahli		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex, roeselii, Carinogrammarus*))	epizoic	Europe
Z. kentii (syn. *Z. hentscheli*)	50-90 x 30-45	freshwater and marine, attached to inanimate substrates, detritus, and plants	free-living, epiphytic	Eurasia
Z. laomedeae		marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus insensibilis*))	epizoic (legs)	Eurasia
Z. latipedia		freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*))	epizoic	Europe
Z. latipes		freshwater, attached to plants (*Callitriche*)	epiphytic	Europe
Z. limpidum	83	freshwater	free-living	Eurasia

Z. longifilum		aquatic, attached to invertebrates (Amphipoda: corophiid (*Chelicorophium curvispinum*), gammarid (*Gammarus fossarum*/*pulex*))	epizoic	Europe
Z. marinum	95-110 x 50-60	marine, attached to algae (seaweed) and unspecified 'zoophytes' (presumably Cnidaria)	epiphytic, epizoic	Europe
Z. maximum	80-121 x 45-65	marine, attached to inanimate substrates and invertebrates (Decapoda: penaeid (*Penaeus orientalis*))	free-living, epizoic	Yellow Sea
Z. microdiscum		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum*); Isopoda: asellid (*Asellus aquaticus*))	epizoic	Europe
Z. minimum		aquatic, attached to invertebrates (Amphipoda: corophiid (*Chelicorophium curvispinum*), gammarid (*Gammarus roeselii, tigrinus*))	epizoic	Europe
Z. mucedo	50-90 x 30-50	marine, attached to plants and invertebrates (Amphipoda: gammarid (*Gammarus pulex, tigrinus*))	free-living, epiphytic, epizoic	Europe
Z. mysidae		freshwater, attached to invertebrates (Mysida: mysid (*Limnomysis benedeni*, *Paramysis lacustris*))	epizoic	Europe
Z. nanum	30-35	marine, attached to algae (seaweed) and invertebrates (Amphipoda: aorid (*Microdeutopus gryllotalpa*), gammarid (*Gammarus duebeni, locusta, oceanicus, salinus, zaddachi*); Isopoda: idotheid (*Idothea baltica*), janirid (*Jaera albifrons*))	free-living, epiphytic, epizoic	Baltic Sea, Black Sea
Z. nii	70-80 x 40-50	marine	free-living	China
Z. niveum (syn. *Z. plumosum, spirale*)	bimorphic: micro-zooids 60 x 19; macro-zooids 20-150	freshwater; attached to submerged plants (*Adiantum* fronds)	epiphytic	Europe
Z. nutans		marine, attached to algae	epiphytic	Europe
Z. ovifera [type species as *Vorticella*]		marine	free-living	Europe
Z. oviforme	64-84 x 30-44	freshwater, attached to plants (*Potamogeton*) and invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus tigrinus*))	epiphytic, epizoic	Europe
Z. palmphlatum	71-86 x 41-50	estuarine, attached to green algae (*Ulva*)	epiphytic	China
Z. paraentzii	50-80 x 25-45	marine, attached to inanimate substrates and invertebrates (Decapoda: penaeid (*Penaeus chinensis*/*orientalis*))	free-living, epizoic	Yellow Sea
Z. paragammari	36-60 x 21-35	marine, attached to invertebrates (Decapoda: penaeid (*Penaeus chinensis*/*orientalis*)	epizoic	Yellow Sea
Z. parahentschli	50-75 x 30-52	marine and brackish water, attached to algae	free-living, epiphytic	China
Z. parahiketes	60-75 x 15-30	marine	free-living	China
Z. pararbuscula	35-65 x 30-40	marine	free-living	China
Z. parasiticum	70	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Dikerogrammus haemobaphes*, *Gammarus balcanicus*, *fossarum*, *komareki*, *pulex*, *tigrinus*); Copepoda: cyclopid (*Cyclops strenuus*, *Macrocyclops albidus*, *fuscus*), diaptomid	epizoic	Europe

		(*Eudiaptomus vulgaris*): Branchiopoda: daphniid (*Daphnia longispina*))		
Z. pelagicum		marine (pelagic)	free-living	Europe
Z. penaei	54-95 x 38-62	marine, attached to invertebrates (Decapoda: penaeid (*Penaeus aztecus, brasiliensis, chinensis, duorarum, vannamei*), palaemonid (*Palaemon pugio*)	epizoic	Mexico, Yellow Sea
Z. perejaslawzewae	67-74 x 40-47	marine, attached to invertebrates (Decapoda: penaeid (*Penaeus chinensis/orientalis*); Isopoda: spaheromatid (*Spaheroma serratum*), Tunicata: ascidiid (*Phallusia*)	epizoic	Black Sea, Yellow Sea
Z. perlatum		freshwater	free-living	Europe
Z. pictum	16	freshwater	free-living	Europe
Z. plectostylum		freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*)	epizoic	Europe
Z. plicatum		marine	free-living	Europe
Z. plumosum		freshwater and marine	free-living	Eurasia
Z. plumula	50-75 x 30-45	marine, attached to inanimate substrates and invertebrates (Decapoda: pagurid (*Pagurus bernhardus*)	free-living, epizoic	Eurasia
Z. ponticum	50	freshwater, attached to inanimate substrates and invertebrates (Amphipoda: gammarid (Gammarus insensibilis); Decapoda: cambarid (*Cambarellus zemopoalensis*)	free-living, epizoic	Black Sea, Mexico
Z. procerissimum		marine, attached to invertebrates (Hydrozoa: cordylophorid (*Cordylophora*))	epizoic	Europe
Z. procerius	60-80 x 27-46	freshwater attached to inanimate substrates, detritus, plants (algae) and invertebrate animals (molluscs, arthropods, Decapoda: astacid (*Astacus astacus/fluviatilis*); Amphipoda: gammarid (*Gammarus pulex, roeselii*))	free-living, epiphytic, epizoic	Europe
Z. prosperinae		aquatic	free-living	Europe
Z. pygmaeum (syn. *Carchesium, Vorticella*)	10-80	freshwater, attached to invertebrates (Isopoda: asellid (Asellus))	epizoic	Eurasia
Z. ramosissimum	54-88 x 29-50	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Dikerogrammus vilosus, Echinogrammus ischnus, trichiatus, Gammarus pulex*)	epizoic	Europe
Z. rigidum		marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus locusta, oceanicus, pulex*); Isopoda: sphaeromid (*Sphaeroma annandelei, terebrans*); Decapoda: penaeid (*Metapenaeus monoceros*); Tanaidacea: parapseudid (*Ctenapseudes chilkensis*)	epizoic	Europe, India, Baltic Sea
Z. robustum	56-86 x 27-36	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus fossarum, pulex, roeselii*)	epizoic	Europe
Z. sevastopoli		marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus olivii, insensibilis*))	epizoic (appendages)	Black Sea
Z. simplex	64-80 x 29-34	freshwater, attached to plants and invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus tigrinus*); Decapoda: cambarid (*Cambarellus patzcuarensis*))	free-living, epiphytic, epizoic	Europe, Mexico
Z. sinense	3-59 x 30-64	marine and brackish water, attached to	free-living,	North Sea,

(syn. *Z. commune p.p., truncatum*)		inanimate substrates and invertebrates (Decapoda: penaeid (*Penaeus orientalis*); Hydrozoa: cordylophorid (*Cordylophora*))	epizoic	Yellow Sea
Z. sphaeroma		marine, attached to invertebrates (Isopoda: sphaeromatid (*Sphaeroma serratum*))	epizoic (gills)	Black Sea
Z. steueri		marine, attached to invertebrates (Copepoda: metridinid (*Pleuromamma gracilis*)	epizoic	Europe
Z. thiophilum		marine, attached to invertebrates (Decapoda: penaeid (*Penaeus chinensis/orientalis*)	epizoic	Yellow Sea
Z. timidum		freshwater	free-living	Europe
Z. varians	54-60 x 38-42	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Dikerogammarus haemobaphes, Gammarus fossarum, roeselii, tigrinus, Carinogammarus*)	epizoic	Eurasia
Z. vermicola	55-100 x 40-50	marine, attached to inanimate substrates and invertebrates (Bivalvia: hyriid (Castalia punctata); Polychaeta: phyllodocid (*Eteone longa*); Annelida: nephtyid (*Nephthys*), pectinariid (*Lagis koreni*); Echinodermata: ophiurid (*Ophiura albida*))	free-living, epizoic	China
Z. wangi	65-90 x 45-55	marine	free-living	China
Z. weishanicum	55-90 x 30-45	freshwater	free-living	China
Z. wilberti	45-65 x 30-40	marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus*))	epizoic	China
Z. xuianum	30-50 x 25-30	marine	free-living	China
Z. zhanjiangense	80-100 x 45-55	brackish water (mangrove)	free-living	China
Genus: ***Zoothamnopsis*** (prominent stalk, branched bearing small colonies, continuous straight myoneme permeates whole colony, all zooids contract in zig-zag fashion at same time, peristome with lip, with reticulate silverline system)				
Z. liui	65-80 x 35-50	marine	free-living	China
Z. mengi [type species]	50-75 x 20-45	marine	free-living	China
Z. perlata		freshwater	free-living	Europe
Z. sinica	70-105 x 40-55	marine	free-living	China
Z. stillerae (syn. *Zoothamnium*)		freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus roeselii*))	epizoic	Europe

Loricate sessiline peritrichs belong to 2 main families:

- The family Vaginicolidae contains species whose zooids have trumpet-shaped bodies housed in pseudochitinous lorica which are often erect (upright), but are sometimes flattened. The lorica are either attached directly to substrates by their bases or they may have short attachment stalks. The lorica apertures may remain open permanently or may be closed by unique valves (opercula) attached to zooids or to loricae. The family contains 9 genera: *Australana, Cothurnia* (syn. *Daurotheca, Dimorphocothurnia, Pachytrocha p.p., Planicola, Semicothurnia, Sincothurnia, Stylocola, Tesnotheca, Thuricolopsis, Tubularia* p.p.), *Cothurniopsis* (syn. *Pseudothuricola*)*, Cothurnopsis, Platycola*, *Pyxicola* (syn. *Caulicola, Pachtrocha p.p.*), *Thuricola*, *Triacola,* and *Vaginicola* (syn. *Miculopodium*).
- In contrast, the family Lagenophryidae contains species whose zooids have rounded bodies housed in pseudochitinous lorica which are often flattened (discoidal), but sometimes upright. The lorica lack attachment stalks and their apertures may be closed by complex devices involving opposing lips and contractile filaments. The family contains 6 genera: *Chilenophrys, Clistolagenophrys, Lagenophrys* (syn. *Circolagenophrys, Stylohedra*)*, Operculigera, Paralagenophrys,* and *Setonophrys.* Many loricate peritrichs occur as epizoic or ectocommensals on the external surfaces of crustacean hosts, often exhibiting high host specificity and tissue tropism, with infestations restricted to certain locations on particular hosts. Heavy infestations of the carapace and gills may cause unsightly fouling and even respiratory problems for their hosts, thus contributing to economic losses in aquaculture industries.

LORICATE PERITRICHS				
Species	**Lorica size (µm)**	**Habitat/Hosts**	**Life-style [disease]**	**Distribution**
Family: **Vaginicolidae**				
Genus ***Australana*** (round discoid lorica, vaulted apical surface with central elliptical aperture, attached to substrate over rounded basal surface)				
A. kaneis	46-50 x 11-12	freshwater, attached to Decapoda: parastacid (*Euastacus australiensis*)	epizoic	Australia
Genus ***Cothurnia*** (upright erect lorica, vase- to urn-shaped with narrower aperture, with short stalk, open aperture, zooid attached to base of lorica without series of membranes, marine/freshwater)				
C. achtiari		marine, attached to invertebrates (Isopoda: sphaeromatid (*Sphaeroma serratum, Nassa bidentata*))	epizoic (legs)	Black Sea
C. acuta (syn. *Semicothurnis*)	50-56 x 30	marine, brackish water, attached to inanimate substrates and invertebrates (Polychaeta: polynoid (*Harmothoe sarsi, imbricata*))	free-living, epizoic	Europe
C. affinis	65	freshwater, attached to invertebrates (Copepoda: canthocamptid (*Canthocamptus*))	epizoic	Eurasia
C. amoyensis	35-40 x 18-20	marine, attached to algae	epiphytic	Atlantic
C. amphicteis (syn. *Semicothurnia*)	53-56 x 35	marine, attached to worms (Polychaeta: ampharetid (*Amphicteis gunneri*))	free-living, epizoic (setae)	Europe
C. angusta	60 x 15-23	fresh or brackish water, attached to inanimate substrates, sea lettuce (*Enteromorpha intestinalis*) and invertebrates (Ostracoda: cypridid (unspecified))	free-living, epiphytic, epizoic	Europe
C. annulata (syn. *Cothurniopsis*)	40-85 x 11-25	freshwater, attached to filamentous algae (*Bulbochaeta*, *Hydrodictyon reticulatum*, *Melosira*, *Mougeoutia*, *Spirogyra*) and submerged plants (*Enteromorpha intestinalis*, *Myriophyllum*, *Lemna*)	free-living, epiphytic	Eurasia, America
C. anomala	30-40 x 15-25	freshwater, attached to invertebrates (Amphipoda: corophiid (*Corophium curvispinum*))	epizoic	Europe
C. antarctica (syn. *Cothurniopsis*)	50-60 x 30	marine, attached to invertebrates (Ostracoda: philomedid (*Philomedes laevipes*))	epizoic	Antarctica
C. aplatita	45-65 x 25-30	marine, attached to green algae and plants (Campanulariaceae)	free-living, epiphytic	Europe
C. apseudophila (syn. *Sinocothurnia*)	88-92 x 29-31	marine, attached to invertebrates (Malacostraca: apseudid (*Apseudes spinosus*))	epizoic	Europe
C. arcuata (syn. *C. arenata, fusiformis*)	125 x 60-65	marine	free-living	Eurasia
C. astaci	90	freshwater, attached to invertebrates (Decapoda: astacid (*Astacus astacus, leptodactylus*) and unspecified 'entomostraca')	epizoic (appendages, gills)	Europe
C. asymmetrica (syn. *C. asimmetrica*)	48-52 x 25	freshwater, attached to filamentous green algae (*Cladophora*) and plants (*Enteromorpha intestinalis*)	epiphytic	Europe
C. auriculata (syn. *Sinocothurnia, S. flexa p.p.*)	110-150 x 45-60	marine, attached to inanimate substrates and filamentous green algae (*Cladophora*)	free-living, epiphytic	Europe, North America
C. beciformis (syn. *Planicola*)	70	freshwater	free-living	Europe
C. boeckii		freshwater	free-living	Europe
C. borealis		marine (planktonic)	free-living	Europe

(syn. *Tintinnus*, *Amphorides*)				
C. branchiata (syn. *Sinoconthurnia*)	87-112 x 35-45	freshwater, attached to crayfish (Decapoda: astacid (*Astacus leptodactylus*))	epizoic (gills, epipodites)	Ukraine
C. brevistyla	43-55 x 20-25	freshwater, attached to algae	epiphytic	Europe
C. butschlii	53 x 27	marine, attached to kinorhynchs (Cyclorhagida: echinoderid (unspecified mud dragon))	epizoic	Europe
C. camura		freshwater	free-living	Europe
C. canthocampti (syn. *Cothurniopsis*)	80-95 x 40-42	freshwater, attached to invertebrates (Copepoda: canthocamptid (*Canthocamptus minutus*))	epizoic	North America
C. carinogammari	70-72 x 40-42	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus*))	epizoic	Europe
C. ceramicola	60-130 x 20-45	marine, attached to inanimate substrates, algae (*Ceramium*) and invertebrates (Bryozoa: cribrilinid (*Cribrilina punctata*), crisiid (*Crisia eburnea*); Hydrozoa: campanulariid (*Laomedea loveni*); Polychaeta: serpulid (*Spirorbis spirorbis*)	free-living, epiphytic, epizoic	Eurasia
C. cincta (syn. *Planicola*)	50	freshwater, attached to inanimate substrates and plants (*Lemna*)	free-living, epiphytic	Europe
C. clausiens	35-50 x 20-35	freshwater, attached to unspecified arthropods	epizoic	Europe
C. coarctata	66-75 x 30	marine, attached to detritus and green algae	free-living, epiphytic	Europe
C. cohni (syn. *C. pupa p.p.*)	60 x 20	marine	free-living	North Sea
C. collaris	60-100 x 30-45	marine or brackish water, attached to algae	free-living	Europe
C. complanata	78-81 x 32-35	marine, attached to worms (Polychaeta: flabelligerid (*Stylarioides plumosus*))	epizoic	Europe
C. compressa (syn. *Sinocothurnia, C. compressula, flexa p.p.*)	100-140 x 50	marine, attached to algae and invertebrates (Bryozoa (unspecified))	epiphytic, epizoic	Europe, North America
C. cordylophorae	120 x 35	brackish water, attached to invertebrates (Hydrozoa: cordylophorid (*Cordylophora caspia*))	epizoic	Europe
C. corrugata	127	marine, attached to thread-like green algae (Confervae)	epiphytic	Europe
C. cracens (syn. *Planicola*)		freshwater	free-living	Europe
C. curvula	60 x 30	marine, attached to invertebrates (Copepoda: harpacticid (unspecified))	epizoic	Europe
C. cuspidata (syn. *Stylocola*)	19	freshwater, attached to algae	epiphytic	Europe
C. cyathiforme (syn. *Sinocothurnia*)	95-100 x 45	marine	free-living	Europe
C. cyclopis	60 x 25	marine, attached to invertebrates (Copepoda: harpacticid (unspecified))	epizoic	Europe
C. cyclopsinae (syn. *Planicola*)		freshwater, attached to invertebrates (Copepoda: cyclopid (*Cyclops*))	epizoic	Europe
C. cylindrica	61 x 29	freshwater, attached to plants (*Enteromorpha intestinalis*)	epiphytic	Europe
C. cytherideae	70 x 35	marine, attached to invertebrates (Ostracoda: cytherideid (*Cytheridea*); Hydrozoa (unspecified))	epizoic	Baltic Sea
C. dauciformis (syn. *Planicola*)		freshwater, attached to algae	epiphytic	Europe
C. elastica	50-70	freshwater, attached to moss	epiphytic	Europe

(syn. *Cothurniopsis*)				
C. elongata (syn. *Sinocothurnia*)	150 x 65	marine (aquaria)	free-living	Asia
C. exilipes (syn. *Stylocola*)	30	freshwater	free-living	Europe
C. exilis (syn. *Planicola*)		freshwater, attached to algae	free-living, epiphytic	Europe
C. fecunda	110 x 35	brackish water, attached to filamentous algae	free-living, epiphytic	North America
C. felinska	110 x 40	marine, attached to algae	epiphytic	Europe
C. fibripes	60 x 30	marine (aquaria), attached to detritus	free-living	Europe
C. floscularia	85 x 40	freshwater	free-living	Europe
C. gammari (syn. *Sinocothurnia*)	53-55 x 25-34	marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus locusta, oceanicus, duebenii, insensibilis*))	epizoic	Europe
C. gracilis (syn. *Sinocothurnia*)	90-100	marine, attached to invertebrates (Leptostraca: nebaliid (*Nebalia bipes*))	epizoic	Europe, North America
C. guyanensis	76-120 x 59-73	marine, attached to tanaids (Peracarida: tanaidid (*Halmyrapseudes spaansi*))	epizoic	South America
C. halacaricola	70 x 23-35	marine, attached to mites (Trombidiformes: halacarid (*Copidognathus fabriciusi*))	epizoic	Eurasia
C. harpactici	75-88 x 28-35	marine, attached to invertebrates (Copepoda: canthocamptid (*Cletocamptus confluens, Mesochra lilljeborgi*))	epizoic	Europe
C. havniensis	85	marine	free-living	America
C. imberbis (syn. *Sinocothurnia, C. putanea*) [type species]	45-85 x 20-40	freshwater, attached to diatoms, plants (*Ruppia*) and invertebrates (Copepoda: cyclopid (*Cyclops*))	epizoic	Europe, North America
C. inclinans	57 x 40	marine, attached to algae	epiphytic	Europe
C. inflata	60 x 30	brackish water, attached to filamentous algae	free-living, epiphytic	North America
C. inflecta	70 x 35	marine, attached to green algae		Europe
C. innata (syn. *C. hofkeri*)	40-100 x 20-27	marine, attached to red algae and snails (Gastropoda: hydrobiid (*Hydrobia*))	epiphytic, epizoic	Europe
C. irregularis	55 x 35	freshwater	free-living	Europe
C. kahli	43-50 x 21-29	freshwater, attached to filamentous green algae (*Cladophora*)	epiphytic	Europe
C. lapponum	72-116 x 30-49	freshwater (marshes), attached to mosses (Sphagnum)	epiphytic	Eurasia
C. lata	50-70 x 40-45	marine or freshwater, attached to invertebrates (Copepoda: diaptomid (Diaptomus) and other 'entomostraca'	epizoic	North America
C. limanica (syn. *Sinocothurnia*)		freshwater, attached to crayfish (Decapoda: astacid (*Astacus leptodactylus*))	epizoic	Eurasia
C. limnoriae (syn. *Tesnotheca*)	70-90 x 33-40	marine, attached to invertebrates (Isopoda: limnoriid (*Limnoria lignorum*))	epizoic	Eurasia
C. macrodisca	75 x 40	freshwater, attached to green algae (*Spirogyra*)	epiphytic	Europe
C. magna	200 x 56	freshwater	free-living	China
C. maritima (syn. *C. cyathus, marina*)	35-56 x 28-33	estuarine, attached to inanimate substrates and green algae	free-living, epiphytic	Eurasia
C. membranoloricata	40-45 x 18-23	marine, attached to filamentous green algae (*Cladophora repens*, *heteronema*, *Spirogyra*)	epiphytic	Europe, Africa
C. minutissima (syn. *C. sinuata, Cothurniopsis*)	35-50 x 18-27	freshwater, attached to detritus, mosses and plants (*Enteromorpha intestinalis*)	free-living, epiphytic	Europe
C. mobiusi	50 x 30	marine	free-living	North Sea

(syn. *C. maritima p.p.*)				
C. mollis (syn. *Planicola*)		freshwater, attached to plants (*Lemna*)	epiphytic	Europe
C. monoannulata (syn. *Sinocothurnia*)	68 x 32	freshwater, attached to filamentous green algae (*Cladophora*)	epiphytic	Europe
C. nana (syn. *Planicola*)		freshwater	free-living	Europe
C. nebaliae (syn. *Dimorphocothurnia*)	100-120 x 40-55	marine, attached to invertebrates (Leptostraca: nebaliid (*Nebalia bipes*))	epizoic	Europe
C. nereicola (syn. *Sinocothurnia*)	33 x 30	marine, attached to worms (Polychaeta: nereidid (*Nereis diversicolor*))	epizoic	Europe
C. nitocrae	93-97 x 30-35	marine, attached to invertebrates (Copepoda: harpacticoid (*Nitocra spinipes*))	epizoic	Europe
C. obligua	95-96 x 44-45	brackish water, attached to green algae (*Ceramium diapharum*)	epiphytic	Europe
C. oblonga	71-82 x 30-33	freshwater, attached to detritus, filamentous green algae (*Cladophora*) and plants (*Lemna*, *Enteromorpha intestinalis*))	free-living, epiphytic	Europe
C. oliva (syn. *Planicola*)	35	freshwater	free-living	Europe
C. ovalis	40 x 22	marine	free-living	North America
C. ovata (syn. *Cothurniopsis*)	125 x 75	freshwater, attached to algae (*Conferva*)	epiphytic	Europe
C. oviformis	48 x 22	freshwater, attached to filamentous green algae (*Cladophora*)	epiphytic	Europe
C. parva (syn. *Planicola*)	46-50 x 30-34	brackish water, attached to green algae (*Ceramium diaphanum*)	epiphytic	Eurasia
C. parvula (syn. *Sinocothurnia*)	50-62 x 24	marine, attached to algae	free-living	Europe
C. patula	55 x 45	freshwater, attached to algae	free-living	Europe
C. pediculata		freshwater, attached to algae	free-living, epiphytic	Europe
C. peloscolicis	81 x 27-41	marine, attached to worms (Oligochaeta: naidid (*Peloscolex benedeni*))	epizoic	Europe
C. physaloides (syn. *Planicola*)	15	freshwater	free-living	Europe
C. plachteri	127 x 30	freshwater, attached to crayfish (Decapoda: astacid (*Astacus astacus, Austropotamobius torrentium*))	epizoic (appendages)	North America
C. planorbicula (syn. *Planicola*)		freshwater, attached to invertebrates (Gastropoda: planorbid (*Planorbis complanatus*))	epizoic	Europe
C. plectostyla (syn. *Cothurniopsis canthocampti*)	80-100 x 30-40	freshwater, attached to invertebrates (Copepoda: canthocamptid (*Canthocamptus*))	epizoic	Europe
C. poculum	40	marine	free-living	North America
C. procera (syn. *Planicola*)	50	freshwater, attached to algae	epiphytic	Europe
C. propinqua	60 x 23	estuarine, attached to invertebrates (Copepoda: cyclopid (*Cyclops*), harpacticid (unspecified))	epizoic	Eurasia
C. pupa		freshwater	free-living	Europe
C. radicosa		freshwater	free-living	Europe
C. recurva	75 45-75 x 17-35	estuarine, attached to invertebrates (Copepoda: cyclopid (*Cyclops*), harpacticid (unspecified), Insecta (unspecified aquatic species)	epizoic	Eurasia
C. recurvata	100 x 50	brackish water, attached to algae	epiphytic	Europe
C. reniformis		freshwater	free-living	Europe

C. rhabdota (syn. *Sinocothurnia*)	125-130 x 40-42	marine, attached to red algae (*Polysiphinia nigrescens*)	epiphytic	Europe
C. richtersi (syn. *Cothurniopsis*)	45-60 x 30-35	freshwater, attached to moss	epiphytic	Europe, Antarctica
C. ruthae	66 x 30	freshwater	free-living	Europe
C. sahrhagei		marine	free-living	Europe
C. salina	80-98 x 12-19	hypersaline lake	free-living	China
C. scyphoides	22	freshwater swamp, attached to algae	free-living, epiphytic	Europe
C. sevastopoli		marine, attached to invertebrates (Amphipoda: gammarid (*Gammarus olivii*))	epizoic, body, legs)	Black Sea
C. sieboldii	113-132 x 30-49	freshwater, attached to crayfish (Decapoda: astacid (*Astacus astacus*, *Austropotamobius torrentium*) and other 'entomostraca'	epizoic (branchial appendages)	Europe
C. simplex	50-60 x 23	marine, attached to algae	epiphytic	Europe
C. sinuosa (syn. *Sinocothurnia*)	90-100 x 35-40	marine, attached to algae	epiphytic	North America
C. soldida	68 x 30	freshwater, attached to detritus and plants	free-living, epiphytic	Eurasia
C. spinosa		marine	free-living	Europe
C. spissa (syn. *C. calix*)	50-60 x 30-35	marine and freshwater, attached to thread-like green algae	epiphytic	North America
C. striata		marine	free-living	Europe
C. stylarioides	121 x 32	marine, attached to worms (Polychaeta: flabelligerid (*Stylarioides plumosus*))	epizoic	Eurasia
C. subglobosa (syn. *Cothurniopsis*)	45-50 x 46-52	marine, attached to invertebrates (Ostracods: cytherid (*Cythereis*))	epizoic	Antarctica
C. subtilis	65-72 x 28	marine, attached to mussels (Bivalvia: mytilid (*Mytilus edulis*))	epizoic	Eurasia
C. tekirghiolica	80 x 30	freshwater, attached to filamentous green algae (*Cladophora*)	epiphytic	Eurasia
C. tenuicula (syn. *Planicola*)		freshwater, attached to algae	epiphytic	Europe
C. tespa (syn. *Daurotheca*)	86-92 x 58-64	freshwater, attached to crayfish (Decapoda: astacid (*Pacifastacus leniusculus*))	epizoic (gills)	Asia
C. tincta (syn. *Planicola*)		freshwater	free-living	Europe
C. transoceanica (syn. *Daurotheca*)	69-74 x 60-75	freshwater, attached to crayfish (Decapoda: astacid (*Pacifastacus lenisculus*))	epizoic	Holarctic
C. triangula	45 x 18	marine, attached to invertebrates (Trombidiformes: halacarid (*Copidognathus fabriciusi*); Ostracoda: cytherid (*Cythereis tuberculata*))	epizoic	Europe
C. trophoniae (syn. *C. pedunculata, nodosa, sahrhagei, Vorticella pedunculata*)	60-140 x 26-50	marine, attached to algae (*Polysiphonia violacea*) and invertebrates (Polychaeta: flabelligerid (*Trophonia plumosa*, *Stylarioides plumosus*); Hydrozoa: campanulariid (*Laomedea loveni*); Pantopoda: callipallenid (*Pallene brevirostris*))	epiphytic, epizoic	Europe
C. trophonicola	60-85 x 31-35	marine, attached to worms (Polychaeta: flabelligerid (*Trophonia plumosa*))	epizoic	Asia
C. ussurina (syn. *Daurotheca*)	69-74 x 42-46	freshwater, attached to crayfish (Decapoda: astacid (*Pacifastacus*), cambarid (*Cambarus*, *Cambaroides*, *Orconectes*)	epizoic	Eurasia
C. vaga	100 x 45	freshwater, attached to invertebrates (Copepoda: cyclopid (*Cyclops*);	epizoic	Eurasia

		Amphipoda: gammarid (*Gammarus*))		
C. variabilis (syn. *Daurotheca, D. marginata*)	75-130	freshwater, attached to invertebrates (Decapoda: astacid (*Astacus leptodactylus, fluviatilis*), cambarid (*Cambarus affinis, bartonii, diffinis, propinquus, Orconectes limosus*)	epizoic (gills)	Europe, North America
C. vas		marine, attached to invertebrates (Amphipoda: crypturopodid (*Crypturopus pachytus*))	epizoic	Eurasia
C. ventosa (syn. *Planicola*)		freshwater, attached to algae	epiphytic	Europe
C. vestita (syn. *Planicola*)		freshwater	free-living	Europe
C. viridis (syn. *Planicola*)	45	freshwater	free-living	Europe
C. vorticelloides		freshwater	free-living	Europe
C. vulgaris		freshwater	free-living	Europe
C. zhytomirensis (syn. *Pachytrocha*)	62-78 x 20-28	freshwater (sewage treatment plant)	free-living	Ukraine
Genus: ***Cothurniopsis*** (upright erect pseudochitinous lorica, urn-shaped with irregular basal ridges, short stalk, aperture closed by internal valve (operculum) attached to lorica when zooid contracts)[recently suggested this genus be synonymized with *Cothurnia* on the basis of molecular studies]				
C. dyonisii (syn. *Pseudothuricola, Thuricola*)	90-100 x 30-35	freshwater, attached to moss	epiphytic	Europe
C. valvata (syn. *Cothurnia, C. elastica, Planicola*)	50-70 x 25-35	estuarine, attached to filamentous algae and moss	epiphytic	Europe
Genus ***Cothurnopsis*** (upright pseudochitinous lorica, urn-shaped, with short stalk, aperture closed by flexible rim when zooid contracts, often on crustacea)				
C. astaci (syn. *Cothurnia*) [type species]	65-90 x 35-45	freshwater, attached to inanimate substrates and invertebrates (Decapoda: *Astacus fluviatilis, leptodactylus*) and other 'entomostraca')	epizoic (carapace)	Europe
C. aurea (syn. *Baikalotheca*)		freshwater	free-living	Russia
C. bavarica (syn. *Cothurnia*)	85-93 x 49-59	freshwater, attached to crayfish (Decapoda: astacid (*Astacus leptodactylus*), cambarid (*Orconectes limosus*))	epizoic (appendages)	Europe
C. curva (syn. *Cothurnia*)	70-100 x 35-40	freshwater, attached to plants (*Ruppia*) and crayfish (Decapoda: astacid (*Astacus leptodactylus*), cambarid (*Orconectes limosus*) and other 'entomostraca')	epizoic (branchial appendages)	Europe, North America
C. entzi (syn. *Cothurnia, Pyxicola*)	70-80 x 26-40	marine, attached to filamentous green algae (*Cladophora*)	epiphytic	Europe
C. minutissima (syn. *Cothurnia*)		terrestrial (soil)	free-living	Holarctic
C. richtersi		terrestrial (soil)	free-living	Holarctic
C. sieboldii		freshwater, attached to crayfish (Decapoda: astacid (*Astacus fluviatilis, torrentium*))	epizoic	Europe
Genus: ***Platycola*** (decumbent pseudochitinous lorica, attached along one side, simple aperture bends upwards diagonally)				
P. baikalica (syn. *Vaginicola*)	90 x 67-70	freshwater, attached to invertebrates (Amphipoda: acanthogammarid (*Brandtia lata, latissima*), gammarid (*Gammarus, Echinogammarus fuscus*), pallaseid (*Pallasea grubei*))	epizoic	Lake Baikal
P. butschlii (syn. *Vaginicola*)	80-100 x 54-110	freshwater, attached to plants and mosses	epiphytic	Europe
P. callistoma	73 x 55	freshwater, attached to cave-dwelling	epizoic	Europe

		invertebrates (Isopoda: sphaeromatid (*Microlistra spinosissima*))		
P. circularis	40-65	marine, attached to invertebrates (Isopoda: limnoriid (*Limnoria*))	epizoic (appendages)	Eurasia
P. coelochila	110-115	freshwater, attached to plants (Lemna)	epiphytic	North America
P. decumbens (syn. *P. amphora, amphoroides, ampulla*, *intermedia, longicollis, regularis*, *reflexa*, *striata*, *truncata*, *Vaginicola*) [type species as *Vaginicola*]	60-170 x 12-110	freshwater, attached to inanimate substrates, detritus, filamentous algae (*Nitella*), submerged plants (*Lemna, Ceratophyllum*), and invertebrates (Amphipoda: gammarid (*Brachiuropus*); Gastropoda: planorbid (*Ancylus fusca*, *Planorbis*), lymnaeid (*Lymnaea stagnalis*); Ephemeroptera: baetid (*Cloeon dipterum* mayfly larvae) and mollusc shells)	free-living, epiphytic, epizoic	cosmopolitan
P. dilatata (syn. *Vaginicola, P. donsi*)	75-80 x 50	freshwater, attached to plants and algae	free-living, epiphytic	Eurasia
P. gracilis (syn. *Vaginicola*)	60 x 37	freshwater, attached to plants and algae	free-living	Europe
P. hydrobiae (syn. *Vaginicola*)	85-90 x 55	marine, attached to snails (Gastropoda: hydrobiid (*Hydrobia*))	epizoic	North Sea
P. lageniformis	120 x 50	freshwater, attached to cave-dwelling invertebrates (Isopoda: sphaeromatid (*Microlistra spinosissima*))	epizoic	Europe
P. mollis (syn. *Vaginicola*)	80-11 x 32	freshwater, attached to plants and algae	free-living, epiphytic	Europe
P. pala (syn. *Vaginicola*)	87-97 x 30-70	freshwater, attached to invertebrates (Amphipoda: gammarid (*Palicarinus* (*Parapallasea*) *puzyllii*))	epizoic	Lake Baikal
P. steineri (syn. *Vaginicola*)	78-88 x 40	freshwater, attached to moss	epiphytic	Europe
Genus: ***Pyxicola*** (upright pseudochitinous lorica, elongate but with irregular outline, short stalk, aperture closed when zooid contracts, operculum (valve) attached to zooid (not lorica)) [no fixed type species]				
P. affinis (syn. *Cothurnia*)	80 x 40	freshwater, attached to plants	epiphytic	Europe
P. carteri (syn. *P. constricta, nolandi*, *annulata, striata*)	60-96 x 12-34	freshwater, attached mostly to filamentous algae, sometimes to aquatic plants (*Pontederia*)	free-living, epiphytic	Eurasia, Americas
P. ligiae (syn. *Cothurnia*)	55	marine, attached to invertebrates (Isopoda: ligiid (*Ligia oceanica*))	epizoic (gills)	Europe
P. limbata	75-80	freshwater	free-living	Europe
P. operculigera	45-70 x 22-35	brackish water, attached to plants and invertebrates (Hydrozoa: cordylophorid (*Cordylophora*))	epiphytic, epizoic	Eurasia
P. ovata	40 x 35	freshwater	free-living	China
P. psammata	75-85 x 23-35	freshwater, attached to invertebrates (Isopoda: sphaeromatid (*Microlistra spinosissima*))	epizoic	Eurasia
P. pusilla (syn. *Cothurnia, C. furcifer, P. carteri p.p., eforiana, furcifer, valvata, Caulicola valvata*))	45-80 x 22-46	fresh and brackish water, attached to inanimate substrates and plants	free-living, epiphytic	Eurasia, North America
P. pyxidiformis (syn. *Caulicola*)	160	freshwater, attached to inanimate substrates and plants (water lilies)	free-living, epiphytic	Eurasia
P. socialis (syn. *Cothurnia*)	100	marine	free-living	Europe
Genus: ***Thuricola*** (upright erect pseudochitinous lorica, cylindrical, without stalk, aperture closed by internal valve (operculum) attached to lorica when zooid contracts, some with zoochlorellae				

T. constricta (possible syn. of *T. valvata*)	160-174 x 62-70	marine	free-living	Europe
T. elegans (syn. *Cothurnia*)	65-75 x 30	brackish water, attached to algae	epiphytic	Europe
T. folliculata (syn. *Cothurnia regalis p.p., crystallina p.p., obliqua*)	125-420 x 15-25	freshwater and marine, attached to inanimate substrates, detritus, filamentous algae (*Enteromorpha intestinalis, Cladophora fracta*), sometimes submerged plants (incl. moss), and occasionally terrestrial (peat bogs)	free-living, epiphytic	Europe, America, Australia
T. gracilis (syn. *T. pediculata, viridis*)	140-220	freshwater, attached to algae and plants	epiphytic	Europe
T. inflata	72-76 x 31-34	freshwater, attached to filamentous algae (*Cladophora*)	epiphytic	China
T. kellicottiana (syn. *T. amphora, innixa, gruberi, amphora p.p., Thuricolopsis, Cothurnia castellensis, crystallina p.p., regalis p.p.*)	140-435 x 20-35	freshwater, attached to inanimate substrates and submerged plants (incl. moss)	free-living, epiphytic	Eurasia, Americas
T. obconica (syn. *T. fimbriate, kamptostoma*)	195-310 x 15-25	brackish water, attached to inert substrates and plants	free-living, epiphytic	Europe
T. parafolliculata	360-400 x 50-60	marine	free-living	China
T. similis	158-248	freshwater (activated sludge)	free-living	Europe
T. valvata (syn. *T. aestuarii, operculata*) [type species as *Vaginicola*]	120-360 x 20-30	marine	free-living	cosmopolitan
T. vasiformis	160-300 x 30-59	freshwater, attached to inanimate substrates, and detritus	free-living	Europe
Genus ***Triacola*** (fossil taxon, erect pseudochitinous lorica fossilized, short stalk with basal disc, attached to fossilized ostracods)				
T. ostracodarum	95-110 x 50-57	attached to fossilized ostracods		Europe
Genus ***Vaginicola*** (upright erect lorica, cylindrical to vase- to urn-shaped, without stalk, open aperture, marine/freshwater)				
V. amadelpha		freshwater	free-living	Europe
V. amphora (syn. *Cothurnia, Platycola, Thuricola amphora p.p.*)	90-100	marine, attached to algae (*Vaucheria*) and invertebrates (Amphipoda: gammarid (*Brachyuropus reicherti*))	epiphytic, epizoic	Eurasia
V. amphorella (syn. *Cothurnia*)	66	freshwater, attached to algae	epiphytic	New Zealand
V. ampulla (syn. *Stylocola*)	60-200	freshwater, attached to algae	epiphytic	Europe
V. annulata	120	freshwater	free-living	Europe
V. angusta	70-95	freshwater	free-living	China
V. attenuata (syn. *Planicola, Cothurnia*)	80	freshwater, attached to plants	epiphytic	Europe
V. calceola		freshwater	free-living	Europe
V. cementata		freshwater, attached to cave-dwelling invertebrates (Isopoda: sphaeromatid (*Microlistra spinosissima*))	epizoic	Europe
V. ceratophylli (syn. *Cothurnia*)	115-145 x 65-80	freshwater, attached to plants (*Ceratophyllum*)	epiphytic	Europe
V. chaperoni (syn. *Cothurnia*)	120	freshwater, attached to moss	epiphytic	Europe
V. compressa	140	marine, attached to algae and invertebrates (Bryozoa (unspecified))	epiphytic, epizoic	Eurasia
V. crassa		freshwater	free-living	Europe

V. cratera (syn. *Cothurnia*)	150	freshwater, attached to invertebrates (Amphipoda: acanthogammarid (*Acanthogammarus victoria, Parapallasea puzilli*), gammarid (*Gammarus*, *Echinogammarus lividus*, *cyaneus*, *verrucosus, Axelboeckia rubra*), pallaseid (*Pallasea gruberi*, *kessleri*))	epizoic	Lake Baikal
V. cristata		freshwater	free-living	Europe
V. cylindrica (syn. *Platycola*)		freshwater	free-living	Europe
V. doliolum	61	freshwater, attached to moss	epiphytic	Eurasia
V. donsi (syn. *Cothurnia grandis*)	120-150	marine	free-living	Europe
V. elegans	160-170	freshwater, attached to invertebrates (Amphipoda: acanthogammarid (*Acanthogammarus victorii*, *albus*), gammarid (*Gammarus*))	epizoic	Eurasia
V. elongata (syn. *Planicola*)	60	freshwater	free-living	Europe
V. festivus	100-106 x 34-46	freshwater	free-living	Asia
V. galericulata		freshwater	free-living	Europe
V. gigantea (syn. *Cothurnia*)	200-460	freshwater, attached to plants	epiphytic	Europe
V. globosa (syn. *Cothurnia*)		freshwater	free-living	Europe
V. gracilis		freshwater, attached to algae	free-living, epiphytic	Europe
V. grandis	230	freshwater, attached to plants	epiphytic	Europe
V. incisa (syn. *Cothurnia, Thuricola*)	160-180	freshwater, attached to planktonic cyanobacteria colonies (*Gomphosphaeria. Microcystis aeruginosa*)	free-living	Africa
V. inclinata (syn. *Planicola, Cothurnia*)	50	freshwater	free-living	Europe
V. ingenita (syn. *Trichoda*, *Planicola, Cothurnia*) [type species as *Trichoda*]	35-65	freshwater, attached to inanimate substrates, diatoms (*Melosira granulata, Fragilaria crotonensis*), filamentous algae (*Spirogyra*), and plants (*Lemna*)	free-living, epiphytic	Eurasia, America
V. leptosoma	160	freshwater, attached to plants	epiphytic	Europe
V. lobata (syn. *Cothurnia*)	200	freshwater	free-living	Europe
V. longipes	280	freshwater, attached to plants	epiphytic	Europe
V. longistyla		freshwater	free-living	Eurasia
V. ovata	80	marine	free-living	Europe
V. paguri (syn. *Cothurnia*)	100	marine, attached to hermit crabs (Decapoda: pagurid (*Pagurus bernhadus*))	epizoic (surface)	Europe
V. pala		freshwater, attached to invertebrates (Amphipoda: acanthogammarid (*Parapallasea puzilli*))	epizoic	Lake Baikal
V. parallela (syn. *Cothurnia*)	100	freshwater, attached to algae	epiphytic	New Zealand
V. parva		freshwater	free-living	Europe
V. plicata	120-150 x 35-42	marine	free-living	Asia
V. pontica (syn. *Cothurnia*)	171	marine	free-living	Europe
V. sediculum (syn. *Cothurnia*)	52-57	freshwater, attached to moss (*Sphagnum*)	epiphytic	Eurasia
V. striata (syn. *Stylocola*)	55	freshwater	free-living	Europe
V. subcrystallina	100-120	freshwater, attached to algae and plants	epiphytic	Europe, North

(syn. *V. crystallina, Planicola*)		(*Cladophora glomerata*)		America
V. sulcata (syn. *Cothurnia*)	60-70	marine, attached to yellow-green algae (Vaucheria)	epiphytic	Eurasia
V. swarczewskyi (syn. *Cothurnia crystallina p.p.*)	195	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus*))	epizoic	Russia
V. terricola (syn. *Cothurnia*)	56	freshwater, attached to moss	epiphytic	Europe
V. tincta (syn. *V. lagena*)	75-175 x 28-71	freshwater, attached to inanimate substrates, filamentous algae (*Spirogyra*), submerged plants (*Myriophyllum, Lemna, Pontederia, Utricularia*, *Spirodela*, and water lilies)	free-living, epiphytic	Eurasia, Americas
V. undata		freshwater	free-living	Europe
V. vas (syn. *Cothurnia*)	115-125	freshwater, attached to invertebrates (Amphipoda: gammarid (*Crypturopus pachytus*))		Lake Baikal
V. vestita (syn. *Planicola*)	60	freshwater	free-living	Europe
V. virgula (syn. *Cothurnia*)	51	freshwater, attached to moss	epiphytic	Europe
V. wangi	155	marine, attached to algae	epiphytic	Europe
Family: **Lagenophryidae**				
Genus: ***Chilenophrys*** (body rounded, within flat hemispherical lorica, without stalk, lorica aperture an invaginated tube (loricastome) perpendicular to long axis, aperture closed by operculum)				
C. allendei (syn. *Stylohedra, Lagenophrys*)	62-67 x 48-52 x 22-24	freshwater, attached to crayfish (Decapoda: parastacid (*Parastacus pugnax, chilensis*))	epizoic	South America
Genus: ***Clistolagenophrys*** (body rounded, within flat discoid lorica, lorica aperture an invaginated tube (loricastome) perpendicular to long axis, aperture closed by loricastome retraction bringing together bases of flexible opposing lips)				
C. primitiva [type species as *Lagenophrys*]	100 x 90 x 30	freshwater, attached to invertebrates (Amphipoda: pallaseid (*Pallasea cancellus*))	epizoic (appendages)	Lake Baikal
Genus ***Lagenophrys*** (body rounded, within flat hemispherical lorica, without stalk, lorica aperture an invaginated tube (loricastome) perpendicular to long axis, aperture closed by drawing together flexible opposing lips)				
L. aegleae	53-62 x 59-65 x 12-18	freshwater, attached to crabs (Decapoda: aegleid (*Aegla castro, franca, laevis*))	epizoic (gills)	South America
L. amupulla	50-75	freshwater, attached to invertebrates (Amphipoda: acanthogammarid (*Acanthogammarus victorii, albus, godlewskii, Brandtia latissima, Diplacanthus brevispinus, Dorogammarus castaneus, Garjajewia cabanisii, Hyalellopsis czyrnianskii, variabilis, Parapallasea puzilli*), crangonyctid (*Crangonyx*), crypturopodid (*Crypturopus inflatus, pachytus, rugosus, tuberculatus, Echiuropus macronychus*), eulimnogammarid (*Eulimnogammarus aheneus, capreolus, cruentus, cyaneus, cyanoides, fuscus, lividus, maackii, olivaceus, sophianosi, verrucosus, viridis, Heterogrammus sophianosii, Odontogammarus calcaratus, margaritaceus*), gammarid (*Axelboeckia carpenteri, potanini, Carinogammarus cinammomeus, rhodophthalmus, Echinogammarus berilloni, Eucarinogammarus wagii, Gammarus annandalei, lacustris, duebeni, pulex*), micuropodid (*Gmelinoides fasciatus, Micruropus fixsenii, glaber, klukii,*	epizoic (gills)	Eurasia, Americas

		littoralis, rugosus, talitroides, wahlii, vortex), ommatogammarid *(Ommatogammarus flavus*), pallaseid (*Pallasea cancellus*, *cancelloides*, *grubei*, *kessleri*); Isopoda: asellid (*Asellus aquaticus*)		
L. andos (syn. *Circolagenophrys*)	95-102 x 72-76 x 9-12	freshwater, attached to crayfish (Decapoda: parastacid (*Parastacus pugnax, chilensis*))	epizoic (gills)	South America
L. anisogammari (syn. *Circolagenophrys*)	65-72 x 64-68	marine, attached to invertebrates (Amphipoda: anisogammarid (*Anisogammarus locustoides*))	epizoic (branchial plates)	Asia
L. anticthos	42-79 x 50-94 x 15-23	freshwater, attached to crayfish (Decapoda: parastacid (*Parastacus defossus, varicosus, nicoleti, pugnax, saffordi*))	epizoic (gills)	South America
L. aselli	80-95 x 78-87	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus, Caecidotea attenuata, communis, forbesi, laticauda, occidentalis, racovitzai, Lirceus lineatus*))	epizoic (gills, appendages)	Europe, North America
L. awerinzewi		freshwater, attached to crabs (Decapoda: gecarcinucid (*Barytelphusa guerini*, *cunicularis*, *Esanthelphusa dugasti*, *Maydelliathelphusa falcidigitis*), potamid (*Apotomonautes hainanensis*, *Demanietta manii*, *Isolapotamon kinabaluense*, *Potamon denticulatus*, *dehaani*, *fluviatilis*, *Sinopotamon davidi*), potamonautid (*Liberonautes latidactylus*, *Potamonautes niloticus*))	epizoic (gills)	cosmopolitan
L. branchiarum	58 x 63	freshwater, attached to shrimp (Decapoda: palaemonid (*Macrobrachium* (*Palaemon*) *nipponense*))	epizoic (gills)	China
L. callinectes	53-65 x 51-60 x 10-21	marine, attached to crabs (Decapoda: portunid (*Callinectes sapidus, bocourti, maracaiboensis*), and shrimp (Decapoda: palaemonid (*Palaemonetes*))	epizoic (gills)	North America
L. cochinensis	42-73 x 46-73	marine, attached to invertebrates (Isopoda: sphaeromatid (*Sphaeroma terebrans, walkeri, annandalei, triste, quoyanum, Exosphaeroma planulum*); Tanaidacea: parapseudid (*Ctenapseudes chilkensis*))	epizoic (appendages)	cosmopolitan
L. commensalis	90 x 60 x 35	freshwater, attached to invertebrates (Amphipoda: acanthogammarid (*Carinurus solsky*))	epizoic (maxillipeds)	Lake Baikal
L. crutchfieldi (syn. *Circolagenophrys*)	60-76 x 55-72 x 18-26	estuarine, attached to invertebrates (Amphipoda: hyalid (*Parhyale hawaiensis, penicillata*))	epizoic (gills)	Americas
L. darwinia	42 x 55	freshwater, attached to crayfish (Decapoda: parastacid (*Cherax quadricarinatus*))	epizoic (gills)	Australia
L. dennisi	51-72 x 40-66 x 15-29	freshwater, attached to crayfish (Decapoda: cambarid (*Cambarellus patzcuarensis, Cambarus bartonii, chasmodactylus, Orconectes illinoiensis*))	epizoic (carapace)	North America
L. deserti	50 x 57	freshwater, attached to crayfish (Decapoda: parastacid (*Cherax quinquecarinatus, tenuimanus*))	epizoic (gills)	Australia
L. diogenes (syn. *Circolagenophrys, L. incompta*)	55-77 x 53-73 x 19-39	freshwater, attached to crayfish (Decapoda: cambarid (*Cambarus diogenes, Orconectes illinoiensis*))	epizoic (gills)	North America

L. discoidea (syn. *L. labiata p.p., wallengreni, Circolagenophrys entocytheris*)	46-70 x 33-63 x 18-19	fresh and brackish water, attached to invertebrates (Ostracoda: candonid (*Candona elliptica, neglecta*), cyclocypridid (*Cyclocypris ovum, sharpei*), cypridid (*Chlamydotheca arcuata*, *Cypria ophthalmica, obesa, Cypridopsis vidua, Heterocypris similis*), entocytherid (*Ankylocythere hobbsi, ancyla, Dactylocythere daphnoides, jeanae, Donnaldsoncythere donnaldsonensis, Thermastrocythere riojai*); Amphipoda: crangonyctid (*Crangonyx gracilis*), gammarid (*Gammarus fossarum, daiberi, fasciatus, tigrinus, pulex*); Decapoda: astacid (*Pacifastacus nigrescens*), cambarid (*Cambarus chasmodactylus*, *bartonii*, *Orconectes illinoiensis*)	epizoic (carapace, appendages)	Eurasia, Americas
L. dungogi	70 x 69	freshwater, attached to crayfish (Decapoda: parastacid (*Euastacus clydensis*))	epizoic (gills)	Australia
L. engaei	54-63 x 54-55	freshwater, attached to crayfish (Decapoda: parastacid (*Engaeus hemicirratus, victoriensis, Paranephrops planifrons*))	epizoic (gills, appendages)	Australia, New Zealand
L. eupagurus (syn. *L. paguri, lunatus, articularis*)	39-75 x 39-77 x 10-23	freshwater or marine, attached to invertebrates (Decapoda: pagurid (*Pagurus longicarpus, Eupagrus*), palaemonid (*Macrobrachium nipponense, rosenbergii, ohione, Palaemonetes varians, pugio, intermedius, kadiakensis, paludosus, vulgaris, Palaemon paucidens, Leander paucidens*), penaeid (*Farfantepenaeus brasiliensis, Litopenaeus setiferus, vannamei*), upogebiid (*Upogebia affinis*); Amphipoda: corophiid (*Apocorophium acutum*)	epizoic (gills, appendages)	Eurasia, Americas
L. foxi	54-67 x 58-68 x 15-26	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus minus, pseudolimnaeus, trogophilus*))	epizoic (gills)	North America
L. hokkaidos (syn. *L. ampulla p.p., Circolagenophrys*).)	50-65 x 62	freshwater, attached to invertebrates (Amphipoda: gammarid (*Jesogrammarus annandalei, Gammarus pulex, roeseli*))	epizoic (gills, appendages)	Eurasia
L. inflata (syn. *Circolagenophrys*)	67 x 59 x 25	freshwater, attached to invertebrates (Amphipoda: acanthogammarid (*Brandtia* (*Gmelinoides*) *fasciata*))	epizoic (pleopods)	Lake Baikal
L. jacobi (syn. *Stylohedra*) [*nomen dubium*, possiblemixture of species]	-	freshwater, attached to crayfish (Decapoda: parastacid (*Engaeus fultoni, hemicirratus, Euastacus, Cherax rotundus*); Isopoda: phreatoicid (*Colubotelson*))	epizoic (setae, appendages)	Australia
L. johnsoni (syn. *L. labiata p.p.*)	56-70 x 44-62 x 12-22	fresh and brackish water, attached to invertebrates (Amphipoda: gammarid (*Gammarus fasciatus, daiberi, tigrinus*), crangoncytid (*Crangonyx gracilis*))	epizoic (gills)	North America
L. leniusculus (syn. *Circolagenophrys, L. oregonensis*)	56-70 x 58-63 x 14-23	freshwater, attached to crayfish (Decapoda: astacid (*Pacifastacus connectens, leniusculus*))	epizoic (gills)	Europe, North America
L. lenticula (syn. *Stylohedra, L. lenticulata*)	60	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus lacustris, pulex*), crangoncytid (*Crangonyx gracilis*), hyalellid (*Hyalella*	epizoic (pereiopods)	Eurasia, Americas

		azteca, curvispina, dentata))		
L. limnoriae (syn. *Circolagenophrys circularis, Platycola*)	39-51 x 38-46 x 15-27	marine, attached to invertebrates (Isopoda: limnoriid (*Limnoria lignorum*, *tripunctata*))	epizoic (pleopods)	North America, Europe
L. machaerigera (syn. *Circolagenophrys*)	74-84 x 64-71 x 18-28	freshwater, attached to crabs (Decapoda: potamonautid (*Foza goudoti*))	epizoic (gill)s	Madagascar
L. macrostoma (syn. *Circolagenophrys*)	80 x 65 x 23	freshwater, attached to invertebrates (Amphipoda: gammarid (*Carinogammarus/Coniurus radoschkowskii*))	epizoic (gills)	Lake Baikal
L. matthesi	65-82 x 60-78 x 30-40	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex, zaddachi, roeselii*))	epizoic (appendages)	Europe
L. maxillaris (syn. *Circolagenophrys*)	66-88 x 57-78 x 15-30	marine and brackish water, attached to invertebrates (Amphipoda: gammarid (*Gammarus locusta, oceanicus*))	epizoic (maxillipeds)	Europe
L. metopauliadis	80 x 94	freshwater (tank bromeliads), attached to bromeliad crab (Decapoda: sesarmid (*Metopaulis depressus*))	epizoic (gills)	Jamacia
L. missouriensis	62-69 x 53-60 x 14-28	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pseudolimnaeus*))	epizoic (appendages)	North America
L. monolistrae	55-85	freshwater, attached to invertebrates (Isopoda: asellid (*Caecidotea* (*Monlistra*) *berica*, *racovitzai*, *caeca*))	epizoic (pleopods)	Europe
L. nassa	60-85 x 48-75 x 20-30	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus pulex, lacustris, roeseli, Eogrammarus confervicolus, Echinogrammarus berilloni*))	epizoic (carapace, appendages)	Europe, North America
L. novazealandae	52-61 x 59-68 x 17-27	freshwater, attached to crayfish (Decapoda: parastacid (*Paranephrops setosus, zealandicus*))	epizoic (gills)	New Zealand
L. oblonga (syn. *Circolagenophrys*)	70 x 45 x 48	freshwater, attached to invertebrates (Amphipoda: gammarid (*Gammarus hyacinthinus*))	epizoic (antennae)	Lake Baikal
L. orchestiae	65 x 55	estuarine, attached to invertebrates (Amphipoda: talitrid (*Orchestia cavimana, uhleri*))	epizoic (gills)	Europe, North America
L. ornata (syn. *Circolagenophrys*)	80 x 54 x 30	freshwater, attached to invertebrates (Amphipoda: gammarid (*Echinogrammarus cyanoides, Carinogrammarus rhodophthalmus sablotzkii*))	epizoic (pereiopods)	Lake Baikal
L. ovalis (syn. *Circolagenophrys*)	85 x 71 x 32	freshwater, attached to invertebrates (Amphipoda: acanthogammarid (*Hyalellopsis variabilis*), eulimnogammarid (*Eulimnogrammus cyanoides*, *Macropereiopus wagneri*), micruropodid (*Micruropus littoralis*, *talitroides*))	epizoic (pereiopods)	Lake Baikal
L. parva (syn. *Circolagenophrys*)	56 x 23	freshwater, attached to invertebrates (Amphipoda: crypturopodid (*Crypturopus pachytus*), eulimnogammarid (*Eulimnogammarus fiscus*))	epizoic (pereiopods)	Lake Baikal
L. patina (syn. *L. labiata p.p.*)	50-75 x 50-78 x 13-25	freshwater, attached to invertebrates (Amphipoda: acanthogammarid (*Hyalella azteca*, *curvispina*), crangonyctid (*Crangonyx gracilis*), gammarid (*Gammarus lacustris*, *pulex*), talitrid (*Orchestia cavimana*))	epizoic (body)	Eurasia, North America
L. petila	93-126 x 32-45	freshwater, attached to crayfish (Decapoda: parastacid (*Parastacoides*	epizoic (gills, pleopods)	Australia

		tasmanicus))		
L. platei	56 x 60	freshwater, attached to invertebrates (Isopoda: asellid (*Asellus aquaticus*); Amphipoda: gammarid (*Gammarus pulex*))	epizoic (gills)	Europe
L. pontocaspica	50-65 x 50-65 x 29-33	freshwater, attached to invertebrates (Amphipoda: gammarid (*Amathillina cristata, Chaetogrammarus ischnus, Dikerogrammarus haemobaphes, villosus, Obesogrammarus crassus, Pontogrammarus abbreviatus, maeoticus, robustoides*))	epizoic (gills, oostegites)	Europe
L reflexa (syn. *Stylohedra*)	-	freshwater, attached to invertebrates (Isopoda: amphisopodid (*Mesamphisopus capensis*))	epizoic (setae)	Africa
L. rugosa	53 x 69	freshwater, attached to crayfish (Decapoda: parastacid (*Engaeus marmoratus, Geocharax falcata*))	epizoic (gills)	Australia
L. shiftus (syn. *Circolagenophrys*)	54-60 x 44-46 x 24-27	freshwater, attached to crayfish (Decapoda: parastacid (*Parastacus pugnax, chilensis*))	epizoic (gills)	South America
L. similis (syn. *Circolagenophrys*)	85 x 38	freshwater, attached to invertebrates (Amphipoda: acanthogammarid (*Hyalellopsis czyrnianskii*), eulimnogrammarid (*Eulimnogammarus verrucosus*))	epizoic (gills)	Lake Baikal
L. simplex (syn. *Circolagenophrys*)	75 x 35	freshwater, attached to invertebrates (Amphipoda: acanthogammarid (*Dorogammarus castaneus*), pallaseid (*Pallasea bicornis*))	epizoic (pereiopods)	Lake Baikal
L. solida	105 x 77 x 33	freshwater, attached to invertebrates (Amphipoda: gammarid (*Plesiogammarus gerstaeckeri*))	epizoic (pereiopods)	Lake Baikal
L. stammeri	88-104 x 88-97 x 40-45	freshwater, attached to invertebrates (Ostracoda: cypridid (*Cypria ophthalmica*))	epizoic (carapace)	Europe
L. stokesi	100 x 42	freshwater, attached to invertebrates (Amphipoda: gammarid (*Axelboeckia potanini*), eulimnogammarid (*Odontogammarus calcaratus*), ommatogammarid (*Ommatogammarus flavus*, *carneolus*))	epizoic (gills)	Lake Baikal
L. stygia (syn. *L. labiata p.p.*, *Circolagenophrys*)	45-73 x 44-68 x 14-22	freshwater, attached to invertebrates (Amphipoda: crangoncytid (*Bactrurus mucronatus*))	epizoic (gills)	North America
L. tattersalli	50-70 x 50-70 x 20-25	marine, attached to invertebrates (Amphipoda: gammarid (*Echinogammarus marinus*))	epizoic (gills)	Europe
L. turneri (syn. *Circolagenophrys*)	51-62 x 54-67 x 13-21	freshwater, attached to shrimps (Decapoda: palaemonid (*Macrobrachium rosenbergii*))	epizoic (gills)	Australasia
L. vaginicola (syn. *L. obovata*) [type species]	45-80 x 42	freshwater, attached to invertebrates (Copepoda: cyclopid (*Cyclops minutus*), canthocamptid (*Bryocamptus minutus*, *Canthocamptus staphylinus*), harpacticoid (unspecified); Isopoda: asellid (*Asellus aquaticus*))	epizoic	Eurasia, America
L. verecunda	61-93 x 70-99 x 19-25	freshwater, attached to shrimp (Decapoda: palaemonid (*Palaemonetes kadiakensis, paludosus*))	epizoic (gills)	North America
L. willisi	44-55 x 64-80	freshwater, attached to crayfish (Decapoda: parastacid (*Cherax albidus, destructor, rotundus, setosus*))	epizoic (gills)	Australia

Genus: ***Operculigera*** (body rounded, with flat discoid lorica, without stalk, aperture a simple opening with a flap-like operculum used for closure, on marine/freshwater crustacea)				
O. asymmetrica	69-80 x 67-81 x 20-31	freshwater, attached to crayfish (Decapoda: parastacid (*Parastacus pugnax, Samastacus spinifrons*))	epizoic (gills	South America
O. carcini	75-81 x 67-75 x 17-27	freshwater, attached to crabs (Decapoda: potamonautid (*Foza goudoti*))	epizoic (gills)	Madagascar
O. haswelli	70-83 x 74-89 x 14-21	freshwater, attached to invertebrates (Isopoda: phreatoicid (*Mesacanthotelson tasmaniae*))	epizoic (pleopods)	Australia
O. inornata	60-76 x 53-76 x 15-23	freshwater, attached to invertebrates (Isopoda: phreatoicid (*Phreatoicopsis terricola, Colubotelson chiltoni*))	epizoic (pleopods)	Australia
O. insolita	97-113 x 101-118 x 30-46	freshwater, attached to crayfish (Decapoda: parastacid (*Parastacus pugnax*))	epizoic (gills)	South America
O. madagascarensis	62-73 x 69-83 x 16-25	freshwater, attached to crayfish (Decapoda: astacid (*Astacoides granulimanus*))	epizoic (gills)	Madagascar
O. montanea [type species]	54-62 x 57-71 x 34-41	freshwater, attached to invertebrates (Isopoda: phreatoicid (*Colubotelson joyneri, searlei*))	epizoic (pleopods)	Australia
O. obstipa	58-71 x 66-79 x 19-28	freshwater, attached to invertebrates (Isopoda: phreatoicid (*Metaphreatoicus australis*))	epizoic (pleopods)	Australia
O. parastacis	84-87 x 86-92 x 45	freshwater, attached to crayfish (Decapoda: parastacid (*Parastacus pugnax/chilensis* (as *nicoleti*))	epizoic (gills)	South America
O. seticola	71-81 x 47-56 x 33-43	freshwater, attached to crayfish (Decapoda: parastacid (*Parastacus pugnax*))	epizoic (setae)	South America
O. striata	50-70 x 95-104 x 26-28	freshwater, attached to crayfish (Decapoda: parastacid (*Parastacus pugnax/chilensis*))	epizoic (gills)	South America
O. taura	66-79 x 82-95 x 26-43	freshwater, attached to crayfish (Decapoda: parastacid (*Parastacus pugnax*))	epizoic (gills)	South America
O. velata	78-85 x 73-77	freshwater, attached to invertebrates (Decapoda: aeglid (*Aegla laevis*))	epizoic (gills)	South America
O. zeehanensis	74-82 x 78-89 x 29-33	freshwater, attached to invertebrates (Isopoda: phreatoicid (*Phreatoicoides longicollis*))	epizoic (pleopods)	Australia
Genus: ***Paralagenophrys*** (body rounded, with discoidal lorica, lorica aperture an invaginated tube (loricastome) at oblique angle to long axis, aperture closed by drawing together flexible opposing lips, monotypic)				
P. singularis [type species as *Lagenophrys*]	78-94 x 70-82 x 21-32	freshwater, attached to detritus, aquatic plants (*Lemna, Myriophyllum, Utricularia*), mosses (on cypress *Ludwigia*), snails (Gastropoda: amnicolid (*Amnicola*), barnacles Cirripedia: cyprid (*Cypris*) and crayfish (Decapoda: cambarid (*Cambarus bartonii*))	epiphytic, epizoic	North America
Genus: ***Setonophrys*** (body rounded, within flat discoid lorica, lorica aperture an invaginated tube (loricastome) perpendicular to long axis, aperture closed by bringing together rigid anterior lip and flexible posterior retractable lip)				
S. bispinosa (syn. *Lagenophrys*)	94 x 95	freshwater, attached to crayfish (Decapoda: parastacid (*Cherax rotundus*))	epizoic (appendages)	Australia
S. communis (syn. *Lagenophrys, L. latispinosa, lawrii*)	59-102 x 55-96 x 15-28	freshwater, attached to crayfish (Decapoda: parastacid (*Cherax albidus, destructor, quadricarinatus, Engaeus marmoratus, Euastacus armatus, nobilis*) and isopods (Isopoda: amphisopid (*Synamphisopus ambiguous*))	epizoic (gills, appendages)	Australia
S. lingulata (syn. *Lagenophrys*)	50-60 x 58-84 x 20-27	freshwater, attached to crayfish (Decapoda: parastacid (*Cherax albidus,*	epizoic (gills)	Australia

		depressus, destructor, rotundus))		
S. nivalis (syn. *Lagenophrys*, *Circolagenophrys*)	90-103 x 75-86 x 22-30	freshwater, attached to isopods (Isopoda: phreatoicid (*Colubotelson searlei*))	epizoic (carapace, appendages)	Australia, Russia
S. occlusa (syn. *Lagenophrys*)	67-75 x 64-71	freshwater, attached to crayfish (Decapoda: parastacid (*Cherax albidus, destructor, rotundus, Geocharax falcata*))	epizoic (gills)	Australia
S. seticola [type species as *Lagenophrys*]	100-119 x 36-43 x 23-29	freshwater, attached to crayfish (Decapoda: parastacid (*Cherax albidus, destructor, rotundus setosus, Engaeus fultoni, Euastacus nobilis, Geocharax falcata*))	epizoic (setae)	Australia
S. spinosa (syn. *Lagenophrys*)	78-80 x 77-80	freshwater, attached to crayfish (Decapoda: parastacid (*Cherax destructor*))	epizoic (carapace)	Australia
S. tricorniculata	89-105 x 85-102 x 19-28	freshwater, attached to crayfish (Decapoda: parastacid (*Geocharax falcata*))	epizoic (pleopods)	Australia

Parasite morphology: Sessiline peritrichous ciliates form 3 basic life-cycle stages: feeding trophonts (zooids); dispersal swarmers (telotrochs); and some species form resistant cysts. Trophonts vary considerably in size, shape and appearance depending on the species and their state of nutrition (well-fed individuals being larger and more robust). Most species form trophonts ranging in size from 10-80 µm, although some species also form macrozooid stages measuring up to 150 µm long. Trophonts may be ovoid to cylindrical to discoid in shape, but they all possess anterior oral cilia. Like all peritrichs, the trophonts have specialized mouthparts with peristomial ciliary wreaths (spirals of cilia) winding counter-clockwise around the apical funnel-shaped buccal cavity down into the cytostome. The ciliary wreaths comprise a prominent paroral membrane (outer haplokinety) accompanied by a smaller series of membranelles (inner polykinety, often triple). Trophonts are sessile as they attach themselves to substrates using a variety of posterior holdfast structures, including small flat adhesive discs (scopulae), short-elongate stalks (solitary or branched) or vase- to disc-like loricae (upright or flat). The stalks of some species may also contain straight or sinusoidal contractile myonemes that allow them to rapidly contract in spiral or zig-zag fashion when disturbed. Species with branched stalks may form large tree-like colonies comprising up to hundreds of individual zooids. When starved, the trophonts of several species have been observed to form small ovoid cysts (10-30 µm in diameter) that are surrounded by tough membranous coats, mostly smooth but some irregular or granular. Telotroch stages are formed often in adverse conditions when trophonts detach from their substrates, stalks or loricae, round up (often barrel-shaped) and form motile unattached swarmer stages. These stages are often mouthless but may retain inert or retracted oral cilia or their primordia. Cell motility occurs by the development of a ring of somatic cilia usually around the posterior body.

Site of infection: Peritrichous ciliates live in aquatic habitats (freshwater, estuarine and marine waters) as free-living species (attached to inanimate objects), epiphytic species (attached to plants) or epizoic species (attached to animals). Infestations have been reported on the superficial surfaces of vertebrates (mainly fish and some amphibians) and invertebrates (crustaceans (decapods, branchiopods, isopods, copepods, amphipods, ostracods), molluscs (gastropods, bivalves), insects, annelids (polychaetes, oligochaetes, leeches), bryozoa and hydrozoa). Infestations may occur on the skin, fins or gills of vertebrates, or on the carapace, brachial chambers or legs (feeding maxillipeds, walking pereiopods, swimming pleopods (swimmerets)) of crustaceans. Infestations have been found in wild and cultured animals, and significant biofouling may occur in intensive aquaculture systems when animals are overcrowded in organically-enriched waters.

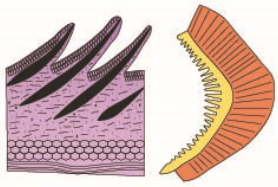
Pathogenesis: Peritrichous ciliates are filter-feeders which use their oral ciliary wreaths to create minute water currents drawing material into the buccal cavity. They feed on solutes and particulates in water, especially bacteria which can often be seen in food vacuoles in the ciliate cytoplasm. They attach themselves to substrates by their posterior ends so that their anterior mouths project outwards into the water column. Many species are considered to be opportunistic ectocommensals of fish and shellfish, but their presence may sometimes cause problems. While ciliates attached to hard surfaces (such as crustacean exoskeletons) do not cause tissue lesions, heavy infestations may cause significant fouling of external surfaces resulting in the unsightly appearance of animals (and reducing their marketability), while fouling of the mouthparts and associated appendages may interfere with host feeding leading to loss of condition. In comparison, ciliates attached to soft tissues (such as gills and skin) may cause some attachment-associated pathologies, with irritation and inflammation leading to gill congestion or skin lesions. Animals may exhibit in respiratory disorders, particularly those infested by ciliate species that form loricae cemented to gill filaments thus reducing functional surface areas resulting in hypoxia. Skin lesions reduce the marketability of fish, and make the hosts more prone to secondary infections by bacteria or fungi. Infestations by sessile peritrichs are more severe on small animals (especially fish fry), and are more abundant during the winter months when hosts are more sedentary. They may become problematic in aquaculture systems when waters become organically enriched resulting in bacterial blooms on which ciliates feed voraciously allowing for rapid population growth.

Developmental cycle and mode of transmission: These peritrichs are free-living ciliates occurring in aquatic habitats, but the feeding stages (trophonts or zooids) attach themselves directly or via stalks or loricae to solid substrates (the surfaces of inanimate objects, plants or animals) where they filter-feed. When conditions are suitable (abundant food, good water quality), the ciliates multiply asexually by binary fission involving the transverse splitting of trophonts into 2 daughter cells. Cell division may continue every few days allowing ciliate populations to grow exponentially. When food becomes scarce, some species initiate sexual reproduction by a unique process of conjugation where mating pairs involve the permanent fusion of a motile microconjugant with a sessile macroconjugant. Sexual reproduction enhances genetic diversity which is thought to promote the chances of survival of at least some offspring. The transmission of ciliates from one host to another is direct via water-borne stages. Some trophonts may detach from hosts in close contact or crowded conditions and subsequently reattach to new hosts. However, in adverse conditions (depleted food, poor water quality, mechanical disturbances), trophonts detach and form swarmer stages (telotrochs) which swim erratically in the water column seeking better substrates. Some species have also been observed to form resistant cysts to survive poor environmental conditions. Transmission of infestations between animal hosts is therefore direct via trophont transfer, via swarmers seeking new hosts, or via stages released from cysts.

Differential diagnosis: Infestations may be indicated by the visual detection of fouled carapaces or body surfaces, with the most conspicuous peritrich species appearing as slimy greenish colonies. However, many species are not green and do not form colonies, but heavy infestations by large numbers of solitary ciliates may cause minor disfigurement evident as discolourations, flecking and even some opacities. Infestations are confirmed by the microscopic detection of ciliates on specimens collected from live or dead hosts, including skin scrapings, fin snips, gill filaments, excised carapace sections, leg segments, or tissue fragments. Samples may be initially screened as wet mounts under the dissecting microscope looking for live ciliates as evidenced by active oral cilia or contractility of zooids and/or stalks. Specimens may then be collected by pipette and transferred to drops on glass slides and examined by compound light microscopy to reveal finer cellular details. Live ciliates are best observed using high-contrast bright-field, phase-contrast or interference-contrast microscopy, and counterstains may be used to reveal internal cellular details (e.g. methyl-green pyronin and methylene blue used to stain nuclei). Most genera can be identified by the morphological characteristics of the attachment apparatus (scopula, stalks, loricae), oral ciliation, pellicular adornments and nuclear configurations. However, specific identification is reliant on the silver impregnation of fixed specimens that have been enrobed onto albuminized slides and stains with silver proteinate (protargol), silver nitrate or silver carbonate to reveal the argentophilic basal bodies (kinetosomes), nuclei and pellicular striations. Researchers often use scanning electron microscopy to reveal topographical features or transmission electron microscopy to identify organelles and patterns of infraciliature. Free-living peritrichous species may be readily cultivated *in vitro* in a range of plant infusions or semi-defined media containing plentiful feeder bacteria, but those species only found in association with specific hosts and specific host tissues are difficult to maintain. Several *in vivo* animal models have been used experimentally to study particular ciliates, but not for long-term propagation. Molecular characterization studies initially used isoenzyme electrophoresis to profile several peritrichous species, but modern molecular biological techniques have now been used to characterize species and determine phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (mainly small subunit (18S) ribosomal DNA, and internal transcribed spacer regions).

Treatment and control: Infestations by peritrichous ciliates on fish or shellfish have been treated by washing fouled animals in clean water or by bathing them in hypo- or hyper-tonic solutions (e.g. freshwater baths for marine species and saltwater baths for freshwater species) or chemical solutions (including formalin, potassium permanganate, copper sulphate, malachite green). However, some treatments had adverse side-effects on the hosts and many of the chemicals are prohibited for use in food animals due to concerns over toxic residues. Various preventive measures have been used to reduce contamination by fouling organisms, particularly in closed aquaculture systems. Animals should be regularly inspected for biofouling, with affected animals removed for treatment, quarantine or culling. Tanks and ponds should be decontaminated by draining and drying or chemical disinfection. Peritrichous ciliates proliferate when bacteria are abundant so every effort should be made to reduce organic enrichment of holding facilities, including clearing overgrowth by aquatic plants and even grassy verges, avoiding over-feeding, and periodic flushing to remove accumulated wastes and prevent stagnation and eutrophication. It is also essential to keep animals healthy and avoid stressful (immunocompromising) situations that increase host susceptibility, such as over-crowding or over-handling stock, and not maintaining good water quality (temperature, pH, oxygenation).

Peritrichous ciliates



skin, gills
(unsightly fouling,
sometimes congestion)

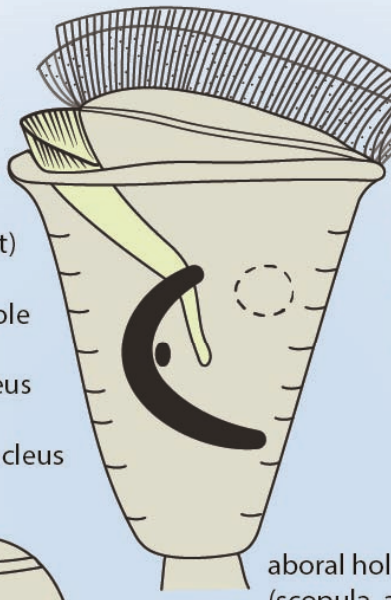
may reproduce asexually
(by transverse binary fission)
or sexually (by conjugation)

mostly free-living aquatic organisms that
opportunistically attach to host surfaces
as epizoic/ectocommensal organisms



Vertebrate Hosts
(freshwater and
marine fish,
crustaceans)

sessile filter-feeding trophont/zooid
(10-80 µm) (stalked, stalkless or loricate)



peristomial disc

peristomial lip

infundibulum (gullet)

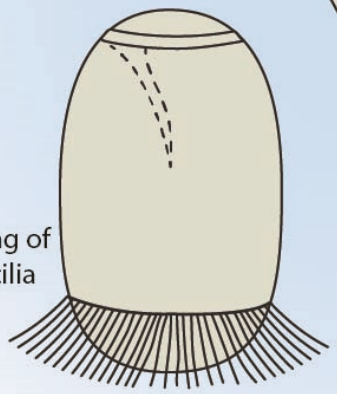
contractile vacuole

micronucleus

macronucleus

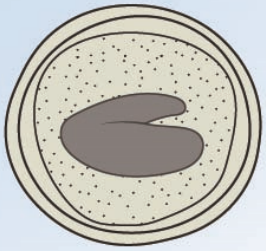
peritrichous oral ciliature:
counter-clockwise (lefthand)
peristomial ciliary wreath with:
- outer circlet (paroral
  undulating membrane)
- inner circlets (series of
  membranelles)

aboral holdfast organelle
(scopula, adhesive disc, stalk or lorica)



aboral ring of
somatic cilia

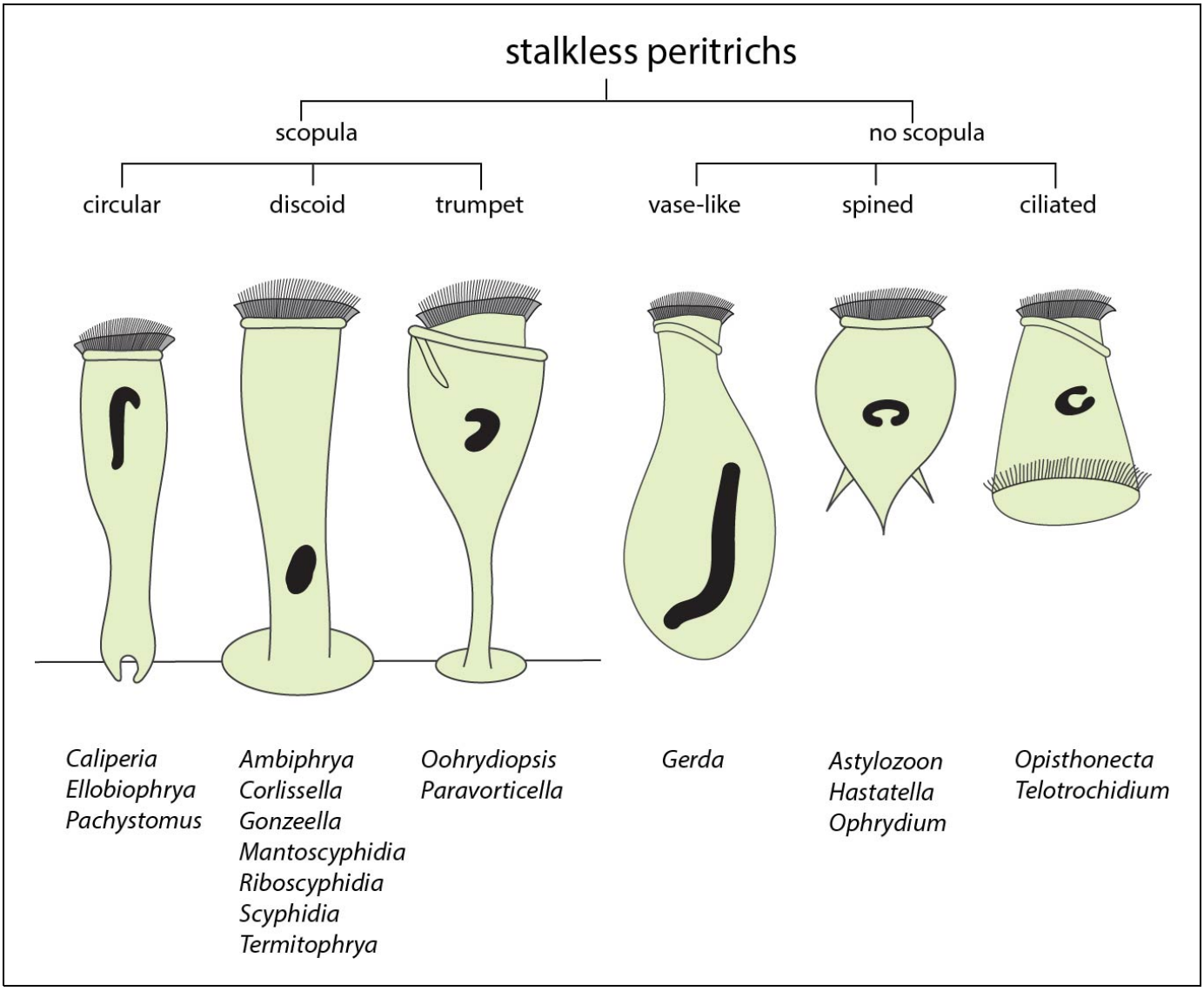
telotroch/swarmer
(nonfeeding dispersal
stage) (10-50 µm)

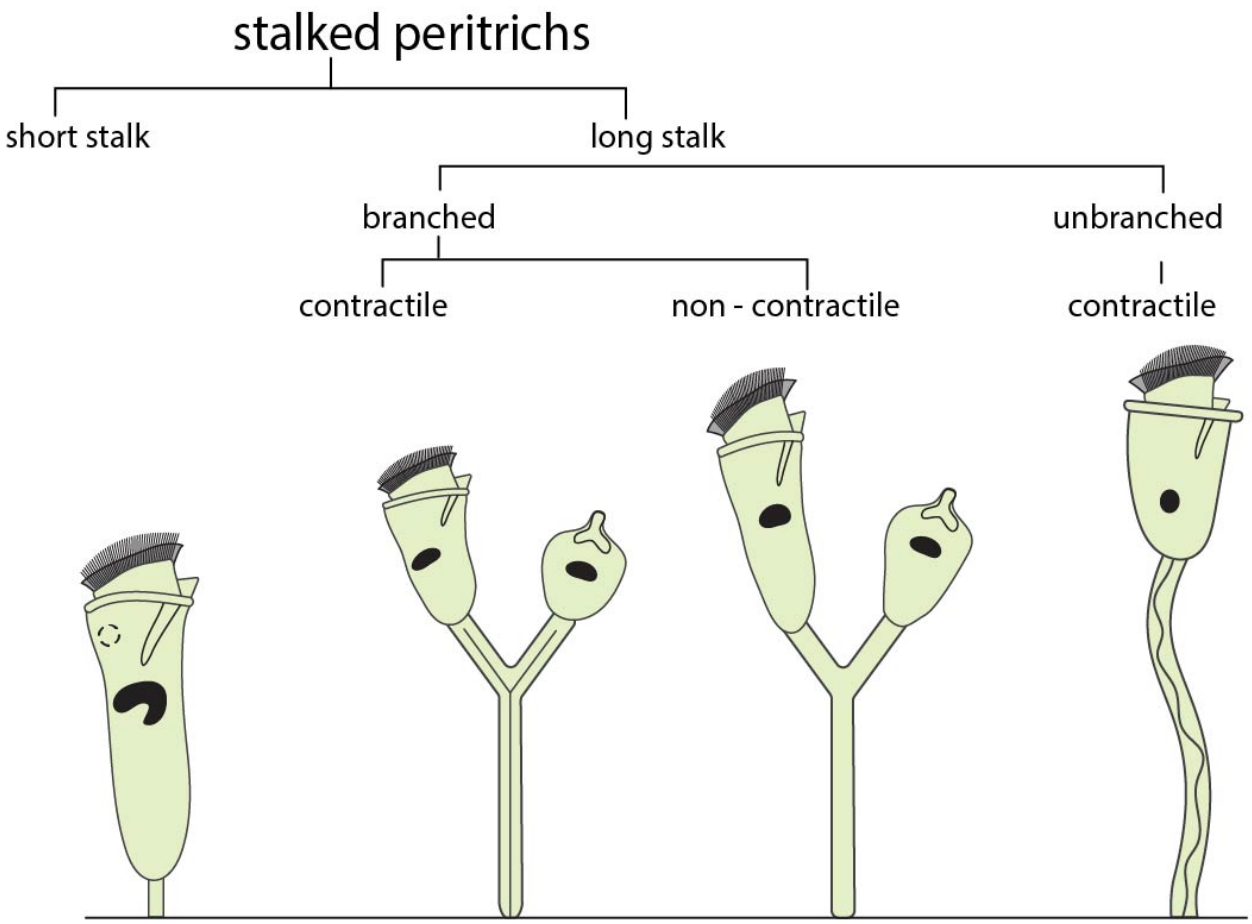


nonmotile

cyst (10-30 µm)
(only observed for
several species)

transmission via free-swimming swarmers in water column
attaching to substrates (incl. host surfaces)


stalkless peritrichs
scopula
no scopula
circular
discoid
trumpet
vase-like
spined
ciliated
Caliperia
Ellobiophrya
Pachystomus
Ambiphrya
Corlissella
Gonzeella
Mantoscyphidia
Riboscyphidia
Scyphidia
Termitophrya
Oohrydiopsis
Paravorticella
Gerda
Astylozoon
Hastatella
Ophrydium
Opisthonecta
Telotrochidium

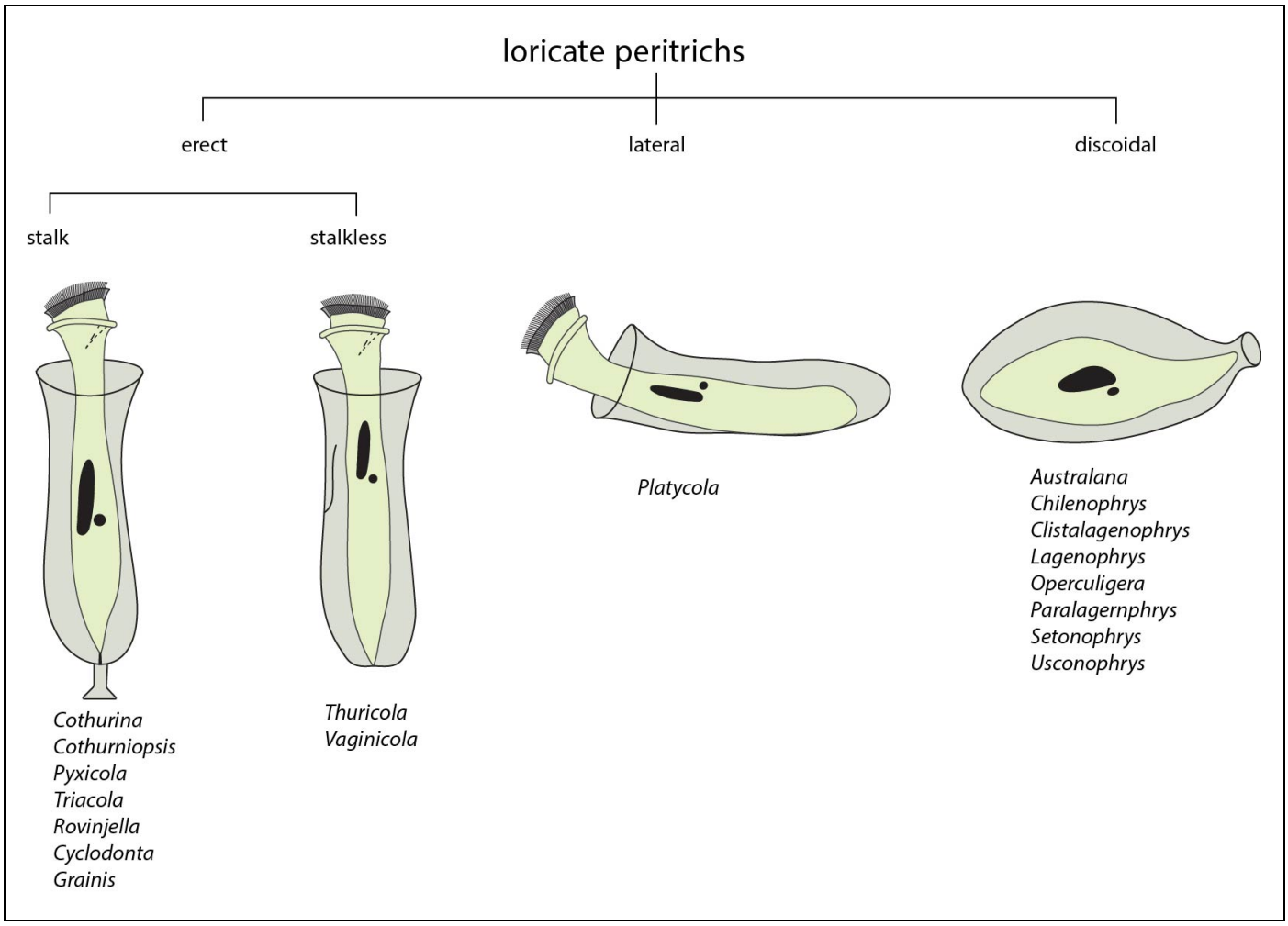


Apiosoma
Foissnerella
Orborhabdostyla
Rhabdostyla
Nuchterleinella
Ballodora
Orbopyxidiella
Propyxidium
Triadopercularia

Carchesium
Entziella
Epicarchesium
Intrastylum
Pseudocarchesium
Rithiella
Craspedomyoschiston
Mesothamnium
Myoschiston
Zoothamniodes
Zoothamnium
Zoothamnopsis

Campanella
Epistylis
Heteropolaria
Pseudepistylis
Bezedniella
Opercularia
Operculariella
Orbopercularia
Systylis

Apocarchesium
Baikalonis
Baikalaster
Cotensita
Parazoothamnium
Pelagovorticella
Piesika
Planeticovorticella
Pseudovorticella
Spinivorticella
Tucolesca
Vorticella
Vorticellides
Haplocaulus
Pseudohaplocaulus


loricate peritrichs
erect
lateral
discoidal
stalk
stalkless
Cothurina
Cothurniopsis
Pyxicola
Triacola
Rovinjella
Cyclodonta
Grainis
Thuricola
Vaginicola
Platycola
Australana
Chilenophrys
Clistalagenophrys
Lagenophrys
Operculigera
Paralagernphrys
Setonophrys
Usconophrys



Epistylis zooids attached to yabby carapace



Vorticella zooids attached to yabby carapace



Lagenophrys loricae attached to yabby gill



Lagenophrus loricae attached to yabby gill (sEM)



Vaginicola loricae attached to yabby carapace



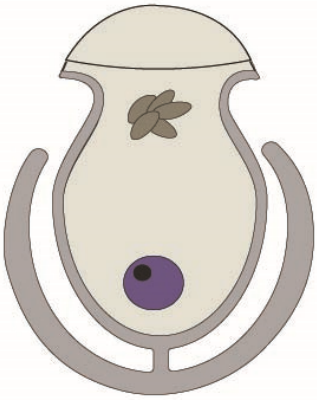
Vaginicola loricae attached to yabby carapace

Ascetospora
(haplosporeans, paramyxeans)

Ascetospora

haplosporidia

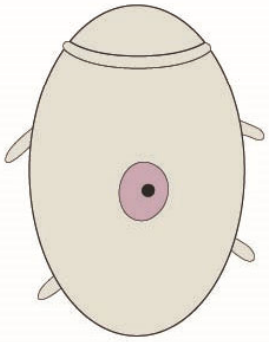
Haplosporidium
(3-8 µm)



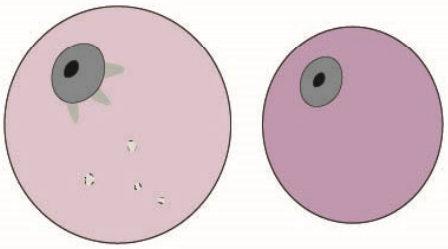
Minchinia
(3-8 µm)



Bonamia
(4-6 µm)

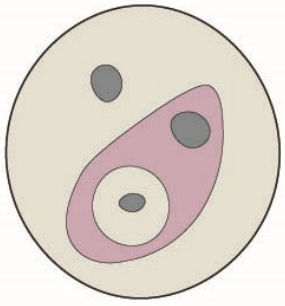


Mikrocytos
(2-5 µm)



paramyxean

Marteilia
(4-10 µm)



Haplosporidium*, *Minchinia
(protist: haplosporidian)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Two major rhizarian groups are recognized: retarians (with reticulopodia) and cercozoans (with filopodia). An enigmatic cercozoan group is the Ascetospora which contains the spore-forming Haplosporidia and Paramyxea. Haplosporidia are characterised by the formation of unicellular spores (without polar capsules or polar filaments) that contain a single sporoplasm and several dense organelles (known as haplosporosomes). The complete developmental cycles of most species are not known. Most have two developmental stages: multinucleate plasmodia and spores (although *Mikrocytos* (and some *Bonamia* spp.) form microcells). The multinucleate plasmodia undergo modified schizogony giving rise to sporonts which eventually differentiate into spores. The spore orifice is covered by an external hinged operculum and spores often have elaborate spore wall ornamentations appearing as filamentous tails or wrappings. Most species are histozoic or coelozoic parasites of aquatic molluscs, annelids, crustaceans and helminths. Several species cause significant diseases and mortality in oysters around the world.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Rhizaria (various amoebae and flagellates)
Division:	Cercozoa (biflagellated and/or amoeboid, usually with filopodia, plus ascetospora)
Phylum:	Ascetospora (haplosporidian and paramyxean parasites forming unique spores)
Class:	Haplosporea (haplosporosomes present)
Order:	Haplosporida (spore with one sporoplasm, spore orifice covered externally by operculum or internally by diaphragm)
Family:	Haplosporididae (spores with operculum)
Genus:	*Haplosporidium* (parasitic in tissues of bivalves and crustaceans)
Genus:	*Minchinia* (parasitic in tissues of bivalves)
Species:	various species cause mortalities in oysters and blemishes in other shellfish

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Two major rhizarian groups are recognized: retarians (with reticulopodia) and cercozoans (with filopodia). An enigmatic cercozoan group is the Ascetospora which contains the spore-forming Haplosporidia and Paramyxea that lack flagella and pseudopodia. Haplosporidia are usually characterised by the formation of unicellular spores (without polar capsules or polar filaments) that contain a single sporoplasm and several membrane-bound electron-dense organelles (known as haplosporosomes), while paramyxeans form unique multicellular (nested) spores. Most species occur as histozoic or coelozoic parasites of aquatic invertebrates (including molluscs, annelids, crustaceans, ascidians and helminths), and several species cause significant diseases and mortality in oysters around the world.

The identification and classification of haplosporidians has a complex and turbulent history. The complete developmental cycles of most species are not known, but various members of the genera *Haplosporidium*, *Minchinia* and *Urosporidium* were shown to form 2 developmental stages: multinucleate plasmodia which undergo modified schizogony to form sporonts that eventually differentiate into uninucleate spores. The spores were surrounded by a spore wall with an orifice (micropyle) and the enclosed endosporoplasm contained a complex membranous system known as a spherulosome (or spherule). Members of several other genera (*Bonamia* and *Mikrocytos*) which produced microcells (but not spores) were nonetheless recognized as haplosporidians on the basis of perceived structural and biological similarities. However, subsequent ultrastructural and molecular characterization studies have now removed *Mikrocytos* to a separate order Mikrocytida as they do not produce plasmodia, spores or haplosporosomes, while *Bonamia* was retained with the Haplosporida as they produced haplosporosomes. Recent studies have since shown that one *Bonamia* species (*B. perspora*) does produce spores, and conversely, that a few *Haplosporidium* spp. (e.g. *H. littoralis*) do not actually produce spores as supposed. Ultrastructural studies conducted on spores demonstrated that the orifice was covered either by an external hinged operculum (adopted as a key characteristic for the family Haplosporidiidae containing the genera *Haplosporidium*, *Minchinia* and *Bonamia*) or occluded by an internal flap-like lingula (taken to characterize the monotypic family Urosporidiidae). Many spores also possessed elaborate external ornamentations, described variously as tails, filaments, folds, projections, extensions or wrappings. It was initially thought that their presence and structure could be used to differentiate taxa, but studies demonstrated considerable variation both between and within taxa. Most *Minchinia* spores lacked ornaments, but some

isolates were found with epispore cytoplasmic extensions, albeit transiently as they disappeared during the spore maturation process. It was speculated that genera could be discerned by the origins (rather than the structure) of the ornamentations, being derived from either spore wall material (as found for many *Haplosporidium* spp. and one *Bonamia* sp.) or from epispore cytoplasmic extensions (observed for *Urosporidium* spp. and a few *Minchinia* isolates). However, molecular characterization studies did not reveal any strong correlations with morphotypic (phenetic) characters. Instead, phylogenetic analyses revealed a series of polyphyletic clades, including: a basal clade of diverse *Haplosporidium* isolates; a more derived clade containing most *Urosporidium* isolates from helminths; 2 sister clades containing *Minchinia* and *Bonamia* isolates respectively; and a clade containing many *Haplosporidium* isolates from gastropods. [Note that various spore-forming organisms detected in cockroaches, copepods, rotifers, polychaetes and toads that were originally thought to be other haplosporidian genera (e.g. *Bertramia, Coelospora, Coelosporidium, Nephridiophaga*) are now considered to be fungi on the basis of molecular phylogenetic studies.]

Family	Genus	Biodiversity	Characters	Hosts
Order: Haplosporida (form unicellular spores/microcells with haplosporosomes)				
Haplosporidiidae (spores with operculum)	*Haplosporidium*	33	spores with external hinged lids, spores with filaments of spore wall material	oligochaetes, molluscs, crustacea, urochordates, echinoderms, polychaetes
	Minchinia	6	spores with external hinged lids, some spores with transient extensions of epispore cytoplasm	oysters, chitons, clams, tusk shells, shipworms
	Bonamia	4	microcells formed, one species forming spores with external hinged lids and filamentous projections of spore wall material	oysters
Urosporidiidae (spores without operculum)	*Urosporidium*	7	spores occluded with internal lingula (plug, flap, diaphragm)), spores with tapering extensions of epispore cytoplasm	hyperparasitic in helminths of molluscs and crabs
Order: **Mikrocytida** (form microcells without haplosporosomes)				
Mikrocytidae	*Mikrocytos*	5	form microcells, no spores, no plasmodia, no haplosporosomes	oysters, clams
	Paramikrocytos	1	form microcells, no spores, no plasmodia, no haplosporosomes	crabs

Haplosporean infections have been detected throughout the world in aquatic invertebrates in coastal waters (freshwater, marine and brackish waters). The genus *Haplosporidium* is a diverse group of species, most of which form operculate spores with elaborate spore wall ornamentations. Over 30 species have been described from freshwater oligochaetes and marine molluscs, crustacea, urochordates, echinoderms and polychaetes. Several species infect commercially important bivalves, sometimes causing epizootic mortalities in oysters, notably *H. nelsoni* and *H. costale* causing MSX (= multinucleate sphere unknown) and SSO (= seaside organism) diseases respectively, particularly in eastern oysters. A range of nominal species have also been assigned *sensu latu* (in the broadest sense) to the genus *Haplosporidium,* including some that apparently do not form spores and others that form spores without orifices (pores) or lids (opercula, clapet). Some of these enigmatic species have since been transferred to other assemblages on the basis of comparative morphological or molecular studies (notably to novel ascetosporan groups, and even to several fungal genera), while the remainder are considered *species inquirenda*, *incertae sedis* or *nomen dubium.* Members of the genus *Minchinia* form operculate spores without ornamentations and some 6 species have been described from chitons, clams, pearl oysters and shipworms. [The third haplosporidiid genus *Bonamia* is considered separately in the next section as these unique parasites form 'microcells' in oysters and generally do not produce spores, although one species has recently been reported to do so].

Parasite species	Spore size	Hosts	Location [Clinical signs]	Distribution
Haplosporidium (operculate spores with ornaments derived from spore wall)				
H. armoricanum (syn. *Minchinia*)	5.0-5.5 x 3.1-4.5 µm	Bivalvia: ostreid (European flat oyster, southern mud oyster)	viscera [brown meat disease]	Europe
H. ascidiarum (syn. *Minchinia*)		Ascidiacea: cionid (vase tunicate), polyclinid (sea-strawberry)	stomach	Mediterranean
H. caulleryi		Polychaeta: nereidid (*Neanthes* (*Nereilepas*) *fucata*)		Europe
H. cernosvitovi	10-11 x 6-7 µm	Clitellata: naidid (aquatic worm *Opisthocysta flagellum*)		South America

H. comatulae	6 x 4 µm	Crinoidea: colobometrid (sawtoothed feather star)	haemal spaces in intestinal wall	Australia
H. costale (syn. *Minchinia*) [SSO = seaside organism]	3.1 x 2.6µm	Bivalvia: ostreid (eastern oyster, Pacific oyster)	connective tissues, digestive gland	North America, Eurasia
H. diporeiae	4-7 x 3-5 µm	Amphipoda: pontoporeiid (*Diporeia* sp.)	coelom, connective tissue, digestive tissue, muscle	North America
H. edule	3.2 x 2.2 µm	Bivalvia: cardiid (common cockle)	digestive gland	Europe
H. heterocirri (syn. *Minchinia*, *Aplosporidium*)	not stated	Polychaeta: cirratulid (*Heterocirrus viridis*)		Europe
H. hinei	3.5-4.0 x 2.5-3.0 µm	Bivalvia: pteriid (South Sea pearl oyster)	connective tissue of digestive gland	Australia
H. limnodrilli	10-12 x 8-10 µm	Clitellata: naidid (worm *Limnodrilus udekemianu*)		Europe
H. louisiana (syn. *H. cadomensis*, *Minchinia*)	12 x 8 µm	Decapoda: panopeid (dwarf crab, Atlantic mud crab)	gut wall	North America, Europe
H. lusitanicum	3.0 x 2.1 µm	Gastropoda: patellid (limpet *Helicon pellucidus*)	gills, viscera	
H. marchouxi		Polychaeta: serpulid (tubeworm *Salmacina dysteri*)		Europe
H. meligethi	3.3-4.8 x 1.6-2.6 µm	Coleoptera: nitidulid (rape blossom beetle)	intestines	Europe
H. montforti	2.4 x 2.3 µm	Gastropoda: haliotid (green ormer)	connective tissue, gill, digestive gland, foot muscle	Europe
H. nelsoni (syn. *Minchinia*) [MSX = multinucleate sphere unknown]	5-11 x 5-8 µm	Bivalvia: ostreid (eastern oyster, Pacific oyster)	gills, gonads, digestive gland [blemishes, mortalities]	North America, Asia
H. nemertis	7 x 4 µm	Nemertea: lineid (ribbonworm *Lineus hilineatus*)		Europe
H. parisi	not stated	Polychaeta: serpulid (calcareous tubeworm)		Atlantic
H. patagon	4.2 x 2.5 µm	Gastropoda: siphonariid (false limpet)	digestive gland	South America
H. pickfordi	8-11 x 4-5 µm	Gastropoda: lymnaeid (great pond snail), physid (broadshoulder physa), planorbid (bell-mouthed ramshorn)	digestive gland	North America
H. pinnae	3.6-5.7 x 2.7-4.5 µm	Bivalvia: pinnid (fan mussel)	digestive gland tubules	Mediterranean
H. potamillae	?	Polychaeta: sabellid (tubeworm *Potamilla torelli*)		Europe
H. raabei	6-9 x 4-6 µm	Bivalvia: dreissenid (zebra mussel)	gills, gonads, digestive gland	Europe
H. scolopli (syn. *Aplosporidium*)	not stated	Polychaeta: orbiniid (bristleworm *Scoloplus mulleri*)		Europe
H. simulii	4.8 x 3.6 µm	Diptera: simuliid (white-stockinged black fly larva)	viscera	North America
H. tipulae	2.4 x 1.8 µm	Diptera: tipulid (crane fly larva)	viscera	Europe
H. tumefacientis	8-11 x 5-8 µm	Bivalvia: mytilid (California mussel)	digestive gland [tumefactions = swellings]	North America
H. tuxtlensis	3.6 x 2.7 µm	Gastropoda: siphonariid (striped false limpet)	visceral tissues	North America
H. vejdovskii	10-12 x 8-10 µm	Clitellata: enchytraeid (iceworm)		Europe
Minchinia (spores without ornaments)				
M. chitonis	9-11 x 6-8 µm	Polyplacophora: tonicellid (gray	digestive gland,	Europe

		chiton)	muscles, gills [brown colourations]	
M. dentali	4.6 x 2.8 µm	Scaphopoda: dentaliid (tusk shell)	radula and connected tissues	Mediterranean
M. mercenaria	5.4 x 3.7 µm	Bivalvia: venerid (hard clam)	connective tissues, muscles	North America
H. orchestiae	not observed	Amphipoda: talitrid (sandhopper *Orchestia* sp.)	connective tissues of digestive glands and other organs [tissue disruption]	Europe
M. occulta	4.5-5.0 x 3.5-4.1 µm	Bivalvia: ostreid (hooded oyster)	connective tissue of gills, mantle, reproductive follicles, digestive gland	Pacific
M. teredinis	fresh 10-11 x 8-9 µm fixed 5.5-7.5 x 4.5-6.0 µm	Bivalvia: teredinid (Bartsch shipworm, Naval shipworm, deepcleft shipworm)	gill, visceral tissues [shipworm disease]	North America
Species inquirenda				
H. aulodrili	spores without orifice or lid	Clitellata: naidid (tubificid bloodworm Aulodrilus)		Europe
H. aselli (transferred to ascetosporan genus *Claustrosporidium*)	spores without orifice or lid	Isopoda: asellid (pond slater)		North America
H. babyloniae	not stated	Gastropoda: babyloniid (sea snail *Babylonia areolata*)	internal organs [tissue disruption]	Asia
H. bayeri	spores without orifice or lid	Ephemeroptera: heptageniid (unspecified mayfly)		Europe
H. carcini	not observed	Decapoda: carcinid (European green crab)	haemolymph, gills, hepatopancreas	Europe
H. cranc	not observed	Decapoda: carcinid (European green crab)	haemolymph, gills, hepatopancreas	Europe
H. ecdyonuris (transferred to fungal genus *Polycarum* then *Endoblastidium*)	spores without operculum	Ephemeroptera: heptageniid (mayfly *Ecdyonurus lateralis*)	connective tissues	Europe
H. echinogammari	not observed	Amphipoda: gammarid (scud *Echinogammarus marinus*)	connective tissues of internal organs [tissue disruption]	Europe
H. gammari (transferred to ascetosporan genus *Claustrosporidium*)	spores up to 10 µm long, without orifice, operculum or lingula	Amphipoda: gammarid (*Rivulogammarux pulex*)	adipose tissue [destroy fat cells]	Europe
H. guarani	?	Oligochaeta: enchytraeid (worm *Guaranidrilus oiepe*)		South America
H. littoralis	not observed	Decapoda: carcinid (European green crab)	haemolymph, gill, hepatopancreas	Europe
H. malacobdellae	3.5 x 2.5-3.0 µm, spores without orifice	Nemertea: amphiporid (ribbonworm *Amphiporus lactifloreus*), lineid (ribbonworm *Lineus bilineatus*)		Europe
H. mesnili (transferred to the ichthyosporean genus *Caullerya*)	10-16 x 8-12 µm	Branchiopoda: daphniid (water fleas, *Daphnia pulex, D. longispina, D. magna, D. galeata, D. obtusa* and *D. galeata x hyalina* hybrid*)*	gut epithelia	Europe
H. mytilovum (transferred to the microsporan genus *Steinhausia* or *Chytridiopsis*)	1-2 µm, spores without orifice	Bivalvia: mytilid (blue mussel, Mediterranean mussel)	ova [mussel egg disease]	Atlantic, Pacific, Mediterranean
H. periplanetae	spores without orifice	Blattodea: blattid (cockroach)		Europe

(syn. *Nephridiophaga*) (now considered to be fungi)	or lid			
H. prostomae	6.5 x 4.5 µm, spores without orifice	Nemertea: prostomatid (ribbonworm *Prostoma eilhardi*)		Europe
H. typographi	spores without orifice or lid	Coleoptera: curculionid (European spruce bark beetle)		Europe
*M. tapetis** (syn. *Haplosporidium*)	4-6 µm, spores without operculum	Bivalvia: cardiid (common cockle), venerid (Palourde clam, European littleneck clam)	gills, mantle, digestive gland tubules	Europe

*Not to be confused with *Urosporidium tapetis* hyperparasitic in trematode from Manila clams.

Parasite morphology: Haplosporidian parasites generally form 4 different types of developmental stages: namely, invasive uninucleate stages; vegetative multinucleate plasmodia; sporonts (yielding sporoblasts); and unicellular spores. The invasive stages are small rounded cells measuring 4-6 µm in diameter and they have a single central nucleus, although diplokaryotic cells are sometimes observed. The multiplicative stages are spherical to amorphous (plasmodial) in shape ranging in size from 4-100 µm in diameter. It sometimes appears that smaller plasmodia form by cleavage of larger plasmodia. These stages are multinucleate, containing up to 60 nuclei in some *Haplosporidium* spp. and up to 24 nuclei in some *Minchinia* spp. The nuclei are usually spherical measuring from 1.5-2.0 µm in diameter. The plasmodia divide by irregular multiple fission (plasmotomy) to form daughter cells (sporonts). Division begins when Golgi bodies and irregular membranes form in the cytoplasm amongst the nuclei, and culminates when each nucleus and some surrounding cytoplasm becomes encircled by limiting membranes arising from fusion of the Golgi vesicles. The resultant sporonts undergo sporoblastogenesis to form sporoblasts which are characterized by gradual thickening of their external membranes (which ultimately become spore walls), the appearance of a pre-operculum (which later differentiates into an operculum) and the formation of haplosporosomes and a spherulosome in the endosporoplasm. The sporoblasts differentiate into spores (sporogenesis) which undergo a maturation process with the development of spore wall ornamentation, degradation of the episporoplasm, rupture of the sporocyst and liberation of mature spores. Haplosporidian spores lack polar capsules (present in myxozoans) and lack polar filaments (present in microsporans). The spores are oval-ellipsoidal in shape and range in size from 3-8 x 2-5 µm (those of several species range up to 13 x 9 µm). The spores are unicellular and possess a single endosporoplasm and a small (2-3 µm) nucleus with an endosome. A rudiment of the intranuclear spindle (known as the 'kernstab') often persists in interphase nuclei. The cytoplasm bears a spherulosome (sometimes called a spherule), mitochondria with tubular cristae, and several dense organelles (known as haplosporosomes). The spores are operculate and have an orifice covered by an external lid in the genera *Minchinia* and *Haplosporidium* (whereas the orifice is occluded by an internal lingula (tongue-like plug, flange or flap) in the genus *Urosporidium*). The mature spores of *Haplosporidium* display elaborate ornamentations appearing as filamentous wrappings of spore wall material, whereas those of *Minchinia* lack ornaments, although some may have transient extensions of epispore cytoplasm during their development. In contrast, the mature spores of most *Urosporidium* spp. have long caudal extensions of epispore cytoplasm.

Site of infection: Haplosporidian parasites infect the soft tissues of aquatic invertebrates, particularly the gills, palps, suprabrachial chambers, connective tissues and epithelia of the intestines and digestive gland (hepatopancreas), with many infections eventually becoming systemic and distributed throughout host tissues. Parasites have been recorded in a wide range of animals (molluscs, crustacea, urochordates, echinoderms, polychaetes and oligochaetes) from a variety of habitats (mostly marine and estuarine, but also from some freshwater regions). Most parasite species appear to be oioxenous and only infect one or a few closely-related hosts.

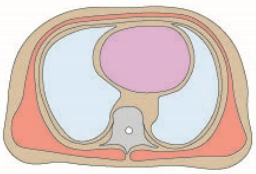
Pathogenesis: Several species are notorious parasites of oysters around the world, causing significant disease and mortalities in both wild and cultured oysters. Infections may cause a range of lesions, from destruction of the gills, gonads or digestive gland to general destruction of all associated tissue, often resulting in tissue discolouration. *H. nelsoni* causes MSX (= multinucleate sphere unknown) disease characterized by pale discolouration of the digestive gland due to the presence of numerous spores in the tubule epithelia. *H. costale* causes SSO (= seaside organism) disease in oysters typified by darker discolouration of the digestive gland due to the presence of spores in the connective tissues between tubules. *H. armoricana* causes brown meat disease in flat oysters, and *M. tapetis* causes discolourations in the tissues of cockles and clams. In many cases, the first signs of infection in shellfish are mortalities. Post-mortem examination often reveals emaciation, retracted mantle with failure of shell growth, rarely brown patches of peristracum opposite lesions on the mantle surface, reduced meat yield, impaired gonadal development and lower fecundity (often a threefold increase in the proportion of females infected, possibly due to inhibition in the development of male gametes). Oysters often start to die within a month of infection, with peak mortalities occurring for 1-3 months over summer. Disease is reduced (suppressed?) by low temperatures over winter and by low salinities. There is some evidence of resistance developing in oysters that survive the first year of infection, as they were often able to suppress or rid themselves of parasites in late spring as temperatures approached 20°C in their second year. Remission was characterized by diminution of infection with localization of parasites to external epithelia and diapedesis resulting in the deposition of moribund parasites and necrotic tissues against the shell followed by external conchiolinous encapsulation.

Developmental cycle and mode of transmission: The complete developmental cycles of most haplosporidian species are not known. Recent studies indicate that amoebulae released from spores undergo modified schizogony (exosporulation of the endosporoplasm) giving rise to multinucleate plasmodia. The plasmodia undergo irregular multiple fission (plasmotomy) to produce sporonts which cleave into uninucleate sporoblasts that eventually differentiate into spores. Sporoblast membranes become thickened during sporoblastogenesis, spore walls become ornamented during sporogenesis, and mature operculate spores are thought to be liberated by rupture of the sporocyst. Despite spore production, most epidemiological and experimental evidence suggests that direct transmission occurs via host-to-host contact during cohabitation. Transmission has been shown to be facilitated by oyster translocations, either deliberate by growers and/or scientists, or accidental via the fouling of ships hulls or via ballast water. Attempts to transmit infections by the experimental transplantation of infected tissues have failed, initially suggesting that another host may be involved (either as a reservoir for infective stages or as an intermediate host for development). No alternate hosts have yet been found even though environmental DNA studies were able to detect haplosporidian signals in planktonic and benthic water samples, suggesting the presence and dissemination of water-borne stages. However, several experiments attempting to transmit infections by injecting spore suspensions have been unsuccessful, suggesting that a maturation period may be required for spores to become infectious. MSX and SSO diseases in oysters usually occur when salinities are greater than 15-20 parts per thousand (ppt), and some outbreaks have been associated with drought conditions which caused estuaries to become more saline and oysters to be more susceptible.

Differential diagnosis: Infections are difficult to recognize ante-mortem as shellfish exhibit few clinical signs before death, although some may become moribund and others appear to gape due to mantle recession. At post-mortem, infected tissues often become watery-translucent and appear to be discoloured or have blemishes. Diagnosis is facilitated by the microscopic examination of host tissues for the presence of parasite developmental stages (plasmodia, sporonts, spores); either in stained haemolymph smears, tissue squash preparations or in histological sections. The sporoplasm of mature spores stains bright red with modified Ziehl-Neelsen carbol fuchsin stains. Careful examination is required to differentiate haplosporidian genera: with *Haplosporidium* spp. forming unicellular operculate ornamented spores (3-12 μm) distributed throughout host tissues, *Minchinia* spp. forming unicellular operculate unornamented spores (4-11 μm) widespread in tissues, and *Bonamia* spp. forming microcells (2-5 μm) usually within host haemocytes. Related *Mikrocytos* spp. also form microcells (2-4 μm) but usually within vesicular connective tissue cells. Transmission electron microscopy is often required to confirm haplosporidian spore identity through the detection of haplosporosomes (notably absent in *Mikrocytos*). In comparison, the paramyxean *Marteilia* spp. infecting oysters forms multicellular nested spores (4-10 μm), with haplosporosomes, usually in digestive tubules. At present, there are no techniques available to culture parasites *in vitro*. Molecular biological techniques have been used to detect, identify and characterize haplosporidian taxa following polymerase chain reaction (PCR) amplification of nuclear gene sequences, predominantly ribosomal RNA and actin genes.

Treatment and control: There is currently no effective treatment for haplosporidian infections in shellfish. Nonetheless, control programmes based on epidemiological observations have been successful in curtailing and preventing infections. Disease outbreaks exhibit a strong seasonal pattern, being most prevalent during summer when water temperatures are warmer and salinity levels are higher due to water evaporation. Spore stages also develop primarily in juvenile oysters, and studies have shown that culture in low salinity areas (< 10 ppt) reduced parasite pathogenicity and enhanced oyster survival. It is therefore recommended that growers plant and culture oysters in areas of low salinity by placing racks in intertidal zones or estuaries, and only moving them during cooler months to high salinity areas to take advantage of better growth. Stocks should be continually monitored for infections in enzootic areas so that informed decisions can be made on when to plant and harvest oysters. Some success has been made with mathematical prediction models simulating infection cycles in oyster populations under different environmental conditions and forecasting conditions that can initiate and end epizootics. Relevant factors include water temperature, salinity, turbidity, available food, host filtration, respiration, assimilation, parasite doubling times, crowding effects and mortality rates to predict disease occurrence, prevalence and intensity. Some success has also been reported selecting oysters for disease resistance based on those with increased haemocyte counts being better able to plug lesions, remove debris, repair tissue and help oysters survive infection. Triploid eastern oysters are more resistant to MSX than diploid cohorts, and some sympatric wild oyster populations appear to be more resistant than their cultured counterparts.

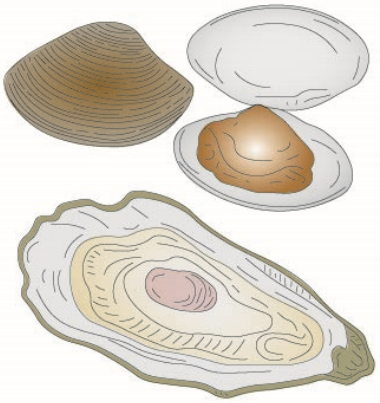
Haplosporidium, Minchina



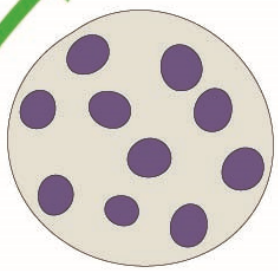
viscera, coelom
(lesions, mortalities)
(MSX disease)
(SSO disease)
(brown meat disease)

form unicellular spores
with single sporoplasm
and haplosporosomes

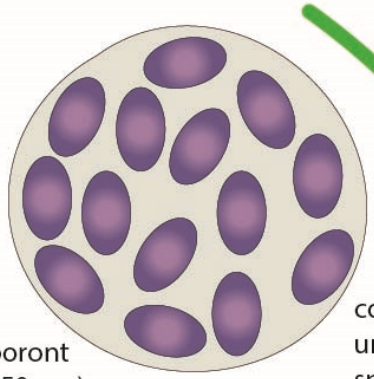
multiply by modified schizogony
within multinucleate plasmodia



Invertebrate Hosts
(aquatic molluscs)



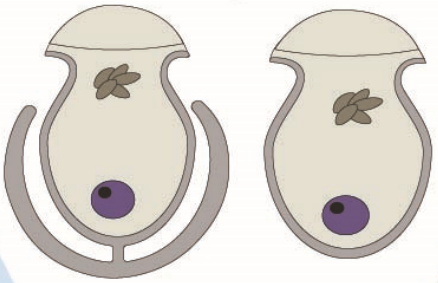
multinucleate
plasmodium
(4-100 µm)



sporont
(~ 50 µm)

containing
uninucleate
sporoblasts

spores (3-8 µm)
(with hinged lids)



Haplosporidium

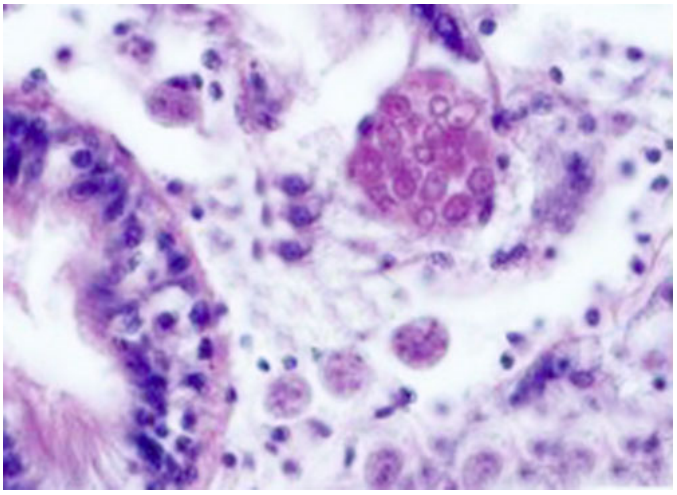
Minchinia



uninucleate
invading
stage
(4-6 µm)

?

despite spore formation, transmission between hosts
is often direct via close contact (co-habitation)



Haplosporidium plasmodia in oyster tissues

Bonamia
(protist: haplosporidian)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Two major rhizarian groups are recognized: retarians (with reticulopodia) and cercozoans (with filopodia). An enigmatic cercozoan group is the Ascetospora which contains the spore-forming Haplosporidia and Paramyxea. Haplosporidia are characterised by the formation of unicellular spores (without polar capsules or polar filaments) that contain a single sporoplasm and several dense organelles (known as haplosporosomes). The complete developmental cycles of most species are not known but most have two developmental stages: multinucleate plasmodia and spores. *Bonamia* (and *Mikrocytos*) are unique in that they form microcells and most species do not form spores. Most are histozoic or coelozoic parasites of aquatic molluscs, annelids, crustaceans and helminths. *Bonamia* spp. infect the haemocytes of oysters and may cause wasting disease and mortality in cultured oysters.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	SAR (Stramenopiles + Alveolata + Rhizaria)
Group:	Rhizaria (various amoebae and flagellates)
Division:	Cercozoa (biflagellated and/or amoeboid, usually with filopodia, plus ascetospora)
Phylum:	Ascetospora (haplosporidian and paramyxean parasites forming unique spores/microcells)
Class:	Haplosporea (haplosporosomes present)
	incertae sedis
Genus:	*Bonamia* (parasitic in tissues of bivalves, most species do not form spores)
Species:	various species cause mortalities in oysters

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Two major rhizarian groups are recognized: retarians (with reticulopodia) and cercozoans (with filopodia). An enigmatic cercozoan group is the Ascetospora which contains the spore-forming Haplosporidia and Paramyxea that lack flagella and pseudopodia. Haplosporidia are usually characterised by the formation of unicellular spores (without polar capsules or polar filaments) that contain a single sporoplasm and several membrane-bound electron-dense organelles (known as haplosporosomes), while paramyxeans form unique multicellular (nested) spores. Most species occur as histozoic or coelozoic parasites of aquatic invertebrates (including molluscs, annelids, crustaceans, ascidians and helminths), and several species cause significant diseases and mortality in oysters around the world.

The identification and classification of haplosporidians has a complex and turbulent history. The complete developmental cycles of most species are not known, but various members of the genera *Haplosporidium*, *Minchinia* and *Urosporidium* were shown to form 2 developmental stages: multinucleate plasmodia which undergo modified schizogony to form sporonts that eventually differentiate into uninucleate spores. The spores were surrounded by a spore wall with an orifice (micropyle) and the enclosed endosporoplasm contained a complex membranous system known as a spherulosome (or spherule). Members of several other genera (*Bonamia* and *Mikrocytos*) which produced microcells (but not spores) were nonetheless recognized as haplosporidians on the basis of perceived structural and biological similarities. However, subsequent ultrastructural and molecular characterization studies have now removed *Mikrocytos* to a separate order Mikrocytida as they do not produce plasmodia, spores or haplosporosomes, while *Bonamia* was retained with the Haplosporida as they produced haplosporosomes. Recent studies have since shown that one *Bonamia* species (*B. perspora*) does produce spores, and conversely, that a few *Haplosporidium* spp. do not actually produce spores as supposed. Ultrastructural studies conducted on spores demonstrated that the orifice was covered either by an external hinged operculum (adopted as a key characteristic for the family Haplosporidiidae containing the genera *Haplosporidium*, *Minchinia* and *Bonamia*) or occluded by an internal flap-like lingula (taken to characterize the monotypic family Urosporidiidae). Many spores also possessed elaborate external ornamentations, described variously as tails, filaments, folds, projections, extensions or wrappings. It was initially thought that their presence and structure could be used to differentiate taxa, but studies demonstrated considerable variation both between and within taxa. Most *Minchinia* spores lacked ornaments, but some isolates were found with epispore cytoplasmic extensions, albeit transiently as they disappeared during the spore maturation process. It was speculated that genera could be discerned by the origins (rather than the structure) of the ornamentations, being derived from either spore wall material (as found for many *Haplosporidium* spp. and one *Bonamia* sp.) or from epispore cytoplasmic extensions (observed for *Urosporidium* spp. and a few *Minchinia* isolates). However, molecular characterization studies did not reveal any strong correlations

with morphotypic (phenetic) characters. Instead, phylogenetic analyses revealed a series of polyphyletic clades, including: a basal clade of diverse *Haplosporidium* isolates; a more derived clade containing most *Urosporidium* isolates from helminths; 2 sister clades containing *Minchinia* and *Bonamia* isolates respectively; and a clade containing many *Haplosporidium* isolates from gastropods. [Note that various spore-forming organisms detected in cockroaches, copepods, rotifers, polychaetes and toads that were originally thought to be other haplosporidian genera (e.g. *Bertramia, Coelospora, Coelosporidium, Nephridiophaga*) are now considered to be fungi on the basis of molecular phylogenetic studies.]

Family	Genus	Biodiversity	Characters	Hosts
Order: Haplosporida (form unicellular spores/microcells with haplosporosomes)				
Haplosporidiidae (spores with operculum)	*Haplosporidium*	33	spores with external hinged lids, spores with filaments of spore wall material	oligochaetes, molluscs, crustacea, urochordates, echinoderms, polychaetes
	Minchinia	6	spores with external hinged lids, some spores with transient extensions of epispore cytoplasm	oysters, chitons, clams, tusk shells, shipworms
	Bonamia	4	microcells formed, one species forming spores with external hinged lids and filamentous projections of spore wall material	oysters
Urosporidiidae (spores without operculum)	*Urosporidium*	7	spores occluded with internal lingula (plug, flap, diaphragm)), spores with tapering extensions of epispore cytoplasm	hyperparasitic in helminths of molluscs and crabs
Order: **Mikrocytida** (form microcells without haplosporosomes)				
Mikrocytidae	*Mikrocytos*	5	form microcells, no spores, no plasmodia, no haplosporosomes	oysters, clams
	Paramikrocytos	1	form microcells, no spores, no plasmodia, no haplosporosomes	crabs

Haplosporean infections have been detected throughout the world in aquatic invertebrates in coastal waters (freshwater, marine and brackish waters). While *Haplosporidium* and *Minchinia* spp. have been recorded from a wide range of hosts (e.g. molluscs, crustacea, oligochaetes, polychaetes), infections by *Bonamia* spp. have only been recorded in oysters (both flat and cupped oysters). Two species (*B. ostreae* and *B. exitiosa*) have been associated with mortalities in farmed and wild oysters in the Northern and Southern Hemispheres, with the parasites forming microcells (but not plasmodia or spores) within host haemocytes. Another species (*B. perspora*) has recently been found to form microcells, plasmodia and operculate spores in the tissues of crested oysters, thus being unique as the only *Bonamia* species exhibiting the basic haplosporean convention of extracellular infection and spore formation. On the basis of ultrastructural and molecular characterization studies, another microcell parasite (*Mikrocytos roughleyi*) is now considered to be *Bonamia roughleyi*, with parasites infecting haemocytes in farmed Sydney rock oysters apparently causing winter mortalities (Note that the aetiology of this disease may be more complex than previously thought, as recent studies have indicated that some isolates of *B. roughleyi* may actually be mis-identified *B. exitiosa,* while other isolates may not be *Bonamia* or *Mikrocytos* at all, thus necessitating further study).

***Bonamia* species**	**Hosts**	**Microcell size**	**Location [Clinical signs]**	**Distribution**
B. ostreae	Bivalvia: ostreoid (European flat oyster, Australian flat oyster, dredge oyster, Puelchean oyster, Olympia oyster, Pacific oyster, Portuguese oyster, Suminoe oyster)	2-3 µm	haemocytes [haemocyte lysis]	North America, Europe, New Zealand
B. exitiosa	Bivalvia: ostreoid (European flat oyster, Australian flat oyster, dredge oyster, Puelchean oyster, Olympia oyster, Suminoe oyster, crested oyster, eastern oyster, Sydney rock oyster)	2-7 µm	haemocytes [haemocyte lysis]	New Zealand, Australia, Americas, Europe
B. perspora	Bivalvia: ostreoid (crested oyster)	2.4-5.6 µm [spores 4.3-6.4 µm]	connective tissues, haemocytes [tissue congestion, infiltration]	North America
B. roughleyi (syn. *Mikrocytos*	Bivalvia: ostreoid (Australian flat oyster, Sydney rock oyster)	2-5 µm	haemocytes [haemocyte lysis,	Australia

roughleyi)			winter mortality]	

Parasite morphology: *Bonamia* is an unusual haplosporidian representative as most species have developmental stages restricted to the formation of 'microcells' that do not produce typical haplosporidian spores. Microcells are typically uninucleate, small (2-7 µm in diameter), irregular in shape, and may occur singly or in groups of up to 10 per host cell. Two morphological forms are often evident: the most frequent being small dense forms (2-3 µm) with basophilic cytoplasm forming a pale halo around the nucleus; and larger clear forms (3-7 µm) with less dense cytoplasm. The former usually occurs extracellularly within host tissues, whereas the latter is found intracellularly mostly within host haemocytes and branchial epithelial cells. Both forms have a single nucleus which is eccentric in *B. ostreae* and centrally-located in *B. exitiosa* (imparting a fried-egg appearance). The microcells possess several mitochondria and they have Golgi bodies arising from the nuclear envelope and associated with a *trans*-Golgi network from which haplosporosomes form. It is thought that microcells may divide by binary fission as binucleate (diplokaryotic) cells are sometimes observed. There have also been rare reports of multinucleate stages measuring from 7-18 µm and containing around 5 nuclei. The uninucleate and multinucleate stages closely resemble the presporogonic stages of other haplosporidians. Recent studies on one species (*B. perspora*) have described 4 different morphological stages: microcells, plasmodia, sporonts and spores. The microcells occurred within connective tissues and measured 2-6 µm and had central to slightly eccentric nuclei. The plasmodia varied in size from small (<8 µm) to large (up to 16 µm) and they contained <5 nuclei per electron microscope (EM) section. The sporonts (also called sporocysts) measured up to 26 µm and possessed 4-14 sporoblasts. The unicellular spores measured 4.3-6.4 x 2.8-4.6 µm and contained an orifice with a hinged operculum and unique spore wall ornamentation comprising numerous short thin flat ribbons projecting from the spore wall and terminating in a capped structure. Spore formation has not been observed for other *Bonamia* spp.

Site of infection: *Bonamia* spp. infect oysters, forming microcells in haemocytes which typically accumulate in the vascular sinuses around the digestive gland, intestine and stomach. In heavy infections, microcells may be found throughout most host tissues, especially connective tissues in the mantle and gills. Following haemocyte lysis, parasites may be observed free (extracellular) amongst host tissues. *Bonamia* spp. were initially thought to exhibit high zoogeographic specificity, with *B. ostreae* infecting flat oysters in the Northern Hemisphere and *B. exitosa* infecting flat and rock oysters in the Southern Hemisphere. However, field and experimental studies have now found infections to be more cosmopolitan than previously thought with most species being able to infect a small range of sympatric related hosts.

Pathogenesis: Most infections are asymptomatic or subclinical with no or few gross or clinical signs present. Heavy infections, however, may cause disease (known as bonamiosis) resulting in high mortalities (up to 60%) in certain oyster beds. Concurrent infections with more than one *Bonamia* spp. may also occur. Parasites infect host haemocytes forming microcells within cytoplasmic vacuoles where they are able to survive and multiply. Even though haemocytes are phagocytic immune cells, the parasites appear to be able to down-regulate reactive oxygen species (ROS) production thus partly disabling their destructive metabolic capability. In susceptible oysters, infections often become systemic when infected haemocytes gather in vascular sinuses where they ultimately lyse releasing microcells into necrotic host tissues, often coincident with host death. In oysters thought to be partly resistant, infections are usually restricted to epithelia demarked by conspicuous haemocyte responses. Clinical signs of disease are inconspicuous with the first indication of infection being increased mortality with dead gaping oysters observed at the farm, tank or pond level. Detailed studies have shown gross pathological signs to include thin watery flesh, pale-yellow atrophied digestive glands, mantle recession with weakened shell closure leading to slight gaping accentuated by deformities to the gill margins and algae-covered shell lips. Infected oysters show stunted growth (including reduced shell growth), poor condition, emaciation and death. Infections are often accompanied by dense focal haemocyte infiltrates into the connective tissues of the gills and mantle and around the gut, sometimes resulting in tissue lesions with occasional perforated ulceration of the gills and mantle. The heart often appears enlarged and darkened by the presence of numerous granulocytes. Experimental studies have shown that lethal infections may develop within 3-6 months, but often require 2 years for disease development. Infections may be detected in spat and larvae, but older or larger oysters have the heaviest infections. Mortalities may occur year-round, but are more prevalent in spring and summer. Epidemiological studies indicate that mortality rates may be influenced by genetic differences in host susceptibility, environmental conditions (particularly those leading to host stress) as well as by differences in parasite virulence (both inter- and intra-specific). Mortalities have been correlated with higher water temperatures (heavier infections in spring when waters are warming) and oysters seemed to be more susceptible to infection after seasons with lower food availability, lower salinity levels or following stressful situations such as dredging. Infections by *B. roughleyi* may cause winter mortality in Sydney rock oysters with disease characterized by focal abscess-like lesions in the gills, connective and gonadal tissues and alimentary tract, especially in high salinity waters (30-35 parts per thousand).

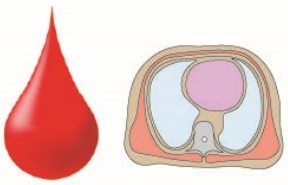
Developmental cycle and mode of transmission: The life-cycles of most *Bonamia* spp. are not known as only microcell formation has been observed in all but one species. Nonetheless, it has been mooted that 2 sequential stages may be involved in parasite development: firstly, uninucleate amoeboid cells (large clear morphological forms) occurring within host haemocytes (possibly representing multiplicative stages); followed by free microcells (small dense forms) being released into host tissues (possibly transmissive stages). There is some evidence that intracellular stages may multiply by fission, as some diplokaryotic forms and a few multinucleate forms (with up to 5 nuclei) have occasionally been observed. However, the occurrence of large multinucleate

plasmodia (20-60 nuclei) and the formation of spores typically found for other haplosporidians (e.g. *Haplosporidium*, *Minchinia*) have not been observed for *Bonamia*, except for one species (*B. perspora*) described from crested oysters in North America. In this species, microcells formed comparatively small multinucleate plasmodia (with <5 nuclei per EM section) which divided to form sporonts/sporocysts with 4-14 sporoblasts that matured to operculate ornamented spores. Despite the formation of spores by one *Bonamia* species, the transmission of most infections appears to be via direct contact. Experimental studies have successfully transmitted infections between oysters held in the same aquaria (cohabitation) and by the *in vivo* inoculation of infected haemocytes or purified parasite suspensions. Transmission apparently occurs year-round, but is greatest during the summer. Epidemiological studies have indicated that human activities may facilitate transmission, particularly when oysters are translocated by farmers, growers or scientists, and possibly via biofouling of ship hulls or ballast waters.

Differential diagnosis: Infections often only become apparent when oysters die and postmortem examination reveals tissue discolouration and sometimes ulcerative lesions. Few clinical signs develop prior to death other than poor condition and sometimes gaping exacerbated by mantle recession. However, similar lesions and signs may be found in oysters infected with other haplosporidian parasites, especially *Mikrocytos* spp. Definitive diagnosis requires the direct detection of parasites in host tissues, usually by microscopy of hemolymph smears, tissue imprints (including ventricular heart imprints) or histological sections of tissues. Parasites are usually found in haemocytes, but may also occur in or near epithelia, and in vesicular connective tissues. They are evident as small (2-5 μm) basophilic spherical-ovoid uninucleate microcells. Transmission electron microscopy is required to detect haplosporosome organelles (absent in *Mikrocytos* microcells). Other haplosporidian parasites (such as *Haplosporidium* and *Minchinia*) typically form multinucleate plasmodia and operculate spores within host tissues (similar stages have only been observed for one *Bonamia* species, *B. perspora* in crested oysters). In comparison, paramyxean parasites of oysters (including *Marteilia* spp.) form multicellular nested spores (4-10 μm) usually in digestive tubules. Several studies have developed monoclonal antibodies against *B. ostreae* and incorporated them into immunological assays (fluorescent-antibody and enzyme-linked assays) to detect parasites in oyster tissues and extracts. More recently, molecular biological studies have been used to diagnose infections, characterize parasites and infer phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (especially ribosomal RNA) and the incorporation of specific probes into restriction fragment length polymorphism (RFLP), realtime PCR, and fluorochrome- and chromogenic-based *in situ* hybridization (ISH) assays.

Treatment and control: There is no effective treatment known for bonamiasis in oysters. Although disease outbreaks may occur rapidly (developing over several weeks to months), various preventive measures have been used to great effect to mitigate the occurrence and spread of infections. *Bonamia* spp. are generally considered to be notifiable pathogens and strict quarantine regulations have been applied to limit translocations of oysters or spat from known endemic areas. Zoning systems have been implemented around foci, with disease-free areas regarded to be protected areas. Regular screening programmes have been recommended and any infected stocks should be destroyed with waste going into landfill rather than being returned to the water. Experimental and field observations have also led to several management strategies being adopted to help control infections, including reducing stocking densities, using suspension cultures, overwintering smaller oysters on up-river leases where lower salinities and higher racks protect them, on-growing in deeper waters, harvesting oysters at a young age (15-18 months), culling and fallowing beds where infection prevalence exceeds 10%, and thoroughly cleansing sites and fishing gear. Studies have also indicated that some oyster species (e.g Pacific oysters) or strains (Rossmore flat oysters) may be more resistant to infection, but inbreeding and population bottlenecks have proven problematic.

Bonamia

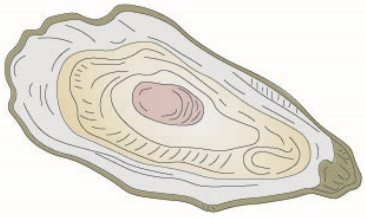


haemozoic/histozoic/coelozoic
(haemocytes, soft tissues)
(lesions, wasting disease,
mortalities)

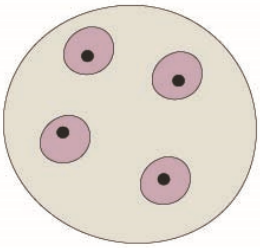
all species form micro-cells within hosts

one species forms unicellular spores
with haplosporosomes and a sporoplasm

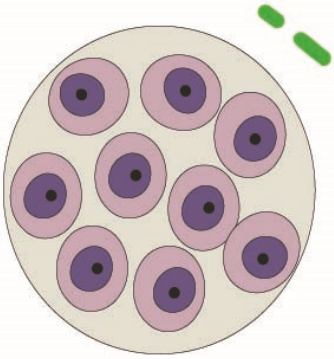
apparently multiplies by modified schizogony
within multinucleate plasmodia



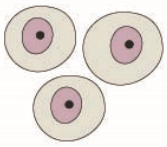
Invertebrate Hosts
(oysters, flat
and cupped)



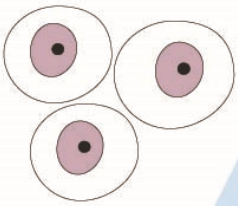
multinucleate
plasmodium
(7-18 µm)



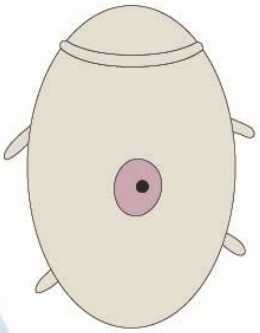
sporont (~ 20 µm)
with uninucleate
sporoblasts



extracellular
(small dense)
(2-3 µm)



intracellular
(large clear)
(3-7 µm)



hinged lid

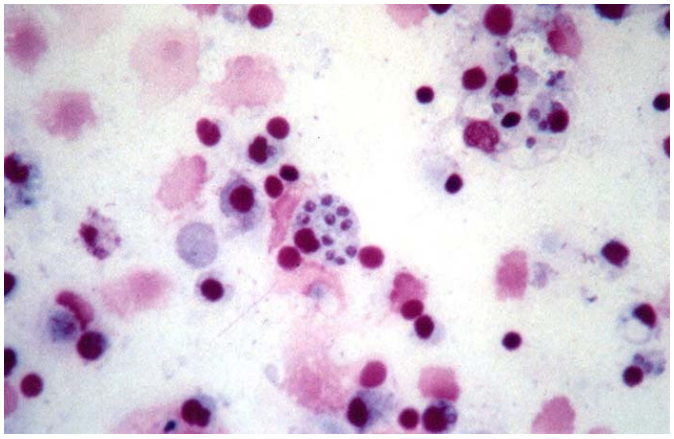
filamentous
projections

spores (4-6 µm)

uninucleate
micro-cells

?

most life-cycles not known
but transmission between hosts is often direct
via close contact (co-habitation)



Bonamia microcells in oyster haemolymph

Mikrocytos
(protist: microcells)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Two major rhizarian groups are recognized: retarians (with reticulopodia) and cercozoans (with filopodia). An enigmatic cercozoan group is the Ascetospora which contains the spore-forming Haplosporidia and Paramyxea. *Mikrocytos mackini* is an unusual amitochondriate protistan previously thought to be related to the haplosporidia, but it does not form spores or multinucleate plasmodia. The only known stages are uninucleate microcells that do not contain haplosporosomes. Infections have been associated with pustule formation and mortalities (Denman Island disease) in commercial oyster beds in North America.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria)
Group: Rhizaria (various amoebae and flagellates)
Division: Cercozoa (biflagellated and/or amoeboid, usually with filopodia, plus ascetospora)
Phylum: Ascetospora (haplosporidian and paramyxean parasites forming unique spores/microcells)
Class: Haplosporea (haplosporosomes present)
incertae sedis
Genus: *Mikrocytos* (parasitic in tissues of bivalves, spores not formed, no haplosporosomes)
Species: various species cause mortalities in oysters

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Two major rhizarian groups are recognized: retarians (with reticulopodia) and cercozoans (with filopodia). An enigmatic cercozoan group is the Ascetospora which contains the spore-forming Haplosporidia and Paramyxea that lack flagella and pseudopodia. Haplosporidia are usually characterised by the formation of unicellular spores (without polar capsules or polar filaments) that contain a single sporoplasm and several membrane-bound electron-dense organelles (known as haplosporosomes), while paramyxeans form unique multicellular (nested) spores. Most species occur as histozoic or coelozoic parasites of aquatic invertebrates (including molluscs, annelids, crustaceans, ascidians and helminths), and several species cause significant diseases and mortality in oysters around the world.

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	Minchinia	6	spores with external hinged lids, some spores with transient extensions of epispore cytoplasm	oysters, chitons, clams, tusk shells, shipworms
	Bonamia	4	microcells formed, one species forming spores with external hinged lids and	oysters

			filamentous projections of spore wall material	
Urosporidiidae (spores without operculum)	*Urosporidium*	7	spores occluded with internal lingula (plug, flap, diaphragm)), spores with tapering extensions of epispore cytoplasm	hyperparasitic in helminths of molluscs and crabs
Order: **Mikrocytida** (form microcells without haplosporosomes)				
Mikrocytidae	*Mikrocytos*	5	form microcells, no spores, no plasmodia, no haplosporosomes	oysters, clams
	Paramikrocytos	1	form microcells, no spores, no plasmodia, no haplosporosomes	crabs

Mikrocytos spp. produce uninucleate microcells (2-4 µm) that appear as quiescent, vesicular or endosomal cells in connective tissue cells, myocytes and haemocytes of oysters. Infections by *M. mackini* have been associated with pustule formation and mortalities (Denman Island disease) in commercial oyster beds in North America. Several others *Mikrocytos* spp. and isolates have also been associated with lesions and mortalities in other oysters and clams. Novel isolates from crabs were found to produce multinucleate plasmodia (but not spores) and they were named *Paramikrocytos canceri*. [Note that the species *Mikrocytos roughleyi* associated with winter mortality in Sydney rock oysters has recently been transferred to the genus *Bonamia* on the basis of ultrastructural and molecular studies. However, the aetiology of winter mortality may be more complex than previously thought, as recent studies have indicated that some isolates of *B. roughleyi* may actually be mis-identified *B. exitiosa,* while other isolates may not be *Bonamia* or *Mikrocytos* at all, thus necessitating further study].

Parasite species	**Hosts**	**Microcell size**	**Location [Clinical signs]**	**Distribution**
Mikrocytos boweri	Bivalvia: ostreid (Olympia oyster, Pacific oyster)	2.0-3.8 µm	connective tissue cells	North America
Mikrocytos donaxi	Bivalvia: donacid (wedge clam)	1.8-3.2 x 1.1-2.4 µm	muscles, nerves, digestive gland, gut, gills, gonads [mortality]	Europe
Mikrocytos mackini	Bivalvia: ostreid (eastern oyster, European flat oyster, southern Olympia oyster, Pacific oyster, Kumamoto oyster)	2-4 µm	connective tissue cells, myocytes, haemocytes [abscess/pustule formation, mortalities, Denman Island disease]	North America
Mikrocytos mimicus	Bivalvia: ostreid (Pacific oyster)	2-5 µm	connective tissue cells, muscles, haemocytes	Europe
Mikrocytis mytilicoli	Hyperparasitic in Copepoda: mytilicolid (*Mytilicola intestinalis*) from gut of Bivalvia: mytilid (Mediterranean mussel)	1.3-3.5 µm	somatic organs	Europe
Mikrocytos veneroides	Bivalvia: donacid (wedge clam)	2.0-4.7 x 1.3-4.0 µm	muscles, digestive gland, gut, gills, gonads, neurons, haemocytes [mortality]	Europe
Mikrocytos sp.	Bivalvia: venerid (Manila clam)	2.4-3.8 µm	muscles, gills, siphon, visceral mass	Asia
*Paramikrocytos canceri**	Decapoda: cancrid (edible crab)	3 µm	antennal gland, bladder, gills [hypertrophy]	Europe

*Only species for which plasmodial stages have been detected. Molecular screening studies have also detected DNA sequences in other decapods (shore crabs), molluscs (mussels, nudibranch), and annelids (tubificids).

Parasite morphology: *Mikrocytos* spp. are unusual haplosporidian parasites that form unicellular microcells in host tissues, but other developmental stages such as plasmodia and spores have not been detected. The microcells are small spherical or ovoid stages measuring 2-5 µm in diameter. They are uninucleate with each containing an eccentric polymorphic nucleus ranging in size from 1.3 x 1.0 µm (occasionally binucleate forms may be found). The microcell cytoplasm contains round vesicles, Golgi bodies, both smooth and rough endoplasmic reticulum, but haplosporosomes and mitochondria are absent (note that some cells possess small membrane-bound organelles ~0.5 µm in diameter which are thought to be putative mitochondria-related organelles (MROs)). It is noteworthy that intracellular microcells are often surrounded by host cell mitochondria, suggesting that they may usurp host organelles for energy production. Many microscopic studies have described 2 morphological forms of microcells: small dense spheroidal forms predominating (with eccentric nuclei and dark granular cytoplasm); and some larger clear forms (with lighter

granular cytoplasm). Several electron microscopic studies have also described 3 ultrastructural forms of microcells (especially for *M. mackini* and *M. mimicus*): namely quiescent, endosomal and vesicular cells. Quiescent cells (apparently corresponding to the small dense morpho-forms) are found predominantly in haemocytes and myocytes and are characterized by the presence of a nucleus with a granular nucleolus as well as a Golgi apparatus that is not budding. In contrast, endosomal cells have well-developed anastomosing endoplasmic reticulum arising from the nuclear membrane budding into the cytoplasm. Vesicular cells (corresponding to the larger clear morpho-forms) are usually found in vesicular cells and myocytes and typically have some dilation of the nuclear membrane forming cisternae as well as large vesicles scattered throughout the cytoplasm.

Site of infection: Microcells of *Mikrocytos* spp. have been detected in oysters and clams mainly in coastal waters around Europe and North America. The parasites may be located intracellularly in haemocytes, vesicular connective tissue cells and myocytes, or extracellularly in connective tissues or sinuses (presumably following host cell rupture). Infections have been recorded in the palps, gills, digestive gland, gut epithelia, mantle epithelia, heart and kidney. Most parasite species have only been detected in individual host species (oioxenous), but laboratory and field challenges have found that the species infecting oysters may occur in a small range of related host species (stenoxenous).

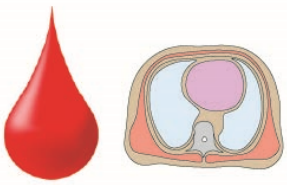
Pathogenesis: Infections by *M. mackini* may cause a disease in oysters known as Denman Island disease (or mikrocytosis). Parasites form microcells within host cells which ultimately rupture resulting in focal green lesions or abscesses in host tissues, mainly the mantle, body wall, labial palps and adductor muscles. Histologically, lesions are sometimes associated with intense inflammatory reactions particularly in connective tissues and parasites are often found adjacent to focal haemocytic infiltrates. Oysters may recover from mild infections but their market value is significantly reduced due to the presence of unsightly discoloured lesions. Heavy infections, however, have been associated with high levels of morbidity and mortality. Although juvenile oysters have been shown to be susceptible to infection, they usually do not show any signs of disease until they are older (2-3 years old). Epidemiological studies demonstrate a strong seasonal pattern to infections and disease apparently linked to water temperature (with peak disease occurring in cooler spring months). Infections by *M. donaxi* and *M. veneroides* have been associated with mortalities in wedge clams, with parasites detected throughout most host tissues.

Developmental cycle and mode of transmission: The complete life-cycles of *Mikrocytos* spp. are not known. Infections in oysters and clams involve up to 3 types of microcells, with quiescent, endosomal and vesicular cells possibly representing invasive, multiplicative and disseminating stages. There is no evidence of spore formation nor spore-like stages that would facilitate parasite survival outside of hosts. Infections appear to be transmitted directly between hosts via close contact (cohabitation), and experimental studies have successfully transmitted infections between oysters by the intramuscular inoculation of purified parasites. It has been noted that disease will only develop in oysters held in cooler waters <10°C for several months, and water temperatures >15°C effectively prevent disease development even though parasites persist within host tissues.

Differential diagnosis: Infections may be strongly suspected by gross signs of abscesses or green pustules on the palps and mantle, but these lesions are not pathognomonic. Diagnosis is generally made by the direct detection of parasites in host tissues, usually by microscopic examination of haemolymph smears, tissue/lesion imprints or histological sections of tissues. When stained with haematological stains (Wright's, Giemsa or equivalent Romanowsky stains such as Hemacolor and Diff-Quik), parasites are evident as small basophilic cells (2-4 μm) with eosinophilic nuclei. Transmission electron microscopy is required to confirm that *Mikrocytos* microcells do not possess haplosporosomes (whereas those of *Bonamia* do). *Mikrocytos* spp. also do not form unicellular spores (like typical haplosporidians such as *Haplosporidium* and *Minchinia*) nor multicellular nested spores (like the paramyxean genus *Marteilia*). Researchers have developed monoclonal antibodies against *M. mackini*, but immunodiagnostic tests have not been developed commercially. Molecular biological techniques have been used to detect infections, characterize species and determine phylogenetic relationships following the polymerase chain reaction (PCR) amplification of ribosomal RNA gene sequences (including 18S-ITS1-5.8S-ITS2-28S) and the incorporation of specific probes into restriction fragment length polymorphism (RFLP) and fluorochrome- and chromogenic-based *in situ* hybridization (ISH) assays.

Treatment and control: There is no known effective treatment for *Mikrocytos* infections in oysters or clams. Various preventive strategies have been utilized to limit disease spread amongst shellfish stocks, based on regular screening programmes with strict quarantine of translocated stocks, destroying infected stock with waste material not being returned to the water, timing plantings with respect to season and tide levels to avoid cooler waters, and harvesting stocks when they are <3 years old.

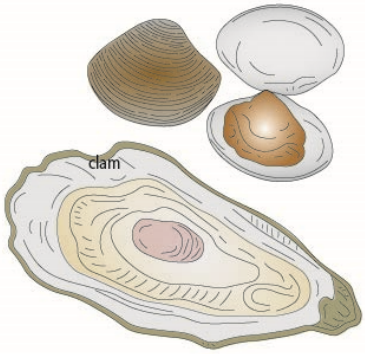
Mikrocytos



haemozoic/histozoic
(haemocytes, viscera)
(pustular lesions,
mortalities)

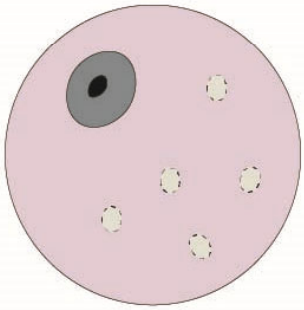
all species form micro-cells within hosts

parasites lack haplosporosomes
spore formation not observed
plasmodial stages not observed



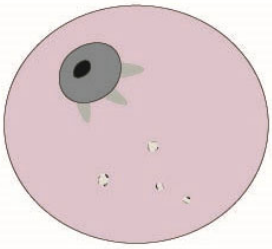
Invertebrate Hosts
(bivalves)

uninucleate
micro-cells
(2-5 µm)



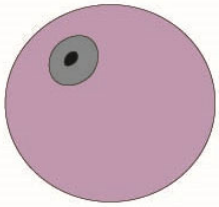
vesicular form
(large clear)

[invasive
stage?]



endosomal form
(plentiful endo-
plasmic reticulum)

[multiplicative
stage?]

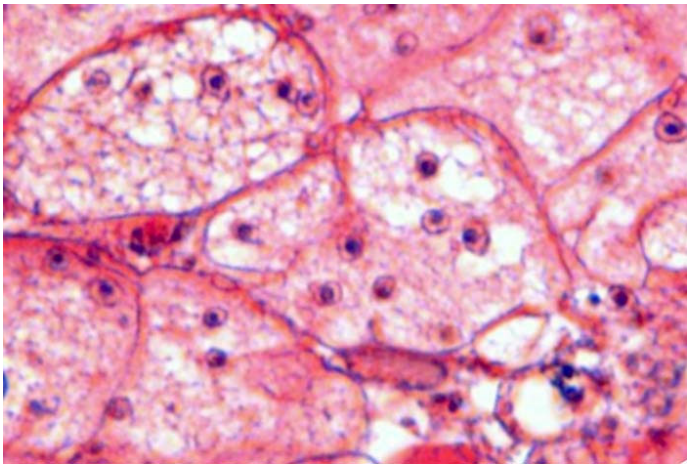


quiescent form
(small dense)

[disseminating
stage?]

?

life-cycles not known
transmission between hosts apparently occurs direct
via close contact (co-habitation)



Mikrocytos microcells in oyster tissues

Marteilia
(protist: paramyxean)

Overview

Protists are single-celled organisms with membrane-bound nuclei (eukaryotes). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Two major rhizarian groups are recognized: retarians (with reticulopodia) and cercozoans (with filopodia). An enigmatic cercozoan group is the Ascetospora which contains the spore-forming Haplosporidia and Paramyxea. The Paramyxea exhibit both protistan and metazoan characters. They form unique multicellular spores where the daughter cells remain enclosed within the parent cells (up to four cells may be enclosed within each other). All species are parasitic in marine invertebrates (polychaetes, molluscs and crustaceans) and different taxa are distinguished by the number of spores and sporal cells within sporonts. Development begins with the enlargement of small amoeboid primary (stem) cells and the internal cleavage of uninucleate secondary cells; sporulation begins with internal cleavage of a third cell (spore primordium) within each secondary cell (sporont). Several species cause mortalities (QX and Abers disease) in oysters.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: SAR (Stramenopiles + Alveolata + Rhizaria)
Group: Rhizaria (various amoebae and flagellates)
Division: Cercozoa (biflagellated and/or amoeboid, usually with filopodia, plus ascetospora)
Phylum: Ascetospora (haplosporidian and paramyxean parasites forming unique spores)
Class: Paramyxea (form unique multicellular spores with cells enclosed within each other)
Order: Marteilida (internal cleavage of secondary cells then sporonts)
Family: Marteiliidae (sporonts contain 2-4 tricellular spores)
Genus: *Marteilia* (parasitic in tissues of oysters)
Species: various species cause QX and Abers disease in oysters

Parasite biodiversity and host range: Protists are unicellular eukaryotes that move using undulipodia (flagella or cilia), pseudopodia (false-feet) or a unique gliding motion. Cells with different modes of locomotion do not form separate monophyletic assemblages as previously thought, but rather are distributed across several disparate supergroups (as evidenced by recent molecular phylogenetic analyses). One protistan supergroup known as SAR comprises the Stramenopiles (with heterokont flagella), Alveolata (with cortical alveoli) and Rhizaria (with fine pseudopodia). Two major rhizarian groups are recognized: retarians (with reticulopodia) and cercozoans (with filopodia). An enigmatic cercozoan group is the Ascetospora which contains the spore-forming Haplosporidia (producing uninucleate spores) and Paramyxea (producing curious multicellular 'nested' spores).

The Paramyxea exhibit a curious combination of both protistan (unicellular) and metazoan (multicellular) characters in that they divide by endogeny forming unique multicellular nested spores where the daughter cells remain enclosed within the parent cells (up to four cells may be enclosed within each other). Most paramyxean developmental stages contain haplosporosomes so they have generally been regarded as a sister taxon to the Haplosporida, a placement confirmed by molecular characterization studies. Paramyxeans are endoparasitic within the tissues of marine invertebrates, including molluscs, crustaceans and polychaetes. Their developmental cycles involve the invasion and enlargement of small amoeboid primary (stem) cells which undergo internal cleavage (sporogony) to form uninucleate secondary cells (sporonts) which subsequently undergo internal cleavage (sporulation) to form tertiary cells (spore primordia), each stage nested within its predecessor. Different taxa have been distinguished primarily by the numbers and types of sporonts and spores formed, but it has proven difficult to provide consensus definitions for several genera because the cognate species vary considerably in their development. In the case of *Paramyxa* and *Paramyxoides* spp., it is relatively straightforward as their primary cells produce 2-4 secondary cells, each of which produces 4 tetracellular spores. However, species belonging to the remaining genera (*Marteilia, Martioides, Paramarteilia* and *Eumarteilia*) have been shown to produce variable numbers of secondary cells (1-16) producing variable numbers of spores (1-14) which may be bicellular or tricellular. While molecular characterization studies have helped resolve phylogenetic relationships between genera and species, they have not strongly supported any conspicuous morphotypic species groups or zoogeographic assemblages.

Family	Genus	Biodiversity	Characters	Hosts
Paramyxida (form unique multicellular spores)				
Marteiliidae	*Marteilia*	9	primary cells produce variable number (1-16) of secondary cells, each producing variable number (2-14)	oysters, mussels, cockles, scallops

			tricellular spores	
	Marteilioides	2	primary cells produce variable number (2-12) of secondary cells, each producing one tricellular (or bicellular) spore	oysters
	Paramarteilia	2	primary cells produce variable number (2-3) of secondary cells, each producing a variable number (2-4) of bicellular spores	oysters, crabs, amphipods
	Eomarteilia	1	primary cells produce 8 secondary cells, each producing 4 tricellular spores	clams
Paramyxidae	*Paramyxa* (incl. *Paramyxoides*)	2	primary cell produces 2-4 secondary cells, each producing 4 tetracellular spores	polychaetes

The multiplication of paramyxean parasites primarily in the digestive glands of their hosts may interfere significantly with digestive processes leading to emaciation and seasonal mass mortalities, resulting in serious economic losses for both wild and farmed fisheries. *M. refringens* (O-type) causes Aber disease in flat oysters in Europe, America and Australia, *M. pararefringens* (M-type, previously *M. maurini*) causes mortalities in northern Europe, and *M. sydneyi* causes QX (= Queensland unknown) disease in Sydney rock oysters in Australia. National and international agencies have imposed quarantine regulations on stock translocations and growers have adopted a range of management procedures to mitigate outbreaks.

Parasite species	**Hosts**	**No. secondary cells**	**No. spores**	**Spore structure**	**Location [Clinical signs]**	**Distribution**
Genus ***Marteilia***						
Marteilia christenseni	Bivalvia: semelid (peppery furrow shell)	8	4	?	digestive gland	France
Marteilia cochillia	Bivalvia: cardiid (common cockle)	4-8	6	?	digestive gland [mortalities]	Spain
Marteilia cocosarum	Bivalvia: cardiid (common cockle)	1-3	?	?	digestive gland	United Kingdom
Marteilia lengehi	Bivalvia: ostreid (hooded oyster)	8	up to 14	?	digestive gland	Persian Gulf, Australia
Marteilia refringens (= O-type)	Bivalvia: ostreid (European flat oyster, Pacific oyster, dredge oyster, Australian flat oyster, Puelchean oyster, crested oyster), solenid (grooved razor shell), cardiid (common cockle), venerid (striped venus clam), mytilid (blue mussel, Mediterranean mussel)	8	4	tricellular	digestive gland [discoloration, emaciation, mortalities, Aber disease, digestive gland disease]	Europe, Americas, Australia
Marteilia octospora	Bivalvia: solenid (grooved razor shell)	4	8	?	digestive gland	Spain
Marteilia pararefringens (formerly M-type *M. refringens*, syn. *M. maurini*)	Bivalvia: mytilid (blue mussel, Mediterranean mussel, axehead mussel), solenis (grooved razor shell)	8	4	tricellular	digestive gland [mortalities]	northern Europe, Australia
Marteilia sydneyi	Bivalvia: ostreid (Sydney rock oyster, blacklip oyster); Polychaeta: nephtyid (*Nephtys australiensis*)	8-16	2-3	tricellular	digestive gland [mortalities, QX disease]	Australia
Marteilia tapetis	Bivalvia: venerid (Manila clam)	4	2-4	tricellular	digestive gland	Asia
Marteilia sp.	Bivalvia: pectinid (Atlantic calico scallop)	8	3-4	?	digestive gland [mortality]	North America
Genus ***Eomarteilia***						
Eomarteilia granula	Bivalvia: venerid (Manila clam)	8	4	tricellular	digestive gland [mortalities]	Asia

(syn. *Marteilia*)						
Genus ***Marteilioides***						
Marteiliodies branchialis	Bivalvia: osterid (Sydney rock oyster)	2-6 (sometimes 12)	1	bicellular	digestive gland, connective tissue cells, haemocytes [mortalities]	Australia
Marteilioides chungmuensis	Bivalvia: ostreid (Pacific oyster, Iwagaki oyster, black-lip oyster)	2 (sometimes 3)	1	tricellular	ovary [tumour-like nodules]	Australasia
Genus ***Paramarteilia***						
Paramarteilia canceri	Decapoda: cancrid (edible crab, velvet crab)	2-3	2-4	bicellular	systemic [shrunken organs]	Europe
Paramarteilia orchestiae	Amphipoda: talitrid (*Orchestia gammarellus, aestuarensis*), gammarid (*Echinogammarus marinus*)	2-3	2	bicellular	testis [males become female or intersex]	Europe
Genus ***Paramyxa***						
Paramyxa paradoxa	Polychaeta: poecilochaetid (*Poecilochaetus serpens*)	2-4	4	tetracellular	gut	Europe
Paramyxa (*Paramyxoides*) *nephtys*	Polychaeta: nephtyid (*Nephtys caeca*)	2-4	4	tetracellular	gut	Europe

Parasite morphology: Paramyxean parasites are characterized by the formation of unique multicellular spores where the daughter cells remain enclosed within the parent cells (up to four cells may be enclosed within each other, somewhat like nested Russian or babushka dolls). The developmental process varies for different taxa but involves the sequential formation of at least 4-6 cell types. Primary (stem) cells invade host epithelia and multiple by binary fission and internal cleavage producing more primary cells which disseminate throughout host tissues, some becoming nurse cells in the digestive gland where they produce spores. During sporulation, primary cells (known variously as C1 cells or sporangiosori) bud endogenously to form secondary cells (C2 cells, sporont primordia, sporonts or sporangia), in which tertiary cells (C3 cells, spore cells, spore wall cells, spore primordia or intermediate cells) bud to form the outer spore wall in which further cells bud and mature as nested spores (C4-C6). Morphological details of these small developmental stages are often difficult to determine by light microscopy so recourse is made to electron microscopy to determine their ultrastructural characteristics. The primary stem cells are amoeboid but often ovoid ranging in size from 4-16 µm. They are uninucleate and contain smooth endoplasmic reticulum, ribosomes, and unique haplosporosomes (membrane-bound organelles with a glycoprotein core). The cells sometimes develop external dendritic membranous extensions and internal multivesicular inclusion bodies. Primary cells also contain a secondary uninucleate daughter cell within a cytoplasmic vacuole. The mother cell become enlarged as the daughter cell divides by binary fission to produce 4 new daughter cells, each of which divides by internal cleavage to also contain a uninucleate cell. These new daughter cells are released and disseminate into host tissues to become new primary cells. In some species, daughter cells lodging beneath the epithelium of digestive gland tubules have been reported to form nurse cells (notably for *M. sydneyi*, but not for *M. chungmuensis* which develops in the ovary). Sporogony begins when primary cells (C1) bud endogenously to form 1-16 (generally 4 or 8) secondary cells (C2). Secondary cells are usually ovoid and grow from 5 µm up to 30 µm in diameter. They contain ribosomes, vesicles, centrioles, cytoplasmic refringent granules but consistently lack haplosporosomes (this also occurs for most haplosporidians as haplosporosome-like bodies disappear in early vegetative stages but reform in spores). Secondary cells contain tertiary cells (C3) which bud endogenously to form the outer spore wall. Tertiary cells contain ribosomes, smooth endoplasmic reticulum, vesicles, and most species have re-acquired haplosporosomes. The cells form the outer layer of the spore which is sometimes underlain by a cytoskeleton of microtubules. The spore wall varies in thickness depending on the species, and sometimes displays striated projections (often attributed to shrinkage artefacts) although *M. sydneyi* produces a thick layer of concentric membranes. Within the spore wall, further cells bud endogenously (internal cleavage) to form spore precursors (C4 cells). These cells are spherical-ellipsoidal in shape and range in size from 5-20 µm in length. They are rich in ribosomes and smooth endoplasmic reticulum, possess haplosporosomes and mitochondria, and some have numerous flattened vermiform vesicles. They divide internally (endosporulation) to form 1-8 spores (C5-C6) which are ovoid, measure from 4-10 µm and often contain spherical refringent inclusion bodies. The spores of most marteiliid species are tricellular as they contain 3 nested (outer, intermediate and inner) cells; i.e., 3 uninucleate sporoplasms of graded sizes with each smaller sporoplasm being enclosed within the cytoplasm of the next largest. In comparison, *Paramyxa* spp. form tetracellular spores and some *Paramarteilia* spp. form bicellular spores.

Site of infection: Paramyxeans are endoparasitic in aquatic invertebrates, including bivalves (oysters, mussels, clams, cockles, scallops, razor shells), decapods (crabs), amphipods and polychaetes. They invade and multiply in epithelial tissues (gills, gut) and then disseminate throughout internal tissues typically undergoing sporulation in the digestive gland (an exception is *Marteilioides chungmuensis* which develops in the gonads). Most parasite species are specific for particular hosts (oioxenous) but experimental

and field studies have shown some to be able to infect closely-related hosts (stenoxenous) or rarely sympatric unrelated hosts (euryxenous). The geographic distributions of most species were initially confined to local confined regions, but subsequent studies have found some to be more widely distributed, particularly throughout oyster growing regions.

Pathogenesis: Infections vary markedly in their pathogenicity, even when parasites may be present in hosts for extended periods (years). Light infections may remain asymptomatic in some hosts, but may cause clinical signs in others. Conversely, heavy infections may cause mortalities in some hosts but not others. Such variation is thought to arise from differences in host susceptibility (e.g. innate genetic factors, immunocompetence, physiological responses to stress) and parasite virulence (invasion, reproduction, and toxicity). Infections by *M. refringens* (O-type) progress from benign to lethal in flat oysters, with rampant parasite multiplication and sporulation leading to destruction of much of the epithelium of the digestive gland resulting in host starvation and death (condition known as Aber disease, or marteiliosis). The gross signs of disease include discolouration (pale brown), inflammation and necrosis of the digestive gland, discolouration (pale yellow) of visceral tissues which appear shrunken and watery/slimy, poor condition index with significant glycogen loss (progressive emaciation), cessation of growth (including the shell), and recession of the mantle with moribund oysters appearing to gape. Infections by *M. pararefringens* (formerly M-type *M. refringens*, or *M. maurini*) also inhibit gonad regeneration after the first spawning in mussels, thus leading to population collapses. Infections by *M (Marteiliodies) chungmuensis* are restricted to the ova of oysters, where they may cause unsightly nodule formation, watery flesh from depleted glycogen reserves, and reduced reproductivity (infected oysters spawning later than normal, and infected oocytes being rendered sterile). Infections in cockles have involved the digestive gland, stomach, gills and labial palps, cumulatively resulting in poor uptake and absorption of organic matter with subsequent loss of condition and mortality. Infections by *M. sydneyi* cause seasonal mortalities (called QX disease) in Sydney rock oysters, with parasite sporulation resulting in degeneration of the digestive gland, visceral tissues becoming colourless and translucent, resorption of the gonads, poor body condition and death (sometimes within 6 weeks). The development of most paramyxean parasites appears to be directly related to water temperature (especially > 17°C), with disease becoming most severe around the end of summer coincident with parasite sporulation. Epidemiological studies have also suggested an association with sudden changes in salinity, but this may reflect host stress responses to rapid environmental changes rather than parasites succumbing to high or low salinity levels.

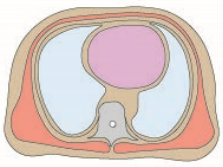
Developmental cycle and mode of transmission: The complete life-cycles of paramyxeans are not known but their development within molluscan hosts has been deduced from detailed studies on several species (notably M. *refringens, M. sydneyi* and *M.* (*Marteilioides*) *chungmuensis*). Infection begins when small amoeboid primary (stem) cells invade host epithelia (gills, palps, gut) and multiply by binary fission and internal cleavage to produce more uninucleate primary cells, each containing a secondary uninucleate daughter cell within a cytoplasmic vacuole. Following replication in epithelia, new primary cells are released into the surrounding connective tissues and haemolymph where they disseminate into host tissues, especially into digestive gland tubules (where some species (e.g. *M. sydneyi*) form nurse cells in the subepithelia). Stages in the digestive gland undergo sporogony (sporont formation) to produce prespores that undergo maturation (sporulation) to form multicellular spores. This process may vary for different species, particularly with regard to the numbers of sporonts and spores formed and their structural composition (remember that these are nested spores where cells occur within cells within cells). During sporulation, primary cells (C1) bud endogenously (unique process of internal cleavage, also known as endosporulation) to form 1-16 secondary cells (C2, sporangial primordia which mature to sporonts), in which 2-4 tertiary cells (C3, spore primordia) bud to form the outer spore wall within which further cells (C4-C6) bud by consecutive internal cleavage forming 1-8 nested spores (most tricellular and a few bicellular in marteiliid species, but tetracellular in paramyxiid species). When mature, each nested spore is surrounded by a continuous spore wall without an operculum, orifice or pore. Spores are released from the digestive tract with host faeces either free or enclosed within propagules (sporonts) singly or in clusters depending on the species (or released from the genital tract in ova in the case of *M. chungmuensis*). The transmission of infections was initially thought to be direct, but attempts to directly infect oysters by feeding or injecting infected homogenized digestive gland, by cohabitation with infected stock, or by introduction of oysters into the field after a disease event, have consistently failed to produce infections. The production of spores and their release into the water column could support either direct or indirect transmission, but the fate of free spores is unknown (although some experiments suggest they are not long-lived). Molecular screening studies have detected parasite DNA in other planktonic and benthic invertebrates (copepods, polychaetes, appendicularians, echinoderms, crustacean larvae), but it is not known whether this was the result of filter-feeding activity or actual infection (with these hosts acting as obligate, facultative, opportunistic or paratenic hosts). Further studies are required to determine the complete life-cycles of paramyxean parasites.

Differential diagnosis: Infections are generally not evident ante-mortem as they elicit few overt clinical signs in bivalves (gape and poor condition often not obvious). Infections may be suspected at post-mortem by the occurrence of watery flesh and discoloured organs (particularly the digestive gland) in moribund or dead animals, but these findings are not pathognomic for marteiliosis. Definitive diagnosis is made by the microscopic detection of parasites in host tissues, usually in impression smears of the digestive gland or in histological sections of the digestive gland, gills or palps. Differential diagnosis is made by careful examination of the parasite developmental stages, as haplosporidian parasites infect similar tissues and may be of similar sizes. *Marteilia* spp. form multicellular nested spores ranging in size from 4-10 µm usually in digestive tubules. The spores contain haplosporosomes but electron microscopic examination is required to detect them. In contrast, haplosporidian parasites form unicellular spores or microcells ranging in size from 3-12 µm. Both *Haplosporidium* and *Minchinia* spp. form operculate spores throughout host tissues

(the former bearing unique spore wall ornamentations, absent in the latter). Both *Bonamia* and *Mikrocytos* spp. form microcells within host cells (haemocytes and connective tissue cells respectively) and *Mikrocytos* spp. lack haplosporosomes. Attempts made to develop specific histological or immunological stains for these different parasites have lacked specificity and sensitivity. For example, polyclonal antibodies raised against *M. sydneyi* sporulating stages were incorporated into fluorescent-antibody assays but they failed to detect presporulation stages in connective tissues of recently infected oysters. Better success was achieved using parasite DNA markers in fluorescent *in situ* hybridization (FISH) assays to track infections in host tissues. Molecular biological studies have been used to characterize parasite species and infer phylogenetic relationships following the polymerase chain reaction (PCR) amplification of ribosomal DNA genes (with various developed for 18S, internal transcribed spacer 1 (ITS-1), 5.8S, ITS-2, 28S and intergenomic spacer (IGS) regions).

Treatment and control: There are no known treatments for *Marteilia* infections in bivalves. Nonetheless, a range of preventive measures have been employed to limit the occurrence and spread of infections in cultured stocks. National and international authorities have introduced strict quarantine protocols prohibiting the transport of oysters or spat within and between endemic areas, with regular monitoring and health surveillance mandated. Growers have adopted several farm management procedures designed to minimize risk, including not planting oysters in endemic areas during summer, harvesting large oysters prior to onset of peak transmission periods, and even holding oysters in high salinity waters where they grow more slowly but remain free of infection. To avoid QX disease, oyster growers have taken to emptying estuarine leases in late spring and restocking in early autumn. Field studies have also indicated that some oyster species appear to be more resistant to infection (e.g. Pacific oysters are more resistant to *M. refringens*) so some stock replacements have occurred. Some success has also been reported in selectively breeding Sydney rock oysters for QX resistance, with survivors having higher numbers of granulocytes in their haemolymph which appear to confer enhanced abilities to kill parasites.

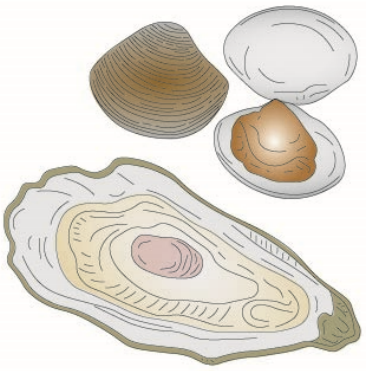
Marteilia



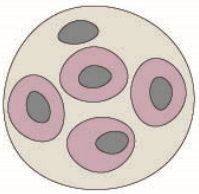
viscera, esp. digestive gland
(emaciation, mortalities)
(QX disease,
Abers disease)

form unique multicellular spores
where daughter cells remain
enclosed within parent cells

all species parasitic in marine invertebrates

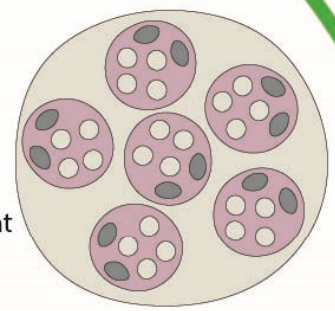


Invertebrate Hosts
(bivalves)



secondary cells
(sporangia)
(5-30 µm)



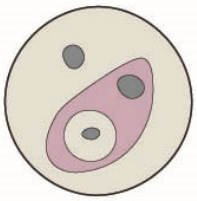


sporont
(refringent
bodies)

tertiary cells
(spore primordia)
(5-20 µm)



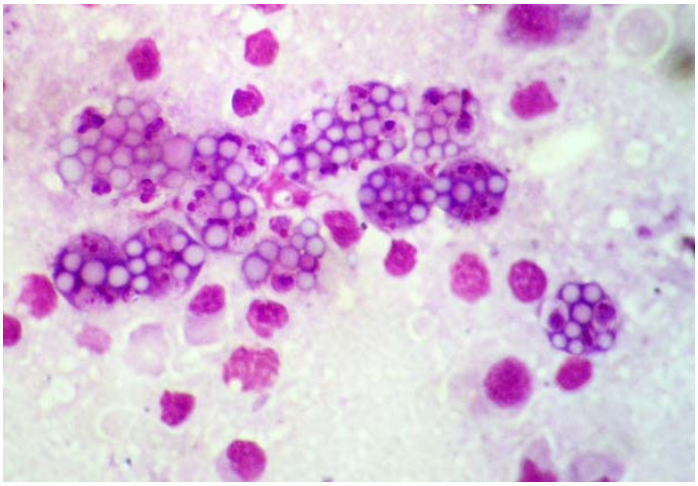
primary cells
(sporangiosori)
(4-16 µm)



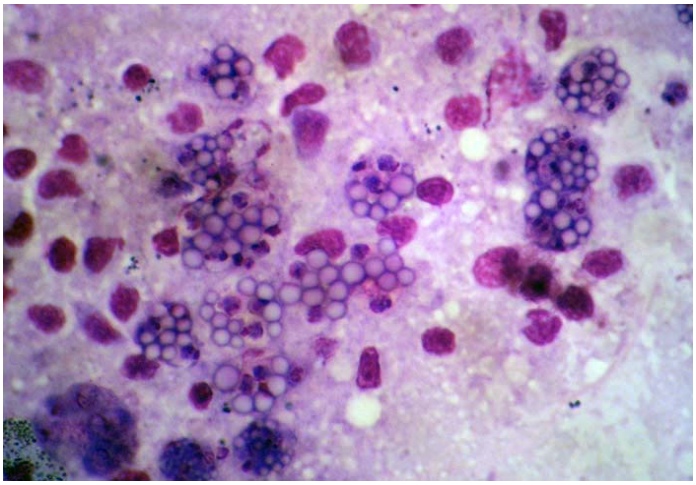
multicellular
(tricellular)
spore
(4-10 µm)

?

despite spore formation and host co-habitation,
actual mode of tranbsmission between hosts unknown



Marteilia sporangia in oyster digestive gland

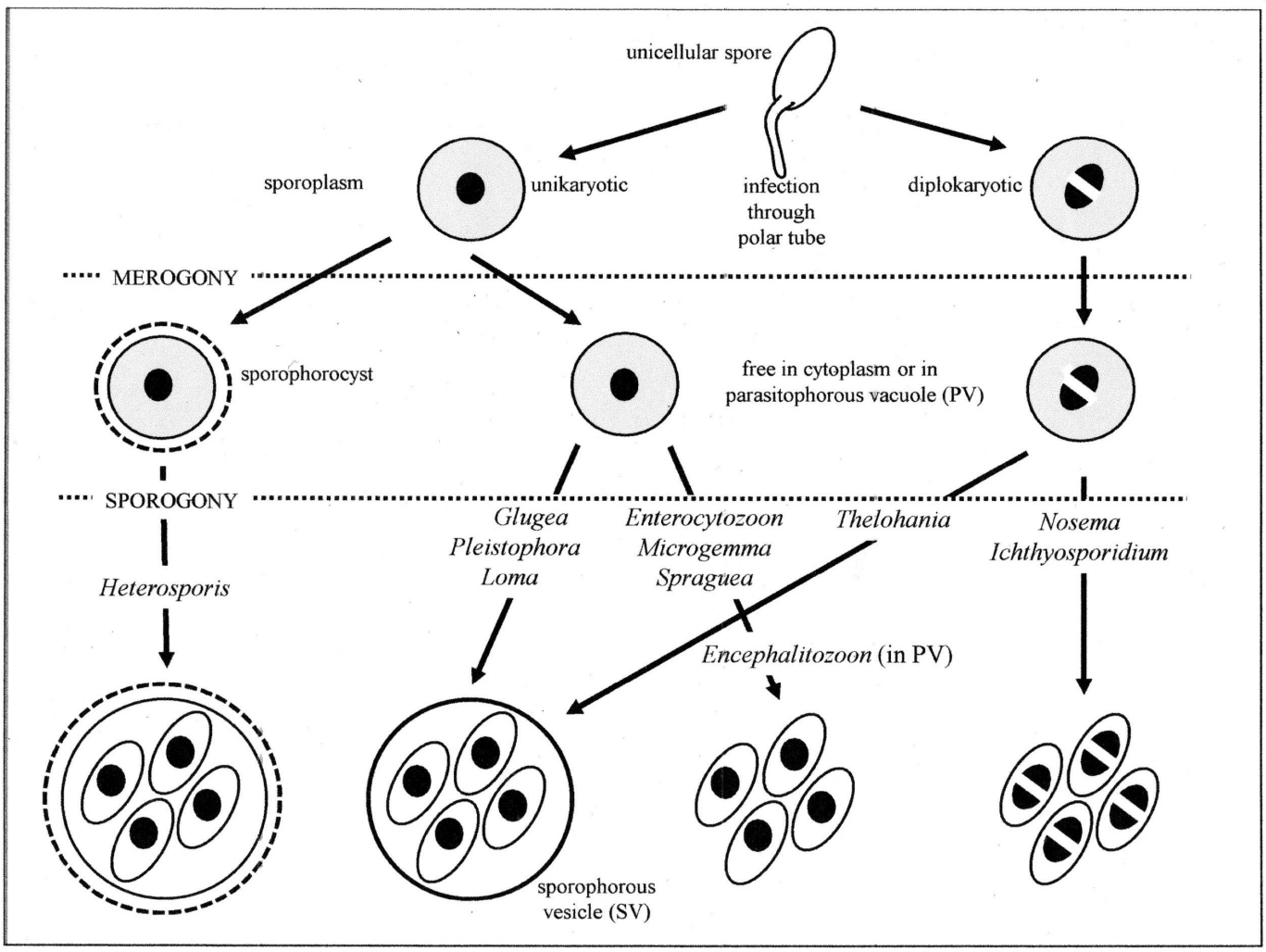


Marteilia sporangia in oyster digestive gland

Fungi
(microsporidia)

MICROSPORAN CYCLES

(with exemplars)



MICROSPORA IN FISH

Glugea, Pleistophora*, *Loma, Heterosporis, Kabatana, Microgemma, Tetramicra, Ichthyosporidium et al.
(fungus: microsporidian)

Overview

Microsporidia are obligate intracellular parasites which lack mitochondria and form small unicellular spores. They were long considered to be a primitive basal group of Protista, but molecular phylogenetic studies have revealed many similarities in biochemical pathways and structural components to fungi, where they are now classified. Numerous species have been described in invertebrates (especially insects) and lower (rarely higher) vertebrates. The parasites proliferate in host tissues by merogony (asexual division) followed by sporogony (often involving plasmotomy prior to sporoblastogenesis). Developmental stages may be monokaryotic (single nucleus) or diplokaryotic (paired nuclei) and sporonts may be surrounded by a membranous sporophorous vesicle (pansporoblast) or lie free in the host cell cytoplasm. All spores contain a unique coiled polar tube which can be extruded to inject the infective sporoplasm into host cells. Infections may be disseminated throughout host tissues or they may cause focal lesions and inflammation involving cysts, granulomas or tumour-like xenomas (enlarged host cells). Various species are found in insects (some causing dysentery in honey bees), crustaceans (some denaturing muscles), fish (some forming lesions or deformities) and even humans (some causing diarrhoea, myositis, encephalitis or corneal lesions).

Classification

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Fungi (with chitinous walls, includes microsporidia)
Division:	Microsporidia (form unicellular spores, with coiled polar tubes, amitochondriate, all parasitic)
Class:	Microsporea (polar filament well-formed, oval spores)
Order:	Microsporida (polaroplast present)
Suborder:	Pansporoblastina (sporophorous vesicle present)
Family:	Glugeidae (all stages monokaryotic, numerous sporoblasts formed in sporophorous vesicles)
Genera:	*Glugea/Pleistophora/Loma/Heterosporis* (parasitic in tissues of fish)
Suborder:	Apansporoblastina (sporophorous vesicle absent)
Family:	Unikaryonidae (all stages monokaryotic, in cell cytoplasm or in parasitophorous vacuole)
Genera:	*Kabatana/Microgemma/Tetramicra/Ichthyosporidium* (parasitic in tissues of fish)
Species:	various species cause lesions, cysts or xenomas in freshwater and marine fish

Parasite biodiversity and host range: Microsporidia possess a remarkable apomorphic adaptation to life as intracellular parasites, their unicellular spores have polar tubes coiled up inside which can be forcibly everted to penetrate host cells and inject their infective germs (sporoplasm). Microsporidia have reduced cellular complexity, they have small genomes, they are amitochondriate and they have metabolomes partway between 'prokaryotes' (archae- and eu-bacteria) and eukaryotes (nucleated cells). They were long considered to be a primitive basal group of Protista but molecular phylogenetic studies have revealed many similarities in nuclear genes, biochemical pathways and structural components to fungi, where they are now classified.

The systematics of microsporidia has progressed over decades from phenotypic classifications based on spore morphology, developmental cycles and host range to genotypic classifications based on comparative gene sequences. Classical studies divided the microsporidia into those with or without an envelope (sporophorous vesicle) around sporoblasts (Pansporoblastina and Apansporoblastina respectively) and recognized families on the basis of vegetative growth, genera on the process of spore formation and species on the basis of spore morphology. The subsequent inclusion of ultrastructural features led to the recognition of three major assemblages: 'primitive' groups with rudimentary polar tubes and no polaroplasts; 'intermediate' groups with short polar tubes and rudimentary polaroplasts; and 'higher' groups with well-developed polar tubes and polaroplasts. Families continued to be identified on the basis of type of reproduction (merogony and sporogony) and nuclear condition (mono- or diplo-karyotic). More recently, chromosome cycles were used to separate microsporidia into Dihaplophasea (diplokaryon in some phase of life-cycle) and Haplophasea (unpaired nuclei in all life-cycle stages). It is thought that the developmental cycle of Dihaplophasea involves a pairing of gametes which proliferate and undergo haplosis either by meiosis (order Meiodihaplophasida) or by nuclear dissociation (order Dissociodihaplophasida), whereas the development of Haplophasea is entirely haplophasic. Molecular phylogenetic studies, however, have not provided good support for conventional classifications but have separated representative species into three major clades mostly correlated with host habitat: including the Aquasporidia (in freshwater insects, crustaceans and bryozoans), Marinosporidia (in marine fish and crustaceans) and Terresporidia (in terrestrial insects and vertebrates). Although many taxa have yet to be analysed and classified, most clades are polyphyletic with conventional genera split within and between clades. It is not known whether this reflects an evolutionary history of parasites switching hosts or habitats, or even hosts switching habitats: events quite likely to have occurred considering that many invertebrate hosts have aquatic origins and

many have retained aquatic stages in their life-cycles. Further studies are required to reconcile phenotypic and genotypic classifications.

Numerous microsporidian species have been described in invertebrates (especially insects and crustaceans) and lower (rarely higher) vertebrates. Over 1,400 species belonging to ~200 genera have been described; with some 800 species in 109 genera infecting insects, 400 species in 62 genera infecting crustaceans, 120 species in 26 genera infecting fish, 17 species in 11 genera infecting mammals, 5 species in 3 genera infecting birds, reptiles and amphibians, 40 species in 27 genera infecting invertebrates (8 genera in annelids, 7 in arachnids, 4 in molluscs, 4 in bryozoans, 2 in ciliates, one in helminths and one in kinorhynchs) and another 20 species in 14 genera being hyperparasitic in other parasites (8 genera in gregarines, 3 in trematodes, 2 in myxozoans and one in mesozoa). The key characteristics of the microsporidian genera are tabulated below:

Microsporidian genera	**Hosts**	**No. nuclei (meronts, spores)** [1= monokaryotic, 2 = diplokaryotic, 1-2 = both]	**Spore types** [1 = mono-morphic, 2 = di-morphic, 3 = poly-morphic]	**Intracellular location** [CY = cytoplasm, NU = nucleoplasm, PV = parasitophorous vacuole, SP = sporophorocyst, SV = sporophorous vesicle]	**Spores per SV** [n = numerous, na = not applicable]	**Xenoma formation**
Abelspora	decapoda	1,1	1	PV	2	xenoma?
Aedispora	diptera	1-2,1-2	2	PV, SV	2-8	absent
Agglomerata	branchiopoda	1,1	1	SV	8-32	absent
Agmasoma	decapoda	2,1	?	SV	8	absent
Alfvenia	copepoda, maxillopoda	2,1	1	SV	1-2	absent
Alloglugea	anura	1,1	1	PV	na	xenoma
Amazonspora	fish	1,1	1	CY	na	xenoma
Amblyospora	copepoda, amphipoda, maxillopoda, diptera	2,1-2	3	SV	8	absent
Ameson	decapoda, diptera	2,1	1	CY	na	absent
Amphiacantha	hyperparasitic in gregarines in polychaetes	1,1	1	SV	n	absent
Amphiamblys	hyperparasitic in gregarines in polychaetes	1,1	1	SV	32-50	absent
Andreanna	diptera	2,2	1	PV, SV	8	absent
Anisofilariata	diptera	1,1	1	SV	2-16	absent
Anncaliia	diptera, coleoptera, humans	2,2	1	CY	na	absent
Antonospora	hymenoptera, psocoptera	?,2	1	CY	na	absent
Areospora	decapoda	1,1	1	SV	8	xenoma
Auraspora	collembola	2,1-2	2	CY, SV	n	absent
Bacillidium	oligochaeta, thysanura, diptera	2,2	1	CY	na	absent
Baculea	branchiopoda	1,1	1	PV, SV	n	absent
Becnelia	heteroptera	1,1	2	SV	8	absent
Berwaldia	branchiopoda	1,1	1	SV	1	absent
Binucleata	branchiopoda	1-2,1	1	SV	8	absent
Binucleospora	ostracoda	2,2	1	PV	na	absent
Bohuslavia	diptera	2,1	1	SV	8-16	absent
Brachiola	diptera, humans	2,2	1	CY	na	absent
Bryonosema	bryozoa	2,2	1	CY	na	absent
Burkea	oligochaete	1,1	1	PV	na	absent
Burunella	hymenoptera	1-2,1-2	2	PV, SV	8	absent
Buxtehudea	thysanura	1,1	1	PV	na	absent
Campanulospora	diptera	2,2	1	PV	na	absent
Canningia	coleoptera	1,1	1	CY	na	absent
Caudospora	diptera	2,2	1	CY	na	absent
Chapmanium	decapoda, diptera	2,1		SV	8	absent
Chytridiopsis	coleoptera	1,1	1	PV, SV	n	absent
Ciliatosporidium	ciliophora	1,1	1	CY	na	absent

Coccospora	diptera	2,1	1	SV	8	absent
Cougourdella	copepoda, maxillopoda, diptera	1,1	1	SV	4	absent
Crepidulospora	diptera	1,1	1	CY	na	absent
Crispospora	diptera	?,1-2	2	PV	na	absent
Cristulospora	diptera	2,1-2	2	CY, SV	8	absent
Cryptosporina	acari	1,1-2	1	SV	8	absent
Cucumispora	amphipoda	2,2	1	CY	na	absent
Culicospora	diptera	1-2,1-2	2	PV, SV	2-8	absent
Culicosporella	diptera	1-2,1-2	3	PV, SV	2-8	absent
Cylindrospora	diptera	2,1	1	PV, SV	8	absent
Cystosporogenes	lepidoptera	1,1	1	SV?	<60	absent
Dasyatispora	elasmobranch	1,1	1	SV	n	absent
Desmozoon	maxillopoda, copepoda, fish	1-2,1	1	CY	na	absent
Desportesia	hyperparasitic in gregarine in echiurid	1,1	1	CY, SV	32	absent
Dictyocoela	amphipod	2,1-2	1	SV	8	absent
Dimeiospora	diptera	1,1	2	SV	8	absent
Duboscqia	branchiopoda, copepoda, isoptera, diptera	1,1	1	SV	16	absent
Edhazardia	diptera	2,1-2	3	PV, SV	1-8	absent
Encephalitozoon	maxillopoda, orthoptera, acari, birds, mammals (incl. humans)	1,1	1	PV	na	absent
Endoreticulatus	lepidoptera, coleoptera, decapoda	1,1	1	PV	na	absent
Enterocytozoon	mammals (inc. humans), fish	1,1	1	CY	na	absent
Enterospora	decapoda, fish	2,2	1	CY, NU	na	absent
Episeptum	trichoptera	1,1	1	SV	4	absent
Euplotespora	ciliophora	1,1-2	1	SV	1	absent
Evlachovaia	diptera	2,1-2	2	PV, SV	2	absent
Facilispora	maxillopoda, copepoda	1,1	1	CY	na	absent
Fibrillanosema	amphipoda, branchiopoda	1,1	1	CY	na	absent
Flabelliforma	copepoda, ostracoda, cladocera, diptera	1,1	1	CY, SV	n	absent
Geussia	hyperparasitic in gregarine of ephemeroptera	?		SV	6-8	absent
Glugea	amphipoda, fish	1,1	1	SV	n	xenoma
Glugoides	branchiopoda	1,1	1	PV, SV	16	absent
Golbergia	diptera	2,1-2	2	CY	na	absent
Gurleya	branchiopoda, copepoda, decapoda, cladocera, diptera, ephemeroptera, isoptera, lepidoptera, odonata, trichoptera	1,1	1	SV	4	absent
Gurleyides	branchiopoda	?	2	SV	1,4	absent
Hamiltosporidium	branchiopoda	1,2	2	SV	8	absent
Hazardia	diptera	1-2,1-2	2	CY	na	absent
Helmichia	diptera	2,1-2	1	SV?	8	absent
Hepatospora	decapoda	1,1	1	PV	na	absent
Hessea	diptera	2,1-2	1	SV	n	absent
Heterosporis	fish, seasnakes	1,1	3	SP, SV	n	absent
Heterovesicula	orthoptera	2,1-2	2	SV	8-n	absent
Hirsutosporos	diptera	2,2	1	CY	na	absent
Holobispora	copepoda, maxillopoda	?,1	1	CY	na	absent
Hrabyeia	oligochaeta	2,2	1	CY	na	absent
Hyalinocysta	diptera, copepoda	2,1	1	SV	8	absent

Ichthyosporidium	fish	2,2	1	PV	na	xenoma
Inodosporus	decapoda	2,1	1	SV	8	absent
Intexta	acari	1,1	2	PV	na	absent
Intrapredatorus	diptera	2,1-2	3	SV	8	absent
Issia	trichoptera, diptera	2,2	2	SV?	2	absent
Janacekia	diptera, coleoptera	2,1-2	1	SV	1	absent
Jirovecia	fish, oligochaete	2,2	1	CY, PV?	na	xenoma
Jiroveciana	oligochaete	1,1	1	PV	na	absent
Johenrea	orthoptera	1,1	1	SV	8,16	xenoma
Kabatana	fish	1,1	1	CY	na	absent
Kneallhazia	hymenoptera	1-2,1	1	SV	8	absent
Kinorhynchospora	kinorhyncha	1,1	2	SV	n	absent
Krishtalia	diptera	2,1-2	2	CY	na	absent
Lanatospora	branchiopoda, maxillopoda, copepoda	1,1	1	SV	6-16	absent
Larssonia	branchiopoda	1,1	1	SV	4-32	absent
Larssoniella	lepidoptera	1,1	1	CY	na	absent
Liebermannia	orthoptera	2,2	1	PV	na	absent
Loma	fish	1,1	1	SV	4	xenoma
Marssoniella	maxillopoda	1,1	2	SV	4-8	absent
Merocinta	diptera	2,1-2	2	PV	na	absent
Metchnikovella	hyperparasitic in gregarine in polychaete	1,1	1	PV, SV	8-32	absent
Microfilum	fish	1,1	1	CY	na	xenoma
Microgemma	fish	1,1	1	PV	na	xenoma
Microsporidium (often used for *species inquirenda, incertae sedis*)	branchiopoda, copepoda, cirripedia, isopoda, amphipoda, mollusca, insecta, fish, mammals (incl. humans)	?	?	?	?	?
Mitoplistophora	ephemeroptera	1,1	1	PV	na	absent
Mockfordia	psocoptera	?,1	1	PV	na	absent
Mrazeckia	isopoda	2,2	1	CY	na	absent
Multilamina	isoptera, diptera	1,1	1	SV	1	absent
Myospora	decapoda	2,2	1	CY	na	absent
Nadelspora	decapoda	1,1	1	CY	na	absent
Napamichum	diptera, acari	2,1	1	SV	8	absent
Nelliemelba	copepoda, maxillopoda	1,1	1	SV	1	absent
Nematocida	nematode	1,1	1	PV	na	absent
Neoflabelliforma	oligochaete, hyperparasitic in myxozoa in oligochaete	1,1	1	SV?	?	absent
Neonosemoides	fish	2,1	1	CY	na	xenoma
Neoperezia	diptera	2,1	2	SV	2	absent
Nolleria	siphonoptera	1,1	1	PV, SV	n	absent
Norlevinea	branchiopoda	1,1	1	SV	4	absent
Nosema	branchiopoda, copepoda, decapoda, amphipoda, mollusca, hymenoptera, lepidoptera, acari, fish, mammals (incl. humans); hyperparasitic in myxozoa in fish, trematodes in snails, oysters, fish	2,2	2	CY	na	absent
Nosemoides	branchiopoda, fish, hyperparasitic in gregarine in nemertean	1,1	1	CY	na	xenoma
Novothelohania	diptera	1,1	1	SV	8	absent
Nucleospora	fish	1,1	1	NU	na	absent
Nudispora	odonata	2,1	1	CY	na	absent
Obruspora	fish	1,1	1	CY	na	xenoma

Octosporea	branchiopoda, isopoda, amphipoda, cladocera, diptera, ephemeroptera, hemiptera, lepidoptera, collembola	2,2	1	SV	8	absent
Octotetraspora	diptera	2,1	1	SV	4,8	absent
Oligosporidium	acari, opiliones	1,1	2	CY	na	absent
Ordospora	branchiopoda	1,1	1	PV	na	absent
Ormieresia	decapoda	2,1	1	CY, SV	8	absent
Orthosomella	lepidoptera, coleoptera	1,1	1	CY	na	absent
Ovavesicula	coleoptera	2,1	1	CY, SV	32	absent
Ovipleistophora	fish, hyperparasitic in trematode in fish	1,1	2	CY, SV	na	absent
Pankovaia	ephemeroptera	1,1	11	CY, SV	1	absent
Paradoxium	decapoda	1-2,1	1	CY	na	absent
Paraepiseptum	trichoptera	1,1	1	SV	4	absent
Parahepatospora	decapod	1,1	1	PV	na	absent
Paranosema	coleoptera, orthoptera	1-2,2	1	CY	na	absent
Paranucleospora	maxillopoda, fish	1-2,1-2	2	CY, NU	na	absent
Parapleistophora	diptera	1,1	1	SV	48-64	absent
Parastempellia	diptera	2,1-2	2	SV	4,8,16	absent
Parathelohania	maxillopoda, diptera	2,1-2	2	SV	8	absent
Pegmatheca	diptera, tricoptera	2,1	1	SV	8	absent
Perezia	branchiopoda, decapoda, lepidoptera, coleoptera, hymenoptera, orthoptera, plus hyperparasitic in gregarine of tunicate	2,1	1	CY	na	absent
Pernicivesicula	diptera	2,1	1	SV	24-64	absent
Pilosporella	diptera	2,1-2	2	SV	8	absent
Pleistophora (Plistophora)	branchiopoda, copepoda, decapoda, blattaria, coleoptera, diptera, lepidoptera, orthoptera, mollusca, fish, mammals (incl. humans	1,1	2	SV	n	absent
Pleistophoridium	hyperparasitic in gregarine in ephemeroptera	1,1	1	CY, PV	na	absent
Polydispyrenia	diptera	2,1	2	PV, SV	n	absent
Potaspora	fish, decapod	1,1	1	CY	na	xenoma
Pseudoloma	fish	1,1	1	SV	16	atypical xenoma
Pseudonosema	bryozoa	2,2	1	CY	na	absent
Pseudopleistophora	lepidoptera, polychaete	2,2	1	PV, SV?	n	absent
Pulicispora	siphonoptera	1,1-2	1	SV	8,16,32	absent
Pyrotheca	copepoda, maxillopoda	1,1	1	CY, SV	4	absent
Rectispora	oligochaeta	2,2	1	CY	na	absent
Resiomeria	odonata	2,1	1	SV	8	absent
Ringueletium	diptera	2,2	1	CY	na	absent
Schroedera	bryozoa	1-2,2	1	CY	na	xenoma
Scipionospora	diptera	2,2	1	SV	4	absent
Semenovaia	diptera	?,1-2	2	CY	na	absent
Senoma	diptera	2,2	1	PV	na	absent
Septata	human	1,1	1	PV	na	absent
Simuliospora	diptera	2,1	2	SV	6,32	absent
Spherospora	diptera	2,1-2	2	SV	8-32	absent
Spiroglugea	diptera	?	1	SV?	8	absent
Spraguea	fish	1-2,1-2	2	CY	na	xenoma
Steinhausia	bivalve, gastropod	1,1	1	PV, NU	na	absent
Stempellia	copepoda, amphipoda, opiliones,	1,1	2	PV, SV	4	absent

	ephemeroptera, diptera, coleoptera, isoptera					
Striatospora	diptera	2,1	1	SV	8	absent
Systenostrema	diptera	2,1-2	1?	SV	8	absent
Tabanispora	diptera	1-2,2	2	SV	1-10	absent
Takaokaspora	diptera	1-2,1-2	2	CY, SV	?	absent
Tardivesicula	trichoptera	1,1	1	SV	16-32	absent
Telomyxa	ephemeroptera, diptera, coleoptera	1,1	1	SV	2	absent
Tetramicra	fish	1,1(2?	1	PV	na	xenoma
Thelohania	branchiopoda, copepoda, decapoda, amphipoda, diptera, collembola, ephemeroptera, hemiptera, lepidoptera, hymenoptera, odonata, trichoptera, fish	1-2,1	1	SV	8	absent
Toxoglugea	branchiopoda, diptera, plecoptera, odonata, hemiptera, homoptera	2,1	1	SV	8	absent
Toxospora	diptera	?,1-2	1	SV	8	absent
Trachipleistophora	mammals (incl. human)	1,1	1	PV, SV	2-n	absent
Trichoctosporea	diptera	2,1	2	SV	8	absent
Trichodubosquia	ephemeroptera	2,1	1	SV	16-32	absent
Trichonosema	bryozoa	2,2	1	CY	na	absent
Trichotuzetia	copepoda, maxillopoda	1,1	1	SV	1	absent
Tricornia	diptera	2,1-2	1	SV	8	absent
Triwangia	decapoda	1,1	1	SV	n	xenoma
Tubulinosema	diptera, orthoptera, hymenoptera, coleoptera, mammals (humans)	2,2	1	CY	na	absent
Tuzetia	branchiopoda, copepoda, maxillopoda, ephemeroptera	1,1	1	SV	1	absent
Unikaryon	coleoptera, acari, hyperparasitic in trematode in bivalve	1,1	1	SV	2	absent
Vairimorpha	decapod, lepidoptera, hymenoptera, diptera	2,1-2	2	CY, SV	8	absent
Vavraia	ostracoda, decapoda, diptera, coleoptera, lepidoptera	1,1	1	SV	16-64	absent
Vittaforma	mammals (humans)	2,2	1	PV	na	absent
Weiseria	diptera	2,2	1	CY	na	absent
Wittmania	hyperparasitic in mesozoan in cephalopod	1-2,2	1	CY	na	absent
Zelenkaia	trichoptera	1,1	1	SV	2	absent

Although many microsporidian species have been described on the basis of presumed host specificity, recent molecular characterization studies have demonstrated that the host ranges for some species can be very broad, encompassing not only hosts from disparate taxa (e.g. insects and mammals) but also hosts from disparate environments (e.g. marine and terrestrial). While considerable work remains to determine the host ranges and phylogenetic affinities of most microsporidia, the following text considers microsporidia from one of three perspectives associated primarily, but not exclusively, with different host groups; namely, arthropods (mainly insects and crustaceans), fish (bony and cartilaginous), and tetrapods (mammals, birds, reptiles and amphibians). This section considers the microsporidia of fish, notably those kept and managed for economic benefit; including ornamental species (aquarium trade), farmed species (freshwater and marine aquaculture) as well as wild fisheries.

Microsporidian infections have been found in both wild and farmed fish from freshwater, estuarine and marine habitats around the world. Most species appear to be oioxenous (host specific) or stenoxenous (infecting closely-related hosts), although a few have been found to be euryxenous (infecting a broad range of hosts). Many infections are disseminated throughout various host

tissues, while others may cause focal space-occupying lesions which may become visible (macroscopic) as cysts or tumour-like xenomas (hypertrophic host cells). Infections have been associated with significant morbidity and mortality, especially in salmonid culture. Microsporidia of fish may be divided into two groups, comprising pansporoblastic and apansporoblastic species whose spores do or do not develop within sporophorous vesicles, respectively. Most pansporoblastic genera are monokaryotic and monomorphic (e.g. *Glugea, Loma, Pseudoloma*), although *Thelohania* forms diplokaryotic meronts and some *Pleistophora* spp. are dimorphic. A notable exception is the genus *Heterosporis* which may undergo three sporulation sequences, all enveloped within a unique sporophorocyst (parasite-derived envelope). The pansporoblastic genera *Glugea, Loma* and *Pseudoloma* form xenomas, while the remainder cause disseminated infections or tissue-bound cysts. Most apansporoblastic genera are monokaryotic and monomorphic (e.g. *Microgemma, Kabatana, Tetramicra, Potaspora, Microfilum*), although several are diplokaryotic and monomorphic (*Ichthyosporidium, Jirovecia*) or diplokaryotic and dimorphic (*Nosema, Spraguea*). Xenomas are formed by most apansporoblastic genera, except *Kabatana* and *Nosema* which form tissue cysts. Meronts of most genera develop either directly within the host cell cytoplasm or within parasitophorous vacuoles, but two notable exceptions are the genera *Nucleospora* and *Enterospora* which develop within the nucleoplasm of host cells.

Parasite species	**Spore dimensions** (mi = microspores; ma = macrospores; me = meiospores)	**Hosts**	**Location**	**Distribution**
Suborder PANSPOROBLASTINA (sporophorous vesicle (SV) present)				
Family GLUGEIDAE (monokaryotic, variable but large number spores produced)				
Genus ***Glugea*** (sporogony by multiple then binary fission, spores in SV with membrane-like wall, xenomas)				
forming large xenomas with numerous branched peripheral nuclei				
G. anomala	3.0-6.0 x 1.9-2.7 µm	freshwater fish (sticklebacks, killifish)	xenomas in connective tissues	North America, Eurasia
G. atherinae	3.5-5.7 x 2.2-2.9 µm	estuarine fish (smelt, silversides, smallmouth hardyhead, short-snout hardyhead, pikehead hardyhead, silver fish)	xenomas in connective tissues of gut, body cavity and mesenteries	Mediterranean, Australia
G. capverdensis	3.6-4.8 x 1.8-2.6 µm	marine fish (lanternfish)	xenomas in intestine, mesentery, ovary	Atlantic
G. cepedianae	4.9 x 2.3 µm	freshwater fish (shad)	xenomas in body cavity	North America
G. fennica	7.4 x 2.8 µm	freshwater fish (lingcod)	xenomas in subcutaneous tissues	Northern Europe
G. heraldi	3.6-4.5 x 1.8-2.3 µm	marine fish (seahorses)	xenomas in connective tissues	Atlantic
G. hertwigi	4.6-5.4 x 2.2-2.3 µm	marine and freshwater fish (smelts, whitefish)	xenomas in intestines, organs	Holarctic
G. pimephales	4.5-6.0 x 2.0-3.0 µm	freshwater fish (minnows)	xenomas in body cavity	North America
G. plecoglossi	5.8 x 2.1 µm	freshwater fish (ayu sweetfish, rainbow trout)	xenomas in visceral organs	Japan
G. sardinellensis	5-5.5 x 2.5-3 µm	marine fish (round sardinella)	xenomas in connective tissue	Tunisia
G. stephani	3.0-3.9 x 1.5-1.7 µm	marine fish (plaice, flounder, sole, turbot)	xenomas in intestines, liver	Europe, North Atlantic
G. vincentiae	ma 7.5-12.0 x 2.0-4.0 µm (12-14 coils) mi 4.5-6.0 x 2.0-2.7 µm (12-14 coils)	marine fish (cardinalfish)	xenomas in subcutaneous tissues	Australia
forming small xenomas with a centrally located nucleus				
G. berglax	6.4 x 2.7 µm	marine fish (rattails)	xenomas in intestines, gall bladder	Canada
G. destruens	3.6 x 2 µm	marine fish (dragonets)	xenomas in muscles	France
G. luciopercae (syn. *G. dogieli*)	4.5 x 2.1 µm	freshwater fish (perch, pike)	xenomas in intestines	Eurasia
G. machari (syn. *Octosporea*)	3.7 x 1.1 µm	marine fish (sea bream)	xenomas in liver	Adriatic

G. tisae	4.5 x 2.4 µm	freshwater fish (catfish)	xenomas in intestines	Europe
G. truttae	5 x 1.5 µm	freshwater fish (brown trout)	yolk sac	Europe
Genus ***Pseudoloma*** (atypical xenomas)				
P. neurophila	4.8-5.9 x 2.3-3.1 µm (13-16 coils)	freshwater fish (zebrafish)	muscles, nervous tissue	North America
Genus ***Pleistophora*** (polysporoblastic sporogony, SV, macro-, medium-, micro-spores (ma, me, mi)				
species infecting skeletal muscle				
P. atretti	4.8-5.4 x 1.8-2.5 µm	freshwater snake	muscles	India
P. duodecimae	ma 6.2 x 3.3 µm mi 4.3 x 2.7 µm	marine fish (rattails)	cysts in muscles	Southern Atlantic
P. ehrenbaumi	ma 7.5 x 3.5 µm mi 3.0 x 1.5 µm	marine fish (wolf fish)	cysts in muscles	North Sea
P. finisterensis	4.0 x 2.0 µm	marine fish (blue whiting)	cysts in muscles	Europe
P. hippoglossoides	4.7 x 2.7 µm	marine fish (flatfish, sole)	cysts in muscles	North Sea
P. hyphessobryconis	ma 6.5-7.0 x 4.0 µm (34 coils) mi 4.0-6.0 x 2.0-3.3 µm (up to 34 coils)	freshwater fish (tetras, danios, barb, goldfish)	cysts in muscles, internal organs, testes, subcutaneous	worldwide (aquarium trade)
P. littoralis	ma 7.7 x 3.8 µm (39 coils) mi 3.9 x 2.3 µm (17 coils)	marine fish (blennies)	cysts in muscles	England
P. macrozoarcidis	ma 8 µm mi 5.5 x 3.5 µm	marine fish (ocean pout)	cysts in muscles	North Atlantic
P. mulleri		marine amphipod (scuds)	muscles	Atlantic
P. typicalis	ma 6.3-8.3 x 3.0-3.3 µm (33-39 coils) mi 3.0-5.6 x 1.5-3.0 µm (10-22 coils)	freshwater fish (sculpins, blennies, sticklebacks)	cysts in muscles	Europe
low organ specificity				
P. aegyptiaca	1.5-2.7 x 1.2-1.8 µm (26-32 coils)	marine fish (lizardfish)	cysts in peritoneum	Red Sea
P. dammami	ma 6.0 x 3.0 µm (20-24 coils) mi 2.5 x 2.0 µm (6 coils)	marine fish (lizardfish)	gi tract	Arabian Gulf
P. pagri	1.5-2.7 x 1.2-1.8 µm (3-5 coils)	marine fish (bream)	viscera	Egypt
P. peponoides	3.6 x 2.0-2.3 µm	freshwater fish (sleeper)	connective tissue	Russia
P. priacanthicola	ma 8.2 x 3.8 µm me 5.4 x 3.1 µm mi 2.9 x 1.9 µm	marine fish (bigeyes)	cysts in gi tract, heart, gonads, visceral organs	South China Sea
species infecting ovaries transferred to new genus *Ovipleistophora*				
O. longifilis (syn. *P. longifilis*)	ma 12 x 6 µm mi 3 x 2 µm	freshwater fish (barbels, roaches)	spore masses in ovaries, ova	Europe, Asia
O. mirandellae (syn. *P. mirandellae, P. oolytica, P. elegans*)	ma 7.3-12.0 x 3.5-6.4 µm me 4.0-6.5 x 2-3.5 µm mi 3.0-7.5 x 1.5-4.0 µm	freshwater fish (cyprinids, esp. barbels, bream, dace, roach, pike, huchen, bleak)	spore masses in ovaries, ova	Europe, Asia
O. ovariae (syn. *P. ovariae*)	8.4 x 4.2 µm	freshwater fish (shiners, minnows)	spore masses in ovaries, ova, liver, kidneys	North America
Genus ***Dasyatispora*** (species in rays)				
D. levantinae	3.8-4.3 x 2.6-2.8 µm (9-12 coils)	marine elasmobranchs (stingrays)	muscle	Turkey
Genus ***Loma*** (polysporoblastic sporogony, up to 8 spores in SV, xenomas up to 1mm with central nucleus)				
L. acerinae (syn. *Glugea*)	2.3-4.5 x 1.6-3.4 µm (10-14 coils)	freshwater fish (perch, gobies)	xenomas in connective tissues, intestines	Central Europe
L. branchialis (syn. *L. morhua,*	4.8 x 2.3 µm	marine fish (haddock, cod)	xenomas in gills, viscera	North Atlantic

Nosema, Glugea)				
L. camerouensis		freshwater (Nile tilapia)	xenomas in gut	Africa
L. dimorpha	4.5 x 1.9 µm	marine fish (gobies)	xenomas in intestines	Mediterranean
L. embiotocia	4.0-5.0 x 2.0-3.0 µm (14-18 coils)	marine fish (perch)	xenomas in gills	Canada
L. kenti	4.0-5.0 x 1.9-4.4 µm (14-16 coils)	marine fish (tomcod)	xenomas in gills, viscera	Canada
L. myrophis		freshwater fish (worm eel)	xenomas in midgut	South America
L. psittaca	4.2 x 2.8 µm (10-12 coils)	freshwater fish (pufferfish)	xenomas in gi tract	Amazon River
L. salmonae	3.0-7.5 x 1.6-2.8 µm	freshwater fish (trout)	xenomas in gills	North America, Japan, Europe
Genus ***Heterosporis*** (stages encased within sporophorocyst wall, polysporoblastic sporogony in SV)				
H. anguillarum	ma 6.7-9.0 x 3.3-5.3 µm (33-46 coils) mi 2.8-5.0 x 2.0-2.9 µm (33-36 coils)	marine fish (eels) [also recorded in garter snakes?]	muscles, skin	Japan, Taiwan, Korea
H. finki	ma 7.0-9.0 x 2.0-5.0 µm (30-36 coils) mi 3.0 x 1.5 µm (7 coils)	freshwater fish (angelfish)	muscles, connective tissues	Germany, France (aquaria)
H. saurida	ma 5.0-6.0 x 3.0-3.8 µm (20-21 coils) mi 3.0-3.8 x 1.5-2.5 µm (5-6 coils)	marine fish (lizardfish)	muscles	Arabian Gulf
H. schuberti	ma 5.4-8.8 x 2.9-4.9 µm mi 3.4-4.9 x 2.4-3.4 µm	freshwater fish (mouthbrooder, Jumbie tetra)	muscles	worldwide (aquaria)
H. sutherlanda	4.8-6.3 x 3.2-3.6 µm	freshwater fish (walleye, yellow perch, northern pike)	muscles	North America
Family THELOHANIIDAE (meronts usually diplokaryotic, spores monokaryotic, 8 spores in SV)				
Genus ***Thelohania*** (uninucleate spores with isofilar polar tube)				
T. baurei	5.4 x 2.7 µm	marine fish (sticklebacks)	spore masses in ovaries	Baltic Sea
T. ovicola	7.0 x 5.0 µm	freshwater fish (whitefishes)	spore masses in ovaries	Switzerland
Suborder APANSPOROBLASTINA (sporophorous vesicle (SV) absent)				
Family UNIKARYONIDAE (monokaryotic, diplo- to poly-sporoblastic sporogony)				
Genus ***Nosemoides*** (polysporoblastic sporogony, sporoblasts in rosette formation)				
N. syacii	2.9-4.9 x 1.8-2.7 µm (4-5 coils)	marine fish (turbot)	xenomas in gut, liver	Senegal
N. tilapiae	2.5-3.0 x 1.5-2.0 µm (4-5 coils)	freshwater fish (cichlids)	xenomas in gills, mesentery	Africa
Genus ***Microgemma*** (sporogonial plasmodia produce sporoblasts by exogenous budding)				
M. carolinus	3.8 x 2.4 µm (8-9 coils)	marine fish (carangids)	xenomas in liver	Brazil
M. caulleryi (syn. *Glugea*)	2.6 x 1.2 µm (7-9 coils)	marine fish (greater sand eel)	xenomas in liver	Spain
M. hepaticus	4.2 x 2.4 µm (7-10 coils)	marine fish (mullet)	xenomas in liver	England
M. ovoidea (syn. *Glugea*)	2.5 x 1.5 µm	marine fish (rockling, bandfish, mullet)	xenomas in liver	Europe
M. tincae	3.6 x 1.2 µm (9 coils)	marine fish (wrasse)	xenomas in liver	Tunisia
Genus ***Kabatana*** (infects muscles, no xenoma formation)				
K. arthuri (syn. *Microsporidium*)	3.1 x 2.1 µm	freshwater fish (catfish)	muscles	Thailand
K. newberryi	2.8 x 1.9 µm (9-10 coils)	marine fish (gobies)	muscles	North America
K. rondoni	4.2 x 2.4 µm	freshwater fish (knifefish)	muscles	Amazon River

	(8-10 coils)			
K. takedai (syn. *Glugea, Nosema, Microsporidium*)	2.8-4.9 x 1.7-2.3 µm	marine fish (salmonids)	muscles, heart	Japan
Genus ***Tetramicra*** (tetrasporoblastic sporogony, xenomas with single central nuclei)				
T. brevifilum	3.7-4.8 x 2.0-2.7 µm (3-4 coils)	marine fish (turbot, anglerfish)	xenomas in connective tissues, muscles	England, Spain
Genus ***Unikaryon*** (disporoblastic sporogony)				
U. nomimoscolexi	3.4 x 1.5 µm (6-8 coils)	hyperparasitic in cestode (*Nomimoscolex,* but probably *Proteocephalus*) in gut of freshwater fish (whitehead catfish)	parenchymal cells	Africa
Genus ***Potaspora*** (tetrasporoblastic sporogony, spore with manubrium, xenoma formation)				
P. aequidens	3.4 x 1.9 µm (8-9 coils)	freshwater fish (cichlid)	xenomas in muscles	Brazil
P. morhaphis	2.8 x 1.5 µm (9-11 coils)	freshwater fish (needlefish)	xenomas in body cavity	Amazon River
Genus ***Microfilum*** (tetrasporoblastic sporogony, spore with manubrium, xenoma formation)				
M. lutjani	4.5 x 2.6 µm	marine fish (snapper)	xenomas in gills	Africa
Family SPRAGUEIDAE (dimorphic species)				
Genus ***Spraguea*** (two developmental sequences, monokaryotic forming oval spores, diplokaryotic forming curved spores)				
S. gastrophysus	3.4 x 1.7 µm (5-6 coils)	marine fish (anglerfish)	xenomas in ganglia, kidneys	Brazil
S. lophii (syn. *Nosema, Glugea, G. americanus*)	oval 4.2 x 2.5 µm (5-6 coils) curved 3.7 x 1.4 µm (3-4 coils)	marine fish (anglerfish)	xenomas in ganglion cells	Mediterranean, Atlantic
Family NOSEMATIDAE (diplokaryotic, diplosporoblastic, monomorphic)				
Genus ***Nosema*** (no xenomas, species in fish include hyperparasites of myxozoans)				
N. branchiale	6.3 x 3.5 µm	marine fish (cod)	gills, viscera	Eurasia, North America
N. ceratomyxae	ns	in myxozoan (*Ceratomyxa*) in gall bladder of marine fish (rabbitfish)	in myxozoan plasmodia	Red Sea
N. girardini	2.0-2.5 x 1.0-1.5 µm	marine fish (poeciliids)	gi tract	Brazil
N. marioni	8.0 x 3.0 µm	in myxozoan (*Ceratomyxa*) in gall bladder of marine fish (wrasses)	in myxozoan plasmodia	Mediterranean
N. notabilis	3.3 x 2.0 µm	in myxozoan (*Ortholinea*) in urinary bladder of marine fish (toadfish)	in myxozoan plasmodia	Atlantic
N. pimephales	3.8-4.4 x 1.9-3.3 µm	freshwater fish (minnows)	abdomen	Canada
N. podocotyloidis	3.1-4.0 x 1.8-3.3 µm	in trematode (Podocotyloides) in marine fish (African striped grunt)	in trematode parenchyma	Atlantic
Genus ***Ichthyosporidium*** (forming lobose xenomas)				
I. giganteum (syn. *Pleistophora gigantea*)	6.0-7.3 x 4.0-5.2 µm (32-46 coils)	marine fish (wrasses, spot croaker)	xenomas in subcutaneous tissues, liver	Atlantic, Black Sea
I. hertwigi	6.0 x 4.5 µm	marine fish (wrasses)	xenomas in gills	Black Sea
I. weissii	ma 7.1-10.1 x 4.8-6.2 µm (36-50 coils) mi 4.9-7.0 x 2.9-5.3 µm (36-50 coils?))	marine fish (gobies)	xenomas in gonads	North America
Family BACILLIDIIDAE (diplokaryotic, disporoblastic, cylindrical spores)				
Genus ***Jirovecia*** (basal polar tube thickened into rod)				
J. piscicola	20.0 x 6.0 µm	marine fish (whiting)	skin	France, India

Family ENTEROCYTOZOONIDAE (monokaryotic, sporogony with formation of electron-dense discs)				
Genus ***Nucleospora*** (multinucleate merogony and sporogony, stages in host cell nuclei)				
N. salmonis (syn. *Enterocytozoon salmonis*)	2.0 x 1.0 µm (8-12 coils)	marine fish (salmonids)	haematopoietic cells, kidney (intranuclear)	Atlantic
N. secunda	1.6 x 0.8 µm (4-5 coils)	freshwater fish (redfin notho)	enterocytes (intranuclear)	Europe
Genus ***Enterospora*** (develop in nucleoplasm)				
E. nucleophila	1.7 x 1.1 µm (5-6 coils)	marine fish (bream)	enterocytes	Spain
Microspora *incertae sedis*				
Genus ***Amazonspora*** (xenoma formation)				
A. hassar	2.7 x 1.8 µm	freshwater fish (thorny catfish)	xenomas in gills	South America
Genus ***Neonosemoides*** (two merogonial phases in host cell cytoplasm, one diplokaryotic, one monokaryotic)				
N. tilapiae	2.5-3.2 x 1.5-2.2 µm (4-5 coils)	freshwater fish (cichlids)	xenomas in gut, gills	Africa

Various reports have also not been able to assign microsporidian species to particular genera, so they have been reported as belonging to a collective group called *Microsporidium s.l.* (*sensu latu* = in the broadest sense).

Parasite species	Spore dimensions	Hosts	Location	Distribution
Genus ***Microsporidium*** (collective group, depository for unidentified microspora)				
forming xenomas				
M. aurata	1.5-2.5 x 1.0-2.0 µm (5-11 coils)	marine fish (bream)	xenomas in muscles, viscera	Egypt
M. cotti	9 x 3 µm	marine fish (sculpins)	xenomas in testes	France
M. hepaticum	4.2-5.0 x 2.1-2.9 µm (6-10 coils)	marine fish (greenback flounder, bridled leatherjacket, sixspine leatherjacket, brown-striped leatherjacket)	xenomas in liver	Australia
M. merluccius	2.5-3.3 x 1.8-2.1 µm (11-12 coils)	marine fish (hake)	xenomas in muscles	Namibia
not forming xenomas				
M. ovoideum	2.5 µm	marine fish (cod, bandfish, mullet)	liver	France
M. prosopium	5.0-7.0 x 3.0-4.0 µm (13-16 coils)	freshwater fish (whitefish)	muscle	Canada
M. rhabdophilia (possibly *Enterocytozoon salmonis*)	2.3-3.5 x 0.8-1.2 µm	marine fish (salmonids)	skin, gills, gi tract (intranuclear)	North America
M. seriolae (possibly *Kabatana*)	3.3 x 2.2 µm	marine fish (yellowtails)	muscles (Beko = myoliquefaction)	Japan
M. sulci (syn. *Cocconema, Pleistoiphora*)	2.5 x 2.5 µm	freshwater fish (sturgeon, sterlet)	ovaries	Volga and Danube Rivers

Parasite morphology: Microsporidia form three sequential developmental stages: meronts, sporonts and spores. The unique unicellular spores are spherical, ovoid or cylindrical, most ranging in length from 2-8 µm. They are encased within tough chitinous walls comprising a thin electron-dense exospore and a thicker electron-lucent endospore. Mature spores possess an elongate polar tube coiled up inside; most tubes being isofilar (of uniform diameter) although some are anisofilar (tapered, showing a reduction in diameter over length). The polar tubes are attached to an anterior anchoring disc enveloped by a membranous polar sac. For most microsporidian genera, the wall of the polar tube and its central canal are inserted into the polar sac, but for chytridiopsid genera (*Buxtehudea, Chytridiopsis* and *Nolleria*), only the central canal surrounded by a honeycomb layer is inserted into the polar sac. The anterior section of the polar tube is straight and surrounded by the polaroplast, which may be lamellar, tubular or both. Mature spores (especially in piscine microsporans) contain a prominent posterior vacuole (often visible by light microscopy) and an amoeboid nucleated sporoplasm. Spores may be monokaryotic (uninucleate) or diplokaryotic (with two closely-appressed nuclei).

Many microsporidia form only one type of spore (monomorphic), while others are heterosporous (dimorphic or polymorphic) forming several different types (usually micro-spores and macro-spores, sometimes meio-spores). Following host cell invasion, parasites undergo asexual merogony (schizogony) and then 1-3 sporulation (sporogony) sequences forming sporoblasts (sporoblastogenesis) which mature to form infective spores (sometimes referred to as germination). Meronts are located either directly within the host cell cytoplasm (often surrounded by host endoplasmic reticulum and sometime host mitochondria) or bound within parasitophorous vacuoles (membranous envelopes of host origin). They appear as clusters of small nucleated intracellular parasites that have divided by binary or multiple fission, although several species form multinucleated plasmodial stages. Sporonts also appear as small clusters of parasitic cells but are characterized by thickened plasmalemmas due to the deposition of parasite secretions on their surface membranes. Pansporoblastic species also form an isolating envelope (thick- or thin-walled membranous sporophorous vesicle, special thick-walled sporophorocyst in the case of *Heterosporis*) whereas apansporoblastic species lie direct in the host cell cytoplasm or within parasitophorous vacuoles. Sporonts divide internally one or more times by binary or multiple fission or plasmotomy to form sporoblasts which then mature into spores. Sporonts of a few species (mostly in insects) are also thought to divide by meiosis to form uninucleate meiospores.

Site of infection: All microsporidian species are histozoic parasites with obligative intracellular development within host cells; either being in direct contact with the host cell cytoplasm (a few even occurring in the nucleoplasm) or being enclosed within parasitophorous vacuoles (membrane of host origin), sporophorocysts or sporophorous vesicles (envelopes of parasite origin). Many species exhibit tissue tropism with development occurring within particular tissues (including gut, gills, subcutis, muscles, connective tissues, visceral organs or gonads) or they may be disseminated throughout multiple tissues, some being systemic.

Pathogenesis: During development, microsporidia are metabolically dependent on host cells and are able to mobilize host cell organelles to meet their demands. Infected cells become swollen and the host cell nucleus becomes enlarged or fragmented. The parasites ultimately cause lysis of infected host cells, thereby resulting in both structural and functional deficits. Infections in tissues may be diffuse, spreading from cell to cell, or localized within cysts. Some microsporidia cause infected host cells to undergo massive hypertrophy forming tumour-like xenomas (xenoparasitic complexes, xenoparasitomes) occupying part or all of the cell volume, surrounded by a simple plasmalemma or a thick wall with surface modifications (microvilli, invagination), and containing a single central hypertrophic host cell nucleus or multiple peripheral (syncytial) nuclei. Disseminated infections, cysts and xenomas are responsible for tissue displacement/replacement, inflammation, space-occupying lesions and pressure atrophy as well as causing structural/growth deformities and disfigurement. Microsporidial spores are highly refractile due to their chitinous walls so heavy infections may cause tissue opacities and unsightly lesions. Host cell lysis often leads to cellular infiltration of the tissues (slow to develop) and sometimes granuloma formation. Host reactions may eventually lead to the destruction of spores, with both humoral and cellular immune responses implicated in parasite clearance. Surviving hosts are left with space-occupying lesions filled with connective tissue fibres, host cellular infiltrates and parasite fragments. Some infections have also been linked to post-mortem (and putatively ante-mortem) liquefaction of muscles. Infected fish have been shown to have reduced fitness, longevity and fecundity, as well as being more susceptible to predation by piscivores. Microsporidial infections therefore not only adversely affect fish health and survival but also cause significant economic losses in aquaculture due to production-limiting diseases in aquaculture as well as reducing the commercial value of wild and farmed fish due to poor quality product.

Xenoma formation has been documented in a variety of fish tissues: often progressing through 3 phases from ‘weakly-reactive’ stages (local proliferation of connective tissue leading to collagenous envelope, usually multilaminate in appearance) to ‘ripe and productive’ stages (prominent inflammation with degenerative changes in xenoma wall) to ‘granuloma involution’ stages following xenoma rupture (involving phagocytes and hyalinization of fibrous connective tissue). Several *Glugea* spp. form synchronous xenomas (enclosed parasites at similar stages of development) with multilaminate walls in submucosal intestinal cells; *Loma* spp. may form asynchronous xenomas (enclosed parasite at different stages of development) in endothelial cells throughout vascularized organs (esp. gills); *Tetramicra* spp. may form xenomas without multilaminate walls throughout the skeletal musculature; *Ichthyosporidium* spp. may form massive multilobate (syncytial-type) xenomas in connective tissues throughout the abdominal cavity and gills, and *Spraguea* spp. may form massive thin-walled xenomas in the hindbrains of fish. Non-xenoma-forming genera may also cause extensive tissue damage as they disseminate throughout host tissues. *Pleistophora* spp. often cause diffuse infections in skeletal muscles with musculature destruction or liquefaction, deformity and the production of tumour-like masses (but not granulomas). *Kabatana* spp. may cause massive infections of the trunk musculature (Beko disease) with cyst formation, fibrosis, deformities and liquefaction. *Heterosporis* spp. mainly infect the muscles of eels forming unique sporophorocysts (thick dense envelope of parasite origin). *Ovipleistophora* spp. infect oocytes and mature eggs causing macroscopic lesions with proliferative granulomatous inflammatory responses that reduce host fecundity. *Nucleospora* spp. infect the nuclei of haemoblasts (particularly lymphoblasts or plasmablasts) causing massive proliferation of immature cells (suggestive of neoplasia), often associated with plasmacytoid leukaemia in salmon. A *Paranucleospora* sp. has recently been found in copepods on salmon in association with ‘proliferative gill disease’.

Infections in fish by different microsporidial species have been associated with reduced growth rates, weight loss, inappetance, anorexia to the point of starvation, and emaciation (*Pseudoloma neurophilia* causing ‘skinny disease’). Infected fish

have demonstrated unusual behaviours associated with respiratory distress and impaired swimming ability, occasionally associated with spinal curvature (scoliosis and kyphosis). Infections of the skin and subcutis can result in focal swellings, loss of body coloration, development of pale patches, bristled scales and ragged fins. Systemic infections have been associated with anaemia and myeloencephalitis, while infections of the gonads have been associated with reduced reproductive capacity (reduced fertility and fecundity) and occasionally parasitic castration (mostly involving ova, rarely testes). Infections are also more prevalent and severe in cultured fish, particularly those confined within small aquaria or ponds at higher stocking densities. Clinical infections usually involve younger fishes, as older fish either develop resistance or do not become infected because of differing feeding habits or physical environments (note that infected fish probably do not survive to older age groups). Various host defense mechanisms have been observed in experimentally and naturally infected fish; including phagocytosis of spores by macrophages, humoral responses (esp. agglutinating antibodies), mononuclear cellular responses, and even premunitive immunity (persistence of some parasites contributing to resistance to super-infection, rather than clearance of infection as occurs in sterile immunity). Microsporidia have also been shown to evade host immune responses by preventing phagosome-lysosome fusion, the production of immunomodulatory serum factors, and the suppression of host inflammatory responses (paradoxically, host stress leading to elevated cortisol levels and immunosuppression has also been associated with more severe infections).

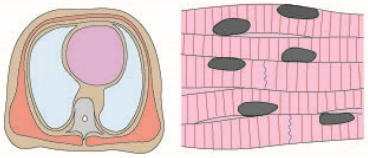
Developmental cycle and mode of transmission: The life-cycles of microsporidia vary considerably. Most piscine microsporidia have simple asexual monoxenous life-cycles, while some insect microsporidia have complex heteroxenous life-cycles with both asexual and sexual reproduction involving successive host generations or crustacean intermediate hosts. Mature spores have tough resistant walls which allow them to survive moderate ranges of various physical and chemical factors encountered in host environments (temperature, moisture, UV radiation, salinity, pH), but they are still susceptible to extremes of heat, cold, desiccation, sunlight, hypersalinity, acidity or alkalinity. Each spore contains an infective sporoplasm which is injected into a host cell through the polar tube when it is forcibly everted by swelling of the posterior vacuole and polaroplast (triggered by changes in calcium influx, osmotic pressure, pH, mechanical compression, etc.). The parasites then undergo vegetative reproduction by merogony (schizogony) by binary or multiple fission, although cytokinesis is sometimes delayed thus forming multinucleate plasmodia which divide by plasmotomy to form more plasmodia or segment into uninucleate meronts again. Meronts may lie direct in the host cell cytoplasm or be contained within membranous parasitophorous vacuoles (the exception being *Heterosporis* which forms a unique sporophorocyst envelope). The parasites then form thickened cell membranes and/or enveloping sporophorous vesicles and undergo further division called sporogony. Sporonts have electron-dense coats and undergo sporoblastogenesis by dividing through binary fission (disporoblastic sporogony) to form sporoblasts, or first forming multinucleated sporogonial plasmodia that divide by multiple fission, by gradual fragmentation, or sometimes producing intermediary mother cells (e.g. genus *Glugea*), to form sporoblasts. The sporoblasts subsequently mature to form spores (completing sporulation). The developmental stages of many microspora have single isolated nuclei throughout their development, ultimately giving rise to uninucleate sporoblasts and spores. Others have paired nuclei which divide synchronously and remain closely appressed throughout their development into diplokaryotic sporoblasts. Some diplokaryotic sporonts also appear to undergo meiotic reduction forming monokaryotic spores. The number of spores formed by each sporont (di-, tetra-, octo-, poly-sporous) can be a defining characteristic for many genera, particularly those developing within sporophorous vesicles. Merogony and sporogony may take place within the same or different tissues of individual hosts. Many microsporidian species are monomorphic (forming only one type of spore) while other species may produce different types of spores (macro-, medi-, micro-, meio-spores) at different stages of development, each type probably having a different function, such as autoinfection (facilitating dissemination within the same host), horizontal transmission (from host to host) and vertical transmission (from mother to offspring). Most infections in fish appear to be transmitted directly between hosts by contact with mature infective spores (skin or gill epithelia) or following their ingestion (gut epithelia). Microsporidian spores have been shown to be liberated from infected hosts from eruptive lesions in the gills and skin, from the digestive and urinary tracts and from degenerating tissues in decomposing carcases. Direct transmission by spore ingestion has been recorded for many species, while some apparently require spores to be primed or concentrated in invertebrate paratenic hosts (water fleas, brine shrimp, amphipods). Fish-to-fish transmission has been achieved experimentally via cohabitation, predation, scavenging, cannibalism and feeding on crustaceans. Vertical transmission has also been demonstrated for microsporidia infecting fish gonads, involving both intra-ovum (transovarial) transmission within eggs and extra-ovum (transovum) transmission on eggs (the latter occurring much more frequently in insect microsporidia during oviposition).

Differential diagnosis: Infections may sometimes be suspected on clinical grounds, with visible cyst-like lesions (sometimes discoloured) on body surfaces and/or erratic fish behaviours (impaired swimming, feeding, respiration). Infections are best diagnosed by the direct detection of parasites within host tissues, using both macroscopic techniques to detect visible cysts/xenomas and microscopic techniques to detect spores. Visual examination of fish tissues during dissection may reveal the presence of distinctive white cysts, tumour-like xenomas or unnatural opaque tissues (pale porcelain discolourations due the presence of numerous spores). Microscopic examination of wet tissue mounts, squash preparations, impression smears or histological sections may reveal the presence of characteristic microsporidian spores. Unstained samples are best examined at medium to high power (400X magnification) by bright-field microscopy with a suboptimal illumination system (introduce diffraction/contrast through specimen by racking down condenser and/or partially closing diaphragm) or alternatively using phase-contrast or differential interference-contrast microscopy. Mature spores are highly refractile, phase-bright, Gram-positive, acid-fast, and have a PAS-positive polar granule. Treatment of spores with dilute hydrogen peroxide can induce mature spores to evert their polar tubes.

Histological sections are best stained using Ziehl- Neelson acid-fast, Periodic acid Schiff or Giemsa stains to highlight merogonous and sporogonous stages. Given the small spore size and their homogenous appearance, transmission electron microscopy is often conducted to reveal the presence of the coiled polar tube within spores and/or the presence of a sporophorous vesicle. Some species have been successfully propagated *in vitro*, e.g. *Nucleospora salmonis* in chinook salmon leucocyte cultures. More recently, immunodiagnostic procedures have been developed to detect host antibodies or parasite antigens, including the use of polyclonal and monoclonal antibodies, fluorescent-labels and enzyme immunoassays. Considerable success has been achieved in detecting parasite DNA by polymerase chain reaction (PCR) amplification of internal transcribed spacer (ITS) regions and small subunit (SSU) ribosomal RNA (rRNA) gene sequences. Molecular characterization techniques are facilitating not only more sensitive and specific diagnoses but also allowing more comprehensive phylogenetic analyses of relationships between taxa.

Treatment: Most drug treatments for microsporidian infections of fish have been applied in experimental situations or in intensive rearing facilities. The antimicrobial agent fumagillin was developed to treat infections in bees, and has been widely used to treat infections in fish although high concentrations or prolonged treatment has adverse effects on the hosts. Fumagillin is not heat stable so foodstuffs must be coated after milling. The anticoccidial triazinone, toltrazuril, has also proven effective as a systemic treatment for some infections. Limited success in treating fish has been reported using other anticoccidial drugs (amprolium, nitrofurazone) and anthelmintic benzimidazole derivatives (albendazole, mebendazole, fenbendazole). Quarantine and disinfection procedures may be used to control and prevent the spread of infections. Translocations of live fish (and source waters) between geographic zones should be avoided to prevent spreading infections. All new stock introduced into aquaculture facilities should be held in quarantine pending satisfactory screening. It is also important to isolate or cull infected fish as soon as possible after disease presentation to prevent water contamination by faeces, necrotic lesions or decaying carcases and spore transmission by contact or ingestion (including scavenging and cannibalism). At present, there are no practical ways of removing infections from wild fish populations without complete extirpation of all fishes in the water body. When processing fish, it is recommended not to dispose of offcuts, heads, entrails or skeletons into source waters, but to dispose of them by burning or burying in landfill. The prevention of infections is based on maintaining good water quality and minimising environmental stressors. Spores have been shown to remain infective under suitable conditions for up to one year, so if infections persist, aquaria or tanks need to be drained and disinfected (chemical treatment with monoaminoacridine or trypaflavine, or liming and drying over summer). Partial success has also been reported in killing spores in water by adjusting the pH to 7.5-8.0, treating with moderate levels of ozonation, or using ultraviolet (UV) sterilisation in water recirculation systems. Fish have been shown to develop some resistance to infection, so several studies developed and tested experimental vaccines in cultured fish. While several preparations (live low-virulence or inactivated whole spores) were found to provide partial protection against microsporidial gill disease in salmonids, as determined by better survival and reduced xenoma formation, no commercial vaccines are yet available. Some promising results have also been obtained when using small interfering RNA molecules (siRNAs) for *in vitro* silencing of microsporidial genes (ATP/ADP antiporter and methionine aminopeptidase) in cultured lizardfish.

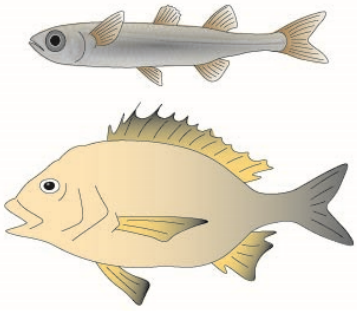
Microspora (piscine hosts)
e.g. *Glugea*



histozoic (viscera, muscles)
(lesions, cysts, sometimes
tumour-like xenomas)

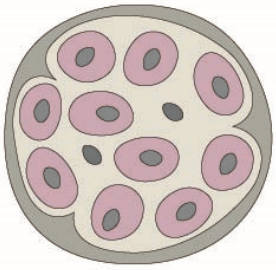
simple monoxenous cycles
most monokaryotic

form unicellular spores
with unique polar tubes

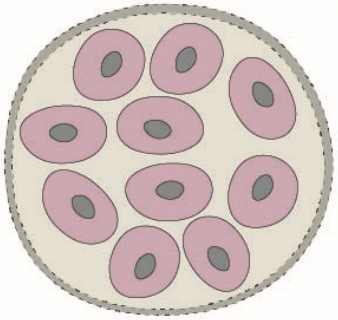


Vertebrate Hosts
(freshwater, marine
and estuarine fish)

development may occur direct in host cell cytoplasm
or in parasitophorous vacuole (membrane of host origin)
or in sporophorous vesicle (envelope of parasite origin)
[a few form thick-walled sporophorocysts (parasite membranes)]

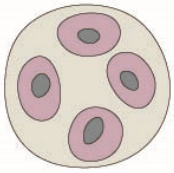


multiplication by merogony
(binary or multiple fission, although
several form multinucleated plasmodia)



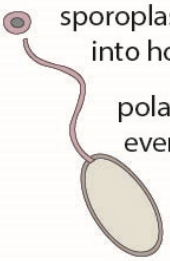
spore formation by sporogony
(binary or multiple fission,
a few by plasmotomy)

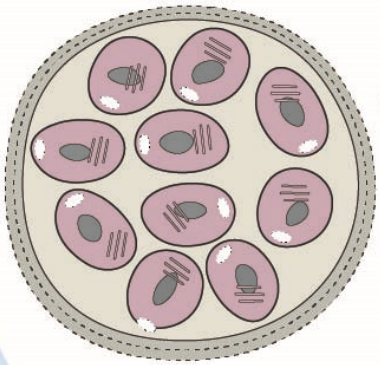
meront



sporoplasm injected
into host cell

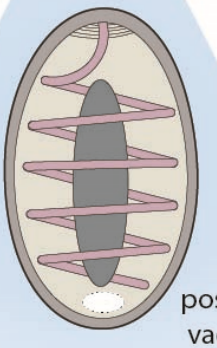
polar tube
eversion





sporont

some form xenomas
with multilaminate
walls



coiled
polar
tube

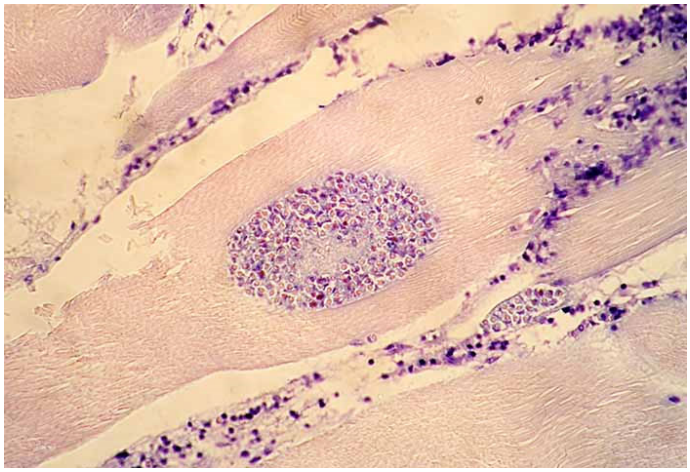
posterior
vacuole

microspore
(2-8 µm)

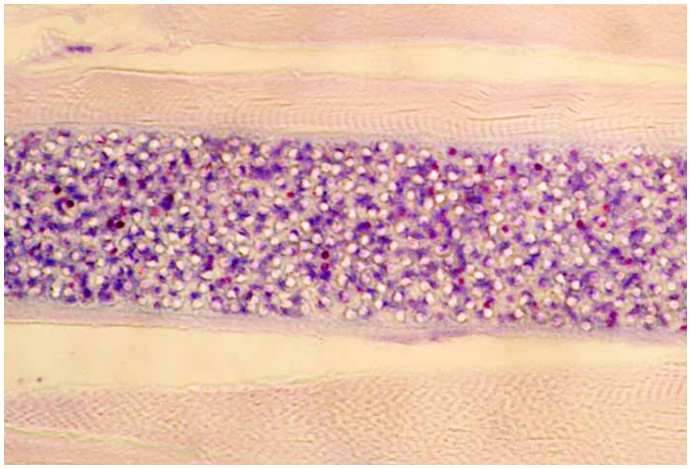
infective spores
ingested/inhaled

mature spores
released

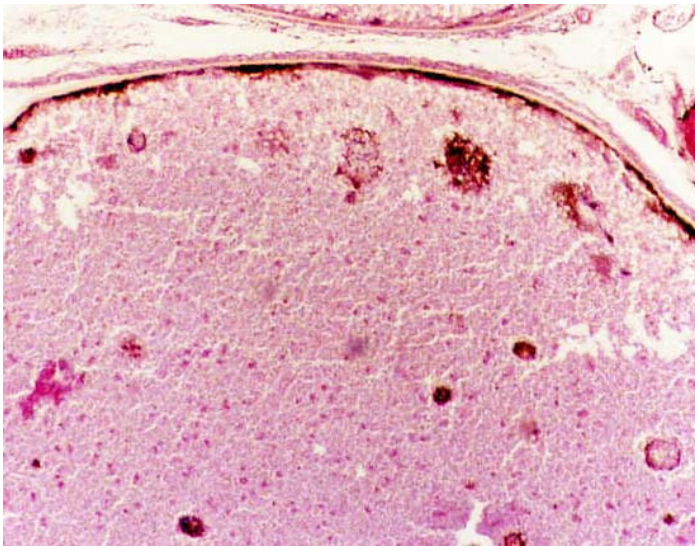
most transmission between hosts direct
via contamination of water by microspores



Pleistophora cyst in fish muscle



Pleistophora cyst in fish muscle



Glugea cyst (xenoma) in fish viscera

MICROSPORA IN ARTHROPODS (insects, crustacea)

Nosema, Ameson, Thelohania, Vavraia, Amblyospora et al.
(fungus: microsporidian)

Overview

Microsporidia are obligate intracellular parasites which lack mitochondria and form small unicellular spores. They were long considered to be a primitive basal group of Protista, but molecular phylogenetic studies have revealed many similarities in biochemical pathways and structural components to fungi, where they are now classified. Numerous species have been described in invertebrates (especially insects) and lower (rarely higher) vertebrates. The parasites proliferate in host tissues by merogony (asexual division) followed by sporogony (often involving plasmotomy prior to sporoblastogenesis). Developmental stages may be monokaryotic (single nucleus) or diplokaryotic (paired nuclei) and sporonts may be surrounded by a membranous sporophorous vesicle (pansporoblast) or lie free in the host cell cytoplasm. All spores contain a unique coiled polar tube which can be extruded to inject the infective sporoplasm into host cells. Infections may be disseminated throughout host tissues or they may cause focal lesions and inflammation involving cysts, granulomas or tumour-like xenomas (enlarged host cells). Various species are found in insects (some causing dysentery in honey bees), crustaceans (some denaturing muscles), fish (some forming lesions or deformities) and even humans (some causing diarrhoea, myositis, encephalitis or corneal lesions).

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Fungi (with chitinous walls, includes microsporidia)
Division:	Microsporidia (form unicellular spores, with coiled polar tubes, amitochondriate, all parasitic)
Class:	Microsporea (polar filament well-formed, oval spores)
Order:	Microsporida (polaroplast present)
Suborder:	Pansporoblastina (sporophorous vesicle present)
Family:	Thelohaniidae (meronts diplokaryotic, spores monokaryotic, 8 spores formed in each vesicle)
Genus:	*Thelohania* (parasitic in tissues of crustaceans/insects)
Species:	various species cause cotton-tail in crayfish
Suborder:	Apansporoblastina (sporophorous vesicle absent)
Family:	Nosematidae (all stages diplokaryotic)
Genus:	*Nosema* (parasitic in gut/tissues of invertebrates)
Species:	*N. apis* (causes bee dysentery in honeybees)

Parasite biodiversity and host range: Microsporidia possess a remarkable apomorphic adaptation to life as intracellular parasites, their unicellular spores have polar tubes coiled up inside which can be forcibly everted to penetrate host cells and inject their infective germs (sporoplasm). Microsporidia have reduced cellular complexity, they have small genomes, they are amitochondriate and they have metabolomes partway between 'prokaryotes' (archae- and eu-bacteria) and eukaryotes (nucleated cells). They were long considered to be a primitive basal group of Protista but molecular phylogenetic studies have revealed many similarities in nuclear genes, biochemical pathways and structural components to fungi, where they are now classified.

The systematics of microsporidia has progressed over decades from phenotypic classifications based on spore morphology, developmental cycles and host range to genotypic classifications based on comparative gene sequences. Classical studies divided the microsporidia into those with or without an envelope (sporophorous vesicle) around sporoblasts (Pansporoblastina and Apansporoblastina respectively) and recognized families on the basis of vegetative growth, genera on the process of spore formation and species on the basis of spore morphology. The subsequent inclusion of ultrastructural features led to the recognition of three major assemblages: 'primitive' groups with rudimentary polar tubes and no polaroplasts; 'intermediate' groups with short polar tubes and rudimentary polaroplasts; and 'higher' groups with well-developed polar tubes and polaroplasts. Families continued to be identified on the basis of type of reproduction (merogony and sporogony) and nuclear condition (mono- or diplo-karyotic). More recently, chromosome cycles were used to separate microsporidia into Dihaplophasea (diplokaryon in some phase of life-cycle) and Haplophasea (unpaired nuclei in all life-cycle stages). It is thought that the developmental cycle of Dihaplophasea involves a pairing of gametes which proliferate and undergo haplosis either by meiosis (order Meiodihaplophasida) or by nuclear dissociation (order Dissociodihaplophasida), whereas the development of Haplophasea is entirely haplophasic. Molecular phylogenetic studies, however, have not provided good support for conventional classifications but have separated representative species into three major clades mostly correlated with host habitat: including the Aquasporidia (in freshwater insects, crustaceans and bryozoans), Marinosporidia (in marine fish and crustaceans) and Terresporidia (in terrestrial insects and vertebrates). Although many taxa have yet to be analysed and classified, most clades are polyphyletic with conventional genera split

within and between clades. It is not known whether this reflects an evolutionary history of parasites switching hosts or habitats, or even hosts switching habitats: events quite likely to have occurred considering that many invertebrate hosts have aquatic origins and many have retained aquatic stages in their life-cycles. Further studies are required to reconcile phenotypic and genotypic classifications.

Numerous microsporidian species have been described in invertebrates (especially insects and crustaceans) and lower (rarely higher) vertebrates. Over 1,400 species belonging to ~200 genera have been described; with some 800 species in 109 genera infecting insects, 400 species in 62 genera infecting crustaceans, 120 species in 26 genera infecting fish, 17 species in 11 genera infecting mammals, 5 species in 3 genera infecting birds, reptiles and amphibians, 40 species in 27 genera infecting invertebrates (8 genera in annelids, 7 in arachnids, 4 in molluscs, 4 in bryozoans, 2 in ciliates, one in helminths and one in kinorhynchs) and another 20 species in 14 genera being hyperparasitic in other parasites (8 genera in gregarines, 3 in trematodes, 2 in myxozoans and one in mesozoa). The key characteristics of the microsporidian genera are tabulated below:

Microsporidian genera	**Hosts**	**No. nuclei (meronts, spores)** [1= monokaryotic, 2 = diplokaryotic, 1-2 = both]	**Spore types** [1 = mono-morphic, 2 = di-morphic, 3 = poly-morphic]	**Intracellular location** [CY = cytoplasm, NU = nucleoplasm, PV = parasitophorous vacuole, SP = sporophorocyst, SV = sporophorous vesicle]	**Spores per SV** [n = numerous, na = not applicable]	**Xenoma formation**
Abelspora	decapoda	1,1	1	PV	2	xenoma?
Aedispora	diptera	1-2,1-2	2	PV, SV	2-8	absent
Agglomerata	branchiopoda	1,1	1	SV	8-32	absent
Agmasoma	decapoda	2,1	?	SV	8	absent
Alfvenia	copepoda, maxillopoda	2,1	1	SV	1-2	absent
Alloglugea	anura	1,1	1	PV	na	xenoma
Amazonspora	fish	1,1	1	CY	na	xenoma
Amblyospora	copepoda, amphipoda, maxillopoda, diptera	2,1-2	3	SV	8	absent
Ameson	decapoda, diptera	2,1	1	CY	na	absent
Amphiacantha	hyperparasitic in gregarines in polychaetes	1,1	1	SV	n	absent
Amphiamblys	hyperparasitic in gregarines in polychaetes	1,1	1	SV	32-50	absent
Andreanna	diptera	2,2	1	PV, SV	8	absent
Anisofilariata	diptera	1,1	1	SV	2-16	absent
Anncaliia	diptera, coleoptera, humans	2,2	1	CY	na	absent
Antonospora	hymenoptera, psocoptera	?,2	1	CY	na	absent
Areospora	decapoda	1,1	1	SV	8	xenoma
Auraspora	collembola	2,1-2	2	CY, SV	n	absent
Bacillidium	oligochaeta, thysanura, diptera	2,2	1	CY	na	absent
Baculea	branchiopoda	1,1	1	PV, SV	n	absent
Becnelia	heteroptera	1,1	2	SV	8	absent
Berwaldia	branchiopoda	1,1	1	SV	1	absent
Binucleata	branchiopoda	1-2,1	1	SV	8	absent
Binucleospora	ostracoda	2,2	1	PV	na	absent
Bohuslavia	diptera	2,1	1	SV	8-16	absent
Brachiola	diptera, humans	2,2	1	CY	na	absent
Bryonosema	bryozoa	2,2	1	CY	na	absent
Burkea	oligochaete	1,1	1	PV	na	absent
Burunella	hymenoptera	1-2,1-2	2	PV, SV	8	absent
Buxtehudea	thysanura	1,1	1	PV	na	absent
Campanulospora	diptera	2,2	1	PV	na	absent
Canningia	coleoptera	1,1	1	CY	na	absent
Caudospora	diptera	2,2	1	CY	na	absent
Chapmanium	decapoda, diptera	2,1		SV	8	absent

Chytridiopsis	coleoptera	1,1	1	PV, SV	n	absent
Ciliatosporidium	ciliophora	1,1	1	CY	na	absent
Coccospora	diptera	2,1	1	SV	8	absent
Cougourdella	copepoda, maxillopoda, diptera	1,1	1	SV	4	absent
Crepidulospora	diptera	1,1	1	CY	na	absent
Crispospora	diptera	?,1-2	2	PV	na	absent
Cristulospora	diptera	2,1-2	2	CY, SV	8	absent
Cryptosporina	acari	1,1-2	1	SV	8	absent
Cucumispora	amphipoda	2,2	1	CY	na	absent
Culicospora	diptera	1-2,1-2	2	PV, SV	2-8	absent
Culicosporella	diptera	1-2,1-2	3	PV, SV	2-8	absent
Cylindrospora	diptera	2,1	1	PV, SV	8	absent
Cystosporogenes	lepidoptera	1,1	1	SV?	<60	absent
Dasyatispora	elasmobranch	1,1	1	SV	n	absent
Desmozoon	maxillopoda, copepoda, fish	1-2,1	1	CY	na	absent
Desportesia	hyperparasitic in gregarine in echiurid	1,1	1	CY, SV	32	absent
Dictyocoela	amphipod	2,1-2	1	SV	8	absent
Dimeiospora	diptera	1,1	2	SV	8	absent
Duboscqia	branchiopoda, copepoda, isoptera, diptera	1,1	1	SV	16	absent
Edhazardia	diptera	2,1-2	3	PV, SV	1-8	absent
Encephalitozoon	maxillopoda, orthoptera, acari, birds, mammals (incl. humans)	1,1	1	PV	na	absent
Endoreticulatus	lepidoptera, coleoptera, decapoda	1,1	1	PV	na	absent
Enterocytozoon	mammals (inc. humans), fish	1,1	1	CY	na	absent
Enterospora	decapoda, fish	2,2	1	CY, NU	na	absent
Episeptum	trichoptera	1,1	1	SV	4	absent
Euplotespora	ciliophora	1,1-2	1	SV	1	absent
Evlachovaia	diptera	2,1-2	2	PV, SV	2	absent
Facilispora	maxillopoda, copepoda	1,1	1	CY	na	absent
Fibrillanosema	amphipoda, branchiopoda	1,1	1	CY	na	absent
Flabelliforma	copepoda, ostracoda, cladocera, diptera	1,1	1	CY, SV	n	absent
Geussia	hyperparasitic in gregarine of ephemeroptera	?		SV	6-8	absent
Glugea	amphipoda, fish	1,1	1	SV	n	xenoma
Glugoides	branchiopoda	1,1	1	PV, SV	16	absent
Golbergia	diptera	2,1-2	2	CY	na	absent
Gurleya	branchiopoda, copepoda, decapoda, cladocera, diptera, ephemeroptera, isoptera, lepidoptera, odonata, trichoptera	1,1	1	SV	4	absent
Gurleyides	branchiopoda	?	2	SV	1,4	absent
Hamiltosporidium	branchiopoda	1,2	2	SV	8	absent
Hazardia	diptera	1-2,1-2	2	CY	na	absent
Helmichia	diptera	2,1-2	1	SV?	8	absent
Hepatospora	decapoda	1,1	1	PV	na	absent
Hessea	diptera	2,1-2	1	SV	n	absent
Heterosporis	fish, seasnakes	1,1	3	SP, SV	n	absent
Heterovesicula	orthoptera	2,1-2	2	SV	8-n	absent
Hirsutosporos	diptera	2,2	1	CY	na	absent
Holobispora	copepoda, maxillopoda	?,1	1	CY	na	absent

Hrabyeia	oligochaeta	2,2	1	CY	na	absent
Hyalinocysta	diptera, copepoda	2,1	1	SV	8	absent
Ichthyosporidium	fish	2,2	1	PV	na	xenoma
Inodosporus	decapoda	2,1	1	SV	8	absent
Intexta	acari	1,1	2	PV	na	absent
Intrapredatorus	diptera	2,1-2	3	SV	8	absent
Issia	trichoptera, diptera	2,2	2	SV?	2	absent
Janacekia	diptera, coleoptera	2,1-2	1	SV	1	absent
Jirovecia	fish, oligochaete	2,2	1	CY, PV?	na	xenoma
Jiroveciana	oligochaete	1,1	1	PV	na	absent
Johenrea	orthoptera	1,1	1	SV	8,16	xenoma
Kabatana	fish	1,1	1	CY	na	absent
Kneallhazia	hymenoptera	1-2,1	1	SV	8	absent
Kinorhynchospora	kinorhyncha	1,1	2	SV	n	absent
Krishtalia	diptera	2,1-2	2	CY	na	absent
Lanatospora	branchiopoda, maxillopoda, copepoda	1,1	1	SV	6-16	absent
Larssonia	branchiopoda	1,1	1	SV	4-32	absent
Larssoniella	lepidoptera	1,1	1	CY	na	absent
Liebermannia	orthoptera	2,2	1	PV	na	absent
Loma	fish	1,1	1	SV	4	xenoma
Marssoniella	maxillopoda	1,1	2	SV	4-8	absent
Merocinta	diptera	2,1-2	2	PV	na	absent
Metchnikovella	hyperparasitic in gregarine in polychaete	1,1	1	PV, SV	8-32	absent
Microfilum	fish	1,1	1	CY	na	xenoma
Microgemma	fish	1,1	1	PV	na	xenoma
Microsporidium (often used for *species inquirenda, incertae sedis*)	branchiopoda, copepoda, cirripedia, isopoda, amphipoda, mollusca, insecta, fish, mammals (incl. humans)	?	?	?	?	?
Mitoplistophora	ephemeroptera	1,1	1	PV	na	absent
Mockfordia	psocoptera	?,1	1	PV	na	absent
Mrazeckia	isopoda	2,2	1	CY	na	absent
Multilamina	isoptera, diptera	1,1	1	SV	1	absent
Myospora	decapoda	2,2	1	CY	na	absent
Nadelspora	decapoda	1,1	1	CY	na	absent
Napamichum	diptera, acari	2,1	1	SV	8	absent
Nelliemelba	copepoda, maxillopoda	1,1	1	SV	1	absent
Nematocida	nematode	1,1	1	PV	na	absent
Neoflabelliforma	oligochaete, hyperparasitic in myxozoa in oligochaete	1,1	1	SV?	?	absent
Neonosemoides	fish	2,1	1	CY	na	xenoma
Neoperezia	diptera	2,1	2	SV	2	absent
Nolleria	siphonoptera	1,1	1	PV, SV	n	absent
Norlevinea	branchiopoda	1,1	1	SV	4	absent
Nosema	branchiopoda, copepoda, decapoda, amphipoda, mollusca, hymenoptera, lepidoptera, acari, fish, mammals (incl. humans); hyperparasitic in myxozoa in fish, trematodes in snails, oysters, fish	2,2	2	CY	na	absent
Nosemoides	branchiopoda, fish, hyperparasitic in gregarine in nemertean	1,1	1	CY	na	xenoma
Novothelohania	diptera	1,1	1	SV	8	absent
Nucleospora	fish	1,1	1	NU	na	absent

Nudispora	odonata	2,1	1	CY	na	absent
Obruspora	fish	1,1	1	CY	na	xenoma
Octosporea	branchiopoda, isopoda, amphipoda, cladocera, diptera, ephemeroptera, hemiptera, lepidoptera, collembola	2,2	1	SV	8	absent
Octotetraspora	diptera	2,1	1	SV	4,8	absent
Oligosporidium	acari, opiliones	1,1	2	CY	na	absent
Ordospora	branchiopoda	1,1	1	PV	na	absent
Ormieresia	decapoda	2,1	1	CY, SV	8	absent
Orthosomella	lepidoptera, coleoptera	1,1	1	CY	na	absent
Ovavesicula	coleoptera	2,1	1	CY, SV	32	absent
Ovipleistophora	fish, hyperparasitic in trematode in fish	1,1	2	CY, SV	na	absent
Pankovaia	ephemeroptera	1,1	11	CY, SV	1	absent
Paradoxium	decapoda	1-2,1	1	CY	na	absent
Paraepiseptum	trichoptera	1,1	1	SV	4	absent
Parahepatospora	decapod	1,1	1	PV	na	absent
Paranosema	coleoptera, orthoptera	1-2,2	1	CY	na	absent
Paranucleospora	maxillopoda, fish	1-2,1-2	2	CY, NU	na	absent
Parapleistophora	diptera	1,1	1	SV	48-64	absent
Parastempellia	diptera	2,1-2	2	SV	4,8,16	absent
Parathelohania	maxillopoda, diptera	2,1-2	2	SV	8	absent
Pegmatheca	diptera, tricoptera	2,1	1	SV	8	absent
Perezia	branchiopoda, decapoda, lepidoptera, coleoptera, hymenoptera, orthoptera, plus hyperparasitic in gregarine of tunicate	2,1	1	CY	na	absent
Pernicivesicula	diptera	2,1	1	SV	24-64	absent
Pilosporella	diptera	2,1-2	2	SV	8	absent
Pleistophora (Plistophora)	branchiopoda, copepoda, decapoda, blattaria, coleoptera, diptera, lepidoptera, orthoptera, mollusca, fish, mammals (incl. humans	1,1	2	SV	n	absent
Pleistophoridium	hyperparasitic in gregarine in ephemeroptera	1,1	1	CY, PV	na	absent
Polydispyrenia	diptera	2,1	2	PV, SV	n	absent
Potaspora	fish, decapod	1,1	1	CY	na	xenoma
Pseudoloma	fish	1,1	1	SV	16	atypical xenoma
Pseudonosema	bryozoa	2,2	1	CY	na	absent
Pseudopleistophora	lepidoptera, polychaete	2,2	1	PV, SV?	n	absent
Pulicispora	siphonoptera	1,1-2	1	SV	8,16,32	absent
Pyrotheca	copepoda, maxillopoda	1,1	1	CY, SV	4	absent
Rectispora	oligochaeta	2,2	1	CY	na	absent
Resiomeria	odonata	2,1	1	SV	8	absent
Ringueletium	diptera	2,2	1	CY	na	absent
Schroedera	bryozoa	1-2,2	1	CY	na	xenoma
Scipionospora	diptera	2,2	1	SV	4	absent
Semenovaia	diptera	?,1-2	2	CY	na	absent
Senoma	diptera	2,2	1	PV	na	absent
Septata	human	1,1	1	PV	na	absent
Simuliospora	diptera	2,1	2	SV	6,32	absent
Spherospora	diptera	2,1-2	2	SV	8-32	absent
Spiroglugea	diptera	?	1	SV?	8	absent
Spraguea	fish	1-2,1-2	2	CY	na	xenoma

Steinhausia	bivalve, gastropod	1,1	1	PV, NU	na	absent
Stempellia	copepoda, amphipoda, opiliones, ephemeroptera, diptera, coleoptera, isoptera	1,1	2	PV, SV	4	absent
Striatospora	diptera	2,1	1	SV	8	absent
Systenostrema	diptera	2,1-2	1?	SV	8	absent
Tabanispora	diptera	1-2,2	2	SV	1-10	absent
Takaokaspora	diptera	1-2,1-2	2	CY, SV	?	absent
Tardivesicula	trichoptera	1,1	1	SV	16-32	absent
Telomyxa	ephemeroptera, diptera, coleoptera	1,1	1	SV	2	absent
Tetramicra	fish	1,1(2?	1	PV	na	xenoma
Thelohania	branchiopoda, copepoda, decapoda, amphipoda, diptera, collembola, ephemeroptera, hemiptera, lepidoptera, hymenoptera, odonata, trichoptera, fish	1-2,1	1	SV	8	absent
Toxoglugea	branchiopoda, diptera, plecoptera, odonata, hemiptera, homoptera	2,1	1	SV	8	absent
Toxospora	diptera	?,1-2	1	SV	8	absent
Trachipleistophora	mammals (incl. human)	1,1	1	PV, SV	2-n	absent
Trichoctosporea	diptera	2,1	2	SV	8	absent
Trichodubosquia	ephemeroptera	2,1	1	SV	16-32	absent
Trichonosema	bryozoa	2,2	1	CY	na	absent
Trichotuzetia	copepoda, maxillopoda	1,1	1	SV	1	absent
Tricornia	diptera	2,1-2	1	SV	8	absent
Triwangia	decapoda	1,1	1	SV	n	xenoma
Tubulinosema	diptera, orthoptera, hymenoptera, coleoptera, mammals (humans)	2,2	1	CY	na	absent
Tuzetia	branchiopoda, copepoda, maxillopoda, ephemeroptera	1,1	1	SV	1	absent
Unikaryon	coleoptera, acari, hyperparasitic in trematode in bivalve	1,1	1	SV	2	absent
Vairimorpha	decapod, lepidoptera, hymenoptera, diptera	2,1-2	2	CY, SV	8	absent
Vavraia	ostracoda, decapoda, diptera, coleoptera, lepidoptera	1,1	1	SV	16-64	absent
Vittaforma	mammals (humans)	2,2	1	PV	na	absent
Weiseria	diptera	2,2	1	CY	na	absent
Wittmania	hyperparasitic in mesozoan in cephalopod	1-2,2	1	CY	na	absent
Zelenkaia	trichoptera	1,1	1	SV	2	absent

Although many microsporidian species have been described on the basis of presumed host specificity, recent molecular characterization studies have demonstrated that the host ranges for some species can be very broad, encompassing not only hosts from disparate taxa (e.g. insects and mammals) but also hosts from disparate environments (e.g. marine and terrestrial). While considerable work remains to determine the host ranges and phylogenetic affinities of most microsporidia, the following text considers microsporidia from one of three perspectives associated primarily, but not exclusively, with different host groups; namely, arthropods (mainly insects and crustaceans), fish (bony and cartilaginous), and tetrapods (mammals, birds, reptiles and amphibians). This section considers the microsporidia of arthropods, notably those arthropods kept and managed for economic benefit; including colonies of insects (silkworms, honeybees) and farmed shellfish (crayfish, shrimp, prawns, crabs).

Microsporidian infections are common in insect and crustacean host species throughout the world, particularly those that are aquatic (freshwater, brackish and marine) or those that complete part of their life-cycle in aquatic environments (notably freshwater diptera). Many parasite species appear to be oioxenous (host specific) or stenoxenous (infecting closely-related hosts), although a few have been found to be euryxenous (infecting a broad range of hosts). Infections have been recorded in all insect orders; notably Diptera (73 genera in flies and mosquitoes), Coleoptera (15 genera in beetles), Lepidoptera (13 genera in butterflies, moths) and Hymenoptera (8 genera in bees). In crustaceans, infections have been recorded in the classes Malacostraca (20 genera in crabs, shrimp, lobsters, amphipods and isopods), Maxillopoda (15 in free-living cyclopid copepods and parasitic calagid copepods), Branchiopoda (13 in cladoceran hosts) and Ostracoda (2 in seed shrimp). Microsporidia in arthropods often demonstrate unique morphological and biological adaptations (including bizarre ectospore appendages, polymorphic spore development, polyxenous life-cycles) with profound impacts on their hosts (altering host behaviour, sex ratios, population dynamics). The life-cycles of arthropod microsporidia range from relatively simple with a single sporulation sequence in one host (such as *Nosema* in silkworms and honeybees) to extremely complex with multiple sporulation sequences involving more than one generation of the host and sometimes an intermediate host (as shown by polymorphic microsporidia of aquatic diptera, e.g. *Amblyospora* in mosquitoes).

Several microsporidian species are notorious pathogens of arthropods of commercial significance, causing devastating diseases in insects (collapse of European silkworm industry, dysentery in honeybees) and crustacea ('cotton-tail' in commercial shellfish species). Infections of economic significance in insects are mostly diplokaryotic and polymorphic, undergoing 2-3 sporulation sequences and being disseminated throughout host tissues without causing xenomas. Infections involve pansporoblastic (e.g. *Amblyospora*) and apansporoblastic genera (e.g. *Nosema*) which often disseminate throughout host tissues. Infections in crustacea of economic significance, including freshwater crayfish, marine prawns, shrimp and crabs, mostly form monokaryotic spores, although some species do have diplokaryotic merogonous stages (such as *Thelohania*, *Ameson*, *Agmasoma*, *Vairimorpha*). Most form monomorphic spores, except *Vairimorpha* which forms dimorphic spores, and none form xenomas but rather disseminate throughout host tissues. Microsporidia have also been used experimentally as biological control agents for some terrestrial insect pests and several species are thought to have potential for controlling aquatic insect pests or vectors of other diseases e.g. several *Amblyospora* spp. markedly reduce host fitness (vigor, longevity, fertility) in mosquitoes.

Parasite species	**Spore dimensions** (mi = microspore, ma = macrospore, me = meiospore)	**Hosts**	**Location [IH]**	**Distribution**
Suborder: Pansporoblastina (sporophorous vesicle (SV) present)				
Family: Amblyosporidae (diplokaryotic meronts, octonucleate sporonts, monokaryotic spores)				
Amblyospora connecticus	me 8-9 x 3-3.2 µm (9-10 coils) [IH 8-10 x 5-6 µm 11-12 coils]	insect (saltmarsh mosquito), crustacean IH (copepod)	fat bodies, oenocytes, ovaries, gut, muscles [ovaries]	North America
Amblyospora albifasciati	me 7.2 x 4.4 µm (4-5 coils)	insect (floodwater mosquito), crustacean IH (copepod)	ovaries, fat bodies [ovaries]	South America
Parathelohania anophelis	me 4-5.5 x 2.5-3.6 µm (3-5 coils)	insect (common malaria mosquito)	fat bodies, oenocytes, ovaries	Americas
Family: Glugeidae (monokaryotic, variable but large number spores produced)				
Vavraia parastacida	5.5 x 2.6 µm (9-11 coils)	freshwater crayfish (yabbies, marron, redclaw, gilgies)	muscles	Australia
Vavraia culicis	ma 5.9 x 3.7 µm mi 4.0 x 2.6 µm (11-13 coils)	insect (many mosquito species)	systemic	Europe, Africa, North America
Pleistophora cargoi		marine blue crab	muscles	North America
Pleistophora miyairii		freshwater shrimp	digestive tract	Japan
Pleistophora sogandaresi		freshwater swamp dwarf crayfish	muscles	North America
Family: Culicosporidae (diplokaryotic, polymorphic)				
Culicospora magna	me 12-16.5 x 4.6 µm	insect (mosquito)	fat body, oenocytes	North America
Edhazardia aedis	me 7.6 x 6 µm	insect (yellow fever mosquito)	caeca, oenocytes, fat body, ovaries	cosmopolitan
Family: Burenellidae (diplokaryotic reducing to monokaryotic, polymorphic)				
Vairimorpha austropotamobii	3.9 x 2.2 µm (11-14 coils)	freshwater crayfish (white-clawed crayfish)	muscles	Europe
Vairimorpha cheracis	3.4 x 1.9 µm (10-12 coils)	freshwater crayfish (yabbies)	muscles	Australia

Vairimorpha disparis		insect (spongy moth)		Eurasia
Vairimorpha necatrix		insect (white-specked moth)		Eurasia
Family: Thelohanidae (meronts usually diplokaryotic, spores monokaryotic, 8 spores in SV)				
Agmasoma penaei (syn. *Thelohania*)	mi 2.5-5 x 2-3.5 µm ma 5.5-8.2 x 3.5-4.2 µm	marine white shrimp	muscles, connective tissues	worldwide
Hyalinocysta chapmani jordani	me 4.5 x 2.8 µm (7-8 coils) [5.3 x 3.5 µm (6-7 coils)]	insect (black-tailed mosquito) [crustacean IH (copepod)]	fat body [ovaries]	North America
Thelohania butleri		marine shrimp		Atlantic
Thelohania californica	6 x 3 µm	insect (mosquitoes)	fat body, intestines	North America
Thelohania cambari		freshwater crayfish (Appalachian brook crayfish, Cajun dwarf crayfish, northern koura, redclaw crayfish)	muscles	North America, New Zealand
Thelohania contejeani	3.8 x 1.8 µm (9-10 coils); some diplokaryotic spores (5-6 coils)	freshwater crayfish (European crayfish, Danube crayfish, white-clawed crayfish, signal crayfish, spinycheek crayfish, virile crayfish, northern koura)	muscles	Europe, North America, New Zealand
Thelohania duorara	4.7-6.8 x 3-4.2 µm	marine brown shrimp	muscles, connective tissue	worldwide
Thelohania giardi		marine brown shrimp	muscles	North America
Thelohania macrocystis		freshwater river shrimp	muscles	North America
Thelohania maenadis		marine green crab	muscles, ovary	North America
Thelohania montirivulorum	4.9-7.2 x 2-3.1 µm (20-22 coils)	freshwater crayfish (yabbies)	muscles	Australia
Thelohania octospora		marine prawns	muscles	Europe
Thelohania paguri		hermit crab	body cavity	Europe
Thelohania parastaci	3.2-4.9 x 1.5-2.7 µm (6-8 coils)	freshwater crayfish (yabbies)	muscles	Australia
Thelohania penaei		marine white shrimp	gonad	North America
Thelohania petrolisthis		marine green porcelain crab	muscles	North America
Thelohania solenopsae		insect (fire-ants)	tissues	Americas
Suborder: Apansporoblastina (sporophorous vesicle (SV) absent)				
Family: Nosematidae (diplokaryotic, diplosporoblastic, monomorphic)				
Nosema apis	6.0 x 3.0 µm (18-44 coils)	insect (honeybees)	midgut (dysentery)	worldwide
Nosema bombi	4.2-5.4 x 2.1-3.5 µm (14-18 coils)	insect (bumblebee)	midgut	worldwide
Nosema bombycis	3-4 x 2-2.5 µm (11-12 coils)	insect (silkworms)	systemic (pebrine, pepper disease)	worldwide
Nosema ceranae	4.7 x 2.7 µm (20-23 coils)	insect (honeybees)	midgut (dysentery)	Eurasia
Nosema disstriae		insect (forest tent caterpillar moth)	body tissues	North America
Nosema empoascae		insect (potato leafhopper)	body tissues	North America
Nosema fumiferanae		insect (light brown apple moth)	body tissues	Pan-Pacific
Nosema furnacalis		insect (Asian corn borer)	body tissues	Asia
Nosema granulosis		freshwater crustacea (amphipods)		Europe
Nosema lymantriae		insect (gypsy moth)		Europe, Africa, North America
Nosema oulemae		insect (cereal leak beetle)	body tissues	cosmopolitan

Nosema pyrausta		insect (European corn borer)	body tissues	Europe
Nosema trichoplusiae		insect (Asian honeybee)	body tissues	Asia
Nosema tyriae		insect (cinnabar moth)	body tissues	Eurasia
Ameson nelsoni (syn. *Nosema, N. pulvis*)	2-3.5 x 1.2-2.3 µm	marine crustacea (penaeid shrimp)	muscles	worldwide
Ameson michaelis (syn. *Nosema, N. sapidi*)	2.2 x 1.7 µm	marine crustacea (blue crabs)	muscles	North America
Anncaliia algerae (syn. *Nosema, Brachiola*)	4 x 2.7 µm (8-11 coils)	insect (mosquito), primates (human)	disseminated	North America, Australia
Family: Enterocytozoonidae (monokaryotic, develop in host cell cytoplasm, precocious development of spore organelles)				
Enterocytozoon hepatopenaei	1.1 x 0.7 µm (5-6 coils)	black tiger shrimp	hepatopancreas	South-East Asia

Parasite morphology: Microsporidia form three sequential developmental stages: meronts, sporonts and spores. The unique unicellular spores are spherical, ovoid or cylindrical, most ranging in length from 2-8 µm. They are encased within tough chitinous walls comprising a thin electron-dense exospore and a thicker electron-lucent endospore. Mature spores possess an elongate polar tube coiled up inside; most tubes being isofilar (of uniform diameter) although some are anisofilar (tapered, showing a reduction in diameter over length). The polar tubes are attached to an anterior anchoring disc enveloped by a membranous polar sac. For most microsporidian genera, the wall of the polar tube and its central canal are inserted into the polar sac, but for chytridiopsid genera (*Buxtehudea, Chytridiopsis* and *Nolleria*), only the central canal surrounded by a honeycomb layer is inserted into the polar sac. The anterior section of the polar tube is straight and surrounded by the polaroplast, which may be lamellar, tubular or both. Mature spores contain a prominent posterior vacuole (often visible by light microscopy) and an amoeboid nucleated sporoplasm. Spores may be monokaryotic (uninucleate) or diplokaryotic (with two closely-appressed nuclei). Many microsporidia form only one type of spore (monomorphic), while others are heterosporous (dimorphic or polymorphic) forming several different types (usually micro-spores and macro-spores, sometimes meio-spores). Following host cell invasion, parasites undergo asexual merogony (schizogony) and then 1-3 sporulation (sporogony) sequences forming sporoblasts (sporoblastogenesis) which mature to form infective spores (sometimes referred to as germination). Meronts are located either directly within the host cell cytoplasm (often surrounded by host endoplasmic reticulum and sometime host mitochondria) or bound within parasitophorous vacuoles (membranous envelopes of host origin). They appear as clusters of small nucleated intracellular parasites that have divided by binary or multiple fission, although several species form multinucleated plasmodial stages. Sporonts also appear as small clusters of parasitic cells but are characterized by thickened plasmalemmas due to the deposition of parasite secretions on their surface membranes. Pansporoblastic species also form an isolating envelope (membranous sporophorous vesicle) whereas apansporoblastic species lie direct in the host cell cytoplasm or within parasitophorous vacuoles. Sporonts divide internally one or more times by binary or multiple fission or plasmotomy to form sporoblasts which then mature into spores. Sporonts of a few species (mostly in insects) are also thought to divide by meiosis to form uninucleate meiospores.

Site of infection: All arthropod microsporidia are histozoic parasites with obligative intracellular development within host cells; either being in direct contact with the host cell cytoplasm (a few even occurring in the nucleoplasm) or being enclosed within parasitophorous vacuoles (membrane of host origin) or sporophorous vesicles (envelopes of parasite origin). Infections in arthropods often involve cells in the midgut (including the hepatopancreas), skeletal musculature, connective tissues (fibrous and/or spongy) and/or gonads (ovaries). Various parasite species demonstrate some tissue tropism within their hosts, particularly within the midgut (*Nosema*), fat bodies and ovaries (*Amblyospora*) of insects and the muscles (*Thelohania*, *Ameson*) of crustacea. Infections of the gut are common for those microsporidian species relying on horizontal transmission, while infections of the gonads are mandatory for those relying on vertical transmission.

Pathogenesis: Microsporidian infections cause a wide variety of diseases in arthropods, most being chronic in nature (slow onset, long duration) and rarely acute (rapid onset, short duration). During development, the parasites are metabolically dependent on host cells and are able to mobilize host cell organelles to meet their demands. Infected cells become swollen and the host cell nucleus becomes enlarged or fragmented. The parasites ultimately cause lysis of infected host cells, and the spores replace host tissue resulting in both structural and functional deficits for the host. Heavily infected tissues often become opaque in appearance due to the presence of numerous refractile spores (hence the condition being colloquially called porcelain-, cotton-, milk- or cooked-tail in crustaceans). Infections may be disseminated throughout host tissues leading to systemic degenerative changes although some species cause focal lesions, inflammation and granulomas. Only a few species form tumour-like xenomas (hypertrophic host cells) in insects: either syncytial-like (fusion of infected host cells to form large multinucleated plasmodia) or neoplastic (parasite-induced increase in number of infected cells (hyperplasia) with hypertrophic, fragmented or branched nuclei and highly modified cell surface). Both adult and pre-adult arthropods (larvae, pupae, nauplius, zoea) may be clinically affected, particularly when parasites compete for nutrients during critical stages of host development (moulting and pupation). Clinical signs of disease are often

progressive in severity and include conspicuous tissue manifestations (opacities, inflammation, deformities, lesions, cysts) and parasite-mediated changes in host phenotype, development and behaviour; all serving to diminish host fitness (reduced vigour, poor stress resistance, lower fertility (sometimes sterility) and poor survival, especially following capture/handling).

In insects, infections of the midgut and fat bodies results in swollen distended tissues that are porcelain white in appearance due to large masses of refractile spores. Infected larvae and pupae are lethargic, stunted and deformed, while infected adults show loss of vigour, shortened lifespans and lower fertility. *Nosema* infections in silkworms have high mortality in late larval instars and survivors spin poor quality silk. *Nosema* infections in worker bees cause dysentery with high mortalities at the onset of winter. Infections in queen bees cause atrophy of the ovaries and reduced fecundity. *Nosema* infections in bumblebees may result in smaller adults, queens with distended abdomens, fewer gynes (reproductive females), crippled and/or infertile males, and reduced hibernation survival. *Amblyospora* spp. vary in their pathogenicity at different stages of their life-cycles in order to complete their transmission: infections in larval mosquitoes and copepod intermediate hosts often being fatal so that spores are released into water for horizontal transmission; whereas infections in adult mosquitoes are not fatal so that vertical (transovarial) transmission may occur. In aquatic crustaceans (marine shrimp, prawns, crabs, freshwater crayfish), microsporidian infections may cause significant economic losses in commercial aquaculture or fisheries due to unsightly tissue lesions, production-limiting diseases and mortalities. Infections of the musculature by various genera (*Ameson, Nadelspora, Thelohania, Myospora*) have been associated with progressive opacity in myofibers due to sarcoplasm replacement by spores, rupture of infected muscle fibres, infiltration by host haemocytes, granulomatous lesions, generalized lethargy and reduced tail-flick responses (poorer avoidance of predators). Heavily infected muscles become porcelain white in appearance, unsightly and unpalatable, thus being rejected from human consumption. Infections of both fibrous and spongy connective tissues in the interstitial spaces of crustacea have been associated with the formation of syncytia (multinucleated giant cells) rather than xenomas. Infections of the midgut and hepatopancreas may cause intracellular inclusions, disruption of hepatopancreatic tubules and pronounced haemocytic infiltration. Some infections in the gonads have also been associated with reduced fecundity as well as distorting host sex ratios through male killing or feminization. Invertebrates often respond to infections by melanization processes involving the formation of dark-pigmented foci within the tissues and haemolymph. Microsporidia have also developed sophisticated mechanisms to evade host responses, including modification of phenol-oxidase cascades, inhibition of apoptosis, accumulation in specialized haemocytes and adipocytes, and stimulating host cells to grow into giant cells with prolonged cell cycles (cysts in insects, xenomas in fish) apparently by differentially influencing gene expression and metabolism.

Developmental cycle and mode of transmission: The life-cycles of microsporidia vary considerably. Most species have simple asexual monoxenous life-cycles, although some species in insects have complex heteroxenous life-cycles with both asexual and sexual reproduction involving successive host generations or crustacean intermediate hosts. Mature spores have tough resistant walls which allow them to survive moderate ranges of various physical and chemical factors encountered in host environments (temperature, moisture, UV radiation, salinity, pH), but they are still susceptible to extremes of heat, cold, desiccation, sunlight, hypersalinity, acidity or alkalinity. Each spore contains an infective sporoplasm which is injected into a host cell through the polar tube when it is forcibly everted by swelling of the posterior vacuole and polaroplast (triggered by changes in calcium influx, osmotic pressure, pH, mechanical compression, etc.). The parasites then undergo vegetative reproduction by merogony (schizogony) by binary or multiple fission, although cytokinesis is sometimes delayed thus forming multinucleate plasmodia which divide by plasmotomy to form more plasmodia or segment into uninucleate meronts again. Meronts may lie direct in the host cell cytoplasm or be contained within membranous parasitophorous vacuoles. The parasites then form thickened cell membranes and/or enveloping sporophorous vesicles and undergo further division called sporogony. Sporonts divide by binary or repeated fission or plasmotomy to form sporoblasts (sporoblastogenesis) which subsequently mature to form spores (sporulation). The latent period may be as short as 1-2 weeks but could last the entire lifespan of the arthropod (whose longevity may be significantly reduced by infection). The developmental stages of many microspora have single isolated nuclei throughout their development, ultimately giving rise to uninucleate sporoblasts and spores. Others have paired nuclei which divide synchronously and remain closely appressed throughout their development into diplokaryotic sporoblasts. Some diplokaryotic sporonts also appear to undergo meiotic reduction forming monokaryotic spores. The number of spores formed by each sporont (di-, tetra-, octo-, poly-sporous) can be a defining characteristic for many genera, particularly those developing within sporophorous vesicles. Merogony and sporogony may take place within the same or different tissues of individual hosts. Many microsporidian species are monomorphic (forming only one type of spore) while other species may produce different types of spores (macro-, medi-, micro-, meio-spores) at different stages of development, each type probably having a different function, such as autoinfection (facilitating dissemination within the same host), horizontal transmission (from host to host) and vertical transmission (from mother to offspring). The polymorphic microsporidia of aquatic diptera (esp. mosquitoes) have complex life-cycles involving asexual (merogony and sporogony) and sexual (karyogamy, gametogenesis and plasmogamy) reproduction, the formation of multiple spore types, and both horizontal and vertical transmission. Most species require two successive host generations to complete their life-cycles, and at least three genera (*Amblyospora, Hyalinocysta* and *Parathelohania*) require obligatory development in an intermediate copepodid host. Copepods acquire infections through the ingestion of spores released into water following the death of infected mosquito larvae. Different types of spores formed in copepods are released into water following the death of the copepods and are infective to mosquito larvae.

Horizontal transmission between arthropod hosts occurs predominantly by contact with infectious spores contaminating the immediate environment (water, soil and plant materials). This may occur by oral ingestion of foodstuffs (including scavenging of carcases and cannibalism of weak or moribund individuals), by trophallaxis (where adults pass food directly to other adults) or during grooming behaviours (especially in eusocial insects). Aquatic hosts may also be infected by spores contacting respiratory surfaces. Infective spores have been shown to be voided into the environment with host faeces, oral secretions (including regurgitates), larval silk as well as from decomposing carcasses. Spores are not motile so their dispersal is dependent on host behaviours (sometimes including parasitoids and predators) and physical factors (wind and water movements). Indeed, water is vitally important for many microsporidian species of invertebrates, particularly hosts that are aquatic or have aquatic larval stages. Some aquatic microsporidia even have 'floatation' devices (coverings or appendages) that allow them to remain suspended in the water column. Spores have been found to remain viable under favourable environmental conditions for extended periods (weeks to months, but usually not longer than a year). Viability is significantly reduced by exposure to high temperatures (over 35°C), low moisture (to the point of desiccation) and direct sunlight (high UV radiation). Spores remain viable and infective for longer when kept in shaded aqueous or semi-solid media (water, faeces, cadavers, etc.) at low temperatures just above freezing (2-10°C). Mature spores of microsporidia infecting terrestrial invertebrates typically have thick chitinous endospore layers that provide protection against environmental insults, while those of microsporidia infecting aquatic invertebrates have thinner endospore walls and are not tolerant of drying or freezing. Some microsporidia have developed more sophisticated strategies to survive in hosts of limited availability (e.g. hosts in ephemeral pools or those with prolonged diapause): including delayed development (overwintering), synchronizing their development to host reproduction (using hormonal cues), and adopting vertical transmission (usually maternally-mediated by trans-ovum contamination of eggs during ovipositioning or transovarial infection within oocytes, rarely paternally-mediated via venereal transmission during mating). Parasite virulence also appears to be associated with transmission modalities: species undergoing horizontal transmission being more virulent so hosts die to release spores; while species undergoing vertical transmission are less virulent so female hosts survive to reproduce.

Differential diagnosis: Infections are best diagnosed by the direct detection of parasites within host tissues, using both macroscopic techniques to detect visible cysts/xenomas and microscopic techniques to detect spores. Visual examination of tissues may reveal the presence of distinctive white cysts, tumour-like xenomas, unnatural tissue opacities (due to presence of refractile spores) or focal dark discolourations (due to focal melanization deposits). Microscopic examination of wet tissue mounts, squash preparations, impression smears or histological sections may reveal the presence of characteristic microsporidian spores. Unstained samples are best examined at medium to high power (400X magnification) by bright-field microscopy with a suboptimal illumination system (introduce diffraction/contrast through specimen by racking down condenser and/or partially closing diaphragm) or by using phase-contrast or differential interference-contrast microscopy. Alternatively, fluorescence microscopy may be used as the spores are autofluorescent at particular ultraviolet (UV) wavelengths. Spores may be concentrated from tissue homogenates by centrifugation and microscopic examination of the spore pellet, which can be quantitated by haemocytometer counts. Mature spores are highly refractile, phase-bright, Gram-positive, acid-fast, and have a PAS-positive polar granule. Treatment of spores with dilute hydrogen peroxide can induce mature spores to evert their polar tubes. Histological sections are best stained using Ziehl- Neelson acid-fast, Periodic acid Schiff, Giemsa or trichrome stains to highlight merogonous and sporogonous stages. Given the small spore size and their homogenous appearance, transmission electron microscopy is often conducted to reveal the presence of the coiled polar tube within spores and/or the presence of a sporophorous vesicle. Various insect microsporidia have also been established in tissue culture systems using established cell lines or tissue explants. More recently, immunodiagnostic procedures have been developed to detect host antibodies or parasite antigens, including the use of polyclonal and monoclonal antibodies, fluorescent-labels and enzyme immunoassays. Considerable success has been achieved in detecting parasite DNA by polymerase chain reaction (PCR) amplification of nuclear gene sequences (notably, small subunit ribosomal RNA and internal transcribed spacers, large subunit RNA polymerase II). Molecular characterization techniques are facilitating not only more sensitive and specific diagnoses but also allowing more comprehensive phylogenetic analyses of relationships between taxa.

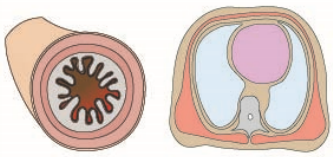
Treatment and control: Infections in colonies of cultured arthropods have been ameliorated (but often not eradicated) by treatment with antimicrobial (fumagillin, fumidil, benomyl), antiprotozoal (quinine, toltrazuril, buquinolate) and even anthelmintic drugs (albendazole, thiabendazole). Insects are often treated with drugs administered in sugar solutions, while aquatic arthropods are treated with drugs added to water baths or aquaria. Some success has been reported using heat therapy where insect hosts exhibit a higher heat tolerance than the parasites, despite poor host survival at temperatures required (e.g. 47°C for 30-45 minutes). Recourse is made to the control of outbreaks by the complete destruction of infected colonies and the disinfection of all equipment. Spores in bee hives have been killed by acetic acid fumigation, gamma radiation, ultrasound and heat treatment (49°C for 24 hours). In aquaculture, contaminated aquaria and tanks need to be drained, cleaned with disinfectants or steam cleaned, or even limed and dried over summer before restocking. Colonies should be constantly monitored and screened for the presence of disease. Infected individuals should be isolated or culled as soon as possible after disease presentation to prevent environmental contamination by spores from faeces, necrotic lesions or decaying carcases. When processing shellfish, it is recommended not to dispose of shells, entrails or offcuts into source waters, but to dispose of them by burning or burying in landfill. Translocations of hosts between geographic zones should be avoided where possible, and all new stock introduced into culture should be held in quarantine pending satisfactory screening. Colonies can be initiated by selecting uninfected progeny (Pasture method) and instituting good sanitation procedures. There is little evidence that arthropods develop any resistance to infections so the prospect for vaccines is poor.

Nonetheless, recent studies have indicated that some future novel therapies may be based on gene silencing using small interfering RNA molecules (siRNAs) possibly involving ADP/ATP transporter genes.

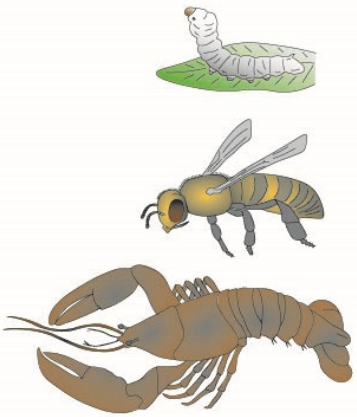
Microspora (arthropod hosts)
e.g. *Thelohania*

most diplokaryotic at some stage
most with monoxenous life-cycles
some with complex heteroxenous cycles

form unicellular spores
with unique polar tubes



histozoic (gut, viscera)
(lesions, cysts, mortalities)



Invertebrate Hosts
(insects, crustaceans)

development may occur direct in host cell cytoplasm
or in parasitophorous vacuole (membrane of host origin)
or in sporophorous vesicle (envelope of parasite origin)

meronts

multiplication by merogony
(binary or multiple fission, although
several form multinucleated plasmodia)

spore formation by sporogony
(binary or multiple fission,
a few by plasmotomy)

sporont

most cycles
direct

some cycles
indirect
(via IH)

some cycles
involve sexual
development
in mosquitoes

diplokaryotic
(paired nuclei)

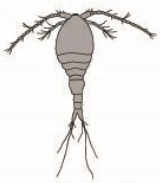
polar tube
eversion

coiled
polar
tube

microspore
(2-8 µm)

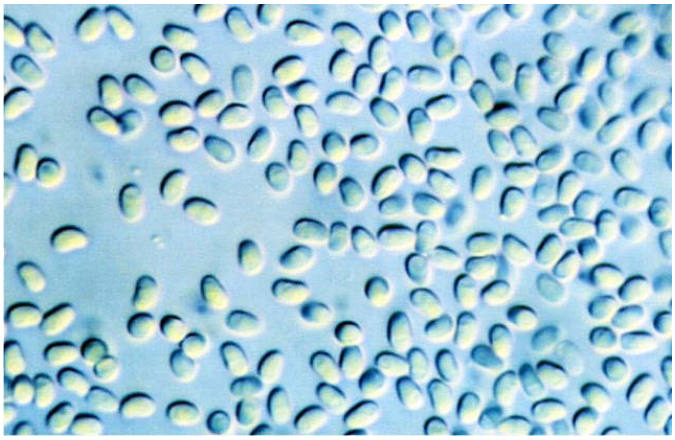
spores
ingested

mature spores
released

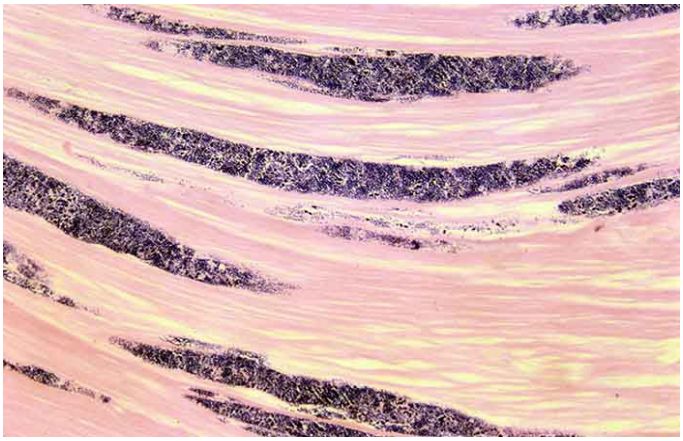


Intermediate Hosts (IH)
(copepods)

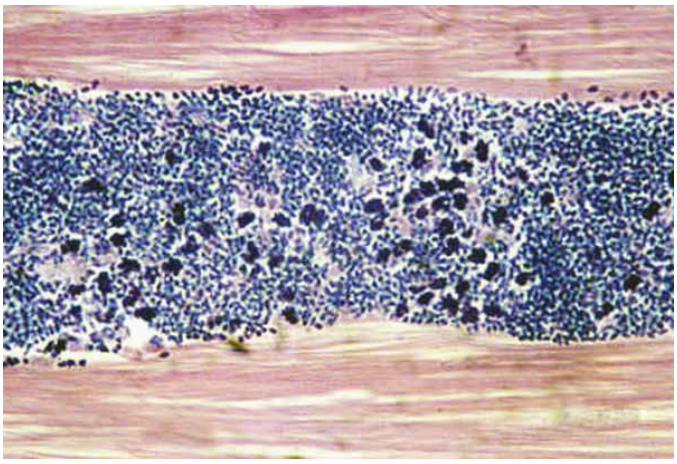
most transmission direct (horizontal, sometimes vertical) via microspores,
some cycles indirect involving copepod IHs, and some in aquatic Diptera
very complex (with sexual development in alternate mosquito generations)



Thelohania microspores from yabby



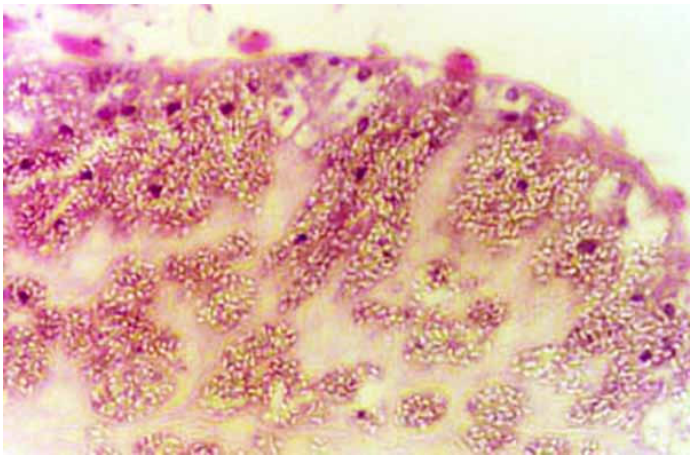
Thelohania cysts in yabby muscle



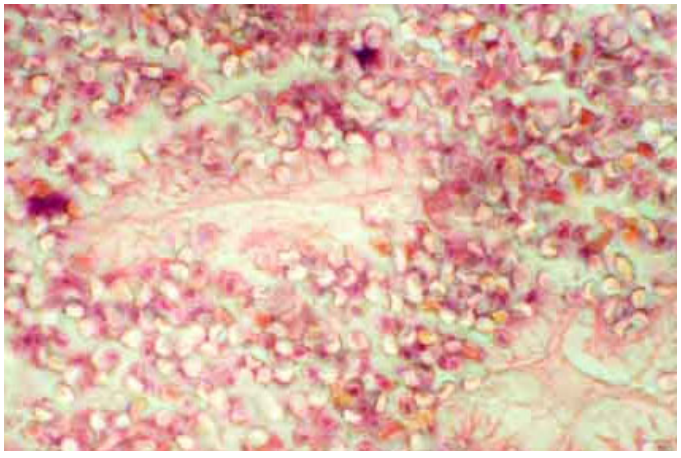
Thelohania cyst in yabby muscle



Thelohania cotton-tail appearance of yabby musculature (L)



Nosema disseminated infection in in bee gut



Nosema refractile spores in bee gut

MICROSPORA IN TETRAPODS (mammals, birds, reptiles, amphibia)

Encephalitozoon, Anncaliia, Nosema, Vittaforma, Enterocytozoon, Trachipleistophora et al.
(fungus: microsporidian)

Overview

Microsporidia are obligate intracellular parasites which lack mitochondria and form small unicellular spores. They were long considered to be a primitive basal group of Protista but molecular phylogenetic studies have revealed many similarities in biochemical pathways and structural components to fungi, where they are now classified. Numerous species have been described in invertebrates (especially insects) and lower (rarely higher) vertebrates. The parasites proliferate in host tissues by merogony (asexual division) followed by sporogony (often involving plasmotomy prior to sporoblastogenesis). Developmental stages may be monokaryotic (single nucleus) or diplokaryotic (paired nuclei) and sporonts may be surrounded by a membranous sporophorous vesicle (pansporoblast) or lie free in the host cell cytoplasm. All spores contain a unique coiled polar tube which can be extruded to inject the infective sporoplasm into host cells. Infections may be disseminated throughout host tissues or they may cause focal lesions and inflammation involving cysts, granulomas or tumour-like xenomas (enlarged host cells). Various species are found in insects (some causing dysentery in honey bees), crustaceans (some denaturing muscles), fish (some forming lesions or deformities) and even humans (some causing diarrhoea, myositis, encephalitis or corneal lesions).

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Fungi (with chitinous walls, includes microsporidia)
Division:	Microsporidia (form unicellular spores, with coiled polar tubes, amitochondriate, all parasitic)
Class:	Microsporea (polar filament well-formed, oval spores)
Order:	Microsporida (polaroplast present)
Suborder:	Pansporoblastina (sporophorous vesicle present)
Family:	Glugeidae (monokaryotic, variable but large number spores produced)
Genus:	*Pleistophora/Trachipleistophora* (parasitic in tissues of mammals)
Suborder:	Apansporoblastina (sporophorous vesicle absent)
Family:	Unikaryonidae (all stages monokaryotic, in cell cytoplasm or in parasitophorous vacuole)
Genus:	*Encephalitozoon* (parasitic in tissues of mammals)
Family:	Nosematidae (diplokaryotic, diplosporoblastic, monomorphic)
Genus:	*Anncaliia/Nosema/Vittaforma* (parasitic in tissues of mammals)
Family:	Enterocytozoonidae (monokaryotic, sporogony with formation of electron-dense discs
Genus:	*Enterocytozoon* (parasitic in tissues of mammals)
Species:	various species cause microsporidiosis in tissues of mammals

Parasite biodiversity and host range: Microsporidia possess a remarkable apomorphic adaptation to life as intracellular parasites, their unicellular spores have polar tubes coiled up inside which can be forcibly everted to penetrate host cells and inject their infective germs (sporoplasm). Microsporidia have reduced cellular complexity, they have small genomes, they are amitochondriate and they have metabolomes partway between 'prokaryotes' (archae- and eu-bacteria) and eukaryotes (nucleated cells). They were long considered to be a primitive basal group of Protista but molecular phylogenetic studies have revealed many similarities in nuclear genes, biochemical pathways and structural components to fungi, where they are now classified.

The systematics of microsporidia has progressed over decades from phenotypic classifications based on spore morphology, developmental cycles and host range to genotypic classifications based on comparative gene sequences. Classical studies divided the microsporidia into those with or without an envelope (sporophorous vesicle) around sporoblasts (Pansporoblastina and Apansporoblastina respectively) and recognized families on the basis of vegetative growth, genera on the process of spore formation and species on the basis of spore morphology. The subsequent inclusion of ultrastructural features led to the recognition of three major assemblages: 'primitive' groups with rudimentary polar tubes and no polaroplasts; 'intermediate' groups with short polar tubes and rudimentary polaroplasts; and 'higher' groups with well-developed polar tubes and polaroplasts. Families continued to be identified on the basis of type of reproduction (merogony and sporogony) and nuclear condition (mono- or diplo-karyotic). More recently, chromosome cycles were used to separate microsporidia into Dihaplophasea (diplokaryon in some phase of life-cycle) and Haplophasea (unpaired nuclei in all life-cycle stages). It is thought that the developmental cycle of Dihaplophasea involves a pairing of gametes which proliferate and undergo haplosis either by meiosis (order Meiodihaplophasida) or by nuclear dissociation (order Dissociodihaplophasida), whereas the development of Haplophasea is entirely haplophasic.

Molecular phylogenetic studies, however, have not provided good support for conventional classifications but have separated representative species into three major clades mostly correlated with host habitat: including the Aquasporidia (in freshwater insects, crustaceans and bryozoans), Marinosporidia (in marine fish and crustaceans) and Terresporidia (in terrestrial insects and vertebrates). Although many taxa have yet to be analysed and classified, most clades are polyphyletic with conventional genera split within and between clades. It is not known whether this reflects an evolutionary history of parasites switching hosts or habitats, or even hosts switching habitats: events quite likely to have occurred considering that many invertebrate hosts have aquatic origins and many have retained aquatic stages in their life-cycles. Further studies are required to reconcile phenotypic and genotypic classifications.

Numerous microsporidian species have been described in invertebrates (especially insects and crustaceans) and lower (rarely higher) vertebrates. Over 1,400 species belonging to ~200 genera have been described; with some 800 species in 109 genera infecting insects, 400 species in 62 genera infecting crustaceans, 120 species in 26 genera infecting fish, 17 species in 11 genera infecting mammals, 5 species in 3 genera infecting birds, reptiles and amphibians, 40 species in 27 genera infecting invertebrates (8 genera in annelids, 7 in arachnids, 4 in molluscs, 4 in bryozoans, 2 in ciliates, one in helminths and one in kinorhynchs) and another 20 species in 14 genera being hyperparasitic in other parasites (8 genera in gregarines, 3 in trematodes, 2 in myxozoans and one in mesozoa). The key characteristics of the microsporidian genera are tabulated below:

Microsporidian genera	**Hosts**	**No. nuclei (meronts, spores)** [1= monokaryotic, 2 = diplokaryotic, 1-2 = both]	**Spore types** [1 = mono-morphic, 2 = di-morphic, 3 = poly-morphic]	**Intracellular location** [CY = cytoplasm, NU = nucleoplasm, PV = parasitophorous vacuole, SP = sporophorocyst, SV = sporophorous vesicle]	**Spores per SV** [n = numerous, na = not applicable]	**Xenoma formation**
Abelspora	decapoda	1,1	1	PV	2	xenoma?
Aedispora	diptera	1-2,1-2	2	PV, SV	2-8	absent
Agglomerata	branchiopoda	1,1	1	SV	8-32	absent
Agmasoma	decapoda	2,1	?	SV	8	absent
Alfvenia	copepoda, maxillopoda	2,1	1	SV	1-2	absent
Alloglugea	anura	1,1	1	PV	na	xenoma
Amazonspora	fish	1,1	1	CY	na	xenoma
Amblyospora	copepoda, amphipoda, maxillopoda, diptera	2,1-2	3	SV	8	absent
Ameson	decapoda, diptera	2,1	1	CY	na	absent
Amphiacantha	hyperparasitic in gregarines in polychaetes	1,1	1	SV	n	absent
Amphiamblys	hyperparasitic in gregarines in polychaetes	1,1	1	SV	32-50	absent
Andreanna	diptera	2,2	1	PV, SV	8	absent
Anisofilariata	diptera	1,1	1	SV	2-16	absent
Anncaliia	diptera, coleoptera, humans	2,2	1	CY	na	absent
Antonospora	hymenoptera, psocoptera	?,2	1	CY	na	absent
Areospora	decapoda	1,1	1	SV	8	xenoma
Auraspora	collembola	2,1-2	2	CY, SV	n	absent
Bacillidium	oligochaeta, thysanura, diptera	2,2	1	CY	na	absent
Baculea	branchiopoda	1,1	1	PV, SV	n	absent
Becnelia	heteroptera	1,1	2	SV	8	absent
Berwaldia	branchiopoda	1,1	1	SV	1	absent
Binucleata	branchiopoda	1-2,1	1	SV	8	absent
Binucleospora	ostracoda	2,2	1	PV	na	absent
Bohuslavia	diptera	2,1	1	SV	8-16	absent
Brachiola	diptera, humans	2,2	1	CY	na	absent
Bryonosema	bryozoa	2,2	1	CY	na	absent
Burkea	oligochaete	1,1	1	PV	na	absent
Burunella	hymenoptera	1-2,1-2	2	PV, SV	8	absent
Buxtehudea	thysanura	1,1	1	PV	na	absent

Campanulospora	diptera	2,2	1	PV	na	absent
Canningia	coleoptera	1,1	1	CY	na	absent
Caudospora	diptera	2,2	1	CY	na	absent
Chapmanium	decapoda, diptera	2,1		SV	8	absent
Chytridiopsis	coleoptera	1,1	1	PV, SV	n	absent
Ciliatosporidium	ciliophora	1,1	1	CY	na	absent
Coccospora	diptera	2,1	1	SV	8	absent
Cougourdella	copepoda, maxillopoda, diptera	1,1	1	SV	4	absent
Crepidulospora	diptera	1,1	1	CY	na	absent
Crispospora	diptera	?,1-2	2	PV	na	absent
Cristulospora	diptera	2,1-2	2	CY, SV	8	absent
Cryptosporina	acari	1,1-2	1	SV	8	absent
Cucumispora	amphipoda	2,2	1	CY	na	absent
Culicospora	diptera	1-2,1-2	2	PV, SV	2-8	absent
Culicosporella	diptera	1-2,1-2	3	PV, SV	2-8	absent
Cylindrospora	diptera	2,1	1	PV, SV	8	absent
Cystosporogenes	lepidoptera	1,1	1	SV?	<60	absent
Dasyatispora	elasmobranch	1,1	1	SV	n	absent
Desmozoon	maxillopoda, copepoda, fish	1-2,1	1	CY	na	absent
Desportesia	hyperparasitic in gregarine in echiurid	1,1	1	CY, SV	32	absent
Dictyocoela	amphipod	2,1-2	1	SV	8	absent
Dimeiospora	diptera	1,1	2	SV	8	absent
Duboscqia	branchiopoda, copepoda, isoptera, diptera	1,1	1	SV	16	absent
Edhazardia	diptera	2,1-2	3	PV, SV	1-8	absent
Encephalitozoon	maxillopoda, orthoptera, acari, birds, mammals (incl. humans)	1,1	1	PV	na	absent
Endoreticulatus	lepidoptera, coleoptera, decapoda	1,1	1	PV	na	absent
Enterocytozoon	mammals (inc. humans), fish	1,1	1	CY	na	absent
Enterospora	decapoda, fish	2,2	1	CY, NU	na	absent
Episeptum	trichoptera	1,1	1	SV	4	absent
Euplotespora	ciliophora	1,1-2	1	SV	1	absent
Evlachovaia	diptera	2,1-2	2	PV, SV	2	absent
Facilispora	maxillopoda, copepoda	1,1	1	CY	na	absent
Fibrillanosema	amphipoda, branchiopoda	1,1	1	CY	na	absent
Flabelliforma	copepoda, ostracoda, cladocera, diptera	1,1	1	CY, SV	n	absent
Geussia	hyperparasitic in gregarine of ephemeroptera	?		SV	6-8	absent
Glugea	amphipoda, fish	1,1	1	SV	n	xenoma
Glugoides	branchiopoda	1,1	1	PV, SV	16	absent
Golbergia	diptera	2,1-2	2	CY	na	absent
Gurleya	branchiopoda, copepoda, decapoda, cladocera, diptera, ephemeroptera, isoptera, lepidoptera, odonata, trichoptera	1,1	1	SV	4	absent
Gurleyides	branchiopoda	?	2	SV	1,4	absent
Hamiltosporidium	branchiopoda	1,2	2	SV	8	absent
Hazardia	diptera	1-2,1-2	2	CY	na	absent
Helmichia	diptera	2,1-2	1	SV?	8	absent
Hepatospora	decapoda	1,1	1	PV	na	absent
Hessea	diptera	2,1-2	1	SV	n	absent

Heterosporis	fish, seasnakes	1,1	3	SP, SV	n	absent
Heterovesicula	orthoptera	2,1-2	2	SV	8-n	absent
Hirsutosporos	diptera	2,2	1	CY	na	absent
Holobispora	copepoda, maxillopoda	?,1	1	CY	na	absent
Hrabyeia	oligochaeta	2,2	1	CY	na	absent
Hyalinocysta	diptera, copepoda	2,1	1	SV	8	absent
Ichthyosporidium	fish	2,2	1	PV	na	xenoma
Inodosporus	decapoda	2,1	1	SV	8	absent
Intexta	acari	1,1	2	PV	na	absent
Intrapredatorus	diptera	2,1-2	3	SV	8	absent
Issia	trichoptera, diptera	2,2	2	SV?	2	absent
Janacekia	diptera, coleoptera	2,1-2	1	SV	1	absent
Jirovecia	fish, oligochaete	2,2	1	CY, PV?	na	xenoma
Jiroveciana	oligochaete	1,1	1	PV	na	absent
Johenrea	orthoptera	1,1	1	SV	8,16	xenoma
Kabatana	fish	1,1	1	CY	na	absent
Kneallhazia	hymenoptera	1-2,1	1	SV	8	absent
Kinorhynchospora	kinorhyncha	1,1	2	SV	n	absent
Krishtalia	diptera	2,1-2	2	CY	na	absent
Lanatospora	branchiopoda, maxillopoda, copepoda	1,1	1	SV	6-16	absent
Larssonia	branchiopoda	1,1	1	SV	4-32	absent
Larssoniella	lepidoptera	1,1	1	CY	na	absent
Liebermannia	orthoptera	2,2	1	PV	na	absent
Loma	fish	1,1	1	SV	4	xenoma
Marssoniella	maxillopoda	1,1	2	SV	4-8	absent
Merocinta	diptera	2,1-2	2	PV	na	absent
Metchnikovella	hyperparasitic in gregarine in polychaete	1,1	1	PV, SV	8-32	absent
Microfilum	fish	1,1	1	CY	na	xenoma
Microgemma	fish	1,1	1	PV	na	xenoma
Microsporidium (often used for *species inquirenda, incertae sedis*)	branchiopoda, copepoda, cirripedia, isopoda, amphipoda, mollusca, insecta, fish, mammals (incl. humans)	?	?	?	?	?
Mitoplistophora	ephemeroptera	1,1	1	PV	na	absent
Mockfordia	psocoptera	?,1	1	PV	na	absent
Mrazeckia	isopoda	2,2	1	CY	na	absent
Multilamina	isoptera, diptera	1,1	1	SV	1	absent
Myospora	decapoda	2,2	1	CY	na	absent
Nadelspora	decapoda	1,1	1	CY	na	absent
Napamichum	diptera, acari	2,1	1	SV	8	absent
Nelliemelba	copepoda, maxillopoda	1,1	1	SV	1	absent
Nematocida	nematode	1,1	1	PV	na	absent
Neoflabelliforma	oligochaete, hyperparasitic in myxozoa in oligochaete	1,1	1	SV?	?	absent
Neonosemoides	fish	2,1	1	CY	na	xenoma
Neoperezia	diptera	2,1	2	SV	2	absent
Nolleria	siphonoptera	1,1	1	PV, SV	n	absent
Norlevinea	branchiopoda	1,1	1	SV	4	absent
Nosema	branchiopoda, copepoda, decapoda, amphipoda, mollusca, hymenoptera, lepidoptera, acari, fish, mammals (incl. humans); hyperparasitic in myxozoa in fish, trematodes in snails, oysters, fish	2,2	2	CY	na	absent

Nosemoides	branchiopoda, fish, hyperparasitic in gregarine in nemertean	1,1	1	CY	na	xenoma
Novothelohania	diptera	1,1	1	SV	8	absent
Nucleospora	fish	1,1	1	NU	na	absent
Nudispora	odonata	2,1	1	CY	na	absent
Obruspora	fish	1,1	1	CY	na	xenoma
Octosporea	branchiopoda, isopoda, amphipoda, cladocera, diptera, ephemeroptera, hemiptera, lepidoptera, collembola	2,2	1	SV	8	absent
Octotetraspora	diptera	2,1	1	SV	4,8	absent
Oligosporidium	acari, opiliones	1,1	2	CY	na	absent
Ordospora	branchiopoda	1,1	1	PV	na	absent
Ormieresia	decapoda	2,1	1	CY, SV	8	absent
Orthosomella	lepidoptera, coleoptera	1,1	1	CY	na	absent
Ovavesicula	coleoptera	2,1	1	CY, SV	32	absent
Ovipleistophora	fish, hyperparasitic in trematode in fish	1,1	2	CY, SV	na	absent
Pankovaia	ephemeroptera	1,1	11	CY, SV	1	absent
Paradoxium	decapoda	1-2,1	1	CY	na	absent
Paraepiseptum	trichoptera	1,1	1	SV	4	absent
Parahepatospora	decapod	1,1	1	PV	na	absent
Paranosema	coleoptera, orthoptera	1-2,2	1	CY	na	absent
Paranucleospora	maxillopoda, fish	1-2,1-2	2	CY, NU	na	absent
Parapleistophora	diptera	1,1	1	SV	48-64	absent
Parastempellia	diptera	2,1-2	2	SV	4,8,16	absent
Parathelohania	maxillopoda, diptera	2,1-2	2	SV	8	absent
Pegmatheca	diptera, tricoptera	2,1	1	SV	8	absent
Perezia	branchiopoda, decapoda, lepidoptera, coleoptera, hymenoptera, orthoptera, plus hyperparasitic in gregarine of tunicate	2,1	1	CY	na	absent
Pernicivesicula	diptera	2,1	1	SV	24-64	absent
Pilosporella	diptera	2,1-2	2	SV	8	absent
Pleistophora (Plistophora)	branchiopoda, copepoda, decapoda, blattaria, coleoptera, diptera, lepidoptera, orthoptera, mollusca, fish, mammals (incl. humans	1,1	2	SV	n	absent
Pleistophoridium	hyperparasitic in gregarine in ephemeroptera	1,1	1	CY, PV	na	absent
Polydispyrenia	diptera	2,1	2	PV, SV	n	absent
Potaspora	fish, decapod	1,1	1	CY	na	xenoma
Pseudoloma	fish	1,1	1	SV	16	atypical xenoma
Pseudonosema	bryozoa	2,2	1	CY	na	absent
Pseudopleistophora	lepidoptera, polychaete	2,2	1	PV, SV?	n	absent
Pulicispora	siphonoptera	1,1-2	1	SV	8,16,32	absent
Pyrotheca	copepoda, maxillopoda	1,1	1	CY, SV	4	absent
Rectispora	oligochaeta	2,2	1	CY	na	absent
Resiomeria	odonata	2,1	1	SV	8	absent
Ringueletium	diptera	2,2	1	CY	na	absent
Schroedera	bryozoa	1-2,2	1	CY	na	xenoma
Scipionospora	diptera	2,2	1	SV	4	absent
Semenovaia	diptera	?,1-2	2	CY	na	absent
Senoma	diptera	2,2	1	PV	na	absent
Septata	human	1,1	1	PV	na	absent

Simuliospora	diptera	2,1	2	SV	6,32	absent
Spherospora	diptera	2,1-2	2	SV	8-32	absent
Spiroglugea	diptera	?	1	SV?	8	absent
Spraguea	fish	1-2,1-2	2	CY	na	xenoma
Steinhausia	bivalve, gastropod	1,1	1	PV, NU	na	absent
Stempellia	copepoda, amphipoda, opiliones, ephemeroptera, diptera, coleoptera, isoptera	1,1	2	PV, SV	4	absent
Striatospora	diptera	2,1	1	SV	8	absent
Systenostrema	diptera	2,1-2	1?	SV	8	absent
Tabanispora	diptera	1-2,2	2	SV	1-10	absent
Takaokaspora	diptera	1-2,1-2	2	CY, SV	?	absent
Tardivesicula	trichoptera	1,1	1	SV	16-32	absent
Telomyxa	ephemeroptera, diptera, coleoptera	1,1	1	SV	2	absent
Tetramicra	fish	1,1(2?	1	PV	na	xenoma
Thelohania	branchiopoda, copepoda, decapoda, amphipoda, diptera, collembola, ephemeroptera, hemiptera, lepidoptera, hymenoptera, odonata, trichoptera, fish	1-2,1	1	SV	8	absent
Toxoglugea	branchiopoda, diptera, plecoptera, odonata, hemiptera, homoptera	2,1	1	SV	8	absent
Toxospora	diptera	?,1-2	1	SV	8	absent
Trachipleistophora	mammals (incl. human)	1,1	1	PV, SV	2-n	absent
Trichoctosporea	diptera	2,1	2	SV	8	absent
Trichodubosquia	ephemeroptera	2,1	1	SV	16-32	absent
Trichonosema	bryozoa	2,2	1	CY	na	absent
Trichotuzetia	copepoda, maxillopoda	1,1	1	SV	1	absent
Tricornia	diptera	2,1-2	1	SV	8	absent
Triwangia	decapoda	1,1	1	SV	n	xenoma
Tubulinosema	diptera, orthoptera, hymenoptera, coleoptera, mammals (humans)	2,2	1	CY	na	absent
Tuzetia	branchiopoda, copepoda, maxillopoda, ephemeroptera	1,1	1	SV	1	absent
Unikaryon	coleoptera, acari, hyperparasitic in trematode in bivalve	1,1	1	SV	2	absent
Vairimorpha	decapod, lepidoptera, hymenoptera, diptera	2,1-2	2	CY, SV	8	absent
Vavraia	ostracoda, decapoda, diptera, coleoptera, lepidoptera	1,1	1	SV	16-64	absent
Vittaforma	mammals (humans)	2,2	1	PV	na	absent
Weiseria	diptera	2,2	1	CY	na	absent
Wittmania	hyperparasitic in mesozoan in cephalopod	1-2,2	1	CY	na	absent
Zelenkaia	trichoptera	1,1	1	SV	2	absent

Although many microsporidian species have been described on the basis of presumed host specificity, recent molecular characterization studies have demonstrated that the host ranges for some species can be very broad, encompassing not only hosts from disparate taxa (e.g. insects and mammals) but also hosts from disparate environments (e.g. marine and terrestrial). While considerable work remains to determine the host ranges and phylogenetic affinities of most microsporidia, the following text considers microsporidia from one of three perspectives associated primarily, but not exclusively, with different host groups; namely, arthropods (mainly insects and crustaceans), fish (bony and cartilaginous), and tetrapods (mammals, birds, reptiles and amphibians).

The host range suggests that microsporidia evolved as parasites of aquatic invertebrates, and then fish. A few species, however, have become established in endothermic birds and mammals despite the temperature barrier and advanced immune defenses. This section considers the microsporidia of tetrapods, mostly mammals (including humans), some birds, several amphibia and a few reptiles.

In mammals, microsporidial infections have been detected worldwide, in rodents, lagomorphs, carnivores, artiodactyls, perissodactyls and primates, including humans. A growing number of clinical infections have been detected in humans, especially in immunocompromised individuals and children. Some infections in humans are similar to species found in animals (possible zoonoses) but some are unique and only found in humans (anthroponoses). To date, 15 species belonging to 9 diverse genera have been detected in human patients. Most species found in humans form monomorphic spores, except some *Nosema* and *Pleistophora* species. Infections involve both monokaryotic genera (pansporoblastic *Pleistophora* and *Trachipleistophora* as well as apansporoblastic *Encephalitozoon* and *Enterocytozoon*) and diplokaryotic genera (apansporoblastic *Nosema*, *Anncaliia*, *Vittaforma* and *Tubulinosema*), all infections being associated with focal lesions in specific tissues and sometimes systemic disseminated infections, but not xenoma formation. Molecular studies have identified several microsporidian clades with representatives infecting tetrapods as well as arthropods. Three clades of predominantly insect microsporidia have been associated with opportunistic infections in immunocompromised humans (clades *Vittaforma/Endoreticulatus/Cystosporogenes, Anncaliia/Tubulinosema* and *Trachipleistophora/Vavraia*) while another specialized clade is widely distributed among animals (*Enterocytozoon/Encephalitozoon*) causing enteric and/or disseminated infections in humans. Molecular characterisation studies have identified over 90 *Enterocytozoon bieneusi* genotypes; some associated with a single host species, others with two or more hosts. Several genotypes have been found to infect only humans, others only particular animal hosts, although a few infect both humans and animals (suggesting their zoonotic potential).

Parasite species	**Spore dimensions**	**Hosts**	**Location**	**Distribution**
Suborder: Pansporoblastina (sporophorous vesicle (SV) present)				
Family: Glugeidae (monokaryotic, variable but large number spores produced)				
Pleistophora ronneafiei	3.2-4 x 2-3 µm (10-12 coils)	Primates (human)	muscle	North America
Trachipleistophora hominis	4.0 x 2.4 µm (11 coils)	Primates (human), experimental infection in Rodentia (mice)	muscles, sinus, eye	Australia, Europe
Trachipleistophora anthropophthera	ma: 3.7 x 2.0 µm (9 coils) mi: 2.2- 2.5 x 1.4-2.0 µm (3-5 coils)	Primates (human)	disseminated	North America, Europe
Pleistophora myotrophica	3.0-6.7 x 1.9-3.0 µm	Anura (common toad, African spotted toad)	muscles	Europe, Africa
Pleistophora bufonis	nr	Anura (toad)	ovary	Africa
Alloglugea bufonis	1.3-1.6 x 0.6-0.8 µm (5-6 coils)	Anura (cane toad)	gut, liver, spleen, kidney	South America
Glugea danilewskyi	3-4 µm	Anura (grass frog), Serpentes (grass snake)	muscles, connective tissue	Europe
Family: Thelohaniidae (meronts usually diplokaryotic, spores monokaryotic, 8 spores in SV)				
Thelohania apodemi	4.2 x 2.3 µm (11 coils)	Rodentia (wood mouse, house mouse)	brain, muscle	Europe
Suborder: Apansporoblastina (sporophorous vesicle (SV) absent)				
Family: Unikaryonidae (monokaryotic, diplo- to poly-sporoblastic sporogony)				
Encephalitozoon cuniculi	2.5 x 1.5 µm (4-7 coils)	Primates (human, chimpanzee, western gorilla, mountain gorilla, squirrel monkey, titi, Goeldi's monkey, bonobo, tamarins, vervet, baboon, ring-tailed lemur), Lagomorpha (rabbit, cottontail, hare), Rodentia (brown rat, house mouse, wood mouse, field mouse, muskrat, guinea pig, hamster, lemming, common vole, water vole, grass vole), Eulipotyphla (shrew), carnivora (mink, dog, wild dog, blue fox, red fox, arctic fox, stone marten, otter, cat, polecat, meerkat, snow leopard, coati), Artiodactyla (sheep, goat, cattle, buffalo, duiker, alpaca, pig), Perissodactyla (horse), birds (Psittaciformes:	brain, eye, kidney, gut, disseminated	cosmopolitan

		mealy amazon, Tucuman amazon, red-crowned amazon, red-lored amazon, bronze-winged parrot, scaly-headed parrot, dusky parrot, red-fan parrot, Senegal parrot, African grey parrot, turquoise parrot, eclectus parrot, crimson rosella, green rosella, eastern rosella, budgerigar, Major Mitchell cockatoo, Solomon's cockatoo, monk parakeet, red-crowned parakeet, rose-ringed parakeet, green-cheeked parakeet, cockateil, Australian ringneck, Fischer's lovebird, rosy-faced lovebird, yellow-collared lovebird, blue-streaked lory, chestnut-fronted macaw, red-shouldered macaw; Passeriformes: red-billed firefinch, zebra finch, Brahminy starling, canary; Suliformes: great cormorant; Podicipediformes: crested grebe; Ciconiiformes: white stork; Falconiformes: gyrfalcon)		
Encephalitozoon hellem	1.5-2.5 x 1 µm (4-9 coils)	Primates (human, chimpanzee, western gorilla, moustached monkey, agile mangabey, bonobo), Carnivora (dog, coati), Rodentia (house mouse, wood mouse, field mouse, grass vole), Chiroptera (fruit bat), Lagomorpha (hare), birds (Psittaciformes: yellow-streaked lory, galah, superb parrot, elegant parrot, red-rumped parrot, festive amazon, yellow-crowned amazon, red-lored amazon, rose-ringed parakeet, green-cheeked parakeet, peach-fronted parakeet, peach-faced lovebird, Fischer's lovebird, rosy-faced lovebird, yellow-collared lovebird, African grey parrot, budgerigar, turquoise parrot, blue-fronted parrot, blue-headed parrot, mealy parrot, eclectus parrot, scaly-headed parrot, umbrella cockatoo, white cockatoo, little corella, Australian ringneck, eastern rosella, blue-streaked lory, chestnut-fronted macaw, red-shouldered macaw, blue-and-yellow macaw; Apodiformes: hummingbirds; Passeriformes: Gouldian finch, zebra finch, yellow finch, saffron finch, crow, blue-eared starling, sparrow, canary, double-collared seedeater, blackbird; Anseriformes: mallard duck, greylag goose, mute swan, black-necked swan, black swan, Coscoroba swan; Gruiformes: black-crowned crane; Columbiformes: Nicobar pigeon; Struthioniformes: ostrich), Crocodilia (crocodile)	eye, lungs, disseminated	cosmopolitan
Encephalitozoon intestinalis (syn. *Septata*)	2.0 x 1.2-1.5 µm (4-7 coils)	Primates (humans, bonobo, mountain gorilla, red-ruffed lemur, ring-tailed lemur), Carnivora (dog, cat, red fox, coati), Lagomorpha (hare), Rodentia (house mouse, wood mouse, grass vole), Artiodactyla (pig, cattle, goat), Perissodactyla (donkey), birds (Struthioniformes: ostrich; Passeriformes: pigeon)	gut, kidney, eye, disseminated	cosmopolitan
Encephalitozoon lacertae	2.9 x 1.2 µm	Sauria (wall lizard, African skink)	gut	Europe, Africa
Encephalitozoon pogonae	1-2 µm	Sauria (bearded dragons)	disseminated	Europe, North America, Asia
Family: Tubulinosematidae (diplokaryotic, diplosporoblastic, thickened plasmalemma, surface tubular network)				
Tubulinosema acridophagus	3.3-3.9 µm	Primates (human)	muscles, disseminated	North America
Anncaliia algerae (syn. *Nosema*, *Brachiola*)	4 x 2.7 µm (8-11 coils)	Diptera (mosquito), Primates (human)	eye, skin, muscle, disseminated	North America, Australia
Anncaliia connori	4-4.5 x 2-2.5 µm	Primates (human)	disseminated	Europe

(syn. *Nosema, Brachiola*)	(10-12 coils)			
Anncaliia vesicularum (syn. *Brachiola*)	2.9 x 2 µm (8-10 coils)	Primates (human)	muscles, skin, eye	North America
Family: Nosematidae (diplokaryotic, diplosporoblastic, monomorphic)				
Vittaforma corneae (syn. *Nosema corneum*)	3.5-4 x 1-1.5 µm (5-6 coils)	Primates (human)	cornea, bladder	North America, Europe
Nosema ocularum	5 x 3 µm (9-12 coils)	Primates (human)	cornea	North America
Nosema tritoni	nr	Urodela (newt)	skin	Europe
Family: Enterocytozoonidae (monokaryotic, sporogony with formation of electron-dense discs)				
Enterocytozoon bieneusi	1.1-1.6 x 1 µm (5-8 coils)	Primates (humans, gorilla, macaques, marmosets, baboon, langur), Artiodactyla (cattle, goat, deer, llama, kudu, pig), Perissodactyla (horse), Rodentia (muskrat, guinea pig, mice, beaver, squirrel, chipmunk, woodchuck, vole), Lagomorpha (rabbit), Carnivora (dog, fox, cat, raccoon, otter, ermine, coati, black bear), birds (Falconiformes: falcon; Columbiformes: pigeon)	intestines, liver, kidney, eye	tropics
Incertae sedis				
Microsporidium ceylonensis	3.5 x 1.5 µm	Primates (human)	cornea	Sri Lanka
Microsporidium africanum	4 x 1.5 µm (15-16 coils))	Primates (human)	cornea	Africa
Microsporidium buyukmichi	4 x 1.5 µm (15-16 coils)	Carnivora (cat)	cornea	North America
Microsporidium simiae	2-4 µm	Primates (titi monkey)	intestines	Europe
Microsporidium schuetzi	7 x 2 µm	Anura (ranid frogs)	oocytes	North America

Parasite morphology: Microsporidia form three sequential developmental stages: meronts, sporonts and spores. The unique unicellular spores are spherical, ovoid or cylindrical, most ranging in length from 2-8 µm. They are encased within tough chitinous walls comprising a thin electron-dense exospore and a thicker electron-lucent endospore. Mature spores possess an elongate polar tube coiled up inside; most tubes being isofilar (of uniform diameter) although some are anisofilar (tapered, showing a reduction in diameter over length). The polar tubes are attached to an anterior anchoring disc enveloped by a membranous polar sac. For most microsporidian genera, the wall of the polar tube and its central canal are inserted into the polar sac, but for chytridiopsid genera (*Buxtehudea, Chytridiopsis* and *Nolleria*), only the central canal surrounded by a honeycomb layer is inserted into the polar sac. The anterior section of the polar tube is straight and surrounded by the polaroplast, which may be lamellar, tubular or both. Mature spores contain a prominent posterior vacuole (often visible by light microscopy) and an amoeboid nucleated sporoplasm. Spores may be monokaryotic (uninucleate) or diplokaryotic (with two closely-appressed nuclei). Many microsporidia form only one type of spore (monomorphic), while others are heterosporous (dimorphic or polymorphic) forming several different types (usually micro-spores and macro-spores, sometimes meio-spores). Following host cell invasion, parasites undergo asexual merogony (schizogony) and then 1-3 sporulation (sporogony) sequences forming sporoblasts (sporoblastogenesis) which mature to form infective spores (sometimes referred to as germination). Meronts are located either directly within the host cell cytoplasm (often surrounded by host endoplasmic reticulum and sometime host mitochondria) or bound within parasitophorous vacuoles (membranous envelopes of host origin). They appear as clusters of small nucleated intracellular parasites that have divided by binary or multiple fission, although several species form multinucleated plasmodial stages. Sporonts also appear as small clusters of parasitic cells but are characterized by thickened plasmalemmas due to the deposition of parasite secretions on their surface membranes. The exception is *Enterocytozoon* whose sporonts do not immediately secrete an electron-dense coat, but are identified by early (precocious) development of organelle precursors of polar tubes (electron-dense discs that accumulate in stacks). Pansporoblastic species (e.g. *Trachipleistophora*) also form an isolating envelope (membranous sporophorous vesicle) whereas apansporoblastic species lie direct in the host cell cytoplasm (e.g. *Anncaliia*, *Enterocytozoon*) or within parasitophorous vacuoles (e.g. *Encephalitozoon*). Sporonts divide internally one or more times by binary or multiple fission or plasmotomy to form sporoblasts which then mature into spores.

Site of infection: All microsporidian species in tetrapods are histozoic parasites with obligative intracellular development within host cells; either being in direct contact with the host cell cytoplasm or being enclosed within parasitophorous vacuoles (membrane of host origin) or sporophorous vesicles (envelopes of parasite origin). Many infections have exhibited some tissue tropism with development occurring preferentially within particular tissues: including the gut (*Enterocytozoon bieneusi, Encephalitozoon*

intestinalis), muscles (*Pleistophora ronneafiei, Trachipleistophora hominis*, *Anncaliia algerae*, *Anncaliia vesicularum, Tubulinosema acridophagus*), central nervous system (*Encephalitozoon cuniculi*, *Trachipleistophora anthropophthera*, *Encephalitozoon hellem*) and eye (*Nosema ocularum*, *Vittaforma corneae*, *Anncaliia connori, Microsporidium ceylonensis, Microsporidium africanum*). However, more extensive studies have since found most infections to be more widely disseminated throughout host tissues, involving a variety of organ systems.

Pathogenesis: During development, microsporidia are metabolically dependent on host cells and are able to mobilize host cell organelles to meet their demands. Infected cells become swollen and the host cell nucleus becomes enlarged or fragmented. The parasites ultimately cause lysis of infected host cells (subacute presentation), contributing progressively to both structural and functional deficits (with acute and/or chronic presentation). Infections in tissues may be diffuse, spreading from cell to cell, or localized within cysts. Parasites are responsible for tissue displacement/replacement, inflammation and space-occupying lesions. Infections in humans involving pansporoblastic (*Pleistophora* and *Trachipleistophora*) and apansporoblastic genera (*Nosema, Enterocytozoon, Encephalitozoon, Anncaliia, Vittaforma* and *Tubulinosema*) have variously been associated with neurologic (convulsions, vomiting, headaches, fever, coma), ocular (keratoconjunctivitis, chronic sinusitis), muscular (atrophy, muscle fibre degeneration), enteric (diarrhoea, fever, malaise, weight loss) and pulmonary (respiratory) signs. Most patients have been immuno-compromised due to HIV-AIDS, immunosuppressive chemotherapy or organ transplantation, but some infections have also been detected in immunocompetent individuals. Infections are typically chronic and subacute in immunocompetent hosts but severe and even fatal in immunocompromised hosts.

In animals and humans, *Encephalitozoon cuniculi* has been associated predominantly with three clinical syndromes: encephalitis (granulomatous and nonsuppurative lesions with torticollis, ataxia, circling, paresis, paralysis), renal dysfunction (interstitial nephritis), and ocular lesions (keratoconjunctivitis, cataract formation, phacoclastic uveitis). Disseminated infections have also involved the digestive (enteritis, peritonitis, hepatitis), urinary (urethritis, cystitis) and respiratory tracts (rhinitis, sinusitis). Young animals (esp. rabbits and puppies) often develop a mixed encephalitis-nephritis syndrome with anorexia, weight loss, behavioural changes, weakness, loss of awareness, incoordination, ataxia, tremors, convulsions and blindness. In birds, *Encephalitozoon* spp. infections have been associated with illthrift, diarrhoea, dehydration, weight loss and respiratory difficulties. *Encephalitozoon hellem* has been associated with ocular (keratoconjunctivitis), respiratory (sinusitis, rhinitis, pneumonitis, bronchiolitis) and urinary signs (nephritis, ureteritis, cystitis, urethritis, prostatitis) in immunocompromised humans, while *Encephalitozoon intestinalis* has been associated mostly with gastrointestinal perturbations (chronic diarrhoea, enteritis, small bowel perforation, cholangitis, cholecystitis) but sometimes extending to urinary (nephritis, urethritis, cystitis), respiratory (sinusitis, rhinitis, bronchitis) and ocular signs (keratoconjunctivitis). *Enterocytozoon bieneusi* most often causes intestinal signs (enteritis, villous atrophy, malabsorption, watery diarrhoea), sometimes with biliary tract involvement (cholangitis, cholecystitis), all contributing to general malaise, dehydration, malnutrition and weight loss in (almost exclusively) immuno-compromised patients. Rarely, it has been associated with respiratory symptoms involving chronic cough and dyspnoea. Microsporidial infections of the eye are common in both immuno-compromised and immuno-competent patients, possibly because the eye is an immuno-privileged site at a lower temperature and thus more susceptible to opportunistic infections. Several microsporidial species infect the corneal stroma and keratocytes causing keratoconjunctivitis involving follicular papillary conjunctivitis and coarse punctate epithelial lesions in three patterns (diffuse, peripheral, paracentral) progressing to nummular keratitis. Symptoms include ocular redness, eye pain, foreign body sensation, light sensitivity, excessive tearing, astigmatism and blurred vision due to corneal ulceration and opacification due to scarring. Infections in the brain have resulted in encephalitis and seizures due to lesions in the hippocampus and cerebrum, while infections in the heart and skeletal muscles have been associated with necrotizing myositis, cellular infiltrates, weakness, myalgia, fever and progressive weigh loss despite maintaining regular food intake.

Developmental cycle and mode of transmission: Microsporidia infecting humans and other tetrapod animals have simple asexual monoxenous life-cycles, involving sequential multiplication and sporulation within host tissues. Most infections are thought to be initiated by the ingestion of infective spores contaminating food and/or water supplies. Mature spores have tough resistant walls which allow them to survive in the external environment under suitable climatic conditions (excluding temperature extremes, desiccation and direct solar radiation). Each spore contains an infective sporoplasm which is injected into a host cell through the polar tube when it is forcibly everted by swelling of the posterior vacuole and polaroplast (triggered by changes in calcium influx, osmotic pressure, pH, mechanical compression, etc.). The parasites then undergo vegetative reproduction by merogony (schizogony) by binary or multiple fission, although cytokinesis is sometimes delayed thus forming multinucleate plasmodia which divide by plasmotomy to form more plasmodia or segment into uninucleate meronts again. Meronts may lie direct in the host cell cytoplasm or be contained within membranous parasitophorous vacuoles. The parasites then form thickened cell membranes and/or enveloping sporophorous vesicles and undergo further division called sporogony. Sporonts divide by binary or repeated fission or plasmotomy to form sporoblasts (sporoblastogenesis) which subsequently mature to form spores (sporulation). The developmental stages of many microsporans have single isolated nuclei throughout their development, ultimately giving rise to uninucleate sporoblasts and spores (e.g. *Pleistophora, Encephalitozoon, Enterocytozoon*). Others have paired nuclei which divide synchronously and remain closely appressed throughout their development into diplokaryotic sporoblasts (e.g. *Anncaliia, Nosema, Vittaforma, Tubuliosema*). The number of spores formed by each sporont (di-, tetra-, octo-, poly-sporous) can be a defining characteristic for many genera, particularly those developing within sporophorous vesicles. Merogony and sporogony may take place within the same or different

tissues of individual hosts. Most tetrapod microsporidia form monomorphic spores, although some *Pleistophora* and *Nosema* species form two types of spores during their development. Mature spores are released by host cell lysis and may infect neighbouring cells (auto-infection and dissemination) or be voided from the host digestive, urinary or respiratory tract to contaminate the environment. Spores have been detected in drinking, recreational and irrigation waters as well as in wastewater from treatment plants (including biosolids). Contaminated foods have included strawberries, raspberries, mung bean sprouts, parsley, curly lettuce, celery, cilantro, cucumbers, mangoes and milk. Spores are thought to access the eye via contaminated contact lenses, fingers or aerosols. There is some epidemiological evidence to also suggest transmission through the skin via insect bites and rarely by sexual transmission. Vertical transmission has not been documented for infections in humans, but transplacental transmission has been observed in other mammalian hosts.

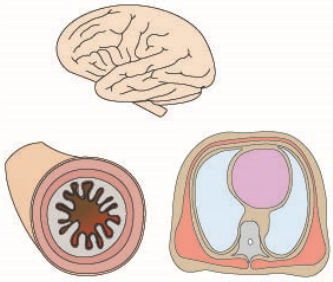
Differential diagnosis: Infections are best diagnosed by the detection of parasites within host tissues, by conventional light microscopy to detect spores or contemporary molecular techniques to detect parasite DNA. Microscopic examination of wet mounts (faecal concentrates, urinary sediments, gut or respiratory aspirates, cerebrospinal fluid) and squash preparations, impression smears or histological sections (of tissue biopsies or autopsy samples) may reveal the presence of characteristic microsporidian spores. Unstained samples are best examined at medium to high power (400X magnification) by bright-field microscopy with a suboptimal illumination system (introduce diffraction/contrast through specimen by racking down condenser and/or partially closing diaphragm), by phase-contrast or differential interference-contrast microscopy, or by fluorescence microscopy with ultraviolet illumination (the chitinous spores are often autofluorescent or can be stained with calcofluor white or Uvitex 2B). Mature spores are highly refractile, phase-bright, Gram-positive, acid-fast, have a PAS-positive polar granule, and exhibit autofluorescence. Treatment of spores with dilute hydrogen peroxide can induce mature spores to evert their polar tubes. Histological sections are best stained using Ziehl-Neelson acid-fast, Periodic acid Schiff, Giemsa, chromotrope or silver stains to highlight merogonous and sporogonous stages. Given the small spore size and their homogenous appearance, transmission electron microscopy is often conducted to reveal the presence of the coiled polar tube within spores and/or the presence of a sporophorous vesicle. Some microsporidian species have also been successfully established in tissue culture monolayers using several mammalian cell lines. A range of immunodiagnostic procedures have been developed to detect host antibodies against microsporidia, including India-ink immunoreaction assays (CIA), complement fixation tests (CFT), indirect fluorescent-antibody tests (IFAT), direct agglutination tests (DAT), enzyme-linked immunosorbent assays (ELISA) and intradermal skin test. Test sensitivity and specificity has been variable and most tests cannot differentiate between current infection and previous exposure. Several polyclonal and monoclonal antibody preparations have been applied to the detection of parasite antigens in host and environmental samples using fluorescent-labels, enzyme-substrate interactions or immunomagnetic bead separation techniques. Pulsed-field gel electrophoresis (PFGE) has also been used for karyotype profiling of several microsporidian species. More recently, considerable success has been achieved in detecting parasite DNA by polymerase chain reaction (PCR) amplification of specific gene sequences (small subunit (SSU) ribosomal RNA (rRNA), internal transcribed spacers (ITS) and polar tubule protein (PTP) genes). Molecular characterization techniques are facilitating not only more sensitive and specific diagnoses but also allowing more comprehensive phylogenetic analyses of relationships between taxa.

Treatment and control: No drug treatments have proven totally effective against microsporidial infections in tetrapods, but symptomatic improvement and/or partial clearance have been reported when treating human infections with albendazole, fumagillin (ocular, intestinal and disseminated infections), nitzaoxanide, metronidazole (intestinal infections) and trimethoprim-sulfamethoxazole (disseminated infections). Albendazole and fumagillin are most effective against *Encephalitozoon* spp. and fenbendazole has also been used to treat *E. cuniculi* infections in rabbits. Nitazoxanide is used for the primary treatment of *Enterocytozoon bieneusi* in humans but side effects are common, including abdominal pain, vomiting, nausea and diarrhoea. The oral administration of fumagillin can also produce thrombocytopenia (reduced platelet counts). The controversial drug thalidomide has helped alleviate diarrhoea and improved weight gain in patients with *E. bieneusi* but it is highly toxic and should only be considered when all other treatments have failed. Enteric infections in many HIV-AIDS patients showed clinical improvement following highly-active anti-retroviral therapy (HAART), although relapses were observed when treatment was discontinued. Symptomatic relief for persistent enteric infections is also afforded by fluid replacement therapy, either orally or parenterally. Myalgias caused by *Trachipleistophora* spp. have responded well to combination therapy with albendazole, pyrimethamine, sulfadiazine and folinic acid. Infections of the eye have been ssuccessfully treated with topical fluoroquinolone monotherapy or oral albendazole and topical fumagillin. Keratoconjunctivitis has also improved using topical prednisolone and chloramphenicol. Permanent damage to the eye or deep stromal infections may require corneal transplantation, preferably using full-thickness penetrating grafts over lamellar grafts to avoid recurrent infection. The prevention of infections in human and animal populations is dependent on good hygienic practices not only to minimize environmental contamination by spores but also restrict their uptake by susceptible hosts. The small size of microsporidian spores and their hardy resistance to adverse environmental conditions means they may survive some routine sewage and water treatment procedures. Comprehensive experimental studies are required to assess the efficacies of various decontamination (sedimentation, coagulation, filtration) and disinfection (heat, chlorination, ozonation, irradiation) processes. Immuno-compromised individuals at risk of developing life-threatening infections are recommended to drink bottled or boiled water, cook all meat products and wash fruit and vegetables prior to consumption, and practice elevated levels of sanitation and hygiene (especially with respect to toilet habits and hand-washing).

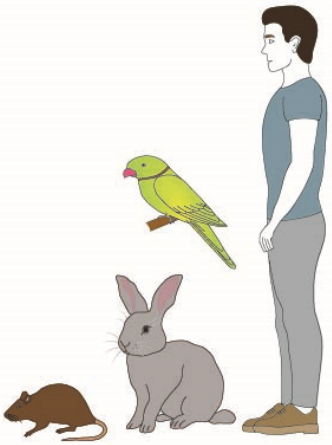
Microspora (tetrapod hosts)
e.g. *Encephalitozoon*

most with simple monoxenous cycles
most monokaryotic

form unicellular spores
with unique polar tubes

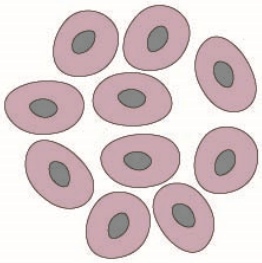


histozoic (gut, viscera, brain)
(lesions/cysts, inflammation,
dysfunction, mortalities)

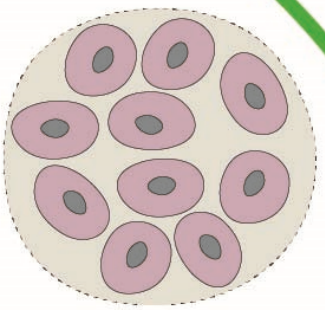


Vertebrate Hosts
(mammals, birds)

development may occur direct in host cell cytoplasm
or in parasitophorous vacuole (membrane of host origin)
or in sporophorous vesicle (envelope of parasite origin)



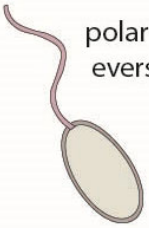
multiplication by merogony
(binary or multiple fission, although
several form multinucleated plasmodia)



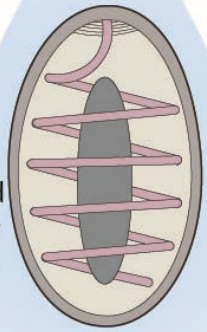
spore formation by sporogony
(binary or multiple fission,
a few by plasmotomy)



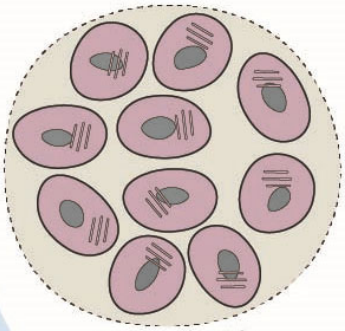
sporoplasm injected
into host cell



polar tube
eversion



coiled
polar
tube



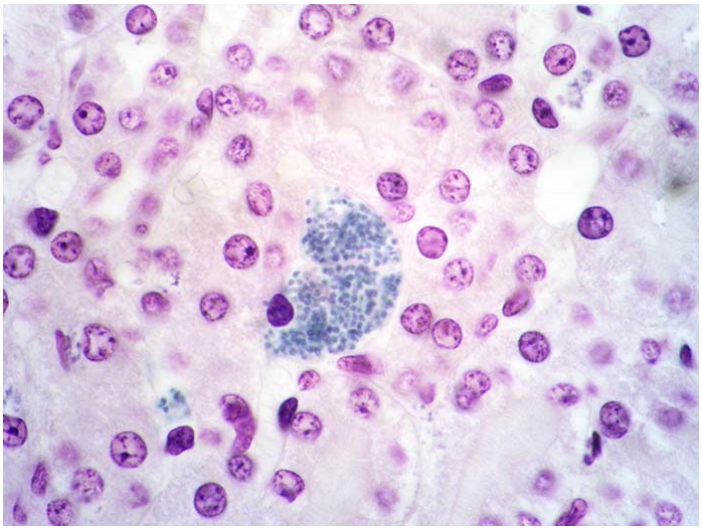
sporont with
sporoblasts

infective spores
ingested/inhaled

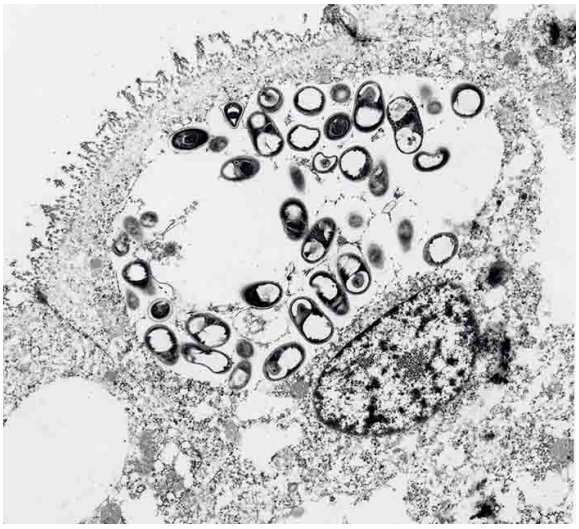
microspore
(2-8 µm)

mature spores
released

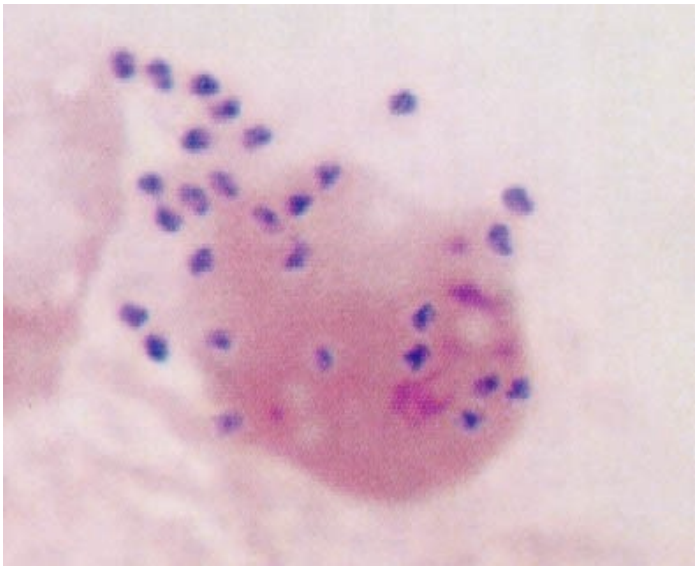
most transmission between hosts direct via spores
contaminating external environment (soil, water, food)



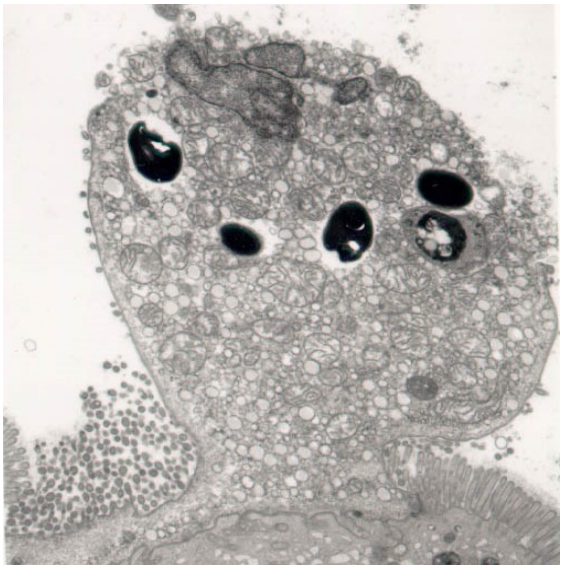
Encephalitozoon cyst in rabbit brain



Encephalitozoon cyst in koala (tEM)

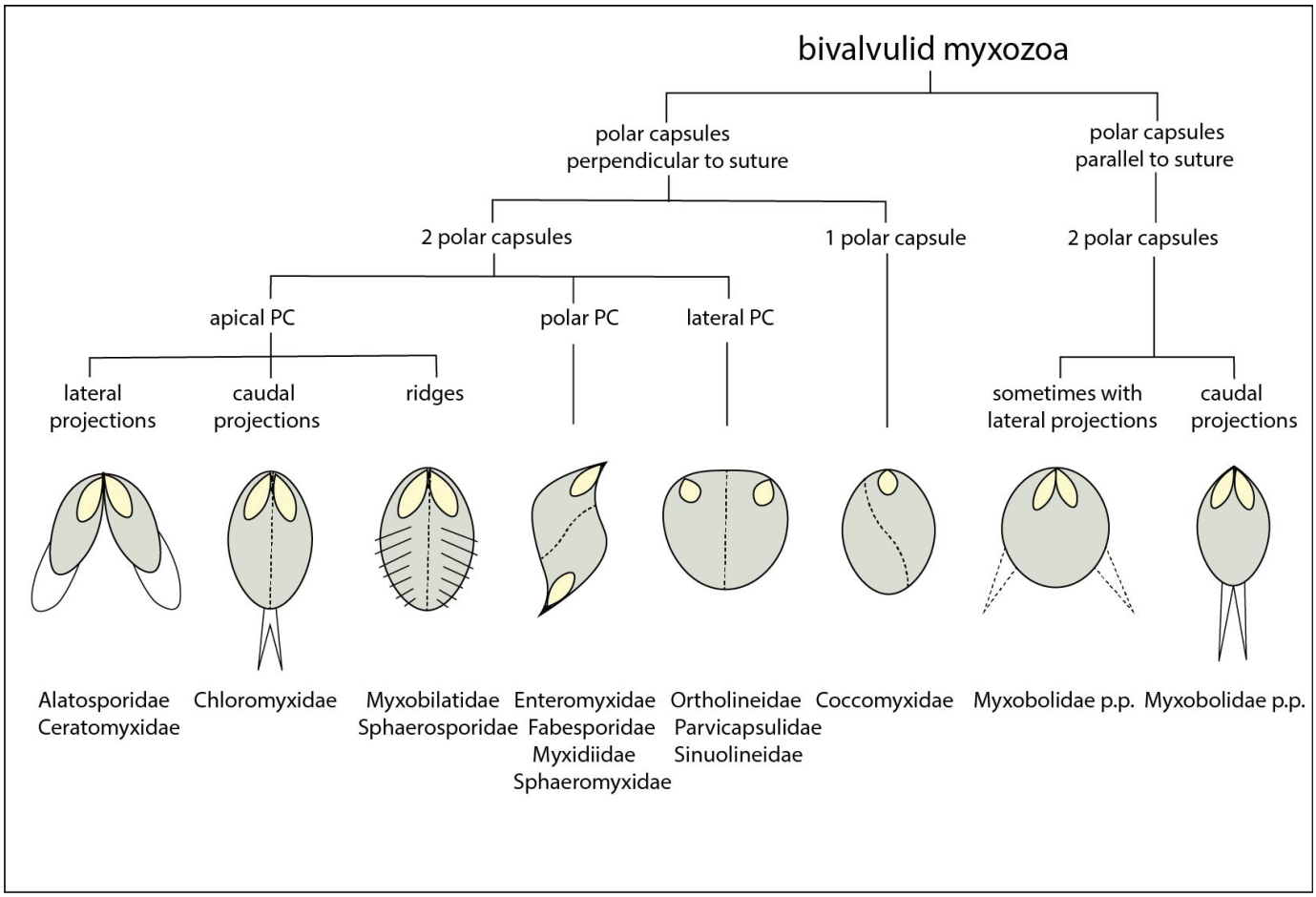


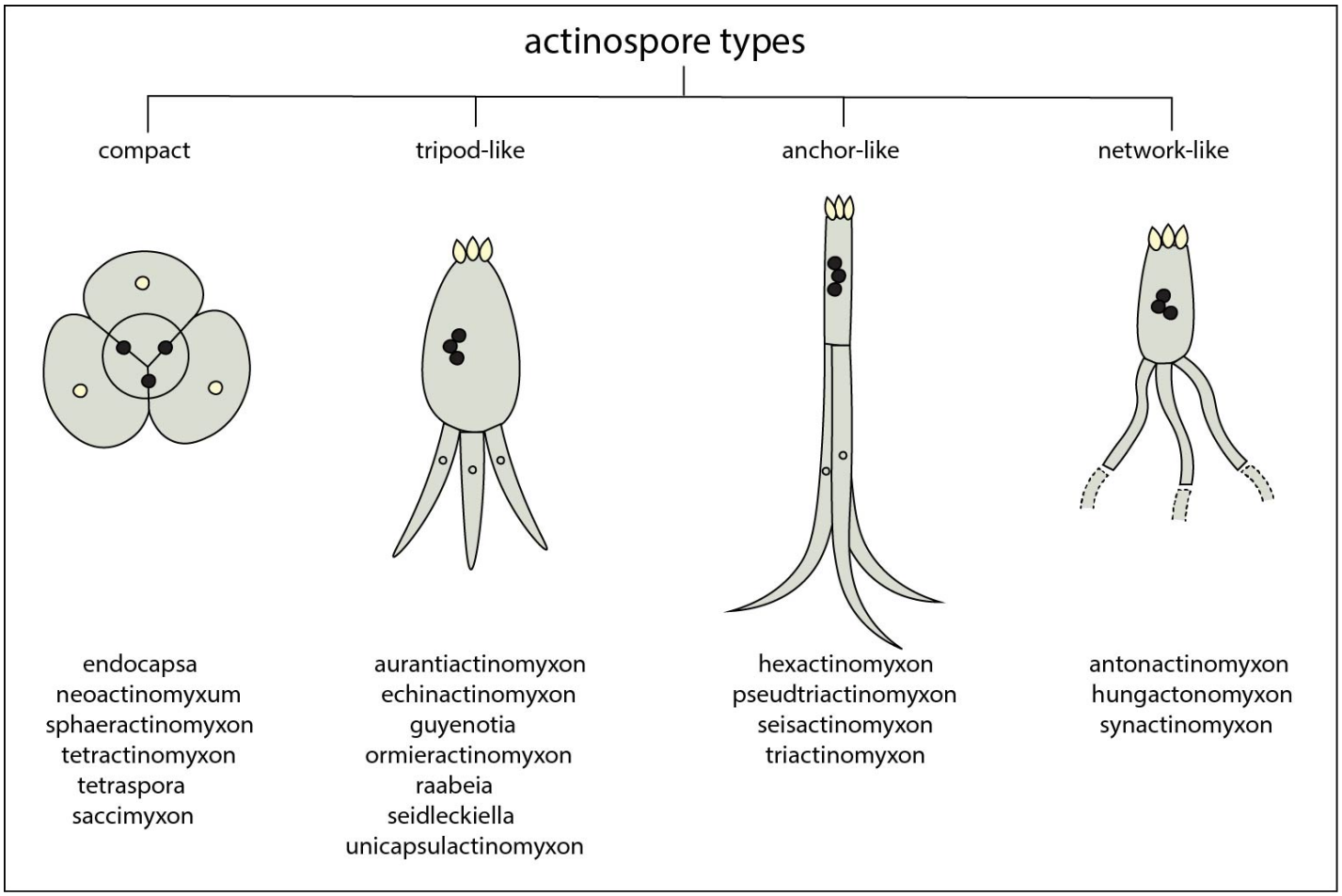
Enterocytozoon spores in human gut



Enterocytozoon spores in human gut (tEM)

Cnidaria
(myxozoa)


bivalvulid myxozoa
polar capsules perpendicular to suture
polar capsules parallel to suture
2 polar capsules
1 polar capsule
2 polar capsules
apical PC
polar PC
lateral PC
lateral projections
caudal projections
ridges
sometimes with lateral projections
caudal projections
Alatosporidae Ceratomyxidae
Chloromyxidae
Myxobilatidae Sphaerosporidae
Enteromyxidae Fabesporidae Myxidiidae Sphaeromyxidae
Ortholineidae Parvicapsulidae Sinuolineidae
Coccomyxidae
Myxobolidae p.p.
Myxobolidae p.p.


actinospore types
compact
tripod-like
anchor-like
network-like
endocapsa
neoactinomyxum
sphaeractinomyxon
tetractinomyxon
tetraspora
saccimyxon
aurantiactinomyxon
echinactinomyxon
guyenotia
ormieractinomyxon
raabeia
seidleckiella
unicapsulactinomyxon
hexactinomyxon
pseudtriactinomyxon
seisactinomyxon
triactinomyxon
antonactinomyxon
hungactonomyxon
synactinomyxon

BIVALVULID MYXOZOA

Myxobolus, Ceratomyxa, Chloromyxum, Myxidium, Zschokkella, Sphaeromyxa, Henneguya, Thelohanellus et al.
(animal: myxozoan)

Overview

Myxozoans are obligate parasites which produce unique multicellular spores comprised of valvogenic, sporoplasmic and capsulogenic cells. The latter form polar capsules with extrudible filaments (similar to cnidarian nematocysts — but used for attachment). They were originally classified as protistan organisms, but ultrastructural and molecular studies have indicated that they are bilateral metazoans, and are now classified as animals (cnidarians). Many species have been described as coelozoic or histozoic parasites in fish and some in amphibia, reptiles and various invertebrates (especially oligochaetes, polychaetes and sipunculids). Parasite development is characterized by vegetative proliferation of trophozoites (by formation of multinucleate plasmodia containing generative cells) followed by spore morphogenesis (by formation of pansporoblasts through the union of pericyte and sporogonic cells and differentiation of the latter to form valvogenic, capsulogenic and sporoplasmic cells which produce the spore valves, nematocyst-like polar capsules and amoeboid infective sporoplasms). The life-cycles of several myxozoan species have been found to involve cyclic development between myxospore stages in fishes and actinospore stages in worms. Two major myxosporean orders are recognized: the Bivalvulida (spores with two shell valves) and the Multivalvulida (spores with more than two shell valves). Numerous bivalvulid species occur as histozoic or coelozoic parasites of freshwater and marine fish. Some infections have been associated with severe lesions and disease in host tissues, including *Myxobolus cerebralis* in cartilage causing whirling disease in salmonids.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Phylum:	Cnidaria (diploblastic, radial symmetry, cnidocytes with nematocysts, sea anemones, corals, jellyfish, hydrozoa, myxozoa)
Subphylum:	Myxozoa (form multicellular valved spores with polar filaments)
Class:	Myxosporea (spores with 1-2 sporoplasms, 1-13 polar capsules)
Order:	Bivalvulida (spores with two valves)
Suborder:	Platysporina (polar capsules in sutural plane)
Family:	Myxobolidae (spores flattened, suture forms elevated ridge, one polar capsule smaller than the other)
Genus:	*Myxobolus* (histozoic parasites in fish)
Species:	*M. cerebralis* (causes whirling disease in salmonid fish)

Parasite biodiversity and host range: Myxozoans are unique parasites that form multicellular (pluricellular) spores (with valves, polar capsules and infective sporoplasms) in cold-blooded vertebrates and worm-like invertebrates. Despite their multicellularity, they were often classified together with the unicellular spore-forming protozoa (Protista), more for convenience than for phylogenetic relationships. Contemporary ultrastructural and molecular studies have now shown that they are bilateral metazoan animals, and are now classified with the Cnidaria (jellyfish and allies). Myxozoa polar capsules contain extrudible filaments similar in structure to cnidarian nematocysts, but they are used for attachment to host cells during the infection process (rather than for stinging). Numerous myxozoan species have been described as coelozoic or histozoic parasites predominantly in fish (marine and freshwater) throughout the world, as well as in some amphibia, reptiles, annelids (oligochaetes and polychaetes) and sipunculids. Conventional taxonomic classification schemes recognized two major myxozoan assemblages which were quite different in morphology and biology: the classical Myxosporea in fish, and the enigmatic Actinosporea in annelids. Little was known about their complete life-cycles and modes of transmission, until recent studies demonstrated that several species had heteroxenous (2-host) life-cycles alternating between myxospores in fish (acting as intermediate hosts) and actinospores in annelids (acting as definitive hosts). This prompted most taxonomists to suppress actinosporean nomenclature pending recognition of complete life-cycles. The anchor-shaped actinospores found in annelids have subsequently been assigned to 20 collective groups with vernacular names (anton-, auranti-, echin-, hex-, hung-, ormier-, pseudtri-, sphaer-, seis-, syn-, tetra-, tri-, unicapsul-actinomyxon, neoactinomyxum, saccimyxon, endocapsa, guyenotia, raabeia, siedleckiella, and tetraspora), whose affinities to myxosporean stages have yet to be determined. Contemporary classification schemes now recognize 2 myxozoan classes: the Malacosporea containing species with soft shell valves and enigmatic worm- and sac-like trophic stages; and the Myxosporea containing species with hardened shell valves enclosing sporoplasmic and capsulogenic cells. Two major myxosporean orders are recognized: the Bivalvulida (spores with 2 shell valves) and the Multivalvulida (spores with more than 2 shell valves).

No. families	No. genera	No. species	Hosts	Location
Class: MALACOSPOREA (spores with soft (unhardened) shell valves)				

Order: Malacovalvulida (worm-like (myxoworm) and sac-like trophic stages)				
1	2	3	bryozoa, salmonid fish	histozoic, coelozoic
Class: MYXOSPOREA (myxospores with hardened shell valves enclosing sporoplasmic and capsulogenic cells)				
Order: Bivalvulida (spores with two valves)				
Suborder: Platysporina (polar capsules at one pole in sutural plane)				
1	13	1,622	fish (mostly freshwater)	histozoic
Suborder: Variisporina [Eurysporina (Unipolariina) + Bipolarina] (polar capsules perpendicular to sutural plane)				
15	48	1,323	fish (mostly marine), some amphibians	mostly coelozoic, some histozoic
Order: Multivalvulida (radially symmetrical spores, 3-13 valves (rarely 2), polar capsules grouped together at apex)				
3	5	163	fish (marine)	mostly histozoic, some coelozoic

Collectively, around 3,110 species of myxozoan parasites have been described in over 2,000 species of fish (belonging to 332 families in 89 orders) as well as in some amphibians, a few reptiles, and rarely in shrews, birds and even as hyperparasites in some trematodes. Myxospores have been recorded in over 800 species of marine fish (from 233 families in 64 orders) and over 1,120 species of freshwater fish (from 124 families in 35 orders). Myxozoan classification still depends largely on myxospore structure (principally shape, number and position of shell valves and polar capsules), and sometimes on their presumed specificity (host occurrence and tissue tropism). With improvements in microscopic techniques, there have been many reports and reviews of myxozoan taxa over the last century. With the recent advent and utilization of molecular characterization techniques, new light has been cast on phylogenetic relationships, which sometimes do not agree with morphotypic and biologic classifications. Many myxozoan groups have been found to be polyphyletic, with broader host specificities than previously thought and many clades aligned with host habitats. For example, molecular studies on members of the bivalvulid genus *Leptotheca* showed them not to be monophyletic, but to align variously with the genera *Ceratomyxa, Ellipsomyxa, Sphaerospora*, and *Myxobolus*, to which they were subsequently re-assigned. Similarly, genotypic characterization of multivalvulid species with 5-13 valves and polar capsules (originally placed in the diverse genera *Pentacapsula*, *Hexacapsula* and *Septemcapsula*) have grouped them together with the genus *Kudoa* (typically with 4 polar capsules), to which they have all been re-assigned. The identity of many more species (and genera) have been reappraised following comparative molecular studies, so the contemporary literature has become riddled with numerous revisions resulting in many synonyms. All attempts have been made in the following tables to record such nomenclatural changes. The Bivalvulida are divided into three suborders depending on the location and orientation of the polar capsules: Platysporina with apical polar capsules parallel to the sutural plane; Eurysporina (Unipolariina) with apical polar capsules perpendicular to the sutural plane; and Bipolarina with polar capsules located at opposite ends of the spore [although recent studies have united the latter two into a single suborder Variisporina].

TAXON	**# spp.**	**Site**	**Hosts**	**Spore**		**Capsules**	
				shape	**size**	**site**	**size**
Order: **Bivalvulida** (two valves meeting in circumsporal suture)							
Suborder: Variisporiina [Bipolarina + Eurysporina] (polar capsules not in sutural plane, usually perpendicular)							
Family: Alatasporidae (triangular spores with lateral projections, two apical polar capsules)							
Alataspora	17	coelozoic	mar fish	triangular	7-15x10-90	apical	=
Pseudalataspora	17	coelozoic	mar fish	triangular	5-15x10-40	apical	=
Renispora	1	coelozoic	mar fish	reniform	10-25	apical	≠
Family: Ceratomyxidae (spores laterally elongate, two apical polar capsules)							
Ceratomyxa (syn. *Leptotheca*)	319	coelozoic, histozoic	fish, frogs, reptiles	ellipsoid, crescent	4-20x10-90	apical	=
Ceratonova	2	histozoic	fish	crescent	6-8 x 14-22	apical	=
Ellipsomyxa	18	coelozoic	mar fish	ellipsoid	5-10x6-18	lateral	=
Meglitschia	1	coelozoic	mar fish	V-shaped	11x16	apical	≠
Family: Chloromyxidae (spherical spores, four apical polar capsules)							
Agarella	1	histozoic	fw fish	spindle	30x10	apical	=
Caudomyxum	2	coelozoic	fw fish, amphibia	spherical	10-18x4-7	apical	=
Chloromyxum	140	coelozoic	fish, amphibia	spherical	4-13	apical	≠
Family: Coccomyxidae (spores with asymmetrical unequal smooth valves, single polar capsule)							
Auerbachia	11	coelozoic	mar fish	club-like	10-35x6-12	apical	na
Coccomyxa (syn. *Thelohanelloides*)	13	coelozoic	mar fish	ellipsoid	8-14x4-10	polar	na
Globospora	1	coelozoic	mar fish	spherical	10	apical	=
Family: Enteromyxidae (sigmoidal spores, 2 polar capsules, tangential at opposite ends, histozoic in intestines of fish)							
Enteromyxum	4	histozoic	fish	crescent	9-25x5-14	polar	=
Family: Fabesporidae (valves elongated perpendicular to sutural plane, two polar capsules at opposite ends)							

Fabespora	2	coelozoic	mar fish digenea	elongate	3-9x4-7	polar	=
Family: Gastromyxidae (sigmoidal spores, 2 polar capsules at opposite poles, in stomach of marine fish)							
Gastromyxum	2	histozoic	mar fish	sigmoidal	7-11x5-6	polar	=
Family: Monomyxidae (sigmoidal spores, 2 polar capsules at opposite poles, histozoic in gill monogeneans)							
Monomyxum	1	histozoic	monogenea	sigmoidal	11x5	polar	=
Family: Myxidiidae (spores elongate, 2 polar capsules at opposite poles)							
Cystodiscus	10	coelozoic	amphibians	ellipsoid	10-18x5-10	polar	=
Myxidium	238	coelozoic histozoic	fish reptiles amphibia	fusiform	6-20x4-10	polar	=
Paramyxidium	4	histozoic coelozoic	fish	lemon	6-12x4-8	polar	=
Sigmomyxa	2	coelozoic	mar fish	ellipsoid	15-20x6-12	polar	=
Soricimyxum	2	coelozoic	shrews	ovoid	6-13x 5-9	polar	=
Zschokkella (syn. *Parazschokkella*)	99	coelozoic histozoic	fish reptiles amphibia	ellipsoid	8-30x5-18	polar	=
Family: Myxobilatidae (elongate spores, pointed anteriorly)							
Acauda	2	coelozoic	fw fish	pyriform	15-22x5-11	apical	=
Hoferellus (syn. *Hoferia, Mitraspora*)	28	coelozoic	fw fish amphibia	spherical	6-16x5-12	apical	=
Myxobilatus	40	coelozoic histozoic	fish	spindle	5-40x4-9	apical	=
Family: Ortholineidae (spores ovoid, two polar capsules wide apart)							
Cardimyxobolus	3	histozoic	fw fish	spindle	8-12x11-15	polar	=
Kentmoseria (syn. *Paraortholinea*)	11	coelozoic	mar fish	elongate	7-14x6-13	lateral	=
Neomyxobolus	2	coelozoic	fw fish	ovoid	6-12x10-12	subapical	=
Ortholinea	15	coelozoic	mar fish	spherical	6-11x5-13	subapical	=
Triangula	7	histozoic	fw fish	triangular	6-14x4-12	subapical	=
Triangulamyxa	2	coelozoic	fw fish	triangular	8x8	subapical	=
Family: Parvicapsulidae (asymmetrical elongate spores, two apical polar capsules)							
Gadimyxa	3	coelozoic	mar fish	round	5-7x6-12	apical	=
Neoparvicapsula	3	coelozoic	mar fish	elongate	12-16x7-10	apical	=
Parvicapsula	17	histozoic coelozoic	mar fish	asymm.	8-15x4-10	apical	=
Family: Sinuolineidae (spherical spores with lateral projections, two polar capsules set apart)							
Bipteria	7	coelozoic	mar fish	pyramid	6-14x6-13	lateral	=
Latyspora	1	coelozoic	mar fish	ellipsoid	9x10	apical	=
Myxodavisia (syn. *Davisia*)	33	coelozoic	mar fish	ovoid	6-14x8-30	apical	=
Myxoproteus (syn. *Conispora*)	19	coelozoic	mar fish	pyramid	6-22x6-14	apical	=
Neobipteria	2	coelozoic	mar fish	pyramid	5-14x8-16	lateral	=
Noblea	1	coelozoic	mar fish	pyramid	17x13	apical	=
Paramyxoproteus	3	coelozoic	mar fish	pyramid	12-30x11-25	apical	=
Schulmania	7	coelozoic	mar fish	spherical	13-24x8-21	subapical	=
Sinuolinea	25	coelozoic	mar fish	spherical	7-20x4-22	subapical	=
Family: Sphaeromyxidae (two polar capsules at opposite poles of fusiform spores)							
Sphaeromyxa	58	coelozoic	mar fish	fusiform	12-27x4-10	polar	=
Family: Sphaerosporidae (spherical spores sometimes ridged, two apical polar capsules)							
Palliatus	6	coelozoic	mar fish	spherical	10-30x7-30	apical	≠
Sphaerospora (syn. *Podospora, Polysporoplasma*)	119	coelozoic histozoic	fish amphibia	spherical	5-12x5-18	apical	=
Wardia	2	histozoic	fw fish	oval	8-11x8-12	lateral	=
Suborder: Platysporina (apical polar capsules lie in sutural plane)							
Family: Myxobolidae (spores ovoid, two apical polar capsules)							
Dicauda	2	histozoic	fw fish	ovoid	9-15x9-11	apical	≠
Hennegoides	7	histozoic	fw fish	elongate	8-18x3-8	apical	≠
Henneguya	290	histozoic	fish	spindle	8-20x4-12	apical	≠
Laterocaudata	2	histozoic	fw fish	ellipsoid	8-9x5-7	apical	=

Myxobolus (syn. *Disparospora, Facieplatycauda, Gyrospora, Lentospora, Mixosoma, Myxosoma, Myxosporidium, Rudicapsula*)	1,143	histozoic	fish amphibia	ovoid	7-20x4-12	apical	≠
Neohenneguya	1	histozoic	fw fish	spindle	18x5	apical	=
Neothelohanellus (syn. *Lomosporus*)	3	histozoic	fw fish	ovoid	9-12x6-8	apical	na
Phlogospora	3	histozoic	fw fish	pyriform	14-24x3-5	apical	=
Spirosuturia	3	histozoic	fw fish	ovoid	8-16x6-9	apical	=
Tetrauronema	2	histozoic	fw fish	spindle	11-14x6-7	apical	≠
Thelohanellus	133	histozoic	fw fish	pyriform	10-35x 5-15	apical	na
Trigonosporus	2	histozoic	mar fish	triangular	7-10x3-18	apical	=
Unicauda	31	histozoic	fw fish	ovoid	7-22x3-10	apical	=
Order **Multivalvulida** (considered in separate section)							

Many bivalvulid species occur as coelozoic and some histozoic parasites of freshwater and marine fish, some amphibians and reptiles, and rarely birds and mammals. Some 16 bivalvulid families have been recognized, containing over 2,945 species classified into 61 genera. Infections in fish have been associated with various clinical diseases that have serious economic consequences for both wild-catch and cultured fish stocks with production losses occurring due to tissue lesions, poor growth, sickness and death. Bivalvulid species exhibit variable host specificity: with many apparently host-specific for individual hosts (oioxenous); while others have broader specificity and may infect closely-related hosts (stenoxenous) rather than unrelated hosts (euryxenous). Infections in fish are scattered throughout marine, estuarine and freshwater environments globally, and phylogenetic studies suggest that marine taxa branched separately from freshwater taxa. Experimental studies conducted to determine life-cycles have only succeeded in a few instances, with some implicating direct fish-to-fish transmission (mostly in crowded aquaculture facilities), and others discovering indirect cyclic transmission between fish (acting as intermediate hosts producing myxospores) and annelids (acting as definitive (rather than alternate) hosts producing actinospores). Molecular characterization studies have since helped provide evidence for around 100 life cycles by linking the DNA profiles of myxospore stages in fish with actinospore stages from annelids.

Some exemplars of the most speciose bivalvulid genera in fish include:

- *Myxidium*, with 238 species forming elongate myxospores with 2 opposing polar capsules;
- *Ceratomyxa* with 319 species forming elongate myxospores with 2 apical polar capsules;
- *Chloromyxum* with 140 species forming spherical myxospores with 4 apical polar capsules;
- *Henneguya* with 290 species forming spindle-shaped myxospores with 2 apical polar capsules; and
- *Myxobolus* with 1,143 species forming ovoid myxospores with 2 apical polar capsules (including the notorious *M. cerebralis* causing whirling disease in salmonid fish).

Parasite species	**Spore dimensions (µm)***	**Vertebrate hosts [life-cycles where known]**	**Location**	**Distribution**
*Dimensions are given as length x breadth (and thickness if available) with ranges (or means) expanded to include different populations or subspecies. Measurements given for spores with caudal or lateral processes include those processes (while measurements without processes are given in parentheses).				
Order **BIVALVULIDA** (two valves meeting in circumsporal suture, 1-4 (usually 2) polar capsules)				
Suborder **Variisporina** (polar capsules not in sutural plane)				
Family **Alatasporidae** (triangular spores, two polar capsules perpendicular to suture line)				
Genus ***Alataspora*** [not to be confused with the aquatic hypomycete *Alatospora*, despite many mis-spellings] (elongate triangular spores with lateral wing-like projections)				
A. adelia	6.5-8.5 x 40-56	marine Pleuronectiformes: pleuronectid (blackfin flounder)	gall bladder	Sea of Japan
A. africana	11.7-13.9 x 32.2-34	marine Spariformes: callanthiid (parrot seaperch)	gall bladder	eastern Atlantic
A. bialata	7-11 x 24-38	marine Pleuronectiformes: pleuronectid (Pacific rock sole)	gall bladder	northern Pacific
A. budegassai	12-14.4 x 86-159.6 (32-39.6)	marine Lophiiformes: lophiid (black-bellied anglerfish)	gall bladder	Portugal
A. caproi	7.3-9.3 x 20-29.3	marine Acanthuriformes: caproid	gall bladder	Celtic Sea

		(boarfish)		
A. contrariocapsularia	6.4-6.5 x 18-26	marine Syngnathiformes: syngnathid (slender snipefish)	gall bladder	eastern Atlantic
A. dracoidea	6.4-8.6 x 16-18.2	marine Aulopiformes: chlorophthalmid (shortnose greeneye)	gall bladder	eastern Atlantic
A. lepidum	6-6.6 x 42.6-58.5	marine Perciformes: triglid (grey gurnard)	gall bladder	Celtic Sea
A. longialata	12-14 x 80-112	marine Pleuronectiformes: pleuronectid (flathead flounder, blackfin flounder, scale-eye plaice)	gall bladder	Sea of Japan
A. merluccii	8.7-11.2 x 11.2-15	marine Gadiformes: merlucciid (southern hake, Argentine hake)	gall bladder	South America
A. opisthocentri	5-7 x 14-17	marine Perciformes: opisthocentrid (ocellated blenny)	gall bladder	Sea of Japan
A. parvicapsula	5.9-6.4 x 9.7	marine Aulopiformes: aulopid (Guinean flagfin)	gall bladder	eastern Atlantic
A. samaroidea [type species]	7.5-12.8 x 32.4-47.1	marine Aulopiformes: chlorophthalmid (Atlantic greeneye)	gall bladder	eastern Atlantic
A. serenum	5-6.1 x 12-16	marine Carangiformes: carangid (Atlantic horse mackerel)	gall bladder	Celtic Sea
A. solomoni	5.9-7.3 x 17.4-21.4	marine Carangiformes: carangid (Mediterranean horse mackerel)	gall bladder	Black Sea
A. subtilis	3.5-5 x 25-37.2	marine Perciformes: epinephelid (white grouper)	gall bladder	eastern Atlantic
A. tetricum	9-12 x 29.3-43.9	marine Pleuronectiformes: pleuronectid (lemon sole)	gall bladder	Celtic Sea
Genus ***Pseudalataspora*** [note several mis-spellings as *Pseudoalatospora, Pseudoalataspora* or *Pseudalatospora*] (triangular spores with lateral projections forming parachute-like pockets)				
P. atlantica	6.7-10 x 34.6-42.5	marine Aulopiformes: chlorophthalmid (shortnose greeneye, Atlantic greeneye); Carangiformes: carangid (false scad); Syngnathiformes: fistulariid (cornetfish)	gall bladder	eastern Atlantic
P. beryxi	5.3-8.7 x 14.6-30.6	marine Beryciformes: berycid (splendid alfonsino)	gall bladder	Atlantic
P. indecora	3.3-4.7 x 13.4-20	marine Eupercaria: sparid (Angolan dentex)	gall bladder	eastern Atlantic
P. insolita	5.3-6 x 14.6-17.3	marine Carangiformes: carangid (false scad)	gall bladder	eastern Atlantic
P. kovalevae	8-10.5 x 14-20 x 8.8-11.6	marine Gadiformes: macruronid (Patagonian grenadier)	gall bladder	South America
P. lophii	7.2-10 x 21.6-28.8 (16.8-22.6)	marine Lophiiformes: lophiid (white-bellied anglerfish)	gall bladder	Scotland
P. meridionalis	6.7-9.5 x 16-20	marine Perciformes nototheniid (marbled rockcod)	gall bladder	Antarctic
P. misrae	8.2-9.7 x 22.5-25.5	marine Scombriformes: scombrid (Indian mackerel)	gall bladder	India
P. originalis	10-12 x 27-36	marine Pleuronectiformes: pleuronectid (flathead flounder, blackfin flounder)	gall bladder	Sea of Japan
P. pacifica	8-12.6 x 27.9-35.9	marine Gadiformes: macrourid (Patagonian grenadier)	gall bladder	South America
P. pontica	5.5-6.5 x 16-19.9	marine/estuarine Mugiliformes: mugilid (golden grey mullet)	gall bladder	Black Sea
P. scomberomorusi	6-7.8 x 16.5-21.5	marine Scombriformes: scombrid (unspecified mackerel)	gall bladder	India
P. scombri [type species]	4.6-6 x 7.9-10.6 x 6.6	marine Scombriformes: scombrid (chub mackerel)	gall bladder	eastern Pacific
P. sebastei	13.3 x 22.6	marine Perciformes: sebastid (golden redfish, beaked redfish, lesser redfish, Acadian redfish)	gall bladder	northern Atlantic

P. squamifrons	5.3-6.7 x 19.9-21.3	marine Perciformes: nototheniid (grey rockcod)	gall bladder	Antarctic
P. umbraculiformis	8-9.3 x 14.6-17.3 x 14.6-17.3	marine/estuarine Gadiformes: gaidropsarid (shore rockling)	gall bladder	Atlantic
P. vanderlingi	12.2-15.3 x 18.2-23.4	marine Gadiformes: merlucciid (Cape hake)	gall bladder	South Africa
Genus ***Renispora*** (reniform spores with lateral membranous processes)				
R. simae [type species]	8-13 x 16-28	marine Perciformes: nototheniid (cod icefish)	gall bladder	Falkland Islands
Family **Ceratomyxidae** (spore valves with large elongations, 2 polar capsules)				
Genus ***Ceratomyxa*** (syn. *Leptotheca*) (ellipsoidal-crescentic spores, coelozoic mainly in marine fish)				
C. abbreviata (syn. *Leptotheca*)	14 x 17	marine Carcharhiniformes: carcharhinid (Atlantic sharpnose shark)	gall bladder	North America
C. acadiensis	7-8 x 40-50	marine Gadiformes: phycid (red hake, white hake); Perciformes: zoarcid (ocean pout)	gall bladder	Canada
C. acanthopagri (syn. *Leptotheca*)	8.7-10 x 16-20	marine Eupercaria: sparid (blackhead seabream)	gall bladder	China
C. acanthuri	10-12 x 16-18	marine Acanthuriformes: acanthurid (Monrovia doctorfish)	gall bladder	Senegal
C. acuta	5-6 x 39-52	marine/estuarine Acropomatiformes: lateolabracid (Japanese seabass)	gall bladder	Sea of Japan
C. adeli (syn. *Leptotheca*)	12-13 x 18.6-20	marine Perciformes: sebastid (golden redfish, beaked redfish, lesser redfish)	gall bladder	North Atlantic
C. aegyptiaca	8-11 x 48-58	marine Pleuronectiformes: soleid (Egyptian sole)	gall bladder	Tunisia
C. aggregata	6-12 x 50-70	marine Acanthuriformes: sciaenid (spot croaker, Atlantic croaker)	gall bladder	Atlantic
C. aglomerata	5 x 24-28	marine/estuarine Aulopiformes: synodontid (inshore lizardfish)	gall bladder	North America
C. agilis (syn. *Leptotheca*)	6-7 x 11-12	marine Myliobatiformes: dasyatid (common stingray)	gall bladder	Mediterranean
C. allantoidea	6-6.6 x 29.3-38.6	marine/estuarine Perciformes: ammodytid (small sand eel)	gall bladder	Bay of Biscay
C. amatea (syn. *Leptotheca*)	9.2-10 x 13-15	marine Pleuronectiformes: pleuronectid (marbled flounder)	gall bladder	Japan
C. amazonensis	6.2-7.6 x 15-16.7	freshwater Cichliformes: cichlid (red discus)	gall bladder	Brazil
C. americana	4.4-5.2 x 8.8-11.1 x 5-5.6	marine Scombriformes: scombrid (Atlantic mackerel)	gall bladder	North America
C. ammodytis		marine/estuarine Perciformes: ammodytid (Pacific sand lance)	gall bladder	China
C. amorpha	11 x 27	marine Aulopiformes: synodontid (inshore lizardfish)	gall bladder	North America
C. ampla (syn. *Leptotheca*)	14.7-17.3 x 25.3-29.3	marine Perciformes: nototheniid (grey rockcod)	gall bladder	Antarctica
C. anguillae	25-30	freshwater Anguilliformes: anguillid (European eel)	gall bladder	Mediterranean
C. angusta	4.7-6.5 x 34.2-57.8	marine Perciformes: anthiadid (tiger seaperch), sebastid (red gurnard perch); Scombriformes: stromateid (silver pomfret)	gall bladder	China, New Zealand
C. anko	9.7-11.9 x 36.9-47.2	marine Lophiiformes: lophiid (yellow goosefish)	gall bladder	Japan
C. anoplopoma	7.5-10 x 53-65	marine Perciformes: anoplopomatid (sablefish)	gall bladder	North America
C. annulata (syn. *Leptotheca*)	4.5-6.7 x 7.9-12.3	marine Perciformes: arripid (kahawai); Scombriformes: gempylid	gall bladder	New Zealand

		(barracouta, silver gemfish)		
C. antarctica	6.2-6.7 x 30.3-47.8	marine Perciformes: nototheniid (grey rockcod)	gall bladder	Antarctica
C. apogoni (syn. *Leptotheca*)	16.8-18.2 x 24.6-26.2	marine Eupercaria: nemipterid (Japanese threadfin bream); Kurtiformes: apogonid (ring-tailed cardinalfish)	(gills, intestines, gall bladder)	India
C. appendiculata	5-8.5 x 27-50	marine Lophiiformes: lophiid (northern European anglerfish, southern European anglerfish)	gall bladder	Europe
C. arabica	7-9 x 10-14	marine Eupercaria: sparid (two bar seabream)	gall bladder	Saudi Arabia
C. archamiae	4.2-5.7 x 8.8-12.4	marine Kurtiformes: apogonid (orange-lined cardinalfish)	gall bladder	Australia
C. arcuata (incl. var. *scorpaenarum*)	5-13.5 x 20-40	marine Eupercaria: labrid (corkwing wrasse), pomacentrid (chromis); Gadiformes: gadid (Atlantic cod, merling), lotid (three-bearded rockling); Gobiiformes: gobiid (rock goby); Ophidiiformes: ophidiid (baldracca); Perciformes: scorpaenid (black scorpionfish, red scorpionfish, small red scorpionfish), serranid (orange perch); Spariformes: sparid (blackspot seabream); Trachiniformes: uranoscopid (Atlantic stargazer)	gall bladder	Mediterranean
C. arripica	4.8-5.1 x 9.3-11.3	marine Perciformes: arripid (Australian salmon)	gall bladder	Australia
C. artedielli	7.2-10.8 x 16.2-23.4	marine Perciformes: cottid (European sculpin)	gall bladder	Barents Sea
C. aspera	8-10 x 38-69	marine Pleuronectiformes: pleuronectid (yellowfin sole, yellow-striped flounder)	gall bladder	Russia
C. assymmetrica (syn. *Leptotheca*)	5.7-7.9 x 8.6-10	freshwater Cypriniformes: cyprinid (bonylip barb)	gills, intestines, gall bladder	India
C. asymmetrica	4-6 x 12.5-17	marine Gadiformes: macrourid (popeye grenadier)	gall bladder	Alaska
C. atkinsoni	4.4-5.8 x 11.2-19.5	marine Spariformes: lethrinid (Pacific yellowtail emperor)	gall bladder	Australia
C. attenuata	9 x 115	marine Carcharhiniformes: carcharhinid (Atlantic sharpnose shark)	gall bladder	North America
C. auerbachi	7-13 x 57-92	marine Clupeiformes: clupeid (Atlantic herring) [cycle involves tetractinomyxon-type actinospores in Polychaeta: sabellid (*Chone infundibuliformis*)	gall bladder	North Sea
C. auratae	5.3-7.6 x 19.7-31.2	marine Spariformes: sparid (gilt-head bream)	gall bladder	Portugal
C. australis	4-5.3 x 13.3-15	marine Carangiformes: carangid (Cape horse mackerel)	Namibia	South Africa
C. ayami	9-11.5 x 15-18.5	marine Tetraodontiformes: monacanthid (unicorn leatherjacket)	gall bladder	Malaysia
C. azevedoi	5-7 x 10-14	marine Eupercaria: lutjanid (blackspot snapper)	gall bladder	Saudi Arabia
C. azonusi	7-9 x 24-30	marine Scorpaeniformes: hexagrammid (Atka mackerel)	gall bladder	Russia
C. barnesi	3.9-5.9 x 13.6-18.4	marine Perciformes: siganid (golden-lined spinefoot)	gall bladder	Australia
C. bartholomewae	4.7-6.2 x 13.5-21.7	marine Beloniformes: hemiramphid (Dussumier's halfbeak)	gall bladder	Australia

C. bassoni	5-7 x 15-20	marine Eupercaria: haemulid (blackspotted rubberlip)	gall bladder	Egypt
C. beloneae	6.7-7.5 x 14-18	marine Beloniformes: belonid (garfish)	gall bladder	Adriatic Sea
C. beveridgei (syn. *Leptotheca*)	8-10 x 15-18 x 7-8	marine Perciformes: scorpaenid (bandfin scorpionfish)	gall bladder	Australia
C. binhthuanensis	10.8-16 x 4.8-6.9	marine Perciformes: epinephelid (blacktip grouper)	gall bladder	Vietnam
C. blennius	26 x 10	marine Perciformes: chaetodontid (unspecified butterflyfish)	gall bladder	Asia
C. bohari	3-4 x 16-19	marine Eupercaria: lutjanid (two-spot red snapper)	gall bladder	Saudi Arabia
C. brasiliensis	5.1-7.5 x 37.1-47.6	freshwater Cichliformes: cichlid (tucanare peacock bass)	gall bladder	Brazil
C. brayi	4.5-6 x 19-27.5	marine Perciformes: epinephelid (chocolate hind)	gall bladder	Australia
C. bryanti	4.5-6.9 x 10.1-19.4	marine Ovalentaria: pomacentrid (Whitley's sergeant)	gall bladder	Australia
C. burgerae	4.5-5.7 x 11-19.3	marine Ovalentaria: pomacentrid (whitetail dascyllus)	gall bladder	Australia
C. buri	5.5-7.5 x 11-16.5	marine Carangiformes: carangid (Japanese amberjack)	gall bladder	Australia, Japan
C. californica	7.5-9 x 48-59	marine Myxiniformes: myxinid (Pacific hagfish)	gall bladder	North America
C. capricornensis	4.7-8 x 21.6-35.7	marine Ovalentaria: pomacentrid (white damsel)	gall bladder	Australia
C. carcharhini	9-11.5 x 44-77.5	marine Carcharhiniformes: carcharhinid (blacktip reef shark)	gall bladder	Australia
C. cardinalis	4.2-6.5 x 10.1-14.6	marine Kurtiformes: apogonid (wolf cardinalfish)	gall bladder	Australia
C. caspia	11.5 x 19.5	marine/estuarine/freshwater Gobiiformes: gobiid (monkey goby, racer goby, Caspian tadpole goby, Kessler's goby)	(renal tubules)	Caspian Sea
C. castigata	5.1-5.9 x 9.2-15.3	marine Perciformes: congiopodid (southern pigfish)	gall bladder	New Zealand
C. castigastoides	5.1-7.3 x 9.8-17.8	marine Labriformes: labrid (scarlet wrasse)	gall bladder	New Zealand
C. centriscopsi (replacement name for *C. constricta*)	5.6-9 x 23.6-29.3	marine Syngnathiformes: centriscid (banded yellowfish)	gall bladder	Australia, New Zealand
C. centropoma (mis-spelling *cantopona*)	6-7.5 x 25.5-31.5	marine/estuarine Perciformes: latid (barramundi)	gall bladder	India
C. cheilinae	10.3-14.7 x 25.3-40.6	marine Eupercaria: labrid (floral wrasse)	gall bladder	Australia
C. choleospora	4-5 x 15-23	freshwater/estuarine Carangaria: centropomid (common snook)	gall bladder	North America
C. choerodonae	4.2-5.8 x 15.8-26.7	marine Euparcaria: labrid (blue tuskfish)	gall bladder	Australia
C. chromis	7-8 x 20-27	marine Ovalentaria: pomacentrid (Mediterranean chromis)	gall bladder	Adriatic Sea
C. coelorhyncha (syn. *Leptotheca*)	6-8 x 9-13	marine Gadiformes: macrourid (hollowsnout grenadier)	gall bladder	Ireland
C. collarae	5.2 x 16.2	marine Acanthuriformes: chaetodontid (redtail butterflyfish)	gall bladder	India
C. constricta (syn. *Leptotheca*)	5.6-10 x 10 x 19-29.3	marine Perciformes: sebastid (broadbanded thornyhead); Syngnathiformes: centriscid (banded yellowfish)	gall bladder	Japan, New Zealand
C. coris (syn. *Leptotheca macrospora*)	10.5 x 26	marine Labriformes: labrid (Mediterranean rainbow wrasse)	gall bladder	Europe

C. cornuti	7 x 25.6	marine Acanthuriformes: zanclid (Moorish idol)	gall bladder	Arabian Sea
C. coryphaenoida	10-16 x 20-28 x 11-13	marine Gadiformes: macrourid (popeye grenadier)	gall bladder	Canada
C. costata	11-14.2 x 22-30 x 10-12	marine Pleuronectiformes: pleuronectid (marbled flounder)	gall bladder	Sea of Japan
C. cottoidii	6.5-8 x 17-22	marine Blenniiformes: clinid (bluntnose klipfish)	gall bladder	South Africa
C. crassa	7.5-9.5 x 27.5-32	marine Scorpaeniformes: cottid (Pacific staghorn sculpin)	gall bladder	North America
C. cretensis	5.5-8.9 x 21.5-38.9	marine Aulopiformes: synodontid (Atlantic lizardfish)	gall bladder	Greece
C. cribbi	3.4-5.6 x 12.4 x 17.4	marine Ovalentaria: pomacentrid (whitetail damsel)	gall bladder	Australia
C. curvata	12 x 24	marine Carcharhiniformes: carcharhinid (sand tiger shark)	gall bladder	Brazil
C. cutmorei	5-8.5 x 12-21.5	marine Perciformes: epinephelid (blacktip grouper)	gall bladder	Australia
C. cyanoglossi	8.5-9.5 x 47-58	estuarine Pleuronectiformes: cynoglossid (long tongue sole)	gall bladder	India
C. cyanosomae	5-8 x 16.7-24.2	marine Kurtiformes: apogonid (yellow striped cardinalfish)	gall bladder	Australia
C. daysciaenae	5.5-7 x 55-75	marine/estuarine Eupercaria: sciaenid (Bengal corvina)	gall bladder	India
C. declivis	5.1-6.8 x 13.5-15.2 x 5.1-6.2	marine Zeiformes: cyttid (New Zealand dory)	gall bladder	New Zealand
C. dehoopi	4-5.5 x 12-17.5	marine Blenniiformes: clinid (super klipfish)	gall bladder	South Africa
C. delicatula	12-13.6 x 16-32	marine Beryciformes: berycid (splendid alfonsino)	gall bladder	Atlantic
C. dennisi	4.3-6.4 x 9.3-17.3	marine Ovalentaria: pomacentrid (spiny chromis)	gall bladder	Australia
C. diamanti	4.2-5.4 x 9.9-14.7	marine Carangaria: polynemid (king threadfin)	gall bladder	Australia
C. diloba	7-8 x 15-20	marine Tetraodontiformes: tetraodontid (Japanese puffer, panther puffer)	gall bladder	Sea of Japan
C. diplodae	5-7 x 18-22	marine Eupercaria: sparid (annular seabream)	gall bladder	Adriatic Sea
C. dissimilaris	9.2-11.8 x 36.4-45.8	marine Eupercaria: nemipterid (mauvelip threadfin bream)	gall bladder	India
C. dissostichi	3.2-4.5 x 15.4-22.8	marine Perciformes: nototheniid (Patagonian toothfish)	gall bladder	Falkland Islands
C. drepanopsettae	7.2-15.3 x 45-92	marine Pleuronectiformes: pleuronectid (American plaice, European plaice, Atlantic halibut, Greenland halibut, summer flounder, European flounder, common dab)	gall bladder	Arctic Seas
C. dubia	17.5 x 8	marine/estuarine Perciformes: cottid (long spined bullhead)	gall bladder	England
C. durusa	8-10 x 100-112	marine Pleuronectiformes: pleuronectid (yellowfin sole, yellow striped flounder)	gall bladder	North America
C. elegans	6-7.5 x 23-29.6	marine Batrachoidiformes: batrachoidid (plainfin midshipman); Gadiformes: macrourid (Fernandez whiptail); Scorpaeniformes: scorpaenid (black scorpionfish, canary rockfish, rosy rockfish)	gall bladder	North America, Black Sea
C. ellipsoidea	8-8.6 x 20-26.6	marine Perciformes: nototheniid (grey rockcod)	gall bladder	Antarctica
C. elongata	12-20 x 10-20	marine Gadiformes: gaidropsarid	gall bladder	France

(syn. *Leptotheca*)		(three-bearded rockling); merlucciid (European hake)		
C. entzerothi	9-11 x 30-46	marine Mugiliformes: mugilid (bluespot mullet)	gall bladder	Egypt
C. epinephela	3.6-5.6 x 23.3-37.5	marine Perciformes: epinephelid (Hong Kong grouper, yellow grouper, kelp grouper)	gall bladder	South America, China
C. ernsti	4.7-6.8 x 9.5-14.8	marine Eupercaria: sillaginid (sand whiting)	gall bladder	Australia
C. etroplusi	4.5-6 x 12.3-18	freshwater/estuarine Cichliformes: cichlid (orange chromide)	gall bladder	India
C. etrumuci (syn. *Leptotheca*)	7 x 7	marine Clupeiformes: dussumieriid (sardine)	gall bladder	Russia
C. faba (syn. *Leptotheca*)	5.6-6.7 x 10.7-14.1 x 6.1-7	marine Pleuronectiformes: bothid (witch)	gall bladder	New Zealand
C. falcatus	3.3-4.3 x 9.3-17.3	marine Ovalentaria: pomacentrid (Whitley's sergeant)	gall bladder	Australia
C. filamentosi	7.1-9.6 x 29.7-48.9	marine Aulopiformes: aulopid (royal flagfin)	gall bladder	Greece
C. filiformis	5 x 16-17	marine Clupeiformes: alosid (blue pilchard)	gall bladder	Sea of Japan
C. fisheri (syn. *Leptotheca*)	5.1-7.1 x 9.3-13.3	marine Chimaeriformes: chimaerid (spotted ratfish)	gall bladder	North America
C. fistulariae	10-12 x 38.8-40	marine Syngnathiformes: fistulariid (red cornetfish)	gall bladder	Senegal
C. flagellifera	12 x 118	marine Carcharhiniformes: carcharhinid (unspecified requiem shark)	gall bladder	North America
C. flexa	5.6-11.9 x 13.6-27	marine Pleuronectiformes: pleuronectid (Patagonian flounder); Perciformes: emmelichthyid (rubyfish)	gall bladder	Argentina, New Zealand
C. fonsecai	2.3-3.9 x 24.3-32.5	freshwater Characiformes: hemiodontid (einflecksalmer, bananinha)	gall bladder	Europe
C. fujitai (syn. *Leptotheca, L. limandae*)	14-16 x 24-26	marine Mugiliformes: mugilid (long finned mullet); Pleuronectiformes: pleuronectid (speckled flounder, yellowfin sole, dotted flounder)	gall bladder, muscle	Japan, China
C. fukuiensis	11-13 x 37-75	marine Pleuronectiformes: pleuronectid (sohachi)	gall bladder	Russia, Japan
C. furcata	11-15 x 45-80	marine Osmeriformes: osmerid (Japansk smelt); Pleuronectiformes: pleuronectid (yellowfin sole, yellow striped flounder); Scorpaeniformes: pholid (penpoint gunnel)	gall bladder	Pacific
C. galeata (syn. *Leptotheca*)	6.6-8.7 x 11.6-14.7	marine Myxiniformes: myxinid (Pacific hagfish)	gall bladder	North America
C. gemmaphora	5.9-8.3 x 14.2-23 x 5.6-6.6	marine Perciformes: serranid (butterfly perch)	gall bladder	New Zealand
C. ghaffari	6-9 x 25-33	marine Beloniformes: belonid (Red Sea houndfish)	gall bladder	Red Sea
C. gibba	1.9-3.3 x 1.5-2.2	marine Scorpaeniformes: congiopodid (southern pigfish)	gall bladder	New Zealand
C. gleesoni	5-7 x 16-22	marine Perciformes: serranid (leopard coral grouper)	gall bladder	Australia
C. globulifera	5-10 x 22-50	marine Gadiformes: merlucciid (European hake); Ophidiiformes: ophidiid (Roche's snake blenny)	gall bladder	Mediterranean
C. gobioidesi	4-5 x 14-15	marine Gobiiformes: oxudercid (rubicundus eel goby); Ophidiiformes: ophidiid (cusk-eel)	gall bladder	India

C. gracilis	4-5.6 x 11-14	marine Blenniiformes: clinid (spotted kelpfish)	gall bladder	North America
C. gracillima	3-5.7 x 6-7.2	freshwater Siluriformes: pimelodid (gilded catfish)	gall bladder	Brazil
C. gunterae	4.4-7.5 x 17.2-29.6	marine Kurtiformes: apogonid (fourline cardinalfish)	gall bladder	Australia
C. gurnardi	4.9-7.4 x 20.3-31.1	marine Scorpaeniformes: triglid (grey gurnard)	gall bladder	Shetland Islands
C. hallettae	3.7-5.9 x 13.9-24.5	marine Spariformes: lethrinid (thumbprint emperor)	gall bladder	Australia
C. hama	6.8-8.3 x 18.5-29.8 x 7-8.3	marine Pleuronectiformes: bothid (witch)	gall bladder	New Zealand
C. hamour	608 x 15-18	marine Perciformes: serranid (orange-spotted grouper)	gall bladder	Saudi Arabia
C. heinigerae	4.8-6.3 x 16.7-32.3	marine Eupercaria: labrid (purple tuskfish)	gall bladder	Australia
C. hemitriptera	8.8-9.5 x 80-88.9	marine Scorpaeniformes: agonid (sea raven)	gall bladder	China
C. hepseti (syn. *Leptotheca*)	7-8 x 12-15	marine Atheriniformes: atherinid (Mediterranean sand smelt)	gall bladder	France
C. heronensis	4-6.2 x 10.3-15.1	marine Kurtiformes: apogonid (orange-lined cardinalfish)	gall bladder	Australia
C. herouardi	nr	marine Spariformes: sparid (Salema porgy)	gall bladder	Mediterranean
C. hilsae	10 x 25-40	freshwater Clupeiformes: dorosomatid (hilsa herring)	gall bladder	India
C. hippocampi	7 x 27	freshwater Siluriformes: loricariid (cascudo)	gall bladder	Brazil
C. hokarari	11-13.2 x 24.2-48.4	marine Ophidiiformes: ophidiid (pink cusk-eel)	gall bladder	New Zealand
C. honckenii	7.5-8 x 18-21	marine Tetraodontiformes: tetraodontid (evileye pufferfish)	gall bladder	South Africa
C. hongtzensis	4.4-9 x 9.7-17.5	freshwater Siluriformes: bagrid (korakinos)	gall bladder	China
C. hooperi	4-5.5 x 10-15.5	marine Perciformes: serranid (longfin grouper)	gall bladder	Australia
C. hopkinsi	5.7-7.5 x 28.7-39	marine Pleuronectiformes: cyclopsettid (longfin sanddab), pleuronectid (English sole, Pacific Dover sole)	gall bladder	North America
C. huanghaiensis	5.5-7.5 x 29-40	marine Perciformes: platycephalid (bartail flathead)	gall bladder	China
C. huangheensis	3.3-5.5 x 8.5-13.3	marine Siluriformes: bagrid (yellowhead catfish)	gall bladder	China
C. hungarica	10-10.5 x 18.5-19.5	marine/estuarine Gobiiformes: gobiid (tubenose goby)	renal tubules, Bowman's capsules	Hungary
C. hurghadensis	8-11 x 46-52	marine Syngnathiformes: fistulariid (blue spotted cornetfish)	gall bladder	Egypt
C. husseini	8-9 x 14-18	marine Perciformes: serrannid (yellowfin hind)	gall bladder	Saudi Arabia
C. inaequalis (syn. *Leptotheca*)	5-16 x 12-15 x 23.5-37	marine Labriformes: labrid (axillary wrasse, East Atlantic peacock wrasse); Pleuronectiformes: pleuronectid (barfin flounder, marbled flounder, dusky sole, roughscale sole)	gall bladder	Eurasia
C. inconstans (syn. *Leptotheca*)	5.4-7.6 x 11.2-13.3	marine Scomberiformes: scombrid (chub mackerel)	gall bladder	North America
C. informis (syn. *Leptotheca*)	9-12 x 15-21	marine Gadiformes: gadid (merling); Tetraodontiformes: molid (sunfish)	gall bladder	Atlantic, North Sea
C. insolita	7-13 x 2.5-4	marine Dactylopteriformes: dactylopterid (flying gurnard)	gall bladder	New Zealand

C. intexua	3.4-5.4 x 9.3-20.1 x 3.5-4.3	marine Acanthuriformes: emmelichthyid (rubyfish); Scombriformes: scombrid (wahoo)	gall bladder	New Zealand
C. inversa	6.9-9.3 x 51.1-73.7 x 7.7-10	marine Ophidiiformes: ophidiid (pink cusk-eel)	gall bladder	New Zealand
C. ireneae	5.2-8.3 x 11.4-17.8	marine Kurtiformes: apogonid (orange-lined cardinalfish, girdled cardinalfish, fragile cardinalfish); Pleuronectiformes: pleuronectid (sohachi)	gall bladder	Australia
C. jamesoni (syn. *C. taenia p.p.*)	7.5-9.5 x 95-117	marine Carcharhiniformes: triakid (leopard shark)	gall bladder	North America
C. japonica	11-13 x 65-75 x 11-13	marine Pleuronectiformes: pleuronectid (Bering flounder, pointhead flounder, yellowfin sole, yellow-striped flounder, marbled flounder, blackfin flounder, shotted halibut)	gall bladder	Sea of Japan
C. jellae	15-18 x 30-39	marine Siluriformes: ariid (blackfin sea catfish)	gall bladder	India
C. jonesi	4.1-6.1 x 11.2-16.5	marine Labriformes: labrid (Gunther's wrasse)	gall bladder	Australia
C. kareus	10-11.8 x 38.2-46	marine Pleuronectiformes: pleuronectid (stone flounder), soleid (zebra sole)	gall bladder	China
C. kenti	4-5.8 x 11.6-21.1	marine Ovalentaria: pomacentrid (scissortail sergeant)	gall bladder	Australia
C. koieae	4.9-6.7 x 28.6-41.2	marine Carangaria: sphyraenid (bigeye barracuda)	gall bladder	Australia
C. kovaljovae (syn. *Leptotheca*)	13.3 x 21.3	marine Perciformes: sebastid (Norway redfish)	gall bladder	North Atlantic
C. kudoi	2.7-4 x 12.9-19.8	marine/estuarine Mugiliformes: mugilid (longarm mullet)	gall bladder	India
C. labracis	5-8 x 75-233	marine/estuarine Eupercaria: moronid (European seabass)	gall bladder	Europe
C. lagocephali	9-10.5 x 20-22.5	marine Tetraodontiformes: tetraodontid (smooth puffer)	gall bladder	Senegal
C. lata	17 x 7	marine Caproiformes: caproid (boarfish)	gall bladder	England
C. lateolabrax	6.3-7.3 x 15.3-18	marine Perciformes: lateolabracid (Japanese sea bass)	gall bladder	China
C. latesi (syn. *Leptotheca*)	6.2 x 10.3-12.4	marine/estuarine Perciformes: latid (barramundi)	gall bladder	India
C. laxa	7.8-9.8 x 20.8-30.3	marine Pleuronectiformes: pleuronectid (large scale flounder)	gall bladder	New Zealand
C. leatherjacketi	5.8-6.5 x 24.5-31	marine Tetraodontiformes: monacanthid (unicorn leatherjacket)	gall bladder	Malaysia
C. lepidopusi (replacement name for *C. elongata*)	9 x 90	marine Scombriformes: trichiurid (silver scabbardfish); Ophidiiformes: ophidiid (unspecified cusk-eel)	gall bladder	South America
C. leucosternoni	7.3 x 24.3	marine Acanthuriformes: acanthurid (powder blue tang)	gall bladder	India
C. lianoides	7-10 x 30-40	marine Perciformes: stichaeid (nagazuka prickleback)	gall bladder	Sea of Japan
C. limandae	11-13 x 9-10 x 43-45	marine Pleuronectiformes: pleuronectid (yellow striped flounder, blackfin flounder, shotted halibut, dusky sole)	gall bladder	Japan
C. limensis	8-15 x 36-86	marine Gadiformes: merlucciid (Peruvian hake)	gall bladder	Peru
C. linospora	12 x 70 x 5	marine Labriformes: labrid (green wrasse)	gall bladder	Italy

C. lizae	7.5-9.9 x 40.5-46.3	marine Mugiliformes: mugilid (goldspot mullet)	gall bladder	India
C. lobata (syn. *Parvicapsula*)	6.3-7 x 14-14.7	marine Atheriniformes: atherinopsid (silverside)	urinary bladder	Argentina
C. lomi	4-6.4 x 48.6-69	marine Acropomatiformes: lateolabracid (Japanese seabass)	gall bladder	China
C. longipes (syn. *Leptotheca*)	7.5-8.5 x 12.5-16.5	marine Gadiformes: gadid (haddock), lotid (cusk)	gall bladder	North Sea
C. longispina	3.5-7 x 16-41	marine Scorpaeniformes: cottid (shorthorn sculpin, fourhorn sculpin)	gall bladder	Barents Sea, White Sea
C. lophii	5.6-8.7 x 18-39.6	marine Lophiiformes: lophiid (European angler)	gall bladder	Europe
C. lovei (syn. *Leptotheca, L. sebasta*)	7.5-8.5 x 13-15	marine Scorpaeniformes: scorpaenid (olive rockfish)	gall bladder	North America
C. lubati (syn. *Leptotheca, L. chromis*)	5.5-7 x 12.5-15	marine Ovalentaria: pomacentrid (Mediterranean chromis)	gall bladder	France
C. lunata	7-9 x 15-38	marine Carcharhiniformes: galeocerdonid (tiger shark)	gall bladder	North America
C. lunula	2.9-4 x 12.8-17.8	marine Ovalentaria: pomacentrid (black damsel)	gall bladder	Australia
C. macapaensis	4.2 x 22.7	freshwater Cichliformes: cichlid (flag cichlid)	gall bladder	South America
C. macroformis (syn. *Leptotheca*)	10.7012.2 x 20-21	marine Scorpaeniformes: scorpaenid (Norway redfish)	gall bladder	North Atlantic
C. macronesi (syn. *Leptotheca*)	6.2-7.2 x 10-14.4	freshwater/estuarine Siluriformes: bagrid (long whiskers catfish)	gall bladder	India
C. macrospore	10.5-15 x 21-27	marine Scorpaeniformes: scorpaenid (Norway redfish, rosefish, sea ruffe)	gall bladder	Europe, China
C. macrouridonum (syn. *Leptotheca, L. minuta*)	4-6.5 x 5-8.5	marine Gadiformes: macrourid (swordsnout grenadier, Japanese pugnose grenadier)	gall bladder	Asia
C. maenae	8 x 20	marine Spariformes: sparid (blotched picarel)	gall bladder	Mediterranean
C. majimae	16-17 x 46-50	marine Pleuronectiformes: cynoglossid (black cow-tongue)	gall bladder	Japan
C. mandii	3.4-5.5 x 26.2-36.3	marine Siluriformes: pimelodid (fura calca)	gall bladder	Europe
C. marine	12-13.3 x 65-75.5	marine Pleuronectiformes: pleuronectid (Pacific rock sole)	gall bladder	Russia
C. markewitchi		In: European register of marine species		
C. maxima	16.6 x 740	marine Beryciformes: berycid (splendid alfonsino)	gall bladder	Atlantic
C. meglitschi	4.6-5.3 x 9.3-10.6	marine Carangiformes: carangid (Chilean jack mackerel)	gall bladder	Chile
C. mehlhorni	7-9 x 10-14	marine Carangiformes: carangid (golden trevally)	gall bladder	Saudi Arabia
C. melanopteri	10-13.5 x 28-58.5	marine Carcharhiniformes: carcharhinid (blacktip reef shark)	gall bladder	Australia
C. merlangi	5.6-8 x 30-53.7	marine Gadiformes: gadid (merling)	gall bladder	Black Sea
C. mesospora	8 x 50-65	marine Carcharhiniformes: sphyrnid (smooth hammerhead, bonnethead)	gall bladder	North America
C. miajimae	17 x 45-60	marine Pleuronectiformes: cynoglossid (black cow-tongue)	gall bladder	Sea of Japan
C. microcapsularis	11-13 x 13-14 x 53-72	marine Pleuronectiformes: pleuronectid (blackfin flounder)	gall bladder	Japan
C. microlepis	5.2 x 35.5	freshwater Characiformes: hemiodontid (bananinha)	gall bladder	Brazil
C. microstomi	11-13 x 51-84	marine Pleuronectiformes: pleuronectid (blackfin flounder)	gall bladder	Japan

C. militarisa	5.5-7 x 47-52	marine Siluriformes: ariid (soldier catfish)	gall bladder	India
C. milleri	4.1-5.4 x 11.4-20.9	marine Eupercaria: lutjanid (blackspot snapper)	gall bladder	Australia
C. minima (syn. *Leptotheca*)	5.1-6.2 x 7.9-11.2	marine Perciformes: arripid (kahawai)	gall bladder	New Zealand
C. minuta	5-7.9 x 9.6-14.2 x 5.4-5.9	marine Scombriformes: gempylid (barracouta, southern kingfish)	gall bladder	New Zealand
C. moenei	4.5-7.1 x 25.3-35.5 x 5.1-6.8	marine Perciformes: serranid (bass grouper)	gall bladder	New Zealand
C. monospora	5-6 x 18-25	marine Scombriformes: stromateid (harvestfish)	gall bladder	North America
C. moseri	3.5-5.9 x 8.9-14.2	marine Ovalentaria: pomacentrid (Ward's damsel)	gall bladder	Australia
C. mylionis (syn. *Leptotheca*)	6.2 x 13.3	marine Spariformes: sparid (blackhead seabream)	gall bladder	Japan
C. myoxocephala	6.7-8 x 12.5-28	marine Perciformes: cottid (Steller's sculpin)	gall bladder	Sea of Japan
C. navicularia	5-7.5 x 14-22	marine Pleuronectiformes: paralichthyid (summer flounder, Gulf flounder); Tetraodontiformes: tetraodontid (northern puffer)	urinary bladder	North America
C. nebulifera (syn. *Leptotheca*)	5.6-6.3 x 10-13	marine Perciformes: pholid (tidepool gunnel)	gall bladder	China
C. negaprioni	10-12.5 x 20.5-58.5	marine Carcharhiniformes: carcharhinid (sicklefin lemon shark)	gall bladder	Australia
C. nengae	6.8-10.2 x 33.1-42.5	marine Siluriformes: ariid (kata)	gall bladder	India
C. nitida	10.8-13.7 x 52.9-63	marine Pleuronectiformes: pleuronectid (New Zealand sole)	gall bladder	New Zealand
C. noblei (syn. *Leptotheca, L. elegans*)	9 x 17	marine Blenniiformes: clinid (spotted kelpfish)	gall bladder	North America
C. nolani	3.5-7 x 12.5-29.5	marine Perciformes: serranid (longfin grouper)	gall bladder	Australia
C. nowakae	5.2-8.3 x 16.2-23.6	mar Spariformes: lethrinid (collared large-eye bream)	gall bladder	Australia
C. obesa	4.5-5.9 x 12.4-14.8	marine Scorpaeniformes: cottid (woolly sculpin)	gall bladder	North America
C. obovalis (syn. *Leptotheca*)	6-9 x 12-18	marine Blenniiformes: blenniid (horned blenny)	gall bladder	South Africa
C. obtusa	9-10 x 44-46 x 9-10	marine Tetraodontiformes: tetraodontid (bullseye puffer)	gall bladder	Sea of Japan
C. opisthocentri	5-7 x 14-17	marine Perciformes: opisthocentrid (ocellated blenny)	gall bladder	Sea of Japan
C. opisthocornata (syn. *Leptotheca*)	6.4-8 x 9.6-14.4	marine Atheriniformes: atherinopsid (cornal)	gall bladder	Argentina
C. oplegnathus	7.9-9.2 x 39-48.4	marine Perciformes: oplegnathid (striped beakfish)	gall bladder	Korea
C. orientalis	7-11 x 33-72	marine Clupeiformes: alosid (Japanese pilchard), clupeid (Pacific herring)	gall bladder	Pacific, White Sea, Sea of Japan
C. orthospora	6.7-7.8 x 40-53	marine Perciformes: channichthyid (spiny icefish)	gall bladder	Antarctica
C. ostorhinchi	5.3-8.6 x 21.2-27.5	marine Kurtiformes: apogonid (ring-tailed cardinalfish)	gall bladder	Australia
C. ovalis (syn. *Leptotheca*)	6-6.7 x 10-10.6	marine Carangiformes: carangid (Chilean jack mackerel)	gall bladder	Chile
C. oxycheilinae	8.3-10 x 22.8-33.9	marine Labriformes: labrid (cheek-lined wrasse)	gall bladder	Australia
C. pacifica	6.6-7.8 x 5.1-5.3 x 10.6-14	marine Clupeiformes: alosid (Japanese pilchard)	gall bladder	Peru

C. pallida	2 x 25-30	marine Spariformes: sparid (bogue, Salema porgy)	gall bladder	France
C. pantherini	7.3-9.1 x 17.9-24.6	marine Pleuronectiformes: bothid (leopard flounder)	gall bladder	Australia
C. parva (syn. *Leptotheca, L. scombri*)	3-9 x 8-14	marine Scombriformes: scombrid (Atlantic mackerel)	gall bladder	Atlantic, Black Sea
C. peculiaria	6.5-8.5 x 21-29.3	marine Eupercaria: sparid (gerle)	gall bladder	Black Sea
C. pegusae (syn. *Leptotheca*)	6.7-9 x 11.2-13.5	marine Pleuronectiformes: soleid (sand sole)	gall bladder	Africa
C. physiculus (replacement name for *C. polymorpha*)	10-12 x 18-20	marine Gadiformes: morid (red codling)	gall bladder	France
C. pinguis (syn. *Leptotheca*)	8.3-11 x 13.7-19	marine Pleuronectiformes: bothid (witch), pleuronectid (New Zealand sole)	gall bladder	New Zealand
C. platichthytis (syn. *Leptotheca*)	7.1-13 x 23.4-36.8 x 9.1-10.5	marine Pleuronectiformes: paralichthyid (olive flounder), pleuronectid (starry flounder, speckled flounder, Far Eastern smooth flounder, yellowfin sole, kurogarei, sohachi)	gall bladder	Sea of Japan
C. polymorpha (syn. *Leptotheca*)	10-21 x 9.5-14.5 x 11.2-18	marine Gadiformes: phycid (forkbeard)	gall bladder	France, New Zealand
C. porrecta	2.3-5 x 25.5-64 x 23-34	marine Scorpaeniformes: cottid (shorthorn sculpin, snowy sculpin, black-edged sculpin, elegant sculpin, bero)	gall bladder	Arctic
C. priacanthi	5.4-8 x 15.6-28.8	marine Eupercaria: priacanthid (moontail bullseye)	gall bladder	India
C. protopsettae	10-12 x 12-13 x 48.6-65	marine Clupeiformes: dorosomatid (spotted sardinella); Pleuronectiformes: paralichthyid (olive flounder), pleuronectid (barfin flounder, stone flounder, blackfin flounder, Bering flounder, shotted halibut, sohachi, dusky sole, yellowfin sole, roughscale sole)	gall bladder	Sea of Japan
C. puntazzi	8-10.7 x 23.8-34.5	marine Spariformes: sparid (sharpsnout seabream)	gall bladder	Europe
C. qingdaoensis	6-7 x 42-48	marine Eupercaria: sciaenid (silver croaker)	urinary bladder	China
C. quadritaenia (syn. *Leptotheca*)	8-9.3 x 12-13.3	marine Perciformes: epigonid (black cardinalfish)	gall bladder	Atlantic
C. ramosa	12-20 x 50-80	marine Pleuronectiformes: pleuronectid (Atlantic halibut)	gall bladder	North Sea, Barents Sea
C. rara	16-17.3 x 85.1-89.1 x 15-16	marine Gadiformes: macrourid (giant grenadier)	gall bladder	Russia
C. recta	6.8-8.8 x 14.7-16.7 x 6.8-8.3	marine Ophidiiformes: ophidiid (pink cusk-eel)	gall bladder	New Zealand
C. recurvata	8-9 x 16	marine Carcharhiniformes: sphyrnid (smooth hammerhead)	gall bladder	North America
C. reidi	5.8-7.5 x 14.3-20.7	marine Perciformes: chaetodontid (vagabond butterflyfish)	gall bladder	Australia
C. renalis	7.3-8.5 x 22.5-33.4 x 7.7-9.3	marine Pleuronectiformes: bothid (witch)	gall bladder. urinary bladder	New Zealand
C. reticulatus	12-15 x 45-50	marine Trachiniformes: trachinid (greater weever)	gall bladder	France
C. robertsthomsoni	4-5.9 x 12.2-24	marine Mugiliformes: mugilid (squaretail mullet)	gall bladder	Australia
C. robusta	18-20 x 115-120	marine Pleuronectiformes: pleuronectid (willowy flounder,	gall bladder	Sea of Japan

		Kamchatka flounder, dusky sole)		
C. rohdei	4.5-5.9 x 40-45 x 5	marine Blenniiformes: blenniid (yellow sabretooth blenny)	gall bladder	Australia
C. rueppellii	5.2-7.3 x 17.3-28.3	estuarine Perciformes: apogonid (western gobbleguts)	gall bladder	Australia
C. sagarica	3.3-4.1 x 26.5-36.3	estuarine Gobiiformes: oxudercid (Boddart's goggle-eyed goby)	gall bladder	India
C. sagarsampadae	14.2-18.4 x 68.6-82.4	estuarine Pleuronectiformes: cynoglossid (unspecified tongue sole)	gall bladder	India
C. sardinellae	6.7-9 x 13.5-15.7	marine Clupeiformes: dorosomatid (Indian oil sardine)	gall bladder	India
C. saurida	9-10.5 x 39.5-47	marine Aulopiformes: synodontid (slender lizardfish)	gall bladder	China
C. scatophagi	4.2-7.2 x 16-26	marine/estuarine Acanthuriformes: scatophagid (spotted scat)	gall bladder	India
C. schulmani	17 x 120	marine Alepocephaliformes: alepocephalid (small scaled brown slickhead)	gall bladder	South Africa
C. scissura (syn. *Leptotheca*)	22 x 11	marine Myliobatiformes: dasyatid (whip stingray), gymnurid (smooth butterfly ray)	gall bladder	North America
C. scorpaeni	7.2-8 x 21.6-44	marine Scorpaeniformes: scorpaenid (black scorpionfish)	gall bladder	Tunisia
C. sebasta	13-16 x 25-35	marine Scorpaeniformes: sebastid (gopher rockfish)	gall bladder	North America
C. sebastisca (syn. *Leptotheca*)	10-10.5 x 19.4-22.5	marine Scorpaeniformes: scorpaenid (unspecified sea ruffe)	(gall bladder)	China
C. seriolae	6-7.5 x 28-41.5	marine Carangiformes: carangid (Japanese amberjack)	gall bladder	Australia, Japan
C. sewelli	3.5-5 x 14.1-23.6	marine Perciformes: pomacentrid (Ward's damsel)	gall bladder	Australia
C. simplex	5-6.5 x 13-17	marine Perciformes: stichaeid (fusaginpo)	gall bladder	China
C. spari	50-60 x 12-15 x 12-15	marine Spariformes: sparid (goldsilk seabream)	gall bladder	Mozambique
C. sparusaurati	4.5-7.5 x 14-17.5	marine Spariformes: sparid (gilt-head seabream)	gall bladder	Spain
C. spectabilis	9-13 x 10-13	marine Scorpaeniformes: apogonid (sea raven), stichaeid (ame-gaji)	urinary bladder	Sea of Japan
C. sphaerulosa [type species]	10-12 x 90-100	marine Carcharhiniformes: triakid (common smooth-hound, school shark)	gall bladder	France
C. sphairophora	12 x 115-119	marine Carcharhiniformes: carcharhinid (Atlantic sharpnose shark)	gall bladder	North America
C. spinosa	7 x 80	marine Pleuronectiformes: paralichthyid (Gulf flounder)	urinary bladder	North America
C. sprenti	4-8 x 14-23 x 3.5-5	marine Eupercaria: labrid (Venus tuskfish); Perciformes: chaetodontid (golden butterflyfish, Rainford's butterflyfish, melon butterflyfish), lutjanid (yellow-banded snapper); Scorpaeniformes: platycephalid (smalleye flathead)	gall bladder	Australia
C. starksi	6.2-8 x 20-28	marine Perciformes: sebastid (rosy rockfish)	gall bladder	North America
C. streptospora	4 x 34-39	marine Acanthuriformes: ephippid (Atlantic spadefish)	urinary bladder	North America
C. subelegans (syn. *Leptotheca*)	8.3-12.5 x 16.2-26.2	marine Gobiiformes: gobiid (New Zealand black goby); Gobiesociformes: gobiesocid (orange clingfish)	gall bladder	New Zealand

C. subequalis	6-9 x 50-59	marine Siluriformes: ariid (Gagora catfish)	gall bladder	India
C. subtilis	3.4-4.5 x 15.7-26 x 3.9-4.5	marine Gadiformes: macrourid (southern whiptail)	gall bladder	New Zealand
C. swaisi	7-9 x 43-55	marine Aulopiformes: synodontid (brushtooth lizardfish)	gall bladder	Egypt
C. syacii	9-9.5 x 22.5-25	marine Pleuronectiformes: cyclopsettid (channel flounder)	gall bladder	Senegal
C. sympetala	10-16 x 38-45.2	marine Pleuronectiformes: pleuronectid (Pacific rock sole)	gall bladder	Russia
C. synaphobranchi	6-7 x 22-32	Anguilliformes: synaphobranchid (Kaup's arrowtooth eel)	gall bladder	Atlantic
C. taenia	6 x 140-150	marine Carcharhiniformes: carcharhinid (Atlantic sharpnose shark)	gall bladder	North America
C. talboti	4.1-6.8 x 10.1-15.9	marine Ovalentaria: pomacentrid (white-spot damsel, white-tail damsel, bowtie damselfish, blue devil, singlebar devil)	gall bladder	Australia
C. tartoori	14-19 x 167-234	marine Clupeiformes: pristigasterid (tardoore)	gall bladder	India
C. tenualosae	8-10 x 26-33	marine Clupeiformes: dorosomatid (toli shad)	gall bladder	India
C. tenuis	10-15 x 10-15 x 108-112	marine Pleuronectiformes: pleuronectid (Bering flounder, yellowfin sole, lemon sole)	gall bladder	Sea of Japan
C. tenuispora (syn. *C. magna*)	8.4-10.7 x 308-504 x 8.6-9.3	marine Scombriformes: trichiurid (black scabbardfish)	renal tubules	North Sea
C. thalassomae	3.3-6.4 x 16.4-22.2	marine Labriformes: labrid (moon wrasse)	gall bladder	Australia
C. thrissoclesi	8.6-10.3 x 81.7-98.7	marine Clupeiformes: engraulid (moustached thryssa)	gall bladder	India
C. thunni	3.9 x 13.4	marine Scombriformes: scombrid (Atlantic bluefin tuna)	gall bladder	Adriatic Sea
C. tienensis	8.4-9 x 4.5-5	marine Siluriformes: pangasiid (striped catfish)	gall bladder	Vietnam
C. toitae	13 x 13 x 30-42	marine Pleuronectiformes: pleuronectid (spotted halibut)	gall bladder	Japan
C. torquata	7.8-9.5 x 20.5-30.3 x 8.3-10.1	marine Pleuronectiformes: pleuronectid (large scald flounder)	gall bladder	New Zealand
C. trachinocephali	10-12 x 48-50	marine Aulopiformes: synodontid (snakefish)	gall bladder	Senegal
C. triacantha	6-7 x 13-16.5	marine Tetraodontiformes: triacanthid (short-nosed tripodfish)	gall bladder	China
C. trichiuri	10-12 x 98-100	marine Scombriformes: trichiurid (largehead hairtail)	gall bladder	Senegal
C. truncata	5 x 25	marine Clupeiformes: alosid (European pilchard)	gall bladder	France
C. tunisiensis	20-25 x 5-8	marine Carangiformes: carangid (false scad, Atlantic horse mackerel)	gall bladder	Tunisia
C. tylosuri	40-50 x 124-140 x 25-30	marine Beloniformes: belonid (houndfish)	gall bladder	Indian Ocean
C. uncinata	10.9-14.1 x 27.8-36	marine Pleuronectiformes: pleuronectid (southern lemon sole)	gall bladder	New Zealand
C. undulata	6 x 22-44	marine Pleuronectiformes: paralichthyid (Gulf of Mexico ocellated flounder)	gall bladder	North America
C. urophysis	5-7.5 x 25-39.1	marine Gadiformes: phycid (white hake)	gall bladder	Canada
C. venusa	4-6 x 63-78	marine Acanthuriformes: sciaenid (white seabass)	gall bladder	North America
C. vepallida	7.8-9.6 x 16-21.4 x	marine Pleuronectiformes:	gall bladder	New Zealand

	8.1	pleuronectid (large scald flounder)		
C. vermiformis	4.2-4.8 x 7.9-9.3	freshwater Characiformes: serrasalmid (tambaqui)	gall bladder	Brazil
C. verudaensis	6-7 x 13-16	marine Scorpaeniformes: scorpaenid (black scorpionfish)	gall bladder	Mediterranean
C. vikrami (syn. *Leptotheca*)	10.3-13.7 x 17.1-20-6	marine Zeiformes: zeid (John Dory)	gall bladder	England
C. whippsi	4.5-6.5 x 11.5-18.5	marine Gadiformes: morid (rock cod); Kurtiformes: apogonid (cardinalfish); Ovalentaria: pomacentrid (sergeant-major, chromis, damselfish, anemonefish, clownfish); Perciformes: serranid (chocolate hind)	muscles, gall bladder	Australia
C. xanthopteri	4.6-6.7 x 11.5-20.1	marine Acanthuriformes: acanthurid (yellowfin surgeonfish)	gall bladder	India
C. yoichiensis (syn. *Leptotheca*)	9 x 21	marine Scorpaeniformes: scorpaenid (three stripe rockfish, fox jacopever)	gall bladder	Japan
C. yokoyamai	4.5-6.5 x 20.5-31	marine Perciformes: epinephelid (highfin grouper)	gall bladder	Australia
C. zancli	9.6 x 25.2	marine Acanthuriformes: zanclid (Moorish idol)	gall bladder	Arabian Sea
Genus ***Ceratonova*** (wedge-shaped spores, histozoic in intestines mainly of anadromous fishes)				
C. shasta (syn. *Ceratomyxa*) [type species]	6-8 x 14-17	freshwater/estuarine Salmoniformes: salmonid (chinook salmon, pink salmon, chum salmon, sockeye salmon, Atlantic salmon, rainbow trout, cutthroat trout, sea trout, brook trout) [cycle involves tetractinomyxon-type actinospores in Polychaeta: fabriciid (*Manayunkia speciosa*)]	gut, gills, spleen, liver, gall bladder, kidneys, urinary bladder, muscle, gonads, connective tissue	North America
C. gasterostea	5.2 x 22.4	freshwater Scorpaeniformes: gasterosteid (three-spine stickleback)	intestines	North America
Genus ***Ellipsomyxa*** (ellipsoidal spores, polar capsules opposite laterally)				
E. adlardi	7.1-8.8 x 11.3-14.4	marine Gobiiformes: gobiid (naked goby)	gall bladder	North America
E. amazonensis	6.7-8.7 x 12.3-13.6	freshwater Siluriformes: pimelodid (gilded catfish)	gall bladder	South America
E. apogoni	6-9.1 x 8.8-11.1	marine Kurtiformes: apogonid (fourline cardinalfish)	gall bladder	Australia
E. arariensis	6.7-8 x 12-13.4	freshwater Characiformes: serrasalmid (red-bellied piranha); Siluriformes: pimelodid (ornate pim)	gall bladder	South America
E. ariusi	6.3-8.2 x 9-12 7.1-8.7	marine Siluriformes: ariid (threadfin sea catfish)	gall bladder	India
E. arothroni	9.9-13.6 x 12.3-17.7	marine Tetraodontiformes: tetraodontid (white-spotted puffer fish)	gall bladder	Australia
E. boleophthalmi	6-7.8 x 9-10.7	marine Gobiiformes: oxudercid (Dussumier's mudskipper)	gall bladder	India
E. fusiformis (syn. *Leptotheca*)	9 x 16	marine Carcharhiniformes: sphyrnid (smooth hammerhead)	gall bladder	North America
E. gobii [type species]	6.6-7.5 x 8-9	brackish water Gobiiformes: gobiid (common goby) [cycle involves tetractinomyxon-type actinospores in Polychaeta: nereidid (*Nereis diversicolor, succinea*)]	gall bladder	Europe
E. gobioides	6.5-7 x 6.5-7.5 x 12.8-13.5	brackish water Gobiiformes: oxudercid (violet goby)	gall bladder	South America
E. kalthoumi	10-15 x 13-21	marine Mugiliformes: mugilid (leaping mullet)	gall bladder	Mediterranean

E. manilensis	10.2-13.3 x 13.8-17.1	marine Tetraodontiformes: tetraodontid (narrow-lined puffer)	gall bladder	Australia
E. mugilis	5.5-8 x 10-13.5	marine Mugiliformes: mugilid (thninlip mullet, leaping mullet, flathead grey mullet) [cycle involves tetractinomyxon-type actinospores in Polychaeta: nereidid (*Nereis* spp.)	gall bladder	Europe
E. nigropunctatis	8-12.9 x 11.9-16.3	marine Tetraodontiformes: tetraodontid (blackspotted puffer)	gall bladder	Australia
E. papantla	7.6-9.9 x 11.6-15 x 6.1-8.2	freshwater Gobiiformes: eleotrid (fat sleeper)	gall bladder	Mexico
E. paraensis	6.6-8.6 x 10.5-12.4	freshwater Cichliformes: cichlid (tucanare peacock bass)	gall bladder	South America
E. plagioscioni	5.6-7.6 x 10.2-12.8	freshwater Acanthuriformes: sciaenid (South American silver croaker)	gall bladder	South America
E. syngnathi	6.3-7.2 x 7.2-8.6	marine Syngnathiformes: syngnathid (broad nosed pipefish)	gall bladder	Europe
Genus ***Meglitschia*** (V-shaped spores with axial polar capsules)				
M. insolita [type species]	11.5 x 16.2	marine Perciformes: serranid (orange-spotted grouper); Scorpaeniformes: triglid (unspecified gurnard)	gall bladder	New Zealand, Vietnam
Family **Chloromyxidae** (spores bisected by meridional suture, some with caudal appendages, 4 polar capsules)				
Genus ***Agarella*** (spindle-shaped spores with 2 caudal projections)				
A. gracilis [type species]	28-35 x 4-16.5	freshwater Ceratodontiformes: lepidosirenid (South American lungfish)	testes	South America
Genus ***Caudomyxum*** (subspherical spores with 1-2 caudal projections)				
C. caudatum (syn. *Chloromyxum*)	18 x 6-7	freshwater Urodela: salamandrid (northern crested newt)	gall bladder	France
C. nanum [type species]	9.6-17 x 4-6.5 x 4-6.5	freshwater Gadiformes: lotid (burbot)	kidneys	Eurasia
Genus ***Chloromyxum*** (spherical spores, smooth or ridged, rarely with caudal appendages)				
C. aegypticum	9-9.2 x 7.8-8	freshwater Anura: bufonid (Egyptian toad)	testes	Egypt
C. alii	5-7.6 x 6-7.3	freshwater Siluriformes: schilbeid (African butter catfish)	gall bladder	Egypt
C. amphipnoui	8.2-10.3 x 8.2-10.3	freshwater Cypriniformes: cyprinid (mola carplet); Siluriformes: heteropneustid (Asian stinging catfish); Synbranchiformes: synbranchid (cuchia)	gall bladder	India
C. argusi	8.3-11.5 x 8.2-12.2	freshwater/estuarine Perciformes: scatophagid (spotted scat)	urinary bladder, ureters	India
C. auratum	12.5-14 x 10.8-14.1 x 11.4-14	freshwater Cypriniformes: cyprinid (goldfish) [cycle involves antonactinomyxon-type actinospores in Oligochaeta (unspecified)	gall bladder	North America
C. barbi	12-13 x 12 x 12	freshwater Cypriniformes: cyprinid (common barbel, Aral barbel, Dnieper barbel), xenocypridid (silver carp)	gall bladder	Eurasia
C. baueri	6.5-8.6 x 5.4-8 x 7.2-7.6	freshwater Cypriniformes: cyprinid (Sattar snowtrout, David's marinka)	gall bladder	Russia, China
C. birgii	6.5-8.7 x 6.3-8.8	freshwater Cypriniformes: cyprinid (martorelli pardkala)	gall bladder	Cameroon
C. bychowskii	5.5-6 x 5.5-6	freshwater Cypriniformes: cyprinid	gall bladder	Korea

		(barbel chub)		
C. carassii (syn. *C. ornatum, sarcochilichthydis*)	7-9 x 7-9 x 7.2	freshwater Cypriniformes: cyprinid (goldfish, mud carp, Prussian carp), gobionid (Chinese lake gudgeon)	gall bladder	Amur Basin, Korea
C. careni	7.2-9 x 4.8-5.9	Anura: megophryid (long-nosed horned frog)	kidney	Indonesia
C. catostomi	8 x 7 x 5-6	freshwater Cypriniformes: catostomid (white sucker), cyprinid (central stone roller, bigmouth shiner, bluntnose minnow, fathead minnow, creek chub)	gall bladder	North America
C. caudatum	10 x 6-7	Urodela: salamandrid (northern crested newt)	gall bladder	France
C. chitosense	8 x 8 x 9	freshwater/estuarine Salmoniformes: salmonid (chum salmon)	gall bladder	Japan
C. chondrostomi	7-8.7 x 6.5-8 x 6.8-8	freshwater Cypriniformes: cyprinid (Iberian nase)	gall bladder	Spain
C. clariasum	7-11 x 8-9	freshwater Siluriformes: clariid (walking catfish)	gall bladder	India
C. clariatis	11.6-13.5 x 9.7-12.2 x 7.7-8.4	freshwater Siluriformes: clariid (walking catfish)		China
C. colchicum	6.6-7.3	freshwater Cypriniformes: cyprinid (common roach)	gall bladder	Russia
C. complicatum	7-8.1 x 6.9-8.4 x 6-8	freshwater Cypriniformes: cyprinid (Iberian barbel)	gall bladder	Spain
C. coregoni	6-6.5 x 6-6.5	freshwater Osmeriformes: osmerid (European smelt); Salmoniformes: salmonid (sockeye salmon, Atlantic salmon, brown trout, Arctic char, sardine cisco, European cisco, Arctic cisco, common whitefish, Amur whitefish, Lagoda whitefish, Valaam whitefish, muksun, tugun)	gall bladder	Holarctic
C. cristatum (syn. *C. cyprini p.p.*)	8-13 x 10-11	freshwater Cypriniformes: cyprinid (common carp, grass carp, common roach, common bream, white-eye bream, common bleak, ide, zope), tincid (tench), xenocypridid (silver carp)	gall bladder, liver	Eurasia
C. cyprini (syn. *C. ctenopharyngodonis, hypophthalmichthydis, insignis, mylopharyngodonis*)	6-13.5 x 6-13.5	freshwater Cypriniformes: cyprinid (koi carp, grass carp, black carp), nemacheilid (Siberian stone loach), xenocypridid (silver carp, black Amur bream)	gall bladder	Amur Basin, Japan
C. dogieli	10.6-12 x 8-8.3	marine Rajiformes: rajid (brown ray)	gall bladder	Russia
C. dubium	10-11 x 10-11	freshwater Gadiformes: lotid (burbot)	gall bladder	Switzerland
C. dzalilovi	8-9 x 7-8	freshwater Cypriniformes: cyprinid (Sattar snowtrout)	gall bladder	Russia
C. ellipticum	7.2-8.4 x 6.9-7.2 x 6-7.2	freshwater Cypriniformes: cyprinid (goldfish, grass carp, mud carp, bighead carp, black carp, sharpbelly, redfin culter, topmouth culter, lake skygazer, white Amur bream), xenocypridid (silver carp, barbel chub)	gall bladder	China
C. erythroculteri	14-15 x 14-15	freshwater Cypriniformes: cyprinid (Mongolian redfin)	urinary bladder	Amur Basin
C. esocinum	8 x 8	freshwater Cypriniformes: cyprinid (golden shiner, Allegheny pearl dace, eastern blacknose dace); Esociformes: esocid (northern pike)	gall bladder	Russia
C. externum	7.9-10.3	freshwater Anabantiformes: channid (blotched snakehead); Cypriniformes:	gills	China, North America

		cyprinid (Allegheny pearl dace)		
C. fluviatile	6-9 x 5-8.5 x 5-8.5	freshwater Cypriniformes: cyprinid (goldfish, crucian carp, Prussian carp, common roach, Caspian roach, common dace, ide, common chub, common bleak, Kura bleak, ziege, common bream, white bream, zope, Kura nase), tincid (tench), xenocypridid (silver carp)	gall bladder	Eurasia
C. fujitai	10-12 x 8-10	freshwater Cypriniformes: cobitid (pond loach)	gall bladder	Japan
C. gibbosum	8.8-11.2 x 8-9.6 x 7.2-8.8	freshwater Perciformes: centrarchid (pumpkinseed)	gall bladder	North America
C. giganteum	14-16 x 13-14 x 13-14	freshwater Salmoniformes: salmonid (pink salmon)	gall bladder	Japan
C. gilekulense	6.5 x 5.4 x 2.7	freshwater Cypriniformes: cyprinid (ziege)	gall bladder	Russia
C. granulosum	7 x 7	marine Beloniformes: belonid (Atlantic needlefish); Cypriniformes: catostomid (largescale sucker); Scorpaeniformes: cottid (shorthorn sculpin)	urinary bladder, gall bladder	North America
C. hemibarbi	10-11 x 10-11	freshwater Cypriniformes: cyprinid (barbel steed)	gall bladder	Russia
C. hemiscyllii	11.8 x 9.5 x 9.8	marine Orectolobiformes: hemiscylliid (epaulette shark)	gall bladder	Australia
C. heteropneustesi	8.3-10.5 x 6-7.5	freshwater Siluriformes: heteropneustid (Asian stinging catfish)	gall bladder	India
C. hoarei	5.7-7.1 x 5.7-7.1	freshwater Cypriniformes: cyprinid (mustuim-narmasmokk)	gall bladder	India
C. hupehensis (*hupehense*)	6-8 x 5.4-7.6 x 6.1-6.8	freshwater Cypriniformes: cyprinid (stone moroko, Chinese false gudgeon, silver minnow, lake skygazer), acheilgnathid (hiina morukas), botiid (ringelschmerle), xenocypridid (hiina laikviidikas)	gall bladder	China
C. incertum	10-11.4 x 10-11.4	freshwater Salmoniformes: salmonid (grayling)	gall bladder	Germany
C. incisum sp. inq	8	marine Rajiformes: rajid (common skate)		Europe
C. inexpectatum	8.4-9.3 x 8-8.7	freshwater Acipenseriformes: acipenserid (sterlet)	renal tubules, ureters, urinary bladder	Europe
C. kabatai	16-18 x 15.5-17	marine Gadiformes: macrourid (Pacific grenadier)	gall bladder	North America
C. koi	16 x 10 x 10	freshwater Cypriniformes: cyprinid (common carp, koi carp)	gall bladder	Eurasia
C. kotorense	8-9.2 x 8-9.2	marine Mugiliformes: mugilid (golden grey mullet)	renal tubules	Montenegro
C. kovaljovae	8.7-9 x 8.2-8.5 x 8	freshwater Gadiformes: lotid (burbot)	urinary bladder	Russia
C. kuhlii	11.4 x 9.1 x 8.8	marine Myliobatiformes: dasyatid (blue-spotted stingray)	gall bladder	Australia
C. kurisi	8.7-9.2 x 7.9-8.3 x 7.6-8.2	marine Atheriniformes: atherinopsid (topsmelt silverside)	kidney	North America
C. labricum	9-10.8 x 7.2-8.8 x 5.4-6.3	freshwater Cypriniformes: cyprinid (Mongolian redfin)	gall bladder	China
C. legeri	7.5 x 7.5 x 6	freshwater Cypriniformes: cyprinid (common carp, common roach, common nase, common rudd, common bream, white bream)	gall bladder	Europe
C. leiosporum	5.8-6.5 x 5.8-6.5 x	freshwater Cypriniformes: cyprinid	gall bladder	Amur Basin

	4.3-5	(Chinese false gudgeon, Amur whitefin gudgeon)		
C. lenorae	8.1 x 6.7	freshwater Gadiformes: lotid (burbot)	(kidneys)	Europe
C. lesteri	10.4 x 8.2 x 8.4	marine Carcharhiniformes: scyliorhinid (Australian swellshark)	gall bladder	Australia
C. leuciscus	6-6.7 x 6-6.7	freshwater Cypriniformes: cyprinid (Amur ide)	gall bladder	China
C. levigatum	11-13 x 8-10	marine Squatiniformes: squatinid (Pacific angelshark)	gall bladder	North America
C. leydigi [type species]	6-12.6 x 5-11	marine Carcharhiniformes: carcharhinid (blacktip shark, Atlantic sharpnose shark), scyliorhinid (small-spotted catshark), sphyrnid (smooth hammerhead, shovelhead), triakid (starry smooth-hound); Myliobatiformes: dasyatid (common stingray, Atlantic stingray, roughtail stingray), gymnurid (smooth butterfly ray); Rajiformes: rajid (bottlenose skate, thornback ray, brown ray, undulate ray, common skate, thorny skate, Rio skate, little skate, winter skate, ocellate spot skate); Squaliformes: etmoptertid (velvet belly lanternshark), squalid (spiny dogfish, picked dogfish); Squatiniformes: squatinid (angelshark); Salmoniformes: salmonid (brook trout); Torpediniformes: torpedinid (Pacific electric ray, marbled electric ray, common torpedo)	gall bladder	cosmopolitan
C. liae	4.4-5.2 x 3.7	marine Carcharhiniformes: carcharhinid (blue shark)	gall bladder	Argentina
C. linghuense	9-12.6 x 9-13.5 x 9-12.6	freshwater Cypriniformes: cyprinid (goldfish, Prussian carp)		China
C. lissosporum	12-13.3 x 6.6-8	marine Squatiniformes: squatinid (smoothback angelshark)	gall bladder	Guinea-Bissau
C. magnum	40-48 x 30-38	marine Squaliformes: squalid (longnose spurdog)	gall bladder	South Africa
C. majori	7-8 x 7-8	freshwater Salmoniformes: salmonid (rainbow trout)	kidneys	North Pacific
C. mapienensis	8-10 x 7.2-8.8 x 8	freshwater Cypriniformes: cyprinid (yunnani silemokk)	gall bladder	China
C. marinum	7.1-7.5 x 6.5-6.8 x 5.8-6.2	marine Beloniformes: belonid (Japanese halfbeak)	urinary bladder	Sea of Japan
C. martjanovae	12 x 10.5-11	freshwater Cypriniformes: xenocypridid (silver carp)	kidneys	Russia
C. megalobramis	10-11	freshwater Cypriniformes: cyprinid (black Amur bream)	gall bladder	Russia
C. meglitschi	7-8.5 x 6-8	brackish water Anabantiformes: channid (spotted snakehead)	gall bladder	India
C. menticirrhi	10.5 x 9.8 x 10.1	marine Acanthuriformes: sciaenid (southern kingfish)	urinary bladder	Brazil
C. mingazzini	11.1 x 8.7 x 8.8	marine Pristiophoriformes: pristiophorid (shortnose sawshark)	gall bladder	Australia
C. misgurni	8-9 x 6-7 x 5-6	freshwater Cypriniformes: cobitid (weatherfish, spined loach)	gall bladder	Asia
C. mitchelli	18-22 x 16.5-21	marine Perciformes: terapontid (crescent grunter)	kidney	India
C. mitenevi	6-7 x 6-7	freshwater Cypriniformes: leuciscid (Eurasian minnow)	gall bladder	Russia

C. montschadskii	6.5-7 x 5.5-6 x 5.5-6	freshwater Cypriniformes: cyprinid (bitterling, Khanka spiny bitterling)	gall bladder	Korea
C. mrigalae	7-10 x 7-10	freshwater Cypriniformes: cyprinid (reba carp, mrigal carp)	gall bladder	India
C. mucronatum (syn. *Myxobolus*)	7-8	freshwater Gadiformes: lotid (burbot)	urinary bladder, ureters	Eurasia
C. multicostatum	5.9-7.4 x 4.4-5.2	marine Squatiniformes: squatinid (angelshark)	gall bladder	Argentina
C. myolibati	11.9 x 9.6 x 10	marine Myliobatiformes: myliobatid (Australian bull ray)	gall bladder	Australia
C. nanum	3.5-5 x 3.5-5	freshwater Cypriniformes: cyprinid (grass carp)	kidneys	Amur Basin
C. noblei	8-10 x 8-10 x 6-7	marine Myliobatiformes: dasyatid (bluespotted ribbontail ray); Orectolobiformes: hemiscylliid (epaulette shark)	gall bladder	Australia
C. ompokii	13-16.1 x 11.9-15.3	freshwater Siluriformes: silurid (butter catfish)	gall bladder	India
C. oncorrhynchi	10 x 9.5 x 9.5	freshwater Salmoniformes: salmonid (masu salmon)	gall bladder	Japan
C. ophiocephali	8.4-9 x 8.4-8.6 x 8.4-8.8	freshwater Anabantiformes: channid (blotched snakehead)	gall bladder	China
C. opladeli	6.5-8 x 6-7.5 x 5.5-7	freshwater Siluriformes: ictalurid (flathead catfish)	gall bladder	North America
C. opsariichthysi	9-10.8 x 8.4-10	freshwater Cypriniformes: cyprinid (Chinese hooksnout carp)	liver	China
C. orbiculatum	9 x 9	freshwater Cypriniformes: cyprinid (silver carp)	gall bladder	Russia
C. orientale	10-12 x 9-10.5 x 9-10.5	freshwater Salmoniformes: salmonid (masu salmon)	gall bladder	Amur Basin
C. ornatum	9 x 9	freshwater Cypriniformes: cyprinid (Chinese lake gudgeon)	liver	Russia
C. osmanovi	5.8-6.5 x 5.6-6	marine Syngnathiformes: syngnathid (narrow-snouted pipefish)	gall bladder	Ukraine
C. ovatum	10-3-13.6 x 7.7-10.9	marine Squaliformes: squalid (Pacific spiny dogfish)	gall bladder	North America
C. oviforme		marine Perciformes: serranid (swallowtail)	gall bladder	Japan
C. parabrami	9-10 x 9-10	freshwater Cypriniformes: cyprinid (white Amur bream)	gall bladder	Russia
C. parasiluri	7.5-12 x 7.5-12 x 6-12	freshwater Siluriformes: silurid (Soldatov's catfish, Amur catfish)	gall bladder	Amur Basin
C. partistriatum	10.5-11.9 x 8.6-9.3	marine Rajiformes: rajid (thornback ray)	gall bladder	Ukraine
C. parvicostatum	5.2-5.9 x 4.4-4.6	marine Rajiformes: arhynchobatid (broadnose skate)	gall bladder	Argentina
C. paulini	11.7-13.4 x 10.5-12.9	freshwater Cypriniformes: cyprinid (common bleak)	gall bladder	Czech Republic
C. pelteobagrus	6.9-10.4 x 6.9-8.1 x 5.8-8.1	freshwater Siluriformes: bagrid (yellowhead catfish)	gall bladder	China
C. pholidapi	7-11 x 12-14 x 12-14	marine Perciformes: stichaeid (rearspined prickleback)	urinary bladder	Sea of Japan
C. phoxini	8-9 x 7-8	freshwater Cypriniformes: leuciscid (common minnow)	gall bladder	England
C. pristiophori	11 x 8-9	marine Pristiophoriformes: pristiophorid (longnose sawshark)	gall bladder	Australia
C. protei	10-13 x 10-13	Urodela: proteid (olm)	renal tubules	Europe
C. proterorhini	8-9 x 6.5-7.5	brackish water Gobiiformes: gobiid (tubenose goby)	gall bladder	Hungary
C. psetti	10.7-13 x 9.4-10.6	marine Pleuronectiformes: scophthalmid (Black Sea turbot)	gall bladder	Ukraine
C. pseudomucronatum	8.7 x 10 x 7.4-9	freshwater Gadiformes: lotid (burbot)	urinary bladder	Russia

C. puntii	11-13.6	freshwater Cypriniformes: cyprinid (ticto barb)	gall bladder	India
C. puntiusi	7-9 x 4-6	freshwater Cypriniformes: cyprinid (scarlet-banded barb)	gall bladder	India
C. quadriforme	10 x 10 x 12	freshwater Salmoniformes: salmonid (chum salmon, pink salmon, masu salmon)	gall bladder	Japan
C. renale	6-7 x 5.5-7.7 x 5.1-6	marine Cyprinodontiformes: fundulid (striped killifish)	kidney	North America
C. reticulatum	7.9-8.9 x 7.9-8.9	freshwater Gadiformes: lotid (burbot)	gall bladder	Europe
C. richardsonii	9-10 x 9-10	freshwater Cypriniformes: cyprinid (redside shiner)	gall bladder	Japan
C. riorajum	11.4 x 8.4 x 5.9	marine Rajiformes: arhynchobatid (Rio skate)	gall bladder	Brazil
C. rostowstschikowi	6.9 x 6.9	freshwater Cypriniformes: cyprinid (sattar snowtrout)	gall bladder	Russia
C. rotunds	7.1-8 x 6.4-7.2 x 6-7.1	freshwater Cypriniformes: cyprinid (golden-line barbel)	gall bladder	China
C. rutili	7.3-7.8 x 7.3	freshwater Cypriniformes: cyprinid (common roach)	gall bladder	Hungary
C. salamandrae	7.8-8.8 x 7-8.2	Urodela: plethodontid (many-ribbed salamander, Texas salamander)	gall bladder	North America
C. salvelini	10-13 x 10-13	freshwater Salmoniformes: salmonid (whitespotted char (kundzha))	gall bladder	Japan
C. sarcochilichthydis	7-8 x 7-8	freshwater Cypriniformes: cyprinid (Chinese lake gudgeon)	liver	Russia
C. schulmani	9.7-10.6 x 6.6-8	marine Rajiformes: rajid (spotted skate)	gall bladder	eastern Atlantic
C. schurovi	5-5-6.6 x 5.5-6.6	freshwater Salmoniformes: salmonid (brown trout, Atlantic salmon) [cycle involves neoactinomyxum-type actinospores in Oligochaeta: lumbricid (*Eiseniella tetraedra*)	kidney	Europe
C. scyliorhinum	9.2-10.6	marine Carcharhiniformes: scyliorhinid (cloudy catshark)	gall bladder	Korea
C. sinense	8-9.2 x 8-9.2	freshwater Cypriniformes: cyprinid (lake stargazer)	gall bladder	China
C. sinilabi	7.5-9 x 4.1-6.1	freshwater Cypriniformes: cyprinid (rendahlovo)	gall bladder	China
C. spanovskajae (syn. *C. hemibarbi, orbiculatum, parabramis*)	7-11 x 6.5-10 x 6.5-10	freshwater Cypriniformes: cyprinid (grass carp, Chinese false gudgeon, barbel steed, spotted steed, white Amur bream)	gall bladder	Amur Basin, Korea
C. sphericum	8-9 x 8-9	freshwater Cypriniformes: cyprinid (pale chub); Siluriformes: silurid (Amur catfish)	gall bladder	Japan
C. sphyrnae	15 x 13	marine Carcharhiniformes: sphyrnid (bonnethead)	gall bladder	Brazil
C. squali	11.4 x 9.3 x 9.4	marine Squaliformes: squalid (spiny dogfish)	gall bladder	Australia
C. striatellus	10.6-11.2 x 6.7-10.6	marine Carcharhiniformes: scyliorhinid (small-spotted catshark)	gall bladder	eastern Atlantic
C. subsphaericum	10.5-13 x 11.7-14.5 x 11.7-14.5	marine Scorpaeniformes: stichaeid (rearspined prickleback)	gall bladder	Sea of Japan
C. tanakai	9.3 x 9.3 x 8.5	freshwater/estuarine Salmoniformes: salmonid (chum salmon)	gall bladder	Japan
C. thompsoni	6-8 x 6-7.5 x 5.5-7	freshwater Cypriniformes: catostomid (smallmouth buffalo)	gall bladder	North America
C. thymalli	7-9.5 x 7-9.5	freshwater Salmoniformes: salmonid (European grayling, Arctic grayling)	gall bladder	Eurasia
C. trachuri	3.6-4 x 3.6-4	marine Carangiformes: carangid (Mediterranean horse mackerel)	gall bladder	eastern Atlantic

C. transversocostatum	5.8-5.9 x 3.7	marine Squaliformes: squalid (spiny dogfish)	gall bladder	Argentina
C. trijugum	8-10 x 8-10 x -7	freshwater Perciformes: centrarchid (longear sunfish, bluegill sunfish, black crappie)	gall bladder	North America
C. tripathii	10.8-12 x 10.8-12	marine Perciformes: terapontid (crescent grunter)	gall bladder [hypertrophy]	India
C. truttae	8-9 x 8-9	freshwater/estuarine Salmoniformes: salmonid (brown trout, sea trout, rainbow trout, brook trout, Atlantic salmon, coho salmon) [cycle involves aurantiactinomyxon-type actinospores in Oligochaeta: lumbriculid (*Stylodrilus heringianus*)	gall bladder, hepatic bile ducts [emaciation]	Eurasia, North America
C. tuberculatum	8 x 9.5 x 7-8.8	freshwater Salmoniformes: salmonid (Arctic grayling)	gall bladder	Russia
C. vanasi	5.9-6.9 x 5.4-6.8	freshwater Siluriformes: bagrid (bayad)	gall bladder	Egypt
C. varicorhini	7.6-9.2 x 6.5-8.3	freshwater Cypriniformes: cyprinid (Samarkand khramulya)	gall bladder	Amur Basin
C. wardi	7.5-10.5 x 7.5-10.5	freshwater Salmoniformes: salmonid (rainbow trout, brook trout, Dolly Varden trout, sockeye salmon, cutthroat salmon)	gall bladder	North Pacific
C. wushingensis	7.4-8.6 x 6-7.2 x 6.2-7.2	freshwater Cypriniformes: cyprinid (common carp, black carp)	gall bladder	China
Family **Coccomyxidae** (spores with asymmetrical unequal smooth valves, single polar capsule)				
Genus ***Auerbachia*** (club-like spores broader anteriorly)				
A. anomala [type species]	20.7-24.3 x 7.8-9	marine Ophidiiformes: ophidiid (pink cusk-eel)	gall bladder	New Zealand
A. bajadi	19-21 x 7-9	marine Carangiformes: carangid (orange-spotted trevally)	gall bladder	Red Sea
A. caranxi	14.2-18.8 x 6-7.9	marine Carangiformes: carangid (brassy trevally)	gall bladder	Australia
A. chaetodoni	26.9-37.7 x 8-10.1	marine Perciformes: chaetodontid (teardrop butterflyfish)	gall bladder	Australia
A. chakravartyi	14-21 (8.4-12.6) x 7-9.8	marine Carangiformes: carangid (torpedo scad)	gall bladder	India, Vietnam
A. chorinemusi	15.5-18 x 6-9.5	marine Carangiformes: carangid (needle scaled queenfish)	gall bladder	India
A. hepatica	31.4-37.4 x 13.6-17.9	marine Carangiformes: carangid (brown back trevally)	liver, gall bladder	India
A. monstrosa	21.1-28.9 x 9.3-10.3	marine Gadiformes: macrourid (javelinfish)	gall bladder	New Zealand
A. pulchra	26-34 x 11-12	marine Gadiformes: macrourid (rock grenadier, roughhead grenadier)	gall bladder	North Atlantic
A. scomberoidi	17.5-25.2 x 6.3-10	marine Carangiformes: carangid (doublespotted queenfish)	gall bladder	Australia
A. sphaerica	9.8-11.2 x 11.2-11.8	marine Atheriniformes: atherinopsid (laterino de ojos negros)	gall bladder	Argentina
Genus ***Coccomyxa*** (syn. *Thelohanelloides*) (spores ellipsoidal, single polar capsule, sigmoidal suture)				
C. baleswarensis	10-13 x 4.5-6	freshwater Clupeiformes: dorosomatid (hilsa herring)	gall bladder	India
C. bengalensis (syn. *Thelonanelloides*)	11.5-14 x 5-6.5	marine Siluriformes: ariid (Sagor sea catfish)	gall bladder	India
C. bragantinensis	8.2-10 x 3.5-5	marine Siluriformes: ariid (Coco Sea catfish)	gall bladder	Brazil
C. claviforme	14 x 5-6	marine/estuarine Tetraodontiformes: diodontid (brown burrfish)	gall bladder	Brazil

C. colurodontidis	10.2-14.3 x 5.2-7.1	marine Tetraodontiformes: monacanthid (Paxman's leatherjacket)	gall bladder	Australia
C. gobiodoni	8.4-12.4 x 5.5-7.5	marine Gobiiformes: gobiid (poison goby)	gall bladder	Australia
C. hoffmani	7.5-9.5 x 6-7.5	marine Siluriformes: plotosid (striped eel catfish)	gall bladder	Philippines
C. jirilomi	9-11.3 x 5-7	marine Gobiiformes: gobiid (spotted frill goby)	gall bladder	Red Sea
C. leiognatha	16-25 x 6-9 x 6.2-8.5	marine Acanthuriformes: leiognathid (shortnose ponyfish)	gall bladder	China
C. meridiei	9.2-11.8 x 5.3-7.8	marine Clupeiformes: dorosometid (Castelnau's herring)	gall bladder	Australia
C. morovi [type species]	14-16 x 5-7	marine Clupeiformes: alosid (European pilchard)	gall bladder	Mediterranean
C. ovale	10.6-12 x 4.8-6.7	marine Beryciformes: berycid (splendid alfonsino)	gall bladder	Atlantic
C. tenuiparies	8.8-12.5 x 7.3-10.8	marine Blenniiformes: clinid (Whitelegg's weedfish)	gall bladder	Australia
Genus ***Globospora*** (subspherical spores, curved suture)				
G. sphaerica [type species]	10.5 x 11.5	marine Atheriniformes: atherinid (silverside)	gall bladder	South America
Family: **Enteromyxidae** (sigmoidal spores, 2 polar capsules, tangential at opposite ends, histozoic in intestines of fish)				
Genus ***Enteromyxum*** (cresentic spores, large elongate equal polar capsules, histozoic in intestines of fish)				
E. caesio	8.5-9.5 x 5-6.3 x 5.7-6.3	marine Perciformes: caesionid (redbelly yellowtail fusilier)	stomach	Malaysia
E. fugu (syn. *Myxidium*)	13.5-15.5 x 8-10	marine Tetraodontiformes: tetraodontid (tiger puffer)	intestines	Japan
E. leei (syn. *Myxidium*)	13.2-19.6 x 5-11	marine Acanthuriformes: sciaenid (red drum); Batrachoidiformes: batrachoidid (Lusitanian toadfish); Blenniiformes: blenniid (peacock blenny); Gobiiformes: gobiid (black goby); Labriformes: labrid (Mediterranean rainbow wrasse, East Atlantic peacock wrasse, ocellated wrasse, axillary wrasse, point-snouted wrasse, five-spotted wrasse, grey wrasse, corkwing wrasse, ornate wrasse, green wrasse, brown wrasse, Ballan wrasse, pearly razorfish); Mugiliformes: mugilid (golden grey mullet, thicklip grey mullet, thinlip mullet, leaping mullet, striped red mullet); Ovalentaria: pomacentrid (damselfish); Scorpaeniformes: scorpaenid (black scorpionfish); Spariformes: sparid (common two-banded sea bream, sargo, gilthead sea bream, sharpsnout sea bream, red sea bream, blotched picarel); Tetraodontiformes: molid (ocean sunfish), tetraodontid (tiger puffer)	intestines [enteromyxosis, enteritis, emaciation]	Mediterranean
E. scophthalmi [type species]	20-25 x 9.2-14.1 x 14	marine Pleuronectiformes: scophthalmid (turbot)	intestines [enteromyxosis, enteritis, emaciation]	Mediterranean
Family **Fabesporidae** (spores with valves elongated perpendicular to central suture line)				
Genus ***Fabespora*** (elongate spores, central transversal suture, lateral polar capsules)				

F. nana [type species]	2.6-3.9 x 6.5-7.8	marine Gobiiformes: gobiid (unspecified goby); Scorpaeniformes: scorpaenid (unspecified scorpionfish)	gall bladder	Black Sea
F. vermicola	7.5-9.8 x 4-5.2	marine, hyperparasitic in digenean trematode Plagiorchiida: megaperid (*Crassicutis archosargi*) in Spariformes: sparid (sheepshead seabream)	integument, parenchyma	North America
Family: **Gastromyxidae** (sigmoidal spores, 2 polar capsules at opposite poles, histozoic in stomach of marine fish)				
Genus ***Gastromyxum*** (spores without striations, inconspicuous suture)				
G. bulani	7.8-11.6 x 4.7-6.8	marine Elopiformes: megalopid (Indo-Pacific tarpon)	stomach wall	Malaysia
G. rafii	7.1-8.5 x 4.9-5.9	marine Elopiformes: elopid (tenpounder)	stomach wall	Malaysia
Family: **Monomyxidae** (sigmoidal spores, 2 polar capsules at opposite poles, histozoic in gill monogeneans)				
Genus ***Monomyxum*** (spores without striations, inconspicuous suture)				
M. incomptavermi (syn. *Myxidium*)	11.3-11.8 x 4.2-5.6	marine, hyperparasitic in trematode Monogenea: diplectanid (*Diplectanocotyla gracilis*) in Elopiformes: megalopid (Indo-Pacific tarpon)	monogenean parenchyma, fish gills, kidney, spleen, intestines	Malaysia
Family **Myxidiidae** (2 polar capsules at opposite ends of elongated spores)				
Genus ***Cystodiscus*** (oval spores with transverse depressions, raised sutural ridge, coelozoic in amphibians)				
C. australis	12-18 x 8-10.5	Anura: hylid (dainty green tree frog, green-and-golden bell frog), limnodynastid (striped marsh frog), bufonid (cane toad)	bile ducts, gall bladder	Australia
C. axonis	12-17 x 7.1-10.5	Anura: bufonid (dwarf American toad, Fowler's toad, cane toad), hylid (dainty green tree frog, Cajun chorus frog, Blanchard's cricket frog, southern bell frog, green-and-golden bell frog, Peron's tree frog), limnodynastid (striped marsh frog), ranid (green frog, Coastal Plains leopard frog); Gymnophiona: typhlonectid (rubber eel, Cayenne caecilian)	gall bladder, liver, brain, gut, gonads	Americas, Europe, Australia
C. elachistocleis	9.8-11.2 x 5.6-6.6	Anura: microhylid (South American narrow-mouthed frog)	gall bladder	South America
C. haldari (syn. *Myxidium*)	10-12 x 6.5-7	Anura: hylid (Jerdon's tree frog)	gall bladder	India
C. immersus (syn. *Myxidium immersum*) [type species]	11.8-14 x 7.5-10	Anura: bufonid (common toad, cane toad, Dorbigny's toad, redbelly toad), hylid (Montevideo tree frog, Carrizo's tree frog, Tyler's tree frog, Spix's snouted tree frog, red snouted tree frog, Australian green tree frog, Peron's tree frog, robust bleating tree frog, eastern dwarf tree frog, desert tree frog, broad-palmed frog, Lesueur's frog, striped rocket frog, mountain mist frog, revealed frog, whistling tree frog, lesser swimming frog), leptodactylid (oven frog, butter frog, Girard's dwarf frog, four-eyed frog), alsodid (rapids frog),	gall bladder	South America, Australia

		odontophrynid (American ground frog), myobatrachid (eastern sign-bearing froglet, smooth toadlet, great barred frog), limnodynastid (ornate burrowing frog, striped marsh frog, spotted grass frog, northern banjo frog)		
C. lesminteri (syn. *Myxidium*)	9.5-15 x 5-8	Anura: bufonid (eastern olive toad), heleophryind (Natal ghost frog), ranid (knocking sand frog, common sand frog)	gall bladder	Africa
C. lyndoyense sp. inq. (syn. *Myxidium lindoyense,* probable syn. of *C. immersus*)	11-12 x 7.5-8	Anura: bufonid (cane toad)	gall bladder	Brazil
C. melleni (syn. *Myxidium*)	12-13.5 x 7-9 x 6.8-8	Anura: bufonid (Fowler's toad), hylid (western chorus frog, upland chorus frog, Cajun chorus frog, spring peeper, Blanchard's cricket frog, northern cricket frog); Urodela: ambystomatid (marbled salamander, spotted salamander, ringed salamander, small-mouth salamander)	gall bladder	North America
C. serotinus (syn. *Myxidium serotinum*)	16-18 x 9	Anura: bufonid (green toad, southern toad, American toad, Texas toad, Gulf Coast toad, Woodhouse's toad), hylid (spotted chorus frog, Strecker's chorus frog, Cajun chorus frog, spring peeper, northern cricket frog, bird-voiced tree frog, Cope's gray treefrog, American green tree frog), ranid (green frog, southern leopard frog, northern leopard frog, Rio Grande leopard frog, Plains leopard frog, American bullfrog, pickerel frog), eleutherodactylid (Rio Grande chirping frog), microhylid (eastern narrow-mouthed toad, western narrow-mouthed toad); Urodela: ambystomatid (small-mouth salamander, ringed salamander, marbled salamander, tiger salamander), plethodontid (northern two-lined salamander, southeastern dwarf salamander, northern dusky salamander, four-toed salamander, Caddo Mountain salamander, Rich Mountain salamander, southern red-backed salamander), salamandrid (eastern newt), sirenid (lesser siren)	gall bladder	North America
C. typhonius (syn. *Myxidium*)	9.8-12.2 x 5.7-8.9	Anura: bufonid (cane toad, South American common toad), hylid (crump treefrog, yellow-toed treefrog, Koechlin's treefrog, white leaf frog, merian frog), aromobatid (dull rocket frog), leptodactylid (white-lipped frog, Wagner's white-lipped frog, Bolivian white-lipped frog, pointed-belly frog), leiuperid (Perez's snouted frog), microhylid (Bolivian bleating frog)	gall bladder	Peru
Genus ***Myxidium*** (fusiform-crescentic spores, 2 pyriform polar capsules at opposite poles, mostly coelozoic in fish and reptiles)				

M. abbottinae	12-12.3 x 5.6-6.4 x 4-5.2	freshwater Cypriniformes: gobionid (kiating gudgeon)	gall bladder	China
M. abudefdufi	9.1 x 6.7-7.2	marine Ovalentaria: pomacentrid (sergeant-major)	gall bladder	Africa
M. acanthobramae	13.8-14.5 x 6-7.1 x 3.3-4	freshwater Cypriniformes: xenocypridid (pseudobream)	gall bladder	China
M. acinum	5.1-5.8 x 2.5-3.9 x 2.1-2.9	freshwater Anguilliformes: anguillid (short-finned eel, New Zealand longfin eel)	gills	Australia, New Zealand
M. acrossocheilus	dimorphic 16-19.2 x 8-8.8 x 7.5 5-5.6 x 4-4.8 x 4	freshwater Cypriniformes: cyprinid (yunnani silemokk)	gall bladder	China
M. adriaticum	14-16 x 7-8	marine Scorpaeniformes: scorpaenid (small red scorpionfish)	gall bladder	Europe
M. alataiense	12.8-13.2 x 4.9-5.2 x 4.3-4.7	freshwater Cypriniformes: cyprinid (ide)	kidneys	China
M. alosae	11 x 6.3	freshwater Clupeiformes: alosid (agone)	gall bladder	France
M. amazonense	16.1-17.9 x 3-4.4 x 8	freshwater Siluriformes: callichthyid (bandit corydoras)	gall bladder	Brazil
M. americanum	15-16 x 5.5-6	Testudines: trionychid (spiny softshell turtle)	urinary tubules	North America
M. anabariliusi	9-9.6 x 6-6.4 x 5.5	freshwater Cypriniformes: cyprinid (silver minnow)	gall bladder	China
M. anatidum	21.3-24.3 x 10.3-11.5 x 10.2-12.2	Anseriformes: anatid (mallard duck)	liver bile ducts	North America
M. andongense	8.1-8.8 x 8.1-8.8 x 7-7.7	freshwater Gobiiformes: oxudercid (Asian freshwater goby)	urinary bladder	China
M. aori	11.4-13.6 x 5.4-7.1	freshwater Siluriformes: bagrid (long-whiskered catfish)	gall bladder	India
M. aplodinoti	11-12 x 5-6 x 5-6	freshwater Acanthuriformes: sciaenid (freshwater drum)	gall bladder	North America
M. apocryptae	30.7-38.2 x 4.2-6.6	freshwater Gobiiformes: oxudercid (mudskipper)	gall bladder	India
M. arcticum	10-13 x 5.5-8.2	marine Scorpaeniformes: cottid (Arctic sculpin, slimy sculpin)	gall bladder	Barents Sea
M. aristichthysi	12.1-14.4 x 5.8-6.2 x 5-6	freshwater Cypriniformes: cyprinid (bighead carp)	gall bladder	China
M. asymmetricum	18.6-19.9 x 6.6-9.3	marine Gadiformes: morid (tadpole codling)	gall bladder	Russia
M. attuum	23.8-28.9 x 9.5-11.9	freshwater Siluriformes: silurid (helicopter catfish)	gall bladder	India
M. aydai	22-24 x 5-6	marine Perciformes: caesionid (Suez fusilier)	gall bladder	Egypt
M. bajacalifornium	3-5 x 19.2-32	marine Alepocephaliformes: alepocephalid (sharpchin slickhead); Beryciformes: berycid (splendid alfonsino)	gall bladder	North America, Atlantic
M. barbatulae	12-15 x 6	freshwater Cypriniformes: nemacheilid (stone loach)	kidneys	France
M. barbodesi	13.6-14.4 x 5.6-7.2 x 4.8-5.6	freshwater Cypriniformes: cyprinid (yunnani silemokk, chonglingchungi)	gall bladder	China
M. batae	14-17 x 6-8	freshwater Cypriniformes: cyprinid (bata)	gall bladder	India
M. baueri	14.4-24 x 4-11 x 3.2-5.3	marine Gadiformes: macrourid (Patagonian grenadier, bigeye grenadier), merlucciid (southern hake, Argentine hake); Perciformes: nototheniid (cod icefish)	gall bladder	Atlantic
M. bellum	1.5-17.5 x 4-5	freshwater Siluriformes: ictalurid (channel catfish)	gall bladder	North America

M. benthophili		Listed in: European register of marine species		Europe
M. bergense	14.5-19 x 5.5-12	marine Gadiformes: gadid (Atlantic cod, polar cod, saithe, pollock, haddock, merling); Pleuronectiformes: pleuronectid (European plaice, common dab); Scorpaeniformes: cottid (shorthorn sculpin), scorpaenid (blackbelly rosefish, Norway redfish)	gall bladder	Atlantic, Barents Sea, White Sea
M. biliare	12-15 x 6-8 x 6-9	freshwater Galaxiiformes: galaxiid (common galaxias)	gall bladder	Argentina
M. binguelai	11.1-12.9 x 4.8-5.8	freshwater Osteoglossiformes: mormyrid (Kingsley elephantfish)	kidney	Cameroon
M. birgii	17.7-22.5 x 7-11	freshwater Cyprinodontiformes: nothobranchiid (twostripe lyretail)	gall bladder	Africa
M. boddaerti	133.3-166.8 x 6.4-8.3	brackish water Gobiiformes: oxudercid (Boddart's goggle-eyed goby)	gut	India
M. bouixi	14 x 4	brackish water Siluriformes: mochokid (upsidedown catfish)	gall bladder	Africa
M. boulengeri		Anura: dicroglossid (spiny-bellied frog)	gall bladder	China
M. brienomyri	12.2-16.2 x 5.5-9	freshwater Osteoglossiformes: mormyrid (baby whale fish)	gall bladder	Africa
M. calcariferi	23-27 x 6-8	freshwater/estuarine Perciformes: latid (barramundi)	gall bladder	India
M. camerounense	19.2-25.5 x 5-8.4	freshwater Characiformes: distichodontid (Ansorge's neolebias)	gall bladder	Africa
M. carinae	12-14.8 x 5-7 x 5.5-8	freshwater Cypriniformes: cyprinid (Iberian barbel)	gall bladder	Spain
M. ceccarelli	17.1-18.1 x 9.8-10.3 x 9.6-10.4	freshwater Characiformes: anostomid (piau)	gall bladder	Brazil
M. chelonarum	12.5-16 x 3-5 x 4-7	Testudines: chelydrid (common snapping turtle), emydid (painted turtle, chicken turtle, pond slider, Alabama map turtle, river cooter, Florida red-bellied cooter, coastal plain cooter), geoemydid (brown roofed turtle), kinosternid (common musk turtle, Sonara mud turtle)	gall bladder, bile ducts	Asia, North America
M. chengkiangense	7.4-7.5 x 6.8-7.5 x 6-6.5	freshwater Cypriniformes: xenocypridid (kanglang fish)	gall bladder	China
M. chilomycteri	10-13 x 6-8	marine Tetraodontiformes: diodontid (Guinean burrfish)	gall bladder	Senegal
M. chiluense	12-13.6 x 5.8-6.6 x 5.8-6.2	freshwater Cypriniformes: cyprinid (Chinese false gudgeon), xenocypridid (kanglang fish)	gall bladder	China
M. cholecysticum	12-15.9 x 6.4-9.6	freshwater Characiformes: characid (mojarra)	gall bladder	Brazil
M. chongquingense	16.2-17.6 x 5.9-7.4 x 4-6	freshwater Cypriniformes: cyprinid (common carp)	gills	China
M. cirrhinae	12.2-15.3 x 5.3-6.8 x 4.8	freshwater Cypriniformes: cyprinid (mud carp)	kidney	China
M. clariae	13.4-15.1 x 4.5-6	freshwater Siluriformes: clariid (African sharptooth catfish)	gall bladder	Israel
M. clidodermatis	16-19 x 7-10 x 6-8	marine Pleuronectiformes: pleuronectid (roughscale sole)	gall bladder	Japan
M. cochleatum	11.3-13.1 x 6.3-6.9 x 4-6	marine Pleuronectiformes: scophthalmid (Black Sea turbot)	gall bladder	Russia
M. commersoni	10-12 x 5.5-7 x 5-5.5	freshwater Cypriniformes: cyprinid (white sucker)	gall bladder	Canada

M. contortum	21-24 x 5-8	marine Blenniiformes: blenniid (horned blenny)	gall bladder	South Africa
M. coryphaenoidium	3-7 x 17-28.5	marine Gadiformes: macrourid (roundnose grenadier)	gall bladder	Mexico
M. crassum	19-21 x 9 x 10-12	marine Perciformes: stichaeid (grigorjevi ridakala)	gall bladder	Japan
M. cruzi	17-18 x 5-7	freshwater Characiformes: triportheid (sardinha)	gall bladder	Brazil
M. ctenopharyngodonis	18-23 x 5-6.5	freshwater Cypriniformes: cyprinid (grass carp)	kidneys, urinary tract, gall bladder	Amur Basin
M. cuneiforme	12-16.3 x 3.8-7 x 5.9-6.9	freshwater Cypriniformes: cyprinid (common carp, koi carp, Japanese crucian carp, goldfish)	gall bladder	China, Korea, Japan
M. danilewskyi	12 x 3-4	Testudines: emydid (European pond turtle)	kidneys	France
M. depressum	12-14 x 5.5-6 x 2.5-3	marine Pleuronectiformes: citharid (spotted flounder)	gall bladder	Italy
M. distichodi	16-17 x 6-7	freshwater Characiformes: distichodontid (grass-eater perch)	gall bladder	Tchad
M. djolonensis	15.5-18 x 5-7.1	freshwater Osteoglossiformes: mormyrid (Kingsley elephantfish)	gall bladder, urinary bladder	Cameroon
M. durum	6.5-8 x 3.5-4.5	freshwater Anguilliformes: anguillid (short-finned eel)	gills	Australia
M. elopsi	7-10 x 4.5-8	marine Elopiformes: elopid (Senegalese ladyfish)	intestines	Senegal
M. eminentis	11.6-14.9 x 6.1-8.3	marine Gobiiformes: gobiid (flat-headed goby)	gall bladder	Japan
M. enchelypterygii	6.2-9 x 3.7-5.1 x 3.7-5.1	freshwater Anguilliformes: anguillid Japanese eel)	fins	China
M. euzeti	9.5-10.3 x 8-9	marine Eupercaria: sparid (annular seabream)	gall bladder	Montenegro
M. fasciatum	14.4-17.6 x 5.6-6.4	freshwater Anabantiformes: osphronemid (banded gourami)	gall bladder	India
M. finnmarchium	13.1-22.4 x 6.4-10.1 x 3.2-9.7	marine Gadiformes: gadid (merling); Scorpaeniformes: cottid (shorthorn sculpin)	gall bladder	Arctic
M. folium	10-12 x 5-6	brackish water Cyprinodontiformes: fundulid (mummichog)	gall bladder, liver	North America
M. fonsecai	7-9 x 2.5-3	freshwater Gymnotiformes: gymnotid (naked-back knifefish)	gall bladder	Brazil
M. fusienense	9.6-10.4 x 9.4-9.7 x 5.9-6.1	freshwater Cypriniformes: cyprinid (yunnani silemokk)	gall bladder	China
M. fusiforme	30 x 9	marine Anguilliformes: anguillid (Japanese eel); Perciformes: sebastid (flame red rockfish)	gall bladder	Japan
M. gadi	8-14 x 4-8	marine Gadiformes: gadid (Atlantic cod, Baltic cod, White Sea cod, pollack, saithe, merling, haddock); Pleuronectiformes: pleuronectid (European flounder), soleid (common sole, black sole); Scorpaeniformes: cottid (shorthorn sculpin)	gall bladder	Arctic
M. gasterostei	7-8 x 14-15	freshwater Scorpaeniformes: gasterosteid (three-spine stickleback, ninespine stickleback)	gall bladder	North America, Russia
M. giganteum	19-28 x 8-10	marine Rajiformes: rajid (brown ray, Mediterranean starry ray)	gall bladder	Italy
M. gigantissimum	42.5-97.5 x 5-8.5	marine Alepocephaliformes: alepocephalid (small scaled brown slickhead)	gall bladder	South Africa
M. glossogobi	12-15 x 8.5-10	marine Gobiiformes: gobiid (tank goby)	gall bladder	India

M. glutinosum	10-11 x 6	marine Acanthuriformes: sciaenid (weakfish)	gall bladder	North America
M. glyptothoraxi	12.1-13.6 x 5.4-6.1 x 4.6-6.1	freshwater Siluriformes: sisorid (kiinanvirtamonni)	kidney	China
M. gracile	9.8-10.1 x 3.9-5.2	freshwater Salmoniformes: salmonid (Arctic grayling)	gall bladder	Russia
M. gurgeli	14.6 x 8.5	freshwater Characiformes: characid (unspecified characin)	gall bladder	Brazil
M. hardella	14.9-20 x 4.5-5.7	Testudines: geoemydid (Brahminy river turtle)	gall bladder, kidney	North America, Pakistan
M. hemiculteri	11.5-13 x 6.8-7 x 3-3.2	freshwater Cypriniformes: cyprinid (sharpbelly)	gall bladder	China
M. heteropneustesi	14.4 x 6.2	freshwater Siluriformes: heteropneustid (Asian stinging catfish)	gall bladder	India
M. histophilum	15	freshwater Cypriniformes: leuciscid ('vairon' = common minnow?)	kidney, ovary	France
M. hokiangense	12.8-15.1 x 5.2-6.9 x 5.9	freshwater Cypriniformes: cyprinid (hiina astelparrak); Siluriformes: bagrid (yellowhead catfish)	gall bladder	China
M. huidongense	13.6-14.4 x 6-8 x 7.5	freshwater Cypriniformes: cyprinid (marinka tsunynska)	gall bladder	China
M. hupehense	13.2-15.6 x 4.8-5.4 x 3.6-4.2	freshwater Cypriniformes: cyprinid (goldfish, jangste kraapmokk, hele hoberunt)	gall bladder. kidney	China
M. hyseleotris	12-14.4 x 6.6-7.8 x 5.8-6.2	freshwater Gobiiformes: odontobutid (Swinhon's freshwater goby)	kidney	China
M. illinoisense	12.7-15.3 x 7.6-9.3	freshwater Anguilliformes: anguillid (American eel)	kidney	North America
M. incurvatum	7.2-20 x 4-8.8	marine Blenniiformes: blenniid (peacock blenny, shanny), tripteryglid (New Zealand topknot); Callionymiformes: callionymid (common dragonet); Cyprinodontiformes: fundulid (striped mummichog), poeciliid (western mosquitofish); Gadiformes: gadid (merling); Gobiesociformes: gobiesocid (orange clingfish, striped clingfish); Mugiliformes: mugilid (flathead grey mullet); Ovalentaria: plesiopid (New Zealand rockfish); Perciformes: ammodytid (small sandeel); Pleuronectiformes: pleuronectid (common dab, European flounder); Scorpaeniformes: cottid (fluffy sculpin, shorthorn sculpin, fourhorn sculpin), cyclopterid (lumpfish), scorpaenid (red scorpionfish, copper rockfish, gopher rockfish, rosethorn rockfish, olive rockfish, Bocaccio rockfish); Syngnathiformes: syngnathid (snake pipefish, greater pipefish, spotted pipefish, worm pipefish, straightnose pipefish, broad-nosed pipefish, Pacific seaweed pipefish, short-snouted seahorse); Trachiniformes: trachinid (greater weever)	gall bladder	cosmopolitan
M. inflatum	20.8-23.4 x 13-15.6	marine Scorpaeniformes: cyclopterid (lumpfish)	gall bladder	Norway
M. intermedium	12 x 6-7	marine Pleuronectiformes: pleuronectid (European flounder)	gall bladder	England

M. ischikauiae	9 x 5	freshwater Cypriniformes: cyprinid (vataka)	gall bladder	Japan
M. islampurium	8.5-12 x 3-6	freshwater Anabantiformes: channid (bullseye snakehead)	gall bladder	India
M. iwamotoi	26-31 x 5-7	marine Gadiformes: macrourid (Carapine grenadier, chiri-kosokodara)	gall bladder	Americas, Asia
M. japonicum	12-18.3 x 4-8.2	marine Scorpaeniformes: agonid (sea raven), cottid (snowy sculpin, antlered sculpin, Herzenstein's sculpin, bero)	gall bladder	Sea of Japan
M. kagayamai	13.6-18 x 5.3-7 x 4.8	freshwater Cypriniformes: cobitid (weatherfish)	gall bladder	Amur Basin, Japan
M. kudoi	8.5-12 x 4-6	freshwater Siluriformes: ictalurid (blue catfish)	gall bladder	North America
M. kwangtungense	20.6-22.8 x 8.4-9 x 7.4-8.4	freshwater Cypriniformes: cyprinid (Chinese barb)	gall bladder	China
M. labeonis	11-14x 5-7	freshwater Cypriniformes: cyprinid (kalabans, boalla)	gall bladder	India
M. lapipiscis	6.1-7.9 x 3.1-4	marine Scorpaeniformes: scorpaenid (estuarine stonefish, reef stonefish)	biliary tract	Australia
M. latesi	15-16 x 8-9	freshwater Perciformes: latid (Nile perch)	gall bladder	Tchad
M. laticurvum (syn. *M. trachinorum*)	11-16.5 x 6.5-8.7	marine Trachiniformes: trachinid (greater weever, lesser weever)	gall bladder	North Sea
M. lentiforme (syn. *M. fusiforme*)	19 x 5	freshwater Anguilliformes: anguillid (Japanese eel)	kidney	Japan
M. lepidocephalicthysum	13-14.1 x 5-6	freshwater Cypriniformes: cobitid (common spiny loach)	kidney	India
M. lesminteri	11-15 x 5-7	Anura: bufonid (eastern olive toad), heleophrynid (Natal ghost frog), pyxicephalid (knocking sand frog)	gall bladder	South Africa
M. licodae	12.8-16.6 x 8-9.4	marine Perciformes: zoarcid (marbled eelpout)	gall bladder	Russia
M. lieberkuehni (*lieberkuhnii*, *lieberkuhni*) (syn. *M. mukundae*) [type species]	12.4-22.4 x 4.5-9.6	freshwater Acipenseriformes: acipenserid (European sea sturgeon); Anabantiformes: anabantid (climbing perch); Cypriniformes: cobitid (pond loach), cyprinid (common carp, crucian carp, goldfish, rosy bitterling, Chinese false gudgeon), gobionid (hele hoberunt), xenocypridid (hiina laikviidikas); Esociformes: esocid (northern pike, Amur pike, chain pickerel); Gadiformes: lorid (burbot); Gobiiformes: oxudercid (Boddart's goggle-eyed goby); Ophidiiformes: ophidiid (slender cuskeel); Perciformes: percid (European perch)	kidney, ureters, urinary bladder, gall bladder [xenomas]	Eurasia, North America
M. lindoyense	11-12 x 7.5-8	Anura bufonid (cane toad), hylid (red-snouted treefrog, blue-headed snouted treefrog), leptodactylid (butter frog), myobatrachid (common froglet)	gall bladder	Brazil
M. longiovaformis	12-12.8 x 6.4-7.2 x 6-6.7	freshwater Cypriniformes: cyprinid (yunnani silemokk)	gall bladder	China
M. maamouni	12-15 x 7-9	marine Beloniformes: exocoetid (blacksail flyingfish)	gall bladder	Egypt
M. mackiei	16-17 x 5	Testudines: trionychid (Indian soft-shelled turtle, Indian flap-shelled turtle)	urinary tract, kidneys	India
M. macrocapsulatum	9.8-11.6 x 2.8-5.3	freshwater Cypriniformes: cyprinid (common rudd)	kidney	Netherlands
M. macrocapsulare	10-12 x 5.4-6 x	freshwater Acanthuriformes: sciaenid	gall bladder,	Eurasia

	3.6-3.8	(freshwater drum); Cypriniformes: cyprinid (common roach, Black Sea roach, ide, common rudd, common bleak, common barbel, Bulatmai barbel, ziege, common bream, white bream), leuciscid (Kura nase), xenocypridid (silver carp); Perciformes: centrarchid (bluegill sunfish); Scorpaeniformes: zoarcid (viviparous eelpout); Siluriformes: bagrid (yellowhead catfish, darkbarbel catfish)	hepatic ducts	
M. macrocheili	10-14.4 x 5.5-8	freshwater Cypriniformes: catostomid (largescale sucker)	gall bladder	North America
M. macropodus	12-14.4 x 6.2-7.2 x 6-6.2	freshwater Anabantiformes: osphronemid (fork-tailed paradise fish)	gall bladder	China
M. macrourium	27-34 x 3.5-4.5	marine Gadiformes: bathygadid (Vaillant's grenadier)	gall bladder	Surinam
M. mapienense	12-12.8 x 4.8-5.2 x 4.9	freshwater Siluriformes: amblycipitid (torrent catfish)	kidneys	China
M. matsuii	9-13 x 6.5-9 x 7-8	freshwater Anguilliformes: anguillid (Japanese eel); Cypriniformes: catostomid (largescale sucker)	dermis	Japan
M. mavori	14-15 x 6-7.5	marine Pleuronectiformes: pleuronectid (winter flounder)	gall bladder	Canada
M. melanocetum	19.8 x 4.5	marine Lophiiformes: melanocetid (humpback anglerfish)	gall bladder	India
M. melanostomi		freshwater/marine Gobiiformes: gobiid (round goby)		Russia
M. melanostigmum	3-6.5 x 20-26	marine Perciformes: zoarcid (midwater eelpout)	gall bladder	North America
M. melleni	12-13.5 x 7-9	Anura: hylid (western chorus frog, Blanchard's cricket frog)	gall bladder	North America
M. melum	11-12 x 5-6	freshwater Siluriformes: ictalurid (black bullhead); Perciformes: centrarchid (black crappie)	gall bladder	North America
M. mendehi	7.8-13.2 x 3.1-4.9	freshwater Cypriniformes: cyprinid (African blackfin barb, martorelli barb)	kidneys	Cameroon
M. menodae	15-19.5 x 9-10.5 x 6-9	freshwater Siluriformes: bagrid (Menoda catfish)	gall bladder	India
M. microcapsulare	16-19 x 8-11 x 9-12	marine Pleuronectiformes: pleuronectid (Kamchatka flounder)	gall bladder	Japan
M. microstomi	14-19 x 8-9 x 8-9	marine Pleuronectiformes: pleuronectid (blackfin flounder)	gall bladder	Japan
M. milleri	9.2 x 5.2 x 6	marine Syngnathiformes: syngnathid (Schultz's pipefish)	gall bladder	Europe
M. mindanoense	5.5-6 x 3-4	freshwater Anguilliformes: anguillid (Indian shortfin eel)	gills	Philippines
M. minteri	9.3-12.6 x 4.5-7	freshwater Salmoniformes: salmonid (coho salmon, chinook salmon, silver salmon, steelhead, rainbow trout, cutthroat trout, brook trout, mountain whitefish)	kidney, liver, gall bladder	North America
M. minutum	8.1 x 4.6	freshwater Anabantiformes: channid (blotched snakehead)	intestines	China
M. misgurni	10.2-13.9 x 4.3-5.6	freshwater Cypriniformes: cobitid (pond loach)	kidneys	China
M. molnari	8.3-10.1 x 2.9-5	freshwater Cypriniformes: cyprinid (reba carp)	gall bladder	India
M. monopteri	19-22.3 x 5.1-6.8 x	freshwater Synbranchiformes:	gall bladder,	China

	3.7-5.6	synbranchid (Asian swamp eel)	kidney	
M. monstruosum	8.4-12.6 x 7-10.6 x 6.7-8.4	freshwater Gobiiformes: odontobutid (Swinhon's freshwater goby); Siluriformes: sisorid (kiinanvirtamonni)	urinary bladder	Korea
M. moxostomatis	8.5-10.5 x 5-6 x 5-6	freshwater Cypriniformes: catostomid (unspecified redhorse)	gall bladder	North America
M. myoxocephali	13.3-17.5 x 6.6-8	marine Scorpaeniformes: cottid (longhorn sculpin)	gall bladder	Canada
M. mystusium	11-16.5 x 5-7.4	freshwater Siluriformes: bagrid (striped mystus catfish)	gall bladder	India
M. nanhaiense	16.8-20.4 x 6.6-8.4 x 7.2-7.8	freshwater Cypriniformes: cyprinid (mud carp)	gall bladder	China
M. nasalis	11.2-12 x 7.2-8 x 7.4	freshwater Cypriniformes: cyprinid (pingi)	nares	China
M. neimongolia	9.6-10.8 x 5.2-6 x 4.2-4.8	freshwater Cypriniformes: cyprinid (Amur ide)	gall bladder	China
M. ningnanense	16-16.8 x 7.2 x 5.6	freshwater Cypriniformes: cyprinid (tomp koukloug)	gall bladder	China
M. nkamense	24-27.5 x 10-13	freshwater Siluriformes: clariid (abugu)	gall bladder	Cameroon
M. noblei	9.3-12 x 4.5-5,3 x 3.6-4.7	marine/freshwater Salmoniformes: salmonid (European grayling)	urinary bladder	Russia
M. notopterum	13.5-16.5 x 7-9	freshwater Osteoglossiformes: notopterid (bronze featherback)	liver	India
M. nyongense	10.8-14.4 x 4.7-9.4	freshwater Cypriniformes: cyprinid (Jae barb)	gall bladder	Cameroon
M. obliquelineolatum	12.6-13.3 x 5.3-6.6	marine Scorpaeniformes: scorpaenid (beaked redfish, Norway redfish)	gall bladder	Russia
M. obscurum	13-16 x 6.1-7.7 x 6.6-8.5	freshwater Salmoniformes: salmonid (sockeye salmon, chum salmon, pink salmon); Scorpaeniformes: gasterosteid (three-spined stickleback, ninespine stickleback)	intestines, occasionally urinary bladder	Russia, Alaska
M. ochengense	9.4-10.8 x 4.8-5.4 x 4.8	freshwater Cypriniformes: cyprinid (goldfish)	gall bladder, kidney, urinary bladder	China
M. ochotense	12-14 x 7 x 6	marine Gadiformes: gadid (Pacific cod)	gall bladder	Japan
M. octospinum	9-11.4 x 4.8-6 x 4.8-5	freshwater Cypriniformes: cyprinid (grass carp)	ureters	China
M. odontobutis	8.9-10.7 x 7.2-10 1 x 5.5-6.9	freshwater Gobiiformes: odontobutid (donko)	intestines, urinary bladder	China
M. oliviforme	16.6-17.9 x 6.6-8.3 x 7.1-8.3	freshwater Siluriformes: bagrid (catfish 'albomarginatus')	intestines	China
M. omuli	15-16 x 5.6-7	freshwater Salmoniformes: salmonid (omul)	ureters	Lake Baikal
M. oncorhynchi	11-12 x 5-8 x 3-5	freshwater Salmoniformes: salmonid (masu salmon)	gall bladder	Japan
M. onychostomatis	13.6-14.4 x 6-7.2 x 5.6-6	freshwater Cypriniformes: cyprinid (tomp koukloug)	gall bladder	China
M. ophiocephali (syn. *Zschokkella*)	11-15.6 x 3-8 x 6-6.2	freshwater Anabantiformes: channid (northern snakehead, blotched snakehead, snakehead murrel); Cypriniformes: cyprinid (bighead carp, pale chub), xenocypridid (silver carp); Siluriformes: bagrid (Pratt's Yangtze catfish), silurid (Amur catfish)	bile ducts, gall bladder, intestines, liver, urinary bladder	Amur Basin, India, Caribbean
M. opsariichthysi	12.2-13.8 x 5.6-6 x 4.3-4.8	freshwater Cypriniformes: cyprinid (Chinese hooksnout carp)	liver	China
M. orientale	7.5-11 x 6-7 x 5-	freshwater Anguilliformes: anguillid	gall bladder	Amur River

	6.1	(Japanese eel); Cypriniformes: botiid (loach), cyprinid (Amur whitefin gudgeon, yunnani silemokk)		
M. oshoroense	16-21 x 8-11 x 7-10	marine Pleuronectiformes: paralichthyid (olive flounder), pleuronectid (dusky sole, yellowfin sole, starry flounder, blackfin flounder, Bering flounder)	gall bladder	Japan
M. osteochili	11.8 x 4.4 x 4.1	freshwater Cypriniformes: cyprinid (Salsbury's barb)	kidney	China
M. ovatum	13 x 6.5	marine Gadiformes: lotid (three-bearded rockling)	gall bladder	England
M. oviforme	10-13 x 7-9	marine Gadiformes: gadid (Atlantic cod); Kurtiformes: apogonid (cardinalfish); Labriformes: labrid (Mediterranean rainbow wrasse); Ovalentaria: embiotocid (white seaperch, shiner perch, pile perch, rainbow surf perch); Salmoniformes: salmonid (Atlantic salmon, chum salmon, chinook salmon, sockeye salmon, pink salmon, brown trout, lake trout, rainbow trout, Arctic char)	gall bladder	Europe
M. pagelli	22-28 x 9-11.5	marine Spariformes: sparid (white steenbras)	gall bladder	South Africa
M. papernae	9.6-14.4 x 4.8-8	marine Mugiliformes: mugilid (largescale mullet)	gall bladder	India
M. parvoviforme	8-11 x 5.5-7	marine Acanthuriformes: sciaenid (southern meagre)	gall bladder	South Africa
M. parvum	6.9-7.3 x 4.3-4.7 x 4.3-4.5	marine Blenniiformes: blenniid (tentacled blenny)	gall bladder	Russia
M. pearcyi	12-18 x 4.5-8.5	marine Gadiformes: macrourid (longarm grenadier)	gall bladder	Japan
M. percae	14.5-20.9 x 2.3-6	freshwater Perciformes: percid (yellow perch)	skin	Canada
M. perniciosum	12-13 x 6-7	freshwater Salmoniformes: salmonid (Arctic cisco); Scorpaeniformes: cottid (Baikal oilfish, little Baikal oilfish, Herzenstein's rough sculpin, Kessler's sculpin, vitim sculpin, bighead sculpin, longfin Baikal sculpin, red Baikal sculpin, Baikal yellowfin, Baikal sculpins (*bergianus, godlewskii, insularis, pallidus, werestschagini*))	gall bladder	Lake Baikal
M. petrocephali	21.5-27 x 6.5-9.8	freshwater Osteoglossiformes: mormyrid (mormyre)	gall bladder	Cameroon
M. pfeifferi (syn. *M. cyprini, pseudogobii p.p.*)	12-18 x 3-6 x 3-4.5	freshwater Cypriniformes: cobitid (spined loach), cyprinid (common carp, crucian carp, koi carp, goldfish, common bream, blue bream, white bream, common roach, Caspian roach, common dace, ide, asp, ziege, common rudd, common bleak, Kura bleak, sunbleak, Bulatmai barbel), nemacheilid (stone loach), tincid (tench); Perciformes: percid (European perch, ruffe)	gall bladder	Eurasia
M. phyllium	11 x 8	freshwater Cyprinodontiformes: poeciliid (western mosquitofish)	gall bladder	North America
M. polymorphum	12-14.2 x 5.5-6 x 4.6-5.2	freshwater Anabantiformes: osphronemid (round-tailed paradisefish); Beloniformes:	gall bladder	China

		adrianichthyid (Japanese rice fish); Cypriniformes: cyprinid (grass carp, bighead carp, mud carp, black carp, Chinese hooksnout carp, three-lips, goldfish, Wuchang bream, black Amur bream, white Amur bream, topmouth culter, lake skygazer, sharpbelly, Chinese false gudgeon, stone moroko), gobionid (longfin rhino gudgeon, gokuraku-haze), xenocypridid (hiina laikviidikas, silver carp)		
M. procerum	21.6-27 x 3.6-6.1	marine Argentiniformes: argentinid (greater argentine); Beryciformes: berycid (splendid alfonsino); Perciformes: latid (barramundi)	gall bladder	Atlantic, Indian Ocean
M. procyprisi	12.2-12.8 x 4.8-5.2 x 4.9	freshwater Cypriniformes: cyprinid (rock carp)	kidney	China
M. profundum [replacement name for *M. noblei* Zubtschenko]	30.6-34.6 x 6.6-8.2	marine Gadiformes: macrourid (roundnose grenadier)	gall bladder	Russia
M. pseudobagrusi	11.4-14.4 x 5.4-6 x 4.8-5.4	freshwater Siluriformes: bagrid (yellowhead catfish)	kidney	China
M. pseudocuneiforme	12-13.1 x 4.8-6.1 x 4.9-6.2	freshwater Cypriniformes: cyprinid (common carp)	gall bladder	China
M. pseudogobii	10.6-14 x 4.5-5.4 x 4.8-5	freshwater Anguilliformes: anguillid (Japanese eel); Cypriniformes: cyprinid (Chinese false gudgeon)	kidney	China, Russia
M. pseudolaubuca		freshwater Cypriniformes: xenocypridid (hiina laikviidikas)		China
M. pseudomacrocapsulare	11-12 x 6-8	freshwater Cypriniformes: cyprinid (gudgeon)	ureters	Russia
M. pulchrum	8.2-13.8 x 5.2-17.5	marine Gobiesociformes: gobiescid (two-spotted clingfish, Connemarra clingfish)	gall bladder	Russia
M. puntius	12-13.2 x 7-7.6 x 6-6.7	freshwater Cypriniformes: cyprinid (gold barb)	gall bladder	China
M. qiantangense	6.1-6.5 x 6.5-6.9	marine Perciformes: lateolabracid (Japanese seabass)	urinary bladder	China
M. queenslandicum	13.3-21.5 x 6.1-9.6	marine Ovalentaria: pomacentrid (scissortail sergeant, Indo-Pacific sergeant)	gall bladder	Australia
M. rarum	13-16 x 3-4	marine Perciformes: sebastid (hatsume)	gall bladder	Russia
M. rhinogobides	132.2-14.4 x 6.2-7.2 x 6.5	freshwater Cypriniformes: gobionid (harilik-nospelrunt)	liver	China
M. rhinogobie	11.3-12.1 x 3.1-3.7 x 2.2-3	freshwater Cypriniformes: gobionid (suuruim-nospelrunt)	kidney	China
M. rhodei	11-18 x 3.5-6.5 x 4.6-5.8	freshwater Cypriniformes: botiid (imperial flower loach), cyprinid (goldfish, Prussian carp, Japanese crucian carp, common carp, koi carp, common roach, Caspian roach, common dace, Danilevskii's dace, ide, Amur ide, rudd, asp, gudgeon, rainbow gudgeon, Chinese false gudgeon, common bleak, spirlin, ziege, European bitterling, Amur bitterling, Khanka spiny bitterling, common bream, white bream, blue bream, barbel steed, spotted steed), tincid (tench)	kidney, ureters, occasionally liver, muscles	Eurasia
M. rhomboideum	7.7 x 6.4	freshwater Scorpaeniformes:	kidney	Netherlands

		gasterosteid (ninespine stickleback)		
M. rimskykorsakowi	12-13 x 6.5-7 x 5	freshwater Gobiiformes: odontobutid (Chinese sleeper)	urinary bladder	Amur Basin
M. rostowstschikowi	12-13 x 6-6.5	freshwater Cypriniformes: cyprinid (Sattar snowtrout, Kura chub)	gall bladder	Russia
M. salvelini	12-16 x 5.2-6.4 x 4.6-6	freshwater Salmoniformes: salmonid (whitespotted char, Arctic char, rainbow trout)	urinary bladder, ureters	Russia
M. sangei	12-14.5 x 3.5-5	freshwater Anabantiformes: channid (obscure snakehead)	gall bladder	Cameroon
M. sarcocheilichthysi	16-18.5 x 5.1-6	freshwater Cypriniformes: cyprinid (rainbow gudgeon)	gall bladder	China
M. scardini	10.5-12 x 4-5	freshwater Cypriniformes: cyprinid (common rudd)	gall bladder	India
M. schalli	10.8-12.6 x 4.5-6.3	freshwater Siluriformes: mochokid (wahrindi)	gall bladder	Egypt
M. schilba	12.7-14.9 x 4.9-6.1	freshwater Siluriformes: schilbeid (African butter catfish)	gall bladder	Egypt
M. schizothoraxi	14.4-16 x 5.6-7.4 x 6.5	freshwater Cypriniformes: cyprinid (marinka tsunynska)	gall bladder	China
M. schulmani	13.3-14 x 7.3 x 8	freshwater Cypriniformes: cyprinid (common roach)	kidney	Russia
M. sciaenae	19.3 x 5.3	marine Eupercaria: sciaenid (Amoy croaker)	gall bladder	India
M. scorpii	8-10 x 4-5	marine Scorpaeniformes: cottid (shorthorn sculpin, fourhorn sculpin)	urinary bladder	White Sea
M. scripta	16.6-20.4 x 4.6-5.9	Testudines: emydid (red-eared slider)	renal tubules, gall bladder	North America
M. semilabei	9.6-12.8 x 5.6-8 x 5.2-5.6	freshwater Cypriniformes: cyprinid (jangtse kraapmokk)	gall bladder, kidney, ureter, urinary bladder	China
M. serum	9.8-12.4 x 3.7-5.4 x 3-4.3	freshwater Anguilliformes: anguillid (New Zealand longfin eel)	gut wall	Australia
M. shamama	14.8-16.8 x 5.6-7.2	freshwater Cypriniformes: cyprinid (Nile carp)	kidney	Egypt
M. shulmani	12-16 x 5.2-6.4 x 4.6-6	freshwater Salmoniformes: salmonid (Arctic char)	urinary bladder, ureters	Russia
M. sinilabi	15.5-18 x 5-7	freshwater Cypriniformes: cyprinid (rendahli bangaan, jangtse kraapmokk)	gall bladder	China
M. songtaoense	12-16 x 6.9-7.5	freshwater Cypriniformes: cyprinid (stone moroko)	gall bladder	China
M. sphaericum (syn. *M. sphericum*)	14-20 x 7-10	marine Beloniformes: belonid (garfish); Carangiformes: carangid (snubnose pompano); Perciformes: zoarcid (checker eelpout, Newfoundland eelpout); Pleuronectiformes: pleuronectid (American plaice, Atlantic halibut, Greenland halibut, witch); Scorpaeniformes: anarhichadid (Atlantic wolffish, spotted wolffish), liparid (Atlantic snailfish), scorpaenid (beaked redfish, Acadian redfish)	gall bladder	France
M. spinosum	6.4-8.4 x 7.2-10.8 x 6-6.8	freshwater Cypriniformes: cyprinid (bighead carp), gobionid (hele-hoberunt), xenocypridid (silver carp); Tetraodontiformes: tetraodontid (obscure pufferfish)	urinary bladder, kidney, ureters	China
M. streisingeri	7.4-9.3 x 4.5-5.6 x 3.6-4.9	freshwater Cypriniformes: cyprinid (zebrafish)	kidney	North America
M. striatum	10-14 x 6-8	marine Acanthuriformes: sciaenid	gall bladder	Brazil

		(southern kingfish, ground croaker)		
M. striatusi	11.1-18.7 x 4.7-7	freshwater Anabantiformes: channid (snakehead murrel)	gall bladder	India
M. theragrae	16-17 x 5-7	marine Gadiformes: gadid (Alaska pollock); Scorpaeniformes: liparid (polka-dot snailfish)	gall bladder	Sea of Japan
M. therapon	9-12 x 4	marine Perciformes: terapontid (coal grunter, leathery grunter)	gall bladder	England, Australia
M. tictoi	11.5-14.2 x 4.4-5.3	freshwater Cypriniformes: cyprinid (ticto barb)	kidneys	India
M. tongrenense	10.5-12 x 5.5-6.5	freshwater Cypriniformes: cyprinid (hele-hoberunt)	gall bladder	China
M. trachinorum	17.2 x 8.8	marine Trachiniformes: trachinid (lesser weever)	gall bladder	England
M. triangulum	8-8.5 x 5.6-6.6 x 4.2-4.7	marine Perciformes: lateolabracid (Japanese seabass)	urinary bladder	Korea
M. truttae (syn. *M. salmonis*)	10.5-13.9 x 5.5-7.3 x 4.5-7	freshwater Cypriniformes: cyprinid (rendahli bangaan); Salmoniformes: salmonid (brown trout, coho salmon, Amur whitefish, sharp-snouted lenok) [cycle involves raabeia-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)]	gall bladder, liver	Eurasia, North America
M. tsudae	14-19 x 5-9	marine Scorpaeniformes: scorpaenid (white-edged rockfish, broadbanded thornyhead)	gall bladder	Sea of Japan
M. tuanfengense	18-20.8 x 9.1-10.4 x 8.8-9.2	freshwater Cypriniformes: botiid (honeycomb loach)	liver, intestines	China
M. uchiyamae	13.5 x 8 x 6	freshwater Anguilliformes: anguillid (Japanese eel)	kidney	Japan
M. umblae	12 x 7.5	freshwater Salmoniformes: salmonid (Arctic char)	urinary bladder, ureters	France
M. umbri	12-14.4 x 2.4-4.8	freshwater Esociformes: umbrid (central mudminnow)	kidney, renal tubules	North America
M. ventricosum	10.4-13 x 6.5-7	freshwater Salmoniformes: salmonid (Arctic grayling)	urinary tract, renal tubules	Amur Basin
M. virensi	13.3-14.6 x 6.6	marine Gadiformes: gadid (saithe)	gall bladder	Russia
M. volitans	21.3-22 x 5.2-5.9	marine Syngnathiformes: dactylopterid (flying gurnard)	gall bladder	Brazil
M. yibinense	11-12 x 7.2-8 x 6-6.4	freshwater Cypriniformes: cyprinid (pingi logsucker)	gills, kidneys, liver, testes, mesentery, gall bladder	China
M. yinjiangensis	14.2-15 x 6.2-7	freshwater Cypriniformes: cyprinid (yunnani silemokk)	gall bladder	China
M. yunnanense	12.8-13.6 x 4.8-5.6 x 4.8-5.7	freshwater Cypriniformes: cyprinid (silver minnow)	gall bladder	China
M. zapotecus	10.8-14.6 x 6.9-11.3 x 5.6-7.1	freshwater Characiformes: characid (unspecified astyanax); Gobiiformes: oxudercid (river goby); Mugiliformes: mugilid (mountain mullet)	gall bladder	Mexico
M. zealandicum	6.4-10.5 x 3.3-4.5	freshwater Anguilliformes: anguillid (short-finned eel, New Zealand longfin eel)	gills	Australia
Genus ***Paramyxidium*** (lemon-shaped spores, with valvular striations, 2 polar capsules at opposite ends)				
P. branchialis	10.7-12.3 x 6.6-7.8	freshwater Anguilliformes: anguillid (European eel)	gills	Iceland
P. bulaniillinois	6.1-6.9 x 4.2-5.1	marine Elopiformes: megalopid (Indo-Pacific tarpon)	kidney tubules	Malaysia
P. giardi (syn. *Myxidium, M.*	9-15 x 5-7.5 x 2.9-6	freshwater Anguilliformes: anguillid (European eel, American eel,	gills, skin, fins, kidney, gut,	cosmopolitan

anguillae, enchelypterygii, illinoisense, serum, zealandicum) [type species]		Japanese eel, speckled longfin eel, African longfin eel, New Zealand longfin eel, short-finned eel, Indian shortfin eel); Perciformes: percid (European perch) [cycle involves aurantiactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)	gonads, gall bladder, urinary bladder, swim bladder	
P. magni	10.8-12.9 x 7-8.4	freshwater Anguilliformes: anguillid (European eel)	stomach wall	Iceland
Genus ***Sigmomyxa*** (ellipsoidal spores, thin protrusion at tips of polar capsules, coelozoic in marine fish)				
S. sphaericum (syn. *Myxidium*) [type species]	15-20 x 6-12.8 x 7.9-9.1	marine Beloniformes: belonid (garfish); Blenniiformes: blenniid (rippled rockskipper, lawnmower blenny, unspecified combtooth blenny); Gadiformes: gadid (merling) [cycle involves tetractinomyxon-type actinospores in Polychaeta: nereidid (*Nereis pelagica*)]	gall bladder	Mediterranean, Australia
S. elmatboulii (syn. *Myxidium*)	19-23 x 9-12 x 8.5-12	marine Beloniformes: belonid (Red Sea houndfish)	gall bladder	Egypt
Genus ***Soricimyxum*** (ovoid spores with rounded ends, coelozoic in bile ducts of terrestrial mammals)				
S. fegati [type species]	6.3-7.5 x 4.3-6 x 3.5	terrestrial Eulipotyphla: soricid (common shrew)	bile ducts	Europe
S. minuti	12.3-13.3 x 8.4-9.6 x 7.4-8.4	terrestrial Eulipotyphla: soricid (pygmy shrew)	bile ducts, gall bladder	Europe
Genus ***Zschokkella*** (ellipsoidal spores with blunt ends, 2 subspherical polar capsules at opposite poles, mostly coelozoic in fish and reptiles)				
Z. acheilognathi	10-14 x 6-7 x 6-7	freshwater Cypriniformes: cyprinid (slender bitterling)	gall bladder, bile ducts	Japan
Z. admiranda	10.6-12.5 x 7.5-8.8	marine Mugiliformes: mugilid (flathead grey mullet)	gall bladder	Russia, Ukraine
Z. anguillae	9.7-11 x 4.8-5.5 x 4.8-5.5	freshwater Anguilliformes: anguillid (Japanese eel); Cypriniformes: gobionid (hele hoberunt), xenocypridid (hiina laikviidikas)	urinary bladder, liver, kidney	China
Z. atlantica	19.9-21.3 x 12-13.3	marine Gadiformes: macrourid (roundnose grenadier)	gall bladder	Russia
Z. auerbachi (syn. *Parazschokkella*)	11 x 6	Anura: bufonid (Asian common toad)	gall bladder	China
Z. auratis	8.7-10.3 x 6.5-8 x 6.5-8	marine Spariformes: sparid (gilthead seabream)	gall bladder	Portugal
Z. australis	16-20 x 10.6-12	marine Perciformes: channichthyid (mackerel icefish)	gall bladder	Antarctic
Z. balistoidi	9.8-12.3 x 5.4-7.8	marine Tetraodontiformes: balistid (titan triggerfish)	gall bladder	Australia
Z. bicarinatis	10.3-12.1 x 6.8-8.7	marine Scombriformes: scombrid (shark mackerel)	gall bladder	Australia
Z. botia	9-11.4 x 6.3-7.6 x 6.1	freshwater Cypriniformes: botiid (ringelschmerle)	gall bladder	China
Z. candia	10.3-12.2 x 6.8-8.8	marine Labriformes: scarid (Mediterranean parrotfish); Scorpaeniformes: scorpaenid (black scorpionfish)	gall bladder	Greece
Z. carassii	13.2-15.6 x 8.4-9 x 7.8	freshwater Cypriniformes: cyprinid (common carp, Japanese white crucian carp, goldfish, spotted steed)	gall bladder. kidney, urinary bladder, liver, spleen	China
Z. cardinalis	9-11.6 x 6.1-8.5	marine Kurtiformes: apogonid (five-lined cardinalfish)	gall bladder	Australia

Z. cascasiensis	8-10.5 x 6.5-8	marine Mugiliformes: mugilid (yellowtail mullet)	gall bladder	India
Z. channae	16.5-18.7 x 8.5-11.1	freshwater Anabantiformes: channid (spotted snakehead)	kidney tubules	India
Z. chiliensis	17.8-18.6 x 8.4-9 x 7.7-8.2	freshwater Centrarchiformes: sinipercid (slender mandarinfish)	intestines	China
Z. chungshanensis	9-12 x 6 x 6	freshwater Anguilliformes: anguillid (Japanese eel)	foregut	China
Z. cirrhinae	20.4-23.8 x 10.2-12.7	freshwater Cypriniformes: cyprinid (reba carp)	gall bladder	India
Z. coelatusae	12-14.8 x 8.9-11.6	marine Siluriformes: ariid (engraved catfish)	gall bladder	India
Z. compressis	8.5-11.3 x 6.2-7.2	marine Kurtiformes: apogonid (ochre-striped cardinalfish)	gall bladder	Australia
Z. costata	9-10.5 x 5-6.5 x 3.9-5	freshwater Cypriniformes: cyprinids (common roach)	gall bladder, urinary bladder, ureters, kidneys	Europe
Z. ctenopharyngodonis	15.4-16.2 x 7.7 x 7.8	freshwater Cypriniformes: cyprinid (grass carp)	gall bladder	China
Z. cyprini	11-15 x 7-10	freshwater Cypriniformes: cyprinid (common carp)	gall bladder, bile ducts	United Kingdom
Z. dogieli	15-16 x 9	marine Mugiliformes: mugilid (unspecified mullet)	gall bladder	Russia
Z. donecae (occasional mis-spelling '*donetzae'*)	14.4-17.1 x 5.4-6.3 x 5-6	freshwater Cypriniformes: cyprinid (largescale silver carp)	gall bladder	Vietnam
Z. egyptica	12.2-15.4 x 9.5-11	marine Mulliformes: mullid (freckled goatfish); Siluriformes: plotosid (striped eel catfish)	gall bladder	Egypt
Z. embiotociddis	13-17 x 9.5-13 x 9-11	marine Ovalentaria: embiotocid (pile perch, striped surfperch)	gall bladder	North America
Z. epinepheli	8-11 x 6.6-7.5	marine Perciformes: epinephelid (white grouper)	gall bladder	Tunisia
Z. flexosasuturalis	12-15 x 6.4-8 x 7.7-9.8	marine Pleuronectiformes: paralichthyid (Patagonian flounder)	urinary bladder	Argentina
Z. floridanae	12-17 x 8-17	marine Cyprinodontiformes: cyprinodontid (goldspotted killifish)	gall bladder	North America
Z. fossilae	10.3 x 4.1-5.2	freshwater Clupeiformes: dorosomatid (hilsa herring); Siluriformes: heteropneustid (Asian stinging catfish)	gall bladder	India
Z. fujitai	13.5-6.5 x 6.5	estuarine Gobiiformes: oxudercid (dusky tripletooth goby)	gall bladder	Japan
Z. ganapatii	11.2-15.5 x 7.7-10.3	marine Mugiliformes: mugilid (largescale mullet)	gall bladder	India
Z. globulosa	9-17 x 7-13	marine Gadiformes: bathygadid (bullseye macrops), macrourid (arrowtooth grenadier, blackfin grenadier, longarm grenadier, largenose grenadier, spearnose grenadier, abyssal grenadier, carapine grenadier, longbear grenadier, marlin-spike grenadier, ghostly grenadier, pugnose grenadier, smooth grenadier, California grenadier, Humboldt grenadier, Japanese grenadier, Misaki grenadier, Mugura grenadier, Pacific grenadier, Peruvian grenadier, western Atlantic grenadier, 'macrolepis' grenadier, 'striatulus' grenadier, notable whiptail, furry whiptail, chiri-kosokodara, kyushu-hige, sujidara); Tetraodontiformes:	gall bladder, urinary bladder, kidney	cosmopolitan

		tetraodontid (northern puffer)		
Z. glossogobii	9.6-11.4 x 6.4-8	freshwater Gobiiformes: gobiid (tank goby)	gall bladder	India
Z. gobidiensis	10-13.5 x 6-9	freshwater Gobiiformes: gobiid (tank goby)	gall bladder	India
Z. gobii	10.5-11 x 6.2-7 x 6-6.8	freshwater Cypriniformes: gobionid (Siberian gudgeon)	kidney	China
Z. guelaguetza	9.1-11.9 x 5.6-7.5 x 6.1-7.3	freshwater Characiformes: characid (unspecified astyanax); Gobiiformes: oxudercid (river goby)	gall bladder	Mexico
Z. helmii	10-11 x 7-8	marine Perciformes: siganid (marbled spinefoot)	gall bladder	Egypt
Z. heronensis	10-11 x 7	marine Perciformes: chaetodontid (blueblotch butterflyfish)	gall bladder	Australia
Z. hildae [type species]	16-19 x 12-18	marine Gadiformes: gadid (Atlantic cod, Baltic cod, White Sea cod, Arctic cod, small-headed cod, winter cod, saffron cod, Alaska pollock, saithe, haddock), phycid (greater forkbeard)	gall bladder, urinary bladder, kidney	Atlantic, Barents Sea, White Sea
Z. hongtsensis	11.2-12.3 x 5.4-5.8 x 4.6-5.4	freshwater Siluriformes: bagrid (‘albomarginatus’ catfish)	gall bladder	China
Z. icterica	11.9-12.9 x 6.6-8 x 3.8-4.9	marine Perciformes: siganid (dusky spinefoot)	gall bladder, liver	Israel
Z. illishae	12.4 x 6.2	marine Clupeiformes: dorosomatid (hilsa herring)	gall bladder	India
Z. iskovi	9.3-10.7 x 6-6.7 x 6.7	marine Gadiformes: lotid (shore rockling); Spariformes: sparid (annular seabream); Trachiniformes: uranoscopid (Atlantic stargazer)	gall bladder	Russia, Ukraine
Z. jaimeae	9.7-13.8 x 6.4-7.8	marine Beloniformes: belonid (stout longtom)	gall bladder	Australia
Z. kudoi	12-17 x 7-11	marine Gadiformes: macrourid (roughhead grenadier)	kidney	Canada
Z. labeonis	9.3-12.9 x 4.3-7.1	freshwater Cypriniformes: cyprinid (mustuim-narmasmokk)	gall bladder	India
Z. leptatherinae	13-17 x 9.5-14 x 9-13	marine Atheriniformes: atherinid (silver fish, small mouth hardyhead, small scale hardyhead, short snout hardyhead, pikehead hardyhead)	gall bladder, bile ducts	Australia
Z. linghuensis	9.4-9.6 x 5.8-6.2 x 5.6-6.2	freshwater Cypriniformes: cyprinid (common carp)	gall bladder	China
Z. lissemysi (syn. *Parazschokkella*)	18.5-22.6 x 14.4-16.4	Testudines: trionychid (Indian flapshell turtle)	gall bladder	India
Z. lophii	16.8-24 x 12.7-16.8	marine Lophiiformes: lophiid (yellow goosefish)	urinary bladder	Japan
Z. macrocapsula	14-17.5 x 12.6-14,6	marine Atheriniformes: atherinid (small mouth hardyhead, silver fish)	gall bladder	Australia
Z. macrouri	14.6-16 x 9.3-11.9	marine Gadiformes: macrourid (roundnose grenadier, longfin grenadier)	urinary bladder	Russia
Z. magna	20.4-22.3 x 15.4-18.5 x 13.5-15.4	freshwater Mugiliformes: mugilid (so-iuy mullet)	gall bladder	China
Z. mahseni	7.8-10.4 x 10.7-11.6	marine Eupercaria: letherinid (sky emperor)	gall bladder	Egypt
Z. meglitschi	7-13.5 x 14-26 x 9.8-11	marine Gadiformes: macrourid (abyssal grenadier, longfin grenadier, western softhead grenadier, spinnaker grenadier, Aloha grenadier, California grenadier, Chilean grenadier, ‘gladius’ grenadier, filamented rattail, pectoral rattail, itodara)	urinary bladder, kidney, gall bladder	Americas, Asia
Z. melanosticti	9.5-10.5 x 6-7 x 6-	Anura: bufonid (Asian common toad)	gall bladder	India

	6.4			
Z. menopterusi	18-22 x 9.3-12.7 x 8.8-10	freshwater Synbranchiformes: synbranchid (Asian swamp eel)	intestines	China
Z. microcapsula	7-12 x 4-8.3	marine Gadiformes: macrourid (Mugara grenadier, 'macrolepis' grenadier, 'velifer' grenadier)	gall bladder	Asia
Z. minuta	7.8-9 x 4.8-6 x 4.8-5.2	freshwater Anguilliformes: anguillid (Japanese eel); Cypriniformes: cyprinid (common carp, goldfish, sharpbelly); Siluriformes: silurid (Amur catfish); Tetraodontiformes: tetraodontid (obscure puffer)	gall bladder, kidney, urinary bladder, intestines	China
Z. mugilis	9.2-11.3 x 5.4-7.7 x 6-7.2	marine Mugiliformes: mugilid (flathead grey mullet, thinlip mullet, leaping mullet)	gall bladder	Eurasia
Z. mugilidae	13.5-18 x 9-13.5	marine Mugiliformes: mugilid (leaping African mullet)	gall bladder	Senegal
Z. mystae	15.3-20.2 x 6.5-9	marine Siluriformes: bagrid (long whiskers catfish)	gall bladder	India
Z. nanhaiensis	9.2-10.8 x 6.9-7.7 x 5.8-6.3	freshwater Gobiiformes: odontobutid (dark sleeper)	urinary bladder	China
Z. nilei	9-11.2 x 5.5-7.5 x 6-6.8	freshwater Cichliformes: cichlid (Nile tilapia)	kidney	Egypt
Z. nova	8-12 x 5-7 x 3.6-6.5	freshwater Anguilliformes: anguillid (Japanese eel); Cypriniformes: cyprinid (grass carp, crucian carp, Prussian carp, goldfish, common bream, vimba bream, common bleak, common chub, common rudd, common roach, common dace, ide, Amur ide, ziege, white bream, Kura nase, striped bystranka, gudgeon), tincid (tench); Mugiliformes: mugilid (golden grey mullet, flathead grey mullet); Perciformes: percid (European perch, ruffe); Salmoniformes: salmonid (European cisco, lavaret, brown trout); Scorpaeniformes: cottid (European bullhead) [cycle involves siedleckiella-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)]	gall bladder	Eurasia
Z. ohlalae	8.9-10.7 x 6.4-7.9	marine Kurtiformes: apogonid (yellow-striped cardinalfish)	gall bladder	Australia
Z. orientalis	9-13 x 6-7.8 x 5.2-6	freshwater Salmoniformes: salmonid (pink salmon, coho salmon, chinook salmon, chum salmon, rainbow trout, Arctic char, whitespotted char); Anabantiformes: osphronemid (three spot gourami)	gall bladder	Russia, Vietnam
Z. ovata	13 x 6.5	marine Gadiformes: lotid (shore rockling)	gall bladder	United Kingdom
Z. oviformis	13.6-17 x 8.5-11.9 x 6.8-9.1	freshwater Cypriniformes: acheilognathid (hiina morukas), cyprinid (Chinese false gudgeon), gobionid (loshani nokisrunt)	gall bladder, bile ducts	China
Z. parasiluri	11-15 x 4-6 x 5.6-6	freshwater Siluriformes: bagrid (yellowhead catfish), pangasid (basa), silurid (Asian redtail catfish, Amur catfish, Soldatov's catfish, Yangtze catfish); Anabantiformes: osphronemid (three spot gourami)	gall bladder	Asia

Z. platystomusi	10.5-12.2 x 6.5-7.4	marine Siluriformes: ariid (flatmouth sea catfish)	gall bladder	India
Z. pleomorpha	14.4-17.6 x 6.4-7.9	freshwater Tetraodontiformes: tetraodontid (green puffer)	urinary tract	Europe (ex: Asia)
Z. polymorpha	14.4-17.6 x 6.4-7.9	freshwater Tetraodontiformes: tetraodontid (green puffer)	gall bladder	Czech Republic
Z. pseudolaubuci	8.8-10.4 x 4.8-5.8 x 2.8-4	freshwater Cypriniformes: xenocypridid (hiina laikviidikas)	gall bladder	China
Z. pseudosciaena	9.5-13.5 x 4.5-7	marine Euparcaria: sciaenid (Ganges jewfish)	renal tubules, ureters	India
Z. pulchella	22.7-24 x 13.3-14.6	marine Gadiformes: morid (Patagonian cod)	urinary bladder	Argentina
Z. rhinogoboides (syn. *Myxidium*)	12-13.6 x 7.2-8.4 x 5.6-7.2	freshwater Cypriniformes: cyprinid (Chinese false gudgeon); Gobiiformes: oxudercid (gokuraku-haze)	skin, liver	China
Z. rovignensis	18-30 x 15 x 10-15	marine Gadiformes: bathygadid (blackmouth rattail), macrourid (arrowtooth grenadier, shoulderspot grenadier, Mexican grenadier, furry whiptail); Scorpaeniformes: scorpaenid (black scorpionfish, red scorpionfish)	urinary bladder, ureters, kidneys	Croatia, Mexico, China
Z. russelli	13.2-16.6 x 8.6-9.9	marine Gadiformes: lotid (shore rockling, five-bearded rockling)	gall bladder	Britain
Z. salvelini	19.1-21 x 10.9-14.5 x 10.2-11.5	freshwater Salmoniformes: salmonid (brook trout)	kidney	Canada
Z. saurogobionis	17.9-19.2 x 9-10.8 x 10.2-11.5	freshwater Cypriniformes: gobionid (dumerili sisalrunt)	gall bladder	China
Z. schizothoraxi	10.4-11.2 x 6.8-7.2 x 7	freshwater Cypriniformes: cyprinid (marinka tsunynska)	gall bladder	China
Z. scomberosis	16.5-19.5 x 9-12	marine Carangiformes: carangid (Talang queenfish)	gall bladder	India
Z. shulmani	15.3-16 x 9.3-10.6	marine Gadiformes: macrourid (roundnose grenadier)	urinary bladder	Russia
Z. sichuanensis	24.5-26.6 x 13.8-15.1 x 13.6-15	freshwater Cypriniformes: xenocypridid (silver carp)	kidney	China
Z. siegfriedi	16.7-18.2 x 9.2-11.6 x 8.5-11	marine Gadiformes: gadid (polar cod)	urinary tract	Arctic
Z. sinocylochilusi	11.2-12 x 5.6-6.4 x 5.6	freshwater Cypriniformes: cyprinid (golden-line barbel)	gall bladder	China
Z. soleae	13.6-14,4 x 10.4-11.2	marine Pleuronectiformes: soleid (common sole)	gall bladder	Tunisia
Z. stettinensis	9.6-11.6 x 7.2-10 x 7.6-8	freshwater Anguilliformes: anguillid (European eel)	urinary bladder	Poland
Z. striata	13-14 x 6-7 x 5.5-6	freshwater Cypriniformes: cyprinid (grass carp, Chinese false gudgeon)	gall bladder	Asia
Z. sturionis	10-14.5 x 6-9.3 x 6-7	marine/freshwater Acipenseriformes: acipenserid (European sea sturgeon, Russian sturgeon, starry sturgeon)	gall bladder	England, Russia
Z. tetrafluvi	10.5-11.3 x 6.8-7.8	freshwater Tetraodontiformes: tetraodontid (green puffer)	gall bladder	Europe (ex: Asia)
Z. tilapiae	15.6-16.8 x 8.6-10 x 9.6-10	freshwater Cichliformes: cichlid (Mozambique tilapia)	intestines	China
Z. trachini	14.4-16 x 9-10.8	marine Trachiniformes: trachinid (greater weever)	gall bladder	Tunisia
Z. tunghuensis	13.6-17 x 7.7-8.8	freshwater Cypriniformes: cyprinid (stone moroko)	gall bladder	China
Z. variabile	14-16 x 7.3-9.3 x 7	marine Gadiformes: macrourid (bigeye grenadier)	urinary bladder	Argentina
Z. yangkiangensis	12-14.4 x 8.4-10.8 x 7.4-8.6	freshwater Gobiiformes: oxudercid (gokuraku-haze)	skin	China

Family **Myxobilatidae** (elongate spores, pointed anteriorly)				
Genus ***Acauda*** (pyriform spores with ridged valves)				
A. elongata (syn. *Mitraspora, Hoferellus*)	15-17 x 5-6 x 4.5-5.5	freshwater Perciformes: centrarchid (green sunfish, bluegill, largemouth bass)	urinary tubules, kidney	North America
A. hoffmani [type species]	17.9-21.8 x 6.9-11	freshwater Cyprinodontiformes: fundulid (banded killifish); Perciformes: centrarchid (bluegill)	kidney tubules	North America
Genus ***Hoferellus*** (syn. *Hoferia, Mitraspora*) (spores anteriorly pointed with filaments at posterior end, 2 polar capsules)				
H. alosae	9.1-10.3 x 7.7-9.2	freshwater/marine Clupeiformes: alosid (Allis shad)	urinary bladder	France
H. anguilli (syn. *Mitraspora*)	8.5-10.2 x 7.3-8.8	freshwater Anguilliformes: anguillid (Japanese eel)	urinary tract	China
H. anurae	7-8.9 x 6-7.9 x 4.5-5.2	Anura: hyperoliid (common reed frog, variable reed frog, Kivu reed frog, striped spiny reed frog)	renal tubules, ureters, intestines	Nigeria
H. azevedoi	5.2-5.6 x 6.3-7.7	freshwater Cichliformes: cichlid (kunapari)	urinary bladder	Brazil
H. carassii (syn. *H. conifer, Mitraspora*)	10.2-17.3 x 5-11.8 x 3.6-7.4	freshwater Cypriniformes: cyprinid (goldfish, Prussian carp) [cycles involving aurantiactinomyxon-type actinospores in Oligochaeta: naidid (*Nais* cf. *elingius*) and neoactinomyxum-type actinospores in Oligochaeta: naidid (*Branchiura sowerbyi*)]	urinary tract, kidney [kidney bloater disease, kidney enlargement disease]	Eurasia, North America
H. caspialosum (syn. *Mitraspora*, *Sphaerospora*)	8.5 x 7.7	marine Clupeiformes: alosid (Caspian shad, Pontic shad, Twait shad, Black Sea shad)	renal tubules	Caspian Sea, Black Sea
H. caudatus (syn. *Mitraspora, Sphaerospora*)	10-11	freshwater/marine Clupeiformes: alosid (agone, Twait shad), engraulid (European anchovy, Azov anchovy)	renal tubules, urinary bladder	Italy, Black Sea
H. changkiangensis	6.8-7.2 x 6.4 x 6.8-7.2	freshwater Siluriformes: sisorid (kiinanvirtamonni)	urinary bladder	China
H. cyprini (syn. *Hoferia, Mitraspora, Sphaerospora*) [type species]	7.4-13.5 x 5.2-9 x 4.8-8	freshwater Cypriniformes: cyprinid (common carp, Crucian carp, koi carp, Amur carp, Prussian carp, goldfish) [cycle involves aurantiactinomyxon-type actinospores in Oligochaeta: naidid (*Nais* sp.)]	urinary tract, kidney	Eurasia, Australasia
H. donecii (syn. *Mitraspora, Sphaerospora*)		marine Clupeiformes: ehiravid (anchovy sprat, Black Sea sprat)	ureters	Russia
H. dubinini (syn. *Mitraspora, Sphaerospora*)	8-10.5 x 7.7-8.5 x 7.3-8.5	freshwater Siluriformes: bagrid (Ussuri catfish)	urinary bladder	Korea
H. gilsoni (syn. *Sinuolina, Sphaerospora*)	7.2-8.7 x 6.7-8.7	freshwater Anguilliformes: anguillid (European eel)	urinary tract	Hungary
H. glyptothoraxi (syn. *Mitraspora*)	9.1-10.6 x 6-7.6 x 7.6-9.1	freshwater Siluriformes: sisorid (kiinanvirtamonni)	urinary bladder, kidneys	China
H. gnathonemi	10.3-14.3 x 9.9-12.7 x 6.3-9.4	marine Osteoglossiformes: mormyrid (Peter's elephantnose fish)	kidney tubules	Europe
H. hunanensis (syn. *Mitraspora*)	7.8-8.4 x 7.4-8.4 x 3.6-4.2	freshwater Cypriniformes: cyprinid (goldfish)	urinary bladder	China
H. hupehensis	9-10.8 x 7.2-8.4 x 6-7.2	freshwater Cypriniformes: cyprinid (goldfish)	urinary bladder	China
H. jurachni	8.5-12.5 x 6.4-7.5	marine Clupeiformes: alosid (Black Sea shad)	urinary bladder	Ukraine

H. jutubensis	6.1 x 5.5	freshwater Siluriformes: auchenipterid (mandube)	urinary bladder	Brazil
H. liocasis (syn. *Mitraspora*)	8.2-8.8 x 7-9 x 7.2-7.4	freshwater Siluriformes: bagrid (Brashnikov's catfish)	gills	China
H. minuta (syn. *Mitraspora*)	7-8 x 6	freshwater Cypriniformes: cyprinid (common carp)	urinary tract	China
H. plecoglossi (syn. *Mitraspora*)	nr	freshwater Osmeriformes: plecoglossid (ayu sweetfish)	kidney	Asia
H. pulvinatus	6-7.2 x 4.7-5.3	freshwater Siluriformes: pangasiid (striped catfish)	urinary bladder	Eurasia
H. reichenowi (syn. Sphaerospora)	9 x 10	freshwater Anguilliformes: anguillid (European eel)	urinary bladder, gut	Europe
H. sichuanensis (syn. *Mitraspora*)	10.6-16.3 x 6.1-8.2 x 6-7.6	freshwater Cypriniformes: cyprinid (goldfish)	urinary tract	China
H. schulmani	8-10 x 7-8 x 4.5-5	freshwater Cypriniformes: cyprinid (crucian carp)	gall bladder	Russia
H. sinensis (syn. *Mitraspora*)	7.2-9 x 6.2-7.2 x 5.8-7.8	freshwater Cypriniformes: cobitid (pond loach), cyprinid (bighead carp); Siluriformes: bagrid (yellowhead catfish, korakinos)	urinary bladder, ureters, kidney	China
H. wuchangensis (syn. *Mitraspora*)	8.4-13.2 x 7-8.4 x 6.6-7.8	freshwater Cypriniformes: cyprinid (goldfish)	urinary bladder	China
H. yiduensis (syn. *Mitraspora*)	7.2-8.4 x 4.8-5.5 x 5.8-6.2	freshwater Perciformes: sinipercid (mandarin fish)	kidney	China
Genus ***Myxobilatus*** (spindle-shaped spores, with 2 long posterior projections)				
M. accessobranchialis	11-12.5 x 4.4-4.6 x 2.8-3.1	freshwater Siluriformes: clariid (African catfish)	arborescent accessory breathing organ	Africa
M. anguillaris	5-7.5 x 3.3-4.2	estuarine Gobiiformes: gobiid (eel worm goby)	gills	India
M. anteronippus	11.4-13.5 x 6.1-6.9 x 6.7-7.2	estuarine Gobiiformes: gobiid (bearded worm goby)	opercula, fins	India
M. asymmetricus	10 x 22	freshwater Perciformes: percid (walleye)	urinary bladder	North America
M. baicalensis (syn. *Henneguya*)	24-30 x 5.5-7.5	freshwater Scorpaeniformes: cottid (bighead sculpin, stone sculpin, vitim sculpin, Herzenstein's rough sculpin, Kessler's sculpin, Baikal yellowfin)	urinary bladder	Lake Baikal
M. carassii	40-42 x 11.4-12.6 x 5-5.5	freshwater Cypriniformes: cyprinid (goldfish)	urinary tract	China
M. caudalis	7 x 6	freshwater Acanthuriformes: sciaenid (freshwater drum)	urinary bladder	North America
M. channi	16.5-20.1 x 4.6-6.7 x 4.5-6.8	freshwater Anabantiformes: channid (northern snakehead)	alimentary tract	China
M. cheni	15.6-26.6 x 5.1 x 6-6.4	freshwater Cypriniformes: cyprinid (David's schizothoracin)	urinary bladder	China
M. convexum	19-38 (8.2-9.3) x 7.3-8.2	marine Blenniiformes: blenniid (tentacled blenny)	urinary tract	Russia
M. cotti	9.8-14.4 x 4.8-7.2 x 6-7.2	freshwater Perciformes: centrarchid (pumpkinseed); Scorpaeniformes: cottid (slimy sculpin, mottled sculpin)	urinary bladder	North America
M. fossilis	26.7-40.5 (13.2-18) x 5.9-9	freshwater Siluriformes: heteropneustid (Asian stinging catfish)	urinary bladder	India
M. fragilicaudus	4.3-6.4	freshwater Scorpaeniformes: cottid (European bullhead)	ureters	Russia
M. gasterostei (syn. *Henneguya*) [type species]	33-48 (15) x 5.6-6.5 x 6.5-7.6	freshwater Scorpaeniformes: gasterosteid (three-spined stickleback, ninespine stickleback) [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid	urinary bladder, ureters, kidney	Eurasia, North America

		(*Nais communis*)]		
M. gobii	26.3-30 (11.2-12.5) x 7-7.5 x 6-6.2	freshwater Cypriniformes: cyprinid (gudgeon)	urinary system	Russia
M. hemiculteri	11.4-13.2 x 5.4-7.2 x 6-6.5	freshwater Cypriniformes: cyprinid (sharpbelly)	ureter, kidneys	China
M. legeri (syn. *Henneguya*)	12-22.5 (11.5-14) x 6-8 x 5-7	freshwater Cypriniformes: cyprinid (common roach, common bleak, ide, common bream, white bream, zope, golden shiner), nemacheilid (stone loach); Scorpaeniformes: cottid (European bullhead)	urinary bladder, ureters, kidney	Europe
M. mastacembeli	8.5-12.5 x 4.6-6.2	freshwater Synbranchiformes: mastacembelid (zig-zag eel)	intestines	India
M. medius (syn. *Henneguya*)	24-30 x 5-7.5 x 7-9	freshwater Scorpaeniformes: gasterosteid (three-spined stickleback, ninespine stickleback, Ukrainian stickleback)	renal tubules	Eurasia
M. mictosporus (syn. *Henneguya mictospora*)	13.5-15 x 8-9 x 6-7.5	freshwater Perciformes: centrarchid (green sunfish, orange-spotted sunfish, largemouth bass)	urinary bladder	North America
M. minutus	7-8 x 3.8-4.8	marine Pleuronectiformes: paralichthyid (Patagonian flounder)	gall bladder	Argentina
M. nostalgicus	11 x 8.1	freshwater Cypriniformes: tincid (tench)	urinary tract	Europe
M. notopterus	30.8-39.2 (8.4-9.8) x 4.2-5.6	freshwater Osteoglossiformes: notopterid (bronze featherback)	gall bladder	India
M. noturi	7.2-10.8 x 6-7.2 x 6-7.2	freshwater Siluriformes: ictalurid (tadpole madtom)	urinary bladder	North America
M. odontamblyopusi	8.1-10.3 x 4.8-6.3	estuarine Gobiiformes: oxudercid (rubicundus eel goby)	gills	India
M. ohioensis (syn. *Henneguya, Myxobolus*)	11.2-13.6 x 4.8-6.4 x 4.8-6.4	freshwater Perciformes: centrarchid (pumpkinseed)	urinary bladder	North America
M. paragasterostei (syn. *M. gasterostei p.p.*)	31-36.5 x 5.6-7	freshwater Cypriniformes: cyprinid (Siberian dace); Scorpaeniformes: cottid (bighead sculpin, vitim sculpin, spotty-fins sculpin, Kessler's sculpin)	urinary bladder, ureters	Lake Baikal
M. platessae (syn. *Henneguya*)	21.8-30.4 x 3.4-3.6 x 4.8-7	marine Pleuronectiformes: pleuronectid (European plaice, European flounder, Arctic flounder), scophthalmid (turbot)	urinary bladder	Baltic, Barents, White Seas
M. polymorphus	36-38 x 10-11.2 x 4.8-5.4	freshwater Perciformes: sinipercid (mandarin fish)	urinary tract	China
M. pseudorasborae	13-34.8 x 7-8 x 5-6.5	freshwater Cypriniformes: cyprinid (stone moroko)	urinary bladder	Amur Basin, Korea
M. rupestris (syn. *Henneguya*)	11 x 8 x 6	freshwater Perciformes: centrarchid (white crappie, rock bass)	urinary bladder	North America
M. schulmani	13-16 x 3.5-4 x 4.7-5.5	freshwater Scorpaeniformes: gasterosteid (ninespine stickleback)	kidney	Russia
M. semotilii	7.5-10 x 4.5-6 x 6-6.5	freshwater Cypriniformes: cyprinid (creek chub, golden shiner)	kidney, ureters	Canada
M. sichuanensis	27.2-34.3 x 4.7-4.8 x 4.2-4.8	freshwater Cypriniformes: cyprinid (goldfish)	ureters, urinary bladder	China
M. sinipercae (syn. *Henneguya*)	22.2-51 x 6-7.2 x 5.6-8.5	freshwater Cypriniformes: cyprinid (goldfish); Perciformes: sinipercid (mandarin fish, golden mandarin fish)	urinary bladder	Amur Basin, China
M. synodontis	20-25 x 5	marine Siluriformes: bagrid (unspecified catfish)	gills	Africa
M. varicorhini	28-31 x 6-7	freshwater Cypriniformes: cyprinid (khramulya)	urinary bladder	Russia
M. wisconsinensis (syn. *Henneguya*)	11.5 x 7	freshwater Perciformes: percid (yellow perch)	urinary bladder	North America

M. yukonensis	16.7-36.2 x 9.5-14,3 x 5.306.9	freshwater Scorpaeniformes: cottid (slimy sculpin), gasterosteid (three-spined stickleback)	kidney, urinary tract	Canada
M. yunnanensis	52-93.9 x 4.8-5.6 x 5.6-6.4	freshwater Cypriniformes: cyprinid (goldfish)	urinary tract	China
Family **Ortholineidae** (spherical spores, 2 polar capsules wide apart)				
Genus ***Cardimyxobolus*** (oval to spindle-shaped spores, polar capsules opposite laterally, in freshwater fishes)				
C. japonensis	8.8-10.4 x 11.3-12.5 x 5.2-6.7	freshwater Gobiiformes: odontobutid (dark sleeper)	gut wall	Japan
C. leshanensis [type species]	7.7-8.4 x 11.7-12.2 x 5.6-7	freshwater Cypriniformes: cyprinid (pingi logsucker)		China
C. rhodeus	11-12.5 x 13.6-15.2 x 9-10	freshwater Cypriniformes: cyprinid (Chinese bitterling)	gills	China
Genus ***Kentmoseria*** (syn. *Paraortholinea*) (elongate spores with lateral projections extending posteriad)				
K. alata (syn. *Ortholinea, Paraortholinea*) [type species]	11.2-14.3 x 9.2-10.2 x 9.7-10.2	marine Perciformes: chaetodontid (northern butterflyfish)	renal tubules and collecting ducts	Australia
K. asymmetrica (syn. *Ortholinea*)	8-10 x 7.5-9.3	marine Carangiformes: carangid (false scad)	gall bladder	Sierra Leone
K. australis (syn. *Ortholinea*)	7.8-10.4 x 7.3-9.5 x 6.2-7.3	marine Spariformes: sparid (yellowfin bream, tarwhine)	gall bladder, bile ducts	Australia
K. basma (syn. *Ortholinea*)	12-15 x 11.8-13	marine Blenniiformes: clinid (agile klipfish)	urinary bladder	South Africa
K. clupeidae (syn. *Ortholinea*)	7.4-9.5 x 5.5-6.3	marine Clupeiformes: clupeid (Pacific herring), dorosomatid (dotted gizzard shad)	urinary bladder, ureters	Russia
K. fluviatilis (syn. *Ortholinea*)	7.9-8.4 x 7.3-8	freshwater Tetraodontiformes: tetraodontid (green puffer)	urinary tract	Europe (ex: Asia)
K. gadusiae (syn. *Ortholinea*)	9-11.7 x 9-9.9 x 7.2-9	freshwater Clupeiformes: clupeid (Indian river shad)	urinary bladder, kidney	India
K. indica (syn. *Ortholinea*)	6.5-9 x 5.5-8	marine Acanthuriformes: sciaenid (cuja bola)	urinary bladder, kidney	India
K. macruri (syn. *Ortholinea*)	9.3-10.6 x 6.5-7 x 809	marine Gadiformes: macrourid (banded whiptail)	urinary bladder	Namibia
K. striateculus (syn. *Ortholinea*)	9.1-10.5 x 8.9-10.4	marine Atheriniformes: atherinid (silver fish)	ureters	Australia
K. visakhapatnamensis (syn. *Ortholinea*)	5.1-6.9 x 5.1-6.1	freshwater/estuarine Mugiliformes: mugilid (largescale mullet)	body cavity	India
Genus ***Neomyxobolus*** (ovoid spores, slightly flattened parallel to sutural plane)				
N. olae	6.2 x 9.7	freshwater Cypriniformes: cyprinid (unspecified minnows)	urinary tract	Crimea
N. ophiocephalus [type species]	7.4-12 x 7.4-11.9 x 5.5-7.9	freshwater Anabantiformes: channid (northern snakehead, blotched snakehead); Cypriniformes: catostomid (longnose sucker, white sucker, largescale sucker)	urinary tract, kidney	China, Canada
Genus ***Ortholinea*** (subspherical spores slightly flattened, in marine fishes)				
O. africanus	6.9-8.5 x 6.9-8.5 x 3.8-4.6	freshwater Cichliformes: cichlid (Nile tilapia)	urinary bladder	Egypt
O. antipae	6.8-7.5 x 5-5.4 x 6.2-7.2	marine Clupeiformes: alosid (Caspian shad)	urinary bladder	Ukraine
O. auratae	8.2-10.1 x 7.5-9.1 x 6.3-8.4	marine Spariformes: sparid (gilthead seabream)	urinary bladder	Portugal
O. concentrica	8.2-11 x 7.9-11 x 7.7-9	marine Perciformes: anthiadid (Patagonian seabass)	urinary system	Argentina
O. divergens	9.2-12 x 9.4-12 x 8	marine Blenniiformes: blenniid	urinary bladder,	Eurasia, North

(syn. *Sphaerospora*) [type species]		(smooth blenny); Gobiiformes: gobiid (Bucchich's goby); Labriformes: labrid (corkwing wrasse, five-spotted wrasse, East Atlantic peacock wrasse); Pleuronectiformes: pleuronectid (American plaice, hornyhead turbot)	renal tubules	America
O. gobiusi	8.8 x 7.1-8.4	marine Gobiiformes: gobiid (grass goby)	urinary tract	Black Sea
O. labracis	6.8-8.7 x 6.7-7.7 x 5.8-7.7	marine Moroniformes: moronid (European seabass) [cycle involves triactinomyxon-type actinospores in Oligochaeta: tubificid (*Tectidrilus*)]	urinary bladder	Portugal
O. lauquen	6.6-8.8 x 6.5-8.3 x 6.3-8.8	freshwater Galaxiiformes: galaxiid (common galaxias)	kidney	Argentina
O. mullusi	9-9.7 x 8.2-9.3 x 7.5-7.9	marine Perciformes: mullid (red mullet)	kidney, urinary bladder	Black Sea
O. nupchi	6.4-9 x 6.3-7.2 x 6.2-8.5	marine Pleuronectiformes: paralichthyid (olive flounder)	urinary bladder	Korea
O. orientalis (syn. *Sphaerospora*)	7.5-11.5 x 7.5-9.8 x 5-8	marine Clupeiformes: clupeid (Atlantic herring, Pacific herring, European sprat); Gadiformes: gadid (navaga, saffron cod)	urinary bladder, rarely gall bladder	Atlantic, Pacific, White Sea
O. polymorpha (syn. *Sphaerospora*)	6.5-11 x 7-10	marine Batrachoidiformes: batrachoidid (oyster toadfish, Gulf toadfish)	urinary bladder	North America
O. saudii	9-11 x 11-13	marine Perciformes: siganid (marbled spinefoot)	kidney	Saudi Arabia
O. scatophagi	6.2-8.7 x 6.1-6.8 x 5.9-8.2	marine Perciformes: scatophagid (spotted scat)	urinary bladder, ureters	India
O. undulans	7-10 x 6-9	marine Pleuronectiformes: bothid (witch), pleuronectid (New Zealand sole)	urinary tract, oviducts	New Zealand
Genus ***Triangula*** (triangular spores, rounded edges, smooth surface, without projections, 2 polar capsules)				
T. cirrhini	6.4-7 x 6.1-7.1	freshwater Cypriniformes: cyprinid (reba carp)	gills	India
T. egyptica	11.5-14.6 x 9.2-12.3 x 6.2-7.7	freshwater Cichliformes: cichlid (Nile tilapia)	kidney	Egypt
T. illinoisensis	10.2 x 12.8	freshwater Cypriniformes: catostomid (smallmouth buffalo)	gills	North America
T. ludhianae (syn. *Myxobolus*)	7.9-8.6 x 6.5-7.3	freshwater Cypriniformes: cyprinid (reba carp)	gills	
T. percae	10.6 x 10.4	freshwater Perciformes: percid (redfin perch)	brain [lordosis]	Australia
T. percotti (syn. *Myxosoma percotti, Myxobolus, Sphaerospora*)	8 x 4	freshwater Gobiiformes: odontobutid (Chinese sleeper)	gills, fins	Asia
T. yangkiangensis [type species]	9.6-10.8 x 8.4-10.8 x 6.2-7.8	freshwater Gobiiformes: oxudercid (bar cheek goby)	gills, skin	China
Genus ***Triangulamyxa*** (triangular spores, rounded edges, ridged surface, 2 equal polar capsules)				
T. amazonica [type species]	8.5 x 7.6 x 3.8	marine/estuarine Tetraodontiformes: tetraodontid (checkered puffer)	intestines	Brazil
T. psittaca	8.8 x 8.4	marine/estuarine Tetraodontiformes: tetraodontid (banded puffer)	urinary bladder	Amazon
Family **Parvicapsulidae** (elongate asymmetrical spores, unequal valves meeting in curved suture)				
Genus ***Gadimyxa*** (bimorphic, wide semicircular spores and thick-walled subspherical (round) spores, 2 polar capsules)				
G. atlantica	wide spores: 5-5.4	marine Gadiformes: gadid (Atlantic	urinary bladder,	Europe

[type species]	x 6.8-8.1 x 5-5.9 round spores: 6.1-7 x 7-7.8 x 5.7-6.1	cod) [cycle involves tetractinomyxon-type actinospores in Polychaeta: spirorbid (*Spirorbis spirorbis, inornatus, tridentatus, corallinae*)]	kidneys	
G. sphaerica	wide spores: 4.5-5.4 x 9-11.3 x 3.6-4.5 round spores: 5-5.4 x 5-5.9 x 5-5.4	marine Gadiformes: gadid (Atlantic cod)	urinary bladder, kidneys	Europe
G. arctica	wide spores: 5.4-6.3 x 9-12.5 x 5.4-5.9 round spores: 5.9-6.8 x 6.8-7.7 x 5.4-6.3	marine Gadiformes: gadid (Arctic cod)	urinary bladder, kidneys	Europe
Genus ***Neoparvicapsula*** (elongate curved spores, 4 polar capsules)				
N. monoalata	12.5-16 x 7-10	marine Acanthuriformes: sciaenid (cuja bola)	urinary bladder [nephrosis, obstruction]	India
N. ovalis [type species]	14.6 x 8.2	marine Perciformes: nototheniid (cod icefish)	urinary tract	South Atlantic
N. subtile		marine Perciformes: nototheniid (Patagonian toothfish)	urinary tract	Patagonia
Genus ***Parvicapsula*** (elongate curved spores, 2 anterior polar capsules open sideways)				
P. anisocaudata	16.7-22 (12-14.4) x 4.9-5 x 4.9-5	marine Pleuronectiformes: paralichthyid (olive flounder)	urinary bladder	Korea
P. asymmetrica [type species]	10-17 x 6-9	marine Scorpaeniformes: cyclopterid (lumpfish)	urinary bladder	White Sea
P. bicornis (syn. *Sphaerospora irregularis p.p.*)	6-8 x 5-6	marine Pleuronectiformes: pleuronectid (European plaice)	urinary bladder, renal tubules	Denmark
P. curvatura	9.6-11.6 x 3.9-5.8	marine Pleuronectiformes: paralichthyid (olive flounder)	urinary bladder	Korea
P. hoffmani	8.5-10.3 x 5.6-6.5	marine Mugiliformes: mugilid (largescale mullet)	intestinal epithelium	India
P. irregularis (syn. *Myxoproteus*, *Ortholinea*, *Sphaerospora*)	8-15.1 x 6-10.4 x 7.4-9	marine Pleuronectiformes: pleuronectid (American plaice)	urinary tract	North Sea
P. kabatai	6.8-14 x 4.9-8	freshwater Salmoniformes: salmonid (pink salmon)	renal interstitium	Canada
P. kareii	11.7-15.6 x 7-8.9	marine Pleuronectiformes: pleuronectid (stone flounder)	urinary bladder	Yellow Sea
P. limandae	8-11 x 4-5.4	marine Pleuronectiformes: pleuronectid (common dab)	urinary bladder, renal tubules	Denmark
P. lobata	14-14.7 x 6.3-7	marine/freshwater Atheriniformes: atherinopsid (Uruguayan silverside)	urinary bladder	Argentina
P. minibicornis	9.7-12.6 x 5.5-8 x 6.5-7	marine Salmoniformes: salmonid (pink salmon, sockeye salmon) [cycle involves tetractinomyxon-type actinospores in Polychaeta: fabriciid (*Manayunkia speciosa*)]	renal tubules	Canada
P. petuniae	9.9-12.3 x 7.4-8.3 x 6.7-11.9	marine Scorpaeniformes: cottid (Arctic staghorn sculpin)	urinary tract	Europe
P. pseudobranchicola	11.1-13.8 x 5.2-7.3	marine Salmoniformes: salmonid (Atlantic salmon)	gills, liver, kidney [gill lesions]	Norway
P. renalis	9.5 x 4-5	marine Acanthuriformes: sciaenid (red drum)	renal tubules	North America
P. schulmani	10.6-14.9 x 4.2-5.3	marine Beryciformes: berycid (splendid alfonsino)	gall bladder	North Atlantic

P. spinachiae	9-12 x 407	marine Scorpaeniformes: gasterosteid (sea stickleback)	kidney, urinary bladder	Denmark
P. unicornis	12 x 4	marine Callionymiformes: callionymid (sailfin dragonet); Pleuronectiformes: pleuronectid (common dab), scophthalmid (megrim)	urinary tract	North Sea
Family **Sinuolineidae** (spherical-pyramidal spores, some with caudal/lateral projections, 2 polar capsules set apart, urinary tract)				
Genus ***Bipteria*** (pyramidal spores, sinuous suture line, wing-like projections)				
B. admiranda [type species]	11-14 x 11-12	marine Spariformes: sparid (axillary seabream)	urinary bladder	Atlantic
B. indica	5.6-6.8 x 5.4-6.8 x 4.8-5.2	marine Mugiliformes: mugilid (flathead grey mullet, largescale mullet)	gall bladder	India
B. magna	16-19 x 13-16	marine Gadiformes: macrourid (giant grenadier)	urinary bladder	Russia
B. merluccii	10-11	marine Gadiformes: merlucciid (Benguela hake)	gall bladder	Guinea Bissau
B. minima	10-13 x 11 x 11-13	marine Gadiformes: macrourid (giant grenadier)	urinary bladder	Russia
B. nototheniae	10.7-12 x 10.7-15	marine Perciformes: notothenid (longtail southern cod)	kidney tubules	Falkland Islands
B. vetusta	8.5-10 x 10.8-13 (8.2-10.3)	marine Chimaeriformes: chimaerid (rabbit fish)	gall bladder	Scotland
Genus ***Latyspora*** (symmetrical spores, anterior polar capsules set obliquely to sinuous sutural line)				
L. scomberomori [type species]	8.1-10.4 x 7.9-12.9 x 14.8-17	marine Scombriformes: scombrid (Indo-Pacific king mackerel)	kidney	Malaysia
Genus ***Myxodavisia*** (syn. *Davisia*) (spherical spores, with hollow horn-like lateral projections)				
M. amoena (syn. *Davisia*)	10.6-13.9 x 10.7-13.9	marine Pleuronectiformes: pleuronectid (American plaice)	urinary tract	Canada
M. anoplopoma (syn. *Davisia*)	12-14 x 13-17	marine Scorpaeniformes: anoplopomatid (sablefish)	urinary tract, renal tubules	North America
M. aurita (syn. *Davisia*)	13.3-15 x 13.3-15.2	marine Gadiformes: macrourid (giant grenadier)	urinary bladder	Okhotsk Sea
M. bidens (syn. *Davisia, Sinuolinea*)	6.5-9 x 8-11.5	marine Batrachoidiformes: batrachoidid (plainfin midshipman)	urinary bladder	North America
M. brachiophora (syn. *Davisia, Sinuolinea*)	9-11 x 9	marine Pleuronectiformes: paralichthyid (Gulf flounder)	urinary bladder	North America
M. bulani	6.8-7.8 x 31-43 (12-13.5)	marine Elopiformes: megalopid (Indo-Pacific tarpon)	gall bladder	Malaysia
M. cella (syn. *Sinuolinea*)	9-13 x 8-10	marine Batrachoidiformes: batrachoidid (plainfin midshipman)	urinary bladder	North America
M. cornuta (syn. *Davisia*)	8.8-10.6	marine Gobiiformes: gobiid (monkey goby)	urinary bladder	Azov Sea
M. coryphaenoidia (syn. *Davisia*)	17-23 x 9-14	marine Gadiformes: macrourid (giant grenadier)	urinary bladder	North America
M. cynoglossi (syn. *Davisia*)	12.6-16.8 x 32.2-42.2 (11.4-15.4)	marine Pleuronectiformes: cynoglossid (unspecified tongue sole)	gall bladder	India
M. diplocrepis (syn. *Davisia*)	9-12 x 12-14	marine Gobiesociformes: gobiesocid (orange clingfish)	urinary tract	New Zealand
M. donecae (syn. *Davisia*)	11 x 10.6	marine Carangiformes: carangid (Cape horse mackerel)	urinary tract	Africa
M. filiformis (syn. *Davisia*)	12-14 x 120-176 (16-20)	marine Clupeiformes: engraulid (longjaw thryssa)	gall bladder	India
M. galeiforme (syn. *Davisia*)	12-17.3 x 5.3-8	marine Perciformes: zoarcid (australis eelpout)	urinary bladder	Falkland Islands
M. haldarae	12-15 x 7.5-9	marine Clupeiformes: dorosomatid (Indian oil sardine)	gall bladder	India

M. hexagrammi (syn. *Davisia*)	9.5-10.5 x 10-12	marine Scorpaeniformes: hexagrammid (fat greenling, spotty-bellied greenling)	urinary bladder	China
M. jejuensis	13.1 x 13.1 x 17.2	marine Pleuronectiformes: paralichthyid (olive flounder)	urinary bladder	Korea
M. longibrachia (syn. *Davisia*)	12-15 x 12	marine Callionymiformes: callionymid (common dragonet); Pleuronectiformes: pleuronectid (lemon sole, American plaice); Scorpaeniformes: agonid (hooknose)	gall bladder	Pacific, North Sea
M. longifilus (syn. *Davisia*)	10.5-13.5 x 11.7-13	marine Pleuronectiformes: pleuronectid (flathead flounder)	urinary bladder	Japan
M. murtii (syn. *Davisia*)	11.2-17.6 x 4.8-11.2	marine Mugiliformes: mugilid (largescale mullet)	gall bladder [inflammation, discoloration]	India
M. narvi (syn. *Davisia*)	10-11.5 x 11.5-14.4	marine Scorpaeniformes: cottid (snowy sculpin)	urinary bladder	Japan
M. newfoundlandia (syn. *Davisia*)	9.6-14 x 7.5-12.8	marine Gadiformes: macrourid (roughhead grenadier, bigeye grenadier)	kidney, urinary bladder	Canada
M. nototheniae (syn. *Davisia*)	12-13 x 12-13.3	marine Perciformes: notothenid (painted notie)	renal tubules	Antarctic
M. opacita (syn. *Davisia, Sinuolinea*)	12-13 x 12-13	marine Pleuronectiformes: paralichthyid (Gulf flounder)	urinary bladder	North America
M. ophidii (syn. *Davisia*)	9-11.7 x 13	marine Ophidiiformes: ophidiid (snake blenny)	urinary bladder	Black Sea
M. ophidioni (syn. *Davisia*)	9.1-11.7 x 13	marine Ophidiiformes: ophidiid (Roche's snake blenny)	urinary bladder	Black Sea
M. pectoralis (syn. *Davisia*)	10-17 x 11-17 x 9-10	marine Gadiformes: macrourid (giant grenadier)	urinary bladder, renal tubules	North America
M. reginae (syn. *Davisia*)	11-15 x 12-20 x 11.5	marine Ovalentaria: embiotocid (striped seaperch, silvery perch); Scorpaeniformes: scorpaenid (olive rockfish, quillback rockfish)	urinary bladder	North America
M. sauridae (syn. *Davisia*)	7.2-10.8 x 17.4-28 (14.8-22.6)	marine Aulopiformes: synodontid (greater lizardfish)	gall bladder	India
M. sebastisca	12.7-13.6 x 10.9-13.5	marine Scorpaeniformes: scorpaenid (false kelpfish)	urinary bladder	China
M. sonae	6.5-8.8 x 7-8	marine Siluriformes: ariid (Sona sea catfish)	gall bladder	India
M. spectabilis (syn. *Ceratomyxa, Davisia*)	10-13	marine Perciformes: stichaeid (forkline prickleback); Scorpaeniformes: agonid (sea raven)	urinary bladder	Japan
M. spinosa (syn. *Davisia, Ceratomyxa*) [type species]	13 x 7	marine Pleuronectiformes: paralichthyid (Gulf flounder)	urinary bladder	North America
Genus ***Myxoproteus*** (syn. *Conispora*) (pyramidal spores with rounded outlines, sometimes with projections)				
M. abyssus	9-12.5 x 9-12	marine Gadiformes: macrourid (abyssal grenadier)	urinary tract	North America
M. ambiguus (syn. *Myxosoma ambiguum*) [type species]	18-20 x 10	marine Lophiiformes: lophiid (European angler)	urinary tract	Europe
M. biliaris	9.6-10 x 6.4 x 7.5-8	marine Pleuronectiformes: paralichthyid (Patagonian flounder)	gall bladder	Argentina
M. californicus	12-17 x 8-11 x 6-10	marine Gadiformes: macrourid (Pacific grenadier)	urinary ducts, urinary bladder	North America
M. caudatus	11-21.6 x 8.5-14	marine Pleuronectiformes: pleuronectid (common dab)	urinary bladder	Barents Sea, White Sea
M. cheni	12.8-15.3 x 11.2-15	marine Tetraodontiformes:	urinary bladder	China

	x 11.2-15	monacanthid (greenfin horse-faced filefish)		
M. cordiformis	12 x 10-11 x 6	marine Acanthuriformes: ephippid (Atlantic spadefish)	urinary bladder	North America
M. cornutus	12 x 9	marine Acanthuriformes: sciaenid (American silver perch)	urinary bladder	North America
M. cujaeus	9-12 x 8-10	marine Acanthuriformes: sciaenid (cuja bola)	urinary bladder	India
M. elongatus	10-13.5 x 6-7 x 7-8.5	marine Salmoniformes: salmonid (sheefish); Scorpaeniformes: anarhichadid (Atlantic wolffish)	urinary bladder	Barents Sea, White Sea
M. hubbsi	5-7 x 4.2-7.5 x 3.5-4.5	marine Gadiformes: macrourid (longnose grenadier)	gall bladder	Surinam
M. inexpectatus	11.7-14 x 5.2-6.5 x 7.8	marine Pleuronectiformes: pleuronectid (dark flounder)	urinary bladder	Sea of Japan
M. innae	10.4 x 9.6 x 8.8-9.6	marine Atheriniformes: atherinopsid (silverside)	gall bladder	Argentina
M. meridionalis (syn. *M. renalis*)	10-13.6 x 7.7-9.7	marine Gadiformes: merlucciid (Argentine hake)	urinary tract	Argentina, Canada
M. moseri	9.5-13.3 x 9-11.9	marine Gadiformes: morid (tadpole codling)	gall bladder	Atlantic
M. myoxocephali	8.4-11.7 x 5.8-8.3	marine Scorpaeniformes: cottid (shorthorn sculpin, longhorn sculpin)	gall bladder	Canada
M. ovale	16.6-19.5 x 14-15.6	marine Scorpaeniformes: agonid (tokubire)		Sea of Japan
M. rosenblatti	15-22 x 9-13.5 x 8.5-11	marine Gadiformes: macrourid (Pacific grenadier, Humboldt grenadier, abyssal grenadier, filamented rattail)	gall bladder	North America
M. scoleciformis	12.5 x 8.7	marine Zeiformes: zeid (John Dory)	urinary tract	Ireland
Genus ***Neobipteria*** (spores with wing-like projections and meridional keel-like extensions)				
N. coramandelensis	4.8-6.8 x 7.2-10.4	marine Eupercaria: nemipterid (mauvelip threadfin bream)	gall bladder	India
N. macrouri [type species]	13.3-14.4 x 14.6-17.3 x 13.3-14.4	marine Gadiformes: macrourid (Pacific grenadier)	urinary bladder	Bering Sea
Genus ***Noblea*** (spores with 2 keel-like extensions and two thickenings)				
N. admiranda [type species]	16-18.6 x 12-14.6	marine Gadiformes: phycid (red hake)	urinary bladder	Canada
Genus ***Paramyxoproteus*** (pyramidal spores with stiff keel-like valvular projections)				
P. chlorophthalmusi	24-32 x 18.6-26.4	marine Aulopiformes: chlorophthalmid (spotted greeneye)	gall bladder	India
P. cordiformis (syn. *Myxoproteus*)	12 x 10-11	marine Acanthuriformes: ephippid (Atlantic spadefish)	urinary bladder	
P. reinhardti [type species]	25 x 20	marine Pleuronectiformes: scophthalmid (turbot)	urinary bladder	Atlantic
Genus ***Schulmania*** (spores with 4 longitudinal keel-like extensions)				
S. aenigmatosa	17.2-23.1 x 12-19.5 x 14.9-18	marine Pleuronectiformes: pleuronectid (American plaice, Bering flounder, flathead sole)	urinary bladder	Arctic
S. albinae	13.3-16 x 8.6-9.3	marine Scorpaeniformes: scorpaenid (rosethorn rockfish)	urinary bladder	Okhotsk Sea
S. japonica	16.8-18.2 x 10.6-12	marine Perciformes: psychrolutid (spinyhead sculpin)	urinary bladder	Japan
S. ovale [type species]	18-20 x 16.5-21.3 (13.3-1.6)	marine Scorpaeniformes: zoarcid (Esmark's eelpout)	urinary bladder	Canada
S. pacifica	16-22.3 x 9.4-13.3	marine Gadiformes: macrourid (longfin grenadier)	urinary bladder	Russia
S. quadriolobata	21.3-24.4 x 10.9-	marine Pleuronectiformes:	urinary bladder	Atlantic, Bering

	13.3 x 5.4	pleuronectid (Greenland halibut, black halibut, flathead flounder, Kamchatka flounder)		Sea, Okhotsk Sea, Sea of Japan
S. simplicificata	14-16 x 6.6-8	marine Gadiformes: macrourid (Pacific grenadier)	urinary bladder	Russia
Genus ***Sinuolinea*** (spherical spores, sinuous suture line, without projections, 2 polar capsules)				
S. andameni	9.6-12.8 x 8-12.8	marine Ophidiiformes: ophidiid (slender cusk-eel)	gall bladder	India
S. arborescens	15 x 12	marine Syngnathiformes: syngnathid (dusky pipefish)	urinary bladder	North America
S. arctica	14.7-16.6 x 14.2-16.6 x 14-18.1	marine Scorpaeniformes: cottid (shorthorn sculpin)	urinary bladder	Arctic
S. argyrosomi	17-20 x 18-22	marine Eupercaria: sciaenid (silver croaker)	urinary bladder	China
S. capsularis	12-14 x 12-14	marine Pleuronectiformes: paralichthyid (Gulf flounder, summer flounder); Tetraodontiformes: tetraodontid (northern puffer)	urinary bladder	North America
S. contrariocapsularis	9.6-11.2 x 8-9.6 x 8-9.6	marine Pleuronectiformes: paralichthyid (Patagonian flounder)	gall bladder	Argentina
S. cyclopterina	14-16 x 13-15	marine Scorpaeniformes: cyclopterid (lumpfish)	urinary bladder	Barents Sea, White Sea
S. dimorpha (syn. *Sphaerospora*) [type species]	15-16 x 4-5	marine Acanthuriformes: sciaenid (weakfish)	urinary tract	North America
S. indica	10-13.5 x 10-13.5	marine Eupercaria: sciaenid (Ganges jewfish)	urinary bladder	India
S. lesteri	15-19 x 15-19	marine Orectolobiformes: hemiscylliid (epaulette shark)	gall bladder	Australia
S. magna	17.5-30 x 19-30	marine Gadiformes: macrourid (Pacific grenadier, pectoral rattail)	urinary bladder	North America
S. mai	21.7-23 x 18.8-20.2	marine Tetraodontiformes: monacanthid (greenfin horse-faced filefish)	urinary bladder	China
S. markevitshi (syn. *S. schulmani*)	8-9.6 x 7.6-8.5	marine Atheriniformes: atherinid (bigscale sand smelt)	gall bladder	Russia
S. murmanica	12-14 x 12-14	marine Trachiniformes: ammodytid (lesser sand eel)	urinary bladder, renal tubules	Barents Sea
S. niloticus	9.1-14.3 x 9.1-14.3	freshwater Cichliformes: cichlid (Nile tilapia)	intestines, stomach, heart, kidney, liver, muscles, spleen	Brazil
S. phyllopteryxa	17.1 x 15.6	marine Syngnathiformes: syngnathid (weedy sea dragon)	kidneys	North America
S. platycephali	14-15 x 4.4.5	marine Scorpaeniformes: platycephalid (bartail flathead)	urinary bladder	China
S. rebae	6.5-12-13.2	marine Gadiformes: macrourid (hollowsnout grenadier, mook-torukarss, softhead grenadier, furry whiptail, unspecified trachyrincus); Pleuronectiformes: soleid (common sole)	urinary bladder, gall bladder	Atlantic
S. renalis	17.4 x 17.4	marine Eupercaria: sciaenid (bronze croaker)	kidney tubules	India
S. sakinachanumae (syn. *Ortholinea*)	6.8-8.2 x 5.7-6.8	marine Syngnathiformes: syngnathid (black-striped pipefish)	gall bladder	Black Sea, Caspian Sea
S. shandongensis	15-20 x 15-18	marine Eupercaria: sciaenid (yellow drum)	urinary bladder	China
S. sinuosa	9-12 x 9-12	marine Gadiformes: gadid (polar cod)	urinary bladder	White Sea
S. tetraodoni	9.3 x 9.3	freshwater Tetraodontiformes: tetraodontid (green puffer)	urinary tract	Europe (ex: Asia)

S. triangularis	10-16	marine Gadiformes: macrourid (rattail); Pleuronectiformes: soleid (common sole)	urinary tract	Japan Sea, Atlantic
S. triangulata	9-16 x 15-18.5	marine Gadiformes: macrourid (giant grenadier, Pacific grenadier, abyssal grenadier, filamented rattail); Tetraodontiformes: tetraodontid (purple puffer)	urinary bladder, kidney	Japan, North America
Family **Sphaeromyxidae** (2 polar capsules at opposite ends of fusiform spores)				
Genus ***Sphaeromyxa*** (polar filament tapering, folded rather than coiled)				
S. arcuata	21.3-23.3 x 3.7-5	marine Gobiiformes: gobiid (frillfin goby); Scombriformes: gempylid (black gemfish); Spariformes: sparid (carpenter seabream)	gall bladder	Namibia
S. argentinensis	23.2-27.5 x 4.5-5.3 x 4.5-5.3	marine Clupeiformes: engraulid (Argentine anchoita)	gall bladder	Argentina
S. artedielli	16.5-18.7 x 4.9-6.2	marine Perciformes: cottid (Atlantic hookear sculpin, moustache sculpin)	gall bladder	Norway
S. atherinae	14.4-16.8 x 3.6-4	marine Atheriniformes: atherinid (Black Sea sand-smelt)	gall bladder	Black Sea
S. azevedoi	20.5-30.1 x 3.5-4.4	marine/freshwater Gobiiformes: gobiid (Graham's goby)	gall bladder	Amazon
S. balbiani [type species]	13-23 x 5-9.5	marine Acropomatiformes: epigonid (pencil cardinal); Alepocephaliformes: alepocephalid (bluntsnout smooth-head); Blenniiformes: blenniid (peacock blenny, rusty blenny); Clupeiformes: alosid (Allis shad, European pilchard); Gadiformes: lotid (three-bearded rockling, fivebeard rockling); Gobiiformes: gobiid (caboz); Perciformes: cepolid (red bandfish), chaetodontid (four-banded butterflyfish), cottid (kirikajika); Scorpaeniformes: cottid (moustache sculpin); Syngnathiformes: syngnathid (dusky pipefish, chain pipefish)	gall bladder	Eurasia, North America
S. bengalensis	25-30 x 4.7-6.8	marine Eupercaria: lutjanid (Bengal snapper)	gall bladder	India
S. bonaerensis	16.5-18.8 x 3.7-4.8 x 3.4-4.5	marine Clupeiformes: engraulid (Marini's anchovy)	gall bladder	Argentina
S. cannolii	16.6-20 x 5-7.1	marine Syngnathiformes: syngnathid (lined seahorse)	bile ducts	North America
S. chacundae	20.5-23.5 x 5.5-6.5	marine/freshwater Clupeiformes: dorosomatid (Chacunda gizzard shad)	gall bladder	India
S. clini	17.4-20.6 x 4.5-6.1 x 4-6	marine Blenniiformes: clinid (sad klipfish, bluntnose klipfish, super klipfish, nosestripe klipfish)	gall bladder, bile ducts	South Africa
S. cornuti	19.2-24.7 x 4.1-5.7	marine Acanthuriformes: zanclid (Moorish idol)	gall bladder	Arabian Sea
S. cottidarum	33-35 x 7-8	marine Scorpaeniformes: agonid (sea raven, unspecified *Blepsias* sculpin), cottid (antlered sculpin, unspecified *Enophrys* sculpin)	gall bladder	Bering Sea, Sea of Japan
S. curvula	19-22 x 4-6	marine Scorpaeniformes: scorpaenid (blackbelly rosefish), Spariformes: sparid (hottentot seabream)	gall bladder	South Africa
S. diacanthusa	18.2-22.7 x 4.6-5.9	marine Acanthuriformes: sciaenid (blackspotted croaker)	gall bladder	India

S. dighae	21-25 x 28-4.5	freshwater Clupeiformes: dorosomatid (hilsa herring)	gall bladder	India
S. elegini	15-23.5 x 4-6.5	marine Gadiformes: gadid (saffron cod)	gall bladder	Sea of Japan
S. exneri	75-80 x 18-20	marine Perciformes: agonid (longnose poacher), platycephalid (Japanese flathead)	gall bladder	Indian Ocean
S. ganapatii	16-19 x 4-4.8	marine Perciformes: terapontid (crescent grunter)	gall bladder	India
S. gasterostei	nr	marine Scorpaeniformes: gasterosteid (sea stickleback)	bile ducts	Europe
S. gibbonsia	27 x 5.2	marine Blenniiformes: clinid (spotted kelpfish, striped kelpfish)	gall bladder	North America
S. hareni	23.3-28.9 x 4.7-8.9	marine Siluriformes: ariid (flatmouth sea catfish)	gall bladder	India
S. hellandi	16.2-30 x 3.5-7.5	marine Gadiformes: gadid (haddock, merling), lotid (cusk, common ling); Perciformes: sebastid (blackbelly rosefish); Scorpaeniformes: pholid (rock gunnel); Syngnathiformes: centriscid (longspine snipefish)	gall bladder	Atlantic
S. hexagrammi	18.2 x 3.5	marine Perciformes: hexagrammid (masked greenling, whitespotted greenling, Okhotsk atka mackerel)	gall bladder	Sea of Japan
S. horrida	12.2-13.9 x 4.2-4.8 x 4.2-4.7	estuarine Scorpaeniformes: scorpaenid (estuarine stonefish)	biliary tract	Australia
S. immersa	12-14 x 9-10	Anura: bufonid (Aegean toad), leptodactylid (Bolivian white-lipped frog)	gall bladder	Europe
S. incurvata	30-35 x 8	marine Blenniiformes: blenniid (butterfly blenny); Pleuronectiformes: soleid (blackhand sole, sand sole)	gall bladder	Mediterranean
S. intermediata	17.5-24 x 3.5-7.5	marine Gadiformes: macrourid (western softhead grenadier, twelve-rayed grenadier, longbeard grenadier, slimehead grenadier)	gall bladder	Americas
S. japonica	18.5-23.7 x 4.3-4.5	marine Perciformes: cottid (spectacled sculpin, Jordan's sculpin)	gall bladder	Japan
S. kenti	17.5-19.8 x 3.8-5.2	freshwater Gobiiformes: gobiid (naked goby)	gall bladder	North America
S. lateralis	26 x 8	marine Scorpaeniformes: cottid (smoothhead sculpin)	gall bladder	North America
S. limocapitis	26.7-30.1 x 5.6-6.7 x 4.1-5.7	marine Trachichthyiformes: trachichthyid (Darwin's slimehead)	gall bladder	Java
S. lomi	23-29 x 3.5-5	marine Gadiformes: macrourid (western softhead grenadier)	gall bladder	Borneo
S. longa	20 x 5	marine Gadiformes: gadid (poor cod)	gall bladder	Europe
S. lycodi	19.6-25.3 x 4.6-6.9 x 4.5-6.2	marine Perciformes: zoarcid (pale eelpout, Arctic eelpout, longear eelpout, doubleline eelpout, Vahl's eelpout)	gall bladder	Iceland
S. magna	22-24 x 5.5-6.4	marine Scorpaeniformes: liparid (polka-dot snailfish)	gall bladder	Barents Sea
S. maiyai	23-30 x 5-7	marine Gadiformes: gadid (Pacific tomcod)	gall bladder	North America
S. minuta	13.5-16.2 x 2.7-3.6	marine Gadiformes: macrourid (silver whiptail); Pleuronectiformes: pleuronectid (Atlantic halibut)	gall bladder	Barents Sea, Philippines
S. nesogobii	22 x 7	marine Gobiiformes: gobiid (sand goby)	gall bladder	Australia
S. noblei	18.5-21.5 x 5.2-6 x 4.8-5.2	marine Blenniiformes: clinid (banded weedfish)	gall bladder	Australia

S. opisthopterae	9-12.7 x 3.3-4.6	marine Clupeiformes: pristigasterid (tardoore)	gall bladder	India
S. ovata	13 x 6.5	marine Gadiformes: gaidropsarid (shore rockling)	gall bladder	Europe
S. ovula	14 x 4.3	marine Gobiesociformes: gobiesocid (California clingfish)	gall bladder	North America
S. parva	15-17 x 4	marine Beloniformes: scomberesocid (Pacific saury); Perciformes: pholid (painted gunnel)	gall bladder	Sea of Japan
S. photopectoralis	19.6-24.8 x 8-11.8	marine Acanthuriformes: leiognathid (orangefin ponyfish)	gall bladder	China
S. pultai	28.8-30 x 5-5.5	marine/estuarine Gobiiformes: oxudercid (rubicundus eel goby)	gall bladder	India
S. reinhardti	21.2-23.3 x 3.7-5	marine Clupeiformes: engraulid (northern anchovy)	gall bladder	North America
S. sabrazesi	16.8-30 x 3-5.5 x 4.8-5.4	marine Beloniformes: exocoetid (black wing flyingfish); Clupeiformes: engraulid (ungeo); Gadiformes: lotid (three-bearded rockling); Syngnathiformes: syngnathid (short-snouted seahorse, long-snouted seahorse, greater pipefish, broadnosed pipefish, spotted pipefish)	gall bladder	Mediterranean, Atlantic
S. schulmani	18.6-20 x 4-6	marine Gadiformes: moronid (Patagonian cod)	gall bladder	Atlantic
S. scorpaena	13.8-15.1 x 4.9-5.8	marine Scorpaeniformes: scorpaenid (longfingered scorpionfish)	gall bladder	China
S. sebastisa	11.5-13.7 x 3.9-5.3	marine Scorpaeniformes: scorpaenid (false kelpfish, weedy stingfish)	gall bladder	China
S. sevastopoli	18-18.3 x 4-4.6	marine Gobiiformes: gobiid (monkey goby)	gall bladder	Black Sea
S. solomoni	25-27.7 x 5.4-7.2	marine Perciformes: cottid (threaded sculpin, antlered sculpin)	gall bladder	Japan
S. theraponi	15.5-19.8 x 4.1-5.9	marine Perciformes: terapontid (tiger perch)	gall bladder	India, China
S. tripterygii	17.2-21.1 x 3.4-3.8	marine Blenniiformes: tripterygiid (variable triplefin, twister)	gall bladder	New Zealand
S. tuanfengensis	20-7-23.8 x 4.7-6.8 x 6.9-8.8	marine Clupeiformes: engraulid (ungeo)		China
S. xiamenensis	19-23 x 3-5	marine Acanthuriformes: siganid (mottled spinefoot)	gall bladder	China
S. zaharoni	13.7-15.1	marine Scorpaeniformes: scorpaenid (devil firefish)	gall bladder	Israel
Family **Sphaerosporidae** (rounded spores, tapering anterior end)				
Genus ***Palliatus*** (subspherical spores enveloped in membranous veil)				
P. binus	17-20 x 17-19.5	marine Pleuronectiformes: pleuronectid (flathead flounder, sohachi, smallscale plaice)	gall bladder	Japan
P. grandis	22-30 x 20-30	marine Alepocephaliformes: alepocephalid (small scaled brown slickhead, bluntsnout smooth-head)	gall bladder	Africa
P. indecorus	23.5 x 20-22	marine Alepocephaliformes: alepocephalid (Risso's smooth-head, Baird's slickhead)	gall bladder	Africa
P. indicus	9.1-10.5 x 7-7.7	marine Mugiliformes: mugilid (largescale mullet)	pancreas [weight loss]	India
P. magellanicus	9.6-19.2 x 10.2-22.4 x 14-20	marine Gadiformes: macrourid (Patagonian grenadier)	gall bladder	Chile
P. mirabilis	15.7-23.2 x 23.5	marine Alepocephaliformes:	gall bladder	Africa

[type species]		alepocephalid (bluntsnout smooth-head)		
Genus ***Sphaerospora*** (syn. *Podospora, Polysporoplasma*) (subspherical spores, valvular diameter shorter than sutural diameter, 2 polar capsules, coelozoic in excretory system of fishes and amphibians)				
S. abrami	12.2-14.1 x 14-15.3	freshwater Cypriniformes: cyprinid (common bream)	renal tubules	Europe
S. aldrichettae	7 x 6	marine Mugiliformes: mugilid (unspecified mullet)	gall bladder	Australia
S. amurensis	7.2-11 x 6.6-10 x 6.6-9.6	freshwater Cypriniformes: cyprinid (grass carp, black carp), xenocypridid (silver carp)	gills, renal tubules	Amur Basin
S. anguillae	5.6-6.8 x 5.6-6.8	freshwater Anguilliformes: anguillid (European eel)	urinary bladder	Poland
S. angulata (syn. *Leptotheca*)	7-12 x 5 x 6-9	freshwater Cypriniformes: cyprinid (common carp, koi carp, Prussian carp, goldfish)	urinary bladder, ureters, renal tubules	Amur Basin
S. araii	14.3-18.4 x 16.2	marine Rajiformes: rajid (longnose skate)	urinary tract	Canada
S. armatura (syn. *Leptotheca*)	10-16 x 17-26	marine Gadiformes: macrourid (pectoral rattail, ghostly grenadier)	urinary bladder, renal tubules	North America
S. bliccae	9.7-11.1 x 9.3-10.1	freshwater Cypriniformes: cyprinid (white bream)	renal tubules	Europe
S. bramae	4.4-5.4 x 4.3-5.4	freshwater Cypriniformes: cyprinid (common bream)	renal tubules, glomeruli	Europe
S. brevis (syn. *Leptotheca, Myxoproteus*)	10-12 x 11.7-12.6	marine Scorpaeniformes: cottid (shorthorn sculpin)	urinary bladder	Barents Sea
S. brevoides (syn. *Leptotheca*)	6-8 x 7-10	marine Perciformes: stichaeid (fusaginpo)	urinary bladder	China
S. carassii (syn. *Leptotheca*)	8-13 x 8-13	freshwater Cypriniformes: cyprinid (common carp, grass carp, crucian carp, Prussian carp, goldfish, common roach)	gills	Eurasia
S. caudata (syn. *Mitraspora*)	10-11 x 28	marine Clupeiformes: alosid (Twaite shad), engraulid (European anchovy)	urinary bladder, renal tubules	Blatic Sea, Black Sea
S. chagasi (syn. *Leptotheca*)	10-11 x 15	Anura: leptodactylid (lesser foam frog)	urinary ducts	Brazil
S. chinensis (syn. *S. branchialis*)	6.3 x 6.3	freshwater Cypriniformes: cyprinid (common carp, goldfish)	gills [gill sphaerosporosis]	China, Russia
S. colomani	8.4-8.7 x 9.7-10.5	freshwater Acipenseriformes: acipenserid (sterlet)	renal tubules, renal glomeruli	Europe
S. compressa (syn. *Leptotheca*)	12.2 x 10.5	marine Gobiesociformes: gobiesocid (slender clingfish)	urinary bladder	North America
S. coregoni	8.2 x 11.3 x 7.1	freshwater Salmoniformes: salmonid (common whitefish)	kidney	Europe
S. corsulae	4.8-5 x 4.7-4.8	marine Mugiliformes: mugilid (corsula)	gall bladder [gel-like bile]	India
S. cristata	9-10 x 8.5-10 x 8.3-10	freshwater Gadiformes: lotid (burbot)	urinary bladder, ureters	Lake Baikal
S. ctenopharyngodoni	13.2-15.6 x 12-13.2 x 10.8-12.6	freshwater Cypriniformes: cyprinid (grass carp)	gills	China
S. danubialis	9.5-11 x 8.5-10	freshwater Perciformes: percid (zander)	renal tubules	Europe
S. dentata	9.4-9.8 x 9.4-9.6	freshwater Cypriniformes: cyprinid (common rudd)	renal tubules	Europe
S. dicentrarchi (syn. *S. mugili p.p.*)	4,5 x 3.9	marine Moroniformes: moronid (spotted seabass, European seabass); Mugiliformes: mugilid (golden grey mullet, flathead grey mullet, thicklip grey mullet, thinlip mullet, leaping	gall bladder, gut, kidney	Europe

		mullet); Spariformes: sparid (gilt-head bream)		
S. diminuta	5.0-8.7 x 6.7-9.7	freshwater Perciformes: centrarchid (pumpkinseed)	kidney	Canada
S. dissostichi	11.2-14.2 x 9.6-11.8 x 9.6-11.8	marine Perciformes: nototheniid (Patagonian toothfish)	kidney	South America
S. diversa	5.9-6.7 x 6.4-7.9	freshwater Cypriniformes: cyprinid (common dace, ide, common chub)	renal tubules	Europe
S. dogieli	7-7.5 x 7-7.5 x 5.7-6	freshwater Siluriformes: silurid (Soldatov's catfish, Amur catfish)	urinary bladder	Korea
S. dubinini	8-10.2 x 7.3-8.5	freshwater Siluriformes: bagrid (Ussuri catfish)		China
S. dykovae (replacement name for *S. renicola*)	7.3 x 7.2	freshwater Cypriniformes: cyprinid (common carp, goldfish) [cycle involves neoactinomyxum-type actinospores in Oligochaeta: naidid (*Tubifex tubifex, Brachiura sowerbyi*)]	urinary tract, kidneys, swim bladder, blood	Europe, Middle-East
S. elegans (syn. *Chloromyxum*) [type species]	7-12 x 7-12	freshwater and marine Cypriniformes: leuciscid (common minnow, lake minnow); Gadiformes: lotid (burbot); Pleuronectiformes: pleuronectid (European flounder); Scorpaeniformes: gasterosteid (three-spined stickleback, fourspine stickleback, ninespine stickleback, Ukrainian stickleback)	ovarian connective tissue, urinary bladder, renal tubules	Eurasia
S. elopi	5.8-6.6 x 8.9-10.5	marine Elopiformes: elopid (ladyfish)	renal tubules	North America
S. elwhaiensis	9.3-12 x 9.9-14.3	freshwater Salmoniformes: salmonid (sockeye salmon)	renal tubules	North America
S. epinepheli	7-10 x 7-9.5 x 12.3-14.5	marine Perciformes: epinephelid (Malabar grouper)	kidney	Thailand
S. erythroculteri (syn. *Podospora*)	6.5-8.2 x 6.5-7.5	freshwater Cypriniformes: cyprinid (topmouth culter)		China
S. festivius	5.2-5.6 x 6.3-7.7	freshwater Cichliformes: cichlid (flag cichlid)	urinary bladder	Brazil
S. formosa (syn. *Bipteria, Myxoproteus*)	6.6-10.4 x 8.5-12	marine Gadiformes: gadid (merling)	urinary bladder	Celtic Sea, Denmark
S. fugu (syn. *Leptotheca*)	8.3-9.5 x 13-15 x 7-8	marine Tetraodontiformes: tetraodontid (Japanese puffer)	digestive tract, gall bladder	Japan
S. galinae	8.8 x 8.4	freshwater Cypriniformes: tincid (tench)	urinary tract, kidneys, blood	Europe
S. gasterostei	6.7 x 7	freshwater Scorpaeniformes: gasterosteid (three-spined stickleback, ninespine stickleback)	renal tubules, urinary bladder, ovaries	Europe
S. glomerosa (syn. *Leptotheca*)	9 x 4.5	marine Pleuronectiformes: paralichthyid (Gulf flounder)	urinary bladder	North America
S. gobionis	6.5-8 x 6.4-7.7	freshwater Cypriniformes: cyprinid (gudgeon)	renal tubules	Europe
S. gutta	6.2-6.6 x 6.3-6.7	freshwater Cypriniformes: cyprinid (common rudd)	renal tubules	Europe
S. hangzhouensis	6-6.4 x 6.4-6.9	freshwater Cypriniformes: cyprinid (common carp)		China
S. hankai	5.4-6.6 x 5.4-6.5	freshwater Siluriformes: ictalurid (brown bullhead)	kidney	Canada
S. hunanensis	8.4-9.6 x 9.6-10.8 x 6	freshwater Cypriniformes: cyprinid (goldfish)	gills	China
S. hupehensis	6.6-9 x 6.6-8.4 x 7.5	freshwater Cypriniformes: cyprinid (unspecified bitterling)	gills	China
S. hypophthalmichthydis (syn. *Podospora*)	9.6-12 x 9.6 x 9.6-10.8	freshwater Cypriniformes: xenocypridid (silver carp)		China
S. ictaluri	5.8 x 5.6 x 6.5	freshwater Siluriformes: ictalurid	kidney, gills,	North America

		(channel catfish)	blood ['hamburger gill disease']	
S. inaequalis	7.4 x 6.9	freshwater Siluriformes: unspecified catfish	urinary tract	Middle-East
S. johnae	9.5-12 x 8.8-12.5	marine Eupercaria: sciaenid (Belanger's croaker)	kidney tubule	India
S. koreana (syn. *Leptotheca*)	8.6 x 13.4 x 8.1	marine Scorpaeniformes: scorpaenid (Korean rockfish)	kidney tubules	Korea
S. krogiusi (syn. *Leptotheca*)	5.8-7.5 x 7.5-8 x 7.5-11.5	freshwater Salmoniformes: salmonid (chum salmon, pink salmon, sockeye salmon, coho salmon, chinook salmon, Arctic char, whitespotted char, rainbow trout)	urinary bladder	Russia
S. kuangtungensis	9.4-9.6 x 7.3-7.7 x 7.6-8.2	freshwater Cypriniformes: cyprinid (grass carp)	gills	China
S. leuciscusi	5.1-6 x 5.4-6.7	freshwater Cypriniformes: cyprinid (common dace)	renal tubules	England
S. lieni	11-12 x 10-11	freshwater Cypriniformes: xenocypridid (silver carp)		China
S. lobosa (syn. *Leptotheca*)	16-18 x 9-10	marine Pleuronectiformes: paralichthyid (summer flounder)	urinary bladder	North America
S. luciopercae	7.2-9.6 x 5-7	freshwater Perciformes: percid (zander)	ovary	Russia
S. lutjani (syn. *Leptotheca*)	4.5-7.6 x 6.7-10.1	marine Perciformes: lutjanid (golden African snapper)	kidney	Africa
S. mackenzii (syn. *Leptotheca*)	8.8-11.6 x 14.4-18	Anura: dicroglossid (rice field frog)	urinary bladder	India
S. markewitschi	10.8-11.2 x 10.8-11.7 x 9.5-10.8	freshwater Perciformes: percid (ruffe, Donets ruffe)	renal tubules	Russia
S. masovica	8 x 8	freshwater Cypriniformes: cyprinid (common bream)	gall bladder, intestines	Canada
S. mayi	2-6 x 4-5 x 2-3.5	marine Atheriniformes: unspecified hardyhead; Mugiliformes: mugilid (flathead grey mullet)	gall bladder, intestines, peritoneum, gills, blood [slimy flesh]	India, Australia
S. melenensis	9-11 x 7-10	freshwater Cichliformes: cichlid (Nile tilapia)	kidneys	Africa
S. minima	6-7.7 x 5.4-6	freshwater Cypriniformes: cyprinid (common roach)	urinary bladder, renal tubules	Russia
S. minuta	8-9	freshwater Cypriniformes: cyprinid (Mongolian redfin)		China
S. molnari	10.3 x 10.5	freshwater Cypriniformes: cyprinid (common carp)	gills, skin [gill sphaerosporosis]	Europe
S. motemarini	13.8-18.4 x 18-2-21.7 x 18.8-22	brackish water Perciformes: lutjanid (mangrove snapper)	glomerular capillaries	North America
S. mugili	4.5-5.8 x 3.8-4.3 x 4.1-6.2	marine Mugiliformes: mugilid (flathead grey mullet)	gall bladder	Russia
S. mugilis (syn. *Polysporoplasma*)	24 x 20.5	marine Mugiliformes: mugilid (leaping mullet, thinlip mullet, thicklip grey mullet, golden grey mullet, so-iuy mullet)	kidney	Atlantic, Mediterranean
S. mystus	10 x 8.9 x 8.7	freshwater Siluriformes: bagrid (Chinese catfish)	kidney	China
S. notropis	9-11.4 x 9.9.5	freshwater Cypriniformes: catostomid (white sucker), cyprinid (common shiner)	mouth, muscles	Canada
S. ohlmacheri (syn. *Chloromyxum*, *Ceratomyxa, Wardia,*	9.5-12.6 x 10.9-14.5	Anura: bufonid (American toad), ranid (common frog, green frog, edible frog, northern leopard frog,	renal tubules, Bowman's capsules	North America

Leptotheca, L. ranae, S. ranae)		Cape River frog, agile frog, American bullfrog)		
S. ojiroveci	6.9-9.1 x 6.5-7.4	freshwater Siluriformes: pangasiid (iridescent shark)	kidney	Asia
S. olsoni	5.2-7.1 x 5.7-6 x 5.8-8.4	marine Atheriniformes: atheriopsid (topsmelt silverside)	kidney	North America
S. oncorhynchi	8.2-10.2 x 7.8-9.2 x 10.2-11.2	freshwater Salmoniformes: salmonid (sockeye salmon)	kidney	North America
S. ousei	7.6-9.1 x 7.5-8.9	freshwater Cypriniformes: cyprinid (common roach)	renal tubules	England
S. ovophila	7.2-8.4 x 6-7 x 7.4-8.2	freshwater Perciformes: centrarchid (pumpkinseed)	ovary [cysts]	Canada
S. paulini	8-8.5	freshwater Cypriniformes: cyprinid (creek chub)	kidney	Canada
S. pectinacea	8.5 x 10	freshwater Perciformes: percid (unspecified perch)	urinary tract, kidneys	Europe
S. periophthalmi	6.6 x 10.4-11.5	marine Gobiiformes: oxudercid (Atlantic mudskipper, Dussumier's mudskipper)	gall bladder	Europe
S. perlata (syn. *Leptotheca, Myxobolus*)	nr	freshwater Perciformes: percid (ruffe)	nr	France
S. pernicialis		freshwater Cypriniformes: tincid (tench)		France
S. petruschewskii	9-12.5 x 7-7.5 x 5.5-6	freshwater Cypriniformes: cobitid (weatherfish)	urinary bladder	Korea
S. plagiognathopsis (syn. *Podospora*)	6.2-7.7 x 6.1-6.3 x 7.3-8.1	freshwater Cypriniformes: xenocypridid (yellowfin)	ovary	China
S. platessae	8-9	marine Pleuronectiformes: pleuronectid (European plaice)	eyes	Europe
S. poljanskii	9.5-10 x 9-10	freshwater Cypriniformes: cyprinid (common roach)	renal tubules	Europe
S. renalis	9.5 x 9	estuarine Cyprinodontiformes: fundulid (mummichog)	urinary tract	England
S. renicola (syn. *Leptotheca*)	6-8 x 6.4-10	marine Scombriformes: scombrid (Atlantic mackerel); freshwater Cypriniformes: cyprinid (common carp)	kidney tubules	France
S. rostrata	10 x 12	estuarine Mugiliformes: mugilid unspecified mullet)	kidney	France
S. rota	8.4-11 x 8.4-11 x 9.1-9.8	freshwater Cypriniformes: cobitid (spined loach), cyprinid (common dace, Siberian dace); Salmoniformes: salmonid (sharp-snouted lenok)	urinary bladder, ureters, renal tubules	Lake Baikal
S. rutili	8.3-9.8 x 8.8-9.3	freshwater Cypriniformes: cyprinid (common roach)	renal tubules	Europe
S. sangmelimaensis		freshwater Characiformes: hepsetid (African pike characin); Osteoglossiformes: mormyrid (baby whale, mbungo)	kidney	Africa
S. sapae	6-9 x 5.7-8.1 x 5.4-7.2	freshwater Cypriniformes: cyprinid (white-eye bream)	renal tubules	Ukraine
S. saurogobii	9.6-12.3 x 8-9.7 x 6.4-9.7	freshwater Cypriniformes: cyprinid (Chinese lizard gudgeon)	gills, scales, nose	
S. scardinii	6-7.3 x 5.3-6.3	freshwater Cypriniformes: cyprinid (common rudd)	kidney, ureters	Europe
S. schulmani (syn. *Leptotheca*)	6.5-7.5 x 7.5-8.5	marine Salmoniformes: salmonid (common whitefish, vendace)	gall bladder, urinary bladder	Russia, Africa
S. sebasta (*sebastis*)	14.7-15.7 x 14.7-16.7 x 14.7-15.3	marine Scorpaeniformes: scorpaenid (Korean rockfish)	gall bladder	China
S. siluri	6.6-6.9 x 6.7-6.9	freshwater Siluriformes: silurid (wels catfish)	renal tubules	Europe

S. simplex (syn. *Leptotheca*)	5-12.5 x 13-17	marine Perciformes: sciaenid (fusaginpo); Pleuronectiformes: pleuronectid (Atlantic halibut)	urinary bladder	Atlantic, China
S. sinensis (syn. *S. branchialis*)	7.8-8.4 7.8-8.2 x 8.4-9	freshwater Anabantiformes: channid (blotched snakehead); Cypriniformes: cyprinid (common carp, bighead carp, goldfish, hiina astelparrak), xenocypridid (silver carp)	gills	China
S. sparidarum (syn. *Leptotheca*)	5-7.1 x 8.8-12.3 x 5.9-6.2	marine Spariformes: sparid (common dentex, gilthead sea bream)	kidney tubules, intestines	Spain
S. sparis (syn. *Polysporoplasma*)	19.8 x 18.1 x 21.3	marine Spariformes: sparid (gilthead sea bream)	kidney	Europe
S. sphaerica	10 x 10 x 10	marine Tetraodontiformes: tetraodontid (panther puffer)	urinary bladder	Sea of Japan
S. sphaerocapsularae (syn. *Ortholinea*)	8.4-12.8 x 8-12 x 8-9.2	freshwater Anguilliformes: anguillid (European eel)	urinary bladder	Poland
S. sphaerula (syn. *Leptotheca*)	13 x 13	marine Blenniiformes: clinid (striped kelpfish)	urinary bladder	North America
S. squalii	6.1-7.1 x 6.2-7	freshwater Cypriniformes: cyprinid (common chub)	renal tubules	Europe
S. subelegans	9-13.6 x 9-13.6	marine Gadiformes: merlucciid (shallow-water Cape hake)	gall bladder	Africa
S. subsphaerica (syn. *Leptotheca*)	7-8.4 x 9.8-10.5	freshwater Salmoniformes: salmonid (omul, Arctic grayling)	ureters, renal tubules	Lake Baikal
S. testicularis	12 x 15	marine Moroniformes: moronid (European seabass)	testes, intestines [reduced reproductivity]	Mediterranean
S. tilapiae	7-8 x 7-9	freshwater Cichliformes: cichlid (Nile tilapia)	kidneys	Africa
S. tincae (syn. *S. pernicialis*)	7-9 x 6-7.7	freshwater Cypriniformes: tincid (tench)	urinary tract, kidneys, head [swollen belly disease]	Europe
S. tongrenensis	6 x 6 x 6	freshwater Perciformes: sinipercid (golden mandarin fish)	kidney	China
S. toxabramis	5.2-6.4 x 5.6-6 x 5.2-6.4	freshwater Cypriniformes: cyprinid (swinhoe amblatikas)		China
S. truttae	6.6-8.7 x 8.2-10.1	freshwater Salmoniformes: salmonid (brown trout, grayling, Atlantic salmon) [cycle involves echinactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex, Limnodriulus variegatus*)	urinary tract, kidneys	Europe
S. umbrae	6.3 x 6.2 x 6.2	freshwater Esociformes: umbrid (European mudminnow)	kidney	Europe
S. undulans	7-10 x 6-9 x 5-8	marine Pleuronectiformes: bothid (witch), pleuronectid (New Zealand sole)	urinary bladder, ureters, oviducts	New Zealand
S. xenocypris	8.9 x 8.7 x 8.8	freshwater Cypriniformes: xenocyprinid (yellowfin)	gall bladder	China
S. yiduensis (syn. *Podospora*)	5.9-6.5 x 7.6-7.8 x 5.2-6	freshwater Cypriniformes: cyprinid (barbel chub)	gall bladder	China
S. zingeli	10 x 7.5	freshwater Perciformes: percid (zingel)	kidneys	Europe
Genus ***Wardia*** (oval-triangulate spores with 2 large spherical polar capsules)				
W. lucii	8-9 x 8-8.5 x 5-6	freshwater Esociformes: esocid (chain pickerel)	kidney	North America
W. ovinocua [type species]	9-11 x 10-12 x 6	freshwater Perciformes: centrarchid (orange spotted sunfish)	ovaries	North America
Suborder **Platysporina**				

(polar capsules in sutural plane of bilaterally symmetrical spore)				
Family **Myxobolidae** (spore flattened, suture ridged, some with projections)				
Genus ***Dicauda*** (spores with two caudal appendages extending in opposing directions)				
D. atherinoidi [type species]	8.5-12.5 x 8.5-11 x 7-9	freshwater Cypriniformes: cyprinid (emerald shiner)	subcutis	North America
D. manipurensis	12.1-15.2 x 7.1-7.6 x 6.1-6.6	freshwater Cypriniformes: cyprinid (Indian flying barb)	gills	India
Genus ***Hennegoides*** (asymmetric spores with 2 non-axial caudal appendages)				
H. berlandi	48-59 (8-9) x 2.5-3	marine Siluriformes: pangasiid (iridescent shark catfish)	gills	Malaysia
H. flockae	35.4-46.4 (15.4-18.7) x 7.1-8.7	freshwater Percopsiformes: aphredoderid (pirate perch)	gills	North America
H. longitudinalis [type species]	10.9-12.2 x 4.7-6.3	freshwater Anabantiformes: osphronemid (gourami)	intestines	Thailand
H. malayensis	36-40.5 (12.5-14.4) x 6.4-7.5	marine Siluriformes: pangasiid (iridescent shark catfish)	gills	Malaysia
H. obpyriformis (syn. *Henneguya*)	20-24.8 (9.6-10.4) x 6.4-6.8 x 4.8-5.2	freshwater Cypriniformes: nemacheilid (stone loach, yingjiangi kivitrulling)	gills, kidneys, liver, spleen	China
H. pangasii	48-72 (24-30) x 12-13.8	marine Siluriformes: pangasiid (iridescent shark catfish)	gills	Malaysia
H. seenghalae	7.5 x 3-4.5	freshwater Siluriformes: bagrid (giant river catfish)	gills	India
Genus ***Henneguya*** (round-spindle spores with 2 divergent caudal projections, 2 anterior polar capsules)				
H. acerinae (syn. *H. creplini p.p., Unicauda nemeczeki*?)	70-82 (20-22) x 5.8-9 x 6-8.1	freshwater Perciformes: percid (ruffe, zander)	gills	Europe
H. acuta	33-66 (14-18) x 4-5 x 4	freshwater Esociformes: esocid (muskellunge)	gills	North America
H. adherens	30.7-35.1 (10.5-13.8) x 5.1-6.5	estuarine Characiformes: acestrorhynchid (red-tailed freshwater barracuda)	gills	Brazil
H. adiposa	45-75 (12-19) x 3.5-4 x 2.5-3.5	freshwater Siluriformes: ictalurid (channel catfish)	fin adipose tissue	North America
H. aegea	10-14.9 x 5.6-10.9 x 5.1-7	marine Spariformes: sparid (red seabream)	bulbus arteriosus, heart	Greece
H. aequidens	39.5-42.5 (14.1-15.9) x 5.2-6.8	freshwater Cichliformes: cichlid (carazinho)	gills	Brazil
H. akule	29-52 (10-14) x 5-9 x 3-7	marine Carangiformes: carangid (bigeye scad)	bulbus arteriosus	North America
H. albomaculata	22-39 (9-11) x 8-10 x 7-8	marine Acanthuriformes: sciaenid (red drum)	gut	North America
H. alestis	17.8 x 6.1	freshwater Characiformes: alestid (African nurse tetra)	gills	Egypt
H. alexandrius	24.2 x 5.1	freshwater Siluriformes: clariid (unspecified catfish)	skin, gills	Egypt
H. alexeevi	40.8-53.4 (19.5-23.4) x 5-8 x 4-5.2	freshwater Cypriniformes: xenocypridid (silver carp); Gobiiformes: odontobutid (Chinese sleeper)	gills, ovaries [cysts]	Amur Basin
H. amazonica	55-65.9 (11.5-14.9) x 5.2-6.3 x 3.3-5	estuarine Cichliformes: cichlid (pike cichlid); Siluriformes: callichthyid (tamuata)	gills, ovaries	South America
H. ameiurensis	38.3-64.8 (23.3) x 4.1 x 3	freshwater Siluriformes: ictalurid (brown bullhead)	skin (barbels)	North America
H. amiae	33.8-50 (15.8-25) x 4.1-6.6	freshwater Amiiformes: amiid (bowfin)	gills	Canada
H. anqingensis	35.4-64.2 (11.6-	freshwater Siluriformes: ictalurid	gills	North America

	16.6) x 3.1-4 x 2.8-3.6	(channel catfish)		
H. arapaima	48.4-53.1 (13.5-15.2) x 5.1-6.1 x 4.7-5.3	freshwater Osteoglossiformes: osteoglossid (pirarucu)	gills, gall bladder	Brazil
H. archosargus	18-26 (9.5-10.9) x 6-6.5 x 4.6-5.2	Marine Spariformes: sparid (sheepshead)	gills	Brazil
H. artigasi	22.4 (16.4) x 4.4	freshwater Characiformes: characid (mojarra)	gills	Brazil
H. assiuti	40.2-50.7 (10.6-13.9) x 4.6-5.7	freshwater Siluriformes: clariid (African sharptooth catfish)	gills	Egypt
H. astyanax	46.4-49.2 (13.7-16.7) x 4.3-7.1 x 4.2	estuarine Characiformes: characid (molok)	gills	Brazil
H. auchenoglanii	52-58 (11-13) x 3-4	freshwater Siluriformes: claroteid (giraffe catfish)	gills	Chad
H. australis	31-35 (11-15) x 3-5 x 3-4	freshwater Perciformes: percichthyid (golden perch)	gills	Australia
H. azevedoi	45-47 (9.9-10.2) x 4-5	freshwater Characiformes: anostomid (boga)	gills	Brazil
H. bagre	19.2-21.8 (10.5-12.4) x 4.6-6.1	freshwater Siluriformes: heptapterid (South American catfish)	gills	Brazil
H. basifilamentalis	39-53 (13-15) x 6-7.5 x 4-5	freshwater Siluriformes: bagrid (Asian redtail catfish)	gills	Malaysia
H. basiri (syn. *Unicauda*)	25.6-39.2 x 3.2-4.4	freshwater Anabantiformes: channid (spotted snakehead)	pharynx	India
H. bayerii	44-56.8 (10-11.8) x 7.9-9.5 x 7.9-8.4	marine Perciformes: cottid (big Baikal oilfish)	kidney	Russia
H. bengalensis (syn. *Unicauda*)	26.4-29.2 x 2.7-3.9	freshwater Anabantiformes: channid (spotted snakehead)	mouth	India
H. bergamini	17-19 (7-8) x 2-2.5	marine Characiformes: characid (banded astyanax)	peritoneal cavity	Brazil
H. bicauda (*bicaudi*)	28.7-31 (20-22) x 5.9-6.5	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
H. bicornuata (syn. *Unicauda*)	26.4-29.2 x 2.7-3.9	freshwater Anabantiformes: channid (spotted snakehead)	gills	India
H. bleekeri	20-25.5 (8.9) x 3.3-5	freshwater Siluriformes: bagrid (Day's mystus)	gills, fins, kidney	India
H. bopeleti	41-48 (15-19) x 5.7-7.1	freshwater Siluriformes: claroteid (belly up)	gills	Cameroon
H. brachydeuteri	36-41 (10-12) x 7-9	marine Eupercaria: haemulid (bigeye grunt)	heart	Senegal
H. brachypomus	52.4-61.6 (11.7-13.8) x 4-4.6	freshwater Characiformes: serrasalmid (pirapitinga)	gills	Brazil
H. branchialis	27.9-41.2 (12-17.5) x 4-7	freshwater Siluriformes: clariid (African sharptooth catfish, mudfish)	gills, intestines	Egypt, Chad
H. brevis	14-15 (10) x 5-6	freshwater Scorpaeniformes: gasterosteid (three-spined stickleback)	ovary, kidney	France
H. breviscauda	15.9-18.7 (9.6-10.8) x 4.4-6.1 x 3.6-3.9	freshwater Siluriformes: heptapterid (South American catfish)	gills	Brazil
H. bulbosus	46.8-66.8 (15-19.3) x 3.7-5.6	freshwater Siluriformes: ictalurid (channel catfish)	gills	North America
H. calcarifer	34-45 (8.3-10) x 4.8-5.5 x 3.7-4	marine/estuarine Perciformes: latid (barramundi)	muscles	Malaysia
H. calcarifera	20.4-23.8 x 8-9.5	marine/estuarine Perciformes: latid (barramundi)	kidney	India
H. camerounensis	13.6-21.7 (9-11) x 3.8-5.5	freshwater Siluriformes: mochokid (upside-down catfish), schilbeid (glass catfish)	gills	Cameroon
H. caquetaia	15-27 x 6.2-10.8 x 6-7.6	freshwater Cichliformes: cichlid (basket cichlid)	opercula, fins, eyes	Brazil

			[cysts]	
H. carolina	28.4-30.4 (12-13.4) x 7.5-9.6 x 5-6.4	marine Carangiformes: carangid (Florida pompano)	intestines	Brazil
H. cartilaginis	33.4-59.6 (9.6-13.5) x 6.5-9.7 x 5.9-6.8	freshwater Salmoniformes: salmonid (masu salmon)	head cartilage	Japan
H. caudalongula	69.6-72.4 (16-17.1) x 4.4-6.6 x 4.6	freshwater Characiformes: prochilodontid (streaked prochilod)	gills	Brazil
H. caudicula	14-16 (11-12) x 5-6 x 3-4	freshwater Characiformes: anostomid (piau)	gills	Brazil
H. cerebralis	26.8-40.7 (7.8-10.7) x 6-8 x 4.2-6	freshwater Salmoniformes: salmonid (Kosogol grayling)	cartilage, connective tissues	Mongolia
H. cesarpintoi	13-14 (5.5-6) x 4-4.5	freshwater Characiformes: characid (banded astyanax)	gills	Brazil
H. chalbulaevi	20.5-23 (12-12.5) x 9-10	marine Cypriniformes: cyprinid (Caspian roach)	muscle	Russia
H. chaudhuryi (syn. *Unicauda*)	26.3-33.2 x 3.3-4.1	freshwater Anabantiformes: channid (spotted snakehead)	gills	India
H. chongqingensis	18.1-42.5 (12.2-15.1) x 7.6-10.6 x 7.6-9.1	freshwater Cypriniformes: cyprinid (goldfish)	ureters, urinary bladder	China
H. chrysichthyi	27-32 (13.7-16) x 4.6-6.3 x 4-4.5	freshwater Siluriformes: claroteid (belly up)	gills	Nigeria
H. chydadea	17.6-20 (8.8-11.2) x 3.2-5.6	freshwater Characiformes: characid (yellowtail tetra)	gill	Brazil
H. clariae	45-107.5 (17.5-28.5) x 5.5-8.5 x 5.5-7.5	freshwater Siluriformes: clariid (African sharptooth catfish)	gills	Nigeria, Egypt
H. clini	43-46 (9-11) x7-8.5	marine Blenniiformes: clinid (super klipfish, bluntnose klipfish)	gills	South Africa
H. collaris	7.1 x 6.3	marine Eupercaria: scarid (Red Sea parrotfish)	kidney	Red Sea
H. corruscans	25-29 (13-15) x 5 x 4	freshwater Siluriformes: pimelodid (spotted sorubim)	gills	Brazil
H. creplini (syn. *Myxobolus. H. acerinae p.p.*)	20-88 (17.3-18.8) x 5.8-6.3	freshwater Perciformes: percid (European perch, ruffe, zander, zingel)	gills [cysts]	Europe
H. ctenopharyngodoni	48.5-57 (16.3-17.9) x 7-8.8 x 6-7.6	freshwater Cypriniformes: cyprinid (grass carp)	gills	China
H. ctenopomae	17-25 (13-17) x 8-10.5	freshwater Anabantiformes: anabantid (dwarf ctenopoma)	gills	Cameroon
H. cuniculator	29.4 (10-14.7) x 4-5.9 x 3.9-4.9	freshwater Siluriformes: pimelodid (spotted sorubim)	gills	Brazil
H. curimata	34.2-36.1 (16-17.4) x 5.8-6.6	estuarine Characiformes: curimatid (branquinha)	kidney	Brazil
H. curvata	36.3-47.1 (14.8-18) x 4.4-5.1	freshwater Characiformes: serrasalmid (speckled piranha)	gills	Brazil
H. cutanea	37-50 (11-15) x 8.5-10	estuarine Cypriniformes: cyprinid (common bream, ide, sabrefish)	skin, fins, muscles, rarely kidneys [cysts, 'nodular skin disease']	Eurasia
H. cynoscioni	34.3-44.1 (9.8-11.7) x 8.8 x 5.9	estuarine Acanthuriformes: sciaenid (spotted seatrout)	bulbus arteriosus	North America
H. cyphocharax	29.6-44.4 (7.7-13.4) x 2.9-6.3	freshwater Characiformes: curimatid (saguiru)	gills	Brazil
H. cyprini	17.3 x 6.3	freshwater Cypriniformes: cyprinid (common carp)	gills	Egypt
H. daoudi	26.4-32.8 (11.4-12.8) x 6.7-7.6 x 4.7-5.7	freshwater Anabantiformes: osphronemid (three spot gourami)	gills	Malaysia
H. dini	27-32 (11-12) x 3-5	freshwater Osteoglossiformes:	gills	Africa

		arapaimid (African bonytongue)		
H. disparis	24-24.8 (11.2-12) x 4.8 x 4	freshwater Anabantiformes: channid (snakehead murrel)	gills	China
H. diversus (*diversis*)	40-62 (13.5-16.5) x 3.2-5 x 3-4.5	freshwater Siluriformes: ictalurid (channel catfish)	skin, fins, liver, kidneys, muscles	North America
H. dogieli (syn. *H. weishanensis*)	26.4-79 (8.5-14) x 4.5-7.2 x 3.2-6.2	freshwater Cypriniformes: cyprinid (topmouth culter); Perciformes: sinipercid (mandarin fish)	gills	Amur Basin, China
H. doneci	32.4-48.2 (8.5-9.5) x 7.2-9.1 x 6.7-7.2	freshwater Cypriniformes: cyprinid (goldfish, Prussian carp), xenocypridid (silver carp)	gills [cysts]	Amur Basin, Korea
H. doori	31-45 (15-24) x 6-16 x 4-8.4	freshwater Perciformes: percid (yellow perch)	gills	North America
H. eirasi	35.3-38.9 (12.1-13.7) x 3.1-3.7 x 3.1	freshwater Siluriformes: pimelodid (spotted sorubim, tiger shovelnose catfish)	gills	Brazil
H. electrica	35-39 (11-13) x 6-8	freshwater Gymnotiformes: gymnotid (electric eel)	electric organs	North America (ex Brazil)
H. episclera	49-81 (16-25) x 7-9 x 7-10	freshwater Perciformes: centrarchid (pumpkinseed)	eyes	North America
H. esocis	34-73.6 (15-23.6) x 3.2-4.6	freshwater Esociformes: esocid (chain pickerel)	gills	Canada
H. exilis	60-70 (18-20) x 4-5 x 3-3.5	freshwater Siluriformes: ictalurid (channel catfish, black bullhead, brown bullhead) [cycle involves aurantiactinomyxon-type actinospores in Oligochaeta: naidid (*Dero digitata*)	gills, skin [interlamellar disease, cysts]	North America
H. extensa	12.6-16.7 x 3.4-4.7 x 2.9-3.9	freshwater/estuarine Siluriformes: ictalurid (channel catfish)	gills	China
H. fastigata	22.3-27.1 (9-10.6) x 2.9-4.1	freshwater Characiformes: curimatid (saguiru)	gills	Brazil
H. fonsecai	23-27 (10-12) x 4.5-5	freshwater Characiformes: anostomid (piaba)	fins, skin	Brazil
H. friderici	28.7-39.3 (9.6-11.8) x 4.8-6.6 x 4.6-5.2	freshwater Characiformes: anostomid (threespot leporinus)	gills, intestines, kidneys, liver	Brazil
H. fusiformis	59-61 (29-33) x 5-7	freshwater Siluriformes: clariid (African airbreathing catfish)	gills	Chad
H. gambusi	22.5-32 (9.5-11) x 5-7 x 4.8-6	freshwater Cyprinodontiformes: poeciliid (western mosquitofish)	skin	North America
H. ganapatiae	9.3-10 x 4-4.8	freshwater Osteoglossiformes: notopterid (bronze featherback)	gills	India
H. garavelli	41.2-51.5 (12-14.4) x 3.9-4.1	freshwater Characiformes: curimatid (saguiru)	gills	Brazil
H. ghaffari	48.1-66.5 (11.8-14) x 6.9-7.9 x 4.9-5.9	freshwater Perciformes: latid (Nile perch)	intestines, caeca, gills	Egypt
H. gigantea	87-110.5 (10.5) x 4-5	freshwater Perciformes: percid (zander)	gills	Europe
H. gigas	37.2-52.8 (10.2-13.2) x 4.6-6.2 x 3.6-4.8	freshwater Anabantiformes: channid (northern snakehead)	gills, intestines, swim bladder, ovary	China
H. gilbert	26-28.4 (11-13.2) x 4.9-5.5	freshwater Characiformes: curimatid (saguiru)	gills	Brazil
H. gracilis	30-40 (10-14) x 2.5-3 x 3	marine Perciformes: terapontid (leathery grunter)	gills	Australia
H. guanduensis	27.3-38.1 (11.4-16.7) x 4.9-7.9	freshwater Siluriformes: callichthyid (tamuata)	gills	Brazil
H. gurleyi	48.7-68.5 (15.7-20.3) x 3.8-6.1 x 3	freshwater Siluriformes: ictalurid (black bullhead)	spines	North America
H. hainanensis	21.5-30 (9.5-12) x 4.5-5.7 x 3-3.7	freshwater Cypriniformes: cobitid (pond loach)	intestines	China

H. hemibagri	24.8-28.4 (9-14) x 2-6.4 x 1.8-3.8	freshwater Siluriformes: bagrid (grey Chinese catfish, Asian redtail catfish)	gills, body	China, Malaysia, Vietnam
H. hemiodopsis	19.7 (10.8) x 3.3 x 2.5	freshwater Characiformes: hemiodontid (bananinha)	gills	Brazil
H. hoimba	24.7 x 7.5 x 4.4	freshwater Characiformes: characid (banded astyanax)	gills	Brazil
H. ictaluri	68.9-106.3 (20.8-26.1) x 4.5-6.4	freshwater Siluriformes: ictalurid (channel catfish) [cycle involves aurantiactinomyxon-type actinospores in Oligochaeta: naidid (*Dero digitata*)]	gills [PGD = proliferative gill disease, hamburger gill disease]	North America
H. iheringi	22 x 6	freshwater Characiformes: serrasalmid (speckled piranha)	gills	Brazil
H. intracornea	36.5-45.9 (18.1) x 5.6-9.9	freshwater Characiformes: characid (piaba)	cornea	Brazil
H. jaczoi	13.2-15.2 x 5.2-7 x 4.8-5.2	freshwater Perciformes: percid (European perch)	mouth, gills	Hungary
H. jariensis	43.9-49.2 (11.9-14.6) x 5.5-7.3	freshwater Cichliformes: cichlid (tucanare peacock bass)	fins	Brazil
H. joalensis	44.5-45 (8.5-9) x 6-7	marine Perciformes: serranid (African hind)	kidneys	Senegal
H. jocu	44-55.3 (10.3-11.4) x 7.8-8.6 x 2.6-3.4	fresh and brackish water Perciformes: lutjanid (dog snapper)	gills	Brazil
H. jundiai	22.9-29.2 (8.8-10) x 4.1-5.5	freshwater Siluriformes: heptapterid (South American catfish)	gills	Brazil
H. kayarensis	52-56.5 (7-9) x 6-7	marine Perciformes: polynemid (lesser African threadfin)	liver	Senegal
H. kwangtungensis	54-82.2 (13.2-15) x 5.5-6 x 4.8-5.2	freshwater Anabantiformes: channid (blotched snakehead); Cypriniformes: cyprinid (goldfish, black carp)	gills, gall bladder	China
H. lacustris	16.1-21 (9.2-12.1) x 4.3-5.8	freshwater Characiformes: characid (tambiu)	gills	Brazil
H. lagodon	25.7-39.3 (7.1-10) x 5.7-7.1 x 4.6-6.8	marine Spariformes: sparid (pinfish)	ocular subcutis	North America
H. lagunensis	29.1 (8.2) x 7.9 x 4.8	marine Eupercaria: gerreid (Brazilian mojarra)	gills	Brazil
H. lambariensis	15.4-24.3 (8.6-12.2) x 3.2-5.8 x 4-4.7	freshwater Characiformes: characid (tambiu)	gills	Brazil
H. laseeae	64.5-79.4 (15.1-17) x 5.1-6.6 x 4.4-4.9	freshwater Siluriformes: ictalurid (flathead catfish)		North America
H. lata	16.5-21.5 (8.9-12.5) x 6.1-7.6 x 4.8-5.4	marine Spariformes: sparid (yellowfin seabream)	gills	Vietnam
H. lateolabracis	48.4 (9.9-11.9) x 6.4-7.8 x 5.9-6.4	marine Perciformes: lateolabracid (unspecified Asian seabass)	bulbus arteriosus	Japan
H. laterocapsulata	29-36.2 (13.8-16) x 3.7-5.3 x 3.3-4.3	freshwater Siluriformes: clariid (African catfish)	skin	Middle-East
H. latesa	22.5-30 (8.5-9) x 5.5-6	estuarine Perciformes: latid (barramundi)	gills	China
H. latiusii	24-26 (12.3-13.7) x 4.2-4.8	freshwater Cypriniformes: cyprinid (Gangetic latia)	gills	India
H. lazerae	14.6 x 5.1	freshwater Siluriformes: clariid (hybrid of African catfish x fattyfin catfish)	gills	Egypt
H. legeri	19.5-22.5 (11.5-14)	freshwater Cypriniformes: nemacheilid (stone loach)	urinary bladder	France
H. leporini	28-33 (13-15) x 5	freshwater Characiformes: anostomid (gra naeselaks)	urinary ducts	Brazil
H. leporinicola	18.4-40.9 (5.5-8.7) x 3.6-4.9	freshwater Characiformes: anostomid (piaucu)	gills	Brazil

H. lepturus	25.1-26.7 (11.2-12.1) x 6-6.9 x 2.2	freshwater Gymnotiformes: hypopomid (bluntnose knifefish)	brain, spinal cord	Brazil
H. lesteri	21.7 (8-10.4) x 4-5 x 2.4-2.6	marine Spariformes: sillaginid (golden lined whiting)	gills	Australia
H. limatula	40-54 (13-17) x 5-6	freshwater Siluriformes: ictalurid (channel catfish, blue catfish)	gall bladder	North America
H. linearis		freshwater Siluriformes: heptapterid (South American catfish, tiger shovelnose catfish), ictalurid (black bullhead)	gills, fins	Americas
H. lobosa (syn. *Myxobolus, H. psorospermica lobosus*)	30-57 (11.5-15) x 4-8 x 4-4.6	freshwater Esociformes: esocid (northern pike, Amur pike); Perciformes: percid (European perch, ruffe)	gills, fins, mouth [cysts]	Eurasia
H. logonensis	33-37 (11-13) x 3-4	freshwater Characiformes: citharinid (moonfish)	gills	Chad
H. longicauda	91-127 (14-17.5) x 3.5-4.5 x 3.5-4	freshwater Siluriformes: ictalurid (channel catfish)	gills	North America
H. longisporoplasma	48.5-59.2 (11.7-13.4) x 4.7-6.5	freshwater Acanthuriformes: sciaenid (South American silver croaker)	gills, fins, kidney	Brazil
H. loretoensis	36.1-36.3 (14.2-14.4) x 4.9-5.3	freshwater Siluriformes: callichthyid (false spotted catfish)	gills	Peru
H. lutjani	47.2-50.4 (11.2-13) x 6-8	marine Perciformes: lutjanid (African red snapper)	gills	Senegal
H. macropodi	20.8-29 (10.7-14) x 3-5.5	freshwater Anabantiformes: osphronemid (round-tailed paradisefish)	skin, scales	Japan
H. maculosus	27.2-38.8 (11.9-14.7) x 3.6-5.2 x 3	freshwater Siluriformes: pimelodid (spotted sorubim, barbed sorubim)	gills	Brazil
H. magna	86.8 (24.8) x 6.2	freshwater Moroniformes: moronid (white bass)	gills	North America
H. mailaoensis	58-63 (15-18) x 5-6	freshwater Osteoglossiformes: mormyrid (elephant snout)	gills	Chad
H. malabarica	26.6-29.8 (11.8-13.1) x 3.6-4.8	estuarine Characiformes: erythrinid (wolf fish)	gills	Brazil
H. malapteruri	42-53 (14-18) x 8.5-11	freshwater Siluriformes: malapterurid (electric catfish)	skin, muscles	Cameroon
H. mandouri	51-56 (11-13) x 6-7.5	estuarine Perciformes: latid (barramundi)	gills	Egypt
H. manipurensis	23.8-28 (12.6-15.4) x 5.6-7	freshwater Anabantiformes: anabantid (climbing perch)	gills, body [ulcers]	India
H. maraensis	11-13 x 7-8	freshwater Perciformes: latid (Nile perch)	gills, intestines	Tchad
H. marcquenskiae	39.5-55.9 (13.9-16.5) x7.1-9	freshwater Percopsiformes: aphredoderid (pirate perch)	liver	North America
H. markewitschi	15.7-18.7 (10.5-12)	freshwater Cypriniformes: cyprinid (gudgeon)	skin, fins	Russia
H. massii	20-23 (8-9) x 5-6	freshwater Perciformes: latid (Nile perch)	gills	Chad
H. mauritaniensis	23.2-42 (11.1-13.5) x 7.2-8.8 x 8	marine Eupercaria: sparid (bluespotted seabream)	bulbus arteriosus	Mauritania
H. mbakaouensis	51.5-69.2 (10-12) x 7-9.9 x 4.8-5.2	freshwater Perciformes: latid (Nile perch)	gills	Cameroon
H. mbourensis	28-33 (10-11) x 6.5-9	marine Eupercaria: sparid (Canary dentex)	kidney	Senegal
H. media	20-22 x 5-6	freshwater Scorpaeniformes: gasterosteid (three-spined stickleback)	kidney	France
H. megalopsi	36.8-40 (11.2-12.8) x 3.2-3.6 x 2.5-3	marine Elopiformes: megalopid (Indo-Pacific tarpon)	gall bladder	India
H. melini	40.3-41.1 (15.3-15.7) x 4.6-4.8	freshwater Siluriformes: callichthyid (false bandit catfish)	gills	Brazil
H. michiganensis	67.3-96.9 (18.6-	freshwater Esociformes: esocid	gills	North America

	22.6) x 5.4-6.9 x 3.5-4	(muskellunge)		
H. minuta (syn. *Myxobolus minutus p.p.*)	28-45 (20-28) x 10-11 x 28-45	freshwater Perciformes: percid (European perch)	gills	Europe
H. mississippiensis	40.7-61.6 (14.4-19.3) x 4.5-5.5	freshwater Siluriformes: ictalurid (channel catfish)	gills	North America
H. miyairii	23-40 (12) x 8	freshwater Cypriniformes: cyprinid (goldfish)	head subcutis	Japan
H. miyazakii	33.1-56.1 (9.6-13.3) x 8.5-11.1 x 4.1-7.3	marine Gobiiformes: oxudercid (fork-tongued goby)	skin	Japan
H. mogurndae	61-62 (26-27) x 5	freshwater Gobiiformes: odontobutid (donko)	gills	Japan
H. mormyri	30-34 (8-9) x 4-5	freshwater Osteoglossiformes: mormyrid (elephant snout)	gills	Chad
H. mueusslini	32 (12) x 8-9	freshwater Salmoniformes: salmonid (brown trout, brook trout) [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)]	skin	Europe
H. multimorpha	15-19.2 (9-10.8) x 4.8-6.1 x3.8-5.4	marine Gobiiformes: gobiid (javelin goby)	gills	China
H. multiplasmodialis	29.5-32.1 (14.2-15.2) x 4.9-5.5 x 4.4	freshwater Siluriformes: pimelodid (spotted sorubim, barred sorubim)	gills	Brazil
H. multiradiatus	43.9-45.1 (16.8-19.6) x 6.6-7.4 x 4.9-5.6	freshwater Siluriformes: callichthyid (hog-nosed catfish)	serosa	Peru
H. mystasi	35.8-53.8 (13-18.7) x 1.6-4	freshwater Siluriformes: bagrid (long whiskers catfish, striped dwarf catfish)	gills	India
H. mystusia	27-40 (11-15) x 3-4 x 2-3	freshwater Cyprinodontiformes: aplocheilid (striped panchax); Siluriformes: bagrid (Asian redtail catfish, unspecified mystus)	gills [haemorrhages]	India, Malaysia
H. nagelii	26.4-39.9 (11.2-11.9) x 4.4-5.5 x 3.6-5.7	freshwater Characiformes: curimatid (saguiru)	gills	Brazil
H. namae	35.2-37.4 (17.6-19.3) x 5.5-6.6 x 4.4-5	marine Ovalentaria: ambassid (elongate glassy perchlet)	gills, heart	India
H. nandi	18-25 (9-11) x 3-5	freshwater Anabantiformes: nandid (Gangetic leaffish)	gills, heart	India
H. nanhaiensis	28-62.4 (13.2-14.4) x 7.2-7.8 x 5-6.4	freshwater Anabantiformes: channid (northern snakehead)	skin, kidneys	China
H. neopolitana	50-60 (8.5-9.5) x 6.3-7	marine Spariformes: sparid (salema porgy)	kidney	Italy
H. nigris	45-60 (22) x 7-8 x 4-5	freshwater Esociformes: esocid (chain pickerel, muskellunge)	gills	North America
H. nilotica	35-45.6 (12.6-17.4)	freshwater Siluriformes: clariid (African catfish)	suprabranchial organ	Egypt
H. nkamensis	36-46 (8010) x 4-5.5	freshwater Characiformes: hepsetid (African pike characin)	gills	Cameroon
H. notopteriae	52-55 (11.5-13) x 4.5-5	freshwater Osteoglossiformes: notopterid (bronze featherback)	gills	India
H. novaerae	23.3-26.8 (10.1-11.6) x 3.2-4.2	freshwater Siluriformes: heptapterid (South American catfish)	gills	Brazil
H. ntemensis	12.5-20.4 (9.2-12) x 7-8.9 x 7	freshwater Osteoglossiformes: mormyrid (baby whale)	gall bladder, kidney, spleen	Cameroon
H. ntondei	24-35 (10.5-14) x 4-7	freshwater Siluriformes: schilbeid (African butter catfish)	gills	Cameroon

H. nuesslini (syn. *H. muesslini*)	27-37 (10-17) x 8-12	freshwater Salmoniformes: salmonid (brown trout, brook trout)	skin	Germany
H. nyongensis	30.5-36.5 (10-14) x 4.5-6.5 x 3-4.2	freshwater Osteoglossiformes: mormyrid (mormyre)	gills, muscles	Cameroon
H. occulta	36-50 (16-20) x 8-10	freshwater Siluriformes: loricariid (unspecified whiptail catfish)	gills	Brazil
H. ocellata	17.2-21.1 (7.3-19.2) x 7.3-8.9 x 5.9-6.6	marine Acanthuriformes: sciaenid (red drum)	intestines, pyloric caeca	North America
H. odzai	29.2-36 (13-16) x 3.3-4.6 x 2.6-3	freshwater Osteoglossiformes: mormyrid (mormyre)	gills	Cameroon
H. ogawai	19.2-23.4 (8.9-12.20 x 6.3-7.5 x 5.2-6.6	marine Spariformes: sparid (blackhead seabream)	intestines	Japan
H. ophiocephali (*ophicephali*) (syn. *Unicauda*)	(41.5-52.5) 23.6-62 x 4.5-7.2 x 3.6-5	freshwater Anabantiformes: channid (northern snakehead, spotted snakehead, dwarf snakehead, giant snakehead)	gills, muscles, swim bladder, walls of blood vessels of visceral organs [cysts]	Amur Basin, Korea, Vietnam, India
H. orientalis	40.2 (12.4-14.5) x 6.5-7 x 6.5	freshwater Anabantiformes: channid (northern snakehead)	gills	China
H. otolothi	35-52 (10-12) x 6-8.5 x 4-5	marine Acanthuriformes: sciaenid (tigertooth croaker, blotched tiger-toothed croaker)	bulbus arteriosus	India
H. ouakamensis	16-24 (9-13) x 5-9	estuarine Mugiliformes: mugilid (flathead grey mullet)	gills, heart	Senegal
H. ovaliformis	17.6-21.6 (10.4-12.2) x 4.8-5.1 x 5	freshwater Anabantiformes: channid (snakehead murrel)	intestines	China
H. ovata	14.7-17.1 (6.1-7.1) x 2.9-4.1 x 2.8-3.3	marine Carangiformes: carangid (ovate pompano)	intestines [enteritis]	China
H. oviperda (syn. *H. psorospermica oviperda, Myxobolus oviperdus, Unicauda*)	19-42 (18) x 5-10 x 5.4	marine Esociformes: esocid (northern pike); Perciformes: percid (zander)	ovaries, testes, rarely intestinal wall, spleen [cysts, reduced fecundity]	Europe
H. pagri	34.7-46.6 (9.9-11.9) x 6.4-8.4 x 5.4-6.4	marine Spariformes: sparid (red seabream)	gills, bulbus arteriosus	Japan
H. papernae [replacement name for *H. latesi*]	9-10.8 x 4-8.2 x 5.4	estuarine Perciformes: latid (barramundi)	gills, mouth	India
H. paraensis	41.6-43 (12.4-13.2) x 8.2-9	freshwater Cichliformes: cichlid (speckled peacock bass)	gills	Brazil
H. paramormyropsi	25.5-32.5 (10.7-12.8) x 3.9-5.9	freshwater Osteoglossiformes: mormyrid (Kingsley elephantfish)	gills, eyes. kidneys	Cameroon
H. paranaensis	56-63 (14-17) x 6-7 x 5	freshwater Characiformes: prochilodontid (streaked prochilod)	gills	Brazil
H. pardensis	24.1-30 (10.8-14.2) x 4-4.9	freshwater Characiformes: curimatid (saguiru)	gills	Brazil
H. pellis	79-124 (11-14.5) x 4.5-5.2 x 4-5	freshwater Siluriformes: ictalurid (blue catfish)	skin	Brazil
H. pellucida	30.3-36.3 (10.8-12) x 3.3-4.9	freshwater Characiformes: serrasalmid (small-scaled pacu)	serosa, body cavity, swim bladder	Brazil
H. periophthalmusi	13.3-21 (8.8-10.6) x 5.9-6.7 x 4.4-5.2	marine Gobiiformes: oxudercid (New Guinea mudskipper)	gills	China
H. peruviensis	22.9-25.5 (12.5-14.3) x 3.8-4	freshwater Characiformes: characid (Loreto tetra)	gills	Peru
H. pethericii	40-52 (11-14) x 4.5-5.5	freshwater Anabantiformes: anabantid (marmoreret buskfish)	gills	Cameroon
H. piaractus	47.6-56.3 (11.8-	freshwater Characiformes:	gills	Brazil

	13.6) x 3.2-3.9	serrasalmid (small-scaled pacu)	[respiratory signs]	
H. pilosa	52.3-56 (20-23.1) x 5.5-6.5	freshwater Characiformes: serrasalmid (caribe azul)	gills	Brazil
H. pindaibensis	32.2-39.6 (11.6-14) x 4.3-5.4	freshwater Characiformes: ctenoluciid (bicuda)	gills	Brazil
H. pinnae	21-25 (10-12) x 3-4	freshwater Anabantiformes: anabantid (tailspot ctenopoma)	fins	
H. pisciforme	25.7-36 (17.3-23.2) x 4.4-6.7	freshwater Characiformes: characid (Buenos Aires tetra)	gills	Brazil
H. polarislonga	27.5-37.2 (13.3-18.1) x 5.8-7.9	freshwater Characiformes: characid (tambiu) [cycle involves seisactinomyxon-type actinospores in Oligochaeta: naidid (*Slavina evelinae*)]	gills	Brazil
H. postexilis	42-74.2 (12.1-18.9) x 3.4-4.8 x 2.9-4.4	freshwater Siluriformes: ictalurid (channel catfish)	gills	North America
H. preintestinalis	9-10.2 x 5.1-6.2 x 4-4.5	estuarine Gobiiformes: oxudercid (dusky tripletooth goby)	intestines	Japan
H. priacanthi	36.5-41 (9-9.5) x 6.5-8	marine Perciformes: priacanthid (Atlantic bigeye)	gills	Senegal
H. pseudoplatystoma	31.3-35.1 (9.8-11) x 3-3.8 x 4.5	freshwater Siluriformes: pimelodid (hybrid of spotted sorubim x barred sorubim)	gills	Brazil
H. pseudorhinogobii	39.5-60.7 (14.2-17.8) x 4.7-5.8	freshwater Gobiiformes: oxudercid (unspecified rhinogoby)	gills	Japan
H. psorospermica (syn. *Myxobolus, H. periintestinalis, texta*) [type species]	24-40 (9-14.4) x 4.8-9 x 4-8	freshwater Cypriniformes: cyprinid (ziege); Gadiformes: lotid (burbot); Gobiiformes: oxudercid (dusky tripletooth goby); Esociformes: esocid (northern pike); Perciformes: percid (European perch, zander); Salmoniformes: salmonid (European cisco)	gills, mouth, muscles, intestines [cysts]	Eurasia
H. pungitii	31-37 (13-17) x 4.5-6	freshwater Scorpaeniformes: gasterosteid (ninespine stickleback)	subcutis [cysts]	Russia
H. qadrii	15.4-26.9 (9.2-12.3) x 4.6-5.3	freshwater Anabantiformes: channid (dwarf snakehead)	intestines	India
H. qenabranchiae	51.8-53.3 (14.2-15.9) x 3.9-4.2	freshwater Siluriformes: clariid (African sharptooth catfish)	gills	Egypt
H. qenasuprabranchiae	33.4-44.2 (12.2-14.5) x 4.5-5.3	freshwater Siluriformes: clariid (African sharptooth catfish)	extrarespiratory organs	Egypt
H. quelen	37-42.8 (14.3-16.4) x 3.9-4.4	freshwater Siluriformes: heptapterid (South American catfish)	kidney	South America
H. renalis	19.2-32 (14.4-19.2) x 8-11.2	freshwater Anabantiformes: channid (bullseye snakehead)	kidney	India
H. renicola	12-21.8 (6.6-9.6) x 12-21.8 x 3-5.8	freshwater Scorpaeniformes: gasterosteid (ninespine stickleback)	kidney	Europe
H. rhamdia	48.2-51.8 (12-14.2) x 4.8-5.7 x 2.5	freshwater Siluriformes: heptapterid (South American catfish)	gills	Brazil
H. rhinogobii	34.7-59.3 (15-19.3) x 4.6-6.2 x 4.2-5.4	marine/freshwater Cypriniformes: cyprinid (rosy bitterling); Gobiiformes: gobiid (gokuraku-haze, harilik nospelrunt)	gills, intestines, mesenteries	China, Japan
H. rhomboideus	57.5-69.9 (13.6-16.5) x 6-7.6 x 6-7.6	freshwater Cypriniformes: cyprinid (goldfish)	swim bladder	China
H. ritae	39.9-44.8 x 5-5.8	freshwater Siluriformes: bagrid (rita)	gills	India
H. rondoni	16.9-18.1 (6.8-7.3) x 3-3.9 x 2.2-2.8	freshwater Gymnotiformes: rhamphichthyid (mousetail knifefish)	peripheral nerves	Brazil
H. rotunda	7.1 x 5.6 x 3.7	freshwater Characiformes: characid (dourado)	gills, fins	Brazil
H. rubicundi	24.4-36.7 (11.1-	estuarine Gobiiformes: oxudercid	fins	India

	12.2) x 3.3-8.1	(rubicundus eelgoby)		
H. sacacaensis	46.5 (16.5) x 5.1	freshwater Cichliformes: cichlid (demon eartheater)	gills	Brazil
H. salmonicola	43.5-57 (11.9-14.7) x 7.1-9.5	freshwater Salmoniformes: salmonid (coho salmon)	muscles	North America
H. salmonis	46.8-57.2 (10-11.6) x 5-7.7 x 4.5-5.5	freshwater/estuarine Salmoniformes: salmonid (Atlantic salmon)	skin	Canada
H. salvelini	37.5-52.5 (12.5-15) x 7.5-10 x 6.2-10	freshwater Salmoniformes: salmonid (Arctic char)	skin	Europe
H. samochimensis	47-53 (12.3-15) x 5-7	freshwater Siluriformes: clariid (African sharptooth catfish)	gills	Botswana
H. santae	19.3-22.7 (8.5-10.6) x 4.7-5.8	freshwater Characiformes: characid (piabinha)	gills	Brazil
H. santarenensis	26.3-36.1 (9.6-11.9) x 3.7-4.9 x 3.4-3.7	freshwater Siluriformes: pimelodid (redtail catfish)	gills	Brazil
H. sarotherodoni	39-42 (11-12) x 6-8	freshwater/estuarine Cichliformes: cichlid (mango tilapia)	intestines	Chad
H. schizodoni	27-30 (12-14) x 3.3-3.4	freshwater Characiformes: anostomid (boga)	kidney	Brazil
H. schizura (syn. *Myxobolus*)	12 x 6 x 3	freshwater Anabantiformes: osphronemid (three spot gourami); Esociformes: esocid (northern pike)	gills, eyes	Eurasia
H. schulmani	16.8-20.4 x 4.8-6 x 3.6-4.2	freshwater Anabantiformes: anabantid (climbing perch)	gills	Vietnam
H. sebasta	48.1-82.8 (13-17.5) x 5.6-11 x 5-8.7	marine Scorpaeniformes: scorpaenid (bocaccio rockfish, shortbelly rockfish, greenspotted rockfish, splitnose rockfish, vermilion rockfish, copper rockfish, olive rockfish)	bulbous arteriosus, heart chamber	North America
H. setiuensis	36-41 (8.3-9.5) x 5.8-6 x 4.1-4.2	estuarine Perciformes: latid (barramundi)	gills	Malaysia
H. shackletoni	34.5-65.5 (9.5-14.5) x 7.2-11.2 x 5.4-8.6	marine Perciformes: eleginopid (Patagonian blenny)	gut wall, mesentery, head, gonads	Falkland Islands
H. shaharini	32.4-40.3 (10.6-12.3) x 2.8-3.9 x 2.5-3.4	fresh and brackish water Gobiiformes: butid (marbled sand goby)	gills	Malaysia, Vietnam
H. shariffi	16.2-27.2 (10.3-11.9) x 3.6-3.8 x 3.6-3.8	freshwater Siluriformes: pangasiid (iridescent shark)	gills	Malaysia
H. sichuanensis	19.1-23.8 (6.1-9.8) x 4.3-7.3 x 6	estuarine Cypriniformes: cyprinid (harilik nospelrunt)	urinary bladder	China
H. similis	37-60 (18-32) x 5.7-10.5	freshwater Perciformes: percid (European perch)	gills	Europe
H. sinensis	31.8-52.2 (10.8-16.2) x 4-6 x 3.6-4.5	freshwater Anabantiformes: channid (northern snakehead, blotched snakehead); Cypriniformes: cobitid (pond loach), Siluriformes: clariid (walking catfish)	intestines, swim bladder, ovaries	China
H. singhi	41.1-61.6 (11-13.6) x 3.9-5.7	freshwater Osteoglossiformes: notopterid (bronze featherback)	gills	India
H. sinova	51.5-68 (11.3-12) x 7.3-8.3 x 6.6-6.8	marine Blenniiformes: blenniid (tentacled blenny)	gills	Turkey
H. striolata	39.3-45.6 (14.4-17) x 4.9-5.9	freshwater Characiformes: serrasalmid (piranha mafura)	gills	Brazil
H. suprabranchiae	30.7-56.4 (11-15.7) x 2-7 x 3.9-4.9	freshwater Siluriformes: clariid (Africa sharptooth catfish)	gills, intestines [cysts]	Israel
H. sutherlandi	48.2-90 (12.2-19.3) x 4.5-6.8	freshwater Siluriformes: ictalurid (channel catfish)	skin	North America
H. symphodae	9.5-11 x 6-7.5	marine Labriformes: labrid (grey	bile ducts	Europe

		wrasse, pointed-snout wrasse, axillary wrasse, east Atlantic peacock wrasse)		
H. tachysuri	47-60 (12-15) x7-8 x 5-6	fresh and brackish water Anabantiformes: channid (spotted snakehead)	gills	India
H. tangschensis	53.6-59 (17.6-19.2) x 4.4-5.6 x 3.2-4.8	freshwater Anabantiformes: channid (northern snakehead)	mouth, intestines	China
H. tapajoensis	31.7-62.2 (14.5-19.1) x 5.7-9.3 x 4.8-5.1	freshwater Cichliformes: cichlid (spotted peacock bass)	gills	Brazil
H. tapariensis	47.4-59 (12.5-14.4) x 3.1-3.9 x 1.9-3.2	freshwater Characiformes: serrasalmid (pirapitinga)	gills	Brazil
H. tchangi	24.4-30.8 (9.2-11.6) x 7.2-7.6 x7-8	freshwater Cypriniformes: cyprinid (davidi marinka)	urinary bladder	China
H. tegidiensis	30-68 (8-12) x 8-12 x 6-7	freshwater Salmoniformes: salmonid (powan)	skin	United Kingdom
H. tengchongensis	12.4-16 (8-10) x 4.4-4.8 x 4-4.8	freshwater Siluriformes: sisorid (sucker throat catfish)	gills	China
H. tenuis	4 (3) x 2	freshwater Perciformes: percid (ruffe)	gut connective tissue	France
H. testicularis	27-28.5 (14-14.5) x 6-6.5	estuarine Characiformes: characid (glass tetra)	testes	Brazil
H. texana	43-68 (7-9) x 6-7 x 4-5	marine Acanthuriformes: sciaenid (black drum)	gills	North America
H. texta (syn. *H. psorospermica texta, Myxobolus textus*)	17.5-22 x 7.2-9.6 x 7.2-9.6	freshwater Perciformes: percid (European perch)	gills	Europe
H. theca	40.6-52.6 x 3-4.1	freshwater Gymnotiformes: sternopygid (glass knifefish)	brain	Brazil
H. thermalis	47-60 (12-13.2) x 6-8 x 5	freshwater Cypriniformes: cobitid (common spiny loach)	brain	India
H. tietensis	53.5-57 (15-16.9) x 5.4-5.6	marine Characiformes: prochilodontid (streaked prochilod)	gills	Brazil
H. torpedo	48.3-48.9 (28.3-30.1) x 7-7.5 x 2.9-3.1	freshwater Gymnotiformes: hypopomid (itui)	brain, spinal cord	Brazil
H. travassoi	26.3-28.1 (10.1-10.8) x 3.8-4.8	freshwater Characiformes: anostomid (unspecified *Leporinus*)	muscles	Brazil
H. tridentigeri	53.9 (12.5) x 7.4 x 7.3	marine Gobiiformes: oxudercid (dusky tripletooth goby, yellowfin goby)	skin, gills	Japan
H. tucunarei	36.1-49.6 (12.1-15.7) x 4.9-7.8	freshwater Cichliformes: cichlid (tucanare peacock bass)	gills	Brazil
H. tunghuensis	59.2-87.2 (15.6-19.2) x 6-6.4 x 4.6-4.8	freshwater Anabantiformes: channid (northern snakehead)	body cavity	China
H. tunisiensis	38-50 (13-14) x 9-10 x 7.5-8.5	marine Labriformes: labrid (East Atlantic peacock wrasse)	gills	Tunisia
H. umbri	35.6-56.4 (15.6-20.4) x 5.4-7 x 4.8-6	freshwater Esociformes: umbrid (central mudminnow)	gills	North America
H. unitaeniata	20.1-25.8 (13.2-15.6) x 4.3-5.7	freshwater Characiformes: erythrinid (gold wolf fish)	gills	Brazil
H. varicorhinusi	40.4-44.2 (13.2-15.2) x 7-8 x 7	freshwater Cypriniformes: cyprinid (tomp koukloug)	gills	China
H. visceralis	22-24 (11-12) x 5-6.5 x 4.5	freshwater Gymnotiformes: gymnotid (South American electric fish)	mesentery, liver, kidney, heart	Americas
H. visibilis	10.8 x 3.9	freshwater Characiformes: anostomid (boga)	connective tissues	Brazil
H. vitiensis	34.8-51.3 (12.1-	marine Acanthuriformes: leiognathid	heart	Fiji

	15.8) x 6.7-8.8	(striped ponyfish)		
H. voronini	35-39 (9.5-10.3) x 5.8-6	estuarine Perciformes: latid (barramundi)	gills	Malaysia
H. vovki	22.4-35 (10-11) x 4.8-7 x 4-5.5	freshwater Anabantiformes: channid (northern snakehead, striped snakehead)	body cavity	Amur Basin, China
H. waltairensis	55-65 (14.6-15.5) x 3.2-4	freshwater Anabantiformes: channid (spotted snakehead, striped snakehead)	gills [haemorrhages]	India
H. wenyoni	28-32 (20) x 4.5-6	freshwater Characiformes: characid (unspecified characin)	gills	Brazil
H. wolinensis	62.3-66.2 (24-26) x 7-8.4 x 6.6.4	freshwater Perciformes: percid (European perch)	scales	Poland
H. yoffensis	37-50 (12-15) x 8-11	marine Spariformes: sparid (bluespotted seabream)	gills, heart	Senegal
H. yokoyamai	21.9-29.2 (10.1-13.7) x 6.6-7.5 x 4.5-6.4	marine Spariformes: sparid (blackhead seabream)	gall bladder, mesentery	Japan
H. yunannensis	19.2-27.2 (8.8-12.8) x 9.6 x 4.8-5.6	freshwater Siluriformes: sisorid (three-lined catfish)	abdomen, tail	China
H. zahoori	20-30.6 (8-12) x 2.1-3	freshwater Anabantiformes: channid (spotted snakehead)	gills, pharynx	India
H. zikawiensis	16-49.2 (8.4-10.8) x 7.2-9.6 x 4.9-6.6	freshwater Cypriniformes: cyprinid (goldfish, Prussian carp)	gills, skin, cornea, intestines, gall bladder, heart, kidney	Amur Basin, Korea, Japan
H. zschokkei (syn. *H. kolesnikovi, salminicola, tegidiensis, Myxobolus zschokkei*)	36-55 (11-15) x 7-14 x 4.7-8	freshwater Cypriniformes: cyprinid (common bream, white bream, vimba bream, common bleak, sabrefish, longnose dace, redside shiner, common roach); Esociformes: esocid (northern pike); Gadiformes: lotid (burbot); Perciformes: percid (European perch); Salmoniformes: salmonid (chum salmon, sockeye salmon, chinook salmon, coho salmon, pink salmon, rainbow trout, lake trout, Arctic char, Arctic grayling, sharp-snouted lenok, fera, vendace, sardine cisco, Arctic cisco, omul, peled, common whitefish, broad whitefish, round whitefish, mountain whitefish, autumn whitefish, pygmy whitefish, Ladoga whitefish, Siberian whitefish, Valaam whitefish, muksun); Scorpaeniformes: cottid (slimy sculpin); Siluriformes: silurid (wels catfish)	muscles, gills, subcutis [cysts, milky flesh, tapioca disease]	Eurasia, North America
Genus ***Laterocaudata*** (ellipsoid spores with long thin curved projections)				
L. armati (syn. *Unicauda*)	7.5-9 (+ tail 8-15) x 5.6-7	freshwater Synbranchiformes: mastacembelid (zig-zag eel)	gills	India
L. mastacembela [type species]	8.1-9.2 (+ tail 13.1-21.6) x 4.6-5.4 x 3.9-4.2	freshwater Synbranchiformes: mastacembelid (spiny eel)	gills	China
Genus ***Myxobolus*** (syn. *Disparospora, Facieplatycauda, Gyrospora, Mixosoma, Myxosoma* (*Lentospora*)*, Myxosporidium, Rudicapsula*) (ovoid-ellipsoidal biconvex spores, 2 polar capsules, with (*Myxosoma*) or without (*Myxobolus*) iodinophilous vacuole in sporoplasm)				
M. abdominalis	6.5-7.7 x 5.2-6.8 x 4.2-5.5	marine Mugiliformes: mugilid (thicklip grey mullet)	peritoneum [cysts]	Portugal
M. abitus	7.2-8.6 x 8.4-9.8 x	freshwater Cypriniformes: cyprinid	gills, body	China

	4.8-5.4	(common carp, bighead carp), xenocypridid (silver carp)	surface, kidneys	
M. absonus	15.7 x 10.2	freshwater Siluriformes: pimelodid (spotted pim)	opercular cavity	Brazil
M. acanthogobii (syn. *M. buri*)	9.6-10.8 x 7.8-9.6 x 5.8-6.6	freshwater/marine Carangiformes: carangid (Japanese amberjack); Cypriniformes: cyprinid (grass carp, black carp); Gobiiformes: oxudercid (yellowfin goby)	brain, gills, intestines, kidneys, spleen, swim bladder [scoliosis]	Asia
M. acanthopagri	9-10.2 x 7.1-7.8 x 5.4-6.5	marine Spariformes: sparid (yellowfin bream)	subepithelial intestines	Australia
M. acanthorhodi	9.6-12 x 6-7.8 x 4.8-6	freshwater Cypriniformes: cyprinid (Khanka spiny bitterling, giant Chinese bitterling, rosy bitterling)	kidneys, spleen	China
M. acheilognathi (syn. *Leptotheca*)	9 x 6 x 12	freshwater Cypriniformes: cyprinid (goldfish, slender bitterling)	skin	Japan
M. acheilognathusi	8.8-11.2 x 6.4-8.8 x 5.4-5.6	freshwater Cypriniformes: cyprinid (omei paljaslong, Chinese false gudgeon)	gills	China
M. achmerovi (syn. *M. oviformis p.p.*)	12-14 x 8.6-10 x 5-6	freshwater/estuarine Cypriniformes: cyprinid (koi carp, goldfish, gold barb, Khanka spiny bitterling); Mugiliformes: mugilid (flathead grey mullet, so-iuy mullet)	fins, mesenteries	Amur Basin, Japan, Vietnam
M. acinosus	9.6-13.2 x 5.4-7.2 x 4.8-6	freshwater Cypriniformes: cyprinid (common carp, koi carp, goldfish)	gills	China
M. acrossocheilusi (syn. *Myxosoma*)	8-9.6 x 7-7.3 x 3.2-4.8	freshwater Cypriniformes: cyprinid (yunnani silemokk)	kidneys	China
M. acutus (syn. *Myxosoma, Lentospora, Sphaerospora*)	8-14.3 x 7-11.2 x 6-8.1	freshwater Anabantiformes: channid (northern snakehead); Cypriniformes: cyprinid (common carp, crucian carp, Prussian carp, Chinese hooksnout carp, goldfish, yunnani silemokk)	gills, intestinal wall, rarely liver	Asia
M. adeli	5.5-6.7 x 6.5-7.7 x 3.5-5.2	marine Mugiliformes: mugilid (golden grey mullet)	gut, swim bladder, gills, muscles	Spain
M. adiposus	8.7-9.3 x 8.7-9.3	marine Mugiliformes: mugilid (thinlip mullet)	ocular adipose tissue, urinary bladder	Portugal
M. adlardi	7.8-8.1 x 4.7-4.9	freshwater Cypriniformes: cyprinid (rohu)	gills	India
M. adrianoi	22.4 x 16.3	freshwater Siluriformes: callichthyid (Schwartz's catfish)	gut serosa	Brazil
M. aeglefini (syn. *M. esmarkii, lairdi*)	9-13 x 8-12 x 5-9	marine Gadiformes: gadid (haddock, Atlantic cod, Baltic cod, Norway pout, merling), lotid (common ling), macrourid (roundnose grenadier); Pleuronectiformes: pleuronectid (European plaice); Salmoniformes: salmonid (Atlantic salmon)	cartilage, skull, eye orbit, brain [cysts]	Atlantic, North Sea, Baltic Sea
M. aestuarium	7.3-8.3 x 6-8 x 4.4-5.8	estuarine Mugiliformes: mugilid (thicklip grey mullet)	gills [cysts]	Portugal
M. africanus	13.6-17.5 x 5.7-9	freshwater Characiformes: hepsetid (African pike characin)	brain	Cameroon
M. agolus	9-11 x 9-10	freshwater Cichliformes: cichlid (banded jewelfish, Nile tilapia, mango tilapia, spotted tilapia, mvogoi tilapia, Cameroon tilapia, hybrid of blue tilapia x Nile tilapia)	gills, viscera	Africa
M. akhmerovi		freshwater Cypriniformes: cyprinid (koi carp); Mugiliformes: mugilid (flathead grey mullet, so-iuy mullet)		Vietnam
M. alacaudatus	13.7-15.8 x 7.4-9.5	freshwater Cypriniformes: cyprinid	gills, fins,	Amur Basin

	x 7.3-9.5	(goldfish, Prussian carp)	muscles	
M. aligarhensis	11.4-15 x 6-7.9	freshwater Anabantiformes: channid (spotted snakehead)	accessory respiratory membrane [cysts]	India
M. albi	8.3–10.0 x 7.7–10.0 x 5.8–7.4	freshwater Gobiiformes: gobiid (common goby)	gills	Scotland
M. albovae	10.5-13 x 8-9.5 x 6-6.5	freshwater Cypriniformes: cyprinid (Siberian dace, common nase)	gills	Russia
M. alburni	12-15.3 x 10-12 x 5.5-6.5	freshwater Cypriniformes: cyprinid (common bleak, Kura bleak)	fins	Russia
M. aldrichetti	9.7 x 7.7	marine Mugiliformes: mugilid (yelloweye mullet)	gills	Australia
M. aletaiense	12.8-13.2 x 4.9-5.2 x 4.3-4.6	freshwater Cypriniformes: cyprinid (ide)	kidney	China
M. algonquinensis	13.6-15.4 x 10.1-12.1 x 5-6.9	freshwater Cypriniformes: cyprinid (golden shiner)	ovary [cysts]	Canada
M. alienus	9.5-11 x .3-9.5 x 6.6-7	freshwater Esociformes: esocid (northern pike)	gall blader wall	Russia
M. alievi	14-15 x 11-12 x 8	brackish Cypriniformes: cyprinid (Caspian roach)	muscles	Russia
M. aligarhensis (syn. *M. ophiocephali, punctatus*)	12-14 x 5.7-7.8	freshwater Anabantiformes: channid (spotted snakehead)	accessory respiratory membrane, pharyngeal epithelia, fins	India
M. allami	11-13 x 7-8 x 10-12	marine Eupercaria: sparid (Sobaity seabream)	intestines	Arabian Gulf
M. allotypica	10.2-12 x 7.2-9.6 x 5.3-6.7	freshwater Cypriniformes: xenocypridid (silver carp)	gills	China
M. altgarhensis	12-14 x 6-7.5	freshwater Anabantiformes: channid (spotted snakehead)	accessory respiratory membrane	India
M. alvarezae	11.3–12.6 x 6.5–7.6 x 6.1–6.9	freshwater Cypriniformes: cyprinid (ide, asp)	gills	Hungary
M. alvigae	9.5-10.5 x 7-8 x 4.8-5.2	freshwater Cypriniformes: nemacheilid (Siberian stone loach)		Russia
M. amieti	11.3-15.8 x 5.4-8.7	freshwater Anabantiformes: anabantid (dwarf ctenopoma)	gills, eye	Cameroon
M. ampullaceus	8.6-10.7 x 6.4-7.9	freshwater Cypriniformes: cyprinid (kolus barb)	fins	India
M. ampullicapsulatus	16.5–19.5 x 8.5–10.0 x 7.0	freshwater Cypriniformes: cyprinid (goldfish)	gills	China
M. amurensis	9-13.5 x 7.8-12.5 x 5.8-6.2	freshwater Cypriniformes: cobitid (pond loach), cyprinid (common carp, koi carp, bighead carp, stone moroko)	gills, fins, intestinal walls, gonads [cysts]	Amur Bason, Korea
M. analfinus (syn. *M. analfnus*)	11.1-13.4 x 7.8-9.3 x 6-6.5	freshwater Siluriformes: heteropneustid (Asian stinging catfish)	fins	India
M. anatolicus	9.4-10.7 x 6.6-7.2 x 4.4-4.6	freshwater Cypriniformes: cyprinid (western fourbarbel scraper)	gills	Turkey
M. andhrae (syn. *Myxosoma*)	12.1-15.7 x 5.7-8.6	freshwater Anabantiformes: channid (spotted snakehead)	intestinal wall	India
M. angustus	14-15 x 7-8 x 6-7	freshwater Cypriniformes: cyprinid (bullhead minnow, fathead minnow, common shiner, golden shiner)	gills	North America
M. anili	9.8-11.1 x 7.9-9.8	estuarine Mugiliformes: mugilid (corsula, largescale mullet)	intestines, mesenteries	India
M. anisocapsularis	14.2-15.6 x 7.7-9.6 x 6-7.1	freshwater Cypriniformes: cyprinid (common carp, barbel steed, spotted steed, salsbury luumokk, davidi	gills	Amur Basin, Korea, Vietnam

		marinka)		
M. anomaliformis	10.8-13.2 x 7.6-8.6 x 6-6.2	freshwater Cypriniformes: cyprinid (goldfish, bighead carp, Chinese false gudgeon)	gills, spleen, intestines, urinary bladder	China
M. anurus (syn. *Myxosoma*)	12-13 x 7-8	freshwater Esociformes: esocid (northern pike, Amur pike); Perciformes: percid (European perch)	gills, fins	Eurasia
M. arabicus	8-10 x 6-7	marine Eupercaria: haemulid (minstrel sweetlips)	body cavity	Qatar
M. arapiunsus	11.6-13.7 x 6.8-8.2 x 5.1-5.6	freshwater Characiformes: serrasalmid (pirapitinga)	pyloric caecum	Brazil
M. arariensis	10.7-12.6 x 6.4-7.9	freshwater Siluriformes: heptapterid (South American catfish)	muscles	Brazil
M. aravalae (syn. *Myxosoma*)		freshwater Cypriniformes: cyprinid pool barb)	kidney	India
M. arcasii	9.3-10.7 x 8-8.7 x 6.3-6.7	freshwater Cypriniformes: cyprinid (bermejuela)	kidneys, gonads	Portugal
M. arcticus	15.4	freshwater Salmoniformes: salmonid (sockeye salmon, coho salmon, masu salmon, chinook salmon, Atlantic salmon, rainbow trout, lake trout, Dolly Varden trout, neiva, white-spotted char, European grayling, Arctic grayling, lake whitefish, round whitefish) [cycle involves triactinomyxon-type actinospores in Oligochaeta: lumbriculid (*Stylodrilus heringianus, Lumbriculus variegatus*)]	brain, spinal cord [compromised swimming behaviour]	North America, Asia
M. argentatus (syn. *M. gnathopogoni*)	10.6-11.3 x 7.2-8.4 x 5.5	freshwater Cypriniformes: gobionid (hele hoberunt)	spleen	China
M. argenteus	12.6-14.7 x 8.6-9.7 x 5.7-7.4	freshwater Cypriniformes: cyprinid (golden shiner)	subdermal connective tissues	North America
M. argus (syn. *M. elliptica, Myxosoma*)	13-15 x 9.4-9.8 x 7	freshwater Anabantiformes: channid (northern snakehead)	intestines	China
M. ariae	15-18 x 10.5-12.8	marine Siluriformes: ariid (threadfin sea catfish)	gall bladder	India
M. aristichthydis	14.4-18.6 x 12-14.4 x 9.6-12	freshwater Cypriniformes: cyprinid (bighead carp), xenocypridid (silver carp)	intestines, heart, kidneys, urinary bladder	China
M. arrabonensis	8.4-10 x 7.6-8 x 5.4-5.6	freshwater Cypriniformes: cyprinid (common nase)	gills	Hungary
M. artus	4.8-8.5 x 6.6-12 x 4.8-5.7	freshwater Cypriniformes: cyprinid (common carp, koi carp, bighead carp, grass carp, silver carp, goldfish); Siluriformes: bagrid (grey Chinese catfish)	intestines, muscles, fins [cysts]	Amur Basin, Korea, Vietnam, China
M. asianensis	10.8-12 x 9.4-10 x 6-6.6	freshwater Cypriniformes: cyprinid (grass carp, goldfish); Gobiiformes: gobiid (gokuraku-haze)	gills, skin, intestines	China
M. associatus	15 x 10	freshwater Characiformes: anostomid (gra naeselaks)	kidney	Brazil
M. asymmetricus (syn. *Lentospora*)	10-11 x 6.5-7	marine Eupercaria: labrid (east Atlantic peacock wrasse)	kidney	Italy
M. atkinsoni	7.4 x 6.8	freshwater Cypriniformes: cyprinid (rohu)	gills	India
M. attui	12.8-15.2 x 7.5-9.6	freshwater Siluriformes: silurid (attu catfish)	gut	India
M. atypicus	13.2-16.8 x 8.4-10.8 x 7-8.4	freshwater Cypriniformes: cyprinid (bighead carp), xenocypridid (silver carp)	gills, intestines, gall bladder, spleen, kidneys,	China

			ureters, urinary bladder	
M. auctus	15 x 10.5-11 x 6.5	freshwater Cypriniformes: cyprinid (silver carp)	body cavity	Amur Basin
M. auratus (syn. *M. orbiculatus*)	9-16.2 x 6-14.4 x 6.5-9.6	freshwater Cypriniformes: cyprinid (eastern shiner, bigmouth shiner, goldfish)	muscles, kidneys	North America, China
M. aureatus	12-14.4 x 5.4-7.5 x 5-6	freshwater Cypriniformes: cyprinid (common carp, pugnose shiner, redside shiner, redmouth sucker, bluntnose minnow, fathead minnow), leuciscid (northern pikeminnow); Gadiformes: lotid (burbot); Siluriformes: bagrid (yellowhead catfish, shining catfish); Perciformes: percid (European perch)	fins, gills, kidneys, brain, gut, swim bladder	China, North America
M. aureus	12.6 x 8.3 x 5.5	freshwater Characiformes: characid (dourado)	liver	Brazil
M. australis	18-19.2 x 12-14.4 x 9.6-10.2	freshwater Anabantiformes: channid (blotched snakehead)	skin, stomach	China
M. avagbodjiensis	3-11 x 5-6	freshwater Characiformes: citharinid (moonfish), hepsetid (African pike characin)	gills	Benin
M. awadhii	7.7-11.6 x 5.7-7.3 x 4.4-5.1	freshwater Siluriformes: clariid (walking catfish)	gills	India
M. axelrodi	19-21.8 x 5.7-7.9 x 4.8-5.9	freshwater Characiformes: characid (cardinal tetra)	brain, eye	Americas
M. azerbajdzanicus	18.4-20 x 13.8-15.7	freshwater Cypriniformes: cyprinid (Kura barbel)	gills	Caucasus
M. bagri	8.5 x 5.3	freshwater Siluriformes: bagrid (bayad)	gills	Egypt
M. balantiocheili	10.6-13.3 x 9.2-10.9 x 6.7-7.1	freshwater Cypriniformes: cyprinid (tricolour sharkminnow)	brain [abnormal swimming behaviour]	
M. balatonicus	10.1-12.2 x 8.8-10.1 x 7.1-7.8	freshwater Cypriniformes: cyprinid (common carp)	gills	Hungary
M. bandyopadhyayi	8.3-8.8 x 5.2-7.5 x 4.3-5.4	freshwater Cypriniformes: cyprinid (rohu)	scales	India
M. bankimi	10-11 x 8-9	estuarine Mugiliformes: mugilid (yellowtail mullet)	gall bladder	India
M. baoshanensis	10.4-11.2 x 8-8.8 x 5.6-6.4	freshwater Cypriniformes: cyprinid (Wayanad mahseer)	kidneys	China
M. barakensis	9.4-9.9 x 5.2-6.3 x 3.8-4.6	freshwater Beloniformes: belonid (freshwater garfish)	gills, ovaries	India
M. bartai	10.3-11.4 x 10-11.3 x 6.1-7.5	freshwater Cypriniformes: cyprinid (common shiner)	muscles	Canada
M. bartoni	6.4-8 x 4-4.8	marine Galaxiiformes: galaxiid (common galaxias)	muscles	Falkland Islands
M. basilamellaris	8.5 x 9.9	freshwater Cypriniformes: cyprinid (common carp)	gills [blockages]	Europe
M. baskai	13.5-15 x 10.5-11 x 6.8	freshwater Siluriformes: pangasiid (iridescent shark)	gills	Malaysia
M. basuhaldari	6.8-7.8 x 5.1-6.2 x 3.5-3.8	freshwater Cypriniformes: cyprinid (rohu)	gills	India
M. basui	12.1-14.6 x 4.6-7.4	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. batae	9.6-11.2 x 7.2-8.8	freshwater Cypriniformes: cyprinid (bata)	gills	India
M. batalhensis	14-15.4 x 8-8.7 x 5-5.2	freshwater Characiformes: characid (dourado)	liver, ovaries [cysts]	Brazil
M. baueri	14-16 x 9.3-12	freshwater Cypriniformes: tincid	gills, heart, liver,	Russia

		(tench)	kidneys	
M. beibeiensis	16-19.1 x 10.2-13 x 7.1-9.5	freshwater Cypriniformes: cyprinid (goldfish)	gill	China
M. bejeranoi	9.6-11.8 x 5.7-8.6	freshwater Cichliformes: cichlid (hybrid of blue tilapia x Nile tilapia)	gills	Israel
M. belligobie	14.4-17.6 x 10.4-12.8 x 8-8.8	freshwater Cypriniformes: gobionid (munt-kirevrunt)	gills	China
M. bellus	10-11 x 6.5-7	freshwater Cypriniformes: cyprinid (common carp)	skin	North America
M. bengalensis	8.5-9.4 x 6.4-6.8 x 4.3	freshwater Cypriniformes: cyprinid (major South Asian carp)	gills	India
M. beninensis	10-15 x 5.5-9	freshwater Cichliformes: cichlid (blackchin tilapia, mango tilapia)	gills	Benin
M. bhadrensis	8-11 x7-8 x 6	freshwater Cypriniformes: cyprinid (rohu)	muscles	India
M. bhadurius (syn. *Myxosoma*)	8.8-11.2 x 4.8-6.7	freshwater Siluriformes: silurid (attu)	gall bladder	India
M. bibullatus (syn. *Myxosoma bibullatum*)	13.2-15.6 x 9.6-12.5 x 6–7.5	freshwater Cypriniformes: catostomid (white sucker), cyprinid (goldfish)	gills, skin, heart, kidney, gall bladder	North America, China
M. bicostatus		freshwater Cypriniformes: tincid (tench)	gills	North America
M. bilineatum	10-12 x 9-10 x 9-10	marine Cyprinodontiformes: fundulid (mummichog)	brain	North America
M. bilis	8.4-9.6 x 8.4-9 x 6	freshwater Cypriniformes: cyprinid (goldfish, Prussian carp)	intestines, gall bladder, swim bladder, kidneys, urinary bladder	Amur Basin
M. bilobus	20.0–22.1 x 7.5–9.3 x 6	freshwater Cypriniformes: cyprinid (golden shiner)	gills	Canada
M. bilongi	14-17 x 11.3-14	freshwater Cypriniformes: cyprinid (unspecified *Labeo*)	gills, fins	Cameroon
M. binnakandiensis	10.2-11.2 x 8.1-10.2	freshwater Siluriformes: clariid (walking catfish)	gills, skin, intestines	India
M. bivacuolatus	8-11 x 8-11	freshwater Siluriformes: clariid (walking catfish)	intestinal wall	India
M. bizerti	14-14.5 x 14-14.5	estuarine Mugiliformes: mugilid (flathead grey mullet)	gills	Tunisia
M. bjoerknae	16.2-18.4 x 11.9-13.9 x 10-11	freshwater Cypriniformes: cyprinid (white bream)	gills	Hungary
M. bladderia	9.8-10.8 x 8.4-9.8 x 6.6-7.2	freshwater Cypriniformes: cyprinid (goldfish)	swim bladder, urinary bladder, kidney, intestines, gall bladder, skin	China
M. bliccae	10.3-14 x 8.2-11.8 x 6.5	freshwater Cypriniformes: cyprinid (white bream, white-eye bream, blue bream, common rudd, common nase), leuciscid (taran)	gills	Ukraine
M. bondi (syn. *M. muelleri p.p.*)	12-13.5 x 7 x 4.5	freshwater Esociformes: esocid (muskellunge)	gills	North America
M. bottliformis	12-13.2 x 8.6-9.6 x 5-6	freshwater Cypriniformes: cyprinid (Chinese barb)	skin	China
M. bouixi	10.8-12 x 9-10.5	freshwater Siluriformes: claroteid (belly up)	gills	Cameroon
M. brachycystis		freshwater Cypriniformes: tincid (tench)	spleen, kidney	Europe
M. brachysporus	7-9 x 11-14	freshwater Cichliformes: cichlid (Nile tilapia, mango tilapia, mvogo tilapia, Cameroon tilapia, Singida tilapia, Victoria tilapia, fivespot cichlid, ruskoraitatilapia, pungu)	kidneys, ovaries, liver	Africa
M. bragantinus	5.9-6.3 x 5.9-6.3	marine Mugiliformes: mugilid (redeye	gills	Brazil

		mullet)		
M. bramae (syn. *M. balleri, scardinii, mulleri p.p.*)	9-16 x 8-13 x 4.5-8	freshwater Cypriniformes: cyprinid (common carp, crucian carp, Prussian carp, goldfish, common bream, white bream, white-eye bream, blue bream, vimba bream, Caspian bream, common roach, Caspian roach, Black Sea roach, Caspian kutum, common dace, Siberian dace, ide, asp, ziege, European chub, common rudd, common bleak, Danube bleak, common barbel, Dnieper barbel, Mediterranean barbel, Bulatmai barbel, common nase, common minnow, gudgeon, Amur bitterling), tincid (tench); Perciformes: percid (zander) [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)]	gills, fins, skin, cornea, mouth, intestines, kidney, liver, spleen, heart, muscles, wall of gall bladder and swim bladder [cysts]	Eurasia
M. bramaeformis	11-12 x 7-7.5	freshwater Cypriniformes: xenocypridid (silver carp)	gut, kidneys	Amur Basin
M. branchialis (syn *Myxosoma, Lentospora*)	6.4-9 x 4.5-8.5 x 3.2-4.8	freshwater Cypriniformes: cyprinid (common barbel, Dnieper barbel, Caspian barbel, Bulatmai barbel); Mugiliformes: mugilid (flathead grey mullet)	gills [cysts]	Eurasia
M. branchiarum	8-15.1 x 4-8.9 x 4.7-7.1	freshwater Perciformes: centrarchid (smallmouth bass)	gills	North America
M. branchilateralis	9.4-10.4 x 7.5-9.1 x 5.2-7.2	freshwater Cypriniformes: cyprinid (common barbel)	gills	Hungary
M. branchiofilum	10-12 x 9-11 x 7-9	freshwater Cypriniformes: catostomid (black redhorse)	gills	North America
M. branchiopectum	8-11 x 6-9 x 5-6	freshwater Cypriniformes: catostomid (black redhorse)	gills	North America
M. branchiophilus	10.8-11.6 x 6.2-7.3 x 5	freshwater Cichliformes: cichlid (Nile tilapia)	gills	Egypt
M. braziliensis	9.4-10.9 x 4.7-5.9 x 3.2-4	freshwater Siluriformes: aspredinid (guitarrito)	gills	Brazil
M. brevicauda		freshwater Cypriniformes: cyprinid (Turkestan barbel)	skin	Uzbekistan
M. brevifilis (syn. *M. chengkiangensis, Myxosoma*)	8-15.2 x 6.8-10.5 x 5.3-8	freshwater Cypriniformes: cyprinid (harilik lehthuul, golden-line barbel)	kidneys	China
M. brycon	6.5-7.2 x 3.9-4.8 x 1.9-2.8	freshwater Characiformes: bryconid (piraputanga)	gills	Brazil
M. bubalis	13.1-14.7 x 10.2-11.7	freshwater Cypriniformes: catostomid (smallmouth buffalo)	muscles	North America
M. buccoroofus	11.6-12.7 x 6.4-8.1	freshwater Cypriniformes: cyprinid (bata)	mouth	India
M. buckei	12.6-15.4 x 10.2-12.4	freshwater Cypriniformes: cyprinid (European chub, common roach, common bream)	nervous tissues	Europe
M. bufonis	8.8-9.6 x 8.6-9.4 x 3.6-4.4	Anura: bufonid (flat-backed toad)	testes	Cameroon
M. bulbocordis	17.3-19.6 x 13.8-15.5 x 13-14.4	freshwater Cypriniformes: cyprinid (binni)	heart	Iran
M. bulbulus	10.4-11 x 4.5-5.2	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. buri	9.2-11.8 x 7.9-10.2 x 5.5-7.3	marine Carangiformes: carangid (Japanese amberjack)	brain	Japan
M. burkinei	12.2 x 9.3	freshwater Cypriniformes: cyprinid (African carp)	fins	Burkina Faso

M. burti	9.7-11.3 x 7.1-8.4 x 5.6-6	freshwater Cypriniformes: cyprinid (spottail shiner)	muscles	Canada
M. cabedae (syn. *Myxosoma*)	8.5-8.7 x 6.8-7 x 5-5.2	freshwater Cypriniformes: cyprinid (European chub)	gills	Italy
M. cakmaki	9.3-11.4 x 7.9-9.8 x 6-7	freshwater Cypriniformes: cyprinid (Anatolian khramulya)	gills	Turkey
M. calbasui	12.4-15 x 8.2-10 x 6.2	freshwater Cypriniformes: cyprinid (orangefin labeo, rohu, mrigal carp)	gall bladder	India
M. calcariferum	6.1-7.1 x 5.7-6.5	estuarine Perciformes: latid (barramundi)	gills	India
M. camerounensis	14-22 x 10-16	freshwater Cichliformes: cichlid (Nile tilapia, redbelly tilapia, blackchin tilapia)	gills, skin	Africa
M. cantonensis	10.8-16 x 8.4-11.2 x 7.4-7.8	freshwater Cypriniformes: cyprinid (goldfish)	gills	China
M. capsulatus	10-11 x 16	freshwater Cyprinodontiformes: cyprinodontid (sheepshead minnow)	connective tissues	North America
M. carassii (syn. *M. pfeifferi p.p.*)	11.4-17.5 x 7.2-12.5 x 5.8-8.8	freshwater Cypriniformes: cyprinid (common carp, crucian carp, Prussian carp, goldfish, ide, asp, ziege, common roach, Black Sea roach, Siberian dace, ide, common rudd, common bleak, common nase, common bream, white bream, white Amur bream, Chinese lake gudgeon, Chinese neon golden stripe shark, Chinese lizard gudgeon, poologa-silemokk), xenocypridid (three-lips): Siluriformes: clariid (walking catfish) [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)]	body cavity, liver, intestinal wall, mesentery, muscles, gills, kidney	Eurasia
M. carlhubbsi	12-13.4 x 5-6.6 x 5.1-6	freshwater Cypriniformes: cyprinid (southern striped shiner)	gills	North America
M. carnaticus	8-9 x 6-7 x 5-6	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. cartilaginis (syn. *Myxosoma*)	9.5-12 x 8.4-11 x 6-7.3	freshwater Perciformes: centrarchid (largemouth bass, bluegill sunfish, green sunfish)	cartilage of gills, head, spines [congestion]	North America
M. cataractae	7.1-8.9 x 5.1-6.6 x 3.4-4.4	freshwater Siluriformes: heptapterid (bagrhino)	gills	Brazil
M. catlae	14.5-16.5 x 6.2 x 5.2	freshwater Cypriniformes: cyprinid (catla, rohu, mrigal carp)	gills	India
M. catmrigalae	20-21.8 x 15.7-17.1	freshwater Cypriniformes: cyprinid (hybrid of catla x mrigal carp)	gills	India
M. catostomi (syn *Myxosoma*)	10-15 x 6.8-11.5	freshwater Cypriniformes: catostomid (white sucker, Sonara sucker)	muscles, mouth, intestines, gall bladder, liver, kidney	North America, Russia
M. caudalis	8-8.9 x 6.8-8.4 x 5.1-5.9	estuarine Mugiliformes: mugilid (thicklip grey mullet)	fins [cysts]	Portugal
M. caudatus	16-19.2 x 11-13.6	freshwater Cypriniformes: cyprinid (Niger barb)	fins	Egypt
M. centropomi	7.5-9 x 3.5-5 x 3.5-4	estuarine Perciformes: centropomid (common snook)	gills	North America
M. centropomius	13.5-16.5 x 7.5-9.8	estuarine Perciformes: latid (barramundi)	gall bladder	India
M. cephalis (syn. *M. cephalus*, *Myxosoma*)	14-15 x 10-11 x 8-10	estuarine Mugiliformes: mugilid (flathead grey mullet)	brain, gills	North America
M. cerebralis (syn. *Myxosoma,*	6-10.4 x 6-10.2 x 4-7.4	freshwater Salmoniformes: salmonid (sockeye salmon, chum salmon,	cartilage, heart, kidneys,	Eurasia, Americas,

Lentospora)		chinook salmon, coho salmon, pink salmon, masu salmon, Atlantic salmon, Black Sea salmon, rainbow trout, cutthroat trout, brown trout, river trout, lake trout, brook trout, Dolly Varden trout, whitespotted char, grayling, huchen); Cypriniformes: cyprinid (goldfish, Amur carp, Chinese lake gudgeon); Clupeiformes: clupeid (Atlantic herring); Anabantiformes: unspecified murrel [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)]	intestines, swim bladder, urinary bladder, spinal cord) [whirling disease, twist disease]	Australasia
M. cerveirensis	7.7-8.7 x 6.7-7.3 x 5-5.7	estuarine Mugiliformes: mugilid (thinlip mullet)	intestines	Portugal
M. chakravartyi	12.1-14.3 x 7.7-10.5	freshwater Cypriniformes: cyprinid (catla)	eye muscles	India
M. chandrostomi	13.5-17 x 10-11.7	freshwater Cypriniformes: cyprinid (common nase)	muscles	Ukraine
M. changjiangensis (syn. *Myxosoma*)	26.5-28 x 21-22 x 15	freshwater Cypriniformes: cyprinid (goldfish, lake stargazer, Chinese hooksnout carp)		China
M. changkiangensis	10.8-13.4 x 8.4-9.6 x6.8-7.6	freshwater Cypriniformes: cyprinid (goldfish)	gall bladder	China
M. changshaensis	9.8-12 x 7.8-8.6 x 5.8-6.2	freshwater Cypriniformes: xenocypridid (silver carp)	gills	China
M. changshingensis	9.6-11 x 8.4-9.6 x 6	freshwater Cypriniformes: cyprinid (goldfish), xenocypridid (silver carp)	intestines, gall bladder, kidney, gills, skin	China
M. changshouensis	9.1-10.6 x 11.5-12.1 x 7.6	freshwater Cypriniformes: cobitid (pond loach), cyprinid (common carp)		China
M. chankaensis	8.4-8.7 x 8.1-8.7 x 5.2-5.6	freshwater Cypriniformes: nemacheilid (Siberian loach)		Russia
M. channai (syn. *Myxosoma*)	14.5-18 x 6-6.5	freshwater Anabantiformes: channid (spotted snakehead)	fins, muscles, liver, kidneys	India
M. chanosi	9.8-12 x 7.2-8.5 x 7.3-8.1	marine Gonorynchiformes: chanid (milkfish)	kidney	India
M. chariensis	9-11 x 5-6	freshwater Characiformes: alestid (true bigscale tetra)	gills	Tchad
M. charii	13-15.5 x 10.5-12	freshwater Characiformes: citharinid (moonfish)	skin	Tchad
M. cheisini	12.5-15 x 5.8-8.5 x 4.2-5	freshwater Characiformes: channid (northern snakehead); Cypriniformes: cyprinid (mud carp, Hoven's carp)	gills, skin	Korea, Vietnam
M. chekiangensis	9.6-12 x 8.4-9.6 x 6.2-7	freshwater Cypriniformes: xenocypridid (silver carp)	gills	China
M. chelonari	7.7-8.7 x 6-7.5	estuarine Mugiliformes: mugilid (thicklip grey mullet)	gills [cysts]	Portugal
M. chengkiangensis	13.6-15.2 x 9-10.5 x 8	freshwater Cypriniformes: cyprinid (golden-line barbel)	kidneys	China
M. chengpoensis (syn. *M. hainanensis, Myxosoma*)	10.2-13.4 x 7.4-8.3 x 5-6	freshwater Cypriniformes: cyprinid (gold barb, salsbury luumokk)	skin, kidney	China
M. chenhshiehi (syn. *M. ophiocephali p.p.*)	12-14.4 x 7.2-7.8 x 4.8-5.4	freshwater Anabantiformes: channid (northern snakehead, blotched snakehead)	gills, intestines, swim bladder	China
M. chennai (syn. *M. anguillae, Myxosoma*)	10.8-13.2 x 6-12 x 5.6-6.4	freshwater Anguilliformes: anguillid (Japanese eel)	gills, mouth, intestines	China
M. chernovae (syn. *Myxosoma lomi p.p.*)	12-14 x 9-11	freshwater Cypriniformes: cyprinid (common roach)	gills	Russia

M. chilkensis (syn. *Rudicapsula*)	7.2-8 x 5.6-6.6	freshwater Cypriniformes: cyprinid (rohu)	gall bladder	India
M. chimbuensis	10-13 x 8-9 x 6-7	Anura: hylid (Darlington's Madang tree frog, Treasury Island tree frog)	testes	New Guinea
M. chinensis (syn. *Myxosoma*)	13.2-15 x 7.8-10.8 x 6.4-7.2	freshwater Cypriniformes: cobitid (pond loach): Gobiiformes: odontobutid (freshwater sleeper)	gills, muscles	China
M. chinghaiensis	7.7-13.6 x 5.4-10.9 x 5.8-8.7	freshwater Cypriniformes: cyprinid (przevalsi paljaskarbik)	gills	China
M. chinsurahensis	8-9.7 x 5.1-6.1	freshwater Anabantiformes: anabantid (climbing perch)	scales	India
M. chittali	9 x 6.2	freshwater Cypriniformes: cyprinid (pool barb)	gills	India
M. chiungchowensis	10.2-11.8 x 9.6-11 x 6-6.6	estuarine Mugiliformes: mugilid (flathead grey mullet)	intestines	China
M. chiunghaiensis	13.2-15.6 x 7.8-10.8 x 6.4-7.2	freshwater Cypriniformes: cyprinid (pale chub)	gills	China
M. chondrophilus	6 x 4.5 x 3.5	marine Clupeiformes: dorosomatid (round sardinella)	gills	Brazil
M. chondrostomi	13.5-17 x 10-11.7	freshwater Cypriniformes: cyprinid (common nase)	muscles	Europe
M. chrysichthyi	10.2 x 6.1	freshwater Siluriformes: claroteid (golden Nile catfish)	gills	Egypt
M. chuantungensis	11.4-12.8 x 7.4-8.4 x 7	freshwater Cypriniformes: cyprinid (tomp koukloug)	urinary bladder, ureters, kidneys	China
M. chuatsi (syn. *Myxosoma*)	4.5-6 x 4.5-6	freshwater Perciformes: sinipercid (mandarin fish)	gills [cysts]	Amur Basin
M. chuchowensis	10.8-13.3 x 7.2-9.6 x 5.8-6.2	freshwater Cypriniformes: cyprinid (common carp, bighead carp, goldfish), xenocypridid (silver carp)	gills, skin, urinary bladder	China
M. chuhkiangensis	10.4-11.2 x 7-8 x 7	freshwater Siluriformes: bagrid (shining catfish, yellowhead catfish)	urinary bladder	China
M. chuhsienensis	7.2-8.7 x 6.7-7 x 5-5.6	freshwater Beloniformes: adrianichthyid (Japanese rice fish); Cypriniformes: balitorid (sichuani hiinakink, pikkuim-hannalhink), cyprinid (topmouth culter, lake skygazer, Ya-fish, predatory carp, sharpbelly, karilik lehthuul, rendahli bangaan)	gills, fins, intestines, gall bladder, kidney, urinary bladder	China
M. chungkingensis	8.8-9.6 x 7.4-8.8 x 4-6	freshwater Cypriniformes: xenocypridid (fangi kriipsu)		China
M. chushi	10.6-11.4 x 8.8-9.2 x 6	freshwater Cypriniformes: cyprinid (Alghad snowtrout)	gills	India
M. circulus (syn. *Myxosoma circulus, bilus, confessus, ornatus, vegrandis, branchialis p.p., sphaerica p.p., Lentospora branchialis p.p.*)	8.5-12 x 7.5-12	freshwater Cypriniformes: cyprinid (common carp, koi carp, common roach, Caspian roach, common bream, Caspian bream, Caucasian scraper, Russian bitterling, sattar snowtrout, chramule steindachnerova, gudgeon, sharpray), leuciscid (taran)	gills, muscles, kidneys, rarely liver, pancreas, heart	Eurasia
M. citharinopsi	9-11 x 6-7	freshwater Characiformes: citharinid (moonfish)	gills	Chad
M. clarias	8.8 x 6.9	freshwater Siluriformes: clariid (African sharptooth catfish)	gills	Egypt
M. clariae [*clarii*]	10.2-15.5 x 6.8-12.4 x 7.2	freshwater Cypriniformes: cyprinid (black carp), xenocypridid (silver carp); Siluriformes: clariid (walking catfish, broadhead catfish)	body surface, cornea, intestines, liver, spleen, kidney, liver, abdominal cavity	India, Vietnam, China
M. cloutmani	8.7 x 7.8	freshwater Cypriniformes: catostomid (blue sucker)	gills	North America

M. cochinensis	6.2-7 x 5-6.2	estuarine Mugiliformes: mugilid (largescale mullet)	gills	India
M. coelii	8.3-14.9 x 4.1-8.4	marine Gonorynchiformes: chanid (milkfish)	gall bladder	India
M. cognati	12-14 x 9.5-10.5 x 8-9	freshwater Scorpaeniformes: cottid (slimy sculpin)	operculum	North America
M. colossomati	11.4-12.2 x 6.6-7.2 x 3.5-4	freshwater Characiformes: serrasalmid (tambaqui)	gills, muscles, liver	Brazil
M. commersonii (syn. *Myxosoma*)	9.5-16.5 x 7-11.4	freshwater Cypriniformes: catostomid (white sucker)	skin	Canada
M. comoei	11.8-8.9	freshwater Siluriformes: clariid (mudfish)	gills, fins	Burkina Faso
M. compressus	12-14 x 7-10 x 7-7.5	freshwater Cypriniformes: cyprinid (river shiner)	skin	North America
M. concentricus (syn. *Myxosoma*)	9.2-9.3 x 8.4 x 7.9	freshwater Gobiiformes: oxudercid (dusky tripletooth goby)	urinary bladder	Japan
M. conei	6.7-10 x 7.6-10.4	marine Carangiformes: carangid (trevally)	liver	Australia
M. conesii		freshwater Cypriniformes: leuciscid (lake chub)	eye	Canada
M. confirmatus	9.5 x 9.5	freshwater Cypriniformes: cyprinid (Russian bitterling)	brain	Amur Basin
M. congesticus	9-10 x 8.5-9.5 x 6	freshwater Cypriniformes: catostomid (silver redhorse)	fins	North America
M. conspicuus	9-11.8 x 5.9-8.2 x 4.5-5.5	freshwater Cypriniformes: catostomid (shorthead redhorse, smallmouth redhorse, silver redhorse), cyprinid (finescale dace)	head [tumours]	North America
M. cordeiroi	10.9-11.3 x 7.1-7.5 x 5.3-5.6	freshwater Siluriformes: pimelodid (jau)	gills, skin, eyes, serosa, urinary bladder	Brazil
M. cordis (syn. *M. pseudocordis*)	12 x 10	freshwater Cypriniformes: cyprinid (common barbel, Dnieper barbel, sattar snowtrout)	stomach wall, heart	Eurasia
M. coriumicus	9-10 x 8-9	freshwater Cypriniformes: cyprinid (mrigal carp)	scales [lesions]	India
M. corneus	8-10.5 x 6.5-9	freshwater Perciformes: centrarchid (bluegill)	eyes	North America
M. costatae	8.3-9.9 x 6.1-7.2 x 4.9-5.2	freshwater Cypriniformes: nemacheilid (eightbarbel loach)		Russia
M. cotti (syn. *M. jiroveci*)	12.5-14.1 x 9.4-11	freshwater Scorpaeniformes: cottid (European bullhead) [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid (‘tubifex’)]	brain	Europe
M. couesii	10.4-13.2 x 7.7-9.4	freshwater Cypriniformes: leuciscid (lake chub)	eyes	Canada
M. crassus	15.3-18.6 x 12-15.3	freshwater Cypriniformes: tincid (tench)	gills, intestines	Russia
M. cristatus (syn. *M. mulleri p.p.*)	5-12 x 6-8 x 6-8	freshwater Cypriniformes: cyprinid (sattar snowtrout, Samarkand khramulya spirlin)	gills, skin, muscles	Russia
M. crucifilus (syn. *Gyrospora*)	9-10 x 8-8.5	freshwater Cypriniformes: cyprinid (fringe-lipped peninsular carp)	gills	India
M. ctenopharyngodoni (syn. *M. ovatus*)	11.5-13 x 9-10 x 6-7	freshwater Cypriniformes: catostomid (smallmouth buffalo), cyprinid (grass carp, black carp)	skin	North America, China
M. ctenopomae	12-14 x 7-11	marine Anabantiformes: anabantid (tailspot ctenopoma)	liver	Benin
M. csabai	12.1-14 x 8.2-9.6 x 4.7-5.6	freshwater Cypriniformes: cyprinid (bonylip barb)	kidney	Malaysia
M. cucurbitiformis	7-8.4 x 7.1-8.8	marine Mugiliformes: mugilid	gall bladder	Portugal

		(thicklip grey mullet)		
M. cultrati	9.2-10.4 x 6-6.8	freshwater Cypriniformes: cyprinid (ziege)	eyes	Hungary
M. cultus	9.3-11.3 x 5.2-7.2 x 3.6-4.6	freshwater Cypriniformes: cyprinid (goldfish) [cycle involves raabeia-type actinospores in Oligochaeta: naidid (*Brachiura sowerbyi*)	cartilage, skin, kidneys	Asia
M. cuneatus (syn. *Myxosoma*)	9-10 x 507 x 4.5	freshwater Esociformes: esocid (muskellunge)	gills	North America
M. cuneus	10 x 5.1	freshwater Characiformes: serrasalmid (small-scaled pacu)	gills, fins, liver, gall bladder, spleen, heart, urinary bladder	Brazil
M. cunhai	9-11 x 4-6	freshwater Characiformes: serrasalmid (piraya piranha); Siluriformes: mochokid (mandi), pimelodid (spotted catfish)	intestines	Brazil
M. curemae	5.7-6.9 x 5.1-6.8 x 4.4-5.5	marine/estuarine Mugiliformes: mugilid (white mullet)	gills	Brazil
M. curimatae	12-14.7 x 7-10.8	freshwater Characiformes: prochilodontid (crumata)	gills	Brazil
M. curmucae	8-11 x 7-8 x 5-6	freshwater Cypriniformes: cyprinid (Curmuca barb)	scales	India
M. cuttacki	13-21.1 x 4.9-8.1	freshwater Cypriniformes: cyprinid (common carp)	gills	India
M. cybinae	9.2-14.5 x 8.8-11.2 x 6.6-8	freshwater Cypriniformes: leuciscid (common minnow)	brain	Russia
M. cycloides	12-17 x 5-10	freshwater Cypriniformes: common roach, unspecified bream); Gobiiformes: unspecified goby	gills, skin, swim bladder	Europe
M. cylindricus (syn. *Myxosoma*)	12.8-16.3 x 4.5-6.4 x 3.2-3.5	freshwater Anabantiformes: channid (dwarf snakehead)	kidney	India
M. cyprini	9.6-16 x 6.6-12 x 4.8-6.8	freshwater Cypriniformes: cyprinid (common carp, koi carp, bighead carp, grass carp, silver carp, goldfish, common roach, common chub, Amur ide, Amur whitefin gudgeon, common bream, blue bream, stone moroko, topmouth culter), tincid (tench); Siluriformes: bagrid (Brazhnikov's catfish)	intestinal wall, mesenteries, muscles, skin, liver, pancreas, kidneys, rarely gall bladder [cysts]	Eurasia
M. cyprinicola	9-12 x 7-9 x 5-6.2	freshwater Cypriniformes: cyprinid (common carp, grass carp, rock carp, silver carp, goldfish, bighead carp, Amur ide, pale bleak, Ya-fish), gobionid (niitmokk-haberunt, sile pardrunt)	gills, fins, intestines, gall bladder, kidney, swim bladder, urinary bladder, gonads	Russia, Vietnam, China
M. dahomeyensis (syn. *Myxosoma*)	12 x 6 x 4-5	freshwater Cichliformes: cichlid (redbelly tilapia, blackchin tilapia); Siluriformes: mochokid (upside-down catfish)	oocytes [castration]	Dahomey
M. dajiangensis	13.9-15.6 x 7.2-9.1 x 5.5	freshwater Cypriniformes: cyprinid (common carp)	gills	China
M. danrici	8.1-11.1 x 8.1-10.1 x 6.3	freshwater Cypriniformes: cyprinid (Indian flying barb)	gills, intestines	India
M. dasguptai	11.4-19.5 x 4.9-8.1	estuarine Mugiliformes: mugilid (Tade gray mullet)	gills, muscles	India
M. debsantus	8.9-9.6 x 8.1-8.9 x 6.2-6.7	freshwater Cypriniformes: cyprinid (hybrid of catla x rohu)	fins	India
M. dechtiari	10-14 x 7-9 x 7-8	freshwater Perciformes: centrarchid (pumpkinseed)	gills	Canada

M. deformis	5.8-7.9 x 8-10.6	freshwater Cypriniformes: cyprinid (common carp)	gills	India
M. dentium	11.8-14.5 x 5.5-7.3	freshwater Esociformes: esocid (muskellunge)	mouth	Canada
M. dermatoulcerans	14.3-16.8 x 7.6-10.3 x 6-6.9	freshwater Characiformes: serrasalmid (red-bellied piranha)	dermis	Peru
M. dermiscalis	5.8-7.8 x 3.9-5.9	freshwater Cypriniformes: cyprinid (rohu)	scales	India
M. dermitis (syn. *Myxosoma*)	9-11 x 8-10	freshwater Cypriniformes: cyprinid (rohu); Mugiliformes: mugilid (flathead grey mullet)	scales	India
M. desaequalis	17.6-19.1 x 10.6-11.9 x 4-5	freshwater Gymnotiformes: apteronotid (black ghost knifefish)	gills	Brazil
M. despair	10-12 x 8	freshwater Cypriniformes: cyprinid (common carp)	gills	France
M. destruens	9-12 x 5-7.2 x 4.8	freshwater Cypriniformes: cyprinid (common rudd)	muscles	Europe
M. dhanachandi	17-19.5 x 5.1-6.8	freshwater Anabantiformes: channid (Ceylon snakehead)	fins	India
M. diaphanus (syn. *Myxosoma*)	15.5-20 x 5.2-7.6	freshwater Cyprinodontiformes: fundulid (banded killifish)	testes	Canada
M. diagrammae	9-12 x 5-5.7 x 4.5-5.5	marine Perciformes: haemulid (rubberlip grunt, African striped grunt)	kidneys	Senegal
M. diamaensis	11-12 x 6-8	freshwater Cichliformes: cichlid (blackchin tilapia)	gills	Senegal
M. diaphanus	15.5-20 x 5.2-7.6	freshwater Cyprinodontiformes: fundulid (banded killifish)	testes	Canada
M. dibombensis	15.8-18 x 10-13	freshwater Cypriniformes: cyprinid (parma batesova)	fins	Africa
M. diminitus (syn. *M. minutus p.p.*)	6-9.6 x 4.2-9.9 x 3.6-7.3	freshwater Cypriniformes: balitorid (narmik-hannalhink), catostomid (smallmouth buffalo), cyprinid (bighead carp, common dace, common chub), xenocypridid (silver carp); Mugiliformes: mugilid (so-ing mullet); Perciformes: percid (European perch); Siluriformes: sisorid (kishinouyi catfish)	gills	Eurasia, North America
M. diplurus		freshwater Gadiformes: lotid (burbot)		Europe
M. discapsularis	12.6-13.5 x 9-10.8	freshwater Cypriniformes: cyprinid (largescale silver carp)	gall bladder	Vietnam
M. discogobie	9.6-11.3 x 9.6-10.4 x 6.6-7.3	freshwater Cypriniformes: cyprinid (fuxiani napprunt)	gills	China
M. discrepans	11.4-13.5 x 9.5-11 x 8.5-9.5	freshwater Cypriniformes: catostomid (highfin carpsucker, river carpsucker)	gills	North America
M. dispar (syn. *Disparospora*)	8.4-14 x 7.2-10.2 x 5.4-7	freshwater Cypriniformes: cobitid (spined loach), cyprinid (common carp, koi carp, bighead carp, mud carp, crucian carp, Prussian carp, goldfish, common bream, white bream, blue bream, vimba bream, Caspian bream, common roach, Caspian roach, common dace, Danilevskii's dace, ide, Amur ide, asp, ziege, common rudd, common nase, common bleak, sunbleak, gudgeon, Chinese lake gudgeon, Aral barbel, European bitterling, giant Chinese bitterling, stone moroko), gobionid (niitmokk-haberunt), leuciscid (taran, spirlin, striped bystranka, common minnow), tincid	gills, skin, muscles, kidneys, connective tissues, wall of intestines, gall bladder, swim bladder, urinary bladder [cysts]	Eurasia

		(tench), xenocypridid (silver carp); Perciformes: percid (zander, European perch); Siluriformes: clariid (walking catfish) [cycle involves raabeia-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)]		
M. disparis (syn. *Myxosoma*)	10.4-12.8 x 7-10 x 6.2-8	freshwater Cypriniformes: cyprinid (tomp koukloug)		China
M. disparoides (syn. *M. dispar p.p.*)	9-13.2 x 6-8.4 x 4.8-5.4	freshwater Cypriniformes: cyprinid (grass carp, sattar snowtrout)	gills, kidneys, rarely spleen	Russia
M. distalisensis	10.4-12.6 x 7.5-8.6 x 5.2-5.8	freshwater Siluriformes: bagrid (yellow catfish)	gills	China
M. distichodi	10-11 x 5-6	freshwater Characiformes: distichodontid (grass-eater perch)	gills, intestines, liver	Tchad
M. distoechodontis (syn. *Myxosoma*)	8.8-9.2 x 8.1-8.8 x 5.9-7.4	freshwater Cypriniformes: xenocypridid (mohknina-poiksuu)		China
M. divergens	14.4-16.2 x 9-10	freshwater Cypriniformes: cyprinid (bighead carp, Prussian carp, goldfish)	gills, skin, liver, spleen, kidneys	Vietnam
M. diversicapsularis	12.7 x 12	freshwater Cypriniformes: cyprinid (common roach)	gills	Eurasia
M. diversus	13.2-16.8 x 7.8-9.6 x 5.3-7.2	freshwater Cypriniformes: cyprinid (common carp, Japanese white crucian carp, goldfish, sattar snowtrout); Perciformes: lateolabracid (Japanese sea bass)	gills, intestines, gall bladder, spleen, muscles, kidneys, urinary bladder	China, India
M. djoudjensis	11-13 x 11-13	freshwater Cichliformes: cichlid (Guinean tilapia)	ovaries	Senegal
M. dogieli	9-16 x 8-15 x 6-7	freshwater Cypriniformes: cyprinid (common carp, koi carp, Prussian carp, goldfish, ide, ziege, white bream); leuciscid (lake minnow), tincid (tench)	muscles, heart, kidneys, rarely liver, gall bladder [cysts]	Eurasia
M. dombrovskaya	12 x 10.5-11 x 6	freshwater Cypriniformes: cyprinid (Chinese lake gudgeon)	liver	Amur Basin
M. donecae	10-13.8 x 6-8.7 x 4.8-6	freshwater Cypriniformes: acheilognathid (bitterling), cyprinid (common dace, ide, ziege)	gills, ureters	Russia, China
M. dongshanensis (syn. *M. kiangsuensis, Myxosoma*)	9.8-13.6 x 6.5-9.1 x 5-7.6	freshwater Cypriniformes: cobitid (pond loach), cyprinid (bighead carp)	gills, liver, spleen, intestines	China
M. dossoui	8.5-11 x 8-10.5	freshwater Cichliformes: cichlid (redbelly tilapia)	gill cartilage	Benin
M. doubleae	10.7-12.3 x 7.7-9 x 4.6-5.4	freshwater Perciformes: percid (European perch)	gills	North America
M. douroensis	7.5-9.2 x 6.5-7.9 x 5-6.2	estuarine Mugiliformes: mugilid (thicklip grey mullet)	gills [cysts]	Portugal
M. drjagini (syn. *Disparospora drjagini, hypothalmichthydis*)	10-14.4 x 7-10 x 6-7	freshwater Cypriniformes: cyprinid (bighead carp, silver carp) [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex, Limnodrilus hoffmeisteri*)]	subcutaneous tissues, brain, kidney, swim bladder ['twist disease']	China, Russia
M. dujardini (syn. *Myxosoma, Chloromyxum*)	11-13 x 5-8 x 5.5-6	freshwater Cypriniformes: cobitid (spined loach), cyprinid (common carp, common roach, Caspian roach, common dace, Siberian dace, Danilevskii's dace, ide, asp, ziege, common rudd, common bleak, sunbleak, common minnow, common bream, blue bream, white-eye bream), tincid (tench)	gills, occasionally fins, rarely kidneys, pancreas, gonads	Eurasia
M. dumerilii	13.9-16.5 x 8.3-9.8	freshwater Siluriformes: bagrid	brain	China

	x 6.3-7.9	(Chinese longsnout catfish)		
M. duodenalis	9 x 3.2	freshwater Siluriformes: silurid (attu)	intestinal wall	India
M. duriensis	13-14 x 8-9.7 x 7.3-8	freshwater Cypriniformes: cyprinid (northern straight-mouth nase)	gills	Portugal
M. dykovae	11-12.7 x 5.6-6.7 x 5.7-6	freshwater Cypriniformes: cyprinid (tinfoil barb)	gills	Malaysia
M. dzeufieti	11.4-13.7 x 9.2-10.6 x 5-6	freshwater Cichliformes: cichlid (Nile tilapia, unspecified tilapia)	skin	Cameroon
M. echengensis	13.2-15.6 x 9-10.2 x 7.2	freshwater Cypriniformes: cyprinid (goldfish)	kidneys	China
M. ectopicus	8.2-9.4 x 7-9 x 7	freshwater Cypriniformes: cyprinid (common carp)	urinary bladder	China
M. edellae	10.5-11.5 x 9-10	freshwater Cypriniformes: cyprinid (grass carp)	kidney	India
M. eeli	10.5-14 x 8.2-11.5	freshwater Synbranchiformes: mastacembelid (zig-zag eel)	intestinal wall	India
M. egregius	13.2-21.6 x 12-15.6 x 6-10.8	freshwater Cypriniformes: cyprinid (goldfish)	intestines, gall bladder, kidney	China
M. egyptica (syn. *M. intestinalis p.p.*)	9.5-10.5 x 8-9 x 8.4-9.2	freshwater Cypriniformes: cyprinid (Niger barb); Mugiliformes: mugilid (hornlip mullet)	gills	Egypt
M. eirasi	8.4-8.8 x 6.5-6.9	freshwater Cypriniformes: cyprinid (mrigal carp)	fins	India
M. eirasianus	12.6-13.5 x 9-10.3 x 7.2-9	freshwater Cypriniformes: cyprinid (white bream)	gills	Hungary
M. ekingeni	10-11.2 x 7.7-8.9 x 4.1-4.4	freshwater Cypriniformes: cyprinid (Anatolian khramulya)	gills	Turkey
M. elaiodes	9-11.7 x 5.4-8.4 x 4.8-5.4	freshwater Cypriniformes: acheilognathid (hiina morukas, horavka cinska), cyprinid (mud carp, bighead carp, Khanka spiny bitterling, giant Chinese bitterling, Chinese lake gudgeon), gobionid (hrouz guichenotuv), xenocypridid (silver carp)	muscles, kidneys	China
M. elegans	13.5-17 x 7.4-10 x 7.4-8	freshwater Cypriniformes: cyprinid (common roach, ide)	gills, fins	Russia
M. ellipsoides (syn. *M. auctus, bramaeformis, ctenopharyngodonis, multihospitis, microcapsularis*)	9.6-21 x 5.5-12.6 x 5-7.2 [rarely 3-8 polar capsules]	freshwater Cichliformes: cichlid (redbelly tilapia); Cypriniformes: cobitid (spined loach), cyprinid (common carp, crucian carp, koi carp, grass carp, bighead carp, goldfish, common roach, Caspian roach, ide, asp, ziege, common chub, common rudd, common nase, gudgeon, Chinese false gudgeon, Chinese lake gudgeon, common bream, white bream, white-eye bream, common barbel, Aral barbel, Bulatmai barbel, common bleak, Danube bleak, spirlin, European bitterling, Russian bitterling, Khanka spiny bitterling, spotted steed), tincid (tench), xenocypridid (silver carp); Gadiformes: lotid (burbot); Perciformes: percid (European perch, ruffe); Siluriformes: bagrid (varjokimalaismonni)	gills, fins, kidneys, liver, spleen, pancreas, heart, mesentery, intestinal wall, gall bladder, urinary bladder, gonads, muscles, cornea, connective tissue, swim bladders	Eurasia, Africa
M. ellipticoides (syn. *Myxosoma*)	11.4-14.1 x 6.8-8.2	freshwater Cypriniformes: catostomid (white sucker)	skin	Canada
M. ellipticus (syn. *M. ellipticum, Lentospora*)	12.6-19 x 9-13 x 10-11	freshwater Cypriniformes: cyprinid (Prussian carp, largescale silver carp)	kidney, gills	Japan, Vietnam

M. elliptoides	14-15.9 x 8.8-10.7 x 6.9-7.4	freshwater Cypriniformes: cyprinid (common carp)	fins	China
M. elongatum	13-17.6 x 7-9	freshwater Cypriniformes: cyprinid (bata)	gills	India
M. elongatus	15 x 6 x 9	freshwater Cypriniformes: cyprinid (crucian carp)	kidneys	Japan
M. encephalicus (syn. *Lentospora*)	6.2-12.6 x 5.8-10.65	freshwater Cypriniformes: cyprinid (common carp, bata)	brain [abnormal swimming behaviour]	Europe, India
M. encephaliens (syn. *Lentospora*, *Myxosoma encephalinum*)		freshwater Cypriniformes: cyprinid (common carp)	brain [whirling disease]	Europe
M. endovasus (syn. *Myxosoma*)	9 x 8	freshwater Cypriniformes: catostomid (smallmouth buffalo)	gills	North America
M. enoblei	13.5-15 x 10.5-11.5 x 7.5	freshwater Cypriniformes: catostomid (smallmouth buffalo)	gills	North America
M. epalzeorhynchusi	7.2-7.4 x 6-6.4 x 5.7	freshwater Cypriniformes: cyprinid (bihorned barbel)	gills	China
M. episquamalis (syn. *M. episquammalis*)	6-7.6 x 5.2-5.8	marine Mugiliformes: mugilid (flathead grey mullet, largescale mullet)	gills, skin, fins, peritoneum [lesions]	Australia, Japan, India
M. equatorialis (syn. *Myxosoma*)	12-14 x 6-8	freshwater Cichliformes: cichlid (helmitilapia, 'mvogoi' tilapia, Nile tilapia, hybrid of blue tilapia x Nile tilapia)	kidneys	Africa
M. ergensi	10-11 x 8.5-9 x 6	freshwater Cypriniformes: cyprinid (common bleak)	kidneys	Hungary
M. erythroculteri	12.5-14 x 7.4-9 x 6-6.5	freshwater Cypriniformes: cyprinid (lake skygazer)	gills	China
M. erythrophthalmi	10.4-12 x 8.3-10.2 x 6.3-7.5	freshwater Cypriniformes: cyprinid (common rudd)	liver, kidney, intestinal wall	Hungary
M. esocinum (syn. *Disporospora*)	10-12 x 6-6.3	freshwater Esociformes: esocid (Amur pike)	gills	Amur Basin
M. esomi (syn. *Rudicapsula*)	11.2-12.4 x 6.8-7.2 [one small polar capsule]	freshwater Cypriniformes: cyprinid (unspecified flying barb)	fins	India
M. eszterbaueri (syn. *M. hakyi p.p.*)	14.4-16.8 x 6-12.6 x 5-9	freshwater Siluriformes: pangasiid (iridescent shark)	skin	Thailand
M. etropli	10.2-14.5 x 8.5-11.9	freshwater Cichliformes: cichlid (green chromide)	bulbus arteriosus, heart [necrosis]	India
M. etsatsaensis	12.8-15 x 6.2-8	freshwater Cypriniformes: cyprinid ('thamalanensis' barb)	gills	Botswana
M. eucalii (syn. *Myxosoma*)	12-15.6 x 8.4-10.8 x 6-7.2	freshwater Scorpaeniformes: gasterosteid (brook stickleback)	head, fins	North America
M. evdokimovae	10-11 x 8.7-9.2	freshwater Salmoniformes: salmonid (European cisco)	mouth	Russia
M. exiguus (syn. *Myxosporidium mugilis*)	7.7-12 x 6-9.3 x 4.2-6	freshwater Cichliformes: cichlid (Nile tilapia); Cypriniformes: cyprinid (common carp, predatory carp, common roach, ide, asp, common chub, white bream, common rudd, common bleak, common nase, Kura nase, asp, ziege, common bream, blue bream, Oriental bream, white-eye bream, osman przewalskeho, common nase, sharpbelly, lake stargazer); Mugiliformes: mugilid (flathead grey mullet, golden grey mullet, thicklip grey mullet, thinlip mullet, leaping mullet)	gills, fins, skin, muscles, intestinal wall, mesenteries, kidneys, spleen, gall bladder, gonads [cysts]	Eurasia

M. exsulatus	9.7-9.9 x 9-9.1	freshwater Cypriniformes: catostomid (longnose sucker)	gills	Siberia
M. fahmii	10.8-12 x 6.4-8	freshwater Cypriniformes: cyprinid (Niger barb)	gills	Egypt
M. fallax	12.6-14.6 x 8.3-10.6 x 6.5-7.6	Anura: hylid (eastern dwarf tree frog)	testes	Australia
M. fanthami (syn. *M. grandis p.p.*)	13.2-17.3 x 9.5-10.9	freshwater Cypriniformes: cyprinid (common shiner)	body cavity	Canada
M. farionis	8.5-10 x 6-7.5 x 4.5-5	freshwater Salmoniformes: salmonid (river trout)	brain, spinal cord	Spain
M. feisti	11.5-13.2 x 9.4-10.8 x 6.6-7	freshwater Cypriniformes: cyprinid (common roach)	gill cartilage	Hungary
M. figueirae	9.1-10 x 5.8-6.9 x 4.4-4.5	freshwater Siluriformes: pimelodid (redtail catfish)	skin	Brazil
M. filamentosus (syn. *Myxosoma*)	11.2-17.3 x 8.1-12.2	freshwater Cypriniformes: cyprinid (filament barb)	brain, cartilage	India
M. filamentum	7.5-9.7 x 5.2-7.3 x 4.8-5.7	freshwater Characiformes: bryconid (piracanjuba)	gills	Brazil
M. filamentus (syn. *M. jahnricei, Myxosoma okobojiensis*)	9.5-15.5 x 10.2-11.7 x 4.2-5.2	freshwater Cypriniformes: cyprinid (smallmouth buffalo); Perciformes: centrarchid (black crappie)	gills, intestines	North America
M. flavus	9.2 x 6.5 x 4.2	freshwater Siluriformes: pimelodid (spotted sorubim)	gills	Brazil
M. fobobi (syn. *M. barbi*)	7.3-13.5 x 5-9 x 5.5-6.3	freshwater Characiformes: alestid (characin); Cypriniformes: cyprinid (African carp, African redfinned barb, ticto barb, kameruni pardkala)	gills, skin	Cameroon, India
M. follius	10-12.5 x 9-10.8 x 7-7.2	freshwater Cichliformes: cichlid (Mozambique tilapia); Cypriniformes: leuciscid (redfin); Mugiliformes: mugilid (so-ing mullet)	gills	Amur Basin
M. fomenai	13.1-16.5 x 6.2-9 x 5.2-7	freshwater Cichliformes: cichlid (Nile tilapia)	muscles	Egypt
M. foshanensis	9.6-11.2 x 8.6-9.8 x 6.2-6.8	freshwater Cypriniformes: cyprinid (mud carp)	kidneys	China
M. fossilii (syn. *Myxosoma*)	9-12 x 6.2-8.5 x 5-6	freshwater Siluriformes: heteropneustid (Asian stinging catfish)	brain, cartilage	India
M. fotoi	13-16 x 10-14	freshwater Cichliformes: cichlid (Nile tilapia)	gills, skin	Africa
M. fountainae	7.3-10.7 x 6.2-8.6	freshwater Cypriniformes: cyprinid (creek chub)	gills	North America
M. franciscoi	6-6.9 x 5.8-6.4 x 3.2	freshwater Characiformes: prochilodontid (curimata)	fins	Brazil
M. freitasi	17.7-19.8 x 8.4-9	freshwater Gymnotiformes: hypopomid (electric knifefish)	brain	Brazil
M. fryeri	12.9 x 8.6 x 7.2	freshwater Salmoniformes: salmonid (coho salmon)	nerves in muscles	North America
M. fujitai (syn. *M. anguilli, Lentospora anguillae*)	9.2-12.4 x 8.4-12 x 4.9-6.4	freshwater Anguilliformes: anguillid (Japanese eel)	fins, dorsal body	Japan
M. fundamentalis	14.4-17 x 11.2-13.2 x 9-9.6	freshwater Cypriniformes: cyprinid (common roach)	gills	Hungary
M. funduli (syn. *Myxosoma, M. musculi p.p.*)	14 x 8 x 6	freshwater Cyprinodontiformes: fundulid (mummichog, striped killifish, banded killifish)	gills, muscles	North America
M. funsienensis (syn. *Myxosoma*)	8.8-10.4 x 6.8-7.2 x 5.6-6.4	freshwater Cypriniformes: cyprinid (phoenix barb)	gills	China
M. gadopsii	13 x 7.5-8 x 5.5-6	freshwater Perciformes: percichthyid (river blackfish)	subcutis	Australia
M. galaicoportucalensis	11.3-12.7 x 10-10.7 x 6-9	freshwater Mugiliformes: mugilid (flathead grey mullet)	intestines	Portugal

M. galaxii	13-15 x 8.8-10	freshwater Galaxiiformes: galaxiid (common galaxias, mountain galaxias)	all organs except gills	South America, Australia
M. galilaeus	12-14 x 10-11	freshwater Cichliformes: cichlid (mango tilapia, hybrid of blue tilapia x Nile tilapia)	ovaries, intestines, spleen	Africa, Israel
M. gallaicus	8.5-11 x 8.2-9.5 x 5-6	freshwater Cypriniformes: cyprinid (Iberian nase)	gill veins	Spain
M. gandiolensis	10-12 x 9-12	freshwater Cichliformes: cichlid (Guinean tilapia)	kidneys	Africa
M. gangulli (syn. *Myxosoma*)	8-10.5 x 4.8-6.5 x 5-6	marine Spariformes: sillaginid (trumpeter whiting)	head cartilage	India
M. gariepinus	13.7-15 x 10-11.2	freshwater Siluriformes: clariid (African sharptooth catfish)	ovary	Botswana
M. garrae	8.8-9.6 x 8-9.6 x 5.6-6.4	freshwater Cypriniformes: cyprinid (pingi logsucker)	fins, mouth	China
M. gayerae	13.7-16.5 x 11.5-13.7 x 7.3-8.7	freshwater Cypriniformes: cyprinid (common chub)	intestines	Hungary
M. gibelio	10.5-12.6 x 7.4-10 x 6	freshwater Cypriniformes: cyprinid (goldfish, Prussian carp)	gills, fins, kidneys	Amur Basin
M. gibelioi	9-11.7 x 9.5-13.5 x 5.4-8.1	freshwater Cypriniformes: cyprinid (goldfish, Prussian carp)	gills	China
M. gigas	17-21.6 x 12.8-16.2 x 9-12.4	freshwater Cypriniformes: cyprinid (common bream, white bream, ide, common chub, common bleak, Fuxian-lake golden-line barbel), tincid (tench)	subcutis, gills, fins, rarely kidneys, pancreas, gall bladder [cysts]	Europe
M. gigi (syn. *Lentospora, Myxobolus multilococapsularis, pseudobagri, miyarii p.p.*)	12-14.8 x 6-10 x 5-6	freshwater Cypriniformes: cyprinid (common carp, goldfish, Japan bouviere); Siluriformes: bagrid (yellowhead catfish, gigi, Ussuri catfish, Braznikov's catfish), silurid (Amur catfish)	gills, gall bladder, kidneys	Amur Basin, Korea, Japan
M. ginbuna	11.7-13.9 x 8.5-9.8 x 6.7-7.3	freshwater Cypriniformes: cyprinid (ginbuna)	gills	Japan
M. girellae	11.8-13 x 7.7-8.4 x 5.5-6.5	marine Perciformes: kyphosid (luderick)	kidney, caeca	Australia
M. globosus	7-8 x 6 x 5	freshwater Cypriniformes: catostomid (lake chubsucker, creek chubsucker)	gills	North America
M. gnathopogonae (syn. *Myxosoma*)	9.3-13.4 x 7.2-10.3 x 5.7-8.2	freshwater Cypriniformes: cyprinid (willow shiner)	cranial skin	Japan
M. gobii (syn. *M. naedenovae*)	9.8-10.7 x 9.8-10 x 7	freshwater Gobiiformes: gobiid (grass goby)	nares	Ukraine
M. gobiorum	11-13 x 9-10 x 5.5-6	freshwater Cypriniformes: cyprinid (gudgeon)	fins	Ukraine
M. goensis	9.5-10.5 x 6-7.5 x 5-6	freshwater Mugiliformes: mugilid (flathead grey mullet)	gills	India
M. gomtii	7.2-8.9 x 4-5.1	freshwater Cypriniformes: cyprinid (rohu)	kidney	India
M. goreensis	10-13 x 10-13	freshwater Mugiliformes: mugilid (flathead grey mullet)	gills	Senegal
M. gorhami	10-12 x 10-10.5	freshwater Cypriniformes: cyprinid (catla, golden mahseer)	gills, opercula	India
M. gourdiformis	12-14.4 x 8.4-10.6 x 6.6-7.4	freshwater Cypriniformes: cyprinid (bighead carp, marinka davidova), xenocypridid (silver carp)	gills, intestines, kidneys	China
M. gracilis	12-14.5 x 6-7 x 5	freshwater Cypriniformes: cyprinid (common carp)	urinary bladder	China
M. grandiintercapsularis	14.4-16.1 x 10-10.5 x 7.7-8.2	freshwater Gobiiformes: odontobutid (swinhonis goby, unspecified goby)	muscles, intestinal wall, kidneys	North America, Korea
M. grandis		freshwater Cypriniformes: cyprinid	abdomen	North America

(syn. *Myxosoma*)		(silverjaw minnow, common shiner, spottail shiner, blacknose dace)		
M. grassi	6-11.1 x 3.9-7.5 x 4.9-6	freshwater Cypriniformes: cyprinid (grass carp)	gills, liver	India
M. gravidus	12-14 x 9.5-10 x 7	freshwater Cypriniformes: catostomid (silver redhorse)	skin, fins	North America
M. groenlandicus	8.5-11 x 4.9-7.1 x 4.9-7.1	marine Pleuronectiformes: pleuronectid (Greenland halibut)	cartilage	Greenland
M. guangzhouensis	8.8-9.7 x 7.8-8.4 x 5.2-5.7	freshwater Cypriniformes: cyprinid (mrigal carp)	scales	China
M. guanqiaoensis	18.2-22 x 9-13.2 x 8-9	freshwater Cypriniformes: cyprinid (silver crucian carp, hybrid of common carp x Prussian carp)	liver, abdominal cavity	China
M. gulio (syn. *M. variformis, variabilis*)	11-17.9 x 4.9-8.1	freshwater Siluriformes: bagrid (long whiskers catfish)	gills, muscles	India
M. gutturocola	11.6-13.7 x 8.4-10.7 x 6.8-7.3	freshwater Cypriniformes: xenocypridid (silver carp)	throat serosa	China
M. guyenoti	14.5-16 x 11-12	freshwater Perciformes: percid (European perch)	gills	Switzerland
M. gylactiformae (syn. *Myxosoma*)	9.2-11 x 7.2-8.9 x 7-8.5	freshwater Gobiiformes: gobiid (Asian freshwater goby)		China
M. gymnocypris	8.7-14.1 x 7.6-9.8 x 6-7.6	freshwater Cypriniformes: cyprinid (hiina herzensteinia, osman przewalskeho)	gills	China
M. haematopterus	11.5-12.6 x 10.6-11.5 x 6.5-6.8	freshwater Cypriniformes: cyprinid (koi carp)	gills, skin, fins	Amur Basin
M. haichengensis	10.2-12 x 7.6-9.6 x 6.2-6.6	freshwater Cypriniformes: cyprinid (Chinese false gudgeon); Siluriformes: bagrid (yellowhead catfish)	gills, kidneys	China
M. haikowensis	14.3-15.8 x 12-13.2 x 7.7-8.7	freshwater Cypriniformes: cyprinid (pale chub)	intestines	China
M. haldari	9-10 x 7-8.5	freshwater Cypriniformes: cyprinid (mrigal carp, rohu, bata, boalla)	gills, fins	India
M. haldi	17-18.7 x 5.1-7.6	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. hanchuanensis	12-13.7 x 9-11 x 5.8-6	freshwater Cypriniformes: acheiloganthid (hiina morukas bittlerling), cyprinid (common carp)	gills, abdominal cavity	China
M. hani	7-9.1 x 7-8	estuarine Mugiliformes: mugilid (white mullet)	branchial spines	Senegal
M. hankiangensis (syn. *M. saurogobii*)	11-12 x 8.5-9.1 x 4.5-5.5	freshwater Cypriniformes: gobionid (dumerili sisalrunt)		China
M. hannensis	13-15 x 13-15	estuarine Mugiliformes: mugilid (flathead grey mullet)	gills	Senegal
M. hardevi	8.9 x 6.2	freshwater Cypriniformes: cyprinid (bata)	gills	India
M. harikensis	10.1 x 8.5	freshwater Cypriniformes: cyprinid (mrigal carp)	fins	India
M. harmandi	12.6-14.4 x 9-10.8	freshwater Cypriniformes: cyprinid (largescale silver carp)	gills	Vietnam
M. harpreetae	11.4-13.8 x 4.9-7.8	freshwater Cypriniformes: cyprinid (bata)	gills	India
M. hearti	13.2-15.8 x 10.4-12 x 7.2-7.8	freshwater Cypriniformes: cyprinid (goldfish)	heart	China
M. heckelii	12.2-13.1 x 6.3-6.9 x 3.7-4.4	freshwater Siluriformes: auchenipterid (pirillo)	gills	Brazil
M. hemibarbi	10-14.5 x 9.4-11.5 x 6-8.5	freshwater Cypriniformes: cobitid (pond loach), gobionid (barbel steed, spotted steed)	gills	Amur Basin, China
M. hendricksoni	13.1 x 12.3	freshwater Cypriniformes: cyprinid	brain	North America

		(fathead minnow)	[cysts)	
M. hepatobiliaris	6-7 x 4.7-5.7 x 4-4.3	marine Mugiliformes: mugilid (thinlip mullet)	liver, gall bladder wall	Portugal
M. heterocapsularis	12-15.6 x 9.6-12 x 7-8.6	freshwater Anabantiformes: channid (northern snakehead, blotched snakehead)	gills	China
M. heterocapsulatus	11-14.1 x 7.5-7.6 x 6	freshwater Cypriniformes: cyprinid (asp)	intestines	Hungary
M. heterofilamentosus	9.2-10.8 x 6.2-7.5 x 5.1-5.9	freshwater Siluriformes: clariid (Africa sharptooth catfish)	gills, liver, spleen, kidneys	Israel
M. heterolepis	12.5-14.5 x 8.5-10.5 x 9	freshwater Cypriniformes: cyprinid (blacknose shiner)	brain, eyes	Canada
M. heteromorpha	9.1-11.8 x 8.8-10.3 x 5-7	freshwater Cypriniformes: cyprinid (common carp)	heart, kidneys	China
M. heterospora (*heterosporus*) (syn. *Myxosoma*)	13-16 x 7-9.2	freshwater Cichliformes: cichlid (mango tilapia, Cameroon tilapia, Nile tilapia, mvogoi tilapia, helmitilapia, Singida tilapia, Victoria tilapia)	gills, kidneys	Cameroon
M. heterotisi	11.5-13 x 9.5-10	freshwater Osteoglossiformes: osteoglossid (African arowana)	gills	Burkina Faso
M. hilarii	9.8-13.4 x 9.7-12.4 x 6.7-9	freshwater Characiformes: bryconid (piraputanga)	renal tubules	Brazil
M. himalayaensis	9.6 x 7.1	freshwater Cypriniformes: cyprinid (common snowtrout)	gills	India
M. hoabinhensis	11.4-12.6 x 7.9-9 x 5.8-6.3	freshwater Cypriniformes: cyprinid (goldfish)	muscles	Vietnam
M. hochingensis	8.4-9.2 x 7.2-8.4 x 5.7-6.3	freshwater Cypriniformes: cyprinid (grass carp, gold barb)	skin, spleen, kidney	China
M. hoffmani (syn. *Myxosoma*)	8.6-10.8 x 7.8-8.9 x 5.9-6.5	freshwater Cypriniformes: cyprinid (bluntnose minnow, fathead minnow)	eyes	North America
M. hokiangensis	12.1-14.2 x 7.6-10.3 x 6.1-6.5	freshwater Cypriniformes: cyprinid (goldfish)	ureters, urinary bladder	China
M. holzerae	7.6-7.7 x 4.1-4.3	freshwater Cypriniformes: cyprinid (rohu)	gills	India
M. homei (syn. *M. abbottinae*, *Myxosoma*)	13.8-17 x 8.5-14.4 x 8.5-9.7	freshwater Cypriniformes: gobionid (tompkoon-abbottiin, loshani nokisrunt)	intestines, gall bladder, kidneys	China
M. homeospora (*homeosporus*) (syn. *Myxosoma*)	13.5-17 x 8.5-11	Freshwater Cichliformes: cichlid (Nile tilapia, unspecified tilapia)	gills, subcutis	Africa
M. honghuensis	15.1-19.5 x 9-11.3 x 7.9-9.1	freshwater Cypriniformes: cyprinid (Prussian carp)	pharynx	China
M. hopehensis	10.8-15 x 7.2-10.8 x 6-7.2	freshwater Cypriniformes: cyprinid (bighead carp), xenocypridid (silver carp)	gills, intestines, gall bladder	China
M. hosadurgensis	9-11 x 5-8	freshwater Cypriniformes: cyprinid (mrigal carp)	gills, muscles	India
M. hoshinae (syn. *M. dermatobius, soldatovi, Lentospora, Myxosoma*)	6.3-12.5 x 6-10.5 x 2-6.9	freshwater Anguilliformes: anguillid (Japanese eel); Cypriniformes: cyprinid (common carp, predatory carp, goldfish), xenocypridid (silver carp); Salmoniformes: salmonid (chum salmon, coho salmon)	subcutaneous tissue [cysts]	Amur Basin, Japan, England
M. huananensis	16.8-19.2 x 8.4-9.6 x 6.2-7.2	freshwater Cypriniformes: cyprinid (goldfish)	skin, gills	China
M. huasaensis	11.6-13.9 x 6.7-9.2 x 5.4	freshwater Cypriniformes: cyprinid (grass carp)	gall bladder, kidneys	China
M. hubeiensis	11.6-12.4 x 10.7-12.1 x 8.6-9.1	freshwater Cypriniformes: gobionid (Chinese lizard gudgeon)		China
M. huchowensis	18-19.8 x 9.6-10.8 x 7.2-8.4	freshwater Cypriniformes: cyprinid (goldfish)	gills	China
M. hudsonis	11.5-12.5 x 7	marine Cyprinodontiformes: fundulid	scales	North America

(syn. *Myxosoma*)		(mummichog)		
M. huitungensis (syn. *M. omeiensis p.p., Myxosoma*)	7.2-12.8 x 5.6-10.4 x 4.8-5.6	freshwater Cypriniformes: cyprinid (ya-fish, marinka tsunynska, longchuani marinka), gobionid (Chinese lizard gudgeon)	gills, kidneys	China
M. humilis	8.1-9 x 6.3-7.2	freshwater Cypriniformes: cyprinid (largescale silver carp)	spleen	Vietnam
M. hunanensis	9.6-11.5 x 7.2-8.4 x 4.8-5.2	freshwater Cypriniformes: xenocypridid (silver carp)	gall bladder	China
M. hungaricus	7.3-9.3 x 4.8-6.8	freshwater Cypriniformes: cyprinid (common bream) [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex, Limnodrilus hoffmeisteri*)]	gills	Europe
M. hupehensis (syn. *Myxosoma*)	9.6-11 x 6-7.2	freshwater Cypriniformes: cyprinid (common carp, bighead carp), xenocypridid (silver carp); Siluriformes: bagrid (yellowhead catfish), clariid (walking catfish)	gills, skin, fins, eyes, intestines, gall bladder, kidney, spleen, heart, muscles, urinary bladder	China
M. hwangkangensis (syn. *M. symmetricus*)	10.8-12 x 7.2-9.6 x 4.6-5	freshwater Cypriniformes: cyprinid (common carp, bighead carp, hiina astelparrak, hollandi astelparrak, tomp koukloug), xenocypridid (silver carp); Perciformes: centrarchid (black crappie)	gills	China
M. hwangshihensis	8.4-9.6 x 7-7.8 x 5	freshwater Cypriniformes: xenocypridid (yellowtail)	heart, kidneys	China
M. hyborhynchi	9.1-10.9 x 7.3-8.6	freshwater Cypriniformes: cyprinid (bluntnose minnow, fathead minnow)	mandibular bone	Canada
M. hydrabadense (mis-spelling *hyderabadense*) (syn. *Myxosoma*)	9.3-11.5 x 5-8	freshwater Cypriniformes: cyprinid (filament barb, olive barb)	gills	India
M. hydrocyni	13-14 x 8-10	freshwater Characiformes: alestid (elongate tigerfish)	gills	Tchad
M. hylae	8.8-15.5 x 8-10.7 x 6.7-7.8	Anura: hylid (spotted-thighed tree frog)	testes, oviducts, kidneys	Australia
M. hypophthalmichthydis (syn. *Disparospora*)	12-15 x 9.6-11.4 x 7.9-8.9	freshwater Cypriniformes: cyprinid (koi carp, goldfish), xenocypridid (silver carp)		China
M. hypseleotris	12.6-15.6 x 8.4-10.8 x 6-7.2	freshwater Cypriniformes: cyprinid (goldfish); Gobiiformes: eleotrid (Swinhone's carp-gudgeon)	muscles, intestines	China
M. iarakiensis	6.7-8.6 x 4.5-6.3 x 2.7-4.7	freshwater Characiformes: prochilodontid (kissing prochilodus)	gills	Brazil
M. ibericus	9-11 x 8-9.5 x 6-7	freshwater Salmoniformes: salmonid (river trout)	liver, spleen, kidneys, ureters	Spain
M. ichkeulensis	8.2-14 x 6-13	freshwater/estuarine Cypriniformes: cyprinid (goldfish); Mugiliformes: mugilid (flathead grey mullet)	gills, fins	Tunisia, India
M. ictiobus	12.7-14.5 x 10.7-13.6 x 10.3-14.8	freshwater Cypriniformes: catostomid (smallmouth buffalo)	gills	North America
M. iecoris	11.4-14.2 x 7.7-9.9 x 6.5-7.5	freshwater Characiformes: bryconid (dourado)	liver	Brazil
M. imami	10.4-11.6 x 7.2-8	freshwater Perciformes: latid (Nile perch)	kidneys	Egypt
M. imparfinis	7.1-8.4 x 4.5-6.2 x 3.1-3.8	freshwater Siluriformes: heptapterid (bagrinho)	gills	Brazil
M. impressus	9.6-12.8 x 8-9.6 x 5.6-7.2	freshwater Cypriniformes: cyprinid (common chub, Crimean barbel, pingi	gills, fins	China

		logsucker)		
M. improvisus	6.5-7.7 x 7.5-9.3 x 4.6-5.6	freshwater Cypriniformes: cyprinid (crucian carp, ide)	muscles	Ukraine
M. inaequalis (*inequalis*)	11 x 7	freshwater Siluriformes: mochokid (mandi)	head	Surinam
M. inaequus	15.6-22 x 7.8-9.3 x 7.7-8.5	freshwater Gymnotiformes: sternopygid (South American knife fish)	brain	Brazil
M. indiae (syn. *Myxosoma*)	12.4-15 x 6.4-8.6	freshwater Cypriniformes: cyprinid (olive barb)	gills	India
M. indica	5.6-7.2 x 3.5-4.9	freshwater Cypriniformes: cyprinid (goldfish)	gills	India
M. indicus	9.5-10.8 x 7.5-8.2 x 5.5	freshwater Cypriniformes: cyprinid (mrigal carp)	intestinal wall, muscles, liver	India
M. indirae (syn. *Myxosoma*)	11-14 x 9-11	freshwater Cypriniformes: cyprinid (mrigal carp)	scales, cranial cartilage	India
M. inflatus	13.2-15.6 x 9.6-10.8 x 5.4-7.5	freshwater Cypriniformes: cyprinid (goldfish); Gobiiformes: eleotrid (Swinhoe's carp-gudgeon)	gills, urinary bladder, kidneys	China
M. infundibulatus	13.4-15.4 x 11-13	freshwater Cypriniformes: cyprinid (European chub)	kidneys, swim bladder wall	Europe
M. inornatus	12.3 x 8.2 x 5.8	freshwater Perciformes: centrarchid (smallmouth bass, largemouth bass, largemouth black bass)	muscles	North America
M. insidiosus	11.5-17.3 x 7.5-11.9 x 6.4-9	freshwater Cypriniformes: catostomid (Lost River sucker); Salmoniformes: salmonid (chinook salmon, coho salmon, cutthroat trout, rainbow trout)	muscles	North America
M. insignis	14-15 x 11-12 x 7-8	freshwater Characiformes: prochilodontid (kissing prochilodus)	gills	Brazil
M. intestinalis	12-13 x 10-12.5 x 8	freshwater Perciformes: centrarchid (black crappie)	intestines	North America
M. intestinicola	7.1-8.1 x 5.8-7.2 x 5.2-5.8	estuarine Mugiliformes: mugilid (thicklip grey mullet)	intestines [cysts]	Portugal
M. intimus	12.5 x 10	freshwater Cypriniformes: cyprinid (common roach) [cycle involves aurantiactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex, tubifex, Limnodrilus hoffmeisteri*)]	gills	Europe
M. intrachondrealis	9-11 x 6-7 x 3.7-4.2	freshwater Cypriniformes: cyprinid (common carp)	gill cartilage	Hungary
M. intramusculi (syn. *M. procerus*)	9.9-17 x 4.6-8 x 5-6	freshwater Percopsiformes: percopsid (trout-perch)	skin, fins, muscles	North America
M. invictus	8.1-9 x 7.4-8.2	estuarine Mugiliformes: mugilid (thicklip grey mullet)	gills [cysts]	Portugal
M. iowensis	12.2-12.9 x 10.6-11.4 x 7.6	freshwater Perciformes: centrarchid (black crappie)	gills	North America
M. iquitoensis	16.2-19.8 x 9.8-12	freshwater Siluriformes: loricariid (zebra oto)	gills	Peru
M. iranicus	13.2-14 x 7.5-9.2 x 5.6-6.3	freshwater Cypriniformes: cyprinid (yellow barbel)	spleen	Iran
M. irinae	9.4-10.6 x 7-7.7	freshwater Cypriniformes: cyprinid (Turkestan barbel, Herat khramulya)	kidneys	Asia
M. isakovi	13-14 x 8.4-8.8	freshwater Cypriniformes: cyprinid (common chub, itaturb, blue bream)	spleen, kidneys	Russia
M. israelensis	14-16 x 8-10	freshwater Cichliformes: cichlid (mango tilapia, Nile tilapia, Cameroon tilapia, mvogoi tilapia, hybrid of Nile tilapia x blue tilapia)	gills, gut, kidneys, muscles	Africa
M. iucundus	11-14.5 x 10.5-11 x 7.1-8.1	freshwater Galaxiiformes: galaxiid (common galaxias)	muscles	New Zealand

M. jialingensis	15.4-17 x 7.8-8.9	freshwater Siluriformes: bagrid (yellowhead catfish)	hepatopancreas, urinary bladder	China
M. jianouensis	8.8-9.6 x 6.6-7.4 x 4.4-5.5	freshwater Cypriniformes: botiid (sekavka tientajska)	gills	China
M. jingangensis	12-14 x 10-11	freshwater Cypriniformes: cobitid (pond loach)	kidneys	China
M. jollimorei	10.5-11.5 x 12-14.5 x 6.5-8	freshwater Perciformes: centrarchid (bluegill sunfish)	bulbus arteriosus	North America
M. junchisi	9.7-12.6 x 8.4-9.2 x 5.2-7.3	freshwater Cypriniformes: cyprinid (common carp)	gills, muscles, kidneys	Amur Basin
M. kainjiae	9-11 x 6-9	freshwater Cichliformes: cichlid (ruskoraitilapia)	ovaries, ureters	Africa
M. kalarfi (syn. *M. garrai*)	11.3-15.5 x 6.8-8.3 x 5-7	freshwater Cypriniformes: cyprinid (hijaz garra)	muscles	Saudi Arabia
M. kalavatiae	6.8-7.7 x 4.8-5.8 x 3.5-3.8	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. kanjali	9.5 x 7.7	freshwater Cypriniformes: cyprinid (mrigal carp)	scales	India
M. kalyaniensis	9-10 x 8-8.5	freshwater Cypriniformes: cyprinid (mrigal carp)	scales	India
M. karaeri	9.3-10.3 x 7.9-9 x 5.5-5.6	freshwater Cypriniformes: cyprinid (Anatolian khramulya)	fins, opercula, gills, skin	Turkey
M. karelicus	7-13 x 6-10 x 7	freshwater Perciformes: percid (European perch, ruffe, zander, zingel)	gills, spleen, kidneys	Europe
M. karnatakae (syn. *Myxosoma*)	16.3-19 x 10.9-13.6	freshwater Cypriniformes: cyprinid (swamp barb)	muscles	India
M. karuni	13-14.9 x 9.7-10.4 x 6.5-7.8	freshwater Cypriniformes: cyprinid (shabout, Mesopotamian himri)	gills	Iran
M. kashingensis	10-13 x 8-10 x 7	freshwater Cypriniformes: cyprinid (grass carp)	gills	China
M. kashmirensis	9.2 x 3.3	freshwater Cypriniformes: cyprinid (Chirruh snowtrout)	gills	India
M. kawabatae (syn. *Lentospora, Myxobolus grandicapsularis, liocassis, tunicatus*)	15-18 x 8-10.6 x 5.6-7	freshwater Siluriformes: bagrid (yellowhead catfish, Ussuri catfish, Braznikov's catfish)	kidneys	Amur Basin, Korea, Japan
M. khaliji	7.2-9.5 x 5.1-7.4 x 8.3-10.2	marine Spariformes: sparid (twobar seabream)	intestines	Saudi Arabia
M. kianghanensis	9.6-13.2 x 8.4-12 x 8.4-8.6	freshwater Cypriniformes: cyprinid (stone moroko)	kidneys	China
M. kiangsiensis	10.8-15.6 x 6.6-8.4 x 5.2-6	freshwater Siluriformes: bagrid (yellowhead catfish)	intestines	China
M. kiangsuensis	11.4-13.6 x 7.6-9.1 x 6.1-7.6	freshwater Cypriniformes: cobitid (pond loach_	gills, mouth	China
M. kiangtsingensis	9.1-10.6 x 5.2-7.6 x 5.3-6.1	freshwater Cypriniformes: cyprinid (rosy bitterling)	heart, spleen, kidney	China
M. kiatingensis	10.4-11.2 x 8-8.8 x 7.5-7.9	freshwater Cypriniformes: gobionid ('kiatingensis' gudgeon)	swim bladder	China
M. kidneyi (syn. *M. capoeta, Myxosoma*)	7.9-14.8 x 6-9.6 x 5-6.4	freshwater Cypriniformes: cyprinid (gold barb)	kidneys, gills	China
M. kienweiensis	11.4-13 x 9.5-11 x 5.6-5.9	freshwater Cypriniformes: cyprinid (marinka davidova)	gills, mouth, fins, intestines, gall bladder, heart, spleen, liver, kidney, urinary bladder	China
M. kingchowensis	9.6-12 x 7.2-8.4 x 6	freshwater Cypriniformes: cyprinid (goldfish, silver carp, bighead carp, Japanese white crucian carp, black	gills, skin, intestines, kidney, liver, heart,	China

		Amur bream, Khanka spiny bitterling)	muscles, urinary bladder, gall bladder, swim bladder	
M. kingsleyae	10-11.5	freshwater Anabantiformes: anabantid (tailspot ctenopoma)	gills	Africa
M. kisutchi	7-8.5 x 6.5-7 x 3.5-3.8	freshwater Salmoniformes: salmonid (chinook salmon, coho salmon)	spinal cord	North America
M. kiuchowensis	16.2-16.8 x 12-12.6 x 8.5-9	freshwater Cypriniformes: cyprinid (bighead carp)	gills, nose, kidney, urinary bladder, gall bladder	China
M. klamathellus	13-15 x 9.5-10 x 7.5-8	freshwater Cypriniformes: leuciscid (blue chub)	head, body	North America
M. knobii	5.8 x 4.2	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. kodjii	7-9 x 5.5-6.6 x 3.5-4.2	freshwater Cypriniformes: cyprinid (African carp)	eyes	Cameroon
M. koi	12-16 x 5-9 x 4.8-6.7	freshwater Cypriniformes: cyprinid (common carp, koi carp, mud carp, mrigal carp, goldfish, rohu, barbel chub, Russian bitterling, Khanka spiny bitterling, tomp koukloug, labeo secuanske), gobionid (Chinese neon golden stripe shark), xenocypridid (silver carp); Gobiiformes: odontobutid (Swinhoe's freshwater goby); Siluriformes: clariid (walking catfish)	gills, skin [gill clubbing]	Eurasia
M. kolesnikova		freshwater Salmoniformes: salmonid (true fera)		Europe
M. koli	7.1-9.6 x 5-6.4	freshwater Cypriniformes: cyprinid (kholus, filament barb)	fins	India
M. korjakovii		freshwater Scorpaeniformes: cottid (Baikal oilfish, little Baikal oilfish)	kidney	Lake Baikal
M. kosteri		freshwater Perciformes: centrarchid (bluegill sunfish)		North America
M. kostiri	8.8-11.2 x 6.4-8 x 4.9-5.8	freshwater Perciformes: centrarchid (small-mouth black bass, bluegill sunfish)	subcutis	North America
M. kotlani	10.3 x 7.6	freshwater Anguilliformes: anguillid (European eel)	subcutaneous tissues	Europe
M. koumingensis	15-16.2 x 8.4-10.8 x 6.2-6.5	freshwater Siluriformes: clariid (walking catfish)	gills, liver, spleen, kidney, gonads	China
M. kouoptamoensis	8-10 x 8-10	freshwater Cypriniformes: cyprinid (African carp)	gills, kidney, spleen	Cameroon
M. kovali	7.5-9 x 6-10 x 7	freshwater Cypriniformes: cyprinid (Samarkand khramulya, Turkestan barbel, sattar snowtrout)	gills	Asia
M. kozloffi (*kosloffi*)	13.5-15.5 x 8-9.5 x 6.5-7.5	freshwater Cypriniformes: catostomid (Lost River sucker)	kidney	North America
M. kribiensis	20.2-23 x 9-10	freshwater Characiformes: alestid (long-fin tetra)	skin, sclera	Cameroon
M. krokhini	9-12 x 7.5-10.5 x 4.8-6.9	freshwater Salmoniformes: salmonid (sockeye salmon, Arctic char); Cypriniformes: cyprinid (pacu)	mesenteries, intestines	Russia, Alaska
M. kubanicus (*kubanicum*) (syn. *M. platyrostris*)	9.6-13.3 x 7-9.6 x 4.8-8	freshwater Anabantiformes: channid (northern snakehead); Cypriniformes: cobitid (pond loach), cyprinid (common carp, koi carp, Japanese crucian carp, Prussian carp, bighead	gills, fins, intestinal wall, muscles, kidneys, urinary bladder, swim bladder	Amur Basin, Korea, China

		carp, goldfish, Chinese lizard gudgeon, stone moroko), gobionid (boulengeri voorikrunt), xenocypridid (silver carp)		
M. kudoi	8.5-8.9 x 6.5-7.3	freshwater Siluriformes: pimelodid (unspecified *Nemathognata*)	skin	Brazil
M. kuleminae (syn. *M. grandis p.p.)*	15-19.5 x 12-15 x 8-9.1	freshwater Cypriniformes: cyprinid (common dace, ide, asp, ziege)	muscles	Ukraine
M. kunmingensis	8.2-8.6 x 8-8.4 x 5.9-6.2	freshwater Cypriniformes: cyprinid (ogauim-nagarmokk)	gills	China
M. kwangsiensis	10-11.5 x 6.4-7.3 x 6	freshwater Cypriniformes: cyprinid (rohu)	kidney	China
M. kwangtungensis (syn. *Myxosoma*)	15.8-18.6 x 10.8-13.2 x 7.8-8.6	freshwater Cypriniformes: cyprinid (mud carp), xenocypridid (silver carp); Siluriformes: clariid (walking catfish)	gall bladder, skin, gills	China
M. kyi (syn. *M. hakyi p.p.*)	14.4-16.8 x 6-12.6 x 5-9	freshwater Cypriniformes: cyprinid (largescale silver carp)	kidneys	Vietnam
M. labeoi	16-17 x 10-12	freshwater Cypriniformes: cyprinid (African carp)	fins	Burkina Faso
M. labeosus	8-10 x 6.5-9	freshwater Cypriniformes: cyprinid (fringe-lipped peninsula carp)	mesentery	India
M. labiae	10 x 7.5	freshwater Cypriniformes: cyprinid (Nile carp)	gills	Egypt
M. labicola	8.1-8.7 x 7.4-8.3 x 5.4-6.2	estuarine Mugiliformes: mugilid (thicklip grey mullet)	top lip [cysts]	Portugal
M. labracis		marine Moroniformes: moronid (European seabass)	gills	Egypt
M. labrosus	9.7-10.3 x 7.7-8.7 x 5.7-6	estuarine Mugiliformes: mugilid (thicklip grey mullet)	urinary bladder	Portugal
M. ladogensis (syn. *M. pelecicola*)	14.9-18 x 11.6-13,3 x 7.4-8.3	freshwater Cypriniformes: cyprinid (ziege)	muscles	Russia
M. lagowskii	12.9-15 x 8.1-9.4 x 6.9-7.2	freshwater Cypriniformes: leuciscid (Chinese minnow)		Russia
M. lalithae	9-11 x 8-9	freshwater Cypriniformes: cyprinid (orangefin labeo)	gills	India
M. lalbaghensis	7.6-11.9 x 5.1-8.5	freshwater Cypriniformes: cyprinid (bata)	gills	India
M. lalithae	9-11 x 8-9	freshwater Cypriniformes: cyprinid (orangefin labeo)	gills	India
M. lalithakumarii (syn. *Myxobolus asymmetricus, Leptotheca asymmetrica*)	8.6-10 x 5.7-7.9	freshwater Cypriniformes: cyprinid (Hasselt's bony-lipped barb)	gallbladder, gills, intestines	India
M. lamellobasis	9.1-10.8 x 8.6-10.5 x 5.2-6.1	freshwater Cypriniformes: cyprinid (white bream)	gills	Hungary
M. lamellus	9.5-13.5 x 9-12 x 5-8	freshwater Cypriniformes: catostomid (white sucker)	gills	Canada
M. lampiformis	14-15 x 11-13 x 9	freshwater Cypriniformes: cyprinid (bighead carp)	gills	China
M. lancangensis (syn. *M. obovoides, Myxosoma*)	8.8-14.4 x 7.5-14.4 x 5.6-8.4	freshwater Cypriniformes: cyprinid (common carp, Chinese false gudgeon, ogauim-nagarmokk, yunnani silemokk); gobionid (dumerili sisalrunt)	gills, fins, urinary bladder	China
M. lanfyongi	10.8-11.7 x 10.8-11.7	freshwater Cypriniformes: cyprinid (phoenix barb)	intestinal wall	Vietnam
M. laterobranchialis	9.4-10.4 x 7.5-9.1 x 5.2-7.2	freshwater Cypriniformes: cyprinid (common barbel)	gills	Hungary
M. latipinnacola	12-14 x 7.1-9.8 x 5.7-7.3	freshwater Cyprinodontiformes: poecilid sailfin molly)	gall bladder	North America
M. latesi	26.2-36.2 (9-10.8)	freshwater Perciformes: latid (Nile	gills, intestines	Tchad

	x 6.3-8.2	perch)		
M. latis	21.2 x 17.2	freshwater Perciformes: latid (Nile perch)	gills	Egypt
M. latus	7-10 x 8.4-11 x 5.2-5.6	freshwater Cypriniformes: xenocypridid (silver carp)	kidneys	Amur Basin
M. lazera (syn. *M. clarii*)	9-13 x 7.5-12 x 6.2-7.2	freshwater Cichliformes: cichlid (Nile tilapia, Guinean tilapia); Cypriniformes: cyprinid (black carp), xenocypridid (silver carp); Siluriformes: clariid (walking catfish, African sharptooth catfish)	gills, gall bladder, liver, gonads, fat bodies	India, China, Africa
M. leafa	11.8-15.3 x 13.6-15.3	freshwater Cypriniformes: cyprinid (bata)	gills	India
M. leiobagrusi	9.6-10 x 7.2-8 x 5.6	freshwater Siluriformes: amblycipitid (margined bullhead)	gills	China
M. leipoensis	8.8-9.6 x 6.4-8 x 4.8	freshwater Cypriniformes: cyprinid (yunnani silemokk)	kidneys	China
M. lentisuturalis	11.2-12.4 x 7.2-8.4 x 5.2	freshwater Cypriniformes: cyprinid (Prussian carp)	muscles [swellings]	China
M. lepomicus	12.5-16.5 x 9-11.5 x 7-7.5	freshwater Perciformes: centrarchid (pumpkinseed)	gills, intestines, gall bladder, heart, muscles, ureters, swim bladder	Canada
M. lepomis	16.8-21.3 x 7-8.8 x 5.3-6.1	freshwater Perciformes: centrarchid (dollar sunfish, redspotted sunfish)	gills	North America
M. leptobarbi	14.8-17 x 8.4-9.6 x 5.5-6.5	freshwater Cypriniformes: cyprinid (mad barb)	muscles	Malaysia
M. leptobotiae	6.8-7.4 x 5.9-6.5 x 4-6	freshwater Cypriniformes: botiid (imperial flower loach)	gills	China
M. lepturichthys	7-9.4 x 5.6-8.7 x 5.6-5.8	freshwater Cypriniformes: balitorid (Nicholski's river loach)	kidneys	China
M. leqingensis	12.9-14.2 x 9-9.7 x 5.1-5.9	freshwater Siluriformes: clariid (walking catfish)	gills, intestines	China
M. leshanensis	9.6-12 x 8-8.8 x 4.8-5.6	freshwater Cypriniformes: cyprinid (pisisuu-koukloug)	kidney	China
M. leuciscini	10-12 x 7.5-9.5 x 5-7.5	freshwater Cypriniformes: cyprinid (Iberian nase, common chub, bermejuela)	gills	Spain
M. leuciscusi	11.6-13.1 x 6.9-8.5 x 5.4-6.2	freshwater Cypriniformes: cyprinid (Amur ide)	spleen, gall bladder, kidney, urinary bladder	China
M. leucogobianus (syn. *Lentospora*)	12 x 10 x 7.5	freshwater Cypriniformes: cyprinid (Japanese gudgeon)	kidneys	Japan
M. liangshanensis (syn. *Myxosoma*)	8.1-11.2 x 7.3-8.8 x 5.1-7	freshwater Cypriniformes: cyprinid (pingi logsucker, marinka tsunynska)	kidneys, ureter, urinary bladder, liver, ovary	China
M. liaoningensis	7.8-8.4 x 9.6-12,8 x 6.6-7.2	freshwater Cypriniformes: cyprinid (common carp, goldfish), xenocypridid (silver carp)	gills, intestines, kidneys	China
M. lieni (syn. *Myxosoma*)	7.2-7.4 x 7.2-7.4 x 4.8-5	freshwater Cypriniformes: acheilognathid (hiina morukas), cyprinid (bighead carp, grass carp, goldfish, rainbow gudgeon, pingi logsucker, poologa-silemokk, stone moroko), xenocypridid (silver carp)	brain, spinal cord, intestines, muscles, gall bladder, spleen, urinary bladder	China
M. lienis	10.3-13.8 x 6.8-9.3 x 6-7	freshwater Characiformes: bryconid (piracanjuba)	spleen	Brazil
M. lii	9-11.5 x 9-12.5 x 5-7.5	freshwater Perciformes: centrarchid (pumpkinseed)	kidney, muscle, spleen, ureters, swim bladder	Canada
M. linearis		freshwater Siluriformes: pimelodid		Europe

		(barred sorubim)		
M. linghuensis	10.2-13.2 x 8.4-9.6 x 6-7.2	freshwater Cypriniformes: cyprinid (common carp, bighead carp)	gills, intestines	China
M. lintoni	13.9 x 11	estuarine Cyprinodontiformes: cyprinodontid (sheepshead minnow)	skin, muscles	North Atlantic
M. linzhiensis	10.1-13 x 10-11.3 x 6.2-7	freshwater Cypriniformes: cyprinid (yarlungi marinka)	gills	China
M. liocassii	14-16 x 6.8-8 x 5-5.5	freshwater Siluriformes: bagrid (Ussuri catfish)	gall bladder	Amur Basin
M. liptoni		Listed in Bulletin of the United States Fish Commission		North America
M. lizae (syn. *M. lairdi, Myxosoma*)	4.6-5.2 x 9-9.5 (9-11 x 9-11 x 5-7)*	estuarine Mugiliformes: mugilid (largescale mullet) marine Gadiformes: macrourid (roundnose grenadier)*	intestinal wall (brain, eyes)*	India, Norway*
M. lobatus (syn. *Myxosoma branchilais p.p.*)	7.5-9.5 x 6-6.5	freshwater Cypriniformes: cyprinid (common barbel, Aral barbel, Bulatmai barbel, Caspian barbel, Dnieper barbel, Mediterranean barbel, Turkestan barbel, common nase, common dace, asp)	gills, intestinal wall [cysts]	Russia
M. lokiaensis (syn. *M. lochiaensis*)	10.8-12 x 8.4-8.6 x 6.2-7.8	freshwater Cypriniformes: cyprinid (goldfish)	urinary bladder	China
M lomi	9-13 x 7-9.6 x 5-7.9	freshwater Cypriniformes: cyprinid (grass carp, common minnow)	gills, intestines, gall bladder, kidneys	Hungary
M. longi (syn. *M. acrossocheilusi, Myxosoma*)	8-10.6 x 7-7.3 x 3.2-5.6	freshwater Cypriniformes: cyprinid (yunnani silemokk)	kidneys, urinary bladder	China
M. longissimus	18-20 x 8.6-10.4 x 7.6-8.9	freshwater Characiformes: serrasalmid (tambaqui)	gut wall, gills	Brazil
M. longisporus	16-17.5 x 6.5-7 x 6	freshwater Cypriniformes: cyprinid (common carp)	gills	China
M. lotae	8.4-10.4 x 6.2-6.5	freshwater Gadiformes: lotid (burbot)	gills	Russia
M. lubati	9-11 x 7-9	marine Spariformes: sparid (haffara seabream)	intestinal wall	Egypt
M. luciogobii (syn. *Myxosoma*)	7.7-10.7 x 6.9-9.2 x 5-7.9	estuarine Gobiiformes: gobiid (flat-headed goby)	urinary bladder	Japan
M. lucknowii	7.1-9.1 x 7-8.4	freshwater Siluriformes: clariid (walking catfish)	kidney	India
M. ludhianae	10 x 9-9.5	freshwater Cypriniformes: cyprinid (boalla)	fins	India
M. luguensis (syn. *Myxosoma*)	9.6-11.4 x 7.6-8.4 x 7.3-7.8	freshwater Cypriniformes: cyprinid (kozlovi marinka)	gills	China
M. lussi	9.5-15 x 7.4-9.1 x 4.8-6.7	freshwater Cypriniformes: cyprinid (bighead carp, silver carp, goldfish, Amur whitefin gudgeon, Siberian gudgeon, Mongolian redfin)	gills, fins [cysts]	Amur Basin
M. lutzi	10 x 7	freshwater Cyprinodontiformes: poeciliid (eye spot toothcarp, January toothcarp)	testes [castration?]	Brazil
M. mabianensis (syn. *M. schizothoraxi, Myxosoma*)	8.8-13.6 x 6.4-8.8 x 6.4-8.2	freshwater Cypriniformes: cyprinid (ya-fish, marinka tsunynska, marinka iravadska, marinka davidova)	gills, fins, heart, spleen, liver, gall bladder, kidneys, urinary bladder	China
M. maceioenensis	6.2-7.7 x 6-8 x 4.1-4.9	estuarine Mugiliformes: mugilid (white mullet)	gills	Brazil
M. machidai	8.1-9.4 x 7.5-8.3 x 5.1-6	marine Centrarchiformes: oplegnathid (spotted knifejaw)	oesophagus	Japan
M. macrocapsularis (syn. *M. marinus, marinum, multiplex,*	12-14.4 x 6.6-9.6 x 6-8.4	freshwater/estuarine Cypriniformes: cyprinid (common carp, crucian carp, black carp, mud carp, goldfish,	gills, fins, swim bladder, intestinal wall, mesenteries,	Eurasia

oviformis p.p., physophilus, vescus, branchialis p.p. [Osmanov])		common bream, white bream, white Amur bream, blue bream, Wuchang bream, common nase, common rudd, common bleak, common dace, common roach, common chub, ide, asp, ziege, gudgeon, Chinese false gudgeon, Chinese lake gudgeon, common barbel, Java barb, European bitterling, sattar snowtrout), gobionid (loshani nokisrunt), leuciscid (spirlin, Pacific redfin, taran), xenocypridid (three-lips, silver carp); Scorpaeniformes: gasterosteid (three-spined stickleback); Siluriformes: bagrid (yellowhead catfish, shining catfish) [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)]	rarely kidneys, spleen, gall bladder, urinary bladder [cysts]	
M. macrolepi	5.2-6.9 x 4.3-6.9	estuarine Mugiliformes: mugilid (largescale mullet)	intestines	India
M. macroplasmodialis	10.5-12 x 8-9 x 5-5.5	freshwater Characiformes: bryconid (dorado)	body cavity	Brazil
M. macropodusi (syn. *Myxosoma*)	15.4-17.7 x 5.4-6.9 x 4.4-4.8	freshwater Anabantiformes: osphronemid (round-tailed paradise fish)	skin	China
M. maculatus	9.7-23 x 7.9-9.5 x 7.2-7.9	freshwater Characiformes: serrasalmid (spotted metynnis)	kidney	Brazil
M. macrurus	10-11 x 6-8 x 4	freshwater Cypriniformes: cyprinid (Mississippi silvery minnow)	subcutis	Europe
M. magai	9-12 x 5.5-7	freshwater Cypriniformes: cyprinid (batesi narmasmokk)	gills	Africa
M. magauddi (syn. *Myxosoma*)	10.8-11.7 x 8.3-10	freshwater Anabantiformes: osphronemid (banded gourami)	gills	India
M. magellanicus	10-13 x 8.1-8.8	freshwater Galaxiiformes: galaxiid (common galaxias)	gills	Argentina
M. magnaspherus	16-22 x 18-22 x 11-13	freshwater Perciformes: centrarchid (pumpkinseed)	kidney	Canada
M. magnus	10-11 x 7-8.5 x 6.5-7.8 [38-45 x 32-38 x 28-35]*	freshwater Perciformes: percid (ruffe*, Donet's ruffe, zander)	eyes	Russia, Germany*
M. magurii	13-15 x 6.5-8	freshwater Siluriformes: clariid (murgodu)	accessory respiratory organ	India
M. mahendrae	11.5-14 x 9.8-10.5	freshwater Cypriniformes: cyprinid (catla)	gills [retarded growth]	India
M. mai	9.7-11 x 8.1-9.5 x 5.6-8	freshwater Cypriniformes: xenocypridid (silver carp)	kidney	China
M. maiai	12.5-14.8 x 11.4-13.8 x 6.4-7.7	freshwater Characiformes: prochilodontid (kissing prochilodus)	gills	Brazil
M. mailaoensis		freshwater Siluriformes: mochokid (wahrindi)	kidney	Tchad
M. majraiensis	8.5 x 5.2	freshwater Cypriniformes: cyprinid (catla)	gills	India
M. mamaevi	10.7-11.9 x 8-9.4 x 5.8-6.1	freshwater Cypriniformes: cyprinid (koi carp)		Russia
M. manoramae	10.7-13.1 x 4.8-6.3	freshwater Cypriniformes: cyprinid (hybrid of catla x rohu)	fins	India
M. manueli	10-11 x 8-10 x 6.5-7	freshwater Perciformes: centrarchid (black crappie)	bulbus arteriosus	Canada
M. mapei	10.5-16.5 x 6-9	freshwater Cichliformes: cichlid (Nile tilapia)	liver, kidneys	Africa

M. maraensis		freshwater Characiformes: citharinid (moonfish)	gills	Brazil
M. marajoensis	10-11.6 x 4.2-5.4	freshwater Siluriformes: heptapterid (South American catfish)	intestinal wall	Brazil
M. marginatus	8.5-10 x 5-7 x 4	freshwater Cypriniformes: cyprinid (common roach)	skull bones	Russia
M. margitae	13-14 x 9.5-10 x 5.5-6	freshwater Cypriniformes: cyprinid (common bleak)	gills	Hungary
M. markiwi	5.6-7.4 x 4.3-6.3	freshwater Cypriniformes: cyprinid (rohu)	gills	India
M. martini	16.4-19.5 x 10.3-13.5 x 7.3-9.5	freshwater Cypriniformes: cyprinid (golden shiner)	eyes	Canada
M. maruliensis (syn. *Myxosoma*)	12-17.5 x 2.5-5	freshwater Anabantiformes: channid (bullseye snakehead)	kidney	India
M. marumotoi	13.3-15 x 14.2-15 x 10-11.7	freshwater Gobiiformes: odontobutid (dark sleeper)	muscles	Japan
M. mathurii	8.7-23.5 x 5.1-10.1	freshwater Cypriniformes: cyprinid (olive barb)	gills	India
M. matosi	9.1-10.8 x 6.5-7.6 x 4.6-5.5	freshwater Characiformes: serrasalmid (tambaqui)	operculum	Brazil
M. mauriensis	11.1 x 12 x 7.8	freshwater/estuarine Clupeiformes: alosid (blueback herring, alewife)	cartilage, body cavity	North America
M. mbailaoi	11-12 x 7.2-8	freshwater Characiformes: citharinid (moonfish)	operculum, skin, intestines	Tchad
M. medius (syn. *Myxosoma media*)	11-16.8 x 7.7-10.4	freshwater Cypriniformes: cyprinid (common shiner)	body cavity	Canada
M. meerutensis	8.8-9.6 x 6.4-7.2 x 4.9-5.1	freshwater Cypriniformes: cyprinid (rohu)	gills	India
M. megalobramae	8.8-9.3 x 8.4-8.9 x 4.8-5.7	freshwater Cypriniformes: cyprinid (Wuchang bream)	intestines	China
M. meglitschi (syn. *Myxosoma rotundus*)	8.4-14 x 7.8-13 x 3-8.5	freshwater Anabantiformes: channid (northern snakehead); Cypriniformes: catostomid (quillback), cyprinid (common carp, koi carp, grass carp, goldfish, common dace, common bream, white Amur bream, gudgeon, barbel chub, davidi marinka, osman przewalskeho), xenocypridid (silver carp)	skin, gills [cysts]	Europe, North America
M. meglitschus	8-9.5 x 6-7.5	freshwater Osteoglossiformes: notopterid (bronze featherback)	gills	India
M. mehlhorni	8.9 x 6.8	freshwater Cypriniformes: cyprinid (hybrid of catla x mrigal carp)	gills	India
M. meijiangensis	10.4-11.6 x 9.6-11	freshwater Cypriniformes: cyprinid (goldfish)	gills	China
M. melenensis	10.2-12.1 x 10-11	freshwater Cichliformes: cichlid (fivespot cichlid)	gills, palate	Cameroon
M. merlucii sp. inq.		listed in European register of marine species		Europe
M. mesentericus	8.6-11.5 x 6-9.5 x 5.2-6.5	freshwater Anabantiformes: channid (northern snakehead); Cypriniformes: cyprinid (grass carp, stone moroko, Rendahl's labeo), xenocypridid (silver carp); Perciformes: centrarchid (green sunfish)	mesentery, liver, spleen	North America, China
M. mesopotamiae	8.9-9.4 x 7.8-8.5 x 5.2-6	freshwater Cypriniformes: cyprinid (shabout)	fins	Iran
M. metynnis	12.9-13.5 x 7.5-8.3 x 3.4-4.5	freshwater Characiformes: serrasalmid (silver dollar)	orbicular connective tissue	Brazil
M. mexicanus	7.5-12 x 5.5-8.5 x 4-7.5	marine Gadiformes: macrourid (common Atlantic grenadier, shoulderspot grenadier, abyssal	kidney, gall bladder	North America

		grenadier, arrowtooth grenadier)		
M. microcystus (*microcystis*)	11-14 x 7-10 x 5-7	freshwater Perciformes: centrarchid (largemouth bass)	gills	North America
M. microlatus	6-8.4 x 7.4-11.4 x 6-7.2	freshwater Cypriniformes: cyprinid (common carp, Chinese hooksnout carp, goldfish)	gall bladder, kidneys	China
M. micropterii	9.1-12.2 x 9-11.7 x 5.2-8.6	freshwater Perciformes: centrarchid (largemouth bass)	gills	North America
M. microsporus	9.6-12 x 6.2-8.2 x 4.6-5.5	freshwater Cypriniformes: cyprinid (common carp, grass carp, goldfish, tomp koukloug)	gills, spleen, kidneys, urinary bladder	China
M. microthecus (*microthecum*) (syn. *Myxosoma*)	10-12.5 x 8.3-11.4 x 4.3-5.2	freshwater Cypriniformes: catostomid (spotted sucker, redside shiner, longnose dace)	mesentery, peritoneum, gall bladder, kidney	North America
M. mineirus	12.8-14.2 x 10-10.6 x 6-6.9	freshwater Characiformes: bryconid (piracanjuba)	mesentery	Brazil
M. minkiangensis	11.2-12 x 7.6-8 x 5.9-6.2	freshwater Cypriniformes: cyprinid (yunnani silemokk)	kidneys	China
M. minor	9.6-11.4 x 7.2-8.4 x 6	freshwater Cypriniformes: cyprinid (common carp, bighead carp)	gall bladder	China
M. minutus (syn. *M. minutissimus*)	6-13.5 x 4.2-11.7 x 4.6-8.6	freshwater Cypriniformes: cyprinid (mrigal carp, rohu, common dace, common chub, common bleak), xenocypridid (silver carp); Perciformes: percid (European perch)	gills, intestines, gall bladder, kidneys, liver, spleen, ureters, urinary bladder	Eurasia
M. mississippiensis	40.7-61.6 (14.4-19.3) x 3.9-6.2 x 4.7-6.2	freshwater Perciformes: centrarchid (bluegill)	gills	North America
M. miyairii	10.2-15 x 4.8-6.7 x 3.4-5	freshwater Cypriniformes: cyprinid (grass carp, topmouth culter, rainbow gudgeon, bihorned barbel); Siluriformes: bagrid ('analis' catfish), pangasiid (striped catfish), silurid (Amur catfish, Soldatov's catfish, Yangtze catfish)	body surface, gills, intestinal wall, mesentery, kidneys, spleen, swim blader	Amur Basin, Korea, Japan, Vietnam, China
M. miyunensis	10.8-12 x 8.4-9.6 x 6	freshwater Cypriniformes: cyprinid (common carp, mud carp)	kidneys	China
M. mokhayeri	14.4-16.6 x 11.6-13.3 x 8.3-9.1	freshwater Cypriniformes: cyprinid (longspine scraper)	fins	Iran
M. molae	8.5-9.5 x 7-8.5	freshwater Cypriniformes: danionid (mola carplet)	kidney	India
M. molnari	13.3-14.6 x 10.4-11.6 x 6.9-7.8	freshwater Cypriniformes: cyprinid (longspine scraper)	gills	Iran
M. mongolicus	11-12 x 8-11 x 4-6	freshwater Cypriniformes: leuciscid (Altai osman)	brain, gut, kidneys, testes	Russia
M. monopterus (syn. *Myxosoma*)	7.8-9.6 x 7-7.4 x 6	freshwater Synbranchiformes: synbranchid (Asian swamp eel)	intestines	China
M. montanus	11-13.2 x 8.8-10.7 x 6-7.2	freshwater Cypriniformes: cyprinid (false osman)	gills	Asia
M. morostomi		freshwater Cypriniformes: catostomid (shorthead redhorse sucker)	snout	North America
M. morrisonae	9.6-10.5 x 9.1-10.3 x 5	freshwater Cypriniformes: catostomid (smallmouth buffalo)	gills	North America
M. moshanensis	12-13.4 x 11.4-13.4 x 7.9-8.5	freshwater Cypriniformes: cobitid (pond loach)	kidney	China
M. moxostomi	6.2-9.4 x 5.5-9.4 x 3.1-4.7	freshwater Cypriniformes: catostomid (pealip redhorse)	skin	North America
M. moyangensis	8.6-10.8 x 6.7-7.8 x 4.6-4.8	freshwater Cypriniformes: acheilognathid (hiina morukas), cyprinid (silver carp)	intestines	China
M. mrigalae	7.2-8.4 x 7.2-8.4 x 6.2	freshwater Cypriniformes: cyprinid (mrigal carp)	scales	India

M. mrigalhitae	10.8-11.3 x 7.6-8.1	freshwater Cypriniformes: cyprinid (hybrid of rohu x mrigal carp)	gills	India
M. mucosus	12.8-14.2 x 10.3-11.4 x 7.2-8.3	freshwater Cypriniformes: cyprinid (common roach)	gills	Russia
M. muelleri (syn. *M. cycloides p.p., lintoni p.p., uzbekistanicus*) [type species]	8-14.5 x 6-11 x 4.5-6	freshwater/estuarine Cypriniformes: cyprinid (crucian carp, Prussian carp, goldfish, common bream, vimba bream, white bream, blue bream, white-eye bream, common roach, Caspian roach, Kura roach, kutum, Caspian kutum, common dace, Siberian dace, ide, common chub, common rudd, common barbel, Aral barbel, Dnieper barbel, Mediterranean barbel, Turkestan barbel, gudgeon, Chinese false gudgeon, Chinese lizard gudgeon, asp, ziege, common bleak, sunbleak, Danube bleak, spirlin, striped bystranka, common nase, European bitterling, Khanka spiny bitterling), leuciscid (taran, common minnow, lake minnow), nemacheilid (stone loach, grey stone loach, brook loach, plain thicklip loach, spotted thicklip loach), tincid (tench); Gadiformes: lotid (burbot); Gobiiformes: gobiid (gokuraku-haze); Labriformes: labrid (corkwing wrasse); Mugiliformes: mugilid (flathead grey mullet, golden grey mullet, leaping mullet); Perciformes: cottid (European bullhead), percid (European perch, aspro, zander); Salmoniformes: salmonid (grayling, Siberian taimen); Scorpaeniformes: cottid (shorthorn sculpin); Siluriformes: bagrid (yellowhead catfish, shining catfish, ‘vachelli’ catfish, varjokimalaismonni), silurid (wels catfish)	gills, fins, skin, brain, eyes, mesentery, liver, spleen, kidneys, gonads, wall of intestines, gall bladder and urinary bladder [cysts]	Eurasia, North America
M. muellericus	9.5-10 x 8-8.2 x 5-5.2	freshwater Cypriniformes: cyprinid (common chub)	gills	Hungary
M. muelleriformis	7.9-12 x 7.2-10.8	freshwater Gadiformes: lotid (burbot)	gills	Russia
M. mugcephalus (syn. *Myxosoma microspora*)	4.8-5.2 x 4.8-5.2	estuarine Mugiliformes: mugilid (flathead grey mullet)	gills	India
M. mugiliensis	11-11.7 x 9-10.3 x 6-6.7	estuarine Mugiliformes: mugilid (flathead grey mullet)	gills	Portugal
M. mugilii	8.1-16.3 x 4-7.3	estuarine Mugiliformes: mugilid (flathead grey mullet)	gills	India
M. multiplicatus (syn. *Myxosoma, Lentospora*)	12-12.5 x 9.2-9.5 x 6-6.5	freshwater Cypriniformes: catostomid (smallmouth buffalo), cyprinid (common roach, common chub, common dace, ide)	muscles, gills	Russia
M. multivaderis	5-10.3 x 3.3-7.3	freshwater Cypriniformes: cyprinid (catla)	gills, mouth, intestines, brain	India
M. muralidharani	13-14 x 4.9-6	freshwater Cypriniformes: cyprinid (rohu)	gills	India
M. murukamii	10.3-12.1 x 9.2-10.9 x 6.2-8.6	freshwater Salmoniformes: salmonid (masu salmon)	nerve cells	Japan
M. musajevi	11.5-14 x 10-11	freshwater Cypriniformes: cyprinid (Caucasian scraper)	gills, rarely kidneys, gall bladder	Russia

			[cysts]	
M. muscularis	8-10 x 6-8.7 x 4.7-6	estuarine Mugiliformes: mugilid (thinlip mullet)	muscles, heart	Portugal
M. musculi	9-13 x 8-11 x 5.3-6.7	freshwater Cypriniformes: cyprinid (crucian carp, Prussian carp, goldfish, common bream, white bream, vimba bream, blue bream, white-eye bream, common barbel, Bulatmai barbel, Caspian barbel, Dnieper barbel, Romanian barbel, Turkestan barbel, ide, Amur ide, common chub, common rudd, common roach, Black Sea roach, Caspian roach, Kura roach, common dace, Siberian dace, asp, ziege, gudgeon, common bleak, common nase, sattar snowtrout, ya-fish, marinka tsunynska), leuciscid (taran, lake minnow, Manchurian lake minnow, striped bystranka), tincid (tench)	skin, muscles, intestines, kidneys, liver, spleen, gallbladder, heart, swim bladder [cysts]	Eurasia
M. musculosus	13-15 x 10-11.5 x 8-8.5	freshwater Cypriniformes: catostomid (white sucker)	muscle	North America
M. musseliusae	10.5-11.1 x 8.8-10 x 7.2	freshwater Cypriniformes: cyprinid (common carp)	gills	Russia
M. mutabilis (syn. *M. mutabilus*)	9.5-12 x 7.5-9 x 4	freshwater Anabantiformes: channid (blotched snakehead); Cypriniformes: cyprinid (bluntnose minnow)	skin	North America, China
M. myleus	19-20 x 7.5-9 x 3.5-4.5	freshwater Characiformes: serrasalmid (redhook myleus)	gall bladder	Brazil
M. mylopharyngodoni	12-15.6 x 10.8-12 x 8.4-9.8	freshwater Cypriniformes: cyprinid (black carp)	gills, kidneys	China
M. mystusius	12.2-14 x 8.7-10.5	freshwater Siluriformes: bagrid (striped dwarf catfish)	scales	India
M. naffari	10.8-13.2 x 7.8-9.8	freshwater Cypriniformes: cyprinid (Nile carp)	gills	Egypt
M. nagaraensis	10.5-13.5 x 8-10 x 6-7	freshwater Gobiiformes: gobiid (unspecified orange-type goby)	body cavity	Japan
M. naini	13.6-16.6 x 7.9-10.5	freshwater Cypriniformes: cyprinid (bata, rohu)	gills	India
M. nainit	12.9 x 8.2	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. najdenovae		marine Gobiiformes: gobiid (unspecified gobies)		Black Sea
M. nanhaiensis (syn. *Myxosoma*)	12-13.8 x 8-8.6 x 5.4-7	freshwater Cypriniformes: cyprinid (thin-banded barb)	kidney	China
M. nankuensis	9-10.8 x 7.2-8.4 x 6	freshwater Cypriniformes: cyprinid (pale chub)	gills	China
M. nanokiensis	9.2 x 5.7	freshwater Cypriniformes: cyprinid (rohu)	gills	India
M. nanyangensis (syn. *M. carassii p.p., Myxosoma*)	12.5-17.5 x 8.7-12.5 x 7.5-8.7	freshwater Cypriniformes: cyprinid (goldfish)	gills	China
M. nanyuensis	18-19.2 x 8.4-9.6 x 7.2-8.4	freshwater Cypriniformes: cyprinid (goldfish)	gills	China
M. narasii (syn. *Myxosoma intestinalis*)	12.5-13.5 x 8.6-9.5	estuarine Mugiliformes: mugilid (squaretail mullet)	intestines	India
M. narzikulovi	10.8-13.2 x 6.8-7.6 x 4-5.8	freshwater Cypriniformes: nemacheilid (Tibetan stone loach), xenocypridid (silver carp)	kidneys	China
M. naylori	10-12 x 7-9 x 5-6	freshwater Cypriniformes: catostomid (sicklefin redhorse)	stratum spongiosum	North America

M. nayuensis		listed in Fauna Sinica book		China
M. nchoutnounensis	11-13 x 8.5-10	freshwater Cypriniformes: cyprinid (African carp)	gills, scales, fins, eyes, liver, spleen, kidney	Cameroon
M. ndjamenaensis	13-14 x 10-11	freshwater Characiformes: citharinid (moonfish)	kidneys	Tchad
M. negmgoda (syn. *M. synodontis*)	10.5 x 6.2	freshwater Siluriformes: mochokid (wahrindi)	gills	Egypt
M. nemacheili (*nemachili*)	9-12 x 8-9 x 4.2-6	freshwater Cypriniformes: cyprinid (common carp, rock carp, goldfish, Chinese lake gudgeon, Chinese mahseer, spotted steed), nemacheilid (stone loach, Kura loach)	head connective tissue, gills, urinary bladder [cysts]	Eurasia
M. nemachilusi (syn. *Myxosoma*)		listed in Animal Taxonomy Journal		China
M. nemeczeki (syn. *Myxosoma lobatum*)	11-12.5 x 6.5-8 x 4.3-5.3	freshwater Cypriniformes: cyprinid (common dace, ide, asp, common bleak)	gills	Eurasia
M. nephroides	9-10.8 x 8.4-10.8 x 5.4-7	freshwater Cypriniformes: cyprinid (bighead carp, grass carp), gobionid (Chinese neon golden stripe shark), xenocypridid (silver carp)	gall bladder, spleen, kidneys, intestines	China
M. neurobius	10-14 x 7.5-9.2 x 5-6.5	freshwater Salmoniformes: salmonid (Atlantic salmon, sockeye salmon, coho salmon, brown trout, grayling, Arctic grayling, Arctic char, whitespotted char)	brain, spinal cord [cysts]	Eurasia
M. neurofontinalis	12-16.9 x 8-12 x 7-10	freshwater Salmoniformes: salmonid (brook trout)	brain	North America
M. neurophilus (syn. *Myxosoma*)	12-16 x 6-8.5 x 4-6	freshwater Perciformes: percid (yellow perch, Johnny darter)	brain	North America
M. ngassami	10.7-12.8 x 8.3-10.5	freshwater Cypriniformes: cyprinid (clipper barb)	skin, fins, eye	Africa
M. niei	9.5-10.8 x 8.2-9.8 x 5.2-6.8	freshwater Cypriniformes: cyprinid (silver carp), Gobiiformes: odontobutid (Chinese sleeper)	skin	Korea
M. nielii	8-12 x 8.4-9.6 x 6	freshwater Cypriniformes: cyprinid (common carp)	viscera	China
M. niger	11.3 x 6.8 x 4.1	freshwater Siluriformes: callichthyid (false bandit catfish)	gills	Brazil
M. nigerae	6.3-6.9 x 4.8-5.2	freshwater Cypriniformes: cyprinid (Alghad snowtrout)	gills	India
M. nile (syn. *M. mugilis*) [incl. *M. mugauratus* Pogoreltseva and *M. mugchelo* Parenzan]	7.4 x 7.3	estuarine Mugiliformes: mugilid (flathead grey mullet, golden grey mullet, thicklip grey mullet)	gills	Egypt, Europe
M. nijnei	14-20 x 11.6-18	freshwater Cypriniformes: cyprinid (African redfinned barb)	gills	Cameroon
M. nilimae	15.9-17 x 6.2-7	freshwater Cypriniformes: cyprinid (rohu)	gills	India
M. niloticus	10.2-25.1 x 6.3-7.8	freshwater Cypriniformes: cyprinid Nile carp)	fins	Egypt
M. ningnanensis	12.8-13.2 x 5.6-6.4 x 4.8-5.2	freshwater Cypriniformes: cyprinid (labeo secuanske)	gills	China
M. ningpoensis	9-10.5 x 10-12 x 5.6-6	freshwater Anguilliformes: anguillid (Japanese eel); Cypriniformes: cyprinid (sharpbelly)	gills	China
M. njoyai	9-10.5 x 7.8-9	freshwater Cypriniformes: cyprinid (African carp)	gills, scales, fins, spleen, kidney	Cameroon
M. nkolyaensis	8-11 x 7.2-11.5	freshwater Cypriniformes: cyprinid (Jae barb)	muscles	Africa

M. nkondjockei	10-10.9 x 7.3-8.5	freshwater Cypriniformes: cyprinid (batesi narmasmokk)	scales	Cameroon
M. nobillis	12-14 x 10.2-12 x 6.6-6.8	freshwater Cypriniformes: cyprinid (bighead carp), xenocypridid (silver carp)	gills, urinary bladder	China
M. noblei (syn. *Myxosoma*)	11.5-14.3 x 8.3-10.5	freshwater Anabantiformes: channid (striped snakehead)	gall bladder	India
M. nodosus	9-10.5 x 8.5-9.5 x 7	freshwater Cypriniformes: cyprinid (bluntnose minnow)	skin	North America
M. nodularis	9 x 7.2	freshwater Cypriniformes: cyprinid (slender rasbora)	muscles	India
M. nodulointestinalis	11.7-13 x 7.8-9.1 x 5.2-7.2	freshwater Cypriniformes: cyprinid (binni, Mesopotamian himri)	intestinal wall	Iran
M. noemacheilusi (syn. *Myxosoma*)	10.4-11.2 x 7.2-9.6 x 6.2	freshwater Cypriniformes: nemacheilid (barred loach)	gall bladder	China
M. noguchii	13.6 x 8.5	freshwater Characiformes: serrasalmid (speckled piranha)	gills	Brazil
M. nokouensis	8.1-11.5 x 5-7	freshwater Cichliformes: cichlid (blackchin tilapia); Cypriniformes: cyprinid (African carp)	gills	Benin, Tchad
M. notatus		freshwater Cypriniformes: cyprinid (bluntnose minnow)	muscles	Canada
M. notemigoni	11.8 x 8.9 x 7.5	freshwater Cypriniformes: cyprinid (golden shiner)	skin	North America
M. notropis (syn. *Myxosoma*)	11.8-16.6 x 6.4-11 x 6.4	freshwater Cypriniformes: cobitid (pond loach), cyprinid (Japanese white crucian carp, goldfish, common shiner, redfin shiner, blacknose shiner, golden shiner, rainbow gudgeon)	skin, intestines, liver, kidney, heart	Canada, China
M. nounensis	13-15 x 11.5-14	freshwater Cichliformes: cichlid (mango tilapia)	spleen, kidneys	Cameroon
M. nuevoleonensis	10.7-13.7 x 6.1-7.6 x 6.1	freshwater Cyprinodontiformes: poeciliid (shortfin molly, guppy)	fins	Mexico
M. nukiangensis (syn. *M. nujiangensis*)	7.2-8 x 6.4-6.8 x 4.8	freshwater Cypriniformes: cyprinid (bihorned barbel)	gills	China
M. obesus	11-12 x 7.5-8	freshwater Cypriniformes: cyprinid (common bleak)	gills, kidney	Europe
M. obliquoides	10-12 x 15.6-18.8 x 8.5	freshwater Cypriniformes: cyprinid (black carp)	gills, spleen, kidneys	China
M. oblongus	12.3-17 x 8.5-9.2 x 5-6.8	freshwater Anabantiformes: channid (northern snakehead, giant snakehead); Cypriniformes: catostomid (lake chubsucker), cyprinid (davidi marinka)	head, skin	China, Vietnam, North America
M. obpyriformis (syn. *M. disperans*)	10.6-15 x 7.2-12 x 3.6-6	freshwater Cypriniformes: cyprinid (grass carp, sattar snowtrout); Gobiiformes: odontobutid (dark sleeper)	gills, muscles, kidneys	Russia, China
M. occularis	9.6 x 8.5	freshwater Cichliformes: cichlid (unspecified tilapia)	eye	Egypt
M. ochengensis	13.2-15.6 x 9-10.2 x 7.2	freshwater Cypriniformes: cyprinid (goldfish)	kidneys	China
M. ochowensis	12-13.2 x 8.4-10.2 x 6.6-7.2	freshwater Siluriformes: bagrid (yellowhead catfish)	fins	China
M. ochridensis	17-18 x 6.5-7	freshwater (unspecified lacustrine fishes)	gills	Macedonia
M. odontobutisus	8.4-9.6 x 8.5-9.8 x 6.6-7.2	freshwater Gobiiformes: odontobutid (dark sleeper)	intestines	China
M. ogilbyi (syn. *Myxosoma*)	11-13 x 6-8 x 5	freshwater Perciformes: percichthyid (golden perch)	gills	England, Australia
M. okomurae	12.2 x 4.9	freshwater Cypriniformes: cyprinid	gills	India

		(bata)		
M. olidus	9-10 x 7-8 x 4-5.5	freshwater Galaxiiformes: galaxiid (mountain galaxias)	spinal cord	Australia
M. oliveirai	11.2 x 7.4 x 4.6	freshwater Characiformes: bryconid (piraputanga)	gills	Brazil
M. oloi	6.3-11.5 x 5.1-9.4	freshwater Cypriniformes: cyprinid (kameruni pardkala)	gills, gullet	Cameroon
M. omari	7.2-8.8 x 11-13.9 x 5.2-6.6	freshwater Siluriformes: pangasiid (sutchi catfish, striped catfish)	muscles	Malaysia
M. omeiensis	11-12.8 x 9.6-10.4 x 4.8-5.6	freshwater Cypriniformes: cyprinid (Chinese lizard gudgeon)	kidneys	China
M. ompok	13.6-14.5 x 5.6-6.4 x 5.2-6.4	freshwater Siluriformes: silurid (Pabda catfish)	kidneys	India
M. ophiocarae	9.3-11.4 x 8-9.5 x 4.1-5.2	freshwater Gobiiformes: butid (northern mud gudgeon)	gills	Malaysia
M. ophicephali	11.6-13.3 x 4.6-6.3	freshwater Anabantiformes: channid (spotted snakehead)	accessory respiratory membrane	India
M. ophiocephaili	11.4-13.6 x 6-6.8 x 4.4-4.8	freshwater Anabantiformes: channid (snakehead murrel)	skin, fins, gall bladder	China
M. ophiocephali (syn. *Myxosoma*)	11.4-14.4 x 6-7.8 x 4.4-5.4	freshwater Anabantiformes: channid (northern snakehead, blotched snakehead, snakehead murrel); Cypriniformes: cyprinid (ristvoot-silemokk); Siluriformes: bagrid (varjokimalaismonni)	gills, skin, fins, gall bladder	China
M. ophthalmusculata	6-12 x 6-9	freshwater Cypriniformes: cyprinid (slender rasbora) [also hyperparasitic as spores recorded in metacercariae of the digenean fluke *Diplostomum minutum*]	fins, intestines, gall bladder, muscles, pancreas	India
M. opienensis	11.2-12 x 8.6-9 x 5.5-5.8	freshwater Cypriniformes: cyprinid (rainbow gudgeon)	gills	China
M. opsariichthysi (*opsariichthyi*)	9.4-12 x 6-9.6 x 6-6.2	freshwater Cypriniformes: acheilognathid (hiina morukas, rosy bitterling), cyprinid (Chinese hooksnout carp, Chinese false gudgeon, pale chub, smallscale yellowfin, stone moroko), xenocypridid (three-lips, mohknina-poiksuu, sharpbelly)	gills, kidneys, liver, intestines, spleen, urinary bladder	China
M. opsaridiumi	10-11.5 x 8-10 x 5.6-7.2	freshwater Cypriniformes: danionid (oubangui norjasdaanio)	skin, muscles, spleen	Cameroon
M. opthalmusculata	12.4-14 x 7.4-9.2	freshwater Cypriniformes: cyprinid (mrigal carp)	eye muscles	India
M. oralis	1.8-12.8 x 8.2-9.9 x 6-7.5	freshwater Cypriniformes: cyprinid (Prussian carp)	palate	China
M. orbiculatus	9-1- x 9-10 x 6.5-7	freshwater Cypriniformes: cyprinid (bigmouth shiner)	muscles	North America
M. orbitalis (syn. *Myxosoma*)	13.3-17.5 x 8-12	freshwater Cypriniformes: cyprinid (common shiner)	eyes	Canada
M. oreochrome		freshwater/estuarine Cichliformes: cichlid (redbelly tilapia)	opercula	Egypt
M. orientalis	18-19.8 x 8.4-11 x 8-9	freshwater Cypriniformes: cyprinid (goldfish, Prussian carp)	gills	China, Korea
M. orissae	macrospore: 11.4-19.5 x 3.2-8.1 microspore: 6-9 x 2.5-4.5	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. ornatus (syn. *Myxosoma*)	9.8-12 x 9-10.8 x 7-7.2	freshwater Cypriniformes: cyprinid (common carp, Russian bitterling)	muscles	China

M. orthotaenae	10-11.4 x 7.3-8.6 x 5.3-7	freshwater Characiformes: bryconid (piracanjuba)	liver	Brazil
M. osburni	9.6-11.2 x 9.6-12.8 x 6.4-8	freshwater Perciformes: centrarchid (bluegill, pumpkinseed, smallmouth bass, black crappie)	mesenteries, peritoneum, pancreas	North America
M. osmaniae (syn. *Rudicapsula*)	12.4-15 x 7.1-10	freshwater Cypriniformes: cyprinid (Punjabi puntius)	intestines, liver	India
M. osteochili	12-14 x 8-9 x 4.5-5.5	freshwater Cypriniformes: cyprinid (bonylip barb)	kidney	Malaysia
M. osteochilus (syn. *Myxosoma*)	10.2-12 x 7.2-8.4 x 5.1	freshwater Cypriniformes: cyprinid (Salsbury luumokk)	kidneys	China
M. osteochilusis	10.8-12 x 7.2-7.6 x 5.2-5.6	freshwater Cypriniformes: cyprinid (Salsbury luumokk)	gills	China
M. ovalis (syn. *Lentospora, Myxosoma*)	15-17 x 15 x 11	freshwater Cypriniformes: catostomid (smallmouth buffalo, bigmouth buffalo, highfin carpsucker), cyprinid (golden shiner)	gills	North America
M. ovarium	9.2-11 x 5.6-6.9 x 4.6-5	freshwater Characiformes: bryconid (piracanjuba)	ovary	Brazil
M. oviformis	10-13 x 8-11 x 6-7	freshwater Cypriniformes: cobitid (suurelaiguline hink), cyprinid (common carp, koi carp, crucian carp, goldfish, common bream, vimba bream, white bream, blue bream, common roach, common dace, Siberian dace, ide, asp, common chub, common rudd, common barbel, common bleak, gudgeon, European bitterling, sattar snowtrout, taieani pardpuntius), leuciscid (taran), tincid (tench); Siluriformes: bagrid (yellowhead catfish)	gills, fins, subcutis, kidneys, liver, muscles, mesentery, gonads, rarely spleen, gall bladder [cysts]	Eurasia
M. ovoidalis	18-26 x 8-15	freshwater Cypriniformes: cyprinid (common carp, unspecified barb); Salmoniformes: salmonid (brook trout)	fins	Canada
M. oxycephali	8.9-9.8 x 7-7.7 x 5.5.5	freshwater Cypriniformes: leuciscid (Amur minnow)		Russia
M. paksensis	14.4-15.2 x 10.4-12 x 8.4-9.2	freshwater Cypriniformes: cyprinid (common nase)	swim bladder wall	Hungary
M. paludinosus	11.2-13.7 x 7.5-10	freshwater Cypriniformes: cyprinid (straightfin barb)	gills	Botswana
M. pangasii	13.5-15 x 6-7.8 x 4-5	freshwater Siluriformes: pangasiid (striped catfish)	spleen	Malaysia
M. pantanalis	9.3 x 6.5	freshwater Characiformes: characid (dourado)	gills	Brazil
M. parabotia (syn. *M. obliquus, Myxosoma*)	7.8-11.2 x 7-9.6 x 5-7.2	freshwater Cypriniformes: botiid (voodiline salebootsia), catostomid (highfin carpsucker), cyprinid (common carp, koi carp, goldfish, Chinese false gudgeon, Chinese lake gudgeon); Gobiiformes: odontobutid (dark sleeper)	muscles, kidney, nasal cavity	North America, China
M. paracuta	12.1-13.6 x 9.1-10.6 x 5.5-6	freshwater Cypriniformes: cyprinid (black carp)	gills	China
M. paradiscogobie	8.8-9.6 x 7.208 x 5.6	freshwater Cypriniformes: cyprinid (yunnani napprunt)	mesentery, kidney, urinary bladder	China
M. paradispar	9.6-12 x 8.6-9.6 x 6.1-6.3	freshwater Cypriniformes: cyprinid (bighead carp)	gall bladder	China
M. paradisparoides	15.2-16.8 x 8.8-10.4 x 8	freshwater Cypriniformes: cyprinid (davidi marinka)	gills, skin, fins	China
M. parallipsoides	14-16 x 8.8-10.7 x	freshwater Cypriniformes: cyprinid		China

	6.9-7.8	(common carp)		
M. parakoi	14.5-17.2 x 6.6-9.7	freshwater Cypriniformes: cyprinid (common carp)	gills	China
M. paralintoni	9.5-11.5 x 9-11.5 x 6.5-7.5	freshwater Perciformes: centrarchid (pumpkinseed)	heart	Canada
M. parallelipticoides (syn. *Myxosoma*)	11.4-16.4 x 7.3-10	freshwater Cypriniformes: cyprinid (finescale dace)	body cavity	Canada
M. paramisgurni (syn. *Myxosoma*)	11.2-12.1 x 10.7-11.9 x 6.9-7.4	freshwater Cypriniformes: cobitid (largescale loach)	kidneys	China
M. paranensis	12-15 x 7-8	freshwater Characiformes: characid (river tiger)	kidneys	China
M. paratoyamai	12.5-16.4 x 5.5-7 x 5-6.4	freshwater Cypriniformes: cyprinid (common carp)	gills	Japan, China
M. paratypicus	12.9-14.9 x 9.2-11.1 x 7	freshwater Cypriniformes: cyprinid (silver carp)	gills	China
M. parellipticoides (syn. *Myxosoma*)	11.4-16.4 x 7.3-10	freshwater Cypriniformes: cyprinid (finescale dace)	body cavity [cysts]	Canada
M. parenzani (syn. *M. branchialis p.p.* [Paraezan]*)*	5-6 x 5-6	estuarine Mugiliformes: mugilid (thicklip grey mullet)	gills	Italy, India
M. parodontidis	10.6-12 x 8.7-10.6	freshwater Characiformes: parodontid (canivete)	gills	Brazil
M. parsi	9-9.5 x 8-8.5	estuarine Mugiliformes: mugilid (gold-spot mullet)	gills	India
M. parviformis		freshwater Cypriniformes: cyprinid (common bream) [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid (*Limnodrilus hoffmeisteri*)		
M. parvus	5-7 x 5.4-6.6 x 3.6-4.2	estuarine Cypriniformes: cyprinid (bighead carp, pisisuu-koukloug), xenocypridid (silver carp); Mugiliformes: mugilid (flathead grey mullet, so-iju mullet, so-ing mullet); Siluriformes: silurid (Amur catfish)	gills, intestines, kidney, spleen, urinary bladder	Korea, China, India
M. patialensis	11.2 x 6.6	freshwater Cypriniformes: cyprinid (rohu)	fins	India
M. pavlovskii (syn. *Disparospora*)	7-10.7 x 9.1-10 x 5-8.8	freshwater Cypriniformes: cyprinid (silver carp, largescale silver carp, bighead carp) [cycle involves hexactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)	gills, body [cysts]	Eurasia
M. peachiformis	15.6-16.3 x 11.4-13 x 8.1-8.4	freshwater Cypriniformes: cyprinid (pale chub)	gills, fins	China
M. peculiaris	23-23.2 x 14.4-15.2	freshwater Characiformes: curimatid (saguiru)	gills	Brazil
M. pekingensis	13.2-15.6 x 8.4-13.2 x 7.2-8.4	freshwater Cypriniformes: cyprinid (koi carp, goldfish)	intestines, liver, kidneys, urinary bladder	China
M. peleci	11.6-13.2 x 10.8-12.5 x 5.6-6	freshwater Cypriniformes: cyprinid (ziege)	gills	Hungary
M. pellicides (*pellucides*)	14.5-16.5 x 8-11.5 x 7.5-8	freshwater Cypriniformes: cyprinid (creek chub)	gills	Canada
M. pelteobagrus (syn. *Myxosoma*)	10.4-12 x 7.2-8 x 4-4.8	freshwater Siluriformes: bagrid (yellowhead catfish, shining catfish)	kidneys	China
M. pendula (syn. *M. pellicides p.p., Myxosoma*)	13.2-16.5 x 8.8-12.1 x 6.6-8.8	freshwater Cypriniformes: cyprinid (creek chub)	gills	North America
M. percae	7.3-10.4 x 8.8-12.1 x 6.6-8.8	freshwater Cypriniformes: cyprinid (creek chub); Perciformes: percid (yellow perch)	gills	Canada

M. percarinae	10.8-13 x 7.2-9.6	freshwater Perciformes: percid (percarina)	gills, kidneys	Ukraine
M. percocypris	9.6-10.4 x 8-8.8 x 5.5-5.8	freshwater Cypriniformes: cyprinid (pingi ahvenkarbik)	gills	China
M. percnuri (syn. *Myxosoma*)	12.3-13.1 x 11.8-12.5	freshwater Cypriniformes: leuciscid (Manchurian Lake minnow)		Russia
M. perforata	9.9-11.3 x 4.5-5.9	freshwater Characiformes: alestid (elongate tigerfish)	opercula, swim bladder	Egypt
M. peritonaei	8-9.6 x 6.9-8.4 x 5-7.1	estuarine Mugiliformes: mugilid (thicklip grey mullet)	peritoneum [cysts]	Portugal
M. peritonaeum	7.7-8.7 x 6.7-7.3	estuarine Mugiliformes: mugilid (thicklip grey mullet)	peritoneum	Portugal
M. perlatus		freshwater Perciformes: percid (ruffe)		Europe
M. permagnus	17-20 x 9.2-12 x 8.4	freshwater Cypriniformes: cyprinid (common rudd, Amur ide, barbel chub, goldfish), leuciscid (Manchurian Lake minnow); Perciformes: percid (yellow perch); Siluriformes: bagrid (yellowhead catfish)	gills, swim bladder wall, rarely kidneys, spleen	Eurasia
M. persicus	9.1-10.4 x 6.5-7.8 x 5.2-6.5	freshwater Cypriniformes: cyprinid (shabout, Mesopotamian himri)	gills	Iran
M. petalum	11-13 x 5-7	freshwater Cypriniformes: cyprinid (rohu)	gills	India
M. petenensis	10.1-13.1 x 12-15.8 x 0.7-0.9	marine/estuarine Clupeiformes: dorosomatid (threadfin shad)	orbicular cartilage	North America
M. pethericii	12-14 x 6.5-7.8	freshwater Anabantiformes: anabantid (aklofui)	gills, fins, gut wall, liver, kidney	Cameroon
M. petruschewskii	11-12 x 7-8.2	marine Scorpaeniformes: cottid (Arctic sculpin)	gills [cysts]	Bering Sea
M. pfeifferi	10-14.4 x 8-12 x 6.6-7.4	freshwater Anabantiformes: channid (northern snakehead); Cypriniformes: cyprinid (common carp, common barbel, Bulatmai barbel, Italian barbel, Turkestan barbel, dnepri pardkala, barbel chub, common chub, common dace, common roach); Gobiiformes: oxudercid (unspecified rhinogoby)	skin, gills, muscles, intestinal wall, kidneys, spleen, ovary [cysts, barbel boil disease]	Europe, North America
M. pfrille (syn. *Myxosoma*)	12-19.1 x 7.7-11.4 x 7	freshwater Cypriniformes: cyprinid (common carp, goldfish, finescale dace, unspecified bitterling); Siluriformes: bagrid (yellowhead catfish)	gills, body cavity	Canada, China
M. pharyngeus (syn. *Myxosoma*)	15-17 x 5-6.5 x 4.2-5.5	freshwater Cyprinodontiformes: poeciliid (western mosquitofish)	pharynx, skin	North America
M. pharyngobranchialis	8.7-10 x 7-8 x 4.7-6	estuarine Mugiliformes: mugilid (thinlip mullet)	Portugal	
M. phoxinaceus (syn. *Myxosoma*)	16-17 x 10-11	freshwater Cypriniformes: leuciscid (lake minnow, Czekanowski's minnow)	gills	Russia
M. phylloides	9-10 x 7-7.5 x 5-5.5	freshwater Cypriniformes: cyprinid (bighead carp, hiina astelparrak), xenocypridid (silver carp)	mesentery, kidneys	Amur Basin
M. pinna	14.8-17.1 x 8.6-10 x 7.1-7.6	freshwater Cypriniformes: cyprinid (grass carp)	fins	China
M. pinnaurati	8-11.4 x 6.5-7.9	freshwater Cypriniformes: cyprinid ('*pinnauratis'* barb)	gills	India
M. pinnula	7.3-8.8 x 6.8-8.6 x 4.7-5.9	estuarine Mugiliformes: mugilid (thicklip grey mullet)	fins [cysts]	Portugal
M. piraputingae	10-13.8 x 4-8.7 x 3.5-6.7	freshwater Characiformes: bryconid (piraputanga), serrasalmid	pyloric caecum, kidney	Brazil

		(pirapitinga)		
M. planilizae	7.4-8.8 x 6-6.9	estuarine Mugiliformes: mugilid (largescale mullet)	intestinal muscles	India
M. platanus	10-11 x 10-11 x 5	estuarine Mugiliformes: mugilid (lebranche mullet)	spleen	Brazil
M. platessae (syn. *Sphaerospora*)	9.8-11.2 x 9.6-10.7 x 6.8-8	marine Pleuronectiformes: pleuronectid (European plaice, common dab)	cartilage	England
M. platyrostris	12 x 8	freshwater Cypriniformes: cyprinid (crucian carp, Prussian carp)		Amur Basin
M. plectroplites	10-12 x 7-8	freshwater Perciformes: percichthyid (golden perch)	kidneys, gall bladder	Australia
M. pleuronectidae	14.8 x 11.9	marine Pleuronectiformes: pleuronectid (winter flounder)	skin	North America
M. poecilichthidis	12.3-15.4 x 4.5-6.8	freshwater Perciformes: percid (Iowa darter)	adipose tissue	Canada
M. polati	9.5-10.5 x 7.8-8.7 x 6-6.2	freshwater Cypriniformes: cyprinid (Ankara nase)	gills	Turkey
M. poljanskii	12-16.3 x 8.4-10.2 x 5.6-6.3	freshwater Cypriniformes: cyprinid (Chinese false gudgeon): Siluriformes: silurid (butter catfish)	gills	Korea, China, Vietnam
M. polycentropsis	11.8-14.4 x 5.6-10	freshwater Ovalentaria: polycentrid (African leaffish)	gill cartilage	Cameroon
M. polymorphosporus	13.9-20 x 10.4-14,2 x 10-12.2	freshwater Anabantiformes: channid (northern snakehead, blotched snakehead)	intestines	China
M. polymorphum	8.8-10.4 x 7.2-8 x 4.8-5.6	freshwater Cypriniformes: cyprinid (ya-fish)	gills	China
M. porofilus	5.7 x 4.8	freshwater Characiformes: prochilodontid (streaked prochilod)	body cavity	Brazil
M. portucalensis	11.2-15 x 7.5-10 x 5.6-7.5	freshwater Anguilliformes: anguillid (European eel) [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)]	fins	Portugal
M. potaili	6.3-7.9 x 4.3-6.4	freshwater Cypriniformes: cyprinid (potail-narmasmokk)	intestines, liver	India
M. potularis	8.3-9.3 x 5.4-6.3	freshwater Cypriniformes: cyprinid (orangefin labeo, Kuria labeo, bata, reba carp)	gills	India
M. pratti (syn. *Facieplatycauda*)	17-20.5 x 11-14 x 7.5-8.5	freshwater Cypriniformes: catostomid (Lost River sucker)	kidney	North America
M. problematicus	9.5-11.5 x 5.5-6 x 2.4-4.5	freshwater Cypriniformes: acheilognathid (harilik paljasloug), cyprinid (Khanka spiny bitterling)	liver, gall bladder wall	Korea
M. procerus (syn. *Myxosoma*)	15-17 x 6.5-7 x 5-6	freshwater Cypriniformes: cyprinid (fathead minnow), Percopsiformes: percopsid (trout-perch); Scorpaeniformes: gasterosteid (brook stickleback)	skin, fins	North America
M. prochilodus (syn. *M. lomi*)	9-15.8 x 7-12.5 x 5.4-7.9	freshwater Characiformes: prochilodontid (streaked prochilod); Cypriniformes: cyprinid (common carp, grass carp, black carp, common chub, barbel chub, common minnow, tomp koukloug)	gills	Eurasia, South America
M. procypris	12-12.8 x 8.8-9.6 x 7.5-8	freshwater Cypriniformes: cyprinid (rock carp)	kidney	China
M. pronini	14.3-16.2 x 9.6-10.8 x 6.4-7.4	freshwater Cypriniformes: cyprinid (Prussian carp)	abdominal cavity [cysts]	Russia
M. psephurusi	14.4-19.2 x 9.6-12.4 x 8.4-9	freshwater Acipenseriformes: polyodontid (Chinese paddlefish)	kidneys	China

M. pseudoanurus (syn. *Myxosoma*)	15.5-19.5 x 7.5-10.5	freshwater Esociformes: esocid (northern pike)	gills	Russia
M. pseudobagrus	17-18.7 x 10.2-11.9 x 8.3-8.5	freshwater Siluriformes: bagrid (Pratt's catfish)	mouth	China
M. pseudobpyriformis	12-12.8 x 8-9.6 x 8	freshwater Cypriniformes: cyprinid (ya-fish)	kidneys	China
M. pseudodispar (syn. *Disparospora*)	10-12 x 7-9.5 x 5.3-6	freshwater Cypriniformes: cyprinid cyprinid (common carp, crucian carp, white bream, vimba bream, common roach, Caspian roach, Kura roach, common dace, ide, asp, common chub, common rudd, common bleak, Danube bleak, gudgeon), leuciscid (taran); Perciformes: percid (yellow perch) [cycle involves triactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex, Limnodrilus hoffmeisteri*)]	muscles, kidneys, gills, rarely mesentery, gut wall, gall bladder, liver, pancreas [cysts]	Eurasia
M. pseudogobii	13.5-15 x 8.5-9 x 6	freshwater Cypriniformes: cyprinid (Chinese false gudgeon)	muscles, kidneys	Amur Basin
M. pseudokoi	11.5-14 x 6-7 x 5	freshwater Cypriniformes: cyprinid (common shiner)	gills, skin	Canada
M. pseudomicrosporus	12-13 x 6.4-7 x 6-6.1	freshwater Cypriniformes: cyprinid (yunnani silemokk)	gall bladder	China
M. pseudonobilis	9.3-10.9 x 7.9-9	freshwater Cypriniformes: cyprinid (silver carp)	gills	China
M. pseudoparvus	7.6-9.6 x 7.2-9 x 6-6.6	freshwater Cypriniformes: acheilognathid (hiina morukas), cyprinid (common carp, bighead carp, grass carp, rock carp, Prussian carp, Chinese hooksnout carp, goldfish, sharpbelly, pisisuu-koukloug, davidi marinka), xenocypridid (silver carp, hiina laikviidkas)	gills, skin, intestines, liver, gall bladder, spleen ureters, urinary bladder	China
M. pseudorasborae (syn. *M. cycloides p.p., Myxosoma*)	10.8-17 x 7-12.6 x 4.8-8	freshwater Cypriniformes: acheilognathid (harilik paljasloug), cyprinid (gudgeon, Chinese false gudgeon, stone moroko, European bitterling); Gobiiformes: odontobutid (freshwater sleeper); Siluriformes: bagrid (yellowhead catfish, darkbarbel catfish, shining catfish, Pratt's catfish, Ussuri catfish, vatjokimalaismonni), silurid (Amur catfish)	muscles, fins, kidneys, gall bladder, swim bladder	Amur Basin, Japan, China
M. pseudosquamae	11.2-12 x 8-8.8 x 6-6.4	freshwater Cypriniformes: cyprinid (Chinese false gudgeon)	gills	China
M. pseudosquarae	9.6-12 x 9.6-10.2 x 5.4	freshwater Cypriniformes: cyprinid (common carp, goldfish)	gills, fins	China
M. pseudowulii	12.9-16.2 x 8.1-10.8 x 6.1-8.1	freshwater Siluriformes: bagrid (yellowhead catfish)	skin	China
M. psilorhynchi	9.3-10.7 x 8.6-10	freshwater Cypriniformes: psilorhynchid (Balitora minnow)	gills	India
M. punctatus	12.3-15 x 5.7-7.9	freshwater Anabantiformes: channid (spotted snakehead)	pharynx	India
M. punjabensis	10-12 x 10-11	freshwater Cypriniformes: cyprinid (boalla)	gills, fins	India
M. punjabii	8.9 x 6.9	freshwater Cypriniformes: cyprinid (rohu)	fins	India
M. puntuisii	7.5-7.9 x 5.2-5.4	freshwater Cypriniformes: cyprinid (pool barb)	fins	India
M. pupkoi	7.9-9.7 x 7-8.7 x 4.5-5.5	estuarine Mugiliformes: mugilid (thicklip grey mullet)	gills [cysts]	Portugal

M. purkynjei	10.2-11 x 7.8-9.4 x 6.5-7	freshwater Perciformes: kyphosid (parore)	gills	Australia
M. pygocentrus	15-16 x 9-11	freshwater Characiformes: serrasalmid (piraya piranha)	intestines	Brazil
M. pyramidis	9.6-11 x 8.4-10.8 x 6	freshwater Cypriniformes: cyprinid (goldfish)	gills	China
M. qiankiangensis (syn. *M. chungnanensis, Myxosoma*)	8.4-18 x 8-12 x 6-8.4	freshwater Cypriniformes: cyprinid (grass carp, goldfish)	spleen, abdominal cavity, kidney, gills	China
M. qiaojiensis	8-9.6 x 6.3-7.2 x 6.7	freshwater Cypriniformes: cyprinid (gara junanska)	urinary bladder	China
M. qingyiensis (syn. *M. yaanensis, Myxosoma*)	10-12.8 x 7.2-8.8 x 4.8-6.4	freshwater Cypriniformes: gobionid (davidi marinka, munt-kirevrunt)	gills	China
M. qionghaiensis (syn. *M. rasborae, Myxosoma*)	7.2-11 x 8.2-9.6 x 5-6	freshwater Cypriniformes: danionid (pisterasbora)	gills, intestines	China
M. rachmani	13.5-14.3 x 11.2-12	freshwater Cypriniformes: leuciscid (striped bystranka)	kidneys	Asia
M. raibauti	14-16 x 12-13	estuarine Mugiliformes: mugilid (flathead grey mullet)	liver	Senegal
M. ramadus	7.3-9.3 x 7.3-8.3 x 6-6.7	estuarine Mugiliformes: mugilid (thinlip mullet)	gills	Portugal
M. ranae	11-12 x 8-10	Anura: ranid (common frog)	skin	Europe
M. rangeli	8 x 5.8 x 3.4	freshwater Siluriformes: pimelodid (ornate pim)	bulbus arteriosus	Brazil
M. renalis	6.3-7.3 x 5.3-6 x 4.3-5	estuarine Mugiliformes: mugilid (thinlip mullet)	kidneys	Portugal
M. reniformis	9.5-11.4 x 13-14.3 x 7.9-8.6	freshwater Siluriformes: silurid (Amur catfish)	intestines	China
M. rewensis (*rewansis*)	8.5-9.7 x 6.8-9.7 x 5-5.4	freshwater Cypriniformes: cyprinid (mrigal carp)	scales	India
M. rhinichthidis (syn. *Myxosoma*)	8.6-11.8 x 5.9-8.2	freshwater Cypriniformes: cyprinid (blacknose dace, eastern blacknose dace)	skin	Canada
M. rhinogobii	12-13.8 x 7.4-8.4 x 5.5-6	freshwater Gobiiformes: gobiid (gokuraku-haze)	gills, muscles	China
M. rhodei	9.8-11.8 x 8.4-9.1	estuarine Mugiliformes: mugilid (flathead grey mullet)	gills	Australia
M. richardsoni	11.2 x 7.7	freshwater Cypriniformes: cyprinid (common snowtrout)	gills	India
M. ridgwayi	10-12.1 x 9.5-10.5 x 6.6-6.7	freshwater Cypriniformes: cyprinid (common creek chub)	muscles	North America
M. ridibundae	8.9-11.5 x 7.5-9.1	Anura: ranid (marsh frog)	testes	Egypt
M. ridouti	9.5-10.5 x 9.4-10.9 x 6.7-6.8	freshwater Cypriniformes: cyprinid (bluntnose minnow)	muscles	North America
M. ridgwayi	10-12.1 x 9.5-10.5 x 6.6-6.7	freshwater Cypriniformes: cyprinid (creek chub)	muscles	Canada
M. rigida	10-11 x 7.5-9.5	freshwater Cypriniformes: cyprinid (mola carplet)	kidney	India
M. robustus (syn. *Myxosoma*)	14-16 x 10-11	freshwater Cypriniformes: cyprinid (common shiner)	skin	North America
M. rocatlae	16.9-19.3 x 5.6-6.9	freshwater Cypriniformes: cyprinid (hybrid of catla x rohu)	gills, gut	India
M. rohdei	9.8-11.8 x 8.4-9.1 x 6.5-7	marine Mugiliformes: mugilid (unspecified mullet)	kidneys	Australia
M. rohitae	9.9-12.1 x 8.8-9.9	freshwater Cypriniformes: cyprinid (rohu)	scales	India
M. ropari	12.5 x 4.5	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. rotundatus	7.5-11 x 6.7-10.5 x 5	freshwater Cypriniformes: cyprinid (common carp, koi carp, white Amur	fins, intestinal wall	Amur Basin, Korea

		bream)		
M. rotundus	10 x 9.8 x 3	freshwater Cypriniformes: catostomid (quillback), cyprinid (common bream, gudgeon)	gills	Germany
M. rutili	14-16.5 x 10.5-13.5 x 7.4-9.5	freshwater Cypriniformes: cyprinid (common roach, common rudd), leuciscid (taran)	gills, fins, eyes, muscles	Ukraine
M. rutilus	8-9 x 6-7.8 x 4.8-5	freshwater Cypriniformes: cyprinid (bighead carp, goldfish, hiina astelparrak); Siluriformes: silurid (Amur catfish, Soldatov's catfish)	gall bladder, liver, muscles, kidneys, urinary bladder	China
M. sacchalinensis (syn. *Myxosoma, Lentospora*)	9-12 x 6-8.5 x 5.5-6	freshwater Cypriniformes: cyprinid (Prussian carp, goldfish), xenocypridid (silver carp)	kidneys, rarely gall bladder	Amur Basin
M. saidovi	10 x 9-9.5 x 7	freshwater Cypriniformes: cyprinid (common bleak)	gills, kidneys	Caspian Sea
M. saintlouisiensis	19-21 x 14-16	freshwater Cichliformes: cichlid (Nile tilapia)	gills	Senegal
M. saladensis	10-11.1 x 8.4-9.7 x 2.6-4.9	estuarine Mugiliformes: mugilid (lebranche mullet)	gills	Argentina
M. salminus	9.6-10.5 x 5.8-6.6 x 4.7-5.3	freshwater Characiformes: bryconid (dorado)	gills	Brazil
M. samgoricus	9.1-11 x 7.8-9.2 x 4.9-5.2	freshwater Cypriniformes: cyprinid (common chub, Caucasian scraper)	gills, fins, kidney	Caucasus
M. samsunensis	8.5-9.9 x 7.6-8.2 x 4.7-4.9	freshwater Cypriniformes: cyprinid (Anatolian khramulya)	gills	Turkey
M. sanagaensis	9.4-11 x 6.1-7.3	freshwater Cypriniformes: cyprinid (clipper barb)	heart	Africa
M. sandrae (syn. *M. luciopercae, volgensis*)	8-11 x 7-9 x 4-6.2	freshwater Perciformes: percid (zander, Volga pikeperch, yellow perch, ruffe)	gills, fins, subcutaneous tissue, muscles, cornea, spinal cord [lordosis]	Eurasia
M. sangei	9-10.5 x 6-6.9	freshwater Characiformes: alestid (true bigscale tetra)	gills, skin, kidney	Cameroon
M. sangoricus	9.1-11 x 7.8-9.2 x 4.9-5.2	freshwater Cypriniformes: cyprinid (Caucasian scraper)	gills, fins, kidneys	Caucasus
M. saranae	6-9 x 6-7	freshwater Cypriniformes: cyprinid (olive barb, orangefin labeo)	gills	India
M. saranai (syn. *M. branchialis p.p.* [Tripathi])	6.4-7 x 4.5-5	freshwater Cypriniformes: cyprinid (olive barb)	gills	India
M. saraswatii	10-20 x 7.8-11	freshwater Siluriformes: clariid (walking catfish)	kidney	India
M. sarcocheilichthydis	10.8-12 x 7.2-9 x 5.8-6.2	freshwater Cypriniformes: cyprinid (grass carp, silver carp), gobionid (jarve-kuhvelrunt)	liver	China
M. sarcocheilithysi	11.2-12 x 8.8 x 5.6	freshwater Cypriniformes: cyprinid (rainbow gudgeon)	gills	China
M. sarigi (syn. *Myxosoma*)	11-13 x 8-9	freshwater Cichliformes: cichlid (mango tilapia, Nile tilapia, Guinean tilapia, helmitilapia, hybrid of Nile tilapia x blue tilapia)	intestines, kidneys, ovaries	Africa
M. sarotherodoni	9-13 x 7.5-10	freshwater Cichliformes: cichlid (blackchin tilapia)	gills	Benin
M. saugati	8.3 x 6.6	freshwater Cypriniformes: cyprinid (rohu)	scales	India
M. saurogobii	11-12 x 8.5-9.1	freshwater Cypriniformes: gobionid (dumerili sisalrunt)	kidneys	China
M. saurogobionis	11.7-14.3 x 7.8-10.4 x 6.5-9.1	freshwater Cypriniformes: gobionid (Chinese lizard gudgeon)	muscles	China

M. scardinii	11-12 x 9-9.5 x 4.5-5	freshwater Cypriniformes: cyprinid (common rudd, blacknose shiner)	gills, kidney	Russia, North America
M. scatophagi	11.4-17.9 x 4-8.1	marine Acanthuriformes: scatophagid (spotted scat)	gills	India
M. schizopygopsis	9-13 x 9-11 x 7	freshwater Cypriniformes: cyprinid (false osman)	gills	Asia
M schizothoraxi	13.2-13.6 x 8-8.8 x 6.4-8.2	freshwater Cypriniformes: gobionid (liaoningi abbottiin)	fins, gall bladder, heart	China
M. schuberti	8.5-12.5 x 7.5-10 x 6.5	freshwater Cypriniformes: cyprinid (common shiner)	brain, kidney, muscle, spleen	Canada
M. schulmani	16.1-19 x 12.2-14.4 x 9-10	freshwater Cypriniformes: cyprinid (white-eye bream)	fins	Europe
M. sciades	9.2 x 4.3 x 4.3	estuarine Siluriformes: ariid (Pemecou sea catfish)	gills	Brazil
M. sclerii	7.9-8.5 x 4.3-5.7	freshwater Cypriniformes: cyprinid (catla)	sclera	India
M. scleroperca (syn. *Myxosoma*)	10-19.2 x 7.2-9.6 x 7.2-13	freshwater Perciformes: percid (yellow perch, common logperch)	eye, cartilage	North America
M. semeniformis	13.2-14.4 x 4.8-6 x 3.6-4.2	freshwater Cypriniformes: cyprinid (mud carp, mrigal carp, rohu)	gills, skin	Vietnam
M. semilabei	9.6-10.4 x 6.8-8 x 5.2-5.6	freshwater Cypriniformes: cyprinid (labeo secuanske)	urinary bladder, ureters, kidneys	China
M. senchowensis	7.4-8.4 x 6-7.2 x 3.4-3.5	freshwater Cypriniformes: xenocypridid (silver carp)	gills	China
M. serrasalmi	12.5-18 x 7-10	freshwater Characiformes: serrasalmid (redeye piranha)	liver, spleen, kidneys	Brazil
M. serratus (*serrata*)	8.5-10 x 8-9	freshwater Cypriniformes: cyprinid (common carp)	gills	India
M. seshadri	11.4-12.9 x 8.6-10	freshwater Cypriniformes: cyprinid (fringe-lipped peninsula carp)	gills	India
M. sessabai	12.6-14 x 9.9-11.5	freshwater Cypriniformes: cyprinid (clipper barb)	kidney	Africa
M. shadgani	13.3-14.1 x 13.3-14.1 x 8.3-8.6	freshwater Cypriniformes: cyprinid (hybrid 'rajanorum' barb)	gills	Iran
M. shaharomae	12.1-14.5 x 9-11.3 x 7-7.6	freshwater Cypriniformes: cyprinid (common bleak)	gut, liver, kidney, testes	Hungary
M. shantipuri	6.3-8.2 x 5.1-6.1	freshwater Cypriniformes: cyprinid (hybrid of catla x rohu)	gills	India
M. shantungensis	7.2-8.4 x 9.6-10.8 x 5.8-7.3	freshwater Cypriniformes: cyprinid (common carp, bighead carp)	gills	China
M. shaochingensis	12-15,6 x 7.2-9 x 6-6.7	freshwater Siluriformes: clariid (walking catfish)	kidneys, intestines, stomach	China
M. sharpeyi	9.2-9.8 x 8.6-7.5 x 4.4-5.3	freshwater Cypriniformes: cyprinid (binni)	gill cartilage	Iran
M. sheroidalis	10.8 x 9.2	freshwater Cichliformes: cichlid (unspecified tilapia); Siluriformes: clariid (unspecified catfish)	viscera	Egypt
M. shettii	8-9 x 7-8	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. sheyangensis	10.5-11.9 x 9.2-10.7 x 5.9-6.9	freshwater Cypriniformes: cyprinid (Prussian carp)	gills	China
M. shuifuensis	13.9-17.1 x 10.3-12.3 x 7.6-8.5	freshwater Cypriniformes: cyprinid (mrigal carp)	kidney	China
M. shuleensis (syn. *M. sinkiangensis, Myxosoma*)	10.8-16.5 x 9-10.8 x 4.8-6.5	freshwater Cypriniformes: cyprinid (stone moroko)	gills, skin	China
M. sichangensis	10.4-12 x 8-9.6 x 6.4	freshwater Cypriniformes: cyprinid (unspecified schizothorax)	kidney, gall bladder	China
M. sichuanensis (syn. *Myxosoma*)	9.6-15 x 7.2-11.4 x 5.6-8	freshwater Cypriniformes: cyprinid (davidi marinka, pingi logsucker)	gills, mouth, body cavity, swim bladder, muscles,	China

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M. sichuangensis	13.1-15 x 10-11.4 x 7.1-8	freshwater Cypriniformes: cyprinid (pingi logsucker)	gills, swim bladder	China
M. siddalli	9.3-11.2 x 8.2-9.7 x 5.4-7.1	freshwater Cypriniformes: cyprinid (common shiner)	kidneys	Canada
M. sigini (syn. *Myxosoma*)	9.8-11.3 x 7.2-7.8 x 4.8-6	freshwater Cypriniformes: cyprinid (bighead carp), xenocypridid (silver carp)	gills, body cavity	China
M. sikiangensis	12-12.4 x 7.9-9 x 7.2	freshwater Cypriniformes: cyprinid (gold barb)	skin	China
M. simplex (syn. *Myxosoma*)	8.4-10 x 7.8-8.4	freshwater Cypriniformes: cyprinid (Russian bitterling), xenocypridid (silver carp)	eyes, muscles	China
M. sinensis (syn. *Myxosoma*)	8-12 x 6.6-9.6 x 4.8-6	freshwater Anabantiformes: channid (blotched snakehead); Anguilliformes: anguillid (Japanese eel); Cypriniformes: cyprinid cyprinid (common carp, mud carp, goldfish, hiina astelparrak), xenocypridid (yunnani kriipsuu)	gut wall, spleen, kidneys, urinary bladder, gall bladder	China
M. sinicyclochilusi	11.4-14.4 x 8.8-11.2 x 7-7.3	freshwater Cypriniformes: cyprinid (golden-line barbel)	gills, kidneys	China
M. sitjae	11-13 x 6.8-8.1 x 6.3-6.9	freshwater Cypriniformes: cyprinid (white bream)	gills	Hungary
M. slendrii	13.9-16.1 x 2.7-3.9	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. smithi	9.9-11.4 x 8.3-9.3 x 5.4-6.7	freshwater Cypriniformes: cyprinid (northern redbelly dace)	kidney	Canada
M. soldatovi	8-9.5	freshwater Salmoniformes: salmonid (chum salmon, chinook salmon)	skin	Amur Basin
M. solidus	11-12 x 10-10.5 x 8.4-8.6	freshwater Cypriniformes: cyprinid (Prussian carp, goldfish)	gills	Amur Basin, Korea
M. sommervillae	10.5-13.5 x 8.4-11.2 x 6.6-7.5	freshwater Cypriniformes: cyprinid (common roach)	gills	Hungary
M. sonarpurensis	11-13.2 x 5.9-6.1	freshwater Cypriniformes: cyprinid (bata)	gills	India
M. sophorae	6.4-26.6 x 5.9-10.1	freshwater Cypriniformes: cyprinid (pool barb)	gills, kidneys	India
M. sourouensis	11-14 x 8-10	freshwater Osteoglossiformes: osteoglossid (African arowana)	gills	Burkina Faso
M. spalli (syn. *Myxosoma cyprini p.p.*)	13.5-15.5 x 7.5-9.2 x 6-8	freshwater Cypriniformes: cyprinid (red shiner, golden shiner)	gills	North America
M. sparoidis	11.7-12.4 x 8.8-9.3 x 8.5	freshwater Perciformes: centrarchid (black crappie, calico bass)	intestines	North America
M. spatulatus	9-12 x 6-7	freshwater Perciformes: cottid (stone sculpin)	gills, eyes	Lake Baikal
M. sphaeralis (*spheralis*)	6-7.3 x 6-7.3	estuarine Mugiliformes: mugilid (largescale mullet); Salmoniformes: salmonid (true fera)	gills	India
M. sphaericus (syn *Myxosoma, Lentospora*)	8.5-12 x 9-11 x 6	freshwater Cypriniformes: cyprinid (Prussian carp, goldfish, spotted steed), xenocypridid (silver carp)	kidneys	Amur Basin, Japan
M. sphaerocapsularis	17-18 x 16-17 x 11-12	freshwater Cypriniformes: cyprinid (Khanka spiny bitterling)	muscles	China, Korea
M. sphericum	9-9.5 x 7.2 x 5-5.5	freshwater Cypriniformes: cyprinid (mrigal carp)	scales	India
M. spinocurvatura	10.6-13.6 x 9.6-11.2	estuarine Mugiliformes: mugilid (flathead grey mullet)	brain, spine, cartilage, intestines, liver [lordosis]	Australia, India, Vietnam
M. spinibarbus	8.8-12 x 6-8.5 x	freshwater Cypriniformes: cyprinid	gills, skin	China

(syn. *M. pyriformis, Myxosoma*)	4.8-6.8	(phoenix barb, hiina astelparrak, yunnani napploug)		
M. spirosulcatus	7.5-10 x 7.5-8.5	marine Carangiformes: carangid (Japanese amberjack, greater amberjack)	bile ducts	Japan
M. spleeni (syn. *M. liaohoensis, Myxosoma*)	7.8-10.8 x 6.2-8.4 x 5.5-7.2	freshwater Cypriniformes: cyprinid (thin-banded barb), xenocypridid (silver carp)	kidney, skin	China
M. splendidus (syn. *Myxosoma*)	8.4-10.1 x 7.8-9	freshwater Cypriniformes: cyprinid (gudgeon)	muscles	Russia
M. sporostoni	9.8-13 x 8.4-11.7 x 6	freshwater Cypriniformes: xenocypridid (silver carp); Clupeiformes: engraulid (Yangtse grenadier anchovy); Siluriformes: silurid (Amur catfish, Soldatov's catfish, wels catfish)	intestinal wall, mesentery, heart	Amur Basin
M. squamae	8.4-13.5 x 7.2-10.5 x 5-6	freshwater Cypriniformes: cyprinid (common carp, koi carp, common barbel, Bulatmai barbel, barbel chub, white Amur bream, sattar snowtrout, gold barb, stone moroko, poologa-silemokk, rosy bitterling), xenocypridid (tsan tui); Gobiiformes: gobiid (gokuraka-haze); Perciformes: sinipercid (mandarin fish); Salmoniformes: salmonid (coho salmon)	skin	Europe, North America
M. squamalis (syn. *Myxosoma*)	8.1-9.9 x 7.7-9.9 x 5.6-7.7	freshwater Salmoniformes: salmonid (chinook salmon, chum salmon, rainbow trout)	scales	North America
M. squamaphilus	17-19.5 x 13-14 x 11-12	freshwater Cypriniformes: cyprinid (common bream)	scales	Hungary
M. squamosus	8-9.6 x 7.2-9.9 x 4.8-7.7	freshwater Cypriniformes: cyprinid (river chub, stone moroko); Salmoniformes: salmonid (chinook salmon, coho salmon, chum salmon, rainbow trout)	skin, scales, gills, kidney, gall bladder, intestines	North America
M. stanlii	7.5-11 x 6.3-11.3 x 6.2-8.6	freshwater Cypriniformes: cyprinid (largescale stoneroller)	muscles, connective tissue	North America
M. stellatus	17-19.4 x 8.2-9.3 x 6.7-7.5	freshwater Characiformes: gasteropelecid (silver hatchetfish)	nerves	Columbia
M. stenosus	11-12.5 x 7.5-8.5	freshwater Siluriformes: mochokid (wahrindi, mandi)	gills	Tchad
M. stepanovi	12.7-14.2 x 10.2-11.2 x 6-7.2	freshwater Cypriniformes: cyprinid (sattar snowtrout)	gills, skin, visceral organs	Asia
M. stokesi	8.5 x 5.3	freshwater Siluriformes: pimelodid (unspecified catfish)	snout subcutis	Brazil
M. stomum	7-10 x 5.5-7.5	marine Perciformes: haemulid (blackspotted rubberlip)	mouth, muscles	Egypt
M. strelkovi	8-12.2 x 6-11 x 4-7	freshwater Cypriniformes: cyprinid (common minnow, ide)	gills, liver	Russia
M. stuartae	10.4-12.9 x 9.6-11.4	freshwater Cypriniformes: cyprinid (western creek chubsucker)	fins	North America
M. subcircularis	9.1-11.8 x 8.2-10	freshwater Cypriniformes: catostomid (white sucker)	fins	Canada
M. subepithelialis	8-12 x 6-10	freshwater Cypriniformes: cyprinid (gudgeon)	subcutis	Czech Republic
M. subtecalis (syn. *Myxosoma*)	15-18 x 6.5-8 x 6	marine Cyprinodontiformes: fundulid (mummichog)	fins	North America
M. sujiensis	8.8-12 x 7.2-8.8 x 6.5	freshwater Cypriniformes: cyprinid (hiina astelparrak)	kidneys	China
M. suppamattayai	6.2-7 x 6.2-6.7	estuarine Mugiliformes: mugilid	scales	Thailand

		(bluespot mullet)		
M. susanlimae	10.6-12 x 9.5-10.8 x 8.3-10.1	freshwater Cypriniformes: cyprinid (common bleak)	gill cartilage	Hungary
M. sushmii	9.6 x 8.3	freshwater Cypriniformes: cyprinid (rohu)	eye	India
M. suturalis (syn. *M. dogieli p.p.*)	9.8-12 x 7.5	freshwater Cypriniformes: cyprinid (sattar snowtrout)	heart, kidneys	Russia
M. symmetricus	9.6-10.8 x 7.2-9.3 x 5.8-6	freshwater Cypriniformes: catostomid (smallmouth buffalo), cyprinid (bighead carp), xenocypridid (silver carp); Perciformes: centrarchid (black crappie)	gills, intestines, kidney, spleen, urinary bladder	North America, China
M. synodonti	12-15 x 5.8-6.9	freshwater Siluriformes: mochokid (dwarf synodontis)	stomach	Cameroon
M. szekeli	8.7 x 4.1	freshwater Siluriformes: silurid (attu)	stomach wall	India
M. szekelyianus	13.4 x 9.5	freshwater Cypriniformes: cyprinid (Chirruh snowtrout)	gills	India
M. szentendrensis	8.8-9.6 x 7.6-8 x 6.4-7.1	freshwater Cypriniformes: cyprinid (common nase)	gills	Hungary
M. tachengensis	18-19.4 x 10.2-12 x 8.5-10.1	freshwater Anguilliformes: anguillid (Japanese eel); Cypriniformes: cyprinid (goldfish)	intestines, gall bladder	China
M. tadzhikistanicus	9-12 x 5-8	freshwater Cypriniformes: cyprinid (Caucasian scraper)	kidneys, spleen	Asia
M. taibaiensis	10.2-11.2 x 9.1-9.9 x 6.1-6.6	freshwater Cypriniformes: cyprinid (common carp)	intestinal wall	China
M. taihuensis (syn. *Myxosoma*)	6.8-12.2 x 7.6-10.5 x 4.6-6	freshwater Cypriniformes: cyprinid (black carp), xenocypridid (silver carp)	gills	China
M. taipingensis (syn. *M. cheni, Myxosoma*)	8-9.6 x 5.4-7.2 x 4-6.5	estuarine/freshwater Cypriniformes: cyprinid (bighead carp, marinka iravadska, stone moroko), xenocypridid (silver carp); Mugiliformes: mugilid (flathead grey mullet, so-iju mullet); Siluriformes: silurid (Amur catfish)	muscles, gills, intestines, gall bladder, kidney, urinary bladder	Korea, China
M. taiwanensis (syn. *Lentospora*)	16-18 x 10-11 x 5	freshwater Cypriniformes: cyprinid (crucian carp)	kidney	Taiwan
M. talievi	6.3-12 x 6.3-11 x 3.8-5.7	freshwater Cypriniformes: balitorid (unspecified hillstream loach); Perciformes: cottid (pallid sculpin, flat sculpin, fatty sculpin, bighead sculpin, red sculpin, Kessler's sculpin, stone sculpin, vitim sculpin, short-headed sculpin, osman przewalskeho)	muscles, body cavity, eyes [blindness]	Lake Baikal
M. tambroides	8.8-10.6 x 6.8-7.9 x 7-7.9	freshwater Cypriniformes: cyprinid (empurau)	gills	Malaysia
M. tamingensis	10.8-13.2 x 8.6-10.8 x 6-6.2	freshwater Cypriniformes: cyprinid (bighead carp)	urinary bladder	China
M. tanakai	15.4-16.8 x 6.3-8.4 x 5.9-6.8	freshwater Cypriniformes: cyprinid (common carp)	gills	Japan
M. tapajosi	13.5-17 x 9.6-11.4	freshwater Siluriformes: pimelodid (gilded catfish)	gills	Brazil
M. tasikkenyirensis	11.8-13.8 x 8.3-9.9 x 5.5-6.5	freshwater Cypriniformes: cyprinid (bonylip barb)	muscles	Malaysia
M. tatuensis	9.6-10.4 x 8-9.6 x 6.4	freshwater Cypriniformes: cyprinid (pale chub)	gills, mouth	China
M. tauricus	11.5-14.5 x 9-11	freshwater Cypriniformes: cyprinid (Crimean barbel)	gills, fins, muscles	Ukraine
M. tayehensis	16.8-19.2 x 10.6-12 x 8.4-8.6	freshwater Anabantiformes: channid (northern snakehead); Cypriniformes: cyprinid (grass carp)	gall bladder, intestines	China

M. tchadanayei	14 x 8.7	freshwater Characiformes: citharinid (moonfish)	gills	Chad
M. tchangi	11.5-12.4 x 6.6-8.4 x 4.8	freshwater Cypriniformes: cyprinid (black carp)	intestines, gall bladder	China
M. tchombouei	17.5-25.5 x 7.5-10	freshwater Cypriniformes: cyprinid (clipper barb)	skin	Africa
M. tengchongensis	8.8-9.6 x 6.4-8 x 6.2	freshwater Cypriniformes: cyprinid (yunnani napprunt)	mesentery, kidney, urinary bladder	China
M. terengganuensis	12-13.4 x 6.7-8.3 x 4.8-5.2	freshwater Cypriniformes: cyprinid (bonylip barb)	muscles	Malaysia
M. teres	9.5-11.5 x 9-10.5 x 5-6	freshwater Cypriniformes: cyprinid (steelcolor shiner)	fins, muscles	North America
M. testicularis	8.2-9.1 x 6.7-7.5 x 2.4-3	freshwater Characiformes: hemiodontid (jatuarana)	testes	Brazil
M. thangi	11.5-12.4 x 6.6-8.4 x 4.8	freshwater Cypriniformes: cyprinid (black carp)	intestines, gall bladder	China
M. thelohanellus	12-14 x 9-9.5	freshwater Cypriniformes: cyprinid (crucian carp)	gills [cysts]	Russia
M. thickthecae	9.6-12 x 9-10.8 x 6	freshwater Cypriniformes: cobitid (pond loach)	kidneys	China
M. thymalli	9-11 x 8-10.5 x 5.9-7.2	freshwater Salmoniformes: salmonid (Arctic grayling)	gall bladder	Kamchatka
M. ticto	12.7-15 x 6.8-9	freshwater Cypriniformes: cyprinid (ticto barb)	gills, muscles	India
M. tilapiae	14-16 x 9-12	freshwater Cichliformes: cichlid (Nile tilapia, redbelly tilapia, mango tilapia, helmitilapia, mvogoi tilapia)	gills, fins, mouth, kidneys, spleen	Nigeria
M. tingrelaensis	11-13 x 8-10	freshwater Cichliformes: cichlid (mango tilapia)	fins	Burkina Faso
M. tisae	9-10 x 8 x 6	freshwater Cypriniformes: cyprinid (common barbel)	kidneys	Hungary
M. tonyaensis	9.2-11.6 x 6.2-7.7 x 5.7-6.3	freshwater Gobiiformes: gobiid (gokuraku-haze)	kidneys	China
M. tori	9.6-10.4 x 7.2-8.8 x 6.8-7	freshwater Cypriniformes: cyprinid (harilik lehthuul)	liver, gall bladder, kidney, urinary bladder	China
M. toyamai (syn. *Thelohanellus*)	13.2-16.8 x 4.6-8 x 4.2-6	freshwater Cypriniformes: cyprinid (common carp, koi carp, goldfish)	gills	Asia, North America
M. transovalis	6-7 x 8	freshwater Cypriniformes: catostomid (smallmouth buffalo), cyprinid (rosyside dace)	scales, gills	North America
M. transversalis	7.7-10 x 9.1-10.5	freshwater Cypriniformes: cyprinid (common shiner, brassy minnow)	muscles, kidney	Canada
M. triangulum	10.8-12 x 10.8-12 x 4.2	freshwater Cypriniformes: cyprinid (black carp)	kidneys	China
M. trichogasteri (syn. *Myxosoma*)	14-17 x 8.7-9.9	freshwater Anabantiformes: channid (spotted snakehead), osphronemid (banded gourami)	gall bladder	India
M. tricostatus	8.4-10.8 x 7.2-9 x 6-7.2	freshwater Cypriniformes: cyprinid (grass carp)	gills, spleen	China
M. tripathii	9.8-10.2 x 12-13.5	freshwater Siluriformes: clariid (unspecified catfish)	gut wall, viscera	India
M. tripterygii (syn. *Myxosoma*)	11.7-12.4 x 11.7-12.4	marine Blenniiformes: tripterygid (variable triplefin)	fins, subcutis	New Zealand
M. tripurensis	8.1-9.4 x 6.5-7	freshwater Cypriniformes: cyprinid (reba carp, bata, orangefin labeo)	gills	India
M. tsangwuensis	10.2-12 x 8.4-9.6 x 6.6-7.2	freshwater Cypriniformes: cyprinid (common carp, bighead carp)	gills, kidneys	China
M. tuenfengensis	12-13.6 x 8.4-10 x 6-7	freshwater Cypriniformes: cyprinid (Chinese lizard gudgeon)	gills	China
M. tuberculus	13.6-14.2 x 13-14 x	freshwater Cypriniformes: cyprinid	urinary bladder,	China

	7-7.5	(goldfish)	ureters, heart	
M. tumides	12-14.4 x 16.8-19.6 x 8.4	freshwater Cypriniformes: cyprinid (black carp)	gills, fins, intestines, heart	China
M. tunicatus	16 x 6.5	freshwater Siluriformes: bagrid (yellowhead catfish)	urinary bladder, kidneys	Amur Basin
M. turbinoides	15 x 7	unspecified coastal fishes	gills	Macedonia
M. turpisrotundus	8.6-10 x 8.2-10 x 5.1-6.5	freshwater Cypriniformes: cyprinid (Prussian carp)	skin, fins	China
M. twistus	16.2-17,4 x 8.4-9.6 x 5.4-6.2	freshwater Siluriformes: bagrid (yellowhead catfish)	kidneys	China
M. umidus	13.5 x 7.8 x 7.7	freshwater Characiformes: bryconid (piraputanga)	spleen	Brazil
M. undasuturae	10-11 x 5-6	freshwater Cypriniformes: cyprinid (mola carplet)	urinary bladder	India
M. undulatus	9-10.5 x 7-8.5 x 5-6	freshwater Cypriniformes: leuciscid (common minnow)	gills	Czech Republic
M. uniporus	10.4-12 x 5-8.4 x 3-6	freshwater Cypriniformes: cyprinid (bighead carp), xenocypridid (silver carp); Siluriformes: bagrid (yellowhead catfish, Herzenstein's catfish, Ussuri catfish), silurid (Amur catfish)	intestinal wall, kidney, gonads, subcutis	Amur Basin, Korea, Japan
M. upmae	9.6 x 5	freshwater Cypriniformes: cyprinid (bighead carp)	gills	India
M. urinaris	9.3-10.3 x 7.7-8.7	estuarine Mugiliformes: mugilid (flathead grey mullet)	urinary bladder	Portugal
M. urinarybladderi (syn. *M. tunghuensis, Myxosoma*)	10.2-16.8 x 8.8-10.8 x 5-9	freshwater Cypriniformes: cyprinid (goldfish)	urinary bladder, kidney	China
M. utlouensis	11.9-12.6 x 8.5-9.2	freshwater Siluriformes: clariid (walking catfish)	cornea	India
M. uvuliferus (syn. *M. gibbosus, lii*)	7-12.3 x 9.8-13 x 6-8.2	hyperparasitic in metacercariae of diplostomatid trematode (*Uvilifer ambloplitis*) in tissues* of freshwater Perciformes: centrarchid (pumpkinseed)	skin, gills*	Canada
M. uyeni	9.9-10.8 x 8-8.5	freshwater Cypriniformes: cyprinid (mud carp)	intestines	Vietnam
M. uzbekistanicus	12-14.2 x 9-11.4 x 6-7.5	freshwater Cypriniformes: cyprinid (seven khramulya, Caucasian scraper)	skin	Uzbekistan
M. valatus	8.4-9.6 x 7.4-8.4 x 6-7	freshwater Cypriniformes: cyprinid (goldfish)	gills, skin, intestines, kidneys	China
M. valdogeli (syn. *M. lobatus p.p.*)	7.5-9.5 x 6.6.5	freshwater Cypriniformes: cyprinid (Caspian barbel)	gills	Asia
M. vanivilasae	8-10 x 7-9	freshwater Cypriniformes: cyprinid (mrigal carp)	skin	India
M. variabilis	9.7-12.2 x 7.5-9.8 x 4.9-6.1	freshwater Cypriniformes: cyprinid (common bream)	gills	Hungary
M. varicorhini	11.8-16 x 10.6-11.8	freshwater Cypriniformes: cyprinid (Caucasian scraper)	skin, spleen, kidneys	Asia
M. varicorhinusis	9.6-11.2 x 7-8 x 5.6-6	freshwater Cypriniformes: cyprinid (pisisuu-koukloug)	kidneys, ureters	China
M. varius (syn. *Myxosoma varia*)	9-13 x 6-8.5 x 4.5-6.5	freshwater Cypriniformes: cyprinid (common carp, bighead carp), xenocypridid (silver carp)	gills, body surface, intestines, gall bladder, spleen, kidneys, urinary bladder	China
M. vartanyanae (syn. M. salmonis)	8.2-12.3 x 7.4-10 x 5.5-8.3	freshwater Salmoniformes: salmonid (chum salmon, Sevan trout, rainbow trout, brown trout, lake trout)	scales, muscles, liver, spleen, kidneys	Ukraine

M. vascularis	9.7-11.7 x 3.8-5.8	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. vastus	9-12 x 7.2-8.6 x 4.5-6.2	freshwater Cypriniformes: catostomid (pealip redhorse, shorthead redhorse), cyprinid (common carp, goldfish, barbel chub, Chinese lake gudgeon), xenocypridid (silver carp)	skin, intestines, gall bladder, liver, kidney, ureters, heart	China, Brazil
M. vedavatiensis	13-15 x 8-10	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. vegrandis (syn. *Myxosoma*)	9.6-10 x 7.2-7.8 x 5.4-6	freshwater Cypriniformes: cyprinid (Russian bitterling), xenocypridid (silver carp)	gills	China
M. velatus	8.4-9.6 x 7.4-8.4 x 6-7	freshwater Cypriniformes: cyprinid (goldfish)	gills, body	China
M. venkateshi	9-10 x 7-8	freshwater Cypriniformes: cyprinid (mrigal carp); Siluriformes: heteropneustid (Asian stinging catfish)	gills	India
M. vescus	8.4-11.2 x 4.8-6.3 x 3.1-4.8	freshwater Anguilliformes: anguillid (Japanese eel); Cypriniformes: cyprinid (Chinese lake gudgeon, Chinese false gudgeon), gobionid (kiatingen gudgeon); Siluriformes: bagrid (yellowhead catfish, darkbarbel catfish, Chinese longsnout catfish, varjokimalaismonni)	gills, skin, gut, kidneys	China
M. vesicularis	11.3-12.7 x 10-10.7 x 6-6.7	estuarine Mugiliformes: mugilid (flathead grey mullet)	gall bladder wall	Portugal
M. vesiformis	10.8-15.8 x 6-7.4 x 5	freshwater Cypriniformes: cyprinid (giant Chinese bitterling, Khanka spiny bitterling)	gills, kidneys	China
M. vetuschicanus	10.7-11.5 x 8.1-8.8	freshwater Characiformes: bryconid (dourado)	fins	Brazil
M. voremkhai (syn. *M. pseudorasborae p.p.)*	15-16 x 8-9 x 8	freshwater Cypriniformes: cyprinid (stone moroko); Siluriformes: bagrid (yellowhead catfish)	gills, fins	Amur Basin, China
M. waleckii	8.4-9.4 x 7.3-8.4 x 5.7-6.3	freshwater Cypriniformes: cyprinid (Amur ide)	gills	Amur Basin
M. warniakiensis	9.5-10.8 x 8-9.5 x 6	freshwater Gadiformes: lotid (burbot)	gills	Poland
M. wasjugani	15.1-17.6 x 10-15.1 x 7.1-8.8	freshwater Cypriniformes: cyprinid (goldfish)	muscles	Russia
M. weishanensis	10-12.5 x 7.5-10 x 5-6.3	freshwater Cypriniformes: cyprinid (barbel chub)	gills	China
M. wellerae	12.5-16.5 x 9.5-11.5 x 6.5-7	freshwater Cypriniformes: cyprinid (common shiner)	muscles	Canada
M. widisuturalis (syn. *M. zacconi*)	8.8-9.6 x 7.2-8 x 6.4	freshwater Cypriniformes: cyprinid (pale chub)	gills	China
M. wootteni	11.6-15 x 10.2-13 x 5.5-6	freshwater Cypriniformes: cyprinid (common roach)	fins	Hungary
M. wuchangensis	9.6-11 x 8.4-10.2 x 6-6.6	freshwater Cypriniformes: cyprinid (common carp)	fins	China
M. wucheni (syn. *M. acutus p.p.*)	12.9-14.3 x 9-11.2 x 6.7-8.1	freshwater Cypriniformes: cyprinid (common carp)	gills, kidneys	China
M. wuhanensis	11.4-23 x 8.4-14 x 6.6-7.2	freshwater Cypriniformes: cyprinid (Prussian carp, goldfish)	skin, kidney, liver, heart, intestines, gall bladder [swellings]	Asia
M. wuhuensis	9-9.8 x 6.7-7.1 x 4.3-4.8	freshwater Siluriformes: silurid (Amur catfish)	intestines	China
M. wulii (syn. *Myxosoma magna*)	15.6-19.2 x 8.9-10.8 x 7.2-8.6	freshwater Cypriniformes: cyprinid (goldfish, Chinese hooksnout carp),	hepatopancreas	China

		xenocypridid (silver carp); Siluriformes: bagrid (Braznikov's catfish)		
M. wushingensis	10.8-12 x 8.2-9.6 x 6.2-6.6	freshwater Cypriniformes: cyprinid (goldfish)	intestines, kidneys	China
M. xenocyprisis	11.3-13.3 x 7.3-8 x 6-6.7	freshwater Cypriniformes: xenocypridid (davidi kriipsuu)	gills	China
M. xiaoganensis	5.4-7.1 x 7.5-9 x 5.2-6.2	freshwater Cypriniformes: cyprinid (silver carp)	spleen	China
M. xiantaoensis	11.3-13.9 x 8.4-11.1 x 6.1-7.7	freshwater Siluriformes: bagrid (yellowhead catfish)	fins	China
M. xiaoi	9.8-12.2 x 8.1-9.2 x 5.2-6.9	freshwater Cypriniformes: cyprinid (common shiner)	gill cartilage	Canada
M. xinanensis	9.6-11.8 x 8.8-9.3 x 5-5.6	freshwater Cypriniformes: cyprinid (marinka iravadska), nemacheilid (spotted thicklip loach)	gills, kidneys	China
M. xiningensis	7.1-11.4 x 7.6-10.3 x 5.6-7.6	freshwater Cypriniformes: cyprinid (osman przewalskeho)		China
M. xinyangensis	8.7-10.6 x 7.3-9.5 x 5.8-7.1	freshwater Cypriniformes: cyprinid (Chinese false gudgeon)	operculum	China
M. xiushanensis	11.2-13.2 x 9.5-11.1	freshwater Siluriformes: bagrid (yellowhead catfish)	gills	China
M. yaanensis (syn. *Myxosoma*)	10.4-12.8 x 7.2-8.8 x 4.8	freshwater Cypriniformes: cyprinid (davidi marinka)	kidneys	China
M. yibinensis	8.5-9.8 x 10-12 x 6.8-6.9	freshwater Cypriniformes: cyprinid (common carp)	muscles	China
M. yini	7-8 x 3-3.5 x 2-2.5	freshwater Cypriniformes: cobitid (weatherfish)	kidneys, rarely pancreas	Korea
M. yogendrai (syn. *M. sphericum*)	9-9.5 x 7.2	freshwater Cypriniformes: cyprinid (mrigal carp)	scales	India
M. yueyangensis	9.6-10 x 8-8.5 x 7-7.5	freshwater Cypriniformes: cyprinid (common carp)	intestines	China
M. yunensis (syn. *M. barbodesi*)	8-11.2 x 7.2-8 x 5.6-7.2	freshwater Cypriniformes: cyprinid (parma vernayova, parma junanska)	gills, kidney	China
M. zaccoi	8.8-9.6 x 7.2-8 x 6.4	freshwater Cypriniformes: xenocypridid ('macrolepis' chub)	gills	China
M. zacconis	10.4-11.4 x 6.2-8 x 5.2-5.6	freshwater Cypriniformes: cyprinid (pale chub)	urinary bladder	China
M. zaikae	10.2-14 x 9.6-11 x 5.8-7.1	freshwater Cypriniformes: cyprinid (common roach)	kidney, liver	Lake Baikal
M. zhaltsanovae	11.3-14.8 x 9.1-11.4 x 5.4-7.2	freshwater Cypriniformes: cyprinid (gibel carp, Prussian carp)	gills	Russia
M. zhaoi (syn. *M. mapienensis, Myxosoma*)	11.9-13.6 x 5.6-11 x 4.8-8.5	freshwater Cypriniformes: cyprinid (yunnani silemokk), gobionid (Kiating gudgeon)	gills	China
M. zhenzensis (syn. *M. taihuensis*)	6.8-7.8 x 7.6-8.4 x 4.6-5.3	freshwater Cypriniformes: cyprinid (silver carp)	muscles	China
M. zhujiangensis (syn. *Myxosoma*)	11.7-12.6 x 7.2-8.6 x 5.2-5.8	freshwater Siluriformes: clariid (Hong Kong catfish)	fins, skin	China
M. zillii	10-11 x 5-6	freshwater Cichliformes: cichlid (mango tilapia)	gills, kidneys, spleen	Africa
M. zoohuri	13.2-17.3 x 4.9-7	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
M. zoqueus	7.1-8.6 x 4.7-6.5	freshwater Mugiliformes: mugilid (mountain mullet)	gall bladder	Mexico
Genus ***Neohenneguya*** (spindle-shaped spores with fine caudal projections, 2 polar capsules)				
N. tetraradiata [type species]	16.2-21.6 (+ tail 63-72) x 5.4	freshwater Gobiiformes: oxudercid (rubicundus eel goby)	gills [cysts]	India
Genus ***Neothelohanellus*** (syn. *Lomosporus*) (ovoid spores, single anterior polar capsule opens laterally)				
N. catlae	8.2-8.8 x 7.7	freshwater Cypriniformes: cyprinid	kidney	India

[type species]		(catla)		
N. indicus (syn. *Lomosporus*)	10-11 x 6-7	freshwater Cypriniformes: cyprinid (orangefin labeo)	gills, operculum	India
N. krishnagarensis (syn. *Lomosporus*)	11-12.1 x 7.1-8.2	freshwater Cypriniformes: cyprinid (orangefin labeo)	brain	India
Genus ***Phlogospora*** (pyriform spores with bifurcate caudal process)				
P. gulio		freshwater Siluriformes: bagrid (long whiskers catfish)		India
P. mysti [type species]	35-42 (14-18) x 3.5-5	freshwater Siluriformes: bagrid (Day's mystus)	gills	India
P. oculatus	45-90.8 (13.5-24) x 2.7-3.5	freshwater Siluriformes: bagrid (Malabar mystus)	gills	India
Genus ***Spirosuturia*** (ellipsoidal biconvex spores with sinuous suture)				
S. carassii [type species]	12.6-16.8 x 6.6-8.6 x 2.4-3.4	freshwater Cypriniformes: cyprinid (goldfish)	urinary bladder	China
S. hypophthalmichthydis	7.2-9.2 x 7.7-9.2 x 5.4-5.6	freshwater Cypriniformes: cyprinid (bighead carp, grass carp), xenocypridid (silver carp)		China
S. lhasaensis	10.8-12 x 7-8.1 x 6.8	freshwater Cypriniformes: cyprinid (Younghusband's cyprinid)	gills	China
Genus ***Tetrauronema*** (spores tapering posteriorly, bearing 4 thin projections)				
T. desaequalis	12.5-13.9 (+tail 4.8-14.1) x 6-6.7 x 3.1-4.1	freshwater Characiformes: erythrinid (wolf fish)	fin connective tissue	Brazil
T. macropodus (syn. *T. macropodos*) [type species]	11.4-12.9 (+ tail 13.3-16.2) x 5.9-6.3 x 5.2-5.9	freshwater Anabantiformes: osphronemid (fork tailed paradisefish)	gills	China
Genus ***Thelohanellus*** (pyriform spores, single apical polar capsule)				
T. acuminatus	12.8-21.6 x 5.8-8.1 x 5-5.8	freshwater Cypriniformes: cobitid (pond loach), cyprinid (grass carp, koi carp)	gills	China, Vietnam
T. andhrae	11.2-14.5 x 4.5-5.5	freshwater Cypriniformes: cyprinid (fringe-lipped peninsula carp, greenstripe barb)	gills	India
T. anilae	bimorphic macrospores 32.3-34 x 11.9-13.6 microspores 12.7-13.6 x 6.8	freshwater Cypriniformes: cyprinid (rohu)	gills	India
T. arii	12-13.5 x 6.6	marine/estuarine Siluriformes: ariid (smoothmouth sea catfish)	gall bladder	Senegal
T. assambai	9-12 x 5-7	freshwater Cypriniformes: cyprinid (unspecified labeo)	gills, fins	Cameroon
T. auerbachi	14-15.8 x 4.5-7	marine Siluriformes: ariid (flatmouth sea catfish)	gall bladder	India
T. avijiti	13-14.7 x 9.1-10.2	freshwater Cypriniformes: cyprinid (rohu)	fins	India
T. batae	32.5-35 x 11-14	freshwater Cypriniformes: cyprinid (bata)	fins	India
T. bengalensis	10-12 x 5.5-7.5	freshwater Cypriniformes: cyprinid (catla)	gall bladder	India
T. bicornei	13-14 x 8-9	freshwater Cypriniformes: cyprinid (African carp)	gills	Burkina Faso
T. bifurcata	30-6-40 x 7.5-10	freshwater Cypriniformes: cyprinid (rohu x catla hybrid)	gills	India
T. boggoti	8.4-12 x 4.8-7.5	freshwater Cypriniformes: cyprinid (indigenous carp, minor carp)	gills, fins	India
T. calbasui	9-10.8 x 7.2	freshwater Cypriniformes: cyprinid	scales	India

		(orangefin labeo)		
T. catlae	19-25.5 x 10.2-13.6 x 11-12.5	freshwater Anabantiformes: channid (northern snakehead); Cypriniformes: cyprinid (common carp, catla, Java barb)	gills, kidneys [cysts]	India, Amur Basin, Vietnam
T. caudatus	13-16.6 x 8.5-12.9	freshwater Cypriniformes: cyprinid (rohu)	fins	India
T. chandannagarensis	11.3-13.2 x 6.3-7.1	freshwater Cypriniformes: cyprinid (catla)	gills	India
T. chelae	9-10.3 x 4.6-6	freshwater Cypriniformes: cyprinid (large razorbelly minnow)	gall bladder	India
T. chilkensis	25.8-27.5 x 7.7-9.5	freshwater Cypriniformes: cyprinid (rohu)	gall bladder	India
T. chinensis	21.6-27.6 x 12-14.4 x 10.2-12.6	freshwater Anabantiformes: channid (northern snakehead)	gills	China
T. chrysopomati	10.7-15 x 4.3-7.1	freshwater Cypriniformes: cyprinid (olive barb)	gills	India
T. chuhsienensis	17.6-19.8 x 7.4-8 x 8.8	freshwater Cypriniformes: cyprinid (common carp)	scales	China
T. chukiangensis	26.1-31.2 x 10.8-12 x 9.3-9.8	freshwater Anabantiformes: channid (blotched snakehead)	skin	China
T. citharini	10-12 x 6-7	freshwater Characiformes: citharinid (moonfish)	heart	Tchad
T. coeli	12-13.5 x 6-8	marine Siluriformes: ariid (thinspine sea catfish)	gall bladder	India
T. commersoni	16.5-19.5 x 9-12	marine Carangiformes: carangid (Talang queenfish)	gall bladder	India
T. costeae	9.4 x 5.6	freshwater Cypriniformes: cyprinid (craw-craw nose)	gills	Benin
T. deri	10 x 5	freshwater Cypriniformes: cyprinid (indigenous carp)	fins	India
T. dipaki	13.3-14.8 x 8.8-10.6	freshwater Cypriniformes: cyprinid (goldfish)	fins	India
T. disporomorphus	macrospores: 32.1 x 8.9; microspores: 14.2 x 8.5	freshwater Cypriniformes: cyprinid (mrigal carp)	fins	India
T. dogieli (syn. *T. amurensis, carassi, cyprini, hovorkae p.p., nikolskii p.p., Disparospora thelohanellus p.p.*)	16-24 x 6.8-12.6 x 7.3-12	freshwater Cypriniformes: cyprinid (common carp, koi carp, Prussian carp, goldfish)	gills, fins, skin, mesentery, liver [cysts]	Amur Basin, Korea, Japan, Vietnam
T. dykovi (*dykovae*)	10.7 x 4.1	freshwater Cypriniformes: cyprinid (rohu)	gills	India
T. endodermitus	12.2-15.3 x 4.6-6.1	freshwater Cypriniformes: cyprinid (rohu)	scales	India
T. filli	25.7-28.5 x 10.1-11	freshwater Cypriniformes: cyprinid (rohu)	gills	India
T. fuhrmanni (syn. *Myxobolus, T. acuminatus, saurogobii*)	14-21 x 5-12 x 4.8-8	freshwater Cypriniformes: cobitid (spined loach, weatherfish), cyprinid (common carp, koi carp, mud carp, Japanese crucian carp, goldfish, common roach, common dace, ide, Russian bitterling), gobionid (Chinese lizard gudgeon), nemacheilid (stone loach)	gills, subcutis, muscles, kidneys, liver, urinary bladder, swim bladder [cysts]	Eurasia
T. gabori	8.4-8.7 x 3.6-3.7	freshwater Cypriniformes: cyprinid (Gangetic latia)	gills	India
T. gangeticus	13.8-17.5 x 4.8-7.2 x 4.8-5.5	freshwater Anabantiformes: channid (northern snakehead, blotched snakehead); Cypriniformes: cobitid	muscles, brain, kidney	India, China

		(pond loach), cyprinid (common carp, goldfish, large razorbelly minnow, greenstripe barb, stone moroko)		
T. garrae	10-12.5 x 7.2-9.2 x 5.6	freshwater Cypriniformes: cyprinid (pingi logsucker)	nephric ducts	China
T. globulosus (*globulosa*)	11.1-12.3 x 7.6-8.2	freshwater Cypriniformes: cyprinid (reba carp)	fins	India
T. goldi	8.7-10.3 x 4.1-7.9	freshwater Cypriniformes: cyprinid (goldfish)	fins	India
T. guangdongensis	13.8-17.1 x 23-46.6 x 9.2-13.3	marine Clupeiformes: clupeid (dotted gizzard shad)	muscles [pseudocysts]	China Sea
T. habibpuri	13-14.3 x 8-9	freshwater Cypriniformes: cyprinid (rohu)	fins	India
T. haldari	12.6-17.7 x 6.2-8	freshwater Cypriniformes: cyprinid (reba carp, mrigal carp)	fin, gills	India
T. hanyangensis	25-26.3 x 8-8.5 x 7-7.2	freshwater Cypriniformes: xenocypridid (silver carp)	gills	China
T. hoffmanni	12.2 x 6.4	freshwater Cypriniformes: cyprinid (goldfish)	gills	Europe (ex: China)
T. hokiangensis	22.1-25.5 x 9.3-11 x 9.3-11.9	freshwater Cypriniformes: cyprinid cyprinid (common carp)	intestines, nephric ducts	China
T. hovorkai (*hovorkae*) (syn. *T. hovorskai*) [type species]	18-22.8 x 7.2-12 x 7-10	freshwater Cypriniformes: cyprinid (common carp, koi carp, goldfish) [cycle involves aurantiactinomyxon-type actinospores in Oligochaeta: naidid (*Brachiurua sowerbyi*)]	gills, intestines, kidneys, brain, gall blader, urinary bladder, swim bladder [haemorrhagic thelohanellosis]	Asia
T. huananensis	20.4-24 x 7.8-9 x 7.2-7.4	freshwater Anabantiformes: channid (blotched snakehead, northern snakehead)	skin, intestines	China
T. hupehensis	14-16.5 x 8.4-9.6 x 8	freshwater Cypriniformes: cyprinid (goldfish)	gills, spleen, kidney	China
T. hwangkangensis (syn. *T. pyriformis p.p.*)	19.2-20.5 x 9.6-11 x 10.1	freshwater Anabantiformes: channid (blotched snakehead, northern snakehead); Cypriniformes: cyprinid (Chinese lizard gudgeon)	body surface, gall bladder, swim bladder	China
T. hwangshihensis (syn. *T. rhinogobii p.p.*)	13.2-14.5 x 5.5-6 x 6	freshwater Gobiiformes: oxudercid (gokuraku-haze)	nares, kidney, spleen, gall bladder, gonads	China
T. imphalensis	20.4-22.1 x 8.5-10.2	freshwater Cypriniformes: cyprinid (rohu)	gills	India
T. indiana	12.1-15.2 x 7.5-8.8	freshwater Cypriniformes: cyprinid (goldfish)	gills, skin, fins	India
T. jiroveci	macrospores: 31-36.1 x 11.1-13.8 microspores: 15.5-17.7 x 6.1-8.3	freshwater Cypriniformes: cyprinid (bata)	gills	India
T. kalavatae	11-12 x 4.3-5.5	freshwater Cypriniformes: cyprinid (reba carp)	fins	India
T. kalbensi	9-10 x 4.4-5.4	freshwater Cypriniformes: cyprinid (orangefin labeo)	gills	India
T. kanjalensis	11.4-11.8 x 6.4-6.8	freshwater Cypriniformes: cyprinid (catla)	snout skin	India
T. kitauei (syn. *T. xinyangensis*)	24.9 x 9.6	freshwater Cypriniformes: cyprinid (common carp, Israel carp)	intestines [cysts]	Korea, Vietnam
T. kyi (syn. *T. acuminatus p.p.*)	19.8-21.6 x 7.2-8.1	freshwater Cypriniformes: cyprinid (common carp)	gills	Vietnam
T. lagdoensis	8-9	freshwater Characiformes: citharinid (moonfish)	intestines	Cameroon
T. lamelliformis	10.2 x 4.9	freshwater Cypriniformes: cyprinid (catla)	gills	India

T. lepturus	17.2-18.3 x 8.6-9.7 x 2.3	freshwater Gymnotiformes: hypopomid (bluntnose knifefish)	brain, spinal cord	Brazil
T. leshanensis	14.8-18.4 x 8.8-10.3 x 8.8-9.6	freshwater Cypriniformes: cyprinid (common carp)	skin, fins	China
T. liaohoensis	9.4-21.8 x 6.2-12 x 5.5-10.8	freshwater Cypriniformes: cyprinid (goldfish, gold barb)	skin, gall bladder	China
T. macrovacuolaris	19.3-23.8 x 10.3-13.6 x 9.8-11.8	freshwater Cypriniformes: cyprinid (common carp)	mouth	China
T. magnacysta	13-16 x 6-8 x 5-6	freshwater Cypriniformes: cyprinid (blacktail shiner)	muscles	North America
T. marginatus	17.1 x 6.9 x 5.1	freshwater Siluriformes: pimelodid (mapara)	gills	Brazil
T. misgurni (syn. *Myxobolus*)	12-15.5 x 6-7.8 x 5-6	freshwater Cypriniformes: cobitid (weatherfish), cyprinid (mud carp), nemacheilid (Berezowskii's loach); Gobiiformes: oxudercid (unspecified stream goby)	gall bladder	Korea, Japan
T. mrigalae	10.8-12 x 6.3-7.2	freshwater Cypriniformes: cyprinid (reba carp, mrigal carp)	skin	India
T. muscularis	9.1-9.2 x 3.9-4	freshwater Cypriniformes: cyprinid (rohu)	cranial muscles	India
T. mylopharyngodoni	15.6-21.6 x 7.8-8.4 x 7.2-7.8	freshwater Cypriniformes: cyprinid (black carp)	gall bladder	China
T. nanhaiensis	15.6-18 x 9.6-10.8 x 7.4-8.2	freshwater Cypriniformes: cyprinid (goldfish)	gills	China
T. narasimhamurtius	9-10 x 2.3-3.5	freshwater Cypriniformes: cyprinid (mola carplet)	gills [necrosis]	India
T. ndjamenaensis	10-11 x 7-8	freshwater Cypriniformes: cyprinid (African carp)	gills	Tchad
T. neocyprini	33-35 x 8.5-9.6	freshwater Cypriniformes: cyprinid (catla)	gills	India
T. nemachili	13.2-14.4 x 7.2-7.8 x 5.9-6.1	freshwater Cypriniformes: cyprinid (mud carp)		China
T. nikolskii (syn. *T. callisporis, cyprini*)	16.5-25.2 x 10-16.2 x 12.2	freshwater Cypriniformes: cyprinid (common carp, koi carp, goldfish) [cycle involves aurantiactinomyxon-type actinospores in Oligochaeta: naidid (*Tubifex tubifex*)]	cartilage, gills, skin [fin lesions]	Asia
T. niloticus (syn. *Myxobolus unicapsulatus*)	20.4-27.1 x 11.5-14.2	freshwater Cypriniformes: cyprinid (Nile carp)	gills	Africa
T. njinei	13-16 x 7.3-9	freshwater Siluriformes: schilbeid (African butter catfish)	intestines	Cameroon
T. notatus (syn. *Myxobolus*)	11.8-20 x 5.5-10 x 5.5-6.5	freshwater Cypriniformes: cyprinid (bluntnose minnow, bullhead minnow, common shiner, golden shiner, river shiner, blacknose shiner, spottail shiner, common roach, finescale dace, white sucker, creek chub)	subcutis [tumours]	North America
T. oculileucisci (syn. *Myxobolus*)	7-14 x 4.5-7.1 x 3	freshwater Cypriniformes: cyprinid (koi carp, crucian carp, Prussian carp, goldfish, ide, common dace, Siberian dace, common roach, taran, common bream, white bream, Russian bitterling, gudgeon)	eyes, brain [cysts]	Europe
T. odontobutis	11.8-14.4 x 5.3-6.6 x 3.9-5.3	freshwater Gobiiformes: odontobutid (dark sleeper)	kidney, urinary bladder	China
T. oklahomaensis	11.1-13.3 x 8.2-9.8	freshwater Cypriniformes: catostomid (quillback)	gills	North America
T. oliviformis	10.8-13.5 x 5.4	freshwater Cypriniformes: cyprinid (goldfish, Prussian carp)	muscles	China

T. ophiocephali	18-22.8 x 10.2-12 x 7.2-9	freshwater Anabantiformes: channid (blotched snakehead, northern snakehead)	skin	China
T. ophthalmicus	12.1-13.2 x 6.6-7.7	freshwater Cypriniformes: cyprinid (catla); Gobiiformes: gobiid (tank goby)	eye	India
T. orissae	macrospores: 11.4-16.3 x 3.2-6.5 microspores: 6-9 x 2.5-4.5	freshwater Cypriniformes: cyprinid (mrigal carp)	gills	India
T. otebike	14.4-15.3 x 6.7-7.5	freshwater Cypriniformes: nemacheilid (eastern crested loach)	gills	Uzbekistan
T. oviformis	10.5-14 x 7.5-9.5 x 6.5-7	freshwater Cypriniformes: cyprinid (golden shiner)	eye, muscle	Canada
T. paludicus	14-15.3 x 8-8.7	Freshwater Cypriniformes: cobitid (southern Iberian spined-loach)	intestines	Portugal
T. parasagittarius	22.8-24.6 x 10.2-12 x 10.8	freshwater Cypriniformes: cyprinid (common carp, goldfish)	gills, skin, gall bladder	China
T. parasilurus	12-13.8 x 8.4-9.6 x 6-7.2	freshwater Siluriformes: silurid (Amur catfish)	gall bladder	China
T. parastromataei	10.7-12 x 8.6-10.3	marine Carangiformes: carangid (black pomfret)	gall bladder	India
T. pathankotensis	9.7 x 3.8	freshwater Cypriniformes: cyprinid (indigenous carp)	gills, fins	India
T. pekingensis	20.4-24 x 9.5-11.8 x 7.2-8.4	freshwater Cypriniformes: cyprinid (common carp)	skin, kidneys	China
T. potaili	12.1-16 x 7.9-9.5	freshwater Cypriniformes: cyprinid (Deccan labeo)	fins	India
T. pseudonikolskii	12.3-15.1 x 7.6-9.1	freshwater Cypriniformes: cyprinid (goldfish)	fins	China
T. pyriformis (syn. *Myxobolus piriformis*)	13-24 x 6-12 x 6.5-6.7	freshwater/marine Anabantiformes: channid (northern snakehead); Cypriniformes: cobitid (weatherfish, spined loach), cyprinid (common roach, common rudd, common dace, Siberian dace, ide, asp, tench, common bream); Salmoniformes: salmonid (peled, common whitefish, broad whitefish); Perciformes: percid (yellow perch); Pleuronectiformes: pleuronectid (European flounder)	gills, muscles, subcutis, intestinal wall, liver, gall bladder, swim bladder, kidneys [cysts]	Eurasia
T. qadrii	14.3-17.1 x 5-6	freshwater Cypriniformes: cyprinid (Deccan labeo)	gills	India
T. qinghoensis	15.8-19.8 x 8.6-11.2	freshwater Cypriniformes: cyprinid (koi carp)	body surface	China
T. relortus	15-17.4 x 9.5-9.8 x 8.4-8.6	freshwater Cypriniformes: cyprinid (goldfish)	gills	China
T. rhabdalestus	16.8 x 10.2 x 5.6	freshwater Characiformes: alestid (Okavango robber)	liver, heart	Angola
T. rhinogobii	10.4-13 x 5.6-7.2 x 6.3-7.2	marine/freshwater Gobiiformes: oxudercid (bar cheek goby)	gall bladder, kidneys	China
T. rodgii	31-41 x 10-15	freshwater Cypriniformes: cyprinid (orangefin labeo)	gills	India
T. rohi	14.5 x 7.7	freshwater Cypriniformes: cyprinid (rohu)	fins	India
T. rohitae (syn. *Myxobolus*)	25.8-33 x 7.2-13 x 7.2-8.6	freshwater Cypriniformes: cyprinid (common carp, rohu, bata, orangefin labeo, Kali labeo, white Amur bream, olive bream)	gills, body surface, scales, nasal cavity, ureters, urinary bladder	India, China
T. sagittarius	19.2-20.6 x 8-10.2 x 8	freshwater Cypriniformes: cyprinid (common carp, grass carp, goldfish)	kidney	China

T. sanagaensis	10.5-13.5 x 8.2-10.5	freshwater Cypriniformes: cyprinid (unspecified labeo)	gills, fins	Cameroon
T. sanjibi	12-13 x 8-8.5	freshwater Siluriformes: bagrid (long whiskers catfish)	kidney	India
T. saurogobii	14-15 x 5.8-6	freshwater Cypriniformes: cyprinid (Chinese lizard gudgeon)	eyes	Russia
T. schizothoraxi	12-12.8 x 5.6-6.8 x 6.1	freshwater Cypriniformes: cyprinid (marinka tsunynska)	kidneys	China
T. seni (syn. *Myxobolus*)	12.5-14.9 x 8.6	freshwater Cypriniformes: cyprinid (catla)	gills	India
T. shaochingensis	12-14.4 x 6.6-8.4 x 4.8-6	freshwater Anguilliformes: anguillid (Japanese eel); Cypriniformes: acheilognathid (Japan fish); Gobiiformes: oxudercid (bar cheek goby, Pope's river goby)	gills, fins, skin, intestines, kidneys	China
T. shortii	11.4-12.9 x 6.4-7.1	freshwater Cypriniformes: cyprinid (fringe-lipped peninsula carp)	fins	India
T. sinensis	13.5-16.2 x 9.2-11.1 x 6.8-8	freshwater Anabantiformes: channid (northern snakehead, blotched snakehead); Anguilliformes: anguillid (Japanese eel); Gobiiformes: oxudercid (bar cheek goby, Pope's river goby)	gills, skin, intestines, kidneys	China
T. spirosuturalis	21.6-27.6 x 12-13.2 x 9.6-10.8	freshwater Anabantiformes: channid (northern snakehead)	caecum	China
T. squaliobarbi	35-40 x 15-16 x 13	freshwater Cypriniformes: cyprinid (barbel chub)	gills, intestines	China
T. sudevi	13-15 x 5-6.5	freshwater Cypriniformes: cyprinid (mola carplet)	kidney	India
T. swellengrebeli	10.3-16.2	freshwater Cypriniformes: acheilognathid (European bitterling)	muscles	Netherlands
T. taguii	19-23 x 5-6.5	freshwater Characiformes: citharinid (moonfish)	opercular muscles, gills, intestines, liver	Tchad
T. testidineus	18.6-20.8 x 6.6-8.4	freshwater Cypriniformes: cyprinid (goldfish, Prussian carp)	skin	China
T. thaili	11.6 x 7.2	freshwater Cypriniformes: cyprinid (bata, catla)	gills	India
T. theinensis	8.1-8.4 x 4.2-4.6	freshwater Cypriniformes: cyprinid (bata)	gills	India
T. tilapiae (mis-spelling '*talipiae'*)	24-28.8 x 13.2-15.6 x 7.2-8.4	freshwater Cichliformes: cichlid (Mozambique tilapia); Cypriniformes: cyprinid (Amur carp)	gills, intestines	China
T. tintinus	18-24.5 x 7.8-9.3 x 6.3-7.6	freshwater Anabantiformes: channid (blotched snakehead)	skin	China
T. tripurensis	17-18 x 9.5-11	freshwater Cypriniformes: cyprinid (orangefin labeo, Kuria labeo, bata, reba carp)	fins	India
T. valeti	11-13 x 4-5.2	freshwater Cypriniformes: cyprinid (Jae barb, kameruni pardkala)	gills, stomach	Cameroon
T. wallagoi	8-11.2 x 4-6.4	freshwater Siluriformes: silurid (wallago)	gall bladder	India
T. wananensis	23-25 x 10.5-11 x 14.5-15	freshwater Cypriniformes: cyprinid (common carp)	gills	China
T. wangi	16.5-22.3 x 9.1-10.8 x 8.2-10.4	freshwater Cypriniformes: cyprinid (gibel carp, Prussian carp, goldfish)	gills	China
T. wuhanensis	21-25 x 12-15.5 x 10-12.5	freshwater Cypriniformes: cyprinid (goldfish, Prussian carp)	skin	China
T. wusihensis	15.6-17 x 9.6-12 x 9.6-12	freshwater Cypriniformes: cyprinid (grass carp)	fins	China
T. yangtzensis	10.8-13.1 x 6.2-6.9 x 5.6	freshwater Gobiiformes: oxudercid (bar cheek goby)	gills, skin, intestines, gall	China

			bladder, kidneys	
T. yiduensis	30.5-33.6 x 7.9-10.7 x 6.6-8.2	freshwater Acipenseriformes: acipenserid (Chinese sturgeon); Anabantiformes: channid (blotched snakehead); Cypriniformes: cyprinid (koi carp, Amur carp)	gills, skin	China
T. zahrahae	21.7-26.3 x 8.5-9.4 x 7.5-7.9	freshwater Cypriniformes: cyprinid (Java barb)	gills	Malaysia
Genus ***Trigonosporus*** (triangular spores with long filamentous processes, 2 polar capsules)				
T. acanthogobii [type species]	7.3-10.5 (+ tail 50.4-99.1) x 11-18 x 4.7-6	marine/estuarine/freshwater Gobiiformes: gobiid (yellowfin goby)	gills	Japan
T. zhejiangensis	8.8-10.3 x 3.3-4.1 x 2-2.6	freshwater Gobiiformes: gobiid (Asian freshwater goby)		China
Genus ***Unicauda*** (spores with single caudal appendage, 2 polar capsules)				
U. andhrae	38.4-47.3 (incl. tail 20.8-24.5) x 4-5.4	freshwater Anabantiformes: channid (dwarf snakehead)	gills	India
U. aplocheili	16.8-18.2 x 9.8-11.2 x 5.6-7	freshwater Cyprinodontiformes: aplocheilid (blue panchax)	skin, scales [ulcers]	India
U. aristichthydis	20-24 (9.6-11.2) x 5.6-6.3 x 5.6	freshwater Cypriniformes: cyprinid (bighead carp)	nephritic ducts	China
U. basiri	25.6-39.2 (incl. tail 10-20.3) x 3.2-4.4	freshwater Anabantiformes: channid (spotted snakehead)	pharyngeal epithelium	India
U. bengalensis	26.4-29.2 (incl. tail 11.5-13.8) x 2.7-3.9	freshwater Anabantiformes: channid (spotted snakehead)	buccal cavity	India
U. bicornuata	35.7-45.7 (incl. tail 14.3-27.1) x 2.9-4.3	freshwater Anabantiformes: channid (spotted snakehead)	gills, branchial epithelia	India
U. brachyura (syn. *Henneguya*)	10-11.5 (+ tail up to 17) x 8-8.7 x 4-5	freshwater Cypriniformes: cyprinid (pugnose shiner)	fins	North America
U. carassii (syn. *Henneguya*)	21 (14) x 10	freshwater Cypriniformes: cyprinid (Prussian carp)	kidney	Japan
U. caudatus (syn. *Myxobolus cutanei*)	10.5-12.5 x 8-9.7 x 6-6.5	freshwater Cypriniformes: cyprinid (Iberian barbel, Kura barbel)	scales, skin	Spain
U. chaudhuryi	26.3-33.2 (+ tail 14.5-20) x 3.3-4.4	freshwater Anabantiformes: channid (spotted snakehead)	gills	India
U. clavicauda (syn. *Henneguya*) [type species]	10.5-11.5 (+ tail 20-30) x 8.5-9.5 x 6	freshwater Cypriniformes: cyprinid (river shiner, spottail shiner)	subcutis	North America
U. crassicauda (syn. *Henneguya*)	12-14.5 (+ tail 40-55) x 8.5-10.5 x 6-7	freshwater Cypriniformes: cyprinid (central stoneroller, northern pikeminnow)	skin, fins	North America
U. fimbrethlae	70.9-126 (6.7-7.8) x 6.1-8	freshwater Siluriformes: ictalurid (channel catfish)	intestines	North America
U. fontinalis (syn. *Henneguya*)	18.2-23 (9.1-14.2) x 7.3-10.6 x 18.8-23	freshwater Cypriniformes: cyprinid (common shiner, blacknose shiner); Salmoniformes: salmonid (brook trout)	fins, skin	Canada
U. irregularis	24-39.1 (9.7-19.5) x 4.9-6.5	freshwater Siluriformes: bagrid (striped dwarf catfish)	muscles	India
U. lumae	10-15 (incl. tail 2-8.4) x 8.5-10	freshwater Cypriniformes: cyprinid (shabout)	liver	Iraq
U. macrura	10-11 (+ tail 30-40) x 6-8	freshwater Cypriniformes: cyprinid (Mississippi silvery minnow)	cranial skin	North America
U. magna	14-17 (+ tail 60-154) x 12-14.5 x 10-13	freshwater Cypriniformes: cyprinid (fathead minnow)	fins	North America
U. minuta	16.3-26 (8.1-13) x 3.2-5.7	freshwater Cichliformes: cichlid (green chromide)	gills	India

U. monera (syn. *Myxobolus monurus*)		freshwater Percopsiformes: aphredoderid (pirate perch)	subcutis	North America
U. ophiocephali	41.5-52.5 x 6.2-7.2	freshwater Anabantiformes: channid (spotted snakehead, dwarf snakehead)	muscles, gills	India
U. pelteobagrus	31.2-39.2 (12.5-14.5) x 7-8.5 x 5.2-5.6	freshwater Siluriformes: bagrid (yellowhead catfish, darkbarbel catfish, korakinos)	gills, muscles	China
U. percae (syn. *Henneguya*)	23.6-35 (13.2-16.8) x 9.2-12.3	freshwater Perciformes: percid (yellow perch)	gills	Canada
U. plasmodia (syn. *Henneguya*)	21 (6) x 7-8 x 6	freshwater Cypriniformes: cyprinid (central stoneroller); Siluriformes: ictalurid (channel catfish)	gills	North America
U. ritae	39.9-44.8 (incl. tail 27.2-31.5) x 5-5.8	freshwater Siluriformes: bagrid (rita)	gills	India
U. spatulata (syn. *Henneguya*)	16-16 (+ tail 25) x 13-16	freshwater Cypriniformes: cyprinid (Prussian carp)	spleen, kidney	Japan
U. strongylurus (*strongylura*) (syn. *Henneguya, Myxobolus*)	9 x 5.4	freshwater Siluriformes: mochokid (wahrindi)	cranial skin	Egypt
U. theraponi	27.7-39.1 (14.6-22.8) x 4-8.1	marine Perciformes: terapontid (crescent grunter)	gills	India
U. trentinii	12-18 (7-11) x 4-6)	freshwater Osteoglossiformes: mormyrid (Peter's elephantnose fish)	intestinal wall, kidney, gall bladder	Nigeria
U. wuhanensis	23.5 (10.1-11) x 4.6-5.1 x 2.8-3.3	freshwater Cypriniformes: cyprinid (silver Prussian carp)	skin, nose	China
U. xihuensis	23.3-40.7 (7.3-9.3) x 5.7-6.3 x 4.7-6	freshwater Cypriniformes: cyprinid (Japanese white crucian carp)	muscles	China
Order **MULTIVALVULIDA** (radially symmetrical spores with 3-13 valves (rarely 2), each with a polar capsule)				
considered in separate section				

Another myxozoan class has recently been recognized: the Malacosporea containing species with soft shell valves and rudimentary worm-like (myxoworm) stages in bryozoans or saccular stages (fishmalacospores) in fish.

Parasite species	**Spore dimensions (µm)**	**Hosts**	**Location**	**Distribution**
Class: **MALACOSPOREA** (spores with soft (unhardened) shell valves)				
Order: **MALACOVALVULIDA** (trophic stages worm-like or sac-like)				
Family: **Saccosporidae** (with characters of order)				
Genus ***Buddenbrockia*** (trophic stages irregular elongate shape (myxoworm))				
B. allmani	20	freshwater Bryozoa: lophopodid (*Lophopus crystallinus*)	body cavity	Europe
B. plumatellae (syn. *Tetracapsula bryozoides*) [type species]	10-18	freshwater Bryozoa: plumatellid (*Plumatella repens, fungosa, Hyalinella punctata*), fredericellid (*Fredericella sultana*)	body cavity	Europe
Genus ***Tetracapsuloides*** (trophic stages regular spherical shape (fishmalacospores))				
T. bryosalmonae (syn. *Tetracapsula bryosalmonae, renicola*) [type species]	12 x 7	freshwater Salmoniformes: salmonid (rainbow trout, steelhead trout, brown trout, Arctic char, grayling, Atlantic salmon, chinook salmon, coho salmon); Esociformes: esocid (pike)	kidneys [proliferative kidney disease (PKD/PKX)]	Northern Hemisphere

		[cycle involves fishmalacospores in Bryozoa: plumatellid (*Plumatella fungosa, rugosa, Pectinatella magnifica*), cristatellid (*Cristatella mucedo*), fredericellid (*Fredericella sultana*)]		

It has now been demonstrated that some myxosporean parasites have heteroxenous (2-host) life-cycles involving the formation of actinospores in annelid hosts and myxospores in piscine hosts. Early classification schemes placed all actinospores in the order Actinomyxida, characterized by spore bodies containing 3 apical polar capsules (often with protruding tips) and most with 3 long hollow caudal projections which inflated osmotically in water to provide spore buoyancy for dispersal in water currents. Four families were recognized from oligochaetes and sipunculids: Tetractinomyxidae (*Tetractinomyxon*); Sphaeractinomyxidae (*Neoactinomyxum, Sphaeractinomyxon*); Triactinomyxidae (*Antonactinomyxon*, *Aurantiactinomyxon*, *Echinactinomyxon*, *Guyenotia*, *Raabeia*, *Siedleckiella*, *Synactinomyxon*, *Triactinomyxon*); and Hexactinomyxidae (*Hexactinomyxon*). However, with the discovery that these stages represent different stages in the life cycles of myxosporean parasites, it was suggested that actinosporean classification be suppressed and that actinospores be assigned to collective groups with vernacular names. To date, some 20 groups have been identified: anton-, auranti-, echin-, hex-, hung-, ormier-, pseudtri-, seis-, sphaer-, syn-, tetra-, tri-, unicapsul-actinomyxon, neoactinomyxum, saccimyxon, endocapsa, guyenotia, raabeia, siedleckiella, and tetraspora (with key characters tabulated below).

Actinospore type	**Spore**		**Polar capsules**	**Other characters**	**Hosts**
	Body shape	**Projections**			
antonactinomyxon	ellipsoidal	long, lanceolate, divergent	pyriform (protruding tips)	groups of 8 spores form cuboidal networks	freshwater oligochaetes
aurantiactinomyxon	ellipsoidal	short, stout, curved, leaflike, divergent	pyriform (protruding tips)	spores appear triradiate from above	freshwater oligochaetes
echinactinomyxon	rectangular	straight, tapered, blade-like, divergent	pyriform (slightly protruding)	spores appear stellate	freshwater oligochaetes
endocapsa	subspherical	small, bulge-like caudal swellings	pyriform (not protruding)	spores compact	marine oligochaetes
guyenotia	subspherical	long, stout, blunt, grouped	pyriform (protruding tips)	spores tripod-like	freshwater oligochaetes
hexactinomyxon	rectangular	long, thin, pointed, bifurcate	pyriform (protruding tips)	spores anchor-like	freshwater oligochaetes
hungactinomyxon	subspherical	long, tapering, divergent	rounded (not protruding)	spores form interlaced cuboidal networks	freshwater oligochaetes
neoactinomyxum	subspherical	absent	pyriform (protruding tips)	spores appear triangular from above	freshwater oligochaetes
ormieractinomyxon	ovoid	long, tapering to thin rod, terminal anchor-like structures	pyriform (protruding tips)	groups of spores interlock to form chains	freshwater oligochaete
pseudtriactinomyxon	ovoid	long, blade-like, divergent	pyriform (protruding tips)	projections with longitudinal suture	freshwater oligochaetes
raabeia	ellipsoidal	long, tapering, curved, divergent	pyriform (protruding lips)	spores grapplehook-like	freshwater oligochaetes
saccimyxon	saccular	absent	pyriform (not protruding)	spores appear globular	marine polychaetes and sipunculids
seisactinomyxon	rectangular	long, stout, divergent, bifurcate	pyriform (protruding lips)	spores grapplehook-like	freshwater oligochaetes
siedleckiella	ellipsoidal	long, stout, divergent	pyriform (protruding tips)	groups of spores form interlocked mesh	freshwater oligochaetes
sphaeractinomyxon	subspherical	absent	pyriform (not protruding)	spores solid, rounded	freshwater and marine oligochaetes
synactinomyxon	spherical	each valve with one short anterior and 2 long caudal processes	round (not protruding)	spores stellate with sinuous projections	freshwater oligochaetes
tetractinomyxon	pyramidal	absent	pyriform (not protruding)	spores appear triangular	freshwater and marine polychaetes,

					sipunculids
tetraspora	subspherical	absent	pyriform (not protruding)	spores antero-posteriorly flattened	marine oligochaetes
triactinomyxon	rectangular	long, tapering, pointed, curved	pyriform (protruding tips)	spores anchor-like	freshwater and marine oligochaetes
unicapsulactinomyxon	ovoid	long, thin, pointed, one anterior, 2 posterior	single large polar capsule	polar capsule opens laterally	marine polychaetes

Parasite morphology: Myxozoan parasites are multicellular (sometimes termed 'pluricellular') aquatic parasites that include myxosporeans, actinosporeans and malacosporeans. Myxosporeans develop in vertebrate hosts (mainly fish) where they form 5 different developmental stages: namely, trophozoites, plasmodia, pansporoblasts, sporoblasts and myxospores. The earliest developmental stages are trophic stages which range from the small invasive uninucleate amoebulae (around 10 μm in diameter) to larger multinucleate trophozoites (up to 80-100 μm) which often develop in the same tissues as spore formation (although a few species undergo an 'extrasporogonic' cycle in different tissues). The trophozoites form cell doublets by nuclear division and endogeny whereby secondary daughter cells are formed within vacuoles in primary maternal cells (this enveloped 'cell-in-cell' condition is typical for myxozoa). This generates polymorphic stages in which growth and proliferation of the secondary cells occurs either within host tissues (histozoic) or within body-organ cavities (coelozoic). These stages generally take 3 forms: remaining as small microscopic (~ 10 um) pseudoplasmodia (usually histozoic) initially containing one vegetative nucleus and producing 1-2 spores; growing to small intermediate (~ 100 um) plasmodia (usually coelozoic) that are mictosporic producing 1, 2 or more spores; or growing to form large (up to 2-4 mm) plasmodia typically containing many nuclei and specialized cells producing masses of spores. The plasmodia may vary in shape from flat sheet-like to round sac-like to elongate worm-like stages, and large histozoic plasmodia often becoming ensheathed by host connective tissue cells thus forming whitish 'myxosporean' cysts. Some coelozoic species may adhere to cavity walls by developing temporary cytoplasmic holdfast outgrowths (occasionally called pseudopodia). Plasmodia have been described as undergoing division by plasmotomy, exogenous or endogenous budding. Most species undergo spore formation (sporogenesis) within pansporoblasts formed when vegetative cells (pericytes) envelope generative (sporogonic) cells, although some species forming small pseudoplasmodia undergo direct sporogenesis without pansporoblast formation. Sporogonic cells divide by binary fission giving rise to sporoblast cells that undergo valvogenic, capsulogenic and sporoplasmic differentiation to form hard-shelled myxospores with multiple shell valves joined along suture lines, nematocyst-like polar capsules and amoeboid infective sporoplasms. Conventionally, myxosporean taxonomy has been based on the configuration of the mature spores, with those of bivalvulid species containing 2 shell valves, 1-4 polar capsules (usually 2), and 1-2 sporoplasms (rarely up to 12 as in *Polysporoplasma*), whereas multivalvulid species contain 3-13 valves (rarely 2), 1-13 polar capsules (rarely more) and 1-2 sporoplasms. Bivalvulids have conventionally been divided into 3 suborders depending on the location and orientation of the polar capsules: Platysporina with 2 apical polar capsules parallel to the sutural plane; Eurysporina (Unipolariina) with 2 apical polar capsules perpendicular to the sutural plane; and Bipolarina with 2 polar capsules located at opposite ends of the spore perpendicular to the sutural plane (although recent studies have united the latter two into a single suborder Variisporina). Mature myxospores may be spherical, pyriform, fusiform, crescentic or spindle-shaped and usually range in size from 10-20 μm in length or width (width measured in plane of suture). The shell valves may have smooth or longitudinal/oblique ridged surfaces, often with structures drawn out into lateral or caudal appendages, and sometimes with mucous envelopes. The polar capsules are pyriform or globular measuring 2-10 μm long and have thick-walled vacuoles elongate polar filaments in 4-9 coils although some are layered in zig-zag fashion. Myxospores contain either a single binucleate sporoplasmic cell or 2 uninucleate sporoplasmic cells. Some spores also contain distinctive 'iodinophilous' vacuoles formed by polysaccharide reserves concentrated into round inclusion bodies.

Actinosporeans develop in annelid invertebrates by undergoing asexual merogonous multiplication (plasmotomy) followed by sexual multiplication involving meiosis (gametogony) and then actinospore formation (sporogony). A growing number of actinosporeans from invertebrates have been shown to be alternate stages in the life-cycles of myxosporeans from vertebrates. Actinosporeans form 4 different types of stages: namely, trophozoites, meronts, pansporocysts and actinospores. Trophic stages include uninucleate invasive amoebulae (10-20 μm), multinucleate trophozoites (15-30 μm) and proliferative meronts which undergo plasmotomy to produce numerous uninucleate cells that invade intercellular spaces (some species undergoing multiple merogonic cycles giving rise to more progeny). Cells then form pansporocysts up to 100 μm in diameter which undergo gametogony (sexual multiplication with meiosis) involving the formation of a complex of 4 cells, 2 outer cells enveloping 2 inner cells which divide several times to produce 16 gametes that fuse to form 8 zygotes (4 zygotes for *Tetraspora* spp.). This gametogony is the only known sexual process for myxozoan parasites, so annelids must be considered as definitive hosts (and vertebrates as intermediate hosts). The zygotes develop and mature to form typical actinospores which are often shaped like boat anchors, having shell valves with tri-radiate caudal projections arising from an elongate spore body containing 3 anterior polar capsules and multiple sporoplasms. Actinospores are extremely variable in size, ranging from around 10 μm for members of the collective neoactinomyxum group up to several hundred μm for triactinomyxon and raabeia groups.

Malacosporeans comprise a small number of species shown to develop in bryozoan invertebrates where they form 3 different types of developmental stages: trophozoites, vegetative stages and malacospores. Trophozoites are unicelluar invasive stages which

form larger multinucleate multiplicative stages in either hollow rounded sacs or larger vermiform bodies that may measure up to 2 mm in length. Mature spores, or malacospores, measure around 19 µm in diameter, and are comprised of 8 valvogenic cells, 4 capsulogenic cells with spherical to subspherical polar capsules, and 2 sporoplasmic cells (some of which may contain a secondary cell).

Site of infection: Myxosporean infections in vertebrate hosts may be coelozoic (inhabiting cavities) and/or histozoic (within tissues), with developing stages and spores usually found in specific locations (implying strict tissue tropism) although some species are more disseminated throughout their hosts. Coelozoic species are usually found in the gall bladder but can occur in other body/organ cavities (urinary bladder, swim bladder, intestines), whereas histozoic species may infect a variety of tissues and organs (cutis, gills, muscles, central nervous system, cartilage, kidney, liver, and gut wall). Myxospores have been found in freshwater and marine fish around the world, including anadromous species (that migrate from the sea into freshwater to spawn) and catadromous species (that migrate from freshwater into the sea to spawn), as well as those inhabiting brackish and estuarine waters. Some 2,945 species of bivalvulid myxosporeans have been found in 540 species of marine fish (from 211 families in 61 orders), 1,100 species of freshwater fish (from 126 families in 35 orders), 120 amphibian species (90 frog species from 16 families, 14 toad species from 1 family, 17 urodelan species from 5 families, 1 caecilian species), 17 reptile species (testudines from 5 families), one bird species, 2 shrew species, and 2 trematode species (one monogenean and one digenean, both in fish). In comparison, only around 160 multivalvulid species have been found in 300 species of marine fish (from 105 families in 36 orders) and a dozen species of freshwater fish (from 6 families in 5 orders). Actinosporean infections in annelids are usually coelozoic in the body cavity, although some stages have been detected in association with the gut wall, and rarely with the epidermis. Actinospores have been recorded in a number of freshwater and marine oligochaetes (mainly in genera of the families Tubificidae and Nadidae), a freshwater polychaete (family Fabriciidae), a growing number of marine polychaetes (families Nereididae, Sabellidae, Spionidae and Spirorbidae) and a few sipunculids (family Golfingiidae). The enigmatic malacosporeans have been found in 5 bryozoan species (from 3 families) and some 10 species of freshwater fish (from 2 families in 2 orders).

Pathogenesis: Most myxosporean infections in fish are benign and not associated with any overt clinical disease. Light and moderate infections cause little damage to host tissues and are often considered latent (condition sometimes referred to myxosporidiasis), while heavier infections may cause sufficient tissue damage to manifest in clinical signs (referred to as myxosporidiosis – although disease due to specific genera may be named accordingly, e.g. myxoboliosis, thelohanellosis, etc.). Infections in fish may be coelozoic and/or histozoic in nature, with developing parasites and spores confined to specific body/organ cavities or encased in various host tissues. Infections may cause structural disturbances in infected tissues or organs, which may or may not be accompanied by functional deficits. Coelozoic species in the lumina of tubular organs are usually benign, although heavy infections of the gall bladder or urinary bladder may sometimes cause abnormal appearance in the size and colour of the organ, sometimes resulting in blockage, inflammation, dilatation and/or degeneration of infected ducts or tubules. Histozoic species tend to form multiple developmental stages within specific tissues either as diffuse small pseudoplasmodial infiltrates or as discrete confined plasmodial lesions (usually microscopic but some grow to macroscopic sizes). Most stages cause little associated tissue damage, but numerous and/or large stages may cause space-occupying lesions in infected tissues and organs. Parasite developmental stages usually do not elicit strong host cellular responses, although moderate inflammation and fibrous encapsulation have been reported in some infections. Large lesions may sometimes become encapsulated by connective tissue walls (cells and fibres) forming whitish 'cysts'. Even then, tissue damage and inflammation when present is usually minimal and localized. Nonetheless, infections have been associated with overt disease and death, often involving species that invade vital organs, notably the gills, brain, heart and skeletal system. For example, lesions in nervous tissues may cause behavioural disorders (such as abnormal tail-chasing, called whirling disease), lesions in cartilage may lead to deformities (especially of the head and spine), and lesions in musculature have been associated with tissue myoliquefaction (due to the post-mortem release of parasite proteolytic enzymes during processing by filleting, freezing/thawing, cooking, smoking). The course and severity of disease varies according to parasite pathogenicity (species/strain virulence), host susceptibility (age, physiological and immune status), the intensity of infection, and the organ systems involved. Because many myxosporean species exhibit relatively strong tissue tropism and appear to have predilection sites of infection, it is often pertinent to consider pathological changes and clinical manifestations based on the organs and tissues infected.

- Skin, scales, fins and subcutaneous tissues: While infections at these sites often do not constitute direct health hazards to fish, they can adversely affect fish trades by producing unsightly lesions that reduce their marketability. A number of species have been associated with macroscopic cysts (e.g. *Myxobolus diversus* and *Myxobolus rotundus* in goldfish), tumor-like growths (e.g. *Henneguya rubicundi* in eel gobies, *Myxobolus esomi* in flying barbs, *Myxobolus rohitae* in rohu), gross swellings (e.g. *Thelohanellus wuhanensis* in Prussian carp), dermal erosion/attenuation (e.g. *Myxobolus episquamalis* in mullet), ulcerative lesions (e.g. *Unicauda aplocheili* in blue panchax, *Thelohanellus hovorkai* in koi carp), fin deformation (e.g. *Thelohanellus nikolskii* in cyprinids), and opercular, head and buccal cavity irregularities (e.g. *Myxobolus drjagini* causing twist disease in silver carp).

- Striated musculature: Infections of somatic skeletal muscles are usually confined to focal lesions or pockets, rather than being disseminated. A growing number of species have been associated with clinical conditions affecting the market value of fish products, including surface blemishes and local swellings sometimes leading to pressure atrophy and blockages with necrosis,

discolourations and dropsy (e.g. *Myxobolus artus* and *Myxobolus cyprini* in carp, *Myxobolus pseudodispar* in roach, *Myxobolus musculi* in barbels), gross swellings (e.g. *Myxobolus lentisuturalis* in Prussian carp), 'boils' (e.g. *Myxobolus pfeifferi* in barbels), and myoliquefaction (milky flesh) often discovered during processing (e.g. *Henneguya zschokkei* in whitefish, *Henneguya salminicola* in salmonids). Infections of cardiac muscles, while rare, are often severe with corrosion, hyaline degeneration, granulation and destruction (e.g. *Henneguya otolithi* in croakers, *Myxobolus etropli* in green chromides).

- Gills: Heavy infections can compromise respiratory function when parasites disrupt the epithelium causing hyperplasia, haemorrhages, inflammation, lamellar fusion and space-occupying lesions with pressure atrophy and cellular necrosis. Infections can be intralamellar (e.g. *Myxobolus sophorae* in pool barb, *Henneguya waltairensis* in spotted snakehead) or interlamellar (e.g. *Myxobolus sphaeralis* in largescale mullet, *Henneguya exilis* in catfish), and sometimes extend to pseudobranchs (e.g. *Parvicapsula pseudobranchicola* in Atlantic salmon). Several species have been associated with proliferative gill diseases (e.g. *Henneguya ictaluri* in catfish), severe hyperplasia (e.g. *Sphaerospora molnari*, *Sphaerospora chinensis* and *Myxobolus pavlovskii* in carp), and large cyst formation (e.g. *Henneguya creplini* in zander, *Henneguya psorospermica* in pike and perch, *Myxobolus basilamellaris* and *Myxobolus koi* in carp). Infections may compromise fish health with decreased feeding, lethargy, erratic swimming, loss of equilibrium (e.g. *Henneguya piaractus* in pacu) and sometimes exophthalmia possibly leading to blindness (e.g. *Parvicapsula pseudobranchicola* in Atlantic salmon).

- Central nervous system: A variety of myxosporean species have been found infecting the brain and spinal cord of fish and amphibians. Many infections apparently do not cause clinical signs (e.g. *Myxobolus galaxii* in mountain galaxias, *Myxobolus neurophilus* in yellow perch, *Myxobolus inaequus* in knife fish), but some cause encephalitis and large cystic space-occupying lesions (e.g. *Myxobolus arcticus* in salmonids, *Myxobolus hendricksoni* in fathead minnows, *Myxobolus neurobius* in brown trout, Atlantic salmon and grayling, *Myxobolus encephaliticus* in bata). Other species have been associated with behavioural abnormalities, such as altered orientation and swimming (e.g. *Myxobolus arcticus* in salmonids, *Myxobolus encephalicus* in carp, *Myxobolus balantiocheirli* in sharkminnows).

- Cartilage: Infections in bone are rare and usually contained, while infections in cartilage may result in extensive hypertrophy resulting in deformation with pernicious behavioural changes. A well-known example is *Myxobolus cerebralis* in salmonids where infections cause chronic granulomatous inflammation, necrosis and fibrosis of cartilage resulting in constriction and pressure on the spinal cord and lower brainstem and even producing gross disfiguration. Structural and behavioural abnormalities include shortening of the mandible (lower jaw) and opercula (gill covering), gaping mouths, dorsal humps, discoloured twisted or bent tails, spinal curvatures, swimming in circles and tail-chasing behaviour (colloquially referred to as whirling disease). Other species have been associated with spinal abnormalities (e.g. *Triangula percae* and *Myxobolus sandrae* causing spinal lordosis in redfin perch, *Myxobolus spinacurvatura* causing spinal curvature in mullet, *Myxobolus buri* causing scoliosis in Japanese amberjack, *Myxobolus buckei* in cyprinids), cranial abnormalities (e.g. *Myxobolus aeglefini* in flounder and cod), and even ulcerative syndromes (e.g. *Myxobolus cartiliginus* in carp and murrel).

- Reproductive tissues: Although infections in fish gonads occur infrequently, they may have serious consequences on fish fecundity by causing gonadal regression or parasitic castration. Developmental stages are often located in the seminferous tubules in the testes of males or in the interstitial or connective tissues of ovaries, sometimes in oocytes. Several species have been reported in the testes in association with hyalinization, hypertrophy, tubule occlusion and ascites (e.g. *Sphaerospora testicularis* in seabass, *Myxobolus lutzi* in toothcarp, *Agarella gracilis* in lungfish) while other species invade the ovaries causing significant degeneration of ovarian tissue and oocytes (e.g. *Henneguya oviperda* in pike, *Henneguya amazonica* in catfish, *Sphaerospora ovophila* in pond perch, *Myxobolus dahmeyensis* in tilapia) sometimes with macroscopic cyst formation (e.g. *Myxobolus algonquinensis* in golden shiners).

- Intestines: Several species infect intestinal tissues, but most are not considered to be pathogenic. Proliferative stages of a few species, however, may cause clinical disease characterized by enteritis (e.g. *Enteromyxa scophthalmi* in turbot, *Enteromyxa leei* in gilthead sea bream) and multifocal epithelial degeneration (e.g. *Sphaerospora mayi* in mullet), sometimes leading to anorexia and poor growth (especially *Ceratonova shasta* causing wasting disease in salmonids). Several species also form large cysts that may obstruct and even perforate the intestines (e.g. *Myxobolus nodulointestinalis* in binni, *Thelohanellus kitauei* in carp, *Henneguya suprabranchiae* in catfish).

- Gall bladder and liver: Many species are coelozoic within the gall bladder, particularly in marine fish, but only a few have been associated with clinical conditions including hypertrophy, bile thickening and discolouration (e.g. *Sphaeromyxa therapani* and *Chloromyxum tripathi* in grunters, *Myxidium papernae* in mullet, *Ceratomyxa kudoi* in mullet), atrophy with occlusion (e.g. *Myxidium gadi* in saithe and pollack), and epithelial necrosis and degeneration (e.g. *Chloromyxum trijugum* in sunfish, *Zschokkella mugilis* in mullet). Other species are histozoic and infect cells and ducts within the liver, causing hepatocellular necrosis, pericholangitis, cholangiofibrosis (e.g. *Zschokkella russelli* in rocklings, *Chloromyxum cristatum* in carp), cholestasis, jaundice, ascites and abdominal distension (*Zschokkella icterica* in rabbitfish, *Ceratomyxa sparusaurati* in gilthead sea bream, *Chloromyxum truttae* in brown trout).

- Urinary tract: Different species occur as coelozoic infections in cavities in the kidneys, ureters and urinary bladders of fish, or as histozoic infections within kidney tissues. Most coelozoic infections are benign, but some may cause renal dysfunction due

to tubule hypertrophy (e.g. *Parvicapsula renalis* in red drum, *Parvicapsula minibicornis* and *Sphaerospora truttae* in salmonids), tubule blockage (e.g. *Sphaerospora sparidarum* in gilthead sea bream and common dentex, *Sphaerospora dykovae* and *Myxobilatus legeri* in carp), ureter obstruction (e.g. *Neoparvicapsula monoalata* in cuja bola), and glomerular disruption (e.g. *Chloromyxum majori* in salmonids, *Chloromyxum inexpectatum* in sterlets, *Sphaerospora sparis* in gilthead sea bream, *Sphaerospora epinepheli* in groupers). Histozoic species may cause severe inflammation resulting in proliferative kidney disease (e.g. *Tetracapsuloides bryosalmonae* in salmonids), granulomatous inflammation (e.g. *Paramyxidium giardi* in eels), kidney enlargement or bloater disease (e.g. *Hoferellus carassii* in goldfish), glomerular atrophy (e.g. *Myxidium rhodei* in roach), swollen belly disease (e.g. *Sphaerospora tincae* in tench) and even 'xenoma' formation comprising grossly enlarged cells with hypertrophied nuclei (e.g. *Myxidium lieberkuehni* in pike).

- Swim bladder: Several coelozoic species infect the swim bladder where they cause little harm, but a few histozoic species infect the swim bladder walls where they may cause lesions becoming encapsulated by fibrous tissue and macrophages (e.g. *Myxobolus cycloides* in chub) and sometimes rupturing provoking intense inflammatory responses leading to organ dysfunction, impaired swimming performance, poor growth and even death (e.g. *Sphaerospora dykovae* in carp, especially fingerlings).

Pseudo-parasitism: Myxospores have occasionally been detected in the faeces of human patients presenting with diarrhoea. Spores of *Henneguya salminicola* were found in two patients, in one case being mistaken for human spermatozoa and leading to a suspicion of sexual abuse, while spores of *Myxobolus plectroplites* were found in another three patients. All individuals had eaten infected fish (salmon or perch) and the passage of mature spores unchanged through their alimentary tracts suggests these organisms were 'pseudo-parasites', i.e. incidental findings unrelated to clinical symptoms.

Developmental cycle and mode of transmission: In vertebrates, myxosporeans first undergo vegetative proliferation in pseudoplasmodia or plasmodia followed by myxospore morphogenesis, both processes featuring a characteristic cell-in-cell condition where endogenously produced secondary cells persist inside primary mother cells. Vertebrates become infected when mature actinospores come into contact with external epithelia (skin and/or gills) discharging filaments from their polar capsules to facilitate attachment. The spore shell valves then open releasing the infective germ cells (sporoplasms) which penetrate the epithelial barriers. The sporoplasms are either single binucleate cells (whose nuclei fuse to form a synkaryon) or 2 uninucleate cells (that fuse by autogamy to form a single cell). They transform to trophic stages (trophozoites), initially called amoebulae, as they invade host tissues, often moving deeper via blood or lymph vessels. The trophozoites undergo proliferation by forming cell doublets through nuclear division and endogeny whereby one daughter nucleus becomes enveloped by endoplasmic reticulum cisternae resulting in a secondary cell located within a vacuole in the primary cell (resulting in the enveloped cell-in-cell condition typical for myxozoa). All species undergo sporogonic cycles forming plasmodia (or pseudoplasmodia) involving growth and proliferation of generative secondary cells and vegetative nuclei. These stages are either immobile rounded stages encased in host tissues (histozoic) or occur as flat sheets or rounded balls within body or organ cavities (coelozoic) where they are attached to the walls by cytoplasmic holdfast outgrowths or occur free-floating in the lumina. This plasmodial development is often coupled with sporogony (spore formation) although some species undergo extrasporogonic cycles in tissues other than where sporogony occurs. Extrasporogonic cycles have been reported from several genera, including *Sphaerospora, Hoferellus, Myxidium, Kudoa* and *Myxobolus*. In extrasporogonic cycles, secondary cells undergo a series of mitotic divisions and then endogenous budding to give rise to tertiary cells. The secondary cells are released by rupture of the primary cells allowing parasites to migrate via blood or lymph vessels to their final sites where sporogony occurs. All species undergo plasmodial development that typically involves one or more of three morphological types: numerous small pseudoplasmodia (containing only one vegetative nucleus) that produce 1-2 spores (mono- or di-sporic) often being histozoic (sometimes pervading host tissues as diffuse infiltrates); medium plasmodia that are mictosporic producing 1, 2 or more spores often being coelozoic; and large plasmodia (sometimes macroscopic) that produce masses of spores (poly-sporic) often being histozoic (sometimes encysted by host connective tissue). Spore formation (sporogenesis) then occurs either directly when generative cells form sporoblasts, but most often occurs following pansporoblast formation when vegetative cells (pericytes) envelope generative (sporogonic) cells. The pericytes degrade to form the pansporoblast envelope while the enveloped sporogonic cells divide by binary fission to give rise to sporoblast cells that undergo valvogenic, capsulogenic and sporoplasmic differentiation to form myxospores with multiple shell valves, polar capsules and sporoplasms. Mature myxospores are released into the aquatic environment either by the antemortem rupture of superficial cysts or the postmortem degradation of infected tissues upon the death and decay of the host. Myxospores are highly resilient to external environmental conditions, and some have been shown to retain infectivity for up to 4 months in mud, for 2 months after freezing at -20°C, and even after passage through the alimentary canal of predatory birds and fish. Myxospore infections in fish often show seasonal patterns of infection, with prevalence generally highest in autumn/winter in subtropical regions, or summer/autumn in temperate regions, although patterns can be hard to discern within specific age groups. Epidemiological observations indicate infection prevalence and abundance may vary according to prevailing environmental conditions (notably water temperature and salinity) but also numerous host factors (population density, age cohorts, migratory, breeding, spawning and feeding habits, nutritional, physiological and immunological status). While many myxospore infections appear to be long-lasting in fish (potentially life-long) and do not apparently stimulate any host protective immunity, some infections (e.g. *Tetracapsuloides bryosalmonae*) seem to be short-lived (< 1 year) and fish surviving primary infections become resistant to reinfection and generally do not display clinical disease. Several studies have used myxosporean parasites as potential biological tags for examining fish stocks, recruitment and seasonal migration patterns, as well as responses to pollution. Some results studies appeared promising, but little is known about myxozoan distribution patterns and their transmission cycles.

Initially, it was thought that myxospores were transmitted directly from fish to fish, sometimes with caveats that spores needed to be 'aged' in mud to become infective, or passaged through the digestive tracts of aquatic invertebrates. It was subsequently discovered for several piscine myxosporeans that a secondary or alternate host was required to complete the life-cycles. Myxospores from fish were found to be infective for aquatic invertebrates (annelids) where they underwent development and the formation of different types of spores (namely actinospores) that proved to be infective to fish. Development in annelids involved asexual proliferation (merogony) followed by sexual reproduction (gametogony) where the zygotes differentiated into actinospores. By definition, this makes annelids the final or definitive hosts (in which sexual development occurs) and fish should be considered simply as intermediate hosts. Similar heteroxenous (2-host) life-cycles have now been shown for a growing number of species in some 16 bivalvulid myxosporean genera (*Ceratomyxa, Chloromyxum, Ellipsomyxa, Gadimyxa, Henneguya, Hoferellus, Myxidium, Myxobilatus, Myxobolus, Ortholinea, Paramyxidium, Parvicapsula, Sigmomyxa, Sphaerospora, Thelohanellus, Zschokkella*) with species in freshwater fish tending to infect oligochaetes while those in marine fish infected polychaetes. Previously, taxonomic classification systems had treated the Actinosporea as a separate myxozoan assemblage and numerous species had been described in invertebrate hosts. However, with the recognition that actinospores may be alternate (yet definitive) stages in myxosporean life-cycles, taxonomists elected to suppress actinosporean nomenclature pending further characterization studies, assigning actinosporeans to some 20 collective groups with vernacular names. Experimental studies have now found myxosporean life-cycles involving 10 of those collective groups; namely, antonactinomyxon, aurantiactinomyxon, echinactinomyxon, hexactinomyxon, seisactinomyxon, tetractinomyxon, triactinomyxon, neoactinomyxum, raabeia, and siedleckiella-type actinospores (tabulated below). However, life cycles for the vast majority of myxosporeans have yet to be elucidated. While it is likely that heteroxenous life-cycles may be found for many species, it is nonetheless recognized that some transmission may occur directly between fish, as intimated by various epidemiological studies. Indeed, experimental studies have shown that *Enteromyxum* (= *Myxidium*) *fugu*, *E. leei* and *E. scophthalmi* are capable of direct fish-to-fish transmission through cohabitation with infected fish, via effluent contaminated with myxospores, and by the oral transfer of infected tissues (including sloughed histozoic stages). Because most experimental studies were conducted in intensive aquaculture systems, it has been suggested that hosts kept in crowded stressed conditions may have increased susceptibility to direct transmission. Clearly, further studies are required to establish parasite life-cycles and unravel the complexities of transmission.

Evidence (E = experimental, M = molecular)	**Myxozoan species**	**Fish host**	**Actinospore type**	**Invertebrate host**
M	*Ceratomyxa auerbachi*	*Clupea harengus* (herring)	tetractinomyxon-type actinospores	Polychaeta: sabellid (*Chone infundibuliformis*)
E, M	*Ceratonova shasta*	*Oncorhynchus mykiss* (rainbow trout)	tetractinomyxon-type actinospores	Polychaeta: fabriciid (*Manayunkia speciosa*)
E, M	*Chloromyxum auratum*	*Carassius auratus* (goldfish)	antonactinomyxon-type actinospores	Oligochaeta (unspecified)
M	*Chloromyxum schurovi*	*Salmo trutta* (brown trout)	neoactinomyxum-type actinospores	Oligochaeta: lumbricid (*Eiseniella tetraedra*)
M	*Chloromyxum truttae*	*Salmo salar* (Atlantic salmon)	aurantiactinomyxon-type actinospores	Oligochaeta: lumbriculid (*Stylodrilus heringianus*)
E, M	*Ellipsomyxa gobii*	*Pomatoschistus microps* (common goby)	tetractinomyxon-type actinospores	Polychaeta: nereidid (*Nereis diversicolor, succinea*)
M	*Ellipsomyxa mugilis*	mullet	tetractinomyxon-type actinospores	Polychaeta: nereidid (*Nereis* spp.)
E, M	*Gadimyxa atlantica*	*Gadus morhua* (Atlantic cod)	tetractinomyxon-type actinospores	Polychaeta: spirorbid (*Spirorbis spirorbis, inornatus, tridentatus, corallinae*)
E	*Henneguya exilis*	*Ictalurus punctatus* (channel catfish)	aurantiactinomyxon-type actinospores	Oligochaeta: naidid (*Dero digitata*)
E	*Henneguya ictaluri*	*Ictalurus punctatus* (channel catfish)	aurantiactinomyxon-type actinospores	Oligochaeta: naidid (*Dero digitata*)
E	*Henneguya nuesslini*	*Salmo trutta* (brown trout), *Salvelinus fontinalis* (brook trout)	triactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
M	*Henneguya polarislonga*	*Astyanax lacustris* (tambiu)	seisactinomyxon-type actinospores	Oligochaeta: naidid (*Slavina evelinae*)
E	*Hoferellus carassii*	*Carassius auratus* (goldfish)	aurantiactinomyxon-type actinospores	Oligochaeta: naidid (*Nais cf. elingius*)

E	*Hoferellus carassii*	*Carassius auratus* (goldfish)	neoactinomyxum-type actinospores	Oligochaeta: naidid (*Branchiura sowerbyi*)
E	*Hoferellus cyprini*	*Cyprinus carpio* (common carp)	aurantiactinomyxon-type actinospores	Oligochaeta: naidid (*Nais* sp.)
M	*Myxidium truttae*	*Oncorhynchus kisutch* (coho salmon)	raabeia-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
M	*Myxobilatus gasterostei*	*Gasterosteus aculeatus* (three-spined stickleback)	triactinomyxon-type actinospores	Oligochaeta: naidid (*Nais communis*)
E, M	*Myxobolus arcticus*	*Oncorhynchus nerka* (sockeye salmon), *Oncorhynchus masou* (masu salmon)	triactinomyxon-type actinospores	Oligochaeta: lumbriculid (*Stylodrilus heringianus, Lumbriculus variegatus*)
E	*Myxobolus bramae*	*Abramis brama* (common bream)	triactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
E	*Myxobolus carassii*	*Leuciscus idus* (ide)	triactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
E	*Myxobolus cerebralis*	*Oncorhynchus mykiss* (rainbow trout)	triactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
E	*Myxobolus cotti*	*Cottus gobio* (European bullhead)	triactinomyxon-type actinospores	Oligochaeta: naidid ('tubifex')
E, M	*Myxobolus cultus*	*Carassius auratus* (goldfish)	raabeia-type actinospores	Oligochaeta: naidid (*Brachiura sowerbyi*)
E	*Myxobolus dispar*	*Cyprinus carpio* (common carp)	raabeia-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
E	*Myxobolus drjagini*	*Hypophthalmichthys molitrix* (silver carp)	triactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex, Limnodrilus hoffmeisteri*)
E	*Myxobolus hungaricus*	*Abramis abramis* (common bream)	triactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex, Limnodrilus hoffmeisteri*)
E, M	*Myxobolus intimus*	*Rutilus rutilus* (common roach)	aurantiactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex, Limnodrilus hoffmeisteri*)
E	*Myxobolus macrocapsularis*	*Abramis brama* (common bream)	triactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
E	*Myxobolus pavlovskii*	*Hypophthalmichthys molitrix* (silver carp)	hexactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
E, M	*Myxobolus parviformis*	*Abramis brama* (common bream)	triactinomyxon-type actinospores	Oligochaeta: naidid (*Limnodrilus hoffmeisteri*)
E	*Myxobolus portucalensis*	*Anguilla anguilla* (European eel)	triactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
E	*Myxobolus pseudodispar*	*Rutilus rutilus* (common roach)	triactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex, Limnodrilus hoffmeisteri*)
M	*Ortholinea labracis*	*Dicentrarchus labrax* (European seabass)	triactinomyxon-type actinospores	Oligochaeta: tubificid (*Tectidrilus*)
E	*Paramyxidium giardi*	*Anguilla anguilla* (European eel)	aurantiactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
M	*Parvicapsula minibicornis*	*Oncorhynchus gorbuscha* (pink salmon)	tetractinomyxon-type actinospores	Polychaeta: fabriciid (*Manayunkia speciosa*)
M	*Sigmomyxa sphaericum*	*Belone belone* (garfish)	tetractinomyxon-type actinospores	Polychaeta: nereidid (*Nereis pelagica*)]
E	*Sphaerospora dykovae*	*Cyprinus carpio* (common carp)	neoactinomyxum-type actinospores	Oligochaeta: naidid (*Tubifex tubifex, Brachiura sowerbyi*)
E	*Sphaerospora truttae*	*Salmo trutta* (brown trout)	echinactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex, Limnodriulus variegatus*)

E, M	*Thelohanellus hovorkai*	*Cyprinus carpio* (common carp)	aurantiactinomyxon-type actinospores	Oligochaeta: naidid (*Brachiurua sowerbyi*)
E	*Thelohanellus nikolskii*	*Cyprinus carpio* (common carp)	aurantiactinomyxon-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
E	*Zschokkella nova*	*Carassius carassius* (crucian carp)	siedleckiella-type actinospores	Oligochaeta: naidid (*Tubifex tubifex*)
E	*Zschokkella* sp.	*Carassius auratus* (goldfish)	echinactinomyxon-type actinospores	Oligochaeta: naidid (*Brachiura sowerbyi*)
E, M	*Tetracapsuloides bryosalmonae*	salmonids	fishmalacospores	Bryozoa: plumatellid (*Plumatella fungosa*), fredericellid (*Fredericella sultana*)]

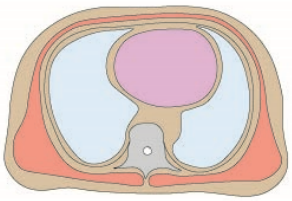
Within annelids, the parasite developmental cycle is characterized by merogonous multiplication (plasmotomy) followed by sexual multiplication involving meiosis (gametogony) and then spore formation (sporogony). Infections are initiated when annelids come into contact with infective myxospores liberated from fish hosts. The myxospores extrude their polar filaments anchoring themselves to host epithelia, and the spore valves separate along their suture lines releasing the enclosed sporoplasms. The sporoplasms are amoeboid and penetrate between the epithelial cells (usually in the gut) and then begin asexual proliferation (merogony or schizogony). Depending on the species, the sporoplasms may be uninucleate or binucleate, but they all undergo several nuclear divisions to produce multinucleate cells which then divide by plasmotomy to produce numerous uninucleate cells. These cells invade intercellular spaces, where some may undergo another schizogonic phase, giving rise to more progeny. Ultimately, the uninucleate cells fuse by plasmogamy to produce a binucleate stage which undergoes gametogony to produce quadrinucleate stages by karyogamy giving rise to 4 uninucleate cells by plasmotomy. Two of these cells become enveloping somatic cells (pericytes) while the other two becoming generative gametocytic cells (designated alpha- and beta-cells). The enveloping pericytes undergo mitosis twice to produce 8 somatic cells, while the alpha- and beta-cells undergo 3 mitotic divisions to produce 16 diploid gametocytes and then one meiotic division to produce 16 haploid gametocytes and 16 polar bodies. Each alpha-cell fuses with a beta-cell to produce a pansporocyst consisting of 8 zygotes surrounded by 8 somatic cells (the exception is the genus *Tetraspora* which has one less mitotic division and only forms 4 zygotes). The fusion of the alpha- and beta-cells is the sexual phase of development, establishing the annelids as final or definitive hosts. The zygotes then begin spore formation (sporogony) by undergoing 2 mitotic divisions to form a 4-cell stage, so that sporocysts now contain 32 cells (in 8 groups of 4). Three cells in each group surround the fourth and divide to produce 6 cells, 3 of which become capsulogenic cells and the other 3 valvogenic cells (note that actinospore groups that have 6 valves, such as pseudotriactinomyxon and hexactinomyxon, involve a further mitotic division to produce 6 valvogenic cells). The enclosed fourth cell in each group becomes the sporoplasm cell, which divides by internal cleavage to produce a generative cell surrounded by a somatic cell. The generative cell divides by mitosis to produce infective germ cells (sporoplasms) in various multiples of 2, normally 2, 4, 8, 16, 32 etc according to the species. The resultant actinospores thus resemble a boat anchor, with an elongate anterior spore body containing three polar capsules and shell valves with posterior caudal projections (often tri-radiate). When mature actinospores are released from annelids into the external aquatic environment by defaecation or postmortem degeneration, the long hollow caudal projections inflate osmotically in water to aid in spore buoyancy and dispersal. Free-living annelids are often associated with substrates in stagnant waters, but populations can survive in many different types of habitats. In general, however, regions with low flow rates and poor water quality (esp. low oxygen content) appear to be detrimental actinosporean infections. Infections may show diurnal, seasonal and annual variations in prevalence and abundance due to a number of factors, particularly the availability of hosts and ambient temperatures. Infections have been shown to persist in oligochaetes for at least a year under laboratory conditions, and possibly for their life-time under natural conditions. Actinospores may be released more frequently at dusk and dawn, particularly during the summer months, and the spores may survive for several weeks in water. There are some indications that actinospores may also be released in response to the presence of mucus from specific fish hosts.

Differential diagnosis: The diagnosis of myxosporean infections in fish on clinical grounds is presumptive, as other aetiological agents or pathological conditions may cause similar signs or behaviours, such as loss of appetite, poor growth, unthriftiness, listlessness, respiratory flaring, swimming at the surface, altered orientation (head-down postures), and tail-chasing (whirling). Even when gross lesions may be evident, other conditions may be responsible for surface erosions, ulcers, haemorrhages, abscesses, swellings, growths and even exophthalmia. The observation of macroscopically visible cysts in host tissues is also not pathognomic as other infectious agents may cause similar encapsulated lesions, especially bacteria. Few infections are diagnosed ante-mortem, other than severe infections with parasite species forming superficial lesions from which biopsy material may be collected. More usually, infections are diagnosed by the direct observation and identification of microscopic myxospores harvested post-mortem from host tissues (organs and flesh) or from the fluid contents of organ cavities (gall bladder, urinary bladder, swim bladder and intestines), body cavities or haemal spaces. Material may be examined microscopically as wet mounts, smears, tissue imprints, squash preparations or sections, preferably using high contrast illumination systems (e.g. phase-contrast, differential interference-contrast). Microscopy is best performed on fresh samples, as preservatives and freezing may distort spore integrity (especially size and shape). Nonetheless, high-volume screening studies often make recourse to the examination of histological sections of fixed tissues. A range of stains have been employed to improve visual acuity, including Giemsa and silver stains, and some fluorochromes

and biotinylated lectins. Several techniques have also been developed to harvest spores from host tissues by maceration, homogenization, enzymatic digestion (pepsin or trypsin), filtration and/or centrifugation. Parasite genera may be identified by the morphological characteristics of their mature spores (size, shape, structure, sutural ridges, spore projections, caudal appendages, ribs, ridges or striae, membranaceous or mucous envelope, iodinophilous vacuoles), polar capsule morphology (number, shape, size and angle, arrangement of coils of the polar filaments, position of capsule opening) and sporoplasms (number, location), but species differentiation often requires additional data on pre-spore developmental stages as well as tissue location, pathological changes, host occurrence and geographic location. Both transmission and scanning electron microscopy may be required to reveal topographical and cellular ultrastructural features. A small range of immunological techniques have also been developed to guide research and aid diagnoses. Monoclonal and/or polyclonal antibodies have been raised against extrasporogonic stages and mature spores of several economically-important myxozoan species (including the bivalvulids *Myxobolus cerebralis, Myxobolus rotundus, Ceratonova shasta, Henneguya salminicola, Myxobolus cerebralis, Sphaerospora dicentrarchi,* the multivalvulid *Kudoa thyrsites,* and the malacosporean *Tetracapsuloides bryosalmonae,*) and used with variable success to detect parasites within fish tissues or tissue extracts, usually by chemiluminescence. Modern molecular biological techniques are now commonly used to characterize species, determine phylogenetic relationships and examine putative life-cycles following the polymerase chain reaction (PCR) amplification of nuclear genes (large and small subunit ribosomal RNA and internal transcribed spacer regions) or by *in situ* hybridization assays or restriction fragment length polymorphism (RFLP) analyses.

Treatment and control: There are almost no chemotherapeutic options available to treat myxozoan infections in fish. Some chemicals may be effective against water-borne stages or superficial infections in fish, but most are ineffective against infections where plasmodia and spores are disseminated throughout host tissues. Considerable variation in treatment efficacy has also been reported depending on parasite species, host species, habitats and husbandry. Early studies trialled a variety of toxic compounds in attempts to manage infections in aquaculture systems. For example, adding the triarylmethane dye malachite green to water had some effect against proliferative kidney disease (PKD) caused by *Tetracapsuloides bryosalmonae* in rainbow trout (but was ineffective against *Ceratonova shasta*). Similarly, adding the pentavalent arsenical compound acetarsol to water partly restricted whirling disease caused by *Myxobolus cerebralis* in trout, and there were a few similar reports using the nitroimidazole dimetridazole. However, most of these compounds have now been withdrawn from commercial use due to concerns over their bioaccumulation and toxicity (ranging from adverse side-effects to carcinogenic properties). More recently, better success was reported using the antibiotic fumagillin (or analogues) in fish feed to treat a range of infections, including *Tetracapsuloides bryosalmonae* in salmonids, *Myxobolus cerebralis* in trout, *Hoferellus carassii* and *Thelohanellus wuhanensis* in goldfish, *Paramyxidium giardi* in eels and *Sphaerospora renicola* in carp. Excessive usage, however, was found to cause toxic side effects (anaemia, anorexia, poor growth), renal tubule disintegration, and atrophy of haematopoietic tissues leading to partial immunosuppression, increased stress and predisposing to secondary bacterial infections. Several anticoccidial drugs (toltrazuril/triazinone, furazolidone, proguanil) have shown some effect against *Myxobolus* infections in trout, bream and carp, as have some traditional herbal treatments with garlic and salt mixtures. Good disease control has been achieved in aquaculture by the adoption of preventive measures designed to minimize the introduction, amplification, survival and spread of parasites amongst fish stocks, with desirable management procedures often mandated by government and/or industry regulations. Various procedures have been used to minimize the introduction of parasites into culture facilities, including deriving stock from certified disease-free eggs/fry/fingerlings, regular health surveillance, particularly of introduced and translocated stock, establishing appropriate quarantine procedures, maintaining temporal and spatial records of parasite distribution and abundance, and implementing education and awareness campaigns for producers and consumers. Protocols employed to avoid contamination of holding facilities include the prompt removal and destruction of diseased fish (by burial or incineration), and regularly cleaning tanks, fomites and equipment using chemicals, heat or desiccation. Some producers recommend using ponds lined with concrete rather than earthen ponds, so that contaminants and sediments (particularly those containing annelids) can be better managed by regularly flushing or draining. A range of chemicals have been used to treat drained and drying ponds to eliminate spores and/or annelids, including calcium hydroxide, potassium hydroxide, calcium oxide, calcium cyanimide, chlorine and quicklime. Good husbandry practices should strive to keep fish in healthy stress-free conditions by providing clean water (through chlorination, ozonation, filtration, ultraviolet irradiation), maintaining good water quality both physico-chemically (appropriate temperature, pH, aeration, turbidity, solutes) and biologically (restricting organic loads, planktonic and benthic plant and animal communities), providing good nutrition without over-feeding, avoiding crowded conditions, separating species and age cohorts, timely stocking (rearing fish outside critical transmission or high prevalence periods, both usually lower in colder winter months), and selectively breeding resistant fish (some prospects based on fish species/strain/stock differences in susceptibility for particular infections, especially amongst salmonids). There are currently no vaccine candidates as many infections do not appear to stimulate strong immune responses, but some infections have been shown to elicit persistent acquired immune responses in fish (e.g. *Tetracapsuloides bryosalmonae, Enteromyxum scophthalmi, Ceratonova shasta*) suggesting possibilities for immuno-activation, supplementation or vaccination.

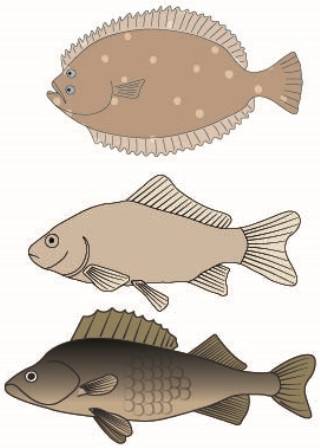
Myxozoa
(bivalvulid species)



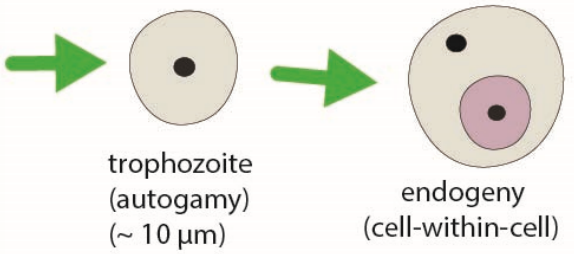
coelozoic/histozoic
(lesions/cysts, inflammation, dysfunction, mortalities)

form unique multicellular spores
(with valvogenic, capsulogenic
and sporoplasmic cells)

discovered to have heteroxenous cycles
with myxospores developing in fish &
actinospores developing in worms



Vertebrate Hosts
[Intermediate Hosts]
(freshwater, marine
and estuarine fish)



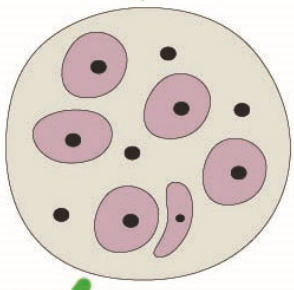
trophozoite
(autogamy)
(~ 10 µm)

endogeny
(cell-within-cell)

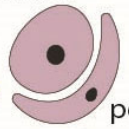
plasmodia or pseudo-
plasmodia (10-4000 µm)

plasmotomy

FISH HOST



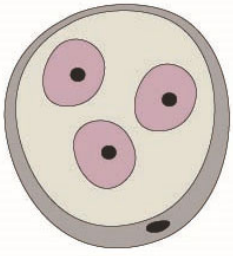
sporogony
(monosporic,
disporic or
polysporic)



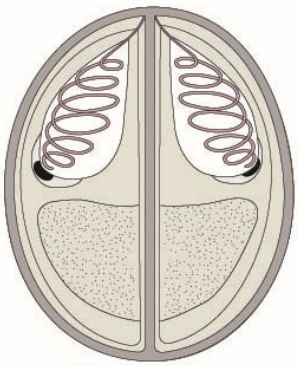
sporoblast

pericyte

pansporoblasts



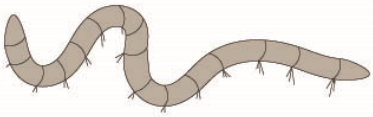
bivalvulid species forming
myxospores with 2 valves
and usually 2 polar capsules



myxospore (10-20 µm)

most life-cycles unknown, but studies have shown myxospores to be infective to aquatic annelids
where they form actinospores infective to fish [actinospore cycle shown separately]

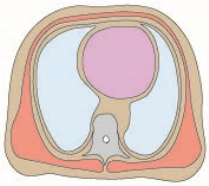
Myxozoa
(actinospore development)



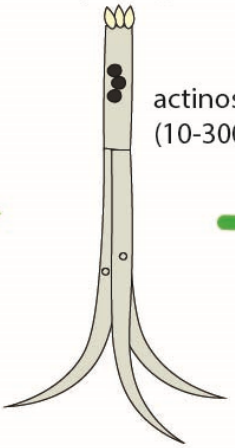
Invertebrate Hosts
(oligochaetes, polychaetes)

form unique multicellular spores
(with valvogenic, capsulogenic
and sporoplasmic cells)

discovered to have heteroxenous cycles
with actinospores developing in worms
and myxospores developing in fish

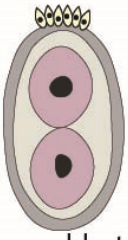


coelozoic
(nonpathogenic)



actinospore
(10-300 µm)

20 types of actinospores
each with 3 polar capsules
and often 3 caudal projections

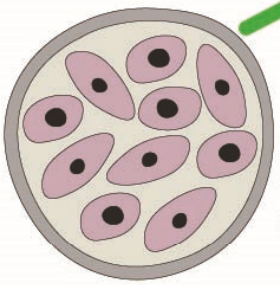


sporoblast



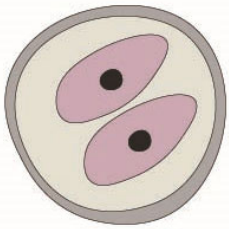
pericytes

sporogony



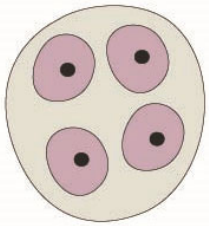
pansporocyst
(enveloping and
gametic cells)

ANNELID HOST

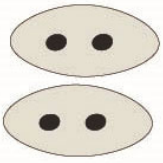


plasmotomy

gamogony
(15-30 µm)



α, β cells



merogony
(10-20 µm)



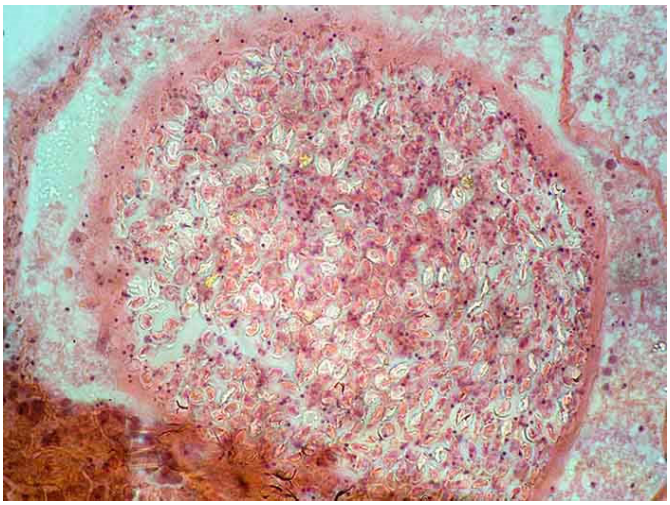
most life-cycles unknown, but studies have shown
actinospores to be infective to fish where they
form myxospores that are infective to annelids
[myxospore cycle shown separately]



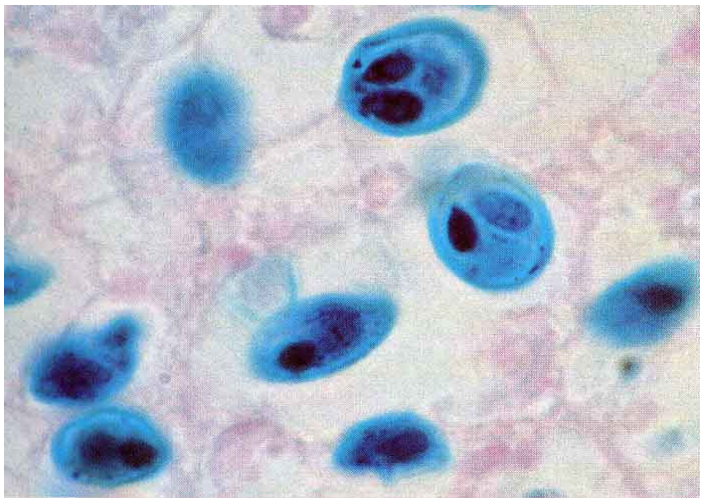
Chloromyxum spores from fish



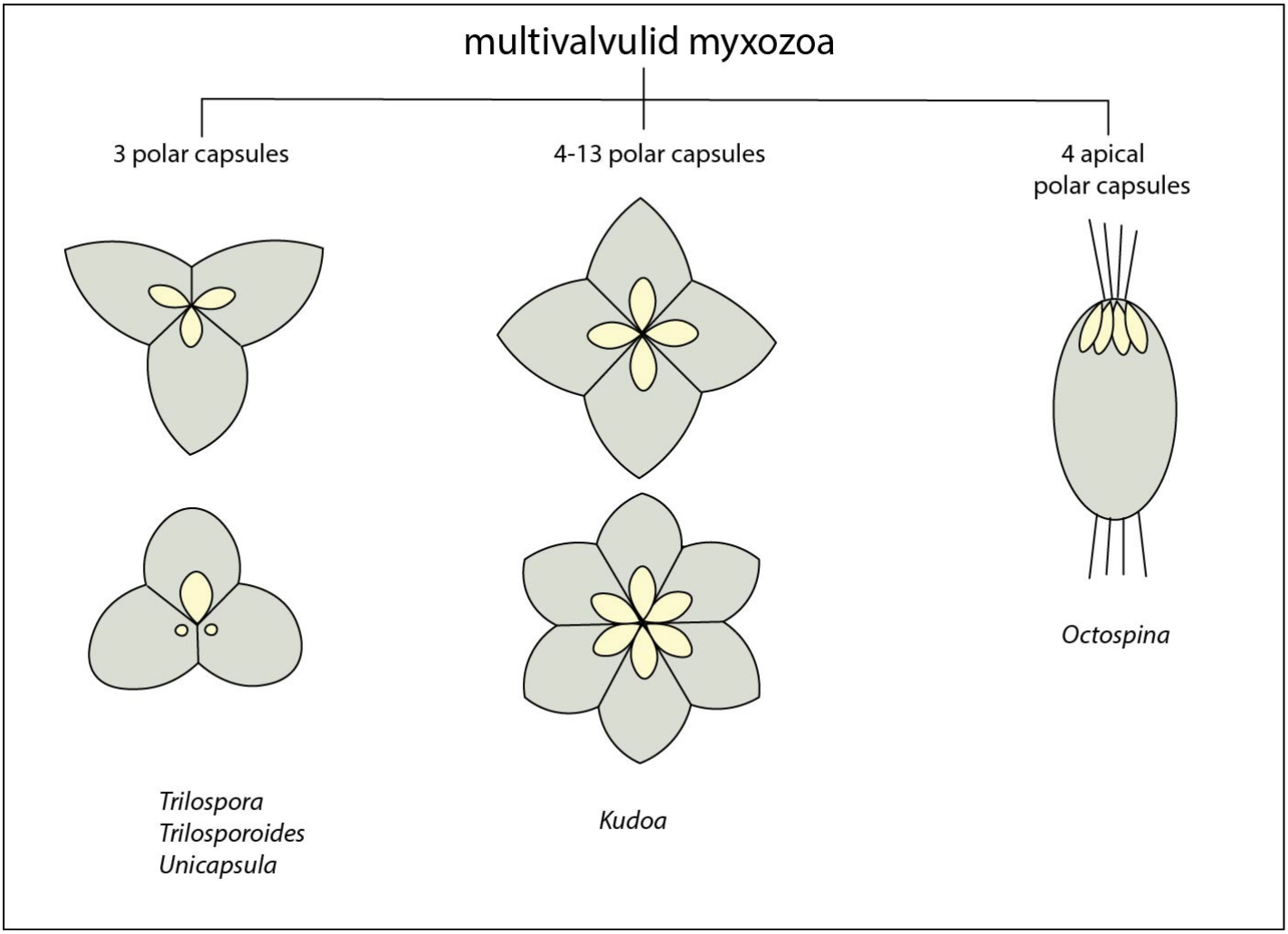
Henneguya spore from fish



Myxobolus cyst in fish tissues



Myxobolus spores from cyst in fish


multivalvulid myxozoa
3 polar capsules
4-13 polar capsules
4 apical polar capsules
Trilospora
Trilosporoides
Unicapsula
Kudoa
Octospina

Kudoa, Unicapsula
(animal: myxozoan)

Overview

Myxozoans are obligate parasites which produce unique multicellular spores comprised of valvogenic, sporoplasmic and capsulogenic cells. The latter form polar capsules with extrudible filaments (similar to cnidarian nematocysts — but used for attachment). They were originally classified as protistan organisms, but ultrastructural and molecular studies have indicated that they are bilateral metazoans, and are now classified as animals (cnidarians). Many species have been described as coelozoic or histozoic parasites in fish and some in amphibia, reptiles and various invertebrates (especially oligochaetes, polychaetes and sipunculids). Parasite development is characterized by vegetative proliferation of trophozoites (by formation of multinucleate plasmodia containing generative cells) followed by spore morphogenesis (by formation of pansporoblast through union of pericyte and sporogonic cells and differentiation of the latter to form valvogenic, capsulogenic and sporoplasmic cells which produce the spore valves, nematocyst-like polar capsules and amoeboid infective sporoplasms). The life-cycles of several myxozoan species have been found to involve cyclic development between myxospore stages in fishes and actinospore stages in worms. Two major myxosporean orders are recognized: the Bivalvulida (spores with two shell valves) and the Multivalvulida (spores with more than two shell valves). Numerous multivalvulid species occur as histozoic or coelozoic parasites of freshwater and marine fish. Kudoid species form stellate spores, most with 4 valves and 4 polar capsules, and infections have been associated with tissue cysts and myoliquefaction, particularly in the muscles of tuna.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Phylum:	Cnidaria (diploblastic, radial symmetry, cnidocytes with nematocysts, sea anemones, corals, jellyfish, hydrozoa, myxozoa)
Subphylum:	Myxozoa (form multicellular valved spores with polar filaments)
Class:	Myxosporea (spores with 1-2 sporoplasms, 1-13 polar capsules)
Order:	Multivalvulida (radially symmetrical spores, 2-13 valves, polar capsules grouped together at apex)
Family:	Kudoidae (4-13 valves and polar capsules (rarely 2), mainly histozoic in muscles of marine fish)
Genus:	*Kudoa* (histozoic parasites in fish)
Species:	various species cause lesions in fish muscles
Family:	Trilosporidae (three valves and polar capsules, coelozoic/histozoic in marine fish)
Genus:	*Unicapsula* (parasitic in muscles of fish)
Species:	various species cause lesions in fish

Parasite biodiversity and host range: Myxozoans are unique parasites that form multicellular (pluricellular) spores (with valves, polar capsules and infective sporoplasms) in cold-blooded vertebrates and worm-like invertebrates. Despite their multicellularity, they were often classified together with the unicellular spore-forming protozoa (Protista), more for convenience than for phylogenetic relationships. Contemporary ultrastructural and molecular studies have now shown that they are bilateral metazoan animals, and are now classified with the Cnidaria (jellyfish and allies). Myxozoa polar capsules contain extrudible filaments similar in structure to cnidarian nematocysts, but they are used for attachment to host cells during the infection process (rather than for stinging). Numerous myxozoan species have been described as coelozoic or histozoic parasites predominantly in fish (marine and freshwater) throughout the world, as well as in some amphibia, reptiles, annelids (oligochaetes and polychaetes) and sipunculids. Some 3,110 species have been described but little is known about their host specificity. Conventional taxonomic classification schemes recognized two major myxozoan assemblages which were quite different in morphology and biology: the classical Myxosporea in fish, and the enigmatic Actinosporea in annelids. Little was known about their complete life-cycles and modes of transmission, until recent studies demonstrated that several species had heteroxenous (2-host) life-cycles alternating between myxospores in fish (acting as intermediate hosts) and actinospores in annelids (acting as definitive hosts). This prompted most taxonomists to suppress actinosporean nomenclature pending recognition of complete life-cycles. The anchor-shaped actinospores found in annelids have subsequently been assigned to 19 collective groups with vernacular names (anton-, auranti-, echin-, hex-, hung-, ormier-, pseudtri-, seis-, sphaer-, syn-, tetra-, tri-, unicapsul-actinomyxon, neoactinomyxum, endocapsa, guyenotia, raabeia, siedleckiella, and tetraspora), whose affinities to myxosporean stages have yet to be determined. Contemporary classification schemes now recognize 2 myxozoan classes: the Malacosporea containing species with soft shell valves and enigmatic worm- and sac-like trophic stages; and the Myxosporea containing species with hardened shell valves enclosing sporoplasmic and capsulogenic

cells. Two major myxosporean orders are recognized: the Bivalvulida (spores with 2 shell valves) and the Multivalvulida (spores with more than 2 shell valves).

No. families	No. genera	No. species	Hosts	Location
Class: MALACOSPOREA (spores with soft (unhardened) shell valves)				
Order: Malacovalvulida (worm-like (myxoworm) and sac-like trophic stages)				
1	2	3	bryozoa, salmonid fish	histozoic, coelozoic
Class: MYXOSPOREA (myxospores with hardened shell valves enclosing sporoplasmic and capsulogenic cells)				
Order: Bivalvulida (spores with two valves)				
Suborder: Platysporina (polar capsules at one pole in sutural plane)				
1	13	1,622	fish (mostly freshwater)	histozoic
Suborder: Variisporina [Eurysporina (Unipolariina) + Bipolarina] (polar capsules perpendicular to sutural plane)				
15	48	1,323	fish (mostly marine), some amphibians	mostly coelozoic, some histozoic
Order: Multivalvulida (radially symmetrical spores, 3-13 valves (rarely 2), polar capsules grouped together at apex)				
3	5	163	fish (marine)	mostly histozoic, some coelozoic

Collectively, around 3,110 species of myxozoan parasites have been described in over 2,000 species of fish (belonging to 332 families in 89 orders) as well as in some amphibians, a few reptiles, and rarely in shrews, birds and even as hyperparasites in some trematodes. Myxospores have been recorded in over 800 species of marine fish (from 233 families in 64 orders) and over 1,120 species of freshwater fish (from 124 families in 35 orders). Myxozoan classification still depends largely on myxospore structure (principally shape, number and position of shell valves and polar capsules), and sometimes on their presumed specificity (host occurrence and tissue tropism). With improvements in microscopic techniques, there have been many reports and reviews of myxozoan taxa over the last century. With the recent advent and utilization of molecular characterization techniques, new light has been cast on phylogenetic relationships, which sometimes do not agree with morphotypic and biologic classifications. Many myxozoan groups have been found to be polyphyletic, with broader host specificities than previously thought and many clades aligned with host habitats. For example, molecular studies on members of the bivalvulid genus *Leptotheca* showed them not to be monophyletic, but to align variously with the genera *Ceratomyxa, Ellipsomyxa, Sphaerospora*, and *Myxobolus*, to which they were subsequently re-assigned. Genotypic characterization of multivalvulid species with 5-13 valves and polar capsules (originally placed in the diverse genera *Pentacapsula*, *Hexacapsula* and *Septemcapsula*) have grouped together with the genus *Kudoa* (typically with 4 polar capsules), to which they have all been re-assigned. The identity of many more species (and genera) have been reappraised following comparative molecular studies, so the contemporary literature has become riddled with numerous revisions resulting in many synonyms. All attempts have been made in the following tables to record such nomenclatural changes. Three multivalvulid families have been recognized, collectively containing around 150 species allocated to 5 genera. Most species are found as histozoic and some coelozoic parasites, mainly in marine fish. Several species have been associated with clinical diseases in their hosts, notably where aggregations of spores form tissue lesions sometimes leading to post-mortem liquefaction (thus causing significant economic losses to fisheries industries).

TAXON	# spp.	Site	Hosts	Spore		Capsules	
				shape	size	site	size
Order: **Multivalvulida** (3-13 valves (rarely 2), one polar capsule per valve, all grouped together)							
Family: Trilosporidae (3 valves, 1-3 polar capsules)							
Unicapsula	16	histozoic	mar fish	pyramid	5-7	1 apical	na
Trilospora	4	coelozoic	mar fish	pyramid	7-16	3 apical	=
Trilosporoides incertae sedis	1	coelozoic	mar fish	triangular	24 x 9	3 lateral	≠
Family: Kudoidae (4-13 valves (rarely 2), 4-13 polar capsules, rarely more)							
Kudoa	141	histozoic	mar fish	stellate	7-15	apical	≠
Family: Spinavaculidae (4 valves, 4 polar capsules)							
Octospina	1	coelozoic	fw fish	spindle		apical	=
Order: **Bivalvulida** (considered in separate section)							

The genus *Trilospora* is characterized by the formation of pyramidal (triradiate) myxospores with 3 valves and 3 apical polar capsules. Four species have been described in the muscles and gall bladders of marine fish. The genus *Trilosporoides* contains a single species forming triangular spores with 3 valves and 3 lateral polar capsules in the gall bladders of marine fish. The genus *Unicapsula* forms small pyramidal spores with 3 unequal valves and one well-developed apical polar capsule. Some 16 species have been reported in the muscles of marine fish, sometimes in association with unsightly lesions which reduces the marketability of infected fish. The genus *Octospina* contains a single species which forms ovoid myxospores with 4 valves, 4 polar capsules and 8 long spines in the gall bladder and swim bladder of freshwater fish. The genus *Kudoa* has traditionally been defined as forming stellate spores with 4 valves and 4 polar capsules within the tissues of marine fish from most oceans around the world. Over 140

species have been described mainly in wild-caught fish, but some have recently been found in fish species being developed for mariculture. Infections have been linked to serious economic losses to the fishing industry as the parasites may cause muscle lesions, neurological or cardiac signs, and post-mortem myoliquefaction (soft flesh, milky condition, jellied meat) in commercially-important species. While many *Kudoa* spp. appear to be highly host specific, several have more extensive host ranges, and their distributions appear to reflect that of their hosts. More recently, morphological, biological and molecular studies have indicated that some widespread species may actually comprise species-complexes and that the genus should be expanded to include several other genera with more complex morphotypic characters; notably genera that form myxospores with > 4 valves and > 4 polar capsules (including *Pentacapsula* (with 5), *Hexacapsula* (with 6), and *Septemcapsula* (with 7). The life-cycles of multivalvulid species remain to be determined but, like bivalvulid myxosporeans, they are thought to involve actinospore stages in annelids (presumably marine polychaetes), even though some species may undergo direct fish-to-fish myxospore transmission.

Parasite species	**Spore dimensions* (µm)**	**Hosts**	**Location [clinical signs]**	**Distribution**
*Dimensions are given as length x breadth (and thickness if available) with ranges (or means) expanded to include different populations or subspecies. Measurements given for spores with caudal or lateral processes include those processes (while measurements without processes are given in parentheses).				
Order **MULTIVALVULIDA** (radially symmetrical spores with 3-13 valves (rarely 2), each with a polar capsule)				
Family Trilosporidae (spores with 3 valves and 3 polar capsules)				
Genus ***Trilospora*** (spores appear as triradiate stars with rounded points, apical polar capsules)				
T. californica [type species]	7.2 x 16	marine Blenniiformes: clinid (spotted kelpfish, striped kelpfish); Gobiiformes: oxudercid (blind goby)	gall bladder	North America
T. minuta	5-6-6.3 x 3.2-3.9	marine Gadiformes: macrourid (rock grenadier)	gall bladder wall	North Atlantic
T. muscularis	6.7-9.8 x 5.2-6.6	marine Gadiformes: lotid (blue ling)	muscles	North Atlantic
T. sphaerica	5.4-6 x 5.4-6	marine Gadiformes: morid (longfin codling)	muscles	Alaska
Genus ***Trilosporoides*** *incertae sedis* (spores with conical posterior end, lateral polar capsules)				
T. platessae	24 x 9	marine Pleuronectiformes: pleuronectid (European plaice)	gall bladder	North Atlantic
Genus ***Unicapsula*** (syn. *Pileispora, Parapileispora*) (subspherical spores, 3 unequal valves, one well-developed polar capsule and sometimes 2 reduced 'rudimentary' polar capsules, exclusively histozoic)				
U. aequilobata	6.7-8.5 x 7.1-8.8	marine Carangiformes: carangid (Japanese scad)	muscles [pseudocysts]	Asia
U. andersenae	4.6-7 x 4.3-6.5	marine/estuarine Acanthuriformes: lobotid (broadbanded velvetchin), sciaenid (Japanese meagre, tigertooth croaker, silver white croaker, donkey croaker, Boeseman croaker); Perciformes: gerreid (whipfin silver biddy), lutjanid (Russell's snapper), polynemid (fourfinger threadfin); Pleuronectiformes: cynoglossid (speckled tonguesole); Spariformes: sparid (yellowfin bream), sillaginid (sand whiting); Tetraodontiformes: monacanthid (Japanese leatherjacket)	muscles [pseudocysts]	Australia, China, Vietnam
U. chirocentrusi	6-6.9 x 6-6.9	marine/estuarine Clupeiformes: chirocentrid (dorab wolf-herring)	muscles	India
U. fatimae	5.5-6.6 x 6.1-7.4	marine Perciformes: siganid (white-spotted spinefoot)	muscles	Arabian Sea
U. galeata	5-6.7 x 5-6.5	marine Clupeiformes: dorosomatid (blacktip sardinella), engraulid (common hairfin anchovy, Hamilton's thryssa); Perciformes: mullid (whitesaddle goatfish); Spariformes:	muscles	Indian Ocean

		nemipterid (forktailed threadfin bream)		
U. marquesi	6.1 x 7.2	marine Percifomes: polynemid (giant African threadfin)	gills	Africa
U. maxima	10-14 x 9-11	marine Acanthuriformes: sciaenid (Ganges jewfish)	kidney	India
U. motomurai	6.1-7.5 x 6.1-7.4	marine Perciformes: polynemid (royal threadfin)	muscles	Africa
U. muscularis [type species]	5.8-7.6 x 6.3-7.8	marine Pleuronectiformes: pleuronectid (Pacific halibut, arrowtooth flounder)	muscles ['wormy halibut']	Pacific
U. pacifica	7.3-8.6	marine Gadiformes: macrourid (giant grenadier)	muscles	Pacific
U. plugfelderi	4-6.9 x 5.3-6.7	marine Perciformes: mullid (West African goatfish); Spariformes: sparid (picarel, sand steenbras)	muscles	Europe, Africa
U. pyramidata	4.7-6.8 x 5-9.6	marine Eupercaria: nemipterid (monogrammed monocle bream, forktailed threadfin bream, Japanese threadfin bream)	muscles [pseudocysts]	India, China, Vietnam
U. schulmani	7.8-10.3	marine Gadiformes: macrourid (giant grenadier)	urinary bladder	Pacific
U. seriolae	5.2-7.4 x 6.3-7.4	marine Carangiformes: carangid (yellowtail amberjack, yellowstripe scad, greater yellowtail); Perciformes: serranid (Malabar grouper, Japanese grouper); Spariformes: sparid (pink snapper)	muscles [pseudocysts, myoliquefaction]	Australia, Asia
U. setoensis	5.6-6.9	freshwater/estuarine Gobiiformes: oxudercid (yellowfin goby)	muscles	Japan
U. trigona	4.4-5.3 x 5.8-7.8	marine Spariformes: nemipterid (golden threadfin bream)	muscles	Asia
Family **Kudoidae** (spores with 4-13 valves (rarely 2), 4-13 polar capsules)				
Genus ***Kudoa*** (syn. *Neochloromyxum, Tetraspina, Pentacapsula, Hexacapsula, Septemcapsula*) (ovoid-quadrate-stellate spores, histozoic in marine/estuarine fishes, 4 polar capsules unless otherwise stated)				
K. aburakarei	6.4-8.3 x 13.2-18.3 x 13.2-16.6	marine Pleuronectiformes: pleuronectid (arrowtooth flounder)	muscles [pseudocysts]	Alaska
K. acentrogobia	4.2-5.3 x 6-6.7 x 5.1-5.9	freshwater/estuarine Gobiiformes: gobiid (greenspot goby)	muscles [pseudocysts]	China Sea
K. aegyptia	9.1-11.4 x 7.1-8.5 x 3.2-5.9	marine Eupercaria: sparid (Haffara seabream)	heart	Egypt
K. aequidens	2.9-3.5 x 6.2-7.1	freshwater Cichliformes: cichlid (carazinho)	muscles [pseudocysts]	South America
K. ajurutellus	6-7.4 x 7.8-9.5	marine Siluriformes: ariid (Bressou sea catfish)	muscles	Brazil
K. akihitoi	5.3-7 x 9.1-12.5 x 6.8-9.4	marine/estuarine Gobiiformes: gobiid (hazekuchi)	muscles [pseudocysts]	Japan
K. alliaria	6.3-8 x 6.3-10 x 6-10	marine Gadiformes: gadid (southern blue whiting), macruronid (Patagonian grenadier); Perciformes: nototheniid (black rockcod, longtail southern cod)	muscles [pseudocysts]	Southern Atlantic
K. amamiensis	4.5-5 x 5-6 x 5-6	marine Acropomatiformes: pempherid (ypsilon bullseye); Carangiformes: carangid (Japanese amberjack, greater amberjack, bigeye trevally); Perciformes: pomacentrid (scissortail sergeant, Bengal sergeant, Whitley's sergeant, Indo-Pacific sergeant, stout chromis, pearlspot chromis, blue damselfish)	muscles) [cysts, muscular kudoasis]	Japan, Australia
K. amazonica	5.0–5.9 x 6.3–7.4 x 7.0–7.9	freshwater Siluriformes: pimelodid (mapara)	oesophageal muscles	Brazil

K. anatolica	3.5-4.1 x 6.7-7.2 x 5.3-6	marine Atheriniformes: atherinid (Mediterranean sand smelt)	muscles, urinary bladder, kidney	Black Sea
K. atropi	8-11 x 8-11.9 x 8-9.5	marine Carangiformes: carangid (cleftbelly trevally)	gills [cysts]	India
K. azevedoi	3-4.2 x 4-5.2 x 3.3-4.8	marine Carangiformes: carangid (Atlantic horse mackerel)	ovaries	Tunisia
K. azoni	5-6 x 6.2-7.2 x 5.2-6	marine Scorpaeniformes: hexagrammid (Arabesque greenling, masked greenling)	muscles	Japan
K. barracudai	4.5-5.5 x 5-6	marine Istiophoriformes: sphyraenid (military barracuda)	muscles	Saudi Arabia
K. bengalensis	7-8.5 x 7-11	marine Siluriformes: ariid (flatmouth sea catfish)	muscles	India
K. boopsi	4-6 x 8-10 x 7-8	marine Spariformes: sparid (bogue)	gills [cysts]	Senegal
K. bora (syn. *Chloromyxum*)	8-9.4 x 9.6-12 x 8.7-12	marine Mugiliformes: mugilid (flathead grey mullet, keeled mullet, long-finned mullet)	muscles [cysts]	Taiwan
K. borimiri	3.3-4 x 4.1-6 x 2.8-4.2	marine Mugiliformes: mugilid (longarm mullet, longfinned mullet)	muscles	Vietnam
K. branchiata	3.8-4.8 x 4.3-4.8 x 4.3-4.8	marine Acanthuriformes: sciaenid (spot croaker)	gills [cysts]	Gulf of Mexico
K. camarguensis	4.4-6 x 6.4-8 x 4.4-6	freshwater/estuarine Gobiiformes: gobiid (common goby, sand goby)	muscles [pseudocysts, myoliquefaction]	France
K. carcharhini	7.2-9.5 x 9.5-11.3 x 7.8-10.6	marine Carcharhiniformes: carcharhinid (nervous shark, pigeye shark, blacktip shark)	muscles	Australia
K. cascasia	6-8 x 7-9 x 7-8	freshwater Mugiliformes: mugilid (yellowtail mullet); Siluriformes: pimelodid (spotted pim)	intestinal mesentery [cysts]	India
K. caudata	5.3-6.7 x 7.9-8.6 x 6.6	marine Scombriformes: scombrid (chub mackerel)	muscles	Peru
K. cerebralis	4.8-5.8 x 5.8-7.2 x 4.8-5.8	marine Moroniformes: moronid (striped bass)	neural connective tissues [cysts]	North America
K. chaetodoni	7.8-10.9 x 15.5-18.3 x 14.0-17.1 [7-9 polar capsules]	marine Perciformes: caesionid (redbelly yellowtail fusilier), chaetodontid (teardrop butterflyfish)	brain [pseudocysts]	Australia
K. cheilodipteri	4.9-7 x 8.3-12.3 x 5.8-7.4	marine Kurtiformes: apogonid (five-lined cardinalfish, yellow-striped cardinalfish, ring-tailed cardinalfish)	muscles	Australia
K. chilkaensis	5.5 x 7.2 x 5.8	marine Beloniformes: belonid (spottail needlefish)	muscles, peritoneum [cysts]	India
K. ciliatae	5-6.3 x 4.7-6.2 x 6.3-7.8	marine Gadiformes: gadid (sand whiting)	intestinal wall [cysts]	Australia
K. clupeidae (syn. *Chloromyxum*) [type species]	4-5.5 x 5-7.8 x 5.5-6.5	marine Clupeiformes: alosid (Atlantic menhaden, alewife, blueback herring, hickory shad), clupeid (Atlantic herring); Labriformes: labrid (cunner); Perciformes: pomatomid (bluefish); Pleuronectiformes: scophthalmid (common topknot); Scombriformes: scombrid (Atlantic bluefin tuna); Scorpaeniformes: zoarcid (ocean pout); Spariformes: sparid (scup)	muscles [pseudocysts, myoliquefaction]	Atlantic
K. coibori	6-7 x 7.5-8.5 x 8.5-9.8	marine Acanthuriformes: sciaenid (Ganges jewfish)	gut wall	India
K. cookii	5.4-7.8 x 7.6-10	Marine Kurtiformes: apogonid	intestinal	Australia

	x 6.4-9.5	(blackbanded cardinal)	submucosa [cysts]	
K. corniculata	7.5-9.1 x 11-14.8 x 9-11.1	marine Perciformes: leiognathid (Jones' ponyfish, common ponyfish)	muscles [pseudocysts]	China Sea
K. crenimugilis	7-9 x 7-8 x 5-6	marine Mugiliformes: mugilid (fringelip mullet)	intestinal wall	Red Sea
K. cruciformum (syn. *Neochloromyxum*)	7-9.1 x 6.3-18.2 x 13.6-18.2	marine Perciformes: lateolabracid (Japanese sea bass)	muscles [myoliquefaction]	Japan
K. crumena	6.8-8.2 x 9.3-10.4 x 8.2-9.7	marine Scombriformes: scombrid (Spanish mackerel, yellowfin tuna)	muscles [cysts]	North America
K. cutanea (syn. *Pentacapsula*)	5.3-6.5 x 12-13.3 x 7.8 [5 polar capsules]	marine Ophidiiformes: carapid (pearlfish)	skin	South Atlantic
K. cynoglossi	5.8-6.5 x 13.8-14.4 x 10-10.6	marine/estuarine Pleuronectiformes: cynoglossid (Senegalese tonguesole)	muscles [cysts]	Nigeria
K. decapterus (syn. *Tetraspina*)	28.8-43,3 x 30.5-50.7	marine Carangiformes: carangid (Japanese scad)	muscle	China Sea
K. dianae	4.5-5.5 x 5.5-6.5 x 5.5-6.5	marine Tetraodontiformes: tetraodontid (bullseye puffer)	oesophagus, intestines [macro-lesions]	Mexico
K. dicentrarchi (syn. *Sphaerospora dicentrarchi p.p.*)	3.5-6 x 3.5-4 x 4.6-8	marine Moroniformes: moronid (European seabass)	gallbladder wall, intestines	Europe
K. eleotrisi	5.5-8	freshwater Gobiiformes: butid (kongontorkkuja)	gills [cysts]	Africa
K. empressmichikoae	5.1-6.1 x 9.2-11.8 x 6.2-9.1	marine/estuarine Gobiiformes: gobiid (hazekuchi)	muscles [pseudocysts]	Japan
K. encrasicoli	5.8-7.5 x 9.1-12.3 x 5.8-7.4	marine Clupeiformes: engraulid (European anchovy)	muscles	Mediterranean
K. eugerres	4.5-6 x 2.7-3.2 x 3.8-4.7 [2 polar capsules]	marine Eupercia: gerreid (Brazilian mojarra)	gall bladder wall	South America
K. fujitai	4.3-5 x 5.4-6.5 x 5.1-5.8	marine Mugiliformes: mugilid (long-finned mullet)	muscles [pseudocysts]	China Sea
K. funduli (syn. *Chloromyxum*)	5.1-7.5 x 6.6-7.4 x 4.3-5	marine/estuarine Cyprinodontiformes: fundulid (mummichog)	muscles, fins [pseudocysts, post-mortem myoliquefaction]	North America
K. guangdongensis	13.8-17.1 x 23-46.6 x 9.2-13.3	marine Clupeiformes: dorosomatid (dotted gizzard shad)	muscles [pseudocysts]	China Sea
K. grammatorcyni	6.3-6.7 x 8-9 x 7.6-8.7 [6 polar capsules]	marine Kurtiformes: apogonid (southern orange-lined cardinal fish); Ovalentaria: pomacentrid (scissortail sergeant, blackspot sergeant, blue green damselfish, monarch damsel, black damsel, whitetail damsel, sapphire devil, banded humbug); Scombriformes: scombrid (shark mackerel)	muscles	Australia
K. gunterae	5-6 x 9.3-10.6 x 5.1-5.9	marine Kurtiformes: apogonid (southern orange-lined cardinal fish); Ovalentaria: pomacentrid (scissortail sergeant, banded sergeant, blackspot sergeant, blue green damselfish, sapphire devil, banded humbug, monarch damsel, bowtie damselfish, singlebar devil, whitetail damsel)	muscles	Australia
K. haridasae	4-5.5 x 9-11	marine/estuarine Mugiliformes: mugilid (goldspot mullet)	gall bladder	India
K. hemiscylli	6.9-9.9 x 9-11 x 7.7-10.5 [occasionally	marine Myliobatiformes: dasyatid (estuary stingray, Kuhl's maskray, bluespotted ribbontail ray);	muscles	Australia

	with 5 polar capsules]	Rhinopristiformes: glaucostegid (common shovelnose ray), rhinobatid (eastern shovelnose ray); Orectolobiformes: hemiscylliid (epaulette shark), orectolobid (western wobbegong, spotted wobbegong, ornate wobbegong)		
K. hexapunctata	6.6-8.3 x 8.9-12.4 x 6.5-10.9 [5-6 polar capsules]	marine Scombriformes: scombrid (Pacific bluefin tuna, yellowfin tuna, longtail tuna)	muscles [myoliquefaction]	Japan, Philippines
K. hirsuta	6.2-8 x 8.7-10.9 x 7.2-9.3	marine Carangiformes: carangid (Japanese jack mackerel, Japanese scad, shortfin scad)	muscles [pseudocysts]	China Sea
K. histolytica (syn. *Chloromyxum histolyticum*)	12-15 x 5-9	marine Scombriformes: scombrid (Atlantic mackerel); Salmoniformes: salmonid (Atlantic salmon)	muscles, gut, kidney [postmortem myoliquefaction, milky salmon]	Atlantic, Mediterranean
K. hoffmani	10-13 x 8-10.5 x 11-13.5	marine Siluriformes: ariid (roughback sea catfish)	gall bladder	India
K. hypoepicardialis	6.5 x 9.3-11.2 x 7.4-9.3	marine Acanthuriformes: sciaenid (black drum); Carangiformes: carangid (blue runner); Perciformes: lutjanid (northern red snapper), pomatomid (bluefish), serranid (Warsaw grouper); Scombriformes: nomeid (bluebottle fish); Spariformes: lobotid (Atlantic tripletail)	heart	North America
K. igami	5.6-8.2 x 9.2-12.7 x 8.5-9.6 [5-9 polar capsules]	marine Labriformes: labrid (yellowtail wrasse, pastel ringwrasse), scarid (starry-eye parrotfish, Japanese parrotfish)	muscles [pseudocysts]	Japan
K. igori	4.2-4.6 x 4.6-6.5 x 3.5-5.1	marine Mugiliformes: mugilid (longarm mullet)	gall bladder	Vietnam
K. iidae	6-7 x 8.6-12.3 x 7-8.9	marine Perciformes: polynemid (royal threadfin)	muscles [pseudocysts]	Atlantic
K. inornata	5.3-5.5 x 5.8-6 x 5.9-6.1	marine Acanthuriformes: sciaenid (spotted seatrout)	muscles [dystrophic muscle disease]	North America
K. insolita	4.2-5.3 x 6.4-7.5 x 5.3-6.4	marine Carangiformes: carangid (greater amberjack)	muscles [cysts]	Europe
K. intestinalis	3-3.5 x 6.3-7 x 5.8-6.5	marine/estuarine Mugiliformes: mugilid (striped mullet)	intestinal musculature	Japan
K. islandica	4.1-6.8 x 6.5-9.5 x 5-8	marine Scorpaeniformes: anarhichadid (Atlantic wolffish, spotted wolffish), cyclopterid (lumpfish)	muscles	Atlantic
K. iwatai	5-9.5 x 6-11.1 x 5-10.7	marine Acanthuriformes: chaetodontid (Eritrean butterflyfish); Beloniformes: hemiramphid (Red Sea halfbeak); Centrarchiformes: oplegnathid (spotted knifejaw, striped beakfish); Eupercaria: priacanthid (moontail bullseye), sparid (soldier bream, goldlined seabream); Kurtiformes: apogonid (flower cardinalfish); Moroniformes: moronid (European seabass); Mugiliformes: mugilid (flathead grey mullet); Ovalentaria: pomacentrid (threespot dascyllus, Miry's demoiselle); Perciformes: lateolabracid (Japanese sea bass), siganid (marbled spinefoot); Scorpaeniformes: platycephalid	intermuscular, adipose tissue [cysts]	Japan, Israel

		(unspecified flathead); Spariformes: lethrinid (spangled emperor, slender emperor), sparid (black porgy, red porgy, gilthead seabream)		
K. javaensis	4.6-6.3 x 6.2-7.9 x 5.1-7.2	marine Carangiformes: carangid (shrimp scad)	muscles [pseudocysts]	Indonesia
K. kabatai	4-5 x 5-7.7 x 5-7.7	marine Pleuronectiformes: scophthalmid (turbot, common topknot)	muscles [pseudocysts]	North Sea
K. kalae	9.5 x 10.5 x 11.2	marine/estuarine Siluriformes: ariid (threadfin sea catfish)	gall bladder	India
K. kenti	5.1-6.1 x 8.4-9.1 x 7-7.6 [occasionally 5 polar capsules]	marine Ovalentaria: pomacentrid (fire clownfish, Barrier Reef anemonefish, white damsel, singlebar devil)	muscles	Australia
K. konishiae	7.1-8.8 x 8.1-9.7 x 7.1-8.8 [6 polar capsules]	marine Scombriformes: scombrid (Japanese Spanish mackerel)	muscles [pseudocysts]	Japan
K. lateolabracis	5.4-6.9 x 9.9-12.9 x 5.9-9.9	marine Labriformes: scarid (Japanese parrotfish); Perciformes: lateolabracid (unspecified seabass); Pleuronectiformes: paralichthyid (olive flounder)	muscles	Japan
K. leiostomi	6.8 x 8-9.8 x 5.8-7	marine Acanthuriformes: sciaenid (spot croaker)	muscles [pseudocysts, dystrophic muscle disease]	North America
K. lemniscati	9.1-9.5 x 14.1-16.6 x 13.1-16.5 [7-8 polar capsules]	marine Perciformes: lutjanid (yellow streaked snapper)	brain	Australia
K. leptacanthae	2.4-7.2 x 7.2-9.6 x 6-8	marine Kurtiformes: apogonid (threadfin cardinalfish, fragile cardinalfish)	pericardial cavity [pesudocysts]	Australia
K. lethrini	4.5-9.3 x 10.1-12.4 x 9.4-11.9 [6-7 polar capsules]	marine Eupercaria: lethrinid (collared large-eye bream, thumbprint emperor)	brain	Australia
K. longichorda	4.3-5.5 x 6-6.8 x 4.8-6.3	marine Carangiformes: carangid (roughear scad, shortfin scad)	muscles [pseudocysts]	Philippines
K. lunata	4.5-6.2 x 9-11.4	marine Pleuronectiformes: bothid (imperial scaldfish, Mediterranean scaldfish, Thor's scaldfish)	muscles [pseudocysts]	Mediterranean
K. lutjanus	6.3-8.4 x 8.8-10.3 x 7.4-9.8	marine/estuarine Eupercaria: gerreid (saddleback silver biddy), lutjanid (crimson snapper), sparid (yellowfin seabream); Ovalentaria: ambassid (estuary glassfish)	brain, eyes, muscles, swim bladder, serosa, organs [pseudocysts]	Taiwan
K. megacapsula	7.9-15.4 x 10.8-12.9 x 25.5-44.7	marine Carangiformes: carangid (Japanese amberjack), sphyraenid (red barracuda)	muscles [pseudocysts, myoliquefaction]	China
K. miniauriculata	4.9-5.8 x 7-8.5	marine Perciformes: sebastid (Bocaccio rockfish, green striped rockfish)	muscles [pseudocysts]	North America
K. minithyrsites	4.3-5.4 x 7.7-9.9 x 5.8-6.8	marine Acropomatiformes: pempherid (ypsilon bullseye)	muscles [pseudocysts]	Australia
K. mirabilis	6.6-8.8 x 10.3-10.4 x 8.1-12	marine/estuarine Scombriformes: trichiurid (largehead hairtail)	muscles [pseudocysts, myoliquefaction]	Yemen
K. miyakoensis	8.2-11.3 x 12,2-15.6 x 11.2-15.1 [7-8 polar	marine Acanthuriformes: acanthurid (bluespine unicornfish)	brain [pseudocysts]	Japan

	capsules]			
K. monodactyli	7.3-9.2 x 7.7-9.1 [5 polar capsules, occasionally 4-10]	marine Eupercaria: monodactylid (silver moony)	muscles [pseudocysts]	Australia, Vietnam
K. muscularis (syn. *Pentacapsula*)	7.5-12 x 5-8 x 4.5-6 [5 polar capsules]	marine Acanthuriformes: chaetodontid (redtail butterflyfish)	muscles [cysts, postmortem myoliquefaction]	Philippines
K. musculoliquefaciens (syn. *Chloromyxum*)	5.3-8.1 x 7.4-10.3 x 7-10	marine Carangiformes: istiophorid (Indo-Pacific sailfish), xiphiid (swordfish)	muscles [pseudocysts, flesh jellification]	Japan
K. neothunni (syn. *Hexacapsula*)	5.3-8.9 x 9.1-13 x 6.8-12 [6-7 polar capsules]	marine Scombriformes: scombrid (yellowfin tuna, longtail tuna, northern bluefin tuna)	muscles [jellied tuna]	Japan
K. neurophila (syn. *Pentacapsula*)	8.6-10.3 x 6.8-8 [4-5 polar capsules]	marine Carangiformes: carangid (yellowtail amberjack); Perciformes: latrid (striped trumpeter)	brain [meningo-encephalo-myelitis, scoliosis]	Australia
K. niluferi	5.7-6.1 x 8.8-9.5 x 7-8.1	marine Gobiiformes: gobiid (round goby)	muscles	Black Sea
K. nova	3.1-7.7 x 4-9.8 x 4-6.8	marine/estuarine Carangiformes: carangid (Atlantic horse mackerel, Cape horse mackerel); Gobiiformes: gobiid (round goby, black goby, grass goby, longtail dwarf goby, toad goby, marbled goby, monkey goby, ratan goby, mushroom goby, sand goby, syrman goby, tubenose goby, flatsnout goby, Pinchuk's goby); Eupercaria: sparid (large-eye dentex); Perciformes: pomatomid (bluefish); Scombriformes: scombrid (little tunny, bigeye tuna); Spariformes: sparid (Spanish seabream)	muscles [pseudocysts]	Atlantic, Mediterranean, Black Sea
K. orbicularis	3.6-5 x 4.2-5.8	freshwater Cichliformes: cichlid (acara tucuma)	muscles	Brazil
K. ocellatus	4.5-4.8 x 6.2-7.2	freshwater Cichliformes: cichlid (oscar)	muscles	Brazil
K. ogawai	8.3-9.6 x 12-14.2 x 9.7-11.7	marine Pleuronectiformes: paralichthyid (olive flounder); Scombriformes: scombrid (Pacific barrelfish)	muscles [cysts]	Japan
K. ovivora	5-7.5 x 6.7-8.3 x 5.8-7.7	marine Eupercaria: scarid (redband parrotfish, redfin parrotfish); Labriformes: labrid (bluehead wrasse, yellowhead wrasse, blackear wrasse, slippery dick)	ovaries [reduced fecundity]	Panama
K. pagrusi	6.5-8.6 x 5.8-7.2 x 5.8-7.2	marine Eupercaria: sparid (red porgy)	heart [cysts]	Suez
K. paniformis	4.5-6 x 6-7 x 5-6.5	marine Gadiformes: merlucciid (North Pacific hake)	muscles [pseudocysts, mushy texture]	Canada
K. paralichthys	4.6-6 x 7.4-8.9 x 6.3-7.7	marine Pleuronectiformes: paralichtyid (olive flounder)	brain	Korea
K. paraquadricornis	7.6-8.6 x 12.2-13.9 x 6.6-7.8	marine Carangiformes: carangid (giant trevally, barcheek trevally, brassy trevally, bigeye trevally)	muscles	Australia
K. parathyrsites	8.1-10.9 x 14-16.8 x 9.7-13.3	marine Tetraodontiformes: monacanthid (black scraper)	muscles	Japan
K. parvibulvosa	4.6-6.4 x 6.3-7.2 x 5.7-6.7	marine Carangiformes: carangid (torpedo scad)	muscles [pseudocysts]	China Sea

K. pericardialis	4-4.2 x 6-7 x 4.5-5	marine Carangiformes: carangid (Japanese amberjack)	pericardial cavity [pericardial kudoasis]	Japan
K. permulticapsula	4.6-6.5 x 8.4-9.9 x 6.3-8.3 [13-15 polar capsules]	marine Scombriformes: scombrid (narrow-barred Spanish mackerel)	muscles [pseudocysts]	Australia
K. peruvianus (syn. *K. hallado*)	4.6 x 5.5-6.5	marine Gadiformes: merlucciid (Peruvian hake)	muscles [cysts, postmortem myoliquefaction]	Peru
K. petala	5.5-8 x 8.5-11.2 x 6.8-10.2	marine Eupercaria: sillaginid (silver sillago)	gall bladder wall [cysts]	Japan
K. pleurogrammi	4.8-6.8 x 6.7-9.1 x 5.6-8.2	marine Scorpaeniformes: hexagrammid (Atka mackerel, Okhotsk Atka mackerel)	muscles	Japan, Alaska
K. prunusi	6.7-8.6 x 8.5-10.3 x 6.7-8.6 [5-6 polar capsules]	marine Scombriformes: scombrid (Pacific bluefin tuna)	brain [pseudocysts, gliosis]	Japan
K. pyramidalis	4.9-6 x 7.1-8 x 6-7.2	marine Carangiformes: carangid (shrimp scad)	gall bladder	China
K. quadratum (syn. *Chloromyxum*)	5-7 x 5	marine Blenniiformes: blenniid (tompot blenny); Callionymiformes: callionymid (common dragonet); Carangiformes: carangid (Atlantic horse mackerel); Labriformes: labrid (Mediterranean rainbow wrasse); Mugiliformes: mugilid (flathead grey mullet); Scombriformes: scombrid (unspecified mackerel); Scorpaeniformes: cottid (shorthorn sculpin); Siluriformes: ariid (white barbel); Syngnathiformes: syngnathid (great pipefish, narrow-snouted pipefish, worm pipefish, snake pipefish)	muscles, kidneys	Atlantic, Indian Ocean, Mediterranean, White Sea
K. quadricornis	7.8-10 x 14-15.3 x 5.9-8.7	marine Carangiformes: carangid (gold-spotted trevally)	muscles [pseudocysts]	Australia
K. quraishii	5.9-6.3 x 5.3-5.7	marine Scombriformes: scombrid (Indian mackerel)	muscles	Saudi Arabia
K. ramsayi	8-10.4 x 4.8-8 x 2.8-4.8	marine Perciformes: nototheniid (longtail southern cod)	muscles	Falklands
K. rayformis	5-5.7 x 4.6-5.7 x 6.1-9.2	marine Scombriformes: scombrid (Pacific sierra)	muscles [pseudocysts]	Panama
K. rosenbuschi (syn. *Chloromyxum*)	6-7 x 6.5 x 5.5	marine Gadiformes: merlucciid (Peruvian hake, Argentine hake)	muscles [myoliquefaction]	Argentina
K. rousseauxii	4.2-6.7 x 6.8-9.6 x 4-6.9	freshwater Siluriformes: pimelodid (gilded catfish)	muscles	Brazil
K. sagarica	12.5-14 x 10-12 x 8.5-10.5	marine/estuarine Mugiliformes: mugilis (goldspot mullet)	gall bladder	India
K. saudiensis	4.3-5.4 x 3.4-4.3	marine Scombriformes: scombrid (Indian mackerel)	ovaries	Saudi Arabia
K. schulmani (syn. *Pentacapsula*)	7-8	marine Spariformes: nemipterid (Japanese threadfin bream)	muscles	Indian Ocean
K. sciaenae	4.8-6.4 x 6.4	marine Acanthuriformes: sciaenid (lorna drum, minor stardrum, louna-tahmkala, Peruvian banded croaker)	muscles [pseudocysts]	Peru
K. scomberi	6.1-6.8 x 8.2-10.5 x 7-8.8	marine Scombriformes: scombrid (chub mackerel)	muscles [cysts]	Japan
K. scomberomori	5-6.8 x 6.8-8.2 x 6.1-7.6 [6 polar capsules]	marine Scombriformes: scombrid (narrow-barred Spanish mackerel, Indo-Pacific king mackerel)	muscles	Australia, Vietnam
K. sebastea	5.4-5.6 x 7.3-8.2 x 5-5.5	marine Perciformes: sebastid (petit perch)	muscles	Japan

K. septempunctata	6.8-10.6 x 11.1-16.4 x 8.9-14.8 [5-8 polar capsules]	marine Pleuronectiformes: paralichthyid (olive flounder); Tetraodontiformes: monacanthid (black scarper)	muscles [pseudocysts]	Korea
K. shiomitsui	5.6-7.4 x 6.7-10.3 x 6.7-9.8	marine Pleuronectiformes: paralichthyid (olive flounder); Scombriformes: scombrid (Pacific bluefin tuna); Tetraodontiformes: monacanthid (thread-sail filefish, unicorn leatherjacket), tetraodontid (Japanese puffer)	heart, pericardial cavity [cysts]	Japan
K. shkae	6.1-6.2 x 7-8.1	marine Siluriformes: ariid (hardhead catfish)	muscles	North America
K. sphyraeni	9-10.2 x 9.5-10.5 x 9.5-10.5	marine Istiophoriformes: sphyraenid (pickhandle barracuda)	intestinal wall, muscles [cysts]	India
K. stellula	5-6.9 x 3.7-4	marine Atheriniformes: atherinid (Mediterranean sand smelt)	kidney	Black Sea
K. surabayaensis	4.6-5 x 6.4-7.6 x 5.8-6.7	marine Mugiliformes: mugilid (flathead grey mullet)	muscles [pseudocysts]	Indonesia
K. tachysurae	4.5-6 x 7-9 x 5-6.5	marine Siluriformes: ariid (thinspine sea catfish)	gall bladder	India
K. tetraspora	8-11 x 8-12 x 8-12	marine/estuarine Mugiliformes: mugilid (striped mullet)	muscles, brain, optic lobes [cysts]	India
K. thalassomi	6.1-10.9 x 9.4-16.1 x 8.5-13.8 [6-7 polar capsules]	marine Acanthuriformes: acanthurid (bluespine unicornfish); Labriformes: labrid (moon wrasse), scarid (Japanese parrotfish); Ovalentaria: pomacentrid (Bengal sergeant)	muscles [pseudocysts]	Australia, Japan
K. thunni	6.4-6.6 x 9.2-9.9 x 7.7-9.9	marine Scombriformes: scombrid (albacore, yellowfin tuna)	muscles [cysts]	Japan
K. thyrsites (syn. *Chloromyxum*)	5.6-9.1 x 6-18.2 x 10.8-19	marine Beloniformes: exocoetid (unspecified flying fish); Beryciformes: berycid (splendid alfonso); Carangiformes: carangid (Indian scad), coryphaenid (mahi-mahi); Clupeiformes: alosid (Australian pilchard, South African pilchard), dorosomatid (Bali sardinella), engraulid (Australian anchovy, Japanese anchovy), spratelloidid (delicate round herring); Gadiformes: gadid (walleye pollock), merlucciid (Cape hake, North Pacific hake, North Pacific hake, Pacific halibut); Perciformes: aulorhynchid (tube-snout), cottid (threadfin sculpin), lateolabracid (Japanese seabass); Pleuronectiformes: paralichtyid (olive flounder), pleuronectid (arrowtooth flounder, Pacific Dover sole, rock sole); Salmoniformes: salmonid (Atlantic salmon, Pacific salmon, coho salmon, brown trout); Scombriformes: gempylid (barracouta), trichiurid (silver scabbardfish); Scorpaeniformes: hexagrammid (lingcod); Tetraodontiformes: monacanthid (black scraper); Zeiformes: zeid (unspecified dory)	muscles [pseudocysts, postmortem myoliquefaction, milky barracouta, pap snoek]	Atlantic, Pacific
K. trachuri	5.5-7.5 x 5.9-8.5 x 4.5-6.2	marine Carangiformes: carangid (Japanese jack mackerel, white trevally, aka-aji, Japanese scad, shortfin scad,	muscles [cysts]	Japan

		roughear scad)		
K. trifolia	13.6-15.4 x 3.3-4 x 13.6-15.5	marine Mugiliformes: mugilid (golden grey mullet, thinlip mullet)	connective tissues, spleen, kidney, intestines, gall bladder, mesenteries, gills	Spain
K. uncinata	5.2-8 x 9.1-13.4 x 5.9-10.8	marine Acanthuriformes: leiognathid (shortnose ponyfish, spotnape ponyfish, orange ponyfish)	muscles [pseudocysts]	China
K. unicapsula	4.7-5.5 x 6.6-8.4 x 4.7-6.9	marine Mugiliformes: mugilid (thinlip mullet, golden grey mullet)	intestines, mesenteries	Spain
K. valamugili	5.2-6.6 x 4.3-5.6 x 5-5.4	marine Mugiliformes: mugilid (longarm mullet)	intestinal muscles	India
K. vesica	5.3-6.6 x 8-9.9 x 8-10.6	marine Scombriformes: centrolophid (southern driftfish)	muscles, urinary bladder	Antarctica
K. viseuensis	7.2 x 5.2	marine Batrachoidiformes: batrachoidid (Pacuma toadfish)	muscles	Asia
K. whippsi	4.2-7.4 x 7.9-15 x 4.7-10.4	marine Kurtiformes: apogonid (southern orange-lined cardinalfish, yellow-striped cardinalfish, ring-tailed cardinalfish, Doederlein's cardinalfish); Mugiliformes: mugilid (longarm mullet, longfinned mullet); Ovalentaria: pomacentrid (Bengal sergeant, Whitley's sergeant, spiny chromis, Barrier Reef anemonefish, fire clownfish, blue green damselfish, bowtie damselfish, whitetail damsel); Perciformes: cheilodactylid (spotted tail morwong)	muscles	Pacific
K. yasai	5.6-7.2 x 7.7-8.6 x 4.2-6	marine Eupercaria: sciaenid (king weakfish)	muscles	Brazil
K. yasunagai (syn. *Septemcapsula*)	4.3-8.4 x 9.4-14.5 x 7.1-14 [5-8 polar capsules]	marine Acanthuriformes: sciaenid (Japanese meagre); Carangiformes: carangid (Japanese amberjack); Eupercaria: lutjanid (blackspot snapper), nemipterid (monogrammed monocle bream); Labriformes: scarid (Japanese parrotfish); Mugiliformes: mugilid (blackfin mullet); Perciformes: lateolabracid (Japanese seabass), oplegnathid (striped beakfish); Pleuronectiformes: paralichtyid (olive flounder); Scombriformes: scombrid (Pacific bluefin tuna); Tetraodontiformes: tetraodontid (Japanese puffer)	brain [pseudocysts]	Japan
Family **Spinavaculidae** (4 valves, 4 polar capsules at one pole, iodinophilous vacuole)				
Genus ***Octospina*** (ovoid to spindle-shaped spores with 8 spines, coelozoic in freshwater fishes)				
O. tongrensis [type species]	12.2-13.5 x 8.5-9.8 x 3.8-4.5	freshwater Cypriniformes: cyprinid (grass carp)	gall bladder, swim bladder	China
Order **BIVALVULIDA** (two valves meeting in circumsporal suture, 1-4 (usually 2) polar capsules)				
considered in separate section				
Class: **MALACOSPOREA** (spores with soft (unhardened) shell valves)				
considered in previous section				

It has now been demonstrated that some myxosporean parasites have heteroxenous (2-host) life-cycles involving the formation of actinospores in annelid hosts and myxospores in piscine hosts. Early classification schemes placed all actinospores in

the order Actinomyxida, characterized by spore bodies containing 3 apical polar capsules (often with protruding tips) and most with 3 long hollow caudal projections which inflated osmotically in water to provide spore buoyancy for dispersal in water currents. Four families were recognized from oligochaetes and spiunculids: Tetractinomyxidae (*Tetractinomyxon*); Sphaeractinomyxidae (*Neoactinomyxum, Sphaeractinomyxon*); Triactinomyxidae (*Antonactinomyxon*, *Aurantiactinomyxon*, *Echinactinomyxon*, *Guyenotia*, *Raabeia*, *Siedleckiella*, *Synactinomyxon*, *Triactinomyxon*); and Hexactinomyxidae (*Hexactinomyxon*). However, with the discovery that these stages represent different stages in the life cycles of myxosporean parasites, it was suggested that actinosporean classification be suppressed and that actinospores be assigned to collective groups with vernacular names. To date, some 20 groups have been identified: anton-, auranti-, echin-, hex-, hung-, ormier-, pseudtri-, seis-, sphaer-, syn-, tetra-, tri-, unicapsul-actinomyxon, neoactinomyxum, saccimyxon, endocapsa, guyenotia, raabeia, siedleckiella, and tetraspora (with key characters tabulated below).

Actinospore type	Spore		Polar capsules	Other characters	Hosts
	Body shape	Projections			
antonactinomyxon	ellipsoidal	long, lanceolate, divergent	pyriform (protruding tips)	groups of 8 spores form cuboidal networks	freshwater oligochaetes
aurantiactinomyxon	ellipsoidal	short, stout, curved, leaflike, divergent	pyriform (protruding tips)	spores appear triradiate from above	freshwater oligochaetes
echinactinomyxon	rectangular	straight, tapered, blade-like, divergent	pyriform (slightly protruding)	spores appear stellate	freshwater oligochaetes
endocapsa	subspherical	small, bulge-like caudal swellings	pyriform (not protruding)	spores compact	marine oligochaetes
guyenotia	subspherical	long, stout, blunt, grouped	pyriform (protruding tips)	spores tripod-like	freshwater oligochaetes
hexactinomyxon	rectangular	long, thin, pointed, bifurcate	pyriform (protruding tips)	spores anchor-like	freshwater oligochaetes
hungactinomyxon	subspherical	long, tapering, divergent	rounded (not protruding)	spores form interlaced cuboidal networks	freshwater oligochaetes
neoactinomyxum	subspherical	absent	pyriform (protruding tips)	spores appear triangular from above	freshwater oligochaetes
ormieractinomyxon	ovoid	long, tapering to thin rod, terminal anchor-like structures	pyriform (protruding tips)	groups of spores interlock to form chains	freshwater oligochaete
pseudtriactinomyxon	ovoid	long, blade-like, divergent	pyriform (protruding tips)	projections with longitudinal suture	freshwater oligochaetes
raabeia	ellipsoidal	long, tapering, curved, divergent	pyriform (protruding lips)	spores grapplehook-like	freshwater oligochaetes
saccimyxon	saccular	absent	pyriform (not protruding)	spores appear globular	marine polychaetes and sipunculids
seisactinomyxon	rectangular	long, stout, divergent, bifurcate	pyriform (protruding lips)	spores grapplehook-like	freshwater oligochaetes
siedleckiella	ellipsoidal	long, stout, divergent	pyriform (protruding tips)	groups of spores form interlocked mesh	freshwater oligochaetes
sphaeractinomyxon	subspherical	absent	pyriform (not protruding)	spores solid, rounded	freshwater and marine oligochaetes
synactinomyxon	spherical	each valve with one short anterior and 2 long caudal processes	round (not protruding)	spores stellate with sinuous projections	freshwater oligochaetes
tetractinomyxon	pyramidal	absent	pyriform (not protruding)	spores appear triangular	freshwater and marine polychaetes, sipunculids
tetraspora	subspherical	absent	pyriform (not protruding)	spores antero-posteriorly flattened	marine oligochaetes
triactinomyxon	rectangular	long, tapering, pointed, curved	pyriform (protruding tips)	spores anchor-like	freshwater and marine oligochaetes
unicapsulactinomyxon	ovoid	long, thin, pointed, one anterior, 2 posterior	single large polar capsule	polar capsule opens laterally	marine polychaetes

Parasite morphology: Myxozoan parasites are multicellular (sometimes termed 'pluricellular') aquatic parasites that include myxosporeans, actinosporeans and malacosporeans (the latter 2 covered in the preceding bivalvulid section). Myxosporeans develop in vertebrate hosts (mainly fish) where they form 5 different developmental stages: namely, trophozoites, plasmodia, pansporoblasts, sporoblasts and myxospores. The earliest developmental stages are trophic stages which range from the small invasive uninucleate amoebulae (around 10 μm in diameter) to larger multinucleate trophozoites (up to 80-100 μm) which often develop in the same tissues as spore formation (although a few species undergo an 'extrasporogonic' cycle in different tissues). The trophozoites form cell doublets by nuclear division and endogeny whereby secondary daughter cells are formed within vacuoles in primary maternal cells (this enveloped 'cell-in-cell' condition is typical for myxozoa). This generates polymorphic stages in which growth and proliferation of the secondary cells occurs either within host tissues (histozoic) or within body-organ cavities (coelozoic). These stages generally take 3 forms: remaining as small microscopic (~ 10 um) pseudoplasmodia (usually histozoic) initially containing one vegetative nucleus and producing 1-2 spores; growing to small intermediate (~ 100 um) plasmodia (usually coelozoic) that are mictosporic producing 1, 2 or more spores; or growing to form large (up to 2-4 mm) plasmodia typically containing many nuclei and specialized cells producing masses of spores. The plasmodia may vary in shape from flat sheet-like to round sac-like to elongate worm-like stages, and large histozoic plasmodia often becoming ensheathed by host connective tissue cells thus forming whitish 'myxosporean' cysts. Some coelozoic species may adhere to cavity walls by developing temporary cytoplasmic holdfast outgrowths (occasionally called pseudopodia). Members of the genera *Kudoa* and *Unicapsula* typically form large polysporic plasmodia within the muscles of fishes (sometimes within cysts), while those of *Trilospora* and *Octospina* are often coelozoic forming smaller plasmodia in organ cavities. Although most myxosporeans species undergo spore formation (sporogenesis) within pansporoblasts (formed when pericytes envelope sporogonic cells), members of the genera *Kudoa* and *Unicapsula* do not form pansporoblasts but rather develop large polysporic plasmodia within which sporogonic cells are capable of producing up to 8 myxospores. Sporogonic cells divide by binary fission giving rise to sporoblast cells that undergo valvogenic, capsulogenic and sporoplasmic differentiation to form hard-shelled myxospores with multiple shell valves joined along suture lines, nematocyst-like polar capsules and amoeboid infective sporoplasms. Conventionally, myxosporean taxonomy has been based on the configuration of the mature spores, with those of multivalvulid species contain 3-13 valves (rarely 2), 1-13 polar capsules (rarely more) and 1-2 sporoplasms, whereas bivalvulid species contain 2 shell valves, 1-4 polar capsules (usually 2), and 1-2 sporoplasms. Most multivalvulid species form spores ranging in size from 4-16 μm with indistinct suture lines, delicate membranous envelopes, apical polar capsules and 2 uninucleate sporoplasms (one sometimes enveloping the other). Amongst the Multivalvulida, members of the family Trilosporidae form spores with 3 valves (*Unicapsula* forming subspherical spores with 1 polar capsule, *Trilospora* forming triradiate spores with 3 polar capsules), while members of the families Kudoidae and Spinacaulidae form spores with 4 valves (*Kudoa** forming rounded, quadrate or stellate spores with 4 polar capsules, *Octospina* forming ovoid to spindle spores with 4 polar capsules and 8 spines). [*Note that recent studies now include spores with 5-13 polar capsules in the genus *Kudoa* rather than the genera *Pentacapsula, Hexacapsula* or *Septemcapsula,* with some species even having multiple spore morphotypes within a single plasmodium (e.g. *K. monodactyli* with 5 or more spore valves and polar capsules and *K. permulticapsula* with up to 13 polar capsules)].

Site of infection: Myxosporean infections in vertebrate hosts may be coelozoic (inhabiting cavities) and/or histozoic (within tissues), with developing stages and spores usually found in specific locations (implying strict tissue tropism) although some species are more disseminated throughout their hosts. Coelozoic species are usually found in the gall bladder but can occur in other body/organ cavities (urinary bladder, swim bladder, intestines), whereas histozoic species may infect a variety of tissues and organs (cutis, gills, muscles, central nervous system, cartilage, kidney, liver, and gut wall). Myxospores have been found in freshwater and marine fish around the world, including anadromous species (that migrate from the sea into freshwater to spawn) and catadromous species (that migrate from freshwater into the sea to spawn), as well as those inhabiting brackish and estuarine waters. Over 160 multivalvulid species have been described mainly in marine fish, being reported in over 300 species (belonging to 105 families in 36 orders), while only a dozen species have been recorded in freshwater fish (belonging to 6 families in 5 orders). In comparison, some 2,945 bivalvulid species have been found in 540 species of marine fish (from 211 families in 61 orders), 1,100 species of freshwater fish (from 126 families in 35 orders), 120 amphibian species (90 frog species, 14 toads, 17 urodelans, 1 caecilian), 17 reptile species (testudines), and rarely mammals (2 shrew species) and birds (one duck species).

Pathogenesis: Infections by myxosporean parasites are generally subclinical in nature, even when developing plasmodia and spores may cause some microscopic lesions, but not severe enough to compromise organ/tissue structure/function. Nonetheless, heavier infections by some species, particularly those forming macroscopic lesions, may result in space-occupying lesions with tissue necrosis and/or hypertrophy, fibrotic encapsulation, inflammation and oedema resulting in pressure atrophy, blockages, ischaemia and anoxia that may be progress to become fatal. The extent of damage inflicted on the host depends on many factors, including host susceptibility (due to variations in innate and acquired resistance), parasite aggressiveness (proliferative potential, tissue tropism) and environmental conditions (temporal and spatial variations in climate and habitat). Most coelozoic infections in organ or body cavities are benign although some have been associated with discolourations and partial blockages, mainly in the gall bladder and upper urinary tract. Histozoic infections vary considerably in their effect on the host depending on the organs involved, the intensity of infection and the sizes of the lesions. A growing number of histozoic species have been found to form cysts or pseudocysts causing space-occupying lesions. Some infections in nervous tissues have been associated with behavioural disorders, some in

cartilage may produce gross deformities, and some infections in somatic musculature may result in visible unsightly lesions which can undergo post-mortem myoliquefaction affecting fillet quality and economic value.

Despite the prevalence and broad host distribution of infections by *Kudoa* spp., most do not cause significant morbidity or mortality as they are often cleared by host immune responses system within a year. Myxospores are ingested by macrophages and destroyed, followed by the repair of host tissues. Any inflammatory responses are generally coincident with myxospore formation, rather than earlier proliferative stages. Mature plasmodia may become surrounded by dense fibrous capsules formed by host connective tissue cells resulting in cavity-like lesions with cyst or pseudocyst formation. Pseudocysts lack an inner parasite-derived lining, and their formation is followed by necrotic changes with the pseudocyst wall formed by reparative inflammation. It has also been shown that the majority of severe infections take place in immunocompromised animals, and even then do not result in anything more than chronic inflammation. Pre-sporogonic developmental stages do not elicit strong immune responses and encysted sporogonic stages are sequestered away from the host immune system. This state of 'immune evasion' generally last until mature myxospores begin to be released, but the resultant immune responses often only lead to the development of multifocal chronic inflammation between muscle fibres that subsides with tissue repair. While developing stages may exhibit low pathogenic potential, their presence does pose a serious threat to fisheries because the cysts may become macroscopically visible as unsightly whitish spots or streaks in the flesh. The cysts may sometimes exhibit dark discolourations initially thought to be due to melanin deposition but now attributed ultrastructurally to the accumulation of breakdown products. The resultant blemishes are aesthetically unappealing and considerably reduce the market value of the fish. They may also severely compromise product quality by causing postmortem myoliquefaction (soft mushy or milky flesh) due to the release of parasite proteolytic enzymes (including cysteine proteases) when cysts are disturbed by processing (filleting, freezing/thawing, cooking/smoking). It has been suggested that myoliquefaction may be a natural process by which mature myxospores are released from host tissues, as anoxic postmortem tissues undergo anaerobic glycolysis with acidic waste products promoting proteolysis. Myoliquefaction has been reported for several multivalvulid species, including *Kudoa thrysites* in Atlantic salmon and coho salmon, *K. clupeidae* in Atlantic herring, *K. cruciformum* in seaperch, *K. funduli* in mummichog, *K. histolytica* in mackerel, *K. mirabilis* in ribbonfish, *K. musculoliquefaciens* in swordfish, *K. neothunni* in yellowfin tuna, *K. paniformis* and *K. peruvianus* in hake, *Unicapsula seriolae* in amberjack, and *U. muscularis* in halibut. Infections in fish muscles are also thought to occasionally cause food poisoning in humans, with a self-limiting diarrhoeic illness developing after the consumption of traditional sushi or sashimi prepared using raw flesh containing *Kudoa* cysts (e.g. *K. septempunctata* in flounder*, K. hexapunctata* and *K. neothunni* in tuna, *K. iwatai* in bream, and *Unicapsula seriolae* in amberjack). Infections in fish may also extend into other tissue and organ systems, including the brain, with several species apparently having little effect (e.g. *K. paralichthys* in olive flounder, *K. tetraspora* in mullet, *K. cerebralis* in striped bass), while others may elicit intense reactions (e.g. *K. neurophila* causing severe granulomatous meningo-encephalo-myelitis in striped trumpeters, *K. yasunagai* forming macroscopic lesions in sea bass and beakfish). One species (*K. ovivora*) was found to reduce the fecundity of wrasse by invading the ovaries and rendering maturing oocytes non-viable. Other species were found to infect the smooth muscle of the intestinal wall, with *K. intestinalis* having little effect on striped mullet, while *K. dianae* formed large cysts that occasionally ruptured.

Developmental cycle and mode of transmission: Myxosporeans in fish first undergo vegetative proliferation in pseudoplasmodia or plasmodia followed by myxospore morphogenesis, both processes featuring a characteristic cell-in-cell condition where endogenously produced secondary cells persist inside primary mother cells. Vertebrates become infected when mature actinospores come into contact with external epithelia (skin and/or gills) discharging filaments from their polar capsules to facilitate attachment. The spore shell valves then open releasing the infective germ cells (sporoplasms) which penetrate the epithelial barriers. The sporoplasms are either single binucleate cells (whose nuclei fuse to form a synkaryon) or 2 uninucleate cells (that fuse by autogamy to form a single cell). They transform to trophic stages (trophozoites), initially called amoebulae, as they invade host tissues, often moving deeper via blood or lymph vessels. The trophozoites undergo proliferation by forming cell doublets through nuclear division and endogeny whereby one daughter nucleus becomes enveloped by endoplasmic reticulum cisternae resulting in a secondary cell located within a vacuole in the primary cell (resulting in the enveloped cell-in-cell condition typical for myxozoa). All species undergo sporogonic cycles forming plasmodia (or pseudoplasmodia) involving growth and proliferation of generative secondary cells and vegetative nuclei. These stages are either immobile rounded stages encased in host tissues (histozoic) or occur as flat sheets or rounded balls within body or organ cavities (coelozoic) where they are attached to the walls by cytoplasmic holdfast outgrowths or occur free-floating in the lumina. This plasmodial development is often coupled with sporogony (spore formation) although some species undergo extrasporogonic cycles in tissues other than where sporogony occurs. Extrasporogonic cycles have been reported for members of the genus *Kudoa,* whereby secondary cells undergo a series of mitotic divisions and then endogenous budding to give rise to tertiary cells. The secondary cells are released by rupture of the primary cells allowing parasites to migrate via blood or lymph vessels to their final sites where sporogony occurs. All species undergo plasmodial development that typically involves one or more of three morphological types: numerous small pseudoplasmodia (containing only one vegetative nucleus) that produce 1-2 spores (mono- or di-sporic) often being histozoic (sometimes pervading host tissues as diffuse infiltrates); medium plasmodia that are mictosporic producing 1, 2 or more spores often being coelozoic; and large plasmodia (sometimes macroscopic) that produce masses of spores (poly-sporic) often being histozoic (sometimes encysted by host connective tissue). *Kudoa* and *Unicapsula* spp. are predominantly histozoic typically forming large polysporic plasmodia within the musculature, while *Trilospora* and *Octospina* spp. are usually coelozoic forming smaller plasmodia in organ cavities. Although most myxosporeans species undergo sporogenesis within pansporoblasts (formed when pericytes envelope sporogonic cells), *Kudoa* and *Unicapsula* spp. do not

form pansporoblasts but rather directly form sporogonic cells that are capable of producing up to 8 myxospores. The sporogonic cells divide by binary fission giving rise to sporoblast cells that undergo valvogenic, capsulogenic and sporoplasmic differentiation to form hard-shelled myxospores with multiple shell valves joined along suture lines, nematocyst-like polar capsules and amoeboid infective sporoplasms. Mature myxospores are released into the aquatic environment either by the antemortem rupture of superficial cysts or the postmortem degradation of infected tissues upon the death and decay of the host. Myxospores are highly resilient to external environmental conditions, and some have been shown to retain infectivity for up to 4 months in mud, for 2 months after freezing at -20°C, and even after passage through the alimentary canal of predatory birds and fish. Myxospore infections in fish often show seasonal patterns of infection, with prevalence generally highest in autumn/winter in subtropical regions, or summer/autumn in temperate regions, although patterns can be hard to discern within specific age groups. Epidemiological observations indicate infection prevalence and abundance may vary according to prevailing environmental conditions (notably water temperature and salinity) but also numerous host factors (population density, age cohorts, migratory, breeding, spawning and feeding habits, nutritional, physiological and immunological status). It was initially thought that many myxospore infections in fish were long-lasting (potentially life-long) but there is growing evidence that infections may cycle seasonally with developing stages not persisting longer than one year. Infections generally do not evoke strong host immune responses, so there may be little protective immunity acquired by fish even after repeated exposure.

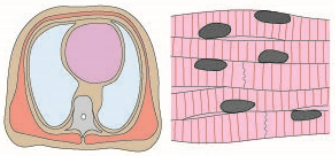
Initially, epidemiological studies suggested that myxospores may be transmitted directly from fish to fish, possibly ascending the food chain when big fish eat little fish, and sometimes with caveats that water-borne spores needed to be 'aged' in sediments to become infective, or passaged through the digestive tracts of aquatic invertebrates. This led to the widespread belief that the feeding of infected ‘trash’ fish to commercial species may be responsible for disease outbreaks, but direct fish-to-fish transmission has not been substantiated for any multivalvulid species (with the possible exception of *Kudoa ovivora* that infects the eggs of wrasse). It was subsequently discovered experimentally that myxosporeans require a secondary or alternate host to complete their life-cycle. Myxospores from fish were found to be infective for aquatic invertebrates (annelids) where they underwent development and the formation of different types of spores (namely actinospores) that proved to be infective to fish. Development in annelids involved asexual proliferation (merogony) followed by sexual reproduction (gametogony) where the zygotes differentiated into actinospores. By definition, this makes annelids the final or definitive hosts (in which sexual development occurs) and fish should be considered simply as intermediate hosts. Heteroxenous (2-host) life-cycles have now been demonstrated for species within 16 bivalvulid genera (see previous section), but not yet for any multivalvulid genera. Clearly, further studies are required to establish parasite life-cycles and unravel the complexities of transmission.

Differential diagnosis: The diagnosis of myxosporean infections in fish on clinical grounds is presumptive, as other aetiological agents or pathological conditions may cause similar symptoms, signs or behaviours. The observation of macroscopically visible cysts in host tissues is not pathognomic as other infectious agents may cause similar encapsulated lesions, especially bacteria. Most infections are diagnosed at post-mortem by the detection and identification of myxospores recovered from host tissues or organ cavities. Samples are usually examined microscopically as wet mounts, smears, tissue imprints, squash preparations or sections, preferably using high contrast illumination systems (e.g. phase-contrast, differential interference-contrast). Microscopy is best performed on fresh samples, as preservatives and freezing may distort spore integrity (especially size and shape). Nonetheless, high-volume screening studies often make recourse to the examination of histological sections of fixed tissues. A range of stains have been employed to improve visual acuity, including Giemsa and silver stains, and some fluorochromes and biotinylated lectins. Several techniques have also been developed to harvest spores from host tissues by maceration, homogenization, enzymatic digestion (pepsin or trypsin), filtration and/or centrifugation. Parasite genera may be identified by the morphological characteristics of their mature spores (size, shape, structure, sutural ridges, spore projections, caudal appendages, ribs, ridges or striae), polar capsule morphology (number, shape, size and angle, arrangement of coils of the polar filaments, position of capsule opening) and sporoplasms (number, location). Specific differentiation often requires further information on pre-spore developmental stages as well as tissue location, pathological changes, host occurrence and geographic location. Both transmission and scanning electron microscopy may be required to reveal topographical and cellular ultrastructural features. A small range of immunological techniques have also been developed to guide research and aid diagnoses. Monoclonal and/or polyclonal antibodies have been raised against extrasporogonic stages and mature spores of several economically important myxozoan species (including the multivalvulid *Kudoa thyrsites*) and used with variable success to detect parasites within fish tissues or tissue extracts, usually by chemiluminescence. Enzyme immunoassays have also been developed to detect host antibodies against *K. thyrsites* antigens in serum samples, yielding specific and sensitive results which allowed reasonable prediction of the degree of postmortem myoliquefaction that may occur. Modern molecular biological techniques are now commonly used to characterize species and determine phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear (large and small subunit ribosomal RNA and internal transcribed spacer regions) or mitochondrial (cytochrome c oxidase subunit I) genes.

Treatment and control: There are few chemotherapeutic agents that work against multivalvulid myxosporean infections in fish. Some successes were observed treating bivalvulid infections using a range of toxic compounds (including malachite green, acetarsol, and dimetridazole) but none worked against multivalvulid *Kudoa* infections and most have since been withdrawn from commercial use due to concerns over their bioaccumulation and toxicity. Similarly, the use of the antibiotic fumagillin showed little effect against *Kudoa* infections despite good success against some bivalvulid infections. There have been a few reports suggesting that dietary supplementation with the coccidiostat nicarbazin may be effective against *K. thyrsites* in Atlantic salmon, but several

problems were encountered with growth retardation, drug residues and some mortalities. Reasonable disease control has been achieved in aquaculture by the adoption of preventive measures designed to minimize the introduction, amplification, survival and spread of parasites amongst fish stocks, with desirable management procedures often mandated by government and/or industry regulations. Procedures used to minimize the introduction of parasites into culture facilities include health screening all source and translocated stocks, establishing appropriate quarantine procedures, maintaining temporal and spatial records of parasite distribution and abundance, and implementing education and awareness campaigns for producers and consumers. Previous recommendations to curtail the feeding of infected trash fish (e.g. pilchards, sardines) to cultured stock have not been supported by experimental studies nor by molecular characterization studies. Protocols employed to avoid contamination of holding facilities include the prompt removal and destruction of diseased fish (by onshore burial or incineration), regularly cleaning fomites and equipment using chemicals, heat or desiccation, and frequently changing netpens and moving them to deeper waters (thus reducing contact with benthos potentially harbouring annelids). Husbandry practices should strive to keep fish in optimal health as they become more susceptible to infection and disease when stressed. Good management involves maintaining water quality (appropriate temperature, pH, aeration, turbidity, solutes), reducing organic loads (monitoring planktonic and benthic plant and animal communities), providing good nutrition without over-feeding, stocking without over-crowding, avoiding conditions where fish become immuno-compromised (by treating concomitant infections, and even removing sexually-mature salmonids as those of some species become partially immuno-suppressed), separating species and age cohorts, harvesting fish before parasite maturation (particularly in colder winter months when prevalence is reduced), and selectively breeding resistant fish (some prospects based on fish species/strain/stock differences in susceptibility for particular infections, especially amongst salmonids). Several studies have also shown that the incidence of post-mortem myoliquefaction can be reduced by implementing post-harvest treatments with potato extracts, egg whites and/or bovine plasma proteins to inhibit parasite proteolytic enzymes released during handling and processing.

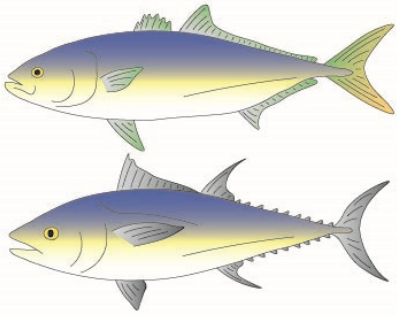
Myxozoa
(multivalvulid species)



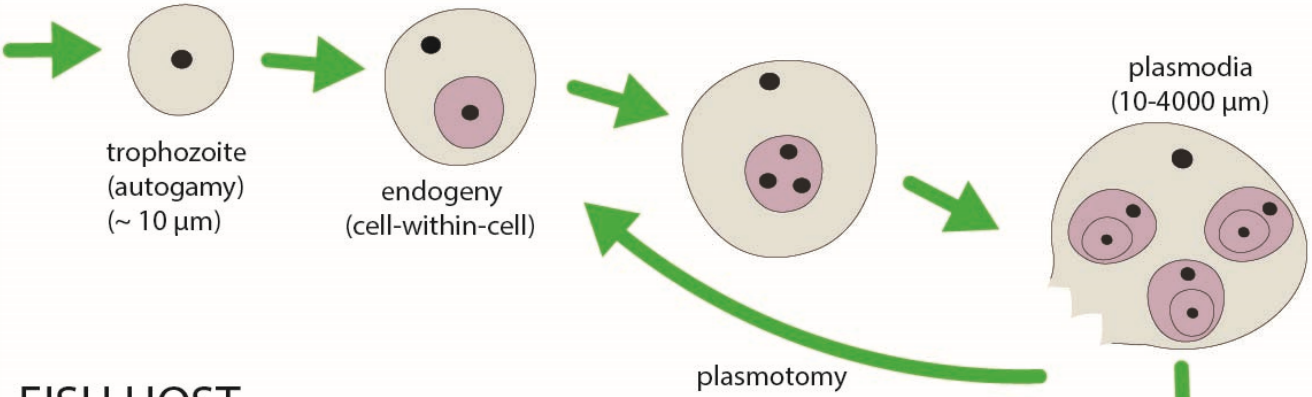
coelozoic/histozoic
(lesions/cysts, inflammation, dysfunction, mortalities)

form unique multicellular spores
(with valvogenic, capsulogenic
and sporoplasmic cells)

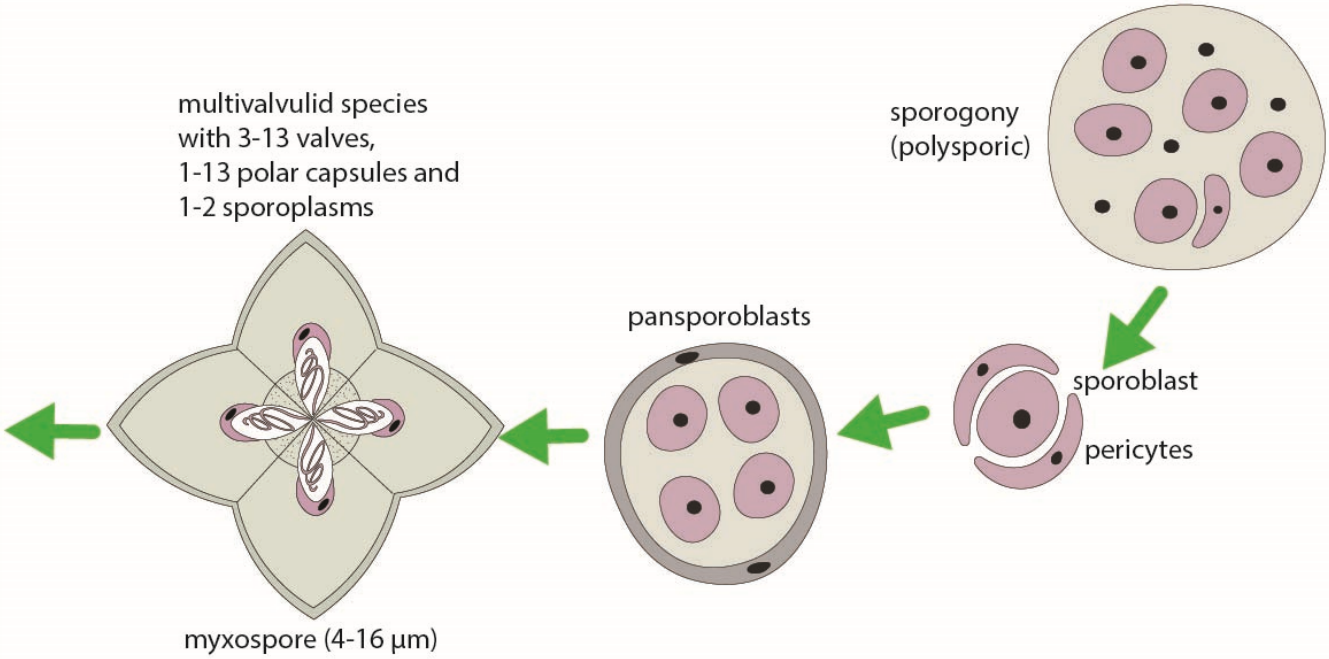
discovered to have heteroxenous cycles
with myxospores developing in fish &
actinospores developing in worms



Vertebrate Hosts
(mainly marine fish)



FISH HOST



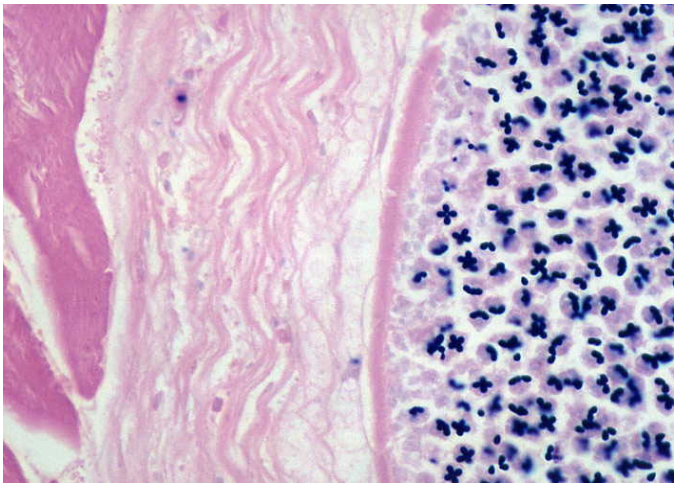
multivalvulid species
with 3-13 valves,
1-13 polar capsules and
1-2 sporoplasms

myxospore (4-16 µm)

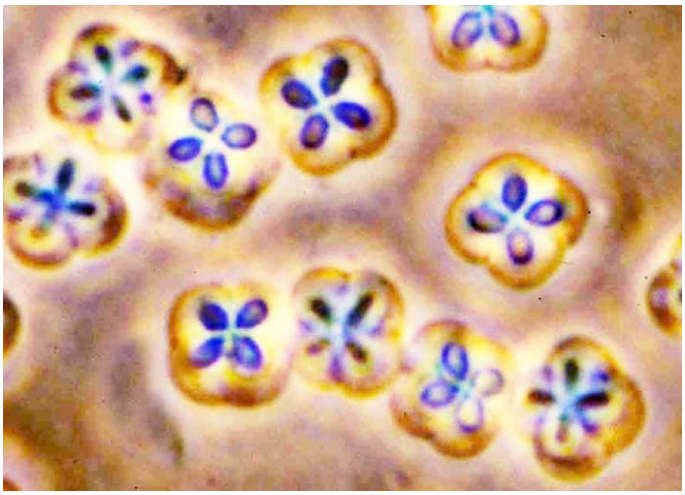
most life-cycles unknown, but studies have shown
myxospores to be infective to aquatic annelids
where they form actinospores infective to fish)
[actinospore cycle shown separately]



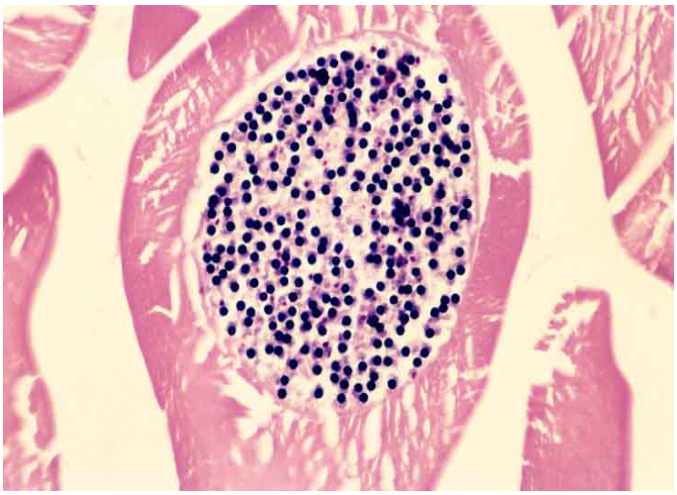
Kudoa cyst in fish muscle



Kudopa cyst wall in fish muscle



Kudoa spores from cyst in fish



Unicapsula cyst in fish muscle

HELMINTHS

HELMINTH PARASITES

The word ‘helminth’ is a general term meaning ‘worm’, but there are many different types of worms. Prefixes are therefore used to designate types: platy-helminths for flatworms and nemat-helminths for roundworms. All helminths are multicellular eukaryotic invertebrates with tube-like or flattened bodies exhibiting bilateral symmetry. They are triploblastic (with endo-, meso- and ecto-dermal tissues) but the flatworms are acoelomate (do not have body cavities) while the roundworms are pseudocoelomate (with body cavities not enclosed by mesoderm). In contrast, segmented annelids (such as earthworms) are coelomate (with body cavities enclosed by mesoderm). Many helminths are free-living organisms in aquatic and terrestrial environments whereas others occur as parasites in most animals and some plants. Parasitic helminths are an almost universal feature of vertebrate animals; most species have worms in them somewhere.

Biodiversity

Five major assemblages of parasitic helminths are recognised: the Nemathelminthes (nematodes), the Acanthocephala (spiny-headed worms), and the Platyhelminthes (flatworms), the latter being subdivided into the Cestoda (tapeworms), the Trematoda (digenetic flukes) and the Monogenea (monogenetic flukes):

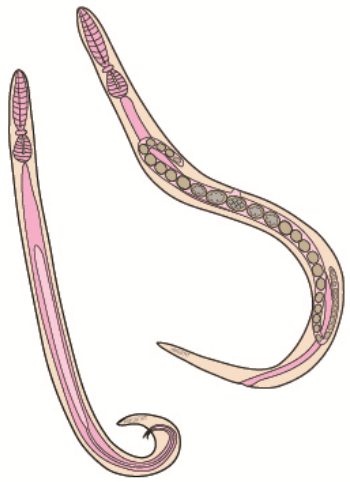
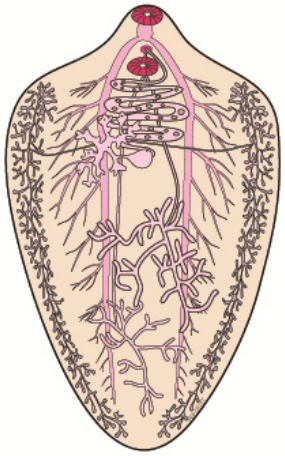
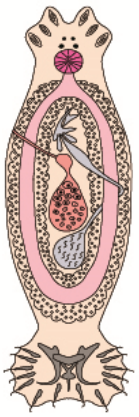
- Nematodes (roundworms) have long thin unsegmented tube-like bodies with anterior mouths and longitudinal digestive tracts. They have a fluid-filled internal body cavity (pseudocoelom) that acts as a hydrostatic skeleton providing rigidity (so-called ‘tubes under pressure’). Worms use longitudinal muscles to produce a sideways thrashing motion. Adult worms form separate sexes with well-developed reproductive systems: females with 1-2 ovaries connected to the uterus via a tubular oviduct, and males with a single testis connected to the vas deferens, seminal vesicle and ejaculatory duct.

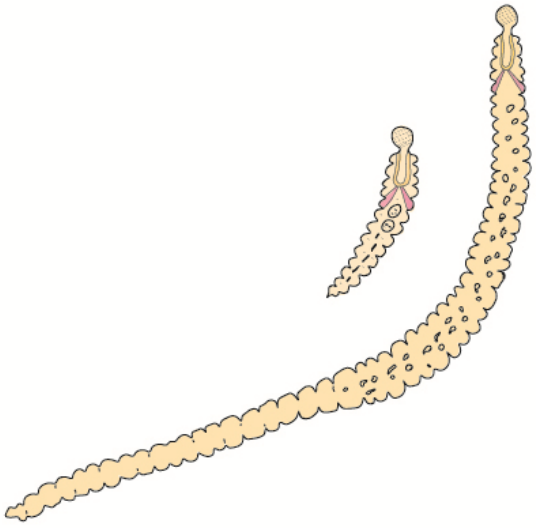
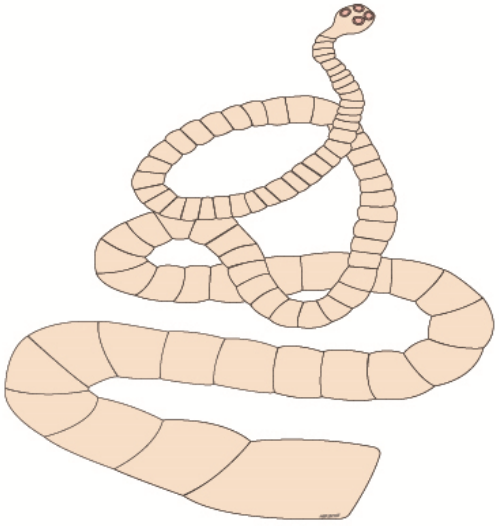
- Acanthocephalans (thorny-headed worms) have elongated flattened bodies with transverse wrinkles and a distinctive cylindrical invaginable proboscis bearing rows of recurved spines. They lack digestive tracts and absorb nutrients through their tegument. Adults form separate sexes: males having 2 testes; and females producing ovarian balls that float free in the pseudocoelom with developing eggs ‘sorted’ by a unique funnel-shaped uterine bell.

- Cestodes (tapeworms) have long flat ribbon-like bodies with a single anterior holdfast organ (scolex) and numerous segments. They do not have a gut and all nutrients are taken up through the tegument. They do not have a body cavity (acoelomate) and are flattened to facilitate perfusion to all tissues. Segments exhibit slow body flexion produced by longitudinal and transverse muscles. Most tapeworms are hermaphroditic and each segment contains both male and female organs.

- Trematodes (digenetic flukes) have small flat leaf-like bodies with oral and ventral suckers and a blind sac-like gut. They are acoelomate and dorsoventrally flattened with bilateral symmetry. They exhibit elaborate gliding or creeping motion over substrates using compact 3-D arrays of muscles. Most species are hermaphroditic (individuals with male and female reproductive systems) although some blood flukes form separate male and female adults. They have indirect life-cycles involving asexual reproduction in molluscs.

- Monogeneans (monogenetic flukes) have leaf-like to cylindrical acoelomate bodies with a prominent posterior attachment organ armed with hooks, suckers and/or clamps. They are hermaphroditic and have direct life-cycles involving free-swimming ciliated larvae (oncomiracidia).

nematode	digenean	monogenean
		

acanthocephalan	cestode
	

Taxonomic classification

Traditionally, most helminths (worms) were classified together with different groups recognised on the basis of body plan, development and habitats. The nematodes (roundworms) were considered a sister group to the platyhelminths (flatworms), the latter comprising cestodes (flat ribbon-like tapeworms) and trematodes (flat leaf-like flukes). The trematodes were further divided into the Monogenea and Digenea on the basis of their monogenetic (1-host) and digenetic (2 or more host) life-cycles. Many textbooks have retained this simplistic classification, which is convenient if not accurate. Modern phylogenetic studies have demonstrated considerable differences between roundworms and flatworms as well as between many flatworm groups. The extent of those differences has facilitated a complete reorganization of extant metazoan groups, with many groups reassigned to new composite taxa.

While Protozoa (Protista) are unicellular eukaryotic organisms, the Metazoa are multicellular eukaryotes with differentiated tissues. They form a major division in the animal kingdom, exclusive of the sponges. Metazoans are triploblastic (with three body germ layers), most have a coelom (body cavity) and they exhibit bilateral symmetry (except the cnidaria (jellyfish) which exhibit radial symmetry). Their embryonic development includes a blastula stage, and two major lineages are recognised depending on the type of cleavage at the 8-cell embryonic stage and the fate of the blastopore: the protostomes (exhibiting determinate cleavage, mostly spiral, and the blastopore becomes the mouth) and the deuterostomes (with indeterminate radial cleavage and the blastopore becomes the anus). The deuterostomes comprise the echinoderms (starfish) and the chordates (including all vertebrates) while the protostomes contain most of the invertebrate animals. Molecular studies found that two major protostome lineages were well supported: Lophotrochozoa and Ecdysozoa.

The Lophotrochozoa was established as a monophyletic group based on molecular evidence and they have few unifying characteristics. The name derives from the frequent possession of a unique feeding structure called the lophophore (ring of ciliated tentacles) or the presence of a planktonic free-swimming stage called a trochophore (ovoid larva with ciliary bands). However, some groups contain neither (particularly the parasitic representatives). The Lophotrochozoa comprise the platyhelminths (flatworms), rotifers, acanthocephalans, lophophorates (bryozoa, branchiopods, phoronids) and spiralians (nemertea, annelids, molluscs). The acanthocephalans are closely related to the rotifers because members of both groups have a eutelic syncytial epidermis (with fixed numbers of nuclei). The platyhelminths are soft-bodied acoelomate flatworms that include free-living 'Turbellaria' (a taxonomically artificial group) and parasitic Trematoda, Monogenea and Cestoda. All the major parasitic groups have Mehlis' (shell) glands surrounding the ootype where the egg is constructed, and ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). The trematodes, monogeneans and cestodes are bound by syncytial (multiple nuclei enclosed within a single cell membrane) teguments (neodermis) and have recently been collectively classified together as the Neodermata which is considered a lineage comprised exclusively of parasites. The endoparasitic trematodes (Aspidogastrea and Digenea) have flattened leaf-like bodies with anterior adhesive organs; of these, the dominant Digenea undergo asexual sporocyst development within molluscan intermediate hosts. The ectoparasitic Monogenea have a posterior adhesive organ and have free-swimming oncomiracidial larval stages in their one-host life-cycles. The endoparasitic cestodes have flattened ribbon-like bodies with an anterior scolex and segmented proglottids that lack digestive tracts. Their life-cycles involve at least 2 hosts.

The Ecdysozoa are organisms which have hard cuticles and can only grow by periodic moulting (ecdysis). They comprise the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). The nematodes are unsegmented tubular worms covered by a collagenous elastic cuticle without microvilli. They have a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have prominent longitudinal muscles which are used to produce a conspicuous thrashing motion. The worms have complex sensory papillae; namely, amphids near the head particularly in free-living species but reduced in parasitic species, and supplemented by phasmids near the tail. Their differential presence has led to the recognition of two major classes: the Secernentea (secretors) with phasmids (= Phasmidea), and the Adenophorea (gland-bearers) without phasmids (= Aphasmidea). However, molecular phylogenetic studies have only partially supported morphotypic classifications and have revealed many unexpected groupings. Studies on ribosomal DNA sequences suggested the existence of five major clades while more comprehensive studies on mitochondrial DNA indicated as many as 12 clades. A revised classification based on both genotypic and phenotypic characters identified three major nematode lineages: Dorylaimia, Enoplia and Chromadoria. The Dorylaimia contains both free-living and parasitic assemblages; many being omnivores or predators and some parasitizing plants and animals (invertebrates and vertebrates). Most possess an odontostyle, a tooth for puncturing food items. The Enoplia are bactivorous or predatory nematodes in moist aquatic or terrestrial habitats or parasitic on plants. They display great osmotic tolerance and many have large hooks or teeth and complex sensory structures such as eyespots and unique stretch receptors (metanemes). The Chromadoria includes several diverse free-living and parasitic lineages whose bodies usually have annules, spiral amphids and three oesophageal glands. The previously-recognised Secernentea (Phasmidea) was found to be deeply nested within the Chromadoria, and has now been relegated to the order Rhabditida. Chromadorian nematodes are common in marine sediments and moist soils (incl. mosses and lichen). They are often small and rapidly reproducing bacterial feeders, although some are predators with sophisticated 'can-opener' teeth. Many species have chemically impermeable cuticles which probably contributed to their success as parasites, colonizers and

extremophiles. Many rhabditids are parasitic in fungi, plants or animals and have been associated with severe diseases and production losses. They possess well-developed pharynxes with one or more rounded muscular bulbs, and their life cycles often involve modified larval ('dauer') stages adapted to long-term survival. Although the phylogenetic relationships between all the disparate nematode groups are slowly being unravelled, most parasitological texts still retain conventional taxonomic classification schemes which provides good group coverage for important human and animal parasites.

Supergroup: Amorphea	(unikonts, with single flagellum, or nonflagellated amoebae)
Opisthokonta	(stages with single posterior flagellum)
Holozoa	(metazoans, filasterans, ichthyosporeans, choanomonads)
Metazoa	(multicellular eukaryotes, heterotrophic)
Protostomia	(triplobastic, spiral cleavage)
▪ Group: Lophotrochozoa	(lophophore feeding structure or trochophore larva or neither)
Phylum: Platyhelminthes	(acoelomate flatworms)
Neodermata	(syncytial tegument = neodermis)
• Class: Trematoda	(leaf-like flukes, anterior sucker, sac-like gut, monoecious)
•• Subclass: Aspidogastrea	(endoparasites with 2-host cycles, no asexual reproduction)
•• Subclass: Digenea	(digenetic endoparasites, asexual reproduction in first int. host)
••• Order: Diplostomatida	(blood and intestinal flukes of all vertebrate classes, cercariae usually penetrate next host)
••• Order: Plagiorchiida	('echinostomatids', plagiorchiids', all vertebrate classes, cercarial behaviour diverse)
• Class: Monogenea	(posterior opisthaptor, oncomiracidia, monoecious, monoxenous)
••• Order: Monopisthocotylea	(opisthaptor with hooks and hooklets)
••• Order: Polyopisthocotylea	(opisthaptor with clamps)
• Class: Cestoda	(tapeworms, without gut, monoecious, heteroxenous, endoparasites)
•• Subclass: Eucestoda	(larvae hexacanth (with six hooks))
••• Order: Caryophyllidea	(aquatic hosts, fish-annelids, simple scolex, one proglottid)
••• Order: Cathetocephalidea	(elasmobranchs, apical pad, papillary band)
••• Order: Diphyllidea	(elasmobranchs, 2 bothria, armed rostellum, cephalic peduncle)
••• Order: Trypanorhyncha	(elasmobranchs, 2-4 bothria, 4 spiny retractile tentacles)
••• Order: Litobothriidea	(elasmobranchs, apical sucker, 3-5 muscular pseudosegments)
••• Order: Lecanicephalidea	(elasmobranchs, 4 small suckers surmounted by globular structure)
••• Order: Rhinobothriidea	(elasmobranchs, 4 stalked loculate bothridia)
••• Order: 'Tetraphyllidea' relics	(elasmobranchs, mammals, 4 stalked bothridia)
••• Order: Spathebothriidea	(marine fish, without bothria or suckers)
••• Order: Haplobothriidea	(marine fish, club-shaped tentacles, bothria)
••• Order: Bothriocephalidea	(fish, amphibians, 2 bothria)
••• Order: Nippotaeniidea	(freshwater fish, scolex with one apical sucker)
••• Order: Tetrabothriidea	(birds, mammals, 4 muscular bothridia)
••• Order: Phyllobothriidea	(elasmobranchs, unarmed bothridia, apical suckers)
••• Order: Oncoproteocephalidea	(cold-blooded vertebrates, 4 loculate bothridia, rostellum)
••• Order: Diphyllobothriidea	(Pseudophyllidea) (aquatic hosts, unarmed scolex, 2 shallow bothria)
••• Order: Cyclophyllidea	(terrestrial hosts, scolex with four suckers, often bearing hooks)
•• Subclass: Cestodaria	(larvae decacanth (with ten hooks))
••• Order: Amphilinidea	(fish hosts, uterus N-shaped, posterior genital pores)
••• Order: Gyrocotylidea	(fish hosts, anterior testes, anterior genital pores)
Phylum: Mesozoa	('middle-animals', parasites of marine invertebrates)
Phylum: Nemertea	(ribbon worms, marine)
Clade: Gnathifera	(small cuticular jaws, except Acanthocephala)
Phylum: Gnathostomulida	(jaw worms, marine sediments)
Phylum: Micrognathozoa	(interstitial sands)

Group: Syndermata (eutelic syncytial epidermis)

Phylum: Rotifera (rotifers, ciliated corona, aquatic, epizoic or parasitic)

Phylum: Acanthocephala (thorny-headed worms, parasitic, arthropod-vertebrate cycles)
- Class: Archiacanthocephala (terrestrial cycles, myriapod/insect intermediate hosts)
  - •• Order: Apororhynchida (intestines, birds, bulbous proboscis)
  - •• Order: Gigantorhynchida (intestines, birds, long proboscis armed with two rows of 6 hooks)
  - •• Order: Moniliformida (intestines, mammals, cylindrical proboscis)
  - •• Order: Oligacanthorhynchida (proboscis subspherical, short rows of hooks, protonephridial organs)
- Class: Palaeacanthocephala (aquatic cycles, malacostracan intermediate hosts)
  - •• Order: Echinorhynchida (fish, long proboscis with 14-22 rows of 10-16 hooks)
  - •• Order: Polymorphida (proboscis bulbous/cylindrical, numerous hooks in rows)
- Class: Eoacanthocephala (aquatic cycles, maxillipod intermediate hosts)
  - •• Order: Gyracanthocephala (freshwater fish, large proboscis with 4 circles of recurved hooks)
  - •• Order: Neoechinorhynchida (freshwater fish, short proboscis with three rows of 6 hooks)

Phylum: Cycliophora (live in mouthparts of marine decapods)

Phylum: Gastrotricha (gastrotrichs, aquatic)

Phylum: Entoprocta (entoprocts, aquatic, some commensals on annelids)

Group: Lophophorates (lophophore mouths, radial cleavage)

Phylum: Ectoprocta (bryozoa, moss animals)

Phylum: Brachiopoda (lamp shells, marine sediments)

Phylum: Phoronida (phoronids, coastal waters)

Phylum: Mollusca ('soft-bodied', chitons, tusk shells, snails, slugs, nudibranchs, sea butterflies, clams, mussels, oysters, squid, octopuses, nautiluses)

Phylum: Annelida (segmented worms, oligochaetes, polychaetes, leeches)

Phylum: Echiura (spoon worms, marine sediments)

Phylum: Sipuncula (peanut worms, marine sediments)

- Group: Ecdysozoa (cuticle moulted = ecdysis)

Group: Nematoidea (collagenous cuticle without microvilli)

Phylum: Nematoda (= Nemata) (pseudocoelomate roundworms, tubular digestive tract, dioecious)

- Class: Enoplea (lacking phasmids, free-living and parasitic)
  - Subclass: Enoplia (free-living, amphids shaped like stirrups, smooth bodies)
    - •• Order: Enoplida (bactivores, algivores, omnivores, predators)
    - •• Order: Triplonchida (aquatic, some phytoparasites)
  - Subclass: Dorylaimia (free-living and parasitic, odontostyle)
    - •• Order: Dorylaimida (phytoparasites, algivores, omnivores, predators)
    - •• Order: Monochida (bactivores, algivores, omnivores, predators)
    - •• Order: Isolaimida (free-living in soils)
    - •• Order: Dioctophymatida (animal parasites)
    - •• Order: Muspiceida (vertebrate parasites)
    - •• Order: Marimermithida (invertebrate parasites)
    - •• Order: Mermithida (invertebrate parasites)
    - •• Order: Trichinellida (vertebrate parasites)

- Class: Chromadorea (free-living and parasitic, spiral amphids, three oesophageal glands)
  - Subclass: Chromadoria (soils, marine and terrestrial)
    - •• Order: Desmoscolecida (marine)
    - •• Order: Chromadorida (bactivores, algivores, omnivores, predators)
    - •• Order: Desmodorida (bactivores, algivores, omnivores, predators)
    - •• Order: Monhysterida (bactivores, algivores, omnivores, predators)
    - •• Order: Araeolaimida (bactivores, algivores, omnivores, predators)
    - •• Order: Plectida (bactivores, algivores, omnivores, predators)
    - •• Order: Rhabditida (= Secernentea, Phasmidea) (with phasmids)
      - ••• Suborder: Spirurina (animal parasites)
        - ••• Infraorder: Gnathostomatomorpha (vertebrate parasites)
        - ••• Infraorder: Oxyuridomorpha (vertebrate and invertebrate parasites)
        - ••• Infraorder: Rhigonematomorpha (invertebrate parasites)
        - ••• Infraorder: Spiruromorpha (vertebrate parasites)
        - ••• Infraorder: Ascaridomorpha (vertebrate parasites)
      - ••• Suborder Myolaimina (bactivores, phytoparasites)
      - ••• Suborder Tylenchina (fungal, plant, animal parasites)
        - ••• Infraorder: Panagrolaimomorpha (bactivores)
        - ••• Infraorder: Cephalobomorpha (bactivores)
        - ••• Infraorder: Tylenchomorpha (fungivores, phytoparasites, invertebrate parasites)
        - ••• Infraorder: Drilonematomorpha (invertebrate parasites)
      - ••• Suborder Rhabditina (often with larval ‘dauer’ stage)
        - ••• Infraorder: Bunonematomorpha (invertebrate parasites)
        - ••• Infraorder: Diplogasteromorpha (omnivores, predators, invertebrate parasites)
        - ••• Infraorder: Rhabditomorpha (entomopathogens, vertebrate/invertebrate parasites)

Phylum: Nematomorpha (horsehair worms, aquatic)

Phylum: Kinorhyncha (spine-necked worms, marine sediments)

Phylum: Priapulida (priapulids, marine sediments)

Phylum: Loricifera (loriciferans, marine sediments)

Group: Panarthropda (haemocoel)

Phylum: Onychophora (velvet worms, litter)

Phylum: Tardigrada (water bears, mosses, lichen, moist soil)

Phylum: Arthropoda (joint-footed, insects, arachnids and allies)

Life-cycles

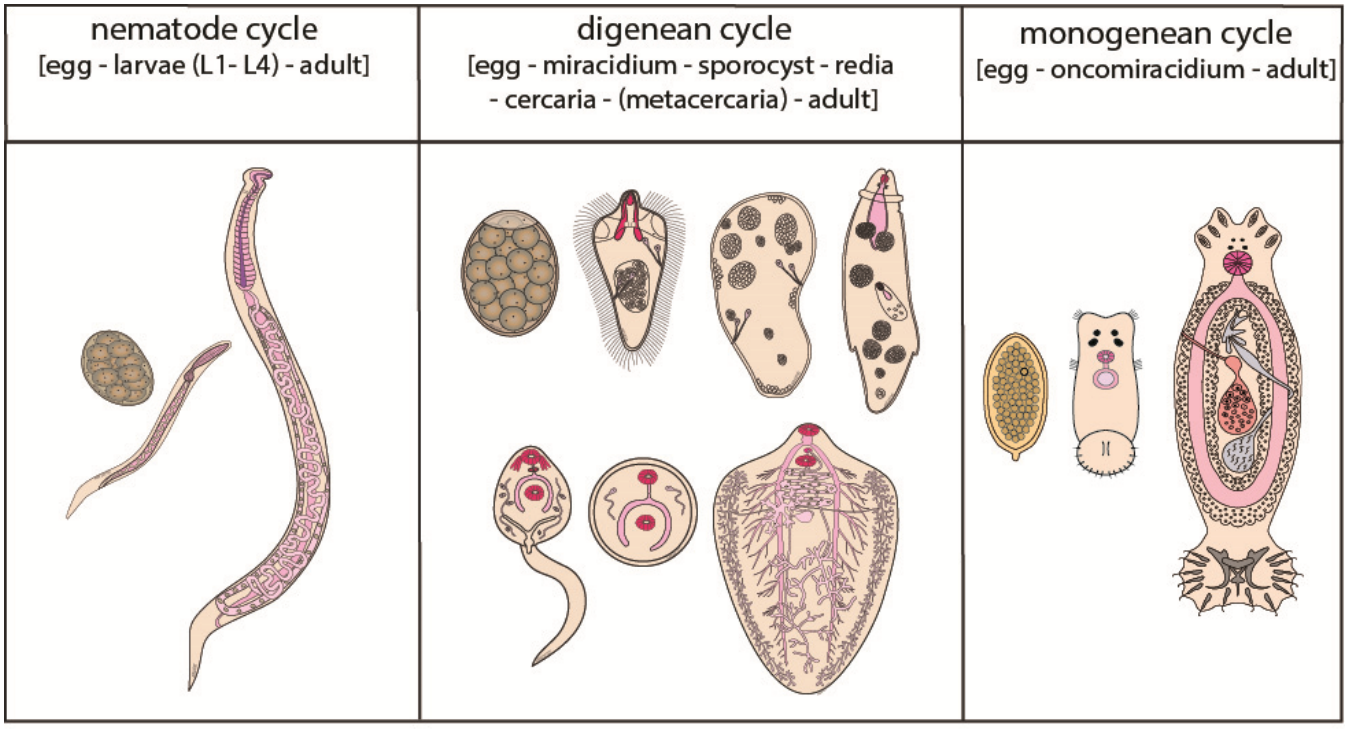
Unlike other pathogens (viruses, bacteria, protozoa and fungi), helminths typically do not proliferate within their hosts. Worms grow, mature and then produce offspring which are voided from the host to infect new hosts. Worm burdens in individual hosts (and often the severity of infection) are therefore dependent on the number of infective stages taken up. Worms also develop slowly compared to other infectious pathogens so any resultant diseases are often slow in onset and chronic in nature. Although most helminth infections are well tolerated by their hosts and are often asymptomatic, subclinical infections may be associated with significant loss of condition in infected hosts. Some helminths cause serious clinical diseases characterized by high morbidity and mortality. Clinical signs of infection vary considerably depending on the site and duration of infection. Larval and adult nematodes lodge, migrate or encyst within tissues resulting in obstruction, inflammation, oedema, anaemia, lesions and granuloma formation. Infections by adult cestodes are generally benign as they are not invasive, but the larval stages penetrate and encyst within tissues leading to inflammation, space-occupying lesions and organ malfunction. Adult flukes usually cause obstruction, inflammation and fibrosis in tubular organs, and the eggs of blood flukes can lodge in tissues causing extensive granulomatous reactions and hypertension.

Helminths form three main life-cycle stages: eggs, larvae and adults. Adult worms infect definitive hosts (those in which sexual development occurs) whereas larval stages may be free-living or parasitize invertebrate vectors, intermediate or paratenic hosts.

- Nematodes produce eggs that embryonate *in utero* or outside the host. The emergent larvae undergo 4 moults before they mature as adult male or female worms.

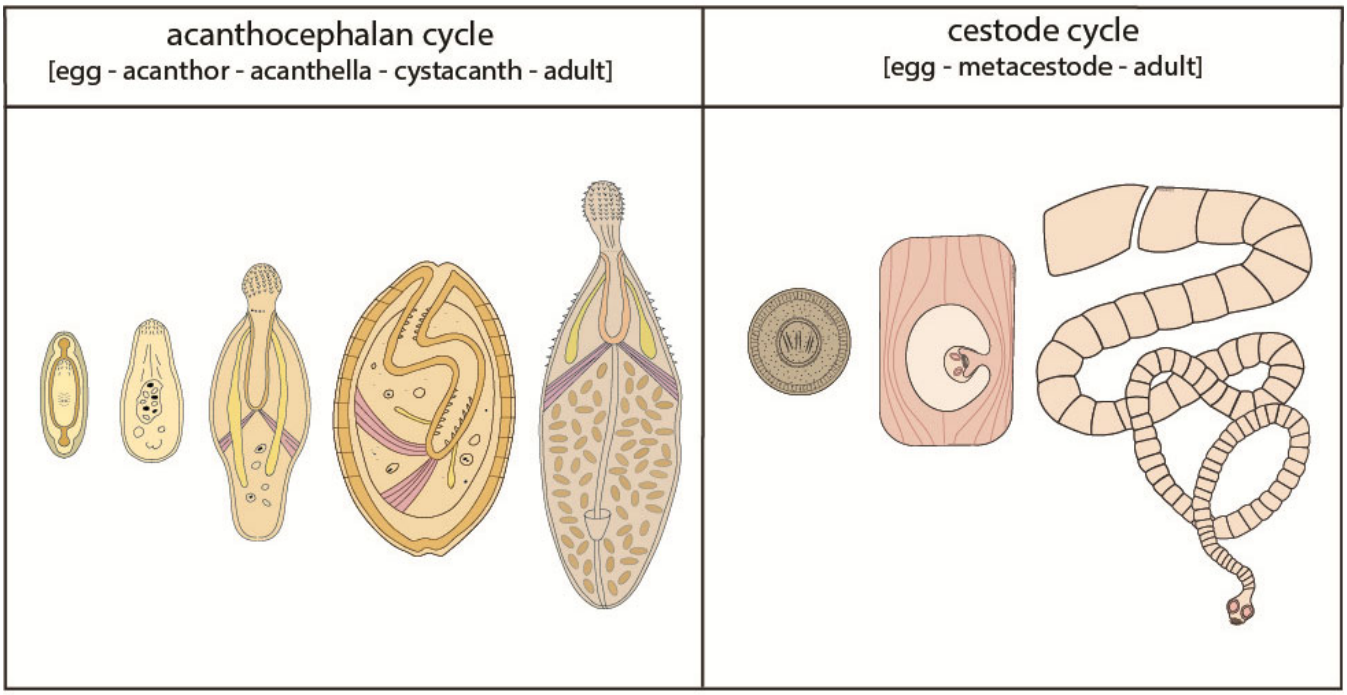
- Digenean trematodes (except for the rare Aspidogastrea) have complex life-cycles involving asexual reproduction in molluscan intermediate hosts. Eggs passed from the vertebrate definitive host hatch to release free-swimming miracidia which actively infect molluscs and develop in sac-like sporocysts to produce numerous rediae. The rediae produce cercariae which emerge from the molluscs and take one or numerous paths to infect the definitive hosts.

- Monogeneans produce eggs which hatch to release free-swimming ciliated larvae (oncomiracidia) that actively seek and attach to hosts.



- Acanthocephalans produce shelled embryos which do not hatch until eaten by an insect intermediate host. The larva (acanthor) develops into a juvenile (cystacanth) which is transmitted to the final host when it eats infected insects.

- Cestode eggs released from gravid segments embryonate to produce six-hooked embryos (hexacanth oncospheres) which are ingested by intermediate hosts. The oncospheres penetrate host tissues and become metacestodes (encysted larvae). When eaten by definitive hosts, they excyst and form adult tapeworms.



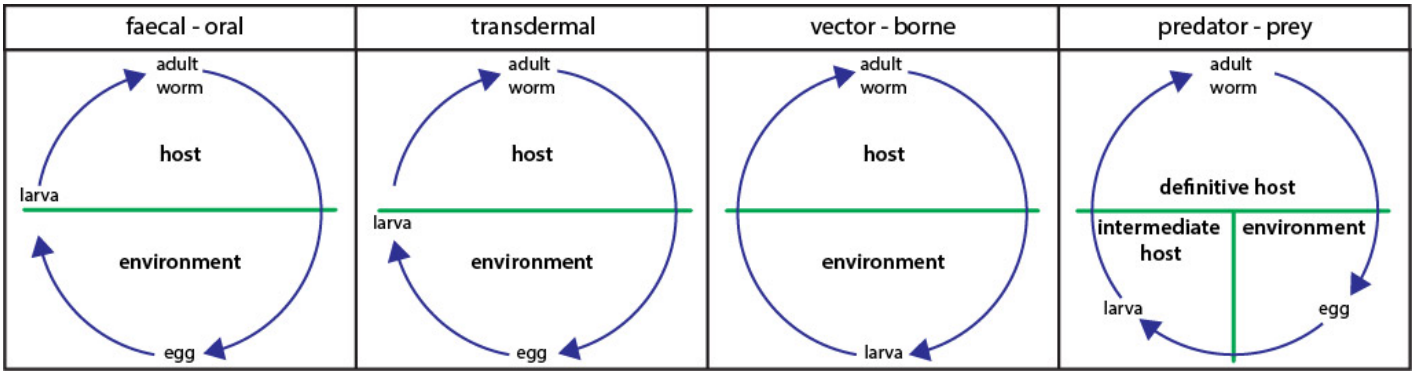
Helminth eggs have tough resistant walls to protect the embryo while it develops. Mature eggs hatch to release larvae either within a host or into the external environment. The four main modes of transmission by which the larvae infect new hosts are faecal-oral, transdermal, vector-borne and predator-prey transmission:

- faecal-oral transmission of eggs or larvae passed in the faeces of one host and ingested with food/water by another (e.g. ingestion of *Trichuris* eggs leads directly to gut infections in humans, while the ingestion of *Ascaris* eggs and *Strongyloides* larvae leads to a pulmonary migration phase before gut infection in humans).

- transdermal transmission of infective larvae in the soil (geo-helminths) actively penetrating the skin and migrating through the tissues to the gut where adults develop and produce eggs that are voided in host faeces (e.g. larval hookworms penetrating the skin, undergoing pulmonary migration and infecting the gut where they feed on blood causing iron-deficient anaemia in humans).

- vector-borne transmission of larval stages taken up by blood-sucking arthropods or undergoing amplification in aquatic molluscs (e.g. *Onchocerca* microfilariae ingested by black flies and injected into new human hosts, *Schistosoma* eggs release miracidia to infect snails where they multiply and form cercariae which are released to infect new hosts).

- predator-prey transmission of encysted larvae within prey animals (vertebrate or invertebrate) being eaten by predators where adult worms develop and produce eggs (e.g. *Dracunculus* larvae in copepods ingested by humans leading to guinea worm infection, *Taenia* cysticerci in beef and pork being eaten by humans, *Echinococcus* hydatid cysts in offal being eaten by dogs).



Overview of major helminth groups parasitizing animals

Nematodes

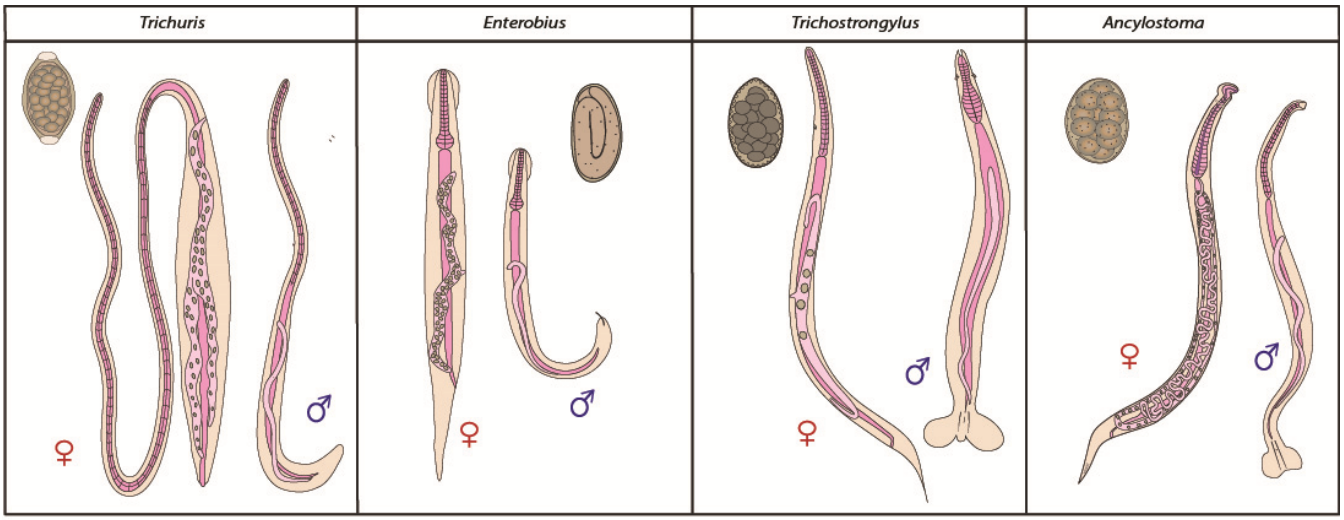
Conventionally, two classes of nematodes are recognised on the basis of the presence or absence of special chemoreceptors known as phasmids: Secernentea (= Phasmidea) and Adenophorea (= Aphasmidea). While many different orders, suborders and infraorders are now recognised in molecular phylogenies, the main parasitic assemblages infecting humans and domestic animals include one aphasmid enoplean order (Trichocephalida = Trichinellida) and three phasmid chromadorean suborders: Rhabditina (infraorder Rhabditomorpha), Spirurina (Dracunculoidea *incertae sedis* and infraorders Ascaridomorpha, Oxyuridomorpha, and Spiruromorpha) and Tylenchina (infraorder Panagrolaimomorpha).

- Trichocephalid 'whipworms' have long thin anterior ends which they embed in the intestinal mucosa of their hosts. They have simple life-cycles where infections are acquired by the ingestion of eggs and emergent larvae moult and mature to adults in the gut. *Trichuris* infections in humans may cause inflammation, tenesmus, straining and rectal prolapse.

- Oxyuridomorphid 'pinworms' have small thin bodies with blunt anterior ends. They have simple life-cycles, but with an unusual modification. Female worms emerge from the anus of their hosts at night and attach eggs to the skin. This causes peri-anal itching and eggs are transferred by hand to mouth. Infections by *Enterobius* cause irritability and sleeplessness in humans, especially children.

- Rhabditomorphid strongyloid 'trichostrongyles' have small bodies with cuticular ridges (synlophe) and males have a well-developed copulatory bursa. They have simple life-cycles where larvae develop on pastures before being ingested by grazing animals. Adult worms infect the gastrointestinal tract and heavy infections by *Trichostrongylus* spp. may cause anaemia, scours, illthrift and death in domestic livestock.

- Rhabditomorphid strongyloid 'hookworms' have dorsally curved mouths armed with ventral cutting plates or teeth which they embed in host tissues to feed on blood. They have complex life-cycles where larvae develop in the external environment (as 'geo-helminths') before infecting hosts by penetrating the skin. Once inside, they undergo pulmonary migration before settling in the gut to feed. Heavy infections by *Ancylostoma* and *Necator* cause severe iron-deficient anaemia in humans, especially children.

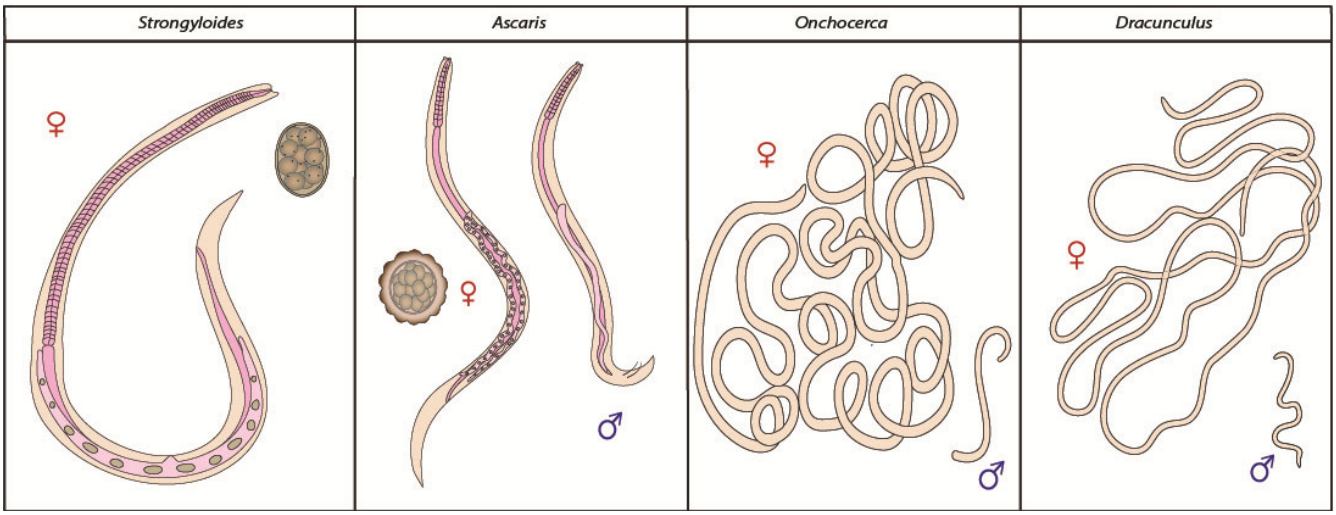


- Panagrolaimomorphid ‘threadworms’ have tiny bodies which become embedded in the host mucosa. Their life-cycle includes parasitic parthenogenetic females producing eggs which may hatch internally (leading to auto-infection) or externally (leading to transmission of infection or formation of free-living male and female adults). Super-infections by *Strongyloides* may cause severe haemorrhagic enteritis in humans.

- Ascaridomorphid ‘roundworms’ have large bodies with 3 prominent anterior lips. Their life-cycles involve a stage of pulmonary migration where larvae released from ingested eggs invade the tissues and migrate through the lungs before returning to the gut to mature as adults. *Ascaris* infections in humans cause gastroenteritis, protein depletion and malnutrition and heavy infections can cause gut obstruction.

- Spiruromorphid filarioid ‘filarial worms’ occur as long thread-like adults in blood vessels or connective tissues of their hosts. The large female worms release live larvae (microfilariae) into the blood or tissues which are taken up by blood-sucking mosquitoes or tissue-feeding flies and transmitted to new hosts. *Onchocerca* infections cause nodules, skin lesions and blindness in humans, while those of *Wuchereria* cause elephantiasis.

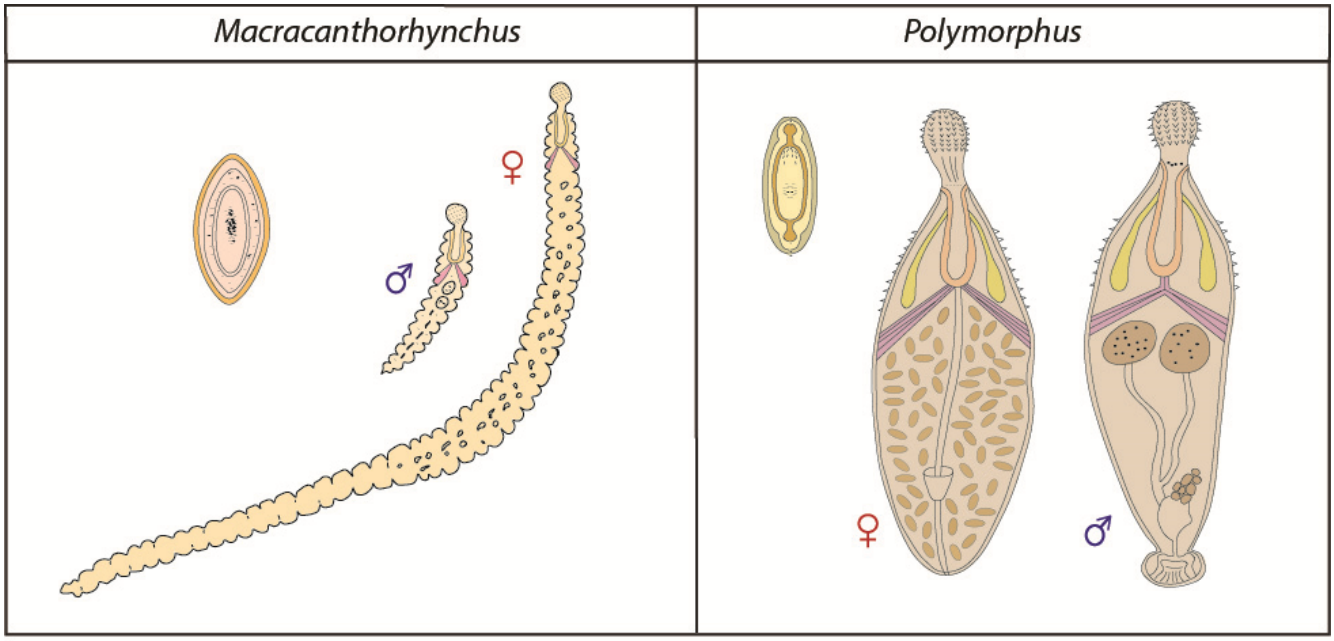
- Dracunculoid ‘guinea worms’ infect host tissues where the large females cause painful blisters on the feet and legs. When hosts seek relief by immersion in water, the blisters rupture releasing live larvae which infect copepods that are subsequently ingested with contaminated drinking water. The ‘fiery serpents’ mentioned in historical texts are thought to refer to *Dracunculus* infections.



Acanthocephalans

Thorny-headed worms have heteroxenous (2-host) life-cycles where adult worms live in the intestines of vertebrate hosts (fish, amphibians, reptiles, birds and mammals) and larval stages develop in arthropod intermediate hosts (insects, crustaceans). Four classes of Acanthocephala are recognised:

- Archiacanthocephala with terrestrial cycles involving mammals/birds and insects (e.g. *Macracanthorhynchus* in pigs and beetles);
- Palaeacanthocephala with aquatic cycles in fish/birds/seals and crustaceans (e.g. *Polymorphus* in ducks and amphipod crustaceans);
- Eoacanthocephala with aquatic cycles in fish/amphibia/reptiles and crustaceans; and
- Polyacanthocephala with aquatic cycles in fish/crocodiles and crustaceans.

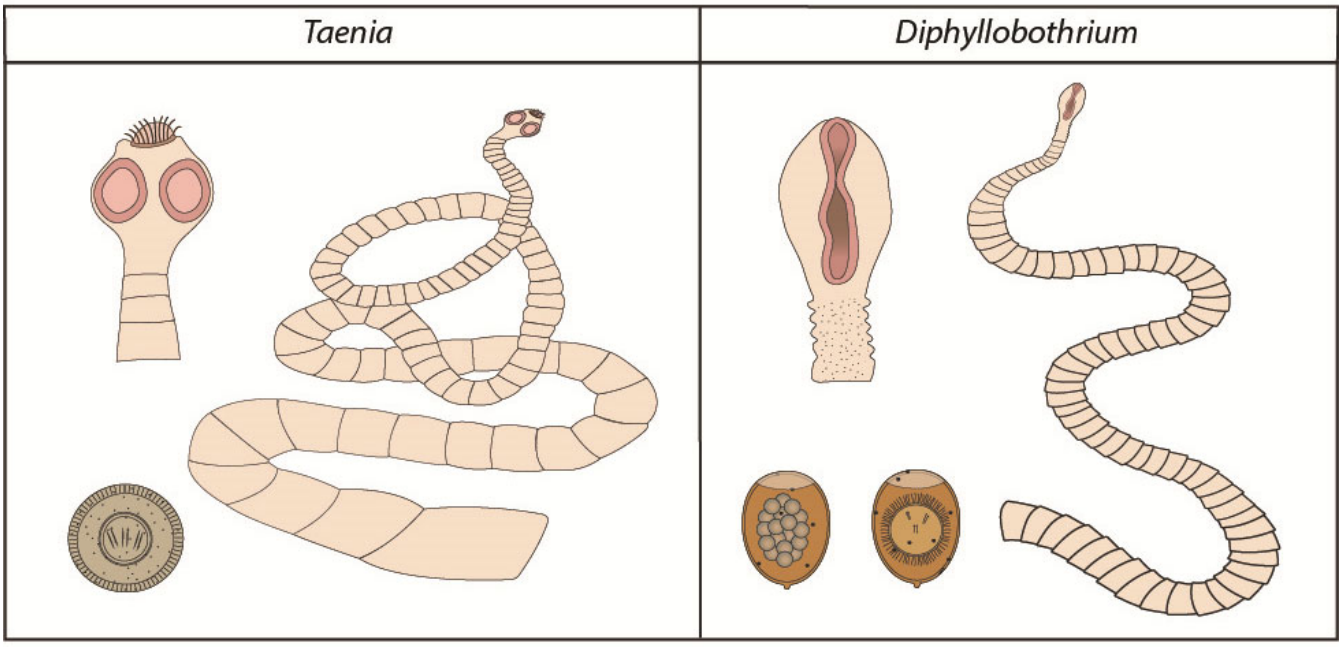


Cestodes

Two subclasses of cestodes are differentiated on the basis of the numbers of larval hooks, the Cestodaria being decacanth (10 hooks) and the Eucestoda being hexacanth (6 hooks). Collectively, 14 orders of cestodes have been identified according to differences in parasite morphology and developmental cycles. Two orders have particular significance as parasites of medical and veterinary importance.

- Cyclophyllidean cestodes have terrestrial 2-host life-cycles where adult tapeworms develop in carnivores (scolex with four suckers and sometimes hooks) while larval metacestodes form bladder-like cysts in the tissues of herbivores. The larvae of *Taenia* spp. cause cysticercosis in cattle, pigs and humans, while those of *Echinococcus* cause hydatid disease in humans, domestic and wild animals.

- Diphyllobothriidean (formerly Pseudophyllidean) cestodes have aquatic 3-host life-cycles, involving the sequential formation of adult tapeworms in fish-eating animals (scolex with two longitudinal bothria), procercoid larval stages in aquatic invertebrates (copepods) and then plerocercoid (spargana) stages in fish e.g. *Dibothriocephalus* (formerly *Diphyllobothrium*) in humans, dogs and cats being transmitted through copepods and fish.

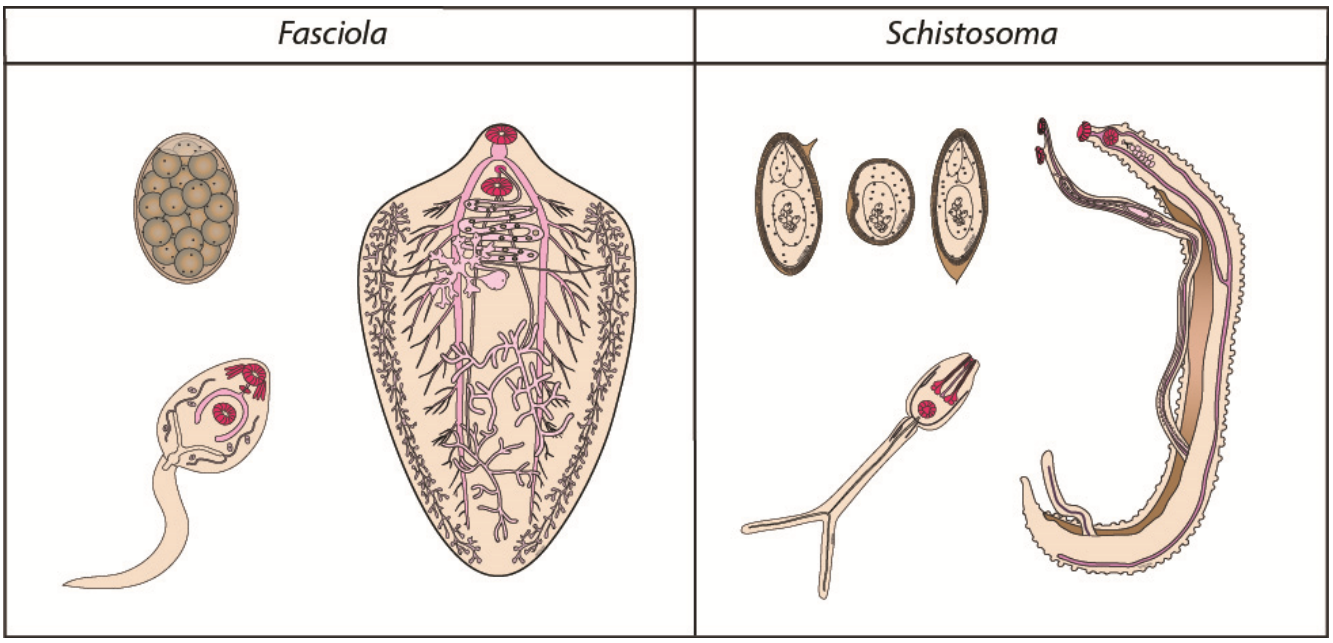


Trematodes

The Trematoda is divided into 2 subclasses: the Aspidogastrea with divided or loculated ventral suckers and the absence of asexual reproduction; and the Digenea with undivided ventral suckers and the occurrence of asexual reproduction in the first intermediate host in addition to sexual reproduction in the definitive host. The Digenea is divided into 2 orders: Diplostomida and Plagiorchiida.

- The Diplostomida contains one suborder which includes the blood flukes of fishes, reptiles, birds and mammals (including humans). The genus *Schistosoma* has multiple species that infect humans by direct penetration of the skin by fork-tailed cercariae. Infections may cause a debilitating disease known as schistosomiasis or bilharzia when fluke eggs become trapped in host tissues and organs resulting in extensive granuloma formation.

- The Plagiorchiida is a much larger and more diverse order containing 14 suborders that include many species of importance in human and animal health; e.g. *Clonorchis* and *Opisthorchis* liver flukes in humans, *Fasciolopsis* intestinal flukes in humans and pigs, *Fasciola* liver flukes in domestic livestock, *Paramphistomum* stomach flukes in ruminants, and *Paragonimus* lung flukes in carnivores and rodents.

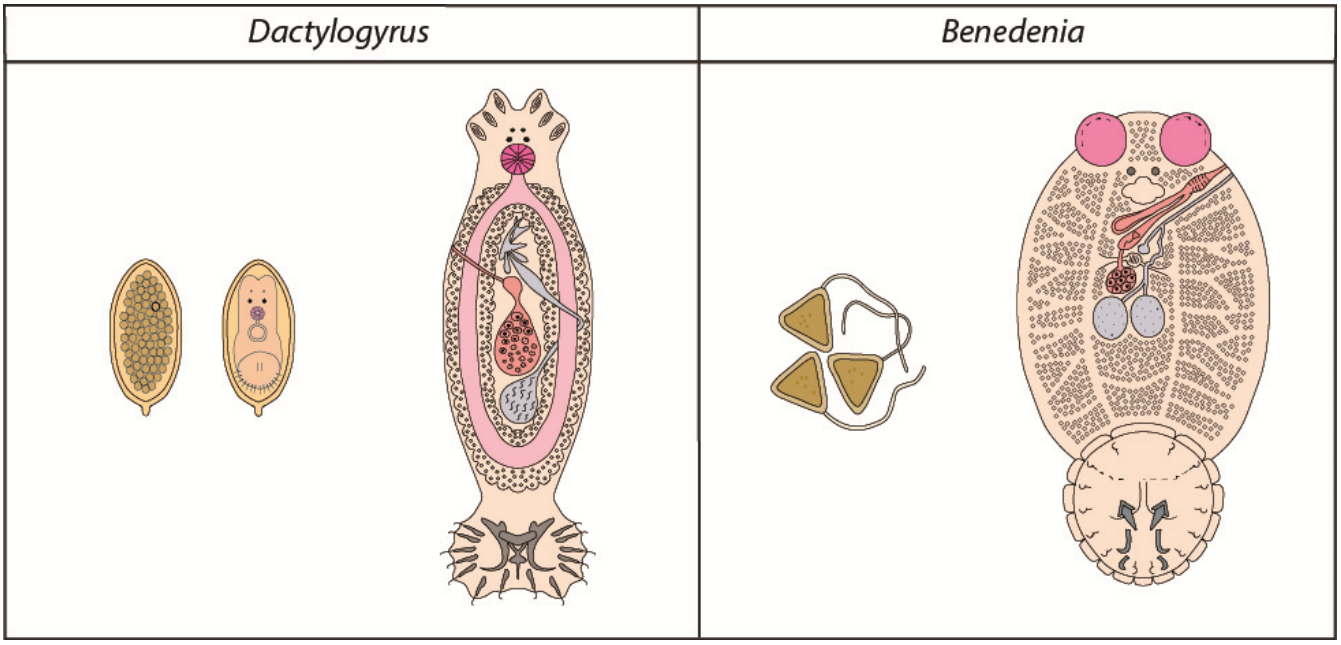


Monogeneans

Monogeneans are almost exclusively ectoparasites of fishes although a few species infect the urinary tracts of some turtles, frogs and birds and the eyes of the hippopotamus. They have direct life-cycles where the oncomiracidium that hatches from the egg swims directly to the host, attaches and begins development to the adult worm. Two subclasses are recognised mainly in the complexity of the posterior attachment structures: the Monopisthocotylea; and the Polyopisthocotylea.

- The Monopisthocotylea have a posterior haptor comprising a single symmetrical attachment unit with hooks and hooklets (but no haptoral clamps). Adults feed on fish epithelia and most species are oviparous and lay eggs (e.g. *Dactylogyrus* gill flukes, and *Benedenia* skin flukes) although some are viviparous and produce live young (e.g. *Gyrodactylus* skin flukes). Infestations may cause morbidity and mortality in fishes, especially in hatcheries, aquaria and intensive aquaculture systems.

- The Polyopisthocotylea have complex opisthaptors with several clamps or suckers used to attach to gill filaments where most feed on blood. Infestations have been recorded on a wide range of freshwater and marine fishes, elasmobranchs, holocephalans and some frogs.

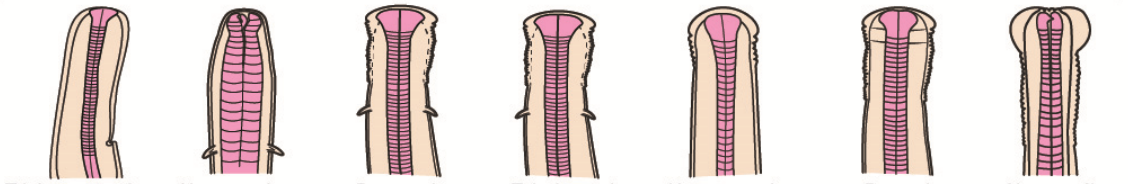


Nematoda
(roundworms)

Nematode heads 1

Strongyloidea

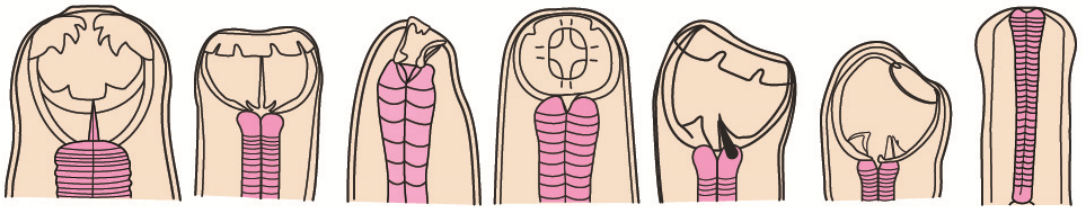
trichostrongyles



Trichostrongylus *Haemonchus* *Ostertagia* *Teladorsagia* *Hyostrongylus* *Cooperia* *Nematodirus*

Strongyloidea

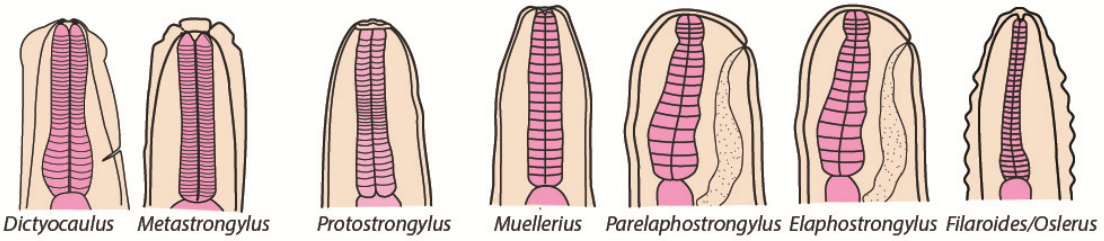
hookworms



Ancylostoma *Globocephalus* *Uncinaria* *Necator* *Bunostomum* *Gaigeria* *Nippostrongylus*

Strongyloidea

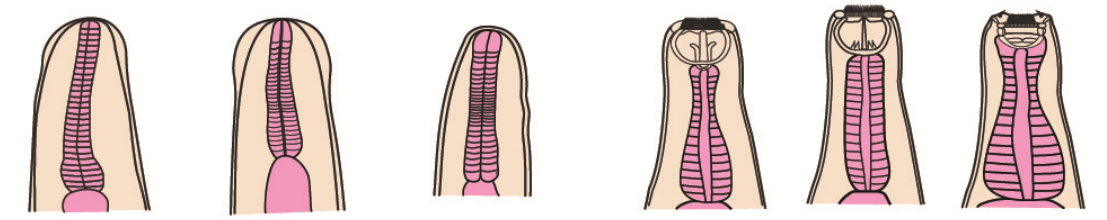
lungworms



Dictyocaulus *Metastrongylus* *Protostrongylus* *Muellerius* *Parelaphostrongylus* *Elaphostrongylus* *Filaroides/Oslerus*

Strongyloidea

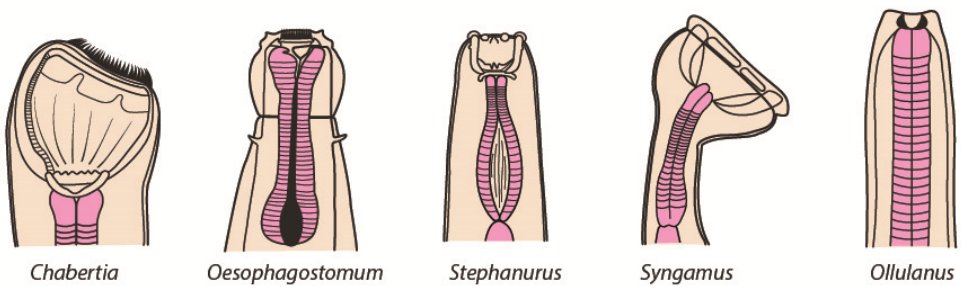
lungworms	strongyles



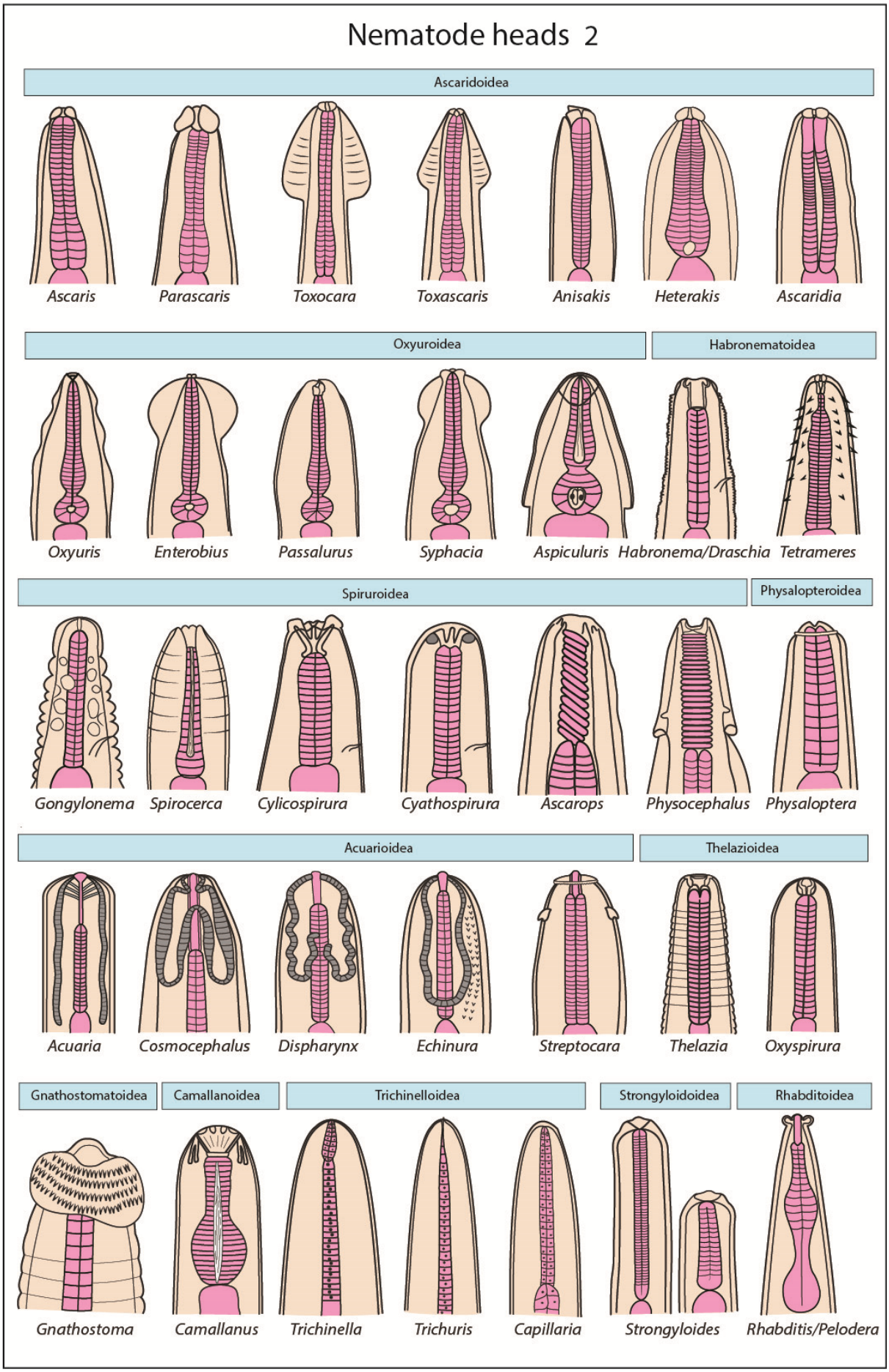
Aelurostrongylus *Angiostrongylus* *Parastrongylus* *Strongylus* *Triodontophorus* *Cyathostomum*

Strongyloidea

nodular worms	kidney worm	gapeworm	stomach worm

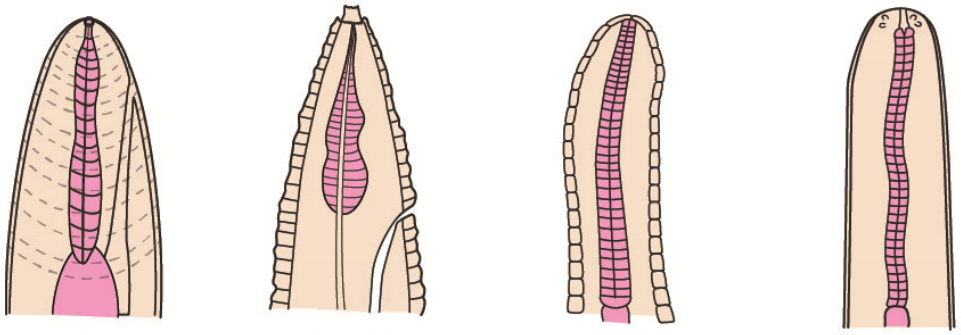


Chabertia *Oesophagostomum* *Stephanurus* *Syngamus* *Ollulanus*


Nematode heads 2
Ascaridoidea
Ascaris
Parascaris
Toxocara
Toxascaris
Anisakis
Heterakis
Ascaridia
Oxyuroidea
Habronematoidea
Oxyuris
Enterobius
Passalurus
Syphacia
Aspiculuris
Habronema/Draschia
Tetrameres
Spiruroidea
Physalopteroidea
Gongylonema
Spirocerca
Cylicospirura
Cyathospirura
Ascarops
Physocephalus
Physaloptera
Acuarioidea
Thelazioidea
Acuaria
Cosmocephalus
Dispharynx
Echinura
Streptocara
Thelazia
Oxyspirura
Gnathostomatoidea
Camallanoidea
Trichinelloidea
Strongyloidoidea
Rhabditoidea
Gnathostoma
Camallanus
Trichinella
Trichuris
Capillaria
Strongyloides
Rhabditis/Pelodera

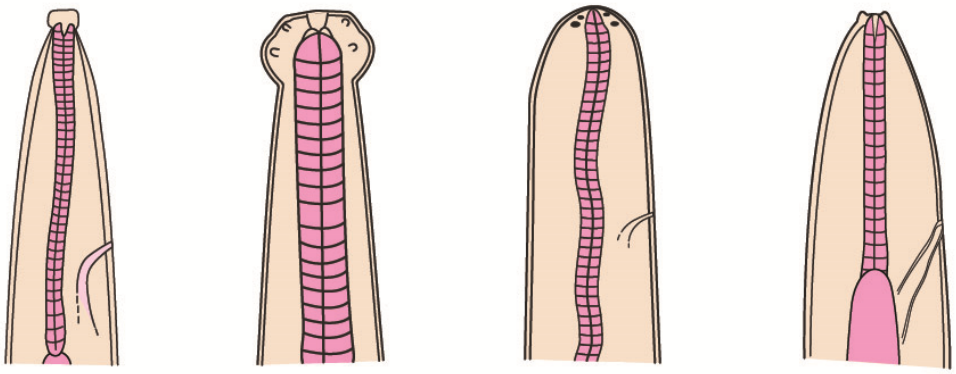
Nematode heads 3

Filarioidea



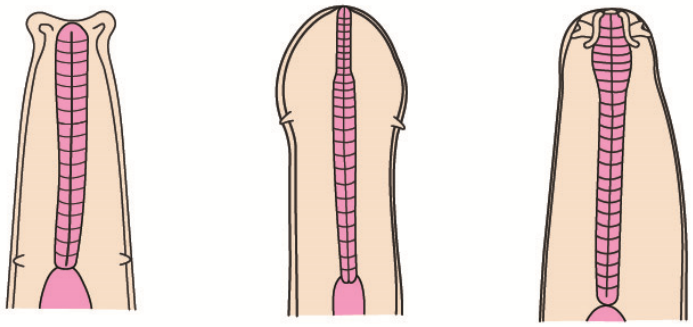
Parafilaria *Stephanofilaria* *Onchocerca* *Mansonella*

Filarioidea



Wuchereria *Brugia* *Loa* *Setaria*

Filarioidea Dracunculoidea



Dipetalonema/ Acanthocheilonema *Dirofilaria* *Dracunculus*

Nematode tails (bursate males)

Strongyloidea

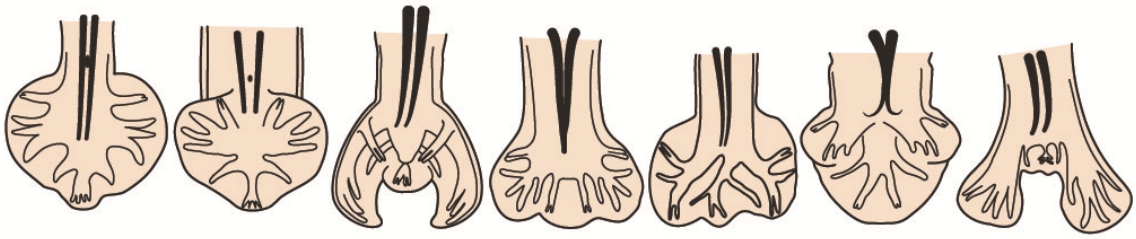
trichostrongyles



Trichostrongylus *Haemonchus* *Ostertagia* *Teladorsagia* *Hyostrongylus* *Cooperia* *Nematodirus*

Strongyloidea

hookworms



Ancylostoma *Globocephalus* *Uncinaria* *Necator* *Bunostomum* *Gaigeria* *Nippostrongylus*

Strongyloidea

lungworms



Dictyocaulus *Metastrongylus* *Protostrongylus* *Muellerius* *Parelaphostrongylus* *Elaphostrongylus* *Filaroides/Oslerus*

Strongyloidea

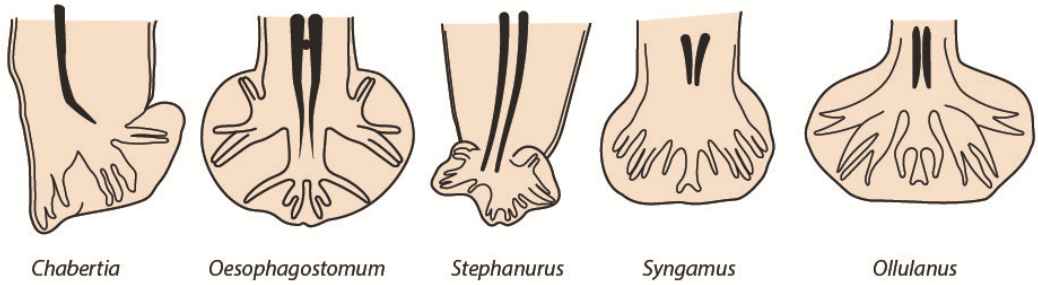
lungworms	strongyles



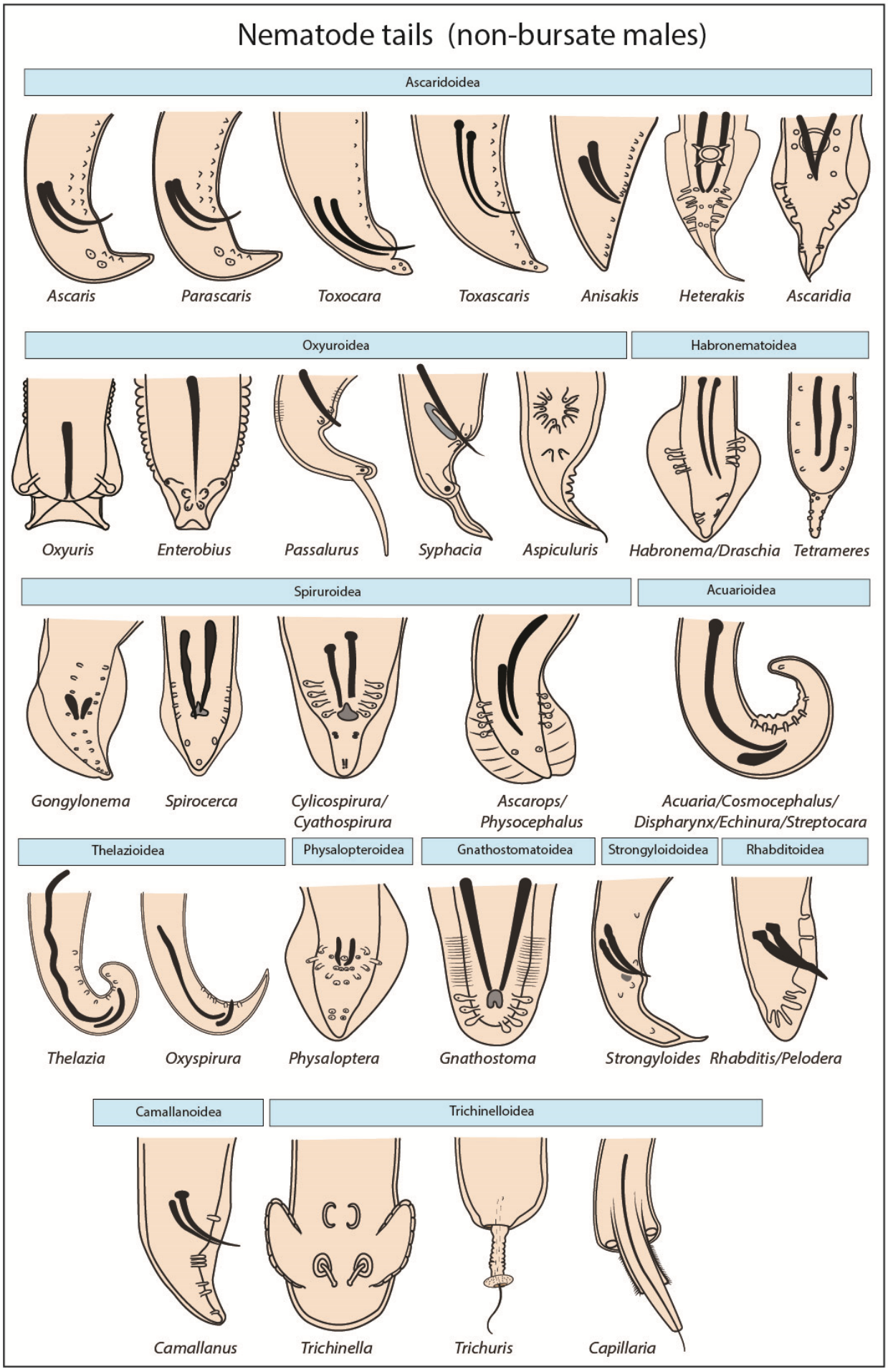
Aelurostrongylus *Angiostrongylus* *Parastrongylus* *Strongylus* *Triodontophorus* *Cyathostomum*

Strongyloidea

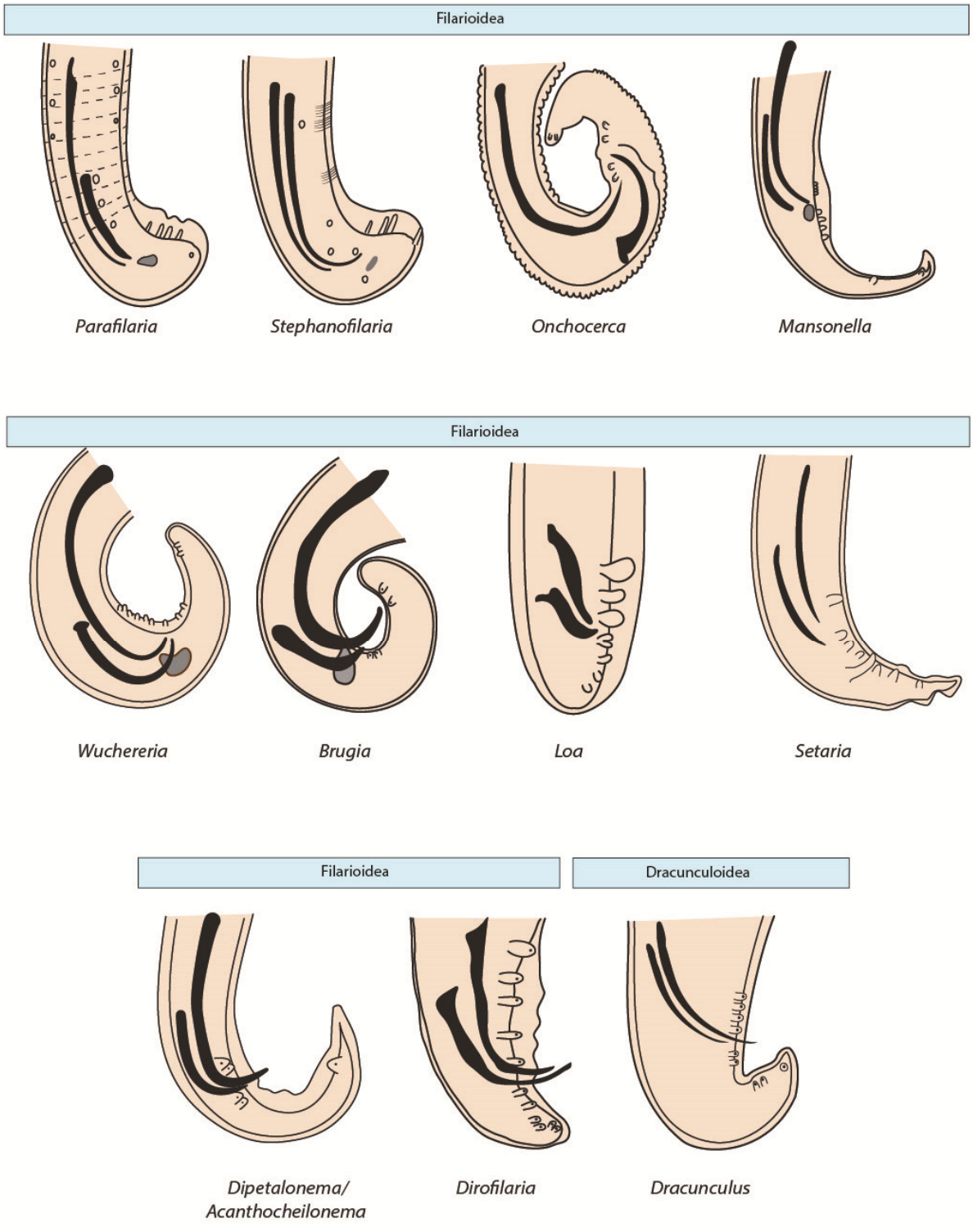
nodular worms	kidney worm	gapeworm	stomach worm

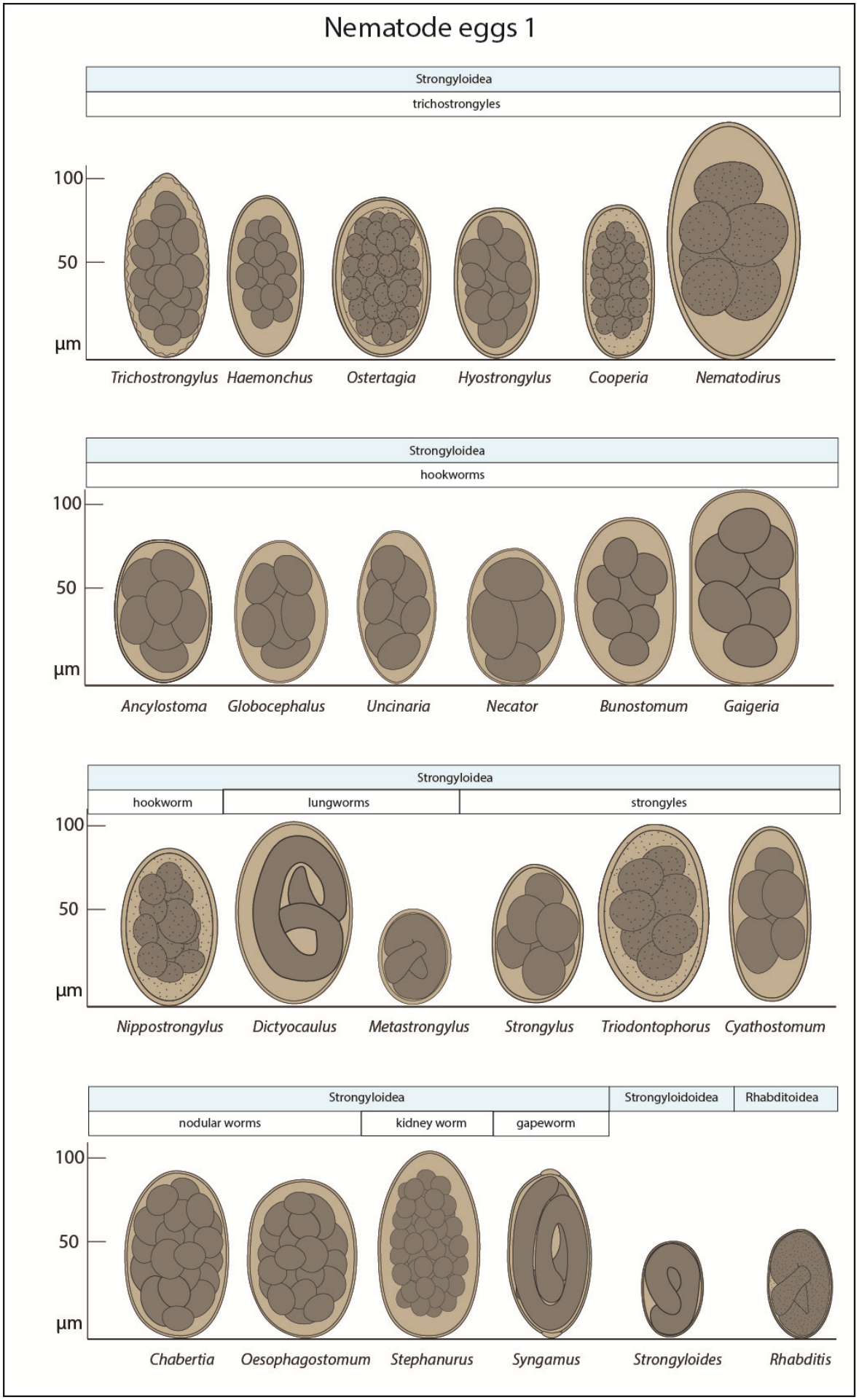


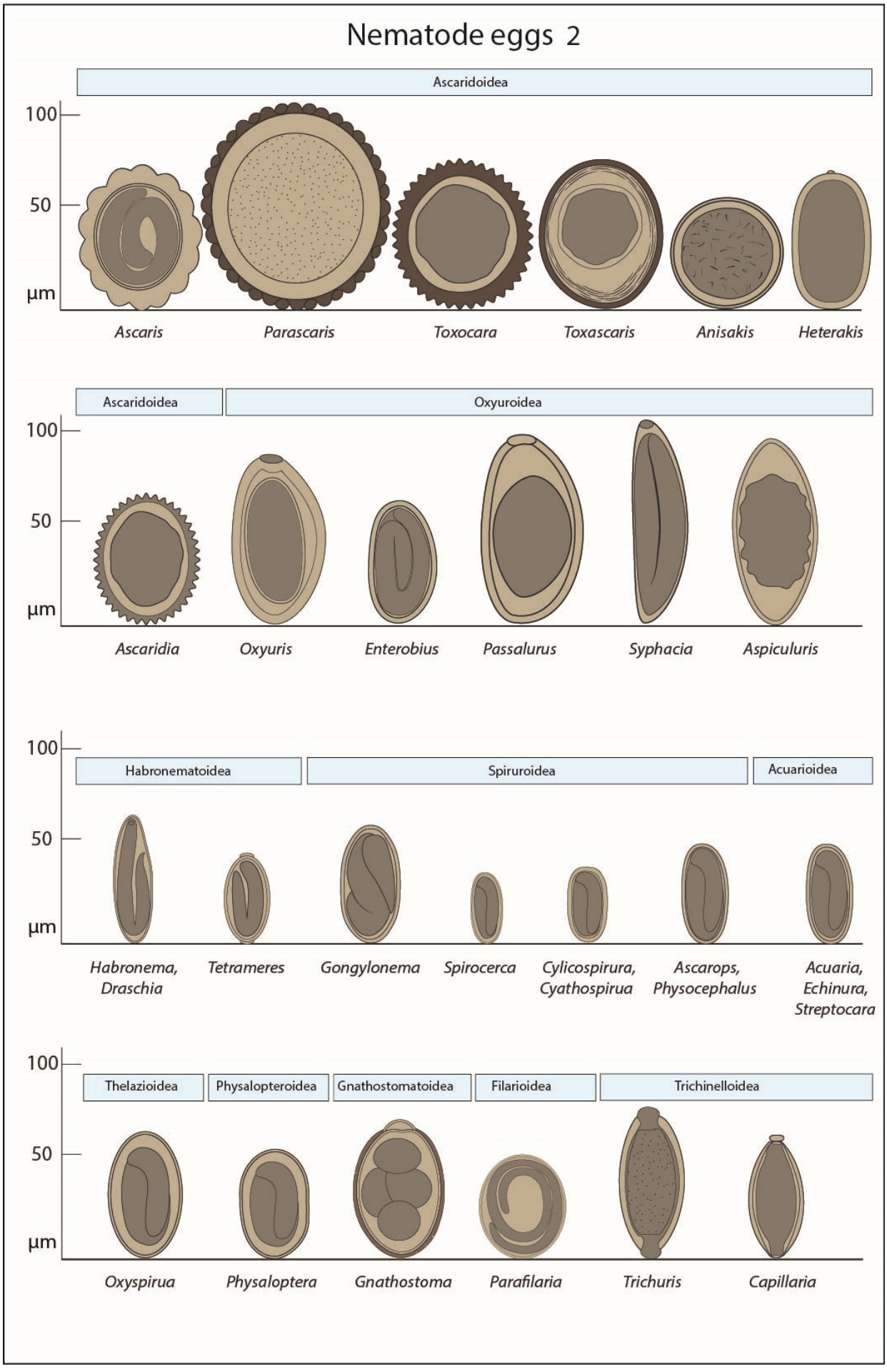
Chabertia *Oesophagostomum* *Stephanurus* *Syngamus* *Ollulanus*


Nematode tails (non-bursate males)
Ascaridoidea
Ascaris
Parascaris
Toxocara
Toxascaris
Anisakis
Heterakis
Ascaridia
Oxyuroidea
Habronematoidea
Oxyuris
Enterobius
Passalurus
Syphacia
Aspiculuris
Habronema/Draschia
Tetrameres
Spiruroidea
Acuarioidea
Gongylonema
Spirocerca
Cylicospirura/
Cyathospirura
Ascarops/
Physocephalus
Acuaria/Cosmocephalus/
Dispharynx/Echinura/Streptocara
Thelazioidea
Physalopteroidea
Gnathostomatoidea
Strongyloidoidea
Rhabditoidea
Thelazia
Oxyspirura
Physaloptera
Gnathostoma
Strongyloides
Rhabditis/Pelodera
Camallanoidea
Trichinelloidea
Camallanus
Trichinella
Trichuris
Capillaria

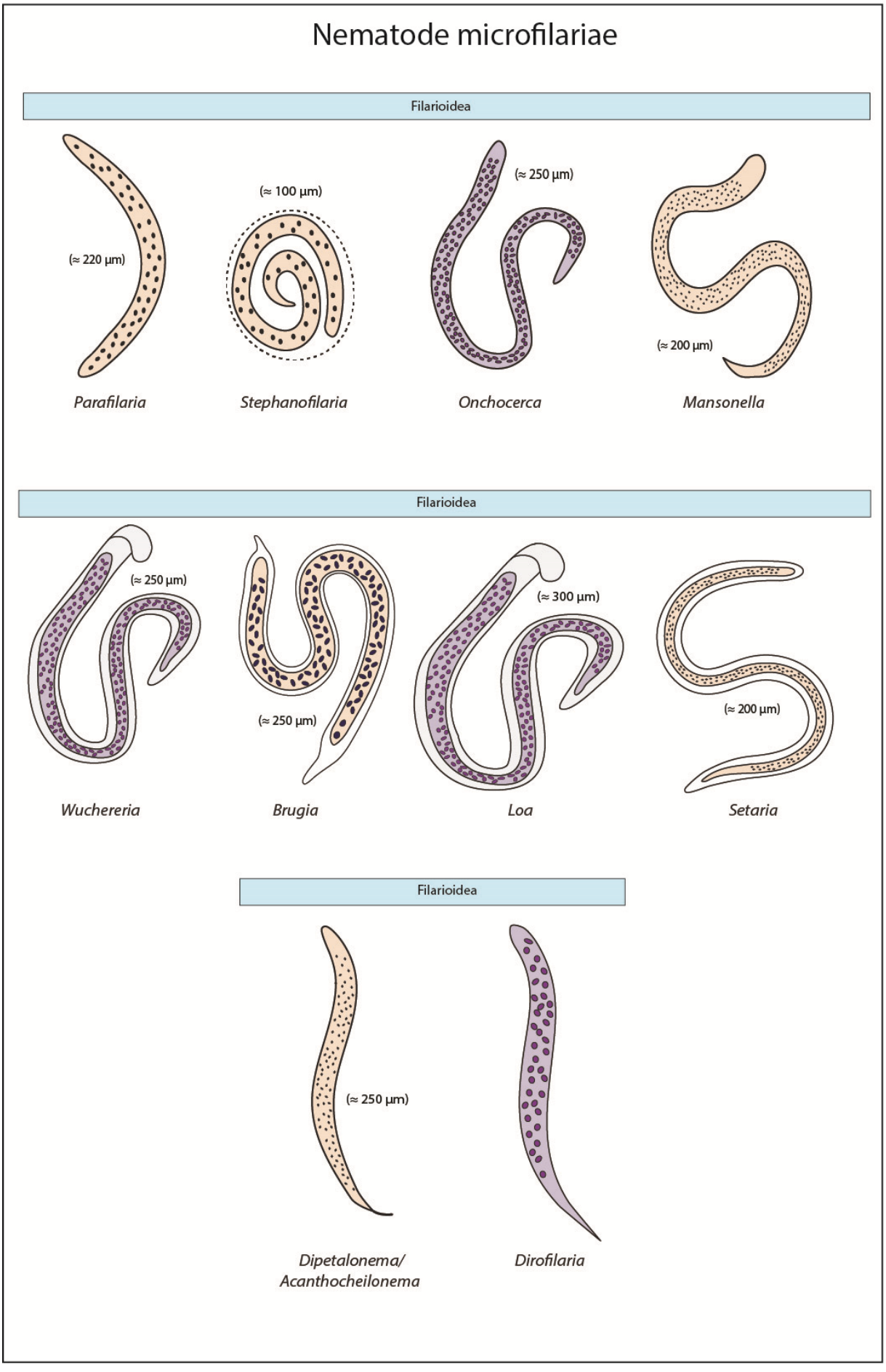
Nematode tails (non-bursate males)




Nematode eggs 1
Strongyloidea
trichostrongyles
100
50
µm
Trichostrongylus
Haemonchus
Ostertagia
Hyostrongylus
Cooperia
Nematodirus
Strongyloidea
hookworms
100
50
µm
Ancylostoma
Globocephalus
Uncinaria
Necator
Bunostomum
Gaigeria
Strongyloidea
hookworm
lungworms
strongyles
100
50
µm
Nippostrongylus
Dictyocaulus
Metastrongylus
Strongylus
Triodontophorus
Cyathostomum
Strongyloidea
Strongyloidoidea
Rhabditoidea
nodular worms
kidney worm
gapeworm
100
50
µm
Chabertia
Oesophagostomum
Stephanurus
Syngamus
Strongyloides
Rhabditis


Nematode eggs 2
Ascaridoidea
100
50
µm
Ascaris
Parascaris
Toxocara
Toxascaris
Anisakis
Heterakis
Ascaridoidea
Oxyuroidea
100
50
µm
Ascaridia
Oxyuris
Enterobius
Passalurus
Syphacia
Aspiculuris
100
Habronematoidea
Spiruroidea
Acuarioidea
50
µm
Habronema, Draschia
Tetrameres
Gongylonema
Spirocerca
Cylicospirura, Cyathospirua
Ascarops, Physocephalus
Acuaria, Echinura, Streptocara
100
Thelazioidea
Physalopteroidea
Gnathostomatoidea
Filarioidea
Trichinelloidea
50
µm
Oxyspirua
Physaloptera
Gnathostoma
Parafilaria
Trichuris
Capillaria

Nematode microfilariae



Strongyloides
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, rhabditinids and tylenchinids. The latter contains the infraorder Panagrolaimomorpha which includes the strongyloidoids which are capable of both parasitic and free-living reproductive cycles. They are small slender cylindrical worms with the long oesophagus and uterus intertwined, giving the appearance of a twisted thread, hence their common name of 'threadworms'. Adults have a small buccal capsule and the males are non-bursate (lack a copulatory bursa). Only parthenogenetic female worms are parasitic, living in the small intestinal mucosa of various mammals, birds, reptiles and amphibians. Transmission involves a geo-helminth phase, where rhabditiform larvae in the soil form infective filariform larvae which penetrate the skin of their hosts. Sometimes, however, larvae develop into male and female worms which undergo one or more free-living cycles in the soil before producing infective larvae. *Strongyloides* infections in humans and some domestic animals have been associated with enteric, dermal, pulmonary and disseminated diseases.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Tylenchina (fungal, plant and animal parasites)
Infraorder:	Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily:	Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)
Family:	Strongyloididae (threadworms, parasitic parthenogenetic females, free-living sexual generations)
Genus:	*Strongyloides* (parasitic in small intestines of mammals/birds)
Species:	various species cause larval currens, diarrhoea and wasting in mammals, including humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial

group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidoidea contains parasitic worms found in insects and other animals and is characterised by diovarial females and monorchic abursate males with small simple mouths (lip region without processes), striated cuticles and the formation of dormant (dauer) stages. It comprises 4 families, including the threadworm family Strongyloididae with 2 genera (*Strongyloides* and *Parastrongyloides*) [early authorities placed the family Strongyloididae in the superfamily Rhabditoidea, until molecular studies indicated their separate classification]. Members of the genus *Strongyloides* are small slender cylindrical worms with the long oesophagus and uterus intertwined, giving the appearance of a twisted thread, hence their common name of ‘threadworms’. Only protandrogonous or parthenogenetic female worms are parasitic, living in the small intestinal mucosa of vertebrate hosts. Transmission involves a geo-helminth phase, where rhabditiform larvae (L1-2) in the soil form infective filariform larvae (L3) which penetrate the skin of their hosts. Sometimes, however, larvae develop into male and female worms which undergo one or more free-living cycles in the soil before producing infective larvae. Around 70 *Strongyloides* spp. have been described throughout the world; mostly in mammals but also in birds, reptiles and amphibians. Whilst *Strongyloides* spp. are commonly known as threadworms, in some countries they are enigmatically called pinworms (a common name generally applied to *Enterobius* spp.). This may cause great confusion when considering treatment options because the drugs used to treat these worms are different. *Strongyloides* infections occur predominantly in tropical and temperate regions with warmer climates favouring the survival of parasite developmental stages in soil. Different species vary in their host-specificity, the species *S. stercoralis* being found in humans and companion animals, and *S. fuelleborni* in primates and humans: thus both species should be considered zoonotic. There is evidence to suggest that geographic strains vary in their infectivity and virulence, thus complicating assessment of their zoonotic and pathogenic potential. It has been estimated that over 100 million people may be infected worldwide. Cross-transmission between humans and dogs has frequently been implicated in epidemiological studies in remote rural communities where sanitation is poor.

***Strongyloides* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
Mammalian hosts			
S. agoutii	Rodentia: dasyproctid (red-rumped agouti)	small intestines	South America
S. akbari	Eulipotyphla: soricid (common Indian shrew, Asian house shrew)	small intestines	Indo-Asia
S. callosciureus	Rodentia: sciurid (Pallas's squirrel, plantain squirrel)	intestines	Asia
S. canis	Carnivora: canid (dog); Primates: hominid (human)	small intestines	Europe
S. cebus	Primates: atelid (southern muriqui), cebid (Panamanian white-faced capuchin, common squirrel monkey), hominid (human)	small intestines	South America
S. chapini	Rodentia: caviid (capybara), echimyid (coypu)	small intestines	South America
S. dasypodis	Cingulata: dasypodid (nine-banded armadillo)	small intestines	Americas
S. elephantis	Probiscidea: elephantid (Indian elephant)	small intestines	Asia
S. erschowi	Carnivora: canid (raccoon dog)	small intestines	Asia
S. felis (syn. *S. cati* p.p.)	Carnivora: felid (cat); Primates: hominid (human)	small intestines	India, Australia
S. ferreirai	Rodentia: caviid (rock cavy)	small intestines	South America
S. fuelleborni (syn. *S. kellyi, S. simiae*, incl. subspp. *S. f. fuelleborni, S. f. kellyi*)	Primates: hominid (human, mountain gorilla, Grauer's gorilla, chimpanzee, orangutan), atelid (Geoffroy's spider monkey), cercopithecid (vervet monkey, blue monkey, Allen's swamp monkey, Japanese macaque, rhesus macaque, Toque macaque, olive baboon, yellow baboon, Chacma baboon, sacred langur)	small intestines [bloody diarrhoea]	Africa, Asia, Americas, Papua New Guinea
S. intestinalis	Primates: hominid (human)	small intestines	Asia
S. longus	Rodentia: murid (brown rat)	small intestines	Europe
S. lutrae	Carnivora: mustelid (North American river otter, Eurasian otter)	small intestines	Holarctic
S. martis	Carnivora: mustelid (Eurasian otter, European polecat, sable, stoat, least weasel, American mink), sciurid (Caucasian squirrel)	small intestines	Europe
S. muris	Eulipotyphla: soricid (Indian musk shrew)	small intestines	Asia
S. mustelorum	Carnivora: mustelid (European polecat, European mink, least weasel)	small intestines	Europe
S. myopotami	Rodentia: echimyid (coypu), procyonid (raccoon); Primates: hominid (human)	small intestines	Americas
S. nasua	Carnivora: procyonid (white-nosed coati)	small intestines	Americas
S. ovocinctus	Artiodactyla: antilocaprid (pronghorn)	small intestines	North America
S. papillosus	Artiodactyla: bovid (sheep, argali, mouflon, goat, cattle, water buffalo, American bison, impala, nyala, blackbuck, greater kudu, red forest duiker, Maxwell's duiker, kob, suni), cervid (roe deer, red deer), camelid (dromedary), suid (pig); Perissodactyla: equid (zebra); Lagomorpha: leporid (snowshoe hare, rabbit); Rodentia: sciurid (squirrel), murid (mouse), echimyid (coypu); Carnivora: mustelid (European polecat); Primates: hominid (human)	small intestines [diarrhoea, anorexia]	worldwide
S. planiceps (syn. *S. cati* p.p.)	Carnivora: felid (cat, flat-headed cat, leopard cat), mustelid (Japanese weasel), canid (dog, Japanese raccoon dog, red fox); Primates: hominid (human)	small intestines	worldwide
S. procyonis	Carnivora: procyonid (raccoon); Primates: hominid (human)	small intestines	North America
S. putorii	Carnivora: mustelid (European polecat)	small intestines	Europe
S. ransomi	Artiodactyla: suid (pig), cervid (red deer); Lagomorpha: leporid (rabbit); Primates: hominid (human)	small intestines [bloody diarrhoea]	worldwide
S. ratti	Rodentia: murid (mouse, Mongolian gerbil, ricefield rat, Polynesian rat, brown rat, black rat, dusky field rat), cricetid (muskrat)	small intestines	Eurasia, North America
S. robustus	Rodentia: sciurid (northern flying squirrel, southern flying squirrel), cricetid (golden hamster), sciurid (eastern gray squirrel, fox squirrel, Richardson's ground squirrel, thirteen-lined ground squirrel, eastern chipmunk, American red squirrel)	small intestines	North America

S. rostombekowi	Eulipotyphla: erinaceid (European hedgehog)	small intestines	Europe
S. sciuri	Rodentia: sciurid (eastern fox squirrel)	small intestines	North America
S. shastensis	Xenarthra: nothrotheriid (Shasta ground sloth)	small intestines	North America
S. sigmodontis	Rodentia: cricetid (hispid cotton rat)	small intestines	Americas
S. spearei	Diprotodontia: vombatid (wombat)	small intestines [enteritis]	Australia
S. stercoralis (threadworm)	Primates: hominid (human, chimpanzee, orangutan), atelid (Geoffroy's spider monkey), hylobatid (Hoolock gibbon, white-handed gibbon), callitrichid (pygmy marmoset), cercopithecid (Patas monkey, rhesus macaque, yellow baboon, golden snub-nosed monkey); Carnivora: canid (dog, Arctic fox, golden jackal), felid (cat, Iberian lynx), mustelid (beech marten), procyonid (raccoon); Rodentia: murid (Mongolian gerbil, mouse); Artiodactyla: suid (pig)	small intestines [bloody diarrhoea]	worldwide
S. suis	Artiodactyla: suid (pig)	small intestines	Europe
S. thylacis	Peramelemorphia: peramelid (northern brown bandicoot)	small intestines	Australia
S. tumefaciens	Carnivora: felid (cat)	small intestines [mucosal tumours]	worldwide
S. ultrajectinus	Rodentia: cricetid (vole)	small intestines	Eurasia
S. venezuelensis	Rodentia: murid (Mongolian gerbil, mouse, Polynesian rat, brown rat, black rat)	small intestines	Americas, Asia
S. vituli	Artiodactyla: bovid (cattle)	intestines	Asia
S. vulpis	Carnivora: canid (Arctic fox, red fox), mustelid (wolverine)	small intestines	Holarctic
S. westeri	Perissodactyla: equid (horse, donkey, zebra); Artiodactyla: suid (pig); Rodentia: caviid (guinea pig), murid (mouse); Lagomorpha: leporid (rabbit)	small intestines [diarrhoea]	worldwide
Avian hosts			
S. ardeae	Pelecaniformes: ardeid (yellow-crowned night heron)	intestines	Americas
S. avium	Galliformes: odontophorid (northern bobwhite quail), phasianid (chicken, turkey); Gruiformes: rallid (water rail); Columbiformes: columbid (rock dove)	intestines	worldwide
S. cubaensis	Pelecaniformes: ardeid (green heron)	intestines	Americas
S. herodiae	Pelecaniformes: ardeid (great blue heron)	intestines	Americas
S. minimum	Anseriformes: anatid (white-cheeked pintail)	intestines	South America
S. oswaldoi	Galliformes: phasianid (chicken)	intestines	Europe
S. pavonis	Galliformes: phasianid (chicken, green peafowl)	intestines	Asia
S. quiscali	Passeriformes: icterid (greater Antillean grackle)	intestines	Central America
S. turkmenica	Gruiformes: rallid (common moorhen, Baillon's crake); Charadriiformes: recurvirostrid (black-winged stilt, stilt-legged plover), scolopacid (Eurasian woodcock)	intestines	Europe
Reptilian hosts			
S. cruzi	Sauria: gekkonid (tropical house gecko)	intestines	Africa
S. darevskyi	Sauria: lacertid (felseneidechse)	intestines	Europe
S. gulae	Serpentes: colubrid (green water snake), pythonid (Burmese python)	intestines	North America, Asia
S. mirzai	Serpentes: colubrid (grass snake, oriental rat snake), viperid (Okinawa habu), typhlopid (European blind snake)	intestines	Eurasia
S. natricis	Serpentes: colubrid (grass snake, viperine water snake)	intestines	Eurasia
S. ophidiae	Serpentes: colubrid (Rio tropical racer)	intestines	South America
S. ophiusensis	Sauria: lacertid (Ibiza wall lizard)	intestines	Europe
S. serpentis	Serpentes: colubrid (green water snake)	intestines	North America
Amphibian hosts			
S. amphibiophilus	Anura: bufonid (Cuban toad)	intestines	Cuba
S. bufonis	Anura: bufonid (natterjack, Asian common toad)	intestines	Eurasia
S. carinii	Anura: leptodactylid (Cerrado oven frog, striped frog, Joly's white-lipped frog)	intestines	South America
S. mascomai	Anura: ranid (Perez's frog)	intestines	Europe
S. pereira	Anura: hylodid (torrent frog)	intestines	South America
S. physali	Anura: bufonid (Gulf Coast toad)	intestines	Central America
S. prokopici	Anura: bufonid (subdesert toad)	intestines	Africa
S. spiralis	Anura: ranid (edible frog, pool frog)	intestines	Europe

The genus *Parastrongyloides* contains 12 species that are parasitic in the small intestines of marsupials, monotremes, moles and shrews, where they form parasitic males as well as females. These species are also able to undergo multiple free-living generations outside of their hosts (> 90 generations recorded for one species).

***Parastrongyloides* species**	**Definitive Hosts**	**Location**	**Distribution**
P. australis	Peramelemorphia: peramelid (southern brown bandicoot, eastern barred bandicoot, long-nosed bandicoot); Dasyuromorphia: dasyurid (brown antechinus, dusky antechinus, white-footed dunnart)	small intestines	Australia
P. caenolesti	Paucituberculata: caenolestid (Tate's shrew opossum)	small intestines	South America
P. callipygus	Afrosoricida: potamogalid (giant otter shrew)	small intestines	Africa
P. chrysochloris	Afrosoricida: chrysochlorid (Congo golden mole); Rodentia: murid (rusty-bellied brush-furred rat)	small intestines	Africa
P. nadgeensis	Dasyuromorphia: dasyurid (agile antechinus, dusky antechinus, fat-tailed dunnart)	small intestines	Australia
P. neotropicalis	Eulipotyphla: soricid (Ecuadorian small-eared shrew)	small intestines	South America
P. peramelis	Peramelemorphia: peramelid (long-nosed bandicoot, northern brown bandicoot); Dasyuromorphia: dasyurid (agile antechinus, brown antechinus)	small intestines	Australia
P. skrjabini	Eulipotyphla: talpid (European mole)	small intestines	Europe
P. tachyglossi	Monotremata: tachyglossid (short-beaked echidna)	small intestines	Australia
P. timbillicensis	Dasyuromorphia: dasyurid (white-footed dunnart, fat-tailed dunnart)	small intestines	Australia
P. trichosuri	Diprotodontia: phalangerid (common brush-tailed possum, short-eared possum, mountain brushtail possum), petaurid (sugar glider)	small intestines	Australia
P. walterae	Dasyuromorphia: dasyurid (dusky antechinus)	small intestines	Australia
P. winchesi	Eulipotyphla: talpid (European mole, Spanish mole, Roman mole, Kobe mole, Sado mole, Japanese mole, blind mole), soricid (northern short-tailed shrew, bicolored shrew, greater white-toothed shrew, lesser white-toothed shrew, Mediterranean water shrew, common shrew, Tien Shan shrew, Shinto shrew, Laxmann's shrew, Eurasian pygmy shrew, long-clawed shrew)	small intestines	Europe, Asia

Parasite morphology: The parasite has an unusual developmental cycle involving the formation of eggs, free-living and parasitic larvae, free-living male and female adult worms, as well as parasitic (protandrogonous or parthenogenetic) female worms. Eggs appear as small oval thin-shelled bodies, measuring 40-60 µm in length by 25-40 µm in width, and may be partially (2-8 cell stage) or fully embryonated (larvated) when passed in faeces. Free-living larvae (L1 and L2) measure up to 380 µm in length and 20 µm in width and they have a short buccal cavity, rhabditiform pharynx and a muscular bulbed oesophagus (ideal for feeding on particulate material, incl. bacteria). Infective third-stage larvae (L3) measure from 524-710 µm in length and 20 µm in width and have a long tubular filariform oesophagus extending over a third of the body length (ideal for sucking fluids after penetrating host tissues). These larvae do not feed in the soil and have closed uneven mouths and pointed tails (sometimes bifid (notched) in some species). Parasitic worms are all females, measuring from 2-9 mm in length by 80-100 µm in width and characterised by the presence of an extremely long cylindrical (filariform) oesophagus (one third of body length), a posterior vulva and a blunt pointed tail. Free-living male and female worms have a tiny buccal capsule, a rhabditiform pharynx and are smaller in size, measuring up to 1 mm in length. Males have two simple spicules and a gubernaculum, and a pointed tail curved ventrally. Females are stout with 2 ovaries and uteri opening into a vulva located around the middle of the body. The uteri of parasitic females only contain a few eggs at a time, while those of free-living females contain far more eggs.

Site of infection: Parasitic female worms become embedded in the small intestinal mucosa, forming tunnels under the epithelium at the bases of villi and in the crypts of the small intestines. Eggs and first-stage larvae are passed with host faeces. Infective third-stage larvae penetrate the skin and undergo pulmonary migration before forming parthenogenetic females in the intestines.

Pathogenesis: Light threadworm infections remain asymptomatic, even though they may persist for years due to auto-infection or re-infection. Heavier infections, however, can cause several forms of disease; including dermal, pulmonary, enteric and disseminated disease. In humans, migrating *S. stercoralis* larvae can race through the skin (up to 10 mm per hour) causing *larval*

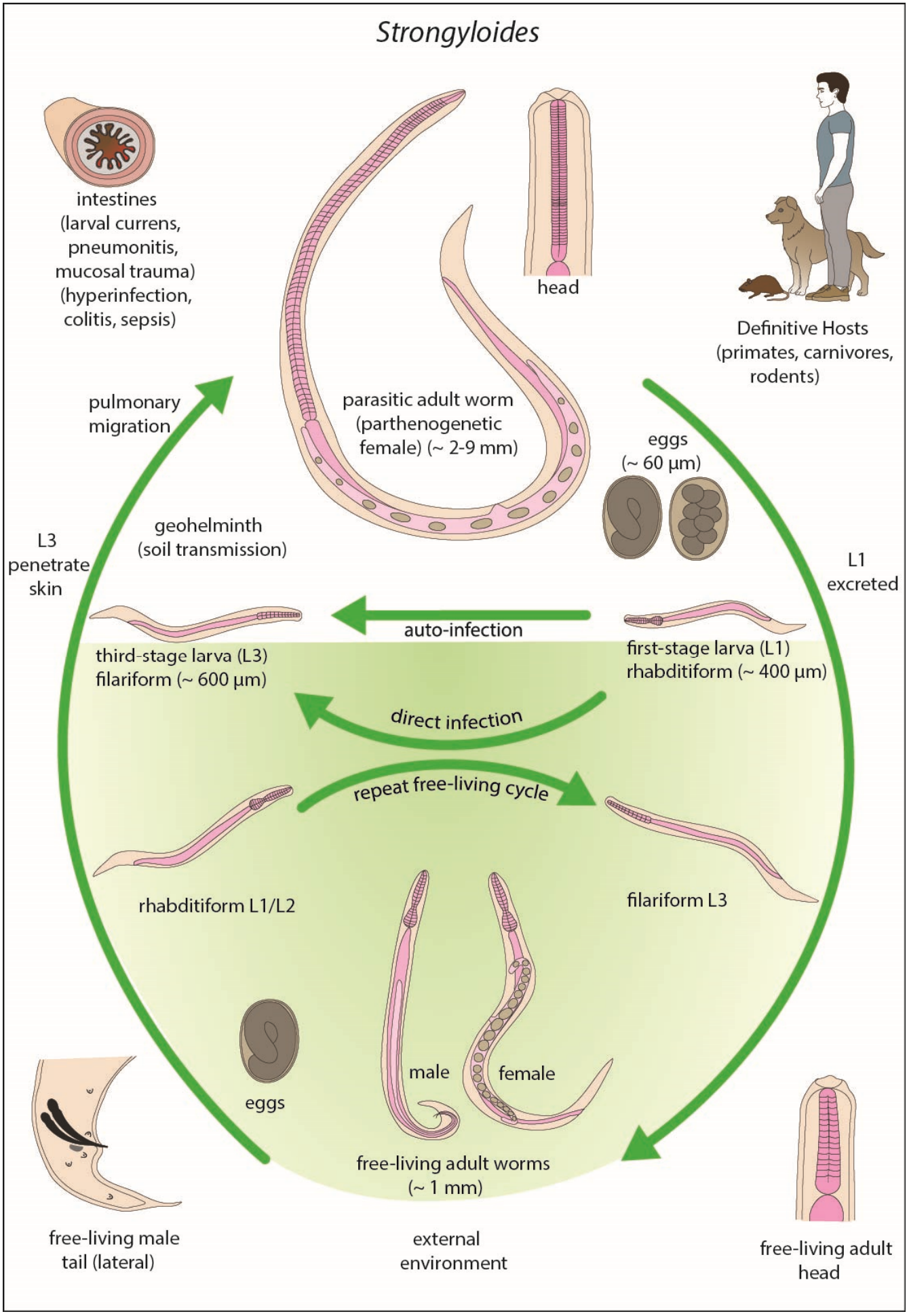
currens, characterised by urticaria, pruritus, eosinophilia, dermatitis, and inflammation. In animals, larvae may cause erythematous lesions where they penetrate the skin. In all cases, pulmonary migration may cause petechiae, mild transient pneumonia or bronchial pneumonitis, with coughing, wheezing, shortness of breath, and transient eosinophilic pulmonary infiltrates (Loeffler's syndrome). Lesions caused by adult worms generally consist of catarrhal inflammation, although severe infections may result in necrosis and sloughing of the mucosa, haemorrhage, epigastric pain (may mimic peptic ulcer or Crohn's disease), vomiting, abdominal distention, diarrhoea with voluminous stools (formerly known as Cochin-China diarrhoea) and a malabsorption syndrome with dehydration and electrolyte disturbance, peripheral eosinophilia, and possibly reactive arthritis. Fulminant hyper-infection syndrome may develop in patients with malnutrition, chronic infections and immunosuppression resulting in severe gastrointestinal and/or respiratory symptoms due to inflammation, haemorrhage and malfunction. Fatal disseminated infection may also develop when large numbers of filariform larvae penetrate the bowel and disseminate, causing colitis, polymicrobial sepsis, pneumonitis or neurological manifestations, such as meningitis and cerebral or cerebellar abscesses. Latent infections may also be reactivated by immunosuppressive chemotherapy leading to hyper-infection syndrome with high worm burdens and disseminated larval migration. In animals, many infections are asymptomatic but some cause diarrhoea and wasting, particularly in neonates infected by transmammary transmission and exacerbated by recurrent autoinfection. Most infections by *S. stercoralis* in puppies and kittens are mild and self-limiting due to the development of a strong protective immunity within weeks, but heavy infections may be associated with pododermatitis, pneumonitis, diarrhoea, catarrhal enteritis, impairment of digestion and absorption, and wasting. Infections in pigs by *S. ransomi* have been associated with erythematous skin reactions, urticaria, pulmonary petechiae, interstitial pneumonia, intestinal inflammation, catarrhal enteritis (with mucosal hyperaemia, petechiae and ecchymoses), villous atrophy, bloody diarrhoea, anaemia, subcutaneous oedema, malabsorption, hypoproteinaemia and emaciation. Infections by *S. westeri* cause enteritis and diarrhoea in foals but are generally asymptomatic in adult horses. Infections by *S. papillosus* may appear early in lambs due to transmammary infection but protective immunity is rapidly acquired and worm burdens decline before weaning. Heavy infections, however, have been associated with sudden death in lambs and calves as well as with a wasting disease in rabbits.

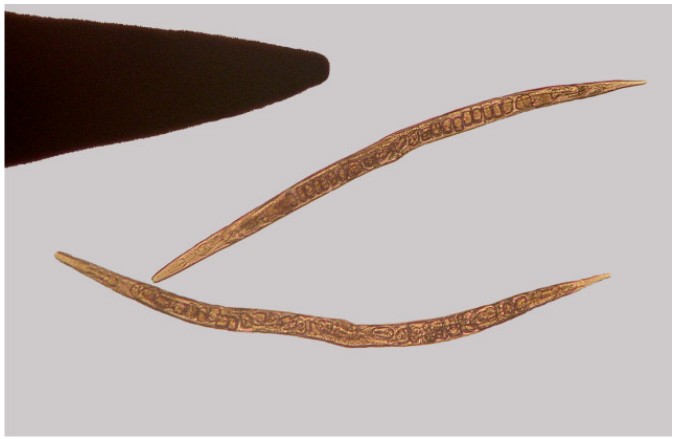
Developmental cycle and mode of transmission: Threadworms have direct life-cycles not involving vectors or intermediate hosts. However, they are unique in that they may form parasitic or free-living adult stages, either as alternating or perpetuating generations. Parasitic stages consist entirely of female worms located in the host intestines, although these worms are protandrogonous (in that male reproductive organs develop first and then disappear) with female reproductive organs then developing and producing larvated eggs (giving the impression of parthenogenetic reproduction). The prepatent period (time from infection to first egg release) often ranges from 25-30 days, but in some species, it may be as short as 6-10 days. The female worms produce several dozen eggs per day, most of which complete embryonation and hatch internally within the host releasing first-stage rhabditiform larvae (L1) which are passed with host faeces. These L1 feed on bacteria and organic debris, moult to second-stage rhabditiform larvae (L2) which feed and then moult to form third-stage filariform larvae (L3). Different L3 strains then undergo free-living (heterogonic) or parasitic (homogonic) development. Heterogonic L3 moult twice to form a generation of free-living males and females which feed on bacteria with their rhabditiform pharynxes. Free-living female worms producing partially-embryonated eggs which eventually hatch releasing rhabditiform L1 that grow and moult twice to form filariform L3. These larvae may give rise to another free-living generation or they may infect hosts as parasites. Infective L3 (homogonic strains and those produced by free-living adults) may survive in moist soil for several weeks (geo-helminth phase) before infecting hosts usually by penetrating the skin (or oral mucosa) although some may simply be ingested. Larvae that are swallowed pass to the intestines where they develop without further migration. Larvae penetrating the skin, however, enter the circulation and are carried to the lungs where they undergo pulmonary migration by penetrating alveoli and moving up the trachea to be swallowed. Other non-pulmonary routes of larval migration have been shown experimentally for several species, mostly involving nasofrontal regions in rodents. After infections have become established in the intestines, further incoming larvae may migrate to deeper tissues and undergo arrested development (hypobiosis) leading to the persistence of chronic infections. Migrating larvae and re-mobilized arrested larvae have been associated with trans-mammary infections by *S. stercoralis, S. ransomi, S. papillosus* and *S. westeri* in dogs, pigs, sheep and horses respectively, as well as prenatal infections by *S. ransomi* and *S. papillosus* in pigs and sheep. Only adult female (parthenogenetic) worms develop in the small intestines and they live for only a few months. Chronic and hyper-infections by *S. stercoralis* and *S. felis* may develop in their hosts because parasitic stages may continue indefinitely through the process of auto-infection [eggs hatching in the intestines may develop into infective L3 which directly penetrate the lower gut (internal auto-infection) or peri-anal region (external auto-infection), thus leading to a new cycle of infection].

Differential diagnosis: Infections are diagnosed by the detection of larvae in faecal samples (or in duodenal endoscopic biopsies), as most eggs hatch internally within the host releasing rhabditiform larvae. Filariform larvae may occasionally be detected, especially during hyper-infection, and they can be identified by their notched tails. Although eggs are rarely detected even in fresh faeces, they are similar in size, shape and appearance to hookworm eggs. Larvae and/or eggs may be present in very low numbers so multiple samples should be examined over a short time course. Larvae may be detected in wet mounts, stained faecal smears, faecal concentrates or cultures. Faecal culture can increase the sensitivity of microscopic diagnosis, by either concentrating larvae (Harada Mori or Baermann technique) or amplifying populations through a generation of free-living males and females. Larval cultures are also used to differentiate between threadworm (*Strongyloides*) and hookworm (*Ancylostoma* and *Necator*) infections, as threadworm larvae have a smaller buccal cavity and a larger genital primordium (such differentiation is crucial as treatment options differ). Non-nutrient agar plate cultures of faeces have also been used to detect motile larvae. The diagnosis of infections by the direct detection of parasites can often be complicated by the sporadic shedding of eggs/larvae, the senescence of parasitic worms (no longer

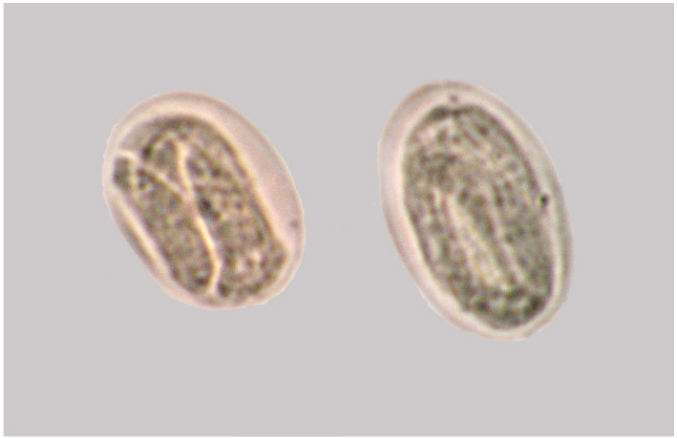
producing eggs), the presence of dormant larvae in tissues (hypobiosis) or extended larval migration (particularly following auto-infection and hyperchronic infections). Recourse is therefore often made to indirect methods of diagnosis. Eosinophilia is a characteristic finding of many helminth infections (including strongyloidiais), but it is relatively nonspecific and also not persistent during hyperinfections Radiology may reveal reflux of oral contrast into the biliary tree, possibly due to inflammation affecting the sphincter of Oddi. Several immunoserological tests (agglutination, fluorescent-antibody, enzyme immunoassays and Western blots) have been developed to detect host antibodies against threadworm antigens, but they have difficulty in distinguishing between past and active infections and may sometimes cross-react with other helminths (such as roundworms, filarial worms and even schistosomes). Several molecular biological tests have recently been developed using polymerase chain reactions (PCR) to amplify parasite DNA sequences, including the hypervariable region (HVR) IV of small subunit (18S) ribosomal DNA, ribosomal protein L10 (rpl-10), mitochondrial cytochrome c-oxidase subunit 1 gene (*cox1*) and β-tubulin gene.

Treatment and control: Several anthelmintics are reasonably effective against threadworm infections, but none are entirely satisfactory. Treating hyperinfections is difficult as drugs are ineffective against migrating auto-infective larvae. Thiabendazole has been widely used but it has unpleasant side-effects, including nausea, vomiting, dizziness, malaise and smelly urine. Other benzimidazoles (albendazole, fenbendazole, flubendazole), imidazothiazoles (levamisole) and macrocyclic lactones (ivermectin, abamectin, doramectin) show good activity, and variable results have been obtained with mebendazole and piperazine. Treatment should be repeated after a week because of difficulty in confirming cure. Immuno-suppressive treatments should be avoided as they can result in rampant auto-infection, as can corticosteroid treatment of mistaken asthmatic respiratory signs. Preventive measures include the wearing of solid shoes in endemic areas, thoroughly washing salad vegetables, prohibiting the use of nightsoil to fertilise gardens, the sanitary disposal of faeces, the provision of latrines in poor areas, and public education campaigns. Infections in animals can be alleviated by improving husbandry, avoiding overcrowded and unhygienic conditions, regularly removing faeces from holding areas, disinfecting pens/stalls, isolating infected individuals and monitoring and treating lactating dams and suckling neonates.


Strongyloides
intestines
(larval currens,
pneumonitis,
mucosal trauma)
(hyperinfection,
colitis, sepsis)
head
Definitive Hosts
(primates, carnivores,
rodents)
pulmonary
migration
parasitic adult worm
(parthenogenetic
female) (~ 2-9 mm)
eggs
(~ 60 µm)
L3
penetrate
skin
geohelminth
(soil transmission)
L1
excreted
auto-infection
third-stage larva (L3)
filariform (~ 600 µm)
first-stage larva (L1)
rhabditiform (~ 400 µm)
direct infection
repeat free-living cycle
rhabditiform L1/L2
filariform L3
eggs
male
female
free-living adult worms
(~ 1 mm)
free-living male
tail (lateral)
external
environment
free-living adult
head



Strongyloides adult worms



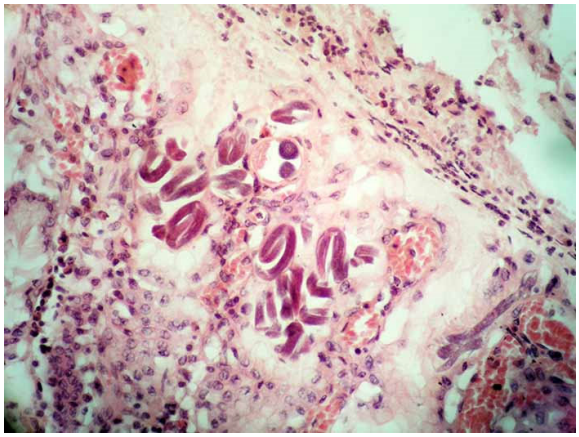
Strongyloides eggs



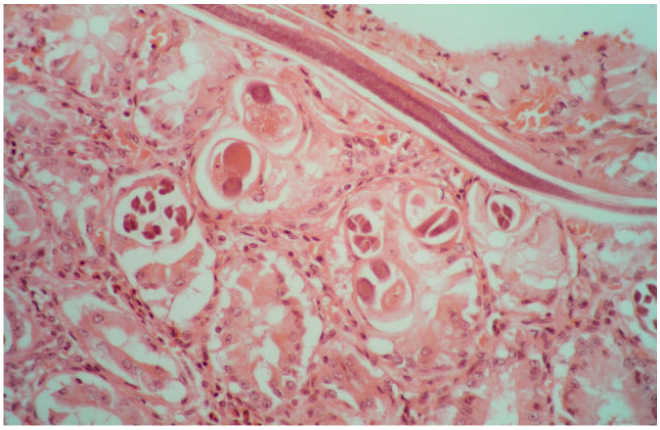
Strongyloides rhabditiform larva



Strongyloides filariform larvva



Strongyloides in gut section



Strongyloides in gut section

Rhabditis, Pelodera
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes rhabditid species which are small slender cylindrical worms with a rhabditiform oesophagus (swollen posteriorly and anteriorly). Adult worms have a small buccal capsule and the males are non-bursate (lack a copulatory bursa). Most rhabditoids are free-living saprophytic nematodes living in warm moist soil/detritus. They have typical life-cycles progressing through eggs, four larval stages and reproductive adults (males being non-bursate). The larvae of some species, however, may opportunistically invade mammalian hosts through hair follicles, orifices or wounds. Several *Rhabditis* and *Pelodera* species have been associated with pruritus, erythema and pustule formation in dogs, cattle and horses.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Rhabditoidea (open tube stoma, excretory system with lateral canals)
Family:	Rhabditidae (protandrous hermaphrodite (male becomes female), parasitic and free-living generations)
Genus:	*Rhabditis/Pelodera* (opportunistic invaders of skin/orifices of animals)
Species:	various species cause skin or udder lesions

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of

most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Rhabditoidea contains worms with phasmids, amphids, an open rod-shaped buccal cavity (stoma), a bulbous oesophagus and an excretory system with lateral canals. Some 12 families are recognised: Agfidae, Alirhabditidae, Angiostomatidae, Brevibuccidae, Carabonematidae, Chambersiellidae, Diploscapteridae, Rhabdiasidae, Rhabditidae, Rhabditonematidae, Steinernematidae, and Syrphonematidae [some authorities include the family Strongyloididae in this superfamily, although recent molecular studies now place it separately in the superfamily Strongyloidoidea]. Rhabditid worms are protandrous hermaphrodites (where male worms becomes female). They are mostly free-living terrestrial nematodes, often living in decaying organic material as bactivores or saprophytes. Several species have been shown to form phoretic relationships with other organisms to aid their dispersal: e.g. dauer larvae may attach themselves to the external surfaces of invertebrates (esp. insects) or invade the tissues of soft-bodied invertebrates (such as earthworms). A few species have also been found to be opportunistically parasitic when special third-stage larvae penetrate the skin of vertebrates (mostly rodents) which are used as paratenic (transport) hosts. These transient infections sometimes cause dermatitis. The family Rhabditidae contains up to 50 genera, including *Rhabditis* and *Pelodera.* Most cases of rhabditic dermatitis in mammals involve some 16 of the 170 described *Rhabditis* spp. and only 2 of the 30 *Pelodera* spp. (note that some authorities regard these 2 genera to be separate, some consider them to be synonymous, and others consider *Pelodera* to be a subgenus of *Rhabditis*). Adult worms have a small buccal capsule, a rhabditiform oesophagus, the integument possesses longitudinal and transverse striae and lateral caudal alae, the males are abursate with medium spicules and the females are oviparous or viviparous.

Rhabditid species	Hosts	Location [Clinical signs]	Distribution
Genus *Pelodera*			
P. strongyloides	free-living (often in manure);	skin	Europe, North

(incl. subsp. *dermatitica*) (syn. *Rhabditis*)	opportunistic infections by L3 in Rodentia: murid (mouse, striped field mouse, yellow-necked mouse, large Japanese field mouse, wood mouse), cricetid (bank vole, field vole, meadow vole, greater long-tailed hamster, northern collared lemming, North American brown lemming, North American deermouse); Carnivora: canid (dog); Primates: hominid (human)	[pruritus, alopecia, dermatitis]	America
P. teres	free-living (in soil); opportunistic infections in Primates: hominid (human)	skin [pruritus]	Europe
Free-living species: *P. arnbomi*, *chitwoodi, coarctata, comandorica*, *conica, cutanea*, *cylindrica, cystilarva, icosiensis, kolbi, lambdiensis, litoralis*, *melisi*, *merionis*, *monohysteroides*, *nidicolis*, *operosa*, *orbitalis*, *par*, *parateres*, *pellio, plicata*, *pseudoteres*, *punctata, serrata, stammeri*, *tretzeli, typica, voelki*			
Genus *Rhabditis* (syn. *Pelodytes*, *Cuticularia*)			
R. adenobia	Coleoptera: scarabaeid (rhinoceros beetles)		Africa
R. axei (syn. *Pelodera, R. usei, R. gracilis, R. tenuicaudala, R. pseudoelongata, R. elongata*)	free-living (in soil); opportunistic infections by L3 in Gastropoda: achatinid (giant African snail, banana rasp snail); Galliformes: phasianid (chicken); Primates: hominid (human)	skin [pruritus]	Africa
R. chabaudi	Gymnophiona: ichthyophiid (common yellow-banded caecilian, brown caecilian)		Sri Lanka
R. cutanea	free-living (often around rodent nests); opportunistic infections by L3 in Rodentia: murid (wood mouse, yellow-necked mouse)	hair follicles	Europe
R. donbass	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
R. elongatus	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
R. esperancensis	Coleoptera: curculionid (white-fringed weevil)		South America
R. gracilis	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
R. inermis (syn. *R. faecalis, R. hominis, R. schachtietla, R. inermoides*)	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
R. macrocerca	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
R. niellyi	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
R. orbitalis	free-living (often around rodent nests); opportunistic infections by L3 in Rodentia: murid (brown rat, mouse, striped field mouse, small Japanese field mouse, large Japanese field mouse, yellow-necked mouse, European wood mouse, Eurasian harvest mouse), cricetid (common mole, field vole, long-tailed vole, European water vole, European snow vole, European pine vole, Tatra pine vole, southern red-backed vole, northern red-backed vole, Hokkaido red-backed vole, grey red-backed vole, Japanese grass vole, bank vole, California vole, northern collared lemming, steppe lemming, Siberian brown lemming), glirid (hazel dormouse)	orbit, conjunctival sac, skin	Eurasia, North America
R. pellio (syn. *Choriorhabditis*, *R. genitalis*)	opportunistic infections by L3 in Primates: hominid (human); Oligochaeta: lumbricid (earthworm)		
R. taurica	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
R. terricola (syn. *R. aspera*)	free-living (in soil); opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	
R. usuii	opportunistic infections by L3 in Primates: hominid (human)	skin [pruritus]	

Free-living species: *R. aberrans, acarta, allgeni*, *anchispora*, *anomala*, *arizonae*, *armata*, *australis*, *bengalensis*, *berolina*, *blumi*, *bonaerensis*, *borealis, bovis, brassicae*, *brevispina*, *buetschlii, cacti*, *caulleryi, ciliata*, *coffeae, colombiana, cornwalli, costai*, *craspedocerca*, *cristata*, *cucumeris*, *curvicaudata*, *dacchensis, dentata, dimorpha, drosophilae, dubia, dudichi*, *duthiersi*, *ehrebaumi*, *elongata*, *entzi, erschowi*, *fertilior*, *filiformis*, *flagellicauda, fluviatilis, formosana, freitasi*, *friderici, fungicola*, *fruticicola*, *gongyloides*, *gracilicauda*, *guenini*, *guignardi*, *gurneyi*, *hartmanni, hermaphrodita*, *heteruroides*, *heterurus*, *impar*, *insectivora*, *insolita, insulana*, *intermedia*, *jagdishi*, *johnstoni*, *karachiensis*, *kherai*, *koerneri*, *krylovi*, *lacustris*, *lepida*, *leptodera*, *longicaudata* (syn. *crenatus*), *longipapillata*, *luciani, lumbriculi, macrospiculata*, *macroura*, *maculosus*, *mairei*, *marina, marionis*, *maupasi*, *maxima, membranosa*, *mucronata*, *musicola*, *myriophila, necromena, neopapillosa*, *nidrosiensis*, *obesa, octopleura* (syn. *leptura*), *oculi*, *ocypodis*, *olitorius*, *oxycerca* (syn. *parapillosa*), *papillosa* (syn. *ikedai*), *paraciliata*, *paraelongata*, *parateres, pellioides, pheropsophi, producta*, *pseudoelongata, pseudolichura, pseudoxycerca*, *rainai*, *reciproca*, *regenfussi, regina, resistens*, *rhabditiformis*, *riemanni*, *rovinjensis, rupaekramae*, *scarabaeum, sechellensis*, *sergenti, seurati, silvatica, simplex, sonorae, stasileonovi*, *stalbergi*, *stercorarius, sylvatica, succaris, suecica, synpapillata, terrestris, tripartita*, *typhae*, *typica, uliginosa*, *uncinata*, *valida*, *varsaviensis*, *velata*, *verneti*, *viguieri, voigti*, *wohlgemuthi*, *zarinae*

Parasite morphology: Rhabditid nematode species form 3 different stages in their developmental cycles: eggs, larvae (4 stages designated L1-L4) and adult worms. All stages are free-living, but in some instances, third-stage larvae (L3) may invade invertebrate or vertebrate hosts. Several worm species have been shown to form 3 different types of L3 (process known as triphenism): regular L3 (free-living); arrested (dauer) L3 (sometimes on or in invertebrate transport hosts); and special parasitic L3 (invade superficial tissues of vertebrate transport hosts). The parasitic L3 are long and thin, measuring from 600-750 µm in length by 30-65 µm in diameter. The larvae do not develop further within their hosts but may undergo modest growth (up to 940 µm in length). They are surrounded by a flexible cuticle with transverse striations, lateral alae and a short-pointed tail (65-100 µm long). The mouth bears lips and opens into a short buccal cavity (20-30 µm long) connected to a rhabditiform oesophagus (with 2 characteristic bulbs) and tubular intestines (cells often become packed with lipid droplets giving the body an opaque appearance). When parasitic L3 are excised from host tissues and cultured, they may establish a free-living generation of adults which mate and produce small round eggs which larvate after oviposition. Adult worms are cylindrical (0.5-2.0 mm long by 35-100 µm wide) and surrounded by a weakly annulated cuticle (with longitudinal and transverse striae). The head is tapered and bears lips which are closed and do not form an open cup. The oesophagus is rhabditiform with 2 swellings, an elongate one near the middle and a rounded terminal one with a simple valvular apparatus. The tail is often pointed (leptoderan), sometimes bluntly rounded (peloderan), and bears membranous caudal alae supported by sets of rays. Adult worms are sexually dimorphic, with males being shorter than females (0.5-1.5 mm cf. 1.0 -2.0 mm). Males have a small posterior accessory piece (no gubernaculum) and 2 curved spicules which may protrude from the cloaca. Females have 2 ovaries, opposed and reflexed, a bifid uterus and median vulva. Most species are oviparous and lay small round-ellipsoidal eggs (55-72 x 25-40 µm) although some species may be viviparous and release first-stage larvae.

Site of infection: These nematodes are free-living in soil or water, but some species may produce special L3 that opportunistically infect the skin (especially hair follicles), and sometimes the conjunctival sacs, of various vertebrate hosts (mostly rodents, but sometimes domestic and companion animals and humans).

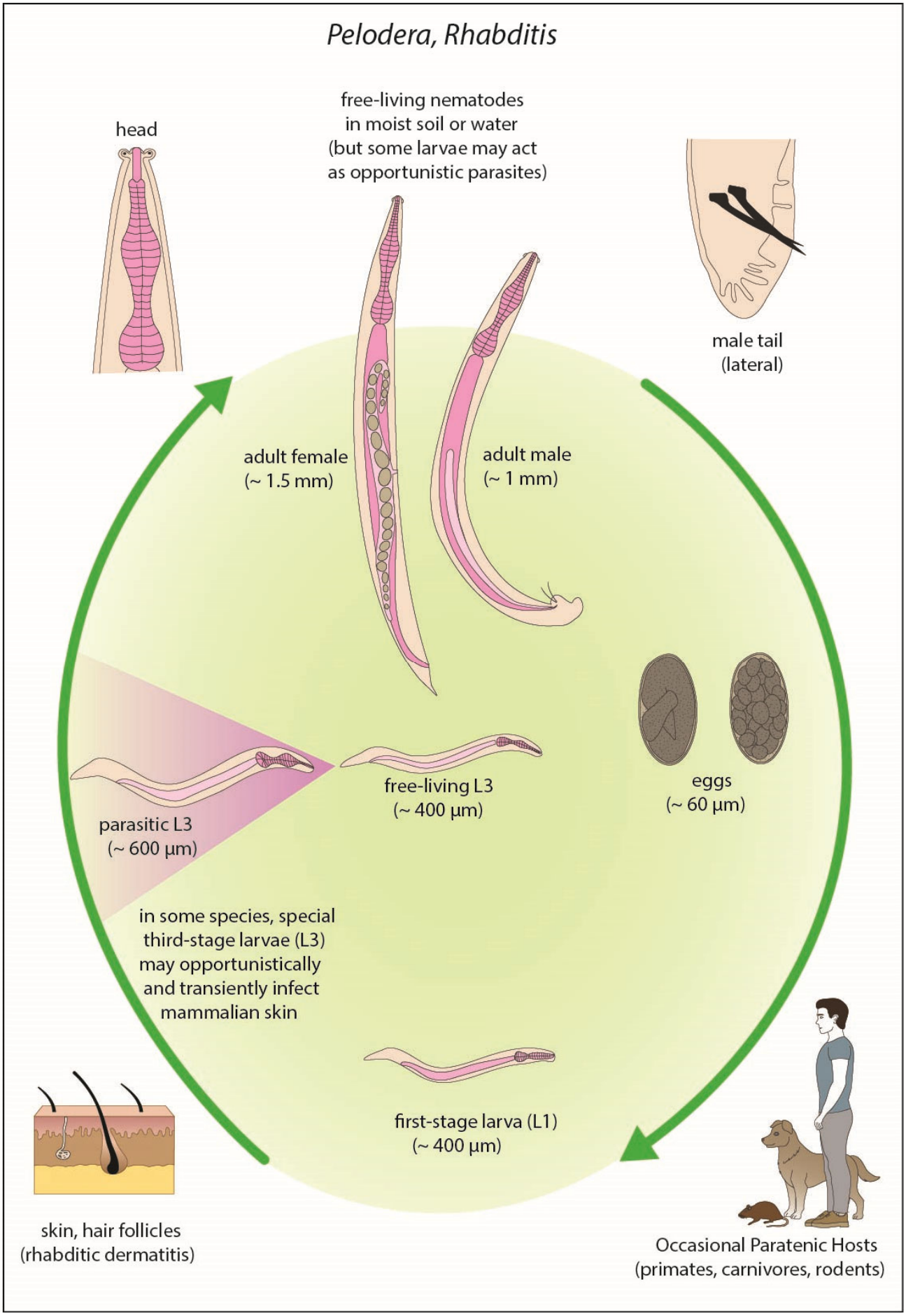
Pathogenesis: Infections by parasitic L3 may cause mild to severe dermatitis in mammals whose skin has come into contact with the ground, notably limb extremities, ventral abdomen and thorax, and perineum. While larvae are ubiquitous as free-living organisms in decaying organic matter especially in moist soil, only some larvae are opportunistically parasitic and may penetrate mammalian skin. Invasion may be facilitated by pre-existing dermatoses, wounds, sores, or when the integrity of the skin is compromised by adverse environmental conditions (e.g. by prolonged exposure to mud or damp bedding). Rhabditic dermatitis has been reported as a rare nonseasonal acute disease in dogs, cows, horses, sheep, guinea pigs and people. Clinical signs include erythema and alopecia with papules, pustules, crusts, erosions or ulcerations. Most individuals experience intense pruritus, although it may be moderate or episodic in others. Histopathological examination frequently reveals acanthotic epidermis, follicular hyperkeratosis, folliculitis with perifollicular infiltrates of eosinophils, mast cells and lymphocytes, furunculosis and sometimes pyogranuloma formation. Infections in dogs in Europe and North America have been associated with severe ulcerative dermatitis and deep pyoderma, notably in animals housed outdoors on damp straw bedding. Infections in cattle in tropical Africa and South America have been associated with otitis externa, media and interna, otorrhea, and occasionally meningitis with depression, abnormal behaviours (circling), recumbency and death. Transient ocular infections in some rodent species in Europe have involved up to 100 larvae per eye without producing any noticeable clinical signs.

Developmental cycle and mode of transmission: These nematodes are normally free-living with life-cycles involving eggs hatching to release larvae which undergo 4 moults to form adult worms. Most species live in moist soil or water where they feed on bacteria and decaying organic material. In addition to forming transient free-living L3, some species have been shown to form dauer L3 which undergo developmental arrest, retaining their L2 cuticle and surviving in low moisture conditions. Dauer larvae of several species have been found attached to the exoskeletons of invertebrates (notably insects) and sometimes within the tissues of soft-

bodied invertebrates (notably earthworms), utilizing them simply as paratenic (transport) hosts for dispersal. However, a few species may also form larger special L3 which can opportunistically parasitize the superficial tissues of mammalian hosts. These larvae are longer and thinner than their free-living counterparts, and are highly active without requiring a film of moisture to move. They are sensitive to heat and vibration and can invade mammalian tissues where they reside apparently deriving nourishment by endosmosis. They may undergo some modest growth but otherwise do not develop further in host tissues, thus effectively utilizing them as paratenic (transport) hosts. When the larvae leave host tissues, under suitable environmental conditions they resume free-living development and moult to form adult worms, thus completing their cycle.

Differential diagnosis: Rhabditic dermatitis is frequently indicated on the basis of clinical symptomatology (characteristic skin lesions) and history of exposure (esp. contact with damp bedding). However, many other parasitoses may cause similar signs, such as demodicosis, scabies, dermatophytosis, pyoderma, and cutaneous larval migrations involved in hookworm dermatitis, dirofilariasis, dipetalonemiasis and strongyloidiasis. Infections may be confirmed by the microscopic detection of characteristic larvae in skin scrapings or biopsies (motile intact larvae from fresh tissues or cross-sections of larvae from fixed tissues). Larvae are readily cultured on ordinary blood agar plates, forming adults a few days after the initial bacterial bloom. One strain has been kept in culture for over 3 decades, with routine weekly subculturing.

Treatment and control: Most infections resolve spontaneously as the larvae are only transient residents in host tissues. Short-term corticosteroids have been used primarily to relieve intense pruritus. Some relief has also been afforded to affected animals by the regular application of insecticidal preparations (dips or sprays), although this may have been protective against secondary infections. Infection control should include improving hygiene by removing and destroying infested bedding materials (esp. moist straw) and moving animals to clean dry surroundings.


Pelodera, Rhabditis
free-living nematodes
in moist soil or water
(but some larvae may act
as opportunistic parasites)
head
male tail
(lateral)
adult female
(~ 1.5 mm)
adult male
(~ 1 mm)
eggs
(~ 60 µm)
free-living L3
(~ 400 µm)
parasitic L3
(~ 600 µm)
in some species, special
third-stage larvae (L3)
may opportunistically
and transiently infect
mammalian skin
first-stage larva (L1)
(~ 400 µm)
skin, hair follicles
(rhabditic dermatitis)
Occasional Paratenic Hosts
(primates, carnivores, rodents)



Rhabditis adult worm



Rhabditis egg



Rhabditis larva

Trichostrongylus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida, including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the trichostrongyles which are small hair-like worms with a small buccal capsule. Adults are usually found in the stomach/abomasum or small intestines of mammals or birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 (some may undergo arrested development, termed hypobiosis) before returning to the lumen to moult into adults. *Trichostronglyus* spp. (black scour and stomach hair worms) cause diarrhoeal diseases that markedly impact production in ruminants worldwide. Considerable efforts are made to control infections through chemical interventions (drenching), husbandry and environmental management.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Trichostrongylidae (hair-like, lips absent/reduced, oesophagus lacking bulb, thin-shelled eggs, direct cycles)
Genus:	*Trichostrongylus* (parasitic in gut of herbivorous mammals/birds)
Species:	various species cause black scours in ruminants

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognise strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal	reduced buccal capsule, cephalic vesicle, female tail with spine or	mammals, birds, reptiles	ingestion of L3	61

worms)	cusps, oviparous/viviparous			
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

The family Trichostrongylidae contains small hair-like worms that infect the gastrointestinal tracts of herbivorous animals, many species causing disease and production losses in ruminant livestock worldwide. Adult worms have a rudimentary buccal cavity with reduced or absent lips but some taxa possessing teeth. Male worms have a well-developed bursa and spicules, and the larger female worms lay thin-shelled eggs that are in the morula stage. Trichostrongyles have direct life-cycles whereby eggs embryonate and hatch in the external environment releasing rhabditiform larvae which grow in soil or on vegetation. These larvae moult to form infective filariform larvae (L3) which are ingested by grazing animals. Various anatomical features have been used to characterise taxa, including patterns of longitudinal ridges (synlophe) on the external cuticular surface as well as structure of the male bursa (arrangement of dorsal, ventral and lateral lobes and supporting rays) and spicules (number, size and shape). Over 50 trichostrongylid genera have been allocated to 8 subfamilies: Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules, 6 genera in mammals and birds); Amidostomatinae (with buccal teeth or extra-buccal appendages, 8 genera in birds); Filarinematinae (neodont formation, long bursa, 3 genera in marsupials); Haemonchinae (well-developed synlophe, neodont formation, 5 genera in ungulates); Ostertagiinae (well-developed synlophe, modified bursa, 15 genera in mammals); Cooperiinae (symmetrical synlophe, bursa with symmetrical dorsal rays, 12 genera in ruminants); Libyostrongylinae (without synlophe, modified bursa, 5 genera in mammals and birds); and Obeliscoidinae (without synlophe, symmetrical bursa, 5 genera in mammals and birds). Note that some taxonomic classifications have split these 8 subfamilies between 3 separate sister families: with Trichostrongylinae, Amidostomatinae and Filarinematinae allocated to a restricted Trichostrongylidae (cephalic vesicle absent, synlophe reduced or absent, male bursa with short dorsal ray and long lateral lobes); Haemonchinae and Ostertagiinae assigned to the Haemonchidae (cephalic vesicle absent, synlophe present without any specific orientation, male bursa with short dorsal rays, often asymmetrical); and Cooperiinae, Libyostrongylinae and Obeliscoidinae placed in the Cooperiidae (cephalic vesicle present, synlophe bilaterally symmetrical or absent, large male bursa with curved lateral rays). Several other genera have recently been transferred to other taxa on the basis of cladistic or molecular phylogenetic studies, mostly those in the subfamily Nematodirinae (6 genera in mammals) now classified in the family Molineidae. Specific trichostrongylid genera of veterinary and medical importance are compared in the following table.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Subfamily Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules)					
Trichostrongylus (hairworm, black scour worm)	56	artiodactyls, lagomorphs, rodents, birds	small intestines, stomach	2-10 mm long, rudimentary buccal cavity, distinct excretory notch in oesophageal region, male bursa with long lateral lobes	75-125 x 31-72 µm, ellipsoidal, thin-shelled

Subfamily Haemonchinae (well-developed synlophe, neodont formation)					
Haemonchus (barber's pole worm)	15	artiodactyls	abomasum	10-40 mm long, buccal capsule with tooth, white spiral ovaries, prominent vulval flap, bursa with asymmetrical dorsal ray, larval hypobiosis	62-90 x 40-50 µm, ellipsoidal, thin-shelled
Subfamily Ostertagiinae (well-developed synlophe, modified bursa)					
Ostertagia (brown stomach worm)	32	artiodactyls	abomasum	6-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-1-2) and proconus, larval hypobiosis	60-100 x 38-50 µm, ellipsoidal, thin-shelled
Teladorsagia (brown stomach worm)	9	artiodactyls	abomasum	10-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-2-1) and proconus, larval hypobiosis	60-100 x 40-50 µm, ellipsoidal, thin-shelled
Hyostrongylus (red stomach worm)	4	suids, lagomorphs	stomach	4-10 mm long, red coloration, well-developed bursa, gubernaculum, telamon, larval hypobiosis	60-90 x 31-42 µm, ovoid, thin-shelled
Subfamily Cooperiinae (symmetrical synlophe, bursa with symmetrical rays)					
Cooperia (wire worm)	24	artiodactyls	small intestines, stomach	4-15 mm long, often coiled, bulbous cephalic vesicle, large bursa, large spicules, larval hypobiosis	65-95 x 29-44 µm, ellipsoidal, thin-shelled

The subfamily Trichostrongylinae contains 6 genera (*Trichostrongylus* (syn. *Buckleya*, *Cobboldostrongylus*, *Gilesia*, *Probostrongylus*); *Graphidioides*, *Graphinema*, *Parostertagia*, *Travassosius*, and *Trichostrongyella*) parasitic in the gastric or intestinal mucosa of ruminants, camelids, rodents, or the caeca of birds. The genus *Trichostrongylus* contains some 60 species of small reddish worms whose excretory pores open into a distinctive ventral notch on the cervical body surface. Infections have been recorded worldwide, particularly in grazing animals, and many species have euryxenous or stenoxenous host ranges often infecting multiple closely-related host species. Most *Trichostrongylus* spp. infect the small intestines of their hosts, although several species infect the stomach (notably *T. axei*). Infections are common in tropical and temperate regions, especially in rural areas with moist loamy soils suitable for egg and larval development. Several species cause considerable problems in domestic livestock industries where morbidity and mortality reduce productivity and treatment is costly. In particular, *T. colubriformis, T. vitrinus* and *T. rugatus* affect sheep production in warm, cool and dry areas respectively, *T. axei* mainly affects cattle production, and *T. tenuis* affects fowl production. Approximately 10 species are known to accidentally infect humans (*T. orientalis* most frequently) when larvae are ingested with unwashed vegetables (some outbreaks traced to farms practising organic farming methods with poorly composted manure). While most infections in humans are not severe, it is estimated that approximately 5.5 million people may be infected annually, with the prevalence being highest in the Middle-East and Asia.

***Trichostrongylus* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
T. affinis	Lagomorpha: leporid (European rabbit, eastern cottontail); Rodentia: cricetid (marsh rice rat, hispid cotton rat, cotton mouse, Oldfield mouse, Florida mouse); Primates: hominid (human)		North America, Europe
T. andreevi	Artiodactyla: cervid (roe deer)		Europe
T. angistris	Artiodactyla: bovid (impala, blue duiker, red forest duiker, bushbuck); Copepoda: cyclopid (*Megacyclops viridis*)		Africa
T. anomalus	Artiodactyla: bovid (suni, blue duiker, red forest duiker)		Africa
T. askivali	Artiodactyla: cervid (roe deer, red deer, sambar deer, fallow deer, white-tailed deer), bovid (sheep)	abomasum	Eurasia
T. assadovi	Artiodactyla: bovid (sheep)		Asia
T. asymmetricus	Diprotodontia: macropodid (un-named wallaby sp.)	stomach	zoo
T. auriculatus	Artiodactyla: bovid (steenbok)	small intestines	Africa
T. axei (syn. *Strongylus extenuatus, gracilis, tenuissimus*) (stomach hairworm, stomach bankrupt worm)	Artiodactyla: bovid (cattle, water buffalo, American bison, European bison, sheep, argali, bighorn sheep, mouflon, Cyprus mouflon, goat, mountain goat, chamois, alpine ibex, Iberian ibex, blackbuck, bushbuck, common duiker, blue duiker, red forest duiker, roan antelope, sable antelope, Sharpe's grysbok), antilocaprid (pronghorn), antilocaprid (pronghorn), cervid (moose, roe deer, red deer, fallow deer, marsh deer, mule deer, white-tailed deer, reindeer, caribou, chital), camelid (llama), suid (pig); Perissodactyla: equid (horse, donkey, mule, onager); Lagomorpha: leporid (rabbit); Rodentia: caviid (capybara), sciurid (Richardson's ground squirrel);	abomasum, stomach [weight loss, diarrhoea, illthrift]	worldwide

	Diprotodontia: phalangerid (common brushtail possum); Primates: hominid (human)		
T. brevis	Artiodactyla: bovid (goat); Carnivora: felid (wildcat); Primates: hominid (human)		
T. calcaratus	Artiodactyla: cervid (roe deer ,white-tailed deer), bovid (sheep); Lagomorpha: leporid (European rabbit, eastern cottontail, black-tailed jackrabbit, volcano rabbit); Rodentia: cricetid (muskrat, Florida mouse), sciurid (fox squirrel); Primates: hominid (human)		North America
T. capricola	Artiodactyla: bovid (European bison, sheep, argali, mouflon, Cyprus mouflon, goat, alpine ibex, Iberian ibex, chamois, Pyrenean chamois), cervid (roe deer, moose); Lagomorpha: leporid (Cape hare); Primates: hominid (human)		Europe, North America
T. cesticillus	Primates: cebid (tufted capuchin)		South America
T. chiapensis (syn. *Boehmiella wilsoni*)	Rodentia: sciurid (Deppe's squirrel)		South America
T. colubriformis (syn. *T. instabilis*) (black scour worm, bankrupt worm)	Artiodactyla: bovid (cattle, water buffalo, sheep, bighorn sheep, argali, mouflon, goat, mountain goat, alpine ibex, Iberian ibex, chamois, common tsessebe, impala, goitered gazelle, dama gazelle, Soemmerring's gazelle, sable antelope, lechwe, blackbuck, bushbuck, Maxwell's duiker, common duiker, Sharpe's grysbok), antilocaprid (pronghorn), cervid (roe deer, red deer, mule deer, marsh deer, moose), camelid (llama, bactrian camel, dromedary), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (European rabbit, Cape hare, European hare, Granada hare, mountain hare); Rodentia: murid (Mongolian gerbil), echimyid (coypu), sciurid (European ground squirrel), cricetid (bank vole, muskrat); Diprotodontia: phalangerid (common brushtail possum); Primates: hominid (human)	duodenum [weight loss, diarrhoea, illthrift]	worldwide
T. cramae	Galliformes: phasianid (northern bobwhite quail, turkey, greater prairie chicken); Anseriformes: anatid (Canada goose); Gruiformes: gruid (sandhill crane)	caecum	North America
T. deflexus	Artiodactyla: bovid (cattle, goat, common tsessebe, waterbuck, impala, steenbok, Cape grysbok, common duiker, grey duiker, common eland, nyala, Cape bushbuck, grey rhebok, greater kudu, suni, oribi), suid (desert warthog); Lagomorpha: leporid (scrub hare)		Africa
T. delicatus	Rodentia: sciurid (Abert's squirrel)		North America
T. dosteri	Artiodactyla: cervid (white-tailed deer)		North America
T. drepanoformis	Artiodactyla: bovid (sheep, goat)	duodenum	Australia
T. duretteae	Rodentia: ctenomyid (Talas tuco-tuco)	small intestines	South America
T. extenuatus	Artiodactyla: bovid (cattle, mouflon, gazelle), cervid (roe deer, red deer)		Europe
T. falculatus	Artiodactyla: bovid (sheep, goat, impala, blue duiker, grey duiker, common tsessebe, sable antelope, Cape grysbok, southern reedbuck bushbuck, grey rhebok, nyala, greater kudu), suid (desert warthog); Lagomorpha: leporid (scrub hare); Primates: cercopithecid (Chacma baboon)		Africa
T. fiberius	Rodentia: cricetid (American muskrat)		North America
T. gaibovi	Artiodactyla: bovid (sheep)		
T. hamatus	Artiodactyla: bovid (common tsessebe)		Africa
T. hypsokysta	Artiodactyla: suid (desert warthog)		Africa
T. instabilis	Artiodactyla: bovid (sheep, impala), suid (desert warthog); Primates: hominid (human)		Africa
T. leiperi	Artiodactyla: bovid (eland)	abomasum, duodenum	Africa
T. lerouxi	Artiodactyla: bovid (cattle); Primates: hominid (human)		Europe
T. longispicularis	Artiodactyla: bovid (cattle, sheep, goat, Pyrenean chamois), cervid	small intestines	Australia,

	(roe deer, mule deer, white-tailed deer, moose), camelid (llama)	[diarrhoea]	Americas, Europe
T. longispiculatum	Artiodactyla: bovid (chamois), cervid (moose)		North America
T. magna	Artiodactyla: bovid (greater kudu)		Africa
T. medius	Anseriformes: anatid (mallard, greylag goose), Galliformes: phasianid (black grouse)	small intestines, caecum	Eurasia
T. minor	Artiodactyla: cervid (roe deer)		
T. monnigi	Artiodactyla: bovid (cattle, sheep, roan antelope)		Africa
T. moschatus	Artiodactyla: bovid (suni)	small intestines	Africa
T. orientalis	Artiodactyla: bovid (sheep); Rodentia: hystricid (Indian crested porcupine); Primates: hominid (human)		Asia, Middle East
T. ostertagiaeformis	Artiodactyla: bovid (argali), cervid (roe deer, red deer)		
T. pietersei	Artiodactyla: bovid (goat, Cape grysbok)		Africa
T. pigmentus	Lagomorpha: leporid (Indian hare)		Asia
T. probolurus	Artiodactyla: bovid (sheep, broad-tailed sheep, goat, blackbuck, dorcas gazelle, dama gazelle, dorcas gazelle, Soemmerring's gazelle, Speke's gazelle, goitered gazelle), cervid (roe deer), camelid (bactrian camel, dromedary); Primates: hominid (human)		Africa
T. qilianensis	Artiodactyla: bovid (bharal)		Asia
T. qinghaiensis	Artiodactyla: bovid (yak)		Asia
T. ransomi	Lagomorpha: leporid (eastern cottontail, European rabbit)	small intestines	North America
T. retortaeformis	Lagomorpha: leporid (European rabbit, volcano rabbit, European hare, Granada hare, mountain hare, Tolai hare, snowshoe hare, Cape hare Rodentia: dipodid (great jerboa), murid (yellow-necked mouse, wood mouse), echimyid (coypu), cricteid (muskrat, common vole, Japanese grass vole, southwestern water vole, European water vole, bank vole), caviid (Patagonian mara, Spix's yellow-toothed cavy), chinchillid (southern viscacha), castorid (American beaver), sciurid (red squirrel); Diprotodontia: phalangerid (common brushtail possum); Artiodactyla: bovid (goat), cervid (roe deer)	small intestines [enteritis, mucous exudates]	worldwide
T. rugatus	Artiodactyla: bovid (sheep, bighorn sheep, goat, blue duiker, red duiker, grey rhebok, Cape grysbok); Diprotodontia: phalangerid (common brushtail possum)	duodenum [weight loss, diarrhoea, illthrift]	Africa, Australasia, North America
T. sigmodontis	Rodentia: cricetid (hispid cotton rat, marsh rice rat, golden hamster), echimyid (coypu), murid (Mongolian gerbil)	lower small intestine, caecum	North America
T. skrjabini	Artiodactyla: bovid (sheep, argali, mouflon), cervid (roe deer); Rodentia: sciurid (European ground squirrel); Primates: hominid (human)	abomasum, small intestines	Russia
T. subtilis	Artiodactyla: bovid (sheep, broad-tailed sheep, dorcas gazelle), camelid (bactrian camel, dromedary); Primates: cercopithecid (hamadryas baboon), hominid (human)		Africa
T. suis	Artiodactyla: suid (pig)		
T. tenuis (syn. *T. pergracilis*)	Galliformes: phasianid (chicken, Indian peafowl, turkey, ring-necked pheasant, grey partridge, rock partridge, chukar, red-legged partridge, willow ptarmigan, rock ptarmigan, common quail, northern bobwhite quail, mountain quail, black grouse, red grouse); Anseriformes: anatid (mottled duck, mallard, greater white-fronted goose, greylag goose, snow goose, mute swan); Casuariiformes: casuariid (emu)	caecum, small intestines [enteritis, diarrhoea]	North America, Eurasia
T. texanus	Rodentia: sciurid (black-tailed prairie dog)	small intestines	North America
T. thomasi	Artiodactyla: bovid (impala, red forest duiker, bushbuck, common tsessebe, greater kudu), suid (desert warthog); Lagomorpha: leporid (scrub hare)		Africa
T. vitrinus (black scour worm)	Artiodactyla: bovid (cattle, European bison, sheep, broad-tailed sheep, argali, goat, mouflon, Cyprus mouflon, chamois, Pyrenean chamois, alpine ibex, Iberian ibex, Cuvier's gazelle, dama gazelle, dorcas gazelle, goitered gazelle), cervid (roe deer, red deer, fallow	duodenum [weight loss, diarrhoea, illthrift]	temperate regions

	deer, mule deer, reindeer, moose), camelid (bactrian camel, dromedary, llama); Lagomorpha: leporid (European rabbit); Diprotodontia: phalangerid (common brushtail possum); Primates: hominid (human)		
T. yoshidai	Rodentia: caviid (Brazilian guinea pig)		South America

Parasite morphology: Trichostrongylid nematodes form 3 different morphological stages in their developmental cycles: eggs; larvae; and adult worms. Freshly laid eggs are described as being typically 'strongyle' in that they are ellipsoidal with slightly pointed uneven poles, bound by thin smooth colourless shells (the inner membrane sometimes wrinkled) and contain a discrete central morula (early-stage embryo) usually consisting of 8-32 cells (blastomeres). Eggs vary in size from 73-125 x 31-72 µm, with narrower size ranges recorded for individual species (e.g. *T. colubriformis* 79-101 x 39-47 µm, *T. retortaeformis* 85-91 x 46-56 µm, *T. vitrinus* 93-118 x 41-52 µm, *T. axei* 79-92 x 31-41 µm). There are 4 sequential larval stages (designated L1-L4), the first 3 being exogenous (developing in the external environment) and the fourth being endogenous (occurring within the host). The first 2 larval stages (L1 and L2) are free-living pre-parasitic stages measuring from 320-400 µm in length. They are characterized by the possession of a rhabditiform pharynx or oesophagus (stout with a caudal bulb) used to feed on bacteria and particulate material. Although the third larval stage (L3) is free-living, it is ensheathed (retains the L2 cuticle as a thin protective sheath) and does not feed externally. They measure from 619-796 µm in length and are characterized by having tapering round heads, a strongyliform (flask-shaped) oesophagus, intestines comprising 16 cells, tapering tails (smooth in the abomasal species *T. axei*, digitate in the intestinal species) and short tail sheath extensions (18-56 µm). L3 are infective to their final hosts in which they develop to L4 and then immature worms (sometimes called pre-adults or L5) which subsequently mature. Adults are slender hair-like worms measuring from 2-10 mm long with rounded heads and tapering tails. Most species are colourless although some may be grey, light brown or pale red in colour. Trichostrongyles have rudimentary or no buccal capsules (compared to well-developed buccal capsules of strongyles) usually lacking lips and teeth are rarely present. *Trichostrongylus* spp. lack cephalic vesicles (unlike *Nematodirus* and *Cooperia*) and they have very small or no cervical papillae. Adult worms are characterized by the presence of a conspicuous ventral notch in the cervical region where the excretory pore is located (notch absent in *Haemonchus* and *Ostertagia*). Worms are surrounded by a thick cuticle with a synlophe (pattern of longitudinal ridges) reduced to annular striations. The oesophagus is relatively short and lacks a caudal bulb while the intestines have well-developed microvilli and a distinctive zig-zag lumen. Mature worms are sexually dimorphic, with females being larger than males (3-10 mm x 55-80 µm cf. 2-9 mm x 50-70 µm). Male worms have a well-developed symmetrical bursa (copulatory clasping organ) with a short dorsal lobe supported by 3 simple rays (comprising muscular elements following nerve channels to terminal papillae) and 2 long lateral lobes each supported by 6 rays (in a popular annotation system the rays have a 1-4 configuration with the ventroventral ray separated from the next 4 rays, while in another annotation scheme ray 2 is separated from rays 3-6). They also have a boat-shaped gubernaculum and 2 stout ridged brown spicules measuring 74-156 µm in length. The spicules vary in morphology depending on the species and may be equal in length (*T. capricola*), unbranched and barbed (*T. colubriformis*) or pointed (*T. vitrinus*); subequal in length and barbed (*T. falculatus*) or blunted (*T. longispicularis*); or markedly unequal in length (*T. axei, T. rugatus*) and barbed (*T. retortaeformis*). Female worms have blunted conical tails and are didelphic with 2 opposed uteri and paired genital tubes opening into a vulva (lacking a flap) usually located just posterior to the midbody. Gravid worms only contain a few (4-5) eggs aligned pole-to-pole *in utero*.

Site of infection: Adult worms of different *Trichostrongylus* species vary in their predilection site of infection: many species (such as *T. colubriformis, T. rugatus, T. vitrinus*) infecting the mucosal lining of the anterior small intestine (usually the duodenum of ruminants); several species (e.g. *T. tenuis, T. sigmodontis*) infecting the caecum (mainly in birds and rodents), and several species (esp. *T. axei*) infecting the stomach (glandular part in monogastrics (pigs, horses) or the abomasum (fourth stomach) in ruminants).

Pathogenesis: Infections by *Trichostrongylus* spp. vary considerably in their impact on their hosts; ranging from subclinical to clinical and even fatal. Pathogenesis depends on the intensity of infection (larval challenge and worm burden), host susceptibility (greatest in young naive animals) and parasite virulence (some species being more pathogenic than others). Parasite developmental stages burrow and feed in the gut mucosa causing traumatic damage and provoking host inflammatory responses. Light to moderate infections often remain subclinical even though various host production parameters may be affected, including impaired growth and weight gain, inferior wool production, reduced milk production and poor reproductive performance. Heavier infections may result in mild-severe gastroenteritis with significant morbidity (especially weaner illthrift) and mortality. Most *Trichostrongylus* spp. infect the small intestines (especially the duodenum and proximal jejunum) where larval and adult worms burrow between villi forming subepithelial tunnels, often congregating in small focal areas. Structural changes include epithelial metaplasia with increased cell turnover, mucous hyperplasia, oedema, catarrhal inflammation and villous atrophy. Functional changes include protein loss into the intestine (leading to hypoalbuminaemia and hypoproteinaemia), reduced levels of brush border enzymes (alkaline phosphatase, dipeptidase), maldigestion and malabsorption, altered levels of gut hormones (secretin), increased gastrointestinal motility, episodic diarrhoea in young animals (black scours, soft dark-coloured faeces producing dags) or chronic diarrhoea in older animals leading to dehydration, inappetence, anorexia and illthrift. Intestinal disease is worsened when tunnels rupture (often synchronously) to release young adults resulting in petechial haemorrhages and the further loss of plasma proteins contributing to mild anaemia. Reduced calcium and phosphorus levels may also result in osteoporosis and osteomalacia. Heavy infections (> 20,000 worms) may cause

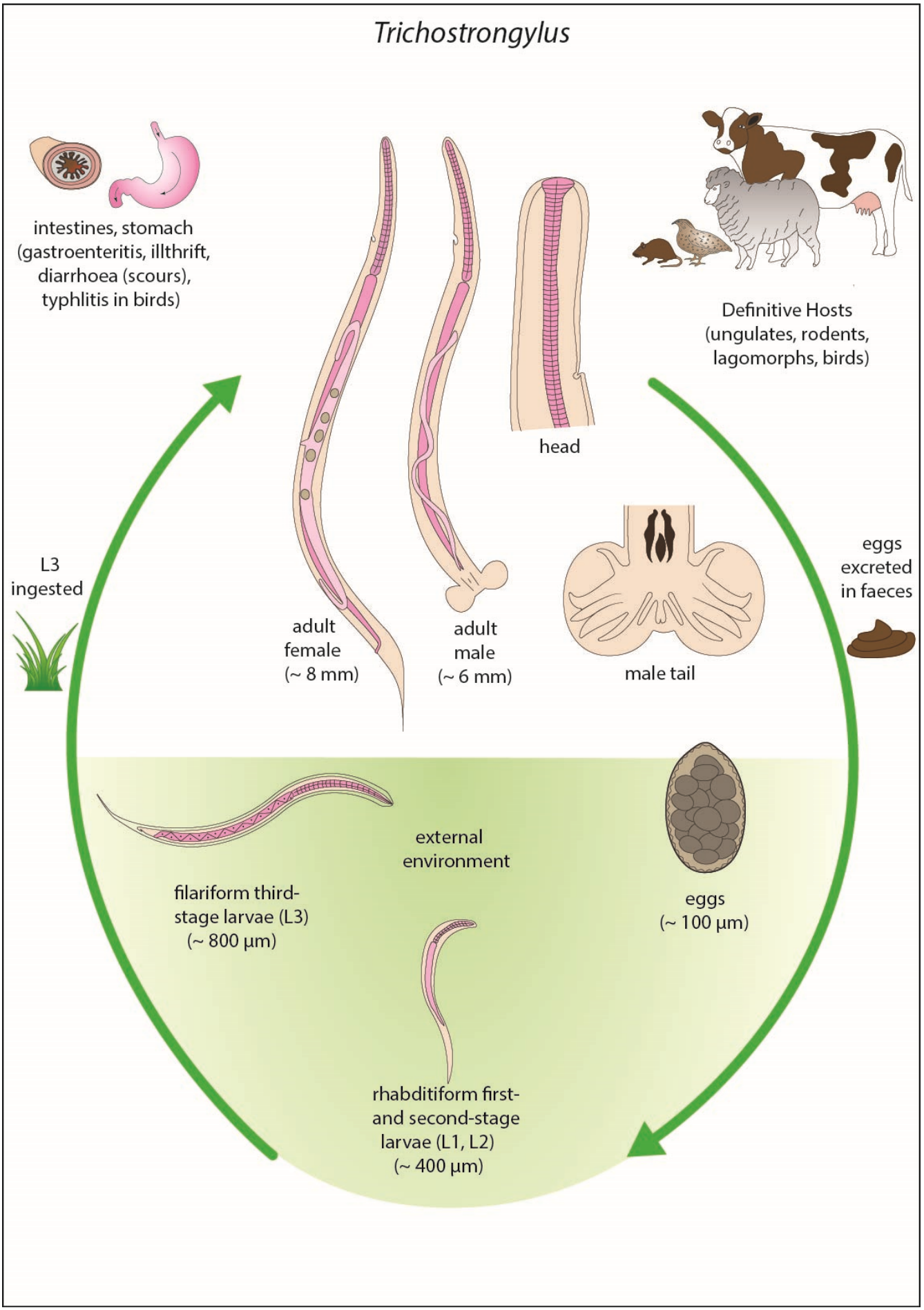
high mortalities, particularly in undernourished weaners. In sheep, the disease is common in lambs under 5 months of age whereas older animals exposed to > 3,000 worms develop a solid cell-mediated immunity which is premunitive (leading to worm expulsion) and protective (resistance to larval challenge). Immune sheep have increased numbers of basophils, eosinophils and mast cells in the lamina propria and they secrete substances in the intestinal mucus which paralyses larvae. Some *Trichostrongylus* spp. (notably *T. axei*) infect the stomach of their hosts (abomasum in ruminants) where developing stages burrow in the gastric mucosa causing hyperaemia and gastritis. Heavy infections are required to produce disease and studies have shown that challenges with > 40,000 larvae may be fatal in certain sheep breeds. Larval stages cause catarrhal gastritis/abomasitis whereas adult worms cause wart-like mucosal thickenings and gastric erosions covered with tenacious mucus. Affected areas may coalesce to present as a diffuse hypertrophic gastritis, evident macroscopically as circumscribed proliferative areas later devoid of epithelium. Chronic infections in horses may result in pale raised thickenings, occasionally with pedunculated or polypoid growths, projecting into the gastric lumen. Functional changes include increases in abomasal pH, abomasal and serum pepsinogen, and a decrease in available nitrogen with the development of foul-smelling ingesta, mucosal oedema, hypoproteinaemia, sometimes diarrhoea and/or anaemia. Clinical signs may develop rapidly and include reduced appetite, anorexia, progressive weight loss, general loss of body condition, emaciation, weakness and death. Infections by *T. tenuis* may cause severe typhlitis in a range of birds, particularly ground-feeding galliform birds (including domestic and game birds). Various species have been found to cause transient infections in humans, usually being asymptomatic but sometimes involving gastrointestinal problems (abdominal pain, diarrhoea, anorexia, emaciation) and/or generalized systemic problems (anaemia, eosinophilia, headache, fatigue).

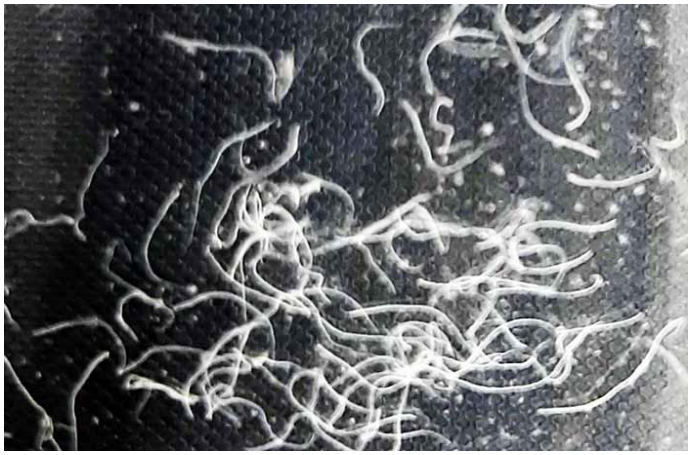
Developmental cycle and mode of transmission: Trichostongyles have simple direct monoxenous life-cycles involving faecal-oral transmission between hosts. Female worms lay eggs which are voided with host faeces into the external environment where they embryonate and hatch within several days. Rhabditiform L1 are released which feed on bacteria and then moult to form rhabditiform L2 which also feed on bacteria. After 5-10 days, the larvae moult to form infective filariform L3 which are ensheathed (retain L2 cuticle), non-feeding and relatively resistant to desiccation (can dry out and become active again when rehydrated). The developmental time from egg to L3 depends on prevailing environmental conditions (especially temperature and moisture), varying from 1-3 weeks in temperate conditions (longer in colder conditions). Rainfall and heavy dew help release larvae from dung pellets and newly hatched larvae are often found on the soil underneath vegetation where they are protected. L3 actively migrate both horizontally over the soil surface (dispersal up to 10 cm) as well as vertically up blades of grass during periods of sunlight (contaminating edible pastures). Definitive hosts become infected by ingesting infective L3 with food or water. The L3 exsheath in the gut and migrate into the mucosa becoming partially embedded where they moult to L4 before returning to the lumen, moulting to young adults (L5) and maturing into male and female adult worms. After mating, mature females lay some 10-200 eggs per day and may live for up to 1 year. The prepatent period (time from infection to first egg production) ranges from 18-28 days. *Trichostronglyus* spp. vary in their geographical distribution and seasonal abundance, mostly in association with regional climatic conditions. For example, species found in sheep vary considerably between regions, with *T. colubriformis* being most prevalent in summer rainfall zones, *T. vitrinus* in winter rainfall zones, and *T. rugatus* in lower rainfall zones. *T. axei* is widespread in temperate zones and has a broader host specificity with cross-transmission occurring when mixed grazing practices are used or when stock are introduced to contaminated paddocks. *T. tenuis* in also prevalent in temperate zones and while parasites develop faster in birds (prepatent period of 7-8 days), infections tend to occur seasonally as some ingested L3 exhibit arrested development (hypobiosis) over winter. Several species may opportunistically infect humans when infective L3 are ingested with contaminated vegetables (raw, unwashed, or washed in contaminated water), particularly crops fertilized in fresh animal manure (widely practiced in rural areas of South-East Asia).

Differential diagnosis: Trichostrongylosis may be suspected on the basis of clinical presentation (gastroenteritis, diarrhoea/scours, anorexia, eosinophilia) and pertinent history (notably afflicting weaners during winter and spring), although other aetiological agents may cause similar diseases (e.g. ostertagiasis, fascioliasis, metabolic disorders, etc). Infections are conventionally confirmed by the direct detection of parasites either antemortem (eggs in faeces) or postmortem (worms in gut). Various coprological techniques may be used to microscopically detect trichostrongyle eggs in faecal samples, usually following concentration by sedimentation in water and then floatation in high specific gravity sugar or heavy-metal salt solutions. Several quantitative techniques have been developed whereby aliquots of diluted faeces are examined in volumetric chambers (McMaster or Whitlock slides) and the number of eggs counted is extrapolated to eggs per gram of faeces (epg). Caution is advised when interpreting faecal egg counts for *Trichostrongylus* infections as they do not correlate well with the intensity of infection; not accounting for larval numbers, male worms, immature or spent female worms, immunological suppression of egg production, nor variable fecundity over time and between species. Egg counts also vary depending on the rate of passage and water content of digesta, often being reduced in diarrhoeic animals and increased in animals starved overnight. Nonetheless, faecal egg counts are routinely used as rough guides to the level of infection when deciding whether to treat animals or not. Faecal egg count reduction tests are also used to determine whether resistance is present to anthelmintic drugs or not. Coprological tests, however, cannot differentiate between many strongyle genera because their eggs are relatively similar in size, shape and appearance (although experienced workers can differentiate trichostrongyle eggs from hookworm eggs (the latter are smaller and do not have pointed ends) and even allocate most trichostrongyle eggs to collective genus-groups (including *Trichostrongylus/Ostertagia*, sometimes separating *Haemonchus*). To differentiate genera, recourse is sometimes made to culturing faecal samples (Baermann apparatus or Petri dishes) until L3 emerge which are then harvested and examined microscopically for characteristic morphotypic features (L3 of *Trichostrongylus* are around 650 μm long, ensheathed, with a tapered head, 16 intestinal cells and a nonpointed tail with a short sheath). Unfortunately,

coproculture takes 1-2 weeks before results become available and it also requires expertise to identify L3s. Infections may also be diagnosed by detecting adult worms in gut samples collected at post-mortem after sacrificing some sick or unthrifty animals. The abomasum and small intestines are collected intact, ligated, preferably filled with warm physiological saline for several hours to help release worms (sometimes the mucosa is digested in pepsin-hydrochloric acid solutions), the washings sieved and examined microscopically for characteristic worms (adult *Trichostrongylus* spp. lacking cephalic vesicles but both sexes with distinctive excretory notches in oesophageal region). The technique can be quantitated by counting the number of worms in aliquots and extrapolating to estimate total worm counts. Infections by 10,000 worms have been associated with significant production losses in sheep, and infections by 20,000 worms have proven fatal in weaners. Several research laboratories have developed serological tests (especially enzyme immunoassays) to detect specific host antibodies against parasite antigens harvested from larval and adult worms, but several problems have been experienced with sensitivity, specificity and cross-reactivity. Modern molecular biological techniques have been used to differentiate species (eggs, larvae and adults) by the polymerase chain reaction (PCR) amplification of parasite DNA (especially the internal transcribed spacer regions (ITS1 and 2) of nuclear ribosomal DNA).

Treatment and control: A range of anthelmintic drugs have been used to effectively treat *Trichostrongylus* spp. infections, but the emergence of drug resistance has become a common problem. In commercial herds/flocks, faecal egg count reduction tests should be conducted to determine drug efficacy. Various authorities recommend regular (periodic) or strategic (as required) dosing, with cyclic rotation of white (benzimidazoles), clear (levamisoles, tetrahydropyrimidines), macrocyclic lactones (avermectins) and even cocktail (mixed) drenches to combat the development of drug resistance. It has also recently been suggested that some animals be left untreated as 'refugia' for susceptible worms as well as allowing for the development of naturally acquired immunity. Anthelmintics act to kill susceptible worms and some are also effective against hypobiotic larvae. Various formulations are either administered orally (drenches), subcutaneously (injected) or even intraruminally (as capsules or boluses that break down to release drugs continuously or in pulses). Careful consideration should be given to regulations and advisory notices concerning drug usage, as some have unpleasant side effects (nausea, bloating, diarrhoea), some have lengthy with-holding periods in production animals, and others are contra-indicated during pregnancy. Infected hosts also respond well to nutrient and protein supplementation during treatment. Regrettably, most anthelmintics have little residual activity, so animals can become re-infected when returned to contaminated pastures - thus giving rise to the conventional practices of 'drench and move to clean pasture' and 'drench at regular intervals'. Studies have shown that the best times to treat sheep is before lambing (to counter the periparturient rise in egg production and minimise pasture contamination) and around weaning (when animals are at their highest risk of disease due to dietary stress, increased grazing and immature immunity) Adult animals generally develop strong protection against challenge infections (concomitant or premunitive immunity rather than sterile immunity as some worms persist within protected hosts). Hosts also exhibit marked variability in their innate genetic resistance to infections, and experimental breeding programs have been successful in selecting resistant livestock, mostly without negatively affecting production parameters. Many environmental factors (especially temperature and moisture) affect the development and survival of eggs, free-living L1 and L2, and ensheathed L3 present in faecal material and on pasture. Nematode control programs should therefore include pasture management practices shown to minimise contamination and reduce the survival/infectivity of free-living stages (rotational grazing of cohorts, mixed grazing with other host species, screening and quarantining introduced livestock, spelling pastures, particularly over dry summers). However, caution is advised when using communal or mixed grazing strategies against *T. axei* infections as this species has a broad host specificity which facilitates cross-transmission between a wide range of herbivores (ruminants and monogastrics). The transmission of infections to humans has been shown to be reduced in regions with proper sewage systems, access to clean water, restricting the use of manure to fertilise vegetable crops, instituting good food hygiene (washing and cooking vegetables) and improving hygiene (washing hands before meals and after contact with animals).


Trichostrongylus
intestines, stomach
(gastroenteritis, illthrift,
diarrhoea (scours),
typhlitis in birds)
Definitive Hosts
(ungulates, rodents,
lagomorphs, birds)
head
adult
female
(~ 8 mm)
adult
male
(~ 6 mm)
male tail
L3
ingested
eggs
excreted
in faeces
external
environment
filariform third-
stage larvae (L3)
(~ 800 µm)
eggs
(~ 100 µm)
rhabditiform first-
and second-stage
larvae (L1, L2)
(~ 400 µm)



Trichostrongylus adult worms



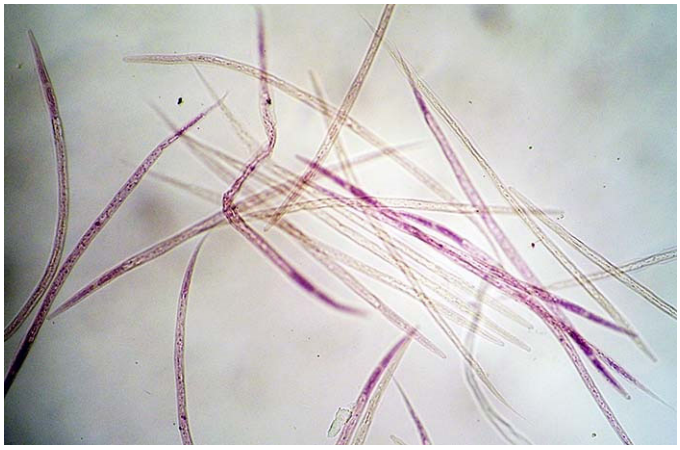
Trichostrongylus adult worm, head



Trichostrongylus adult worm, male bursa



Trichostrongylus egg



Trichostrongylus third-stage larvae

Haemonchus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the trichostrongyles which are small hair-like worms with a small buccal capsule. Adults are usually found in the stomach/abomasum or small intestines of mammals or birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 (some may undergo arrested development, termed hypobiosis) before returning to the lumen to moult into adults. *Haemonchus* spp. (barber's pole worms) cause acute haemorrhagic anaemia (haemonchosis) markedly impacting production in sheep worldwide. Considerable efforts are made to control infections through chemical interventions (drenching), husbandry and environmental management.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Trichostrongylidae (hair-like, lips absent/reduced, oesophagus lacking bulb, thin-shelled eggs, direct cycles)
Genus:	*Haemonchus* (parasitic in abomasum of ruminants)
Species:	*H. contortus* causes anaemia and illthrift in sheep

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61

Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

The family Trichostrongylidae contains small hair-like worms that infect the gastrointestinal tracts of herbivorous animals, many species causing disease and production losses in ruminant livestock worldwide. Adult worms have a rudimentary buccal cavity with reduced or absent lips but some taxa possessing teeth. Male worms have a well-developed bursa and spicules, and the larger female worms lay thin-shelled eggs that are in the morula stage. Trichostrongyles have direct life-cycles whereby eggs embryonate and hatch in the external environment releasing rhabditiform larvae which grow in soil or on vegetation. These larvae moult to form infective filariform larvae (L3) which are ingested by grazing animals. Various anatomical features have been used to characterize taxa, including patterns of longitudinal ridges (synlophe) on the external cuticular surface as well as structure of the male bursa (arrangement of dorsal, ventral and lateral lobes and supporting rays) and spicules (number, size and shape). Over 50 trichostrongylid genera have been allocated to 8 subfamilies: Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules, 6 genera in mammals and birds); Amidostomatinae (with buccal teeth or extra-buccal appendages, 8 genera in birds); Filarinematinae (neodont formation, long bursa, 3 genera in marsupials); Haemonchinae (well-developed synlophe, neodont formation, 5 genera in ungulates); Ostertagiinae (well-developed synlophe, modified bursa, 15 genera in mammals); Cooperiinae (symmetrical synlophe, bursa with symmetrical dorsal rays, 12 genera in ruminants); Libyostrongylinae (without synlophe, modified bursa, 5 genera in mammals and birds); and Obeliscoidinae (without synlophe, symmetrical bursa, 5 genera in mammals and birds). Note that some taxonomic classifications have split these 8 subfamilies between 3 separate sister families: with Trichostrongylinae, Amidostomatinae and Filarinematinae allocated to a restricted Trichostrongylidae (cephalic vesicle absent, synlophe reduced or absent, male bursa with short dorsal ray and long lateral lobes); Haemonchinae and Ostertagiinae assigned to the Haemonchidae (cephalic vesicle absent, synlophe present without any specific orientation, male bursa with short dorsal rays, often asymmetrical); and Cooperiinae, Libyostrongylinae and Obeliscoidinae placed in the Cooperiidae (cephalic vesicle present, synlophe bilaterally symmetrical or absent, large male bursa with curved lateral rays). Several other genera have recently been transferred to other taxa on the basis of cladistic or molecular phylogenetic studies; mostly those in the subfamily Nematodirinae (6 genera in mammals) now classified in the family Molineidae. Specific trichostrongylid genera of veterinary and medical importance are compared in the following table.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Subfamily Haemonchinae (well-developed synlophe, neodont formation)					
Haemonchus (barber's pole worm)	15	artiodactyls	abomasum	10-40 mm long, buccal capsule with tooth, white spiral ovaries, prominent vulval flap, bursa with asymmetrical dorsal ray, larval hypobiosis	62-90 x 40-50 µm, ellipsoidal, thin-shelled
Subfamily Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules)					

Trichostrongylus (hairworm, black scour worm)	56	artiodactyls, lagomorphs, rodents, birds	small intestines, stomach	2-10 mm long, rudimentary buccal cavity, distinct excretory notch in oesophageal region, male bursa with long lateral lobes	75-125 x 31-72 µm, ellipsoidal, thin-shelled
Subfamily Ostertagiinae (well-developed synlophe, modified bursa)					
Ostertagia (brown stomach worm)	32	artiodactyls	abomasum	6-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-1-2) and proconus, larval hypobiosis	60-100 x 38-50 µm, ellipsoidal, thin-shelled
Teladorsagia (brown stomach worm)	9	artiodactyls	abomasum	10-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-2-1) and proconus, larval hypobiosis	60-100 x 40-50 µm, ellipsoidal, thin-shelled
Hyostrongylus (red stomach worm)	4	suids, lagomorphs	stomach	4-10 mm long, red coloration, well-developed bursa, gubernaculum, telamon, larval hypobiosis	60-90 x 31-42 µm, ovoid, thin-shelled
Subfamily Cooperiinae (symmetrical synlophe, bursa with symmetrical rays)					
Cooperia (wire worm)	24	artiodactyls	small intestines, stomach	4-15 mm long, often coiled, bulbous cephalic vesicle, large bursa, large spicules, larval hypobiosis	65-95 x 29-44 µm, ellipsoidal, thin-shelled

The subfamily Haemonchinae was originally erected for genera with one or several teeth in the buccal cavity (neodont formation), large cervical papillae, longitudinal cuticular ridges sometimes restricted to anterior regions, and the male bursa (types 2-2-1 or 2-1-2) with a reduced dorsal lobe and rays 2 and 3 forming a common trunk. The parasites have direct cycles involving faecal-oral transmission whereby eggs voided in faeces contaminate pastures and ultimately produce infective L3 which are ingested and develop in the gastric mucosa. Larval hypobiosis (inhibited or arrested development) in the mucosa is common allowing parasites to persist over adverse seasons. The subfamily Haemonchinae contains 6 genera (*Haemonchus*, *Ashworthius*, *Bigastronema, Boehmiella*, *Leiperiatus*, and *Mecistrocirrus*) parasitic in the stomach of artiodactyls (mainly ruminants) and rarely neotropical rodents. The genus *Haemonchus* forms adults with a small buccal cavity containing a single tooth, a well-developed synlophe restricted to the anterior half of the body. Males have 2 spicules with barbed tips and a bursa with an asymmetrical dorsal lobe, while females have a prominent vulval flap. Some 15 species have been described from the abomasum of a range of ungulates (bovids, camelids, giraffids, cervids), with another 13 species synonymised as *H. contortus* (considered to be a highly polymorphic species). *H. contortus* and *H. placei* causes significant diseases in sheep and cattle respectively, mainly in weaners as a protective immunity develops with age. Infections occur mainly in tropical, sub-tropical and warm temperate zones, particularly those with summer rainfall or irrigated pastures. Parasites abound in the wet season due to the high fecundity of mature females and favourable environmental conditions for the survival of larvae on pastures, whereas parasite numbers decline during dry seasons.

***Haemonchus* species**	**Definitive hosts**	**Location [Clinical signs]**	**Distribution**
H. bedfordi	Artiodactyla: bovid (African buffalo, impala, black wildebeest, blue wildebeest, common tsessebe, sable antelope, kafue lechwe, Limpopo grysbok, Livingstone's eland)		Africa
H. contortus (barber's pole worm, twisted stomach worm, large stomach worm, wire worm) (syn. *H. atectus, bangalorensis, bispinosus, cayugensis, cervinus, fuhrmanni, hispanicus, kentuckiensis, lunatus, okapiae p.p., pseudocontortus, tartaricus, uktalensis*) (incl. subspp. *contortus, cayugensis, bangelorensis, hispanicus,*	Artiodactyla: bovid (sheep, bighorn sheep, mouflon, chamois, Pyrenean chamois, goat, alpine ibex, Iberian ibex, cattle, Bali cattle, zebu, water buffalo, African buffalo, yak, muskox, American bison, addax, impala, blackbuck, bushbuck, water buck, kafue lechwe, common duiker, red forest duiker, blue wildebeest, common tsessebe, Soemmerring's gazelle, Speke's gazelle, nilgiri tahr, sable antelope, Salt's dik-dik, East African oryx, grey rhebok, Cape grysbok, Sharpe's grysbok, southern reedbuck, Bohor reedbuck, Livingstone's eland), antilocaprid (pronghorn), cervid (chital, pygmy brocket, moose, roe deer, red deer, sika deer, sambar deer, fallow deer, marsh deer, white-tailed deer, mule deer, southern mule deer, Columbian black-tailed deer, barasingha, muntjac, Reeve's muntjac), giraffid (Angolan giraffe), camelid (dromedary, llama), suid (pig); Rodentia: hystricid (African brush-tailed porcupine), caviid (guinea pig), murid (Mongolian gerbil, house mouse); Primates: hominid (human); Siluriformes: silurid (helicopter catfish)	abomasum [anaemia, bottle-jaw oedema, illthrift]	worldwide

kentuckiensis, ukatalensis)			
H. dinniki	Artiodactyla: bovid (dik-dik antelope)		Africa
H. horaki	Artiodactyla: bovid (bontebok, grey rhebok)		Africa
H. krugeri	Artiodactyla: bovid (impala, Cape grysbok, Sharpe's grysbok)		Africa
H. lawrencei	Artiodactyla: bovid (impala, blue duiker)		Africa
H. longistipes (camel stomach worm)	Artiodactyla: camelid (Bactrian camel, dromedary), bovid (cattle, zebu, sheep, goat)	abomasum [anaemia]	Afica, Middle East
H. mitchelli	Artiodactyla: bovid (impala, Sharpe's grysbok, common eland, Livingstone's eland, greater kudu), giraffid (Angolan giraffe)		Africa
H. okapiae	Artiodactyla: giraffid (okapi)		Africa
H. ostertagi	Artiodactyla: bovid (American bison)		North America
H. ovis	Artiodactyla: bovid (goat)		
H. placei (now considered to be a cattle strain adaptation of *H. contortus*)	Artiodactyla: bovid (cattle, zebu, yak, European bison, muskox, sheep, bighorn sheep, goat, nilgiri tahr, greater kudu), cervid (roe deer, white-tailed deer), antilocaprid (pronghorn), camelid (dromedary)	abomasum [anaemia, illthrift]	worldwide
H. santomei	Artiodactyla: bovid (cattle)		Europe
H. similis (syn. *H. bubalis*)	Artiodactyla: bovid (cattle, zebu, water buffalo, sheep, goat, common tsessebe, sable antelope, blackbuck), cervid (moose, white-tailed deer)	abomasum [anaemia]	North America, Europe
H. vegliali (syn. *vegliai*)	Artiodactyla: bovid (impala, sable antelope, suni, Sharpe's grysbok, common duiker, grey duiker, Livingstone's eland, nyala, Cape bushbuck, Limpopo bushbuck, greater kudu)		Africa

Parasite morphology: *Haemonchus* spp. form 3 different morphological stages in their developmental cycles: eggs; larvae (4 stages designated L1 to L4); and adult worms (males and females). Gravid females lay thin-walled ellipsoidal eggs ranging in size from 62-90 x 40-50 µm and containing an embryo in the early stages of cleavage (4-32 blastomeres). Fully embryonated eggs hatch to release free-living rhabditiform L1 which measure around 340-350 µm and have a tubular buccal cavity, an oesophagus with a distal valved bulb, and an attenuated sharply pointed tail. L1 moult to form rhabditiform L2 which are longer measuring from 400-450 µm and have developed lateral alae. L2 moult to form infective filariform L3 which retain the L2 cuticle with its attenuated pointed tail generally kinked at the tip (the tail of the ensheathed larva is less attenuated and conical). L3 measure from 650-866 µm in length and have a bullet-shaped head with an anterior shoulder, an elongate buccal cavity closed anteriorly, prominent lateral alae, an elongate strongyliform (non-bulbed) oesophagus, intestines comprising 16 triangular cells (arranged alternately giving the lumen a zigzag appearance as opposed to the straight intestinal lumen in hookworm L3), the gut ending in 2 terminal cells, and finely tapering tails (often appearing kinked or offset) with an elongate tail sheath extension (65-119 µm) of which the last 10-20% is filamentous. Following ingestion and exsheathment, L3 moult to form L4 which escape from the L3 cuticle through a longitudinal slit. L4 measure from 655-840 µm and their buccal capsule opens so they feed and grow, eventually moulting to become young adults (sometimes designated L5). Adult worms are 10-40 mm long and have a rounded head (cephalic vesicle absent) with a small globular buccal capsule containing a single tiny lancet-shaped tooth attached to the dorsal wall (neodont formation used for feeding). They lack the anterior excretory notch present in *Trichostrongylus*, but have a pair of large cervical papillae projecting above the body surface. The synlophe is well-developed with prominent transverse striations at the anterior end followed by numerous longitudinal cuticular ridges restricted to the anterior body. Adult worms are sexually dimorphic with females being larger than males (18-40 mm cf. 10-30 mm in length). Females are characterized by their red-and-white (barber's pole) appearance (white ovaries spiral around the red blood-filled intestines), short vagina, large prominent vulva flap (linguiform in sheep, bulbous in cattle), and short pointed tail without a terminal spine. Females are didelphic and their uteri may contain hundreds of developing eggs. Males have a prominent caudal copulatory bursa with 2 large lateral lobes containing supporting rays (muscular elements following nerve channels to terminal papillae) arranged in a 2-2-1 or 2-1-2 configuration, a smaller asymmetrical dorsal lobe (with a Y-shaped dorsal ray). They also possess a gubernaculum and 2 short thick spicules with distal barbs (left spicule 0.02-0.04 mm, right spicule 0.04-0.06 mm). *H. contortus* in sheep and *H. placei* in cattle were originally distinguished by minor differences in several morphotypic and biological traits (*H. placei* males have longer spicules, females have a knob-like vulva flap, L3 are shorter, and eggs kept at 11°C do not hatch). However, experimental studies succeeded in hybridizing these species with progeny showing some sex-linked dominant traits (notably in vulva morphology and cold resistance of eggs). *H. placei* is now considered by many authorities to be a cattle strain adaptation of *H. contortus.*

Site of infection: Fourth-stage larvae (L4) and adult worms infect the fourth stomach (abomasum) of ungulates or the glandular stomach of monogastric animals. L1 and L2 are free-living stages in faecal material and on soil and pasture, while L3 are the infective stages for grazing animals.

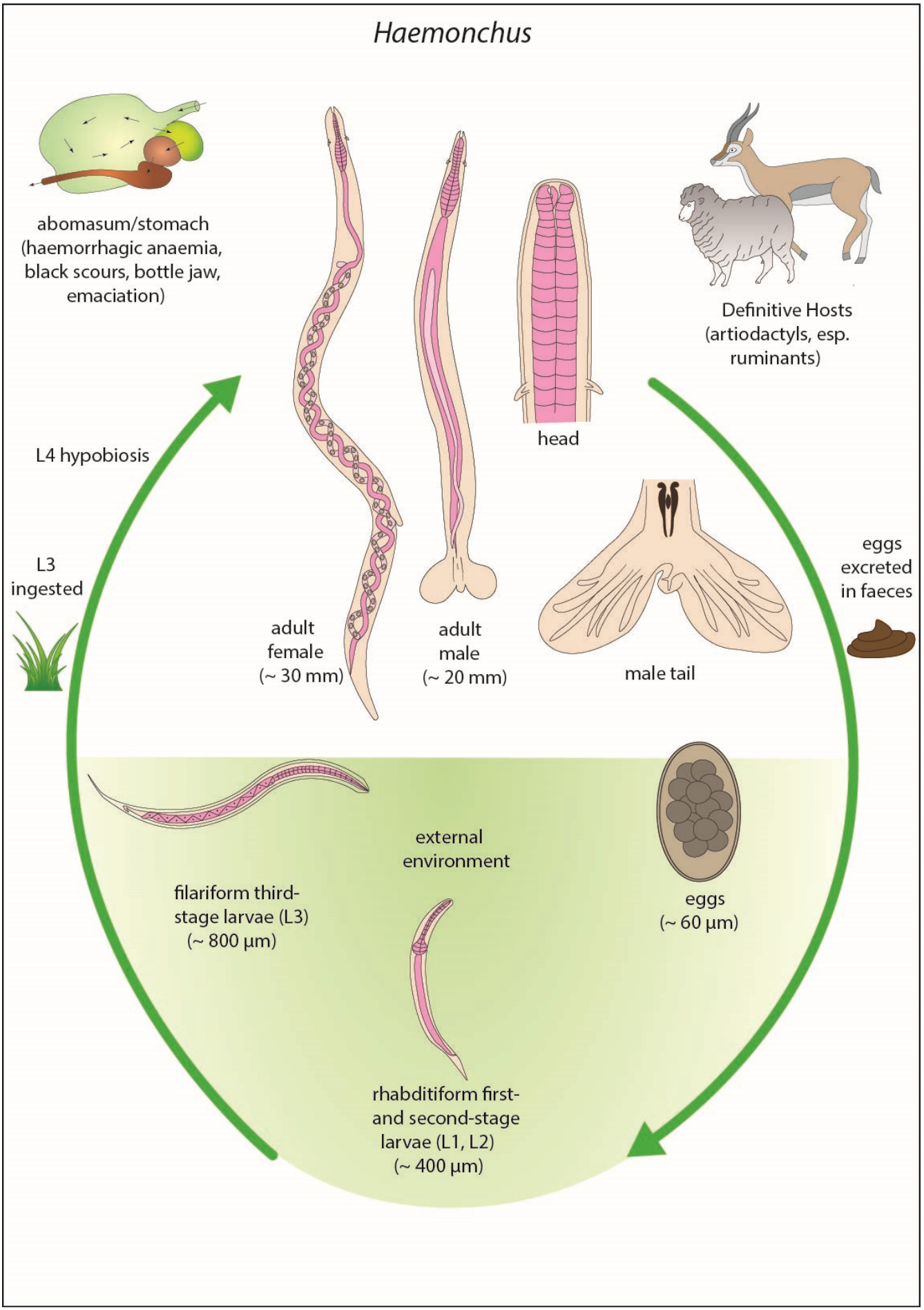
Pathogenesis: Infections by *Haemonchus* spp. vary in their pathogenicity depending on the parasite species, host susceptibility and intensity of infection. Most species are infective for a small range of artiodactyls and a few are notorious pathogens of domestic livestock, particularly young animals. Worms pierce the abomasal mucosa using their oral lancets causing tissue lacerations and blood loss through active feeding (exacerbated by rapid blood transit through worms) and petechial haemorrhages (exacerbated by anticoagulants secreted by feeding worms). While light infections may remain asymptomatic, they may still contribute to significant subclinical production losses (reduced meat, milk and/or fibre). Heavier infections (> 1,000 worms in sheep, > 8,000 worms in cattle) may cause mild to severe clinical disease (haemonchosis), with high morbidity and mortality in susceptible cohorts. Depending on the course and severity of infection, 3 successive stages of disease are recognised; namely, peracute, acute and chronic stages. Early stage (peracute or hyper-acute) infections occur when developing L4 cause petechial haemorrhages resulting in blood loss and anaemia. The onset of disease may be rapid particularly when young susceptible animals ingest large numbers of infective L3 all at once. Infections by > 20,000 *H. contortus* L3 may cause sheep to lose up to 1 litre of blood per day and die suddenly from haemorrhagic gastritis. Later stage infections by young and maturing adults may cause acute or chronic disease syndromes depending on the intensity of infection. Heavy infections may quickly lead to acute disease when feeding worms cause mucosal lacerations, erosions at attachment sites, frank petechial haemorrhages and significant blood loss. Acute signs include severe anaemia, hypoproteinaemia, ascites, subcutaneous oedema (bottle jaw) and only sometimes scouring with darkened faeces due to blood seepage into the gut lumen. Infections by 2,000-20,000 worms may cause animals to lose 100-1,000 ml blood per day (female worms may ingest 0.05 ml blood per day) with clinical anaemia becoming apparent around 2 weeks after infection. Haematocrit values (packed cell volume) may initially stabilise as homeostatic mechanisms (erythropoiesis through bone marrow hyperplasia) begin to compensate, but the continuing loss of blood, iron reserves and serum proteins (esp. albumin) may prove fatal. The abomasal mucosa becomes hyperaemic with many petechiae, focal erosions and some small ulcers, and the submucosa becomes thickened and oedematous. Animals become weak, listless, lose weight (even when food intake may be increased), stunted in growth and emaciated, with high mortality rates in young susceptible animals. Less severe infections (100-2,000 worms) may not result in acute disease, but their protracted course may cause chronic manifestations, particularly during winter when pastures become deficient in nutrients (protein and iron) thus forestalling efficient recovery. The abomasal mucosa exhibits hyperplasia and metaplasia, the submucosa becomes thickened and folded, and there is chronic red bone marrow hyperplasia with reversion to white bone marrow due to iron depletion. Animals do not develop severe anaemia or submandibular oedema but lose weight progressively over several weeks becoming pale, weak and emaciated. While animals may exhibit some age-resistance to disease (developing when > 1 year of age), they do not appear to acquire any effective immunity to infection (unlike many other nematode infections). Nonetheless, animals surviving acute and chronic disease may demonstrate a phenomenon known as self-cure when subject to challenge infections. Adult worms are expelled from the gut by immunological mechanisms involving immediate-type hypersensitivity reactions, but this does not necessarily result in protection against reinfection.

Developmental cycle and mode of transmission: *Haemonchus* spp. have direct monoxenous (1-host) life-cycles involving faecal-oral horizontal transmission (faecal contamination of the external environment by worm eggs, oral ingestion of infective larvae by grazing animals). Gravid female worms may lay 5,000-10,000 eggs per day which are voided with host faeces. The eggs embryonate in faecal material and hatch releasing free-living L1 which feed on bacteria before moulting to form another generation of free-living larvae (L2). These larvae then moult but retain their cuticle to form ensheathed L3 which are non-feeding but are infective to hosts. Depending on prevailing environmental conditions, L3 may develop within 5 days in warm moist conditions but their development may be delayed for weeks in cooler conditions. They survive well on improved or irrigated pastures and those with summer rainfall, migrating horizontally (dispersing outwards from faecal pats) and vertically (ascending blades of grass overnight and descending during the day). Infective L3 on herbage are ingested by grazing animals, mostly in late summer and autumn. Inside their hosts, they exsheath in the stomach and burrow into the abomasal glands where they moult to L4 before re-emerging to the lumen to moult and mature as adults. In certain regions scattered throughout tropical, subtropical and temperate areas, L4 may undergo arrested development (hypobiosis) at the beginning of prolonged dry periods, only resuming development with the onset of seasonal rains when conditions are more favourable for the survival of free-living stages. This often results in a spring rise in egg production and pasture contamination which coincides with host reproduction and is thought to be triggered by the periparturient immunosuppression that occurs during pregnancy. Hypobiosis is by no means a universal feature as it does not occur in regions with more frequent rainfall. The prepatent period (time from infection to first excretion of eggs) ranges from 18-21 days for *H. contortus* in sheep and 23-28 days for *H. placei/contortus* in cattle. Patency (duration of egg production) is often continuous year-round, but may exhibit considerable seasonal fluctuations, particularly in areas where hypobiosis occurs (often resulting in high summer burdens in tropical and subtropical areas and severe outbreaks following summer rains).

Differential diagnosis: Infections may be strongly indicated on the basis of clinical symptomatology (black scours, anaemia, bottle jaw, emaciation) in susceptible animals (esp. weaners) during seasons with warm moist conditions. A variety of technical aids have been developed to indicate and even quantify blood loss, including coloured cards to assess the pallor of mucous membranes, dipsticks for occult blood in faeces, and microhaematocrit tubes for determining packed cell volumes. Infections are conventionally confirmed by the direct detection of parasites in host material, usually worm eggs in faecal samples (antemortem) or adult worms in gut samples (post-mortem). A range of coprological tests have been used to harvest and concentrate worm eggs from faeces, usually by alternate sedimentation in water and floatation in high specific gravity sugar or salt solutions. Some tests have been quantitated by counting the number of worm eggs in known volumes of diluted faeces in chambered McMaster or Whitlock slides, and then calculating the number of eggs per gram of faeces (epg). Egg counts provide a rough guide to the level of infection by a range of

nematode parasites, with considerable variation found in their correlation with the actual numbers of worms (due to differences in fecundity between species and over time, immunosuppression of egg production, changed rates of passage of digesta, and failure to account for larvae, male worms, immature or senescent females). In the case of *Haemonchus* spp. which are prolific egg producers, there is a relatively good correlation between faecal egg counts and the level of infection, so the technique is often used to indicate the need for chemotherapy as well as to screen for drug resistance (by conducting faecal egg count reduction tests pre- and post-treatment). Nonetheless, it is difficult even for trained technicians to differentiate *Haemonchus* eggs from *Trichostrongylus* and *Ostertagia* eggs. When time permits, specific diagnosis may make recourse to culturing eggs over 1-2 weeks to harvest larvae for differentiation. Faecal samples are incubated in funnels (Baermann technique) or petri-dishes (Harada-Mori technique) until L3 emerge which are then collected and examined microscopically for characteristic features (*Haemonchus* L3 have narrow rounded heads, intestines with 16 cells arranged in a zigzag pattern, and a tapering tail with a medium offset sheath). Infections may also be diagnosed by the detection of adult worms in gut samples collected from deceased, euthanized or sacrificed animals. Both male and female worms can be identified by their morphometric features, notably the barber's pole appearance (white ovaries twisted around red intestines) and the prominent vulvar flap of females, and bursa structure in males. Worm burdens can also be quantitated by counting their numbers in aliquots of saline washes of abomasal and/or intestinal mucosa (sometimes digested in pepsin-hydrochloric acid solutions to release hypobiotic larvae). Research laboratories have developed several serological tests (mostly enzyme immunoassays) to detect specific host antibodies against larval and adult worm antigens, but considerable cross-reactivity was detected with other nematode infections. Modern molecular biological techniques have recently been used to characterize several *Haemonchus* spp. by polymerase chain reaction (PCR) amplification of egg, larval and adult worm DNA (18S, 5.8S and 28S ribosomal DNA and internal transcribed spacer regions I and II).

Treatment and control: A broad range of anthelmintics have been used to treat infections in livestock, but the emergence of drug resistance has become a widespread problem. When effective, most anthelmintics kill adult worms and some are also active against hypobiotic larvae. Common drug groups include white drenches (benzimidazoles), clear drenches (imidazothiazoles), salicylanilides (closantel) and macrocyclic lactones (avermectins). Most are available as oral formulations, some as subcutaneous injections and a few as slow-release rumen boluses. Nonetheless, they have little residual activity so animals may be rapidly re-infected if returned to contaminated areas (thus requiring repeat treatments and giving rise to the conventional adage of 'drench and move' to pasture not recently grazed). Many agricultural authorities recommend that drug-resistant testing (faecal egg count reduction tests) be performed to select the most effective formulations for mass treatments, that drugs be used in cyclic rotation or in combination, and that treatments be conducted periodically (around weaning or seasonally) or strategically (only as required). More recently, studies have counter-intuitively shown that leaving some animals untreated may delay the onset of drug resistance (by providing 'refugia' for drug-susceptible worms). Control programmes for gastrointestinal nematodes should also include management practices designed to limit host exposure and minimise the contamination, development and survival of parasites on pastures. Weaners are most at risk due to their increased grazing frequency, their exposure to high numbers of larvae (the result of the periparturient spring rise in worm egg production), the physiological stress accompanying dietary changes (from milk to grass), and their relative immunological immaturity. It is usually recommended that pregnant animals be treated before birth and that weaners be treated before moving onto safe pastures. Studies have shown that some individual hosts (and some native breeds) have an innate resistance to clinical infection and experimental breeding trials have succeeded in selectively breeding resistant sheep without sacrificing production parameters. Pasture contamination can also be minimised by adopting rotational grazing and/or mixed grazing practices, or spelling pastures over dry summers as worm eggs, free-living L1 and L2, and infective L3 are susceptible to adverse environmental conditions (especially lack of moisture).

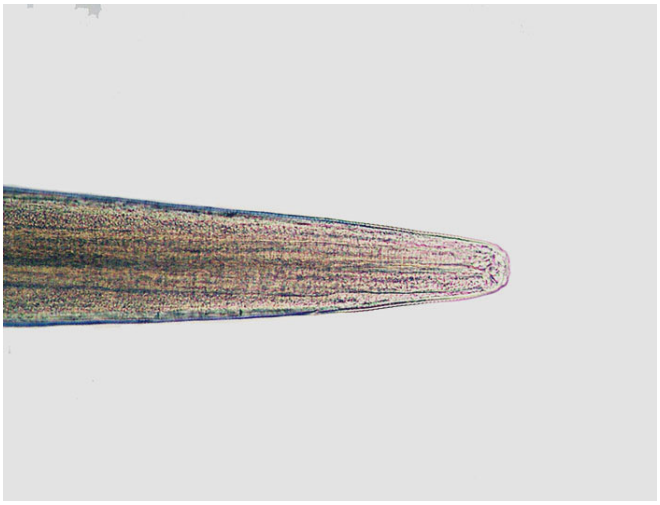

Haemonchus
abomasum/stomach
(haemorrhagic anaemia,
black scours, bottle jaw,
emaciation)
Definitive Hosts
(artiodactyls, esp.
ruminants)
head
L4 hypobiosis
L3
ingested
adult
female
(~ 30 mm)
adult
male
(~ 20 mm)
male tail
eggs
excreted
in faeces
external
environment
filariform third-
stage larvae (L3)
(~ 800 µm)
eggs
(~ 60 µm)
rhabditiform first-
and second-stage
larvae (L1, L2)
(~ 400 µm)



Haemonchus adult worms



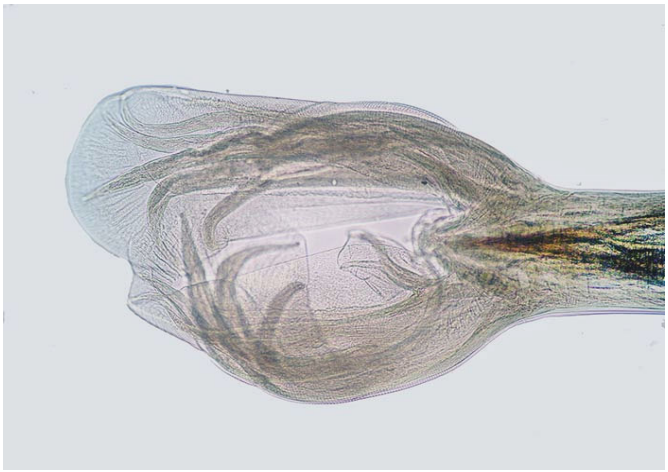
Haemonchus adult worms



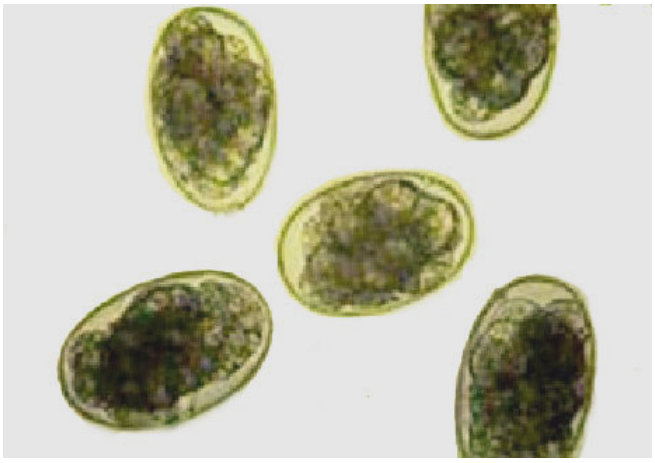
Haemonchus adult worm, head



Haemonchus adult worm, female vulval flap



Haemonchus adult male worm, male bursa



Haemonchus worm eggs

Ostertagia
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the trichostrongyles which are small hair-like worms with a small buccal capsule. Adults are usually found in the stomach/abomasum or small intestines of mammals or birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 (some may undergo arrested development, termed hypobiosis) before returning to the lumen to moult into adults. *Ostertagia* spp. (brown stomach worms) cause diarrhoeal diseases (type I and II ostertagiasis) markedly impacting production in cattle worldwide. Considerable efforts are made to control infections through chemical interventions (drenching), husbandry and environmental management.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Trichostrongylidae (hair-like, lips absent/reduced, oesophagus lacking bulb, thin-shelled eggs, direct cycles)
Genus:	*Ostertagia* (parasitic in abomasum of ruminants)
Species:	various species cause enteric diseases in ruminants (type 1 and type 2 ostertagiasis)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61

Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

The family Trichostrongylidae contains small hair-like worms that infect the gastrointestinal tracts of herbivorous animals, many species causing disease and production losses in ruminant livestock worldwide. Adult worms have a rudimentary buccal cavity with reduced or absent lips but some taxa possessing teeth. Male worms have a well-developed bursa and spicules, and the larger female worms lay thin-shelled eggs that are in the morula stage. Trichostrongyles have direct life-cycles whereby eggs embryonate and hatch in the external environment releasing rhabditiform larvae which grow in soil or on vegetation. These larvae moult to form infective filariform larvae (L3) which are ingested by grazing animals. Various anatomical features have been used to characterize taxa, including patterns of longitudinal ridges (synlophe) on the external cuticular surface as well as structure of the male bursa (arrangement of dorsal, ventral and lateral lobes and supporting rays) and spicules (number, size and shape). Over 50 trichostrongylid genera have been allocated to 8 subfamilies: Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules, 6 genera in mammals and birds); Amidostomatinae (with buccal teeth or extra-buccal appendages, 8 genera in birds); Filarinematinae (neodont formation, long bursa, 3 genera in marsupials); Haemonchinae (well-developed synlophe, neodont formation, 5 genera in ungulates); Ostertagiinae (well-developed synlophe, modified bursa, 15 genera in mammals); Cooperiinae (symmetrical synlophe, bursa with symmetrical dorsal rays, 12 genera in ruminants); Libyostrongylinae (without synlophe, modified bursa, 5 genera in mammals and birds); and Obeliscoidinae (without synlophe, symmetrical bursa, 5 genera in mammals and birds). Note that some taxonomic classifications have split these 8 subfamilies between 3 separate sister families: with Trichostrongylinae, Amidostomatinae and Filarinematinae allocated to a restricted Trichostrongylidae (cephalic vesicle absent, synlophe reduced or absent, male bursa with short dorsal ray and long lateral lobes); Haemonchinae and Ostertagiinae assigned to the Haemonchidae (cephalic vesicle absent, synlophe present without any specific orientation, male bursa with short dorsal rays, often asymmetrical); and Cooperiinae, Libyostrongylinae and Obeliscoidinae placed in the Cooperiidae (cephalic vesicle present, synlophe bilaterally symmetrical or absent, large male bursa with curved lateral rays). Several other genera have recently been transferred to other taxa on the basis of cladistic or molecular phylogenetic studies; mostly those in the subfamily Nematodirinae (6 genera in mammals) now classified in the family Molineidae. Specific trichostrongylid genera of veterinary and medical importance are compared in the following table.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Subfamily Ostertagiinae (well-developed synlophe, modified bursa)					
Ostertagia (brown stomach worm)	32	artiodactyls	abomasum	6-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-1-2) and proconus, larval hypobiosis	60-100 x 38-50 µm, ellipsoidal, thin-shelled
Teladorsagia (brown stomach	9	artiodactyls	abomasum	10-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5	60-100 x 40-50 µm, ellipsoidal,

worm)				lateral rays (2-2-1) and proconus, larval hypobiosis	thin-shelled
Hyostrongylus (red stomach worm)	4	suids, lagomorphs	stomach	4-10 mm long, red coloration, well-developed bursa, gubernaculum, telamon, larval hypobiosis	60-90 x 31-42 µm, ovoid, thin-shelled
Subfamily Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules)					
Trichostrongylus (hairworm, black scour worm)	56	artiodactyls, lagomorphs, rodents, birds	small intestines, stomach	2-10 mm long, rudimentary buccal cavity, distinct excretory notch in oesophageal region, male bursa with long lateral lobes	75-125 x 31-72 µm, ellipsoidal, thin-shelled
Subfamily Haemonchinae (well-developed synlophe, neodont formation)					
Haemonchus (barber's pole worm)	15	artiodactyls	abomasum	10-40 mm long, buccal capsule with tooth, white spiral ovaries, prominent vulval flap, bursa with asymmetrical dorsal ray, larval hypobiosis	62-90 x 40-50 µm, ellipsoidal, thin-shelled
Subfamily Cooperiinae (symmetrical synlophe, bursa with symmetrical rays)					
Cooperia (wire worm)	24	artiodactyls	small intestines, stomach	4-15 mm long, often coiled, bulbous cephalic vesicle, large bursa, large spicules, larval hypobiosis	65-95 x 29-44 µm, ellipsoidal, thin-shelled

The subfamily Ostertagiinae was erected for genera with an accessory bursal membrane and other characters include a head region with a small restricted cephalic vesicle, small cervical papillae and prominent transverse striations, and a body with numerous longitudinal cuticular ridges. Some 23 genera have been reported from ruminants, hippopotami, lagomorphs and suids: namely, *Africanostrongylus, Apteragia, Camelostrongylus, Cervicaprastrongylus, Graphidium, Grosspiculagia* (syn. *Ostertagiella*), *Hamulonema, Hyostrongylus* (syn. *Bergheia*), *Longistrongylus* (syn. *Bigalkea, Bigalkenema, Kobusinema*), *Marshallagia, Mazamastrongylus, Orloffia, Ostertagia* (syn. *Capreolagia, Gruhneria, Muflonagia, Ostertagiana, Sjobergia, Skrjabinagia*), *Ostertamia, Paramecistrocirrus, Pseudomarshallagia, Rinadia, Robustostrongylus, Sarwaria, Spiculopteragia* (syn. *Altaevia*), *Spiculopteroides, Teladorsagia* (syn. *Paramecistocirrus*, *Stadelmania*), and *Tunisostertagia.* Some members of the Ostertagiinae have been allocated to 2 groups; one characterised by bursal type 2-1-2 (ray 2 grouped with ray 3, isolation of ray 4, ray 5 grouped with ray 6) including *Graphidium*, *Marshallagia*, *Longistrongylus* and *Ostertagia*; and another characterised by bursal type 2-2-1 (ray 2 grouped with ray 3, ray 4 grouped with ray 5, isolation of ray 6) including *Hyostrongylus*, *Spiculopteragia*, *Teladorsagia* and *Gazellostrongylus*. The genus *Ostertagia* is further characterised by bursate males with a symmetrical dorsal lobe, an enlarged proconus, spicules with short branches and barbed tips, and a genital cone with short dorsal raylets associated with a simple accessory membrane. Over 25 species have been described from bovids and holarctic cervids, where they have direct life-cycles with faecal-oral transmission. Worms developing and feeding in the abomasal mucosa may cause disease in weaners and the synchronous emergence of hypobiotic larvae may later cause disease in yearlings. Infections contribute to significant economic losses in livestock industries through morbidity, mortality and reduced production (meat, milk, fibre). Several species are important pathogens in cattle in most temperate, and some subtropical, regions with winter rainfall.

***Ostertagia* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
O. angusdunni	Artiodactyla: bovid (giant eland)		Africa
O. arctica (syn. *Sjobergia, Ostertagiella, Skrjabinagia*)	Artiodactyla: bovid (muskox, mouflon), cervid (roe deer, red deer, fallow deer, reindeer, Svalbard reindeer, Siberian reindeer, mountain reindeer, boreal woodland caribou, barren ground caribou)	abomasum	North America
O. boevi	Artiodactyla: bovid (water buffalo)		
O. callis	Didelphimorphia: didelphid (big-eared opossum)		South America
O. cervi	Artiodactyla: bovid (red deer)		Europe
O. delicata (syn *Delicata cameroni*)	Cingulata: chlamyphorid (southern naked-tailed armadillo)		South America
O. dikmansi (syn. *Skrjaninagia*)	Artiodactyla: cervid (white-tailed deer)	abomasum	North America
O. drozdzi	Artiodactyla: bovid (goat, sheep), cervid (red deer, fallow deer, Altai wapiti)		Europe
O. gruehneri (syn. *Gruhneria*))	Artiodactyla: bovid (cattle, muskox, sheep, mouflon), cervid (roe deer, reindeer, Svalbard reindeer, Siberian tundra reindeer, mountain reindeer, boreal woodland caribou, barren ground caribou)	abomasum	Eurasia
O. harrisi	Artiodactyla: bovid (goat, red forest duiker, grey		Africa

	duiker, Cuvier's gazelle, dama gazelle, nyala)		
O. houdemeri	Artiodactyla: cervid (unspecified deer species)		Indo-China
O. kolchida (syn. *O. lasensis, popovi, rubricervi, Mouflongia podjapolskyi, Grosspiculagia, Sjobergia, Skrjabinagia*) [possibly minor morphotype of *O. leptospicularis*]	Artiodactyla: bovid (cattle, European bison, sheep, mouflon, goat, chamois), cervid (roe deer, red deer, Spanish red deer, sika deer, fallow deer, mule deer, Tule elk, Altai wapiti, reindeer, boreal woodland caribou, moose)	abomasum	North America, Eurasia, New Zealand
O. leptospicularis (syn. *O. capreolagi, capreoli, crimensis, paracapreoli, taurica, Capreolagia antipinni, paraskrjabini, skrjabini, Grosspiculagia*)	Artiodactyla: bovid (cattle, European bison, sheep, argali, mouflon, goat, chamois, alpine ibex, blackbuck), camelid (camel), cervid (red deer, Spanish red deer, mule deer, fallow deer, sika deer, roe deer, Siberian roe deer, Tule elk, Altai wapiti, reindeer, boreal woodland caribou, moose)	abomasum [diarrhoea]	worldwide, esp. Europe, New Zealand
O. lyrata (syn. *O. occidentalis, Camelostrongylus lyratus, Grosspiculagia, Sjobergia, Skrjabinagia, Marshallagia*) (now considered to be a morphological variant of *O. ostertagi*)	Artiodactyla: bovid (cattle, American bison, European bison, muskox, sheep, bighorn sheep, Dall sheep, argali, mouflon, chamois, goat, mountain goat, alpine ibex, Iberian ibex), cervid (roe deer, red deer, fallow deer, white-tailed deer)	abomasum [diarrhoea]	worldwide, esp. temperate zones
O. lyrataeformis	Artiodactyla: cervid (roe deer, Siberian roe deer, moose)		Eurasia
O. mossi	Artiodactyla: bovid (sheep), cervid (white-tailed deer, fallow deer, red deer, reindeer)	abomasum	Holarctic
O. muraschkinzevi sp. inq. (syn. *O. nemorhaedi, Grosspiculagia, Camelostrongylus*, *Longistrongylus*)	Artiodactyla: bovid (Himalayan goral)		Eurasia
O. nianqinqtanggulaensis (syn. *Grosspiculagia*, *Camelostrongylus*, possibly *Sarwaria*)	Artiodactyla: bovid (sheep, goat)		Eurasia
O. oreamni	Artiodactyla: bovid (mountain goat), cervid (reindeer)		Holarctic
O. ostertagi (brown stomach worm, medium stomach worm) (syn. *O. caprae, Strongylus*)	Artiodactyla: bovid (cattle, Bali cattle, American bison, European bison, sheep, bighorn sheep, Dall sheep, argali, goat, mouflon, Cyprus mouflon, mountain goat, chamois, alpine ibex, Iberian ibex, Cuvier's gazelle, rhim gazelle, kudu, southern reedbuck), antilocaprid (pronghorn), camelid (llama), cervid (roe deer, red deer, Spanish red deer, mule deer, fallow deer, white-tailed deer, sika deer, reindeer, moose); Perissodactyla: equid (horse); Primates: hominid (human)	abomasum/stomach [diarrhoea, illthrift, type I and II diseases]	worldwide, esp. temperate zones
O. oxidentalis	Artiodactyla: bovid (goat)		Eurasia
O. paleobisonica (syn. *Skrjabinagia*)	Artiodactyla: bovid (frozen prehistoric bison)		Russia
O. ryjikovi	Artiodactyla: bovid (goat, sheep), cervid (fallow deer)		Europe
O. spiculoptera	Artiodactyla: cervid (red deer)		Europe
O. triquetra	Artiodactyla: bovid (grey rhebok)		Africa
O. turkestanica	Artiodactyla: bovid (sheep)		Middle-East
Re-assigned species			
O. aegagri (now *Grosspiculagia*)	Artiodactyla: bovid (sheep, Bezoar goat)		Europe
O. argunica (now *Camelostrongylus*)	Artiodactyla: bovid (sheep)		Europe
O. asymmetrica (syn. *quadrispiculata*)	Artiodactyla: cervid (fallow deer)		Europe

(now *Spiculopteragia*)			
O. belockani (now *Marshallagia*)	Artiodactyla: bovid (wild goat)		Russia
O. bisonis (syn. *O. orloffi, bellae, kazakhstanica*, *Camelostrongylus*) (now *Orloffia*)	Artiodactyla: bovid (cattle, American bison, sheep. Barbary sheep), antilocaprid (pronghorn), cervid (mule deer, moose)	abomasum	North America
O. bubalis (now *Sarwaria*)	Artiodactyla: bovid (cattle)		South America
O. bullosa (now *Pseudostertagia*)	Artiodactyla: antilocaprid (pronghorn), cervid (mule deer), bovid (sheep, bighorn sheep)	abomasum	North America
O. butschnevi (syn. *Skrjabinagia*, *Marshallagia*) (now *Camelostrongylus*)	Artiodactyla: bovid (sheep)		Eurasia
O. dahurica (syn. *O. hsiungi, Orloffia buriatica*) (now *Orloffia*)	Artiodactyla: bovid (goat, sheep, cattle)	abomasum	Asia
O. erschovi (now *Camelostrongylus*)	Artiodactyla: bovid (sheep)		Europe
O. elongata (now *Pseudomarshallagia*)	Artiodactyla: bovid (sheep)		Africa
O. gansuensis (now *Grosspiculagia*)	Artiodactyla: bovid (sheep)		Asia
O. kenyensis (now *Hamulonema*)	Artiodactyla: bovid (Damara dik-dik, Grant's gazelle)		Africa
O. lanceata (now *Grosspiculagia*)	Artiodactyla: bovid (bharal)		Asia
O. marshalli (syn. *O. brigantiaca*, *O. tricuspis*) (now *Marshallagia*)	Artiodactyla: bovid (mountain goat, sheep, bighorn sheep, chamois, Pyrenean chamois)	abomasum, duodenum	Europe, North America
O. mentulata (now *Camelostrongylus*)	Artiodactyla: camelid (dromedary), bovid (rhim gazelle)		Middle-East, Africa
O. mongolica (now *Marshallagia*)	Artiodactyla: bovid (goat, sheep, antelope)		Eurasia
O. ningshaanensis (now *Grosspiculagia*)	Artiodactyla: bovid (takin)		Asia
O. odocoilei (now *Mazamastrongylus*)	Artiodactyla: cervid (white-tailed deer)		North America
O. okapiae (now *Bergheia*)	Artiodactyla: giraffid (okapi)		Eurasia
O. ransomi (now *Delicata*)	Cingulata: chlamyphorid (southern naked-tailed armadillo)		South America
O. sogdiana (now *Marshallagia*)	Artiodactyla: bovid (goat)		Russia
O. trifida (now *Marshallagia*)	Artiodactyla: bovid (sheep, argali, goat, goitered gazelle, steppe saiga), camelid (dromedary)		Asia

Several other *Ostertagia* spp. described in ruminants (*O. bakuriani, O. murmani, O. petrovi, O. tatiani, O. tundra,* and *O. volgaensis*) are considered *species inquirenda* as their descriptions appear to be based on teratologically changed specimens (esp. with respect to spicule and bursa morphology). Several species prevalent in sheep have also been transferred to the genus *Teladorsagia;* notably *T. circumcincta*; *T. davtiana* and *T. trifurcata* (indeed, these 3 species possibly represent a pleomorphic species complex).

Parasite morphology: *Ostertagia* spp. form 3 different stages in their developmental cycles: eggs; larvae (moulting through 4 consecutive stages termed L1 to L4); and adult worms (males and females). Freshly laid eggs have a symmetrical ellipsoidal shape and range in size from 60-100 x 38-50 µm. They are thin-walled and contain a morula (8-16 cell stage) that almost fills the egg. First-stage larvae (L1) are elongate measuring from 300-500 µm in length and have rounded heads and conical pointed tails. L1

have a small buccal capsule and rhabditiform (bulbed) oesophagus used to feed on free-living bacteria. They moult to form L2 which are also free-living rhabditiform larvae but are longer (up to 750 μm). In turn, they moult to form infective L3 which are ensheathed (retain the L2 cuticle) and are thus non-feeding stages. L3 measure from 850-928 μm in length and have a squared head, strongyliform (flask-shaped) oesophagus, intestines comprising 16 cells, the gut ending in a single terminal cell, and a smooth sharply-tapering tail with a short tail sheath extension (45-83 μm) of which the last 10% may be filamentous. Once ingested, L3 exsheath and invade gastric glands where they moult to form L4 almost 1 mm long (some of which may exhibit developmental arrest). Eventually, they re-emerge to the gut lumen and moult to form young adult worms (sometimes designated L5) which mature and mate. Adults are long slender worms ranging in length from 6-15 mm and are brown to red in colour. They have a small cephalic vesicle with a tiny buccal cavity lacking teeth (neodont formation absent). Worms are bound by well-developed cuticular synlophes whose anterior regions have transverse striations while the rest of the body have numerous longitudinal ridges. Adults lack an excretory notch (present in the genus *Trichostrongylus*) and they have 2 small cervical papillae projecting above the body surface (but smaller and located more posteriorly than in the genus *Haemonchus*). They have a strongyliform oesophagus leading to elongate intestines ending in a subterminal anus/cloaca. Adult worms are sexually dimorphic, with females being larger than males (8-15 x 0.14 mm compared to 6-9 x 0.12 mm). Mature females are didelphic with 2 ovaries connected to uteri opening into posterior vulva often covered by small skirt-like flap (unlike the large and prominent vulva flap in *Haemonchus*). Female tails have a small number of annular cuticular bands at the tip but they lack a terminal spine. Mature males have a large copulatory bursa with 2 large lateral lobes and a symmetrical dorsal lobe (cf. asymmetrical in *Haemonchus*). The lateral lobes have 5 lateral rays (comprising muscular elements following nerve channels to terminal papillae) arranged in a 2-1-2 configuration (ventral rays together, anterolateral ray separate, mediolateral and posterolateral rays together). The bursa has an enlarged proconus, and the genital cone has 2 lobes with short dorsal raylets associated with a simple accessory membrane. Males also possess a gubernaculum and have 2 large well-sclerotized spicules usually curved with short branches and barbed tips. Early studies considered spicule morphology to be distinctive for individual *Ostertagia* spp. (e.g. stout and rod-like with expanded tips in *O. ostertagi*, robust and rectangular in *O. lyrata*, or stout and branched near the middle in *O. trifurcata*), but recent studies have indicated that different morphological types ('morphs') may occur within several *Ostertagia* spp.

Site of infection: Infective larvae (L3) invade the gastric pits and glands of their ungulate hosts, mainly in the fundus and pylorus of the abomasum, where they moult to L4 before re-emerging onto the mucosal surface to moult and mature into adult worms. Pastures become contaminated with larvae that hatch from worm eggs voided with host faeces.

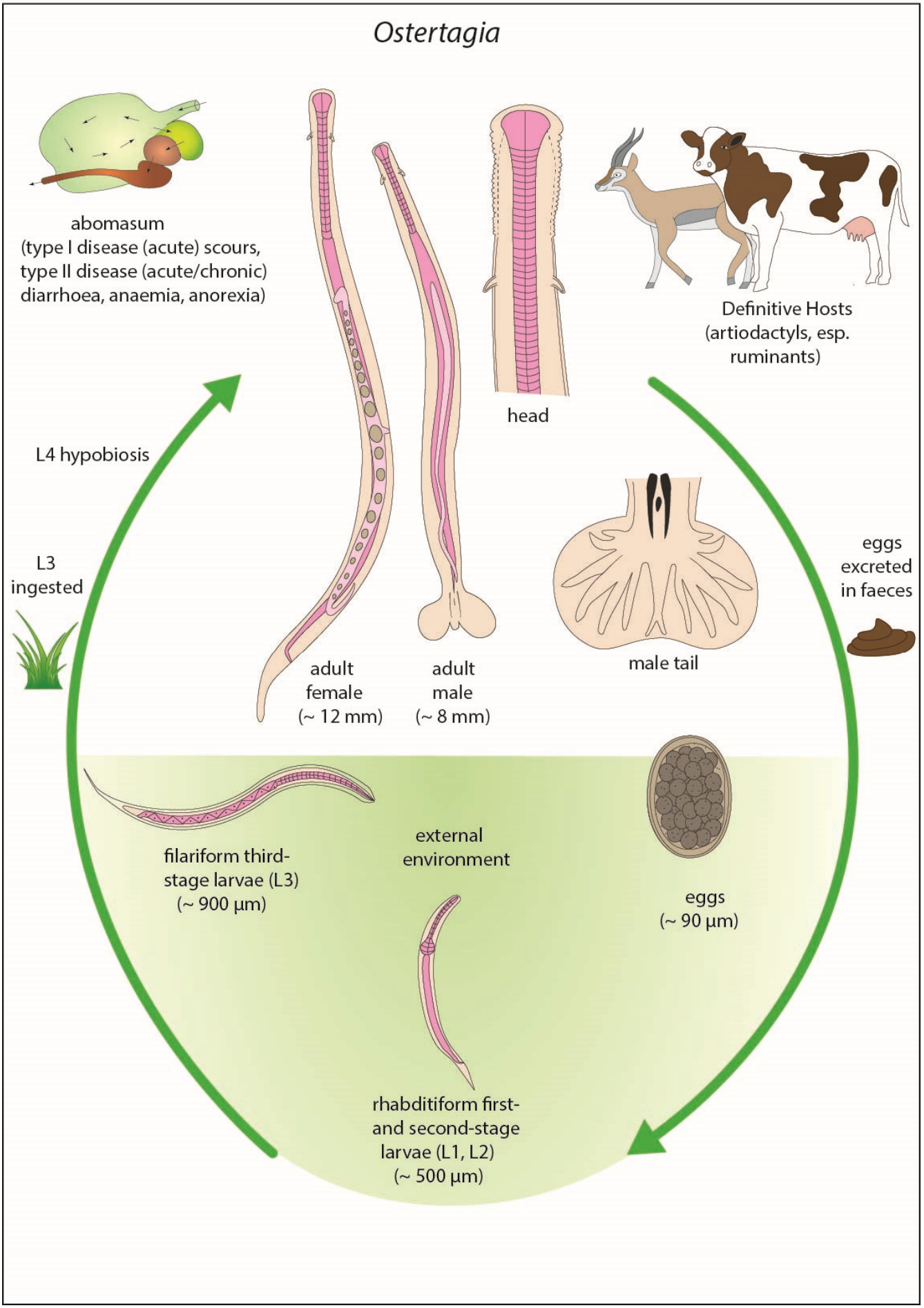
Pathogenesis: Infections by *Ostertagia* spp. may be subclinical but are frequently associated with clinical disease in susceptible grazing animals. While adult worms live on the surface of the abomasum and feed on host blood, most damage is caused by earlier larval stages penetrating, developing and re-emerging from the mucosa resulting in extensive structural and functional changes. L3 invade the gastric pits and glands of the abomasum where they moult and develop to L4 which cause small space-occupying lesions evident as white raised umbilicated nodules 1–2 mm in diameter. Most nodules occur in the fundic region, but they may extend over the whole abomasal mucosa. They are usually found as discrete isolated lesions, but tend to coalesce in heavy infections giving the mucosa a cobblestone appearance. The larvae cause pressure necrosis in the glandular epithelium resulting in hyperplasia (initially focal but becoming more generalized over time) and metaplasia with rapid turnover of mucosal cells. There is a marked loss of zymogen (Chief) cells (which produce pepsinogen) and parietal cells (which produce hydrochloric acid) and they are replaced by rapidly dividing undifferentiated mucus neck cells. The reduction in acid production causes the abomasal pH to rise (from 2 to 7) so pepsinogen is not activated to pepsin and food digestion is impaired. The ensuing maldigestion and rapid transit of poorly processed digesta manifest as watery diarrhoea with loss of body condition. The integrity of the mucosal lining is also compromised as cells in affected glands lose their tight intercellular junctions resulting in the leakage of fluids and proteins into tissues, the circulation and the gut lumen. Such leakage causes local oedema in the abomasum, sometimes extending into the small intestine, as well as generalized oedema with ascites (fluid accumulation in the abdomen) and bottlejaw (submandibular oedema). Collectively, these changes produce a protein-losing gastroenteropathy (PLGE) with malabsorption and watery diarrhoea presenting as scours (with 'dagginess' in sheep and 'dirty-tail' in cattle). The increased abomasal pH stimulates gastrin production, resulting in hypergastrinaemia which exacerbates inappetence and weight loss. Changes in the abomasal environment diminish its bacteriostatic activity leading to bacterial overgrowths and diarrhoea. Adult worms feed on host blood through the mucosa, often causing small petechial haemorrhages with blood loss and progressive anaemia. The combination of diarrhoea, malabsorption, hypoproteinaemia and anaemia results in reduced growth rates, inappetence, anorexia, loss of body condition, emaciation, and even death. Infections contribute to significant production losses (meat, milk, fibre) due to host morbidity, mortality and even reduced reproductive performance. Infections may cause 2 types of disease: most producing type I ostertagiasis (an acute disease occurring several weeks after infection); and some causing type II ostertagiasis in cattle (acute or chronic disease occurring months after infection). Type I disease occurs when larvae undergo normal uninterrupted development in the gastric glands and emerge approximately 18 days after infection. It often occurs in weaners grazing pastures for the first time and is characterised by persistent scours (profuse watery green-coloured diarrhoea) with soiled hindquarters, dull rough coats, bottle jaw and anaemia. It usually occurs simultaneously in many animals (reflecting their common exposure) and is associated with high morbidity but low mortality. Type II disease occurs mostly in cattle when L4 undergo prolonged arrested development (hypobiosis) in gastric glands, eventually emerging (often synchronously) several months later in yearlings. Disease may be acute (profuse diarrhoea, rapid loss of condition, dehydration and often death) or more chronic (progression of signs over several weeks, with intermittent diarrhoea, excessive thirst, anaemia, anorexia, weight loss). It generally occurs only in a few animals within a herd at once (reflecting the irregular development of

larvae), and is associated with lower morbidity but higher mortality. Type II disease occurs more frequently in beef cattle than in dairy cattle, and it varies in its seasonal occurrence (late winter or spring in cool temperate regions, spring and early summer in warm temperate regions, and autumn in regions with hot dry summers). Both types of disease occur mainly in young animals (weaners and yearlings) due not only to their immunological immaturity but also apparently to active impairment or immunosuppression of particular cellular and humoral responses. Adult animals exposed to low dose infections do eventually acquire strong protective immunity, but usually at a slower rate than that found for other nematodes. There is also some evidence that certain stressors may precipitate disease; particularly parturition, lactation, stock translocations, nutritional changes (both decreased and increased levels) and sudden bad weather.

Developmental cycle and mode of transmission: *Ostertagia* spp. have direct monoxenous life-cycles involving faecal-oral transmission. Gravid females produce 50-200 eggs per day which are passed in host faeces to contaminate the external environment. Eggs embryonate and hatch releasing free-living rhabditiform larvae (L1) which feed on bacteria before moulting. The resultant L2 are also free-living rhabditiform stages that feed before moulting, but in this case, the L3 retain the L2 cuticle as an encapsulating protective sheath. L3 do not feed and have a small closed buccal capsule and a strongyliform oesophagus. Eggs and larvae may survive for long periods in faecal material, but are susceptible to desiccation and temperature extremes. Under warm and moist environmental conditions, L3 may develop in as little as 5 days, but typically take longer under suboptimal conditions (usually 10-14 days). They also exhibit horizontal migration (dispersing out of faecal deposits) and vertical migration (ascending herbage into dew droplets when sunlight levels are low). Infective L3 ingested by grazing hosts exsheath in the stomach and invade the gastric glands in the abomasum where they undergo histotrophic development moulting to L4 and subsequently to young adults (sometimes designated L5) after 9-11 days. Young worms emerge from the gastric glands around 18 days after infection and they feed and complete their development to sexually-mature adults on the mucosal surface. The prepatent period (time from infection to first egg excretion) ranges from 18-28 days. The course of infection by certain *Ostertagia* spp. (mostly in cattle) may be greatly prolonged when developing larvae inhibit or arrest their development for several months, usually as early L4 inside gastric glands. This process is known as hypobiosis and usually occurs over seasons when external environmental conditions are not conducive for parasite development and survival on pastures (over winter or summer in temperate and subtropical regions depending on rainfall patterns). The exact mechanisms governing larval hypobiosis are not known, but may involve host physiological changes in response to seasonal reproduction, day length, climatic variation, level of nutrition, abomasal crowding and developing host immunity. Pregnant animals often exhibit a sharp periparturient rise in worm egg production which leads to heavy larval contamination of pastures around the time their weaning offspring begin grazing. Hypobiosis is by no means a universal feature as it does not occur in regions with more frequent rainfall.

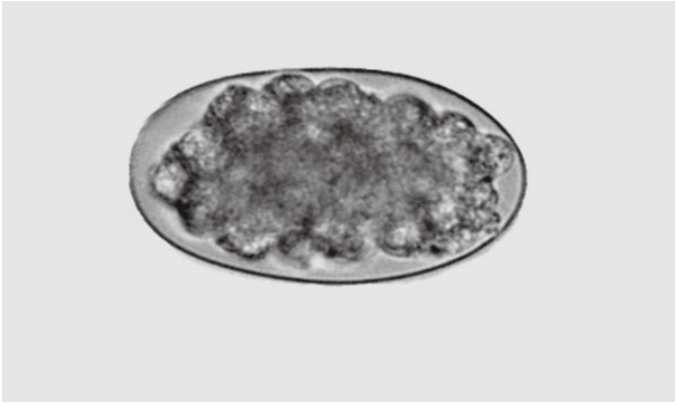
Differential diagnosis: Infections may be strongly indicated on the basis of clinical signs (scours, oedema, anaemia, poor development) and history (appropriate host cohorts, region, season and grazing history), but other aetiological agents may confound diagnosis (notably other gastrointestinal nematodes). Several clinical parameters may provide indirect evidence of infection, including haematology (for progressive anaemia) and blood biochemistry (for hypoalbuminaemia and elevated plasma pepsinogen). There is a strong correlation between the degree of abomasal pathology and the amount of pepsinogen leaking into the circulation, peaking during the course of infection when larvae disrupt mucosal integrity. Coprological tests are best used to confirm infections by the microscopic detection of worm eggs in faecal samples, usually following concentration by sedimentation in water and/or floatation in high specific gravity sugar or salt solutions. Some techniques may be quantitated by counting the number of worm eggs in aliquots of diluted faeces in volumetric McMaster or Whitlock chambers and then calculating the number of eggs per gram of faeces (epg). Faecal eggs counts > 500 epg are often considered to be suggestive for chemotherapeutic intervention, but egg counts do not always correlate well with actual worm burdens as they do not take into account developing larvae, male worms, immature or senescent females or those in which egg production has been reduced by immunological mechanisms, nor hosts experiencing changes in the rate of passage of digesta (egg numbers often higher in diarrhoeic faeces). Clinical signs may also be more evident before egg production occurs (i.e. during the prepatent period) when hosts are infected by developing larvae rather than mature worms. Unfortunately, egg morphometrics cannot be used to differentially diagnose *Ostertagia* infections as their eggs are very similar to those of other trichostrongyle nematodes (particularly *Trichostrongylus*, *Haemonchus* and *Teladorsagia* spp.). For generic diagnosis, recourse is sometimes made to coprocultures whereby faecal material is incubated in funnels or petri dishes for several days to harvest L3 stages which can then be identified by their morphological characteristics (squared head, strongyliform oesophagus, intestines comprising 16 cells, and a tapering tail with a short sheath). Infections may also be diagnosed by the collection and identification of adult worms from gut samples collected at post-mortem from dead or sacrificed animals. Total worm counts may also be conducted by ligating the abomasum and intestines, perfusing them with saline and then counting worm numbers in mucosal washes (and sometimes mucosal digests (warm pepsin-hydrochloric acid) to free larval stages). Several serological tests have been developed to detect specific host antibodies against worm antigens, but problems have been encountered with test sensitivity and specificity, including cross-reactions with other nematodes. Molecular biological techniques have also been used to characterize adult worms, larvae and even eggs of different *Ostertagia* spp. by the polymerase chain reaction (PCR) amplification of specific gene sequences from nuclear DNA (mostly large and small subunit ribosomal DNA and internal transcribed spacers I and II).

Treatment and control: A broad range of anthelmintic drugs have been used to treat livestock with most being effective against adult worms, including benzimidazole-methylcarbamates (albendazole, fenbendazole, oxfendazole, parbendazole), benzimidazole-thiazolyl (thiabendazole), probenzimidazoles (febantel, netobimin, thiophanate), imidazothiazole (levamisole), tetrahydropyrimidine (morantel) and macrocyclic lactones (avermectins such as doramectin, eprinomectin, ivermectin, and milbemycins such as milbemycin and moxidectin). However, only some of these drugs were effective against hypobiotic larvae, including the benzimidazoles (albendazole, fenbendazole, oxfendazole) and macrocyclic lactones (ivermectin, milbemycin) when used at standard dosages, and the probenzimidazole (febantel) when used at higher doses. Anthelmintics do not have any persistent residual activity so to prevent treated animals from quickly becoming re-infected when returned to contaminated pastures, repeat treatments are recommended. Young susceptible animals are generally treated around weaning when they first begin to graze, and are then re-treated after periods when larvae may undergo arrested development (usually as yearlings in the spring/summer in temperate zones, or autumn/winter in subtropical regions). Adult animals are usually not treated as they develop strong protective immune responses. However, the emergence and widespread distribution of drug resistance to benzimidazoles and macrocyclic lactones has presented a significant problem to control programmes. It is recommended that drug resistance testing (faecal egg count reduction tests) be conducted on representative animals to select the most effective drug for mass treatments, that drugs be administered correctly (avoiding under-dosing) and that they be used strategically (as required) or systematically (in cyclic rotation) to avoid the development of drug resistance. Recent studies have also indicated that leaving some animals untreated provides ‘refugia’ for drug-susceptible worms and facilitates low-dose infections for the acquisition of natural protective immunity. Preliminary studies on vaccine development with membrane-bound proteins and excretory-secretory products of *O. ostertagi* have provided some encouraging results with vaccinated animals having lower worm burdens, but sometimes having more hypobiotic larvae. Genetic studies have also shown that individual animals vary in their innate resistance to infection, and experimental breeding programmes have successfully selected some resistant lines of animals without compromising production parameters. Various biological control strategies are under investigation, including seeding pastures with nematode-trapping fungi, and providing supplementary feed rich in tannins. However, the most effective control programmes at the farm level include stock and pasture management practices shown to reduce environmental contamination by worm eggs and decrease the development and survival of larvae on pastures. Treated animals should be immediately moved to clean areas (spelled or recently ungrazed pastures), new livestock should be treated in quarantine, different cohorts should be grazed sequentially or in rotation but young susceptible animals should be separated from adults, stocking rates should be kept low where possible, different host species may be grazed together (mixed grazing) or alternately (e.g. sheep one year, cattle the next), and pastures should be spelled periodically, particularly over adverse seasons (e.g. hot summers).


Ostertagia
abomasum
(type I disease (acute) scours,
type II disease (acute/chronic)
diarrhoea, anaemia, anorexia)
head
Definitive Hosts
(artiodactyls, esp.
ruminants)
L4 hypobiosis
L3
ingested
eggs
excreted
in faeces
adult
female
(~ 12 mm)
adult
male
(~ 8 mm)
male tail
external
environment
filariform third-
stage larvae (L3)
(~ 900 µm)
eggs
(~ 90 µm)
rhabditiform first-
and second-stage
larvae (L1, L2)
(~ 500 µm)



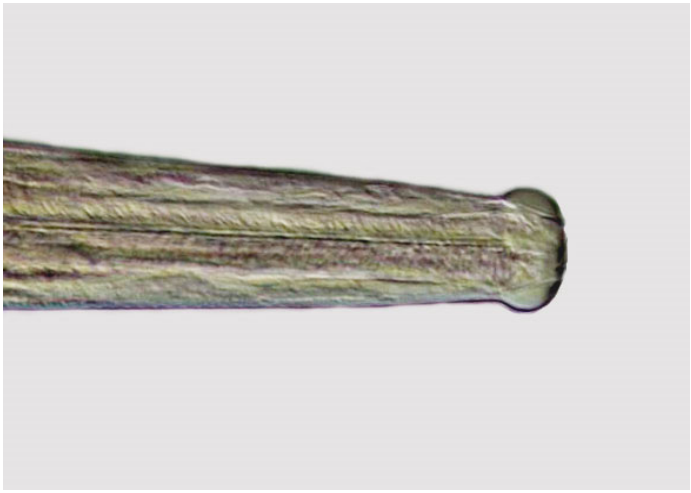
Ostertagia adult worms



Ostertagia worm egg



Ostertagia adult worm, male bursa



Ostertagia adult worm, head

Teladorsagia
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the trichostrongyles which are small hair-like worms with a small buccal capsule. Adults are usually found in the stomach/abomasum or small intestines of mammals or birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 (some may undergo arrested development, termed hypobiosis) before returning to the lumen to moult into adults. *Teladorsagia* spp. (brown stomach worms) cause diarrhoeal diseases markedly impacting production in sheep worldwide. Considerable efforts are made to control infections through chemical interventions (drenching), husbandry and environmental management.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Trichostrongylidae (hair-like, lips absent/reduced, oesophagus lacking bulb, thin-shelled eggs, direct cycles)
Genus:	*Teladorsagia* (parasitic in abomasum of ruminants)
Species:	*T. circumcincta* causes scours and illthrift in sheep and goats

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IH)
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61

Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

The family Trichostrongylidae contains small hair-like worms that infect the gastrointestinal tracts of herbivorous animals, many species causing disease and production losses in ruminant livestock worldwide. Adult worms have a rudimentary buccal cavity with reduced or absent lips but some taxa possessing teeth. Male worms have a well-developed bursa and spicules, and the larger female worms lay thin-shelled eggs that are in the morula stage. Trichostrongyles have direct life-cycles whereby eggs embryonate and hatch in the external environment releasing rhabditiform larvae which grow in soil or on vegetation. These larvae moult to form infective filariform larvae (L3) which are ingested by grazing animals. Various anatomical features have been used to characterize taxa, including patterns of longitudinal ridges (synlophe) on the external cuticular surface as well as structure of the male bursa (arrangement of dorsal, ventral and lateral lobes and supporting rays) and spicules (number, size and shape). Over 50 trichostrongylid genera have been allocated to 8 subfamilies: Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules, 6 genera in mammals and birds); Amidostomatinae (with buccal teeth or extra-buccal appendages, 8 genera in birds); Filarinematinae (neodont formation, long bursa, 3 genera in marsupials); Haemonchinae (well-developed synlophe, neodont formation, 5 genera in ungulates); Ostertagiinae (well-developed synlophe, modified bursa, 15 genera in mammals); Cooperiinae (symmetrical synlophe, bursa with symmetrical dorsal rays, 12 genera in ruminants); Libyostrongylinae (without synlophe, modified bursa, 5 genera in mammals and birds); and Obeliscoidinae (without synlophe, symmetrical bursa, 5 genera in mammals and birds). Note that some taxonomic classifications have split these 8 subfamilies between 3 separate sister families: with Trichostrongylinae, Amidostomatinae and Filarinematinae allocated to a restricted Trichostrongylidae (cephalic vesicle absent, synlophe reduced or absent, male bursa with short dorsal ray and long lateral lobes); Haemonchinae and Ostertagiinae assigned to the Haemonchidae (cephalic vesicle absent, synlophe present without any specific orientation, male bursa with short dorsal rays, often asymmetrical); and Cooperiinae, Libyostrongylinae and Obeliscoidinae placed in the Cooperiidae (cephalic vesicle present, synlophe bilaterally symmetrical or absent, large male bursa with curved lateral rays). Several other genera have recently been transferred to other taxa on the basis of cladistic or molecular phylogenetic studies; mostly those in the subfamily Nematodirinae (6 genera in mammals) now classified in the family Molineidae. Specific trichostrongylid genera of veterinary and medical importance are compared in the following table.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Subfamily Ostertagiinae (well-developed synlophe, modified bursa)					
Teladorsagia (brown stomach worm)	9	artiodactyls	abomasum	10-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-2-1) and proconus, larval hypobiosis	60-100 x 40-50 µm, ellipsoidal, thin-shelled
Ostertagia	32	artiodactyls	abomasum	6-15 mm long, small buccal cavity, ridged	60-100 x 38-50 µm,

(brown stomach worm)				synlophe, small vulval flap, bursa with 5 lateral rays (2-1-2) and proconus, larval hypobiosis	ellipsoidal, thin-shelled
Hyostrongylus (red stomach worm)	4	suids, lagomorphs	stomach	4-10 mm long, red coloration, well-developed bursa, gubernaculum, telamon, larval hypobiosis	60-90 x 31-42 µm, ovoid, thin-shelled
Subfamily Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules)					
Trichostrongylus (hairworm, black scour worm)	56	artiodactyls, lagomorphs, rodents, birds	small intestines, stomach	2-10 mm long, rudimentary buccal cavity, distinct excretory notch in oesophageal region, male bursa with long lateral lobes	75-125 x 31-72 µm, ellipsoidal, thin-shelled
Subfamily Haemonchinae (well-developed synlophe, neodont formation)					
Haemonchus (barber's pole worm)	15	artiodactyls	abomasum	10-40 mm long, buccal capsule with tooth, white spiral ovaries, prominent vulval flap, bursa with asymmetrical dorsal ray, larval hypobiosis	62-90 x 40-50 µm, ellipsoidal, thin-shelled
Subfamily Cooperiinae (symmetrical synlophe, bursa with symmetrical rays)					
Cooperia (wire worm)	24	artiodactyls	small intestines, stomach	4-15 mm long, often coiled, bulbous cephalic vesicle, large bursa, large spicules, larval hypobiosis	65-95 x 29-44 µm, ellipsoidal, thin-shelled

The subfamily Ostertagiinae was erected for genera with an accessory bursal membrane and other characters include a head region with a small restricted cephalic vesicle, small cervical papillae and prominent transverse striations, and a body with numerous longitudinal cuticular ridges. Some 23 genera have been reported from ruminants, hippopotami, lagomorphs and suids: namely, *Africanostrongylus, Apteragia, Camelostrongylus, Cervicaprastrongylus, Graphidium, Grosspiculagia* (syn. *Ostertagiella*), *Hamulonema, Hyostrongylus* (syn. *Bergheia*), *Longistrongylus* (syn. *Bigalkea, Bigalkenema, Kobusinema*), *Marshallagia, Mazamastrongylus, Orloffia, Ostertagia* (syn. *Capreolagia, Gruhneria, Muflonagia, Ostertagiana, Sjobergia, Skrjabinagia*), *Ostertamia, Paramecistrocirrus, Pseudomarshallagia, Rinadia, Robustostrongylus, Sarwaria, Spiculopteragia* (syn. *Altaevia*), *Spiculopteroides, Teladorsagia* (syn. *Paramecistocirrus*, *Stadelmania*), and *Tunisostertagia.* Some members of the Ostertagiinae have been allocated to 2 groups; one characterised by bursal type 2-1-2 (ray 2 grouped with ray 3, isolation of ray 4, ray 5 grouped with ray 6) including *Graphidium*, *Marshallagia*, *Longistrongylus* and *Ostertagia*; and another characterised by bursal type 2-2-1 (ray 2 grouped with ray 3, ray 4 grouped with ray 5, isolation of ray 6) including *Hyostrongylus*, *Spiculopteragia*, *Teladorsagia* and *Gazellostrongylus*. The genus *Teladorsagia* is further characterised by bursate males with a symmetrical dorsal lobe, a small proconus, spicules with sharply pointed branches, and a genital cone with a Sjoberg organ or short dorsal raylets associated with the accessory membrane. Some 9 species have been described from bovids, camelids and cervids, where they have direct life-cycles with faecal-oral transmission. Several species formerly recorded as *Ostertagia* spp. have been transferred to the genus *Teladorsagia* on the basis of phenotypic and genotypic studies; notably *T. circumcincta*; *T. davtiana* and *T. trifurcata* in sheep (in fact, these 3 species possibly represent a pleomorphic species complex). Worms developing and feeding in the abomasal mucosa may cause disease in weaners and the later emergence of dormant larvae may cause disease in young adults. Infections contribute to significant economic losses in livestock industries through morbidity, mortality and reduced production (meat, milk, fibre). Several species are important pathogens in sheep and goats in all temperate regions, particularly those with high rainfall.

***Teladorsagia* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
T. boreoarcticus	Artiodactyla: bovid (muskox, Greenland muskox), cervid (reindeer, barren ground caribou)		Holarctic
T. circumcincta (brown stomach worm) (syn. *Ostertagia, Ostertagiella, Stadelmania, Strongylus, S. vicarius, cervicornis p.p., instabilis, turkestanica*)	Artiodactyla: bovid (cattle, muskox, sheep, bighorn sheep, Dall sheep, argali, mouflon, Cyprus mouflon, goat, mountain goat, chamois, Pyrenean chamois, alpine ibex, Iberian ibex, antelope, common tsessebe, common duiker, red forest duiker, bushbuck, Cuvier's gazelle, Cape grysbok), antilocaprid (pronghorn), camelid (camel, llama), cervid (roe deer, red deer, mule deer, southern mule deer, white-tailed deer, black-tailed deer, reindeer, Svalbard reindeer, mountain reindeer, boreal woodland caribou, barren ground caribou, moose); Rodentia: murid (Mongolian gerbil); Primates: hominid (human)	abomasum [weight loss, diarrhoea]	worldwide
T. dactylospicula (syn. *Skrjabinagia*)	Artiodactyla: bovid (cattle)	abomasum	Asia

T. davtiani (syn. *T. grigoriani*) (considered by some to be a morphological variant of *T. circumcincta*)	Artiodactyla: bovid (sheep, bighorn sheep, Dall sheep, goat, mountain goat, chamois, Iberian ibex, Cuvier's gazelle, muskox), cervid (mule deer, roe deer, reindeer)	abomasum [weight loss, diarrhoea]	worldwide
T. kasakhstanica (syn. *Ostertagia*)	Artiodactyla: bovid (American bison)		North America
T. kegeni	Artiodactyla: bovid (sheep)		Eurasia
T. pinnata (syn. *Ostertagia*)	Artiodactyla: bovid (sheep, mouflon, chamois, alpine ibex, Iberian ibex), cervid (roe deer)		Europe
T. trifurcata (syn. *Ostertagia, Stadelmania*) (considered to be a morphological variant of *T. circumcincta*)	Artiodactyla: bovid (cattle, water buffalo, muskox, Greenland muskox, sheep, bighorn sheep, Dall sheep, argali, mouflon, chamois, Pyrenean chamois, goat, mountain goat, alpine ibex, Iberian ibex), antilocaprid (pronghorn), cervid (roe deer, red deer, fallow deer, mule deer, white-tailed deer, reindeer, Svalbard reindeer, boreal woodland caribou), camelid (llama)	abomasum [weight loss, diarrhoea]	worldwide
T. vietnamica (syn. *Spiculopteragia, Spiculopteroides, Mazamastrongylus*)	Artiodactyla: cervid (Indian muntjac)		Asia
Re-assigned species			
T. hamata (syn. *Ostertagia, Spiculopteragia, Apteragia, Teladorsagia*) (now *Hamulonema*)	Artiodactyla: bovid (springbok, bontebok, Speke's gazelle, gemsbok, grey rhebok)		Africa
T. peruvianus (syn. *Spiculoperagia*) (now *Mazamastrongylus*)	Artiodactyla: camelid (alpaca, vicugna, guanaco)		South America
T. pursglovei (now *Mazamastrongylus*)	Artiodactyla: cervid (white-tailed deer)		North America

Parasite morphology: *Teladorsagia* spp. form 3 different morphological stages in their developmental cycles: eggs; larvae (4 consecutive stages termed L1 to L4); and adult worms. Newly laid eggs have a symmetrical ellipsoidal shape and range in size from 60-100 x 40-50 µm. They are thin-walled and contain a morula (8-16 cell stage) that almost fills the egg. First-stage larvae (L1) are 300-500 µm long and have a rounded head, a bulbed (rhabditiform) oesophagus, and a conical pointed tail. They moult to form L2 which are also rhabditiform but are slightly bigger measuring up to 750 µm in length. These larvae moult to form L3 which retain the L2 cuticle as a close-fitting protective sheath. Infective L3 measure from 797-910 µm in length and have a round head, tubular (strongyliform) oesophagus, intestines comprising 16 cells, and a sharply-tapering tail with a short non-filamentous tail sheath extension (30-60 µm). Following ingestion, L3 exsheath and moult in gastric glands to form L4 around 1 mm long. Eventually, L4 emerge onto the mucosal surface and moult to form young adult worms (sometimes designated L5) which mature and mate. Adults are elongate slender worms 10-15 mm in length and usually appearing brown to red in colour. They have a small cephalic vesicle with a tiny buccal cavity lacking teeth (neodont formation absent). Worms are bound by well-developed cuticular synlophes whose anterior regions have transverse striations while the rest of the body have numerous longitudinal ridges. Adults lack an excretory notch (present in the genus *Trichostrongylus*) but they have 2 small cervical papillae projecting above the body surface (smaller and located more posteriorly than in the genus *Haemonchus*). They have a strongyliform oesophagus leading to elongate intestines ending in a subterminal anus/cloaca. Adult worms are sexually dimorphic, with females being larger than males. Mature males have a large copulatory bursa with 2 large lateral lobes and a small symmetrical dorsal lobe (cf. asymmetrical in *Haemonchus*). The lateral lobes have 5 lateral rays (comprising muscular elements following nerve channels to terminal papillae) arranged in a 2-2-1 configuration (ventral rays together, anterolateral and mediolateral rays close together, and posterolateral rays separate). The genital cone has a small proconus (ventral swelling) and a small accessory bursal membrane. Detailed studies have also shown that male worms of several species may exhibit different morphological types ('morphs') whereby the genital cone may simply be supported by 2 divergent rays (e.g. *T. circumcincta*) or modified to form Sjoberg's organ resembling a pair of posterior sessile papillae (e.g. *T. davtiani, T. trifurcata*). Males also possess a gubernaculum with a telamon and 2 spicules which vary in shape (long and thin or short and broad) but whose posterior ends are split into 2-3 pointed processes (crab-claw like). Mature females are didelphic with 2 ovaries connected to uteri opening into a posterior vulva covered by medium-sized flap (unlike the large and prominent vulva flap in *Haemonchus*). Female tails have a small number of annular cuticular bands at the tip but they lack a terminal spine.

Site of infection: Adult worms occur on the mucosal surface of the abomasum of their ruminant hosts, while developing larvae infect the gastric pits and glands. Pastures become contaminated with worm eggs which release free-living larvae that eventually become infective for grazing animals.

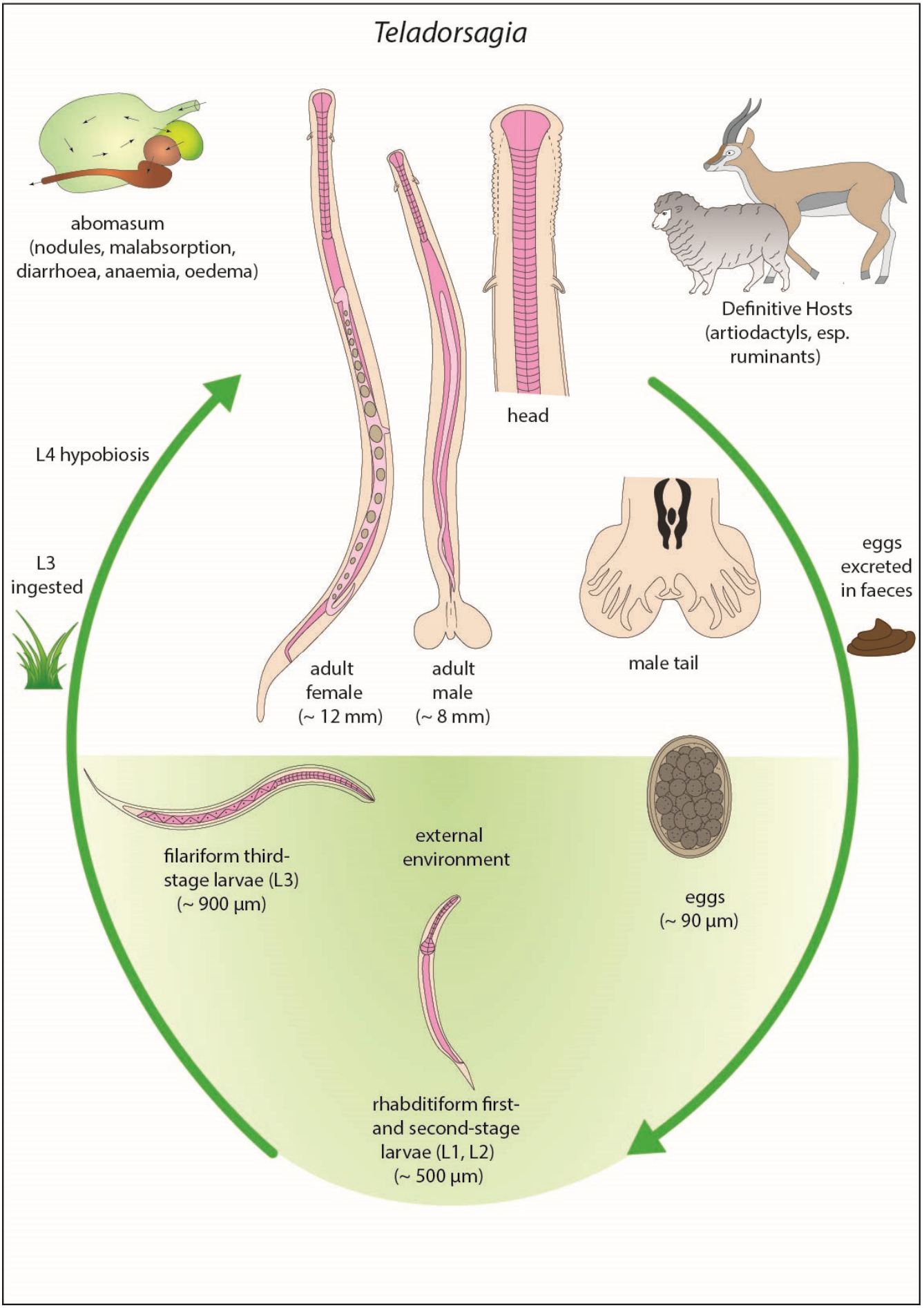
Pathogenesis: Infections by *Teladorsagia* spp. are a significant cause of diarrhoea and ill-thrift in sheep and goats around the world, particularly in cool temperate regions. Light-moderate infections may be symptomatic but still cause subclinical production losses, while heavier infections (> 10,000 worms) may cause severe disease in young susceptible animals (due to their immunological immaturity). While adult worms live on the surface of the abomasum and feed on host blood, most damage is caused by earlier larval stages penetrating, developing and re-emerging from the mucosa resulting in extensive structural and functional changes. L3 invade the gastric pits and glands of the abomasum where they moult and develop to L4 which cause small space-occupying lesions evident as white raised umbilicated nodules 1–2 mm in diameter, each nodule having a central opening. Sometimes the nodules become confluent and covered with tenacious mucus. The abomasal mucosa becomes inflamed and hyperaemic (diffuse hyperplastic abomasitis), sometimes with small abscesses or scar tissue in the gastric pits (rarely imparting a leathery cobblestone appearance). The larvae cause pressure necrosis in the glandular epithelium resulting in hyperplasia and metaplasia with rapid turnover of mucosal cells. There is a marked loss of zymogen (Chief) cells (which produce pepsinogen) and parietal cells (which produce hydrochloric acid) and they are replaced by rapidly-dividing undifferentiated mucus neck cells. The reduction in acid production causes the abomasal pH to rise (from 2 to 7) so pepsinogen is not activated to pepsin and food digestion is impaired. The integrity of the mucosal lining is also compromised as cells in affected glands lose their tight intercellular junctions resulting in the leakage of fluids and proteins into tissues, the circulation and the gut lumen. Such leakage causes local oedema in the abomasum, sometimes extending into the small intestine, as well as generalized swellings such as submandibular oedema (bottle jaw), anasarca and ascites (particularly in Angora goats). Collectively, these changes produce a protein-losing gastroenteropathy (PLGE) with maldigestion and malabsorption leading to an intermittent diarrhoea with hindquarter staining ('dagginess' in sheep and 'dirty-tail' in cattle). The increased abomasal pH stimulates the production of gastrin resulting in hypergastrinaemia which exacerbates inappetence and weight loss. Changes in the abomasal environment diminish its bacteriostatic activity leading to bacterial overgrowths and diarrhoea. Adult worms feed on host blood through the mucosa, often causing small petechial haemorrhages with blood loss and progressive anaemia. The combination of diarrhoea, malabsorption, hypoproteinaemia and anaemia in small ruminants results in reduced growth rates, inappetence, anorexia, loss of body condition, emaciation, and even death. Infections contribute to significant production losses (meat, milk, fibre) due host morbidity, mortality and even reduced reproductive performance. Clinical infections generally cause an acute or subacute disease syndrome (termed type I disease) when larvae undergo normal uninterrupted development in the gastric glands emerging 2-3 weeks later. This disease frequently occurs in weaners grazing pastures for the first time and is characterised by marked weight loss with intermittent diarrhoea. However, infections by a few species may sometimes cause a more chronic form of disease (similar to type II ostertagiasis) when larvae undergo short periods of arrested or protracted development in gastric glands emerging several months later (some consider this to be a prolonged histotrophic stage rather than true hypobiosis). This type II syndrome occurs sporadically in young adult animals in temperate and subtropical regions with winter rainfall, and is typified as progressive loss of condition and emaciation. Adult animals exposed to low dose infections do eventually acquire strong protective immunity, but at a slower rate than that found for other nematodes.

Developmental cycle and mode of transmission: *Teladorsagia* spp. have direct monoxenous life-cycles with horizontal transmission occurring between individuals by the faecal contamination of pastures by eggs and the oral ingestion of infective larvae by grazing animals. Females produce 10-200 eggs per day which are passed in host faeces. The eggs embryonate and hatch releasing rhabditiform larvae (L1) which are free-living and feed on bacteria in faecal material. The larvae moult to form rhabditiform L2 which are also free-living and feed on bacteria. These larvae moult to form strongyliform L3 which retain the L2 cuticle as an encapsulating protective sheath and do not feed. Eggs and larvae may survive for long periods in faecal material, particularly in regions with cooler climates, but they are susceptible to desiccation. L3 may develop from eggs in 10-14 days, but may take longer in suboptimal conditions. When moisture is available (following rainfall or morning dew), mature L3 exhibit horizontal migration (dispersing out of faecal deposits) and vertical migration (ascending herbage into water droplets). Infective L3 are ingested on herbage by grazing hosts and they exsheath in the stomach and invade the gastric glands in the abomasum. Here they form nodules and moult to L4 before emerging onto the mucosal surface some 9-11 days later and moulting to young adults which feed and mature. The prepatent period (time from infection to first egg excretion) ranges from 18-21 days, and adult worms live for several months before dying or being expelled by host immune responses. In infections by certain species, some larvae may still be found in the mucosa 8-12 weeks after infection, apparently undergoing arrested development (hypobiosis) although some authorities consider them to be prolonged histotrophic stages. Their delayed development occurs over seasons when external environmental conditions are not conducive for parasite development and survival on pastures (generally over winter in temperate regions). The exact mechanisms involved are not known, but appear to include host reproductive physiology (pregnancy, parturition and lactation), metabolism (level of nutrition), immunity (innate and acquired responses) as well as external environmental conditions (day length, temperature and rainfall patterns). Pregnant animals often exhibit a sharp periparturient rise in worm egg production which leads to heavy larval contamination of pastures around the time their weaning offspring begin grazing.

Differential diagnosis: Infections may be suggested by clinical symptomatology with appropriate history, but other gastroenteric pathogens may cloud diagnoses. Blood biochemistry may show reduced albumin and elevated pepsinogen levels consistent with

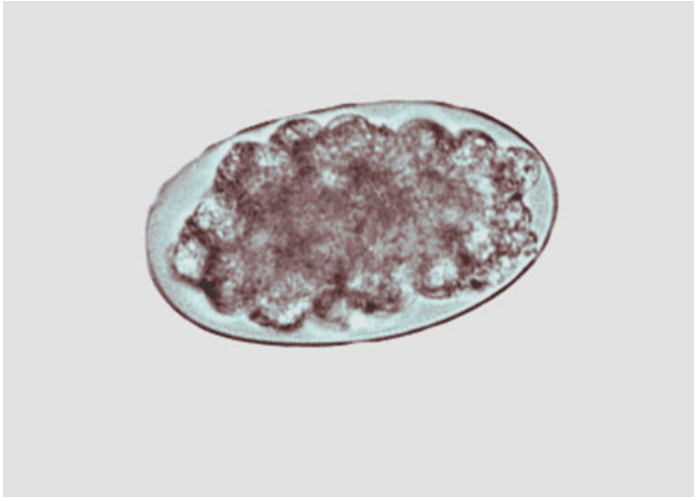
abomasal damage and fluid leakage. While there is a strong correlation between the degree of abomasal pathology and the amount of pepsinogen leaking into the circulation, levels often peak early in the course of infection when only larvae are present. Coprological tests may be used to detect patent infections by the microscopic detection of worm eggs in faecal samples, usually following concentration by sedimentation in water and/or floatation in high specific gravity sugar or salt solutions. Some techniques may be quantitated by counting the number of worm eggs in aliquots of diluted faeces in volumetric McMaster or Whitlock chambers and then calculating the number of eggs per gram of faeces (epg). However, faecal eggs counts do not correlate well with worm burdens as they do not take into account developing larvae, male worms, immature or senescent females or those in which egg production has been reduced by immunological mechanisms. Unfortunately, egg morphometrics cannot be used to differentially diagnose infections as *Teladorsagia* eggs are very similar to those of other trichostrongyle nematodes (particularly *Trichostrongylus*, *Haemonchus* and *Ostertagia*). Recourse is sometimes made to coprocultures whereby faecal material is incubated in funnels or petri dishes for several days to harvest L3 stages which can then be identified by their morphological characteristics (squared head, strongyliform oesophagus, intestines comprising 16 cells, and a tapering tail with a short sheath). Infections may also be diagnosed by the collection and identification of adult worms from gut samples collected at post-mortem from dead or sacrificed animals. Total worm counts may also be conducted by ligating the abomasum and intestines, perfusing them with saline and then counting worm numbers in mucosal washes (and sometimes mucosal digests (warm pepsin-hydrochloric acid) to free larval stages). Several serological tests have been developed to detect specific host antibodies against worm antigens, but problems have been encountered with test sensitivity and specificity, including cross-reactions with other nematodes. Molecular biological techniques have also been used to characterize adult worms, larvae and even eggs of different *Teladorsagia* spp. by the polymerase chain reaction (PCR) amplification of specific gene sequences from nuclear DNA (large and small subunit ribosomal DNA and internal transcribed spacers I and II).

Treatment and control: A broad range of anthelmintic drugs have been used to treat clinical infections in livestock, with most drugs being effective against adult worms, including benzimidazole-methylcarbamates (albendazole, fenbendazole, oxfendazole, parbendazole), benzimidazole-thiazolyl (thiabendazole), probenzimidazoles (febantel, netobimin, thiophanate), imidazothiazole (levamisole), tetrahydropyrimidine (morantel) and macrocyclic lactones (avermectins such as doramectin, eprinomectin, ivermectin, and milbemycins such as milbemycin and moxidectin). However, only some of these drugs were effective against hypobiotic larvae, notably the benzimidazoles (albendazole, fenbendazole, oxfendazole) and macrocyclic lactones (ivermectin, milbemycin). Repeated treatments are required as anthelmintics do not have any persistent residual activity and animals quickly become re-infected when returned to contaminated pastures. Pregnant animals should be treated to avoid a periparturient rise in egg production, and young susceptible animals should be treated around weaning when they first begin to graze, and then re-treated at the end of the season when larval hypobiosis or prolonged development may have occurred (usually late winter or early spring). Adult animals are usually not treated as they gradually acquire strong protective immune responses and show an age-resistance to clinical infection. Regrettably, many countries have now reported the emergence of widespread drug resistance to benzimidazoles and macrocyclic lactones. Authorities recommend that drug resistance testing (faecal egg count reduction tests) be conducted on representative animals to select the most effective drug for mass treatment, that drugs be administered correctly (avoiding under-dosing) and that they are used strategically (as required) or systematically (in cyclic rotation) to avoid the development of drug resistance. Recent work has also shown that leaving some animals untreated provides ‘refugia’ for drug-susceptible worms and facilitates low-dose infections for the acquisition of natural protective immunity. Genetic studies have also shown that individual animals vary in their innate resistance to infection, and experimental breeding programmes have successfully selected some resistant lines of animals without compromising production parameters. However, the most effective control programmes at the farm level include stock and pasture management practices shown to reduce environmental contamination by worm eggs and decrease the development and survival of larvae on pastures. Treated animals should be immediately moved to clean areas (spelled or recently ungrazed pastures), new livestock should be treated in quarantine, different cohorts should be grazed sequentially or in rotation (but young susceptible animals should be kept separate from adults), stocking rates should be kept low, different host species may be grazed together (mixed grazing) or alternately (e.g. sheep one year, cattle the next), and pastures should be spelled periodically, particularly over adverse seasons (e.g. hot summers).

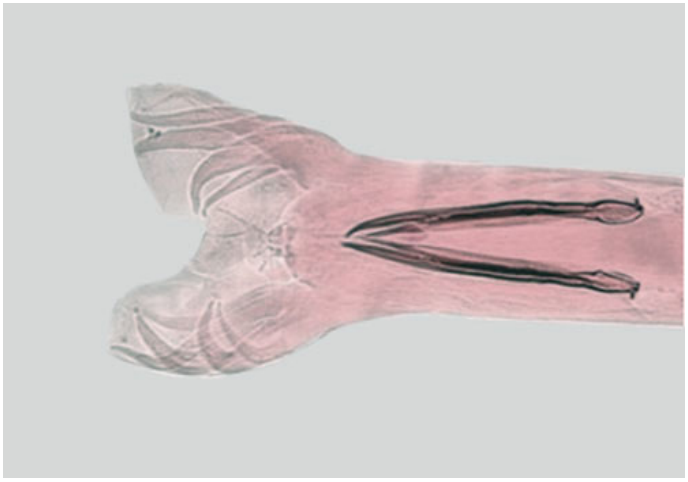

Teladorsagia
abomasum
(nodules, malabsorption,
diarrhoea, anaemia, oedema)
head
Definitive Hosts
(artiodactyls, esp.
ruminants)
L4 hypobiosis
L3
ingested
eggs
excreted
in faeces
adult
female
(~ 12 mm)
adult
male
(~ 8 mm)
male tail
filariform third-
stage larvae (L3)
(~ 900 µm)
external
environment
eggs
(~ 90 µm)
rhabditiform first-
and second-stage
larvae (L1, L2)
(~ 500 µm)



Teladorsagia adult worms



Teladorsagia worm egg



Teladorsagia adult worm, male bursa

Hyostrongylus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the trichostrongyles which are small hair-like worms with a small buccal capsule. Adults are usually found in the stomach/abomasum or small intestines of mammals or birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 (some may undergo arrested development, termed hypobiosis) before returning to the lumen to moult into adults. *Hyostrongylus* (red stomach worm) causes diarrhoea and wasting in pigs, but can be readily controlled in intensive piggeries.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Trichostrongylidae (hair-like, lips absent/reduced, oesophagus lacking bulb, thin-shelled eggs, direct cycles)
Genus:	*Hyostrongylus* (parasitic in stomach of pigs)
Species:	*H. rubidus* causes diarrhoea and wasting in pigs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56

Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

The family Trichostrongylidae contains small hair-like worms that infect the gastrointestinal tracts of herbivorous animals, many species causing disease and production losses in ruminant livestock worldwide. Adult worms have a rudimentary buccal cavity with reduced or absent lips but some taxa possessing teeth. Male worms have a well-developed bursa and spicules, and the larger female worms lay thin-shelled eggs that are in the morula stage. Trichostrongyles have direct life-cycles whereby eggs embryonate and hatch in the external environment releasing rhabditiform larvae which grow in soil or on vegetation. These larvae moult to form infective filariform larvae (L3) which are ingested by grazing animals. Various anatomical features have been used to characterize taxa, including patterns of longitudinal ridges (synlophe) on the external cuticular surface as well as structure of the male bursa (arrangement of dorsal, ventral and lateral lobes and supporting rays) and spicules (number, size and shape). Over 50 trichostrongylid genera have been allocated to 8 subfamilies: Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules, 6 genera in mammals and birds); Amidostomatinae (with buccal teeth or extra-buccal appendages, 8 genera in birds); Filarinematinae (neodont formation, long bursa, 3 genera in marsupials); Haemonchinae (well-developed synlophe, neodont formation, 5 genera in ungulates); Ostertagiinae (well-developed synlophe, modified bursa, 15 genera in mammals); Cooperiinae (symmetrical synlophe, bursa with symmetrical dorsal rays, 12 genera in ruminants); Libyostrongylinae (without synlophe, modified bursa, 5 genera in mammals and birds); and Obeliscoidinae (without synlophe, symmetrical bursa, 5 genera in mammals and birds). Note that some taxonomic classifications have split these 8 subfamilies between 3 separate sister families: with Trichostrongylinae, Amidostomatinae and Filarinematinae allocated to a restricted Trichostrongylidae (cephalic vesicle absent, synlophe reduced or absent, male bursa with short dorsal ray and long lateral lobes); Haemonchinae and Ostertagiinae assigned to the Haemonchidae (cephalic vesicle absent, synlophe present without any specific orientation, male bursa with short dorsal rays, often asymmetrical); and Cooperiinae, Libyostrongylinae and Obeliscoidinae placed in the Cooperiidae (cephalic vesicle present, synlophe bilaterally symmetrical or absent, large male bursa with curved lateral rays). Several other genera have recently been transferred to other taxa on the basis of cladistic or molecular phylogenetic studies; mostly those in the subfamily Nematodirinae (6 genera in mammals) now classified in the family Molineidae. Specific trichostrongylid genera of veterinary and medical importance are compared in the following table.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Subfamily Ostertagiinae (well-developed synlophe, modified bursa)					
Hyostrongylus (red stomach worm)	4	suids, lagomorphs	stomach	4-10 mm long, red coloration, well-developed bursa, gubernaculum, telamon, larval hypobiosis	60-90 x 31-42 µm, ovoid, thin-shelled
Ostertagia (brown stomach worm)	32	artiodactyls	abomasum	6-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-1-2) and proconus, larval hypobiosis	60-100 x 38-50 µm, ellipsoidal, thin-shelled

Teladorsagia (brown stomach worm)	9	artiodactyls	abomasum	10-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-2-1) and proconus, larval hypobiosis	60-100 x 40-50 µm, ellipsoidal, thin-shelled
Subfamily Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules)					
Trichostrongylus (hairworm, black scour worm)	56	artiodactyls, lagomorphs, rodents, birds	small intestines, stomach	2-10 mm long, rudimentary buccal cavity, distinct excretory notch in oesophageal region, male bursa with long lateral lobes	75-125 x 31-72 µm, ellipsoidal, thin-shelled
Subfamily Haemonchinae (well-developed synlophe, neodont formation)					
Haemonchus (barber's pole worm)	15	artiodactyls	abomasum	10-40 mm long, buccal capsule with tooth, white spiral ovaries, prominent vulval flap, bursa with asymmetrical dorsal ray, larval hypobiosis	62-90 x 40-50 µm, ellipsoidal, thin-shelled
Subfamily Cooperiinae (symmetrical synlophe, bursa with symmetrical rays)					
Cooperia (wire worm)	24	artiodactyls	small intestines, stomach	4-15 mm long, often coiled, bulbous cephalic vesicle, large bursa, large spicules, larval hypobiosis	65-95 x 29-44 µm, ellipsoidal, thin-shelled

The subfamily Ostertagiinae was erected for genera with an accessory bursal membrane and other characters include a head region with a small restricted cephalic vesicle, small cervical papillae and prominent transverse striations, and a body with numerous longitudinal cuticular ridges. Some 23 genera have been reported from ruminants, hippopotami, lagomorphs and suids: namely, *Africanostrongylus, Apteragia, Camelostrongylus, Cervicaprastrongylus, Graphidium, Grosspiculagia* (syn. *Ostertagiella*), *Hamulonema, Hyostrongylus* (syn. *Bergheia*), *Longistrongylus* (syn. *Bigalkea, Bigalkenema, Kobusinema*), *Marshallagia, Mazamastrongylus, Orloffia, Ostertagia* (syn. *Capreolagia, Gruhneria, Muflonagia, Ostertagiana, Sjobergia, Skrjabinagia*), *Ostertamia, Paramecistrocirrus, Pseudomarshallagia, Rinadia, Robustostrongylus, Sarwaria, Spiculopteragia* (syn. *Altaevia*), *Spiculopteroides, Teladorsagia* (syn. *Paramecistocirrus*, *Stadelmania*), and *Tunisostertagia.* Some members of the Ostertagiinae have been allocated to 2 groups; one characterised by bursal type 2-1-2 (ray 2 grouped with ray 3, isolation of ray 4, ray 5 grouped with ray 6) including *Graphidium*, *Marshallagia*, *Longistrongylus* and *Ostertagia*; and another characterised by bursal type 2-2-1 (ray 2 grouped with ray 3, ray 4 grouped with ray 5, isolation of ray 6) including *Hyostrongylus*, *Spiculopteragia*, *Teladorsagia* and *Gazellostrongylus*. The bursal characteristics of members of the genus *Hyostrongylus* also include well-developed lateral lobes, a short dorsal lobe (dorsal ray with 3 branches), a genital cone with 2 small dorsal raylets, and elongate tapering spicules. Several species have been described from the stomachs of mammals (artiodactyls, lagomorphs and primates), where developmental stages may damage the mucosa resulting in gastritis, maldigestion, diarrhoea and poor body condition (particularly in free-range pigs infected with *H. rubidus*). The parasites have direct monoxenous life-cycles involving the faecal-oral transmission of larvae on pastures.

***Hyostrongylus* species**	**Definitive hosts**	**Location [Clinical signs]**	**Distribution**
H. rubidus (red stomach worm) (syn. *Strongylus attenuatus, molini, rubida, Ostertagia*)	Artiodactyla: suid (pig), tayassuid (white-lipped peccary), bovid (cattle, sheep, red forest duiker); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig)	stomach [diarrhoea]	worldwide
H. kigeziensis	Primates: hominid (western gorilla, mountain gorilla)		Africa
H. okapiae (syn. *Bergheia*)	Artiodactyla: giraffid (okapi)		Africa
H. vinnica	Artiodactyla: bovid (sheep, cattle)		Russia
Re-assigned species			
H. gabonensis (now *Cervicaprastrongylus*)	Artiodactyla: tragulid (water chevrotain)		Africa
H. malviyai (now *Cervicaprastrongylus*)	Artiodactyla: bovid (blackbuck)		India
H. moreli (now *Cervicaprastrongylus*)	Lagomorpha: leporid (Cape hare)		Africa

Parasite morphology: *Hyostrongylus* spp. form 3 morphologically distinct stages during their development: membrane-bound eggs; fusiform larvae (4 stages coded L1-L4); and sexually dimorphic adults. Gravid females lay thin-walled ovoid eggs ranging in size from 60-90 x 31-42 µm (note that some texts incorrectly give a smaller egg size (45 x 36 µm) found to be due to a scaling error in the original description). Freshly laid eggs are brown in colour and contain a morula (16-64 cell stage) that almost fills the

interior. Eggs hatch releasing free-living (pre-parasitic) first-stage larvae (L1) that initially measure from 280-300 μm but grow up to 550 μm after feeding on bacteria. They have a rounded head, a rhabditiform oesophagus with a posterior bulb, and a slender pointed tail. They moult to form rhabditiform L2 which are similar to L1 but measure up to 700-750 μm in length. L2 moult to form L3 which retain the L2 cuticle as a close-fitting protective sheath. L3 are active but non-feeding free-living stages that are infective to their vertebrate hosts. Infective L3 measure from 715-735 μm in length (sometimes up to 1,000 μm) and have a squared head, a short buccal capsule, a strongyliform (non-bulbed) oesophagus, intestines comprising 16 cells, a tapering tail with a small digitiform process, and a short tail sheath extension. Following ingestion and exsheathment, L3 invade host tissues and moult to L4 which grow up to 2-3 mm in length and begin to show distinct genitalia (esp. male bursa and female vulva). L4 eventually moult to form young adults (sometimes called L5 or subadults) which then develop into reproductive adults. Mature worms are bright red-pink in colour and slender and hair-like in shape ranging from 4-10 mm in length. They have a small cephalic vesicle with a small buccal cavity lacking teeth (neodont formation absent) and are bound by a well-developed synlophe with numerous (40-45) symmetrical longitudinal ridges. Adults lack an excretory notch (present in the genus *Trichostrongylus*) but they have 2 small cervical papillae projecting above the body surface (smaller than those present in the genus *Haemonchus*). They have a strongyliform oesophagus leading to elongate intestines ending in a subterminal anus/cloaca. Female worms are larger than males (6-10 mm cf. 4-7 mm) and they have 2 ovaries (didelphic) connected to uteri opening into a posterior vulva surrounded by irregular cuticular inflations (rather than a vulval flap like other trichostrongyles). Mature males have a large copulatory bursa with 2 large lateral lobes and a short symmetrical dorsal lobe (cf. asymmetrical in *Haemonchus*). The lateral lobes have 5 lateral rays (comprising muscular elements following nerve channels to terminal papillae) arranged in a 2-2-1 configuration (ventral rays together, anterolateral and mediolateral rays close together, and posterolateral rays separate) and the dorsal lobe has a single ray which divides into 3 branches. The genital cone has a small proconus (ventral swelling) and a simple rectangular accessory bursal membrane supported by 2 widely-separated dorsal raylets. Males also possess a gubernaculum with a telamon and 2 short tapering spicules with a main stem and 2 slender distal branches (ventral and dorsal).

Site of infection: Developing larval stages invade the gastric pits and glands in the glandular portion of the stomach, while adult worms occur on the mucosal surface. Free-living stages (eggs and L1-L3) contaminate the external environment and may be found in faecal material, soil or on herbage.

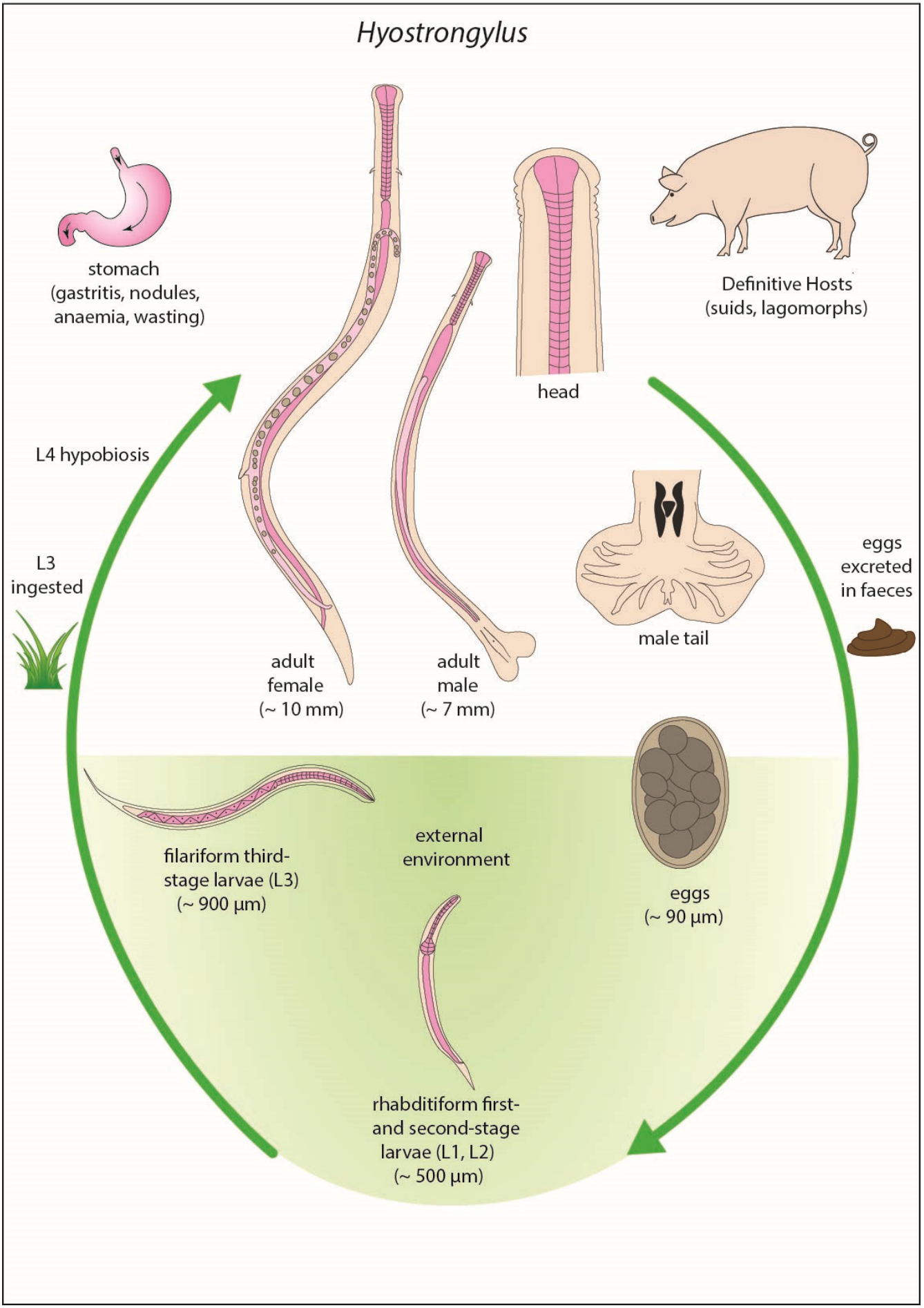
Pathogenesis: Adult worms feed on host blood obtained through the stomach mucosa, while earlier developing larval stages penetrate the mucosa causing structural and functional changes contributing to maldigestion and malnutrition. Light infections are usually asymptomatic, but larger numbers of parasites may damage the mucosa, particularly during the prepatent period when larval stages are prevalent. Larvae penetrating gastric pits and glands cause inflammation (catarrhal gastritis) with excessive mucus production, nodule formation (sometimes confluent), mucosal erosion and ulceration, hyperaemia, haemorrhage, epithelial hyperplasia and metaplasia with loss of acid-producing parietal cells and pepsinogen-producing Chief (zymogen) cells leading to a failure to activate pepsin thereby significantly reducing digestive processes. A breakdown in tight epithelial junctions also results in fluid and protein leakage into the tissues, circulation and gut lumen, contributing to oedema and hypoproteinaemia. Infected animals lose condition and may exhibit pallor, anaemia, inappetence, poor growth, weight loss or wasting with occasional bouts of diarrhoea. On occasion, adult pigs have died suddenly due to massive blood loss when mucosal ulcers perforate. Clinical disease is uncommon in growing pigs but adults may develop illthrift, particularly when exposed to high levels of infection when placed outdoors on contaminated pastures, or when hypobiotic larvae resume development. Animals do not develop a strong protective immunity and infections tend to accumulate with age. Hosts also seem to be more susceptible to clinical disease when stressed by poor nutrition, extended translocation, pregnancy and lactation. The so-called ‘poor-sow’ or ‘thin-sow’ syndrome is often due to persistent *H. rubidus* infection, often concomitantly with *Oesophagostomum* spp.

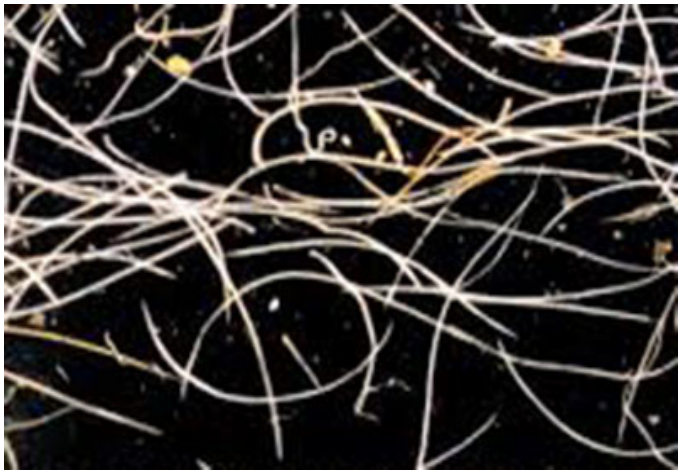
Developmental cycle and mode of transmission: *Hyostrongylus* spp. have direct life-cycles with horizontal transmission occurring between individuals by the faecal contamination of pastures by worm eggs from which infective larvae arise to be ingested by foraging animals. Females worms have a low fecundity and only produce 10-50 eggs per day during patency. The eggs are voided with host faeces into the external environment where they embryonate and hatch around 5 days later releasing free-living rhabditiform L1 which feed on bacteria. L1 moult to form rhabditiform L2 which also feed before moulting to L3 which remain enclosed within the L2 cuticle and thus do not feed. Nonetheless, L3 are highly motile stages and they move out of faecal material into the soil and onto vegetation. Infective L3 may develop within 1-2 weeks under optimum conditions (15-20°C, 80-95% relative humidity) although their development may take longer under less ideal conditions and they are highly susceptible to cold and desiccation. Animals become infected by ingesting infective L3 when foraging or grazing. The L3 exsheath in the stomach and penetrate the mucosa where they moult to L4 in nodules in about 2 weeks. These larvae emerge onto the mucosal surface where they moult to young adults (often designated L5) which feed and mature to adult worms which subsequently mate. The prepatent period (time from infection to first egg production) is 18- 21 days, but may be considerably longer if L4 arrested their development for several months (process known as hypobiosis). Inhibition of larval development usually occurs over seasons when external environmental conditions are not conducive to the development and survival of free-living stages on pastures. How endoparasites know prevailing external conditions is unknown but hypobiosis may be induced by repeated infections (occurs more frequently in older animals), seasonal climatic variation (particularly over winter months in temperate regions) and changes in host physiology (larvae resume development when sows begin lactation). Established infections in pregnant animals also show a periparturient rise

in egg production, presumably due to a relaxation or partial suppression of immunity. This results in a spring rise in environmental contamination which later places weaning animals at their greatest risk of infection as they begin foraging/grazing. Infections are mostly confined to animals raised outdoors or with access to contaminated pastures, whereas those raised indoors under intensive husbandry are least at risk as their stalls/pens are frequently cleaned. It is common practice in some temperate regions to keep breeding stock (gilts and sows) on pasture, resulting in significantly higher levels of infection.

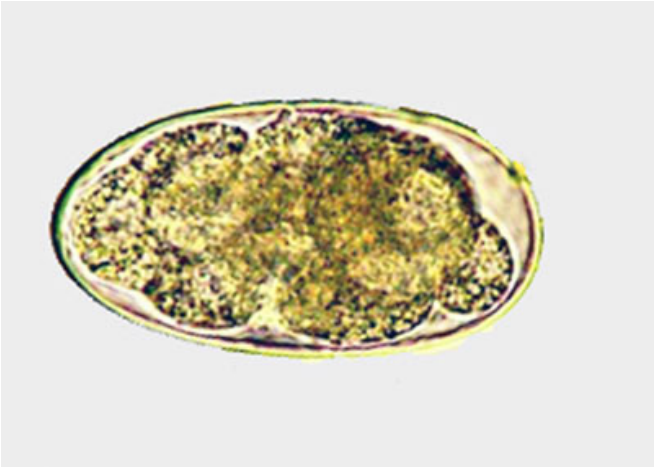
Differential diagnosis: Infections are difficult to diagnose on the basis of clinical symptomatology due to their nonspecific nature (often manifest only as illthrift). Coprological tests are therefore used to detect worm eggs in faecal samples after sedimentation in water and/or floatation in saturated sugar or salt solutions (eggs buoyant in media with high specific gravity). Several techniques are also quantitative in that the number of eggs counted in aliquots of diluted faeces in volumetric chambers (McMaster or Whitlock slides) may be used to calculates the number of eggs per gram of faeces (epg). However, coprological tests frequently demonstrated poor specificity (inconclusive negative results due to irregular egg excretion and low fecundity) and poor correlations with worm burdens (not accounting for developing larvae, males, or females not laying eggs because they are too young or too old). Egg morphology could also not be used for specific or even generic diagnosis, as *Hyostrongylus* eggs are remarkably similar to those of *Oesophagostomum* spp. Recourse can be made to coprocultures whereby faecal samples are incubated for several days in funnels or petri dishes in order to harvest L3 for microscopic examination and identification. *Hyostrongylus* L3 are slender active stages (often exhibiting a 'swimming' motion) with short tails ending in digitiform processes. In contrast, the L3 of *Oesophagostomum* are shorter, sluggish (do not 'swim') and have long filamentous tails without processes. Infections may also be diagnosed by the recovery and identification of adult worms in gut samples collected at post-mortem from dead or sacrificed animals. The stomach and intestines may be ligated, perfused with saline and the numbers of worms counted in gut washes (or sometimes mucosal digests to release tissue-bound larvae). A range of immunological tests (including precipitation, complement fixation, immunofluorescence, and enzyme immunoassays) have been used to detect specific host antibodies against worm antigens, but many demonstrated cross-reactivity problems with other nematodes. More recently, molecular biological techniques have been used to characterize parasites by polymerase chain reaction (PCR) amplification of specific nuclear gene sequences (ribosomal DNA).

Treatment and control: A range of anthelmintic drugs have been used to treat infections, with benzimidazoles (e.g. fenbendazole), probenzimidazoles (e.g. febantel), organophosphonates (e.g. dichlorvos) and macrocyclic lactones (e.g. doramectin, ivermectin) being effective against larval and adult worms, including hypobiotic larvae. Most drugs are available as oral formulations (drenches) although some may be administered percutaneously (injectables). Unfortunately, they do not have any persistent residual activity and animals quickly become re-infected when returned to contaminated pastures, so repeated treatments are required. Pregnant animals are treated to avoid periparturient rises in worm egg production, weaners are treated when they first begin to forage/graze, young adults are treated after seasons in which larval hypobiosis may have occurred (end of winter), and adults on pastures (especially sows) are regularly treated as they acquire little protective immunity and infections accumulate with age. Some drug resistance has been detected in parasite populations in pigs, so it is often recommended that drug resistance testing be conducted to select the most efficacious drug and that drenches be used strategically (as required) or in rotation to curb the development of drug resistance. Because the transmission of infections requires hosts to have access to pastures contaminated with free-living stages, control programmes should integrate stock and pasture management practices shown to minimise environmental contamination by worm eggs and reduce the development and survival of larvae on pastures. Animals should be moved to clean areas (spelled or recently ungrazed pastures) after treatment, but this is often difficult in small holdings and backyard situations where set-stocking on few pastures are involved. Stocking rates should be kept low, new livestock should be treated in quarantine and, if possible, pastures should be rotated with other livestock species or crops, or spelled periodically, particularly over adverse seasons (e.g. hot summers). Studies on biological control options have also shown that supplementary feeds laced with the nematophagous fungus (*Duddingtonia flagrans*) resulted in significant reductions in pasture larvae thus contributing to reduced worm burdens.

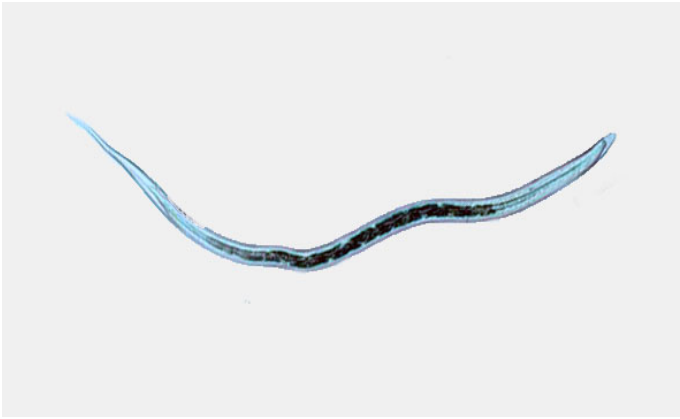

Hyostrongylus
stomach
(gastritis, nodules,
anaemia, wasting)
adult
female
(~ 10 mm)
adult
male
(~ 7 mm)
head
Definitive Hosts
(suids, lagomorphs)
male tail
eggs
excreted
in faeces
L4 hypobiosis
L3
ingested
external
environment
filariform third-
stage larvae (L3)
(~ 900 µm)
eggs
(~ 90 µm)
rhabditiform first-
and second-stage
larvae (L1, L2)
(~ 500 µm)



Hyostrongylus adult worms



Hyostrongylus worm egg



Hyostrongylus third-stage larva

Cooperia
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the trichostrongyles which are small hair-like worms with a small buccal capsule. Adults are usually found in the stomach/abomasum or small intestines of mammals or birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 (some may undergo arrested development, termed hypobiosis) before returning to the lumen to moult into adults. *Cooperia* spp. (wire worms) contribute to illthrift reducing production in sheep and cattle worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Trichostrongylidae (hair-like, lips absent/reduced, oesophagus lacking bulb, thin-shelled eggs, direct cycles)
Genus:	*Cooperia* (parasitic in small intestines of ruminants)
Species:	various species cause scours and illthrift in cattle and sheep

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56

Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

The family Trichostrongylidae contains small hair-like worms that infect the gastrointestinal tracts of herbivorous animals, many species causing disease and production losses in ruminant livestock worldwide. Adult worms have a rudimentary buccal cavity with reduced or absent lips but some taxa possessing teeth. Male worms have a well-developed bursa and spicules, and the larger female worms lay thin-shelled eggs that are in the morula stage. Trichostrongyles have direct life-cycles whereby eggs embryonate and hatch in the external environment releasing rhabditiform larvae which grow in soil or on vegetation. These larvae moult to form infective filariform larvae (L3) which are ingested by grazing animals. Various anatomical features have been used to characterize taxa, including patterns of longitudinal ridges (synlophe) on the external cuticular surface as well as structure of the male bursa (arrangement of dorsal, ventral and lateral lobes and supporting rays) and spicules (number, size and shape). Over 50 trichostrongylid genera have been allocated to 8 subfamilies: Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules, 6 genera in mammals and birds); Amidostomatinae (with buccal teeth or extra-buccal appendages, 8 genera in birds); Filarinematinae (neodont formation, long bursa, 3 genera in marsupials); Haemonchinae (well-developed synlophe, neodont formation, 5 genera in ungulates); Ostertagiinae (well-developed synlophe, modified bursa, 15 genera in mammals); Cooperiinae (symmetrical synlophe, bursa with symmetrical dorsal rays, 12 genera in ruminants); Libyostrongylinae (without synlophe, modified bursa, 5 genera in mammals and birds); and Obeliscoidinae (without synlophe, symmetrical bursa, 5 genera in mammals and birds). Note that some taxonomic classifications have split these 8 subfamilies between 3 separate sister families: with Trichostrongylinae, Amidostomatinae and Filarinematinae allocated to a restricted Trichostrongylidae (cephalic vesicle absent, synlophe reduced or absent, male bursa with short dorsal ray and long lateral lobes); Haemonchinae and Ostertagiinae assigned to the Haemonchidae (cephalic vesicle absent, synlophe present without any specific orientation, male bursa with short dorsal rays, often asymmetrical); and Cooperiinae, Libyostrongylinae and Obeliscoidinae placed in the Cooperiidae (cephalic vesicle present, synlophe bilaterally symmetrical or absent, large male bursa with curved lateral rays). Several other genera have recently been transferred to other taxa on the basis of cladistic or molecular phylogenetic studies; mostly those in the subfamily Nematodirinae (6 genera in mammals) now classified in the family Molineidae. Specific trichostrongylid genera of veterinary and medical importance are compared in the following table.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Subfamily Cooperiinae (symmetrical synlophe, bursa with symmetrical rays)					
Cooperia (wire worm)	24	artiodactyls	small intestines, stomach	4-15 mm long, often coiled, bulbous cephalic vesicle, large bursa, large spicules, larval hypobiosis	65-95 x 29-44 µm, ellipsoidal, thin-shelled
Subfamily Trichostrongylinae (reduced synlophe, wide bursa, short twisted spicules)					
Trichostrongylus (hairworm, black scour worm)	56	artiodactyls, lagomorphs, rodents, birds	small intestines, stomach	2-10 mm long, rudimentary buccal cavity, distinct excretory notch in oesophageal region, male bursa with long lateral lobes	75-125 x 31-72 µm, ellipsoidal, thin-shelled

Subfamily Haemonchinae (well-developed synlophe, neodont formation)					
Haemonchus (barber's pole worm)	15	artiodactyls	abomasum	10-40 mm long, buccal capsule with tooth, white spiral ovaries, prominent vulval flap, bursa with asymmetrical dorsal ray, larval hypobiosis	62-90 x 40-50 µm, ellipsoidal, thin-shelled
Subfamily Ostertagiinae (well-developed synlophe, modified bursa)					
Ostertagia (brown stomach worm)	32	artiodactyls	abomasum	6-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-1-2) and proconus, larval hypobiosis	60-100 x 38-50 µm, ellipsoidal, thin-shelled
Teladorsagia (brown stomach worm)	9	artiodactyls	abomasum	10-15 mm long, small buccal cavity, ridged synlophe, small vulval flap, bursa with 5 lateral rays (2-2-1) and proconus, larval hypobiosis	60-100 x 40-50 µm, ellipsoidal, thin-shelled
Hyostrongylus (red stomach worm)	4	suids, lagomorphs	stomach	4-10 mm long, red coloration, well-developed bursa, gubernaculum, telamon, larval hypobiosis	60-90 x 31-42 µm, ovoid, thin-shelled

The subfamily Cooperiinae was established for genera with a cephalic vesicle and contains 10 genera (*Chabaudstrongylus*, *Cooperia*, *Cooperioides*, *Gazellostrongylus*, *Impalaia* (syn. *Anthostrongylus, Minutostrongylus*), *Megacooperia*, *Minutostrongylus*, *Neocooperia, Ortleppstrongylus*, *Paracooperia* (syn. *Schwartziella*), *Paracooperioides, Pseudostertagia* and *Tapironema*) which are parasitic in the small intestines of ruminants (bovids, giraffids, camelids, cervids). The genus *Cooperia* contains small wire-worms with small cephalic vesicles, reduced buccal capsules with three or fewer cutting plates or teeth, and the males have a fully developed bursa (type 2-2-1) with lyre-shaped dorsal rays, no gubernaculum or telamon, and 2 spicules not joined posteriorly. Some 24 species have been described mainly from bovids, giraffids and camelids. All species have direct life-cycles involving the faecal-oral transmission of pasture stages. Infective larvae do not undergo tracheal migration in their hosts, but some may undergo arrested development (hypobiosis) in host tissues. Several *Cooperia* spp. are important pathogens of domestic ruminants, causing significant production losses through reduced weight gain, poor reproductive performance, morbidity and mortality. Infections are more common in cooler areas with high winter rainfall as the exogenous stages of the parasites (eggs and larvae) prefer moist conditions.

***Cooperia* species**	**Definitive Hosts**	**Location [clinical signs[**	**Distribution**
C. acutispiculum	Artiodactyla: bovid (greater kudu, bushbuck)		Africa
C. asamati	Artiodactyla: bovid (cattle)		
C. aserbaidjanica	Artiodactyla: bovid (cattle)		Asia
C. borgesi sp. inq.	Artiodactyla: bovid (cattle, sheep, reedbuck)		Africa
C. chabaudi	Artiodactyla: bovid (bay duiker)	small intestines	Africa
C. connochaeti	Artiodactyla: bovid (blue wildebeest, Livingstone's eland, impala, puku)	abomasum, small intestines	Africa
C. curticei (syn. *C. fieldingi p.p., Strongylus curticei, ventricosus p.p.*)	Artiodactyla: bovid (cattle, water buffalo, sheep, argali, mouflon, goat, roan antelope, sable antelope, lechwe, Kafue lechwe, Sharpe's grysbok, blesbok, gemsbok, springbok, waterbuck, black wildebeest, impala), cervid (roe deer, red deer, white-tailed deer); Diprotodontia: phalangerid (common brushtail possum)	small intestines [inappetence]	worldwide
C. erschovi sp. inq.	Artiodactyla: bovid (cattle)	pancreas	China
C. fuelleborni	Artiodactyla: bovid (impala, common tsessebe, roan antelope, sable antelope, waterbuck, topi, Sharpe's grysbok, Coke's hartebeest, common duiker, greater kudu, common eland, sheep, cattle, blesbok, African buffalo)	small intestines	Africa
C. hippotragusi sp. inq.	Artiodactyla: bovid (cattle, roan antelope, reedbuck, oribi)		Africa
C. hrenktahnsa	Artiodactyla: bovid (yak)		Asia
C. hungi	Artiodactyla: bovid (goat, sheep, African buffalo, blue wildebeest, Coke's hartebeest, common tsessebe, sable antelope, steenbok, nyala, greater kudu, bushbuck, Sharpe's grysbok, southern reedbuck, waterbuck, common duiker, common eland, impala, topi, suni), suid (desert warthog); Lagomorpha: leporid (scrub hare)	abomasum, small intestines	Africa

C. laterouniformis	Artiodactyla: bovid (blackbuck, water buffalo)	small intestines	Asia
C. minor sp. inq.	Artiodactyla: bovid (cattle)		Africa
C. neitzi	Artiodactyla: bovid (sable antelope, Sharpe's grysbok, Livingstone's eland, kudu, greater kudu, bushbuck, grey duiker, sheep)	small intestines	Africa
C. okapi (syn. *C. okapiae*)	Artiodactyla: giraffid (okapi)	small intestines	Africa
C. oncophora (wire worm) (syn. *C. bisonis, harkeri, Strongylus radiatus p.p., ventricosus p.p., oncophorus*)	Artiodactyla: antilocaprid (pronghorn), bovid (cattle, sheep, bighorn sheep, argali, mouflon, goat, European bison, American bison), camelid (dromedary, llama, vicuna, alpaca), cervid (roe deer, fallow deer, red deer, mule deer, white-tailed deer)	small intestines, stomach [inappetence, diarrhoea]	worldwide
C. pectinata (syn. *C. nicolli*)	Artiodactyla: antilocaprid (pronghorn), bovid (cattle, zebu, European bison, water buffalo, African buffalo, sheep, argali, mouflon, goat, common tsessebe, Livingstone's eland, Coke's hartebeest, greater kudu, bushbuck, sable antelope, impala), camelid (dromedary), cervid (roe deer, fallow deer, red deer, white-tailed deer)	small intestines [inappetence, diarrhoea]	worldwide
C. pigachei	Artiodactyla: bovid (mountain reedbuck)		Africa
C. punctata (cattle bankrupt worm) (syn. *C. africana, brasiliensis, fieldingi p.p., Strongylus punctatus, bovis*)	Artiodactyla: antilocaprid (pronghorn), bovid (cattle, Bali cattle, zebu, water buffalo, African buffalo, European bison, sheep, goat, chamois, Sharpe's grysbok, Coke's hartebeest, greater kudu, sable antelope, Livingstone's eland, suni), cervid (roe deer, fallow deer, red deer, marsh deer, chital, white-tailed deer), suid (pig)	abomasum, small intestines, pancreas [inappetence, diarrhoea]	worldwide
C. reduncai sp. inq.	Artiodactyla: bovid (reedbuck)		Africa
C. rotundispiculum	Artiodactyla: bovid (impala, blue duiker, red forest duiker, grey duiker, suni, gemsbok, common duiker, common eland, nyala, Cape bushbuck, greater kudu, Bohor reedbuck)	abomasum, small intestines	Africa
C. schistopapillatus	Artiodactyla: bovid (greater kudu)		Africa
C. spatula	Artiodactyla: bovid (cattle, sheep), cervid (white-tailed deer)		North America
C. spatulata	Artiodactyla: bovid (cattle, zebu, sheep)	small intestines	Australasia, North America, Africa
C. surnabada (syn. *C. zurnabada, mcmasteri*) (now considered to be a morphological variant of *C. onchophora*)	Artiodactyla: antilocaprid (pronghorn), bovid (cattle, American bison, European bison, sheep, bighorn sheep, goat), camelid (llama), cervid (red deer, roe deer, mule deer)	small intestines [inappetence, diarrhoea]	Europe, Americas, Australia
C. svanetica	Artiodactyla: bovid (cattle)	small intestines	Russia
C. verrucosa	Artiodactyla: bovid (common eland, impala, Coke's hartebeest, Kirk's dik-dik)	abomasum, small intestines	Africa
C. yoshidai	Artiodactyla: bovid (impala, red forest duiker, common tsessebe, sable antelope, Bohor reedbuck, southern reedbuck, greater kudu)	abomasum, small intestines	Africa
Re-assigned species			
C. alata (now *Pithecostrongylus*)	Primates: cercopithecid (macaque)		Africa
C. antidorca (now *Cooperioides*)	Artiodactyla: bovid (springbok, Grant's gazelle, Thomson's gazelle, sheep)		Africa
C. caballeroi (now *Chabaudstrongylus*)	Artiodactyla: tragulid (mouse-deer)		Asia
C. dubosti (now *Chabaudstrongylus*)	Artiodactyla: tragulid (water chevrotain)		Africa
C. elegans (now *Molineus*)	Primates: cebid (Guianan squirrel monkey)	small intestines	South America
C. falsa	Cingulata: chlamyphorid (southern naked-tailed	stomach	South

(now *Macielia*)	armadillo)		America
C. hamiltoni (syn. *C. kenyensis*) (now *Cooperioides*)	Artiodactyla: bovid (impala, suni, sheep)	small intestine	Africa
C. hepaticae (now *Cooperioides*)	Artiodactyla: bovid (impala)		Africa
C. macieli (now *Macielia*)	Cingulata: dasypodid (nine-banded armadillo)	stomach	South America
C. nodulosa (syn. *Schwartziella*) (now *Paracooperia*)	Artiodactyla: bovid (carabao)	small intestines	Philippines
C. serrata (syn. *Schwartziella*) (now *Paracooperia*)	Artiodactyla: bovid (springbok, sheep)		Africa

Parasite morphology: *Cooperia* spp. exhibit sequential development through 3 distinct biological stages: eggs; larvae (4 stages encoded L1-L4); and adult worms. Gravid females lay thin-walled eggs measuring 65-95 x 29-44 µm which are prolate ellipsoidal in shape with nearly parallel sides. Freshly laid eggs contain a morula composed of 16-32 cells almost filling the interior. First-stage larvae (L1) are pre-parasitic free-living feeding stages measuring from 300-375 µm in length. They have a rounded head, rhabditiform (bulbed) oesophagus, intestines dilated anteriorly and posteriorly with an undulating lumen, and sharply pointed tails. L2 are similarly free-living feeding stages but they measure 500-800 µm long and their intestines are less serpentine. In contrast, L3 are non-feeding stages that are still encased in the L2 cuticle as a protective sheath. The ensheathed L3 usually measure from 711-924 µm in length, but those of some species may range from 550-1,050 µm depending on maturity. The sheath has an annulated appearance and a long tail sheath extension (35-116 µm) of which the posterior 20-25% is filamentous. The larvae themselves have a round-square head with 2 distinctive refractile bodies, a strongyliform (non-bulbed) oesophagus, intestines comprising 16 cells, and a blunt tail. Parasitic L4 are elongate measuring from 1.9-4.6 mm in length and their genital primordia have begun to form distinctive reproductive organs (with the vulva and bursa becoming conspicuous). Early L4 of some species may undergo arrested development (hypobiosis) in host tissues. Adult worms are commonly called 'wire-worms' due to their comma or watch-spring appearance (with 1-2 tight coils). They are small slender worms measuring from 4-15 mm in length and are red-brown or pink-white in colour. They typically have an anterior cuticular inflation (cephalic vesicle) giving the head a bulbous or cylindrical appearance, a reduced buccal capsule, tiny cervical papillae, a cylindrical strongyliform oesophagus and a distinctive synlophe with prominent anterior transverse striations giving way to a small number of longitudinal cuticular ridges. Adults have an excretory pore located near the distal oesophagus (but lack the excretory notch characteristic of the genus *Trichostrongylus*). Adult worms are sexually dimorphic, with females being larger than males (5-15 mm cf. 4-9 mm long). Mature females are didelphic with 2 ovaries (rarely some are monodelphic) connected to uteri opening into a posterior vulva with a well-developed ovejector and small vulvar flaps. They have long tapering tails that are sharply pointed and lack terminal spines. Male worms have a large pronounced copulatory bursa with 2 lateral lobes supported by 5 rays (comprising muscular elements following nerve channels to terminal papillae) with a 2-2-1 configuration (divergent ventral and lateral rays separated from posterolateral ray) and a shorter symmetrical dorsal lobe with dorsal rays forming a distinctive lyre-shape. Mature males do not have a gubernaculum or telamon, but have 2 short thick spicules not joined posteriorly. Spicule structure appears to be species-specific (e.g. bow-like with terminal feet for *C. oncophora*, posterior bifurcation and conical tips for *C. surnabada*, medial wing-like projection with ridges for *C. curticei*).

Site of infection: Parasites infect the small intestines of their hosts, particularly the duodenum, but sometimes extending to the large intestines, abomasum, and rarely the pancreas. Larval stages develop in small intestinal crypts (sometimes undergoing development arrest), whereas adult worms coil up amongst mucosal villi. Worm eggs are excreted onto pastures where free-living larval stages eventually develop into infective L3.

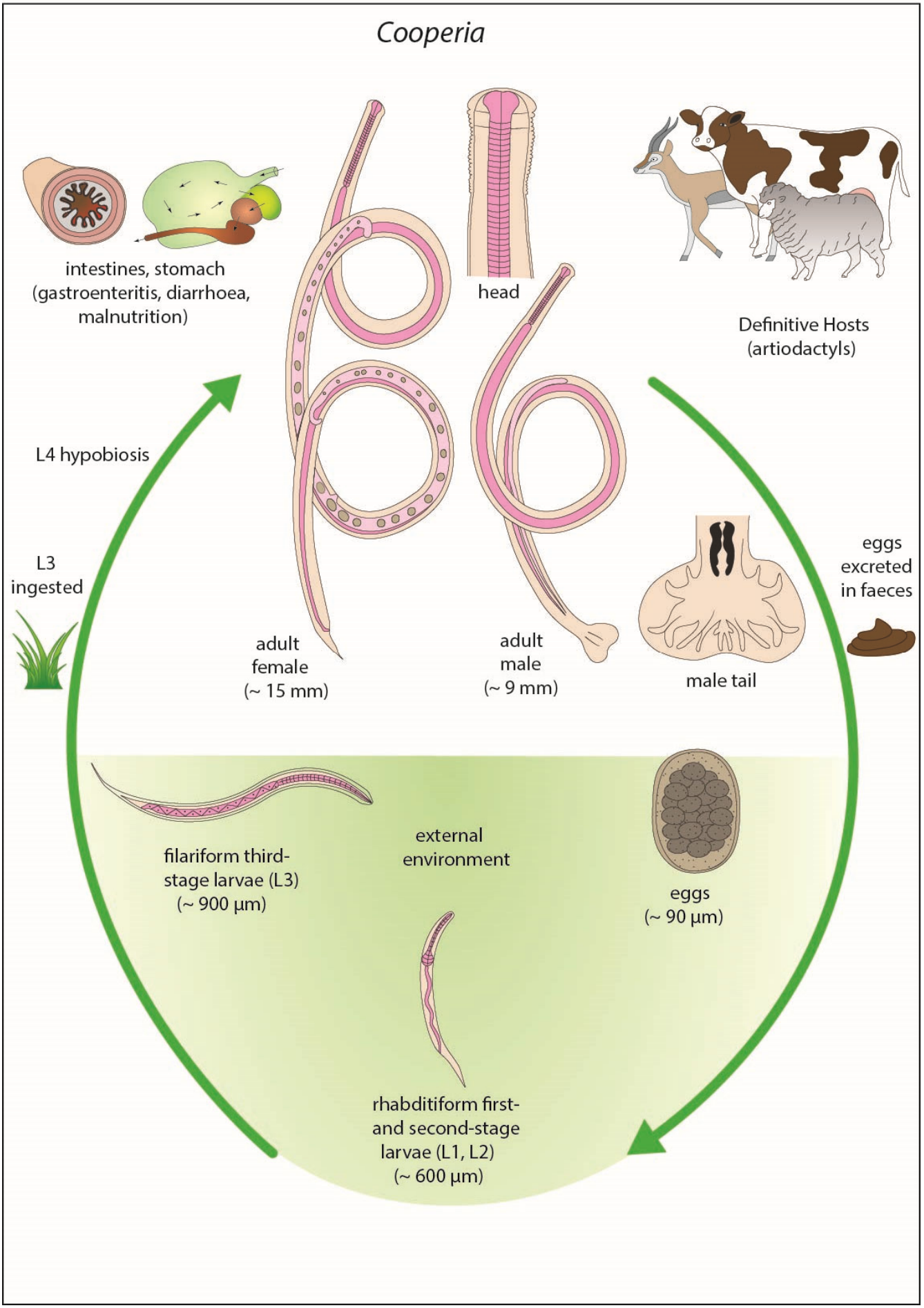
Pathogenesis: While many infections are light and remain asymptomatic, mild-moderate infections may cause significant subclinical production losses and heavy infections (> 40,000 worms) may produce clinical disease. When infections occur concomitantly with other gut nematodes (especially *Haemonchus* and *Ostertagia*), the combined clinical effects (gastroenteritis, diarrhoea, malnutrition) can be severe. Developing larval stages burrow beneath the small intestinal mucosa forming tunnels which eventually rupture to release young adults into the lumen. Adult worms coil among the intestinal villi and forage along the mucosa (earlier reports of them feeding on host blood have not been substantiated, but adults have been observed to bury their bulbous heads in the mucosa apparently for anchorage). Collectively, larval and adult stages cause mucosal damage resulting in inflammation (catarrhal enteritis), cellular infiltration, epithelial loss, lesion formation, villus atrophy and some petechial haemorrhages which contribute to malabsorption with fluid and protein loss. Infected animals exhibit intermittent watery diarrhoea, dehydration, hypoproteinaemia, oedema, inappetence, anorexia and failure to thrive with reduced growth rates and poor weight gain or weight loss. *Cooperia* spp. vary in their pathogenicity, with *C. pectinata* and *C. punctata* considered to be most pathogenic (large numbers can be fatal in calves) and *C. oncophora* to be mildly pathogenic (causing mild diarrhoea). Young animals (< 8 months old) are most susceptible to clinical infections but they rapidly acquire a strong but partial protective immunity by 12 months of age. The

resumption of development of hypobiotic larvae in older animals (yearlings) is not usually associated with a second wave of disease (as occurs for some *Ostertagia* spp.). While adult animals generally show few clinical signs of infection, but may continue to act as carriers with low but persistent egg excretion.

Developmental cycle and mode of transmission: *Cooperia* spp. are monoxenous parasites with direct life-cycles involving the faecal-oral transmission of infective larvae on pastures. Gravid female worms lay 1,000-3,000 eggs per day which are passed into the external environment with host faeces. The eggs embryonate and hatch after several days releasing free-living L1 which feed on faecal bacteria. The larvae then moult to L2 that also feed on bacteria before moulting to ensheathed non-feeding L3 (they retain the L2 cuticle as a protective sheath). L3 are very active stages that migrate outwards from faecal material and upwards onto vegetation. They develop in 1-6 weeks depending on prevailing environmental conditions, with development occurring in moist conditions with temperatures ranging from 5-33°C. Infective L3 may survive on pastures for up to 1 year, and are able to tolerate cold conditions. They are ingested on herbage by grazing animals and exsheath in the gut before invading crypts in the small intestines. Here they moult to L4 and then to young adults over 8-10 days before emerging onto the intestinal mucosa to feed, mature and mate. The prepatent period (time from infection to the first release of eggs) ranges from 11-22 days depending on species (11-19 days for *C. punctata*, 14-15 days for *C. curticei*, and 17-22 days for *C. oncophora*). The larvae of several *Cooperia* spp. may also exhibit arrested development (hypobiosis) at the early L4 stage (particularly when preparasitic L3 are exposed to cold conditions), only resuming development months later when environmental conditions are more suitable. Hypobiosis occurs during late autumn and winter in cool temperate zones, during spring and summer in warm temperate zones, and during prolonged dry seasons in subtropical regions.

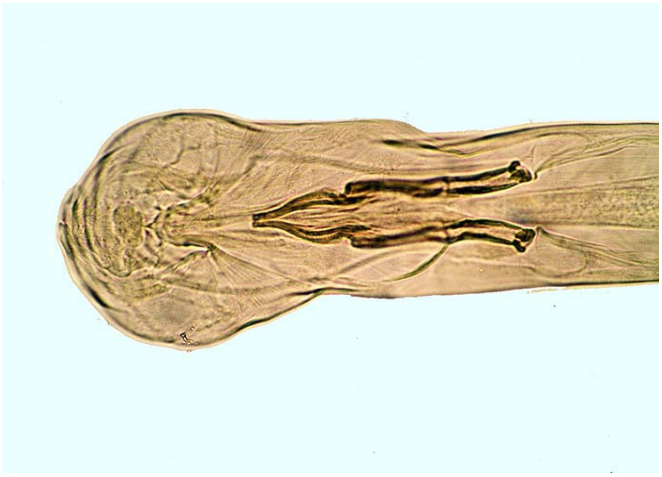
Differential diagnosis: Infections cause nonspecific clinical signs (gastroenteritis) which could be attributed to a wide range of infectious agents. Indeed, *Cooperia* infections often occur concomitantly with other gut nematodes that have similar host ranges and modes of transmission. Infections are often diagnosed by the direct detection of worm eggs in faecal samples, normally following their concentration by sedimentation in water and/or floatation in saturated salt or sugar solutions (eggs are buoyant in media with high specific gravities). Several coprological techniques have been quantitated by counting the number of eggs present in aliquots of diluted faeces in volumetric chambers (McMaster or Whitlock slides) and calculating the number of eggs per gram of faeces (epg). Unfortunately, faecal egg counts show poor correlations with worm burdens and the severity of clinical disease, as they do not account for larval stages, male worms, or females not producing eggs due to their immaturity, senescence or immune-induced suppression of egg production. The eggs of *Cooperia* spp. are small in size and ellipsoidal in shape with flattened sides, but otherwise do not exhibit any reliable characteristics to differentiate species or even other trichostrongyle genera (notably *Trichostrongylus, Haemonchus, Ostertagia* and *Teladorsagia*). Faecal samples may be incubated for several days to harvest L3 which can be identified by their morphological characteristics (annulated sheath with long tapering tail, squared head with refractile bodies, strongyliform oesophagus, and intestines comprising 16 cells). Infections may also be diagnosed by the detection of adult worms in gut samples obtained post-mortem from dead or sacrificed animals. The stomach and intestines may be ligated, perfused with saline and mucosal washes or digests examined for characteristic worms (red colouration, coiled spring appearance, prominent bursa and spicules). More recently, molecular biological techniques have been used to characterize different species by the polymerase chain reaction (PCR) amplification of nuclear genes (encoding ribosomal RNA and internal transcribed spacers I and II).

Treatment and control: A variety of anthelmintic drugs have been used to effectively treat clinical infections, including benzimidazoles (fenbendazole, oxfendazole, albendazole), prebenzimidazoles (febantel, netobimin, thiophanate), imidazothiazole (levamisole), and macrocyclic lactones (ivermectin). Regrettably, drug resistance to benzimidazoles and macrocyclic lactones has become widespread, so it is recommended that drug resistance monitoring be instituted (faecal egg count reduction tests) and that treatments be applied strategically (as required) or systematically (regularly and in rotation). In particular, young livestock should be treated during their first grazing season, whereas adult animals acquire protective immunity and usually do not display clinical signs. Control programmes should also include stock and pasture management practices at the farm level to reduce pasture contamination by worm eggs and larvae. New livestock should be isolated and treated in quarantine, stocking rates should be kept low, different cohorts should be grazed in rotation, treated animals should be placed on clean pastures, different host species may be grazed together or alternately, and pastures should be spelled periodically, particularly over adverse seasons (e.g. hot summers). While some studies have shown that pastures seeded with a nematode-trapping fungus (*Athrobotrys oligospora*) later contained fewer infective larvae, environmental constraints (narrower temperature ranges and moisture requirements) appear to limit widespread application.


Cooperia
intestines, stomach
(gastroenteritis, diarrhoea,
malnutrition)
head
Definitive Hosts
(artiodactyls)
L4 hypobiosis
L3
ingested
adult
female
(~ 15 mm)
adult
male
(~ 9 mm)
male tail
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 900 µm)
external
environment
eggs
(~ 90 µm)
rhabditiform first-
and second-stage
larvae (L1, L2)
(~ 600 µm)



Cooperia adult worm, head



Cooperia adult worm, male bursa



Cooperia worm egg

Nematodirus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the trichostrongyles which are small hair-like worms with a small buccal capsule. Adults are usually found in the stomach/abomasum or small intestines of mammals or birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 (some may undergo arrested development, termed hypobiosis) before returning to the lumen to moult into adults. *Nematodirus* spp. (thin-necked or thread-necked intestinal worms) contribute to diarrhoea and illthrift reducing production in sheep and cattle worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Molineidae (reduced buccal capsule, cephalic vesicle, female tail with spine/cusps, direct cycles)
Subfamily:	Nematodirinae (corona radiata, neodont formation, oviparous, herbivores)
Genus:	*Nematodirus* (parasitic in small intestines of ruminants)
Species:	various species cause scours and illthrift in lambs and calves

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Trichostrongylina (trichostrongyles)				
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb,	artiodactyls, birds	ingestion of L3	50

	thin-shelled eggs			
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Some authorities recognize a superfamily Molineoidea comprising 4 families: Molineidae in mammals, birds and reptiles; Amphibiophilidae mainly in amphibians; Mackerrastrongylidae in monotremes and marsupials; and Strongylacanthidae in bats. These worms have a buccal capsule reduced to an annulus, most have a cephalic vesicle and a bilaterally symmetrical synlophe, the males have an asymmetrical bursa and females have a tail with a caudal spine or numerous tubercles. The family Molineidae contains 6 subfamilies: Nematodirinae (corona radiata, neodont formation, bursa with short dorsal ray split to base, didelphic, oviparous, 6 genera in herbivorous mammals); Ollulaninae (synlophe absent, cephalic vesicle absent, bursa with short dorsal ray, monodelphic, viviparous, female tail with 3-5 tubercles, 1 genus in felids and occasionally suids); Molineinae (bursa with short dorsal ray not split to base, synlophe with perpendicular ridges, 26 genera in amphibians, reptiles and mammals); Dromaeostrongylinae (bursa with elongate dorsal ray, 1 genus in birds); Merstensinematinae (bursa with short dorsal ray not split to base, synlophe absent, 2 genera in reptiles and amphibians); and Anoplostrongylinae (cephalic vesicle with armature, synlophe with dorsoventral ridges, bursa with short dorsal ray not split to base, 25 genera in edentates and bats). Specific molineid genera of veterinary and medical importance are compared in the following table.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs/larvae**
Subfamily Nematodirinae					
Nematodirus (thin-necked intestinal worm)	53	artiodactyls, lagomorphs	small intestines	10-30 mm long, cephalic inflation, thin neck, mid-body spiral coil, female with spiked tail, male with long thin spicules	150-260 x 67-118 µm, eggs ellipsoidal, thin-shelled
Subfamily Ollulanidae					
Ollulanus	1	carnivores	stomach	0.7-1.0 mm long, small buccal capsule, females with trifid tail, viviparous (eggs hatch *in utero*), larvae shed in vomitus (or auto-infection)	larvae 400-500 µm, tail with terminal cusps

The subfamily Nematodiriinae contains 6 genera (*Nematodirus, Lamanema, Murielis, Nematodirella, Nematodiroides,* and *Rauschia*) parasitic in small intestines of ruminants (esp. Holarctic cervids and bovids), camelids and lagomorphs. The genus *Nematodirus* is characterised by medium-sized worms with a distinct cephalic vesicle, synlophe with perpendicular ridges, and males possessing an asymmetrical bursa (type 2-3 tending to 2-1-2) with the dorsal ray divided into 2 projections, and 2 long spicules joining in a membrane at their tips (cf. short and unjoined in *Cooperia*). They are commonly known as thin necked

intestinal worms (sometimes long-necked bankrupt worms, or thread-necked worms) and over 50 species have been described in ruminants particularly in temperate or cold regions, often from elevated mountainous areas. The parasites produce large eggs which are resistant to desiccation and freezing and hosts often become infected in warm months during spring, with mass hatching occurring under suitable conditions of moisture and temperature.

***Nematodirus* species**	**Definitive Hosts**	**Location [clinical signs]**	**Distribution**
N. abnormalis	Artiodactyla: bovid (cattle, sheep, bighorn sheep, mouflon, chamois, goat, alpine ibex, Iberian ibex, common duiker, bushbuck, Cuvier's gazelle, goitered gazelle), antilocaprid (pronghorn), cervid (mule deer), camelid (dromedary); Lagomorpha: leporid (rabbit); Primates: hominid (human)	small intestines [diarrhoea]	worldwide
N. andersoni	Artiodactyla: bovid (bighorn sheep, Dall sheep)		North America
N. andreevi	Artiodactyla: bovid (sheep, goitered gazelle)		Eurasia
N. antilocaprae	Artiodactyla: bovid (mountain goat), cervid (red deer)		North America
N. archari	Artiodactyla: bovid (sheep, bighorn sheep, argali, Dall sheep, mouflon, goat, goitered gazelle)		Eurasia, North America
N. arizonensis	Lagomorpha: leporid (rabbit)	small intestines	North America
N. aspinosus (*Rauschia*)	Lagomorpha: leporid (rabbit, mountain hare)		-
N. aznivi	Artiodactyla: bovid (sheep)		
N. battus (thread-necked worm)	Artiodactyla: bovid (cattle, sheep, chamois, goat), cervid (Reeve's muntjac),	small intestines [diarrhoea]	Europe, North America
N. becklundi	Artiodactyla: bovid (mountain goat)		North America
N. bioccai	Artiodactyla: bovid (sheep)		Iran
N. brevispiculus	Artiodactyla: bovid (sheep)		Kazakhstan
N. centripunctata	Artiodactyla: cervid (roe deer)		
N. chabaudi	Artiodactyla: bovid (Pyrenean chamois)		Europe
N. davtiani (incl. subspp. *davtiani, alpinus*, syn. *N. rufaevastitatis*)	Artiodactyla: bovid (bighorn sheep, Dall sheep, mountain goat, chamois, alpine ibex, Iberian ibex)		Europe, North America
N. dogieli	Artiodactyla: bovid (sheep, argali, saiga antelope)		Eurasia
N. dromedarii	Artiodactyla: bovid (dromedary)		
N. erschovi	Artiodactyla: cervid (roe deer)		Europe
N. europaeus	Artiodactyla: bovid (European bison, mouflon), cervid (roe deer)		Europe
N. filicollis (syn. *N. furcatus*, *Ascaris, Fusaria, Oesophagostomum, Strongylus*) (thread-necked worm)	Artiodactyla: bovid (cattle, sheep, bighorn sheep, argali, mouflon, chamois, Pyrenean chamois, goat, mountain goat, alpine ibex, Iberian ibex, Cuvier's gazelle, dama gazelle, dorcas gazelle, antilocaprid (pronghorn), cervid (roe deer, fallow deer, red deer, mule deer, Columbian black-tailed deer, white-tailed deer, reindeer), camelid (llama, alpaca): Rodentia: ctenodactylid (common gundi)	small intestines [diarrhoea]	worldwide (except Africa), esp. temperate zones
N. furcatus	Artiodactyla: bovid (sheep)		
N. gazellae	Artiodactyla: bovid (sheep, goitered gazelle, saiga antelope)		Eurasia
N. helvetianus (thread-necked worm)	Artiodactyla: bovid (cattle, muskox, American bison, European bison, sheep, bighorn sheep, mouflon, chamois, goat, mountain goat, alpine ibex, Cuvier's gazelle, greater kudu), cervid (moose, roe deer, fallow deer, red deer, mule deer, Hondo sika deer, Yezo sika deer, boreal woodland caribou), camelid (dromedary, llama); Carnivora: canid (coyote)	small intestines [diarrhoea]	worldwide
N. hsuei	Artiodactyla: bovid (sheep)		Asia
N. hugonnetae	Artiodactyla: bovid (chamois)		Europe
N. ibicis	Artiodactyla: bovid (chamois, goat, alpine ibex)		Eurasia
N. iranicus	Artiodactyla: bovid (sheep)		Iran
N. lamae	Artiodactyla: camelid (alpaca, vicuna), bovid (sheep)		South America
N. lanceolatus	Artiodactyla: bovid (goat)		
N. leporis (*Rauschia*)	Lagomorpha: leporid (rabbit, hare)		North America

N. maculosus	Artiodactyla: bovid (mountain goat, bighorn sheep)		North America
N. mauritanicus	Artiodactyla: cervid (moose, roe deer), camelid (dromedary), bovid (sheep, dorcas gazelle, goitered gazelle)		Eurasia
N. molini	Artiodactyla: tayassuid (collared peccary)		South America
N. nachitchivanicus	Artiodactyla: bovid (sheep, goat)		
N. nemorhaedi	Artiodactyla: bovid (long-tailed goral)	small intestines	Asia
N. neomexicanus (*Rauschia*)	Lagomorpha: leporid (rabbit)	small intestines	North America
N. neotoma (syn. *N. tortuosus*)	Rodentia: cricetid (bushy-tailed woodrat)		North America
N. odocoilei	Artiodactyla: cervid (moose, fallow deer, red deer, mule deer, southern mule deer, white-tailed deer, reindeer, boreal woodland caribou), bovid (sheep, bighorn sheep, mountain goat)		North America
N. oiratianus (incl. subspp. *oiratianus, interruptus*, syn. *N. lanceolatus*)	Artiodactyla: antilocaprid (pronghorn), bovid (cattle, sheep, bighorn sheep, Dall sheep, argali, chamois, goat, mountain goat, Iberian ibex, goitered gazelle), camelid (Bactrian camel, dromedary), cervid (roe deer, red deer)		worldwide
N. petrovi (*Rauschia*)	Lagomorpha: leporid (tolai hare)		Eurasia
N. roscidus	Artiodactyla: bovid (European bison, sheep), cervid (red deer, fallow deer)		Europe
N. rupicaprae	Artiodactyla: cervid (roe deer), bovid (mouflon, chamois)		Europe
N. schulzi	Artiodactyla: bovid (sheep)		
N. skrjabini	Artiodactyla: bovid (muskox), cervid (reindeer)		North America
N. spathiger (syn. *Strongylus*) (thread-necked worm)	Artiodactyla: antilocaprid (pronghorn), cervid (moose, roe deer, fallow deer, red deer, mule deer), bovid (cattle, sheep, bighorn sheep, Dall sheep, argali, mouflon, chamois, goat, alpine ibex, Iberian ibex, blackbuck, bushbuck, grey rhebok, Cuvier's gazelle, dama gazelle, dorcas gazelle, goitered gazelle, Cape grysbok, common duiker), camelid (dromedary, llama); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Rodentia: ctenodactylid (common gundi); Galliformes: phasianid (turkey); Struthioniformes: struthionid (ostrich)	small intestines [diarrhoea]	worldwide
N. sugatini	Artiodactyla: bovid (goitered gazelle)		Eurasia
N. tarandi	Artiodactyla: bovid (sheep, muskox), cervid (moose, reindeer, Greenland reindeer)		Eurasia
N. tortuosus	Rodentia: cricetid (pack rat)		North America
N. triangularis (*Rauschia*)	Lagomorpha: leporid (snowshoe hare)		North America
N. urichi	Artiodactyla: cervid (red brocket); Carnivora: procyonid (crab-eating raccoon)		South America
N. weinbergi	Primates: hominid (chimpanzee)		Africa
N. wittenbergi	Artiodactyla: bovid (goat)	intestines	Israel
N. zembrae	Lagomorpha: leporid (rabbit)		

Parasite morphology: *Nematodirus* spp. form 3 different morphological stages in their developmental cycles: eggs, larvae; and adult worms. Eggs laid by gravid female worms are unusual in that they are almost twice the size of other trichostrongyle eggs, measuring 150-260 x 67-118 µm. They are rhomboid in shape with curved sides and rounded poles, surrounded by thin clear-brown shells, and contain a central morula (comprising 2-8 blastomeres) only partially filling the fluid-filled interior. Larval development in the genus *Nematodirus* is also unique because formation of the first 3 larval stages (L1-L3) takes place within the eggs before they hatch. Embryonation generates L1 which moult to L2 which then moult to L3. Larval stages measured from 750-1,250 µm in length, including their long attenuated tails (up to 160 µm long). Upon hatching, L3 are released still encased within the L2 cuticle which appears as a closely-fitting sheath with a long tail sheath extension (207-309 µm) of which the terminal 50-60% is filamentous (the L1 cuticle is often left behind in the eggshell). Infective L3 have broad rounded heads, intestines comprising 8 cells, and their tails vary in morphology according to species, being pointed (*N. helvetianus*), lobed (e.g. *N. filicollis*), notched (e.g. *N. battus*) or stumpy (e.g. *N. spathiger*). Adults are slender red-brown worms measuring from 10-30 mm in length. They have a distinctive swelling or inflation of the head (cephalic vesicle) and thin thread-like anterior ends often coiled, twisted or tangled together. The oral opening is encircled by small perioral denticles (sometimes called the corona radiata) and the dorsal aspect of the anterior oesophagus bears a cuticularized tooth (neodont formation). Worms are bound by a cuticular synlophe with prominent

transverse striations in the cephalic region followed by longitudinal body ridges, restricted to the anterior half in females. Adults are sexually dimorphic, with female worms being larger than males (15-30 mm cf. 10-16 mm). Mature males possess a well-developed copulatory bursa with 2 large lateral lobes, each with 5 supporting rays (comprising muscular elements following nerve channels to terminal papillae) arranged in a 2-3 configuration (sometimes tending to 2-1-2) whereby the 2 ventral rays are separate from the rest), and a smaller symmetrical dorsal lobe (with the supporting ray split into 2 parallel processes for *N. battus* or 4 processes for other species). Males lack a gubernaculum and telamon, but possess 2 long thin filiform spicules (0.9-1.3 mm) whose distal tips are fused and joined in a membrane (in contrast to the short and unjoined spicules of *Cooperia*). The spicule tips also differ in their ornamentation according to species; being heart-shaped (*N. battus*), lanceolate (*N. filicollis*), pointed (*N. helvetianus*) or rounded and spatulate (*N. spathiger*). Mature females are didelphic with 2 functional ovaries (whereas those of the genus *Ollulanus* are monodelphic). They are oviparous and developing eggs are found in the 2 uteri which open into a common vulva located in the posterior third of the body. The tip of the female tail is pointed in the case of *N. battus*, but is truncate with a prominent terminal spine for all other species.

Site of infection: Parasitic larval stages and adult worms infect the mucosa of the small intestines of their hosts, particularly the ileum. Worm eggs are excreted into the external environment with host faeces and produce preparasitic larval stages before hatching.

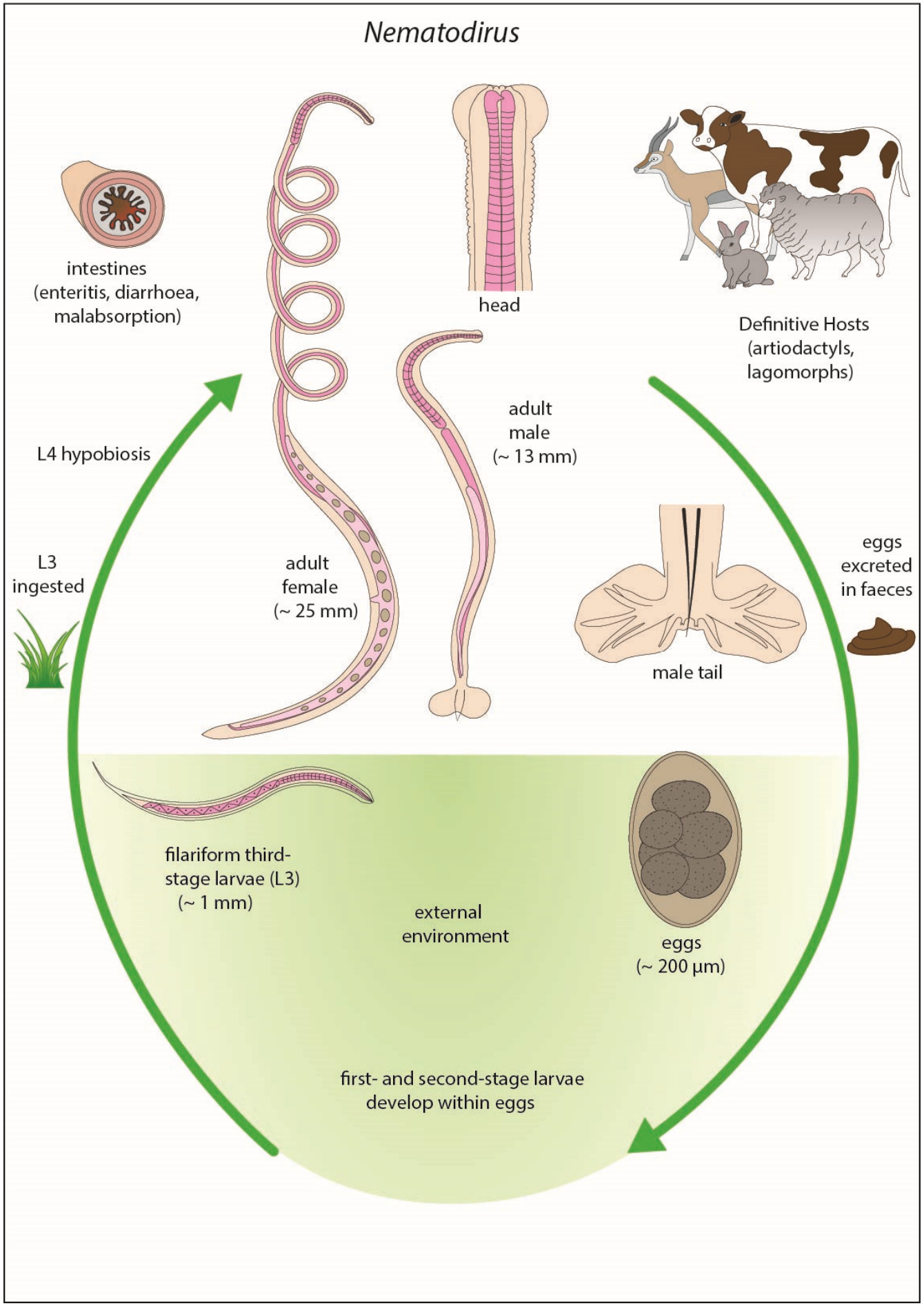
Pathogenesis: Infections by *Nematodirus* spp. are often asymptomatic in adult animals because the hosts acquire strong protective immunity following exposure. It has been suggested that most infections rarely cause disease by themselves, but contribute to the parasitic gastroenteritis observed in concomitant infections with other pathogens (especially other nematodes and some coccidia). Young animals, however, are susceptible to clinical disease due to their immunological immaturity and naivety. The severity of disease depends on the parasite species (*N. battus* being the most pathogenic), the intensity of infection (> 1,000 worms causing clinical disease), and host susceptibility (preweaners most at risk). The disease nematodirosis is characterised by the sudden onset of diarrhoea with marked dehydration, sometimes culminating in mortality. Infective L3 penetrate into the crypts of the small intestines where they develop to L4 and then young adults (L5) which emerge onto the mucosal surface, often coiling superficially around villi. All parasitic stages feed on host blood and tissues causing traumatic damage, erosive lesions, epithelial necrosis, hyperaemia and inflammation (catarrhal enteritis) which significantly alters villous architecture (distortion, compression and atrophy reducing mucosal surface area). The resultant malabsorption may result in profuse watery yellow-green diarrhoea, dehydration, anorexia, lethargy and unthriftiness with growth retardation, poor weight gain or weight loss. Clinical signs are mostly associated with larval development and the emergence of subadults into the lumen some 10-12 days after infection (note that this is during the prepatent period before adults become sexually mature and produce eggs). Disease may occur in calves and lambs as young as 6 weeks of age, but becomes more problematic at 9-15 weeks of age when preweaners begin to graze more regularly. Some larvae may undergo inhibited or arrested development (hypobiosis) in the mucosa over winter months, only resuming development in spring. Young animals placed on heavily contaminated spring pastures may therefore acquire intense infections over a short period of time resulting in acute disease.

Developmental cycle and mode of transmission: Like other trichostrongyles, *Nematodirus* spp. have direct monoxenous life-cycles involving faecal-oral transmission, but in this case infective L3 develop in excreted eggs before they hatch. Gravid female worms produce around 50 eggs per day which are passed into the external environment with host faeces. The large eggs embryonate and form L1, L2 and then L3 stages before hatching. This development may occur over 2-4 weeks in optimal conditions of moisture and temperature, but is often delayed for several months, with some reports extending up to 2 years. The eggs are highly resistant to both desiccation and freezing, so they may survive mild summers and cool winters. Indeed, most infections occur in temperate or cold regions, often in elevated mountainous areas. Eggs hatch in large numbers after rain, or following warming to > 10°C after prolonged cold periods. This may lead to an annual seasonal pattern of infection, predominantly in late spring, although hatching may be extended over a longer period under milder conditions making more than one annual generation possible for some species. Grazing animals become infected when they ingest infective L3 on herbage, either as free-living pasture stages or still contained within eggs. Ingested larvae exsheath in the gut and penetrate into crypts in the small intestines where they moult to L4 and then to subadults (sometimes designated L5). Young worms emerge back into the gut lumen where they become sexually mature. The prepatent period (time from infection to first egg excretion) ranges from 14-28 days.

Differential diagnosis: Infections may be indicated on the basis of clinical symptomatology (sudden diarrhoea) and predisposing history (notably, host age and grazing season), but other aetiological agents may be involved Coprological techniques are often used to detect the large distinctive worm eggs in faecal samples, usually following their concentration by sedimentation in water and/or floatation in saturated sugar or heavy-metal salt solutions. While some tests may be quantitated using volumetric chambers (McMaster or Whitlock slides) to provide eggs counts per gram of faeces (epg), they show poor correlations with worm burdens and the severity of clinical disease, particularly since most clinical signs occur during the prepatent period when immature stages damage the gut before egg production commences. Egg counts also not account for male worms, or for females not producing eggs due to their immaturity, senescence or immune-induced suppression of egg production. Faecal samples may also be cultured to yield L3 which can be identified microscopically by their morphological characteristics (broad rounded heads, intestines comprising 8

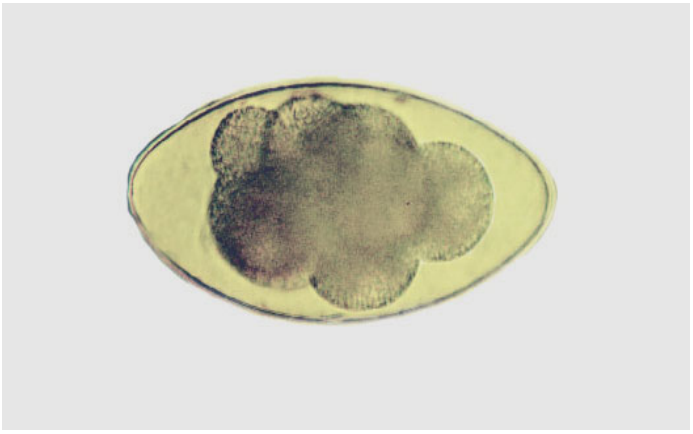
cells, and unique tails, all encased within filamentous sheaths with long tapering tails). Gut samples may also be collected from dead or sacrificed animals and examined for adult worms. However, the numbers of worms are often difficult to enumerate in gut washes as the thin-necked adults may be found in tangled masses. It is also difficult to recover developing larvae from intestinal crypts without resorting to strong acid digestion techniques. Several research laboratories have recently used molecular biological techniques to characterize different species following the polymerase chain reaction (PCR) amplification and sequencing of several nuclear genes (large and small subunit ribosomal RNA and their internal transcribed spacers I and II).

Treatment and control: Several broad-spectrum anthelmintic drugs have been used to effectively treat clinical infections in young livestock, including the benzimidazoles (thiabendazole, mebendazole, fenbendazole, oxfendazole, albendazole), probenzimidazoles (thiophanate, febantel, netobimin), macrocyclic lactones (avermectins, milbemycins), imidazothiazoles (levamisole) and tetrahydropyrimidines (morantel, pyrantel). The macrocyclic lactones were the most effective, even providing some short-term prophylaxis, although oral and parenteral formulations differed in their efficacy (the latter being less effective). The imidazothiazoles and tetrahydropyrimidines also exhibited little activity against hypobiotic larvae. Fortunately, there have been few reports on the emergence of drug resistance in these worms, but treatment protocols should be followed scrupulously to avoid under-dosing or unwarranted repetitive dosing which can select for drug resistance. The best time for treatment can often be predicted on the basis of climatic information (especially soil temperature) conducive to the development and hatching of eggs on pastures, particularly when warm weather follows a prolonged cold period in late winter or early spring. Young animals should be treated as a group and moved to clean pastures (spelled or previously ungrazed pastures) with adequate nutrition. Because animals develop strong protective immunity with age, drug treatments should be used strategically to reduce worm burdens and minimise pasture contamination, but still allow subclinical (low-dose) exposure to stimulate immune responses. Various farm management practices can also be used to help reduce pasture contamination, including rotational and/or mixed grazing (different cohorts or different species at different times), keeping stocking rates low, quarantining new introduced livestock, and periodically spelling or cropping pastures.

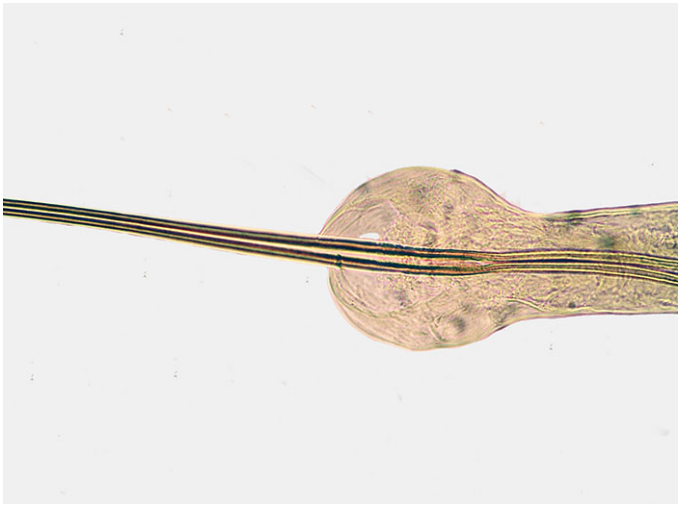

Nematodirus
intestines
(enteritis, diarrhoea,
malabsorption)
head
Definitive Hosts
(artiodactyls,
lagomorphs)
adult
male
(~ 13 mm)
L4 hypobiosis
L3
ingested
adult
female
(~ 25 mm)
eggs
excreted
in faeces
male tail
filariform third-
stage larvae (L3)
(~ 1 mm)
external
environment
eggs
(~ 200 µm)
first- and second-stage larvae
develop within eggs



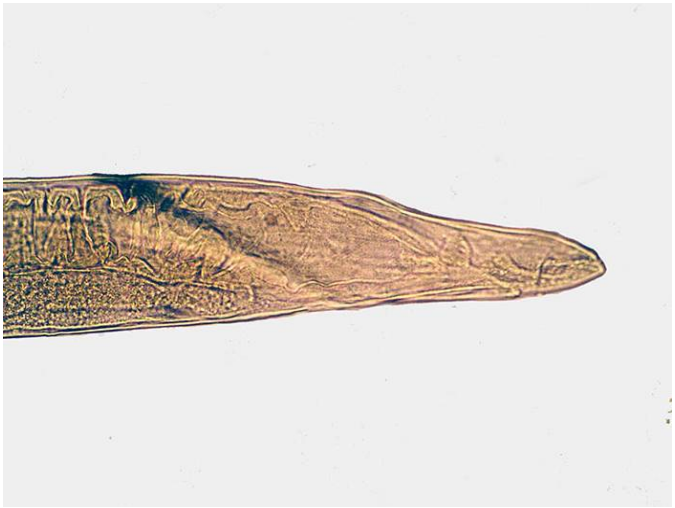
Nematodirus adult worm



Nematodirus worm egg



Nematodirus adult worm, male bursa



Nematodirus adult worm, head

Ollulanus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the molineids which are small hair-like worms with a small buccal capsule. Adults are usually found in the stomach/abomasum or small intestines of mammals or birds. They have direct life-cycles, usually involving eggs passed in faeces developing to L3 which are ingested and subsequently form adults. The monotypic genus *Ollulanus*, however, is unique as the females are viviparous (eggs hatch *in utero*) releasing L3 which may undergo auto-infection or be shed in vomitus to be ingested by new hosts. Infections may cause gastritis, vomiting and emaciation in cats, and occasionally pigs.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Molineidae (reduced buccal capsule, cephalic vesicle, female tail with spine/cusps, direct cycles)
Subfamily:	Ollulaninae (head with spiral coil, female tail with cusps, viviparous (develop to L3 in uterus))
Genus:	*Ollulanus* (parasitic in stomach of cat/fox/pig)
Species:	various species cause gastritis in felids and suids

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Trichostrongylina (trichostrongyles)				
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56

Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Some authorities recognize a superfamily Molineoidea comprising 4 families: Molineidae in mammals, birds and reptiles; Amphibiophilidae mainly in amphibians; Mackerrastrongylidae in monotremes and marsupials; and Strongylacanthidae in bats. These worms have a buccal capsule reduced to an annulus, most have a cephalic vesicle and a bilaterally symmetrical synlophe, the males have an asymmetrical bursa and females have a tail with a caudal spine or numerous tubercles. The family Molineidae contains 6 subfamilies: Nematodirinae (corona radiata, neodont formation, bursa with short dorsal ray split to base, didelphic, oviparous, 6 genera in herbivorous mammals); Ollulaninae (synlophe absent, cephalic vesicle absent, bursa with short dorsal ray, monodelphic, viviparous, female tail with 3-5 tubercles, 1 genus in felids and occasionally suids); Molineinae (bursa with short dorsal ray not split to base, synlophe with perpendicular ridges, 26 genera in amphibians, reptiles and mammals); Dromaeostrongylinae (bursa with elongate dorsal ray, 1 genus in birds); Merstensinematinae (bursa with short dorsal ray not split to base, synlophe absent, 2 genera in reptiles and amphibians); and Anoplostrongylinae (cephalic vesicle with armature, synlophe with dorsoventral ridges, bursa with short dorsal ray not split to base, 25 genera in edentates and bats). Specific molineid genera of veterinary and medical importance are compared in the following table.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs/larvae**
Subfamily Ollulanidae					
Ollulanus	1	carnivores	stomach	0.7-1.0 mm long, small buccal capsule, females with trifid tail, viviparous (eggs hatch *in utero*), larvae shed in vomitus (or auto-infection)	larvae 400-500 µm, tail with terminal cusps
Subfamily Nematodirinae					
Nematodirus (thin-necked intestinal worm)	53	artiodactyls, lagomorphs	small intestines	10-30 mm long, cephalic inflation, thin neck, mid-body spiral coil, female with spiked tail, male with long thin spicules	150-260 x 67-118 µm, eggs ellipsoidal, thin-shelled

The subfamily Ollulaninae contains a single genus (*Ollulanus*) with a single species (*O. tricuspis*) infecting the stomach of felids, and occasionally canids and suids. While infections have been reported sporadically from many countries, they are probably widespread around the world together with their felid hosts. They have unusual cryptic life-cycles as the female worms are viviparous and produce live larvae which are transmitted in host vomitus (rather than being oviparous and laying eggs which are transmitted in host faeces, like many other gastroenteric nematodes).

***Ollulanus* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**

O. tricuspis (syn. *O. suis, O. skrjabini*)	Carnivora: felid (cat, wild cat, lion, tiger, cougar, cheetah), canid (dog, red fox); Artiodactyla: suid (pig)	stomach [gastritis, emaciation, vomiting]	Europe, Americas, Australasia

Parasite morphology: The species *Ollulanus tricuspis* forms 2 different morphological stages in its developmental cycle; namely, larvae (4 stages designated L1-L4); and adult worms. While female worms do produce eggs, they embryonate and hatch internally (*in utero*). Three sequential larval stages develop coiled up within the eggs; rhabditiform L1 measuring around 350 µm long with round blunt tails; rhabditiform L2 measuring around 340 µm long with tails bearing 3 cusps; and strongyliform L3 measuring from 400-500 µm in length and having short tails with at least 3 terminal cusps. Following hatching, L3 uncoil in the uterus of the female and are then released into the gut lumen of the host. Following infection (or auto-infection) by freed L3, the larvae moult firstly to L4 and then to young adults on the gastric mucosa. L4 measure from 625-650 µm in length and have begun to develop male or female genitalia. Adults are small hair-like worms 0.7-1.0 mm long and are not visible to the naked eye. They are surrounded by a tough cuticle with conspicuous longitudinal ridges and cervical papillae. The anterior end usually coils around on itself but does not possess an anterior inflation (cephalic vesicle). They have a cup-like buccal capsule that does not contain teeth, hooks, cutting plates or other ancillary structures. The elongate esophagus is slightly swollen where it joins the tubular intestine. Mature worms are sexually dimorphic, with females being larger than males (0.8-1.0 x 0.03 mm cf. 0.7-0.8 x 0.04 mm). Males have a well-developed copulatory bursa with 2 large lateral lobes, each supported by 5 rays (comprising muscular elements following nerve channels to terminal papillae) arranged in a 2-1-2 configuration, and a smaller dorsal lobe (supported by a single short dorsal ray). They have 2 stout equal spicules 40-50 µm long, each with a longitudinal split, but they do not have a gubernaculum or telamon. Female worms are readily identified by their characteristic tails bearing 3 major bumps (cusps or tubercles) which are occasionally accompanied by up to 3 minor ones. They are monodelphic with a single ovary and uterus opening into a posterior vulva without a muscular ovejector. Mature females are viviparous as they produce 1-3 large eggs at a time that embryonate and hatch internally releasing L3.

Site of infection: Adult worms infect the fundus of the stomach, and are usually found covered in mucus with their anterior ends partly embedded in gastric crypts. There are essentially no free-living stages as female worms do not produce eggs but release L3 which exit the host in vomitus.

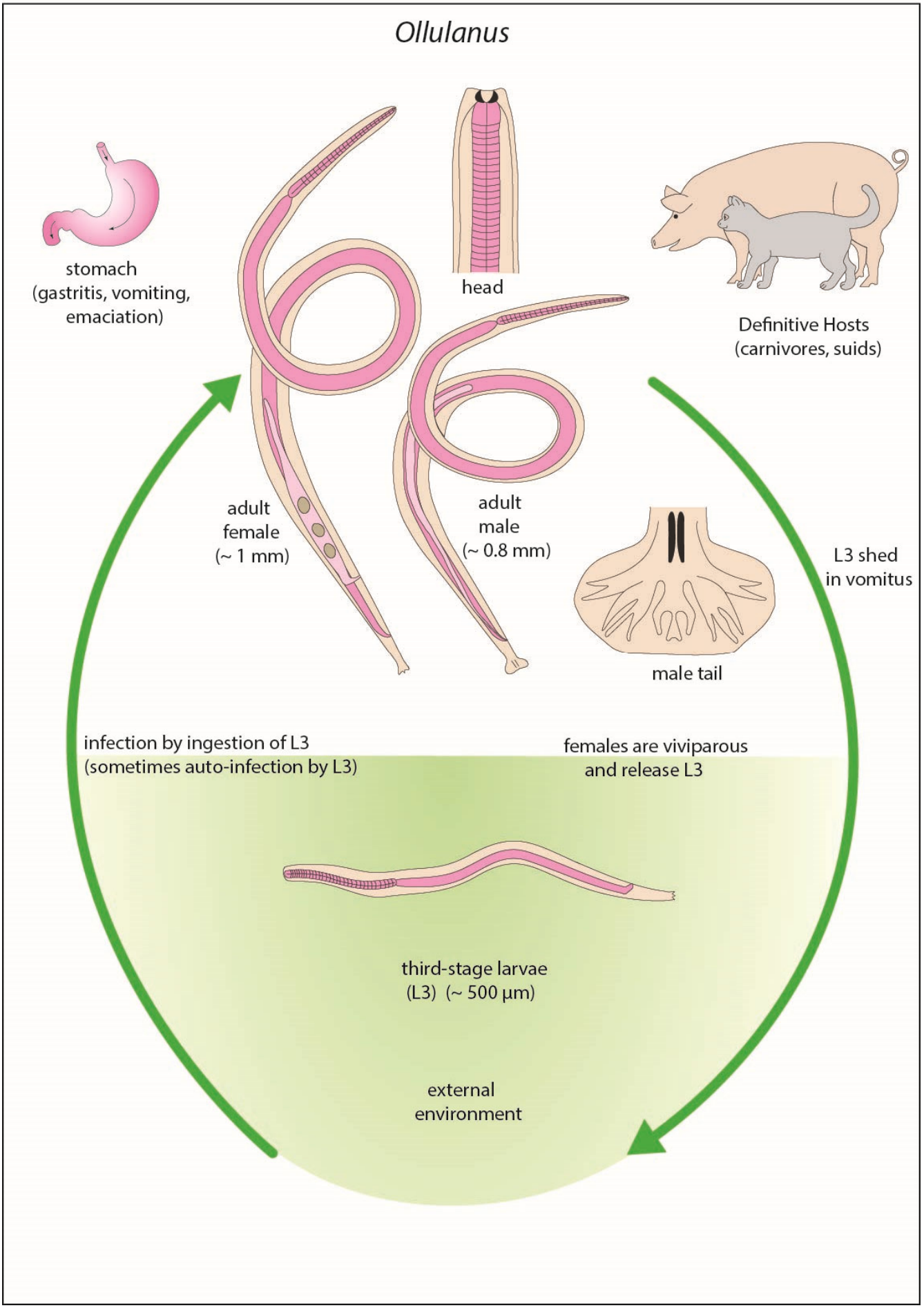
Pathogenesis: Most infections appear to be light and remain asymptomatic, but heavier or prolonged infections have been causally associated with intermittent vomiting in felids, sometimes in suids but rarely in canids. Immature and mature worms bury their heads in the gastric mucosa causing a mild erosive or catarrhal gastritis. The inflammation and excessive mucus production predisposes vomiting, often minutes or hours after eating. Heavy infections may result in severe chronic gastritis with mucosal erosion, hyperplasia, sclerosis and cellular infiltration with lymphoid aggregates and leucocytosis. Animals display recurrent vomiting contributing to dehydration, anorexia, weight loss and emaciation, sometimes culminating in death. Clinical infections have been recorded in domestic and stray cats, as well as in colony-reared cats and captive zoo animals (cheetahs, lions and tigers).

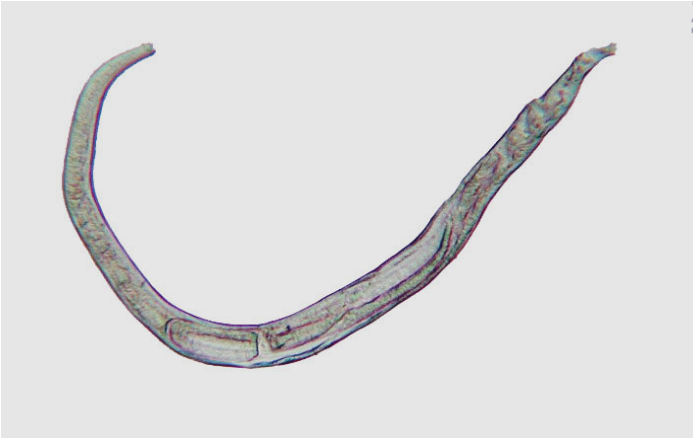
Developmental cycle and mode of transmission: *Ollulanus* has a simple direct monoxenous life-cycle, but its transmission is highly unusual in that infective larvae are transmitted via vomitus (and not by the faecal-oral transmission of worm eggs and the development of infective larvae on pastures). Viviparous females in the stomach mucosa produce and release L3 into the gut lumen which are then passed into the external environment in host vomitus (normally comprising undigested or partly digested food covered in mucus). Infective L3 have been found to survive in vomitus for up to 12 days and horizontal transmission to new susceptible hosts occurs when they ingest contaminated vomitus. The same individual host may also become re-infected by consuming its own vomitus, or when L3 in the stomach directly initiate a new cycle of development. Heavy infections therefore develop in individuals exhibiting regular vomition, although they can also build up by repetitive endogenous auto-infection. Infective L3 moult in the gastric mucosa to L4 and then to subadults (sometimes designated L5) which subsequently mature and mate. The prepatent period (time from infection to first release of L3) was found to range from 28-37 days. Worm burdens in domestic cats may involve only a few worms, although clinical infections often involve several hundred worms (mean intensity of 1,500 reported in several surveys) with occasional reports as high as 11,000 worms. While it has been suggested that long-haired cats may be more likely to transmit infections due to their greater frequency of vomition associated with hairball development after grooming, the most intense and severe infections have been observed in stray cats (that vomit from hunger) and in felids kept in crowded situations (zoos and animal breeding colonies).

Differential diagnosis: Clinical infections may be suspected in animals exhibiting regular vomition and weight loss, but many other gastroenteric pathogens may cause similar nonspecific signs. Diagnosis is usually afforded by the microscopic detection of larvae, sometimes adult worms, in vomitus (natural or following emesis) or in gastric lavages or endoscopic biopsies. Worms may be recovered from digesta and mucus by repeated dilution and sedimentation, or concentrated using sieves and funnels (e.g. Baermann's apparatus) using vomitus instead of faeces (parasites passing posteriad are digested and rarely seen in faeces). Mucosal scrapings can be taken post-mortem from dead or euthanized animals and examined for parasites, often following peptic digestion. In all instances, careful microscopy is required to differentiate larvae and adult worms from a range of other nematode parasites (e.g.

Aelurostrongylus abstrusus, *Aonchotheca* (*Capillaria*) *putorii*, *Physaloptera* and *Trichostrongylus* spp.) and pseudo-parasites (e.g. oxyurids of small prey animals eaten by felids).

Treatment and control: A range of anthelmintic drugs have been used to treat clinical infections in felids and suids, including macrocyclic lactones (ivermectin), benzimidazoles (fenbendazole, oxfendazole) and imidazothiazoles (levamisole, tetramisole). Repeated treatments were recommended to combat cyclic re-infection and auto-infection, although no endogenous developmental stages (L3, L4 and adults) appeared to be resistant to treatment. Control strategies involve restricting host access to infective material by improving hygiene (removing vomitus, disinfecting pens/cages/runs), isolating individuals (for treatment and to prevent unnecessary interactions) and ensuring housing facilities are secure (particularly against strays).


Ollulanus
stomach
(gastritis, vomiting,
emaciation)
head
Definitive Hosts
(carnivores, suids)
adult
female
(~ 1 mm)
adult
male
(~ 0.8 mm)
male tail
L3 shed
in vomitus
infection by ingestion of L3
(sometimes auto-infection by L3)
females are viviparous
and release L3
third-stage larvae
(L3) (~ 500 µm)
external
environment



Ollulanus adult worm, female



Ollulanus adult worm, male

Nippostrongylus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the heligmosomatids which are hookworm-like parasites found in the intestines of small mammals and birds. They have direct life-cycles, usually involving eggs passed in faeces developing to L3 which are ingested by new hosts and develop to adults. *Nippostrongylus* spp., however, may also infect hosts percutaneously, when L3 penetrate the skin, migrate through the lungs and form adults in the gut. Infections in rodents are generally subclinical, but heavy infections may cause verminous pneumonia. *N. brasiliensis* has been used as a laboratory model, although it can become problematic in animal colonies.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Heligmosomatidae (adults filiform, reddish in colour, direct cycle)
Genus:	*Nippostrongylus* (parasitic in small intestines of rodents)
Species:	*N. brasiliensis* causes verminous pneumonia in rodents

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Trichostrongylina (trichostrongyles)				
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61

Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Several families in the superfamily Strongyloidea have been grouped together with the trichostrongyles, while others have placed them in a new superfamily Heligmosomoidea; namely: Heligmonellidae (56 genera in mammals); Heligmosomidae (8 genera in small mammals); Herpetostrongylidae (13 genera in reptiles and marsupials); Nicollinade (2 genera in monotremes and marsupials); Ornithostrongylidae (8 genera in mammals); and Viannaliidae (7 genera in mammals). These worms are generally coiled and their synlophe is not bilaterally symmetrical. The family Heligmonellidae contains small worms with cephalic vesicles, rudimentary buccal capsules (reduced to an annulus), bursate males, and monodelphic oviparous females without spined tails. Worms have a synlophe with conspicuous longitudinal elevations (ridges), some of which are fused (comaretes) and some supported by underlying thickenings (paired thickenings termed carenes). Four subfamilies are recognised: Nippostrongylinae (carene present or absent, lateral ridges poorly developed, synlophe with 4-46 circumferential ridges continuous along length, axis of orientation of ridges 45-67° from sagittal axis); Brevistriatinae (carene present or absent, lateral ridges poorly developed, absent on ventral quadrant, axis of orientation of ridges 67-90° from sagittal axis); Heligmonellinae (carene absent, lateral ridges strongly developed, axis of orientation of ridges < 45° from sagittal axis); and Pudicinae (carene present, cuticular ridges absent on ventral quadrant, axis of orientation of ridges 67-90° from sagittal axis, dorsal ray divided in proximal half or with ventral comaretes).

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Subfamily Nippostrongylinae					
Nippostrongylus	10	rodents	small intestines	2-6 mm long, reddish in colour, reduced buccal capsule, oblique cuticular ridges, bursa asymmetrical (2-2-1), larvae with longitudinal alae	50-70 x 28-35 µm, ellipsoidal, thin-shelled

The subfamily Nippostrongylinae contains 29 genera (*Bunomystrongylus, Carolinensis, Euzetoda, Guerrerostrongylus, Hasanuddinia, Hassalstrongylus, Heligmonina, Heligmonoides, Hypocristata, Malaistrongylus, Malvinmea, Mammanidula, Mawsonema, Maxomystrongylus, Melomstrongylus, Montistrongylus, Neoheligmonella, Nippostrongylus* (syn. *Austroheligmonema*), *Odilia, Orientostrongylus, Paraheligmonelloides, Parasabanema, Rattustrongylus, Sabanema, Spalacina, Stilestrongylus, Suttonema, Trichofreitasia* and *Yatinema*) parasitic in rodents, dermopterans, lagomorphs, primates and insectivores. The genus *Nippostrongylus* is characterised by small red worms with cephalic vesicles, small buccal cavities, synlophes with oblique cuticular ridges and bursate males with asymmetrical dorsal rays. Ten species are recognized in a wide range of rodents and some in lemurs, lagomorphs and talpid insectivores. Infections are more common in temperate and tropical regions where warm moist conditions are more favourable for the survival of free-living stages. The host specificity of individual parasite species varies from narrow (oioxenous) to broad (euryxenous). The species *N. brasiliensis* is frequently found worldwide in rodents and has been used extensively as a laboratory model.

***Nippostrongylus* species**	**Definitive hosts**	**Location [Clinical signs]**	**Distribution**
N. brasiliensis (syn. *N. muris, Heligmosomum muris*) (rat intestinal worm, rat 'hookworm')	Rodentia: murid (black rat, Philippine black rat, brown rat, African grass rat, soft-furred rat, ricefield rat, lesser ricefield rat, Himalayan field rat, dusky field rat, Polynesian rat, Tanezumi rat, chestnut white-bellied rat, bush rat, house mouse, wood mouse, Eurasian harvest mouse, Algerian mouse, typical striped grass mouse, striped field mouse, Natal multimammate mouse, African pygmy mouse, gerbil), cricetid (golden hamster, reed vole, deer mouse), nesomyid (Gambian pouched rat), chinchillid (chinchilla); Eulipotyphla: soricid (greater white-toothed shrew); Lagomorpha: leporid (rabbit)	small intestines [pneumonia]	worldwide
N. djumachani (syn. *Longistriata*)	Rodentia: murid (bandicoot rat)		Asia, North Africa
N. magnus (syn. *Austroheligmonema*)	Rodentia: murid (fawn-footed mosaic-tailed rat, bush rat, brown rat, black rat, dusky field rat)		Australia, New Guinea, Indonesia
N. marhaeniae	Rodentia: murid (Moluccan prehensile-tailed rat)		Indonesia
N. rauschi	Dermoptera: cyanocephalid (Philippine flying lemur)		Philippines
N. rysavyi (syn. *Oswaldonema*)	Rodentia: cricetid (Chinese striped hamster, black rat)		Asia
N. sembeli	Rodentia: murid (yellow-tailed rat)		Indonesia
N. smalesae	Rodentia: murid (Whitehead's spiny rat)	small intestines	Indonesia
N. typicus (syn. *Austroheligmonema*)	Rodentia: murid (bush rat, dusky field rat)		Australia, New Guinea
N. witenbergi	Rodentia: murid (short-tailed bandicoot rat)	small intestines	Asia, North Africa

Parasite morphology: *Nippostrongylus* spp. form 3 different morphological stages in their developmental cycles: eggs, larvae (4 consecutive stages designated L1-L4); and adult worms. Freshly-laid eggs are thin-walled, ellipsoidal in shape measuring 50-70 x 28-35 µm, and contain a morula usually comprising 16-20 cells (sometimes 4-16 cells). First-stage larvae (L1) released from hatched eggs are elongate (280-300 µm long), bound by a thin transparent cuticle with lateral alae and have a rounded head, a rhabditiform (bulbed) oesophagus, and a tapering tail terminating in a sharp point. L2 are larger (470-750 µm long), bound by a thicker cuticle with obvious striations and longitudinal alae, and have rounded heads with an elongate buccal cavity, a rhabditiform oesophagus, darkened intestinal cells, and an attenuated tail. L3 are initially ensheathed in that they retain the L2 cuticle as a protective covering, but over time (days-weeks) the sheath contracts and develops an anterior split through which the L3 slowly and tentatively emerges. Ensheathed larvae measure up to 770-820 µm in length, while freed L3 measure from 600-750 µm. Infective L3 are bound by a thick cuticle with longitudinal alae, and have a rounded head with a small compressed buccal cavity, a thin strongyliform (non-bulbed) oesophagus, and a short tail. L4 are parasitic stages in which the genital primordia have begun to develop into specific male or female organs. Adult worms are small in size measuring from 2-6 mm in length and have a reddish colour due to endogenous haemoglobin present in the cuticle and tissues (and not from feeding on host blood). Their heads have an anterior expansion of the cuticle (cephalic vesicle) up to 50-70µm wide and they have a small buccal capsule without teeth or lips. Worms are bound by a distinctive synlophe with 14 or more oblique cuticular ridges (axis of orientation 45-67° from sagittal) sometimes supported by poorly-developed underlying thickenings (carenes). Adult worms are sexually dimorphic, with females being larger than males (2.5-6.0 x 0.09-0.13 mm cf. 2.1-4.5 x 0.08-0.10 mm). Mature males have an asymmetrical copulatory bursa consisting of two large lateral lobes supported by unequal rays (comprising muscular elements following nerve channels to terminal papillae) arranged in a 2-2-1 configuration, and a small dorsal lobe (supported by a dorsal ray split posteriorly into unequal branches). They also have 2 brown filiform spicules measuring from 0.44-0.55 mm in length. Mature females have a bell-shaped posterior end with a short conical tail, usually curved ventrally and lacking a terminal spine. They are monodelphic with a single ovary and uterus terminating in a posterior vulva overlaid by a small circular cuticular projection.

Site of infection: Adult worms are found in the small intestinal mucosa of their rodent hosts, predominantly in the duodenum and jejunum, but sometimes extending into the ileum. Developing larval stages may be found in various host organs and tissues as infective L3 undertake somatic migration via the circulation and/or lymphatics, with most forming L4 in the lungs and migrating up

the trachea to reach the gut. Worm eggs are voided into the external environment and give rise to free-living larval stages before becoming infective to rodents.

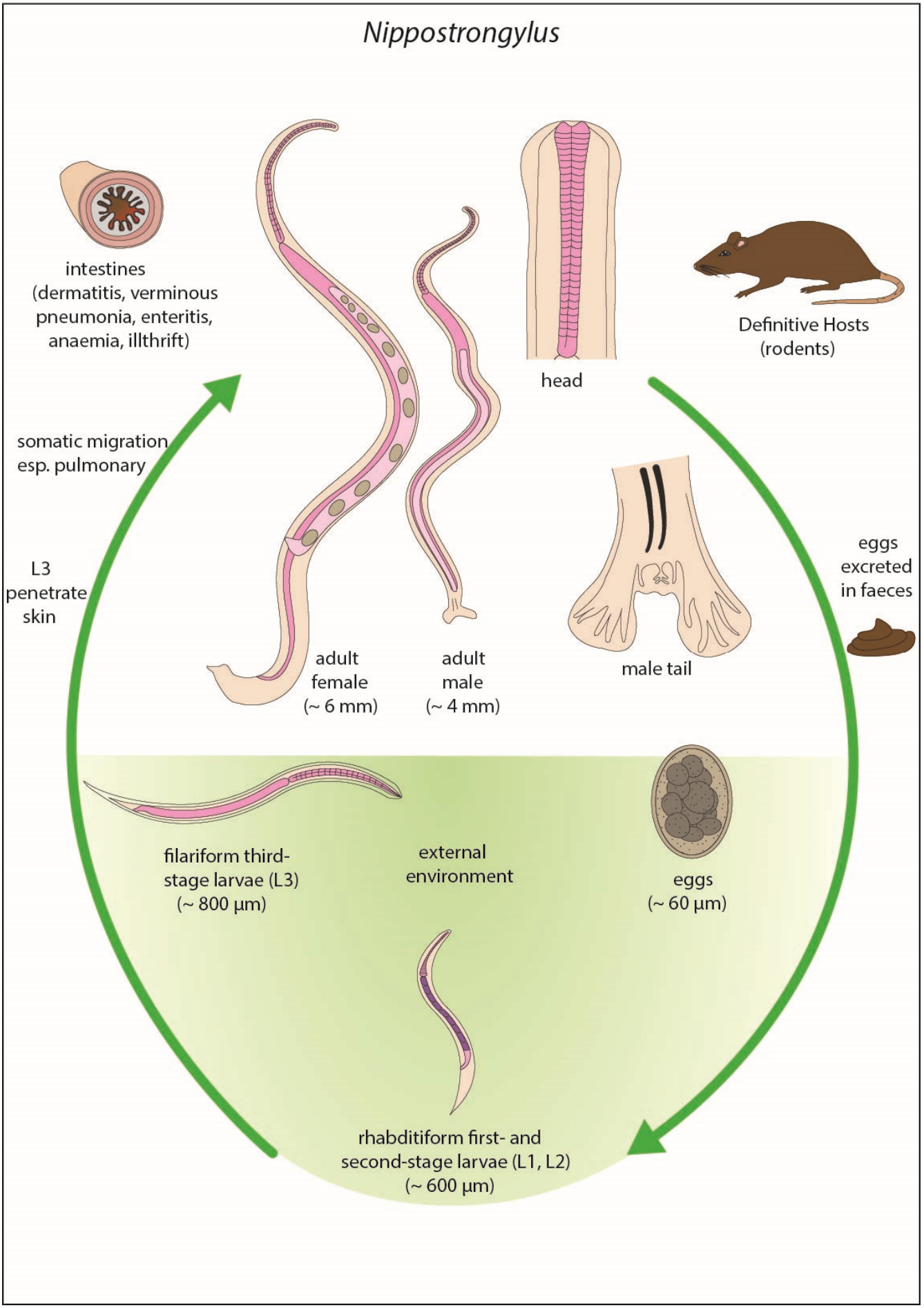
Pathogenesis: Light infections often remain asymptomatic, but heavier infections may cause acute and/or chronic clinical disease, the severity of which depends on parasite burdens (number of infective L3), host susceptibility (young and malnourished (iron and protein deficient) hosts most at risk) and immune status (prior exposure stimulates protective immune responses). There are 3 stages of infection which cause different types of disease: first, skin penetration by larvae causing dermatitis; then pulmonary migration of larvae causing lobar pneumonia and compensating emphysema; and finally, enteric feeding by adults causing malabsorption and anaemia. Infective L3 penetrate the skin and feed on host tissues while migrating through loose connective tissue to subcutaneous veins. Moderate to heavy infections may cause small haemorrhages and mild inflammatory responses in dermal tissues, which usually subside spontaneously within 2-3 days. Many larvae then migrate to the lungs where they feed and develop to L4, causing pulmonary inflammation, petechial haemorrhages, oedema, increased mucus production, alveolar consolidation and airway blockages leading to verminous lobar pneumonia (similar to chronic obstructive pulmonary disease (COPD)) with focal areas of compensating emphysema. L4 then ascend the bronchial muco-ciliary escalator to the trachea where they are swallowed reaching the small intestines after several days. Immature and mature worms burrow in the intestinal villi and crypts, often forming small pockets of worms coiling spirally around villi. Worms have small mouthparts and feed by releasing excretory-secretory (ES) products (including enzymes) and then ingesting the resultant slurry of host tissues and gut content. Feeding lesions may cause small haemorrhages with blood lost in the faeces, sometimes resulting in anaemia, particularly in iron-deficient individuals. However, local T-cell dependent immune responses cause most of the damage to the intestinal mucosa, which becomes grossly thickened and oedematous with red thickened pockets sometimes double normal size. The architecture and integrity of the mucosa changes markedly, with epithelial degeneration, autolysis, crypt hyperplasia, villous atrophy and sprue-like lesions producing a flat mucosa with reduced surface area leading to maldigestion, malabsorption, diarrhoea, anorexia, lethargy, malnutrition, weight loss and reduced growth rate (failure to thrive). Nevertheless, infected animals acquire a strong protective immunity resulting in the expulsion of adult worms, although sometimes a small population may survive for a prolonged period (known as concomitant or premunitive immunity, rather than sterile immunity).

Developmental cycle and mode of transmission: *Nippostrongylus* spp. have direct monoxenous life-cycles involving faecal-oral or transdermal transmission of infective larvae. Gravid female worms may lay up to 1,000 eggs per day which are excreted into the external environment with host faeces. The eggs embryonate in 18-24 hours and then hatch releasing rhabditiform L1 which subsequently moult to rhabditiform L2 and then filariform L3. Free-living larval stages can tolerate a wide range of ambient temperatures (from 7-50°C), but they are highly susceptible to desiccation. In optimal conditions (22-30°C with high humidity), L3 may form as early as 36-48 hours after egg excretion, but take longer in suboptimal conditions (5-6 days). L3 are ensheathed when first formed, but the sheath gradually contracts and splits longitudinally over several days allowing the enclosed larvae egress. Freed L3 are active stages exhibiting both horizontal migration (for dispersal) and vertical migration (ascending vegetation). Infective L3 either ingested orally or they penetrate the skin of the host (transdermal or percutaneous infection). The larvae migrate through superficial tissues and undergo somatic migration via the circulatory and/or lymphatic systems to various tissues (e.g. liver). However, most L3 undertake pulmonary migration to the lungs where they penetrate into alveoli and moult to L4 which ascend the trachea to be swallowed thereby accessing the intestines. Larvae may reach the lungs in as little as 11 hours and reside there up to 72 hours after infection. L4 may reach the intestines in as little as 41 hours but most take at least 72 hours. In the intestinal mucosa, L4 moult to young adults (sometimes designated L5) around 90-108 hours post-infection. They mature over several days and females first produce eggs 6-7 days after infection (= prepatent period) with greatest egg production occurring from 8-10 days. Adult worms usually do not persist long in the intestines as developing host immune responses lead to worm expulsion 7-14 days later, although a few adult worms may sometimes linger in hosts protected against challenge infections. Recurrent infections may become problematic in laboratory animal colonies where sanitation is poor.

Differential diagnosis: Infections are rarely diagnosed on the basis of clinical symptomatology as many aetiological agents may cause similar clinical conditions (pneumonia, diarrhoea, anaemia, anorexia, failure to thrive). Coprological techniques are therefore used to detect worm eggs in faecal samples, usually following their concentration by sedimentation in water and/or floatation in saturated sugar or heavy-metal salt solutions. Some techniques may be quantitated by counting the number of eggs in aliquots of diluted faeces in volumetric chambers (McMaster or Whitlock slides) to calculate the number of eggs per gram of faeces (epg). Worm egg counts provide a rough indication of worm burdens, even though they do not account for larval stages, male worms, or immature or senescent females. It is also difficult to differentially diagnose *Nippostrongylus* infections solely on the basis of egg morphology as the trichostrongyle eggs are similar in morphology to those of other nematodes (such as *Nematospiroides*). Recourse is sometimes taken to coprocultures whereby faecal samples are incubated for several days in moist conditions in order to harvest L3 for microscopic examination and identification by their characteristic features (size, longitudinal alae, compressed buccal cavity, filariform oesophagus, short tail). Infections may occasionally be diagnosed by the microscopic detection of developing worms in saline washes of tissue samples (liver, lungs, small intestines) collected at post-mortem. Infections in laboratory animal models have also been diagnosed using alternative technologies: including medical imaging (although X-rays tend to kill worms, especially males): ultraviolet spectroscopy (of faecal and gut samples taken from animals fed fluorescent dyes); and immunoserology (to detect specific host antibodies against worm antigens). Modern molecular biological techniques have also been used to characterize

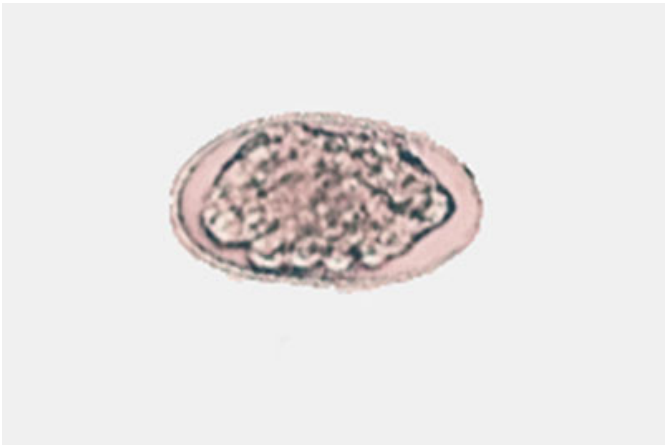
parasites after the polymerase chain reaction (PCR) amplification and sequencing of nuclear gene sequences (ribosomal RNA and internal transcribed spacer regions).

Treatment and control: Considerable experience has been gained in managing *N. brasiliensis* infections in laboratory rodents. Most infections are left untreated because host immune responses lead to the rapid expulsion of worms (self-cure phenomenon) and provide lasting protection against further infection. Nonetheless, a range of anthelmintic drugs have been tested, with benzimidazoles (mebendazole, fenbendazole, albendazole), imidazothiazoles (levamisole, tetramisole), diethylenediamines (piperazine) and tetrahydropyrimidines (pyrantel) found to be effective against enteric stages, and sometimes migrating larvae, without disrupting host immunity. Treatment was most effective when animals were provided with dietary supplements, notably protein and iron. Because hosts acquire solid protective immunity, a range of vaccination studies were conducted, with variable success in that they only stimulated partial protection and some demonstrated toxic side-effects. Various preventive strategies have also been used to help control infections, mostly in laboratory animal colonies where host and environmental management can reduce transmission (through improved hygiene, clean housing and bedding, food hygiene, dietary supplements, preventing unnecessary social interactions between animals and cohorts, and securing facilities against feral rodents).


Nippostrongylus
intestines
(dermatitis, verminous
pneumonia, enteritis,
anaemia, illthrift)
head
Definitive Hosts
(rodents)
somatic migration
esp. pulmonary
L3
penetrate
skin
adult
female
(~ 6 mm)
adult
male
(~ 4 mm)
male tail
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 800 µm)
external
environment
eggs
(~ 60 µm)
rhabditiform first- and
second-stage larvae (L1, L2)
(~ 600 µm)



Nippostrongylus adult worm



Nippostrongylus worm egg

Strongylus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the strongylids which are stout worms with a large buccal capsule often armed with teeth and with a leaf crown around the mouth. Small and large species occur in the intestinal or respiratory tracts of domestic animals and birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 before returning to the lumen to moult into adults. Extra-intestinal migrations of larvae and/or young adults through host organs sometimes occurs. *Strongylus* spp. are migratory large strongyles in the caecum/colon contributing to diseases associated with colic, diarrhoea and anaemia in horses worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Strongylidae (strongyles, large buccal capsules, often with teeth/leaf crown, infection by ingestion of L3, three pairs of branches in dorsal ray, equid hosts,)
Subfamily:	Strongylinae (large strongyles, red-worms, globular buccal capsules)
Genus:	*Strongylus* (parasitic in caecum/colon of equines)
Species:	various species cause diseases associated with colic, diarrhoea and anaemia in horses

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (*per os* or *per cutaneous*), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but

some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22

Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Strongyle worms are characterised by their prominent buccal capsules with lips, leaf crowns or labial collars at the mouth opening, sometimes with teeth or cutting plates. They are parasitic in a variety of organ systems in a range of animals, including the large intestines of mammals (ruminants, suids, elephants, perissodactyls, rodents, marsupials and primates), tortoises and ratite birds, the forestomach of marsupials, the trachea of birds and mammals, and the renal system of suids. Four families are recognised: Strongylidae (buccal capsule globular or cylindrical, oral opening circular, dorsal ray with 6 terminal branchlets, 32 genera in large intestines of mammals, reptiles and birds); Chabertiidae (buccal capsule globular or cylindrical, oral opening circular or oval, with leaf crown or labial collar, with up to 3 teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 22 genera in gastrointestinal tract of mammals); Syngamidae (buccal capsule subglobular, oral opening hexagonal, numerous teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 7 genera in respiratory, urinary and digestive tracts of mammals and birds); and Deletrocephalidae (oral opening hexagonal, dorsal ray with 6 terminal branches, 2 genera in large intestines of birds). The family Strongylidae contains 2 subfamilies conventionally differentiated on worm size and buccal capsule morphology: namely, Strongylinae ('large' strongyles (or strongylins) with globular or funnel-shaped buccal capsules) parasitic in the large intestines of perissodactyls, elephants and ratite birds (sometimes undergoing extra-intestinal migration); and Cyathostominae ('small' strongyles (or trichonemes, cyathostomes, cyathostomines, cyathostomins) with cylindrical or ring-shaped buccal capsules) found in the large intestines of perissodactyls, elephants, hyracoids, tortoises and occasionally some artiodactyls. Contemporary molecular characterization studies, however, do not fully support the separation of these subfamilies as several 'large' strongyles group together with the 'small' strongyles.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Strongylinae ('large' strongyles or strongylins)					
Strongylus (redworms)	13	ungulates, esp. equids	large intestines	10-50 mm long, red colouration, large globular buccal capsule often armed with teeth, leaf crowns, L3 with long filamentous sheath	64-99 x 36-58 µm, ellipsoidal, thin-shelled
Triodontophorus, Oesophagodontus, Craterostomum, Bidentostomum	11	equids	large intestines	6-25 mm long, globular or funnel-shaped buccal capsule often with teeth, leaf crowns [*despite their large strongyle features, molecular studies indicate that they are genetically closer to small strongyles]	66-130 x 33-68 µm. ellipsoidal, thin-shelled
Cyathostominae ('small' strongyles* or cyathostomins)					

Cyathostomum, etc.	6	equids	large intestines	5-30 mm long, red-grey colouration, cylindrical buccal capsule, with labial collar, some with dorsal gutter, external and internal leaf crowns variable	35-150 x 17-68 µm, ellipsoidal, thin-shelled

The subfamily Strongylinae conventionally contains 11 genera: 7 typified as large strongyles (*Strongylus* (syn. *Sclerostoma*, *Sclerostomum*, *Alfortia*, *Delafondia*) in equids; *Choniangium, Decrusia, Equinurbia* in elephants; *Codiostomum* in ostriches; *Macropicola* and *Hypodontus* in macropodid marsupials); and 4 other genera (*Triodontophorus* (syn. *Triodontus*)*, Bidentostomum, Craterostomum,* and *Oesophagodontus* (syn. *Pseudosclerostomum*) in equids, originally considered to be large strongyles. However, recent molecular-genetic studies have grouped them together with the small strongyles. The genus *Strongylus* contains large worms with deep buccal capsules, high collars, corona radiata with fine needle-like elements, buccal teeth if present with rounded points, males with 3 pairs of branches in the dorsal ray of the bursa, and straight spicule tips. Early studies recognised 5 *Strongylus* subgenera on the basis of host occurrence and the variable possession of spicule accessory pieces and buccal teeth: namely *S.* (*Strongylus*)*, S.* (*Alfortia*) and *S.* (*Delafondia*) in equids; *S.* (*Decrusia*) in elephants; and *S.* (*Dicerocola*) in rhinoceros. In contrast, other biotypic studies promoted many subgenera to generic status, but recent genotypic studies did not find significant differences between the subgenera in horses and thus collapsed them into the single genus *Strongylus*. Parasites in equids are commonly known as bloodworms (also redworms, palisade worms or migratory strongyles) and have been associated with thromboembolic colic (verminous arteritis) due to migrating larvae, as well as colonic ulceration and/or diarrhoea due to adult worms. Infections were prevalent in horses around the world until the introduction and widespread application of 'modern' anthelminthics in the 1970s.

***Strongylus* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
S. additictus (now *Decrusia*)	Proboscidea: elephantid (Indian elephant)		India
S. asini (syn. *S.* (*Delafondia*))	Perissodactyla: equid (donkey, horse, Burchell's zebra, Hartmann's mountain zebra, Grevy's zebra)	large intestines, liver [cysts]	Africa
S. auricularis	Anura: bufonid (common toad), ranid (edible frog), pelobatid (common spadefoot)		Eurasia
S. edentatus (syn. *S.* (*Alfortia*))	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan); Proboscidea: elephantid (African bush elephant); Rodentia: nesomyid (Gambian pouched rat)	large intestines [colic, anaemia]	worldwide
S. equinus (syn. *Sclerostonum armatum p.p.*) (syn. *S.* (*Strongylus*))	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, Burchell's zebra)	large intestines [colic, anaemia]	worldwide
S. hypostoma (syn. *Sclerostoma*)	Artiodactyla: bovid (sheep)		
S. micrurus	Perissodactyla: equid (horse, onager)		Asia
S. myoxi	Rodentia: glirid (edible dormouse)		Europe
S. nodularis	Gruiformes: rallid (Eurasian coot)		Europe
S. paradoxus (syn. *S.* (*Alfortia*))	Artiodactyla: suid (pig)		Europe
S. sagittatus (*Varestrongylus*?)	Artiodactyla: cervid (red deer)		Europe
S. tremletti (now *Dicerocola*)	Perissodactyla: rhinocerotid (black rhinoceros)	colon	Africa
S. ventricosus	Artiodactyla: cervid (red deer)		Europe
S. vulgaris (syn. *Sclerostonum armatum p.p.*) (syn. *S.* (*Delafondia*))	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, Burchell's zebra)	large intestines, mesenteries [colic, anaemia]	worldwide

Many early descriptions of enteric bursate nematodes in mammals, reptiles and amphibians recorded species within the genus *Strongylus s.l.* (*sensu latu*, in the broad sense), but most have since been reclassified to other strongylid genera: e.g., species in sheep included *Strongylus contortus* (now *Haemonchus contortus*)*, Strongylus hypostomum* (now *Chabertia ovina*)*,* and *Strongylus filaria* (now *Dictyocaulus filaria*)*.* There are therefore many historical records of *Strongylus* spp. which are no longer valid as they have been synonymized elsewhere or are considered *nomen dubium* or *species inquirenda*.

Parasite morphology: *Strongylus* spp. form 3 different types of developmental stages: eggs; larvae (L1-L4); and adult worms. Freshly-laid eggs are elliptical to ovoid in shape, ranging in size from 64-99 x 36-58 μm depending on species (e.g., *S. vulgaris* eggs: 64-75 × 36-46 μm, *S. asini* eggs: 75 × 45 μm, *S. equinus* eggs: 71-90 × 42-58 μm, *S. edentatus* eggs: 90-99 × 43-51 μm). The eggs are surrounded by a smooth thin eggshell and contain a morula at the 4-8 cell (blastomere) stage of development. The eggs release first-stage larvae (L1) which undergo 3 moults, forming L2, L3 and L4 before moulting to form young adults. L1 and L2 are free-living stages measuring up to 750 μm in length and they have a rounded head, a rhabditiform (bulbed) oesophagus, and a long tapering tail. L3 begin as free-living ensheathed stages but when they become infective and are ingested by a suitable host, they exsheath and become parasitic. The sheath is formed by retention of the L2 cuticle as a protective covering and it characteristically has a long filamentous tail (260-300 μm). Including the sheath, L3 range from 740-1,090 μm in length, but they do exhibit some species-specific variation with respect to size as well as gut structure. *S. edentatus* form short thin L3 (740-840 μm long) with the gut (alimentary tract) comprising 18-20 poorly-defined elongated cells, *S. equinus* form long thin L3 (920–1,020 μm) with the gut comprising 16 poorly-defined rectangular cells, and *S. vulgaris* form long broad L3 (930-1,090 μm) with the gut comprising 28-32 well-defined rectangular cells. All L3 have conical heads with small buccal cavities and a long thin strongyliform (non-divided) oesophagus. L4 are parasitic stages that are 2-5 times the size of L3 and whose genital primordia have begun to display gender-specific organs (notably male bursa and female vulva structures). Adults are large stout tubular worms measuring from 10-50 mm in length by 1.0-2.3 mm in width. They are often dark red to light black in colour due to their uptake of host blood (hence commonly known as red-worms or blood worms). They are bound by a tough cuticle with circular striations but lacking longitudinal ridges (synlophe absent) and lacking an anterior inflation (cephalic vesicle absent). The anterior oral opening is circular and surrounded by well-developed corona radiata with the external leaf crown containing longer but fewer needle-like elements than the internal leaf crown (40-75 cf. 42-80). The buccal capsule is large and subglobular (deeper than wide) and possesses a dorsal gutter (containing the duct of the dorsal oesophageal gland) and a variable number of teeth (e.g. no teeth for *S. edentatus,* 2 rounded teeth for *S. vulgaris,* 2 lobar teeth for *S. asini,* and 3 pointed teeth for *S. equinus*). Adult worms are sexually dimorphic, with females being larger than males (e.g. *S. vulgaris* females 13-25 x 1.0-1.4 mm cf. males 10-19 x 1.0-1.4 mm; *S. edentatus* 28-45 x 1.3-2.2 mm cf. 19-28 x 1.3-2.2 mm; *S. equinus* 35-50 x 1.1-2.3 mm cf. 24-36 x 1.1-2.3 mm. *S. asini* 30-42 mm cf. 18-33 mm). Mature males have a distinctive copulatory bursa comprising 2 medium lateral lobes supported by rays (comprising muscular elements following nerve channels to terminal papillae) arranged in a unique configuration (2 short ventral rays closely adjoined, 3 lateral rays radiating from a common stem, and single externodorsal ray arising from the base of the dorsal ray) and a well-developed rounded dorsal lobe supported by a dorsal ray with 3 pairs of branches. Males have a short conical genital cone, a small gubernaculum and 2 elongate spicules ranging in length from 1.9-3.2 mm with straight or curved tips (fused in the case of *S. vulgaris*). Mature females are didelphic with 2 ovaries and uteri connected to a vagina by paired muscular ovejectors (with a T-shape configuration) which open into a common vulva located in the posterior third of the body but anterior to the anus. The tail of female worms is short and tapers to a fine point. Females are oviparous and they lay numerous eggs.

Site of infection: Adult worms are luminal but attach to the mucosa of the large intestines (caecum and colon); while larval stages (L3 and L4) undergo extensive extra-intestinal migration (varying for each species) before returning to the gut and maturing to adults. Worm eggs deposited on pastures in faecal pats give rise to 2 free-living larval stages (L1-L2) before moulting to infective L3.

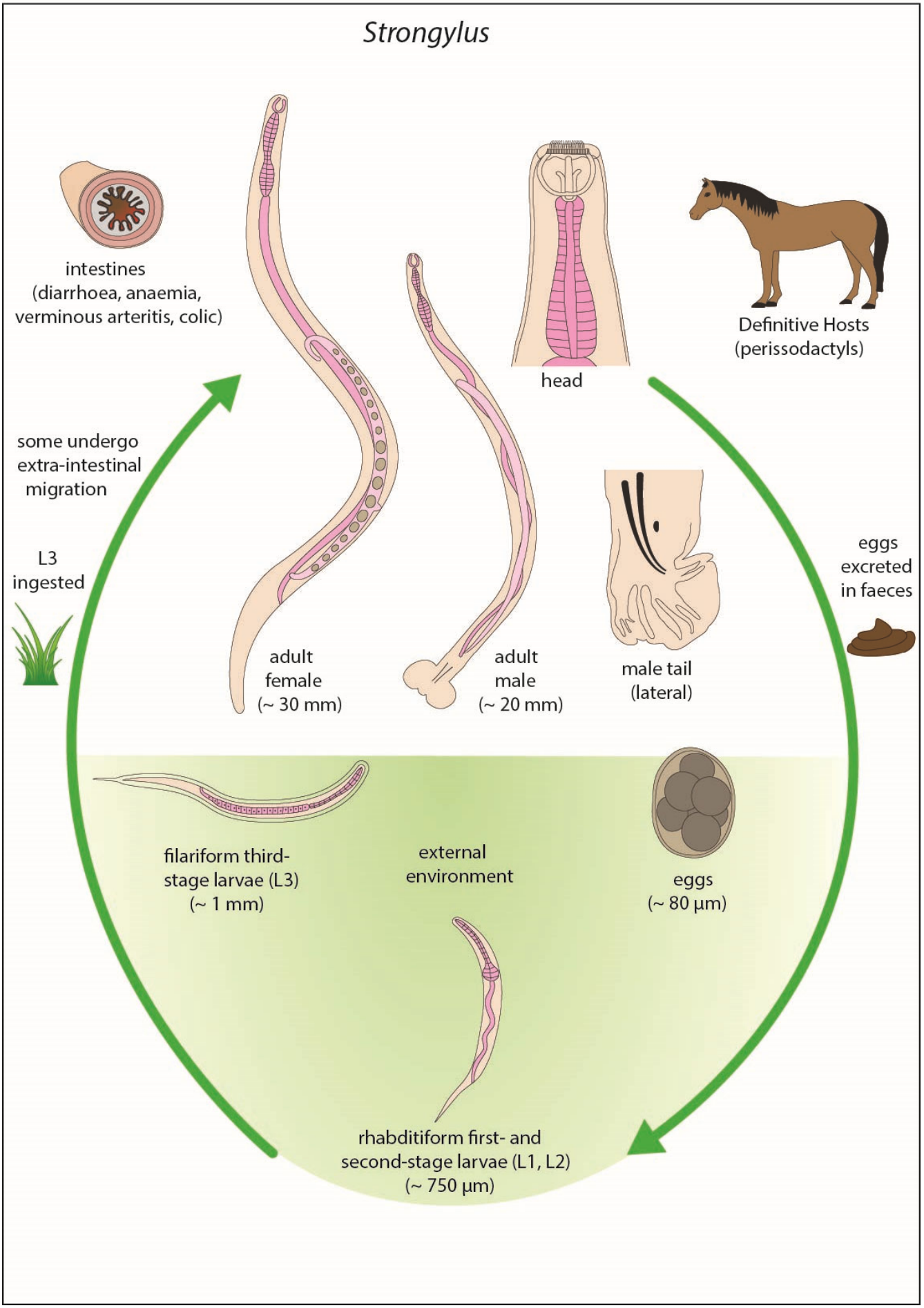
Pathogenesis: Strongylin infections (particularly *S. vulgaris*) can cause serious disease in domestic equids. In the past, the prevalence of disease (strongylosis/strongyliasids) was substantial, but the widespread introduction (from the 1970s onwards) and application of anthelmintic drugs led to a significant reduction in prevalence over time. Nonetheless, animals are still at risk of disease, depending on the pathogenicity of the parasite species involved (*S. vulgaris* being the most pathogenic), the intensity of infection (number of parasites), the stage of infection (migrating larvae cause more serious pathology than feeding adult worms) and host susceptibility (young and naïve animals are most at risk). Adult worms are tissue-plug feeders as they draw a plug of mucosa into their large buccal capsules, where it is broken down by teeth/plates and enzymes secreted via the dorsal gutter. This feeding also causes blood loss as they frequently rupture capillaries ingesting some blood as well as causing petechial haemorrhages and leakage. Worms are aggressive feeders and they frequently move to new feeding sites leaving behind small bleeding ulcers. Heavy feeding may result in significant traumatic damage to the intestinal mucosa, colonic ulceration, mild anaemia (normochromic normocytic), hypoproteinaemia, fluid and protein loss, dehydration, depression, anorexia, weight loss, emaciation, poor condition and performance, and sometimes diarrhoea, fever and/or colic. However, most of the pathogenic effects are associated with the earlier extra-intestinal migration of developing larval stages which cause mechanical damage, inflammation (particularly linked to arteritis), intravascular thrombus formation, emboli, fibrosis and/or colic. The route of migration, and pathological consequences, varies for each *Strongylus* species, but it involves intra-abdominal organs and blood vessels over a period of 6-12 months. *S. vulgaris* larvae migrate along the walls of mesenteric arteries, *S. edentatus* larvae migrate to the liver and then the abdominal walls, and *S. equinus* larvae migrate through the intestinal mucosa to the liver and then the pancreas. For most species, late-stage larvae returning to the caecum/colon form nodules in the intestinal walls which subsequently rupture releasing young adults into the lumen. Encysted larvae provoke minimal inflammatory responses, but the synchronous emergence of large numbers may cause diffuse inflammation. *S. vulgaris* is the most pathogenic species, as the intravascular migration of larvae can cause a severe verminous arteritis with marked intimal thickening, cellular infiltrates, thrombotic lesions and ensuing emboli. Thromboemboli released from the arterial wall can partially or completely block vessels downstream in the large intestines, resulting in ischaemia (as a consequence of restricted blood flow or blockage), infarction, necrosis (sometimes with ensuing gangrene) and associated clinical

signs including anorexia, constipation/diarrhoea, marked pyrexia, and a rapid onset of severe colic (intermittent or persistent pain in the abdominal cavity), substantially elevated respiratory and heart rates, and sudden death (sometimes due to rupture of aneurisms close to the posterior aorta). Thromboemboli released from the arterial wall (of heavily infected equids) can also travel to and intermittently or completely occlude the femoral artery (uni- or bi-laterally – usually unilateral), resulting in hypoxia or ischaemia in the musculature of the rear leg(s). Affected horses exhibit an 'intermittent lameness', as the emboli can dislodge within the artery during exercise (enabling blood to flow and oxygen to get to muscles). The severity of disease usually depends on the number of migrating larvae, although moderate infections by 600 larvae can be fatal in foals with low levels of immunity. Acute disease is often observed in older foals/yearlings when grazed on heavily contaminated pastures, while chronic sporadic disease can become apparent over months to years. *S. equinus* and *S. edentatus* larvae may also cause haemorrhages, oedema, inflammation, fibrosis and/or nodule formation in the tissues through which they move (liver, pancreas, peritoneal cavity), but the lesions not as severe as those caused by *S. vulgaris* larvae. Aberrant larval migrations have been associated with haemorrhages and granulomatous lesions (sometimes with adhesions or 'tags') in the abdominal muscles, omentum, ileum wall (haemomelasma ilei), kidneys, testes, diaphragm or lungs. Changes to clinical parameters during larval migration have included reduced haematocrits, hypoproteinaemia (particularly hypoalbuminaemia), hypergammaglobulinaemia, and leucocytosis (including eosinophilia).

Developmental cycle and mode of transmission: *Strongylus* spp. have direct monoxenous life-cycles involving the faecal-oral transmission of infective larvae (L3) from pastures. Gravid female worms lay many eggs which are excreted with host faeces contaminating the external environment. Eggs embryonate and hatch in faecal pats releasing free-living rhabditiform L1 which feed on bacteria. These larvae moult to free-living L2 which also feed on bacteria. Eventually they moult to form L3 which are ensheathed (encased in L2 cuticle) and therefore do not feed. Development to L3 may be completed in as little as 3 days under optimal conditions (warm and moist), but usually takes 1-2 weeks in suboptimal conditions (cool and/or dry). L3 can survive for months in faecal pats or in the underlying soil, even surviving cold winters under protective snow cover. Given adequate moisture (particularly following rainfall), L3 exhibit horizontal migration (dispersing from faecal pats) and vertical migration (ascending vegetation). Hosts become infected when they ingest infective L3 when grazing. The L3 exsheath in the gastrointestinal tract and undergo extensive somatic (intra-abdominal) migration before returning to the large intestines to mature as adults. The long duration of larval migration accounts for very long prepatent periods (5-12 months) before worms mature and produce eggs. The route of migration also varies for each species. *S. vulgaris* L3 penetrate the intestinal mucosa and moult to L4 in the submucosa over 5-7 days. These larvae penetrate blood vessels and migrate along the endothelium of the mesenteric arterial network for several months before moulting and migrating to the intestinal wall and form nodules which eventually rupture releasing young adult worms into the lumen. The prepatent period (time from infection to first egg production) is 5-7 months and the patent period (duration of egg production) can last up to 18 months. *S. edentatus* L3 migrate via the portal system to the liver where moult to L4 (some within granulomata). Weeks later, they emerge and enter the hepatic ligaments and migrate retroperitoneally through the subperitoneum, mesenteries and abdominal wall (predilection for the flanks). Here they moult to L5 which migrate back to the large intestines forming purulent nodules which rupture releasing young adults into the lumen. The prepatent period is 10-11 months and patency may last for up to 18 months. *S. equinus* L3 form haemorrhagic nodules in the muscular and subserosal layers of the intestines before moulting to L4 and migrating across the peritoneal cavity to the liver where migration continues for several weeks. Then, L4 enter the pancreas and develop and migrate to the gut lumen via the connective tissue adhesion of the pancreas and the head of the caecum. The prepatent period is 8-9 months and patency may last for 18 months. Infections in equids typically involve large mixed populations of numerous strongyle species, so that the epidemiological and clinical pictures can become confounded. Although worms may persist year-round, many infections exhibit annual seasonal cycles, with egg production and pasture larvae development and survival varying markedly depending on climatic conditions and geographic location (higher in spring in temperate regions or in autumn in subtropical regions).

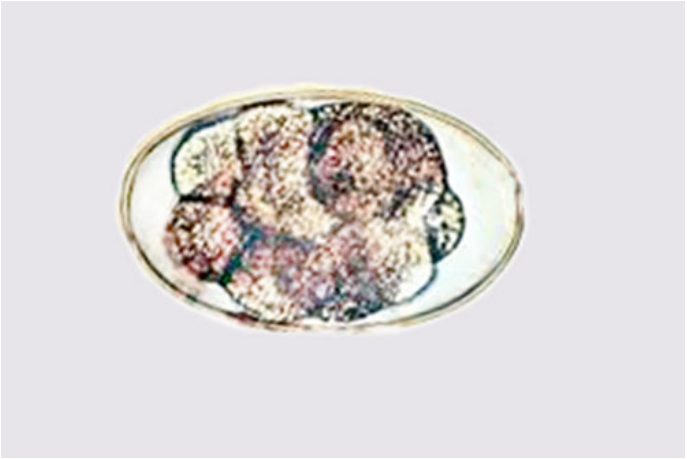
Differential diagnosis: While infections may be suspected on the basis of clinical signs (acute or chronic colic) and appropriate history (e.g., young animals, climate and season), other aetiological agents may be implicated. If verminous arteritis is considered as a cause of colic, physical examination (palpation per rectum) may reveal a painful enlargement of the root of the mesentery. Various clinical parameters are also indicative but not definitive, including changes in serum biochemistry (hypoproteinaemia, hypoalbuminaemia, increased alkaline phosphatase, increased gamma-glutamyl transpeptidase), haematology (anaemia, leucocytosis, eosinophilia) and discolouration of peritoneal fluid (dark yellow). Patent infections are usually diagnosed by the detection of worm eggs in faecal samples, usually following their concentration by sedimentation in water and/or flotation in saturated sugar or salt solutions (with some techniques being quantitative and estimating the number of eggs per gram of faeces (epg)). However, coprological techniques cannot diagnose prepatent clinical infections due to migrating larval stages (as egg production has not yet commenced). The differential diagnosis of infections on the basis of egg morphology is not possible as most strongyle eggs are similar in size, shape and appearance. Instead, faecal samples may be incubated for 10-14 days to harvest L3 for microscopic identification (*Strongylus* spp. form ensheathed L3 with long filamentous tails and intestines comprising 16-32 elongated or rectangular cells, whereas those of small strongyles have intestines comprising 8-16 triangular or pentagonal cells). Serological techniques (enzyme immunoassays) have also been developed to detect host antibodies against specific parasite antigens, but their test specificity and sensitivity remains to be critically validated. Molecular biological techniques have also been used to characterize eggs, larvae and adults of various species by the polymerase chain reaction (PCR) amplification of specific nuclear genes (ribosomal DNA sequences, including internal transcribed spacer regions 1 and 2, and the intergenic spacer).

Treatment and control: Infections have been successfully treated with a range of anthelmintic drugs, with the macrocyclic lactones (ivermectin, moxidectin, abamectin) and benzimidazoles (fenbendazole, thiabendazole, cambendazole, oxibendazole) proving effective against larvae and adults, with tetrahydropyrimidines (pyrantel) being effective against adult worms only. The clinical treatment of severe cases of enteropathy may benefit from the administration of non-steroidal anti-inflammatory drugs. The widespread use of these drugs in domestic and performance horses has dramatically reduced the incidence of strongylosis worldwide, but sporadic outbreaks may occur in untreated feral and wild equid populations. It is recommended that foals be treated regularly due to their high susceptibility, and that drenches be used in cyclic rotation to forestall the emergence of drug resistance (which regrettably has occurred with many small strongyles or cyathostomins). Control programmes (suppressive, strategic and integrated) should include pasture management strategies to reduce faecal contamination by worm eggs, and limit the development and survival of infective larvae on pastures; including stock rotation, mixed grazing, removing and composting faeces, and periodically spelling pastures. Several studies have also demonstrated the utility of biological control using nematophagous fungi to reduce larval contamination of pastures.

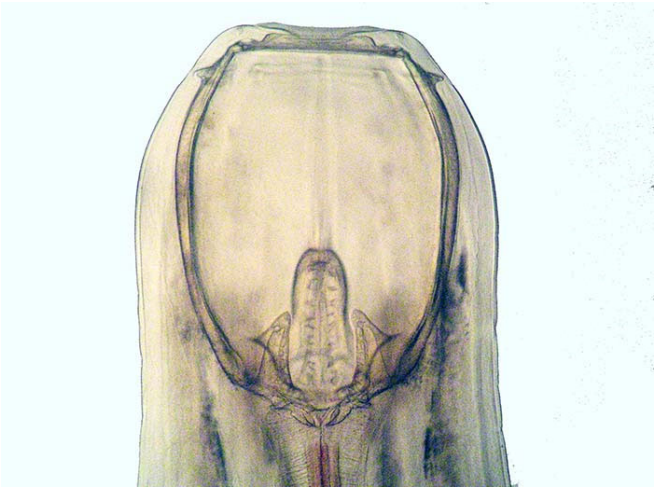

Strongylus
intestines
(diarrhoea, anaemia,
verminous arteritis, colic)
head
Definitive Hosts
(perissodactyls)
some undergo
extra-intestinal
migration
L3
ingested
adult
female
(~ 30 mm)
adult
male
(~ 20 mm)
male tail
(lateral)
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 1 mm)
external
environment
eggs
(~ 80 µm)
rhabditiform first- and
second-stage larvae (L1, L2)
(~ 750 µm)



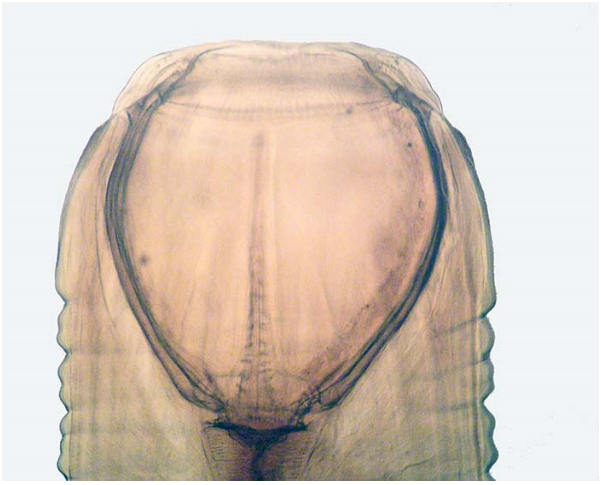
Strongylus adult worms



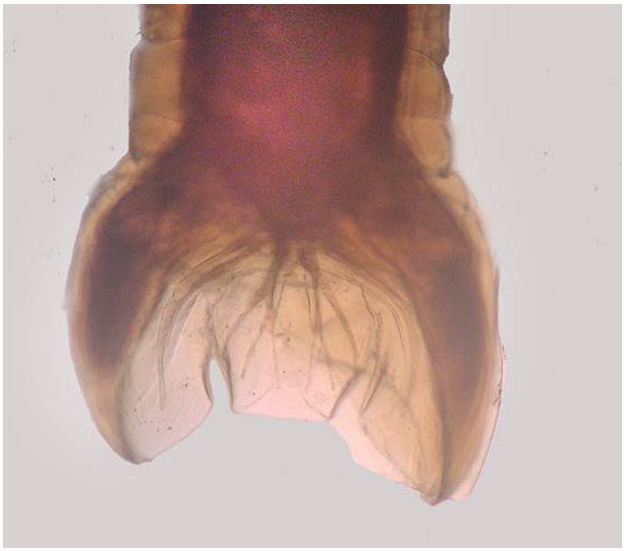
Strongylus worm egg



Strongylus equinus adult worm, head



Strongylus edentatus adult worm, head



Strongylus adult worm, male bursa

Triodontophorus/Oesophagodontus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the strongylids which are stout worms with a large buccal capsule often armed with teeth and with a leaf crown around the mouth. Small and large species occur in the intestinal or respiratory mucosa of domestic animals and birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, invade the mucosa and moult into L4 before returning to the lumen to moult into adults. *Triodontophorus, Oesophagodontus* and *Craterostomum* species are non-migratory strongyles of the caecum/colon, which can contribute to poor body condition in equids worldwide. These genera were conventionally classified together with *Strongylus* as large strongyles, but molecular-genetic studies found them to group together with the small strongyles.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Strongylidae (strongyles, large buccal capsules, often with teeth/leaf crown, equid hosts) [originally classified as large strongyles in the subfamily Strongylinae on the basis of similar morphotypic features, but recently realigned with the small strongyles in the subfamily Cyathostominae on the basis of molecular studies]
Genus:	*Triodontophorus* (parasitic in caecum/colon of equines)
Genus:	*Oesophagodontus* (parasitic in caecum/colon of equines)
Species:	various species cause unthriftiness in horses

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and

Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on microbes in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae	large buccal capsules, leaf crown of	artiodactyls, primates	ingestion of L3	22

(nodule worms)	labial collar, L3 sheathed			
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Strongyle worms are characterised by their prominent buccal capsules with lips, leaf crowns or labial collars at the mouth opening, sometimes with teeth or cutting plates. They are parasitic in a variety of organ systems in a range of animals, including the large intestines of mammals (ruminants, suids, elephants, perissodactyls, rodents, marsupials and primates), tortoises and ratite birds, the forestomach of marsupials, the trachea of birds and mammals, and the renal system of suids. Four families are recognised: Strongylidae (buccal capsule globular or cylindrical, oral opening circular, dorsal ray with 6 terminal branchlets, 32 genera in large intestines of mammals, reptiles and birds); Chabertiidae (buccal capsule globular or cylindrical, oral opening circular or oval, with leaf crown or labial collar, with up to 3 teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 22 genera in gastrointestinal tract of mammals); Syngamidae (buccal capsule subglobular, oral opening hexagonal, numerous teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 7 genera in respiratory, urinary and digestive tracts of mammals and birds); and Deletrocephalidae (oral opening hexagonal, dorsal ray with 6 terminal branches, 2 genera in large intestines of birds). The family Strongylidae contains 2 subfamilies conventionally differentiated on worm size and buccal capsule morphology: namely, Strongylinae ('large' strongyles (or strongylins) with globular or funnel-shaped buccal capsules) parasitic in the large intestines of perissodactyls, elephants and ratite birds (sometimes undergoing extra-intestinal migration); and Cyathostominae ('small' strongyles (or trichonemes, cyathostomes, cyathostomines, cyathostomins) with cylindrical or ring-shaped buccal capsules) found in the large intestines of perissodactyls, elephants, hyracoids, tortoises and occasionally some artiodactyls. Contemporary molecular characterization studies, however, do not fully support the separation of these subfamilies as several 'large' strongyles group together with the 'small' strongyles.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Strongylinae ('large' strongyles or strongylins)					
Triodontophorus, Oesophagodontus, Craterostomum, Bidentostomum	11	equids	large intestines	6-25 mm long, globular or funnel-shaped buccal capsule often with teeth, leaf crowns [*despite their large strongyle features, molecular studies group them with the small strongyles]	66-130 x 33-68 µm. ellipsoidal, thin-shelled
Strongylus (redworms)	13	ungulates, esp. equids	large intestines	10-50 mm long, red colouration, large globular buccal capsule often armed with teeth, leaf	64-99 x 36-58 µm, ellipsoidal,

				crowns, L3 with long filamentous sheath	thin-shelled
Cyathostominae ('small' strongyles* or cyathostomins)					
Cyathostomum, etc.	6	equids	large intestines	5-30 mm long, red-grey colouration, cylindrical buccal capsule, with labial collar, some with dorsal gutter, external and internal leaf crowns variable	35-150 x 17-68 µm, ellipsoidal, thin-shelled

The subfamily Strongylinae conventionally contains 11 genera: 7 typified as large strongyles (*Strongylus* (syn. *Sclerostoma*, *Sclerostomum*, *Alfortia*, *Delafondia*) in equids; *Choniangium, Decrusia, Equinurbia* in elephants; *Codiostomum* in ostriches; *Macropicola* and *Hypodontus* in macropodid marsupials); and 4 other genera (*Triodontophorus* (syn. *Triodontus*)*, Bidentostomum, Craterostomum,* and *Oesophagodontus* (syn. *Pseudosclerostomum*) in equids, originally considered to be large strongyles. However, recent molecular-genetic studies have grouped them together with the small strongyles. The latter 4 genera comprise medium-sized worms with subglobular or funnel-shaped buccal capsules, mouth collars associated with submedian papillae, external and internal leaf crowns with similar or dissimilar elements, males with 3 pairs of branches in the dorsal ray of the bursa, spicules with pick-like or hooked tips, and females with oval or Y-shaped ovejectors. They are parasitic in the large intestines of equids throughout the world and have been associated with poor performance and body condition. Endoparasitic larval stages undergo histotrophic development in the intestinal mucosa but they do not undertake extra-intestinal migration like other large strongyles (*Strongylus* spp.). Infections are transmitted by the contamination of pastures with worm eggs from which infective larvae develop.

Parasite species	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
Triodontophorus			
T. brevicauda	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines [poor condition]	worldwide
T. burchelli	Perissodactyla: equid (donkey, Burchell's zebra)	large intestines	Africa
T. hartmannae	Perissodactyla: equid (donkey, mountain zebra)	large intestines	Africa
T. minor (syn. Triodontus)	Perissodactyla: equid (horse, donkey, onager)	large intestines [poor condition]	worldwide
T. nipponicus (syn. *T. brochotrilobulatus, T. hsiungi)*	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager, mountain zebra)	large intestines [poor condition]	Eurasia, Americas
T. serratus (syn. *T. intermedius, Triodontus*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra, mountain zebra); Artiodactyla: suid (pig)	large intestines [poor condition]	worldwide
T. tenuicollis (syn. *T. popovi)*	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager, plains zebra)	large intestines [poor condition]	worldwide
Oesophagodontus			
O. robustus (syn. *Sclerostomum, Strongylus, Pseudosclerotomum securiferum*)	Perissodactyla: equid (horse, donkey, mule, plains zebra)	large intestines [poor condition]	worldwide
Craterostomum			
C. acuticaudatum (syn. *Cylicostomum, C. mucronatum*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra, Hartmann's mountain zebra)	large intestines [poor condition]	worldwide
C. tenuicauda	Perissodactyla: equid (horse, plains zebra)	large intestines [poor condition]	Africa, Asia
Bidentostomum			
B. ivashkini	Perissodactyla: equid (horse, mule)	large intestines	Asia

Parasite morphology: These strongyles form 3 different morphological stages in their developmental cycles: eggs; larvae (4 stages designated L1-L4); and adult worms. Gravid female worms lay typical strongyle eggs which are ovoid in shape, surrounded by a smooth thin eggshell and containing a morula at the 4-8 cell (blastomere) stage of development. Eggs range in size from 66-130 x 33-68 µm, with some variation observed among genera (see following Table). L1 and L2 are free-living rhabditiform stages, measuring from 480-700 µm in length, with rounded heads, short cylindrical buccal capsules, bulbed oesophagi, and long slender tails. L3 are ensheathed filariform larvae which are initially free-living, but become parasitic when ingested by suitable hosts. The

sheath is formed by retention of the L2 cuticle as a protective covering and it characteristically has a long filamentous tail. L3 are 500-670 µm long and have conical heads with small buccal cavities, a long thin strongyliform oesophagus, and intestines consisting of 16-20 cells. Genera may sometimes be differentiated on the basis of the morphological characteristics of L3: *Triodontophorus* L3 have intestines with 18-20 well-defined rectangular cells; *Craterostomum* L3 have intestines with 16 rectangular cells arranged in a double row anteriorly and a single row posteriorly; and *Oesophagodontus* L3 have intestines with 16-18 elongate or triangular cells in a double row. L4 are parasitic stages that feed on host tissues while growing markedly in size (from 1.2-7.8 mm depending on species) and they have well-developed buccal capsules, 3 stout and pointed oesophageal teeth, and immature genitalia.

Genus	***Triodontophorus***	***Oesophagodontus***	***Craterostomum***	***Bidentostomum***
Egg size	66-122 x 33-68 µm	88-130 x 40-60 µm	120 x 60 µm	101-107 x 51-52 µm
L3 intestines	18-20 rectangular cells	16-18 elongate/triangular cells in a double row	16 rectangular cells	?
Adult mouth collar	inflated round tube	flattened, sharp peripheral ridge	flattened, divided into 2 rings	flattened, divided into 2 rings
Adult oesophageal teeth	3 large projecting teeth	3 lancet non-projecting teeth	3 small non-projecting teeth	3 large projecting teeth
ELC cf. ILC elements (external cf. internal leaf crowns)	equal no. (44-73) but longer	similar but fewer (18 cf. 34-48)	longer, thinner, fewer (8 cf. 23-24)	similar but fewer (8 cf. 16)

Adult worms measure from 6-24 mm in length, being smaller in size than *Strongylus* spp. and similar in size to the small strongyles (cyathostomins). Although molecular-genetic studies group these genera with the small strongyles, they possess morphological features consistent with large strongyles (*Strongylus*), notably a globular buccal capsule (funnel-shaped in *Oesophagodontus*) armed with 3 oesophageal teeth (see Table). Adult worms also have distinctive arrangements of complex cephalic structures, comprising mouth collars, cephalic papillae, corona radiata (external leaf crowns (ELC) and internal leaf crowns (ILC)), extra-chitinous supports, dorsal gutters, and oesophageal funnels. The genus *Triodontophorus* has a mouth collar resembling an inflated round tube, whereas the genera *Oesophagodontus*, *Craterostomum* and *Bidentostomum* have flattened mouth collars, with those of the latter 2 genera divided into inner and outer rings. The buccal capsule of *Triodontophorus* has a thickened anterior rim and is surrounded by 6 plate-like structures, that of *Oesophagodontus* has a posterior collar, and those of *Craterostomum* and *Bidentostomum* are thickened anteriorly. The dorsal gutter is elongate in *Triodontophorus* and *Craterostomum,* button-like in *Bidentostomum,* and inconspicuous in *Oesophagodontus.* The elements of the ELC and ILC may be similar in appearance but fewer in number (*Oesophagodontus, Bidentostomum*), dissimilar and fewer (*Craterostomum*) or dissimilar and equal in number (*Triodontophorus*). The oesophageal teeth of *Triodontophorus* and *Bidentostomum* project up into the buccal capsule, but those of *Oesophagodontus* and *Craterostomum* do not. Adult worms are sexually dimorphic, with female worms being larger than males (*Craterostomum* females 6-11 mm cf. males 6-10 mm; *Bidentostomum* 9-10 cf. 8-9 mm; *Triodontophorus* 10-20 cf. 8-20 mm; and *Oesophagodontus* 19-25 cf. 15-20 mm). Males have a well-developed copulatory bursa consisting of 2 lateral lobes and a long dorsal lobe. The lateral lobes are supported by 6 rays (comprising muscular elements following nerve channels to terminal papillae) where the ventral rays are shorter or equal to the lateral rays, and the externodorsal rays begin at the junction of the dorsal and lateral lobes. The dorsal lobe is supported by an elongate dorsal ray with 6 branches arising from 3 bifurcations. Males also have a narrow gubernaculum with a small handle and an enlarged distal tip (sometimes with a ventral notch or groove), an elongate genital cone extending beyond the bursal edge, and 2 filiform equal spicules with hook-shaped tips (*Triodontophorus*, *Bidentostomum*) or straight tips (*Oesophagodontus*, *Craterostomum*). Female worms are didelphic with 2 ovaries, 2 oviducts, 2 uteri and 2 ovejectors connected through an oval or Y-shaped vestibule to a common vagina leading to a vulva located in the posterior body but anterior to the anus. Females have tails that may be long, short, conical or pointed. Mature females are oviparous in that they produce and lay partially-embryonated eggs.

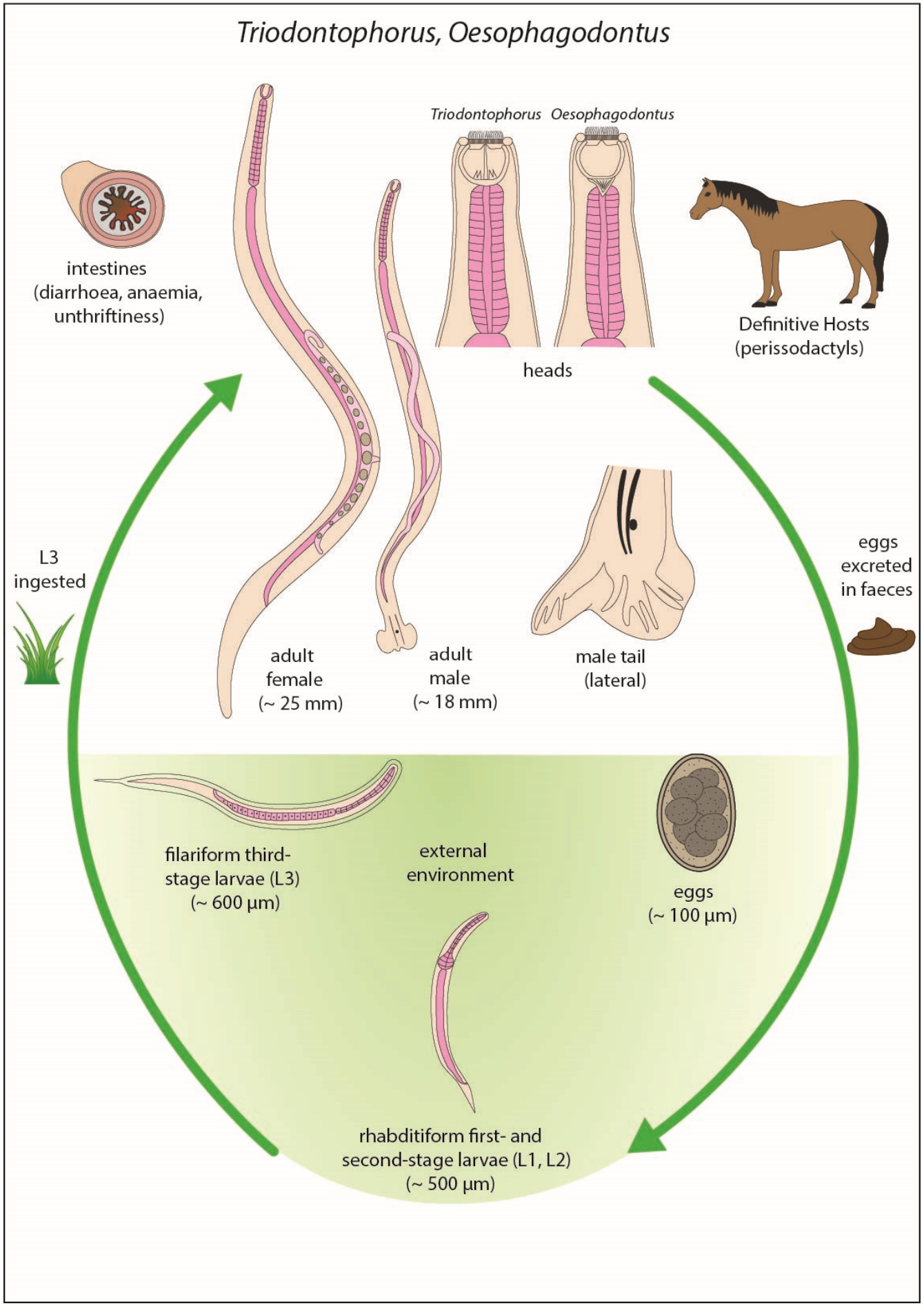
Site of infection: Adult worms infect the large intestines of their hosts, and are found in the lumen of the caecum and colon, whereas larval stages migrate into and develop within the intestinal mucosa. Free-living larval stages emerge from worm eggs deposited on pastures in host faeces.

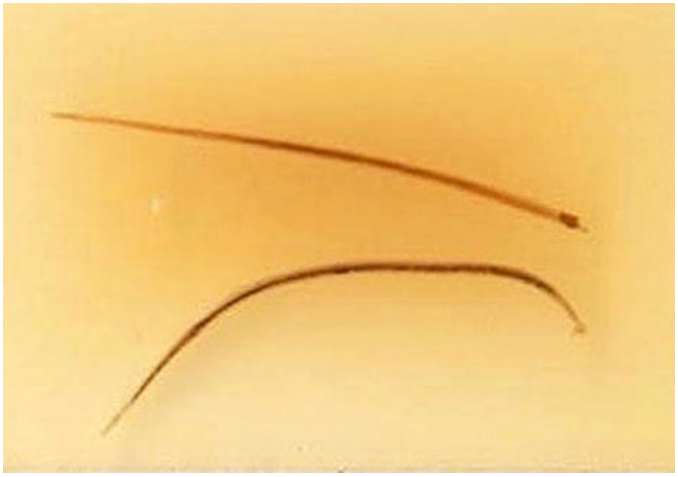
Pathogenesis: Infections by these strongyles have been implicated in loss of condition and ill-thrift in equids, but their contribution is unclear, as they usually occur in mixed infections with other large and small strongyles. Adult worms feed on host mucosa causing traumatic damage, petechial haemorrhages, inflammation and ulceration contributing to anaemia, diarrhoea, weakness and poor condition. *Triodontophorus* worms may cause deep ulceration in the right dorsal colon resulting in significant haemorrhage and blood loss. However, the preceding larval stages do not undertake extensive somatic (extra-intestinal) migrations and appear not to cause severe pathological changes like *Strongylus* spp. Instead, they invade the intestinal mucosa where they encyst and undergo histotrophic development before being released back into the gut lumen. They are often referred to as the large non-migratory strongyles and infections have not been associated with acute morbidity or mortality, but rather with cumulative deleterious health effects attributable to mixed strongyle infections.

Developmental cycle and mode of transmission: These parasites have direct monoxenous life-cycles involving faecal-oral transmission. Gravid female worms lay eggs that are passed into the external environment with host faeces. The eggs embryonate and hatch after several days releasing free-living L1 which feed on microbes before moulting to L2 which also feed. Eventually they moult to L3 but retain the L2 cuticle as a protective sheath which prevents them from feeding. Development from egg to infective L3 usually takes around 2 weeks in temperate zones, but may be more rapid in warmer regions. L3 exhibit both horizontal migration (dispersal from faeces) and vertical migration (ascending vegetation), particularly in moist conditions. Hosts become infected when they ingest infective L3 on pasture when grazing. The ingested L3 exsheath in the gut and invade glands in the wall of the large intestines where they undergo histotrophic development (the larvae migrate into the intestinal wall but do not undergo extra-intestinal migration). L4 are released into the lumen of the intestines where they moult to young adults (sometimes designated L5) which feed, mature and mate. The prepatent period (time from infection to first release of eggs) is around 9 weeks.

Differential diagnosis: Infections are conventionally diagnosed by the direct detection of parasites, usually by the coprological detection of worm eggs in faecal samples following their concentration by sedimentation in water and floatation in saturated sugar or heavy metal salt solutions, and sometimes by the microscopic detection of larvae in faecal samples. Strongyle eggs cannot be identified reliably to species or genus because of their similar morphologies. Faecal samples may be cultured to yield L3 which allows some genera to be identified on the basis of larval morphology (notably gut anatomy involving the number, shape and configuration of intestinal cells). Unfortunately, coprocultures usually take 2 weeks to perform, and they usually yield numerous larvae of different species, which cannot be identified accurately to genus and species. Infections may be diagnosed by the microscopic identification of worms from gut samples collected at post-mortem, with *Triodontophorus* worms reported to cluster together around colonic ulcers. Molecular biological techniques have been used to characterize large non-migratory strongyles following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (ribosomal RNA), with the results showing clear phylogenetic relationships with small strongyles (cyathostomins).

Treatment and control: A range of anthelmintic drugs have been used to treat infections in horses, including benzimidazoles (e.g., fenbendazole, oxfendazole), tetrahydropyrimidines (pyrantel salts), and macrocyclic lactones (ivermectin, moxidectin, abamectin) which have been effective against gut stages of the parasites (in the absence of drug resistance). It has been recommended that drugs be used judiciously to avoid the development and spread of drug resistance in worm populations, including strategic drenching of particular age groups (e.g., foals) and considering time of the year (season, depending on climatic zone), rotation of anthelmintic classes and rotational grazing with species other than horses (e.g. sheep or other ruminants – which only have *Trichostrongylus axei* (parasite of the stomach) in common with equids). Levels of anthelmintic resistance to particular compounds (classes) can be monitored using faecal egg count reduction tests (FECRT), conducted according to internationally accepted guidelines (cf. World Association for the Advancement of Veterinary Parasitology (WAAVP)). At the farm level, integrated control strategies may also include the reduction of environmental contamination by worm eggs and free-living larvae in the environment (by removing and composting faeces, mixed grazing or pasture spelling).

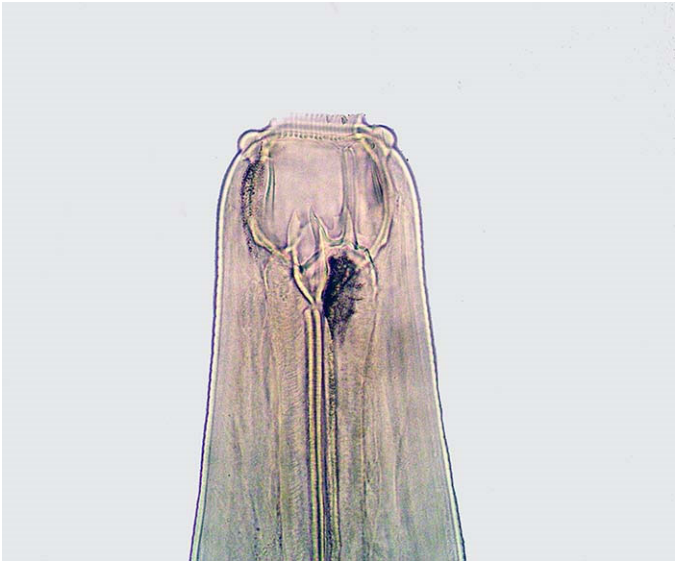

Triodontophorus, Oesophagodontus
Triodontophorus
Oesophagodontus
intestines
(diarrhoea, anaemia,
unthriftiness)
heads
Definitive Hosts
(perissodactyls)
L3
ingested
adult
female
(~ 25 mm)
adult
male
(~ 18 mm)
male tail
(lateral)
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 600 µm)
external
environment
eggs
(~ 100 µm)
rhabditiform first- and
second-stage larvae (L1, L2)
(~ 500 µm)



Triodontophorus adult worms



Triodontophorus worm egg



Triodontophorus adult worm, head

Cyathostomum
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the strongylids which are stout worms with a large buccal capsule often armed with teeth and with a leaf crown around the mouth. Small and large species occur in the intestinal or respiratory mucosa of domestic animals and birds. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult to L4 before they return to the lumen and moult into adults (some L4 undergo arrested development - termed hypobiosis – in the large intestinal wall). More than 40 species of small strongyles (cyathostomes, cyathostomins, trichonemes or red worms) are found in the large intestines, causing catarrhal and/or haemorrhagic enteritis in horses worldwide. Considerable efforts are made to control infections through chemical interventions (drenching), husbandry and environmental management.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Strongylidae (strongyles, large buccal capsules, often with teeth/leaf crown, equid hosts)
Subfamily:	Cyathostominae (small strongyles, cylindrical buccal capsule)
Genus:	*Cyathostomum* (parasitic in caecum/colon of equines)
Species:	various species cause enteritis in horses

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms, but

some are found in freshwater or on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on microbes in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22

Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Strongyle worms are characterised by their prominent buccal capsules with lips, leaf crowns or labial collars at the mouth opening, sometimes with teeth or cutting plates. They are parasitic in a variety of organ systems in a range of animals, including the large intestines of mammals (ruminants, suids, elephants, perissodactyls, rodents, marsupials and primates), tortoises and ratite birds, the forestomach of marsupials, the trachea of birds and mammals, and the renal system of suids. Four families are recognised: Strongylidae (buccal capsule globular or cylindrical, oral opening circular, dorsal ray with 6 terminal branchlets, 32 genera in large intestines of mammals, reptiles and birds); Chabertiidae (buccal capsule globular or cylindrical, oral opening circular or oval, with leaf crown or labial collar, with up to 3 teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 22 genera in gastrointestinal tract of mammals); Syngamidae (buccal capsule subglobular, oral opening hexagonal, numerous teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 7 genera in respiratory, urinary and digestive tracts of mammals and birds); and Deletrocephalidae (oral opening hexagonal, dorsal ray with 6 terminal branches, 2 genera in large intestines of birds). The family Strongylidae contains 2 subfamilies conventionally differentiated on worm size and buccal capsule morphology: namely, Strongylinae ('large' strongyles (strongylins or migratory strongyles) with globular or funnel-shaped buccal capsules) parasitic in the large intestines of perissodactyls, elephants and ratite birds (sometimes undergoing extra-intestinal migration); and Cyathostominae ('small' strongyles (trichonemes, cyathostomes, cyathostomines, cyathostomins or non-migratory strongyles) with cylindrical or ring-shaped buccal capsules) found in the large intestines of perissodactyls, elephants, hyracoids, tortoises and occasionally some artiodactyls. Contemporary molecular-genetic characterization studies, however, do not fully support the separation of these subfamilies as several 'large' strongyles group together with the 'small' strongyles.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Cyathostominae ('small' strongyles* or cyathostomins)					
Cyathostomum, etc.	6	equids	large intestines	5-30 mm long, red-grey colouration, cylindrical buccal capsule, with labial collar, some with dorsal gutter, external and internal leaf crowns variable	35-150 x 17-68 µm, ellipsoidal, thin-shelled
Strongylinae ('large' strongyles or strongylins)					
Strongylus (redworms)	13	ungulates, esp. equids	large intestines	10-50 mm long, red colouration, large globular buccal capsule often armed with teeth, leaf crowns, L3 with long filamentous sheath	64-99 x 36-58 µm, ellipsoidal, thin-shelled
Triodontophorus,	11	equids	large	6-25 mm long, globular or funnel-shaped buccal	66-130 x 33-68 µm.

Oesophagodontus, Craterostomum, Bidentostomum			intestines	capsule often with teeth, leaf crowns [*despite their large strongyle features, molecular studies group them with the small strongyles]	ellipsoidal, thin-shelled

The subfamily Cyathostominae contains small strongyles with single or double corona radiata (leaf crowns) and males with 6 rami in the dorsal ray of their bursa. Some 23-27 genera are recognised in 6 tribes: Cyathostominea (*Caballonema, Coronocyclus, Cyathostomum* (syn. *Trichonema p.p., Ershovinema p.p.*), *Cylicocyclus, Cylicodontophorus, Cylicostephanus* (syn. *Petrovinema, Schulzitrichinema, Cyclicotetrapedon, Trichonema p.p., Ershovinema p.p.*), *Cylicostomias, Cylindropharynx, Gyalocephalus, Hsuingia, Parapoteriostomum, Petrovinema, Poteriostomum* (syn. *Hexodontostomum*), *Skrjabinodentus, Tridentoinfundibulum*) in equids; Eucyathostominea (*Eucyathostomum*) in ruminants; Kilulluminea (*Kiluluma*) in rhinoceros and tapir; Murshidiinea (*Khalilia*, *Murshidia*, *Neomurshidia*) in elephants, rhinoceros, warthogs and tapir; Quiloninea (*Quilonia, Theileriana*) in elephants, rhinoceros and hyracoids; and Sauricolinea (*Chapiniella*, *Sauricola*) in tortoises. Members of the tribe Cyathostominea have internal and external corona radiata, females with well-developed parallel ovejectors, males with pick-like spicules and a large gubernaculum with a longitudinal groove and a flanged ventral notch. The genera *Cyathostomum, Cylicocyclus, Cylicodontophorus, Poteriostomum, Cylicostephanus, Coronocyclus* and *Gyalocephalus* are common cosmopolitan parasites in the large intestines of equids, and have been associated with acute catarrhal and/or haemorrhagic enteritis as well as chronic ill-thrift, particularly in young animals but also in equids of other age groups. Infections are transmitted by the faecal contamination of pastures by worm eggs which produce larvae that develop to infective L3 and are ingested by grazing animals.

Parasite species	Definitive Hosts	Location	Distribution
Cyathostomum			
C. alveatum (syn. *Cylichnostomum, Cylicocerus, Cylicostomum, Erschowinema, Trichonema*)	Perissodactyla: equid (horse, donkey, mule, plains zebra)	large intestines	Africa, Europe, Asia
C. catinatum (syn. *Cylichnostomum, Cylicocerus, Cylicostomum, C. pseudocatinatum, Erschowinema, Petrovinema, Trichonema)*	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, plains zebra, mountain zebra)	large intestines	worldwide
C. equatoriale	Perissodactyla: equid (Grant's zebra)	large intestines	Africa
C. montgomeryi (syn. *Cylicostomum, Cylicotoichus, Erschowinema, Trichonema*)	Perissodactyla: equid (horse, donkey, mule, plains zebra, mountain zebra, Burchell's zebra)	large intestines	Africa
C. pateratum (syn. *Cylicocerus, Cylicodontophorus, Cylicostomum cymatostomum, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, tarpan, plains zebra)	large intestines	worldwide
C. tetracanthum (syn. *C. aegyptiacum, Cylichnostomum, Cylicostoma, Cylicostomum, Strongylus, Sclerostomum, S. quadridentatum, Trichonema, T. arcuata*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager, plains zebra, mountain zebra, Burchell's zebra)	large intestines	worldwide
Species inquirenda			
C. maestrii sp. inq.	Perissodactyla: equid (Grant's zebra)	large intestines	Africa
C. symmetricum sp. inq.	Perissodactyla: equid (Grant's zebra)	large intestines	Africa
C. zavattarii sp. inq.	Perissodactyla: equid (Grant's zebra)	large intestines	Africa

Other small strongyle genera and species in equids

Parasite species	Definitive Hosts	Location	Distribution
Caballonema			
C. longicapsulata (syn. *Sinostrongylus*)	Perissodactyla: equid (horse)	large intestines	Asia

Coronocyclus			
C. coronatus *(syn. Cyathostomum, Cylichnostomum, Cylicocerus, Cylicostomias, Cylicostomum, Erschowinema, Trichonema, T. subcoronatum)*	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, tarpan)	large intestines	worldwide
C. labiatus *(syn. Cyathostomum, Cylichnostomum, Cylicocerus, Cylicostomias, Cylicostomum, Schulzitrichonema, Trichonema)*	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, tarpan, plains zebra)	large intestines	worldwide
C. labratus *(syn. Cyathostomum, Cylichnostomum, Cylicostomias, Cylicostomum, Schulzitrichonmea, Trichonema)*	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, mountain zebra)	large intestines	worldwide
C. sagittatus *(syn. Cylicostomias, Cylicostomum, Cylicodontophorus, Trichonema)*	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule)	large intestines	Eurasia
C. ulambajari	Perissodactyla: equid (horse)	large intestines	Asia
Cylicocyclus			
C. adersi sp. inq. (syn. *Cyathostomum*, *Cylicostomum*, *Trichonema*)	Perissodactyla: equid (horse, donkey, mountain zebra, damaraland zebra)	large intestines	Africa, Asia
C. ashworthi (syn. *C. largocapsulatus, C. matumurai, C. zhidanensis, Cylicobrachytus zhidanensis Trichonema largocapsulatus, T. matumurai*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager)	large intestines	worldwide
C. asini	Perissodactyla: equid (donkey, plains zebra, mountain zebra)	large intestines	worldwide
C. auriculatus (syn. *Cyathostomum, Cylichnostomum, Cylicostomum*, *Trichonema*)	Perissodactyla: equid (horse, donkey, mule, plains zebra, mountain zebra)	large intestines	Africa, Americas, Asia
C. brevicapsulatus (syn. *Cylicobrachytus, Cylicostephanus*, *Cylicostomum, Trichonema*)	Perissodactyla: equid (horse, donkey)	large intestines	Eurasia, Americas
C. elongatus (syn. *Cyathostomum, Cylichnostomum, Cylicostomum*, *Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
C. gyalocephaloides sp. inq	Perissodactyla: equid (donkey, plains zebra, mountain zebra); Proboscidea: elephantid (African bush elephant)	large intestines	Africa
C. insigne (syn. *Cyathostomum, Cylichnostomum, Cylicostomum*, *Cylicostomum zebra, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager, plains zebra)	large intestines	worldwide
C. leptostomum (syn. *Cyathostomum, C. bogoriense, Cylichnostomum, Cylicostomum, Cylicotetrapedon*, *Schulzitrichonema*, *Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, plains zebra)	large intestines	worldwide
C. nassatus (syn. *C. bulbiferus, Cyathostomum, Cylichnostomum, Cylicostomum*, *Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, tarpan, plains zebra, mountain zebra)	large intestines	worldwide
C. radiatus (syn. *Cyathostomum, Cylichnostomum, Cylicostomum, C. prionodes, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
C. triramosus (syn. *Cyathostoma*, *Cylicostomum,*	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager, tarpan, plains zebra,	large intestines	Africa, Asia, North America

Trichonema)	Burchell's zebra, Hartmann's mountain zebra)		
C. ultrajectinus (syn. *Cyathostomum, Cylicodontophorus, Cylicostomum, Trichonema*)	Perissodactyla: equid (horse, donkey, onager, plains zebra)	large intestines	worldwide
Cylicodontophorus			
C. bicoronatus (syn. *Cyathostomum, Cylichnostomum, Cylicostephanus, Cylicostomum, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager)	large intestines	worldwide
C. reineckei	Perissodactyla: equid (plains zebra, Hartmann's mountain zebra)	large intestines	Africa
Cylicostephanus			
C. asymetricus (syn. *Cylicostomum, Cylicotetrapedon, Erschowinema, Schulzitrichonema*)	Perissodactyla: equid (horse, donkey)	large intestines	worldwide
C. bidentatus (syn. *Cylicostomum, Cylicotetrapedon, Schultzitrichonema, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
C. calicatus (syn. *Cyathostomum, Cylichnostomum, Cylicostomum, C. barbatum, Erschowinema, Trichonema, T. tsengi*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, mountain zebra, Burchell's zebra)	large intestines	worldwide
C. goldi (syn. *C. ornatus, Cyathostomum ornatum, Cylichnostomum, Cylicocerus, Cylicodontophorus ornatum, Cylicostomias ornatum, Cylicostomum, C. ornatum, C. tridentatum, Cylicotetrapedon, Schultzitrichonema, Trichonema, T. ornatum, T. parvibursatum*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, plains zebra)	large intestines	worldwide
C. hybridus (syn. *Cyathostomum, Cylicostomum, Erschowinema, Schultzitrichonema, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager)	large intestines	Eurasia, North America
C. longibursatus (syn. *Cylicostomum, C. calicatiforme, C. nanum, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, plains zebra)	large intestines	worldwide
C. minutus (syn. *Cylicocyclus, Cylicostomum, Erschowinema, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, tarpan, onager, plains zebra, mountain zebra, Burchell's zebra)	large intestines	worldwide
Cylindropharynx			
C. brevicauda (syn. *C. aethiopica, Cyathostoma aethiopicum*)	Perissodactyla: equid (donkey, mule, plains zebra, Grant's zebra)	large intestines	Africa
C. intermedia (syn. *C. ornata, C. dolfusi sp. inq. C. rhodesiensis sp. inq*.)	Perissodactyla: equid (plains zebra, Hartmann's mountain zebra)	large intestines	Africa
C. longicauda (syn. *C. asini)*	Perissodactyla: equid (donkey, mule, plains zebra, Hartmann's mountain zebra)	large intestines	Africa
Gyalocephalus			
G. capitatus (syn. G. equi)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
Hsiungia			
H. pekingensis (syn. *Cylicocyclus*)	Perissodactyla: equid (horse, donkey)	large intestines	Asia
Parapoteriostomum			
P. euproctus (syn. *Cylichnostomum, Cylicodontophorus, Cylicostomum,*	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide

Trichonema)			
P. mettami (syn. *Cyathostomum, Cylicocercus, Cylicodontophorus, C. zhongweiensis, Cylicostoma, Trichonema, Cylicostomum ihlei*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager)	large intestines	Africa, Eurasia
P. mongolica (syn. *Cylicodontophorus*)	Perissodactyla: equid (horse)	large intestines	Asia
P. schuermanni (syn. *Cylicodontophorus, Trichonema*)	Perissodactyla: equid (plains zebra)	large intestines	Africa
Petrovinema			
P. poculatum (syn. *Cyathostomum, Cylichnostomum, Cylicostephanus, Cylicostomum, Trichonema*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
P. skrjabini (syn. *Cylicostephanus, Poteriostomum, Trichonema*)	Perissodactyla: equid (horse, donkey)	large intestines	Asia
Poteriostomum			
P. imparidentatum (syn. *P. pluridentatum, Cylicostomum, C. zebrae, Cylichnostomum, Hexodontostomum markusi*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
P. ratzii (syn. *Craterostomum, Cylicostomum, Cylichnostomum*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	large intestines	worldwide
Skrjabinodentus			
S. caragandicus (syn. *Cylicostephanus*, *Trichonema*)	Perissodactyla: equid (horse, mule)	large intestines	Asia
S. longiconus (syn. *Cylicostephanus*)	Perissodactyla: equid (plains zebra, mountain zebra, Hartmann's mountain zebra)	large intestines	Africa
S. tshoijoi (syn. *Cylicostehanus*)	Perissodactyla: equid (horse)	large intestines	Asia
Tridentoinfundibulum			
T. gobi (syn. *Cylicostephanus, C. torbertae*)	Perissodactyla: equid (horse, mule)	large intestines	Eurasia, North America

Parasite morphology: The small strongyles form 3 different morphological stages in their development: eggs; larvae (4 successive stages designated L1-L4); and adult worms (males and females). Freshly laid eggs are ovoid in shape, bound by smooth thin shells, and contain a morula at the 4-8 cell (blastomere) stage. Eggs produced by small strongyles vary considerably in size, collectively ranging from 35-150 x 17-68 μm, although the range is narrower depending on genus and species (see following table). The first 2 larval stages (L1 and L2) are free-living stages that feed on microbes and have rounded heads, rhabditiform oesophagi (with cuticular valves) and tapering tails. L3 are free-living ensheathed stages (they retain the L2 cuticle) and are arrested in development although motile, do not feed on microbes and are infective to their equid hosts. Cyathostomin L3 range in length from 730-890 μm and have characteristic long filamentous tail sheath extensions (2:1 body to tail-sheath ratio), tapering heads, small tubular buccal cavities, long strongyliform oesophagi (without cuticular valves), and intestines comprising 6 or more cells. The identification of L3 is possible for some genera (e.g., *Poteriostomum* and *Gyalocephalus)* but those of the other cyathostomin genera can only be assigned to larval types (primarily on the basis of intestinal anatomy and cell numbers). *Poteriostomum* form broad L3 with intestines having 16 rectangular or pentagonal cells arranged in a double row, whereas *Gyalocephalus* L3 have intestines formed by 12 rectangular or pentagonal cells (the first 6-10 in a double row, and the remainder in a single row). A total of 8 other cyathostomin L3 types have been described: type A having intestines with 8 cells in a 2+6 configuration (first 2 triangular or rectangular cells in double row, remaining 6 trapezoidal or rectangular cells in a single row) often assigned to *Cyathostomum*, *Cylicocyclus*, *Cylicostephanus* and *Petrovinema* spp.; type B having intestines with 8 cells in a 4+4 configuration (triangular or pentagonal cells in double row) often referred to *Cylicocyclus* and *Cylicodontophorus* spp.; type C having intestines with 8 cells in 2+2+4 configuration (first 4 pentagonal, triangular or rectangular cells in double row, remaining 4 trapezoidal cells in single row) usually referred to *Cylicostephanus* spp.; type D having intestines with 8 trapezoidal or triangular cells in single row; type E having intestines with 6 triangular or trapezoidal cells in different configurations of double and single rows; type F having intestines with 7 elongate triangular or trapezoidal cells in different configurations (often 2-4 in double rows, 2-3 in single rows); type G having intestines with 8 elongate triangular or rectangular cells; and type H having intestines with 9 elongate triangular cells in a 6+3 configuration (first 6 in double row, remaining 3 in single row). The parasitic L4 (encysted and hypobiotic stages) grow up to 3-9 mm in length and sometimes show generic and species-specific cephalic and genital structures.

Genus	Egg size	L3 intestines
Cyathostomum	76-105 x 36-49 µm	8 cells (type A)
Caballonema	98-112 x 47-54 µm	
Coronocyclus	86-147 x 39-60 µm	
Cylicocyclus	35-130 x 17-65 µm	8 cells (type A or B]
Cylicodontophorus	76-120 x 39-59 µm	8 cells (type B)
Cylicostephanus	53-114 x 34-56 µm	8 cells (type A or C]
Cylindropharynx	84-106 x 44-61 µm	
Gyalocephalus	90-118 x 50-68 µm	12 cells
Hsiungia	114-150 x 54-72 µm	
Parapoteriostomum	80-128 x 50-62 µm	
Petrovinema	61-130 x 32-56 µm	8 cells (type A)
Poteriostomum	95-115 x 48-57 µm	16 cells
Skrjabinodentus	97-128 x 42-64 µm	
Tridentoinfundibulum	114-133 x 57-65µm	

Adult cyathostomins are commonly known as small red-worms due to their small size (5-30 x 1.5 mm) and their bright red colouration (sometimes yellow-grey). They have round mouths and well developed short cylindrical buccal capsules without buccal teeth but possessing elaborate cephalic structures, including mouth collars, cephalic papillae, corona radiata (internal leaf crowns (ILC) and external leaf crowns (ELC)), extra-chitinous supports, septum intracoronae (from anterior edge of buccal capsule to lateral edge of leaf crowns), dorsal gutters, oesophageal funnels and oesophageal teeth. Some 14 cyathostomin genera are recognised by different combinations of these structures. For example, the genus *Cyathostomum* has a high mouth collar divided into inner and outer rings, submedian papillae extending through the collar, a broad cylindrical buccal cavity (wider than deep) without buccal teeth, a nipple-like dorsal gutter, a shallow oesophageal funnel with inconspicuous oesophageal teeth, the elements of the ELC are longer, thicker and fewer than those of the ILC, the ILC insertion line is sinuous, the ELC has extra-chitinous supports consisting of a sclerotized ring anterior to the buccal capsule (sometimes appearing as a continuation of the buccal capsule but usually connected to it by strands of connective tissue), and the ILC has extra-chitinous supports near the anterior edge. The genus *Coronocyclus* is similar but the extra-chitinous support for the ELC is separated anteriorly from the buccal capsule, and the ILC insertion line is straight. The genera *Cylicocyclus, Cylicodontophorus, Gyalocephalus* and *Hsiungia* also have high mouth collars divided into rings; the genera *Cylicostephanus, Cylindropharynx, Petrovinema, Skrjabinodentus* and *Tridentoinfundibulum* have flattened mouth collars divided into rings; and the genera *Poteriostomum, Parapoteriostomum* and *Caballonema* have mouth collars that are not divided. The buccal capsules of several genera are modified, with the genus *Cylicocyclus* having a posterior hoop, *Hsiungia* a basal ring, *Poteriostomum* and *Petrovinema* posterior thickenings, *Parapoteriostomum* anterior thickenings, and *Cylindropharynx* being elongated. The oesophageal funnel may be shallow or elongate, and usually possesses inconspicuous teeth (although those of *Hsiungia* and *Caballonema* are more prominent, those of *Tridentoinfundibulum* are large, and those of *Gyalocephalus* are sickle-shaped).

Genus	Mouth collar	ELC cf. ILC elements (external cf. internal leaf crowns)	Other	Female length (mm)	Male length (mm)
Cyathostomum	high, divided	longer, thicker, fewer (18-29 cf. 30-90)	sinuous ILC insertion line, extra-chitinous supports connected anteriorly	5-13	4-11
Coronocyclus	high, divided	longer, thicker, fewer (16-28 cf. 40-80)	straight ILC insertion line, extra-chitinous supports separated anteriorly	7-13	5-11
Cylicocyclus	high, divided	longer, thicker, fewer (10-54 cf. 30-150)	buccal capsule (BC) with posterior hoop	7-30	5-17
Hsiungia	high, divided	similar (no. unspecified)	BC with basal ring, prominent teeth	12-17	9-12
Cylicodontophorus	high, divided	shorter, thinner, more (17-30 cf. 15-30)	ILC inserted near anterior edge	11-16	7-12
Gyalocephalus	high, divided	shorter, thinner, more (90-95 cf. 30-34)	3 sickle-shaped teeth	10-11	7-10
Poteriostomum	high, undivided	shorter, thinner, more (60-95 cf. 38-59)	ILC inserted near posterior edge, BC thicker posteriorly	11-21	9-14
Parapoteriostomum	arched, undivided	shorter, fewer (38-60 cf. 25-46)	BC thicker anteriorly	6-16	6-11
Petrovinema	flattened, divided	similar but fewer (28-36 cf. 80-84)	BC thicker posteriorly	10-19	8-15
Cylicostephanus	flattened,	longer, thicker, fewer	depressed mouth collar	5-10	4-8

	divided	(8-22 cf. 18-42)			
Skrjabinodentus	flattened, divided	shorter, thinner, fewer (8-16 cf. 16-23)	bursa with 4 branches (rather than 6)	8-13	8-10
Tridentoinfundibulum	flattened, divided	similar no. (30-40) but longer, thinner	3 prominent teeth	13-16	10-12
Cylindropharynx	flattened, divided	dissimilar and fewer (6 cf. 12)	ELC elements triangular, elongate BC	6-11	5-10
Caballonema	flattened, undivided	dissimilar, longer, fewer (8 cf. 16)	ELC elements triangular	12-16	6-13

Adult worms are sexually dimorphic, with female worms being moderately larger than males (5-30 cf. 4-17 mm). Mature males have a well-developed copulatory bursa, the dorsal lobe of which is usually longer than the lateral lobes (except for *Hsiungia* and *Cylindropharynx* where they are equal in length). The lateral lobes are supported by 6 rays (comprising muscular elements following nerve channels to terminal papillae) varying in branching pattern and length, and the dorsal ray typically has 6 branches (except *Skrjabinodentus* which has 4 branches). Males also have a gubernaculum with a dorsal handle (except *Gyalocephalus*) and a ventral notch (except *Petrovinema, Cylindropharynx* and *Skrjabinodentus* which have enlarged distal tips, and *Parapoteriostomum* which has paired ventral prominences). The genital cone is conical and short (except for *Gyalocephalus, Petrovinema, Parapoteriostomum, Skrjabinodentus* and *Cylindropharynx* where it is elongate, the latter also having finger-like appendages). Males have 2 filiform spicules which are equal in length and have pick-like tips (*Cyathostomum, Coronocyclus, Cylicostephanus, Cylicocyclus, Caballonema*), hook-like tips (*Cylicodontophorus, Poteriostomum, Gyalocephalus, Petrovinema, Parapoteriostomum, Skrjabinodentus, Tridentoinfundibulum, Cylindropharynx*) or straight tips (*Hsiungia*). Mature female worms are didelphic with 2 ovaries, 2 oviducts, 2 uteri and 2 well-developed ovejectors connected to an oval or Y-shaped vestibule (except *Cylindropharynx* where the vestibule is T-shaped) leading to long or short vagina which opens to the exterior through a posterior vulva close or distant to the anus (*Cylicodontophorus* also having a prominent anteroventral vulvar bulge). The tails of female worms may be long, short, conical or digitiform, sometimes with a sharp tip. Females are oviparous as they lay partially embryonated strongyle-type eggs.

Site of infection: Free-living larval stages develop from worm eggs deposited on pastures in host faeces. Parasitic larval stages encyst within the large intestinal wall of their perissodactyl hosts within which they continue development or undergo developmental arrest (hypobiosis). Adult cyathostomins are then found in the lumen of the caecum and the ventral and dorsal colon (not the descending colon or rectum).

Pathogenesis: Infections by small strongyles (cyathostomins) are commonly found in equids and usually occur as mixed infections involving multiple genera and species. Parasites may cause disease when developing or emerging from the tissues as larvae or when residing and feeding in the intestinal lumen as adults. Small strongyles have small buccal capsules which they use to feed superficially on mucosal tissues (they are not plug-feeders like large strongyles with large buccal capsules). Nevertheless, cyathostomin feeding causes traumatic damage to mucosal tissues with petechial haemorrhages and mild ulceration at feeding sites leading to a desquamative catarrhal, haemorrhagic and/or fibrinous enteritis (typhlocolitis), with mucosal thickening and oedema. Heavy infections may result in altered bowel function with diarrhoea, anaemia, unthriftiness with lethargy and sudden weight loss, particularly in animals up to 2-3 years of age. However, the most serious clinical manifestations are associated with larval cyathostomins, which can profoundly damage the gut wall not only when they first invade (causing type I cyathostominosis) but later when encysted stages emerge (causing type II cyathostominosis). L3 penetrate the epithelial lining and glands of the caecum and ventral colon, where they grow in fibrous granulomatous nodules (0.5-5.0 mm in diameter), although some may penetrate the muscularis mucosa and develop in submucosa. Heavy infections may involve thousands of encysted larvae covering the mucosa causing structural and functional changes that markedly reduce digestive processes and nutritional metabolism. The developing larvae do not undergo extra-intestinal somatic migration like the large migratory strongyles (*Strongylus* spp.), but they undergo histotrophic development in the tissues which can be extended for up to 2.5 years when larvae inhibit or arrest their development (process known as hypobiosis). The most devastating damage arises when encysted larvae emerge synchronously from the intestinal wall, causing haemorrhages and ulceration and precipitating severe clinical disease - known as larval cyathostominosis (type II). The condition is characterised by severe inflammation and is associated with a sudden onset of severe diarrhoea, fluid seepage with oedema and protein loss, intermittent colic, pyrexia, sudden and progressive weight loss and wasting, and death is common in outbreak situations. The damaged mucosa also predisposes to endotoxaemia when endotoxins in the intestinal contents enter the bloodstream. Disease relates to the synchronous reactivation, excystation and emergence of larval stages from the mucosa, and can be seasonal (late winter or early spring in temperate zones). Young horses are the vulnerable, particularly those reared on continually or progressively contaminated pastures, although horses of all ages are susceptible to cyathostomin infection because these nematodes do not induce protective immunity.

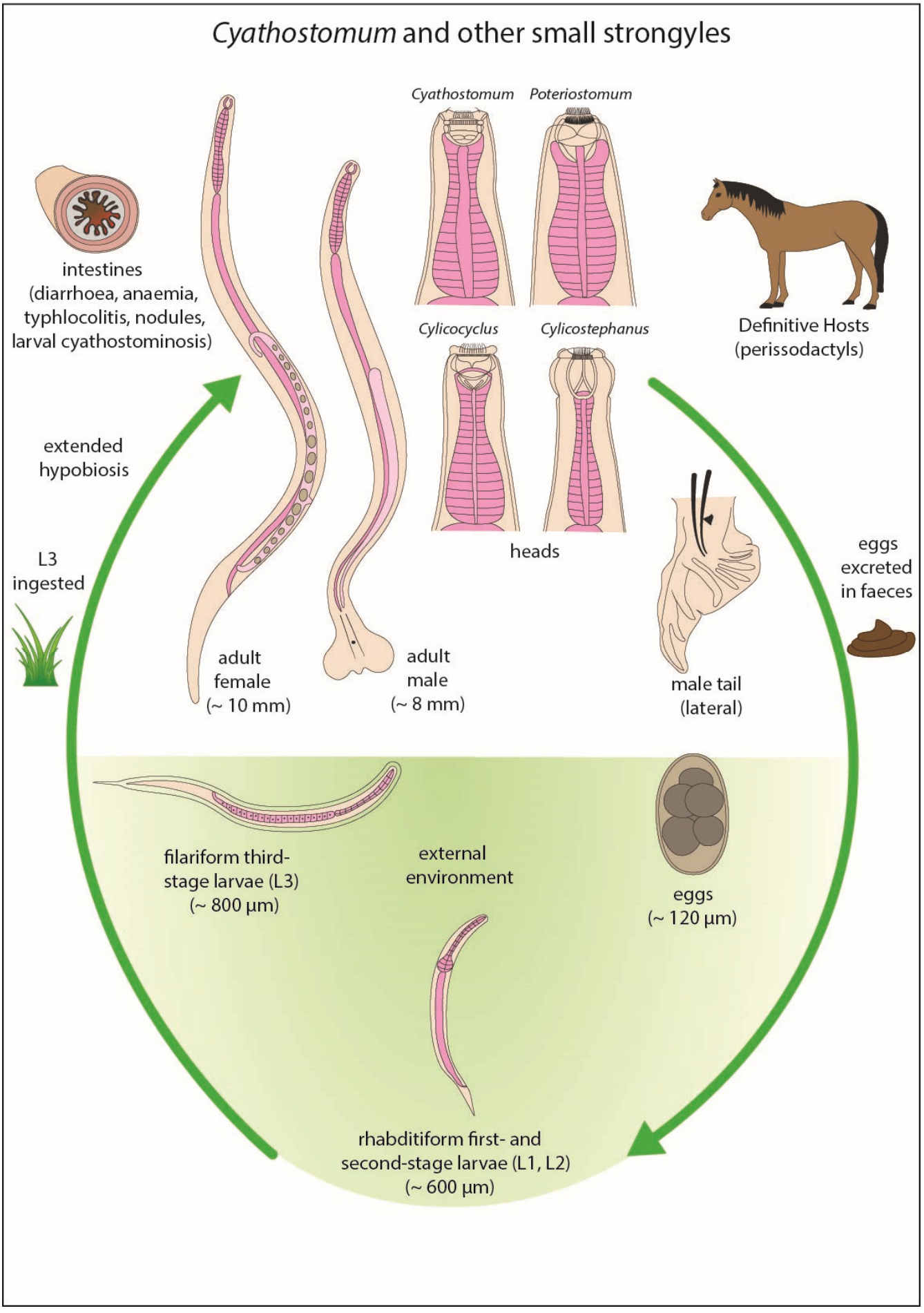
Developmental cycle and mode of transmission: Cyathostomins have direct monoxenous life-cycles involving faecal-oral transmission between hosts. Mature female worms lay eggs in the large intestinal lumen and they are excreted with host faeces into

the external environment. The eggs hatch after several days releasing free-living rhabditiform L1 which feed on bacteria before moulting to similar but larger L2 that also feed. These larvae then moult to form filariform L3 which retain the L2 cuticle as a protective sheath and are thus unable to feed. The time taken from egg hatching to the development of L3 varies depending on the prevailing environmental conditions, but it usually takes 1-2 weeks under favourable conditions (warm and moist in temperate climatic regions). Ensheathed L3 can survive for extended periods even under unfavourable, and given adequate moisture, they exhibit horizontal migration (dispersing from faecal pats) and vertical migration (ascending vegetation). Hosts become infected when they ingest infective L3 on pastures whilst grazing. Ingested larvae exsheath in the stomach and the freed early L3 (EL3) may remain in the intestinal lumen for several weeks before invading the mucosa of the caecum and colon where they become encysted in fibrous capsules (and do not undertake extra-intestinal migration). The EL3 develop over several months to late L3, moult to developing L4 (DL4) and then emerge as late L4 (LL4) – the process of emergence is often referred to as excystment. In the intestinal lumen, the LL4 moult to young adults (sometimes designated L5) which then mature into fecund adults. The prepatent period (time from infection to the first release of eggs) varies from 5-14 weeks, but may be considerably longer if EL3 undergo inhibited or arrested development (hypobiosis). It has been estimated that up to 90% of encysted cyathostomins undergo hypobiosis for periods ranging from 3-4 months up to 2 years. Larval hypobiosis appears to be triggered by a variety of factors, involving host physiological responses to stressors (metabolic and reproductive), adverse environmental conditions, and even pre-existing infections. It is often seasonal in occurrence, usually over winter in temperate regions and over summer in tropical regions, thereby causing outbreaks of larval cyathostomosis in spring or autumn, respectively. Despite such periodicity, comparative studies involving breeding and nonbreeding animals has not provided any evidence for a periparturient rise in worm egg production (as occurs for some trichostrongyle nematodes of some ruminant hosts).

Differential diagnosis: Although infections by small strongyles may be suspected on the basis of symptomatology and pertinent history, most clinical signs are relatively nonspecific (diarrhoea, anaemia, loss of condition). Similarly, changes in various clinical parameters may be suggestive but not definitive: including serum biochemistry (hypoalbuminaemia, hyper-beta-globulinaemia, increased alkaline phosphatase, reduced glycated fructose amines) and haematology (neutrophilia, anaemia with or without eosinophilia and/or lymphocytosis). Infections are conventionally diagnosed by the detection of characteristic (ovoid) worm eggs in faecal samples following their concentration by floatation in saturated sugar or salt solutions (specific gravity > 1.3). Quantitative techniques are usually employed, so that eggs can be counted in aliquots of diluted faeces in volumetric chambers (McMaster or Whitlock slides) and then extrapolated to the number of eggs per gram of faeces (epg). However, faecal egg counts do not correlate well with worm burdens, because they do not consider the stage of infection, the developmental stages that do not produce eggs (e.g., mucosal larval stages, males and immature or senescent females) and the fact that different species of worms commonly present have variable reproductive indices (rates). In addition, most strongylin and cyathostomin eggs appear similar in size and appearance and cannot be unequivocally differentiated even to genus. Recourse is sometimes made to larval coproculture where faecal samples are incubated for at least one week in funnels or petri dishes to harvest L3 for microscopic examination. While several cyathostomin genera can be identified on the basis of L3 characteristics (*Poteriostomum* and *Gyalocephalus*), those of the other 12 genera can only be assigned to larval types (A-H), primarily on the basis of gut anatomy (number, shape and configuration of intestinal cells). Infections can be diagnosed at post-mortem by the detection of adult worms and larvae in the gut lumen, in mucosal scrapings following pepsin-acid digestion, or the detection of encysted larvae in the gut wall via transillumination using a light box. Several serological techniques have been developed to detect serum antibodies to larval antigens (cyathostomin gut-associated larval antigen-1) or parasite copro-antigens. However, the kinetics and dynamics of serological responses to cyathostomins (as a group) and the different developmental stages present during the course of infection remain to be determined. A microchip-based capillary electrophoresis technique has been used to differentiate several cyathostomin species, as have polymerase chain reaction (PCR) amplification techniques for nuclear genes (ribosomal DNA, transcribed spacer regions (ITS) 1 and 2, and intergenic spacer (IGS)).

Treatment and control: The widespread application of anthelmintics has been spectacularly successful in treating large strongyle infections in horses, but the drugs have been less effective against small strongyles due to the limited efficacy of numerous drugs against encysted larval stages and the rapid emergence of drug resistance in cyathostomins. Infections are best treated with macrocyclic lactones (ivermectin, moxidectin, and abamectin). In susceptible worms, these lactones are effective against adults, but only moxidectin was 70-80% effective against inhibited/encysted larvae. In the absence of drug resistance, treatments with benzimidazoles (fenbendazole), tetrahydropyrimidines (pyrantel) and diethylenediamines (piperazine salts) were effective against adult worms but less so against encysted larvae and not against inhibited larvae. Recent treatment may also precipitate disease as killing adult stages may stimulate encysted (hypobiotic) stages to emerge from the gut wall. Some treatments have also caused serious side-effects involving severe inflammation of the colonic mucosa. Numerous veterinary health agencies recommend that anthelmintics be used prudently, with faecal egg count reduction tests used to monitor for drug resistance and to select the most appropriate anthelmintic for strategic dosing (usually seasonal, before and after winter) or selective dosing (treat those with high egg counts, as parasites are over-dispersed with the majority occurring in a small number of hosts). Continuous dosing with in-feed pyrantel has been discontinued due to the high levels of resistance induced, and regular-interval ('suppressive') dosing may also induce resistance and/or interfere with the development of natural protective immune responses (but is still practiced widely, especially in yearlings). Various control strategies may also be implemented to limit the faecal-oral transmission of infections, mainly by reducing the contamination on pastures with worm eggs and larvae (drench and move to clean pastures, collect and compost faeces, avoid overstocking, quarantine new animals, separate age groups, rotational grazing of cohorts so that nursing

mares and foals do not graze the same area in consecutive years, mixed or alternate grazing with other non-susceptible herbivores, or pasture spelling, particularly over hot dry periods). Several studies have also demonstrated the utility of biological control using nematophagous fungi to reduce larval contamination on pastures.

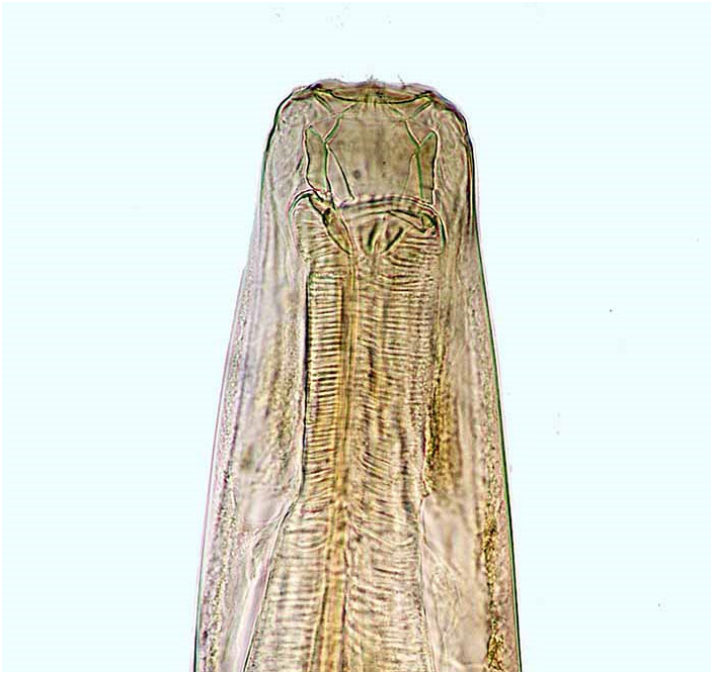

Cyathostomum and other small strongyles
Cyathostomum
Poteriostomum
Cylicocyclus
Cylicostephanus
heads
intestines
(diarrhoea, anaemia,
typhlocolitis, nodules,
larval cyathostominosis)
Definitive Hosts
(perissodactyls)
extended
hypobiosis
L3
ingested
adult
female
(~ 10 mm)
adult
male
(~ 8 mm)
male tail
(lateral)
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 800 µm)
external
environment
eggs
(~ 120 µm)
rhabditiform first- and
second-stage larvae (L1, L2)
(~ 600 µm)



Cyathostomum adult worms



Cyathostomum worm eggs



Cyathostomum adult worm, head

Chabertia
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the chabertiids which have large buccal capsules and infect the large intestines of herbivores. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 before they return to the lumen and moult into adults. *Chabertia* spp. (large-mouthed bowel worms) are found in the large intestines sometimes causing haemorrhagic enteritis in ruminants worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Chabertiidae (bowel and nodular worms, two pairs of branches in dorsal ray)
Genus:	*Chabertia* (parasitic in caecum/colon of ruminants)
Species:	various species cause haemorrhagic enteritis in ruminants and pigs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Strongylina (strongyles)				
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1

Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Strongyle worms are characterised by their prominent buccal capsules with lips, leaf crowns or labial collars at the mouth opening, sometimes with teeth or cutting plates. They are parasitic in a variety of organ systems in a range of animals, including the large intestines of mammals (ruminants, suids, elephants, perissodactyls, rodents, marsupials and primates), tortoises and ratite birds, the forestomach of marsupials, the trachea of birds and mammals, and the renal system of suids. Four families are recognised: Strongylidae (buccal capsule globular or cylindrical, oral opening circular, dorsal ray with 6 terminal branchlets, 32 genera in large intestines of mammals, reptiles and birds); Chabertiidae (buccal capsule globular or cylindrical, oral opening circular or oval, with leaf crown or labial collar, with up to 3 teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 22 genera in gastrointestinal tract of mammals); Syngamidae (buccal capsule subglobular, oral opening hexagonal, numerous teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 7 genera in respiratory, urinary and digestive tracts of mammals and birds); and Deletrocephalidae (oral opening hexagonal, dorsal ray with 6 terminal branches, 2 genera in large intestines of birds). The family Chabertiidae contains 4 subfamilies: Chabertinae (globular buccal capsule with leaf crowns, J-shaped ovejector, 11 genera in large intestines of ruminants, rodents, marsupials and primates); Oesophagostominae (cylindrical buccal capsule with leaf crowns and often cervical collar, J-shaped ovejector, 11 genera in large intestines of ruminants, suids, rodents and primates); Cloacinae (cylindrical buccal capsule wit leaf crowns, J-shaped ovejector, 39 genera in stomach of marsupials); and Phascolostrongylinae (cylindrical or globular buccal capsule without leaf crowns but with teeth or cutting plates, Y-shaped ovejector, 6 genera in stomach and intestines of marsupials).

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Chabertiinae (bowel worms)					
Chabertia (large-mouthed bowel worm)	5	artiodactyls	large intestines	10-26 mm long, stout white body, prominent bell-shaped buccal capsule curved ventrally, vestigial leaf crown in 2 rows, bifurcate dorsal gutter	90-105 x 50-55 µm, ellipsoidal, thin-shelled
Oesophagostominae (nodule worms)					
Oesophagostomum (nodule worms)	52	artiodactyls, primates	large intestines	6-25 mm, white-grey body, cylindrical buccal capsule, prominent leaf crown, cervical collar, larvae provoke nodule formation	58-89 x 34-51 µm, ovoid, thin-shelled

The subfamily Chabertinae contains 11 genera of bowel worms (*Agriostomum, Ancistronema, Castorstrongylus, Chabertia*, *Chabertiella, Colobostrongylus, Corollostrongylus, Cyclodonostomum, Okapistrongylus, Ransomus, Schulzinema,* and *Ternidens*) which are found in mammals worldwide, but are more common in temperate regions where infective larvae are better able to survive mild winters on pasture. Members of the genus *Chabertia* are characterised by their large conspicuous globular buccal capsules which are bent ventrally and associated with 2 rudimentary leaf crowns. Some 5 species have been described from

the large intestines of domestic and wild herbivores, and infections have been implicated in productional losses in livestock and sometimes with clinical disease (parasitic gastroenteritis).

***Chabertia* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
C. esrchowi	Artiodactyla: bovid (sheep, goat); Proboscidea: elephantid (Indian elephant)	large intestines	Asia
C. gaohanensis	Artiodactyla: bovid (sheep, goat)	large intestines	China
C. ovina (large-mouthed bowel worm) (syn. *Strongylus ovinus, hypostomus, cernuus*)	Artiodactyla: bovid (cattle, American bison, European bison, yak, sheep, bighorn sheep, argali, mouflon, chamois, goat, alpine ibex, goitered gazelle), cervid (roe deer, fallow deer, red deer, mule deer, white-tailed deer), camelid (dromedary), suid (pig)	large intestines [anorexia, enteritis, diarrhoea]	worldwide, esp. temperate zones
C. rishati	Artiodactyla: camelid (camel, sheep, goat)	large intestines	Indo-China
C. shaanxiensis	Artiodactyla: bovid (cattle, sheep, goat)	large intestines	China

Parasite morphology: *Chabertia* spp. form 3 different types of developmental stages: eggs; larvae (4 consecutive stages designated L1-L4); and adult worms. Mature females lay eggs which are thin-shelled, clear-coloured, oval-elliptical in shape measuring 90-105 x 50-55 µm and are partially embryonated containing a morula at the 16-32 cell (blastomere) stage of development. L1 are elongate free-living stages measuring around 450 x 20 µm with a striated cuticle bearing a longitudinal lateral line, a cylindrical buccal capsule, a rhabditiform (double-bulbed) oesophagus, intestines comprising 16 cells, and a tapering tail. L2 are similar in morphology but are larger (up to 650 x 30 µm), the cuticle bears 2 lateral lines, and the posterior buccal capsule contains short curved rods. L3 measure around 710-790 µm in length and are ensheathed (retain the L2 cuticle as a protective covering) and have broad round-square heads, small buccal capsules, a strongyliform (non-bulbed) oesophagus, intestines comprising 28-32 rectangular cells, and short conical tails encased in long tail sheath extensions (100-150 µm) of which the last 25% is filamentous. L4 are developing parasitic stages measuring from 1.1-1.8 mm in length and they are beginning to show many adult characteristics, including a well-developed buccal capsule with epaulette-like cranial swellings, an internal cuticular collar, a prominent cervical vesicle near the middle of the oesophageal region, and immature genitalia. Adults are stout white worm ranging in size from 10-26 mm and are readily identified by their enlarged and truncated anterior ends containing a prominent thick-walled buccal capsule which is bent ventrally (visible macroscopically and giving rise to the common name of large-mouthed bowel worm). The buccal capsule is subglobular or bell-shaped (unlike that of *Oesophagostomum* which is cylindrical) and it contains a double row of minute papillae and a dorsal gutter which bifurcates to form the sub-oral canal. The head bears a slightly inflated cephalic vesicle, vestigial corona radiata (internal and external leaf crown much reduced) and a shallow ventral cervical groove. Adult worms are sexually dimorphic, with females being larger than males (14-26 cf. 11-18 mm). Mature males have a well-developed copulatory bursa with 2 long spicules (1.3-1.8 mm) projecting from the posterior end. The bursa comprises 2 lateral lobes supported by 6 rays (comprising muscular elements following nerve channels to terminal papillae) and a dorsal lobe supported by a single ray with 4 terminal branches. Males also possess a gubernaculum (~0.2 mm long) and the tail is often spirally coiled. Mature females are didelphic with 2 ovaries, 2 uteri and 2 opposed J-shaped ovejectors leading to a common vulva opening posteriorly near the anus. They are oviparous and produce unembryonated thin-walled eggs.

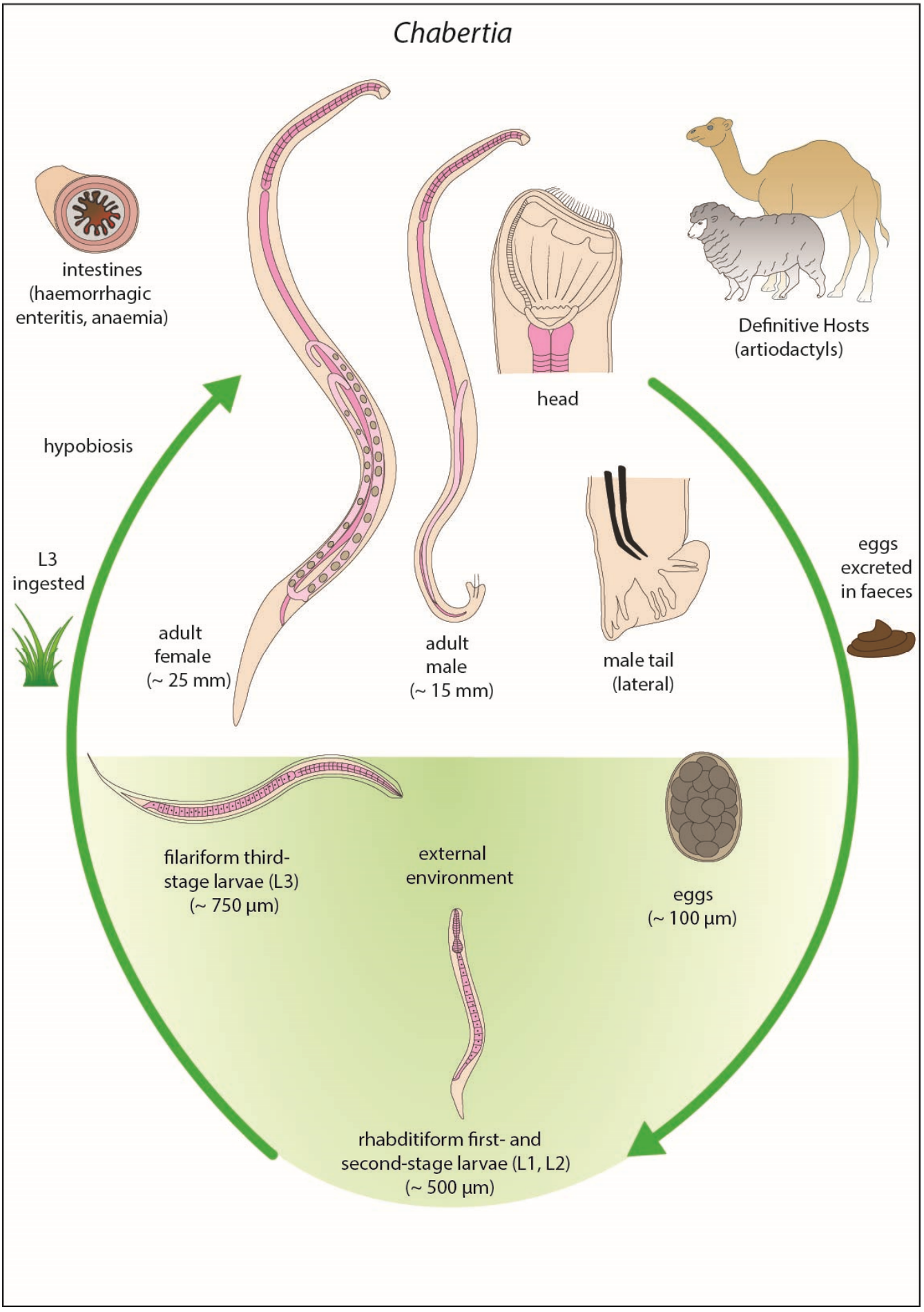
Site of infection: Endoparasitic stages include exsheathed L3, developing and hypobiotic L4 and adult worms which are all found in the large intestines of their ruminant hosts, especially the proximal colon. Free-living stages include worm eggs, L1, L2 and ensheathed L3 which occur on pastures contaminated by host faeces.

Pathogenesis: Infections by *Chabertia* spp. often occur concomitantly with other nematodes and collectively, moderate infections may contribute to subclinical production losses while heavy infections may cause mild to severe clinical disease (parasitic gastroenteritis). Larvae developing in the mucosa and adults in the lumen feed by drawing a plug of tissue into their large buccal capsules where it is digested. This results in significant traumatic damage to host tissues with petechial haemorrhages, oedema and inflammation. Adult worms frequently move to new feeding sites causing further damage and leaving behind haemorrhagic lesions. The walls of the large intestines become oedematous, thickened and congested, with excess mucus production and ulceration. Blood loss may be sufficient to cause anaemia, and disruptions to the intestinal wall lead to protein and fluid loss with soft or diarrhoeic faeces often containing blood and mucus (and sometimes detached worms), hypoalbuminaemia, weight loss, emaciation and sometimes death. Burdens of 300 worms are often considered to be pathogenic, but adult sheep and cattle develop a strong protective immunity leading to worm expulsion, so they rarely harbour large worm burdens. However, clinical signs may develop during the late prepatent period when developing larvae disrupt the mucosa before adult worms have matured, particularly in young animals under stress. Clinical infections are rarely seen in cattle, while those in sheep occur more frequently in temperate regions, particularly those with winter rainfall.

Developmental cycle and mode of transmission: Chabertiid worms have simple direct monoxenous life-cycles involving faecal-oral transmission. Female worms lay partially embryonated eggs (up to 3,000-5,000 per day) which are excreted with host faeces into the external environment. In warm and moist conditions, the eggs hatch in several days releasing free-living L1 which feed on faecal bacteria. These larvae moult to form free-living L2 which also feed on bacteria before moulting to L3 which retain the L2 cuticle as a protective sheath and are thus unable to feed. Development from egg to L3 generally takes around 5 weeks in favourable conditions of warmth and moisture, but may take longer in cooler conditions. Eggs and larvae are also able to survive for long periods in cold conditions, even withstanding temporary freezing. Infections are more prevalent in temperate regions, particularly those with winter rainfall. Sheathed L3 exhibit both horizontal migration (dispersing from faecal pellets) and vertical migration (ascending vegetation) in moist conditions (e.g. following rainfall or heavy dew). Ruminants become infected when they ingest infective L3 on contaminated pastures. Ingested L3 exsheath in small intestine and then invade glands in the ileum, caecum and colon where they moult to L4 around 7 days later (they do not undertake extra-intestinal migration). L4 may be released from mucosal tissues to continue their development, or they may undergo developmental arrest (hypobiosis) in the intestinal wall, emerging much later to resume development. In either case, L4 liberated into the gut lumen congregate in the caecum where moult to young adults (sometimes designated L5). Direct development from infection to L5 takes around 24-25 days, whereas delayed development involving hypobiotic larvae usually occurs over winter, with larvae emerging in early spring. The young adults move to the colon where they mature and mate. The prepatent period (time from infection to first egg excretion) ranges from 42-56 days.

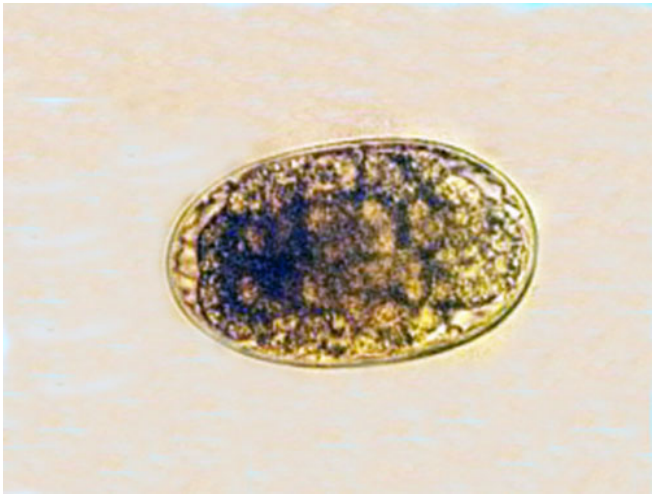
Differential diagnosis: The diagnosis of infections on the basis of clinical symptomatology is difficult as many infectious agents may cause similar nonspecific signs of gastroenteritis and loss of condition. Although expelled worms may be observed in diarrhoeic faeces in heavy acute infections, most diagnoses are based on the microscopic detection of worm eggs in faecal samples, usually following their concentration by sedimentation in water and floatation in saturated sugar or heavy metal salt solutions. Regrettably, the morphological features of the worm eggs are not sufficiently characteristic to differentially diagnose infections, as the eggs appear similar to many other trichostrongyle genera. In addition, many of the clinical signs may be caused by developing larvae before adult worms have matured and thus may appear during the late prepatent period when egg counts are negative or low. Recourse may be made to the coproculture of faecal samples to harvest L3 which can be identified by their morphological characteristics (sheathed L3 with broad rounded head, filariform oesophagus, intestines comprising 32 cells, and long filamentous tail sheath). Infections may also be diagnosed at necropsy by the detection of grey punctate lesions and/or adult worms in mucosal tissues. Molecular biological techniques have been used to differentiate various parasite species following the polymerase chain reaction (PCR) amplification of parasite DNA (nuclear ribosomal DNA, especially internal transcribed spacer regions 1 and 2, and the complete mitochondrial genome).

Treatment and control: A range of broad-spectrum anthelmintics have been used to successfully treat *Chabertia* infections in domestic livestock, including the macrocyclic lactones (avermectins (ivermectin, abamectin), milbemycins (moxidectin)), benzimidazoles (thiabendazole), imidazothiazoles (levamisole) and tetrahydropyrimidines (morantel), with most drugs being effective against adult worms, and less so against larval stages. Many veterinary health agencies recommend that producers monitor for drug resistance using faecal egg count reduction tests, and that they reduce treatment frequency by systematic dosing (seasonally or by cohort) or strategic dosing (on a needs basis). A variety of preventive control measures may also be used at the farm level to reduce the faecal-oral transmission of infections. Pasture contamination by worm eggs and free-living larvae may be minimalized by improving sanitation (draining pastures, providing clean water, and not giving supplementary feed on the ground), reducing stocking rates, quarantining new livestock, moving treated animals to clean ungrazed pastures, using rotational grazing for different cohorts (especially pregnant livestock and neonates) or mixed grazing with other animal species, and periodically spelling pastures, especially over hot dry summers.


Chabertia
intestines
(haemorrhagic
enteritis, anaemia)
Definitive Hosts
(artiodactyls)
head
hypobiosis
L3
ingested
adult
female
(~ 25 mm)
adult
male
(~ 15 mm)
male tail
(lateral)
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 750 µm)
external
environment
eggs
(~ 100 µm)
rhabditiform first- and
second-stage larvae (L1, L2)
(~ 500 µm)



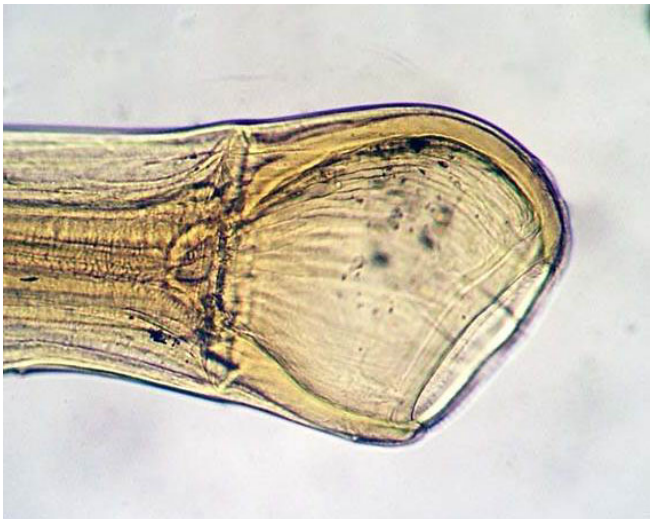
Chabertia adult worms



Chabertia worm egg



Chabertia adult worm, male bursa



Chabertia adult worm, head

Oesophagostomum
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the chabertiids which have large buccal capsules and often form nodules in the large intestines of herbivores. They have direct life-cycles where eggs passed in faeces develop to L3 (L2 cuticle retained as a sheath). Hosts ingest L3 which exsheath, migrate into the mucosa and moult into L4 (some may undergo arrested development, termed hypobiosis) before they return to the lumen and moult into adults. *Oesophagostomum* spp. (nodule worms) are found in the large intestines causing diarrhoea and ulcerative colitis in ruminants and sometimes necrotic colitis in pigs worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Chabertiidae (nodular worms, two pairs of branches in dorsal ray)
Genus:	*Oesophagostomum* (parasitic in caecum/colon of ruminants/pigs/humans)
Species:	various species cause enteritis in ruminants and pigs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Strongylina (strongyles)				
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae	buccal capsule armed with teeth, leaf	suids	transdermal	1

(kidneyworm)	crowns and external epaulettes		penetration or ingestion of L3 or PH	
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Strongyle worms are characterised by their prominent buccal capsules with lips, leaf crowns or labial collars at the mouth opening, sometimes with teeth or cutting plates. They are parasitic in a variety of organ systems in a range of animals, including the large intestines of mammals (ruminants, suids, elephants, perissodactyls, rodents, marsupials and primates), tortoises and ratite birds, the forestomach of marsupials, the trachea of birds and mammals, and the renal system of suids. Four families are recognised: Strongylidae (buccal capsule globular or cylindrical, oral opening circular, dorsal ray with 6 terminal branchlets, 32 genera in large intestines of mammals, reptiles and birds); Chabertiidae (buccal capsule globular or cylindrical, oral opening circular or oval, with leaf crown or labial collar, with up to 3 teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 22 genera in gastrointestinal tract of mammals); Syngamidae (buccal capsule subglobular, oral opening hexagonal, numerous teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 7 genera in respiratory, urinary and digestive tracts of mammals and birds); and Deletrocephalidae (oral opening hexagonal, dorsal ray with 6 terminal branches, 2 genera in large intestines of birds). The family Chabertiidae contains 4 subfamilies: Chabertinae (globular buccal capsule with leaf crowns, J-shaped ovejector, 11 genera in large intestines of ruminants, rodents, marsupials and primates); Oesophagostominae (cylindrical buccal capsule with leaf crowns and often cervical collar, J-shaped ovejector, 11 genera in large intestines of ruminants, suids, rodents and primates); Cloacinae (cylindrical buccal capsule with leaf crowns, J-shaped ovejector, 39 genera in stomach of marsupials); and Phascolostrongylinae (cylindrical or globular buccal capsule without leaf crowns but with teeth or cutting plates, Y-shaped ovejector, 6 genera in stomach and intestines of marsupials).

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Oesophagostominae (nodule worms)					
Oesophagostomum (nodule worms)	52	artiodactyls, primates	large intestines	6-25 mm, white-grey body, cylindrical buccal capsule, prominent leaf crown, cervical collar, larvae provoke nodule formation	58-89 x 34-51 µm, ovoid, thin-shelled
Chabertiinae (bowel worms)					
Chabertia (large-mouthed bowel worm)	5	artiodactyls	large intestines	10-26 mm long, stout white body, prominent bell-shaped buccal capsule curved ventrally, vestigial leaf crown in 2 rows, bifurcate dorsal gutter	90-105 x 50-55 µm, ellipsoidal, thin-shelled

The subfamily Oesophagostominae contains 11 genera of nodular worms which are classified within 3 tribes: Oesophagostominea (*Oesophagostomum, Daubneyia, Wuia*) with the transverse cervical groove confined to ventral side, parasitic in ruminants, rodents and suids; Bourgelatioidinea (*Bourgelatioides*, *Neorhabditostomum*, *Rhabditistomum*) with the transverse

cervical groove completely encircling body, parasitic in ruminants and tragulids; and Bourgelatinea (*Bourgelatia*, *Kuntzistrongylus*, *Lemurstrongylus*, *Phacochoerostrongylus*, *Trachypharynx*) lacking a transverse cervical groove, parasitic in suids, rodents and primates. Over the years, various workers proposed the division of the genus *Oesophagostumum* into various subgenera (*Oesophagostomum, Proteracaecum*, *Hysteracrum*, *Conoweberia, Ihlea, Lerouxiella*, *Bosicola, Hydsonia* and *Pukuia*), but many considered such divisions to be based primarily on host records and not on characteristics of the parasites themselves. At present, the genus *Oesophagostomum* contains over 50 species which occur worldwide in domestic and wild artiodactyls, primates and some rodents. The species *O. radiatum* and *O. columbianum* infect ruminants mainly in tropical or subtropical areas, with heavy parasite burdens seen during periods of high (often summer) rainfall. The species *O. venulosum* also occurs in ruminants but mainly in regions with cooler climates and winter rainfall. The species *O. dentatum* is found in pigs worldwide, but only in free-range animals (and not in intensive feedlot piggeries) as the presence of soil is necessary for larval development. The species *O. bifurcum, O. aculeatum* and *O. stephanostomum* infect primates (including humans) mostly in South-East Asia and western Africa.

***Oesophagostomum* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
O. (*Conoweberia*) *aculeatum*	Primates: cercopithecid (rhesus macaque, Japanese macaque, crab-eating macaque, Togue macaque, Francois' leaf monkey, golden snub-nosed monkey, northern plains grey langur), hominid (human)		Asia
O. aethiopicum	Artiodactyla: suid (bushpig, warthog)		Africa
O. africanum	Artiodactyla: bovid (springbok)		Africa
O. apiostomum	Primates: cercopithecid (rhesus macaque), hominid (human)		
O. (*Hysteracrum*) *asperum*	Artiodactyla: bovid (sheep, bharal, goat, Himalayan goral, nilgai), cervid (sambar deer, Reeve's muntjac, moose), suid (pig)	large intestines [diarrhoea]	Asia, Americas
O. (*Conoweberia*) *bifurcum*	Primates: cercopithecid (grivet, mona monkey, Campbell's mona monkey, crab-eating macaque, rhesus macaque, stump-tailed monkey, olive baboon, yellow baboon, chacma baboon, gray-footed chacma baboon, patas monkey), hominid (chimpanzee, human); Artiodactyla: bovid (goat), suid (pig)	large intestines	Africa, South-East Asia, South America
O. (*Conoweberia*) *blanchardi*	Primates: hylobatid (gibbon), hominid (orangutan)		Asia
O. brevicaudum	Artiodactyla: suid (pig)	large intestines [diarrhoea]	Europe, North America
O. (*Conoweberia*) *brumpti*	Primates: cercopithecid (macaque), hominid (orangutan, human)		Asia
O. cervi	Artiodactyla: cervid (roe deer, fallow deer, red deer, sambar deer, white-tailed deer)		worldwide
O. (*Proteracaecum*) *columbianum*	Artiodactyla: bovid (cattle, sheep, argali, goat, impala, black wildebeest, blue wildebeest, common tsessebe, sable antelope, waterbuck, steenbok, Sharpe's grysbok, southern reedbuck, Limpopo bushbuck, common duiker), cervid (white-tailed deer), camelid (bactrian camel, dromedary, alpaca); Rodentia: caviid (guinea pig)	intestines [diarrhoea]	worldwide, esp. tropics
O. curvatum	Artiodactyla: cervid (sambar deer, Indian muntjac)		Asia
O. dentatum (syn. *O. subulatum*)	Artiodactyla: suid (pig, Indian boar, Sardinian wild boar), tayassuid (collared peccary, white-lipped peccary)	large intestines [diarrhoea]	worldwide
O. dentigerum	Primates: hominid (chimpanzee)		Africa
O. (*Daubneyia*) *eurycephalum*	Artiodactyla: suid (desert warthog), bovid (roan antelope)		Africa
O. farchai	Artiodactyla: suid (desert warthog)		Africa
O. georgianum	Artiodactyla: suid (pig)	large intestines [diarrhoea]	North America
O. (*Daubneyia*) *goodeyi*	Artiodactyla: suid (warthog)		Africa
O. granatensis	Artiodactyla: suid (pig)	large intestines [diarrhoea]	Europe
O. hylochoeri	Artiodactyla: suid (giant forest hog)	colon	Africa
O. lechwei	Artiodactyla: bovid (kafue lechwe)		Africa

O. longicaudatum	Artiodactyla: suid (pig)	large intestines [diarrhoea]	Europe
O. longicaudum	Artiodactyla: suid (pig)	large intestines [diarrhoea]	Europe
O. macacae	Primates: cercopithecid (rhesus macaque)		Africa
O. mocambiquei	Artiodactyla: suid (desert warthog)		Africa
O. mpwapwae	Artiodactyla: suid (desert warthog); Proboscidea: elephantid (African bush elephant)		Africa
O. multifoliatum	Artiodactyla: bovid (sheep, goat, steenbok, Sharpe's grysbok, common duiker)	large intestines [diarrhoea]	Africa
O. (*Hysteracrum*) *muntiacum*	Artiodactyla: cervid (Indian muntjac, Reeve's muntjac)		Asia
O. (*Daubneyia*) *mwanzae*	Artiodactyla: suid (desert warthog), bovid (roan antelope, Livingstone's eland); Proboscidea: elephantid (African bush elephant); Perissodactyla: equid (plains zebra)		Africa
O. okapi	Artiodactyla: giraffid (okapi)		Africa
O. (*Daubneyia*) *oldi*	Artiodactyla: bovid (roan antelope), suid (warthog)		Africa
O. (*Conoweberia*) *ovatum*	Primates: hylobatid (gibbon),		Asia
O. (*Conoweberia*) *pachycephalum*	Primates: cercopithecid (red-tailed monkey)		Africa
O. quadrispinulatum	Artiodactyla: suid (pig, wild boar)	large intestines [diarrhoea]	worldwide
O. radiatum (syn. *Bosicola radiatum, tricollaris, O. inflatum, dilatum, bovos, biramosum, vesiculosum*)	Artiodactyla: bovid (cattle, Bali cattle, zebu, water buffalo, American bison, European bison, sheep, goat, chamois, kob, steenbok, Livingstone's eland), cervid (roe deer, fallow deer, red deer, Javan rusa deer, sambar deer)	intestines [diarrhoea]	worldwide
O. (*Conoweberia*) *raillieti*	Primates: hylobatid (gibbon),		Asia
O. roscoei	Artiodactyla: bovid (blue duiker)		Africa
O. (*Daubneyia*) *roubaudi*	Artiodactyla: suid (warthog)		Africa
O. santosdiasi	Artiodactyla: suid (warthog)		Africa
O. (*Conoweberia*) *selfi* (syn. *Kuntzistrongylus*)	Rodentia: murid (Coxing's white-bellied rat)		Taiwan
O. sikae	Artiodactyla: cervid (roe deer, fallow deer, red deer), tragulid (Java mouse-deer)		Asia
O. (*Daubneyia*) *simpsoni*	Artiodactyla: suid (warthog), bovid (roan antelope); Proboscidea: elephantid (African bush elephant)		Africa
O. (*Ihlea*) *stephanostomum* (incl. subspp. *stephanostomum*, *thomasi*)	Primates: hominid (eastern lowland gorilla, chimpanzee, eastern chimpanzee, human)		Africa, Asia,, South America
O. (*Lerouxiella*) *suzannae*	Rodentia: pedetid (springhare)		Africa
O. (*Protaeracum*) *synceri*	Artiodactyla: bovid (African buffalo)		Africa
O. traguli	Artiodactyla: tragulid (Java mouse-deer)		Asia
O. (*Ihlea*) *ventri*	Carnivora: felid (wild cat)		
O. (*Hysteracrum*) *venulosum* (large bowel worm) (syn. *Strongylus follicularis, O. acutum, inflatum var. ovis, vigintimembrum*)	Artiodactyla: bovid (cattle, zebu, European bison, sheep, argali, mouflon, goat, mountain goat, chamois, nilgai), cervid (roe deer, fallow deer, red deer, Iberian red deer, sika deer, chital deer, water deer, Reeve's muntjac, mule deer, Columbian black-tailed deer, white-tailed deer, boreal woodland caribou, moose), camelid (bactrian camel, dromedary, llama)	large intestines [diarrhoea]	worldwide
O. walkeri	Artiodactyla: bovid (impala, sable antelope, Sharpe's grysbok, common eland, Livingstone's eland)		Africa
O. (*Lerouxiella*) *xeri*	Rodentia: sciurid (African ground squirrel)		Africa
O. (*Daubneyia*) *yorkei*	Artiodactyla: suid (desert warthog); Proboscidea: elephantid (African bush elephant)		Africa
O. (*Conoweberia*) *zukowskyi*	Primates: cercopithecid (baboon)		Africa

Parasite morphology: *Oesophagostomum* spp. form 3 different types of morphological stages in their developmental cycles: eggs; larvae (4 stages designated L1-L4); and adult worms (males and females). Eggs are oval to elliptical in shape measuring 58-89 x 34-

51 µm and contain a morula at the 8-32 cell (blastomere) stage with a clear space between the developing embryo and the very thin eggshell. L1 and L2 are free-living stages with long narrow buccal capsules, a muscular rhabditiform oesophagus (flask-shaped with 2 projections), intestines comprising several cells and long tapering tails. L3 are ensheathed stages that have retained the L2 cuticle as a protective covering. They are elongate stages measuring 600-923 µm in length and have broad squared heads, cylindrical buccal capsules, a strongyliform (club-shaped) oesophagus, intestines comprising 18-22 triangular cells, and tapering rounded tails encased in long tail sheath extension (122-207 µm) of which the terminal 50% is filamentous. Adult worms have stout white-grey bodies 6-25 mm long that are often slightly curled. The anterior oral opening is circular and often forms a high mouth collar (appearing as a truncate cone). The mouth is surrounded by a corona radiata with 9-24 elements in the external leaf crown (ELC) and usually double that number (18-48) in the internal leaf crown (ILC), although their composition varies between species. For example, *O. dentatum* and *O. quadrispinulatum* have 9-12 ELC but poorly developed ILC elements, *O. georgianum* and *O. longicaudum* have 9 ELC elements and 18 ILC elements, *O. brevicaudum* has 14-16 ELC elements and 28-32 ILC elements, *O. venulosum* has 18-20 ELC elements and 36-40 ILC elements, *O. columbianum* has 20-24 ELC elements and 40-48 ILC elements, while *O. radiatum* has 30-40 ILC elements but those of the ELC are highly reduced to small regular protuberances. All *Oesophagostomum* species have a small cylindrical thin-walled buccal cavity which opens forward (as opposed to the large globular buccal capsule of *Chabertia* which is bent ventrally). The head of adult worms then has a distinct anterior inflation of the cuticle (cephalic vesicle) located anteriorly from a transverse constriction (cervical groove) [which in the case of the oesophagostomines is confined to the ventral side]. The location of the lateral cervical papillae (spiny sensory protrusions) varies according to species, but most are located just posterior to the ventral groove. An excretory pore (stoma) is also present in the ventral groove at the level of the oesophagus (thus giving the genus its name). Some species also have well-developed lateral cervical alae arising behind the ventral groove (e.g. *O. columbianum*). Adult worms are sexually dimorphic, with females generally slightly larger than males (6-25 cf. 5-17 mm). Mature males have a bell-like copulatory bursa with 2 lateral lobes supported by 5 rays (comprising muscular elements following nerve channels to terminal papillae) whereby the 2 ventral rays are closely-associated but separate from the 3 lateral rays (with the middle anterolateral ray shorter and separate from the others), and a dorsal lobe supported by a ray with 4 terminal branches. Males also have a gubernaculum and telamon with 2 equal filiform spicules measuring 0.7-1.2 mm in length. Mature females are didelphic with 2 ovaries and 2 uteri connected by J-shaped ovejectors to a common vulva that opens near the anus along the tapering tail. Females are oviparous and lay partially embryonated thin-walled eggs.

Site of infection: Adult worms infect the large intestines (caecum and colon) of their definitive hosts (ruminants, suids, rodents, primates), while developing larval stages (L3 and L4) are found in nodules in the walls of both the small and large intestines. Free-living larval stages (L1, L2 and sheathed L3) are found in the external environment where they contaminate soil and pastures.

Pathogenesis: Infections by several *Oesophagostomum* spp. have been associated with mild to severe disease in ruminants, suids and primates. The severity of disease depends on parasite virulence, the intensity of infection, host susceptibility, and prior exposure. While most infections are light and remain subclinical, heavier infections (> 800 worms in cattle, > 200 worms in sheep) may cause transient diarrhoea and illthrift. Adult worms reside in the lumen of the large intestines and are plug-feeders (ingest host tissues), often causing chronic infections where the intestinal mucosa becomes hyperaemic, mucoid and thickened. In contrast, earlier larval stages may cause acute disease when they damage the intestinal wall. Infective L3 penetrate deep into the wall of the small and large intestines where they become encapsulated in small subserosal nodules (1-2 mm) by host fibroblastic reactions (the exception is *O. venulosum* which does elicit nodule formation). The histotrophic stages develop to L4 which elicit stronger host reactions so the nodules become larger (1-2 cm) and start to mineralize becoming filled with caseous material that may eventually calcify. Nodular lesions render the gut wall unsuitable for use as sausage casings. While L4 may be retained in nodules for long periods, eventually they emerge leaving ulcerative lesions which ooze and bleed, with ecchymoses and petechial haemorrhages leading to fluid, protein and blood loss. It is estimated that worms may cause daily blood loss of 0.1 ml/worm so heavy infections may result in anaemia and hypoproteinaemia (esp. hypoalbuminaemia). Tissue trauma and inflammation alters intestinal function (reduced digestion, absorption and peristalsis) resulting in blood-stained mucoid to projectile fetid diarrhoea, with dehydration, intestinal discomfort, anorexia, unthriftiness, progressive weight loss, retarded growth, general weakness, exhaustion, and starvation. Inflammatory nodular disease may also involve diphtheritic jejunitis, typhlitis and colitis with perforations and adhesions, intussusception, abscess formation and peritonitis. Acute disease involving diarrhoea, dehydration, colic and fever is seldom observed in sheep, as larval challenge elicits strong local protective immune responses in the colon resulting in worm expulsion. Nonetheless, persistent infections may produce chronic disease with intermittent diarrhoea (foul-smelling mucopurulent green faeces), anorexia, weight loss and occasionally intussusception. Cattle also develop strong protective immune responses after 8-12 months of age, but calves older than 7 weeks may develop acute disease with diarrhoea, anaemia, oedema, anorexia and cachexia. Most infections in pigs do not cause overt disease, but rather contribute to ill-thrift with occasional diarrhoea, particularly in older animals in which worm burdens increase with age. However, *O. dentatum* and *O. quadrispinulatum* may cause severe wasting disease in young pigs, with ulcerative colitis, enteritis, widespread haemorrhages, diphtheritic membrane formation and regional lymphadenopathy. In humans, emergent larvae may cause nodule remnants to become ulcerative and haemorrhagic, but in many cases, L4 do not emerge but cause dark pustular abscesses containing numerous eosinophils and macrophages. Oesophagostomiasis in humans may be uni-nodular, with single large nodules (2-11 cm in diameter) projecting from the colon causing hard painful abdominal masses (regionally known as Dapaong disease), or multi-nodular, with numerous tiny nodules forming along the colon causing mild diarrhoea, dysentery or constipation, anaemia, bowel obstructions, anorexia, nausea, fever and

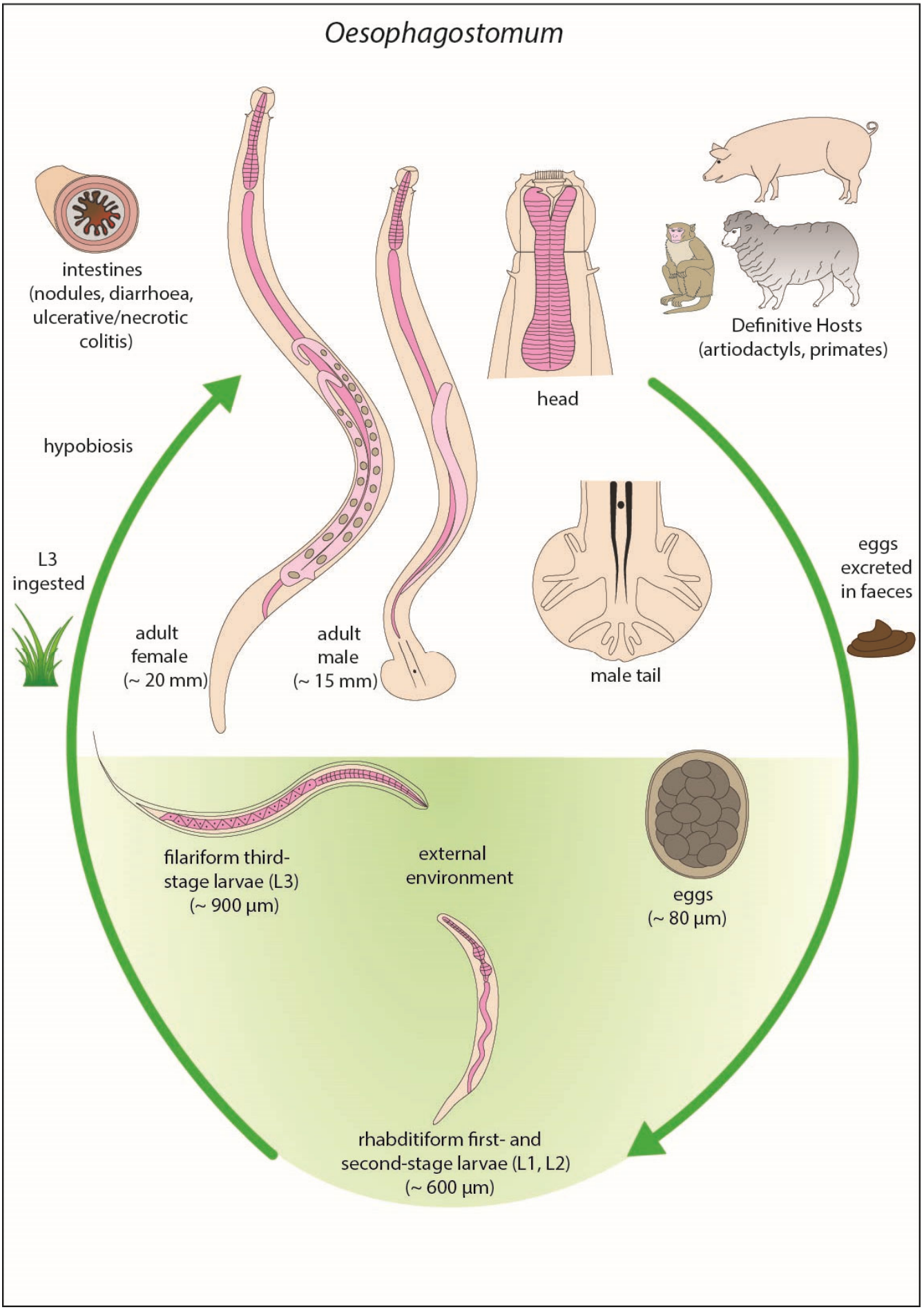
malaise. Infections have also been associated with peritonitis, appendicitis, hepatosplenomegaly, cardiomegaly, emaciation, and occasionally skin lesions.

Developmental cycle and mode of transmission: *Oesophagostomum* spp. have simple direct monoxenous life-cycles involving the faecal-oral transmission of infections between individuals. Gravid female worms lay eggs (several thousand per day) which are excreted in host faeces to contaminate the external environment. In moist shady warm conditions, the eggs hatch after 2 or more days releasing free-living L1 which feed on faecal bacteria before moulting to form free-living L2 which also feed on bacteria. These stages then moult to form L3 which retain the L2 cuticle as a protective sheath and are thus unable to feed. Depending on prevailing environmental conditions, it usually takes several weeks for L3 to develop from eggs. While free-living larvae prefer hot moist conditions found in tropical and subtropical regions (particularly those with summer rainfall), the larvae of some species appear to be very resistant to desiccation and/or freezing, and are able to survive for several months (up to 14 months). Moisture stimulates L3 to migrate horizontally (dispersing from faecal pats) as well as vertically (ascending vegetation during the day but descending during cold nights). Hosts become infected by ingesting infective L3 in contaminated food, water or soil. Ingested L3 exsheath in the gut and penetrate the mucosa of the small or large intestines within a few hours. Here they undergo histotrophic development forming nodules over 6-20 days in which they moult to L4 (the larvae do not undertake any extra-intestinal migration). At this stage, some larvae may exhibit inhibited or arrested development (known as hypobiosis) for several weeks/months before resuming development. There is good evidence for L4 hypobiosis occurring in sows from colder regions, with resumption of development around farrowing resulting in a periparturient rise in egg production. In either case, L4 eventually emerge from the gut wall into the lumen and migrate to the colon where they moult to young adults (sometimes called L5) which feed, mature and mate. The prepatent period (time from infection to first excretion of eggs) ranges from 30-40 days for first infections, increasing to several months for subsequent infections (prior sensitization of the host apparently exacerbates nodule formation and the retention of L4 in the intestinal wall).

Differential diagnosis: Infections may be suspected on the basis of clinical symptomatology (diarrhoea, illthrift) but many other conditions may cause similar signs of disease (especially gastroenteric nematodes). Coprological techniques are conventionally used to detect worm eggs in faecal samples, either in wet mounts or smears but usually following their concentration by sedimentation in water and/or floatation in saturated sugar or heavy metal salt solutions. Regrettably, the thin-shelled eggs deteriorate quickly in floatation media, and they are also remarkably similar in morphology to those of other strongylid nematodes, particularly trichostrongyles (like *Hyostrongylus* in pigs) and hookworms. In addition, faecal egg counts often do not correlate well with the occurrence of clinical signs, as developing larval stages may cause disease before adult worms have matured and begun egg production. Faecal samples may be incubated in moist chambers in order to harvest L3 for morphological identification, but most coproculture techniques take over a week to perform and are frequently contaminated by fungal overgrowths. *Oesophagostomum* L3 are ~ 500 μm long and have broad rounded heads, intestines comprising 32 cells, and tapering tails with long filamentous tail sheaths. These characteristics are similar to those of *Chabertia* L3 but the latter are shorter and have shorter tail sheaths, whereas *Hyostrongylus* L3 are ~ 700 μm and have squared heads, intestines comprising 16 cells, tapering tails with a digitiform process, short tail sheaths, and are highly active (often exhibiting a swimming motion). Modern medical imaging techniques (particularly ultrasound) have also been used to detect intestinal and abdominal wall nodules in humans, sometimes in association with laparoscopy. Uni-nodular (Dapaong) tumours have defined but poorly-reflective walls and echo-free lumens, while multi-nodular disease revealed numerous small colonic lesions and pseudokidney intussusceptions. Investigative surgery has also been used to differentiate colonic carcinoma, amoebiasis or inflammatory bowel disease from oesophagostomiasis by the subsequent microscopic detection of parasites in biopsied nodules. Infections may also be diagnosed post-mortem in domestic animals by the detection of adult worms in the colon. Several enzyme immunoassays have been developed to detect specific host serum antibodies against parasite antigens, but many demonstrated cross-reactivity problems with other nematodes, especially hookworms. Modern molecular biological techniques have been used to characterize adult and larval stages of various species following the polymerase chain reaction (PCR) amplification of parasite DNA, including restriction fragment length polymorphism (RFLP) analyses, rapid amplified polymorphic DNA (RAPD) analyses, single strand conformation polymorphism (SSCP) analyses or partial gene sequencing (nuclear ribosomal DNA and internal transcribed spacer regions, and mitochondrial cytochrome c oxidase subunit I).

Treatment and control: Infections by adult worms have been successfully treated with a variety of anthelmintics, including macrocyclic lactones (abamectin, doramectin, ivermectin), benzimidazoles (albendazole, thiabendazole, fenbendazole, flubendazole), imidazothiazoles (levamisole), tetrahydropyrimidines (pyrantel) and diethylenediamines (piperazine). However, the drugs were less effective against developing or hypobiotic larval stages encapsulated within nodules in the intestinal walls, so treatment needs to be repeated to counter emerging stages as well as re-infections. There have been increasing reports of drug resistance in worm populations, particularly against benzimidazole drugs. Veterinary authorities recommend monitoring for drug resistance using faecal egg count reduction tests, cycling between different drug classes, and using systematic or strategic dosing protocols to treat susceptible and/or infected animals, particularly following rainy seasons when infections are most prevalent. Surgical intervention has been used to incise and drain uni-nodular (Dapaong) tumours as well as to relieve bowel obstruction complications in human patients. Various control strategies can be used to reduce transmission rates, mostly by limiting faecal contamination of the environment and providing clean food and water supplies free of infective larvae. Where possible, faeces should be collected for treatment or sanitary disposal, and should not be used to fertilise edible foods. Strict hygiene should be

maintained in intensive farming situations, with regular cleaning and disinfection of holding facilities, especially farrowing pens. Pasture management practices involve controlled rather than free-range grazing, reducing stocking rates, quarantining new livestock, rotational or mixed grazing, draining pastures of excess moisture, or leaving them ungrazed for a season. In human communities at risk, vegetables and fruits should be washed thoroughly in clean treated water or cooked properly before consumption. Education campaigns may also be used to create public awareness and suggest suitable interventions.


Oesophagostomum
intestines
(nodules, diarrhoea,
ulcerative/necrotic
colitis)
head
Definitive Hosts
(artiodactyls, primates)
hypobiosis
L3
ingested
adult
female
(~ 20 mm)
adult
male
(~ 15 mm)
male tail
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 900 µm)
external
environment
eggs
(~ 80 µm)
rhabditiform first- and
second-stage larvae (L1, L2)
(~ 600 µm)



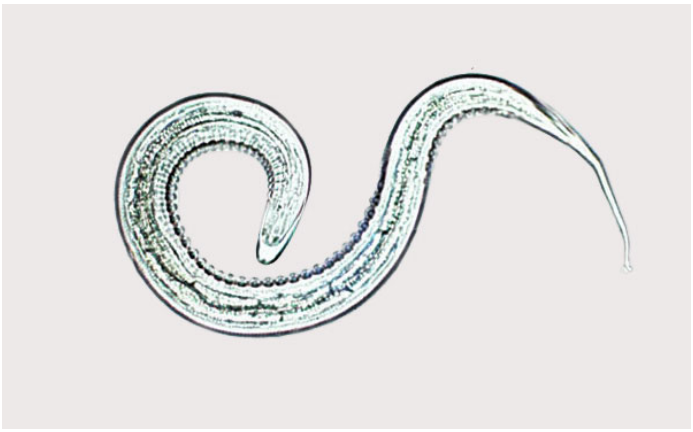
Oesophagostomum adult worms



Oesophagostomum adult worm, head



Oesophagostomum worm egg



Oesophagostomum third-stage larva

Stephanurus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the stephanurids which are stout worms with a prominent buccal capsule often armed with teeth, small leaf crowns and external epaulettes. They have direct life-cycles, usually involving eggs passed in faeces developing to L3 which are ingested by new hosts and develop to adults. *Stephanurus*, however, may also infect hosts percutaneously, when L3 penetrate the skin, moult to L4, wander in the liver parenchyma during maturation before completing development in cysts in peri-renal regions. Worm eggs are voided via the ureter with host urine. Earthworms may also act as paratenic (transport) hosts for L3. *S. dentatus* (pig kidneyworm) causes hepatic cirrhosis in pigs worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Syngamidae (buccal capsule with basal teeth, in respiratory, urinary or digestive tract of mammals/birds)
Subfamily:	Stephanurinae (rudimentary leaf crown, kidney-worm in pigs)
Genus:	*Stephanurus* (parasitic in kidneys of pigs)
Species:	*S. dentatus* causes cirrhosis in pigs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Strongylina (strongyles)				
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32

Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Strongyle worms are characterised by their prominent buccal capsules with lips, leaf crowns or labial collars at the mouth opening, sometimes with teeth or cutting plates. They are parasitic in a variety of organ systems in a range of animals, including the large intestines of mammals (ruminants, suids, elephants, perissodactyls, rodents, marsupials and primates), tortoises and ratite birds, the forestomach of marsupials, the trachea of birds and mammals, and the renal system of suids. Four families are recognised: Strongylidae (buccal capsule globular or cylindrical, oral opening circular, dorsal ray with 6 terminal branchlets, 32 genera in large intestines of mammals, reptiles and birds); Chabertiidae (buccal capsule globular or cylindrical, oral opening circular or oval, with leaf crown or labial collar, with up to 3 teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 22 genera in gastrointestinal tract of mammals); Syngamidae (buccal capsule subglobular, oral opening hexagonal, numerous teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 7 genera in respiratory, urinary and digestive tracts of mammals and birds); and Deletrocephalidae (oral opening hexagonal, dorsal ray with 6 terminal branches, 2 genera in large intestines of birds). The family Syngamidae contains 3 subfamilies: Syngaminae (leaf crown absent, teeth at base of buccal capsule, anterior vulva, 5 genera in trachea of birds and some mammals); Stephanurinae (rudimentary leaf crown, teeth at base of buccal capsule, rudimentary bursa, posterior vulva, 1 genus in urinary system of suids); and Archeostrongylinae (leaf crown absent, teeth absent at base of buccal capsule, 1 genus in intestines of porcupines).

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Stephaurinae					
Stephanurus (kidney-worm)	1	suids	urinary tract	2-5 cm long, stout reddish bodies, white reproductive organs, prominent buccal capsule often armed with teeth, small leaf crowns and external epaulettes, eggs passed in faeces and urine, L3 ingested or percutaneous, earthworm PH	90-136 x 53-70 µm, ellipsoidal, thin-shelled
Syngaminae					
Syngamus (gape worm)	10	birds	respiratory tract	2-30 mm long, hexagonal cup-shaped buccal capsule armed with teeth, no leaf crowns, small male permanently attached to female vulva imparting Y-shape, L3 develop in eggs before hatching, invertebrate PH	70-100 x 42-62 µm, ellipsoidal, operculate

The subfamily Stephanurinae is monotypic and contains a single genus (*Stephanurus*) with a single species (*S. dentatus*) which forms cysts attached to the ureters of suids (commonly known as pig kidneyworms). Worm eggs are passed in urine to the

external environment where they embryonate. Hosts become infected by eating infective L3 or when L3 penetrate the skin resulting in extra-intestinal migration. Infections are common in free-ranging and wild pigs in tropical and sub-tropical areas, and may affect domestic pigs with access to unfloored or outdoor areas (occasionally infecting cattle).

***Stephanurus* species**	**Definitive Hosts [plus Paratenic Hosts (PH)]**	**Location [Clinical signs]**	**Distribution**
S. dentatus (pig kidneyworm) (syn. *S. morai, S. nattereri, Sclerostoma dentatum, pinguicola, renium, Strongylus dentatus, pinguicola*)	Artiodactyla: suid (pig, wild boar, Japanese boar), bovid (cattle); rarely Rodentia: caviid (guinea pig) [plus PH: Clitellata: octochaetid (*Eutypheus waltoni*), megascolecid (*Pheretima diffringens*)]	kidney, perirenal fat [abscesses]	worldwide (except western Europe), esp. tropics

Parasite morphology: The pig kidneyworm forms 3 different types of developmental stages: eggs; larvae (4 successive stages designated L1-L4); and adult worms. Eggs are thin-shelled ovoid stages measuring 90-136 x 53-70 µm with one end broadly rounded and the other narrowly rounded. The contain a multicellular morula (32-64 blastomere stage) which is centrally located but usually surrounded by a clear space. L1 are free-living stages measuring from 360-560 µm with a rhabditiform (bulbed) oesophagus and an elongate tapering tail. L2 are similar but measure from 540-710 µm and have a slender tail. L3 are ensheathed in that the second moult was incomplete and they retained the L2 cuticle as a protective sheath. These larvae measure from 510-610 µm and have a mouth bordered by inconspicuous lips, a spindle-shaped buccal cavity, a strongyliform oesophagus, intestines with 32 cells, and a short conical tail. L4 are parasitic stages that migrate through host tissues. They are initially small (320-790 µm) but grow markedly throughout their development (up to 1-3 mm long). The have a well-developed and heavily-sclerotized buccal capsule, and an elongate tubular oesophagus. Adult worms have stout bodies 20-50 mm long that are pink-red in colour but frequently appear mottled as the light-coloured internal reproductive organs are visible through the translucent cuticle. Adults have a hexagonal oral opening leading to a prominent subglobular (cup-shaped) buccal capsule armed with 6 cusped teeth at the base, and surrounded by small rudimentary leaf crowns (absent in *Syngamus*) and 6 external cuticular thickenings (epaulettes). Mature worms are sexually dimorphic, with females being larger than males (30-50 cf. 20-30 mm). Males have a short rudimentary bursa reduced to short thick blunt rami (the dorsal ray having 4 terminal branches) and 2 dark elongate spicules almost equal in length. Females are didelphic with 2 ovaries and connecting ducts terminating in a common posterior vulva (anterior in *Syngamus*).

Site of infection: Adult worms are usually found encysted within the peri-renal fat or in the pelvis of the kidneys of their suid hosts. Eggs are voided in host urine and give rise to free-living larval stages (L1, L2 and ensheathed L3) that contaminate the external environment. Parasitic L4 migrate through the liver before young adults infect the kidneys.

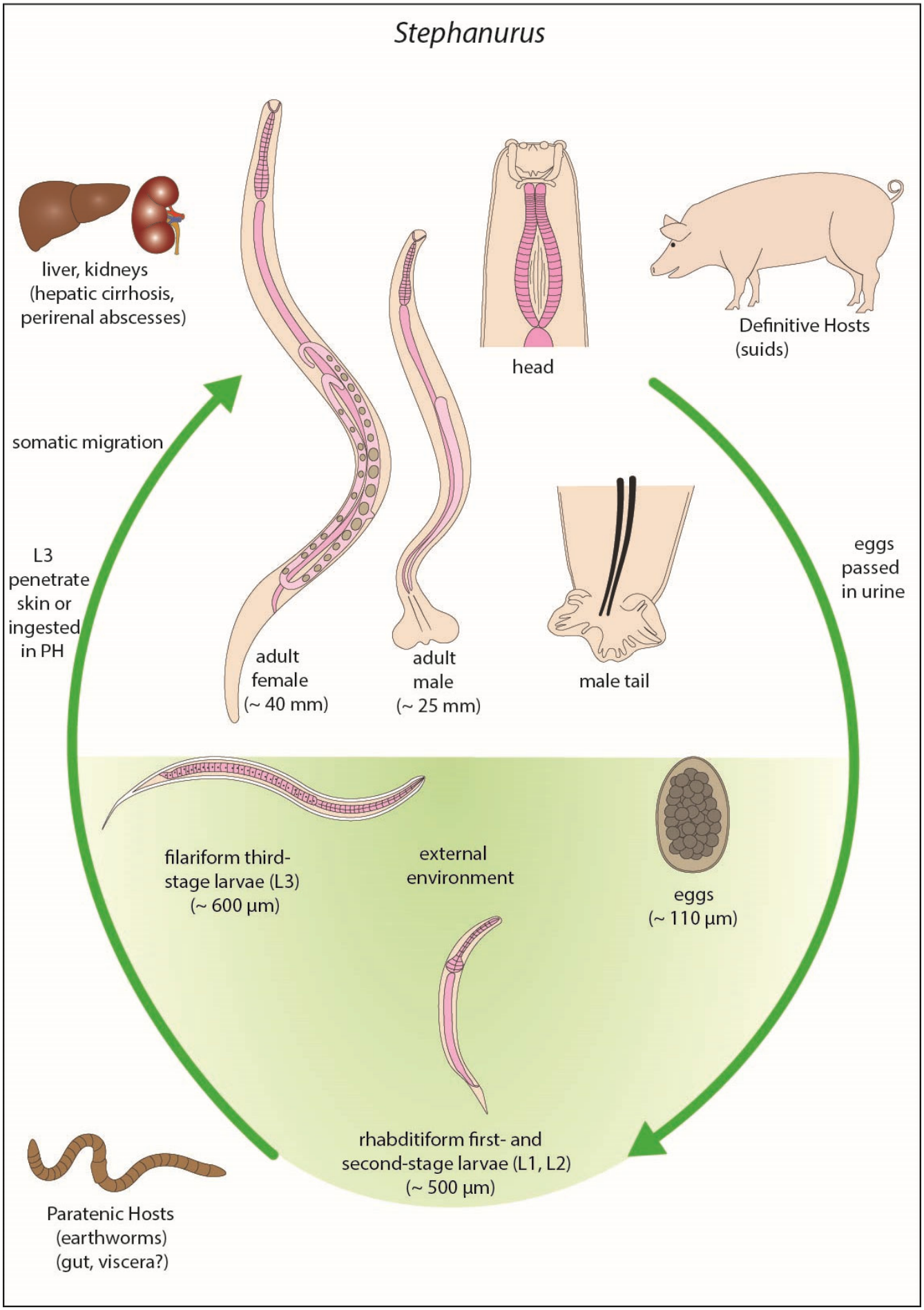
Pathogenesis: Infections by adult worms are generally not associated with disease, even though worms become encysted around the kidneys. The cysts range in diameter from 5-40 mm and usually contain a pair of worms surrounded by inflammatory cells (sometimes greenish pus) and a dense fibrous capsule. In rare cases, the ureters may become thickened and partially occluded or stenosed, with subsequent hydronephrosis. Blood may also be passed occasionally in the urine (haematuria) together with worm eggs. Most of the pathogenic effects, however, are caused by earlier larval stages damaging tissues when feeding and migrating. Percutaneous infections may result in transient inflammation of the skin with oedema and enlarged superficial lymph nodes, but migrating L4 and young adults (often called L5) with their well-developed mouthparts cause significant damage to host tissues, particularly during their obligatory and lengthy development in the liver. Infections cause inflammation (hepatitis) with eosinophilia, abscess formation, extensive fibrosis (evident as patchy cirrhosis), thrombosis of hepatic vessels, and fluid accumulation (ascites), all contributing to liver dysfunction. Clinical signs include anorexia, loss of body condition, illthrift with depressed growth, weight loss, and in severe cases, muscle wasting, emaciation, liver failure and death. Migrating stages may also undertake aberrant migrations to ectopic sites and cause tissue damage and abscess formation in various organs, including pulmonary lesions, portal phlebitis, splenitis, pancreatitis, lymphadenitis, myositis and myelitis leading to paralysis.

Developmental cycle and mode of transmission: *Stephanurus* varies in its route of transmission, with direct cycles involving infective L3 being ingested (faecal-oral transmission) or penetrating the skin (percutaneous or transdermal transmission), or an indirect cycle involving the ingestion of L3 in invertebrate paratenic (transport) hosts. Gravid female worms are very fecund and lay thousands of eggs per day which are excreted in host urine (up to 1.5 million eggs per urination have been recorded). Voided eggs hatch in the external environment in about 30 hours releasing free-living rhabditiform L1 which feed on soil bacteria and then moult to L2 which also feed. These larvae undergo an incomplete moult producing a strongyliform L3 still ensheathed in the L2 cuticle. These stages do not feed but are highly active and migrate through damp soil and onto vegetation. In warm moist conditions, L3 may form in 2-7 days and they may survive for 2-5 months. They are highly susceptible to cold and desiccation, so infections are most prevalent in warm wet countries, often in association with poorly-drained damp soils. Hosts become infected when they ingest infective L3 on pastures or when L3 come into contact with their skin and penetrate dermal tissues. It was also discovered that L3

ingested by earthworms could survive unchanged within them for up to a year, and were still infective for pigs that consumed infected earthworms. Irrespective of route, L3 exsheathed and moulted to L4 within 3 days of infection. However, in the case of oral infections, this moult occurred in the stomach wall and L4 migrated to the liver via the portal veins. In the case of transdermal infections, the moult takes place in the skin or muscles and L4 migrated to the liver via the lungs and systemic circulation. Within the liver, the larvae moult to L5 and the young worms wander in the parenchyma for 3 or more months before piercing the capsule and moving through the peritoneal cavity to the peri-renal region (although some may undertake aberrant migrations to ectopic sites). Adult worms become encapsulated by host reactions in the peri-renal fat or in the kidney, with the cysts communicating with the ureter directly or via fine connecting canals. Inside the cysts, worm pairs mature and mate, with eggs being liberated into the ureter and excreted with host urine. The prepatent period (time from infection to first egg excretion) ranges considerably from 6-19 months (usually 9 months) and the adult worms may live for up to 2-3 years. Pigs of all ages are susceptible to infection, but most patent infections are observed in animals > 2 years of age (usually breeders) due to the long prepatent period. Prenatal infections have also been reported involving the transplacental transmission of migrating larvae.

Differential diagnosis: Infections cannot be diagnosed on the basis of symptomatology due to their vague nonspecific nature (essentially illthrift with liver signs). Diagnosis is usually made at necropsy by the detection of milk spot liver lesions or an extensively-scarred and enlarged liver, or by the detection of cysts or abscesses containing worms. Ante-mortem diagnosis may be made by the microscopic detection of worm eggs in urine sediments, especially those prepared from the first urine passed in the morning. Experimental studies using immunodiffusion and immunoelectrophoretic techniques detected specific antibody responses against both juvenile and adult worms, but they were transient and short-lived compared to the long course of infection. Molecular phylogenetic studies have recently been used to characterize adult worms following the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (small subunit ribosomal DNA).

Treatment and control: Infections have responded well to treatment with several anthelmintic drugs, including macrocyclic lactones (ivermectin) and benzimidazoles (fenbendazole) which were effective against migrating and adult stages, and the imidazothiazole (levamisole) which was effective against adult worms. It is recommended that producers treat breeders before and after farrowing to limit the transmission of infections between generations. Given the long prepatent period, several authorities have recommended that only a single generation be bred from gilts and young boars prior to their slaughter before infections become patent (i.e. before egg production begins). Intensive indoor piggeries usually do not have problems with kidneyworms because the concrete pens are cleaned regularly and pigs have no access to soil or pastures contaminated with larvae. However, infections can become problematic in traditional extensive holdings where pigs are kept outdoors or have access to earthen areas or pastures, particularly those with moist loose soils and earthworms. Nonetheless, some measure of control can be afforded by improving hygiene to reduce environmental contamination by urine, placing feeding and watering equipment on concrete in sunny well-drained locations, rotating livestock between locations, separating cohorts (especially adults from weaners), avoiding mud wallow formation by fencing or draining, and preventing foraging for earthworms.


Stephanurus
liver, kidneys
(hepatic cirrhosis,
perirenal abscesses)
head
Definitive Hosts
(suids)
somatic migration
L3
penetrate
skin or
ingested
in PH
adult
female
(~ 40 mm)
adult
male
(~ 25 mm)
male tail
eggs
passed
in urine
filariform third-
stage larvae (L3)
(~ 600 µm)
external
environment
eggs
(~ 110 µm)
rhabditiform first- and
second-stage larvae (L1, L2)
(~ 500 µm)
Paratenic Hosts
(earthworms)
(gut, viscera?)



Stephanurus adult worms



Stephanurus worm egg

Syngamus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the syngamids which have large cup-shaped buccal capsules armed with teeth but no leaf crowns. Several species parasitize the respiratory mucosa of birds. They have direct life-cycles, usually involving eggs passed in faeces developing to L3 which are ingested by new hosts and develop to adults. Unlike other strongyloids, the L3 of syngamids develop in eggs before hatching. Infections may therefore occur by ingestion of L3 in eggs, L3 that have hatched or L3 taken up by invertebrate paratenic (transport) hosts. *Syngamus* spp. (gape worms) infect the trachea and bronchi causing obstructive respiratory distress in birds worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Syngamidae (buccal capsule with basal teeth, in respiratory, urinary or digestive tract of mammals/birds)
Subfamily:	Syngaminae (gapeworm, in trachea of birds and mammals)
Genus:	*Syngamus* (parasitic in trachea of birds)
Genus:	*Mammomonogamus* (parasitic in frontal airways of ruminants and cats)
Genus:	*Cyathostoma* (parasitic in trachea of waterfowl)
Species:	various species cause respiratory distress

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but

some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
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Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
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Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1

Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Strongyle worms are characterised by their prominent buccal capsules with lips, leaf crowns or labial collars at the mouth opening, sometimes with teeth or cutting plates. They are parasitic in a variety of organ systems in a range of animals, including the large intestines of mammals (ruminants, suids, elephants, perissodactyls, rodents, marsupials and primates), tortoises and ratite birds, the forestomach of marsupials, the trachea of birds and mammals, and the renal system of suids. Four families are recognised: Strongylidae (buccal capsule globular or cylindrical, oral opening circular, dorsal ray with 6 terminal branchlets, 32 genera in large intestines of mammals, reptiles and birds); Chabertiidae (buccal capsule globular or cylindrical, oral opening circular or oval, with leaf crown or labial collar, with up to 3 teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 22 genera in gastrointestinal tract of mammals); Syngamidae (buccal capsule subglobular, oral opening hexagonal, numerous teeth at base of buccal capsule, dorsal ray with 4 terminal branchlets, 7 genera in respiratory, urinary and digestive tracts of mammals and birds); and Deletrocephalidae (oral opening hexagonal, dorsal ray with 6 terminal branches, 2 genera in large intestines of birds). The family Syngamidae contains 3 subfamilies: Syngaminae (leaf crown absent, teeth at base of buccal capsule, anterior vulva, 5 genera in trachea of birds and some mammals); Stephanurinae (rudimentary leaf crown, teeth at base of buccal capsule, rudimentary bursa, posterior vulva, 1 genus in urinary system of suids); and Archeostrongylinae (leaf crown absent, teeth absent at base of buccal capsule, 1 genus in intestines of porcupines).

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**
Syngaminae					
Syngamus (gape worm)	10	birds	respiratory tract	2-30 mm long, hexagonal cup-shaped buccal capsule armed with teeth, no leaf crowns, small male permanently attached to female vulva imparting Y-shape, L3 develop in eggs before hatching, invertebrate PH	70-100 x 42-62 µm, ellipsoidal, operculate
Stephaurinae					
Stephanurus (kidney-worm)	1	suids	urinary tract	2-5 cm long, stout reddish bodies, white reproductive organs, prominent buccal capsule often armed with teeth, small leaf crowns and external epaulettes, eggs passed in faeces and urine, L3 ingested or percutaneous, earthworm PH	90-136 x 53-70 µm, ellipsoidal, thin-shelled

The subfamily Syngaminae contains 5 genera: *Syngamus* (including subgenera *Syngamus* and *Ornithogamus*), *Cyathostoma* (including subgenera *Cyathostoma, Calcaronema* and *Hovorkonema*) and *Boydinema* all of which form adults with buccal capsules with smooth inner walls, eggs with opercula, and are parasitic in birds; while *Mammomonogamus* and *Rodentogamus* form adults with buccal capsules with longitudinal ribs on the inner wall and are parasitic in mammals. [Several early studies suggested that the genus *Cyathostoma* be placed in a separate subfamily Cyathostominae because males and females were not fused *in copula* (as occurs for *Syngamus* spp.), but subsequent studies found this character to be unreliable]. The genus *Syngamus* contains 10 species which infect the trachea of birds causing respiratory distress with birds gaping and struggling for breath (hence the common name of gape worm). The species *S. trachea* occurs worldwide in a range of birds *(*galliforms, anseriforms, passerines, psittacines, columbiforms, birds of prey), being most evident in gamebirds used for sporting purposes. Many infections have been reported in ground-feeding birds, especially those ingesting invertebrates (earthworms, snails, slugs, coprophagous arthropods) which act as paratenic transport hosts. Infected birds can be found any time in the year, mainly in young birds as older birds apparently gain some protective immunity and shed parasites with age. Species in the other genera may also cause upper or lower respiratory disorders in their hosts, especially in tropical and subtropical regions where climatic conditions favour the survival of larval stages in the external environment.

Parasite species	**Definitive Hosts [plus Paratenic Hosts (PH)]**	**Location [Clinical signs]**	**Distribution**
Syngamus [incl. subgenera *S.* (*Syngamus*) (well-developed collar) and *S.* (*Ornithogamus*) (rudimentary collar)]			
S. anterogonimus	Charadriiformes: scolopacid (western sandpiper, red-necked phalarope)		Eurasia, North America
S. (*Ornithogamus*) *arcticus*	Gaviiformes: gaviid (red-throated loon)	trachea	North America
S. dyki	Passeriformes: turdid (common blackbird)	trachea	Europe
S. (*Ornithogamus*) *gibbocephalus*	Charadriiformes: scolopacid (pin-tailed snipe)		Eurasia
S. (*Ornithogamus*) *merulae*	Passeriformes: turdid (varied thrush, song thrush, fieldfare, common blackbird, American robin, Naumann's thrush, redwing), muscicapid (blue rock thrush), passerid (house sparrow), corvid (western jackdaw)		Palearctic
S. palustris	Charadriiformes: scolopacid (ruff, Eurasian woodcock, wood sandpiper)		Eurasia
S. skrjabinomorpha	Galliformes: numidid (helmeted guineafowl), phasianid (chicken); Anseriformes: anatid (goose) [plus PH: Clitellata: lumbricid (*Allolobophora caliginosa, chlorotica, jassyensis, Dendroboena faucium, hortensis, mariupoliensis, schmidti, venata, Eiseniella colchidica, Eophila patriarchalis*)]	trachea	Palearctic
S. taiga	Passeriformes: corvid (spotted nutcracker), acrocephalid (sedge warbler, Eurasian reed warbler), motacillid (white wagtail), muscicapid (bluethroat), corvid (rook), alaudid (Eurasian skylark, woodlark); Galliformes: phasianid (hazel grouse, grey partridge)	trachea	Russia
S. tenuispiculum	Passeriformes: turdid (American robin)		North America
S. trachea (gapeworm, redworm, forked worm) (syn. *S. gracilis, parvus, primitivus, skrjabini, trachealis*)	Galliformes: phasianid (chicken, red junglefowl, willow ptarmigan, northern bobwhite quail, chukar partridge, grey partridge, rock partridge, red-legged partridge, hazel grouse, black grouse, western capercaillie, Caucasian woodcock, ring-necked pheasant), numidid (helmeted guineafowl); Anseriformes: anatid (mallard, goose, bar-headed goose); Pelecaniformes: pelecanid (great white pelican), threskiornithid (American white ibis); Suliformes: phalacrocoracid (double-crested cormorant); Gruiformes: gruid (sandhill crane); Piciformes: picid (European green woodpecker); Charadriiformes: scolopacid (dunlin, sanderling, common snipe, ruff, Eurasian woodcock, common greenshank), charadriid (little ringed plover); Coraciiformes: alcedinid (belted kingfisher); Apodiformes: apodid (common swift); Accipitriformes: accipitrid (besra sparrow hawk); Columbiformes: columbid (pigeon); Passeriformes:	trachea, lungs [respiratory distress]	worldwide

	passerellid (fox sparrow), sturnid (common mynah, common starling), monarchid (black-naped monarch), turdid (song thrush, fieldfare), fringillid (brambling), icterid (red-winged blackbird, common grackle), parulid (northern water thrush), corvid (Eurasian jay, western jackdaw, common raven, hooded crow, carrion crow, large-billed crow, rook, Eurasian magpie, red-billed chough) [plus PH: Clitellata: lumbricid (*Allolobophora calliginosa, rosea, Dendroboena platyura, vejdovskyi, Eisenia foetida, Lumbriculus variegatus, Lumbricus baicalensis, castaneus, rubellus, Nicrodrilus calliginosus, roseus*): Diptera: muscid (*Musca domestica, Lucilia sericata*)]		

Other genera in birds

Parasite species	Definitive Hosts [plus Paratenic Hosts (PH)]	Location [Clinical signs]	Distribution
Cyathostoma [incl. subgenera *C.* (*Cyathostoma*), *C.* (*Calcaronema*) and *C.* (*Hovorkonema*)]			
C. (*Hovorkonema*) *americanum*	Accipitriformes: accipitrid (Cooper's hawk, northern goshawk, red-tailed hawk, eastern red-tailed hawk, broad-winged hawk, western marsh harrier, common buzzard, rough-legged buzzard); Strigiformes: strigid (snowy owl, long-eared owl, little owl)	trachea, air sacs	Europe, North America
C. boularti (syn. *Syngamus*)	Casuariiformes: casuariid (cassowary)	trachea	Australia
C. brantae (syn. *Syngamus*)	Anseriformes: anatid (Canada goose, snow goose, mandarin duck); Casuariiformes: casuariid (emu, zoo animal)	trachea	Eurasia
C. (*Hovorkonema*) *brodskii*	Accipitriformes: accipitrid (western marsh-harrier); Gruiformes: gruid (black crowned crane)		Eurasia
C. (*Hovorkonema*) *bronchialis* (syn. *Syngamus*)	Anseriformes: anatid (mandarin duck, greylag goose, Canada goose, swan): Casuariformes: casuariid (emu) [plus PH: Clitellata: lumbricid (*Eisenia foetida*)]	trachea, bronchi [respiratory distress]	North America, Europe
C. cacatua	Psittaciformes: cacatuid (sulphur-crested cockatoo)	air sacs	New Zealand
C. coscorobae (syn. *Syngamus*)	Anseriformes: anatid (coscoroba swan, spur-winged goose)	trachea, bronchi	Americas
C. ibisi	Pelecaniformes: threskiornithid (Indian white ibis)	trachea	India
C. lari	Charadriiformes: larid (European herring gull, black-headed gull); Falconiformes: falconid (common kestrel); Accipitriformes: accipitrid (Eurasian sparrow hawk, common buzzard)	orbital sinuses	Eurasia
C. sarcidiornis (syn. *Syngamus*)	Anseriformes: anatid (knob-billed duck)	trachea	
C. (*Cyathostoma*) *sphenisci*	Sphenisciformes: spheniscid (African penguin); Gaviiformes: gaviid (common loon); Pelecaniformes: pelecanid (brown pelican, American white pelican)	trachea, lungs, air sacs	Africa, North America
C. (*Hovorkinema*) *tadornae*	Anseriformes: anatid (common shelduck)	trachea	Russia
C. trifurcatum	Ciconiiformes: ciconiid (black stork)	trachea	Europe
C. turemuratovi (syn. *C. microspiculum, Syngamus* (*Ornithogamus*), *S. hexadontus*)	Suliformes: phalacrocoracid (great cormorant, pygmy cormorant)		Asia
C. (*Hovorkinema*) *variegatum*	Anseriformes: anatid (mallard, snow goose, bar-headed goose, black swan): Galliformes: phasianid (Indian peafowl); Casuariformes: casuariid (emu); Gruiformes: gruid (whooping crane, sandhill crane,	trachea, bronchi [respiratory distress]	Eurasia, Australia

	common crane); Ciconiiformes: ciconiid (white stork, black stork); Accipitriformes: accipitrid (northern goshawk, Eurasian sparrowhawk, western marsh harrier, white-tailed sea eagle, common buzzard)		
C. (*Cyathostoma*) *verrucosum* (syn. *Calcaronema, Syngamus*)	Pelecaniformes: pelecanid (Dalmatian pelican, great white pelican); Ciconiiformes: ciconiid (white stork)		Asia
Boydinema			
B. alcyone (syn. *Syngamus*)	Coraciiformes: alcedinid (belted kingfisher)		North America

Other genera in mammals

Parasite species	Definitive Hosts [plus Paratenic Hosts (PH)]	Location [Clinical signs]	Distribution
Mammomonogamus			
M. auris (syn. *Syngamus*)	Carnivora: felid (cat)	middle ear [otitis interna]	Asia, Americas
M. dispar	Carnivora: felid (cat, cougar)		North America
M. felis	Carnivora: felid (tiger)	lungs	Malaya
M. gangguiensis	Artiodactyla: bovid (cattle)		
M. hippopotami	Artiodactyla: hippopotamid (hippopotamus)		Africa
M. ierei	Carnivora: felid (cat)	nasal cavities [sneezing, discharge]	Caribbean
M. indicus (syn. *Syngamus*)	Proboscidea: elephantid (Indian elephant)		Asia
M. laryngeus (syn. *S. laryngeus, S. kingi*)	Artiodactyla: bovid (cattle, water buffalo, sheep, goat); Carnivora: felid (jaguar); Didelphimorphia: didelphid (common opossum); Primates: hominid (human)	larynx [laryngitis, cough]	Asia, Africa, South America
M. loxodontis (syn. *Syngamus*)	Proboscidea: elephantid (African forest elephant); Primates: hominid (western lowland gorilla)		Africa
M. mcgaughei	Carnivora: felid (cat)	sinuses, pharynx [sneezing, discharge]	Sri Lanka
M. nasicola	Artiodactyla: bovid (cattle, African forest buffalo, sheep, goat), cervid (deer); Primates: hominid (human)	nasal cavities [sneezing, discharge]	Americas, Africa
M. okapiae	Artiodactyla: giraffid (okapi)	bronchi	Africa
Rodentogamus			
R. citelli (syn. *Syngamus*)	Rodentia: sciurid (long-tailed ground squirrel)		Russia
R. microtinae (syn. *Syngamus*)	Rodentia: cricetid (grey red-backed vole, northern red-backed vole, tundra vole)		Palearctic
R. ryjikovi	Rodentia: murid (striped field mouse, large Japanese field mouse)		Asia

Parasite morphology: *Syngamus* spp. form 3 different types of morphological stages in their developmental cycles: eggs; larvae (4 stages designated L1-L4); and adult worms. The eggs are elliptical-oval measuring 70-100 x 42-62 µm and are thin-shelled but have 2 thickened polar opercular plugs (except those of *Mammomonogamus*). Freshly-laid eggs contain a morula at the 8-16 cell (blastomere) stage of development. Unlike most other strongyles, larvae develop and moult within the eggs before they hatch (L1 moulting to L2 and then to L3). The early larval stages also lack the rhabditiform (bulbed) oesophagus and filamentous tail common to other strongyles. Following hatching, the emergent L3 measure 278-286 x 13-16 µm and are ensheathed (retain L2 cuticle) and have an elongate oesophagus and a short pointed tail. L4 are transient endoparasitic stages and have not been well described. Adult worms are sexually dimorphic, with female worms being larger than males (5-30 x 0.35 mm cf. 2-10 x 0.2 mm). The adults are highly unusual in that the smaller male attaches permanently to the larger female in permanent copulation (*in copula*) such that they form a characteristic Y-shape (in contrast, *Cyathostoma* males and females are not usually found *in copula*). The worms often appear pink-red in colour due to the presence of host blood in their intestines. Both sexes have large hexagonal mouth openings without leaf crowns but with an orbicular collar, well-developed in the subgenus *S.* (*Syngamus*) but rudimentary in the subgenus *S.*

(*Ornithogamus*) (a collar is also present in the genera *Boydinema* and *Rodentogamus*, but absent in *Cyathostoma* and *Mammomonogamus*). *Syngamus* spp. have large subglobular shallow (cup-shaped) buccal capsules with smooth inner walls and 6-10 teeth at the base (the buccal capsules of *Cyathostoma* and *Boydinema* also have smooth inner walls, while those of *Mammomonogamus* and *Rodentogamus* have longitudinal ribs on the inner wall). Mature males have a short asymmetrical copulatory bursa that appears obliquely truncated with supporting rays (muscular elements following nerve channels to terminal papillae) reduced to short thick blunt rami. The dorsal ray is similar in length to the externolateral ray (but is longer in *Cyathostoma*) and it characteristically has 4 terminal branches. Males also have 2 short slender spicules 53-82 µm long, but their distal ends are not connected (whereas they are connected in *Boydinema*). Female worms are didelphic and have 2 ovaries, 2 oviducts and 2 uteri opening into a common vulva located anterior to the midbody in the subgenus *S.* (*Syngamus*) or near the midbody in the subgenus *S.* (*Ornithogamus*). Females have conical tails with pointed processes and they are oviparous and produce numerous thin-walled operculate eggs. While many species display stable uniform morphological characteristics, some species exhibit considerable pleomorphy in certain characters. For example, *S. trachea* isolates from chickens have been found to vary in egg size, worm length, buccal capsule size and shape, number of buccal teeth, and bursa structure; but the differences have not been enough to delineate new or cryptic species.

Site of infection: Adult worms of species infecting birds (*Syngamus, Cyathostoma, Boydinema*) occur in the lining of the trachea, bronchi and bronchioles, while the preceding larval stages migrate from the gut through the liver to the lungs before forming adults. Adult worms of species infecting mammals (*Mammomonogamus* and *Rodentogamus*) occur in the upper or lower respiratory tract.

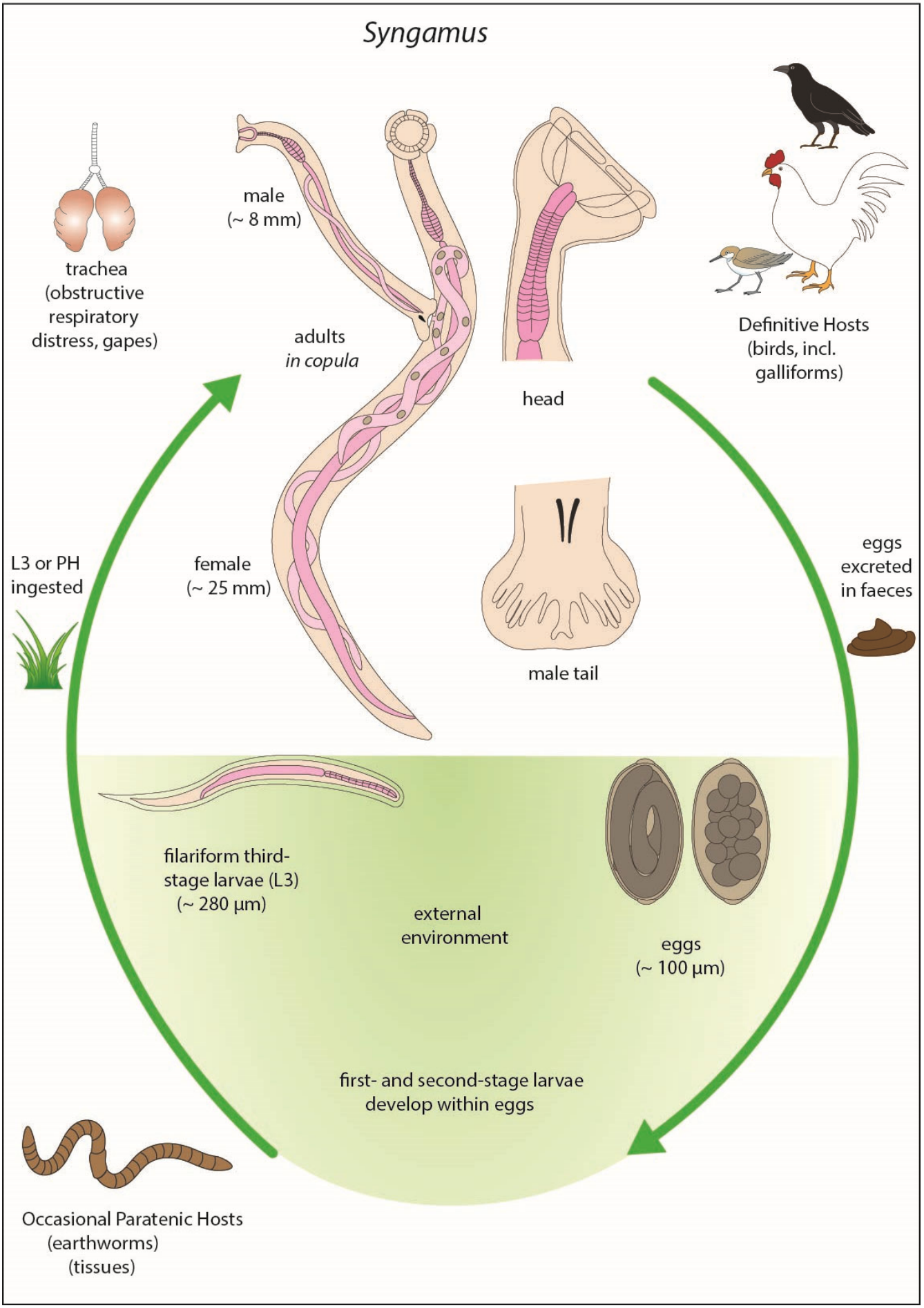
Pathogenesis: Most infections in birds show few signs of clinical disease as only a few worms may be involved. However, heavier infections by a number of *Syngamus* and *Cyathostoma* spp. may cause serious problems in poultry and game bird production. The parasites are known as gapeworms because they partially block the respiratory tree causing birds to gape (open their mouths wide and stretch their necks to gasp for air) and lose condition. Disease severity is dependent on parasite pathogenicity (some species are highly virulent), the intensity of infection (worm burden), host susceptibility (particularly young galliform birds), host size (small birds with small trachea are more severely affected) and the stage of infection (disease due to migrating larvae or adult worms). Clinical respiratory signs that become apparent during the prepatent period (before adults have matured and produced eggs) are due to the migration and development of larvae and young adults through the lungs, causing pulmonary lesions, inflammation, emphysema and oedema which may lead to pneumonia with dyspnoea and depression. Clinical disease that manifests during the patent period (when eggs are being produced) are due to adult worms attaching to the tracheal mucosa to feed on host blood causing haemorrhagic tracheitis with excess mucus production (often bloody) leading to anaemia, tracheal obstruction, dyspnoea, and respiratory distress (agitated coughing, sneezing, head shaking, gaping, and hissing). Birds stop feeding, rapidly lose weight and body condition becoming weak, depressed, emaciated and may die due to asphyxia (suffocation) and/or starvation. Infections are most severe in young birds, particularly domestic chickens < 2-3 months old, game chicks and turkey poults, especially in breeding or rearing enterprises with outdoor pens or runs. Infections by other genera in mammals (including humans) have occasionally been associated with respiratory signs (coughing, haemoptysis, sneezing, nasal discharge) and poor condition when adult worms infect the upper respiratory tract.

Developmental cycle and mode of transmission: Syngamids usually have direct monoxenous life-cycles involving the faecal-oral transmission of infective larvae (sometimes still in eggs), but they may also have indirect life-cycles involving infectious stages being transported in invertebrate paratenic hosts. Female worms deposit partially-embryonated eggs in the respiratory tract where they are carried up the trachea by the mucociliary escalator to be swallowed and excreted with host faeces. Infective L3 develop within the eggs in 2-7 days depending on prevailing environmental conditions (particularly warm moist conditions). The L3 may remain in the eggs for long periods or they may hatch spontaneously after 8-14 days. Both eggs and larvae have been shown to survive in damp soil for up to 9 months. Definitive hosts become infected following the oral ingestion of infective L3 either when larvated eggs are eaten, when released larvae are eaten, or when an invertebrate paratenic host carrying eggs or larvae is eaten. Many infections have been reported in ground-feeding birds, especially those ingesting invertebrates (mainly earthworms, but also including snails, slugs, beetles, and some flies) which act as paratenic hosts in which infective L3 may survive encysted in their tissues for many months (up to 4 years). Ingested L3 exsheath in the duodenum and penetrate the intestinal wall migrating via the venous circulation through the liver to the lungs as early as 4-6 hours after infection. The larvae develop in the lungs over 5-7 days moulting twice to form adults. Males and females copulate after the final moult in the larger bronchi and mated pairs migrate *in copula* to the trachea by day 11. The prepatent period (time from infection to first egg excretion) ranges from 12-21 days and adult worms may live for up to 9 months.

Differential diagnosis: Clinical infections in birds are often diagnosed on the basis of symptomatology when affected birds exhibit the classical signs of gaping for breath and hissing to dislodge obstructions. On rare occasions, dark red worms may be observed in the throat. Coprological techniques can be used to detect worm eggs in faecal samples, either in wet mounts, smears or concentrates (usually faecal floats). The thin-walled operculate eggs can be readily identified but they need to be differentiated from those of *Capillaria* (which are smaller, more robust, have thicker shells, and usually contain a single-celled morula). Adult worms may also be recovered ante-mortem by endoscopic biopsy or post-mortem by dissection, and identified by their red colouration and Y-shaped

paired (*in copula*) configuration. Modern molecular biological techniques have recently been used to determine phylogenetic relationships between various taxa following the polymerase chain reaction (PCR) amplification of nuclear genes (large and small subunit ribosomal DNA, internal transcribed spacers I and 2) and mitochondrial genes (cytochrome c oxidase I).

Treatment and control: Infections in birds have been successfully treated with a range of anthelmintics administered by individual oral doses, in-feed or in-water medications or by subcutaneous injection, including benzimidazoles (thiabendazole, albendazole mebendazole, flubendazole, fenbendazole, cambendazole), imidazothiazoles (levamisole, tetramisole), halogenated monophenols (nitroxynil) and macrocyclic lactones (ivermectin), although the latter was not very effective. Caution is advised in treating heavy infections as birds may be unable to expel numerous dead worms and may suffocate. Repeated treatments may also be required to prevent larval stages from re-establishing infections. Many different control strategies have been used to break transmission cycles in domestic, game and aviary bird facilities, principally involving improved sanitation (removing litter and faeces, cleaning pens/cages), hygiene (clean food and water) and isolation (quarantining new stock, segregating birds of different ages, excluding wild birds as potential carriers, preventing foraging for invertebrate paratenic hosts, and restricting access to contaminated yards and open grounds). Various attempts have been made to treat range soils with chemicals to eliminate worm eggs and larvae and to reduce invertebrate populations, but most were only partially effective and had adverse environmental effects depending on the toxicity of the disinfectants and insecticides. Intensive indoor industries generally do not have problems with gapeworms, although recent trends towards free-range poultry production may experience a resurgence of infections.


Syngamus
trachea
(obstructive
respiratory
distress, gapes)
male
(~ 8 mm)
adults
in copula
head
Definitive Hosts
(birds, incl.
galliforms)
female
(~ 25 mm)
male tail
L3 or PH
ingested
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 280 µm)
external
environment
eggs
(~ 100 µm)
first- and second-stage larvae
develop within eggs
Occasional Paratenic Hosts
(earthworms)
(tissues)



Syngamus adult worms *in copula*



Syngamus adult worms *in copula*



Syngamus worm eggs

Ancylostoma
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the ancylostomatids (hookworms) which are characterised by their bent mouths, the anterior ends being bent dorsally. They have a well-developed buccal capsule with cutting plates or teeth, and are voracious blood-feeders in the small intestines of mammals. They have direct life-cycles, involving a geo-helminth phase. Eggs voided with faeces hatch releasing free-living rhabditiform larvae which subsequently develop into infective filariform L3 that are ingested or actively penetrate the skin of their hosts (some species causing cutaneous larval migrans). Larvae undergo pulmonary migration through the lungs (sometimes causing pneumonitis) before developing into blood-feeding adults in the small intestines. Some larvae may undergo arrested development (hypobiosis) and vertical transmission may occur (transplacental and transmammary). Infections by *Ancylostoma* cause Old World hookworm disease, characterised by iron-deficiency anaemia and growth retardation in humans, particularly in children and malnourished individuals.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Ancylostomatidae (hookworms, buccal capsule bent dorsally, armed with teeth/cutting plates)
Genus:	*Ancylostoma* (parasitic in small intestines of humans/dogs/cats)
Species:	*A. duodenale* [causes Old World hookworm disease in humans]

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but

some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Trichostrongylina (trichostrongyles)				
Trichostrongylidae	reduced buccal capsule, ridged	artiodactyls, birds	ingestion of L3	50

(trichostrongyles)	synlophe, oesophagus lacking bulb, thin-shelled eggs			
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Hookworms are characterised by their dorsally bent heads with prominent buccal capsules containing paired ventral lancets as well as teeth, cutting plates or lateral jaw-like structures. They are parasitic in the small intestines of mammals and reptiles and infections are acquired by the ingestion or skin penetration of infective L3 followed by tracheal migration. Two families are recognised: Ancylostomatidae (dorsally deviated head, buccal capsule usually armed with teeth or cutting plates, 20 genera in intestines of mammals); and Diaphanocephalidae (anteriorly directed head, buccal capsule forming 2 lateral jaw-like structures, 2 genera in intestines of reptiles). The family Ancylostomatidae contains 2 subfamilies: Ancylostomatinae (buccal capsule subglobular, with dorsal gutter, bursa with short dorsal ray, gubernaculum present, posterior vulva, female tail with terminal spine, most in carnivores); and Bunostominae (buccal capsule subglobular, with tooth-like dorsal cone, bursa with long dorsal ray, gubernaculum absent, anterior vulva, female tail without terminal spine, most in herbivores). Ancylostomatid genera of particular medical and/or veterinary significance are tabulated below.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**	**Transmission**
Ancylostominae						
Ancylostoma	32	carnivores, primates	small intestines	5-25 mm long, bent heads, buccal capsule with ventral lancets and fused teeth, larval pulmonary migration, hypobiosis	55-95 x 32-58 µm, ellipsoidal, thin-shelled	oral, transdermal, transplacental, transmammary
Globocephalus	18	artiodactyls, rodents, primates	caecum, small intestines	3-9 mm long, large buccal capsule without cutting plates or teeth, larval pulmonary migration	60-75 x 35-41 µm, ovoid, thin-shelled	oral, transdermal
Uncinaria	22	carnivores	small intestines	3-15 mm long, well-developed buccal capsule with pair of ventral cutting plates, no pulmonary migration	65-98 x 35-58 µm, ovoid, thin-shelled	oral (direct or via PH), rarely transdermal
Bunostominae						
Bunostomum	9	artiodactyls, proboscidea	small intestines	10-30 mm long, buccal capsule with ventral cutting plate and 1-2 pairs subventral teeth, larval pulmonary migration,	79-117 x 40-70 µm, ovoid, thin-shelled	oral, transdermal, transplacental, transmammary

				hypobiosis		
Gaigeria	1	artiodactyls	small intestines	10-45 mm long, buccal capsule with pair ventral cutting plates, elongate lancets and teeth, larval pulmonary migration	108-115 x58-61 µm, ellipsoidal, thin-shelled	transdermal
Necator	7	primates, artiodactyls	small intestines	7-11 mm long, buccal capsule with cutting plates, larval pulmonary migration	55-77 x 35-42 µm, ovoid, thin-shelled	oral, transdermal

The subfamily Ancylostominae contains 8 genera classified in 4 tribes: Ancylostomatinea containing worms with oral openings armed with teeth, and globular buccal capsules not divided into articulating plates (*Ancylostoma* (syn. *Agchylostoma*, *Anchylostomum*, *Ankylostoma*, *Ankylostomum*, *Ceylancylostoma*, *Diploodon, Dochmius*) and *Galoncus*) parasitic in carnivores, primates, edentates, rodents, and suids; Uncinarinea containing worms with oral openings with well-developed cutting plates, and buccal capsule not divided into articulating plates (*Uncinaria* (syn. *Dochmoides*, *Dochmius*, incl. subgenera *Uncinaria*, *Megadeirides*) and *Bioccastrongylus*) parasitic in insectivores, primates, and carnivores; Arthrocephalinea containing worms with buccal capsules divided into articulating plates (*Arthrocephalus*, *Arthrostoma*, and *Placoconus*) parasitic in carnivores; and Globocephalinea containing worms with oral openings lacking teeth and cutting plates (*Globocephalus* (syn. *Characostomum*, *Crassisoma*, *Cystocephalus*, *Raillietostrongylus*)) parasitic in suids, primates, mustelids, rodents, ruminants, and South American marsupials. The genus *Ancylostoma* contains over 30 species which have been described from a range of mammalian species throughout the world, mainly in tropical and subtropical regions because the larvae cannot develop below 22°C. They are most common in rural areas with high annual rainfall and shaded sandy or loam soils ideal for larval development (not clay or gravel). It is estimated that around 450 million people are infected with hookworms (*Ancylostoma* and *Necator*) worldwide, with 1.6 million suffering from anaemia and 55,000 deaths annually. *A. duodenale* is the Old World human hookworm and is entrenched on most continents. Similar hookworm species occur in domestic and wild carnivores, and they vary in their host specificity. *A. ceylanicum* normally occurs in carnivores but has been reported from humans in the Asia-Pacific region. *A. braziliense* has also been found in humans from several countries, but some infections may have been confused with *A. ceylanicum*. The larvae of many species can undergo partial development in humans, and the dog hookworm *A. caninum* can almost complete its development in humans. *A. tubaeforme* occurs worldwide in cats, but only rarely in dogs.

***Ancylostoma* species**	**Oral structures**	**Definitive Hosts**	**Clinical signs**	**Geographic distribution**
A. ailuropodae	4 pairs ventral teeth	Carnivora: ursid (giant panda)	anaemia	China
A. bidens	3 pairs ventral teeth	Carnivora: procyonid (crab-eating raccoon, South American coati)		South America
A. braziliense (hookworm)	2 pairs ventral teeth	Carnivora: felid (cat, bobcat, cheetah, cougar, leopard, leopard cat, lion, African wildcat, serval, jaguarundi, ocelot), canid (dog, wolf, dingo, side-striped jackal, black-backed jackal, fennec fox, bat-eared fox, grey fox), hyaenid (spotted hyena, aardwolf), viverrid (common genet, masked palm civet, large Indian civet), procyonid (crab-eating raccoon); Primates: hominid (human)	diarrhoea, cutaneous larva migrans in humans	Africa, Brazil, India, Sri Lanka, Indonesia, Philippines
A. buckleyi	5 pairs teeth (3 ventral, 2 dorsal)	Carnivora: felid (puma, cougar), canid (short-eared fox, crab-eating fox, Pampas fox, dog)		South America, Australia
A. caninum [canine hookworm]	3 pairs ventral teeth	Carnivora: canid (dog, dingo, coyote, red wolf, red fox, grey fox, fennec fox, bat-eared fox, corsac fox, Atlas fox, Iberian fox, maned wolf, black-backed jackal, side-striped jackal, golden jackal, raccoon dog), hyaenid (spotted hyena, striped hyena), felid (cat, bobcat, lynx, cheetah, jungle cat, wildcat, African wildcat, lion, tiger, leopard, clouded leopard, leopard cat), viverrid (common genet, cape genet, large Indian civet), ursid (American black bear, Florida black bear, polar bear, sloth bear); Cingulata: chlamyphorid (six-banded armadillo); Artiodactyla: suid (pig); Rodentia: murid (mouse); Primates: hominid	pneumonitis, anaemia	worldwide in tropics and temperate zones

		(human); Diptera: muscid (house fly)		
A. ceylanicum	2 pairs ventral teeth	Carnivora: felid (cat, leopard cat, fishing cat), canid (dog, dingo), viverrid (Malabar large-spotted civet, small Indian civet); Rodentia: murid (Natal multimammate mouse), cricetid (golden hamster); Primates: hominid (human)	anaemia, diarrhoea	Sri Lanka, India, Asia, Philippines
A. conepati	3 pairs ventral teeth	Carnivora: mephitid (Molina's hog-nosed skunk)		South America
A. ctenomys	4 pairs teeth (3 ventral, 1 dorsal)	Rodentia: ctenomyid (Steinbach's tuco-tuco, Bolivian tuco-tuco)		South America
A. duodenale [Old World human hookworm]	2 pairs ventral teeth	Carnivora: hyaenid (spotted hyena), felid (cat, lion), canid (dog, golden jackal, black-backed jackal, fennec fox), viverrid (Malabar large-spotted civet, genet); Artiodactyla (suid (pig); Primates: cercopithecid (rhesus macaque), hominid (human); Diptera: muscid (house fly)	pneumonitis, anaemia	Eurasia, Africa, Indo-China, patchy distribution in North and South America
A. galogoi		Primates: galagid (brown greater galago)		Africa
A. genettae	5 pairs teeth (3 ventral, 2 dorsal)	Carnivora: viverrid (common genet)		Africa
A. gilsoni		Rodentia: sciurid (Pallas's squirrel, Berdmore's ground squirrel), murid (Himalayan field rat)		Asia
A. guentini	3 pairs ventral teeth	Carnivora: canid (golden jackal)		Asia
A. hescheleri	1 pair ventral teeth	Tubulidentata: orycteropodid (aardvark)		Africa
A. iperodontatum	6 pairs teeth (3 ventral, 3 dorsal)	Carnivora: felid (cheetah, African wild cat, caracal)		Africa
A. japonica sp. inq.		Primates: hominid (human)		Asia
A. kusimaense	2 pairs ventral teeth	Carnivora: canid (raccoon dog, Japanese red fox), procyonid (raccoon)		Asia, North America
A. longespiculatum	3 pairs ventral teeth	Carnivora: felid (European wildcat)		Europe
A. lucknowense	n pairs teeth (3 ventral, many dorsal)	Carnivora: felid (leopard cat)		Asia
A. malayanum	2 pairs ventral teeth	Carnivora: ursid (Asian black bear); Primates: hominid (human)		Asia
A. martinagliai	5 pairs teeth (3 ventral, 2 dorsal)	Carnivora: canid (black-backed jackal); Cingulata: chlamyphorid (screaming hairy armadillo)		Africa
A. martinezi		Carnivora: viverrid (common genet)		Africa
A. mephitis	2 pairs ventral teeth	Carnivora: mustelid (striped polecat)		Africa
A. minimum	-	Carnivora: felid (rusty-spotted cat)		Asia
A. mucronatum	3 pairs ventral teeth	Cingulata: dasypodid (nine-banded armadillo)		South America
A. mycetis	2 pairs ventral teeth	Primates: atelid (howler monkey)		South America
A. paraduodenale	2 pairs ventral teeth	Carnivora: felid (cheetah, lion, serval, cat, caffer cat, wildcat)		Africa
A. pluridentatum (syn. *Uncinaria*) [feline hookworm]	5 pairs teeth (2 ventral, 3 small dorsal)	Carnivora: felid (bobcat, cougar, tiger, oncilla, maracayo, ocelot, jaguar, jaguarundi, Florida panther, margay cat)	anaemia	Americas
A. protelesis	3 pairs ventral teeth	Carnivora: hyaenid (aardwolf)		Africa
A. somaliense	3 pairs ventral teeth	Carnivora: canid (black-backed jackal)		Africa

A. taxideae	3 pairs ventral teeth	Carnivora: mustelid (American badger)		North America
A. tubaeforme [feline hookworm]	3 pairs ventral teeth	Carnivora: felid (cat, bobcat, cougar, Geoffroy's cat, Iberian lynx, cheetah, lion, wildcat, African wildcat, South African wildcat, caffer cat, caracal, jaguarundi, leopard, leopard cat, ocelot, marbled polecat), canid (dog, black-backed jackal, red fox, grey fox), ursid (black bear), viverrid (common genet); Primates: hominid (human)	anaemia	worldwide

Parasite morphology: Hookworm developmental stages include eggs, four larval stages and adult worms. Eggs appear as oval thin-shelled bodies, measuring 55-95 µm in length by 32-58 µm in width. Freshly-excreted eggs contain a developing embryo (morula) in the early stages of cleavage with 2-8 cells (blastomeres). The first two larval stages (L1 and L2) are free-living stages characterised by a long narrow buccal chamber and a muscular rhabditiform (flask-shaped) oesophagus. Third stage larvae (L3) measure up to 600 µm in length and are non-feeding infective stages characterised by a closed mouth, elongate oesophagus with posterior bulb (strongyliform) and pointed non-notched tail. Fourth-stage larvae (L4) migrate and live in host tissues. Adult hookworms have a creamy-white tough cuticle (synlophe absent), a prominent anterior hook (dorsally deviated) and a large subglobular buccal capsule with specialised structures to aid in feeding; most species having ventral lancets with 2-3 pairs of fused teeth. The buccal capsule also has a dorsal gutter connected to the oesophagus. Adult worms are sexually dimorphic, with females being larger than males (6-25 x 0.4-0.6 mm cf. 5-13 x 0.3-0.5 mm). Females have 2 ovaries connected by oviducts to a posterior vulva and their tails have a terminal spine. Males have a single testis, a conspicuous posterior copulatory bursa consisting of two broad lateral lobes and a smaller dorsal lobe, all supported by fleshy rays consisting of muscular elements following nerve channels to terminal papillae (the short dorsal ray having 4 or 6 branchlets), a gubernaculum and 2 needle-like spicules with simple tips that are not fused distally.

Site of infection: Adult hookworms use their bent mouths to attach to the small intestinal mucosa. Infective larvae invade dermal tissues, particularly in sites which have come into close contact with the ground (feet, hands and buttocks). Migrating larvae move through the lungs (pulmonary migration) and some may undergo arrested development deeper in the gut tissues or in muscles (hypobiotic larvae of *A. duodenale*).

Pathogenesis: Many people may be infected with hookworms but remain asymptomatic. In general, disease development depends on the parasite species involved, the intensity of infection, and the nutritional condition of the individual. Sequential parasite development causes three phases of disease; a cutaneous phase where invading larvae may cause dermatitis, a pulmonary phase where migrating larvae may cause pneumonitis, and an intestinal phase where adult worms may cause gastrointestinal pain and iron-deficiency anaemia. Infective larvae penetrate the skin and invade blood vessels in the dermis, moderate to heavy infections giving rise to an allergic dermatitis with papular, and sometimes vesicular, focal rash and pruritus (condition known as ground itch). Larvae from animal hookworms (especially *A. caninum* and *A. braziliense*) can also penetrate human skin but do not complete their development. Instead, they aimlessly tunnel through the skin for several days or weeks, with *A. braziliense* leaving red itchy wounds that may become secondarily infected. The resultant condition is known as cutaneous *larval migrans* (or ground itch or creeping eruption) and is characterised by local dermatitis, pruritus (itching) and inflammation (oedema, erythema). The next phase of disease occurs when larvae undergo pulmonary migration, having been carried to the lungs where they break out into airspaces (alveoli) causing focal haemorrhages and allergic pneumonia (severity dependent on numbers). Once worms reach the small intestines, they attach to the mucosa by ingesting a tissue plug into their mouths and commence feeding on blood. Moderate to heavy infections result in significant gastrointestinal haemorrhage, iron-deficiency anaemia, and protein malnutrition in heavily infe3cted children, women of reproductive age and malnourished individuals. The adult worms have voracious appetites and individual adult *Ancylostoma* worms may take up to 0.26 ml blood per day. Blood loss from the host may result in an initial normocytic, normochromic anaemia that may worsen to a profound iron-deficiency microcytic, hypochromic anaemia with hypoproteinaemia. *Ancylostoma* spp. appear to be wasteful feeders as not all blood ingested is digested, some is apparently used for respiration and passes through the worm but degrades in the intestines resulting in black tarry faeces (melena). Blood loss is further exacerbated by intestinal lacerations as worms move to new feeding sites from time to time, secreting proteolytic enzymes and anticoagulants, and leaving microscopic ulcers. Infections by as few as 100 worms may cause severe disease in children or malnourished individuals. Hookworm infections are a major cause of anaemia in developing countries, particularly in young children and pregnant women. It is generally considered to be a disease of the poor (low socioeconomic status), with high rates of infection in rural impoverished tropical areas with poor sanitation and barefoot populations. Patients with heavy infections have severe protein deficiency, dry skin and hair, oedema, and potbelly in children with delayed puberty, mental dullness, heart failure and death. Disease is intensified by malnourishment and immunological impairment. Hookworm infections elicit profound humoral and cellular immune responses in their hosts, involving polyclonal antibody production, marked eosinophilia and Th2 lymphocyte proliferation with characteristic cytokine profiles (interleukins 4, 5, 10, 13), but such responses fail to eliminate infections, possibly due to parasites secreting a myriad of proteins that facilitate immune evasion. It is somewhat paradoxical that hookworms elicit allergenic-like responses but

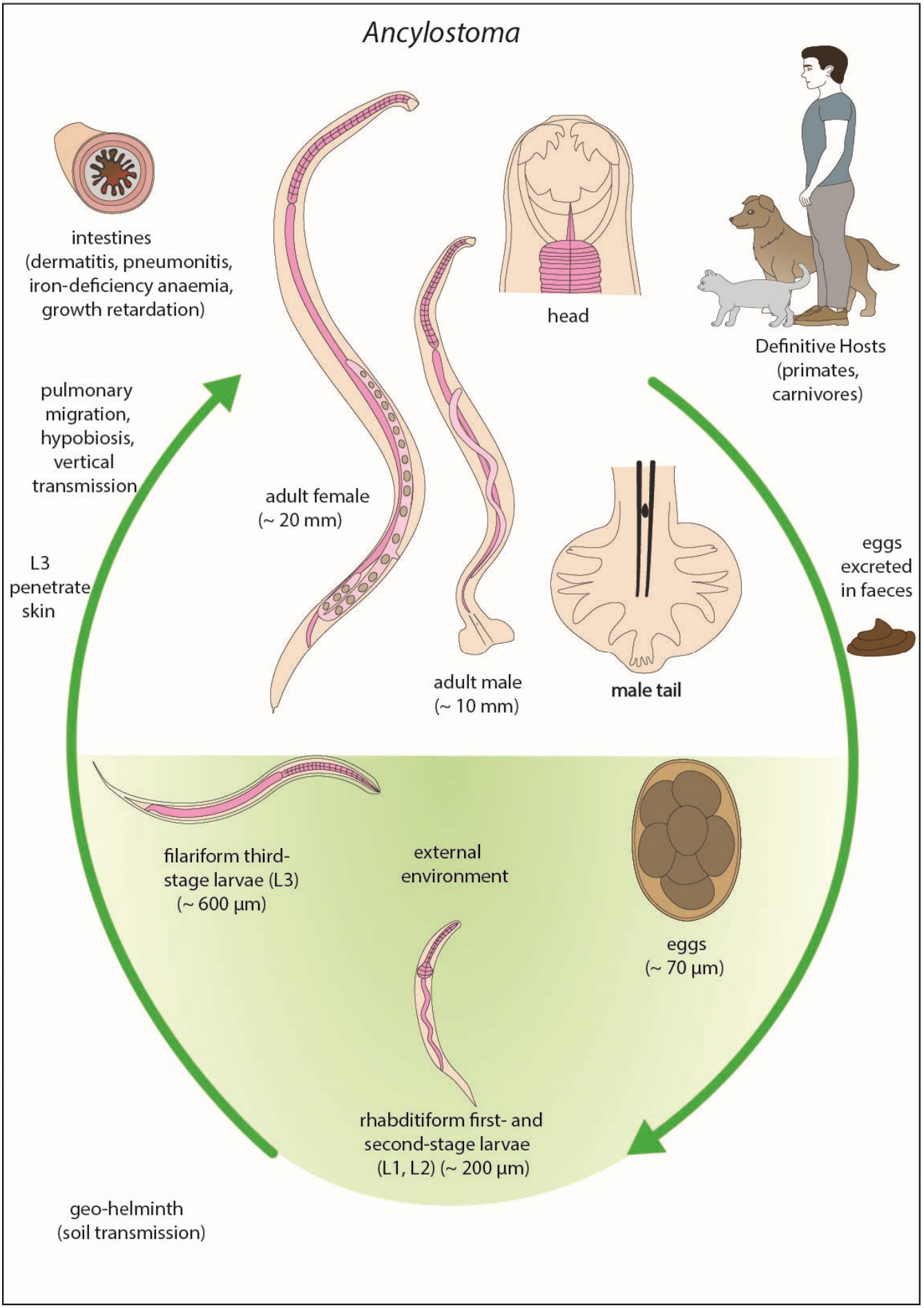
survive by modifying those responses. It is thought that these anti-inflammatory properties may benefit patients suffering from various autoimmune or hypersensitivity conditions. While this might provide the basis for alternative medical treatments using helminths, there have been few independent case-controlled studies to provide any supportive medical evidence. In animals, *A. ceylanicum* causes transient dermatitis, anaemia and bloody diarrhoea in dogs which may develop into a nonregenerative iron deficiency anaemia. This species has become recognised as the most important human hookworm in some areas of the Asia-Pacific region. *A. caninum* causes similar clinical manifestations in dogs, the severity of intestinal disease compounded by multiple haemorrhagic lesions associated with worms changing feeding sites. Peracute infection involving transmammary transmission may cause severe haemorrhagic diarrhoea, anaemia, dehydration, weakness and death in puppies. This species has been associated with several cases of eosinophilic enteritis in humans. *A. tubaeforme* may cause significant blood loss in cats with accompanying anaemia, diarrhoea, inappetence and depression, but this species has not been found to be zoonotic.

Developmental cycle and mode of transmission: Hookworms have direct life-cycles involving a geo-helminth (soil-transmitted) stage where infective larvae in the soil actively penetrate the skin or oral mucosa of their hosts. Female worms produce numerous unembryonated eggs (10,000-30,000 eggs per day) which are excreted with host faeces. The eggs embryonate rapidly in warm moist conditions and hatch within 1-2 days releasing free-living rhabditiform larvae which feed on bacteria and organic debris. The larvae moult once after ~3 days and then transform 2-5 days later into non-feeding ensheathed filariform larvae (L3) which are the infective stages. They remain viable for several weeks in shaded sandy or loamy soils under warm moist conditions. The larvae also exhibit short vertical migration, moving to the surface in moist conditions and host-seeking by rhythmically waving back and forth, but retreating back into the soil in dry conditions. Infective L3 may penetrate the skin to infect their definitive hosts (transdermal or percutaneous transmission), but they can also penetrate the oral mucosa following ingestion (*per os* transmission). Vertical transmission has also been reported for some species when larvae are passed in mother's milk (transmammary transmission) and when they cross the placenta to infect the foetus (transplacental transmission). Some evidence suggests that *A. duodenale* larvae may survive in paratenic (transport) hosts and lead to human infections through the ingestion of undercooked meat, including rabbit, lamb, beef and pork. *A. caninum* and *A. tubaeforme* larvae may infect other small animal species (rodents, birds) where they undergo arrested development until these transport hosts are eaten by canine or feline predators. In the definitive (final) host, ingested larvae may undertake pulmonary migration, but most undergo a histotrophic stage by penetrating mucosal glands before returning to the lumen and maturing into adults. Larvae which penetrate the skin actively secrete collagenase to break down basement membranes and dermal ground substances. The larvae enter the circulation and migrate over 2-7 days to the lungs where they break into respiratory alveoli and move up the trachea to be swallowed. Once they reach the small intestines, they moult, attach to mucosa and become sexually differentiated, moult again and grow into adult worms. The prepatent period (time from infection to first egg excretion) ranges from 2-7 weeks for most species, but intestinal infections by several species may be delayed for months (up to 38 weeks) when migrating larvae undergo developmental arrest (hypobiosis) within somatic tissues. Hypobiotic larvae lay dormant in host tissues (gut or muscles) and only recommence their development coincident with the seasonal return of environmental conditions more favourable to transmission. Larvae may become reactivated by host hormonal cues during the latter stages of pregnancy and migrate to the mammary glands where they are transferred to suckling offspring. Infections may persist for years, with adults of some species living for up 5 years.

Differential diagnosis: The diagnosis of hookworm disease on the basis of clinical symptomatology (notably chronic anaemia and debility) is highly suggestive, but requires confirmation by the detection of parasite eggs in faecal samples by microscopy, preferably after concentration although they can be found in direct smears or wet mounts. Because the eggs of many hookworms (*Ancylostoma* and *Necator*) and threadworms (*Strongyloides*) are virtually identical, faeces should be kept for larval cultures (usually Harada-Mori filter paper technique in closed tubes for a few days) to differentiate genera (hookworm larvae have a larger buccal cavity and smaller genital primordium), since treatment options are quite different for each group. Several studies have also been conducted in attempts to detect drug resistance in hookworms using egg hatch, larval development or larval motility assays. Radiographic findings include intestinal hypermotility, proximal jejunal dilatation and coarsening of the mucosal folds. Several immunoserological tests (enzyme immunoassays and Western blots) have been developed to detect host antibodies against hookworm antigens, but they generally do not discriminate between patent or previous infections and often exhibit some cross-reactivity with other helminths. More recently, several polymerase chain reaction (PCR) tests have been developed to detect specific parasite DNA sequences of nuclear (internal transcribed spacers (ITS-1, ITS-2), ribosomal RNA) and mitochondrial genes (cytochrome oxidase 1 gene, cAMP-dependent protein kinase catalytic subunit), but they have not yet found widespread use outside of research laboratories.

Treatment and control: Various anthelmintic drugs have been used to cure infections, and are best used in conjunction with dietary supplementation, especially iron replacement. While many nematocides are active against adult worms, migrating and arrested larvae might not be affected so it is necessary to treat individuals several times or on a regular basis. The most effective drugs are mebendazole, albendazole and pyrantel pamoate. Levamisole is less effective and treatment has adverse side-effects. Older drugs, such as bephenium and tetrachlorethylene, are still used in many areas throughout the world because they are cheap. Salicylanilides have also proven effective against animal *Ancylostoma* infections and emodepside is active against mature and immature stages. In hosts with severe hookworm disease**,** treatment should be combined with supportive care involving fluid and electrolyte therapy, iron supplementation, high protein diet and even blood transfusion if deemed necessary. While chemotherapy works, mass treatment

programmes are only partly effective as most cured individuals return to heavily contaminated areas and rapidly become re-infected. Infection appears to stimulate little protective immunity. Control programmes must include prophylaxis to prevent infections as well as environmental management to reduce soil contamination. People should be encouraged to wear solid shoes in endemic regions and to thoroughly wash salad vegetables. Building and education campaigns should be introduced to provide latrines/toilets and improve sanitary conditions, as promiscuous defaecation, associated with poverty and ignorance, keeps soil contamination high. Nightsoil (faecal waste) should not be used to fertilise gardens or vegetable crops. Dog faeces should not be left on lawns or parks (especially well-watered ones) where people congregate. Sound hygienic practices should be instituted in animal holding facilities (regular removal of faeces) and concrete surfaces can be sprayed with bleach (hypochlorite) solutions after hosing and scrubbing clean of organic debris. Companion animals should be regularly treated pre- and post-weaning to prevent vertical and horizontal transmission and preventing them from hunting will curb transmission from paratenic (prey) animals. Several countries have successfully controlled infections in human populations, predominantly by using periodic mass treatment programs and encouraging people to wear shoes and use latrines through public education campaigns. Considerable effort has also been made in developing vaccines against hookworm infections, particularly using secreted larval proteins to prevent infections or by inhibiting adult gut enzymes (aspartic proteases, cysteine proteases, haemoglobinases) to reduce worm burdens. Variable results have been obtained, although several formulations are currently undergoing clinical trials.

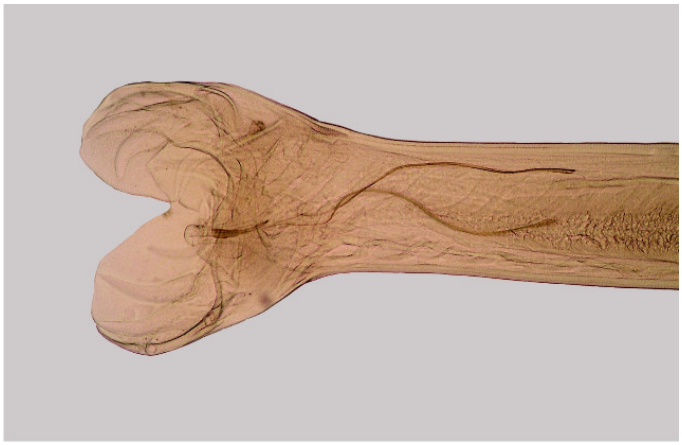

Ancylostoma
intestines
(dermatitis, pneumonitis,
iron-deficiency anaemia,
growth retardation)
head
Definitive Hosts
(primates,
carnivores)
pulmonary
migration,
hypobiosis,
vertical
transmission
adult female
(~ 20 mm)
L3
penetrate
skin
eggs
excreted
in faeces
adult male
(~ 10 mm)
male tail
filariform third-
stage larvae (L3)
(~ 600 µm)
external
environment
eggs
(~ 70 µm)
rhabditiform first- and
second-stage larvae
(L1, L2) (~ 200 µm)
geo-helminth
(soil transmission)



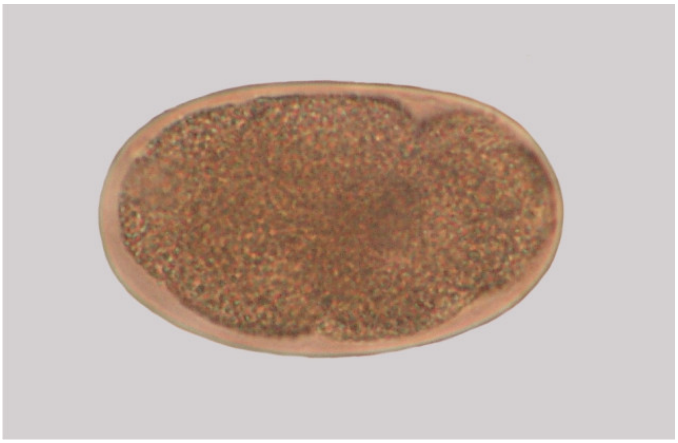
Ancylostoma adult worms



Ancylostoma adult worm, head



Ancylostoma adult worm, male bursa



Ancylostoma worm egg



Ancylostoma rhabditiform larvae



Ancylostoma filariform larva

Globocephalus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the ancylostomatids (hookworms) which are characterised by their bent mouths, the anterior ends being bent dorsally. They have a well-developed buccal capsule with cutting plates or teeth, and are voracious blood-feeders in the small intestines of mammals, esp. humans and companion animals. They have direct life-cycles, involving a geo-helminth phase. Eggs voided with faeces hatch releasing free-living rhabditiform larvae which subsequently develop into infective filariform L3 that are ingested or actively penetrate the skin of their hosts. Larvae undergo pulmonary migration through the lungs (sometimes causing pneumonitis) before developing into blood-feeding adults in the small intestines. *Globocephalus urosubulatus* causes mild hookworm disease (anaemia and diarrhoea) in pigs on most continents, except Australia.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Ancylostomatidae (hookworms, buccal capsule bent dorsally, armed with teeth/cutting plates)
Genus:	*Globocephalus* (parasitic in small intestines of pigs)
Species:	*G. urosubulatus* causes anaemia in pigs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50

Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Hookworms are characterised by their dorsally bent heads with prominent buccal capsules containing paired ventral lancets as well as teeth, cutting plates or lateral jaw-like structures. They are parasitic in the small intestines of mammals and reptiles and infections are acquired by the ingestion or skin penetration of infective L3 followed by tracheal migration. Two families are recognised: Ancylostomatidae (dorsally deviated head, buccal capsule usually armed with teeth or cutting plates, 20 genera in intestines of mammals); and Diaphanocephalidae (anteriorly directed head, buccal capsule forming 2 lateral jaw-like structures, 2 genera in intestines of reptiles). The family Ancylostomatidae contains 2 subfamilies: Ancylostomatinae (buccal capsule subglobular, with dorsal gutter, bursa with short dorsal ray, gubernaculum present, posterior vulva, female tail with terminal spine, most in carnivores); and Bunostominae (buccal capsule subglobular, with tooth-like dorsal cone, bursa with long dorsal ray, gubernaculum absent, anterior vulva, female tail without terminal spine, most in herbivores). Ancylostomatid genera of particular medical and/or veterinary significance are tabulated below.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**	**Transmission**
Ancylostominae						
Globocephalus	18	artiodactyls, rodents, primates	caecum, small intestines	3-9 mm long, large buccal capsule without cutting plates or teeth, larval pulmonary migration	60-75 x 35-41 µm, ovoid, thin-shelled	oral, transdermal
Ancylostoma	32	carnivores, primates	small intestines	5-25 mm long, bent heads, buccal capsule with ventral lancets and fused teeth, larval pulmonary migration, hypobiosis	55-95 x 32-58 µm, ellipsoidal, thin-shelled	oral, transdermal, transplacental, transmammary
Uncinaria	22	carnivores	small intestines	3-15 mm long, well-developed buccal capsule with pair of ventral cutting plates, no pulmonary migration	65-98 x 35-58 µm, ovoid, thin-shelled	oral (direct or via PH), rarely transdermal
Bunostominae						
Bunostomum	9	artiodactyls, proboscidea	small intestines	10-30 mm long, buccal capsule with ventral cutting plate and 1-2 pairs subventral teeth, larval pulmonary migration, hypobiosis	79-117 x 40-70 µm, ovoid, thin-shelled	oral, transdermal, transplacental, transmammary
Gaigeria	1	artiodactyls	small intestines	10-45 mm long, buccal capsule with pair ventral cutting plates, elongate lancets and teeth, larval	108-115 x58-61 µm, ellipsoidal,	transdermal

				pulmonary migration	thin-shelled	
Necator	7	primates, artiodactyls	small intestines	7-11 mm long, buccal capsule with cutting plates, larval pulmonary migration	55-77 x 35-42 µm, ovoid, thin-shelled	oral, transdermal

The subfamily Ancylostominae contains 8 genera classified in 4 tribes: Ancylostomatinea containing worms with oral openings armed with teeth, and globular buccal capsules not divided into articulating plates (*Ancylostoma* (syn. *Agchylostoma*, *Anchylostomum*, *Ankylostoma*, *Ankylostomum*, *Ceylancylostoma*, *Diploodon, Dochmius*) and *Galoncus*) parasitic in carnivores, primates, edentates, rodents, and suids; Uncinarinea containing worms with oral openings with well-developed cutting plates, and buccal capsule not divided into articulating plates (*Uncinaria* (syn. *Dochmoides*, *Dochmius*, incl. subgenera *Uncinaria*, *Megadeirides*) and *Bioccastrongylus*) parasitic in insectivores, primates, and carnivores; Arthrocephalinea containing worms with buccal capsules divided into articulating plates (*Arthrocephalus*, *Arthrostoma*, and *Placoconus*) parasitic in carnivores; and Globocephalinea containing worms with oral openings lacking teeth and cutting plates (*Globocephalus* (syn. *Characostomum*, *Crassisoma*, *Cystocephalus*, *Raillietostrongylus*)) parasitic in suids, primates, mustelids, rodents, ruminants, and South American marsupials. The genus *Globocephalus* contains 18 species of hookworms, 9 species infecting pigs. The species *G. urosubulatus* is found throughout many tropical and sub-tropical regions and infections have tentatively been associated with anaemia in domestic animals.

***Globocephalus* species**	**Hosts**	**Location [Clinical signs]**	**Distribution**
G. amucronatus (syn. *Characostomum*)	Artiodactyla: suid (pig)		Java
G. asmilium (syn. *Characostomum*)	Primates: cercopithecid (southern pig-tailed macaque)		Africa, Asia
G. callosciuri	Rodentia: sciurid (grey-bellied squirrel)		Malaysia
G. connorfilii	Artiodactyla: suid (pig, wild boar); Rodentia: murid (black rat)		
G. gigantospiculatus	Carnivora: mustelid (hog badger)	caecum	Vietnam
G. howelli (syn. *Characostomum*)	Rodentia: nesomyid (Gambian pouched rat)	small intestines	Africa
G. longemucronatus (possible syn. of *G. urosubulatus*)	Artiodactyla: suid (pig, wild boar, Japanese boar); Primates: cercopithecid (Campbell's mona monkey)	small intestines	Africa, Eurasia
G. lutrae	Carnivora: mustelid (Eurasian otter)		Asia
G. macaci (probably *Ternidens deminutus*)	Primates: cercopithecid (southern pig-tailed macaque)		Africa
G. madagascariensis	Artiodactyla: suid (bushpig)		Africa
G. marsupialis	Didelphimorphia: didelphid (southern opossum, grey four-eyed opossum)		South America
G. maplestoni	Artiodactyla: suid (warthog)		Africa
G. mexicanus	Rodentia: geomyid (smoky pocket gopher)		North America
G. samoensis	Artiodactyla: suid (wild boar, Japanese boar)		Asia
G. sichuanensis	Artiodactyla: suid (pig)		Asia
G. simiae	Primates: cercopithecid (macaque)	intestines	
G. urosubulatus (pig hookworm)	Artiodactyla: suid (pig, wild boar, Sardinian wild boar)	small intestines [occasionally anaemia]	Americas, Europe, Africa, Asia
G. versteri	Artiodactyla: suid (bushpig)		Africa

Parasite morphology: *Globocephalus* spp. form 3 different types of morphological stages during their development: eggs; larvae (4 successive stages designated L1-L4); and adult worms. The eggs are thin-shelled and ovoid measuring 60-75 x 35-41 µm and contain an embryo at the 4-8 cell (blastomere) stage of development. L1 are free-living stages measuring 300-360 µm with a cylindrical buccal cavity, a rhabditiform (double-bulbed) oesophagus and a long tail. L2 are similar in morphology but are larger measuring up to 620 µm. L3 are ensheathed stages measuring 630-730 µm with a striated cuticle, a strongyliform (flask-shaped) oesophagus, intestines with a palisade zig-zag appearance comprising > 20 triangular cells, and a long filamentous tail sheath. L4 are transient parasitic stages that are beginning to show adult characteristics, particularly with respect to feeding structures. Adults are small stout white worms measuring 3-9 mm long and have heads bent dorsally like most hookworms. They have large subglobular buccal capsules without lips, leaf crowns, teeth or cutting plates. The buccal capsule contains a pair of large bicuspid subventral lancets near its base, and has an elongate dorsal gutter (containing the duct of the dorsal oesophageal gland) usually

extending to the top margin. Adult worms are sexually dimorphic, with female worms being larger than males (4-9 cf. 3-7 mm). Mature females have 2 large ovaries and uteri that connect to a common vulva located posterior to the midbody, and tails containing a small terminal spine. Mature males have a caudal copulatory bursa with 2 lateral lobes supported by 6 pointed rays (consisting of muscular elements following nerve channels to terminal papillae) and a dorsal lobe (supported by a short dorsal ray with 4-6 branches). They also have a gubernaculum and 2 slender spicules measuring around 400 μm in length.

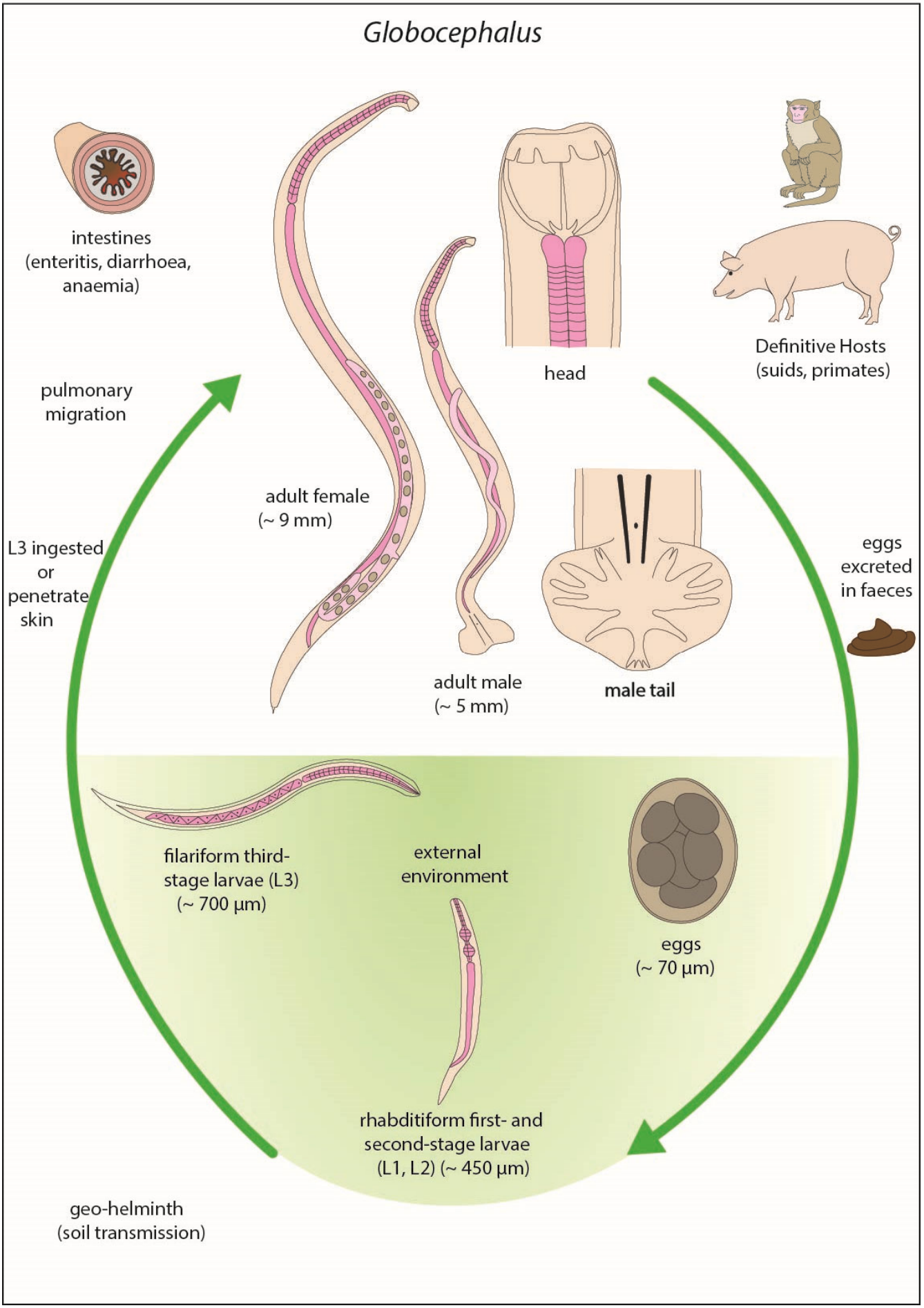
Site of infection: Adult worms infect the small intestinal mucosa of their vertebrate hosts, while developing larval stages undertake a pulmonary migration through the lungs before returning to the gut to mature as adults. Worm eggs excreted into the external environment release free-living (pre-parasitic) larval stages that become infective to their hosts.

Pathogenesis: Infections in pigs are often asymptomatic or subclinical, but heavy infections, particularly in young animals, may cause disease with anaemia and enteritis. Adult hookworms suck blood from the intestinal mucosa and frequently change their sites of attachment leaving behind haemorrhagic lesions that may contribute to anaemia. In addition, mucosal trauma and inflammation disrupt digestive function and fluid flow leading to maldigestion, hypoproteinaemia, oedema, diarrhoea (often black in colour due to the presence of blood), colic, reduced weight gain or weight loss, and sometimes emaciation. On occasion, earlier developing larvae migrating through the lungs may cause pneumonitis predisposing to pneumonia.

Developmental cycle and mode of transmission: *Globocephalus* spp. have direct monoxenous life-cycles involving the uptake of infective larvae (L3) from the external environment by oral ingestion or transdermal penetration. Gravid female worms in the intestines of the hosts lay eggs which are excreted with faeces. The eggs embryonate and hatch in 1-3 days releasing free-living L1 which feed and then moult to free-living L2 which also feed. These larvae moult to form L3 which retain the L2 cuticle as a protective sheath and are thus unable to feed. L3 may be formed in 8-12 days and while they may survive for several weeks in favourable warm moist conditions, they are not very resistant to cold, desiccation or direct sunlight. Hosts become infected when they ingest infective L3 on contaminated foods or when L3 in the soil penetrate the skin. In either case, exsheathed L3 undertake a pulmonary migration whereby they move through host tissues and reach the lungs via the circulation. The larvae then invade the alveolar air-spaces and ascend the respiratory mucociliary escalator to the trachea where they are swallowed and move to the intestines. The larvae attach to the gut mucosa where they develop through 2 moults to form adult worms which mature and mate. The prepatent period (time from infection to first egg excretion) ranges from 4-7 weeks. In endemic subtropical regions, egg production often shows seasonal variation, being highest during summer rainfall months.

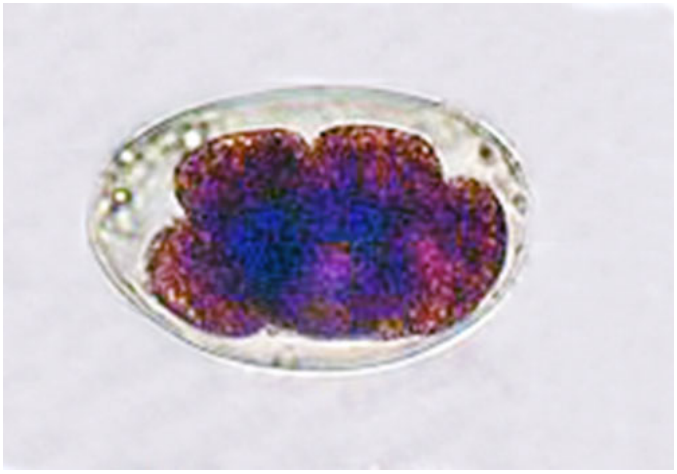
Differential diagnosis: Infections cannot be diagnosed on the basis of symptomatology as most clinical signs are vague and nonspecific (anaemia, illthrift) although the occurrence of black diarrhoea in young piglets may raise suspicions. Coprological techniques are conventionally used to diagnose infections by the detection of hookworm eggs in faecal samples, usually in concentrates following faecal floatation. Regrettably, the eggs are typically strongylid in appearance (elliptical, thin-walled, partially embryonated) and appear similar to those of other hookworms as well as some trichostrongyles, strongyles and metastrongyles. Definitive diagnosis is therefore usually achieved at post-mortem by the detection of adult worms attached to the small intestinal mucosa.

Treatment and control: Clinical infections have been treated with a range of broad-spectrum anthelmintics, including benzimidazoles (albendazole, fenbendazole, flubendazole, mebendazole, oxfendazole), imidazothiazoles (levamisole), macrocyclic lactones (abamectin, doramectin, ivermectin, moxidectin) and even organophosphonates (dichlorvos). The drugs were effective against adult worms, while the macrocyclic lactones were also effective against migrating larvae. Infections are usually not problematic in intensive piggeries due to the higher levels of sanitation and hygiene practiced compared to the conditions experienced by free-range, pastured, feral or wild swine. The regular removal of faeces and cleaning of pens and sties reduces environmental contamination by worm eggs. In addition, many infections occur by the percutaneous transmission of infective larvae when pigs come into direct contact with contaminated soils, so animals housed on solid floors and without access to soil are not at high risk.


Globocephalus
intestines
(enteritis, diarrhoea,
anaemia)
head
Definitive Hosts
(suids, primates)
pulmonary
migration
adult female
(~ 9 mm)
adult male
(~ 5 mm)
male tail
L3 ingested
or
penetrate
skin
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 700 µm)
external
environment
eggs
(~ 70 µm)
rhabditiform first- and
second-stage larvae
(L1, L2) (~ 450 µm)
geo-helminth
(soil transmission)



Globocephalus adult worms



Globocephalus worm egg



*Globocephalus t*hird-stage larva

Uncinaria
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the ancylostomatids (hookworms) which are characterised by their bent mouths, the anterior ends being bent dorsally. They have a well-developed buccal capsule with cutting plates or teeth, and are voracious blood-feeders in the small intestines of mammals. They have direct life-cycles, involving a geo-helminth phase. Eggs voided with faeces hatch releasing free-living rhabditiform larvae which subsequently develop into infective filariform L3 that are ingested or actively penetrate the skin of their hosts. *Uncinaria* infections are usually acquired by carnivores ingesting L3 or by eating paratenic (transport) hosts (such as rodents) harbouring L3. Percutaneous infections rarely mature, larvae do not undergo pulmonary migration and vertical transmission has not been demonstrated. Infections by *U. stenocephala* may cause low grade hookworm disease (anaemia and diarrhoea) in dogs and cats, and contribute to pedal dermatitis in hypersensitive animals.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Ancylostomatidae (hookworms, buccal capsule bent dorsally, armed with teeth/cutting plates)
Genus:	*Uncinaria* (parasitic in small intestines in dogs/foxes/cats)
Species:	*U. stenocephala* causes anaemia/diarrhoea in carnivores

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb,	artiodactyls, birds	ingestion of L3	50

	thin-shelled eggs			
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Hookworms are characterised by their dorsally bent heads with prominent buccal capsules containing paired ventral lancets as well as teeth, cutting plates or lateral jaw-like structures. They are parasitic in the small intestines of mammals and reptiles and infections are acquired by the ingestion or skin penetration of infective L3 followed by tracheal migration. Two families are recognised: Ancylostomatidae (dorsally deviated head, buccal capsule usually armed with teeth or cutting plates, 20 genera in intestines of mammals); and Diaphanocephalidae (anteriorly directed head, buccal capsule forming 2 lateral jaw-like structures, 2 genera in intestines of reptiles). The family Ancylostomatidae contains 2 subfamilies: Ancylostomatinae (buccal capsule subglobular, with dorsal gutter, bursa with short dorsal ray, gubernaculum present, posterior vulva, female tail with terminal spine, most in carnivores); and Bunostominae (buccal capsule subglobular, with tooth-like dorsal cone, bursa with long dorsal ray, gubernaculum absent, anterior vulva, female tail without terminal spine, most in herbivores). Ancylostomatid genera of particular medical and/or veterinary significance are tabulated below.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**	**Transmission**
Ancylostominae						
Uncinaria	22	carnivores	small intestines	3-15 mm long, well-developed buccal capsule with pair of ventral cutting plates, no pulmonary migration	65-98 x 35-58 µm, ovoid, thin-shelled	oral (direct or via PH), rarely transdermal
Ancylostoma	32	carnivores, primates	small intestines	5-25 mm long, bent heads, buccal capsule with ventral lancets and fused teeth, larval pulmonary migration, hypobiosis	55-95 x 32-58 µm, ellipsoidal, thin-shelled	oral, transdermal, transplacental, transmammary
Globocephalus	18	artiodactyls, rodents, primates	caecum, small intestines	3-9 mm long, large buccal capsule without cutting plates or teeth, larval pulmonary migration	60-75 x 35-41 µm, ovoid, thin-shelled	oral, transdermal
Bunostominae						
Bunostomum	9	artiodactyls, proboscidea	small intestines	10-30 mm long, buccal capsule with ventral cutting plate and 1-2 pairs subventral teeth, larval pulmonary migration, hypobiosis	79-117 x 40-70 µm, ovoid, thin-shelled	oral, transdermal, transplacental, transmammary
Gaigeria	1	artiodactyls	small	10-45 mm long, buccal capsule	108-115 x58-61	transdermal

			intestines	with pair ventral cutting plates, elongate lancets and teeth, larval pulmonary migration	µm, ellipsoidal, thin-shelled	
Necator	7	primates, artiodactyls	small intestines	7-11 mm long, buccal capsule with cutting plates, larval pulmonary migration	55-77 x 35-42 µm, ovoid, thin-shelled	oral, transdermal

The subfamily Ancylostominae contains 8 genera classified in 4 tribes: Ancylostomatinea containing worms with oral openings armed with teeth, and globular buccal capsules not divided into articulating plates (*Ancylostoma* (syn. *Agchylostoma*, *Anchylostomum*, *Ankylostoma*, *Ankylostomum*, *Ceylancylostoma*, *Diploodon, Dochmius*) and *Galoncus*) parasitic in carnivores, primates, edentates, rodents, and suids; Uncinarinea containing worms with oral openings with well-developed cutting plates, and buccal capsule not divided into articulating plates (*Uncinaria* (syn. *Dochmoides*, *Dochmius*, incl. subgenera *Uncinaria*, *Megadeirides*) and *Bioccastrongylus*) parasitic in insectivores, primates, and carnivores; Arthrocephalinea containing worms with buccal capsules divided into articulating plates (*Arthrocephalus*, *Arthrostoma*, and *Placoconus*) parasitic in carnivores; and Globocephalinea containing worms with oral openings lacking teeth and cutting plates (*Globocephalus* (syn. *Characostomum*, *Crassisoma*, *Cystocephalus*, *Raillietostrongylus*)) parasitic in suids, primates, mustelids, rodents, ruminants, and South American marsupials. The genus *Uncinaria* contains over 20 species of hookworms with globular buccal capsules armed with 2 ventrolateral and 2 dorsolateral cutting plates. Most species infect wild animals, although the species *U. stenocephala* is commonly found in companion animals, mainly working dogs. Infections are often found worldwide in regions with cooler climates, including temperate and subarctic zones in the Northern and Southern Hemispheres. Occasionally, humans may become infected transdermally with larval stages causing transient cutaneous larval migrans.

***Uncinaria* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Distribution**
U. bauchoti	Afrosoricida: tenerecid (greater hedgehog tenerec)		Madagascar
U. bidens	Carnivora: procyonid (crab-eating raccoon, coati)		Asia
U. brasilensis	Carnivora: canid (dog)		South America
U. carinii	Carnivora: canid (crab-eating fox)		
U. criniformis	Carnivora: mustelid (European badger, Iberian badger, pine marten, beech marten)		Eurasia
U. felidis	Carnivora: felid (cat, leopard cat)		Asia
U. hamiltoni	Carnivora: otariid (brown fur seal, New Zealand fur seal, South American fur seal, Australian sea lion, South American sea lion)	small intestines [anaemia]	Australia, South America
U. hydromyidis	Rodentia: murid (Australian water rat)		Australia
U. longespiculatum (possibly *Arthrocephalus*)	Carnivora: viverrid (masked palm civet, small Indian civet)		Asia
U. lucasi	Carnivora: otariid (northern fur seal, Steller sea lion), phocid (ringed seal)		North America
U. lyonsi	Carnivora: otariid (California sea lion)		North America
U. maxillaris	Carnivora: procyonid (crab-eating raccoon)		Asia
U. maya	Carnivora: felid (iriomote cat)		Asia
U. muridis sp. inq.	Rodentia: murid (Southern African vlei rat)		Africa
U. olseni	Scandentia: tupaiid (treeshrew)		Asia
U. parvibursata	Carnivora: mustelid (honey badger)		Africa
U. philippinensis (possibly *Arthrocephalus longespiculum*)	Carnivora: viverrid (Asian palm civet)		Philippines
U. rauschi	Carnivora: ursid (black bear, brown bear)		North America
U. sanguinis	Carnivora: otariid (Australian sea lion)	intestines [anaemia]	Australia
U. skrjabini	Carnivora: mustelid (sable)		Eurasia
U. stenocephala (Northern hookworm, European hookworm)	Carnivora: canid (dog, dingo, coyote, wolf, maned wolf, red fox, eastern American red fox, arctic fox, Darwin's fox, grey fox, swift fox, corsac fox, Iberian fox, Bengal fox, golden jackal, raccoon dog, culpeo), felid (cat, sand cat, lynx, lion), mustelid (European badger); Artiodactyla:	small intestines [anaemia, diarrhoea]	worldwide, esp. temperate zones

(syn. *Dochmius balsami*, *U. polaris*)	suid (pig); Rodentia: murid (mouse) [plus larval infections in Primates: hominid (human)]		
U. trigonocephala (syn. *Ankylostoma*)	Carnivora: canid (bat-eared fox, red fox)		Africa
U. yukonensis	Carnivora: ursid (American black bear, brown bear)		North America

Parasite morphology: *Uncinaria* spp. form 3 different types of morphological stages in their development: namely, eggs, larvae (4 consecutive stages usually encoded L1-L4), and adult worms. Female worms produce elliptical eggs measuring 65-93 x 35-58 µm that have thin eggshells and contain a central embryonic mass (morula) usually at the 8 cell (blastomere) stage. L1 and L2 are free-living (preparasitic) stages measuring from 300-500 µm in length and they have long narrow buccal capsules, short rhabditiform (double-bulbed) oesophagi and tapering tails. L3 are ensheathed stages (still encased in L2 cuticle) measuring 450-540 µm in length and they have closed mouths, elongate strongyliform oesophagi, and pointed non-notched tails. L4 are transient parasitic stages that have begun to show adult worm characteristics, particularly with regard to mouthparts and developing genitalia. Adult hookworms are small stout white worms ranging in length from 3-15 mm and having heads with a prominent dorsal deviation (hook). They have an enlarged subglobular to funnel-shaped buccal capsule not divided into articulating plates but with a pair of well-developed chitinous cutting plates on the ventral border and a pair of spear-shaped subventral teeth. The buccal capsule has a dorsal gutter on its inner surface containing the duct of the oesophageal gland, and the oesophagus is flask-shaped and elongate occupying the anterior third of the worm. Adult worms are sexually dimorphic, with females being longer and stouter than males (7-15 cf. 3-9 mm long). Mature males have a well-developed copulatory bursa with 2 large separate lateral lobes, each supported by 6 finger-like rays (formed by muscular elements following nerve channels to terminal papillae), and a short dorsal lobe (supported by a short ray bifurcating into 4-6 branches). They also have a gubernaculum around 25 µm long and 2 slender spicules measuring up to 800 µm long. Mature female worms are didelphic, with 2 ovaries and uteri with short wide vaginas and symmetrical longitudinal ovejectors opening into a prominent vulva located posterior to midbody, and they have short tapering tails with terminal spine.

Site of infection: Adult worms infect the small intestines of their definitive hosts (predominantly carnivores), while earlier parasitic larval stages undergo histotrophic development in mucosal tissues (rarely undertaking pulmonary migration). Free-living larval stages develop from excreted eggs and contaminate the external environment.

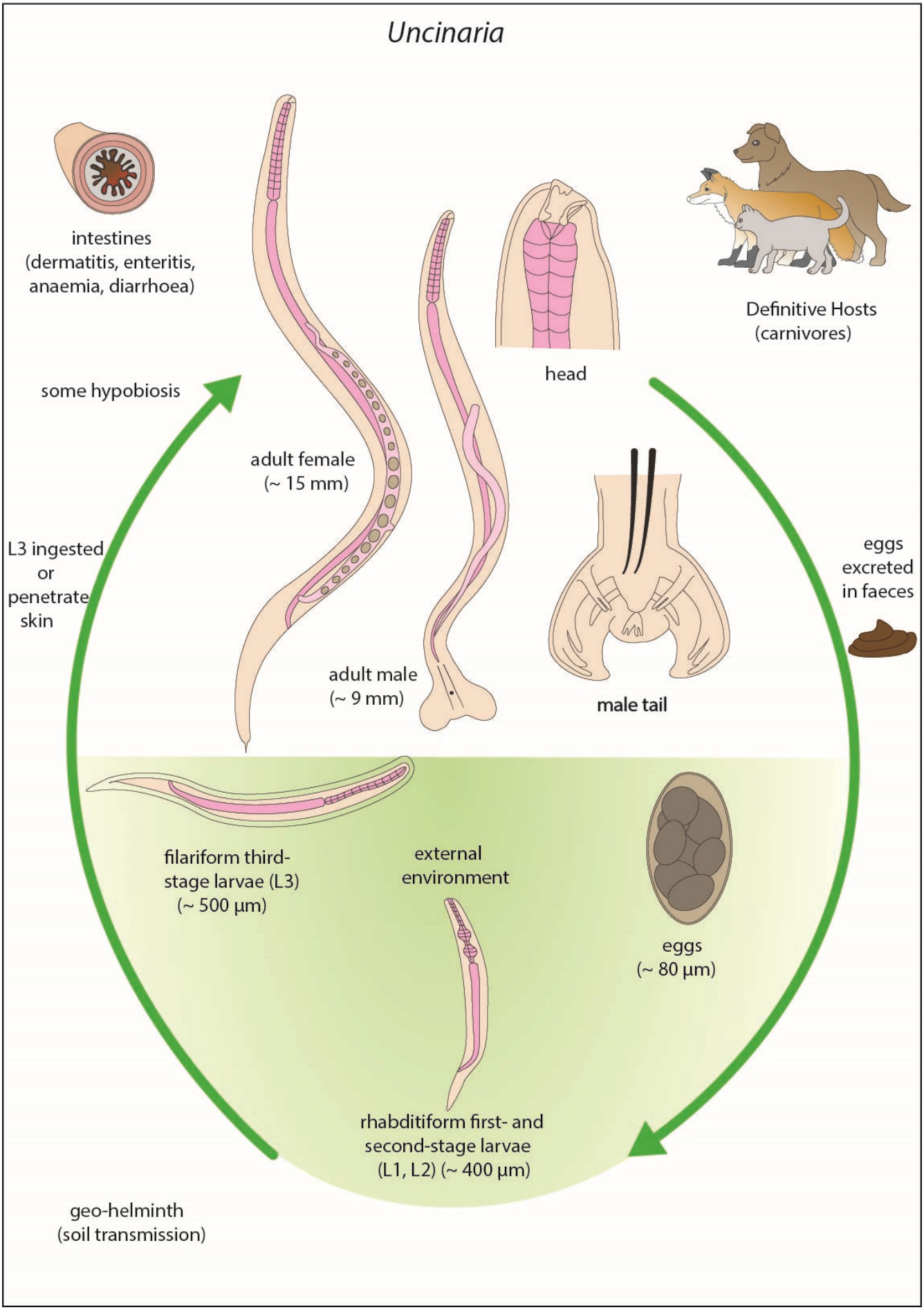
Pathogenesis: Most infections remain asymptomatic because few worms are involved, although heavier infections may cause clinical disease, either when larvae migrate through tissues or when adult worms feed on blood in the intestines. The severity of disease depends on the virulence of the parasite species, the intensity and route of infection, and host susceptibility (young and/or malnourished individuals are most at risk). Infective larvae coming into contact with host skin may penetrate dermal tissues and cause trauma and transient inflammation when migrating through tissues, including erythema, dermatitis with papules and severe pruritus (condition commonly known as cutaneous larva migrans or creeping eruption). Lesions are commonly found in areas with high exposure to contaminated soils, and are often found between the toes or on the forearms, and sometimes on the bellies of resting animals. Migrating larvae only move a few millimeters each day, producing characteristic lesions until they leave the tissues or succumb to host immune responses (innate and acquired, including eosinophilia). Dermal lesions are usually transient and self-limiting, although several cases have reportedly lasted for over a year. Lesions in dogs are often worse in individuals sensitized by prior exposure, resulting in erythematous interdigital skin, pedal dermatitis, swollen and painful pads sometimes with hyperkeratosis and fissures in severe chronic cases. Cutaneous infections in humans are superficial and transient as the larvae are unable to penetrate deeper into dermal tissues and soon die. When adult worms develop in the small intestines, they feed on blood and intestinal mucosa using their large mouths and cutting plates to ingest, lacerate and digest plugs of tissue. Although they are reportedly not as voracious as other hookworms, taking 0.3 µl of blood per worm per day (cf. 100 µl for other hookworms), the blood loss is exacerbated when feeding worms detach and move to new feeding sites leaving behind haemorrhagic lesions. The cumulative blood loss can lead to erythropenia and the development of an acute normocytic normochromic anemia progressing to a hypochromic microcytic anaemia due to iron deficiency. Trauma to the small intestinal mucosa may lead to inflammation, villous atrophy and/or fusion, maldigestion, fluid and protein leakage leading to hypoproteinaemia (esp. hypoalbuminaemia), diarrhoea (often bloody with black tarry stools (melena)), dehydration and anorexia, all contributing to failure to thrive, reduced growth, weakness, lethargy, wasting, emaciation and sometimes death.

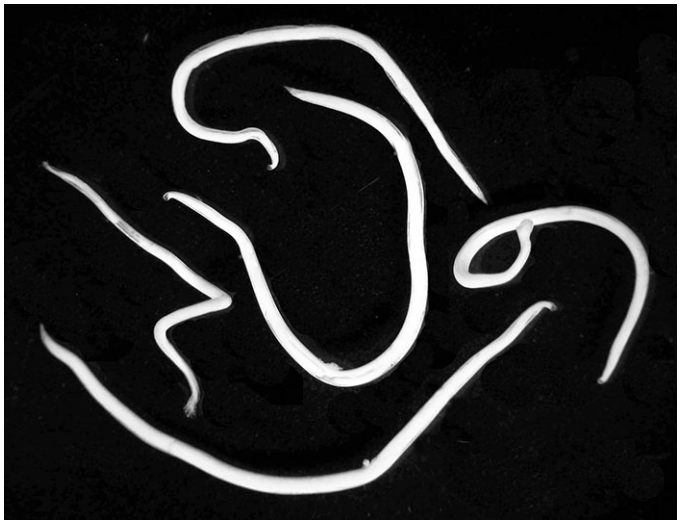
Developmental cycle and mode of transmission: These hookworms have direct monoxenous life-cycles involving the oral ingestion of larval stages from the environment (faecal-oral transmission), or more infrequently and less successfully, by penetration of infective larvae through the skin (percutaneous or transdermal transmission). Gravid females lay eggs (up to 3,000-5,000 per day) which are excreted with host faeces into the external environment. The eggs embryonate and hatch within several days under suitable climatic conditions, optimal in cool moist conditions although they can develop in colder conditions, but do not survive freezing. Hatched eggs release free-living rhabditiform larvae which feed and grow before moulting to L2 which also feed. These larvae then moult forming strongyliform L3 which have retained the L2 cuticle as a protective sheath and are unable to feed. Infective L3 may be formed in as little as 5-10 days and they are able to survive for several weeks in favorable conditions dispersing

from faecal material into the surrounding soil and vegetation. In some species in seals, larval development from L1 to L3 has been reported to occur entirely within eggs before they hatch. Definitive hosts become infected mainly by the oral ingestion of infective L3, which exsheath in the gut and enter gastric glands in the pylorus of the stomach and the crypts and glands in the duodenal mucosal where they undergo histotrophic development (these larvae do not undertake pulmonary migration). The larvae usually emerge after several days to moult and mature as adults in the small intestines. The prepatent period (time from infection to first egg excretion) ranges from 13-21 days, and adult worms have been reported to live from 4 months to 2 years. The larvae of some species (including *U. stenocephala*) have also been reported to undergo developmental arrest (hypobiosis) emerging weeks to months later to resume development. The triggers for hypobiosis are not fully understood but have been associated with climatic changes (particularly sudden drops in temperature) and physiological changes in hosts (notably hormonal changes during pregnancy and lactation). However, there is no substantive evidence that transplacental and transmammary transmission occurs for these hookworm species. Infective L3 in the soil may penetrate host skin and they are well-documented as causes of dermatological lesions in a range of hosts. However, these percutaneous infections by *Uncinaria* spp. rarely mature, although a very small number of larvae are thought to complete pulmonary migration through the circulation to the lungs where they enter alveolar air-spaces and ascend the mucociliary escalator to the trachea to be swallowed and enter the gut. There have also been several reports of carnivores becoming infected by ingesting dormant L3 carried in small vertebrate prey animals (notably mice) which act as paratenic (transport) hosts. The majority of infections in dogs, however, have been associated with infective larvae on pastures used for training purposes, with peaks in seasonal abundance coinciding with the first rainfalls in autumn.

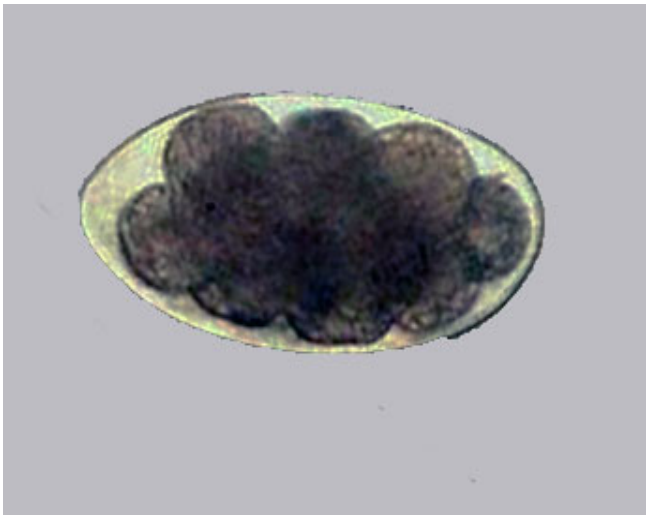
Differential diagnosis: While clinical signs may be highly suggestive of hookworm disease due to migrating larvae (dermatitis) or feeding adults (anaemia, diarrhoea), they are nonspecific and may be attributed to a variety of other conditions or infections. Most infections in dogs also have a history of poor husbandry with dogs housed on dirt runs or grassed areas and not provided with adequate worm control. The differential diagnosis of suspect dermatological cases may be aided by cytological examination of hair plucks and skin scrapings or biopsies, mostly to rule out other aetiological agents (bacteria, fungi, mites) as larvae are rarely found in eruptive tracts and histopathological examination is frequently non-specific (perivascular dermatitis containing eosinophils and neutrophils). Diagnosis is conventionally made by the microscopic detection of worm eggs in faecal samples, usually in concentrates following centrifugal floatation. However, the eggs are not sufficiently characteristic in morphology to discriminate between hookworm genera or from other strongyles, particularly the metastrongyles (lungworms). Recourse is sometimes made to the coproculture of faecal samples to harvest developing larvae, as the L1 of various genera vary in structure (those of *Uncinaria* having long buccal tubes (short in *Strongyloides*) and tapering tails without kinks or spines (kinked in *Filaroides*, kinked and spined in *Aelurostrongylus* and *Angiostrongylus*). Several immunoserological tests have been developed to detect specific host antibodies against hookworm antigens, but many demonstrated considerable cross-reactivity between hookworm genera. Modern molecular biological techniques have been used to characterize hookworm species following the polymerase chain reaction (PCR) amplification and restriction fragment length polymorphism (RFLP) analysis of nuclear genes (ribosomal DNA region spanning the first and second internal transcribed spacers (ITS1 and ITS2) plus the 5.8S gene).

Treatment and control: Infections by adult hookworms have been successfully treated with a range of anthelmintic drugs, including benzimidazoles (fenbendazole, albendazole, mebendazole), tetrahydropyrimidines (pyrantel), isoquinolines (praziquantel), macrocyclic lactones (ivermectin, moxidectin), chloronicotinyles (imidacloprid), substituted isothiocyanates (nitroscanate), diethylenediamines (piperazine), imidazothiazoles (levamisole), and depsipeptides (emodepside) with or without the symmetric triazines (toltrazuril). Cutaneous infections by migrating larvae are usually self-limiting but they have responded well to treatment with albendazole or ivermectin. When treating heavy infections with significant anaemia, supportive therapy may be required in the form of fluid/electrolyte replacement, and dietary supplementation (esp. protein and iron). It is often recommended that puppies and kittens be treated before and after weaning, and that dogs be dewormed on a regular basis as they may be quickly re-infected when returned to contaminated surroundings. A variety of management practices have been used to limit the transmission of infections, primarily through improved sanitation (regular removal of faeces), good hygiene (disinfection of holding pens/cages, provision of clean food, water and bedding), and sensible husbandry (avoid overcrowding, separate cohorts, keep facilities dry, and restrict access to earthen and/or grassy runs). The use of stringent chemicals to disinfect contaminated soils had variable success and no appeal due to concerns over toxic residues and environmental pollution. Preliminary studies on vaccine development have reported restricted adult development and reduced egg counts in dogs given irradiated larvae.


Uncinaria
intestines
(dermatitis, enteritis,
anaemia, diarrhoea)
Definitive Hosts
(carnivores)
head
some hypobiosis
adult female
(~ 15 mm)
L3 ingested
or
penetrate
skin
eggs
excreted
in faeces
adult male
(~ 9 mm)
male tail
filariform third-
stage larvae (L3)
(~ 500 µm)
external
environment
eggs
(~ 80 µm)
rhabditiform first- and
second-stage larvae
(L1, L2) (~ 400 µm)
geo-helminth
(soil transmission)



Uncinaria adult worms



Uncinaria worm egg



Uncinaria adult worm, female tail



Uncinaria adult worm, head

Necator
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the ancylostomatids (hookworms) which are characterised by their bent mouths, the anterior ends being bent dorsally. They have a well-developed buccal capsule with cutting plates or teeth, and are voracious blood-feeders in the small intestines of mammals. They have direct life-cycles, involving a geo-helminth phase. Eggs voided with faeces hatch releasing free-living rhabditiform larvae which subsequently develop into infective filariform L3 that are ingested or actively penetrate the skin of their hosts (some species causing cutaneous larval migrans). Larvae undergo pulmonary migration through the lungs (sometimes causing pneumonitis) before developing into blood-feeding adults in the small intestines. Infections by *Necator* cause New World hookworm disease in humans, characterised by iron-deficiency anaemia and growth retardation in children.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Ancylostomatidae (hookworms, buccal capsule bent dorsally, armed with teeth/cutting plates)
Genus:	*Necator* (parasitic in small intestines of humans/pigs)
Species:	*N. americanus* (causes New World hookworm disease in humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb,	artiodactyls, birds	ingestion of L3	50

	thin-shelled eggs			
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Hookworms are characterised by their dorsally bent heads with prominent buccal capsules containing paired ventral lancets as well as teeth, cutting plates or lateral jaw-like structures. They are parasitic in the small intestines of mammals and reptiles and infections are acquired by the ingestion or skin penetration of infective L3 followed by tracheal migration. Two families are recognised: Ancylostomatidae (dorsally deviated head, buccal capsule usually armed with teeth or cutting plates, 20 genera in intestines of mammals); and Diaphanocephalidae (anteriorly directed head, buccal capsule forming 2 lateral jaw-like structures, 2 genera in intestines of reptiles). The family Ancylostomatidae contains 2 subfamilies: Ancylostomatinae (buccal capsule subglobular, with dorsal gutter, bursa with short dorsal ray, gubernaculum present, posterior vulva, female tail with terminal spine, most in carnivores); and Bunostominae (buccal capsule subglobular, with tooth-like dorsal cone, bursa with long dorsal ray, gubernaculum absent, anterior vulva, female tail without terminal spine, most in herbivores). Ancylostomatid genera of particular medical and/or veterinary significance are tabulated below.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**	**Transmission**
Bunostominae						
Necator	7	primates, artiodactyls	small intestines	7-11 mm long, buccal capsule with cutting plates, larval pulmonary migration	55-77 x 35-42 µm, ovoid, thin-shelled	oral, transdermal
Bunostomum	9	artiodactyls, proboscidea	small intestines	10-30 mm long, buccal capsule with ventral cutting plate and 1-2 pairs subventral teeth, larval pulmonary migration, hypobiosis	79-117 x 40-70 µm, ovoid, thin-shelled	oral, transdermal, transplacental, transmammary
Gaigeria	1	artiodactyls	small intestines	10-45 mm long, buccal capsule with pair ventral cutting plates, elongate lancets and teeth, larval pulmonary migration	108-115 x58-61 µm, ellipsoidal, thin-shelled	transdermal
Ancylostominae						
Ancylostoma	32	carnivores, primates	small intestines	5-25 mm long, bent heads, buccal capsule with ventral lancets and fused teeth, larval pulmonary migration, hypobiosis	55-95 x 32-58 µm, ellipsoidal, thin-shelled	oral, transdermal, transplacental, transmammary
Globocephalus	18	artiodactyls, rodents,	caecum, small	3-9 mm long, large buccal capsule without cutting plates or teeth,	60-75 x 35-41 µm, ovoid,	oral, transdermal

		primates	intestines	larval pulmonary migration	thin-shelled	
Uncinaria	22	carnivores	small intestines	3-15 mm long, well-developed buccal capsule with pair of ventral cutting plates, no pulmonary migration	65-98 x 35-58 µm, ovoid, thin-shelled	oral (direct or via PH), rarely transdermal

The subfamily Bunostominae contains 12 genera classified in 2 tribes: Bunostominea containing worms with anterodorsally directed heads with pronounced dorsal inclination, oral opening with well-developed cutting plates, no buccal collar, long oesophagus (*Bunostomum* (syn. *Bustomum*, *Monodontus*), *Bathmostomum*, *Bunostomoides, Brachyclonus*, *Cameronecator*, *Gaigeria*, *Grammocephalus*, *Monodontus*, *Necator*, *Rhinoceratonema*) in elephants, rhinoceros, procyonids, ruminants, rodents, tayasuids, tapirs, and primates; and Acheilostominea containing worms with anterodorsally directed heads with slight dorsal inclination, oral opening with inconspicuous or no cutting plates, buccal collar, short oesophagus (*Acheilostoma*, *Tetragomphius*) in rodents, mustelids and procyonids. The genus *Necator* comprises hookworms whose buccal capsules contain 2 pairs of cutting plates (subdorsal plates flanking the dorsal cone), females with elongate vestibula in the ovejector, and males with short dorsal rays and deep median fissures in the bursa. Some 7 species that have been described from a small range of mammals from several continents, notably the Americas and Africa. The species *N. americanus* is colloquially called the New World human hookworm, although it probably came to the Americas from Africa with the slave trade. Infections are commonly found in tropical and subtropical regions because the larvae cannot develop below 22°C. They are frequently found in rural areas with high annual rainfall and shaded sandy or loam soils ideal for larval development (not clay or gravel). It is estimated that around 900 million people are infected with hookworms (*Necator* and *Ancylostoma*) worldwide, with 1.6 million suffering from anaemia and 55,000 deaths annually.

***Necator* species**	**Oral structures**	**Hosts**	**Clinical signs**	**Geographic distribution**
N. americanus (syn. *Uncinaria americana*) [New World human hookworm]	2 pairs cutting plates (dorsal and ventral)	Primates: hominid (human, chimpanzee, lowland gorilla), cercopithecid (rhesus macaque, patas monkey, sooty mangabey, Campbells' mona monkey, king colobus, western red colobus, yellow baboon), pithecid (bald uakari); Artiodactyla: suid (pig), rhinocerotid (Indian rhinoceros); Perissodactyla: equid (donkey); Lagomorpha: leporid (rabbit); Pholidota: manid (Chinese pangolin, Indian pangolin); Rodentia: erethizontid (Bahai porcupine), cricetid (Chinese hamster, golden hamster), murid (mouse); Carnivora: canid (dog); Siluriformes: claroteid (bagrid catfish); Cichliformes: cichlid (blackchin tilapia, Guinean tilapia, Nile tilapia)	cutaneous larval migrans, pneumonitis, anaemia	Americas, Africa, India, Asia
N. congolensis	2 pairs cutting plates	Primates: hominid (chimpanzee)	small intestines	Africa
N. exilidens	2 pairs cutting plates	Primates: hominid (chimpanzee)	small intestines	Africa
N. gorillae	2 pairs cutting plates	Primates: hominid (lowland gorilla, bonobo, human)	small intestines	Africa
N. okapi		Artiodactyla: giraffid (okapi)		Africa
N. suillus	2 pairs cutting plates	Artiodactyla: suid (pig)	small intestines	Caribbean
N. urichi	2 pairs cutting plates	Carnivora: procyonid (crab-eating raccoon)	small intestines	South America

Parasite morphology: Hookworm developmental stages include eggs, four larval stages and adult worms. Eggs appear as oval thin-shelled bodies, measuring 55-77 µm in length by 35-42 µm in width. Freshly-excreted eggs contain a developing embryo (morula) in the early stages of cleavage with 2-8 blastomeres (cells). The first two larval stages (L1 and L2) are rhabditiform (free-living) and characterised by a long narrow buccal chamber and flask-shaped muscular oesophagus. Third stage larvae (L3) measure up to 600 µm in length and are filariform, non-feeding infective stages characterised by a closed mouth, elongate oesophagus with posterior bulb (strongyliform) and pointed non-notched tail. Fourth-stage larvae (L4) migrate and live in host tissues. Adult hookworms have a creamy-white tough cuticle (synlophe absent), a prominent anterior hook (head deviated dorsally) and a large oval buccal capsule with a pair of dorsal and a pair of ventral cutting plates surrounding the anterior margin. The buccal capsule also has a pair of

subdorsal and a pair of subventral teeth near the posterior dorsal cone opening into the oesophagus. Adult worms are sexually dimorphic, with females being larger than males (9-11 mm long cf. 7-9 mm). Female worms have 2 ovaries, an anterior or midbody vulva and their tails lack terminal spines. Male worms have a single testis, 2 needle-like spicules with barbed tips fused distally (gubernaculum absent) and a conspicuous posterior copulatory bursa consisting of two broad lateral lobes and a smaller dorsal lobe supported by fleshy rays formed by muscular elements following nerve channels to terminal papillae (the long dorsal ray has 4 or 6 branchlets).

Site of infection: Adult hookworms use their bent mouths to attach to the small intestinal mucosa. Infective larvae invade dermal tissues, particularly in sites which have come into close contact with the ground (feet, hands and buttocks). Migrating larvae undergo pulmonary migration before being coughed up and swallowed to complete their development in the intestines.

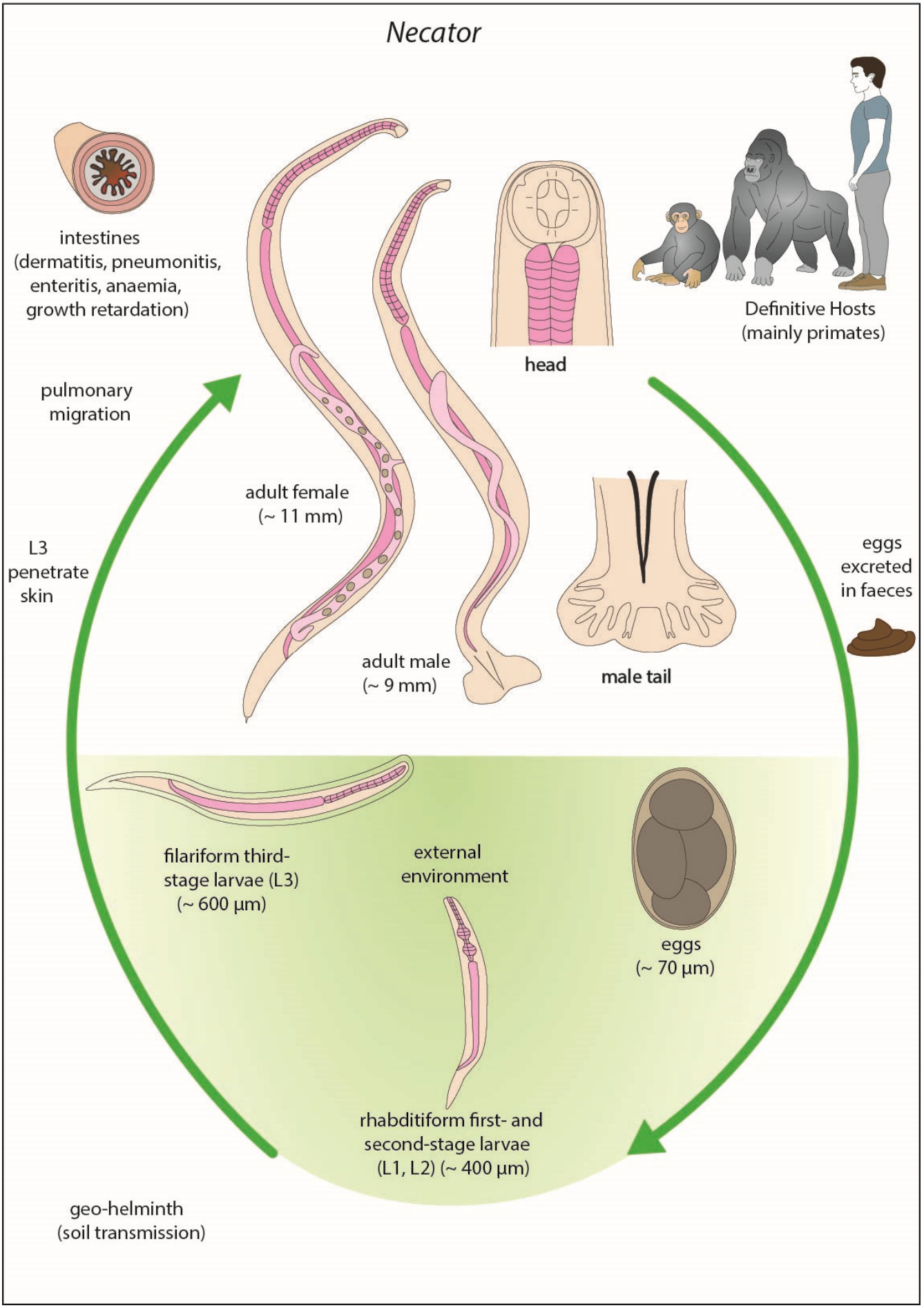
Pathogenesis: Many people infected with hookworms remain asymptomatic. Disease development depends on the parasite species involved, the intensity of infection, and the nutritional condition of the individual. Infections cause three phases of disease; a cutaneous phase where invading larvae may cause dermatitis, a pulmonary phase where migrating larvae may cause pneumonitis, and an intestinal phase where adult worms may cause anaemia. Infective larvae penetrate the skin and invade blood vessels in the dermis, moderate to heavy infections giving rise to an allergic dermatitis with papular, and sometimes vesicular, focal rash and pruritus (condition known as ground itch). The pulmonary phase then occurs when larvae carried to the lungs by the bloodstream break out into airspaces (alveoli) causing focal haemorrhages and allergic pneumonia (severity dependent on numbers). Larvae are coughed up and swallowed and once they reach the small intestines, they attach to the mucosa by ingesting a tissue plug into their mouths and commence feeding on blood. Infections result in significant gastrointestinal haemorrhage, iron-deficiency anaemia, protein malnutrition and intestinal inflammation. The adult worms have voracious appetites and individual adult worms may consume 0.03 ml blood per day. Blood loss from the host may result in an initial normocytic, normochromic anaemia that may worsen to a profound iron-deficiency microcytic, hypochromic anaemia with hypoproteinaemia. The worms ingest substantially less blood than adult *Ancylostoma* spp., but they are nonetheless wasteful feeders as not all blood ingested is digested, some is apparently used for respiration and passes through the worm but degrades in the intestines resulting in black tarry faeces (melena). Blood loss is further exacerbated by intestinal lacerations as worms move to new feeding sites from time to time, secreting proteolytic enzymes and anticoagulants, and leaving microscopic ulcers. Infections involving <100 *Necator* are frequently mild whereas >100 worms produce more damage and >1,000 may be fatal. Hookworm infections are a major cause of iron-deficiency anaemia in developing countries, particularly in young children and pregnant women. It is generally considered to be a disease of the poor (low socioeconomic status), with high rates of infection in rural impoverished tropical areas with poor sanitation and barefoot populations. Patients with heavy infections have severe protein deficiency, dry skin and hair, oedema, and potbelly in children with delayed puberty, mental dullness, heart failure and death. Disease is intensified by malnourishment and immunological impairment. Hookworm infections elicit profound humoral and cellular immune responses in their hosts, involving polyclonal antibody production, marked eosinophilia and Th2 lymphocyte proliferation with characteristic cytokine profiles (interleukins 4, 5, 10, 13), but such responses fail to eliminate infections, possibly due to parasites evading immune responses. It is somewhat paradoxical that hookworms elicit allergenic-like responses but survive by modifying those responses.

Developmental cycle and mode of transmission: Hookworms have direct life-cycles involving a geo-helminth (soil-transmitted) stage where infective larvae in the soil actively penetrate the skin or oral mucosa of their hosts. Female worms produce numerous unembryonated eggs (3,000-9,000 per day) which are excreted with host faeces. The eggs embryonate rapidly in warm moist conditions and hatch within 1-2 days releasing free-living rhabditiform larvae which feed on bacteria and organic debris. The larvae moult twice over 10 days transforming into non-feeding ensheathed filariform larvae (L3) which are the infective stages. They remain viable for 3-4 weeks in moist temperate soils but do not survive freezing or desiccation. *Necator* larvae penetrate the skin to infect their definitive hosts (transdermal or percutaneous transmission). The larvae enter the circulation and are carried to the lungs where they break into respiratory alveoli and move up the trachea to be swallowed (pulmonary migration lasting several days). Once they reach the small intestines, they moult, attach to mucosa and become sexually differentiated, moult again and grow into adult worms. The prepatent period (time from infection to first egg excretion) ranges from 2-7 weeks and adult worms may live for up to 15 years.

Differential diagnosis: The diagnosis of hookworm disease on the basis of clinical symptomatology (notably chronic anaemia and debility) is highly suggestive, but requires confirmation by the detection of parasite eggs in faecal samples by microscopy, preferably after concentration although they can be found in direct smears or wet mounts. Because the eggs of hookworms (*Necator* and *Ancylostoma*) and threadworms (*Strongyloides*) are virtually identical, faeces should be kept for larval cultures (usually Harada-Mori filter paper technique in closed tubes for a few days) to differentiate genera (hookworm larvae have a larger buccal cavity and smaller genital primordium), since treatment options are quite different for each group. Radiographic findings include intestinal hypermotility, proximal jejunal dilatation and coarsening of the mucosal folds. Several immunoserological tests (enzyme immunoassays and Western blots) have been developed to detect host antibodies against hookworm antigens, but they generally do not discriminate between patent or previous infections and often exhibit some cross-reactivity with other helminths. More recently, several polymerase chain reaction (PCR) tests have been developed to detect specific parasite DNA sequences of nuclear (ribosomal

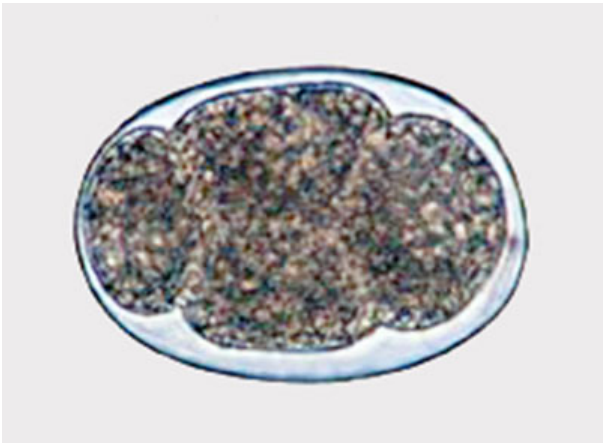
RNA internal transcribed spacers (ITS-1, ITS-2)) and mitochondrial genes (cytochrome oxidase 1 gene, cAMP-dependent protein kinase catalytic subunit).

Treatment and control: Various anthelmintic drugs have been used to cure infections, and are best used in conjunction with supportive care involving fluid and electrolyte therapy, dietary supplementation (especially iron replacement), and even blood transfusion if deemed necessary. The most effective drugs are mebendazole, albendazole and pyrantel pamoate. Levamisole is less effective and treatment has adverse side-effects. Older drugs, such as bephenium and tetrachlorethylene, are still used in many areas throughout the world because they are cheap. Regrettably, mass drug treatment programmes are only partly effective as many individuals return to heavily contaminated areas and rapidly become re-infected. Infection appears to stimulate little protective immunity. Control programmes must include prophylaxis to prevent infections as well as environmental management to reduce soil contamination. People should be encouraged to wear solid shoes in endemic regions and to thoroughly wash salad vegetables. Building and education campaigns should be introduced to provide latrines/toilets and improve sanitary conditions, as promiscuous defaecation, associated with poverty and ignorance, keeps soil contamination high. Nightsoil (faecal waste) should not be used to fertilise gardens or vegetable crops. Several countries have successfully controlled infections in human populations, predominantly by using periodic mass treatment programs and encouraging people to wear shoes and use latrines through public education campaigns. Considerable effort has also been made in developing vaccines against hookworm infections, particularly using secreted larval proteins to prevent infections or by inhibiting adult gut enzymes (aspartic proteases, cysteine proteases, haemoglobinases) to reduce worm burdens. Variable results have been obtained, although several formulations are currently undergoing clinical trials.

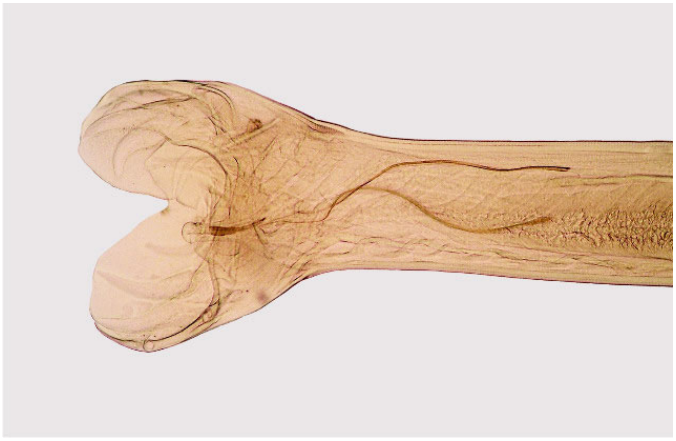

Necator
intestines
(dermatitis, pneumonitis,
enteritis, anaemia,
growth retardation)
head
Definitive Hosts
(mainly primates)
pulmonary
migration
adult female
(~ 11 mm)
adult male
(~ 9 mm)
male tail
L3
penetrate
skin
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 600 µm)
external
environment
eggs
(~ 70 µm)
rhabditiform first- and
second-stage larvae
(L1, L2) (~ 400 µm)
geo-helminth
(soil transmission)



Necator adult worms



Necator adult worms



Necator adult worm, male bursa



Necator adult worm, head

Bunostomum
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the ancylostomatids (hookworms) which are characterised by their bent mouths, the anterior ends being bent dorsally. They have a well-developed buccal capsule with cutting plates or teeth, and are voracious blood-feeders in the small intestines of mammals, esp. humans and companion animals. They have direct life-cycles, involving a geo-helminth phase. Eggs voided with faeces hatch releasing free-living rhabditiform larvae which subsequently develop into infective filariform L3 that are ingested or actively penetrate the skin of their hosts. Larvae undergo pulmonary migration through the lungs (sometimes causing pneumonitis) before developing into blood-feeding adults in the small intestines. Some larvae may also undergo arrested development (hypobiosis) and vertical transmission may occur (transplacental and transmammary). *Bunostomum* spp. cause mild-severe hookworm disease (anaemia and diarrhoea) in cattle and sheep worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Ancylostomatidae (hookworms, buccal capsule bent dorsally, armed with teeth/cutting plates)
Genus:	*Bunostomum* (parasitic in small intestines of ruminants)
Species:	various species cause anaemia/diarrhoea in cattle and sheep

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb,	artiodactyls, birds	ingestion of L3	50

	thin-shelled eggs			
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Hookworms are characterised by their dorsally bent heads with prominent buccal capsules containing paired ventral lancets as well as teeth, cutting plates or lateral jaw-like structures. They are parasitic in the small intestines of mammals and reptiles and infections are acquired by the ingestion or skin penetration of infective L3 followed by tracheal migration. Two families are recognised: Ancylostomatidae (dorsally deviated head, buccal capsule usually armed with teeth or cutting plates, 20 genera in intestines of mammals); and Diaphanocephalidae (anteriorly directed head, buccal capsule forming 2 lateral jaw-like structures, 2 genera in intestines of reptiles). The family Ancylostomatidae contains 2 subfamilies: Ancylostomatinae (buccal capsule subglobular, with dorsal gutter, bursa with short dorsal ray, gubernaculum present, posterior vulva, female tail with terminal spine, most in carnivores); and Bunostominae (buccal capsule subglobular, with tooth-like dorsal cone, bursa with long dorsal ray, gubernaculum absent, anterior vulva, female tail without terminal spine, most in herbivores). Ancylostomatid genera of particular medical and/or veterinary significance are tabulated below.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**	**Transmission**
Bunostominae						
Bunostomum	9	artiodactyls, proboscidea	small intestines	10-30 mm long, buccal capsule with ventral cutting plate and 1-2 pairs subventral teeth, larval pulmonary migration, hypobiosis	79-117 x 40-70 µm, ovoid, thin-shelled	oral, transdermal, transplacental, transmammary
Gaigeria	1	artiodactyls	small intestines	10-45 mm long, buccal capsule with pair ventral cutting plates, elongate lancets and teeth, larval pulmonary migration	108-115 x58-61 µm, ellipsoidal, thin-shelled	transdermal
Necator	7	primates, artiodactyls	small intestines	7-11 mm long, buccal capsule with cutting plates, larval pulmonary migration	55-77 x 35-42 µm, ovoid, thin-shelled	oral, transdermal
Ancylostominae						
Ancylostoma	32	carnivores, primates	small intestines	5-25 mm long, bent heads, buccal capsule with ventral lancets and fused teeth, larval pulmonary migration, hypobiosis	55-95 x 32-58 µm, ellipsoidal, thin-shelled	oral, transdermal, transplacental, transmammary

Globocephalus	18	artiodactyls, rodents, primates	caecum, small intestines	3-9 mm long, large buccal capsule without cutting plates or teeth, larval pulmonary migration	60-75 x 35-41 µm, ovoid, thin-shelled	oral, transdermal
Uncinaria	22	carnivores	small intestines	3-15 mm long, well-developed buccal capsule with pair of ventral cutting plates, no pulmonary migration	65-98 x 35-58 µm, ovoid, thin-shelled	oral (direct or via PH), rarely transdermal

The subfamily Bunostominae contains 12 genera classified in 2 tribes: Bunostominea containing worms with anterodorsally directed heads with pronounced dorsal inclination, oral opening with well-developed cutting plates, no buccal collar, long oesophagus (*Bunostomum* (syn. *Bustomum*, *Monodontus*), *Bathmostomum*, *Bunostomoides, Brachyclonus*, *Cameronecator*, *Gaigeria*, *Grammocephalus*, *Monodontus*, *Necator*, *Rhinoceratonema*) in elephants, rhinoceros, procyonids, ruminants, rodents, tayasuids, tapirs, and primates; and Acheilostominea containing worms with anterodorsally directed heads with slight dorsal inclination, oral opening with inconspicuous or no cutting plates, buccal collar, short oesophagus (*Acheilostoma*, *Tetragomphius*) in rodents, mustelids and procyonids. The genus *Bunostomum* comprises hookworms with globular buccal capsules with subventral lancets, large dorsal cones, males with asymmetrical dorsal rays and filiform spicules, and females with an anterior vulva. Nine species have been described from ruminants and elephants, most species being stenoxenous and found in a small range of related hosts. Infections by *Bunostomum* spp. occur worldwide, but with a patchy distribution favouring regions with warm moist climates more suitable for the development of exogenous stages in the environment. *B. phlebotomum* is a major enteric parasite of cattle (dairy and beef), while *B. trigonocephalum* mainly infects sheep and goats, although cross-infections can occur. Infections may cause severe disease involving anaemia, hypoproteinaemia and diarrhoea, even death. Infections in abnormal hosts (such as guinea pigs, mice and occasionally humans) usually lead to incomplete worm development, although migrating larvae may still cause transient cutaneous lesions (larval migrans).

***Bunostomum* species**	**Definitive hosts**	**Location [Clinical signs]**	**Distribution**
B. bhavanagarense	Artiodactyla: bovid (blackbuck)		Asia
B. brevispiculum	Proboscidea: elephantid (African elephant)		Africa
B. cobi (syn. *B. dentatum*)	Artiodactyla: bovid (kafue lechwe, red lechwe, puku, waterbuck, common reedbuck)		Africa
B. floridanus	Rodentia: cricetid (hispid cotton rat)		Americas
B. foliatum	Proboscidea: elephantid (Indian elephant)		Asia
B. hamatum	Proboscidea: elephantid (African elephant)		Africa
B. phlebotomum (syn. *B. longecirratum*, *radiatum, Monodontus*) (cattle hookworm)	Artiodactyla: bovid (cattle, zebu, Bali cattle, water buffalo, yak, Indian yak, European bison, sheep, argali, blue wildebeest), cervid (roe deer, fallow deer, Reeve's muntjac, moose); Lagomorpha: leporid (Indian hare) [plus larval infections in Primates: hominid (human)]	small intestines [anaemia, occasionally oedema, diarrhoea, pruritus]	worldwide
B. sangeri	Proboscidea: elephantid (Asian elephant)		Asia
B. trigonocephalum (syn. *B. kashinathi, Monodontus*) (grassveld hookworm)	Artiodactyla: bovid (sheep, argali, goat, mouflon, chamois, Iberian ibex, cattle, zebu, European bison, impala, blackbuck, blue wildebeest, dorcas gazelle, Arabian oryx), cervid (fallow deer, red deer, roe deer, sambar deer, moose), camelid (camel); Carnivora: canid (dog); Rodentia: caviid (guinea pig), murid (mouse) [plus larval infections in Primates: hominid (human)]	small intestines [anaemia, occasionally oedema, diarrhoea]	worldwide

Parasite morphology: *Bunostomum* hookworms form 3 different stages in their developmental cycles: eggs; larvae (4 successive stages designated L1-L4); and adult worms (sexually dimorphic males and females). Eggs are asymmetrically oval-elliptical in shape (one side being somewhat flattened) measuring 79-117 x 40-70 µm. They are thin-shelled and contain a morula at the 4-8 cell (blastomere) stage of development when laid. L1 and L2 are free-living (preparasitic) stages with elongate tubular bodies, truncated heads, short buccal capsules with cutting plates, rhabditiform (double-bulbed) oesophagi, and hair-like tails. L1 measure from 360-500 µm in length, while L2 are slightly larger measuring from 360-600 µm in length. Infective L3 are larger still, measuring 450-700 µm in length, but they are ensheathed (encased in L2 cuticle) and have bullet-shaped heads, funnel-shaped buccal capsules, long strongyliform oesophagi with a prominent caudal bulb, intestines comprising 16 cells, and sharply-tapering tails encased in short tail sheath extensions (58-115 µm) that are filamentous for the last 50% of their length. L4 are transient parasitic stages that are developing adult characteristics, particularly with respect to head structures and genitalia. Adult hookworms are stout white-grey worms 10-30 mm long with typically hooked heads and buccal capsules opening anterodorsally. The buccal capsule is large and subglobular, and contains 2 semilunar chitinous cutting plates on the anterior rim, and a large internal tooth-like dorsal cone that

contains the duct of the oesophageal gland (in members of the sister subfamily, the ancylostomins, the duct is contained in an elongate dorsal groove). Dorsal teeth are absent but there are 1-2 pairs of small subventral lancets at the base of the buccal capsule. Adult male worms are smaller than females (10-17 mm cf. 16-30 mm) and are readily identified by their well-developed caudal bursa (copulatory clasping organ). The bursa consists of 2 lateral lobes supported by 6 rays formed by muscular elements following nerve channels to terminal papillae (with the externolateral rays arising at different levels from main stem, and the anterolateral rays diverging from other lateral rays) and a dorsal lobe supported by a long asymmetrical dorsal ray (with 4 or 6 terminal branches). Mature males do not possess a gubernaculum (present in the ancylostomins) but have 2 conspicuous spicules, both either short and twisted (e.g. *B. trigonocephalum*) or long and slender (e.g. *B. phlebotomum*). Mature females are didelphic with 2 ovaries and uteri connected to a common vulva located in the anterior half of the body (posterior half in ancylostomins), and their tails do not have a terminal spine (present in ancylostomins). Females are oviparous producing strongyle-type eggs which are passed into the gut lumen of their hosts.

Site of infection: Adult hookworms infect the mucosa of the small intestines, mainly the duodenum and anterior jejunum, while earlier larval stages migrate through host tissues to develop in the lungs (process called pulmonary or tracheal migration). Free-living preparasitic larval stages are found developing in host faeces in the external environment.

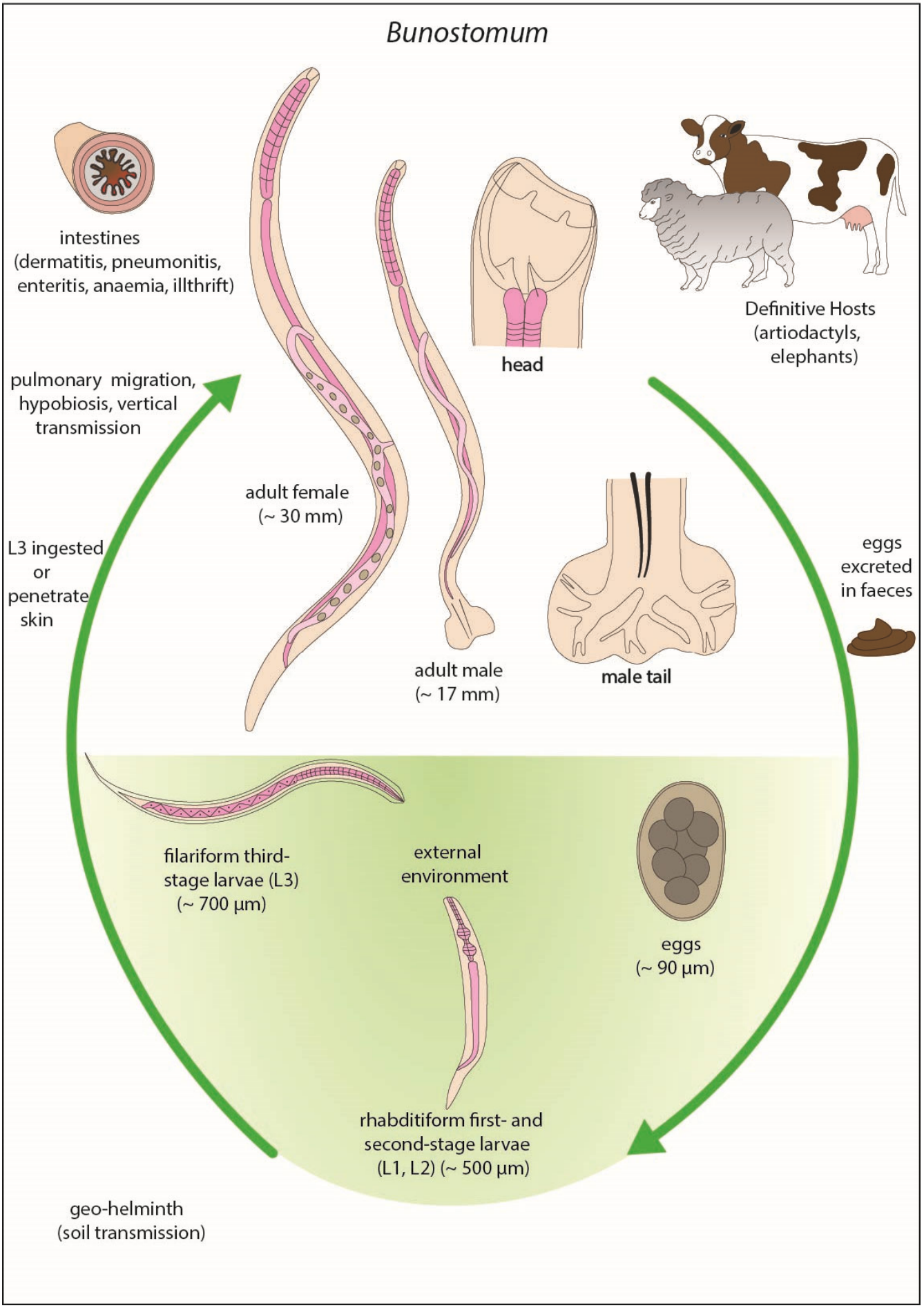
Pathogenesis: Light infections are usually asymptomatic or subclinical, but heavier infections (involving 250 or more worms) may cause significant morbidity and even mortality in domestic animals. The severity of disease depends on a range of factors, including parasite pathogenicity (some species are more virulent), the intensity of infection (number of parasites), host susceptibility (young individuals of permissive species are most at risk), and the stage of infection (peracute, acute or chronic). Three types of disease may be caused during the course of infection: infective larvae penetrating the skin may cause transient cutaneous larval migrans; larvae migrating through the lungs may cause acute pneumonitis; and adult worms feeding in the small intestines may cause chronic manifestations, notably anaemia, enteritis, diarrhoea and illthrift. In normal (permissive) hosts (such as sheep and cattle), penetration and migration of infective L3 through the skin occurs rapidly (within 45 minutes) and often does not produce significant lesions even though the larvae cause traumatic tissue damage and provoke inflammatory responses. However, in some individuals, particularly those sensitized by previous exposure, the larvae may cause dermatitis with pruritus, usually involving the limbs and provoking foot-stamping. In unusual or abnormal (non-permissive) hosts (including humans and laboratory rodents), the infective L3 may persist in the skin for longer periods leading to cutaneous larval migrans with local dermatitis with cellular infiltrates, oedema and hyperaemia. Larvae subsequently undergoing pulmonary migration in normal hosts often do not produce clinical signs, although they may cause small haemorrhages and pneumonitis when they penetrate into alveolar air-spaces. In contrast, larvae reaching the lungs in abnormal hosts generally do not complete their development but may persist longer causing acute local inflammation with cellular infiltrates, epithelial desquamation, and alveolar consolidation. The most common signs associated with infections, particularly in normal hosts, arise when subadult and adult worms attach to the small intestinal mucosa and feed on tissue plugs and blood using their large buccal capsules and cutting plates. Worms frequently detach to move to new feeding sites leaving behind punctate haemorrhagic lesions, with blood, fluid and protein loss contributing to anaemia (progressing to iron deficiency), oedema (ascites and submandibular bottle-jaw), and hypoproteinaemia (esp. hypoalbuminaemia). The mucosa becomes swollen and covered in mucus with villous atrophy and fusion leading to maldigestion, malabsorption, anorexia, cachexia, alternating diarrhoea (sometimes bloody) and constipation, weight loss, emaciation, collapse and even death. Previous infection has been shown to elicit some protective immunity, so older livestock may be refractory to re-infection although worms may be present asymptomatically (concomitant immunity). More severe infections may also occur in stressed hosts experiencing poor nutrition, sometimes coupled with pregnancy.

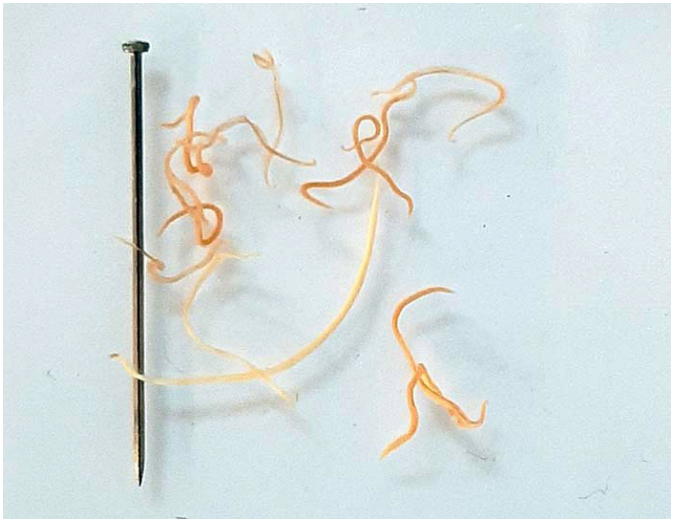
Developmental cycle and mode of transmission: These hookworms have direct monoxenous life-cycles, with hosts becoming infected by the oral ingestion or transdermal penetration of infective larvae contaminating the external environment. Gravid female worms lay eggs (up to 600-1,200 day depending on season) which are excreted with host faeces. The eggs embryonate and hatch releasing free-living (preparasitic) rhabditiform L1 which feed on bacteria in the faecal material. These larvae moult to form similar rhabditiform L2 which also feed on bacteria before they moult forming strongyliform L3 which are ensheathed (encased in L2 cuticle) and are unable to feed. The time taken for embryonation and larval development depends on prevailing environmental conditions, with L3 being formed after several days in warm moist conditions. Development takes longer in cooler conditions but the larvae are highly susceptible to desiccation and cold (< 10°C) conditions. Unlike other hookworms, *Bunostomum* L3 remain in faecal material (surviving for 5-14 days) and do not climb vegetation. Definitive hosts become infected mainly when infective L3 contact and penetrate the skin (percutaneous or transdermal transmission), although infections can sometimes occur when L3 are ingested (oral transmission). Ingested L3 exsheath in the gut and then undergo 2 moults (without any extra-intestinal migration) to form adults which mature and mate producing eggs after 7-10 weeks. However, L3 penetrating the skin undertake a pulmonary migration moving to the lungs via the circulation and possibly the lymphatics. Here, they invade the alveolar air-spaces and moult to L4 which ascend the mucociliary escalator to the trachea to be swallowed reaching the small intestines in 10-12 days. L4 moult to subadult stages (sometimes designated L5) which mature to adults that begin egg production 5-6 weeks after infection. Adult worms may survive in the intestines for 1-2 years. Aberrant migrating larvae are also thought to facilitate transmammary (transcolostral) infections in some hosts. Infections are more prevalent in temperate and subtropical regions supporting wet or habitually moist pastures, particularly in animals which regularly camp at particular sites over winter. Many infections also demonstrate seasonal

transmission coincident with the first rains after the dry season (although desiccation during the dry reduces pasture larval survival, high worm burdens may develop in animals at the end of the dry, presumably due to maturation of hypobiotic larvae, with peak egg production occurring early in the rainy season).

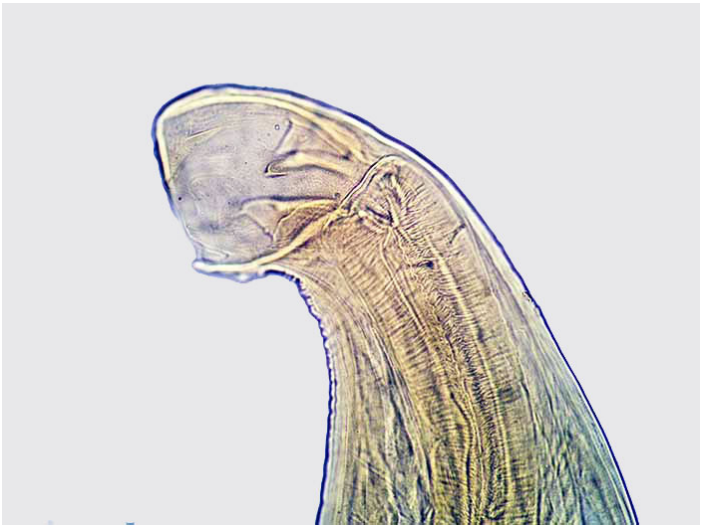
Differential diagnosis: Infections are rarely diagnosed on the basis of symptomatology as most clinical signs (anaemia, diarrhoea) are non-specific (not pathognomic) and may be attributable to other conditions (including fasciolosis in temperate regions and haemonchosis in tropical regions). Coprological examinations may be used to detect and quantitate worm eggs in faecal samples, usually following their concentration by sedimentation in water and floatation in saturated sugar or heavy metal salt solutions, However, faecal egg counts may fluctuate as egg production by female worms is irregular, and clinical disease may be present in some hosts when few eggs are being produced (especially for *B. trigonocephalum* infections). *Bunostomum* eggs are also similar in appearance to those of several trichostrongyles, but are more bluntly rounded than those of *Haemonchus*, and often have sticky eggshells with adherent debris. Faecal samples may be subject to coproculture for several days to harvest L3 which can tentatively be identified by their morphological characteristics (short ensheathed L3 with 16 intestinal cells and short filamentous tails). Adult worms may be detected and quantitated in post-mortem samples of the small intestinal mucosa. Total worm counts of 100-300 worms have been found to cause clinical disease in sheep, goats and cattle, and higher worm burdens have been associated with fatalities. Modern molecular biological techniques have been used to characterize parasite species, examine drug resistance and determine phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (internal transcribed spacers 1 and 2 of ribosomal RNA, beta-tubulin isotype 1) or mitochondrial genomes.

Treatment and control: Clinical infections have been treated effectively using several anthelmintic drugs, including benzimidazoles (albendazole, oxfendazole, fenbendazole, thiabendazole), macrocyclic lactones (ivermectin, doramectin, moxidectin, eprinomectin), imidazothiazoles (levamisole) and tetrahydropyrimidines (morantel). Cutaneous larval migrans in humans has often responded well to treatment with similar anthelmintics, and some success has been reported freezing superficial skin lesions with ethylene chloride to kill migrating larvae. Regrettably, most anthelmintics do not have any persistent residual activity, so hosts may be rapidly re-infected when returned to contaminated environments. In veterinary medicine, it has become standard practice to immediately move treated livestock to clean (ungrazed or spelled) pastures, and/or to repeat treatments at regular intervals. Young animals are usually treated before and after weaning, and dietary supplementation should be considered when levels of nutrition are poor (disease is worse in malnourished hosts). To avoid the emergence of drug resistance in parasite populations, it is recommended that strategic dosing be employed on a needs basis, and that drug classes be rotated on a cyclic basis. Various management strategies can be introduced at the farm level to reduce transmission rates by limiting environmental contamination by worm eggs and larvae, either through improved sanitation and hygiene (regularly clean pens, remove faeces particularly from feeding and resting areas, provide dry bedding), stock management (separate cohorts, cyclic or rotational grazing, mixed grazing, avoid overstocking, quarantine new livestock) and pasture management (drain wet pastures, compact soil around water troughs or salt liberally, and spell pastures over hot dry periods).

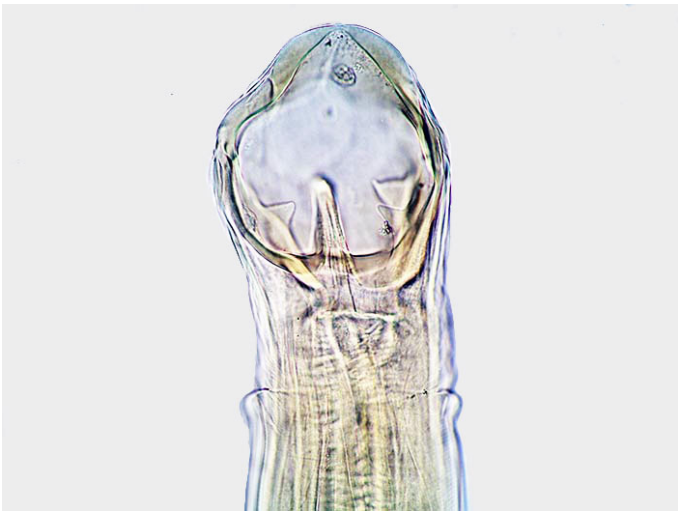

Bunostomum
intestines
(dermatitis, pneumonitis,
enteritis, anaemia, illthrift)
head
Definitive Hosts
(artiodactyls,
elephants)
pulmonary migration,
hypobiosis, vertical
transmission
adult female
(~ 30 mm)
L3 ingested
or
penetrate
skin
adult male
(~ 17 mm)
male tail
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 700 µm)
external
environment
eggs
(~ 90 µm)
rhabditiform first- and
second-stage larvae
(L1, L2) (~ 500 µm)
geo-helminth
(soil transmission)



Bunostomum adult worms



Bunostomum adult worm, head, lateral



Bunostomum adult worm, head, ventral

Gaigeria
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including the ancylostomatids (hookworms) which are characterised by their bent mouths, the anterior ends being bent dorsally. They have a well-developed buccal capsule with cutting plates or teeth, and are voracious blood-feeders in the small intestines of mammals, esp. humans and companion animals. They have direct life-cycles, involving a geo-helminth phase. Eggs voided with faeces hatch releasing free-living rhabditiform larvae which subsequently develop into infective filariform L3 that are ingested or actively penetrate the skin of their hosts. Larvae undergo pulmonary migration through the lungs (sometimes causing pneumonitis) before developing into blood-feeding adults in the small intestines. *Gaigeria* spp. cause mild-severe hookworm disease (anaemia) in sheep in southern continents, except Australia.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Ancylostomatidae (hookworms, buccal capsule bent dorsally, armed with teeth/cutting plates)
Genus:	*Gaigeria* (parasitic in small intestines of sheep)
Species:	*G. pachyscelis* causes anaemia in sheep

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50

Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Hookworms are characterised by their dorsally bent heads with prominent buccal capsules containing paired ventral lancets as well as teeth, cutting plates or lateral jaw-like structures. They are parasitic in the small intestines of mammals and reptiles and infections are acquired by the ingestion or skin penetration of infective L3 followed by tracheal migration. Two families are recognised: Ancylostomatidae (dorsally deviated head, buccal capsule usually armed with teeth or cutting plates, 20 genera in intestines of mammals); and Diaphanocephalidae (anteriorly directed head, buccal capsule forming 2 lateral jaw-like structures, 2 genera in intestines of reptiles). The family Ancylostomatidae contains 2 subfamilies: Ancylostomatinae (buccal capsule subglobular, with dorsal gutter, bursa with short dorsal ray, gubernaculum present, posterior vulva, female tail with terminal spine, most in carnivores); and Bunostominae (buccal capsule subglobular, with tooth-like dorsal cone, bursa with long dorsal ray, gubernaculum absent, anterior vulva, female tail without terminal spine, most in herbivores). Ancylostomatid genera of particular medical and/or veterinary significance are tabulated below.

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm eggs**	**Transmission**
Bunostominae						
Gaigeria	1	artiodactyls	small intestines	10-45 mm long, buccal capsule with pair ventral cutting plates, elongate lancets and teeth, larval pulmonary migration	108-115 x58-61 µm, ellipsoidal, thin-shelled	transdermal
Bunostomum	9	artiodactyls, proboscidea	small intestines	10-30 mm long, buccal capsule with ventral cutting plate and 1-2 pairs subventral teeth, larval pulmonary migration, hypobiosis	79-117 x 40-70 µm, ovoid, thin-shelled	oral, transdermal, transplacental, transmammary
Necator	7	primates, artiodactyls	small intestines	7-11 mm long, buccal capsule with cutting plates, larval pulmonary migration	55-77 x 35-42 µm, ovoid, thin-shelled	oral, transdermal
Ancylostominae						
Ancylostoma	32	carnivores, primates	small intestines	5-25 mm long, bent heads, buccal capsule with ventral lancets and fused teeth, larval pulmonary migration, hypobiosis	55-95 x 32-58 µm, ellipsoidal, thin-shelled	oral, transdermal, transplacental, transmammary
Globocephalus	18	artiodactyls, rodents,	caecum, small	3-9 mm long, large buccal capsule without cutting plates or	60-75 x 35-41 µm, ovoid,	oral, transdermal

		primates	intestines	teeth, larval pulmonary migration	thin-shelled	
Uncinaria	22	carnivores	small intestines	3-15 mm long, well-developed buccal capsule with pair of ventral cutting plates, no pulmonary migration	65-98 x 35-58 µm, ovoid, thin-shelled	oral (direct or via PH), rarely transdermal

The subfamily Bunostominae contains 12 genera classified in 2 tribes: Bunostominea containing worms with anterodorsally directed heads with pronounced dorsal inclination, oral opening with well-developed cutting plates, no buccal collar, long oesophagus (*Bunostomum* (syn. *Bustomum*, *Monodontus*), *Bathmostomum*, *Bunostomoides, Brachyclonus*, *Cameronecator*, *Gaigeria*, *Grammocephalus*, *Monodontus*, *Necator*, *Rhinoceratonema*) in elephants, rhinoceros, procyonids, ruminants, rodents, tayasuids, tapirs, and primates; and Acheilostominea containing worms with anterodorsally directed heads with slight dorsal inclination, oral opening with inconspicuous or no cutting plates, buccal collar, short oesophagus (*Acheilostoma*, *Tetragomphius*) in rodents, mustelids and procyonids. The genus *Gaigeria* is monotypic and contains a single species *G. pachyscelis* infecting ruminants in Africa, India and Indonesia. Adult worms have exceptionally large dorsal bursal lobes, the dorsal cone is not supported by subdorsal plates and the female ovejectors have short vestibula. This species is a voracious bloodsucker and is probably the most pathogenic hookworm.

Parasite species	Hosts	Location [Clinical signs]	Distribution
Gaigeria pachyscelis (syn. *G. ullissiponensis*)	Artiodactyla: bovid (zebu, sheep, goat, blue wildebeest, grey duiker, nyala, impala, nilgai, blackbuck, steenbok), suid (African bush pig); Rodentia: caviid (guinea pig), murid (mouse)	small intestines [anaemia]	Africa, Americas, Asia

Parasite morphology: *Gaigeria* forms 3 different types of morphological stages in its developmental cycle: eggs; larvae (4 consecutive stages designated L1-L4); and adult worms. The eggs are thin-shelled ellipsoidal stages measuring 108-115 x 58-61 µm and contain a developing embryo (morula) at the 4-8 cell (blastomere) stage of development. L1 and L2 are free-living (pre-parasitic) stages measuring from 350-600 µm in length that have rounded heads, rhabditiform (double-bulbed) oesophagi, and tapering tails. L3 are ensheathed stages (still encased in the L2 cuticle) measuring from 630-720 µm in length, including a long sheath tail extension (128-135 µm) which is filamentous for the last 50% of its length. Infective L3 have a bullet-shaped head, strongyliform oesophagus with a prominent caudal bulb, intestines comprising 16 cells, and a sharply-tapering tail. L4 are transient parasitic stages that have begun to show adult worm characteristics, particularly with regard to mouth and genitalia (male bursa and female vulva). Adults are small white hookworms measuring from 10-45 mm long with anterodorsally directed heads with a pronounced dorsal inclination (hook). They have large subglobular to funnel-shaped buccal capsules armed with pair of well-developed ventral cutting plates around the oval mouth and a pair of elongate subventral lancets (each with several cusps). The buccal capsule also contains a short dorsal cone (not supported by subdorsal plates) containing the duct of the dorsal oesophageal gland (in ancylostomins, the duct is contained within a dorsal groove). Adult worms are sexually dimorphic, with males being smaller than females (10-20 x 0.5-0.6 mm cf. 17-45 x 0.6-0.8 mm). Mature males have a well-developed copulatory bursa consisting of 2 short lateral lobes joined together ventrally, each supported by 6 rays (formed by muscular elements following nerve channels to terminal papillae) arranged such that the short anterolateral rays are separated from the other laterals, and the externodorsal rays arise from the main stem of the dorsal ray) and an exceptionally large symmetrical dorsal lobe (supported by a dorsal ray which bifurcates with each short branch terminating in small digitations). Males do not possess a gubernaculum but they have 2 elongate equal spicules (1.2-1.3 mm) with recurved (kinked or barbed) tips. Mature females are didelphic with 2 ovaries and uteri connected by ovejectors with short vestibula to a common vulva located anterior to the midbody. Females have bluntly rounded tails that do not have terminal spines.

Site of infection: Adult worms infect the small intestines (mainly the duodenum) of their herbivorous hosts, while earlier larval developmental stages undergo a pulmonary migration through the lungs before settling in the gut. Free-living larval stages contaminate the external environment after developing from hatched eggs.

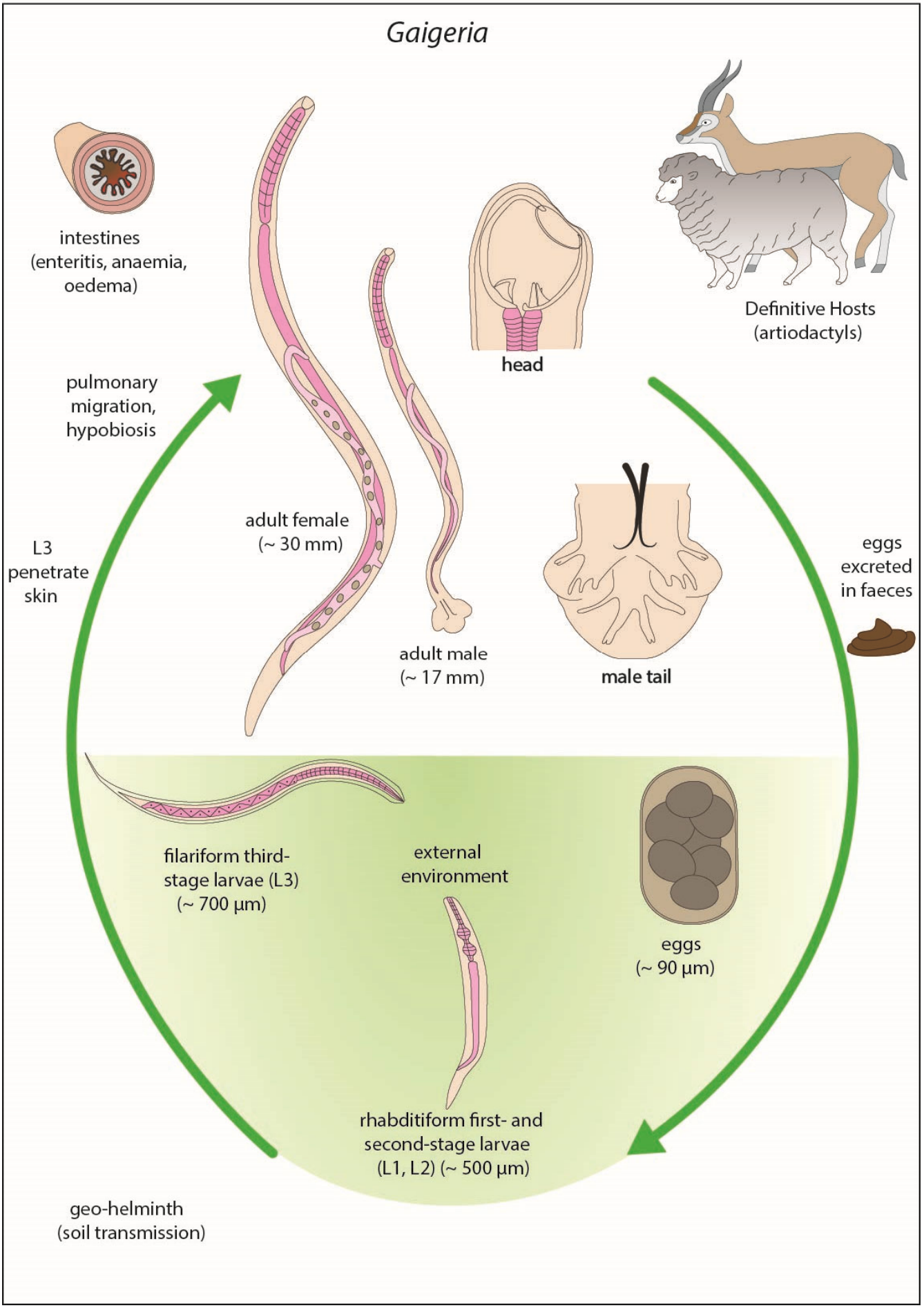
Pathogenesis: The species *G. pachyscelis* has a reputation as a voracious bloodsucker and some consider it to be the most pathogenic hookworm. Infections with < 30 worms have been associated with clinical disease in small ruminants, and infections with > 100 worms may cause death within several weeks. Adult worms attach to the intestinal mucosa and feed on host tissues and blood with their large buccal capsules and cutting plates. Worms frequently detach and move to new feeding sites leaving behind haemorrhagic lesions in a swollen and inflamed mucosa covered with mucus. Blood loss causes a progressive anaemia and disrupted mucosal function contributes to oedema (ascites and submandibular bottle-jaw), maldigestion, hypoproteinaemia, intermittent

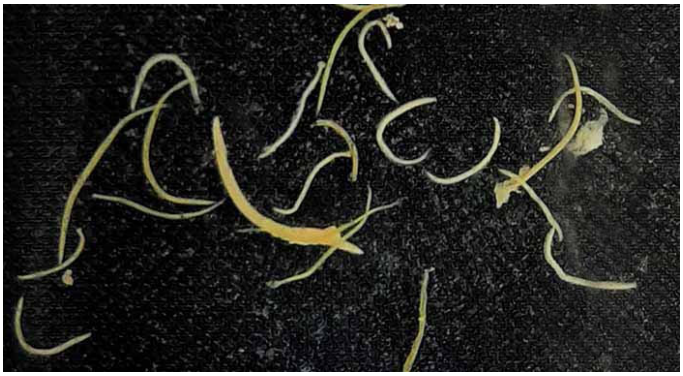
diarrhoea, cachexia, rapid loss of condition, emaciation, weakness and death. Young animals are most susceptible to clinical disease, while prior exposure may provide some protective immunity to surviving adult animals.

Developmental cycle and mode of transmission: Like other hookworms, these parasites have direct monoxenous life-cycles whereby hosts become infected by the percutaneous (transdermal) penetration of infective L3 from the environment. Female worms lay eggs (up to 600-800 per day) which are excreted with host faeces. The eggs hatch under suitable warm and moist conditions releasing free-living rhabditiform L1 which moult to similar L2. These stages then moult to form strongyliform L3 which retain the L2 cuticle as a protective sheath. Nevertheless, these L3 are highly susceptible to desiccation and do not survive long without adequate moisture. Definitive hosts become infected when infective L3 come into contact with their skin which they quickly penetrate invading dermal tissues. The larvae migrate to the lungs via the circulation, penetrate into alveolar air-spaces and moult to L4 which ascend the mucociliary escalator to the trachea where they are swallowed and carried to the gut. They moult in the small intestines to young adults which feed and develop into mature adults over several weeks. The prepatent period (time from infection to first excretion of eggs) ranges from 56-70 days. Transplacental and transmammary transmission has not been reported. High worm burdens are sometimes found in tropical regions at the end of the dry season, apparently due to maturation of hypobiotic larvae. Infections are more common in tropical and subtropical regions where pastures may be moist for most of the year, while heavy infections are uncommon in temperate regions with hot summers.

Differential diagnosis: While infections may be suspected on the basis of clinical signs (severe anaemia), other aetiological agents may be responsible (including other hookworms and some trichostrongyles). Infections are conventionally diagnosed by the detection of the large characteristic eggs in faecal samples, usually following their concentration by sedimentation in water and floatation in saturated sugar or heavy metal salt solutions. Coprocultures may also be used to harvest L3 which can tentatively be identified by their morphological characteristics (short ensheathed L3 with 16 intestinal cells and long filamentous tails), but incubation times of up to a week are often required. Infections may also be diagnosed by the detection of adult worms in gut samples collected post-mortem from dead or sacrificed animals. Several immunoserological tests (mostly enzyme immunoassays) have been developed to detect specific host antibodies against adult worm antigens, but they have varied in their sensitivity and specificity due to some cross-reactivity with other nematodes.

Treatment and control: A range of anthelmintic drugs have been used to treat clinical infections, including benzimidazoles (albendazole, oxfendazole, fenbendazole, mebendazole), macrocyclic lactones (ivermectin, doramectin, moxidectin), and imidazothiazoles (levamisole). Treatment is usually repeated on a regular basis to stop hosts becoming re-infected, although strategic drenching before and after weaning, and then on a needs-basis, have been recommended to combat the emergence of drug resistance. A variety of farm management strategies may be used to minimise transmission between livestock, mostly by reducing environmental contamination by worm eggs and larvae (remove faeces from holding areas, regularly clean pens, provide dry bedding, drain wet pastures, spell pastures over hot dry periods) and managing grazing (separate young and adult cohorts, cyclic or rotational grazing, mixed grazing, avoid overstocking, quarantine new livestock). Preliminary studies on vaccine development using irradiated larvae demonstrated variable protection in some animals as evidenced by reduced worm burdens and less severe disease following pathogenic challenge.


Gaigeria
intestines
(enteritis, anaemia,
oedema)
Definitive Hosts
(artiodactyls)
head
pulmonary
migration,
hypobiosis
adult female
(~ 30 mm)
adult male
(~ 17 mm)
male tail
L3
penetrate
skin
eggs
excreted
in faeces
filariform third-
stage larvae (L3)
(~ 700 µm)
external
environment
eggs
(~ 90 µm)
rhabditiform first- and
second-stage larvae
(L1, L2) (~ 500 µm)
geo-helminth
(soil transmission)



Gaigeria adult worm

Dictyocaulus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Unlike most lungworms, dictyocaulids have direct life-cycles where adults in the lungs lay eggs or larvae which are swallowed and passed in faeces as L1. They develop to L3 in the external environment and are ingested by hosts where they exsheath, penetrate the intestinal wall and migrate via the lymphatic-vascular systems to the lungs. *Dictyocaulus* infections have been associated with respiratory clinical signs in many ruminants, sometimes progressing to pneumonia.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Dictylocaulidae (lungworms, direct cycle, infection by ingestion of L3)
Genus:	*Dictyocaulus* (parasitic in respiratory tract of ruminants)
Species:	various species cause pneumonia in ruminants (incl. husk in cattle)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod His
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Metastrongylina (lungworms)				
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Metastrongylidae	small buccal capsule, 2 trilobed lips,	suids	ingestion of IH carrying	1

(lungworms)	bursa with reduced dorsal lobe		L3	
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 5 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials).

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Larvae**
Dictylocaulidae					
Dictylocaulus (lungworms)	13	ruminants, equids	respiratory tract	25-100 mm long, small buccal capsules, male bursa with large lobes, short stout spicules, direct cycle, eggs laid in lungs swallowed, L1 passed in faeces	larvae 290-450 µm, anterior knob, short tail spike

The family Dictyocaulidae contains 2 subfamilies: Mertensinematinae containing 3 genera (*Mertensinema*, *Borrellostrongylus* (syn. *Parabatrachostrongylus*) and *Zygocaulus*) parasitic in the digestive tracts of amphibians and reptiles; and Dictyocaulinae containing 2 genera (*Dictyocaulus* (syn. *Micrurocaulus*) and *Bronchonema*) parasitic in the trachea, bronchi and bronchioles of ruminants and horses. These lungworms have direct life-cycles with infective larvae on pastures ingested by grazing herbivores. The genus *Dictyocaulus* contains some 13 species, many of which have been associated with respiratory clinical diseases in domestic and wild ruminants, particularly bovids and cervids. The lungworms vary in their host specificity, most being stenoxenous (infect closely-related hosts) but they do demonstrate strong preferences for particular host species. Most parasite species are also considered to be cosmopolitan, presumably due to the widespread translocations of domestic livestock, but they do exhibit variations in their regional distribution and seasonal abundance. For example, the species *D. viviparus* occurs mainly in cattle and buffalo in subtropical and temperate regions, mostly in moist elevated areas (forests and farms at altitudes of 1,000-2,000 m).

***Dictyocaulus* species**	**Hosts**	**Location [Clinical signs**	**Distribution**
D. africanus	Artiodactyla: bovid (hartebeest, tiang)	lungs	Africa
D. arnfieldi (equine lungworm)	Perissodactyla: equid (horse, donkey, onager), tapirid (Indian tapir)	lungs [persistent cough, nasal discharge]	worldwide
D. cameli	Artiodactyla: camelid (bactrian camel, dromedary)	lungs	worldwide
D. capreolus	Artiodactyla: cervid (moose, roe deer), bovid (cattle)	lungs	worldwide
D. cervi	Artiodactyla: cervid (red deer)	lungs	Europe
D. eckerti	Artiodactyla: cervid (roe deer, fallow deer, red deer, sika deer, reindeer, Indian hog deer, Indian muntjac, moose), bovid (cattle, muskox)	bronchi, trachea	worldwide, esp. temperate zones
D. filaria (syn. *D. sibiricus*, *unequalis*) (sheep lungworm)	Artiodactyla: bovid (sheep, mouflon, urial, chamois, argali, goat, Iberian ibex, cattle, water buffalo, American bison, kafue lechwe), cervid (fallow deer, red deer, moose), camelid (dromedary); Lagomorpha: leporid (rabbit); Rodentia: murid (mouse, gerbil)	lungs [cough, unthriftiness]	worldwide
D. hadweni	Artiodactyla: bovid (American bison), cervid (moose)	lungs	North America
D. khawi sp. inq.	Artiodactyla: suid (pig)	lungs	
D. magnus (syn. *Bronchonema*)	Artiodactyla: bovid (blesbok, springbok)	lungs	Africa
D. murmanensis	Artiodactyla: cervid (reindeer)	lungs	Eurasia
D. noerneri (possible syn. of *D. viviparus* or *D. eckerti*)	Artiodactyla: cervid (red deer, roe deer, fallow deer)	lungs	worldwide
D. pandionis	Perissodactyla: equid (onager)	lungs	Africa
D. viviparus (syn. *D. bisonis*) (bovine lungworm)	Artiodactyla: bovid (cattle, zebu, muskox, water buffalo, European bison, sheep, bighorn sheep, mouflon, argali, chamois, Tatra chamois, impala, kafue lechwe, nyala, greater kudu, southern reedbuck, common duiker, red forest duiker, grey duiker), cervid (roe deer, fallow deer, sika deer, Japan rusa, red deer, central European red deer, reindeer, Arctic reindeer, boreal woodland caribou, Rocky Mountain elk, mule deer, black-tailed deer, white-tailed deer, western moose), camelid (bactrian camel)	bronchi, trachea [cough (husk), unthriftiness]	worldwide, esp. temperate zones

Parasite morphology: *Dictyocaulus* spp. form 3 different morphological stages during their development: eggs, larvae (4 successive stages designated L1-L4); and adult worms. Freshly laid eggs are thin-shelled and ovoid measuring 75-138 x 51-90 µm, and are already embryonated containing a fully developed larva. Freed L1 are small stout stages measuring 290-450 µm with rounded heads, a club-shaped oesophagus spanning the anterior third to half of the body, intestinal cells with dark granules (usually obscuring anatomical details), and a smooth round tapering tail (*D. filaria* L1 also possess a small anterior cuticular knob and a short tail spike, while *D. arnfieldi* L1 have a terminal protuberance, and those of other lungworm genera have more elaborate tail ornamentations). L2 are free-living stages measuring up to 500-600 µm with rounded heads, granular intestinal cells and blunt conical tails. L3 differ in that they have retained the L2 cuticle as a close-fitting protective sheath measuring 400-500 µm, and they have a rounded head, an elongate flask-shaped (strongyliform) oesophagus, intestines with few granules, and a short sharply conical tail. L4 are endoparasitic stages which have developed many adult characteristics, with males measuring 800-890 µm and females 780-1,080 µm in length. Adult lungworms are slender milky-white worms 25-100 mm long with an oval oral opening surrounded by a buccal ring (triangular or reniform in shape), a small anterior buccal capsule with heavily chitinized walls, and single basal buccal

tooth. The mouth lacks lips and leaf crowns, but a few species have a small cephalic vesicle (*D. eckerti, D. cervi*). The cuticle bears numerous longitudinal ridges (synlophe) and the intestines often appear as a dark internal band. Adult worms are sexually dimorphic, with males being smaller than females (25-80 cf. 43-100 mm). Mature males have a fully developed caudal copulatory bursa which is non-lobulated and appears bell-shaped (not divided into lateral and dorsal lobes, but confluent). The supporting rays have a unique configuration in that the ventral rays are partly fused and separate from the lateral rays, and the dorsal ray is split to its base. Males have a gubernaculum, telamon and 2 short boot-shaped spicules (0.2-0.6 mm long) made of spongy porous material and bearing either large lateral alae or 1-2 small branching processes. Mature females are didelphic with 2 ovaries and uteri (opposed in amphidelphic configuration) opening into a common midbody vulva, sometimes with raised lips. Females have pointed tails and produce eggs that embryonate *in utero* to contain a fully developed L1.

Site of infection: Adult lungworms infect the respiratory tracts of their hosts, residing mainly in the bronchi, but sometimes extending down to the bronchioles or up to the trachea. Earlier developing larval stages migrate from the gut to the lungs via the circulation and/or lymphatics before invading alveolar air-spaces and forming young adults which ascend the bronchi. Free-living (preparasitic) larval stages develop on pastures and soils contaminated with host faecal material.

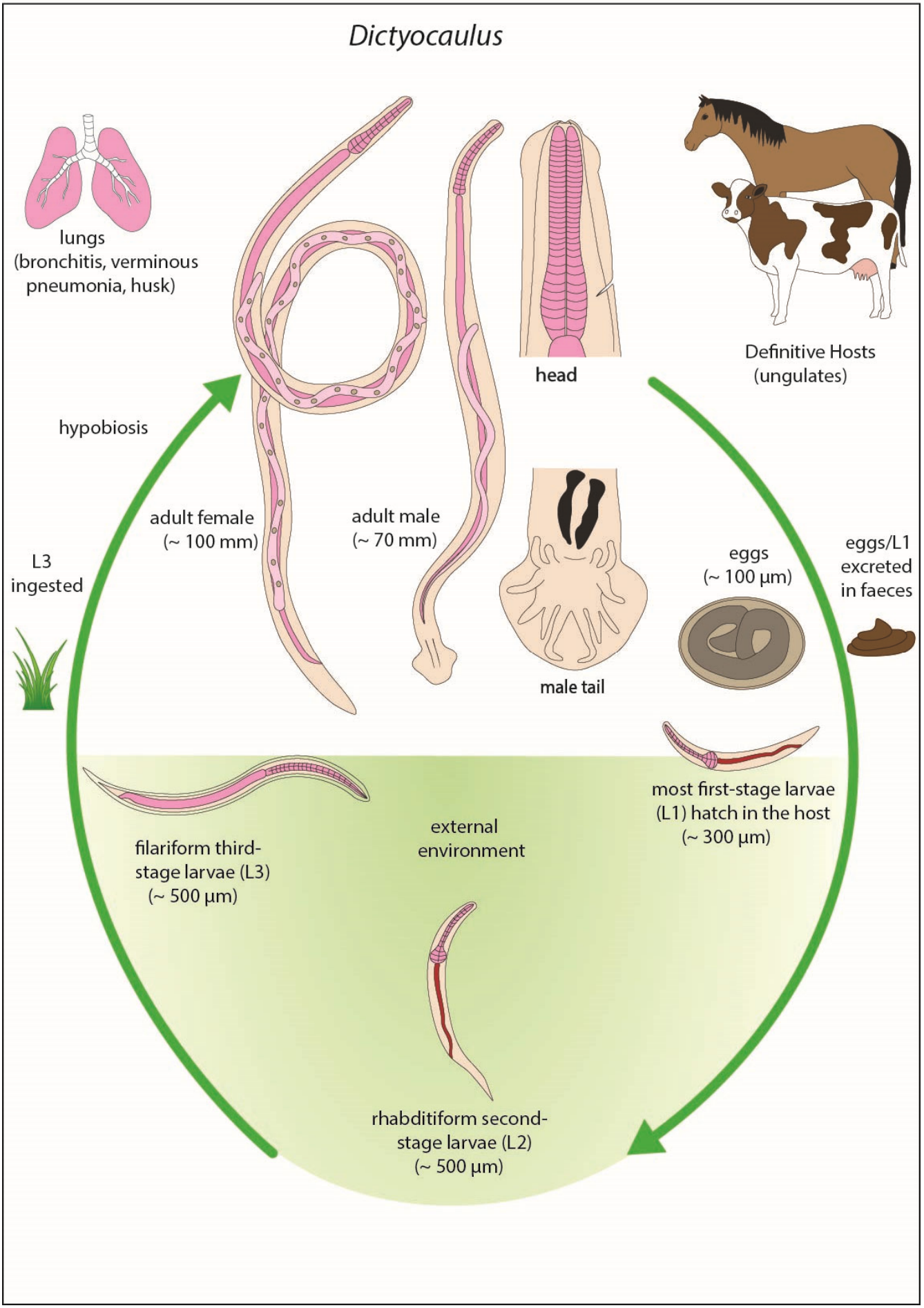
Pathogenesis: Light lungworm infections may remain asymptomatic or cause subclinical conditions possibly contributing to poor growth with associated production losses (reduced meat, milk and/or fibre production). Heavier infections, however, may cause clinical respiratory disease varying in severity depending on the parasite species (some species more virulent than others), host susceptibility (permissive species, young naive animals), and the dynamics (intensity) and kinetics (phase) of infection. The species *D. viviparus* causes parasitic bronchitis in cattle (also known as verminous pneumonia, husk, hoose or fog fever), while other species cause little or sporadic episodic disease in small ruminants and equids. The parasites live in the upper respiratory tract where developing larvae and adult worms cause traumatic damage to the mucosa exacerbated by host inflammatory responses, both leading to partial occlusion of the airways and respiratory distress typified by coughing, dyspnoea (shortness of breath, laboured breathing), hyperpnoea (rapid breathing), pulmonary oedema, emphysema and pneumonia. Hypersensitivity reactions may also develop in hosts following re-infection. Pathogenesis has been associated with 3 consecutive phases of infection: often described as the prepatent, patent and post-patent (or recovery) phases. In the first week after infection, ingested larvae penetrate the gut and migrate to the lungs but rarely cause clinical signs. However, the developing larvae cause damage to alveoli and bronchioles during the prepatent phase (from 8-25 days after infection) with inflammation (alveolitis, bronchiolitis and finally bronchitis) and cellular infiltrates (especially eosinophils) occluding airways and causing atelectasis (alveolar collapse) resulting in tachypnoea and coughing. Heavy infections may be fatal after 15 days due to respiratory failure with severe interstitial emphysema and pulmonary oedema. During the patent phase of infection (from 26-60 days after infection), disease is caused by a combination of bronchitis and pneumonia. The development of worms in the bronchi and distal trachea causes severe catarrhal bronchitis with epithelial hyperplasia, cellular infiltrates and excess mucus production (worms becoming embedded in white frothy mucus). Pneumonia develops when the congestion spreads to the lungs, particularly in areas around infected bronchi which collapse when aspirated eggs and larvae elicit dense cellular infiltrates (polymorphs, macrophages and multinucleated giant-cells) with interstitial emphysema, pulmonary oedema, alveolar epithelialization and hyaline membrane formation. Clinical signs progress from an occasional cough when exercised to a deep harsh cough at rest (with squeaks and crackles on auscultation), dyspnoea (animals adopting an 'air-hunger' disposition with mouth-breathing and outstretched necks), hyperpnoea and tachypnoea (> 60 respirations per minute), tenacious nasal discharges, excessive salivation, anorexia, unthriftiness with poor growth and weight loss, sometimes proving fatal. Most animals recover slowly in a post-patent phase (from 60-90 days after infection) when adult worms are expelled by adaptive (acquired) immune responses and inflammation subsides with improved respiration, less frequent coughing, and animals resuming weight gain. Lesions may persist in some animals, mostly involving bronchial/peribronchial fibrosis with surrounding alveolar epithelialization, sometimes leading to sporadic mortalities due either to post-patent bronchitis (proliferation of type 2 pneumocytes with emphysema and oedema associated with degenerating worms) or acute interstitial pneumonia (due to secondary bacterial infections in damaged lungs). Young animals are most susceptible to clinical infections due to their immature immune systems, while adult animals develop strong protective immune responses unless malnourished or immunocompromised. Infective larvae that have become trapped in lymph nodes generate some resistance to infection (but it rapidly weakens and only lasts around 6 months), whereas developing larvae and worms in the lungs stimulate more persistent cellular and humoral responses (lasting for 2 years or more if maintained by repeated exposure). Occasionally, the massive uptake of larvae may establish infections quicker than the immune system can respond, thus leading to the phenomenon known as re-infection syndrome. Infections are more prevalent and severe in cattle farmed under intensive conditions, particularly dairy or dairy-cross calves during their first grazing season on permanent or semipermanent pastures. Infections in deer are variable in presentation, with animals often tolerating high worm burdens until subject to nutritional or behavioural stress due to poor season or frequent herding. Animals may quickly lose condition and die with little or no warning. Infections in sheep and horses are rarely associated with disease, although some horses may develop atypical lesions involving raised circumscribed pulmonary lesions (30-50 mm in diameter) containing worms and mucopurulent discharge.

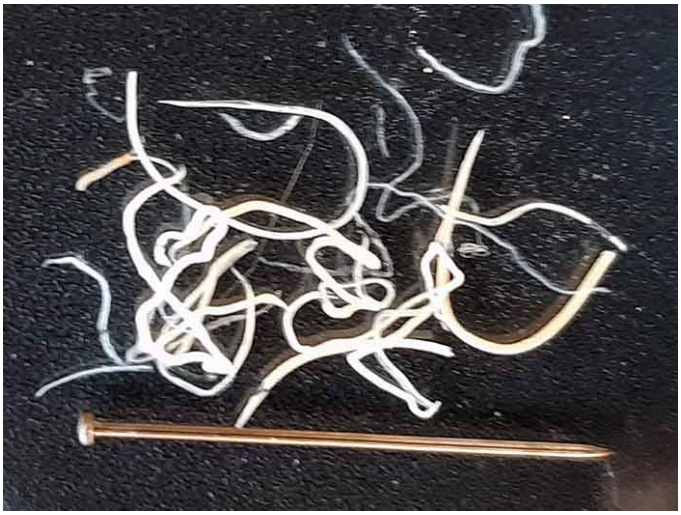
Developmental cycle and mode of transmission: *Dictyocaulus* spp. have direct monoxenous (one-host) life-cycles with faecal-oral transmission involving larval stages on pastures. Gravid female lungworms lay fully embryonated (larvated) eggs which hatch almost immediately in the airways releasing L1 which ascend the trachea to be swallowed and passed in host faeces. Some eggs may

be swallowed intact and hatch in the intestines, while the eggs of a few species (e.g. *D. arnfieldi*) pass through the gut to be shed in faeces where they hatch shortly thereafter. The free-living L1 contain numerous food granules and are not rhabditiform and do not feed on bacteria. They moult to L2 within several hours and then to ensheathed L3 in 4-7 days in favourable environmental conditions, but take longer in suboptimal conditions. L3 are sensitive to heat and desiccation and survive only days in dry conditions, but they are quite resistant to cold and can survive on moist pastures and soils for months (overwintering in temperate regions). Infective L3 migrate horizontally out of faecal material onto surrounding vegetation, with those of some species (mainly in cattle) invading the sporangia of fungi (*Pilobolus* spp.) growing in faeces to be broadcast over several metres when the sporangia explode during sporulation. Grazing animals become infected when they ingest infective L3 on contaminated vegetation. The L3 exsheath in the gut and invade the wall of the abomasum or small intestines. They enter the lymphatics and move to the mesenteric lymph nodes where they remain for 5-6 days and moult to L4 without significant growth. The L4 migrate via the thoracic duct to the anterior vena cava, the heart and then the pulmonary arteries in the lungs where they penetrate into alveoli about 1 week after infection. Here they grow markedly and move to the bronchioles where they moult several days later to young adults (sometimes designated L5). Immature adults move up to the bronchi where they mature and mate, with gravid females laying embryonated eggs. The prepatent period (time from infection to the first excretion of eggs/larvae) varies from 3-5 weeks (8-14 weeks for *D. arnfieldi* in equids), and the adult worms live only for 7-10 weeks before being expelled by host immune responses. In some instances, the prepatent period may be extended for several months when developing stages (late L4 and early L5) undergo delayed maturation (developmental arrest or hypobiosis) overwinter in lymph nodes or bronchioles before resuming development in spring. Most cattle become infected as young animals (2-5 months of age) during their first grazing season on spring pastures, especially dairy or dairy-cross calves turned out after being housed indoors over winter. Clinical infections are more prevalent in livestock in temperate regions with mild climates, high rainfall and abundant permanent grass, whereas disease occurs intermittently in tropical areas particularly after heavy rainfall when animals congregate on raised damp areas.

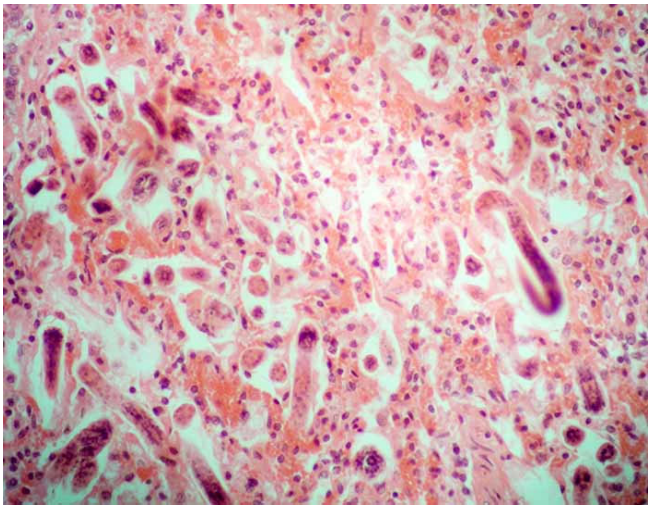
Differential diagnosis: Infections are strongly indicated on the basis of clinical signs (respiratory distress involving coughing) and relevant history (young naive animals, spring grazing, endemic region). However, the occurrence and severity of clinical signs varies considerably according to host species, being worse in cattle, sporadic in deer, and rare in small ruminants and equids. Coughing may be induced or become more pronounced in animals subject to mild exercise (e.g. chasing around a paddock) and physical examinations involving auscultation may help reveal sounds of bronchopneumonia. Infections are conventionally diagnosed by the detection of L1 in faecal samples (usually following their harvest by Baermann filtration), and sometimes by the detection of embryonated eggs in faecal concentrates (usually centrifugal floats). Counts of > 100 larvae per gram of faeces are considered significant, although larger numbers (> 1,000) may be present during patency. L1 appear as lethargic stages with rounded heads, granular intestines and bluntly pointed tails. Tracheal washes may also be examined for eggs, larvae and sometimes adults, and bronchoscopy may reveal parasites in the upper respiratory tract. At necropsy, worms may be detected in the bronchi upon dissection. Several immunoserological tests (mostly enzyme immunoassays) have been developed to detect specific host antibodies against *D. viviparus* antigens. They have generally yielded good sensitivity and specificity, with a few false positives, and seroconversion was shown to take around 4-6 weeks but only persisted for 4-7 months. Molecular biological techniques have been used to characterize parasite species following the polymerase chain reaction (PCR) amplification (including multiplex PCR and real-time PCR) of nuclear gene sequences (particularly the internal transcribed spacer 2 of ribosomal RNA).

Treatment and control: Lungworms infections may be treated with a range of anthelmintic drugs, but care should be taken to avoid excessive dosing which may interfere with the development of natural protective immunity as well as predispose towards the emergence of drug resistance. Treatment appears to be most effective against mature stages within the respiratory tree, but is less effective against developing or hypobiotic stages in host tissues. It is therefore recommended that longer-acting drugs, such as some benzimidazoles (albendazole, oxfendazole, fenbendazole) and macrocyclic lactones (ivermectin, eprinomectin, abamectin, moxidectin) be used, with follow-up treatment as required. Many animal health authorities also recommend that strategic dosing be used to prevent heavy pasture contamination and to protect young animals while they acquire protective immune responses. Treatment may initially worsen clinical signs due to parasite death and host inflammatory responses, so some supportive therapy may be required in the form of non-steroidal anti-inflammatory agents, antibiotics to ameliorate secondary bacterial pneumonia, electrolyte replacement for dehydrated animals, dietary supplementation to reduce nutritional stress, and even sheltered housing in poor weather conditions. Despite treatment, some animals may experience relapses of respiratory signs due to the severity and poor resolution of lung pathology. An alternative, or better yet a supplement, to drug treatment is that of vaccination, as this parasitic disease is one of the few for which effective vaccines have been developed, predominantly for use in cattle. Two doses of live attenuated (gamma-irradiated) larvae 2-4 weeks apart stimulates the development of strong protection against disease, but does not completely eradicate existing infections (generating a concomitant or premunitive immunity, rather than a sterile immunity). Vaccination is primarily targeted at young animals in their first grazing season, but is effective in older animals, including pregnant breeders. It is most effective on farms in endemic areas, particularly when remembering that vaccinated animals need further exposure to infection by low levels of pasture larvae in order to develop a natural acquired immunity. Various preventive strategies have been applied, usually at the farm level, to reduce transmission rates, principally involving improved sanitation (faecal removal, cleaning pens), maintaining good hygiene (clean water, food troughs for supplementary feed), stock management (closed herds, quarantining imports, avoid overstocking, separating cohorts) and pasture management (rotational and/or mixed grazing, draining wet pastures, spelling pastures). Several studies on biological control using nematode-trapping fungi or dung beetles demonstrated modest reductions in pasture larval contamination, but no methods have yet been commercialized.

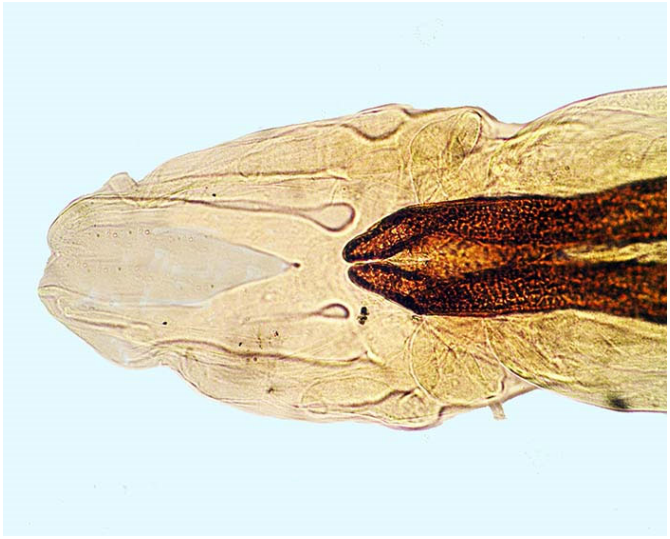

Dictyocaulus
lungs
(bronchitis, verminous
pneumonia, husk)
head
Definitive Hosts
(ungulates)
hypobiosis
adult female
(~ 100 mm)
adult male
(~ 70 mm)
male tail
L3
ingested
eggs
(~ 100 µm)
eggs/L1
excreted
in faeces
most first-stage larvae
(L1) hatch in the host
(~ 300 µm)
filariform third-
stage larvae (L3)
(~ 500 µm)
external
environment
rhabditiform second-
stage larvae (L2)
(~ 500 µm)



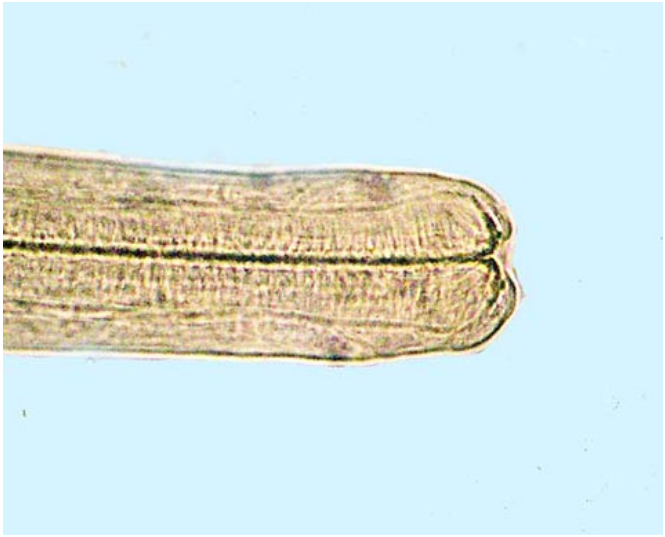
Dictyocaulus adult worms



Dictyocaulus lung lesion



Dictyocaulus adult worm, male bursa



Dictyocaulus adult worm, head

Metastrongylus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Metastrongyles have indirect life-cycles involving the development of L3 in invertebrate intermediate hosts. Adult *Metastrongylus* in the lungs lay eggs which are swallowed and passed in faeces. The eggs hatch and emergent L1 are ingested by earthworms where they develop to infective L3. When eaten by pigs, larvae penetrate to mesenteric lymph nodes and moult to L4 which then migrate via the lymphatic-vascular systems to form adults in the lungs. *Metastrongylus* spp. cause respiratory signs in pigs worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Metastrongylidae (infection of pigs by ingestion of earthworm/molluscan IH carrying L3)
Genus:	*Metastrongylus* (parasitic in lungs of pigs, earthworm IH)
Species:	various species cause respiratory signs in pigs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Metastrongylina (lungworms)				
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	Suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Angiostrongylidae	no or reduced buccal cavity, short	carnivores, rodents	ingestion of IH or PH	28

(lungworms)	club-shaped oesophagus		carrying L3	
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	Suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 2 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm eggs
Metastrongylidae					
Metastrongylus (lungworms)	8	artiodactyls	respiratory tract	10-60 mm long, small buccal capsule, 2 trilobed lips, reduced male bursa, indirect cycle, eggs laid in lungs swallowed, voided, L3 develop in invertebrate IH	41-61 x 26-43 µm, ovoid, thick-shelled

The family Metastrongylidae is monotypic containing a single genus (*Metastrongylus*) characterised by large lungworms with 2 large lateral trilobed labia, thick-shelled sculptured eggs, an atypical bursa, earthworm intermediate hosts and predominantly suid definitive hosts. Some 8 species have been described in domestic, wild and feral swine around the world, many in association with respiratory disease typified as verminous bronchitis. Clinical infections by *M. apri* and *M. salmi* have occasionally been observed in humans.

***Metastrongylus* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Intermediate Hosts**	**Distribution**
M. apri (syn. *M. elongatus*) (pig lungworm)	Artiodactyla: suid (pig, wild boar, central European boar, Japanese boar), bovid (cattle, sheep, goat), cervid (deer); Carnivora: canid (dog); Primates: hominid (human)	bronchi [coughing, dyspnoea, nasal discharge]	Clitellata: lumbricid (*Allolobophora calliginosa, Aporrectodea*, *Bumastus, Dendrobaena rubida*, *Eisenia austriaca*, *Helodrilus caliginosus, foetidus*, *Lumcriculus variegatis, Lumbricus rubellus, terrestris*), megascolecid (*Diplocardia*)	worldwide
M. asymmetricus	Artiodactyla: suid (wild boar, Japanese boar)	Bronchi		Eurasia
M. confusus	Artiodactyla: suid (wild boar)	Bronchi		
M. madagascariensis	Artiodactyla: suid (pig)	Bronchi		Africa
M. pudendodectus (syn. *M. brevivaginatus*)	Artiodactyla: suid (pig, wild boar, central European boar, Sardinian wild boar, Japanese boar)	bronchi [coughing, dyspnoea, nasal discharge]	Clitellata: lumbricid (*Lumbricus rubellus, terrestris*)	worldwide
M. pulmonalis	Artiodactyla: suid (central European boar)	Bronchi		Europe
M. salmi	Artiodactyla: suid (pig, wild boar, Japanese boar), tayassuid (white-lipped peccary); Primates: hominid (human)	bronchi [coughing, dyspnoea, nasal discharge]	Clitellata: lumbricid (*Eisenia phoetida*)	Africa, Asia, Americas
M. tschiauricus	Artiodactyla: suid (wild boar)	Bronchi		Russia

Parasite morphology: *Metastrongylus* spp. form 3 different types of morphological stages during their developmental cycles: eggs; larvae (4 successive stages designated L1-L4); and adult worms. The eggs are grey-brown in colour, ellipsoidal in shape measuring 41-61 by 26-43 µm, and are surrounded by unique thick sculptured shells (with a rough corrugated-wrinkled surface). When laid, they are embryonated and contain a fully developed larva. Free L1 are elongate stages measuring 275-350 µm, but they may grow to 400-540 µm before moulting. They have bullet-shaped heads, a rhabditiform (double-bulbed) oesophagus measuring 110-120 µm, numerous granular intestinal cells and a tail coiled ventrad. L2 are similar stages but are larger measuring 550-650 µm, and have conical truncated heads and tapering tails. L3 are often ensheathed in the L2 cuticle and they measure from 630-685 µm and have a truncated head with 2 characteristic indentations, a club-shaped oesophagus 150-170 µm long and a tapering tail with 2 deep notches near the tip. L4 are transient stout parasitic stages measuring 530-755 µm and have rounded heads, a club-shaped oesophagus 140-160 µm long, an attenuated tail terminating in a knob-like process, and are beginning to show sexual characteristics (notably a developing male bursa and female vulva). Adults are thin slender white worms measuring from 10-60 mm in length and are characterised by an anterior mouth bearing 2 large lateral tri-lobed lips. The cuticle bears longitudinal ridges (synlophe) and the worms have a small vestigial buccal capsule, a short club-shaped oesophagus, and relatively thick intestines terminating in a caudal cloaca in males and a posterior anus in females. Male worms are smaller than females (10-26 x 0.12-0.25 mm cf. 23-60 x 0.45 mm). Mature males have a distinctive copulatory bursa consisting of 2 large broad lateral lobes divided by deep terminal incision, and a highly reduced dorsal lobe. The lateral lobes are supported by an asymmetrical configuration of up to 5 irregular digitiform rays, and the dorsal lobe is supported by a single reduced dorsal ray with a terminal bifurcation. Males lack a gubernaculum but have a

strongly developed genital cone and 2 very long thread-like spicules (400-600 μm) often protruding caudally from the body and ending in a hook (double hooks in *M. pudendotectus* and *M. asymmetricus*). Mature females are didelphic with 2 ovaries and uteri terminating in a posterior vulva usually with a prevulvar swelling. Females of most species also have a well-developed provagina (absent in *M. salmi* and *M. confusus*) and their tails are either straight ((e.g. *M. pudendotectus*) or curved ventrad (e.g. *M. apri*). They are oviparous and produce thick-walled eggs that are fully embryonated when laid.

Site of infection: Infective larvae migrate from the gut to the lungs of their porcine hosts, where adult worms develop to infect the bronchioles and small bronchi, particularly in the posterior lobes, although some species (e.g. *M. apri*) may also extend into the trachea. First-stage larvae contained in eggs or freshly hatched in host faeces are ingested by earthworms where they develop to infective L3 which become encapsulated in earthworm tissues.

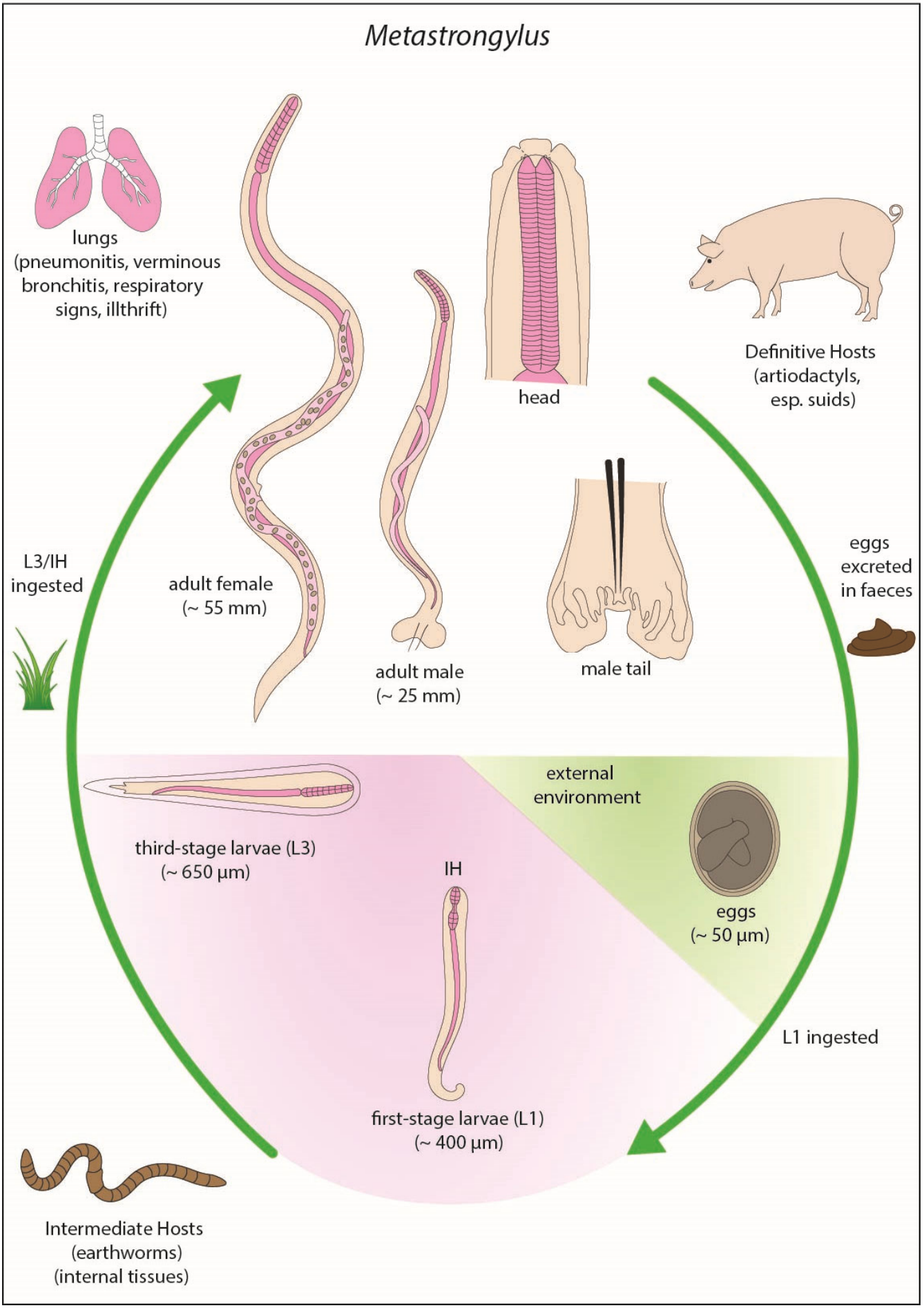
Pathogenesis: Most infections appear benign and remain asymptomatic or subclinical in adult pigs which rapidly acquire a natural protective immunity (some animals may develop burdens of several hundred worms without apparent harm). However, young animals with immature immune systems are susceptible to clinical disease, the severity of which depends on parasite pathogenicity (some species are more virulent), host susceptibility (young pigs 4-8 months of age), and the intensity of infection (numbers of larvae and/or adults). Infections may produce respiratory disease during both the prepatent period when only larval stages are present and during patency when adults are feeding and laying eggs. Early larval stages migrating through the lungs may cause traumatic damage with micro-haemorrhages and inflammation resulting in pneumonitis, pulmonary consolidation, and respiratory signs (dyspnoea and developing cough). Adult worms then develop and feed on bronchial exudates, desquamated epithelial cells and mucus, provoking significant inflammation of the airways, all contributing to lumen occlusion, catarrhal bronchiolitis and bronchitis (also known as verminous bronchitis) with alveolar collapse (atelectasis), bronchopneumonia, and compensatory emphysematous areas surrounding lesions. Worm eggs may also be aspirated into smaller air passages and into the lung parenchyma exacerbating pulmonary consolidation and emphysema. Histopathological changes include bronchial and peri-bronchiole cellular infiltrations (esp. by eosinophils), epithelial hyperplasia and metaplasia with goblet cell formation, hypersecretion of mucus, emphysematous areas with alveolar enlargement, and the development of small dense grey miliary nodules containing degenerating parasites (eggs, larvae or adults). Respiratory disease usually develops chronically, rarely acutely, in young animals with persistent cough, initially dry (thumps) and subsequently productive, dyspnoea and sometimes tachypnoea, bronchial fremitus (palpable vibration) and sibilant rales (crackling) on auscultation, muco-purulent nasal discharge, loss of appetite and body condition with impaired growth and weight loss. Lungworm infections can precipitate or enhance other respiratory diseases, particularly those caused by secondary bacterial infections (e.g. purulent staphylococcal infections with congestion and pneumonia). There have also been several reports that lungworm larvae may also be able to transmit viral infections, such as swine influenza, Teschen disease and hog cholera. There have also been several rare reports of infections by *M. apri* and *M. salmi* causing pulmonary disease in human patients, characterised by progressive dyspnoea, chest pain, fatigue and the production of thick bloody sputum.

Developmental cycle and mode of transmission: These lungworm parasites have indirect heteroxenous life-cycles involving the development of infective larval stages in invertebrate intermediate hosts which are then consumed by vertebrate definitive hosts. Gravid female worms lay embryonated eggs in the airways which ascend the mucociliary escalator to the trachea to be swallowed and passed in host faeces. While the eggs have been shown to be tolerant of cold temperatures (surviving in manure for 6-8 months and in moist soils for 3-18 months), most eggs hatch almost immediately in humid conditions releasing L1 stages into the surrounding soil. Earthworms act as obligate intermediate hosts in which ingested eggs and/or larvae continue their development to infective L3 stages over 10-30 days. L1 penetrate the wall of the crop and invade the calciferous glands where they moult twice to form ensheathed L3. These larvae spread via the earthworm vascular system to numerous tissues and sinuses where they become encapsulated within granulomas by fibrous host reactions. L3 have been shown to remain viable in earthworms for up to 7 years (most earthworms only live for 8-9 years) and infections may accumulate over time (up to 600 larvae have been recorded in some individuals). It has also been demonstrated that L3 may leave the bodies of dying or dead earthworms and are able to survive in moist soils for several months. Definitive hosts become infected when they consume infective L3 either in earthworms or free on pastures or water. Ingested L3 burrow through the gut wall and migrate to the mesenteric lymph nodes where they moult to L4 before moving via the thoracic duct or portal venous system to the heart and pulmonary arteries to reach the lungs. The L4 invade alveolar airspaces and moult to subadults (sometimes designated L5) which move upwards to the bronchioles and bronchi to mature into adult worms. The prepatent period (time from infection to first excretion of eggs) ranges according to species from 2-6 weeks, and adult worms are thought to live for 8-12 months.

Differential diagnosis: Clinical infections may be suspected on the basis of respiratory signs (dyspnoea and coughing) in young piglets with access to pastures, but other conditions may also cause similar signs (e.g. pulmonary ascariosis, strongyloidosis, bacterial or viral pneumonia). Infections are conventionally confirmed by the microscopic detection of worm eggs in faecal samples, usually following their concentration by floatation in saturated sugar or salt solutions with high specific gravities. However, eggs may be passed sporadically in low numbers and they are similar in appearance to thick-walled *Ascaris* eggs which embryonate in aged faecal material. Infections may be diagnosed at necropsy by the detection of adult worms in dissected bronchi, in bronchial exudates or by extrusion of material from incised lung lobes (esp. terminal diaphragmatic lobes). Molecular biological techniques

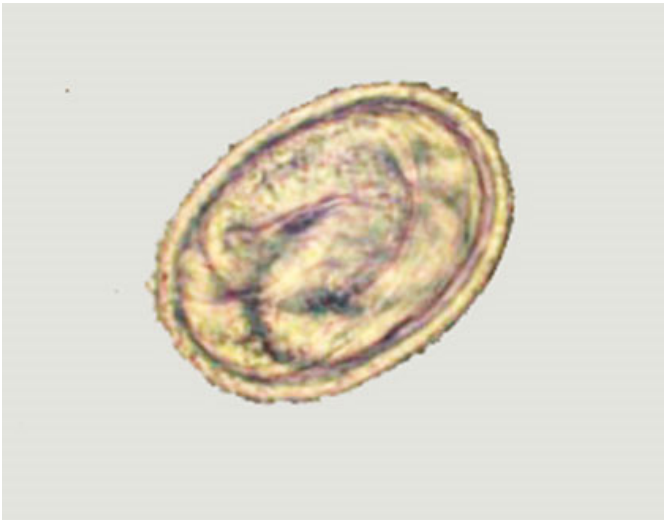
have been used to characterize species and determine phylogenetic relationships following the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (notably internal transcribed spacer 2 (ITS2) of ribosomal RNA) and mitochondrial genes (esp. cytochrome c oxidase subunit 1 (cox1)).

Treatment and control: Clinical infections in pigs have responded well to treatment with various anthelmintic drugs, including benzimidazoles (albendazole, fenbendazole, oxfendazole, flubendazole), imidazothiazoles (levamisole), and macrocyclic lactones (abamectin, doramectin, ivermectin, moxidectin) - the latter also being effective against migrating larvae. Human infections have also been treated successfully with ivermectin. However, treated animals may be rapidly re-infected unless various preventive measures are adopted, particularly on farms where pigs are outdoors and have access to soils containing earthworms. Infections are rarely a problem in intensive piggeries where indoor pens can be regularly cleaned and solid flooring prevents contact with soil. In extensive or semi-intensive systems using outdoor shelters and enclosures, attempts should be made to reduce environmental contamination by pig faeces (raised pens, better sanitation through drainage and/or effluent treatment) and to minimise the uptake of infective larvae in earthworms or soils (provide clean food and water, prevent foraging using barriers or nose rings, pasture rotation involving previously ungrazed areas). Little can be done to control infections in wild or feral pig populations which scavenge widely and tend to congregate around open water sources with moist soils. Epidemiological studies have found infections to be less prevalent in forested areas than open ranges, presumably due to the lower abundance of earthworms.


Metastrongylus
lungs
(pneumonitis, verminous bronchitis, respiratory signs, illthrift)
adult female
(~ 55 mm)
adult male
(~ 25 mm)
head
male tail
Definitive Hosts
(artiodactyls, esp. suids)
eggs excreted in faeces
L3/IH ingested
external environment
third-stage larvae (L3)
(~ 650 µm)
IH
eggs
(~ 50 µm)
L1 ingested
first-stage larvae (L1)
(~ 400 µm)
Intermediate Hosts
(earthworms)
(internal tissues)



Metastrongylus adult worms



Metastrongylus worm egg



Metastrongylus adult worm, head

Protostrongylus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Protostrongyles have indirect life-cycles involving the development of L3 in invertebrate intermediate hosts. Adult *Protostrongylus* in the lungs release L1 which are swallowed and passed in faeces. L1 then penetrate the foot of a snail and develop to L3. When eaten by ruminants, larvae penetrate to the mesenteric lymph nodes and moult to L4 which then migrate via the lymphatic-vascular systems to form adults in the lungs. Infections by *Protostrongylus* spp. in sheep and goats are generally asymptomatic.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Protostrongylidae (infection of ruminants by ingestion of earthworm/molluscan IH carrying L3)
Genus:	*Protostrongylus* (parasitic in lungs of sheep/goats, snail intermediate host)
Species:	various species cause subclinical infections in sheep and goats

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Metastrongylina (lungworms)				
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	Suids	ingestion of IH carrying L3	1
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28

Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	Suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 2 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials). Several protostrongylid genera of significance to livestock production are compared below:

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm larvae**
Protostrongylidae					
Protostrongylus (lungworm)	27	artiodactyls, lagomorphs	respiratory tract	13-80 mm long, small buccal capsule, 6 lip-like elevations, indirect cycle, eggs laid in lungs swallowed, voided, L3 develop in snail IH	250-400 µm, fine striations
Muellerius (lungworm)	4	artiodactyls	respiratory tract	10-30 mm long, small buccal capsule, indirect cycle, eggs laid in lungs, swallowed, voided, L3 develop in snail IH	230-340 µm, dorsal spine, tail kink

Parelaphostrongylus (meningeal worm, brain worm)	3	artiodactyls	brain, lung	17-90 mm long, small buccal capsule, indirect cycle, eggs laid in meninges travel via blood to lungs, swallowed, L1 voided, L3 develop in snail IH	300-380 µm, dorsal spine
Elaphostrongylus (brain worm)	3	artiodactyls	muscles, brain, lung	26-70 mm long, small buccal capsule, indirect cycle, eggs laid in tissues travel to lungs via blood, swallowed, L1 voided, L3 develop in snail IH	288-490 µm, dorsal spine

The family Protostrongylidae contains 17 genera: *Cystocaulus, Dukerostrongylus, Elaphostrongylus* (syn. *Protostrongyloides*)*, Imparispiculus, Mariostrongylus, Muellerius, Neostrongylus, Orthostrongylus, Paraelaphostrongylus* (syn. *Odocoileostrongylus, Neurofilaria*)*, Pneumocaulus, Pneumostrongylus, Protostrongylus* (syn. *Gelanocaulus, Synthetocaulus*)*, Pulmostrongylus, Skrjabinocaulus, Spiculocaulus, Umingmakstrongylus* and *Varestrongylus.* Early works placed some of these genera into separate subfamilies (Elaphostrongylinae, Muelleriinae, Neostrongylinae, Protostrongylinae, Skrjabincaulinae, and Varestrongylinae) but recent molecular studies failed to support them, indicating that several may be monophyletic, and even that the genus *Protostrongylus* may be paraphyletic grouping strongly with *Spiculocaulus* and *Orthostrongylus*. Clearly, further work needs to be conducted to differentiate protostrongylid species, genera and subfamilies. Members of the genus *Protostrongylus* are characterised by males with well-developed bursal rays, telamon with simple plates and arches, gubernaculum with capitulum, corpus and paired crura, short stout spicules, L1 with pointed tail and no dorsal spines. Some 27 species have been described around the world from the lungs of sheep, goats, chamois, antelope, cervids and lagomorphs. Three subgenera have been differentiated on the basis of morphological differences in reproductive organs: *P.* (*Protostrongylus*) (edges of gubernacular crura nodulated or toothed, provagina well-developed)*; P.* (*Davtianostrongylus*) (edges of gubernacular crura nodulated or toothed, provagina weakly-developed or absent); and *P.* (*Pulmostrongylus*) (edges of gubernacular crura smooth). Nonetheless, the subgeneric designation of most species remains undetermined as many descriptions are ambiguous or often incomplete. All protostrongylid lungworms have heteroxenous life-cycles with infective larvae developing in gastropod intermediate hosts. Infections in domestic livestock have been associated with respiratory disease (parasitic bronchitis and pneumonia), particularly in goats and sheep in countries with warm moist climates.

***Protostrongylus* species**	**Definitive hosts**	**Location [Clinical signs]**	**Intermediate hosts**	**Distribution**
P. andrejevi	Artiodactyla: bovid (Amur goral)			Russia
P. boughtoni (syn. *Synthetocaulus leporis*)	Lagomorpha: leporid (snowshoe hare, eastern cottontail, European rabbit)	Bronchi	Gastropoda: euconulid (*Euconolus fulvus*), vallonid (*Vallonia pulchella*), vertiginid (*Columella edentula*, *Vertigo gouldi*, *ovata*)	North America
P. brevispiculatum	Artiodactyla: bovid (sheep, chamois, goat)	Lungs		North America
P. caprae	Artiodactyla: bovid (Siberian ibex)			Russia
P. coburni	Artiodactyla: cervid (white-tailed deer)	Lungs		North America
P. cuniculorum (maybe a variety of *P. rufescens* specific for lagomorphs)	Lagomorpha: leporid (European rabbit, European hare)	Lungs		Europe
P. davtiani	Artiodactyla: bovid (sheep, argali, goat)	Lungs		North America
P. frosti	Artiodactyla: bovid (bighorn sheep)	Lungs		North America
P. hobmaieri	Artiodactyla: bovid (sheep, chamois, goat, alpine ibex)	Lungs		Asia
P. indicus	Artiodactyla: bovid (wild goat)			Eurasia
P. kamenskyi	Lagomorpha: leporid (mountain hare)			
P. kochi	Artiodactyla: cervid (roe deer, red deer), bovid (sheep, mouflon)			Europe
P. macrotis	Artiodactyla: cervid (moose)			North America
P. muraschkinzewi	Artiodactyla: bovid (sheep)		Gastropoda: geometrid (*Cochlicella barbara*), helicid (*Cepaea nemoralis*)	Russia

P. oryctolagi	Lagomorpha: leporid (European hare, European rabbit)	Lungs		Europe
P. ovis	Artiodactyla: bovid (sheep)			
P. pulmonalis (syn. *P. commutatus, terminalis*)	Lagomorpha: leporid (European hare, Cape hare, mountain hare, European rabbit)	Lungs		Europe, Africa
P. raillieti	Artiodactyla: bovid (goat, Siberian ibex, sheep, argali, chamois)			Eurasia
P. rufescens (red lungworm) (incl. subspp. *rufescens*, *boevi*)	Artiodactyla: bovid (water buffalo, sheep, argali, mouflon, goat, chamois, alpine ibex, Iberian ibex)	lungs (small bronchioles)	Gastropoda: chondrinid (*Abida*), enid (*Zebrina*), geometrid (*Cernuella arigonis*, *virgata*, *Cochlicella acuta*, *barbara*, *conoidea*), helicid (*Arianta, Capaea nemoralis, Theba*), hygromiid (*Helicella apicina*, *corderoi*, *itala*, *jamuzensis*, *madritensis*, *ordunensis*, *rugosiuscula*, *valdeona*, *zaratei*, *Perforatella incarnata*)	Africa, Europe, North America, Australia, New Zealand
P. rupicaprae	Artiodactyla: bovid (chamois, Pyrenean chamois)			Europe
P. rushi	Artiodactyla: bovid (sheep, bighorn sheep, goat)	Lungs		North America
P. shiozawai	Artiodactyla: bovid (Japanese serow)	Lungs		Asia
P. skrjabini	Artiodactyla: bovid (sheep, goat)	Lungs		Eurasia
P. stilesi	Artiodactyla: bovid (mountain goat, white-faced muskox, bighorn sheep, Dall sheep)	Lungs		North America
P. sylvilagi	Lagomorpha: leporid (cottontail rabbit, jackrabbit)	Lungs		North America
P. tauricus	Lagomorpha: leporid (European hare, brown hare, European rabbit)	Lungs		Europe
P. vsevolodovi	Artiodactyla: bovid (sheep, Siberian ibex)	Lungs		Russia

Parasite morphology: *Protostrongylus* spp. form 3 different morphological stages during their developmental cycles: eggs; larvae (4 consecutive stages designated L1-L4); and adult worms. Eggs are thin-walled elliptical stages measuring 50-90 x 35-60 µm and are partially embryonated when deposited in lung tissues where they hatch. First-stage larvae (L1) are elongate cylindrical forms ranging in length from 250-400 µm and are often half curled posteriorly. They have rounded heads, cuticles with fine transverse striations and well-developed lateral alae, a long rhabditiform (double-bulbed) oesophagus occupying the anterior 33-50% of the body, intestines without food granules, and a long tapering tail with a pointed terminus (lacking dorsal spines as is characteristic of protostrongylines). L2 are similar in morphology but are slightly larger (300-450 µm) and are often ensheathed in the L1 cuticle. L3 are larger still (400-750 µm) but have a strongyliform (flask-shaped) oesophagus and blunt rounded tails. L3 contained within snail tissues are ensheathed in both the L1 and L2 cuticles, which are shed when the infective L3 are released from host tissues. L4 are transient parasitic stages that have begun to adopt the morphological characteristics of adults, especially in mouth structures and developing genitalia. Adults are thin tubular red-brown worms measuring 13-80 mm in length and the cuticle bears small longitudinal ridges (synlophe). They have a small anterior mouth with 6 elevations or flat perityls that appear like small lips. The buccal capsule is small and unarmed and leads to a stout oesophagus. Adult worms are sexually dimorphic, with females being larger than males (21-80 cf. 13-45 mm). Mature females are didelphic with 2 ovaries and uteri connected to a common posterior vulva where the body abruptly narrows to the conical tail. Most species have a well-developed provagina extending posterior to the vulva but anterior to the anus. Mature males have a small but well-developed copulatory bursa with large lateral lobes (each supported by 6 rays) and a prominent dorsal lobe (supported by a globular dorsal ray with 6 ventral papillae). They also have a highly developed gubernaculum (comprising capitulum, corpus and paired boot-shaped crura with nodulated or toothed edges) and telamon (with simple plates and arches) and 2 stout spicules (250–320 µm long) terminating in membranous alae. Some consider that the genera *Spiculocaulus* and *Orthostrongylus* should be synonymized with *Protostrongylus* as they were differentiated primarily on the basis of longer filiform spicules in *Spiculocaulus* and an elaborately developed telamon in *Orthostrongylus.*

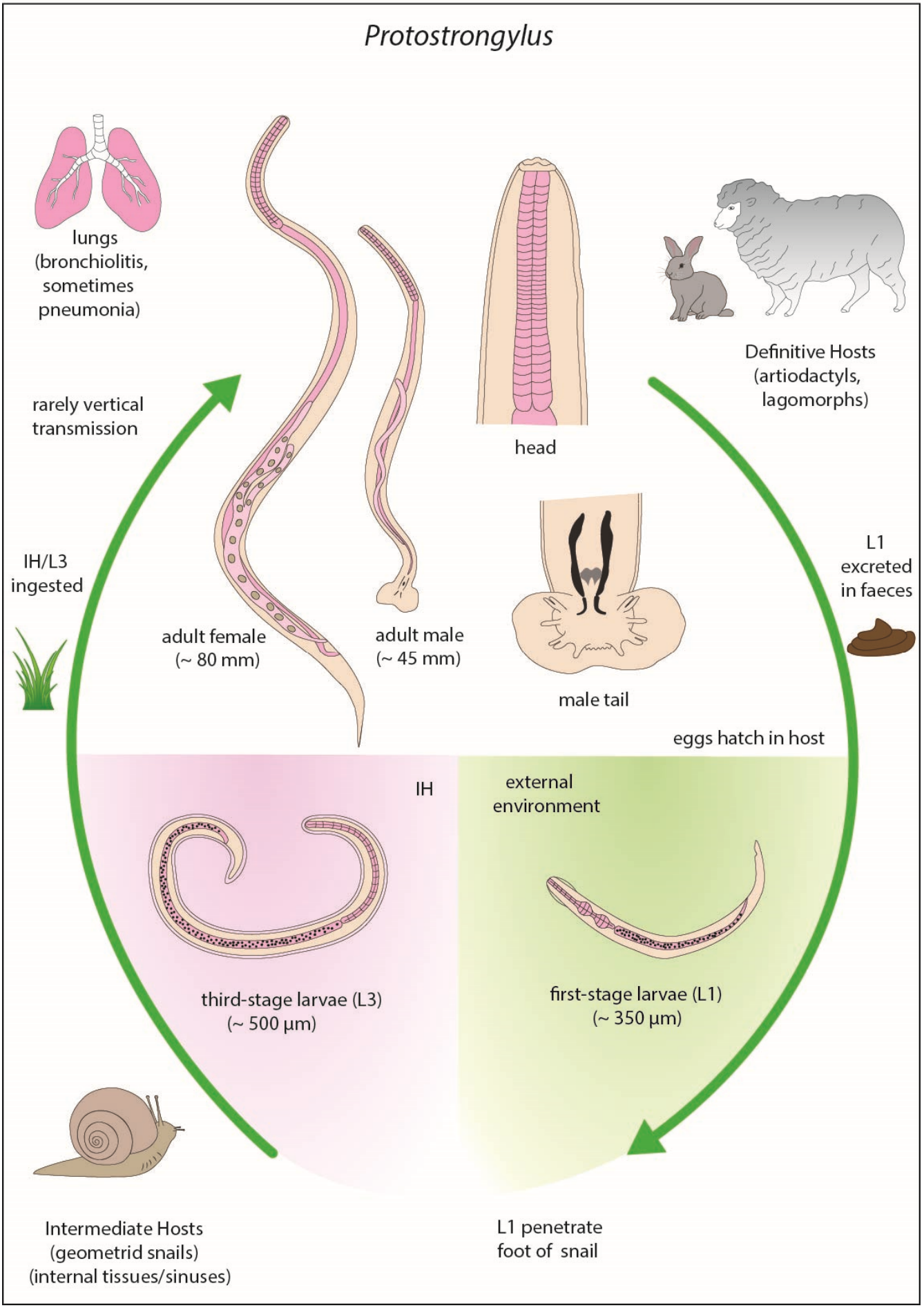
Site of infection: Adult lungworms are found in the air passages of their definitive hosts, ranging from the alveoli and alveolar ducts to the bronchioles and small bronchi. Earlier developing larval stages migrate from the gut to the lungs via the lymphatics and/or circulation. Infective larvae develop in the tissues and sinuses of obligate gastropod intermediate hosts.

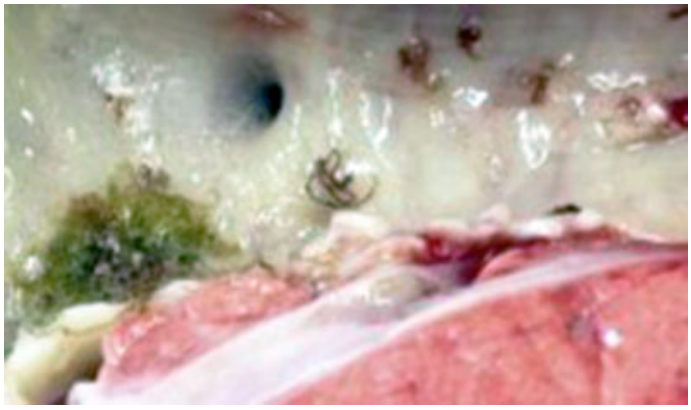
Pathogenesis: Infections by these lungworms cause characteristic discoloured lesions usually seen on the surface of dorsal lobules of the lungs at necropsy. The lesions in the lungs are more extensive than those caused by *Muellerius* infections, as occlusion of the small bronchioles leads to lesser branches filling with eggs, larvae and cellular debris. Occasionally, *Protostrongylus* infections may cause respiratory signs similar to dictyocaulosis, although not as severe and involving localised bronchiolitis and sometimes pneumonia (the latter frequently involving secondary bacterial infections). Worms in alveoli and small air passages cause local inflammation with epithelial desquamation, leucocyte infiltrations, exudate formation and connective tissue proliferation all contributing to occlusion, atelectasis, emphysema, peribronchitis, bronchitis, and small foci of lobular pneumonia with nodular or polygonal plaque-like lesions (up to 1 cm in diameter) appearing as red-gray to yellow discolourations, sometimes progressing to granuloma formation. Respiratory signs are rarely observed, but include dyspnoea (with crackles, crepitation and hypersonority on auscultation), cough (dry then productive), nasal discharge and weight loss, sometimes diarrhoea. Despite intense innate immune responses, hosts tend not to acquire any strong protective immunity, so infections accumulate with age (adults have more prevalent and intense infections). Nonetheless, these lungworm infections are not considered to represent serious health threats to domestic livestock.

Developmental cycle and mode of transmission: *Protostrongylus* spp. have indirect heteroxenous life-cycles involving the faecal contamination of pastures and the formation of infective larvae in obligate gastropod intermediate hosts and their transmission back to herbivorous definitive hosts when grazing. Female worms lay eggs in the airways where they complete embryonation and hatch releasing L1 which migrate up to the trachea via the mucociliary escalator and are swallowed to be passed in host faeces (previous suggestions that L1 moult in the airways with L2 being excreted have not been supported). In the external environment, L1 may survive for months in faecal pellets, eventually migrating outwards onto pastures and into soils, usually following rainfall or flooding. The L1 actively penetrate the foot of gastropods which are used as intermediate hosts in which infective L3 develop in body tissues and cavities over 12-14 days in optimal thermal conditions (20-26°C), but with development being inhibited in colder conditions and in aestivating snails. Infective L3 have been shown to survive in snail tissues for up to 2 years (easily over-wintering). Intermediate host specificity is poorly known but appears to be quite broad involving a range of aquatic and terrestrial snails and slugs. Definitive hosts become infected when they consume infected gastropods with herbage, although some reports suggested that they could also be infected by directly ingesting L3 released from gastropods onto pastures. Ingested L3 penetrate the intestinal wall and migrate to the mesenteric lymph nodes where they moult to L4 and then move to the lungs via the hepatic portal system and heart. The larvae moult to subadults (often designated L5) which settle in the alveoli and bronchioles and mature to adults. The prepatent period (time from infection to first excretion of L1) ranges from 19-54 days, and larval migration have been implicated in transplacental and transcolostral transmission for several species. Infections demonstrate a pronounced seasonality with clinical signs developing over winter and infections becoming more prevalent in spring when humidity and temperatures rise.

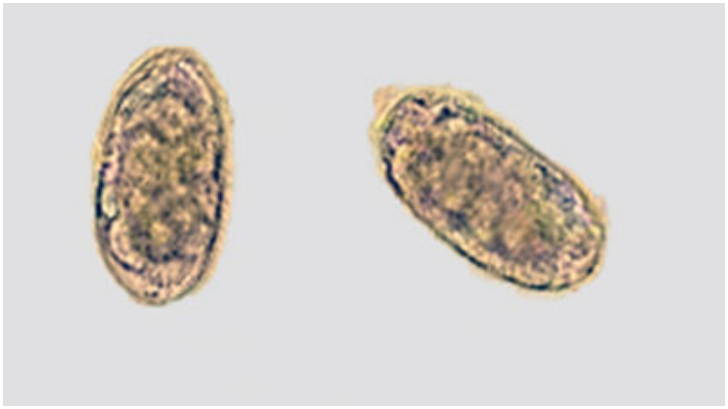
Differential diagnosis: Few infections become symptomatic and are easily confounded with other conditions, including dictyocaulosis, strongyloidosis, pulmonary hydatosis, and viral or bacterial bronchopneumonia. Most infections are diagnosed fortuitously by the detection of L1 in faecal samples usually by Baermann filtration. It should be noted that L1 often occur deep in the core of faecal pellets, so samples need to be wetted and thoroughly mixed. The L1 can be differentiated from those of *Dictyocaulus* by the absence of an anterior protoplasmic knob, and from other metastrongyles by the absence of a dorsal tail spine. Infections can be diagnosed at post-mortem by the detection of characteristic lesions on the dorsal surfaces of the lungs, but recovering intact worms from the lesions can be difficult. Recent molecular biological techniques have been used to characterize protostrongyle species by polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (ribosomal RNA, especially internal transcribed spacer 2) and mitochondrial genes (esp. cytochrome c oxidase subunit 1).

Treatment and control: A range of broad-spectrum anthelmintic drugs have been used to treat infections, mostly benzimidazoles (laxabendazole, albendazole, oxfendazole, fenbendazole, flubendazole) and macrocyclic lactones (abamectin, moxidectin, eprinomectin, ivermectin) at higher doses or with repeated treatments. Care should be taken during treatment as clinical signs may initially worsen due to parasite death and host inflammation, so supportive therapy may be required with anti-inflammatory agents, and possibly antibiotics to prevent secondary bacterial pneumonia. Where possible, preventive measures should be taken to reduce faecal contamination of pastures (improved sanitation and hygiene) and limit transmission by controlling gastropod populations (improved drainage, or employing molluscicides), stock management (quarantining new livestock, reduced stocking rates, separating cohorts) and pasture management (rotational grazing, cultivation, spelling).


Protostrongylus
lungs
(bronchiolitis,
sometimes
pneumonia)
rarely vertical
transmission
IH/L3
ingested
adult female
(~ 80 mm)
adult male
(~ 45 mm)
head
male tail
Definitive Hosts
(artiodactyls,
lagomorphs)
L1
excreted
in faeces
eggs hatch in host
IH
external
environment
third-stage larvae (L3)
(~ 500 µm)
first-stage larvae (L1)
(~ 350 µm)
Intermediate Hosts
(geometrid snails)
(internal tissues/sinuses)
L1 penetrate
foot of snail



Protostrongylus adult worms in lung bronchi



Protostrongylus worm eggs



Protostrongylus larva

Muellerius
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Protostrongyles have indirect life-cycles involving the development of L3 in invertebrate intermediate hosts. Adult *Muellerius* in the lungs release L1 which are swallowed and passed in faeces. L1 then penetrate the foot of a snail or slug and develop to L3. When eaten by ruminants, larvae penetrate to the mesenteric lymph nodes and moult to L4 which then migrate via the lymphatic-vascular systems to form adults in the lungs. Infections by *Muellerius* cause mild respiratory signs in sheep and goats worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Protostrongylidae (infection of ruminants by ingestion of earthworm/molluscan IH carrying L3)
Genus:	*Muellerius* (parasitic in lungs of sheep/goats)
Species:	*M. capillaris* species causes mild respiratory signs in sheep and goats

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Metastrongylina (lungworms)				
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	Suids	ingestion of IH carrying L3	1
Angiostrongylidae	no or reduced buccal cavity, short	carnivores, rodents	ingestion of IH or PH	28

(lungworms)	club-shaped oesophagus		carrying L3	
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	Suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 2 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials). Several protostrongylid genera of significance to livestock production are compared below:

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm larvae**
Protostrongylidae					
Muellerius (lungworm)	4	artiodactyls	respiratory tract	10-30 mm long, small buccal capsule, indirect cycle, eggs laid in lungs, swallowed, voided, L3 develop in snail IH	230-340 µm, dorsal spine, tail kink
Protostrongylus (lungworm)	27	artiodactyls, lagomorphs	respiratory tract	13-80 mm long, small buccal capsule, 6 lip-like elevations, indirect cycle, eggs laid in lungs	250-400 µm, fine striations

				swallowed, voided, L3 develop in snail IH	
Parelaphostrongylus (meningeal worm, brain worm)	3	artiodactyls	brain, lung	17-90 mm long, small buccal capsule, indirect cycle, eggs laid in meninges travel via blood to lungs, swallowed, L1 voided, L3 develop in snail IH	300-380 µm, dorsal spine
Elaphostrongylus (brain worm)	3	artiodactyls	muscles, brain, lung	26-70 mm long, small buccal capsule, indirect cycle, eggs laid in tissues travel to lungs via blood, swallowed, L1 voided, L3 develop in snail IH	288-490 µm, dorsal spine

The family Protostrongylidae contains 17 genera: *Cystocaulus, Dukerostrongylus, Elaphostrongylus* (syn. *Protostrongyloides*)*, Imparispiculus, Mariostrongylus, Muellerius, Neostrongylus, Orthostrongylus, Paraelaphostrongylus* (syn. *Odocoileostrongylus, Neurofilaria*)*, Pneumocaulus, Pneumostrongylus, Protostrongylus* (syn. *Gelanocaulus, Synthetocaulus*)*, Pulmostrongylus, Skrjabinocaulus, Spiculocaulus, Umingmakstrongylus,* and *Varestrongylus.* Early works placed some of these genera into separate subfamilies (Elaphostrongylinae, Muelleriinae, Neostrongylinae, Protostrongylinae, Skrjabincaulinae, and Varestrongylinae) but recent molecular studies failed to support them, indicating that several may be monophyletic. Clearly, further work needs to be conducted to differentiate protostrongylid species, genera and subfamilies. The genus *Muellerius* contains lungworms whose males have a reduced bursa with short ventral and lateral rays but a highly-developed dorsal ray (often trifid), telamon with basal and transverse plates, gubernaculum with 2 plates, split spicules, and L1 with a dorsal spine on the tail. Four species have been described around the world in the airways of sheep, mouflon, goats and chamois. The species *M. capillaris* is widespread in ruminants and is transmitted by infective larvae developing in gastropod intermediate hosts (snails and slugs).

***Muellerius* species**	**Definitive hosts**	**Location [Clinical signs]**	**Intermediate hosts**	**Distribution**
M. capillaris (syn. *Synthetocaulus*) (nodular lungworm, hair lungworm)	Artiodactyla: bovid (sheep, argali, mouflon, Cyprus mouflon, chamois, Tatra chamois, goat, wild goat, alpine ibex, Nubian ibex, Iberian ibex), cervid (roe deer, red deer, chital deer, moose)	lung [sporadic coughing]	Gastropoda: agriolimacid (*Agriolimax agrestis, reticulatus, Deroceras reticulatum*), ariophantid (*Macrochlamys*), arionid (*Arion subfuscus, hortensis, circumscriptus, empericorum* (= *ater*)), camaenid (*Fructicola hispida*), clausilid (*Bulgarica fritilaria*), enid (*Chondrula microtraga*, *Zebrina detrita*), geomitrid (*Candidula interecta*, *Cernuella arigonis*, *cespitum*, *virgata*, *Cochlicella barbara*, *Ponentina*, *Trochoidea seetzenii*), helicid (*Arianta arbustorum*, *Cepaea hortensis, nemoralis*, *vindobonensis*, *Helix aspersa*, *pomatia*, *Theba pisana*), hygromiid (*Euomphalia brigantina*, *Helicella bierzona*, *corderoi*, *itala*, *jamuzensis*, *madritensis*, *obvia*, *ordunensis*, *valdeona*, *zaratei*, *Monacha cartusiana*, *umbrosa, Perforatella incarnata*), limacid (*Limax cinereus* (= *maximus*), *flavus*), lymnaeid (*Lymnaea trunculata*), planorbid (*Planorbis*), polygyrid (*Polygyra*), succineid (*Succinea putris, pfeifferi*), trissexodontid (*Oestophora barbula*), urocyclid (*Atoxon pallens*)	worldwide
M. indicus	Sauria: agamid (Oriental garden lizard)			Asia
M. minutissimus	Artiodactyla: bovid (sheep, goat)			
M. tenuispiculatus	Artiodactyla: bovid (chamois, Tatra chamois)		Gastropoda: helicid (*Cepaea vindobonensis*), succineid (*Succinea putris*)	Europe

Parasite morphology: *Muellerius* spp. form 3 different types of morphological stages during their development: namely, eggs, larvae (4 successive stages encoded L1-L4), and adult worms. The eggs are thin-shelled ovoid stages measuring 60-80 x 40-50 µm

and they are partially embryonated (containing a multicellular morula) when deposited in host tissues where they hatch. Freed L1 are elongate typically measuring 230-340 μm although some may range up to 400 μm long. They have round heads with well-developed lateral alae, a long flask-shaped oesophagus (extending 33-50% body length), and an S-shaped kinked tail with a small dorsal spine adjacent to the tip (dorsal-spined L1 are characteristic of non-protostrongylines). L2 are similar in morphology but are somewhat larger (500-540 μm) and do not have a conspicuous kinked tail. L3 are even larger (600-630 μm) and have truncated heads, an elongate tubular oesophagus and a tapering tail. L4 are transient parasitic stages that have begun to show adult characteristics, particularly in head structures and developing genitalia (male bursa and female vulva). Adults appear as red-grey slender hair-like worms 10-30 mm long with ridged cuticles (synlophe present), simple mouths, small buccal capsules, stout oesophagi and intestines terminating in a subterminal anus/cloaca. Mature worms are sexually dimorphic, with males being smaller than females (10-23 cf. 18-30 mm). Males have a spirally coiled tail with a small reduced copulatory bursa folded inwards. The bursa comprises 2 lateral lobes (each with 6 short ventral and lateral rays) and a prominent dorsal lobe (with a highly-developed dorsal ray, often trifid). Males also have a highly developed gubernaculum (with 2 sclerotized rods or plates) and a telamon (with basal and transverse plates) and 2 spicules (120-170 μm long) each split into a proximal alate section with 2 distal serrated arms. Mature female worms are didelphic with 2 ovaries and uteri connecting to a common vulva located posteriorly. Gravid females are oviparous and lay partly embryonated eggs in host tissues.

Site of infection: Adult worms are tightly coiled in the pulmonary parenchyma, alveoli and small air passages (bronchioles, bronchioli) of the lungs of their vertebrate definitive hosts (herbivores), sometimes extending into subpleural tissue. Infective larvae develop in the tissues of their invertebrate intermediate hosts (gastropods).

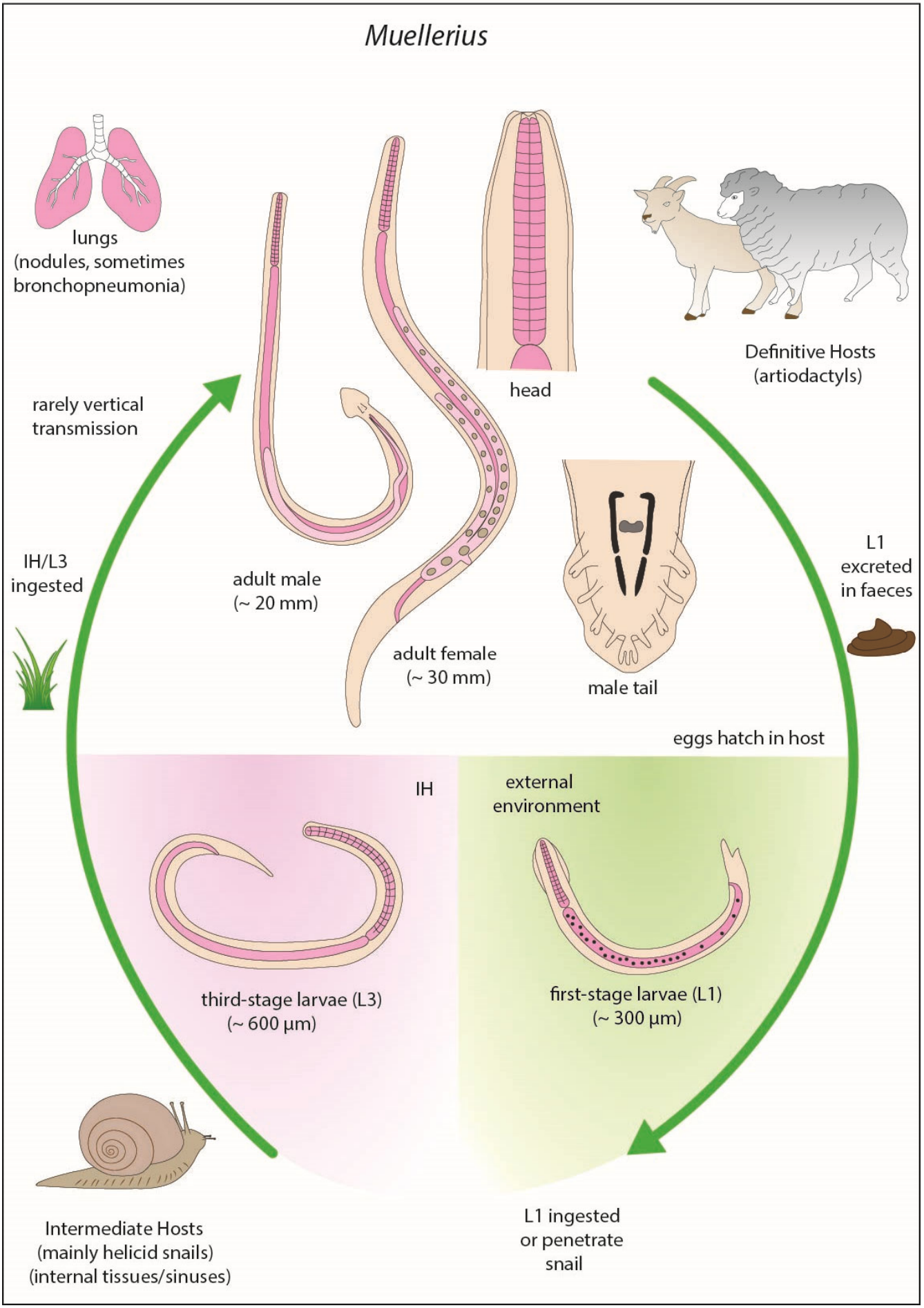
Pathogenesis: Most infections remain asymptomatic, and clinical respiratory signs (dyspnoea, cough, bronchopneumonia) rarely develop even in heavy infections. However, lungworm infections do damage the lungs and predispose hosts to secondary bacterial infections which may also cause pneumonia. Pathogenicity depends largely on host susceptibility (greater in young animals of permissive species, and moderated by levels of innate resistance and acquired immunity), the intensity of infection (numbers of parasites) and the stage of infection (prepatent or patent periods). Early larval stages migrating through the lungs during prepatency cause transient traumatic damage, while patent infections by adult worms may cause chronic disease with nodule formation. Worms living in the small airspaces (alveoli) and airways (bronchioles) cause local inflammation with epithelial desquamation, leucocyte infiltrations, fibrous reactions and exudates contributing to diffuse congestion with airway occlusion, bronchitis, peribronchitis, atelectasis, emphysema, and nodular pneumonia with small firm spherical gray nodules developing usually on the lung surface. The nodules are necrotic granulomatous masses filled with live and degenerating parasites, leucocytes and pulmonary tissue surrounded by fibrous connective tissue and occasional giant cells. They are usually small (2-4 mm diameter) but some may grow larger (up to 20 mm) and begin to calcify. Although emphysemic nodules may be extensive, pneumonic signs are rarely observed, but may include chronic bronchopneumonia with sporadic coughing, lethargy, and weight loss (similar to dictyocaulosis but not as severe). Infections in sheep are usually benign as the parasites are rapidly killed by host immune responses and encapsulated, but without the acquisition of any strong protective immunity so infections accumulate with the age of the sheep. Heavier infections develop in goats apparently due to their broader foraging behaviours, and the infections are more severe due to their poorer immune responses allowing the parasites to cause greater damage over time.

Developmental cycle and mode of transmission: *Muellerius* spp. have indirect heteroxenous life-cycles involving transmission to obligate molluscan intermediate hosts in which infective L3 develop. Gravid female worms lay eggs inside the lung nodules where they complete embryonation and hatch releasing L1. These larvae escape from the nodules and ascend the respiratory tract via the mucociliary escalator to the trachea where they are swallowed and excreted with host faeces. L1 are relatively resistant to desiccation and may survive for months in faecal pellets. They are most active at temperatures ranging from 17-27°C and are not killed by cold conditions, including freezing. L1 are then eaten or penetrate the foot of gastropods (snails and slugs) which act as intermediate hosts supporting the development of infective L3 over 12-21 days. Infective L3 have been found to live as long as their gastropod hosts (several years) and even remain viable for up to 1 week after their death. Herbivorous definitive hosts are infected when they consume infected gastropods on contaminated pastures. Ingested L3 invade the intestinal walls and migrate to the mesenteric lymph nodes where they moult to L4 before moving to the lungs via the lymph and/or blood. The larvae infect pulmonary tissues and moult to young adults (sometimes referred to as L5) which subsequently mature in developing nodules. The prepatent period (time from infection to first excretion of L1) ranges from 6-10 weeks, and adult worms may persist in nodules for up to 2 years. The larvae of some species have been found in the liver and lungs of foetuses and newborn lambs, suggesting that transplacental transmission has occurred, but infections are rarely found in animals younger than 6 months. Infections are very prevalent in sheep in temperate regions, especially those with winter rainfall or cool mountainous regions supporting dense gastropod populations on pastures.

Differential diagnosis: Few infections cause clinical disease, but even then, diagnosis is not easy as symptoms and signs are non-specific and may be caused by other respiratory ailments, including dictyocaulosis, strongyloidosis, pulmonary hydatosis, and viral or bacterial bronchopneumonia. Infections are generally diagnosed by the microscopic detection of L1 in faecal samples, usually following their harvest by Baermann filtration. The L1 can be differentiated from those of *Dictyocaulus* by the absence of an

anterior protoplasmic knob, and from some protostrongyles by the presence of a kinked tail and dorsal spine. Infections may be diagnosed at post-mortem by the detection of characteristic grey 'lead-shot' nodules on the lungs, but the recovery of intact worms is difficult as they are tightly coiled within nodules and many nodules may be pustular or calcified. Molecular biological techniques have been used to determine parasite phylogenetic relationships by the polymerase chain reaction (PCR) amplification of nuclear or mitochondrial genes (internal transcribed spacer 2 of ribosomal RNA and cytochrome c oxidase subunit I, respectively).

Treatment and control: Infections in livestock have been successfully treated using a range of anthelmintic drugs, including benzimidazoles (laxabendazole, albendazole, oxfendazole, fenbendazole, flubendazole), imidazothiazoles (levamisole) and macrocyclic lactones (abamectin, moxidectin, eprinomectin, ivermectin). No drench resistance has yet been reported, but some infections required higher doses and/or repeat treatments. Supportive therapy with anti-inflammatories or antibiotics may also be required to lessen complications due to initial adverse inflammatory reactions to dead parasites or secondary bacterial infections in damaged lungs. Various preventive strategies should also be introduced to reduce transmission rates, by improving sanitation (faecal removal, cleaning pens), maintaining hygiene (clean water, food troughs for supplementary feed), restricting gastropod populations (draining wet pastures, applying molluscicides), grazing management (quarantining new livestock, reducing stocking rates, separating cohorts) and pasture management (rotational and/or mixed grazing, cultivating or spelling pastures).


Muellerius
lungs
(nodules, sometimes
bronchopneumonia)
head
Definitive Hosts
(artiodactyls)
rarely vertical
transmission
IH/L3
ingested
adult male
(~ 20 mm)
adult female
(~ 30 mm)
male tail
L1
excreted
in faeces
eggs hatch in host
IH
external
environment
third-stage larvae (L3)
(~ 600 µm)
first-stage larvae (L1)
(~ 300 µm)
Intermediate Hosts
(mainly helicid snails)
(internal tissues/sinuses)
L1 ingested
or penetrate
snail



Muellerius lung lesion



Muellerius larva

Parelaphostrongylus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Protostrongyles have indirect life-cycles involving the development of L3 in invertebrate intermediate hosts. Adult *Parelaphostrongylus* in the meninges release eggs into the bloodstream where they travel to the lungs, break through to alveoli and are passed in faeces. L1 then penetrate the foot of a snail or slug and develop to L3. When eaten by ruminants, larvae migrate to the central nervous system and develop into adult worms. Infections by *Parelaphostrongylus tenuis* cause neurological signs in deer and moose in North America.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Protostrongylidae (infection of ruminants by ingestion of earthworm/molluscan IH carrying L3)
Genus:	*Parelaphostrongylus* (parasitic in brain of cervids)
Species:	*P. tenuis* causes neurological signs in deer and moose

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Metastrongylina (lungworms)				
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	Suids	ingestion of IH carrying L3	1
Angiostrongylidae	no or reduced buccal cavity, short	carnivores, rodents	ingestion of IH or PH	28

(lungworms)	club-shaped oesophagus		carrying L3	
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	Suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 2 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials). Several protostrongylid genera of significance to livestock production are compared below:

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm larvae**
Protostrongylidae					
Parelaphostrongylus (meningeal worm, brain worm)	3	artiodactyls	brain, lung	17-90 mm long, small buccal capsule, indirect cycle, eggs laid in meninges travel via blood to lungs, swallowed, L1 voided, L3 develop in snail IH	300-380 µm, dorsal spine
Elaphostrongylus	3	artiodactyls	muscles,	26-70 mm long, small buccal capsule, indirect	288-490 µm,

(brain worm)			brain, lung	cycle, eggs laid in tissues travel to lungs via blood, swallowed, L1 voided, L3 develop in snail IH	dorsal spine
Protostrongylus (lungworm)	27	artiodactyls, lagomorphs	respiratory tract	13-80 mm long, small buccal capsule, 6 lip-like elevations, indirect cycle, eggs laid in lungs swallowed, voided, L3 develop in snail IH	250-400 µm, fine striations
Muellerius (lungworm)	4	artiodactyls	respiratory tract	10-30 mm long, small buccal capsule, indirect cycle, eggs laid in lungs, swallowed, voided, L3 develop in snail IH	230-340 µm, dorsal spine, tail kink

The family Protostrongylidae contains 17 genera: *Cystocaulus, Dukerostrongylus, Elaphostrongylus* (syn. *Protostrongyloides*)*, Imparispiculus, Mariostrongylus, Muellerius, Neostrongylus, Orthostrongylus, Paraelaphostrongylus* (syn. *Odocoileostrongylus, Neurofilaria*)*, Pneumocaulus, Pneumostrongylus, Protostrongylus* (syn. *Gelanocaulus, Synthetocaulus*)*, Pulmostrongylus, Skrjabinocaulus, Spiculocaulus, Umingmakstrongylus,* and *Varestrongylus.* Early works placed some of these genera into separate subfamilies (Elaphostrongylinae, Muelleriinae, Neostrongylinae, Protostrongylinae, Skrjabincaulinae, and Varestrongylinae) but recent molecular studies failed to support them, even indicating that several clustering together may be monophyletic. Clearly, further work needs to be conducted to differentiate protostrongylid species, genera and subfamilies. The genus *Parelaphostrongylus* comprises worms whose males have well-developed mound-like dorsal rays with 2-4 branches, a gubernaculum with a wedge-shaped corpus, a well-defined crura but no capitulum, short stout spicules, and L1 with a dorsal spine on the tail. Three species have been found as tissue parasites in the muscles and central nervous system of a range of cervids, notably in North America.

***Parelaphostrongylus* species**	**Definitive hosts**	**Location [Clinical signs]**	**Intermediate hosts**	**Distribution**
P. andersoni (muscle worm)	Artiodactyla: cervid (white-tailed deer, Greenland reindeer, boreal woodland caribou, barren ground caribou, moose, mule deer, fallow deer)	intermuscular blood vessels and connective tissues	Gastropoda: polygyrid (*Mesodon thyroidus*, *Triodopsis albolabris*, *multilineata*), agriolimacid (*Deroceras laeve*)	North America
P. odocoilei (syn *Elaphostrongylus*) (mule deer muscle worm)	Artiodactyla: cervid (mule deer, Columbian black-tailed deer, woodland caribou, moose, western moose), bovid (mountain goat, Dall sheep); Rodentia: caviid (guinea pig)	intermuscular blood vessels and connective tissues	Gastropoda: agriolimacid (*Agriolimax*, *Deroceras laeve*, *reticulatum*), discid (*Discus cronkhitei*, *shimeki*), euconulid (*Euconulus fulvus*), gastrodontid (*Zonitoides arboreus*, *nitidus*), helicid (*Helix aspersa*), monadeniid (*Epigramorpha* (*Monadenia*?) *arrosa*), polygyrid (*Trodopsis multilineata*), vitrinid (*Vitrina limpida*)	North America
P. tenuis (syn. *Odocoileostrongylus, Elaphostrongylus, Neurofilaria cornellensis*) (meningeal worm, brainworm)	Artiodactyla: cervid (white-tailed deer, northern white-tailed deer, Dakota white-tailed deer, Columbian black-tailed deer, mule deer, red deer, fallow deer, reindeer, boreal woodland caribou, wapiti, elk, moose), bovid (cattle, sheep, bighorn sheep, goat, common eland, sable antelope, bongo antelope, scimitar-horned oryx, blackbuck), antilocaprid (pronghorn), camelid (llama, guanaco, alpaca, camel); Carnivora: mephitid (striped skunk); Lagomorpha: leporid (European rabbit); Rodentia: murid (brown rat), caviid	venous sinuses of cranial meninges [neurological signs] [moose sickness]	Gastropoda: agriolimacid (*Deroceras laeve*, *reticulatum*), arionid (*Arion circumscriptus*), cochliocopid (*Cochlicopa lubrica*), discid (*Anguispera alternata*, *Discus cronkhitei*, *patulus*), gastrodontid (*Striatura exigua*), haplotrematid (*Haplotrema concavum*), helicid (*Helicina orbicula*, *orbiculata*), philomycid (*Pallifera dorsalis*, *Phylomycus carolinianus*), polygyrid (*Mesodon inflectus*, *sayanus, thyroidus*, *Polygyra dorenilliana*, *jacksoni*, *Stenotrema fraternum*, *strenotrema*, *Triodopsis albolabris*, *divesta*,	Americas, Africa

	(guinea pig)		*multilineata*, *notata, tridentata*), succineid (*Succinea ovalis*), strobilopsid (*Strobilops labyrithica*), zonitid (*Mesomphix cupreus*, *Ventridens collisella, intertextus*, *Zonitoides arboreus*, *nitidus*)	

Parasite morphology: *Parelaphostrongylus* spp. form 3 different morphological stages during their developmental cycles: eggs; larvae (4 consecutive stages encoded L1-L4); and adult worms. Female worms produce small delicate eggs which are laid in the blood to be carried to the lungs where they appear as round-ovoid stages 40-80 μm in diameter with a central unsegmented embryonic mass clearly separated from the thin surrounding eggshell. L1 are tubular elongate stages measuring 300-380 x 16-36 μm with conical heads, lateral alae, a flask-shaped oesophagus, and curled tails (30-40 μm long) with a subterminal kink and a distinctive triangular dorsal spine (characteristic of non-protostrongyline L1). L2 are similar in morphology but are slightly longer and have non-spined pointed tails. L3 are larger still, measuring from 624-1,323 x 33-52 μm depending on species, (*P. odocoilei* 624-977 μm; *P. andersoni* 911-1,200 μm; *P. tenuis* 900-1,323 μm), and have bullet-shaped heads, rounded lateral thickenings, and short rounded tails usually with a small dorsal swelling. L4 are transient parasitic stages that are beginning to show adult worm characteristics, especially with respect to head structures and developing genitalia (male bursa and female vulva). Adults are slender white worms (17-90 mm long) with thin cuticles bearing fine longitudinal striations, circular anterior mouths bounded by a cuticular ring and 6 inconspicuous perityls (non-movable lips, absent in *Elaphostrongylus*), small conical buccal capsules, a broad muscular club-shaped oesophagus, excretory glands opening subapically, and greenish-yellow to brown-black intestines extending to a subterminal anus (cloaca in males). Adult worms are sexually dimorphic, with females being larger than males (*P. odocoilei* females 40-56 mm, males 20-35 mm; *P. andersoni* females 23-36 mm, males 17-23 mm; *P. tenuis* females 60-90 mm, males 40-60 mm). Mature males have a well-developed copulatory bursa with 2 lateral lobes (each supported by 6 stout rays (2 ventrals partially united, 3 laterals partially united, separate externodorsal ray) and a prominent dorsal lobe (supported by a mound-like dorsal ray with 2-4 branches). Males also have a highly developed gubernaculum with a wedge-shaped bifurcate corpus and a well-defined crura (but no capitulum) and 2 short stout spicules (100-130 μm long) with alae. Mature females are didelphic with 2 ovaries and uteri connected to an ovejector and a common posterior vulva.

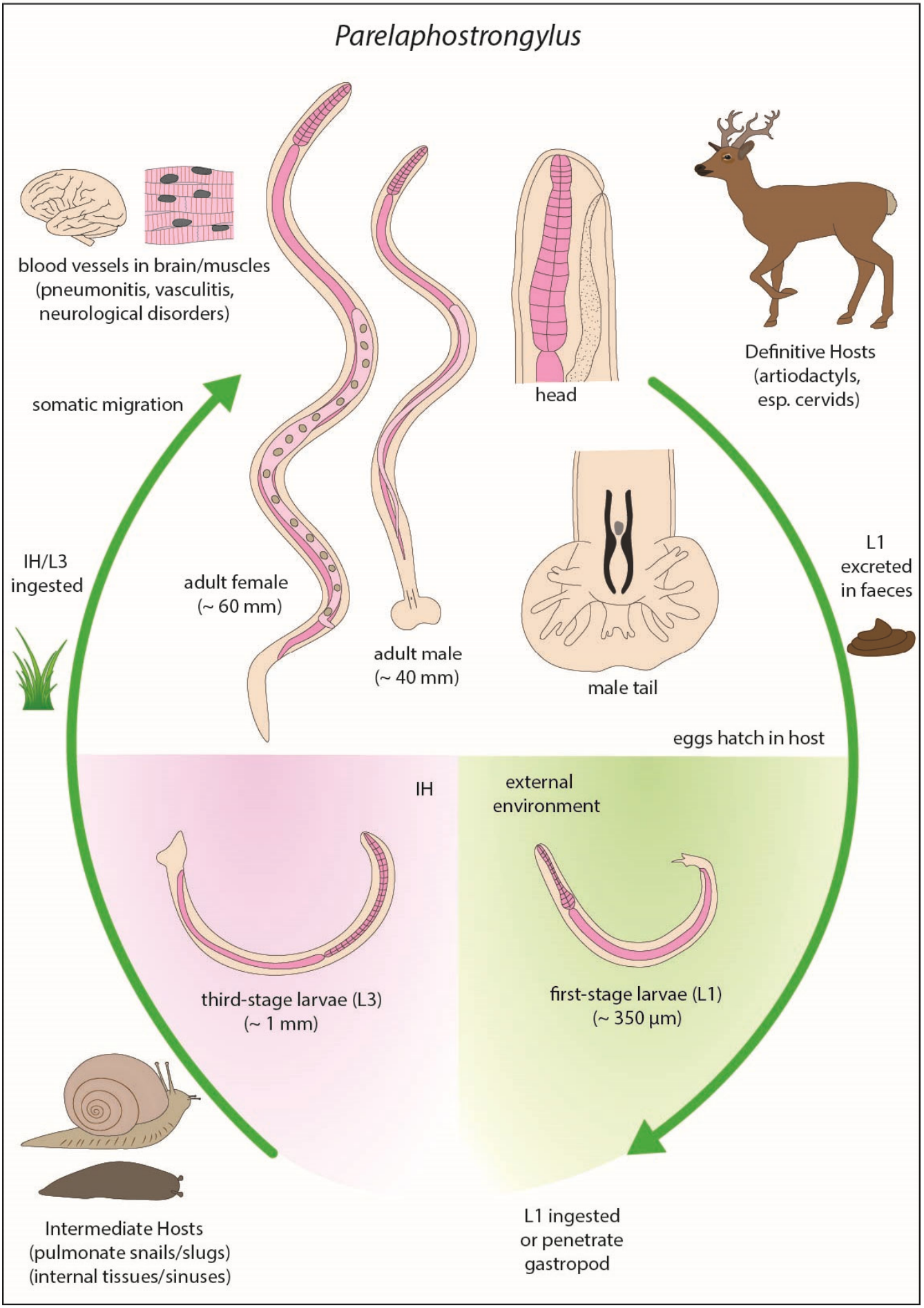
Site of infection: Adult worms infect blood vessels in the brains or muscles of their vertebrate hosts (mostly artiodactyls, especially cervids). *Parelaphostrongylus* spp. differ in their predilection sites: *P. tenuis* infecting veins and venous sinuses in the cranial meninges; *P. odocoilei* infecting veins in connective tissues between muscle bundles; and *P. andersoni* infecting blood vessels and connective tissues deep in the loin and thigh muscles. Infective larvae of each species develop in the tissues and sinuses of invertebrate intermediate hosts (gastropods).

Pathogenesis: Most infections by *Parelaphostrongylus* spp. are relatively nonpathogenic in their normal host species, but when parasites infect aberrant (abnormal) host species they may cause severe neurological diseases. For example, infections by the meningeal worm *P. tenuis* have little effect in most domestic livestock (bovids appear to have innate resistance) and white-tailed deer (which rapidly acquire protective immunity and usually support light infections). However, infections in other cervid species (moose, wapiti (elk), caribou, reindeer, mule deer, black-tailed deer) may lead to debilitating cerebrospinal disease when parasites invade neurological tissues as well as the meninges. Adult worms are frequently associated with space-occupying lesions near cranial nerves causing tissue compression, perineuritis, myelin sheath degeneration, and disruption of axis cylinders. Worms also become embedded in the dura mater over the brain and spinal cord causing minute haemorrhages, perivasculitis with cuffing and infiltrates by lymphocytes, plasma cells and eosinophils, yellowish exudates and meningoencephalitis within weeks of infection. Clinical signs are highly variable in onset, duration and nature involving motor and sensory deficits and numerous behavioural changes, including rapid eye movements (nystagmus), reduced vision (sometimes blindness), torticollis (head tilting), circling, general or hindlimb ataxia (incoordination) with weakness, stiffness, lameness, swaying, difficulty standing, recumbency, paresis (muscle weakening), paraparesis (partial paralysis), paraplegia (paralysis), fearlessness, depression, unthriftiness, anorexia and weight loss. Neurological disease is generally progressive and often fatal, although there may be short periods of remission when animal appear normal. Infections may also cause respiratory signs when worm eggs released in host blood vessels disseminate and accumulate in the lungs where they release larval stages that migrate through tissues causing petechial haemorrhages, fibrosis, atelectasis (alveolar collapse), congestion and pneumonia. Infections by *P. andersoni* and *P. odocoilei* appear to be less pathogenic but have been associated with transient verminous pneumonia, bronchiolitis, bronchitis and vasculitis (esp. arteritis) in the lungs. Adult worms of both species develop in the skeletal muscles and experimental infections in cervids have resulted in disturbances in posture and gait with weakness and recumbency due to petechial haemorrhages and focal necrosis, often with few cellular responses but sometimes with granuloma formation around parasites and their subsequent calcification.

Developmental cycle and mode of transmission: These parasites have indirect heteroxenous life-cycles, involving the development of infective larvae in invertebrate intermediate hosts (gastropods) which are then consumed by vertebrate definitive hosts (usually ruminants). The life-cycles are also unusual in that adult worms live in the host vasculature (rather than the gastrointestinal tract) and produce eggs which are carried to the lungs where they lodge in alveolar capillaries to develop and hatch releasing L1. Adult worms of *P. tenuis* living in subdural spaces may also deposit eggs on the dura mater where they develop and hatch releasing L1 which penetrate small blood vessels and are carried to the lungs. Migrating L1 penetrate into alveolar airspaces and ascend the mucociliary escalator to the trachea to be swallowed and excreted with host faeces. These larvae are often found in the mucus coating faecal pellets and they may survive for several months in cold moist conditions (including subzero temperatures beneath snow, but not repeated freezing and thawing). A range of terrestrial pulmonate gastropods (agriolimacid, arionid and philomycid slugs, and cochliocopid, discid, gastrodontid, haplotrematid, helicid, polygyrid, succineid, strobilopsid and zonitid snails) then act as obligate intermediate hosts. They become infected either when L1 actively penetrate the foot or when L1 in mucus are ingested during feeding. The larvae moult in internal tissues to L2 and then to L3 in 3-4 weeks (longer at lower temperatures), but their development may be arrested in aestivating snails. Most infected gastropods have been found to contain only a few infective L3 (mean 2-6) which may remain viable for the life of the host. Definitive hosts become infected when they consume infected gastropods on vegetation. L3 released in the gastrointestinal tract penetrate the gut wall into the peritoneal cavity. The larvae of each *Parelaphostrongylus* spp. then migrate to their different predilection sites to moult twice and mature into adult worms. Those of *P. andersoni* and *P. odocoilei* penetrate the musculature and move to veins in the intermuscular connective tissues, while those of *P. tenuis* migrate directly to the central nervous system following lateral spinal nerves (mostly lumbar) to the spinal cord (dorsal horns of grey matter) before moving anteriorly in subdural spaces to reach cranial venous sinuses. The prepatent periods (time from infection to first excretion of L1) varies from 49-75 days for *P. andersoni*, 45-62 days for *P. odocoilei*, and 82-137 days for *P. tenuis.*

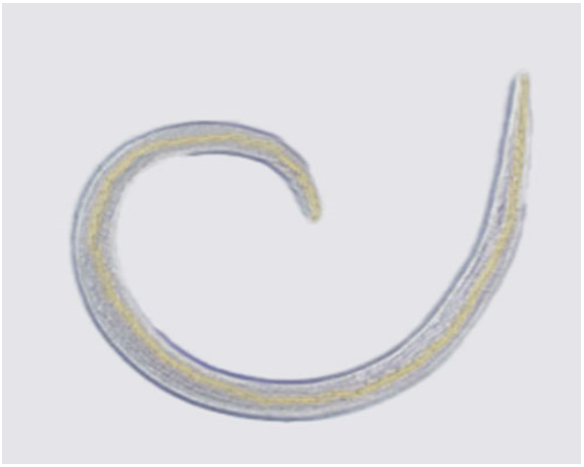
Differential diagnosis: While neurological signs may be suggestive of clinical *Parelaphostrongylus* infections, they are often nonspecific (variable and/or vague) and could be caused by other infectious organisms or toxicological disturbances. Evaluation of various haematological and biochemical parameters proved unfruitful, although an eosinophilic pleocytosis was often detected in cerebrospinal fluid. Most infections are diagnosed during patency when L1 may be detected in faecal samples, usually following their recovery by submerging faecal packets in water (Baermann filtration has been found to be unreliable). Regrettably, the dorsal-spined larvae cannot readily be differentiated from those of other protostrongylids (including *Elaphostrongylus* and *Muellerius*). Infections can be diagnosed at post-mortem by the detection of adult worms in smears or sections of host neural tissues or the detection of worm eggs/larvae in washings (particularly of cranial meninges). Several attempts at xeno-diagnosis have been made whereby laboratory snails have been infected with L1 from faeces and then examined later for L3 which assume a characteristic C- or J-shape when heat-relaxed, but larval dimensions within and between genera vary considerably. Several immunological techniques have been developed to detect specific host antibodies in serum or cerebrospinal fluid by enzyme immunoassays or to detect specific parasite antigens by immunoblot analyses, but the tests demonstrated some cross-reactivity with other nematodes. More recently, modern molecular biological techniques have been used to characterize larvae and adult worms by polymerase chain reaction (PCR) amplification of nuclear gene sequences (especially internal transcribed spacer region 2 of ribosomal RNA).

Treatment and control: Clinical infections in domestic livestock or managed free-range herds have been treated with various anthelmintic drugs, including benzimidazoles (albendazole, fenbendazole), imidazothiazoles (levamisole), diethylenediamines (diethylcarbamazine) and macrocyclic lactones (ivermectin), but with variable efficacy. Most treatments reduced larval excretion, bit it often resumed later without repeated treatment. Parasites appear to be difficult to treat due to their slow development (long prepatent and patent periods), their highly migratory nature within host tissues, their development behind the blood-brain barrier, their encapsulation by host responses, and their swift re-infection on contaminated pastures. Animals may also require supportive treatment with steroids and anti-inflammatory agents to prevent adverse reactions to numerous dying or dead parasites. A range of interventions have also been utilized in attempts to prevent or reduce infections in intensive and extensive farming situations, and even in feral and wild populations as appropriate. Most efforts have involved reducing faecal contamination (through improved sanitation), limiting gastropod populations (by applying molluscicides, building gravel or paved barriers, draining wet pastures), controlling stock (isolation and quarantine of new animals, separate cohorts, exclude wild animals through better fencing or culling by hunting) or pasture management (rotational grazing, cultivating and/or spelling pastures).


Parelaphostrongylus
blood vessels in brain/muscles
(pneumonitis, vasculitis,
neurological disorders)
somatic migration
IH/L3
ingested
adult female
(~ 60 mm)
adult male
(~ 40 mm)
head
male tail
Definitive Hosts
(artiodactyls,
esp. cervids)
L1
excreted
in faeces
eggs hatch in host
IH
external
environment
third-stage larvae (L3)
(~ 1 mm)
first-stage larvae (L1)
(~ 350 µm)
Intermediate Hosts
(pulmonate snails/slugs)
(internal tissues/sinuses)
L1 ingested
or penetrate
gastropod



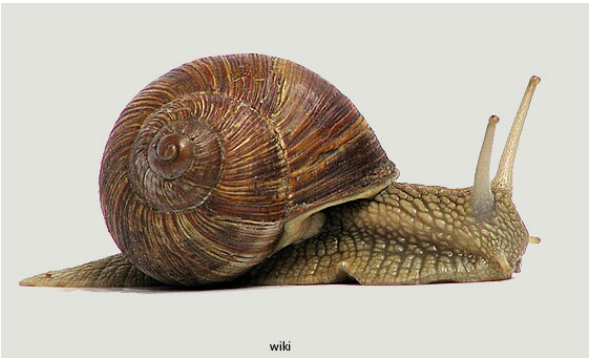
Parelaphostrongylus adult worms



Parelaphostrongylus larva



Parelaphostrongylus vector, agriolimacid slug



Parelaphostrongylus vector, helicid snail

Elaphostrongylus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Protostrongyles have indirect life-cycles involving the development of L3 in invertebrate intermediate hosts. Adult *Elaphostrongylus* in intermuscular connective tissues or brain meninges produce eggs and larvae which travel to the lungs in the bloodstream, break through to alveoli and are passed in faeces. L1 then penetrate the foot of a snail or slug and develop to L3. When eaten by ruminants, larvae migrate to connective/nervous tissues and develop into adult worms. Infections by *Elaphostrongylus cervi* cause acute neurological signs and illthrift in deer in Europe.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Protostrongylidae (infection of ruminants by ingestion of earthworm/molluscan IH carrying L3)
Genus:	*Elaphostrongylus* (parasitic in muscles of cervids)
Species:	various species cause neurological signs in cervids

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Metastrongylina (lungworms)				
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	Suids	ingestion of IH carrying L3	1
Angiostrongylidae	no or reduced buccal cavity, short	carnivores, rodents	ingestion of IH or PH	28

(lungworms)	club-shaped oesophagus		carrying L3	
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	Suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 2 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials). Several protostrongylid genera of significance to livestock production are compared below:

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm larvae**
Protostrongylidae					
Elaphostrongylus (brain worm)	3	artiodactyls	muscles, brain, lung	26-70 mm long, small buccal capsule, indirect cycle, eggs laid in tissues travel to lungs via blood, swallowed, L1 voided, L3 develop in snail IH	288-490 µm, dorsal spine
Parelaphostrongylus (meningeal worm, brain worm)	3	artiodactyls	brain, lung	17-90 mm long, small buccal capsule, indirect cycle, eggs laid in meninges travel via blood to lungs, swallowed, L1 voided, L3 develop in snail IH	300-380 µm, dorsal spine

Protostrongylus (lungworm)	27	artiodactyls, lagomorphs	respiratory tract	13-80 mm long, small buccal capsule, 6 lip-like elevations, indirect cycle, eggs laid in lungs swallowed, voided, L3 develop in snail IH	250-400 µm, fine striations
Muellerius (lungworm)	4	artiodactyls	respiratory tract	10-30 mm long, small buccal capsule, indirect cycle, eggs laid in lungs, swallowed, voided, L3 develop in snail IH	230-340 µm, dorsal spine, tail kink

The family Protostrongylidae contains 17 genera: *Cystocaulus, Dukerostrongylus, Elaphostrongylus* (syn. *Protostrongyloides*), *Imparispiculus, Mariostrongylus, Muellerius, Neostrongylus, Orthostrongylus, Paraelaphostrongylus* (syn. *Odocoileostrongylus, Neurofilaria*), *Pneumocaulus, Pneumostrongylus, Protostrongylus* (syn. *Gelanocaulus, Synthetocaulus*), *Pulmostrongylus, Skrjabinocaulus, Spiculocaulus, Umingmakstrongylus,* and *Varestrongylus*. Early works placed some of these genera into separate subfamilies (Elaphostrongylinae, Muelleriinae, Neostrongylinae, Protostrongylinae, Skrjabincaulinae, and Varestrongylinae) but recent molecular studies failed to support them, even indicating that several clustering together may be monophyletic. Clearly, further work needs to be conducted to differentiate protostrongylid species, genera and subfamilies. The genus *Elaphostrongylus* comprises worms whose males have a bursa not divided into lobes by a terminal cleft and a mound-like dorsal ray with 2-3 branches, a gubernaculum with a boat-shaped corpus but no crura or capitulum, short stout spicules, and L1 with a dorsal spine on the tail. Three species have been described in the muscles and central nervous systems of cervids, mainly from Europe.

***Elaphostrongylus* species**	**Definitive hosts**	**Location [Clinical signs]**	**Intermediate hosts**	**Distribution**
E. alces (syn. *Varestrongylus*) (brain worm)	Artiodactyla: cervid (moose, reindeer), bovid (sheep, goat); Rodentia: caviid (guinea pig)	lungs, central nervous system, intermuscular connective tissue [neurological disease]	Gastropoda: arionid (*Arion subfuscus*), helicid (*Arianta arbustorum*), gastrodontid (*Zonitoides nitidus*), succineid (*Succinea*), vitrinid (*Vitrina pellucida*); agriolimacid (*Deroceras agreste, reticulatum*), limacid (*Limax cinereoniger*)	Europe
E. cervi (*Protostrongyloides, E. panticola*) (tissue worm)	Artiodactyla: cervid (reindeer, Greenland reindeer, boreal woodland caribou, elk, red deer, Central European red deer, Norwegian red deer, Iberian red deer, Siberian red deer (maral), wapiti, sika deer, roe deer, fallow deer, mule deer, moose), bovid (sheep, goat); Rodentia: cricetid (golden hamster), caviid (guinea pig); Anura: ranid (edible frog)	lungs, central nervous system, intermuscular connective tissue [verminous pneumonia, acute neurological disease, chronic illthrift]	Gastropoda: agriolimacid (*Deroceras reticulatum*), bradybaenid (*Bradybaena fruticum*), helicid (*Arianta arbustorum, Cepaea hortensis, vindobonensis, Helix pomatia*), hygromiid (*Euomphalia strigella, Perforatella bidentata, Zenobiella nordenskioldi*), lymnaeid (*Lymnaea stagnalis, Radix ovata*), polygyrid (*Triodopsis multilineata*), succineid (*Succinea altaica*, *putris*)	Eurasia, New Zealand
E. rangiferi (syn. *E. cervi rangiferi*) (brain worm, meningeal worm)	Artiodactyla: cervid (reindeer, Greenland reindeer, boreal woodland caribou, moose, fallow deer), bovid (sheep, goat, muskox, cattle)	lungs, central nervous system, intermuscular connective tissue [verminous pneumonia, staggers, ataxia, stiff-neck]	Gastropoda: agriolimacid (*Deroceras laeve*), arionid (*Arion subfuscus*), euconulid (*Euconulus fulvus*), helicid (*Arianta arbustorum*), lymnaeid (*Lymnaea stagnalis, Galba trunculata*), succineid (*Oxyloma pfeifferi*)	Eurasia, North America

Parasite morphology: *Elaphostrongylus* spp. form 3 distinct morphological stages during their development: eggs; larvae (4 consecutive stages designated L1-L4); and adult worms. Female worms lay eggs in blood vessels to be carried to the lungs where they embryonate and hatch. Eggs initially appear as indistinct round stages 40-50 µm in diameter, but develop to become ovoid

measuring 55-67 x 46-63 μm with a central unsegmented morula clearly separated from the surrounding delicate smooth eggshell. L1 are elongate stages, measuring 288-490 x 15-24 μm depending on species, and they have conical heads, lateral alae, flask-shaped oesophagi, and curved tapering pointed tails (26-53 μm long) with a subterminal kink and a triangular cuticular dorsal spine (dorsal-spined L1 characteristic for non-protostrongylines). L2 are similar in morphology to L1, but are larger and have non-spined tails. L3 vary in size according to species (*E. alces* 675-756 x 34-43 μm; *E. rangifer* 937-1,041 x 42-49 μm; *E. cervi* 687-1,291 x 33-73 μm) and have rounded heads, flask-shaped oesophagi, and rounded tails (33-80 μm long). L4 are temporary parasitic developmental stages that have begun to show adult worm morphological characteristics, particularly in developing genitalia (male bursa and female vulva). Adults are thin slender yellow-brown worms measuring 26-70 mm in length and having round anterior mouths without lips but with 6 peribuccal ridges bearing labial papillae and amphids (perityls or non-movable lips are present in *Parelaphostrongylus*). Adults have thin cuticles with longitudinal ridges (synlophe), excretory glands opening subapically and small short buccal capsules leading to a thick stout muscular oesophagus (bottle-shaped in *E. alces*, club-shaped in *E. rangiferi*, and cylindrical in *E. cervi*). Adult worms are sexually dimorphic, with males being shorter than females (*E. rangiferi* males 26-39 x 0.19-0.25 mm, females 33-55 x 0.20-0.28 mm; *E. cervi* males 29-45 x 0.15-0.28 mm, females 49-62 x 0.20-0.24 mm; *E. alces* males 29-47 x 0.15-0.24 mm, females 60-70 x 0.29-0.32 mm). Mature males have a well-developed copulatory bursa that is not divided into distinct lobes but appears circular (*E. rangiferi* 140-160 μm, *E. cervi* 180-190 μm) or oval (*E. alces* 180-215 x 130-150 μm). The supporting ventral and lateral rays are short and blunt, the externodorsal rays are isolated, and the dorsal ray is mound-like with 2-3 branches. Males also have a highly developed gubernaculum with a boat-shaped corpus measuring 47-110 μm (but without a crura or capitulum), a genital cone with a prominent medial region, and 2 short stout spicules (200-235 μm) with alae. Mature females are didelphic with 2 ovaries and uteri connected to an ovejector (with a strong sphincter split anteriorly) opening into a common vulva on the short rounded tail.

Site of infection: Adult worms infect the intermuscular connective tissues, either beneath the epimysium or in the fasciae between muscle bundles, of their vertebrate hosts (mainly cervids). *Elaphostrongylus* spp. exhibit variable site specificity: with *E. cervi* locating preferentially in the shoulders, chest, back and fore-limbs; *E. rangiferi* in the shoulders, chest, belly and hind-limbs; and *E. alces* in the thorax and thighs. Some worms may also infect the central nervous system and spinal cord (subdural and subarachnoid spaces and occasionally ventricles). Infective larvae of each species develop in the internal tissues of their invertebrate intermediate hosts (gastropods).

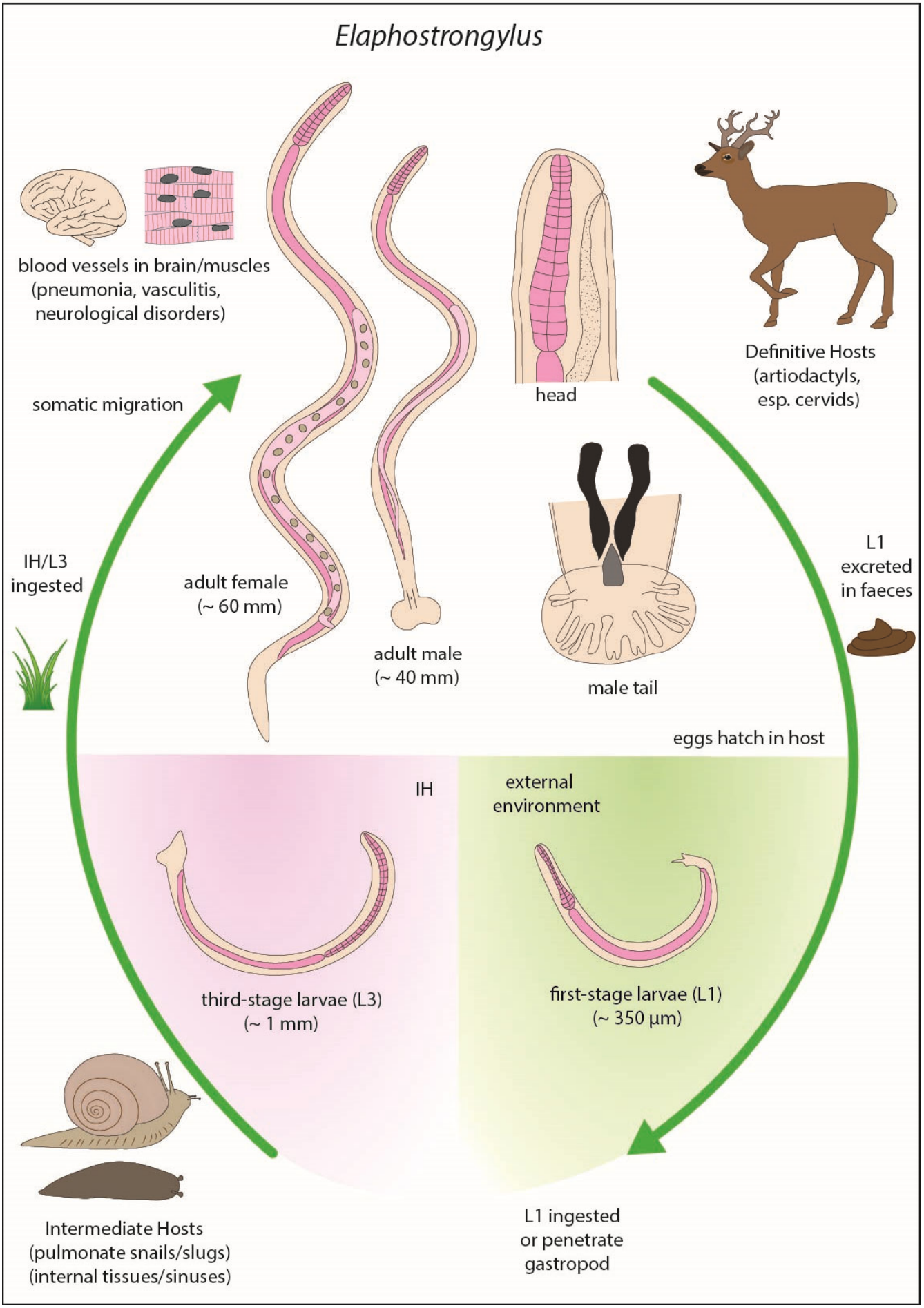
Pathogenesis: The clinical consequences of infection by individual *Elaphostrongylus* spp. varies greatly depending on the host species. Most infections are asymptomatic and subclinical in their normal permissive hosts, but infections in aberrant (abnormal) hosts may cause clinical disease, including periodic epizootics of neurological disorders in semi-domesticated and wild cervids, usually following unusually warm summers. Disease may be caused during the prepatent period when developing larvae (L3, L4) and young adults (L5) are migrating through host tissues, or during the patent period when mature adults produce eggs which are deposited in tissues releasing L1 to migrate through the lungs. Infections have been associated with both subacute respiratory diseases and debilitating neurological diseases, predominantly in young animals (< 1 year old). The former is more common and manifests as verminous interstitial pneumonia due to petechial haemorrhages, cellular infiltrates, alveolar fibrosis, focal emphysema, and eosinophilic granulomas with giant cells surrounding eggs/larvae. Clinical signs include dyspnoea (sometimes coughing), restlessness, weakness and poor condition. Yearlings may sometimes die of inanition (exhaustion caused by lack of nourishment) in winter and early spring. Neurological disease is sporadic in occurrence and severity, ranging from mild oedema and yellowish discolouration of the leptomeninges to firm adhesions between the dura and pia mater scattered over the brain, cellular infiltrates (lymphocytes, plasma cells, eosinophils), scattered axon demyelination, and small haemorrhagic foci in the muscles with green caseous plaques along fascial sheets and chronic granulomatous nodules encapsulating degenerating worms. Clinical signs include sensory and motor deficits and a range of behavioural changes, such as reduced vision (sometimes blindness), head tilting, ataxia, circling, weakness, unsteady gait, lameness, hindlimb incoordination and paralysis, recumbency, mental confusion, fearlessness, somnolence, poor growth, unthriftiness, emaciation, and death. The presence of parasites and inflammatory infiltrates in the host musculature may also produce unsightly discoloured lesions that require trimming, down-grading or condemning carcasses at meat inspection.

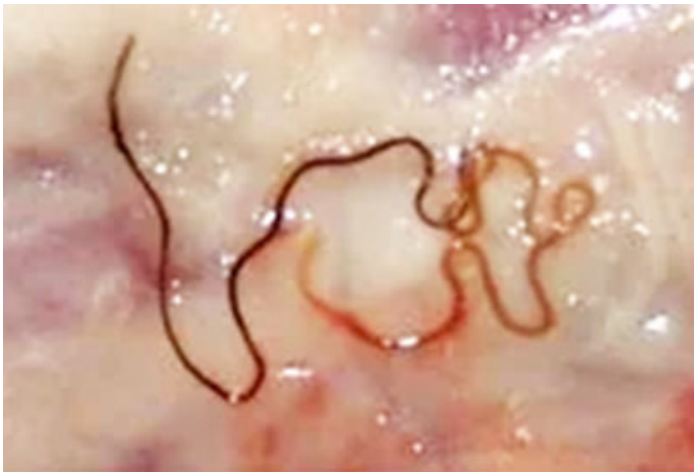
Developmental cycle and mode of transmission: *Elaphostrongylus* spp. have indirect heteroxenous life-cycles involving cyclic transmission between invertebrate intermediate hosts (harbouring infective larvae) and vertebrate definitive hosts (harbouring adult worms). The life-cycle is also unusual as the adult worms live in blood vessels (rather than the gastrointestinal tract) and produce eggs which are carried to the lungs to develop. The eggs hatch releasing L1 which invade alveoli and ascend the respiratory tree to the trachea where they are swallowed and excreted with host faeces. In the external environment, L1 survive well in cool moist conditions (up to 18 months), and even tolerate low temperatures but not freezing. They exhibit horizontal migration (dispersal) out of faecal pellets onto pastures, particularly after rainfall. The larvae infect a range of terrestrial and aquatic gastropods (agriolimacid, arionid and limacid slugs, and bradybaenid, euconulid, gastrodontid, helicid, hygromiid, lymnaeid, polygyrid, succineid and vitrinid snails) which act as obligate intermediate hosts. L1 penetrate foot tissues and moult to L2 and then L3 within 27-50 days, or longer at lower temperatures (but no development below 10°C). L3 survive for long periods in gastropods (up to 2 years), even those species which undergo aestivation. Definitive hosts become infected when they accidentally consume infected gastropods with vegetation when grazing pastures. L3 released in the gastrointestinal tract penetrate the gut wall and then migrate to the central

nervous system either by haematogenous spread or by penetrating the peritoneal/pleural cavities and migrating along lateral nerves. The larvae undergo development to L4 and then young adults (L5) in the nervous system before migrating out to settle in the skeletal muscles. *E. rangiferi* and *E. cervi* develop in the meninges (subarachnoid and subdural spaces) and sometimes the spinal canal, ventricles or neural parenchyma, while *E. alces* does not penetrate beneath the dura mater but develops epidurally near lateral nerves and surrounding fat and connective tissues within the vertebral canal. Adults worms mature in blood vessels in the intermuscular connective tissues and gravid females begin egg production. The prepatent period (time from infection to first excretion of L1) varies according to species: ranging from 39-73 days for *E. alces*, 110-206 days for *E. cervi*, and 84-252 days for *E. rangiferi*. Adult worms may live for up to 2-6 years and larval production exhibits a seasonal cycle, peaking over winter (especially in young animals) and declining over summer. Infections also tend to be more prevalent and intense in young male cervids than in females.

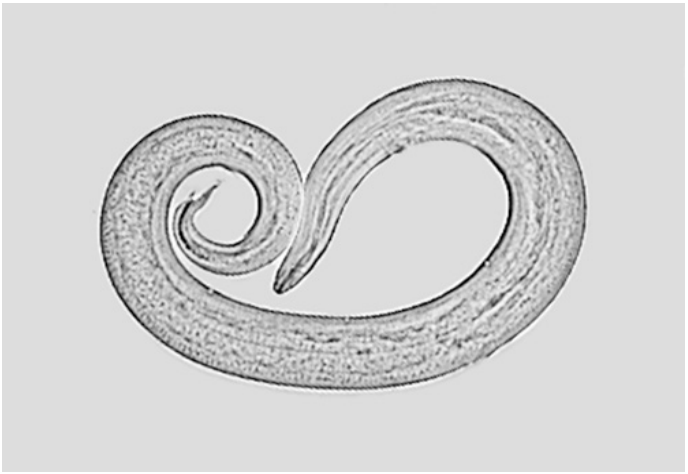
Differential diagnosis: Infections are difficult to diagnose on the basis of symptomatology as clinical signs (pneumonia and neurological disorders) may be broad, vague, transient, intermittent or attributable to a range of conditions. Patent infections are usually diagnosed by the microscopic detection of L1 in faecal samples, usually following their recovery by soaking faecal packets in water or less successfully, by Baermann filtration. However, the dorsal-spined larvae cannot be reliably differentiated from those of other protostrongylids. Infections may be diagnosed at post-mortem by the detection of adult worms in musculature or nervous tissue, but considerable dissection may be required to find coiled worms in lesions. More recently, several immunoserological techniques (indirect fluorescent-antibody tests, enzyme immunoassays, immunoelectrophoresis, Western blotting) have been developed to detect host serum antibodies against larval cuticular, somatic or excretory/secretory (ES) products, but the results have demonstrated variable levels of sensitivity and cross-reactivity. Modern molecular biological techniques have been used to characterize larval and adult stages following the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (notably the internal transcribed spacer 2 or ribosomal RNA).

Treatment and control: The treatment of clinical infections using anthelmintic drugs has yielded conflicting results: with variable efficacies recorded depending on parasite species; host species and age; severity, stage and season of infection; and drug class, dose and route of administration. Infections may be difficult to treat as the parasites undergo extensive migrations in their life-cycles, they have developmental stages in privileged sites (behind the blood-brain barrier, and sometimes encapsulated by host reactions) and re-infections are commonplace on contaminated pastures. Nevertheless, some success has been reported in treating domestic livestock and wild animals with benzimidazoles (mebendazole, fenbendazole, oxfendazole, albendazole, thiabendazole), macrocyclic lactones (ivermectin) and heterocyclic thiazines (phenothiazine, now discontinued). Best results were obtained with repeated drenching, in-feed medications or subcutaneous injections, when drug levels could be sustained to access successive developmental stages. Mebendazole and ivermectin were most effective in reducing larval production, but not in eradicating infections. During treatment, some supportive therapy may be required with steroids and other anti-inflammatory agents to safeguard against adverse reactions to dying or dead parasites. Various preventive strategies have been developed to reduce transmission rates in managed stock, notably through pasture management (avoid seasonal grazing of same pastures, regular pasture rotation (3 year cycle), cultivating and/or draining pastures, chemical control of gastropod intermediate hosts) or stock management (quarantine new livestock, separate cohorts, discourage gregarious behaviours, selectively culling young males, excluding feral animals).


Elaphostrongylus
blood vessels in brain/muscles
(pneumonia, vasculitis,
neurological disorders)
somatic migration
IH/L3
ingested
adult female
(~ 60 mm)
adult male
(~ 40 mm)
head
male tail
Definitive Hosts
(artiodactyls,
esp. cervids)
L1
excreted
in faeces
eggs hatch in host
IH
external
environment
third-stage larvae (L3)
(~ 1 mm)
first-stage larvae (L1)
(~ 350 µm)
Intermediate Hosts
(pulmonate snails/slugs)
(internal tissues/sinuses)
L1 ingested
or penetrate
gastropod



Elaphostrongylus adult worm



Elaphostrongylus larva

Aelurostrongylus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Angiostrongyles have indirect life-cycles involving the development of L3 in invertebrate intermediate hosts, and their carriage in paratenic (transport) hosts. Adult *Aelurostrongylus* in the lungs produce eggs which release L1 that are swallowed and passed in faeces. L1 then penetrate the foot of a snail or slug and develop to L3. These larvae may persist in the tissues of small mollusc-eating animals, such as rodents, birds and lizards. When cats eat intermediate or paratenic hosts, L3 migrate via the lymphatics to the lungs and develop into adult worms. Infections by *A. abstrusus* may cause respiratory signs in cats worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Angiostrongylidae (no buccal cavity, infection of vertebrates by ingestion of earthworm/molluscan IH)
Genus:	*Aelurostrongylus* (parasitic in lungs of cats)
Species:	*A. abstrusus* (causes respiratory signs in cats)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and in bursate species, elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but

some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Metastrongylina (lungworms)				
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	Suids	ingestion of IH carrying L3	1

Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	Suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 2 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials). Genera covered in this resource are tabulated below:

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm larvae
Angiostrongylidae					
Aelurostrongylus (lungworm)	5	carnivores	lungs	4-10 mm long, small buccal capsule, short club-shaped oesophagus, indirect cycle, eggs laid in lungs, swallowed, L1 voided, L3 develop in snail IH, then in small mollusc-eating PH	300-400 µm, dorsal spine
Angiostrongylus	15	carnivores,	lungs,	14-34 mm long, small buccal capsule dorsally	310-400 µm,

(lungworm)		rodents	blood vessels	hooked, indirect cycle, eggs laid in tissues travel to lungs, swallowed, L1 voided, L3 develop in snail IH, then small mollusc-eating PH	long narrow buccal chamber
Parastrongylus (lungworm)	12	rodents, primates	pulmonary arteries	10-42 mm long, vestigial buccal capsule, indirect cycle, eggs laid in vessels enter lungs, swallowed, L1 voided, L3 develop in snail IH, then small mollusc-eating PH	250-300 µm, sheathed

The family Angiostrongylidae contains 28 genera (*Aelurostrongylus, Andersonstrongylus, Angiocaulus, Angiostrongylus, Antechinostrongylus, Cercogylus, Chabaudistrongylus, Cosmostrongylus, Didelpostrongylus, Filostrongylus, Gallegostrongylus, Glirovyngylus, Gurltia, Heterostrongylus, Madafilaroides, Madangiostrongylus, Malayometastrongylus, Marsupostrongylus, Parastrongylus, Procyonostrongylus, Pulmostrongylus, Rauschivyngylus, Rodentocaulus, Sobolevingylus, Stefanskostrongylus, Thaistrongylus, Trilobostrongylus, Viverrostrongylus*) parasitic in the respiratory and vascular systems of Australian and South American marsupials, insectivores, rodents, felids, mustelids, viverrids, canids and lemurs. The genus *Aelurostrongylus* contains worms whose males have a reduced bursa and an undivided dorsal ray, no gubernaculum, stout arcuate spicules, and females with subterminal vulva and anus. Five species have been described from the lungs of felids, mustelids and rodents; and assigned to 2 subgenera on the basis of egg development: *A.* (*Aelurostrongylus*) (oviparous), and *A.* (*Perostrongylus*) (ovoviviparous). The species *A. abstrusus* is cosmopolitan in distribution and primarily infects cats where it may cause chronic cough and weight loss, particularly in cats that hunt (stray, feral and wild cats). Infective larval stages develop in invertebrate intermediate hosts (snails and slugs) and they may also be carried various small vertebrates (birds, reptiles, amphibians and rodents) which act as paratenic (transport) hosts.

***Aelurostrongylus* species**	**Definitive hosts**	**Location [Clinical signs]**	**Intermediate hosts [plus Paratenic hosts (PH)]**	**Distribution**
A. abstrusus (syn. *Sytheocaulus, Strongylus pusillus, nanus*) (cat lungworm)	Carnivora: felid (cat, wild cat, jaguarundi, Eurasian lynx, snow leopard), canid (dog)	lungs [chronic cough]	Gastropoda: achatinid (*Achatina* (*Lissachatina*) *fulica*), agriolimacid (*Agriolimax* (*Deroceras*) *laevis, agrestis, columbianus, obstrusus*), arionid (*Arion circumscriptus*, *lusitanicus*), enid (*Chondrula septemdentata*), helicid (*Cepaea hortensis, Helix aspersa, cavata, Levantina cesareana, hierosolyma, Theba pisana*), helminthoglyptid (*Helminthoglypta* (*Epiphragmophora*) *arrosa*, *californiensis*, *nickliniana tzickliuliniza*), hygromiid (*Cernuella virgata*, *Helicella barbesiana*, *vestalis joppensis, Monacha syriaca*), limacid (*Limax flavus*), planorbid (*Biomphalaria glabtrata*), pleurodontid (*Thelidomus aspera*), subulinid (*Rumina decollata*), zonitid (*Betinella nitellina*) [plus PH: Rodentia: murid (mouse, striped field mouse); Anseriformes: anatid (duck); Galliformes:	worldwide

			phasianid (chicken); Passeriformes: passerid (sparrow); Insecta: blattid (American cockroach); Anura (frog?, toad?); Serpentes (snake?); Sauria (lizard?)]	
A. dubosti (syn. *Stefanskostrongylus*)	Afrosoricida: potamogalid (giant otter shrew)			Africa
A. falciformis	Carnivora: mustelid (European badger)			Europe
A. pridhami	Carnivora: mustelid (European mink, American mink, European badger, stoat), canid (red fox)			Europe, North America
A. pottoi	Afrosoricida: tenrecid (web-footed tenrec)			Madagascar

Parasite morphology: *Aelurostrongylus* spp. form 3 different types of developmental stages: eggs; larvae (4 consecutive stages encoded L1-L4); and adult worms. The eggs are ovoid-ellipsoid in shape measuring from 63-84 x 54-70 µm and contain a central developing embryo surrounded by a thin delicate eggshell. L1 are active cylindrical forms measuring 300-400 x 18-20 µm enclosed by a cuticle covered with fine transverse striations. They have a rounded head, a simple mouth opening surrounded by 6 papillae, a rhabditiform (bulbed) oesophagus extending 33-50% the length of the body, and an undulating S-shaped (kinked) tail with distinct notches and a subterminal dorsal spine. Subsequent larval stages are similar in appearance but are larger (L2 measuring 380-480 x 28-36 µm, L3 450-530 x 26-30 µm, L4 700-880 x 35-45 µm) and their tails have lost their caudal notches and spines. L2 and L3 sometimes appear ensheathed within the cuticles of the preceding stages, but the sheaths are shed during the infection process. Adults are thin elongate brown worms measuring 4-10 mm in length and they have cuticles with longitudinal ridges (synlophe present), rounded heads with small buccal capsules, short club-shaped oesophagi, and tapering tails. Mature worms are sexually dimorphic, with male worms being smaller than females (4-7 x 0.07 mm cf. 9-10 x 0.05-0.08 mm). Males have a significantly reduced caudal bursa without distinct lobes but with visible supporting rays, a gubernaculum with a raised central section and lateral channel, and short stout spicules appearing as curved striated rods 100-130 µm long. Females are didelphic with 2 ovaries and uteri in a prodelphic configuration (parallel and anteriorly directed) connected to a common posterior vulva, sometimes with a prominent sphincter. Mature females are oviparous and produce eggs at various stages of embryonation depending on species.

Site of infection: Adult worms infect pulmonary alveoli, alveolar ducts and the terminal respiratory bronchioles in the lungs of their vertebrate definitive hosts (mainly carnivores). Infective larvae (L3) form in the tissues of invertebrate intermediate hosts (gastropods) and they may also encyst in the viscera of small vertebrate paratenic (transport) hosts (rodents, birds, frogs, lizards, snakes).

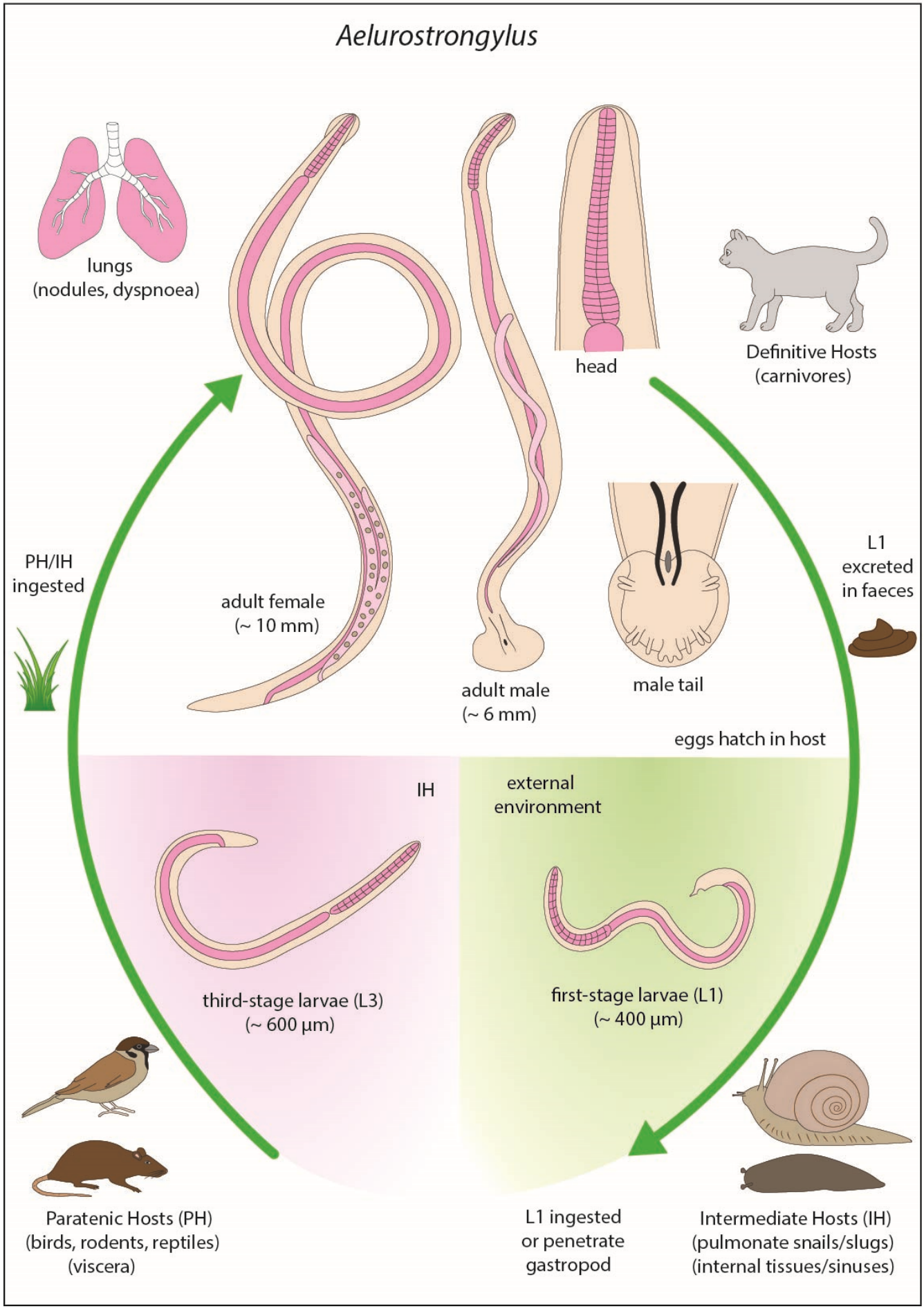
Pathogenesis: While infections are relatively common, particularly in cats, they often remain asymptomatic or subclinical although prolonged exposure may cause a chronic respiratory syndrome, especially in stray cats. The severity of disease depends primarily on parasite virulence, host susceptibility and the intensity of infection. Infective larvae migrate into the lungs, adult worms develop in the small airways and produce eggs which lodge in tissues releasing larvae which migrate out of the lungs. Parasites therefore cause traumatic damage and airway occlusion, exacerbated by strong host inflammatory responses with lesion formation in alveoli, bronchioles and local arteries. Pulmonary arteries may show disrupted endothelia as early as 10 days after infection and severe pulmonary disease may develop over 5-15 weeks with many vessels becoming occluded by 24 weeks due to hypertrophy and hyperplasia of intimal and medial layers. Obstructions and lesions in the alveoli and bronchioles may result in nodular pneumonia, bronchiolitis, peribronchiolitis and compensatory emphysema. Nodules appear as grey raised subpleural lesions 1-10 mm in diameter, which may coalesce producing large foci and confluent areas of consolidation, and even calcify in chronic infections. Clinical signs include coughing and sneezing with a mucopurulent nasal discharge, progressive dyspnoea with production of reddish mucoid sputum, tachypnoea with rapid open-mouth abdominal breathing, bronchial crackles and heart murmur (on auscultation), loss of appetite, anorexia, weight loss, adynamia (lack of strength/vigour) and death.

Developmental cycle and mode of transmission: *Aelurostrongylus* spp. have indirect heteroxenous life-cycles involving the formation of adult worms in vertebrate definitive hosts (carnivores) and the development of infective larvae in invertebrate intermediate hosts (gastropods) and sometimes their carriage in small vertebrate paratenic hosts (rodents, birds, reptiles, amphibians). Female worms lay eggs in the lungs where they embryonate and hatch releasing L1 (eggs deeply embedded in the parenchyma form ducts for larval release). The L1 than move up the mucociliary escalator to the trachea where they are swallowed and excreted in host faeces. Larval production and excretion is often sporadic, but they may remain viable in moist soils for up to 4 weeks. Terrestrial snails and slugs become infected when L1 penetrate foot tissues where they moult twice and form infective L3

which may survive for up to 2 years. The gastropods thus act as obligate intermediate hosts as they are required for larval development. If infected gastropods are eaten by some small vertebrates (birds, rodents, frogs, lizards, snakes), the L3 may invade their viscera and encyst surviving for up to 3 months. These hosts thus act as opportunistic or facultative paratenic (transport) hosts as the parasites are simply carried without undergoing further development. Definitive hosts become infected when they ingest infective L3 contained in the tissues of prey animals, usually paratenic hosts and sometimes intermediate hosts. Ingested L3 penetrate the intestinal mucosa and migrate to the lungs via the bloodstream or lymphatics where they moult twice and grow to adults in alveoli and bronchioles in 8-9 days. Following maturation and mating, female worms begin to lay eggs as early as 25 days after infection. The prepatent period (time from infection to first larval excretion) ranges from 28-42 days, peaking around 3 months but persisting for 6-9 months.

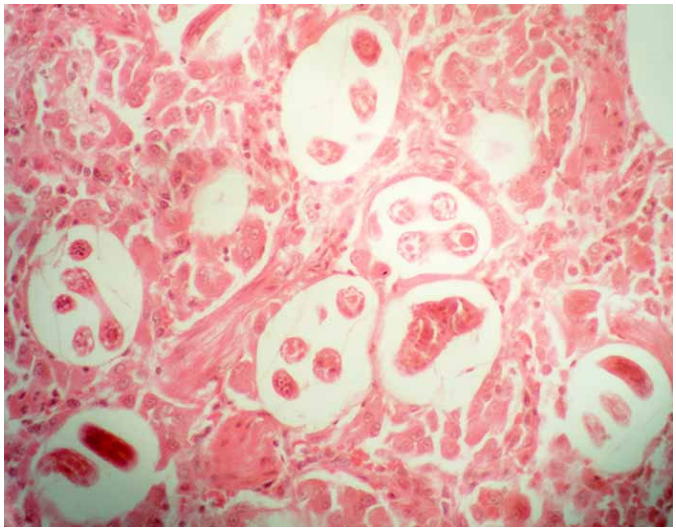
Differential diagnosis: While pulmonary signs may be suggestive of infection, particularly in animals deemed to be most susceptible (e.g. wild or stray felids), most clinical signs are non-specific and may be related to other respiratory conditions. Medical imaging techniques (X-rays and computed tomography (CT) scans) may reveal diffuse broncho-interstitial and patchy alveolar pulmonary patterns due to cellular infiltrations and nodule formation around parasites, sometimes with pleural effusions and thickening. Infections are generally confirmed by the microscopic detection of characteristic L1 (S-shaped tail with subterminal spine) either in faecal samples (smears, floats, or Baermann filtrates) or airway cytology samples (pharyngeal swabs, tracheal washings, bronchoalveolar lavages). Infections may also be diagnosed at necropsy by the detection of nodular pneumonia with multiple small grey foci or larger consolidated granulomas, but recovering the tightly coiled worms from lesions is difficult. Immunoserological tests (enzyme immunoassays) have been developed to detect specific host antibodies against worm antigens, but some cross-reactivity was found with other nematode infections. Molecular biological techniques have been used to examine phylogenetic relationships between various lungworm species following the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (internal transcribed spacer regions of ribosomal RNA).

Treatment and control: Clinical infections have been treated with variable success with several anthelmintics: including benzimidazoles (fenbendazole), macrocyclic lactones (ivermectin, moxidectin, selamectin), isoquinolines (praziquantel) and depsipeptides (emodepside); with some reports claiming complete eradication while others noted the cessation of larval excretion for 2 weeks but its resumption thereafter. Supportive therapy with bronchodilators and corticosteroids was also necessary in many instances to aid respiration and ameliorate host inflammatory reactions to dying and dead parasites. Efforts made to curb transmission by restricting contact between predatory definitive hosts and their smaller prey (particularly paratenic hosts but also including intermediate hosts) may be suitable in domestic urban situations, but are difficult to implement in peri-urban, rural or wild populations. Nevertheless, molluscicides and gravel barriers may be used to reduce gastropod populations in small communal areas, baiting and trapping may be used to control rodent populations, vertebrate pest agencies may be employed to gather feral or stray animals, and free-ranging hosts should be confined or prevented from hunting.


Aelurostrongylus
lungs
(nodules, dyspnoea)
adult female
(~ 10 mm)
adult male
(~ 6 mm)
head
male tail
Definitive Hosts
(carnivores)
PH/IH
ingested
L1
excreted
in faeces
eggs hatch in host
IH
external
environment
third-stage larvae (L3)
(~ 600 µm)
first-stage larvae (L1)
(~ 400 µm)
Paratenic Hosts (PH)
(birds, rodents, reptiles)
(viscera)
L1 ingested
or penetrate
gastropod
Intermediate Hosts (IH)
(pulmonate snails/slugs)
(internal tissues/sinuses)



Aelurostrongylus larva



Aelurostrongylus lung lesion

Angiostrongylus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Angiostrongyles have indirect life-cycles involving the development of L3 in invertebrate intermediate hosts, and their carriage in paratenic (transport) hosts. Adult *Angiostrongylus* in the pulmonary vessels of rodents and dogs produce eggs which hatch in the lungs releasing L1 that break through into alveoli to be swallowed and passed in faeces. L1 then penetrate the foot of a snail or slug and develop to L3. The larvae of some species may also persist in the tissues of small mollusc-eating animals, such as rodents and crustaceans (prawns and crabs). When definitive hosts eat intermediate or paratenic hosts, L3 migrate via the lymphatics to the lungs and develop into adult worms. Infections may cause pulmonary disease in dogs, and sometimes neurological disorders in humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Angiostrongylidae (no buccal cavity, infection of vertebrates by ingestion of earthworm/molluscan IH)
Genus:	*Angiostrongylus* (parasitic in pulmonary artery of dogs)
Species:	various species cause respiratory/neurological disease in dogs, rodents and humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and in bursate species, elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and

Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Metastrongylina (lungworms)				
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Metastrongylidae	small buccal capsule, 2 trilobed lips,	suids	ingestion of IH	1

(lungworms)	bursa with reduced dorsal lobe		carrying L3	
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	Suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 2 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm larvae
Angiostrongylidae					
Angiostrongylus (lungworm)	15	carnivores, rodents	lungs, blood vessels	14-34 mm long, small buccal capsule dorsally hooked, indirect cycle, eggs laid in tissues travel to lungs, swallowed, L1 voided, L3 develop in snail IH, then small mollusc-eating PH	310-400 µm, long narrow buccal chamber

Aelurostrongylus (lungworm)	5	carnivores	lungs	4-10 mm long, small buccal capsule, short club-shaped oesophagus, indirect cycle, eggs laid in lungs, swallowed, L1 voided, L3 develop in snail IH, then in small mollusc-eating PH	300-400 µm, dorsal spine
Parastrongylus (lungworm)	12	rodents, primates	pulmonary arteries	10-42 mm long, vestigial buccal capsule, indirect cycle, eggs laid in vessels enter lungs, swallowed, L1 voided, L3 develop in snail IH, then small mollusc-eating PH	250-300 µm, sheathed

The family Angiostrongylidae contains 28 genera (*Aelurostrongylus, Andersonstrongylus, Angiocaulus, Angiostrongylus, Antechinostrongylus, Cercogylus, Chabaudistrongylus, Cosmostrongylus, Didelpostrongylus, Filostrongylus, Gallegostrongylus, Glirovyngylus, Gurltia, Heterostrongylus, Madafilaroides, Madangiostrongylus, Malayometastrongylus, Marsupostrongylus, Parastrongylus, Procyonostrongylus, Pulmostrongylus, Rauschivyngylus, Rodentocaulus, Sobolevingylus, Stefanskostrongylus, Thaistrongylus, Trilobostrongylus, Viverrostrongylus*) parasitic in the respiratory and vascular systems of Australian and South American marsupials, insectivores, rodents, felids, mustelids, viverrids, canids and lemurs. The genus *Angiostrongylus* contains a variety of lungworms with a typical bursa and posterior vulva infecting the lungs and blood vessels of insectivores, rodents, felids and canids, and using gastropods as intermediate hosts for larval development. Two subgenera are recognised: *A.* (*Angiostrongylus*) syn. *Haemostrongylus, Cardionema,* and *Angiocaulus* (male worms with a bursal externolateral ray separate from the 2 other lateral rays); and *A.* (*Parastrongylus*) syn. *Pulmonema, Rattostrongylus* and *Morerastrongylus* (males with bursal externolateral ray joined with other lateral rays into a common stalk). The latter subgenus has been elevated to generic status by several workers although many reference texts still place species in the genus *Angiostrongylus* rather than *Parastrongylus*, especially those of considerable biomedical importance (*P. cantonensis* and *P. costaricensis,* both considered in the following separate section). The species *A. vasorum* is considered to be a newly emergent or re-emergent disease of dogs, particularly in southern Europe and isolated areas of Africa and North America.

***Angiostrongylus* species**	**Definitive hosts**	**Location [Clinical signs]**	**Intermediate hosts [plus Paratenic Hosts (PH)]**	**Distribution**
A. andersoni	Rodentia: murid (Nigerian gerbil, Kemp's gerbil)	lungs [abscesses]	Gastropoda: helicid (*Helix aspersa*), lymnaeid (*Lymnea stagnalis*), planorbid (*Planorbarius corneus*)	Africa
A. blarini	Eulipotyphla: soricid (northern short-tailed shrew)			North America
A. chabaudi	Carnivora: felid (wild cat)	lungs		Europe
A. daskalovi	Carnivora: mustelid (beech marten, European pine marten, European badger)	pulmonary arteries		Europe
A. felineus	Carnivora: felid (jaguarundi)	pulmonary arteries		South America
A. gubernaculatus	Carnivora: mephitid (striped skunk), mustelid (American badger), canis (Island fox)	heart (right ventricle)		North America
A. lenzii	Rodentia cricetid (montane grass mouse)	pulmonary arteries		South America
A. michiganensis	Eulipotyphla: soricid (common shrew, smoky shrew)			Eurasia
A. minutus	Eulipotyphla: talpid (Japanese shrew mole)			Asia
A. morerai	Rodentia: cricetid (dolorous grass mouse)	pulmonary arteries		South America
A. ondatrae	Rodentia: cricetid (musk rat)			Holarctic
A. raillieti	Carnivora: canid (dog, pampas fox, crab-eating fox), procyonid (South American coati)	pulmonary arteries		South America
A. soricis	Eulipotyphla: soricid (Laxmann's shrew,			Eurasia

	Eurasian pygmy shrew)			
A. ten incertae sedis	Carnivora: mustelid (Japanese marten)	heart		Asia
A. vasorum (French heartworm)	Carnivora: canid (dog, wolf, coyote, jackal, hoary fox, red fox, Iberian fox, pampas fox, hoary fox, crab-eating fox, African desert fox), felid (cat), mustelid (European badger, tayra); Rodentia: murid (African grass rat)	pulmonary arteries, right ventricle [chronic cough, dyspnoea, exercise intolerance]	Gastropoda: achatinid (*Achitina fulica*, *Lissachatina fulica, Prosopeas javanicum, Subulina octona*), agriolimacid (*Deroceras reticulatum*), arionid (*Arion ater, hortensis, rufus, vulgaris* (*lusitanicus*)), bradybaenid (*Bradybaena similaris*), clausiliid (*Cochlodina laminata*), helicid (*Arianta arbustorum, Helix pomatia, Cepaea nemoralis, Cornu asperum*), limacid (*Limax flavus*), physid (*Physa*), planorbid (*Biomphalaria glabrata, pfeifferi, tenagophila*), succineid (*Omalonyx, Succinea putris*), veronicellid (*Laevicaulis alte*), unplaced (*Eceparypha physana*) [plus PH: Rodentia: murid (rat, mouse); Anura: ranid (European common frog); Galliformes: phasianid (chicken); Sauria (lizard?)]	worldwide (except North America)

Parasite morphology: *Angiostrongylus* spp. form 3 different types of morphological stages in their developmental cycles: eggs; larvae (4 stages designated L1-L4); and adult worms. The eggs are ellipsoidal thin-shelled stages measuring 63-67 x 37-42 µm and contain a developing embryo (morula). L1 are elongate cylindrical coiled stages measuring from 310-400 µm in length and they have rounded heads with a small cephalic button, a long narrow buccal chamber, a flask-shaped muscular oesophagus extending 33-50% of the body length, and a sharply-pointed wavy tail with a subterminal dorsal notch (kink) and a small ventral indentation. L2 are similar in morphology but slightly longer, while L3 are longer still measuring 425-524 x 23-34 µm and are characterised by the possession of an anterior rod-shaped structure, and a sharply-pointed tail. L4 are transient parasitic stages that have lost the anterior rod-shaped structure and have blunt tails. Adults are medium-sized white-pink worms measuring 14-34 mm long) and they have dorsally hooked mouths (similar to the hookworms), a round oral opening without adornments, a small rudimentary buccal capsule, and are surrounded by a cuticle with longitudinal ridges (synlophe). Adult worms are sexually dimorphic, with females being longer than males (15-34 x 0.28-0.56 mm cf. 14-25 x 0.25-0.42 mm). Mature females are didelphic with 2 ovaries and uteri in a prodelphic configuration (parallel and anteriorly directed) which appear as white tubules spirally twisted around the red gut (resembling a barber's pole). The oviducts connect to a common posterior vulva, sometimes equipped with a prominent sphincter. Mature males have a small caudal copulatory bursa with lateral lobes supported by 6 rays (2 partly fused ventral rays, 3 lateral rays, separate single externolateral ray) and a dorsal lobes supported by a stout dorsal ray (with stout terminal branches). [Note that differences in bursal ray structure have been used to differentiate *Angiostrongylus* (ventrolateral ray separated) from *Parastrongylus* (ventrolateral ray not separated) either as different genera or subgenera]. Males also possess a rudimentary gubernaculum and 2 elongate curved spicules.

Site of infection: Larval stages undergo extensive migrations through the tissues of their definitive hosts, moulting and developing into subadults along the way, before settling in their final predilection sites and maturing to fertile adult worms. Different species exhibit relatively strict tissue tropism, with larvae moulting either in the lungs (e.g. *A. andersoni*) or lymphatics (e.g. *A. vasorum*). Adult worms then mature in the lung parenchyma (e.g. *A. andersoni*) or in the pulmonary circulation (pulmonary arteries, right ventricle of heart, e.g. *A. vasorum*). Infective larvae (L3) develop in the tissues of various gastropods (aquatic and terrestrial snails and slugs), and they may also be carried in the tissues of various paratenic (transport) hosts, such as amphibians and rodents.

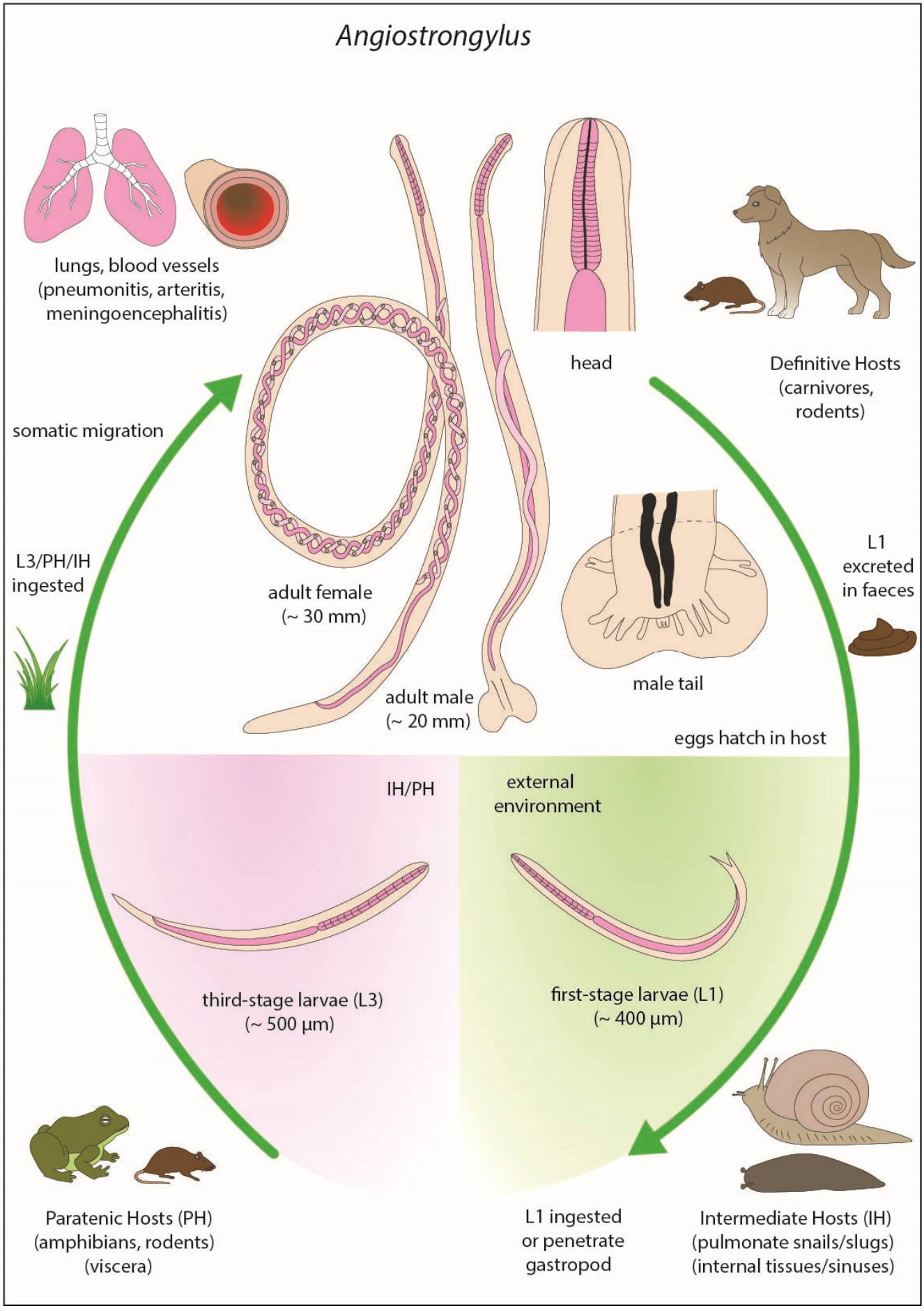
Pathogenesis: Many infections in definitive hosts have been detected fortuitously during post-mortem surveys of small carnivores or rodents, often without any indications of disease. Clinical infections, however, have been reported in wild and domestic

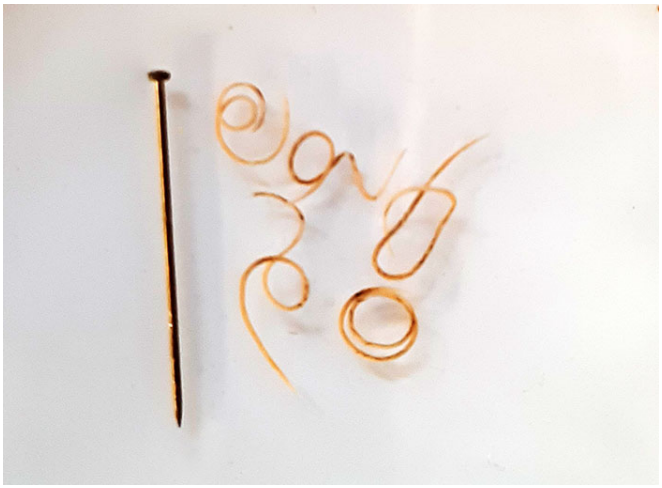
carnivores, particularly canids. Canine angiostrongyliasis rarely presents as an acute disease (dyspnoea, violent cough, white-yellow occasionally bloody sputum), more often as a chronic condition developing over many months with widely varying clinical signs (respiratory, cardiovascular and neurological). Invading migrating larvae cause traumatic damage to host tissues, while adult worms and the eggs and larvae they produce elicit strong inflammatory host responses, all contributing to circulatory occlusions with downstream effects. Infections in the lungs may cause verminous interstitial pneumonia with pulmonary sclerosis and emphysema, while damage to blood vessels leads to arteritis, haemorrhagic conditions and coagulation abnormalities (including thrombotic endarteritis, periarteritis, petechial ecchymoses, bleeding in the abdominal and/or thoracic cavities, subcutaneous haematomas, with oedema, haemothorax, hydropericardium, and ascites). The clinical signs most commonly observed are coughing, exercise intolerance, weight loss and poor general body condition, but they may progress to include severe respiratory distress with dyspnoea, coughing, haemoptysis, gagging, vomiting, nasal discharge, melena, anorexia, depression and stunted growth. Animals may develop cardiac insufficiency and hypertrophy, and die due to congestive heart failure. Aberrant or erratic larval migrations and bleeding in the nervous system may also cause neurological signs, including meningitis, epileptic seizures, ataxia, paraplegia, cranial nerve deficits, vestibular signs, blindness and proprioceptive deficits.

Developmental cycle and mode of transmission: *Angiostrongylus* spp. have indirect heteroxenous life-cycles involving cyclic transmission between vertebrate definitive hosts (in which adult worms develop) and invertebrate intermediate hosts (in which infective larvae develop). Eggs laid by female worms in the bloodstream are carried to the lungs where they lodge to develop and hatch releasing larvae. The L1 penetrate into alveolar air-spaces and ascend the respiratory mucociliary escalator to the trachea where they are swallowed and excreted with host faeces. In the external environment, L1 infect gastropods either by ingestion (e.g. *A. andersoni*) or percutaneous penetration of the foot, or both (e.g. *A. vasorum*). A variety of terrestrial and aquatic gastropods (snails and slugs) act as obligate intermediate hosts in which L1 moult twice and form infective L3 in nodules in the connective tissues and muscles over 15-17 days (longer in cooler conditions). Infections are more prevalent in regions with wet mild climates that are favourable for gastropod development. Infective L3 of *A. vasorum* may also be carried in the tissues of various paratenic (transport) hosts (rodents, amphibians) which have consumed infected gastropods. Definitive hosts become infected when they consume L3 either in intermediate hosts or in paratenic hosts. The routes of infection and sites of development in definitive hosts varies depending on the parasite species: with larvae developing either in the lymphatics or lungs; and adults developing either in the lung parenchyma or in the pulmonary circulation (pulmonary arteries, right ventricle of heart). The simplest cycle is demonstrated by *A. andersoni* when L3 migrate from the gut via the hepatic portal system to the liver within 14 hours and then the lungs within 24-28 hours where they moult to L4 at 2-3 days and then L5 at 5-7 days. The prepatent period (time from infection to first excretion of L1) ranges from 24-31 days. The cycle of *A. vasorum* is more complex as L3 migrate from the gut to visceral lymph nodes where they moult twice in 4-5 days to subadults (L5) before migrating via the hepatic portal vein to the liver and then via the caudal vena cava to the right ventricle and pulmonary arteries by 9-10 days after infection. Here they mature to adult worms which produce eggs that hatch releasing L1 around 45 days (although the prepatent period is highly variable ranging from 28-108 days). It is thought animals may be infected for life with intermittent excretion of L1.

Differential diagnosis: While the occurrence of cardiovascular and pulmonary conditions may be indicative of infection, the clinical signs exhibited are highly variable and nonspecific. Similarly, medical imaging techniques (radiography, computed tomography) may reveal suspicious lesions, including diffuse peribronchial, interstitial and alveolar densities, multiple nodules in peripheral caudal lung lobes, and enlargement of the right heart and pulmonary artery, but other causes may be involved. Infections are therefore generally diagnosed by the microscopic detection of L1 in faecal samples, usually following their recovery by Baermann filtration. Multiple samples should be tested, however, as larval excretion is intermittent. L1 may also be detected in tracheal washes, bronchoalveolar lavages, fine needle lung aspirates and sometimes in urine. Infections may be diagnosed at post-mortem by the detection of lesions and parasites in respiratory tissues, although worms are difficult to remove from tissues. Several research studies have developed immunological tests (enzyme immunoassays and Western blots) to detect specific host antibodies against parasite antigens, but some problems were encountered with cross-reactivity. Molecular biological techniques have been used to characterize parasite species by polymerase chain reaction (PCR) amplification of parasite DNA, including nuclear genes (internal transcribed spacer region 2 of ribosomal RNA) and mitochondrial genes (cytochrome c oxidase subunit I).

Treatment and control: A variety of anthelminthic drugs have been used to treat clinical infections, including benzimidazoles (fenbendazole, albendazole, mebendazole), imidazothiazoles (levamisole) and macrocyclic lactones (ivermectin, moxidectin, milbemycin). Care was required during treatment to avoid exacerbating clinical signs, with corticosteroids, bronchodilators, expectorants and diuretics used to manage adverse reactions. On several occasions, lumbar puncture and analgesics were used to relieve signs of meningitis. Various preventive strategies may be applied in domestic and peri-domestic settings to reduce transmission rates to intermediate hosts (reduce faecal contamination through better sanitation), limit gastropod populations (using barriers or molluscicides), avoid transmission to paratenic hosts (vertebrate pest control, esp. rodents), and to minimise larval uptake by final hosts (improving hygiene, providing clean food and water, preventing hunting). Obviously, such interventions are impractical in larger non-domestic situations, so infections may persist in wild or feral animal populations.

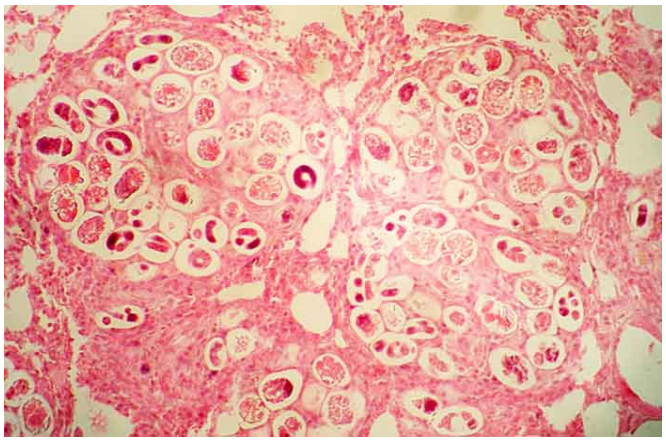

Angiostrongylus
lungs, blood vessels
(pneumonitis, arteritis,
meningoencephalitis)
head
Definitive Hosts
(carnivores,
rodents)
somatic migration
L3/PH/IH
ingested
adult female
(~ 30 mm)
adult male
(~ 20 mm)
male tail
L1
excreted
in faeces
eggs hatch in host
IH/PH
external
environment
third-stage larvae (L3)
(~ 500 µm)
first-stage larvae (L1)
(~ 400 µm)
Paratenic Hosts (PH)
(amphibians, rodents)
(viscera)
L1 ingested
or penetrate
gastropod
Intermediate Hosts (IH)
(pulmonate snails/slugs)
(internal tissues/sinuses)



Angiostrongylus adult worms



Angiostrongylus adult worms



Angiostrongylus lung lesion



Angiostrongylus larva

Parastrongylus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Angiostrongyles have indirect life-cycles involving the development of L3 in invertebrate intermediate hosts, and their carriage in paratenic (transport) hosts. The genus *Parastrongylus* contains the rat lungworm *P. cantonensis* (formerly *Angiostrongylus cantonensis*). Adult worms in the pulmonary vessels of rodents produce eggs which hatch in the lungs releasing L1 that break through into alveoli to be swallowed and passed in faeces. L1 then penetrate the foot of a snail or slug and develop to L3. The larvae may also persist in the tissues of small mollusc-eating animals, such as crustaceans (prawns and crabs). When definitive hosts eat intermediate or paratenic hosts, L3 migrate via the lymphatics to the lungs and develop into adult worms. Infections by migrating stages may cause eosinophilic meningoencephalitis in humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Angiostrongylidae (no buccal cavity, infection of vertebrates by ingestion of earthworm/molluscan IH)
Genus:	*Parastrongylus* (parasitic in pulmonary artery of rats)
Species:	*P. cantonensis* (formerly *Angiostrongylus cantonensis*) causes eosinophilic meningoencephalitis in humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and in bursate species, elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and

Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these ‘bursate’ nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Metastrongylina (lungworms)				
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Metastrongylidae	small buccal capsule, 2 trilobed lips,	suids	ingestion of IH carrying	1

(lungworms)	bursa with reduced dorsal lobe		L3	
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	Suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 2 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Worm larvae
Angiostrongylidae					
Parastrongylus (lungworm)	12	rodents, primates	pulmonary arteries	10-42 mm long, vestigial buccal capsule, indirect cycle, eggs laid in vessels enter lungs, swallowed, L1 voided, L3 develop in snail IH, then small mollusc-eating PH	250-300 µm, sheathed
Angiostrongylus	15	carnivores,	lungs,	14-34 mm long, small buccal capsule dorsally	310-400 µm,

(lungworm)		rodents	blood vessels	hooked, indirect cycle, eggs laid in tissues travel to lungs, swallowed, L1 voided, L3 develop in snail IH, then small mollusc-eating PH	long narrow buccal chamber
Aelurostrongylus (lungworm)	5	carnivores	lungs	4-10 mm long, small buccal capsule, short club-shaped oesophagus, indirect cycle, eggs laid in lungs, swallowed, L1 voided, L3 develop in snail IH, then in small mollusc-eating PH	300-400 µm, dorsal spine

The family Angiostrongylidae contains 28 genera (*Aelurostrongylus, Andersonstrongylus, Angiocaulus, Angiostrongylus, Antechinostrongylus, Cercogylus, Chabaudistrongylus, Cosmostrongylus, Didelpostrongylus, Filostrongylus, Gallegostrongylus, Glirovyngylus, Gurltia, Heterostrongylus, Madafilaroides, Madangiostrongylus, Malayometastrongylus, Marsupostrongylus, Parastrongylus, Procyonostrongylus, Pulmostrongylus, Rauschivyngylus, Rodentocaulus, Sobolevingylus, Stefanskostrongylus, Thaistrongylus, Trilobostrongylus, Viverrostrongylus*) parasitic in the respiratory and vascular systems of Australian and South American marsupials, insectivores, rodents, felids, mustelids, viverrids, canids and lemurs. The genus *Angiostrongylus* contains a variety of lungworms with a typical bursa and posterior vulva infecting the lungs and blood vessels of insectivores, rodents, felids and canids, and using gastropods as intermediate hosts for larval development. Two subgenera are recognised: *A.* (*Angiostrongylus*) syn. *Haemostrongylus, Cardionema* and *Angiocaulus* (male worms with a bursal externolateral ray separate from the 2 other lateral rays); and *A.* (*Parastrongylus*) syn. *Pulmonema, Rattostrongylus* and *Morerastrongylus* (males with bursal externolateral ray joined with other lateral rays into a common stalk). The latter subgenus has been elevated to generic status by several workers although many reference texts still place species in the genus *Angiostrongylus* rather than *Parastrongylus*, especially those of considerable biomedical importance (*P. cantonensis, P. malaysiensis, P. costaricensis* and *P. mackerrasae*). Most species are primarily parasites of rodents and are transmitted by a range of gastropod intermediate hosts and some small vertebrate paratenic hosts. Humans may become accidentally infected when consuming infective L3 in snails, in paratenic hosts, or on contaminated vegetables. Larvae migrate through host tissues, some may moult and develop to sexual maturity producing eggs, but they eventually die. Nevertheless, they may cause severe clinical disease in humans, including eosinophilic meningoencephalitis in South-East Asia, and eosinophilic enteritis in Central and South America.

Parasite species	**Definitive Hosts**	**Location [Clinical sign**	**Intermediate hosts [plus Paratenic Hosts (PH)]**	**Distribution**
Parastrongylus cantonensis (formerly *Angiostrongylus*) [rat lungworm]	Rodentia: murid (black rat, brown rat, Philippine black rat, dusky field rat, yellow-breasted rat, white-bellied rat, Himalayan field rat, Turkestan rat, Ryukyu Island tree rat, lesser bandicoot rat, greater bandicoot rat, Bower's white-toothed rat, Polynesian rat, grassland mosaic-tailed rat, fawn-footed mosaic-tailed rat, house mouse), cricetid (eastern wood rat), capromyid (hutia); Eulipotyphla: soricid (Asian house shrew); Chiroptera: pteropodid (grey-headed flying fox, black flying fox); Perissodactyla: equid (horse); Artiodactyla: bovid (Barbary sheep), camelid (alpaca); Didelphimorphia: didelphid (Virginia opossum); Diprotodontia: macropodid (red-necked wallaby, purple-necked rock wallaby, parma wallaby, western grey kangaroo), potoroid (rufous bettong), pseudocheirid (common ringtail possum), phalangerid (brushtail possum); Peramelemorphia:	pulmonary arteries, right ventricle [eosinophilic meningoencephalitis, neurological lesions]	Gastropoda: achatinid (*Achatina fulica, Archachatina marginata, Subulina octona*), agriolimacid (*Deroceras laeve*, *reticulatum*), ampullariid (*Ampullaria canaliculata*, *Lanistes carinatus, Pila, Pomacea canaliculata, maculata, paludosa, poeyana*), ariophantid (*Macrochlamys indica, loana, Microparmarion malayanus, Parmarion martensi*), bradybaenid (*Acusta despecta, Bradybaena brevispira, circulus, ravida, similaris*), camaenid (*Camaena cicatricosa, Plectotrophis appanata, Satsuma mercatoria, Trichochloris hungertordiana, rufopila*), cepolid (*Jeanneretia bicincta, subtusulcata*), cyclophorid (*Cyclophorus*), discid (*Anguispira alternata*), helicarionid (*Helicarion*), helicid (*Emoda sagrayama, Helicina adspersa, Viana regina*), helminthoglyptid (*Polymita muscarum, picta*), limacid (*Lehmannia poiureri, Limax flavus, maximus, Ambigolimax* (*Lehmannia*) *valentiana*), neocyclotid (*Poteria*), oleacinid (*Oleacina*), orthalicid (*Liguus fasciatus*), philomycid	Asia, Australia, India, Africa, Americas

	thylacomyid (greater bilby); Carnivora: canid (dog, fox); Primates: atelid (black howler), hylobatid (lar gibbon), lemurid (red-ruffed lemur), callitrichid (cotton-top tamarin), cebid (Guianan squirrel monkey), hominid (human); Psittaciformes: cacatuid (yellow-tailed black cockatoo, gang cockatoo); Caprimulgiformes: podargid (tawny frogmouth); Gruiformes: gruid (brolga); Cuculiformes: cuculid (channel-billed cuckoo)		(*Philomycus bilineatus, carolinianus, Meghimatium bilineatum*), planorbid (*Biomphalaria glabrata, Gyraulus spirillus, Hippeutis umbilicalis*), pleurodontid (*Pleurodonte sagemon, Thelidomus aspera, Zachryia auricoma, guanensis*), polygyrid (*Mesodon thyroidus, Polygyra triodontoides*), sagdid (*Sagda*), spiraxid (*Euglandina rosea*), urocoptid (*Tetrentodon filiola*, *perdidoensis*), veronicellid *(Laevicaulis alte, Sarasinula plebeia, Vaginulus alte, ameghini, yuxjsjs, Veronicella alte, cubensis*), viviparid (*Cipangopaludina chinensis, Sinotaia* (*Bellamya*) *aeruginosa*, *quadrata*) [plus PH: Anura: hylid (golden bell frog), ranid (American bullfrog), dicroglossid (Asian grass frog), bufonid (Asian toad), rhacophorid (common tree frog); Sauria: varanid (Bengal monitor); Bivalvia: ostreid oysters (*Crassostrea rizophorae*, *virginica*), Decapoda: coenobitid crab (*Birgus latra*), palaemonid shrimp (*Macrobrachium lar*); Rhabditophora: geoplanid flatworm (*Platydemus manokwari*)]	
Parastrongylus costaricensis (formerly *Angiostrongylus*)	Rodentia: murid (brown rat, black rat, house mouse), cricetid (hispid cotton rat, short-tailed cane rat, Watson's climbing rat, Tome's rice rat, northern pygmy rice rat, black-footed pygmy rice rat, rat-headed rice rat, Costa Rican dusky rat, Mexican deer mouse), echimyid (Tome's spiny rat), heteromyid (Panamanian spiny pocket mouse, Salvin's spiny pocket mouse); Carnivora: procyonid (white-nosed coati, raccoon); Didelphimorphia: didelphid (Virginia opossum); Primates: atelid (black-handed spider monkey), aotid (Nancy Ma's night monkey), callitrichid (moustached tamarin), hylobatid (siamang), hominid (human)	mesenteric arteries [eosinophilic enteritis, necrotic gut lesions]	Gastropoda: achatinid (*Subulina octona*), ampullariid (*Pomacea flagellata*), bradybaenid (*Bradybaena similaris*), bulinid (*Bulinus*), helicid (*Helix aspersa*), limacid (*Limax flavus*, *maximus*), lymnaeid (*Lymnaea*), planorbid (*Biomphalaria glabrata*, *straminea*, *Helisoma trivolvis*), strophocheilid (*Megalobulinus abbreviatus*), succineid (*Succinea*), veronicellid (*Belocaulus angustipes*, *Phyllocaulis soleiformis*, *variegatus*, *Sarasinula marginata*, *plebeia*, *Vaginulus plebeius*) [plus PH: Anura: ranid (frog); Malacostraca: palaemonid (freshwater prawn)]	Americas
P. dujardini	Rodentia: murid (wood mouse, yellow-necked mouse, house mouse), cricetid (European pine vole, bank vole, hamster)	pulmonary arteries, heart	Gastropoda: planorbid (*Biomphalaria glabrata*)	Europe
P. mackerrasae	Rodentia: murid (brown rat,	pulmonary arteries,	Gastropoda: agriolimacid	Australia

	bush rat, Australian swamp rat); Chiroptera: pteropodid (black flying fox); Primates: hominid (human)	right ventricle, lungs	(*Deroceras laeve*), helicarionid (*Helicarion*)	
P. malaysiensis	Rodentia: murid (Malayan field rat, Polynesian rat, brown rat, black rat, Malayan house rat, ricefield rat, Muller's giant Sunda rat, Bower's white-toothed rat, long-tailed giant rat, Annandale's rat, red spiny rat, Whitehead's spiny rat, dark-tailed tree rat); Eulipotyphla: soricid (Asian house shrew); Scandentia: tupaiid (common treeshrew); Primates: cercopithecid (Taiwanese macaque), hominid (human)	pulmonary arteries, right ventricle, lungs	Gastropoda: achatinid (*Achatina fulica*, *Allopeas javanicum*, *Rumina decollata*), ampullariid (*Pila sututu*), ariophantid (*Macrochlamys resplendens*, *Microparmarion malayanus*, *Girasia peguensia*), lymnaeid (*Lymnea rubiginosa*), planorbid (*Biomphalaria glabrata*, *Indoplanorbus exustus*), veronicellid (*Laevicaulis alte*), viviparid (*Bellamyia ingalisiana*)	Asia
P. petrovi	Rodentia: glirid (forest dormouse)	heart, bronchi		Russia
P. ryjikovi	Rodentia: cricetid (northern red-backed vole)	pulmonary arteries		Russia
P. sandarsae	Rodentia: murid (Natal multimammate mouse, Indian gerbil)	pulmonary arteries		Africa
P. schmidti	Rodentia: cricetid (marsh rice rat, hispid cotton rat, white-footed mouse, golden hamster), murid (house mouse, brown rat, Mongolian gerbil)	pulmonary arteries	Gastropoda: planorbid (*Biomphalaria glabrata*), polygyrid (*Polygyra septemvolva*)	North America
P. sciuri	Rodentia: sciurid (red squirrel)	pulmonary arteries		Europe
P. siamensis	Rodentia: murid (house mouse, long-tailed giant rat, small white-toothed rat, black rat, red spiny rat, greater bandicoot rat, Savile's bandicoot rat, Mongolian gerbil), cricetid (hispid cotton rat); Primates: cercopithecid (crab-eating monkey)	mesenteric arteries	Gastropoda: planorbid (*Biomphalaria glabrata*)	Asia
P. tateronae	Rodentia: murid (eastern broad-toothed field mouse)	pulmonary arteries		Africa

Parasite morphology: *Parastrongylus* spp. form 3 different morphological stages in their developmental cycles: eggs; larvae (4 successive stages usually designated as L1-L4); and sexually dimorphic adult worms. Eggs are thin-shelled ovoid stages measuring 60-110 µm in longest diameter and they are partially embryonated containing a central multicellular morula. L1 are elongate cylindrical stages measuring 250-300 x 15 µm and covered by a transversely striated cuticle. They have an anterior triangular oral opening surrounded by six cephalic papillae, broad lateral alae extending along the body, and a sharply-pointed ventrally curved tail. L2 are slightly larger measuring 320-450 x 30 µm and have a distinct anterior structure with a keratinous cap. L3 measure 450-510 x 20 µm and the anterior structure has developed T-bar structures on the anterior tip. Both L2 and L3 may appear ensheathed if they retain the cuticle of the former stage, but the sheaths are shed during the infection process. L4 are transient parasitic stages measuring up to 1-2 mm x 40 µm and subadult stages (sometimes designated L5) measure 2-4 mm x 60 µm before maturing. growing up to 20-40 mm long as mature adults. Adults are slender elongate lungworms 10-42 mm long with filariform bodies tapering at both ends and bound by a tough cuticle with transverse striations (synlophe present). They have a small lipless mouth with a number of small hook-like teeth, a small buccal capsule, a stout oesophagus with a posterior valve leading to the elongate intestines terminating in a subterminal anus/cloaca. Adult worms are sexually dimorphic, with females generally larger than males (17-42 x 0.26-0.56 mm cf. 15-25 x 0.25-0.42 mm for *P. cantonensis,* 27-40 x 0.10-0.35 mm cf. 15-20 x 0.1-0.3 mm for *P. costaricensis*). Mature female worms are didelphic having 2 ovaries and uteri in a prodelphic configuration (parallel and anteriorly directed) and appearing as white tubules spirally wound around the red gut (resembling a barber's pole). The oviducts connect to a

common posterior vulva, sometimes with a prominent sphincter or protective flap, and the tail is conical and slightly curved terminating in a small refringent spine. Mature males have a small but well-developed caudal copulatory bursa comprising 2 lateral lobes each supported by 6 rays (2 fused ventral rays, 4 lateral rays arising from common stalk) and a small dorsal lobe supported by a single dorsal ray (with a terminal branch). [Note that differences in bursal ray structure have been used to differentiate *Parastrongylus* (ventrolateral ray not separated) from *Angiostrongylus* (ventrolateral ray separated) either as different genera or subgenera]. Males also possess a weakly developed gubernaculum (0.01 mm) and 2 slender elongate striated spicules (0.3-1.3 mm) with blunt tips (pointed in *P. costaricensis*).

Site of infection: Different *Parastrongylus* spp. exhibit tissue tropism within their definitive hosts, with larvae and adults infecting specific tissues. Adult worms infect either the lung parenchyma (e.g. *P. dujardini, P. schmidti*), pulmonary circulation (pulmonary arteries, right ventricle of heart) (e.g. *P. cantonensis, P. mackerrasae, P. malaysiensis*) or the mesenteric circulation (mesenteric arteries (e.g. *P. siamensis*) or veins (e.g. *P. costaricensis*)). Pre-adult larval stages undergo extensive migrations through host tissues, moulting either in the lungs (e.g. *P. dujardini, P. schmidti*), lymphatics (e.g. *P. siamensis*), or circulation (e.g. *P. costaricensis*), sometimes becoming trapped in neural parenchyma (e.g. *P. cantonensis, P. mackerrasae, P. malaysiensis*). All species form infective third-stage larvae (L3) in the tissues of a variety of gastropods (aquatic and terrestrial snails and slugs). The infective L3 of *P. cantonensis, P. malaysiensis* and *P. costaricensis* may also be carried without further development in the tissues of various paratenic (transport) hosts, including crustacea (crabs, shrimps), molluscs (oysters), amphibians, lizards and planarians.

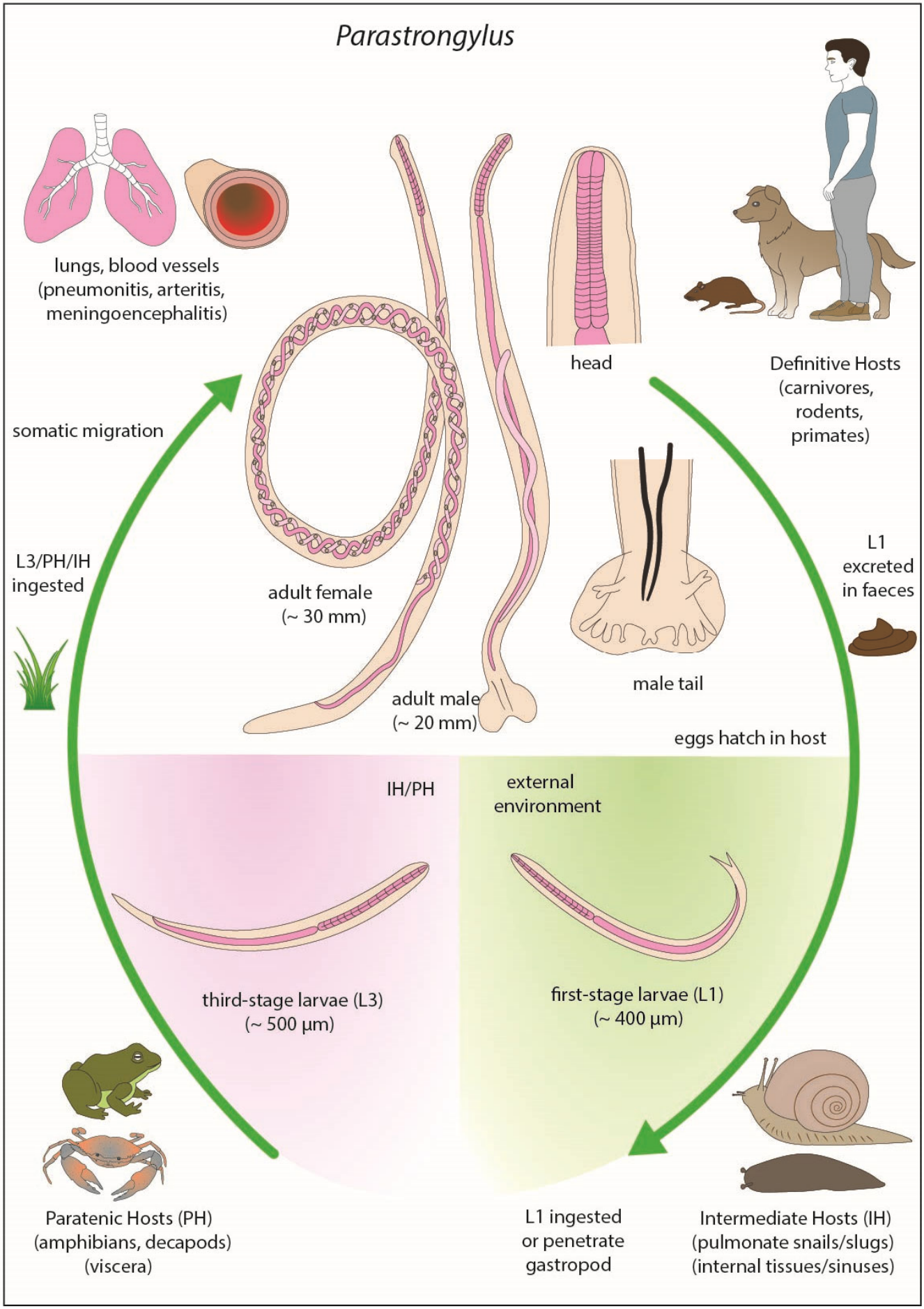
Pathogenesis: Most rat lungworm species appear to be well-adapted to their usual rodent hosts and infections generally do not produce any clinical disease although the parasite life-cycle involves obligate migration and development in host tissues before adults mature in the circulation and produce eggs. However, in accidental or aberrant hosts (including humans), parasites may not complete their development and migrating larvae and worms (alive and dead) elicit intense inflammatory reactions resulting in severe disease, notably eosinophilic meningoencephalitis due to *P. cantonensis* or eosinophilic enteritis due to *P. costaricensis*. Disease development and severity depends on parasites species (some being more virulent under certain conditions), host susceptibility (usual permissive (normal) host species versus unusual aberrant (abnormal) host species, young versus mature individuals, immunologically naive versus exposed individuals), intensity of infection (number of parasites), and stage of infection (prepatent period involving larval migrations, patent period involving worm and egg burdens). Infections by *P. cantonensis* are usually asymptomatic in rats even though larvae migrate and develop in the central nervous system before adults mature in the pulmonary arteries and right heart ventricle. Occasionally, heavy infections may form lesions in the meninges and lungs, with blockages of the pulmonary artery resulting in clinical signs involving coughing, sneezing, ataxia, paraplegia and death. However, in non-permissive hosts, the parasites do not complete their development but cause intense inflammation which may result in eosinophilic meningoencephalitis. Larvae migrate along peripheral nerves and nerve roots to the spinal cord, subsequently moving cranially within the parenchyma or via the subarachnoid space. The parasites cause traumatic damage to nervous tissue involving migratory tracts (sometimes abscesses) with petechial haemorrhages, nerve degeneration, inflammation and cellular infiltrates. Eosinophilia develops in peripheral blood and cerebrospinal fluid (100-2,000 cells/mm^3), the latter leading to high intra-cranial pressures sometimes with hydrocephaly. A range of neurological signs may be observed, including severe headache, neck stiffness, fever, vomiting, inappetence, diarrhoea, faecal incontinence, urinary incontinence, depression, convulsions, ataxia (incoordination), conscious proprioception deficits, paresis (impaired movement), paraesthesia (tingling), facial paralyses, paraplegia, coma, and eye involvement involving ocular pain, keratitis, ocular neuritis, retinal oedema, photophobia, visual impairment, diplopia and blindness. Many light infections are self-limiting with full recovery in a month, but heavier infections can lead to permanent neurological damage and death in domestic animals, wildlife and humans. Infections by *P. costaricensis* are usually nonpathogenic in rodents, even though parasites migrate through gut tissues and develop in the mesenteric circulation where they deposit eggs. However, in non-permissive hosts (including humans), parasites die and degenerate causing intense inflammatory and granulomatous reactions resulting in eosinophilic enteritis. The intestinal wall becomes thickened by granulomatous inflammation with massive infiltrates of eosinophils, sometimes producing palpable tumour-like masses (mimicking malignancy), and sometimes rupturing the intestines. Clinical signs include relapsing periods of severe abdominal pain (resembling acute appendicitis), fever, vomiting, diarrhoea, leucocytosis (esp. eosinophilia) and anorexia. In rare cases, parasites have been associated with testicular obstruction, arthritis, infarction, thrombosis, gastrointestinal haemorrhage, eosinophilic vasculitis and hepatic signs resembling visceral larval migrans.

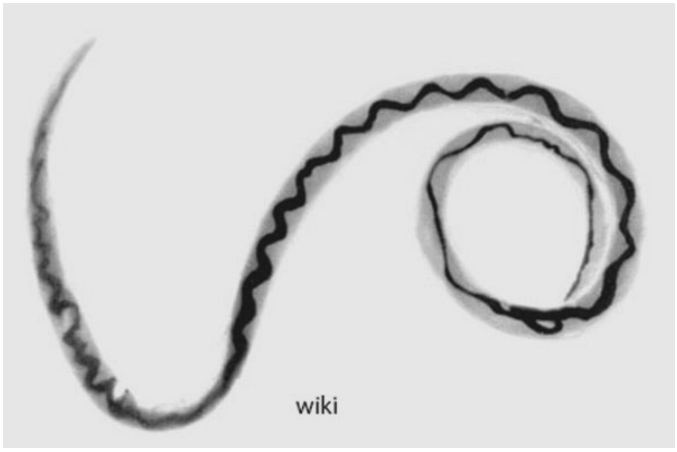
Developmental cycle and mode of transmission: *Parastrongylus* spp. have indirect heteroxenous life-cycles involving the formation of adult worms in vertebrate definitive hosts and the development of infective larvae in invertebrate intermediate hosts, and sometimes their carriage in paratenic (transport) hosts. Eggs laid by gravid female worms in the circulation are carried to the lungs where they develop and hatch releasing L1 which migrate up the respiratory tree to the trachea to be swallowed and excreted in host faeces. L1 infect a range of obligate intermediate hosts (aquatic and terrestrial snails and slugs) in which they moult twice forming L3 in 9-25 days. Infective L3 survive for long periods in gastropod tissues, and those of some species even survive for several days when shed in gastropod mucus trails. A range of animals (including frogs, shrimp, crabs, lizards and planarians) may also act as paratenic hosts for several species when they carry L3 in their internal tissues following the consumption of infected gastropods. Definitive hosts become infected by ingesting infective L3 which penetrate the gut wall and migrate through various host tissues moulting and maturing into adult worms. Several variations in this typical life-cycle have been observed for different

Parastrongylus spp.; mainly in how gastropods become infected (L1 ingested or percutaneous penetration); how final hosts become infected (ingesting L3 shed in mucus or contained within gastropods or paratenic hosts); where larvae develop in final hosts (lungs, lymphatics, circulation or neural parenchyma); where adults mature in final hosts (lung parenchyma, pulmonary circulation or mesenteric circulation); and how L1 emerge from final hosts (via airways to the intestines or direct into the intestines). The most diverse cycles are exhibited by *P. cantonensis, P. mackerrasae* and *P. malaysiensis* whereby gastropods ingest L1, final hosts ingest L3 in mucus or in host tissues, larvae migrate from the stomach to the brain in 2-3 days (via an extensive migration through the lymphatics to the heart, the pulmonary circulation and then the arterial circulation), both moults occur in neural parenchyma over 1-2 weeks, young adults reside in the subarachnoid space for 2 weeks before entering the cerebral vein, adults develop in the right ventricle of the heart and in pulmonary arteries by 3-4 weeks, and eggs release L1 via the airways. The prepatent period (time from infection to first larval excretion) ranges from 32-45 days (*P. malaysiensis* 32 days, *P. mackerrasae* 40-42 days, *P. cantonensis* 42-45 days). Infections by *P. costaricensis* vary in their development in that L1 infect gastropods by ingestion or percutaneous penetration, final hosts ingest L3 in mucus trails or in gastropods, larvae undergo 2 migratory routes within 1-2 weeks moulting twice in the process (usually once in abdominal lymphatics and once in mesenteric arteries, but sometimes both in intrahepatic veins), adults mature in the mesenteric veins, eggs release L1 direct into the intestines, and the prepatent period ranges from 21-28 days. *P. siamensis* infects rodents by the ingestion of L3 in snails, larvae moult twice within a week in mesenteric lymph nodes and vessels, adults mature in mesenteric arteries, eggs release L1 into the intestines, and the prepatent period is 29-34 days. *P. dujardini* and *P. schmidti* infect rodents following the ingestion of L3 in snails, larvae moult twice within a week but in the lungs, adults mature in the lung parenchyma, eggs release L1 in the airways, and the prepatent period is 24-31 days. Humans become infected with *P. cantonensis* and *P. costaricensis* primarily when they consume infected intermediate or paratenic hosts, particularly in regions where shrimp and other crustaceans are traditionally eaten raw. People may also be infected when they consume salad vegetables contaminated with L3 in gastropod mucus trails, and children have been infected when consuming or playing with infected slugs or snails.

Differential diagnosis: Presumptive diagnosis may be made in humans on the basis of symptomatology (meningoencephalitis or enteritis) in individuals with a relevant history (travel to endemic regions, consumption of raw or partially cooked gastropods and/or crustaceans), but other infections may cause similar conditions (e.g. *Gnathostoma*, *Paragonimus*, *Taenia solium*). Infections are accompanied by a profound eosinophilia in the blood and cerebrospinal fluid, but other helminths also elicit eosinophilic responses. Occasionally, larvae or young worms may be detected microscopically in cerebrospinal fluid samples collected by lumbar puncture. Medical imaging techniques may reveal alterations commonly associated with infections, with computed tomography (CT) scans indicating cerebral oedema or ventricular dilatation in the absence of focal lesions, and magnetic resonance imaging (MRI) demonstrating multiple micronodular enhancements in the brain and spine. Regrettably, infections are generally confirmed in humans at necropsy by the detection of parasites (larvae, adults, eggs) in tissue samples. A range of immunological tests (enzyme immunoassays and Western blots) have been developed to detect specific host antibodies against crude, excretory/secretory (ES) or refined antigens from adults and larvae, but many demonstrated some cross-reactivity problems before the introduction of monoclonal antibody reagents. Modern molecular biological techniques have been used to characterize parasite species following the amplification (by polymerase chain reaction (PCR), real-time PCR, or loop-mediated isothermal amplification (LAMP)) of nuclear gene sequences (18S ribosomal RNA and internal transcribed spacer I) and mitochondrial genes (cytochrome c oxidase subunit I, 66 kDa protein).

Treatment and control: Despite the severity of clinical disease in humans, most infections are self-limiting and patients often recover spontaneously over 4-6 weeks, although an increasing number have protracted infections over several months with periodic relapses. Various attempts have been made to treat human infections with anthelmintic drugs, notably benzimidazoles (fenbendazole, albendazole, mebendazole), but such treatment is generally contraindicated as disease often worsens as worms die and degenerate leading to further adverse inflammatory reactions. A variety of supportive care options have been used to provide symptomatic relief, including corticosteroids (anti-inflammatories), lumbar puncture (to reduce intracranial pressure), analgesics and opioids (for pain relief), sedatives (for sensory hyperesthesia), intravenous fluid therapy (restoring fluid volumes), urinary catheterisation, passive physiotherapy and antibiotic treatment (for secondary infections). In exceptional circumstances, surgical intervention has been warranted to remove *P. cantonensis* from the eyes, and to remove inflamed intestinal tissue in *P. costaricensis* infections. A range of preventive measures have been applied in endemic areas in attempts to reduce cyclic transmission between hosts. Rodent control acts to reduce faecal contamination of the environment with parasite larvae as well as to reduce the number of natural final hosts that may acquire sylvatic infections. Controlling gastropod populations using molluscicides and barriers (especially around gardens) acts to reduce the number of infective larvae which may perpetuate infections. Attempts to control aquatic crustacean populations in waterways may help minimise the uptake of infective larvae into potential paratenic hosts. However, the greatest impact on reducing transmission involves changing people's behaviour with respect to food and personal hygiene. Fresh produce (salad and vegetables) should be thoroughly washed in clean water to remove gastropods and their mucus trails, both of which may contain infective larvae. Despite traditional culinary practices, molluscs and crustaceans should not be eaten raw, as cooking them effectively destroys any infective larvae present. Food handlers and cooks should practice strict personal hygiene by wearing gloves or washing hands and utensils in contact with potentially contaminated food items. Children should also be discouraged from playing with live gastropods and never to consume them even if dared to. Several countries have developed successful education campaigns to raise public awareness about infections and make recommendations to curb transmission rates.


Parastrongylus
lungs, blood vessels
(pneumonitis, arteritis,
meningoencephalitis)
head
Definitive Hosts
(carnivores,
rodents,
primates)
somatic migration
L3/PH/IH
ingested
adult female
(~ 30 mm)
adult male
(~ 20 mm)
male tail
L1
excreted
in faeces
eggs hatch in host
IH/PH
external
environment
third-stage larvae (L3)
(~ 500 µm)
first-stage larvae (L1)
(~ 400 µm)
Paratenic Hosts (PH)
(amphibians, decapods)
(viscera)
L1 ingested
or penetrate
gastropod
Intermediate Hosts (IH)
(pulmonate snails/slugs)
(internal tissues/sinuses)



Parastrongylus adult worm



Parastrongylus larva

Filaroides
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Unlike most lungworms, filaroids have direct life-cycles where adults in the lungs produce eggs which hatch releasing L1 to be swallowed and passed in faeces. L1 are ingested by dogs or, more commonly, transferred to pups by maternal grooming or regurgitative feeding. L2 develop in the intestines and then migrate via the lymphatic-vascular route to the lungs and mature into adults. *Filaroides* spp. have been associated with respiratory distress in dogs worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Filaroididae (direct cycle, infection of carnivores by ingestion of L1)
Genus:	*Filaroides* (parasitic in lungs of dogs/mustelids)
Species:	various species cause subclinical infections in dogs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Metastrongylina (lungworms)				
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	Suids	ingestion of IH carrying L3	1
Protostrongylidae	small buccal capsule, bursa with large	artiodactyls	ingestion of IH	17

(lungworms)	lobes, gubernaculum		carrying L3	
Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	Suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 2 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials).

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm larvae**
Filaroididae					
Filaroides (lungworm)	17	carnivores, primates	lungs	2-90 mm long, vestigial buccal capsule, bursa absent, L1 voided in faeces, vomitus or sputum, direct cycle (L1 transferred to young during grooming or regurgitative feeding) or indirect cycle (L1 infect gastropods and form infective L3)	220-325 µm, posterior kink

Oslerus (lungworm)	2	carnivores	trachea	4-64 mm long, small buccal capsule, bursa reduced, L1 voided in faeces, vomitus or sputum, direct cycle (L1 transferred to young during grooming or regurgitative feeding) or indirect cycle (L1 infect gastropods and form infective L3)	230-270 µm, S-shaped tail

The family Filaroididae contains 4 genera (*Filaroides, Filariopsis, Oslerus*) parasitic in the respiratory system of canids, mustelids, pinnipeds, primates and Australian marsupials. The family contains delicate lungworms which are difficult to remove from host tissues and study intact, but they have been separated from the family Angiostrongylidae in that the males are abursate and the females have a subterminal vulva. Their life-cycles are quite varied: some being direct; while others are indirect and use gastropods or fish as intermediate hosts. The genus *Filaroides* contains some 17 spp. classified in 2 subgenera: *F.* (*Filaroides*) (= *Pseudostrongylus*) (males with well-developed caudal papillae and spicules) parasitic in terrestrial carnivores, primates and Australian marsupials with direct cycles or indirect cycles involving gastropod intermediate hosts; and *F.* (*Parafilaroides*) (males lacking caudal papillae, with small spicules and a weakly developed gubernaculum) parasitic in the lung parenchyma of marine pinnipeds with indirect cycles involving coprophagous fishes.

***Filaroides* species**	**Definitive hosts**	**Location [Clinical signs]**	**Intermediate hosts (IH) [plus Paratenic Hosts (PH)]**	**Distribution**
Subgenus *Filaroides*				
F. (*F.*) *athertonensis*	Diprotodontia: macropodid (red-legged pademelon)	Lungs		Australia
F. (*F.*) *bronchialis*	Carnivora: mustelid (sable)	Lungs		Asia
F. (*F.*) *canadensis*	Carnivora: mustelid (North American river otter)	Lungs		North America
F. (*F.*) *hirthi*	Carnivora: canid (dog)	Lungs	no IH (direct)	North America, Europe, Japan, Australia
F. (*F.*) *martis*	Carnivora: mustelid (American mink, American marten, beech marten, European pine marten, European polecat, sable, stoat, Japanese weasel, least weasel, ferret), mephitid (skunk), herpestid (Egyptian mongoose), canid (Iberian fox)	Lungs	Gatropoda: endodontid (*Anguispira alternata*, *Discus cronkhitei*), limacid (*Deroceras gracile*), physid (*Physa integra*), planorbid (*Gyraulus deflexus*), succineid (*Succinea ovalis*), zonitid (*Zonitoides arboreus*) [plus PH: Rodentia: murid (mouse)]	Eurasia, Americas
F. (*F.*) *mephitis*	Carnivora: mephitid (skunk)	Lungs		North America
F. (*F.*) *myonaxi*	Carnivora: herpestid (black-tipped mongoose, slender mongoose)	Lungs		Africa
F. (*F.*) *orientalis*	Carnivora: mustelid (stoat, least weasel, Siberian weasel)	Lungs		Eurasia
F. (*F.*) *pararostratus*	Carnivora: canid (dog)	Lungs		Americas
F. (*F.*) *pilbarensis*	Dasyuromorphia: dasyurid (little red kaluta)	Lungs		Australia
Subgenus *Parafilaroides*				
F. (*P.*) *decorus*	Carnivora: otariid (California sea lion, Steller sea lion, northern fur seal)	Lungs	Perciformes: kyphosid (opaleye fish)	North Pacific
F. (*P.*) *gymnurus* (syn. *Pseudalius*, *Halocercus, F. arcticus*)	Carnivora: phocid (hooded seal, harp seal, ringed seal, harbour seal, spotted seal, grey seal, bearded seal,	lungs		Holarctic

	Baikal seal)			
F. (*P.*) *hispidus*	Carnivora: phocid (ringed seal, grey seal)	Lungs		western Arctic, western Atlantic
F. (*P.*) *hydrurgae*	Carnivora: phocid (leopard seal)	Lungs		Antarctic
F. (*P.*) *krascheninnikovi*	Carnivora: phocid (ringed seal, bearded seal, Baikal seal)	Lungs		Eurasia
F. (*P.*) *nanus*	Carnivora: otariid (Steller sea lion)	Lungs		North Pacific
F. (*P.*) *prolificus*	Carnivora: otariid (Steller sea lion)	Lungs		North Pacific
Species inquirenda				
F. gordius sp. inq.	Primates: cebid (common squirrel monkey)			South America
F. kreisi sp. inq.	Carnivora: canid (Cape hunting dog)			Africa
F. (*P.*) *caspicus sp. inq.*	Carnivora: phocid (Caspian seal)	Lungs		Caspian Sea
Re-assigned species				
F. (*F.*) *cebus* (syn. *Filariopsis arator*) [now *Filariopsis barretoi*]	Primates: cebid (white-faced capuchin, common squirrel monkey)), callitrichid (common marmoset)	Lungs		South America
F. milksi (now *Andersonstrongylus milksi* in family Angiostrongylidae as bursa present]	Carnivora: canid (dog)	Lungs		North America
F. mustelarum [now *Skrjabingylus nasicola*]	Carnivora: mustelid (stoat, weasel), mephitid (skunk)	frontal sinuses, lungs	Gastropoda: agriolimacid (*Deroceras reticulatum*) [plus PH; Eulipotyphla: soricid (common shrew); Rodentia: murid (field mouse), cricetid (bank vole)	North America, Eurasia

Parasite morphology: These lungworms form 3 different types of morphological stages in their developmental cycles: eggs; larvae (4 successive stages encoded L1-L4); and adult worms. The eggs are thin-shelled transparent ellipsoidal stages measuring 49-80 x 39-50 μm and they are fully larvated when laid. L1 are elongate coiled stages measuring from 220-325 μm in length and they have annulated cuticles with lateral alae, rounded heads, narrow buccal capsules, rhabditiform (bulbed) oesophagus extending 33-50% the body length, and undulating tails with a subterminal dorsal indentation (but no dorsal spine) and a terminal lance-like tip. Few descriptions are available for subsequent larval stages for those species with direct cycles, while those with indirect cycles have been described from intermediate hosts, including gastropods (e.g. *F. martis*) and coprophagous fish (e.g. *F. decorus*). L2 measured 320-380 μm long and had cuticles with regular delicate transverse striations (apparently without alae) and blunt conical tails. L3 were more slender and serpentine measuring 318-362 μm and had striated cuticles with narrow lateral alae, well-developed cylindrical buccal capsules, and blunt conical tails, some with tiny digitiform appendages. L2 and L3 often appeared ensheathed as they retained the cuticles of their previous stages, but they were easily shed when larvae were disturbed. L4 were transient parasitic stages with developing male or female genitalia. Adults are small thin pale worms measuring 2-13 mm long (some species in the subgenus *F.* (*Parafilaroides*) measure up to 90 mm long) with inflated cuticles forming voluminous tegumental sheaths (outer cortical layer). They have small mouths surrounded by 4 mound-like excrescences, small buccal capsules, club-shaped oesophagi, intestines terminating in subterminal anus/cloaca, and short blunt rounded tails. Adult lungworms are sexually dimorphic, with females being slightly larger than males (5-90 cf. 2-37 mm long). Mature female worms are didelphic with 2 ovaries and uteri in a prodelphic configuration (parallel and anteriorly directed) connected to a common posterior subterminal vulva. Mature males are abursate and do not possess a distinct caudal copulatory bursa (the family Filaroididae was separated from the family Angiostrongylidae by the absence of a male bursa). The bursal rays are completely reduced to well-developed caudal papillae in members of the subgenus *F.* (*Filaroides*), but they are absent in those of the subgenus *F.* (*Parafilaroides*). Males also have a weakly developed gubernaculum and 2 stout arcuate spicules.

Site of infection: Adult worms infect the lung parenchyma of their carnivorous hosts, usually being tightly coiled up in alveoli and small bronchioles, particularly in diaphragmatic lobes, and sometimes forming granulomatous nodules in mucosa. In parasite species with direct life-cycles, larval stages also develop within the lungs, whereas those of species with indirect cycles develop within the viscera of intermediate hosts (gastropods or coprophagous fishes).

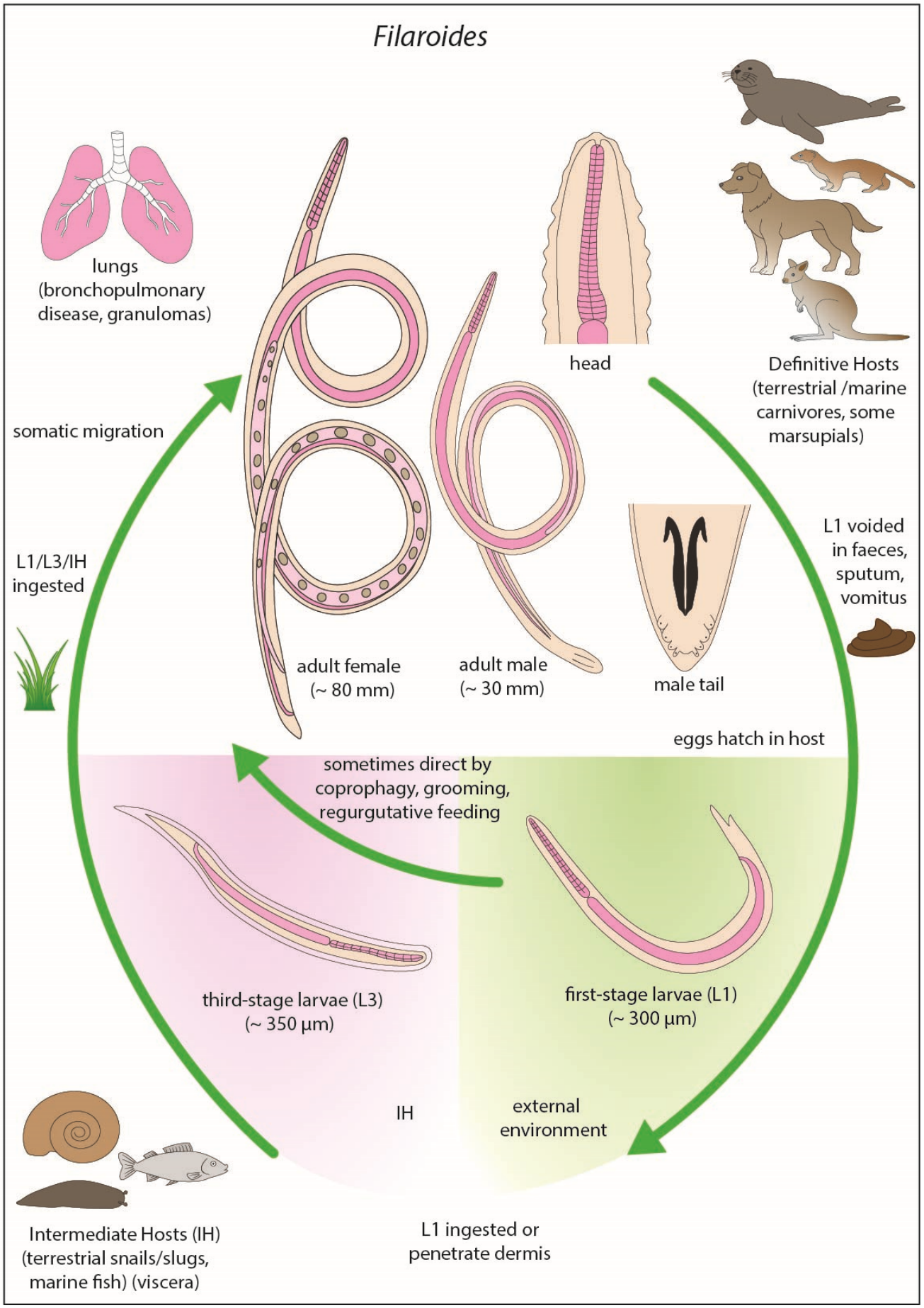
Pathogenesis: *Filaroides* infections are usually asymptomatic, often being detected incidentally during post-mortem examination of lung tissues from captive or wild animals dying of other causes. Heavy infections have been associated with bronchopulmonary disease (verminous pneumonia) in carnivores (mostly canids and pinnipeds) with sporadic chronic development over months, but overwhelming in animals that are immunologically compromised (young or immuno-suppressed individuals) or have complicating conditions (such as canine distemper, adrenal cortical carcinoma, or chronic post-operative stress). Parasites cause tissue destruction during migration and feeding and elicit strong local inflammatory responses. Worms coil into complex knots forming soft grey miliary nodular lesions distributed subpleurally and throughout the lung parenchyma. Four types of nodules may be formed: round subpleural foci 0.5-1.0 mm in diameter; round white raised foci 1-2 mm; irregular white foci 2-10 mm with grey centres; and confluent mottled white-red foci up to 14 mm. The progressively enlarging granulomatous nodules may coalesce and obstruct airflow causing nodular pneumonia with multifocal atelectasis (alveolar collapse) and emphysema as well as epithelial hyperplasia, squamous metaplasia, alveolitis, suppurative bronchiolitis, peribronchiolitis, perivasculitis, pulmonary oedema, and pleural and interstitial fibrosis. Clinical signs include spasmodic attacks of hard dry rasping coughing (precipitated by exercise or exposure to cold air), dyspnoea, tachypnoea, laboured breathing, sero-mucus nasal discharge, difficulty eating, anorexia, emaciation, malaise and death.

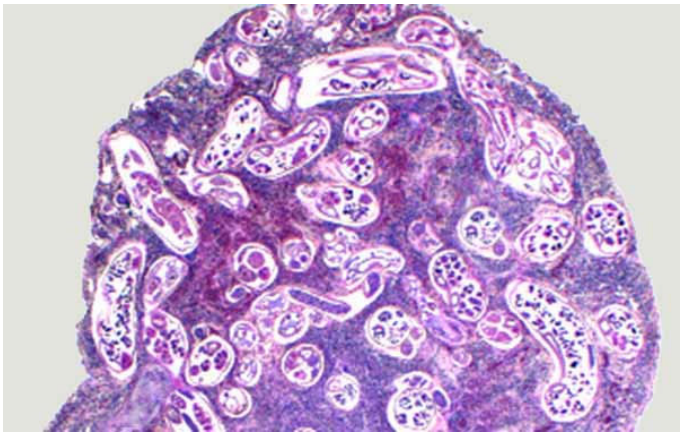
Developmental cycle and mode of transmission: These lungworms are unusual in that some have direct monoxenous life-cycles while others have indirect heteroxenous life-cycles involving intermediate hosts. Direct horizontal transmission occurs for some terrestrial species in the subgenus *F.* (*Filaroides*) (e.g., *F.* (*F.*) *hirthi*). Larvated eggs laid in lungs hatch releasing L1 which migrate up the respiratory tree via the mucociliary escalator and may be voided in faeces, vomitus or sputum. New final hosts become infected when they ingest infective L1 by eating fresh faeces (coprophagy) or vomitus, by regurgitative feeding (more common in some wild animals) or by their transfer in sputum during maternal grooming (licking) of pups. Ingested L1 penetrate the intestinal wall and migrate to the mesenteric lymph nodes where they moult to L2, L3 and then L4. Any of these larval stages may then migrate through the lymph nodes and liver to the lungs where they moult to subadults (often designated L5) which settle in the lung parenchyma to mature. The prepatent period (time from infection to first larval excretion) is 32-35 days, and heavy infections may develop in immuno-compromised hosts by autogenous re-infection when L1 are not excreted but re-invade tissues. In contrast, indirect cycles are exhibited by other terrestrial species in the subgenus *F.* (*Filaroides*) (e.g., *F.* (*F.*) *martis*) where L1 infect terrestrial and aquatic gastropods (snails and slugs) and develop to infective L3 which are consumed by mollusc-eating carnivores and become patent in 41-53 days. All species in marine pinnipeds in the subgenus *F.* (*Parafilaroides*) (e.g., *F.* (*P.*) *decorus*) are thought to have indirect cycles involving larval development in the mesenteries of coprophagous fishes which are subsequently eaten by piscivorous seals becoming patent after 3 weeks. Infections may remain patent for over 1 year and adult worms are thought to live for several years.

Differential diagnosis: While clinical respiratory signs (cough to pneumonia) may be suggestive of infection, they are relatively nonspecific and may be attributed to other conditions. Haematological changes often indicate neutrophilia and eosinophilia, but these are similarly nonspecific. Infections in live animals are usually diagnosed by the detection of larvae (rarely eggs) in faecal samples, often following their concentration by floatation rather than Baermann filtration as the larvae are not very active. Larvae and eggs may also be detected in sputum samples, tracheal washes or bronchial lavages. Bronchoscopy may be used to collect biopsy samples as well as to reveal nodular lesions. Thoracic radiography of verminous pneumonia often reveals diffuse infiltrates throughout the lungs. sometimes with bronchiolar nodules apparent as space-occupying masses. Infections are often diagnosed incidentally at post-mortem by the detection of worm fragments, eggs and larvae in association with nodular lesions in fresh, frozen or fixed lung tissues (sometimes in squeeze preparations from the cut surface of the lungs). Recovering intact worms by dissection is almost impossible as they are tightly knotted within host tissues. However, some success has been reported in recovering *F. Parafilaroides* lungworms in pinnipeds by mincing lung tissues in seawater and allow worms to migrate out. Molecular biological techniques have recently been used to characterize adult worms and larvae by polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (18S, 5.8 S and 28S ribosomal RNA and internal transcribed spacers 1 and 2).

Treatment and control: Clinical infections in canids and pinnipeds have responded well to treatment with various anthelmintic drugs, including benzimidazoles (fenbendazole, oxfendazole, thiabendazole, albendazole), imidazothiazoles (levamisole) and macrocyclic lactones (ivermectin, doramectin), particularly when higher doses were used over extended periods. Preventive measures used in animal breeding or housing facilities include improved sanitation (regular removal of faeces), good hygiene (clean food and water), chemoprophylactic treatment (particularly pregnant and nursing bitches), quarantine and isolation (including

separating pups from older infected animals, sometimes requiring hand-raising or foster-rearing), and excluding molluscs and wild animals from facilities (using chemical or physical barriers).


Filaroides
lungs
(bronchopulmonary
disease, granulomas)
head
Definitive Hosts
(terrestrial /marine
carnivores, some
marsupials)
somatic migration
L1/L3/IH
ingested
adult female
(~ 80 mm)
adult male
(~ 30 mm)
male tail
L1 voided
in faeces,
sputum,
vomitus
eggs hatch in host
sometimes direct by
coprophagy, grooming,
regurgutative feeding
third-stage larvae (L3)
(~ 350 µm)
first-stage larvae (L1)
(~ 300 µm)
IH
external
environment
Intermediate Hosts (IH)
(terrestrial snails/slugs,
marine fish) (viscera)
L1 ingested or
penetrate dermis



Filaroides nodule



Filaroides larva

Oslerus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including spirurinids, tylenchinids and rhabditinids. The latter contains the infraorder Rhabditomorpha which includes strongyloid nematodes characterised by an expansion of the tail of the male known as the copulatory bursa (clasper with one dorsal and two lateral lobes with muscular rays). Many families are recognised: including lungworms with small buccal capsules and reduced male bursae. Adult worms are found mostly in the lungs of their hosts, although some inhabit the pulmonary artery, meninges or connective tissues. Five main groups occur: dictyocaulids in ruminants and horses; metastrongyles in pigs; protostrongyles in ruminants; angiostrongyles in carnivores and rodents; and filaroids in dogs. Unlike most lungworms, filaroids have direct life-cycles where adults in the lungs produce eggs which hatch releasing L1 to be swallowed and passed in faeces. L1 are ingested by dogs or, more commonly, transferred to pups by maternal grooming. L2 develop in the intestines and then migrate via the lymphatic-vascular route to the lungs and mature into adults. *Oslerus osleri* infections have been associated with respiratory distress in dogs worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)
Infraorder:	Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily:	Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Family:	Filaroididae (direct cycle, infection of carnivores by ingestion of L1)
Genus:	*Oslerus* (parasitic in trachea of dogs)
Species:	*O. osleri* causes respiratory distress in dogs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic with 2 ovaries (some monodelphic or polydelphic), 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Strongyloidea comprises a range of worms often with prominent buccal capsules and specialised oral structures well-suited to their feeding habits on host tissues and/or fluids. Adults of most species are parasitic in the gastrointestinal tracts of mammals and some birds, while larval stages feed on bacteria in the external environment, although some larvae may infect invertebrates as intermediate or paratenic hosts. The adult worms are sexually dimorphic, the smaller males characterised by an expansion of the tail (bursa) which is used as a copulatory clasping organ. Many classification schemes group these 'bursate' nematodes into one or more superfamilies in the order Strongylida (with suborders containing the strongyles, trichostrongyles, hookworms and lungworms), although the families essentially remain the same. Many families are recognised on the basis of parasite morphology, biology, life-cycle, host specificity and tissue tropism; including the following which contain many notorious parasites of vertebrates.

Representative Strongyloidea (cf. Strongylida) [with bursate males]				
Family	**Characters**	**Definitive Hosts**	**Transmission***	**No. genera**
Metastrongylina (lungworms)				
Filaroididae (lungworms)	small buccal capsule, reduced male bursa, infective L1	carnivores	ingestion of L1	4
Metastrongylidae (lungworms)	small buccal capsule, 2 trilobed lips, bursa with reduced dorsal lobe	Suids	ingestion of IH carrying L3	1
Protostrongylidae (lungworms)	small buccal capsule, bursa with large lobes, gubernaculum	artiodactyls	ingestion of IH carrying L3	17

Angiostrongylidae (lungworms)	no or reduced buccal cavity, short club-shaped oesophagus	carnivores, rodents	ingestion of IH or PH carrying L3	28
Dictylocaulidae (lungworms)	small buccal capsule, bursa with large lobes, short stout spicules	ungulates, reptiles	ingestion of L3	5
Trichostrongylina (trichostrongyles)				
Trichostrongylidae (trichostrongyles)	reduced buccal capsule, ridged synlophe, oesophagus lacking bulb, thin-shelled eggs	artiodactyls, birds	ingestion of L3	50
Molineidae (stomach/intestinal worms)	reduced buccal capsule, cephalic vesicle, female tail with spine or cusps, oviparous/viviparous	mammals, birds, reptiles	ingestion of L3	61
Heligmonellidae (hookworm-like)	body coiled, cephalic vesicle, ridged synlophe, bursa asymmetrical	mammals, birds	transdermal penetration of L3	56
Strongylina (strongyles)				
Strongylidae (strongyles)	large buccal capsule often armed with teeth, leaf crown around mouth	mammals, reptiles, birds	ingestion of L3	32
Chabertiidae (nodule worms)	large buccal capsules, leaf crown of labial collar, L3 sheathed	artiodactyls, primates	ingestion of L3	22
Syngamidae (gapeworm)	cup-shaped buccal capsule, armed with teeth, male attached to female	birds, mammals	ingestion of L3 or invertebrate PH	7
Stephanurinae (kidneyworm)	buccal capsule armed with teeth, leaf crowns and external epaulettes	Suids	transdermal penetration or ingestion of L3 or PH	1
Ancylostomatina (hookworms)				
Ancylostomatidae (hookworms)	large buccal capsule bent dorsally, armed with teeth/cutting plates	primates, carnivores, artiodactyls	transdermal penetration of L3 (sometimes *per os*)	20

*IH = intermediate host, PH = paratenic (transport) host, L1 = first-stage larva, L3 = third-stage larva

Lungworms are characterised mostly by their unique location within the respiratory systems of their mammalian hosts, although some species also infect cardiovascular, nervous or intermuscular connective tissues. Adult worms have a small buccal capsule, often reduced to an annulus, and sometimes possessing lips. Male worms have a caudal bursa that is variable in structure (often with reduced lobes and/or rays), spicules and a gubernaculum and telamon that are often not highly developed. Female worms have a median or posterior vulva, sometimes with a sphincter, and they are oviparous (releasing eggs) or ovoviviparous (releasing larvae). Many species have direct cycles involving the ingestion of infective larvae, while others have indirect cycles involving the ingestion of larvae in invertebrate intermediate hosts, and sometimes paratenic hosts. Eight metastrongyline families are recognised: Metastrongylidae (mouth with 2 large lateral trilobed lips, bursa with large lateral lobes and reduced dorsal lobe, oviparous, indirect cycle, earthworms used as intermediate hosts, 1 genus in lungs of suids); Angiostrongylidae (mouth with or without lips, bursa well-developed, oviparous, ovoviviparous, indirect cycle, gastropods used as intermediate hosts, 28 genera in respiratory and vascular systems of marsupials, rodents, insectivores, lemurs, mustelids, viverrids, felids and canids); Dictyocaulidae (mouth small, bursa with large lateral lobes and large dorsal lobe (divided to base), ovoviviparous, direct cycle, 2 genera in airways of ruminants and horses); Filaroididae (mouth small, bursa absent or reduced (rays reduced to papillae), ovoviviparous, direct cycle, 4 genera in respiratory system of canids, mustelids, pinnipeds, primates, and marsupials); Protostrongylidae (mouth small, bursa with large lateral lobes and prominent dorsal lobe, highly developed gubernaculum and telamon, oviparous, indirect cycle, molluscs used as intermediate hosts, 17 genera in lungs of ruminants, felids, canids, leporids, and skeletal muscles and central nervous system of cervids); Pseudaliidae (mouth small, bursa reduced (rays fused but not reduced to papillae), ovoviviparous, direct cycle, 7 genera in respiratory, auditory, circulatory systems of delphinids, phocoenids, monodontids and mongoose); Skrjabingylidae (mouth small, bursa modified to form lateral fleshy lobes, ovoviviparous, direct cycle, 1 genus in nasal cavities of mustelids); and Crenosomatidae (mouth small, bursa with large lateral lobes and large dorsal lobe (not divided to base), ovoviviparous, direct cycle, 5 genera in respiratory system of canids, felids, pinnipeds, soricids and marsupials).

Genus	**No. spp.**	**Definitive Hosts**	**Location**	**Adult worms**	**Worm larvae**
Filaroididae					
Oslerus (lungworm)	2	carnivores	trachea	4-64 mm long, small buccal capsule, bursa reduced, L1 voided in faeces, vomitus or sputum, direct cycle (L1 transferred to young during grooming or regurgitative feeding) or indirect cycles (L1 infect gastropods and form infective L3)	230-270 µm, S-shaped tail
Filaroides (lungworm)	17	carnivores, primates	lungs	2-90 mm long, vestigial buccal capsule, bursa absent, L1 voided in faeces, vomitus or sputum, direct cycle	220-325 µm, posterior kink

				(L1 transferred to young during grooming or regurgitative feeding) or indirect cycle (L1 infect gastropods and form infective L3)	

The family Filaroididae contains 4 genera (*Filaroides, Filariopsis, Oslerus*) parasitic in the respiratory system of canids, mustelids, pinnipeds, primates and Australian marsupials. The family contains delicate worms which are difficult to remove from lung tissues and study intact, but they have been separated from the family Angiostrongylidae in that the males are abursate and the females have a subterminal vulva. Their life-cycles are quite varied: some being direct; while others are indirect and use gastropods or fish as intermediate hosts. The genus *Oslerus* contains 2 spp. separated into 2 subgenera: *O.* (*Oslerus*) (females with inconspicuous vaginal sphincter) containing the species *O.* (*O.*) *osleri* with a direct cycle in canids; and *O.* (*Anafilaroides*) (females with highly developed vaginal sphincter) containing the single species *O.* (*A.*) *rostratus* with an indirect cycle in felids and slugs.

***Oslerus* species**	**Hosts**	**Location [Clinical signs]**	**Intermediate Hosts (IH) [plus Paratenic Hosts (PH)]**	**Distribution**
O. (*Oslerus*) *osleri* [formerly *Filaroides osleri*] (dog lungworm)	Carnivora: canid (dog, dingo, wolf, coyote, red fox)	trachea, bronchi [cough]	no IH (direct)	worldwide
O. (*Anafilaroides*) *rostratus*	Carnivora: felid (cat, wild cat, bobcat, leopard cat)	trachea, bronchi	Gastropoda: limacid (*Limax maximus*) [plus PH: Rodentia: murid (mouse); Galliformes: phasianid (chicken)]	Americas

Parasite morphology: *Oslerus* spp. form 3 different types of morphological stages during their development: eggs; larvae (4 consecutive stages encoded L1-L4); and adult worms. The eggs are thin-shelled ovoid-ellipsoid stages measuring 80-120 x 50-70 µm and they are fully embryonated when laid. L1 from hatched eggs are thin elongate larvae, those recovered from bronchial mucus measuring 230-270 µm in length while those recovered from faeces measured 326-412 µm long. They had rounded heads, rhabditiform (bulbed) oesophagi, and short wavy S-shaped tails with a prominent constriction. Descriptions of subsequent endogenous larval stages (L2-L4) of *O. osleri* are lacking, while experimental studies on *O. rostratus* have described L3 from slugs as measuring 469-578 x 24-29 µm with pointed tails and small subterminal surface serrations. Adults are pale slender worms measuring 4-64 mm in length and they have striated cuticles with a well-developed tegumental sheath (inflation of outer cortical layer), small buccal capsules, club-shaped oesophagi, and short blunt rounded tails. Adult worms are sexually dimorphic, with males being smaller than females (4-8 cf. 9-15 mm for *O. osleri*, 28-37 cf. 48-64 mm for *O. rostratus*). Mature males are abursate and do not possess a distinct caudal copulatory bursa (the family Filaroididae was separated from the family Angiostrongylidae by the absence of a male bursa). Instead, the male tail has ill-defined lateral and ventral ray vestiges reduced to small single and sessile papillae, and a dorsal ray divided near its tip. Males also have a small gubernaculum and 2 short curved spicules slightly unequal in appearance (90-113 µm long). Mature females are didelphic with 2 ovaries and uteri arranged in a parallel prodelphic formation and connected to a common vulva located posteriorly near the anus. The 2 *Oslerus* subgenera are recognised primarily on the basis of the differences in the vaginal sphincter, being inconspicuous in *O.* (*Oslerus*) females and highly developed in *O.* (*Anafilaroides*). Females of both subgenera produce eggs that are larvated when laid.

Site of Infection: Adult worms infect the upper air passages of their carnivorous hosts, being located in the tracheal and bronchial mucosa adjacent to the carina (cartilaginous ridge at the tracheal bifurcation). Eggs and larvae are voided with host excretions, and invading larvae migrate through the gut to the lungs. Experimental studies on *O. rostratus* have demonstrated L1 may infect terrestrial slugs as intermediate hosts where they develop into L3 which may be spontaneously shed in mucus trails (whereas *O. osleri* do not involve intermediate hosts).

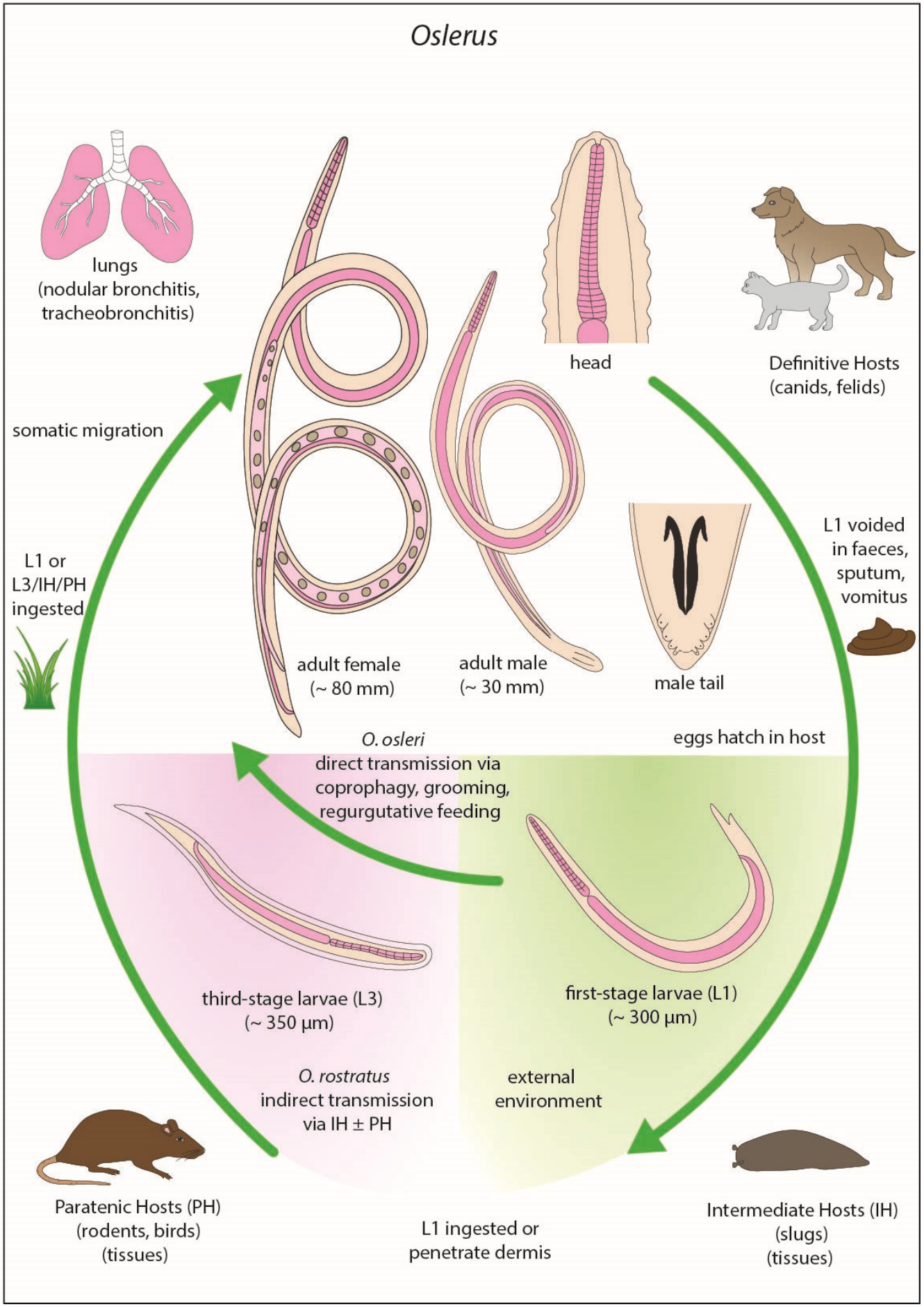
Pathogenesis: Most infections are asymptomatic even though worms produce granulomatous nodules in the trachea and bronchi as early as 2 months after infection. The nodules are located in the submucosa between the supporting cartilage rings near the tracheal bifurcation. They are fibrous and contain tangles of tightly coiled worms (counts ranging from 1-105 worms per nodule). They are covered by intact epithelium except for small pores through which female worms protrude their tails to lay eggs. The nodules appear as grey wart-like masses 2-20 mm in diameter, often flat but sometimes protruding as plaques up to 10 mm into the lumen. Nodules containing live worms may provoke local lymphocytic infiltrations whereas nodules with dead worms elicit strong inflammatory responses with neutrophils and a few giant cells. Heavy infections involving numerous, large or confluent nodules may cause respiratory difficulties, usually chronic in onset with progressive airway obstruction (chronic tracheobronchitis or verminous nodular bronchitis which can appear similar clinically to kennel cough). The main clinical sign is coughing, with spasmodic

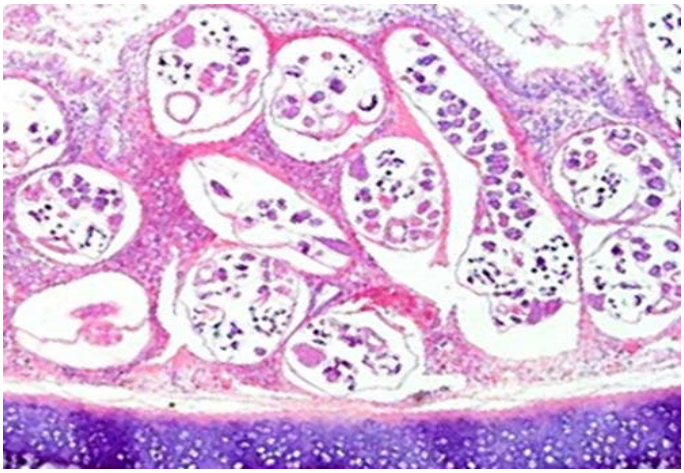
paroxysmal attacks of a hard dry (non-productive) rasping cough, precipitated by exercise or cold air and unresponsive to antibiotic therapy. Other signs include inspiratory respiratory distress with wheezing and acute onset dyspnoea, exercise intolerance, inappetence, anorexia, weight loss, emaciation, and death. The most severe cases occur in young dogs (6-12 months old), particularly in working dogs rather than household pets.

Developmental cycle and mode of transmission: *Oslerus* and *Filaroides* spp. are unique amongst the metastrongyle lungworms because they may have direct or indirect life-cycles, exemplified by *O. osleri* with direct transmission in canids and *O. rostratus* with indirect transmission between felids and gastropods. *O. osleri* females deposit larvated eggs in the trachea where they hatch. Many of the released L1 are coughed up, swallowed, and shed intermittently in host faeces, but are often sluggish, dead or degenerate (suggesting that faecal-oral transmission via coprophagy would be uncommon, even though it has been demonstrated experimentally). Instead, most infections are transmitted when L1 in sputum, expectorations or saliva are transferred to pups during maternal grooming through licking or when L1 in vomitus are transferred during regurgitative feeding (common in wild carnivores) or scavenging. Ingested L1 moult in intestines and L2 migrate to the lungs via the lymphatic and/or vascular systems where they develop to subadults (often referred to as L5) in alveoli and bronchi before settling near the tracheal bifurcation to mature. The prepatent period (time from infection to first larval excretion) ranges from 63-147 days and infections have been found to remain patent for several years, especially when entrenched in breeding kennels. In contrast, experimental studies with *O. rostratus* from felids have shown that L1 may infect leopard slugs which act as intermediate hosts in which L3 develop. Infective L3 have also been shown to be spontaneously shed by slugs in mucus trails, and they have even survived in mice and chickens as experimental paratenic (transport) hosts.

Differential diagnosis: The predominant clinical sign of coughing is nonspecific and physical examination reveals little other than increased tracheal sensitivity (although throat manipulation does not precipitate coughing). Eosinophilia may sometimes be detected by haematology (complete blood count) or cytology (airway washes). Infections are readily detected by endoscopic examination (bronchoscopy) under anaesthesia, which reveals characteristic nodules containing worms in the trachea. Medical imaging techniques (lateral thoracic radiography) may also reveal soft tissue densities (granulomas) in the caudal trachea. Diagnosis may be confirmed by detecting L1 in endoscopic biopsies of sputum, transtracheal washes, bronchoalveolar lavages, and less frequently in fresh faecal samples following floatation or Baermann filtration (but faecal shedding is intermittent). L1 appear as sluggish coiled stages with S-shaped tails. Molecular biological techniques have been used to characterize parasites following the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (ribosomal RNA).

Treatment and control: A range of anthelmintic drugs have been used in attempts to treat infections, including benzimidazoles (fenbendazole, thiabendazole, oxfendazole) and macrocyclic lactones (ivermectin, doramectin). No single therapy was effective in eradicating infections, but extended treatment with several drug combinations led to symptomatic improvement with the amelioration of clinical signs and nodule shrinkage. Preventive strategies applicable to animal breeding or housing facilities involved better sanitation (regular removal of faeces and vomitus, washing/disinfecting cages), good hygiene (washing soiled animals, providing clean food and water), chemoprophylactic treatment (particularly breeding animals), quarantine and isolation (including separating pups from older infected animals, sometimes requiring hand-raising or foster-rearing), and excluding molluscs and wild animals from facilities (using chemical or physical barriers).


Oslerus
lungs
(nodular bronchitis,
tracheobronchitis)
head
Definitive Hosts
(canids, felids)
somatic migration
L1 or
L3/IH/PH
ingested
adult female
(~ 80 mm)
adult male
(~ 30 mm)
male tail
L1 voided
in faeces,
sputum,
vomitus
O. osleri
direct transmission via
coprophagy, grooming,
regurgutative feeding
eggs hatch in host
third-stage larvae (L3)
(~ 350 µm)
first-stage larvae (L1)
(~ 300 µm)
O. rostratus
indirect transmission
via IH ± PH
external
environment
Paratenic Hosts (PH)
(rodents, birds)
(tissues)
L1 ingested or
penetrate dermis
Intermediate Hosts (IH)
(slugs)
(tissues)



Oslerus tracheal lesion

Ascaris
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Ascaridomorpha which includes ascaridoid nematodes (roundworms) characterised by their large size, three prominent anterior lips and the absence of a bursa. They occur in the small intestines of many animals (including humans) and most have simple direct life-cycles involving faecal-oral transmission. Female worms produce numerous eggs which are excreted with host faeces and undergo embryonation to contain infective larvae. When ingested, larvae hatch from the eggs and develop into adult worms in the gut. The larvae of ascaridoid species undergo hepato-pulmonary migration before forming adults, whereas those of heterakoid species do not. Two major ascaridoid families are recognised: ascarids in terrestrial mammals; and anisakids in marine mammals. Infections by *Ascaris* spp. are very common in human and pig populations throughout the world, causing unthriftiness and even gut obstruction.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Ascaridomorpha (large roundworms, mouth surrounded by three large lips, numerous caudal papillae)
Superfamily:	Ascaridoidea (ascarids, eggs thick-shelled, direct cycle but larvae undertake hepato-pulmonary migration)
Family:	Ascarididae (large pale roundworms, in terrestrial mammals)
Genus:	*Ascaris* (parasitic in small intestines of humans/pigs)
Species:	*A. lumbricoides* (causes gut obstruction in humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Ascaridomorpha is characterised by large roundworms with poorly developed buccal cavity with 3 large lips sometimes separated by interlabia, an undivided oesophagus, numerous caudal papillae, nonbursate males often with pre-anal suckers, and females with complex ovejectors. Five superfamilies (conventionally assigned to the order Ascaridida) are recognised as parasites in vertebrates: Ascaridoidea (cylindrical oesophagus often terminated by swelling without bulb, coelomyarian, eggs thick-shelled); Heterakoidea (oesophagus cylindrical or with claviform corpus, short isthmus and valved bulb, coelomyarian, pre-anal sucker, eggs thick-shelled); Seuratoidea (lips absent, oesophagus short, platymyarian, eggs with delicate shells or hatch *in utero*); Cosmocercoidea (oesophagus with cylindrical corpus, elongate isthmus and valved bulb, platymyarian, eggs with delicate shells or hatch *in utero*); and Subuluroidea (well-developed buccal capsule without lips, coelomyarian, pre-anal sucker, eggs thick-shelled). Adult worms of the superfamily Ascaridoidea inhabit the gastrointestinal tract of vertebrate hosts and generally consume food ingested by the host. They may have simple monoxenous life cycles involving faecal-oral transmission, or more complicated heteroxenous life-cycles involving larval development in vertebrate intermediate hosts and sometimes larval transport in invertebrate paratenic hosts. Female worms produce unembryonated eggs which are passed in host faeces into the external environment where they embryonate to first-stage larvae (L1) which grow and moult to infective L2 or L3. Aquatic species produce thin-shelled eggs which hatch in water releasing sheathed L2 that are taken up by suitable hosts, while terrestrial species produce thick-shelled eggs which hatch releasing L3 when ingested by suitable hosts. Ascaridoid larval stages then undertake unique journeys: most involving pulmonary or somatic migration in their definitive hosts before maturing in the gut, sometimes including vertical transmission (transplacental and/or transmammary); many migrating into the tissues of intermediate hosts, sometimes involving larval migrans or encapsulation in ‘unsuitable’ hosts; and a few undergoing precocious development in invertebrate hosts.

Five ascaridoid families are recognised: Ascarididae (lips often with toothed ridge, oesophagus with or without ventriculus, parasites of mammals, birds, reptiles, amphibians, fishes); Anisakidae (lips with tongue-like prolongations with cuticular thickenings, oesophagus with ventriculus with suture-like depressions, parasites of mammals, birds, reptiles and fishes);

Crossophoridae (lips semicircular with toothed combs, fimbriated collar, long oesophagus without ventriculus, parasites of hyracoids); Heterocheilidae (lips with tongue-like prolongations with cuticular thickenings, cylindrical oesophagus without ventriculus, parasites of sirenians); and Acanthocheilidae (lips small with teeth or toothed ridges, oesophagus with ventriculus, parasites of elasmobranchs). The family Ascarididae contains 4 subfamilies: Ascaridinae (oesophagus simple, gubernaculum absent, lips hexagonal with anterior region offset from posterior, parasites of terrestrial mammals); Toxocarinae (oesophagus with globular ventriculus without appendices, gubernaculum absent, parasites of terrestrial or marine mammals or birds); Angusticaecinae (oesophagus simple, gubernaculum absent, lips quadrangular and not divided into anterior and posterior regions, parasites of reptiles and amphibians); and Multicaecinae (oesophagus with globular ventriculus usually with appendices, gubernaculum present, parasites of crocodilians or rarely fish). Ascaridid genera of medical and veterinary significance are compared in the following table.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Ascaridinae						
Ascaris (roundworm)	2 (+ 150 *nomen dubium*)	primates, suids	small intestines	15-50 cm long, 3 small lips, striated cuticle, males with curved tail, simple spicules, females opisthodelphic, larvae undergo hepato-pulmonary migration	50-87 x 35-60 µm, ovoid, thick-shelled	faecal-oral
Parascaris	3	equids	small intestines	10-50 cm long, 3 large lips each with transverse groove, cuticle striated, males abursate, simple spicules, larvae undergo hepato-pulmonary migration	90-120 µm, spherical, thick-shelled	faecal-oral
Toxascaris	2	carnivores	small intestines	2-15 cm long, 3 lips, long thin cervical alae, oesophageal ventriculus absent, males lack terminal digitiform appendage, larvae do not undergo hepato-pulmonary migration	70-85 x 60-75 µm, ovoid, thick-shelled	faecal-oral (sometimes ingestion of infected PH)
Toxocarinae						
Toxocara	26	carnivores, ruminants, rodents	small intestines	3-30 cm long, 3 lips, long thin cervical alae, oesophageal ventriculus present, males with terminal digitiform appendage, larvae undergo somatic migration, hypobiosis	64-91 µm, spherical, thick-shelled	faecal-oral, ingestion of PH, transplacental, transmammary

The subfamily Ascaridinae contains 5 genera of large roundworms with well-defined lips and a simple oesophagus: *Ascaris* (syn. *Fusaria*, *Lombricoides*, *Stomachida*), *Baylisascaris, Lagochilascaris*, *Parascaris* and *Toxascaris.* The genus *Ascaris* contains worms whose lips are only separated into anterior and posterior regions by slight lateral indentations (interlabia, cervical alae and lateral flanges absent) and whose cuticles have longitudinal bracket-like bars not reaching the surface. Over 175 *Ascaris* spp. have previously been described from a range of vertebrate hosts (mammals, birds, reptiles, amphibians and fish), but the number of species in the genus is highly contentious. Nowadays, only 2 *Ascaris* species are considered valid: namely, *A. lumbricoides* and *A. suum*. Over 100 species are considered *nomen dubium*, another 40 species are pending detailed characterization studies (*species inquirenda*) and around 35 species have been reclassified to other genera, e.g. those described from reptiles have been grouped into 3 genera: *Polydelphis* (without interlabia, with 4 uterine branches) in pythons; *Travassosascaris* (with interlabia, with 4 uterine branches) in rattlesnakes; and *Hexametra* (without interlabia, with 6 uterine branches) in lizards and snakes.

A. lumbricoides from humans and *A. suum* from pigs are commonly encountered around the world. They have been differentiated on the basis of host occurrence and possibly some minor morphological differences (in the sizes and shapes of labial denticles and copulatory spicules), but more recently by genetic differences (mitochondrial and nuclear gene sequences). *A. lumbricoides* is common in many human populations around the world, particularly in tropical and subtropical countries with high rainfall, as well as in temperate regions with warm summers. Infections are particularly prevalent in impoverished communities with poor environmental sanitary conditions, including households where nightsoil (human faeces) is used to fertilise vegetable crops. It is estimated that almost one quarter of the world population (1.4 billion people) may be infected with soil-transmitted helminths, with 700 million infected with *Ascaris*. Infections are over-dispersed in local populations, where large numbers of parasites occur in a small number of individuals. Children are most susceptible to clinical infection; although a range of predisposition factors have been reported, involving various combinations of environmental, social, behavioural and genetic factors. *A. suum* is prevalent in pigs, especially in developing countries with free-ranging village or feral pigs. Modern husbandry practices in developed countries have resulted in a significant decline in the incidence of infections in pigs. There is considerable biological and epidemiological evidence to suggest zoonotic transmission of *A. suum* to humans resulting in patent infections, although molecular studies have

shown limited gene flow between human and pig ascarid populations. While the whole life-cycle of *A. suum* may not be completed in other non-porcine hosts, their larvae can undergo extensive migration in a number of hosts (cattle, sheep, rodents and lagomorphs) leading to allergic manifestations and/or respiratory distress.

***Ascaris* species**	**Definitive hosts**	**Location [Clinical signs]**	**Distribution**
A. lumbricoides (giant roundworm, human roundworm)	Primates: hominid (human, gorilla, chimpanzee, orangutan), hylobatid (gibbon), cercopithecid (rhesus macaque, Barbary macaque, Abyssinian black-and-white colobus), atelid (Guatemalan black howler) [plus miscellaneous reports: Carnivora: canid (dog), ursid (Hokkaido brown bear); Rodentia: castorid (Eurasian beaver), sciurid (black giant squirrel, Indian squirrel, Irrawaddy squirrel, grey squirrel, fox squirrel), murid (mouse), cricetid (muskrat); Lagomorpha: leporid (rabbit, cape jumping hare); Artiodactyla: bovid (cattle, water buffalo, sheep, goat, saiga), cervid (roe deer, moose), suid (pig, wild boar), tayassuid (peccary); Siluriformes: claroteid (bagrid catfish); Gadiformes: gadid (Alaska pollock); Cichliformes: cichlid (blackchin tilapia, Guinean tilapia, Nile tilapia); Diptera: muscid (house fly *Musca domestica*)]	small intestines [illthrift, gut obstruction]	worldwide
A. suum (pig roundworm)	Artiodactyla: suid (pig, wild boar, Sardinian wild boar), Primates: hominid (human) [plus miscellaneous reports: Artiodactyla: bovid (cattle, sheep, goat), cervid (roe deer); Rodentia: murid (mouse); Lagomorpha: leporid (rabbit); Galliformes: phasianid (chicken); Clitellata: lumbricid earthworm *Eisenia foetida*)]	small intestines [production losses]	worldwide

Species awaiting characterization:
A. brevicauda (from crested newt), *brevispiculum* (striped field mouse, wood mouse), *bulbosa* (bearded seal), *casta* (golden dorado), *castoris* (Eurasian beaver), *cebi* (Columbian white-faced capuchin), *circumflexa* (leopard), *columnaris* (black bear, wolverine, Pacific marten, beech marten, European pine marten, fisher, sable, European badger, American badger, striped skunk, spotted skunk, mountain weasel, least weasel, Siberian weasel, stoat, Siberian polecat, European polecat, steppe polecat, raccoon, squirrel, mouse, cotton rat hispid cotton rat), *compar* (willow ptarmigan), *dasypodina* (greater naked-tailed armadillo, six-banded armadillo, striped skunk), *depressa* (Eurasian sparrowhawk, Eurasian eagle-owl, white-tailed eagle, falcon), *devosi* (wolverine, American marten, European pine marten, fisher, stoat, least weasel, European polecat, American mink), *ensicaudata* (common starling, northern lapwing), *eperlani* (European smelt), *equorum* (horse), *ferox* (Syrian rock hyrax), *gestri* (checkered keelback), *gracilis* (long-tailed ground squirrel), *hippopotami* (hippopotamus), *joffi* (little ground squirrel, long-tailed ground squirrel), *laevis* (alpine marmot, hoary marmot, Tarbagan marmot, groundhog, Arctic ground squirrel, long-tailed ground squirrel), *linstowi* (wels catfish), *lotae* (common ling), *marginata* (dog, red fox), *megalocephala* (horse), *meleagrinae* (masked triggerfish, starry triggerfish), *mosgovoyi* (reindeer), *mucronata* (burbot), *osmeri* (European smelt), *ovis* (sheep, saiga antelope), *petiti* (aye-aye), *petromyzi* (European river lamprey), *phacochoeri* (desert warthog, common warthog), *phoxini* (common minnow), *rugosa* (Eurasian eagle-owl), *semiteres* (northern lapwing), *siluriglanidis* (wels catfish), *spalacis* (lesser mole rat), *spilaris* (little owl), *suilla* (pig), *suricattae* (meerkat), *tarbagan* (long-tailed ground squirrel, gray marmot, black-capped marmot, long-tailed marmot, Tarbagan marmot, groundhog), *tentaculatus* (rock hyrax), *thymalli* (grayling), *triquetra* (red fox) and *vimbae* (vimba bream).

Species reclassified to other genera:
A. adunca = *Hysterothylacium aduncum*
A. anguillae = *Raphidascaris acus*
A. anoura (syn. *A. attenuata, A. rubicunda*, *A. oculata*) = *Polydelphis anoura*
A. applanata = *Hexametra applanata*
A. aquillae = *Contracaecum haliaeti*
A. bicolor = *Anisakis rosmari* (syn. *Anisakis simplex*)
A. biuncinata = *Hysterothylacium fabri*
A. brachycheilos = *Polydelphis brachycheilos*
A. circularis = *Terranova circularis*
A. clavata = *Contracaecum clavatum* (syn. *Hysterothylacium clavatum, Hysterothylacium aduncum*)
A. decipiens = *Pseudoterranova decipiens*
A. fabri = *Contracaecum fabri* (syn. *Hysterothylacium fabri*)
A. falcigera = *Contracaecum falcigerum* (syn. *Contracaecum radiatum*)

A. filholi (syn. *A. nelsonis*) = *Anisakis simplex* larvae
A. gadi = *Hysterothylacium gadi*
A. gestri = *Hexametra gestri*
A. hexametra = *Hexametra hexametra*
A. leptura = *Kathlania leptura*
A. marina = *Anisakis marina* (syn. *Anisakis simplex*)
A. marina = *Hysterothylacium rigidum*
A. microcephala = *Contracaecum microcephalum*
A. micropapillata = *Contracaecum micropapillatum*
A. multipapillata = *Contracaecum multipapillatum*
A. osculata = *Contracaecum osculatum*
A. ovalis = *Contracaecum ovale*
A. patagonica = *Anisakis patagonica* (syn. *Anisakis simplex*)
A. pedum = *Contracaecum pedum*
A. plagiostomorum = *Contracaecum plagiostomorum*
A. quadrata = *Mawsonascaris pastinacae*
A. quadricornis (syn. *A. quadrangularis, A. quadrilobata*) = *Hexametra quadricornis*
A. radiata = *Contracaecum radiatum*
A. rotundicaudata (syn. *A. brachyura*) = *Hexametra rotundicaudata*
A. scombrica = *Contracaecum scombricum*
A. similis = *Anisakis similis*
A. simplex = *Anisakis simplex*
A. sphaerocephala = *Cucullanus sphaerocephalus*
A. spiculigerum = *Contracaecum spiculigerum* (syn. *Contracaecum rudolphii*)
A. striata = *Ophidascaris* sp.

Nomen dubium:
A. acanthocaudata (from common ling)*, acerinae* (Eurasian ruffe), *aculeati* (three-spined stickleback), *acuta* (tubot, brill, New York flatfish), *affinis* (common smooth hound), *albulae* (maraena whitefish), *alepocephali* (Risso's smooth-head), *anguillae* (European eel), *appendiculata* (Atlantic pomfret, Atlantic bonito), *argentinae* (Mueller's pearlside), *aspidophori* (hooknose), *atherinae* (Mediterranean sand smelt), *balisticola* (triggerfish), *barbatulae* (stone loach), *belonesvulgaris* (needlefish), *blennii* (viviparous eelpout), *boopis* (bogue), *brachyura* (oriental garden lizard), *bramae* (Atlantic pomfret), *capsularia* (allis shad, royal flagfin, European conger, lumpfish, Atlantic cod, silver scabbardfish, oilfish, Atlantic mackerel, ribbonfosh, John Dory), *carpionis* (common carp), *centrisci* (long-spine snipefish), *clupeae* (European sprat, Atlantic herring), *clupearum* (Atlantic herring), *collaris* (turbot), *constricta* (greater weaver), *crassicauda* (East Atlantic peacock wrasse), *cuneiformis* (ziege, ide, monkey goby), *cyclopteri* (lumpfish), *cynaedi* (goldsinny wrasse), *cyprinierythrophthalmi* (common rudd), *dehiscens* (ringed seal), *digitata* (Ballan wrasse), *ecaudata* (European conger, Atlantic salmon), *engraulidis* (European anchovy, European pilchard), *farionis* (Atlantic salmon), *filariformis* (lanternfish), *flesi* (European flounder), *gadiaeglefini* (haddock), *gadibrandti* (Pacific cod), *gadimerlangi* (blue whiting), *gadiminuti* (poor cod), *gasterostei* (three-spined stickleback), *genypteri* (kingklip), *gracilescens* (Atlantic herring, European anchovy, European sprat), *helopis* (starry sturgeon), *heringii* (giant anteater), *hippocampi* (long-snouted seahorse), *hirsuta* (European smelt), *incrassata* (roughtail stingray), *labiata* (European eel, European conger), *labrilusci* (green wrasse), *leucisciidi* (ide), *linguatulae* (spotted flounder), *longestriata* (Atlantic bluefin tuna), *lophiipiscatorii* (angler), *lyrae* (piper gurnard), *macrolabium* (vadigo, dusky grouper), *macruri* (bighead grenadier), *macruroidei* (grenadier), *madagascariensis* (river hog), *maenae* (blotched picarel), *manidis* (Chinese pangolin), *microcerca* (black-bellied angler), *minuta* (brill), *molvae* (blue ling), *morae* (common mora), *mozgovoyi* (reindeer), *mulli* (red mullet), *neglecta* (black-spotted porcupinefish), *novaculae* (pearly razorfish), *ophidiibarbati* (snake blenny), *ophidiiimberbis* (pearlfish), *orthragorisci* (ocean sunfish), *pachyderma* (porbeagle), *papilligera* (bullet tuna, Atlantic mackerel), *phycis* (forkbeard), *pigmentata* (marmot), *prionodora* (moonfish), *rajae* (common skate), *rostrata* (jewfish), *rubicunda* (Indian python, reticulated python), *salmonisomul* (Arctic cisco), *sauri* (Atlantic lizardfish), *scaphirhynchi* (shovelnose sturgeon), *schroederei* (giant panda), *sciaenae* (shi drum), *scombrorum* (chub mackerel), *scorpaenae* (red scorpionfish), *scorpaenaecirrhosae* (scorpionfish, black scorpionfish), *siluri* (wels catfish), *smaris* (picarel), *soleae* (shorthorn sculpin, common sole), *sparoidum* (bogue, sand steenbras, saddled seabream, picarel), *spicrae* (picarel), *squali* (Schmidt's dace), *stictodora* (pink dentex), *succisa* (lumpfish, thornback ray), *tenuissima* (whiting, common ling), *torpedinis* (marbled electric eel), *trigonura* (stone loach), *truncatula* (European perch), *truttae* (Atlantic salmon), *ungulata* (Ballan wrasse), *uranoscopi* (Atlantic stargazer), *velocissima* (ruffe, zander, European perch) and *wedli* (red mullet).

Parasite morphology: The parasite forms several different developmental stages: eggs, larvae [moult from first-stage (L1) through to fourth-stage (L4)], and adults (male and female). Fertilised eggs appear as round-oval tan-coloured (bile-stained) stages measuring from 50-87 µm in length by 35-60 µm in width (*A. lumbricoides* eggs 65-75 x 35-50 µm, *A. suum* eggs 56-87 x 46-57 µm). They are surrounded by a thick albuminous mamillated (lumpy) outer coat. Before insemination or in early stages of oviposition, female worms may also excrete unfertilised eggs which are more elongate (75-95 x 35-50 µm) and decorticated (not mamillated). Fertilised eggs are excreted unembryonated, but then develop L1 which moult twice to form L2 then L3. When

infective eggs are ingested by susceptible hosts, they hatch releasing small stout larvae (170-250 µm long) with conical tails. The larvae invade host tissues and grow in size (500-600 µm long) before undertaking hepato-pulmonary migration. Larvae in the lungs grow up to 1.0-1.7 mm long and then migrate up the trachea to be swallowed. They moult in the intestines to form L4 (1.6-2.7 mm long) which then moult to form juvenile worm (17-23 mm long) which grow and mature. Adult worms are tubular, cream-pink in colour and large: female worms measuring 200-500 x 3-6 mm; while males are smaller, measuring 150-300 x 2-4 mm. Adults have a striated cuticle and an anterior mouth with 3 small fleshy lips (one dorsal, 2 ventrolateral) bearing small denticles along their anterior inner margins. They do not possess interlabia and they do not bear cervical or caudal alae. Mature males have a tail that curls ventrally, a single tubular testis and a pair of equal spicules 2.0-3.5 mm long. Mature females have an opisthodelphic reproductive tract, with two coiled branches running posteriad initially from the anterior vulva. The combined uteri may contain millions of eggs at any one time and gravid females lay thousands of eggs daily. The species *A. lumbricoides* and *A. suum* are considered by many to be virtually indistinguishable. While careful examination by some workers indicated that *A. suum* had larger labial denticles and thinner and sharper spicules than *A. lumbricoides*, others have reported considerable pleomorphy in these characters apparently related to the age of the worms. Molecular characterization studies have tended to support their separate classification, but they are apparently not as host specific as previously thought.

Site of infection: Adult worms live in the lumen of the small intestine, where the females lay numerous eggs which are shed in host faeces. Prior to the development of adult worms, the infective larvae undertake a curious circuitous hepato-pulmonary migration (a phenomenon considered to be an evolutionary relict behaviour preserved from ancestral forms). The larvae migrate through the gut wall and are carried via the portal circulation to the liver and then the lungs where they penetrate into air spaces and move up the respiratory tree to the epiglottis where they are swallowed (ending up in the gut from where they started).

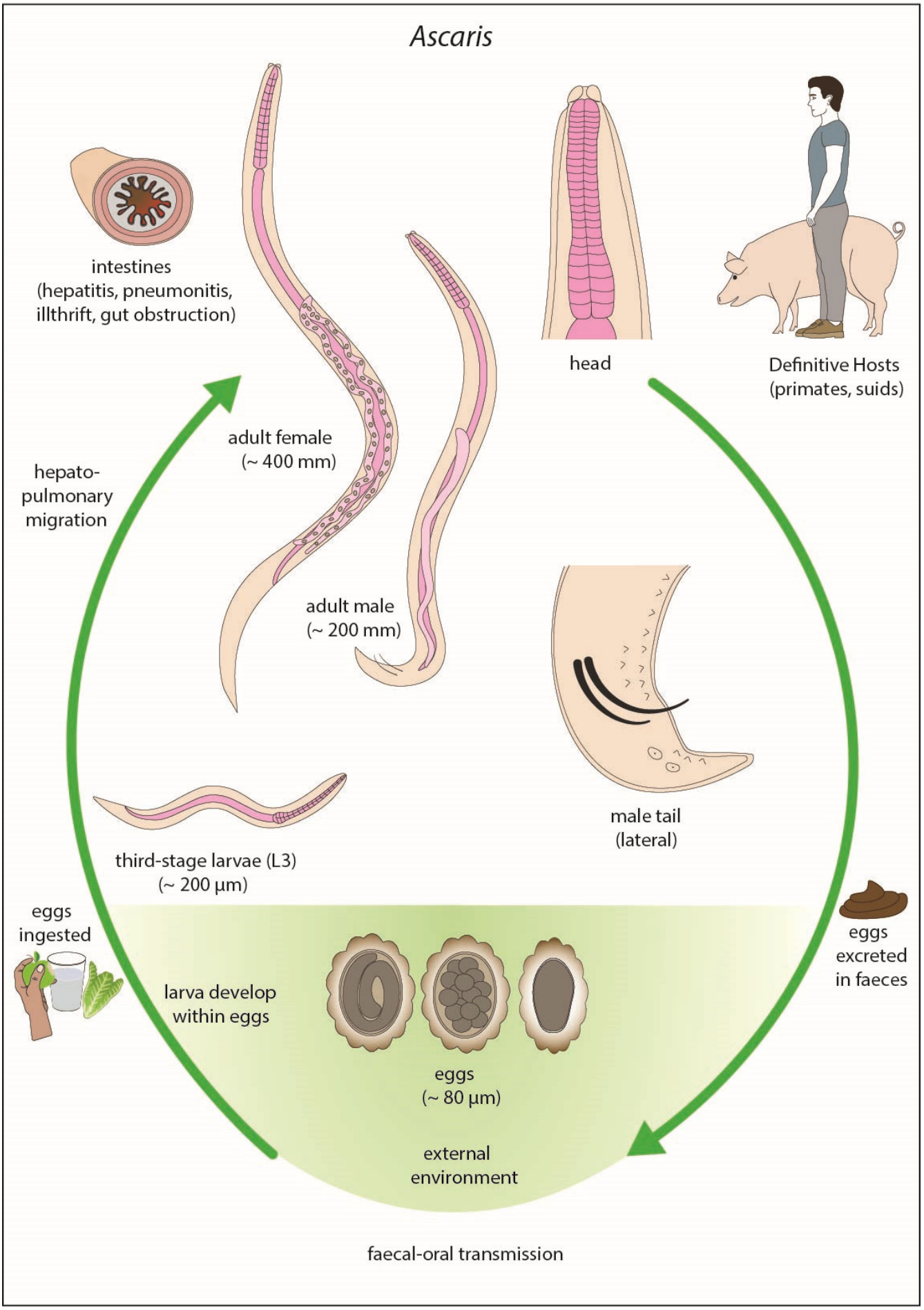
Pathogenesis: Infections by small numbers of worms may remain asymptomatic, although some individuals may develop allergic reactions (urticaria, eosinophilia). Larger numbers of worms, however, can cause significant health problems for the host. Following infection, larvae hatch from eggs in the intestines and invade the intestinal wall to the portal circulation where they pass through the liver and heart to the lungs where L3 are formed. Migrating larvae may cause mucosal haemorrhages in the intestines and white milk-spot lesions up to 1 cm in diameter in the liver (also known as multiple parasitic interstitial hepatitis). Pulmonary migration by larvae may cause petechial haemorrhages, oedema, emphysema, inflammation, and transient pulmonary congestion (pneumonitis, or Loeffler's pneumonia) with cough, chest pain and dyspnoea (difficulty breathing with diaphragmatic thumps or expiratory heaves). Migrating larvae lost or trapped in other tissues often die causing focal inflammation and vague symptoms difficult to diagnose. Adult worms developing in the gut feed on luminal content, they steal liquid nourishment from the host contributing to protein energy malnutrition, impaired carbohydrate absorption and vitamin A malabsorption. Moderate-heavy infections may cause a variety of digestive disorders (abdominal pain, distension, colic, nausea, vomiting, intermittent diarrhoea, anorexia, enterocolitis, mucosal abnormalities) as well as poor growth and development in children with restlessness, insomnia and allergic responses (rashes, asthma). Heavy infections may also cause life-threatening gut obstructions where tangles of worms form a bolus mechanically blocking the gut. To the great consternation of their hosts, worms may also occasionally wander upstream (obstructing biliary or pancreatic ducts, sometimes even being regurgitated) or downstream (infecting the appendix, or being passed in faeces). In pigs, infections by *A. suum* have been associated with reduced productivity through liver damage, reduced feed conversion efficiency, slower live-weight gain, and extended fattening periods. In sheep, and sometimes cattle, grazing on heavily contaminated pastures, migrating larvae may cause eosinophilic granulomas, inflammation and fibrosis in the liver as well as emphysema, oedema and bronchiolitis in the lungs.

Developmental cycle and mode of transmission: The parasite life-cycle is direct and does not involve intermediate hosts or vectors, although paratenic (transport) hosts may sometimes be involved. Infections are passed between definitive hosts by the faecal-oral transmission of eggs containing infective larvae (L3). Freshly-excreted eggs require 9-40 days for embryonation before they become infective. Embryonation occurs faster in warm moist soil (especially clay) and water (~10 days at 30°C). The eggs are very resistant to external environmental conditions and can survive high temperatures (up to 45°C) and dry conditions (down to 6% humidity). Experimental studies have shown that eggs may remain viable in soil for several years. They are also dispersed in the environment by wind, water, earthworms and insects (cockroaches). Eggs in soil/water may be transferred to the mouth by contaminated hands or ingested with foods (uncooked vegetables, washed salads and fruits) or soil (pica = dirt-eating), especially by young children. Once ingested, the eggs hatch in the small and large intestines releasing infective larvae (previously thought to be L2 but now shown to be L3 covered by a loosened L2 cuticle). The L3 invade the mucosa and migrate via the portal circulation to the liver and then to the lungs over 8-10 days. They break into the airspaces (alveoli) of the lungs and move up the bronchi and trachea to the pharynx where they are swallowed. This pulmonary migration is enigmatic as the parasites end up in the intestines from where they started. It has been argued that such migration by various ascarid species may be a remnant genetic trait derived from a vector-borne ancestor, or that it is an adaptive trait strongly associated with enhanced adult body size and fecundity and maintained by selection. Once back in the small intestines, the larvae moult to L4 around 2 weeks after infection and then to L5 (sub-adults) around 3-4 weeks after infection. Worms mature by 6 weeks after infection and females begin egg production 40-65 days after infection (= prepatent period) and produce huge numbers of eggs (up to 200,000 per day). The adult worms may live for 6 months to 2 years, so the entire parasite life-cycle can range from 2 months up to 5-10 years. It has also been shown that eggs of *A. suum* ingested by earthworms or dung beetles may hatch releasing larvae which may remain in their tissues for some time but can

resume development when the paratenic host is ingested by pigs. Suckling piglets have also been found to acquire infections from sows udders contaminated with embryonated eggs and repeated infections have been shown to induce partial immunity.

Differential diagnosis: Infections may be indicated by clinical history and symptomatology but are confirmed by the microscopic detection of eggs in faecal material, often using sedimentation and/or floatation concentration techniques. Ascarid eggs are relatively dense and float better in saturated salt solutions with higher specific gravities (e.g. zinc or magnesium sulphate rather than saturated sodium chloride). Occasionally, intact adult worms may be expelled through the anus, mouth or nose. Haematological tests often reveal marked peripheral eosinophilia during infections but it can be quite variable in strength and duration. Imaging techniques (X-ray, ultrasound, magnetic resonance imaging (MRI) and computed tomography (CT) scans) may be used to discern large worms in tubular organs and ducts. At necropsy, tangles of adult worms may be found in the intestines and small white-spot fibrotic lesions may be visible through the liver. The antemortem diagnosis of infections during the larval migration stage is difficult due to non-specific nature of any clinical signs. Larvae have sometimes been detected in sputum samples but are difficult to identify by untrained personnel. Several immunoserological tests (variants of enzyme immunoassays) have been developed to detect host antibodies against infections but they are generally not clinically useful due to persistent antibody responses and cross-reactivity with other helminths. Various molecular biological techniques using polymerase chain reactions (PCR) to amplify specific gene sequences (mitochondrial cytochrome genes, nuclear ribosomal genes and a range of microsatellite markers) have been used to genotype isolates, trace infections, test egg viability after disinfection and even test coprolites.

Treatment and control: Various anthelmintic drugs have proven effective for the treatment of infections. On a population level, mebendazole and albendazole appear to be the drugs of choice in communities endemic for ascariasis, with chemoprevention targeting school-aged children. Repeated doses of benzimidazoles for individual cases increases efficacy, although it sometimes may cause some worms to wander. Suitable alternatives include pyrantel and levamisole, while ivermectin and moxidectin have also recently been trialled in humans. Piperazine was commonly used but has now been substantively withdrawn due to adverse side-effects. In pigs, suspect ascarid pneumonia may be treated with injectable levamisole or ivermectin. For routine deworming, doramectin, ivermectin, flubendazole, fenbendazole, pyrantel and morantel are effective against ascariasis and have a broader spectrum of activity that piperazine. Although most infections can be successfully treated, the individual often returns to the same heavily contaminated environment and quickly becomes re-infected. Environmental decontamination is difficult because the eggs are very resistant to chemicals; they can embryonate in dilute formalin, potassium dichromate, acid solutions and many commercial disinfectants. Because infections accumulate in their hosts (worms do not multiply in hosts), control measures involve avoiding behaviours conducive to the uptake of eggs; such as improving personal hygiene, maintaining sanitary conditions, and proper disposal of excreta. Fresh faecal material should not be used to fertilise edible crops, but it can be processed by microbial biocomposting before use (high temperature processing destroys egg viability). In piggeries, parasite control should include drenching sows prior to farrowing, regularly treating piglets, maintaining strict hygiene in pens/sties, and proper effluent disposal. Control in free-range operations may be problematic due to the high levels of contamination and the longevity of infective eggs, so paddock rotation/spelling may be necessary.

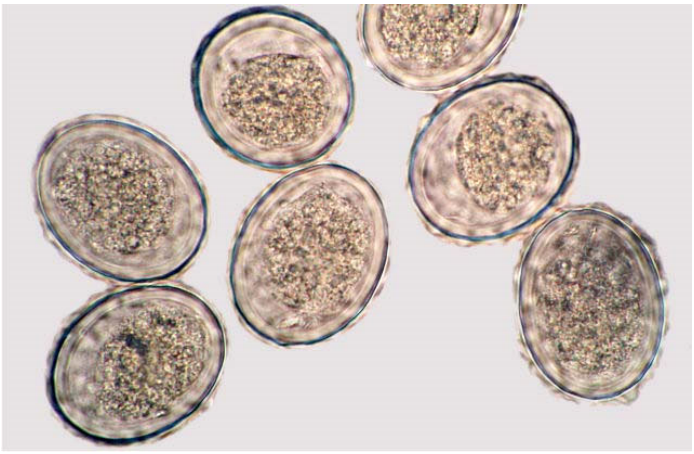

Ascaris
intestines
(hepatitis, pneumonitis,
illthrift, gut obstruction)
adult female
(~ 400 mm)
adult male
(~ 200 mm)
head
Definitive Hosts
(primates, suids)
hepato-
pulmonary
migration
male tail
(lateral)
third-stage larvae (L3)
(~ 200 µm)
eggs
ingested
larva develop
within eggs
eggs
excreted
in faeces
eggs
(~ 80 µm)
external
environment
faecal-oral transmission



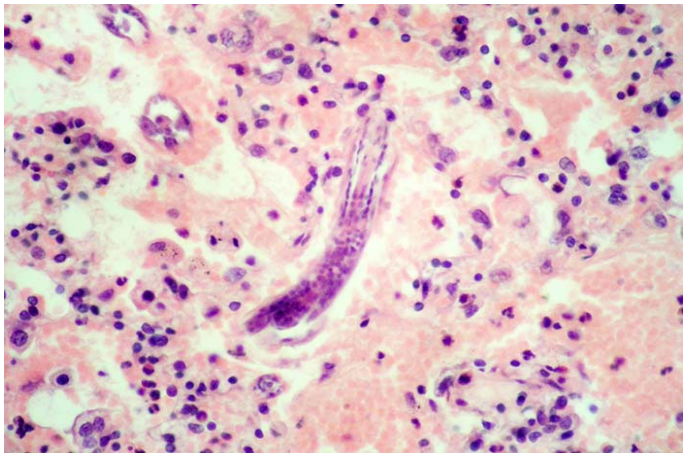
Ascaris adult worms



Ascaris adult worms



Ascaris worm eggs



Ascaris larva in lung

Parascaris
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Ascaridomorpha which includes ascaridoid nematodes (roundworms) characterised by their large size, three prominent anterior lips and the absence of a bursa. They occur in the small intestines of many animals (including humans) and most have simple direct life-cycles involving faecal-oral transmission. Female worms produce numerous eggs which are excreted with host faeces and undergo embryonation to contain infective larvae. When ingested, larvae hatch from the eggs and develop into adult worms in the gut. The larvae of ascaridoid species undergo hepato-pulmonary migration before forming adults, whereas those of heterakoid species do not. Two major ascaridoid families are recognised: ascarids in terrestrial mammals; and anisakids in marine mammals. Infections by *Parascaris* spp. cause enteritis and illthrift in horses worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Ascaridomorpha (large roundworms, mouth surrounded by three large lips, numerous caudal papillae)
Superfamily:	Ascaridoidea (ascarids, eggs thick-shelled, direct cycle but larvae undertake hepato-pulmonary migration)
Family:	Ascarididae (large pale roundworms, in terrestrial mammals)
Genus:	*Parascaris* (parasitic in small intestines of horses)
Species:	several species cause illthrift in foals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Ascaridomorpha is characterised by large roundworms with poorly developed buccal cavity with 3 large lips sometimes separated by interlabia, an undivided oesophagus, numerous caudal papillae, nonbursate males often with pre-anal suckers, and females with complex ovejectors. Five superfamilies (conventionally assigned to the order Ascaridida) are recognised as parasites in vertebrates: Ascaridoidea (cylindrical oesophagus often terminated by swelling without bulb, coelomyarian, eggs thick-shelled); Heterakoidea (oesophagus cylindrical or with claviform corpus, short isthmus and valved bulb, coelomyarian, pre-anal sucker, eggs thick-shelled); Seuratoidea (lips absent, oesophagus short, platymyarian, eggs with delicate shells or hatch *in utero*); Cosmocercoidea (oesophagus with cylindrical corpus, elongate isthmus and valved bulb, platymyarian, eggs with delicate shells or hatch *in utero*); and Subuluroidea (well-developed buccal capsule without lips, coelomyarian, pre-anal sucker, eggs thick-shelled). Adult worms of the superfamily Ascaridoidea inhabit the gastrointestinal tract of vertebrate hosts and generally consume food ingested by the host. They may have simple monoxenous life cycles involving faecal-oral transmission, or more complicated heteroxenous life-cycles involving larval development in vertebrate intermediate hosts and sometimes larval transport in invertebrate paratenic hosts. Female worms produce unembryonated eggs which are passed in host faeces into the external environment where they embryonate to first-stage larvae (L1) which grow and moult to infective L2 or L3. Aquatic species produce thin-shelled eggs which hatch in water releasing sheathed L2 that are taken up by suitable hosts, while terrestrial species produce thick-shelled eggs which hatch releasing L3 when ingested by suitable hosts. Ascaridoid larval stages then undertake unique journeys: most involving pulmonary or somatic migration in their definitive hosts before maturing in the gut, sometimes including vertical transmission (transplacental and/or transmammary); many migrating into the tissues of intermediate hosts, sometimes involving larval migrans or encapsulation in ‘unsuitable’ hosts; and a few undergoing precocious development in invertebrate hosts.

Five ascaridoid families are recognised: Ascarididae (lips often with toothed ridge, oesophagus with or without ventriculus, parasites of mammals, birds, reptiles, amphibians, fishes); Anisakidae (lips with tongue-like prolongations with cuticular thickenings, oesophagus with ventriculus with suture-like depressions, parasites of mammals, birds, reptiles and fishes);

Crossophoridae (lips semicircular with toothed combs, fimbriated collar, long oesophagus without ventriculus, parasites of hyracoids); Heterocheilidae (lips with tongue-like prolongations with cuticular thickenings, cylindrical oesophagus without ventriculus, parasites of sirenians); and Acanthocheilidae (lips small with teeth or toothed ridges, oesophagus with ventriculus, parasites of elasmobranchs). The family Ascarididae contains 4 subfamilies: Ascaridinae (oesophagus simple, gubernaculum absent, lips hexagonal with anterior region offset from posterior, parasites of terrestrial mammals); Toxocarinae (oesophagus with globular ventriculus without appendices, gubernaculum absent, parasites of terrestrial or marine mammals or birds); Angusticaecinae (oesophagus simple, gubernaculum absent, lips quadrangular and not divided into anterior and posterior regions, parasites of reptiles and amphibians); and Multicaecinae (oesophagus with globular ventriculus usually with appendices, gubernaculum present, parasites of crocodilians or rarely fish). Ascaridid genera of medical and veterinary significance are compared in the following table.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Ascaridinae						
Parascaris	3	equids	small intestines	10-50 cm long, 3 large lips each with transverse groove, cuticle striated, males abursate, simple spicules, larvae undergo hepato-pulmonary migration	90-120 µm, spherical, thick-shelled	faecal-oral
Ascaris (roundworm)	2 (+ 150 *nomen dubium*)	primates, suids	small intestines	15-50 cm long, 3 small lips, striated cuticle, males with curved tail, simple spicules, females opisthodelphic, larvae undergo hepato-pulmonary migration	50-87 x 35-60 µm, ovoid, thick-shelled	faecal-oral
Toxascaris	2	carnivores	small intestines	2-15 cm long, 3 lips, long thin cervical alae, oesophageal ventriculus absent, males lack terminal digitiform appendage, larvae do not undergo hepato-pulmonary migration	70-85 x 60-75 µm, ovoid, thick-shelled	faecal-oral (sometimes ingestion of infected PH)
Toxocarinae						
Toxocara	26	carnivores, ruminants, rodents	small intestines	3-30 cm long, 3 lips, long thin cervical alae, oesophageal ventriculus present, males with terminal digitiform appendage, larvae undergo somatic migration, hypobiosis	64-91 µm, spherical, thick-shelled	faecal-oral, ingestion of PH, transplacental, transmammary

The subfamily Ascaridinae contains 5 genera of large roundworms with well-defined lips and a simple oesophagus: *Ascaris* (syn. *Fusaria*, *Lombricoides*, *Stomachida*), *Baylisascaris, Lagochilascaris*, *Parascaris* and *Toxascaris.* The genus *Parascaris* contains worms whose lips are subdivided into anterior and posterior regions by internal transverse grooves forming deep incisions on the lateral margins, small interlabia are present but cervical alae and lateral flanges are absent, and the cuticle has longitudinal bracket-like bars not reaching the surface. Two species, *P. equorum* and *P. univalens,* have been described from equids around the world, mostly in tropical and temperate regions. These species are very similar in morphology, although small differences in spicule structure have been noted (those of *P. equorum* are rounded while those of *P. equorum* are truncated/sharp). Classical and contemporary karyotyping studies differentiated both species, with *P. equorum* having 4 chromosomes with terminal and intercalary heterochromatin, and *P. univalens* having only 2 chromosomes with terminal heterochromatin. More recent molecular characterization studies on nuclear and mitochondrial gene sequences found both species to be closely-related, so close that some authors think they may even be the same species. Irrespective of designation, infections in equids are of clinical significance as a cause of colic, ill-thrift and even death, particularly in foals and yearlings. It is also possible for *P. equorum* eggs ingested by rodents and humans to hatch but the released larvae do not complete their development in these aberrant hosts.

***Parascaris* species**	**Hosts**	**Location [Clinical signs**	**Distribution**
P. equorum (syn. *Ascaris megalocephala bivalens*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra, Burchell's zebra, Hartmann's mountain zebra) [plus miscellaneous reports: Artiodactyla: cervid (white-tailed deer); Rodentia: murid (rat); Primates: hominid (human); Diptera: muscid (house fly *Musca domestica*)]	small intestines [illthrift]	worldwide
P. felis	Carnivora: felid (lion)	5 worms passed	India

		in faeces	
P. univalens (syn. *Ascaris megalocephala univalens*)	Perissodactyla: equid (horse, donkey)	small intestines [illthrift]	Europe, Americas

Parasite morphology: *Parascaris* spp. form 3 different types of developmental stages: eggs; larvae; and adult worms. Freshly laid eggs are spherical to subspherical in shape measuring from 90-120 µm in diameter, brown in colour and surrounded by a thick albuminous (sticky) roughened (finely pitted) eggshell and contain a central single-celled morula. Descriptions of the 4 successive larval stages (L1-L4) are limited as embryonation to L1 and the first moult to L2 occur within the eggs and subsequent moults to L3 and L4 occur within host tissues. Larvae recovered from eggs and host tissues were stout cylindrical forms with rounded heads, thin tubular oesophagi, granular intestines and short tapering tails. Larvae (L3/4) recovered from horse lungs 14 days after infection measured 1.6-2.4 mm long, but 0.7-1.0 mm at 23 days, while young worms (sometimes designated L5) recovered from the intestines at 14 days measured 2.0.-2.5 mm long and 4.2-5.1 mm after 23 days. Adults are exceptionally large white worms with stout rigid cylindrical bodies measuring from 10-50 cm in length. They lack cervical alae and have a small buccal capsule surrounded by 3 large hexagonal- to heart-shaped lips, each divided by a transverse groove (notch) on the medial surface, a short tubular oesophagus connected to the intestines, and short conical tails with a subterminal anus/cloaca. Adults are sexually dimorphic, with females being larger than males (150-500 x 3-8 mm cf. 100-300 x 3-6 mm). Mature females are didelphic and have 2 extensive ovaries and uteri connected to a common vulva located just posterior to the midbody. They have rounded tails terminating in a short conical process. Mature males have rounded or bluntly conical tails with small caudal alae (absent in *P. felis*). They lack a gubernaculum but have 2 long stout spicules (2.0-2.5 mm) whose distal tips are rounded (*P. equorum*) or truncated/sharp (*P. univalens*).

Site of infection: Adults worms infect the small intestines of their equid hosts, being found in the lumen of the duodenum and proximal jejunum, rarely in the stomach. Earlier larval stages undertake hepatic-pulmonary migration from the gut to the liver and then the lungs before being coughed up the trachea and swallowed into the intestines.

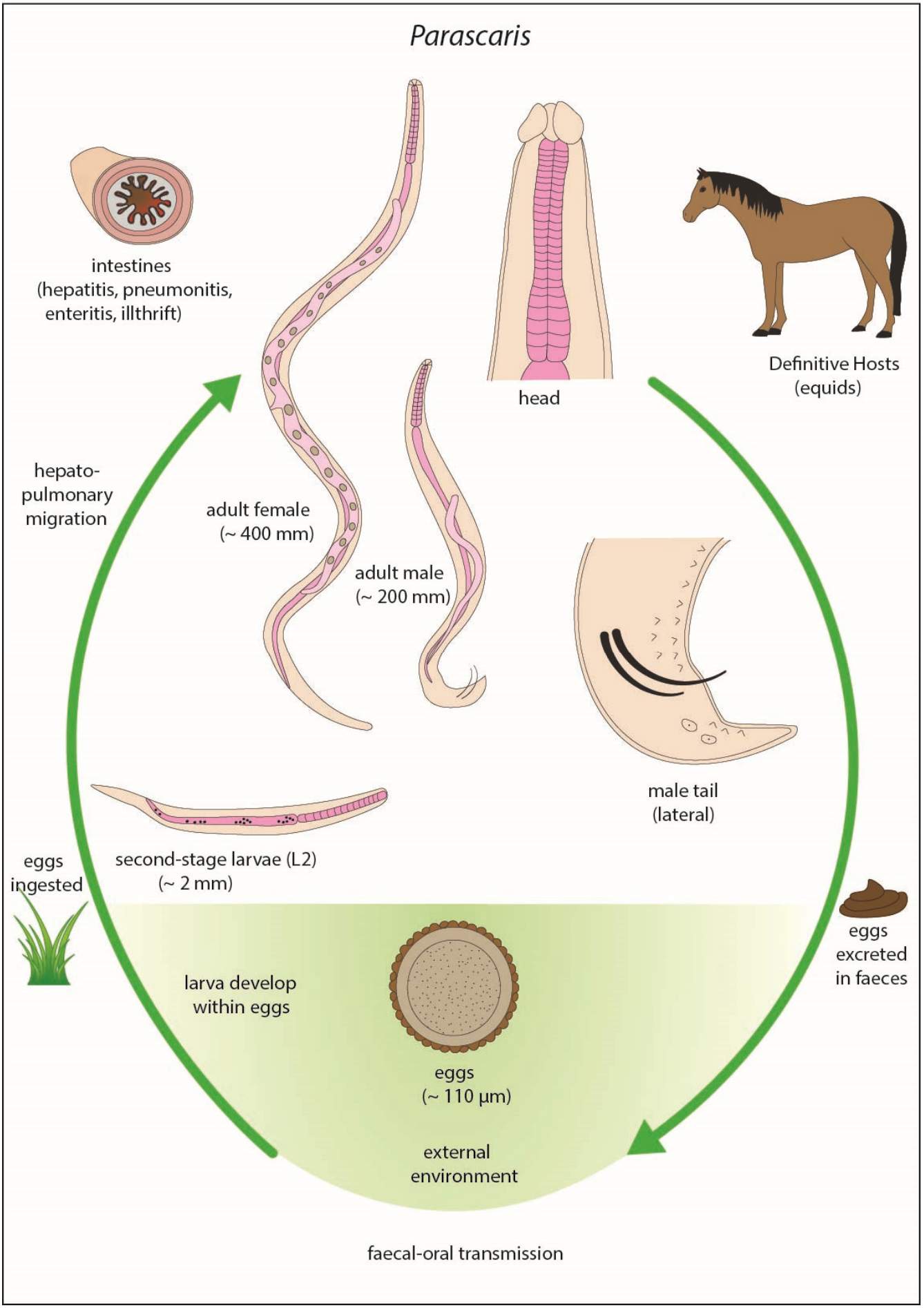
Pathogenesis: Light infections by *P. equorum* and *P. univalens* usually remain asymptomatic, but heavy infections may cause severe disease in suckling and weaning foals as they are highly susceptible due to their immunological immaturity. Foals usually become infected soon after birth and acquire a solid protective immunity over 6-12 months resulting in worm expulsion. Nevertheless, adult horses may harbour some worms and act as carriers, but heavy worm burdens are generally confined to foals and yearlings. Disease develops over 2 phases depending on the stage of infection: developing larvae may cause liver and lung lesions during the prepatent period; while adult worms may cause intestinal disturbances during the patent period. Larvae migrating through the interlobular tissues of the liver form narrow tracts, resulting in traumatic microlesions, haemorrhagic foci, and inflammation (hepatitis) with eosinophilia, later resolving to white fibrotic scars. When they reach the lungs in the pulmonary circulation, they migrate through to alveolar airspaces and ascend the respiratory tree causing pneumonitis, alveolitis, bronchiolitis and bronchitis with interstitial and/or broncho-pneumonia, exacerbated by host immune cells releasing cytotoxic granules which attack worms and damage respiratory tissues (eosinophil infiltrates are later replaced by lymphocytes). Subpleural grey-green lymphocytic nodules develop around dead or dying larvae (nodules more numerous following re-infection). Clinical signs include frequent coughing sometimes with grey nasal discharges, but most foals remain bright and alert although a few may develop fever and anorexia often in association with secondary bacterial infections. Pulmonary signs are most frequent in foals during the spring and autumn. Adult worms living in the intestinal lumen feed on liquid contents competing with the host for food and causing digestive disorders and intestinal disturbances. Gastric motility may be reduced with maldigestion and malabsorption, hypoalbuminaemia, and catarrhal enteritis with abdominal bloating, foul-smelling diarrhoea sometimes alternating with constipation, and colic attacks. Worms and inflammatory responses may also cause intestinal obstruction, impaction, intussusception and sometimes rupture with subsequent peritonitis. Animals may exhibit a variety of clinical signs, mostly involving chronic loss of condition. They develop capricious appetites, sometimes pica, rickets, dull coats, mild anaemia, unthriftiness, reduced growth rates, weight loss, lethargy, weakness, malaise, and emaciation. Aberrant migration of worms can occasionally result in obstruction of the bile and pancreatic ducts which may be life-threatening.

Developmental cycle and mode of transmission: *Parascaris* spp. have direct monoxenous life cycles involving faecal-oral transmission of eggs containing infective larvae. Female worms lay millions of eggs (up to 200,000 eggs per day) which are excreted with host faeces. The eggs embryonate to contain L1 which then moult within the egg to form sheathed L2 over 7-14 days (longer in cooler conditions). The eggs are extremely resistant to external environmental conditions (desiccation, warmth and sunlight) and can survive for up to 10 years in favourable cool climates. Egg development may be arrested over cold winter periods, but they do not survive hot summers unless protected from desiccation in organic matter (such as manure). The eggs are dispersed in the environment by wind and water action and their sticky coats allow them to adhere to many substrates (horses, stables, vegetation, small insects) thus providing many potential sources of infection for foals. Equids become infected by ingesting eggs containing infective L2. Ingested eggs hatch in small intestine and the released larvae penetrate the gut wall and undertake undergo hepato-pulmonary migration. They move to the liver within 2 days via the portal system moulting along the way to L3 which then

migrate through the liver overt the next 7 days (leaving white fibrotic tracts). L3 then re-enter the blood stream through the hepatic vein to the caudal vena cava and subsequently travel through the heart to the pulmonary artery and the pulmonary capillaries to eventually reach the alveoli by 14-23 days. Some workers think the L3 moult to L4 here, while others think it occurs later in intestines. The larvae ascend the mucociliary escalator to the trachea where they are swallowed and return to the small intestine. Here they moult (once or twice) and mature to adults over 7-10 days. The prepatent period (time from infection to first egg excretion) ranges from 63-115 days and the patent period (duration of egg excretion) may last up to 2 years but often declines within several months as acquired immune responses may lead to worm expulsion. There is no evidence of transplacental or transmammary transmission. Infections are abundant in horse populations around the world due to the high fecundity of the females and the extreme resistance of the eggs to external environmental conditions. Infections often demonstrate a seasonal cycle coinciding with the arrival of new susceptible foals in herds with high rates of infections in yearlings (rather than adults).

Differential diagnosis: Clinical signs in foals (cough, intermittent diarrhoea and/or colic) and yearlings (loss of condition) may be suggestive of infection, but a variety of other conditions may cause similar signs. Haematological examinations often reveal elevated white blood cell counts with marked eosinophilia and blood biochemistry may sometimes reveal elevated liver enzymes and hypoalbuminaemia. Medical imaging techniques (thoracic or abdominal radiography) may show inflammation of the airways and/or air sacs and help locate gut obstructions. Endoscopic examination (bronchoscopy) has occasionally been used to detect larvae in the respiratory tract in association with increased mucus production. Infections are conventionally diagnosed by the microscopic detection of characteristic eggs (round with thick pitted walls) in faecal samples, usually following their concentration by sedimentation in water and centrifugal floatation in saturated sugar or heavy metal salt solutions. Infections may also be diagnosed at necropsy by the detection of large white worms inside the small intestines. A range of genotypic characterization techniques have been applied to the identification of parasite species. Karyotyping studies found *P. equorum* to have 4 chromosomes with terminal and intercalary heterochromatin, and *P. univalens* to have 2 chromosomes with terminal heterochromatin. Molecular biological techniques have revealed further differences between these species by polymerase chain reaction (PCR) amplification and restriction fragment length polymorphism (RFLP) analyses or sequencing of nuclear genes (internal transcribed spacer 2 of ribosomal RNA, beta-tubulin) or the entire mitochondrial genome.

Treatment and control: A range of anthelmintic drugs have been used to treat clinical infections in equids, including benzimidazoles (fenbendazole, febantel, oxfendazole, oxibendazole, albendazole, thiabendazole), macrocyclic lactones (ivermectin, abamectin, moxidectin), tetrahydropyrimidines (pyrantel), diethylenediamines (piperazine) and even organophosphonates (dichlorvos, trichlorfon). Most treatments were effective against adult worms in the gut, but care should be taken treating individuals with high worm burdens to avoid subsequent gut obstructions. Few anthelmintics were effective against larval stages in the tissues, therefore repeated treatments are mandated (often monthly from 2-12 months of age). Regrettably, the widespread adoption of regular prophylactic treatment in the horse industries has led to the development of drug resistance in parasite populations, particularly to macrocyclic lactones and pyrantel. It is now recommended by many veterinary authorities that prophylactic treatment not be carried out without diagnosis, that faecal egg count reduction tests be conducted to select the most efficacious drug, that drenches be rotated on a cyclic basis, and that animals be treated systematically (foals and yearlings) or selectively (as required). In order for animals to develop a solid protective immunity against disease, they must still be exposed to low levels of natural infection, so the objective of treatment programmes should be control rather than eradication. Various preventive strategies may also be applied at the farm level to reduce transmission rates; mostly by improved sanitation and hygiene (frequent removal of faeces from pastures, regular cleaning and disinfection of stables and yards, provision of clean food and water), stock management (quarantine and isolation, reducing stocking rates, treating pregnant horses, separating foals and yearlings, stabling or moving to clean pastures after treatment) and pasture management (pasture rotation or spelling, but remembering that worm eggs may remain viable for years).

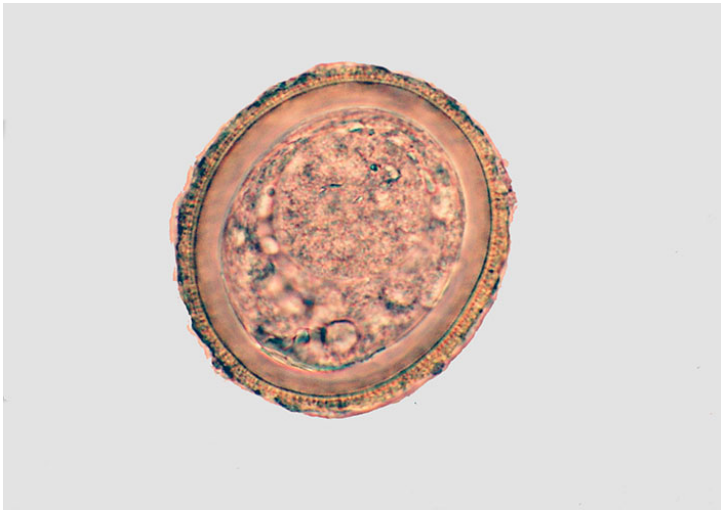

Parascaris
intestines
(hepatitis, pneumonitis,
enteritis, illthrift)
head
Definitive Hosts
(equids)
hepato-
pulmonary
migration
adult female
(~ 400 mm)
adult male
(~ 200 mm)
male tail
(lateral)
second-stage larvae (L2)
(~ 2 mm)
eggs
ingested
eggs
excreted
in faeces
larva develop
within eggs
eggs
(~ 110 µm)
external
environment
faecal-oral transmission



Parascaris adult worms



Parascaris adult worms



Parascaris worm egg

Toxascaris
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Ascaridomorpha which includes ascaridoid nematodes (roundworms) characterised by their large size, three prominent anterior lips and the absence of a bursa. They occur in the small intestines of many animals (including humans) and most have simple direct life-cycles involving faecal-oral transmission. Female worms produce numerous eggs which are excreted with host faeces and undergo embryonation to contain infective larvae. When ingested, larvae hatch from the eggs and develop into adult worms in the gut. The larvae of ascaridoid species undergo hepato-pulmonary migration before forming adults, whereas those of heterakoid species do not. Two major ascaridoid families are recognised: ascarids in terrestrial mammals; and anisakids in marine mammals. Infections by *Toxascaris* spp. are unusual in that larvae may be taken up by paratenic (transport) hosts (usually rodents), and they do not undergo hepato-pulmonary migration in the definitive host. Infections in cats and dogs cause unthriftiness, and occasionally diarrhoea.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Ascaridomorpha (large roundworms, mouth surrounded by three large lips, numerous caudal papillae)
Superfamily:	Ascaridoidea (ascarids, eggs thick-shelled, direct cycle but larvae undertake hepato-pulmonary migration)
Family:	Ascarididae (large pale roundworms, in terrestrial mammals)
Genus:	*Toxascaris* (parasitic in small intestines of dogs/foxes/cats)
Species:	*T. leonina* (causes illthrift in carnivores)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

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CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Ascaridomorpha is characterised by large roundworms with poorly developed buccal cavity with 3 large lips sometimes separated by interlabia, an undivided oesophagus, numerous caudal papillae, nonbursate males often with pre-anal suckers, and females with complex ovejectors. Five superfamilies (conventionally assigned to the order Ascaridida) are recognised as parasites in vertebrates: Ascaridoidea (cylindrical oesophagus often terminated by swelling without bulb, coelomyarian, eggs thick-shelled); Heterakoidea (oesophagus cylindrical or with claviform corpus, short isthmus and valved bulb, coelomyarian, pre-anal sucker, eggs thick-shelled); Seuratoidea (lips absent, oesophagus short, platymyarian, eggs with delicate shells or hatch *in utero*); Cosmocercoidea (oesophagus with cylindrical corpus, elongate isthmus and valved bulb, platymyarian, eggs with delicate shells or hatch *in utero*); and Subuluroidea (well-developed buccal capsule without lips, coelomyarian, pre-anal sucker, eggs thick-shelled). Adult worms of the superfamily Ascaridoidea inhabit the gastrointestinal tract of vertebrate hosts and generally consume food ingested by the host. They may have simple monoxenous life cycles involving faecal-oral transmission, or more complicated heteroxenous life-cycles involving larval development in vertebrate intermediate hosts and sometimes larval transport in invertebrate paratenic hosts. Female worms produce unembryonated eggs which are passed in host faeces into the external environment where they embryonate to first-stage larvae (L1) which grow and moult to infective L2 or L3. Aquatic species produce thin-shelled eggs which hatch in water releasing sheathed L2 that are taken up by suitable hosts, while terrestrial species produce thick-shelled eggs which hatch releasing L3 when ingested by suitable hosts. Ascaridoid larval stages then undertake unique journeys: most involving pulmonary or somatic migration in their definitive hosts before maturing in the gut, sometimes including vertical transmission (transplacental and/or transmammary); many migrating into the tissues of intermediate hosts, sometimes involving larval migrans or encapsulation in 'unsuitable' hosts; and a few undergoing precocious development in invertebrate hosts.

Five ascaridoid families are recognised: Ascarididae (lips often with toothed ridge, oesophagus with or without ventriculus, parasites of mammals, birds, reptiles, amphibians, fishes); Anisakidae (lips with tongue-like prolongations with cuticular

thickenings, oesophagus with ventriculus with suture-like depressions, parasites of mammals, birds, reptiles and fishes); Crossophoridae (lips semicircular with toothed combs, fimbriated collar, long oesophagus without ventriculus, parasites of hyracoids); Heterocheilidae (lips with tongue-like prolongations with cuticular thickenings, cylindrical oesophagus without ventriculus, parasites of sirenians); and Acanthocheilidae (lips small with teeth or toothed ridges, oesophagus with ventriculus, parasites of elasmobranchs). The family Ascarididae contains 4 subfamilies: Ascaridinae (oesophagus simple, gubernaculum absent, lips hexagonal with anterior region offset from posterior, parasites of terrestrial mammals); Toxocarinae (oesophagus with globular ventriculus without appendices, gubernaculum absent, parasites of terrestrial or marine mammals or birds); Angusticaecinae (oesophagus simple, gubernaculum absent, lips quadrangular and not divided into anterior and posterior regions, parasites of reptiles and amphibians); and Multicaecinae (oesophagus with globular ventriculus usually with appendices, gubernaculum present, parasites of crocodilians or rarely fish). Ascaridid genera of medical and veterinary significance are compared in the following table.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Ascaridinae						
Toxascaris	2	carnivores	small intestines	2-15 cm long, 3 lips, long thin cervical alae, oesophageal ventriculus absent, males lack terminal digitiform appendage, larvae do not undergo hepato-pulmonary migration	70-85 x 60-75 µm, ovoid, thick-shelled	faecal-oral (sometimes ingestion of infected PH)
Ascaris (roundworm)	2 (+ 150 *nomen dubium*)	primates, suids	small intestines	15-50 cm long, 3 small lips, striated cuticle, males with curved tail, simple spicules, females opisthodelphic, larvae undergo hepato-pulmonary migration	50-87 x 35-60 µm, ovoid, thick-shelled	faecal-oral
Parascaris	3	equids	small intestines	10-50 cm long, 3 large lips each with transverse groove, cuticle striated, males abursate, simple spicules, larvae undergo hepato-pulmonary migration	90-120 µm, spherical, thick-shelled	faecal-oral
Toxocarinae						
Toxocara	26	carnivores, ruminants, rodents	small intestines	3-30 cm long, 3 lips, long thin cervical alae, oesophageal ventriculus present, males with terminal digitiform appendage, larvae undergo somatic migration, hypobiosis	64-91 µm, spherical, thick-shelled	faecal-oral, ingestion of PH, transplacental, transmammary

The subfamily Ascaridinae contains 5 genera of large roundworms with well-defined lips and a simple oesophagus (ventriculus absent): namely, *Ascaris* (syn. *Fusaria*, *Lombricoides*, *Stomachida*), *Baylisascaris, Lagochilascaris*, *Parascaris* and *Toxascaris.* The genus *Toxascaris* contain the arrow-headed ascaridoids (cervical alae present) which form smooth-shelled eggs. The lips of adult worms are not deeply indented anteriorly, interlabia and lateral flanges are absent, and the cuticle has funnel-shaped bars reaching the surface in the alae region. Transmission cycles are usually direct (ingestion of eggs containing infective L2) but may sometimes be indirect (ingestion of encapsulated larvae in tissues of small paratenic hosts). The genus *Toxascaris* may be monotypic with a single species *T. leonina* being found as a relatively common cosmopolitan parasite in domestic and wild carnivores, notably felids and less frequently canids. Several species described in ursid and procyonid carnivores have recently been transferred to the genus *Baylisascaris* and the sole report of a species in a bird remains doubtful.

***Toxascaris* species**	**Definitive hosts**	**Location [Clinical signs]**	**Paratenic hosts**	**Distribution**
T. centropusi	Cuculiformes: cuculid (greater coucal)	intestines		India
T. leonina (syn. *T. limbata, marginata, Ascaris anterospiralis, canis, cati, crenata, microptera, teres*)	Carnivora: felid (cat, wild cat, rusty spotted cat, Pallas's cat, Kaffir cat, African wild cat, fishing cat, bobcat, Eurasian lynx, Canada lynx, Iberian lynx, cougar, leopard cat, leopard, snow leopard, clouded leopard, ocelot, serval, jaguar, puma, South American tiger cat, Brazilian chati, Bengal tiger, Siberian	small intestines [illthrift]	Rodentia: murid (mouse, rat), cricetid (Siberian brown lemming, tundra vole); Lagomorpha: leporid (rabbit); Diptera: muscid	worldwide

	tiger, lion, Asiatic lion, cheetah), canid (dog, dingo, Cape hunting dog, wolf, Arctic wolf, coyote, golden jackal, culpeo, raccoon dog, red fox, American red fox, Iberian fox, grey fox, corsac fox, Indian fox, Arctic fox), ursid (American black bear), mephitid (Molina's hog-nosed skunk), viverrid (common genet), mustelid (wolverine); Primates: hominid (human)		(house fly *Musca domestica*)	
T. melursus (now *Baylisascaris*)	Carnivora: ursid (sloth bear)			India
T. procyonis (now *Baylisascaris*)	Carnivora: procyonid (raccoon)			North America
T. transfuga (syn. *T. ailuri*, *multipapillata*, *selenarctis*) (now *Baylisascaris*)	Carnivora: ursid (American black bear, brown bear), ailurid (red panda)			North America, Eurasia

Parasite morphology: *Toxascaris* spp. form several different developmental stages: eggs which produce larvae that moult from first-stage (L1) to fourth-stage (L4) before developing into adult worms. Freshly laid eggs are subspherical measuring 70-85 x 60-75 µm, clear and translucent or pale brown in colour, surrounded by a smooth thick shell (rough in *Toxocara*), and are unembryonated containing a central morula. Embryonated eggs contain a coiled L1 which measured from 190-230 µm in length when dissected from eggs and had small cuticular projections around the mouth, lateral alae, and a tapering tail with a small terminal knob. L2 also develop within the egg and upon hatching they ranged in length from 200-600 µm, had rounded heads with conspicuous triangular structures around the mouth (modified lips), a tapering tail with a small terminal knob, and were ensheathed (retained L1 cuticle as protective covering). L3 measured 420-650 µm long and had small lips, a cuticular flange, and a knobbed tail, while L4 ranged in length from 560-1,420 µm and had mouths with distinct lips and sharp dorsally curved tails. Adults are large tan-pink cylindrical worms measuring from 2-15 cm long and they have 2 prominent cervical alae (making them members of the 'arrow-headed' ascaridoids). The alae are lanceolate in shape being long and narrow (those of *Toxocara* are often broader) and the surrounding cuticle has small annulations and funnel-shaped bars reaching to the surface. The worms have 3 lips surrounding the mouth, each with anterior denticulate margins but lacking interlabia and lateral flanges, an inconspicuous buccal capsule, a tubular oesophagus without a posterior bulb (present in *Toxocara*), and short tapering tails. Adult worms are sexually dimorphic, with female worms being larger than males (20-150 x 2 mm cf. 20-70 x 2 mm). Mature females are didelphic with 2 ovaries and uteri lying posteriorly behind the common vulva located in the anterior third of the body. Mature males have simple conical tails without terminal appendages (present in *Toxocara*) and they have 2 subequal curved wingless spicules measuring 0.7-1.5 mm in length.

Site of infection: Adult worms infect the small intestines of their carnivorous hosts, residing within the lumen. Earlier larval stages do not undertake somatic or hepato-pulmonary migration through host tissues, but may undergo a brief histotrophic phase of development in the intestinal wall (sometimes termed local migration). Infective larvae have been detected encysted within the muscles of small vertebrate prey animals which may act as paratenic hosts (carrying L2) or as intermediate hosts (in which L2 develop to L3).

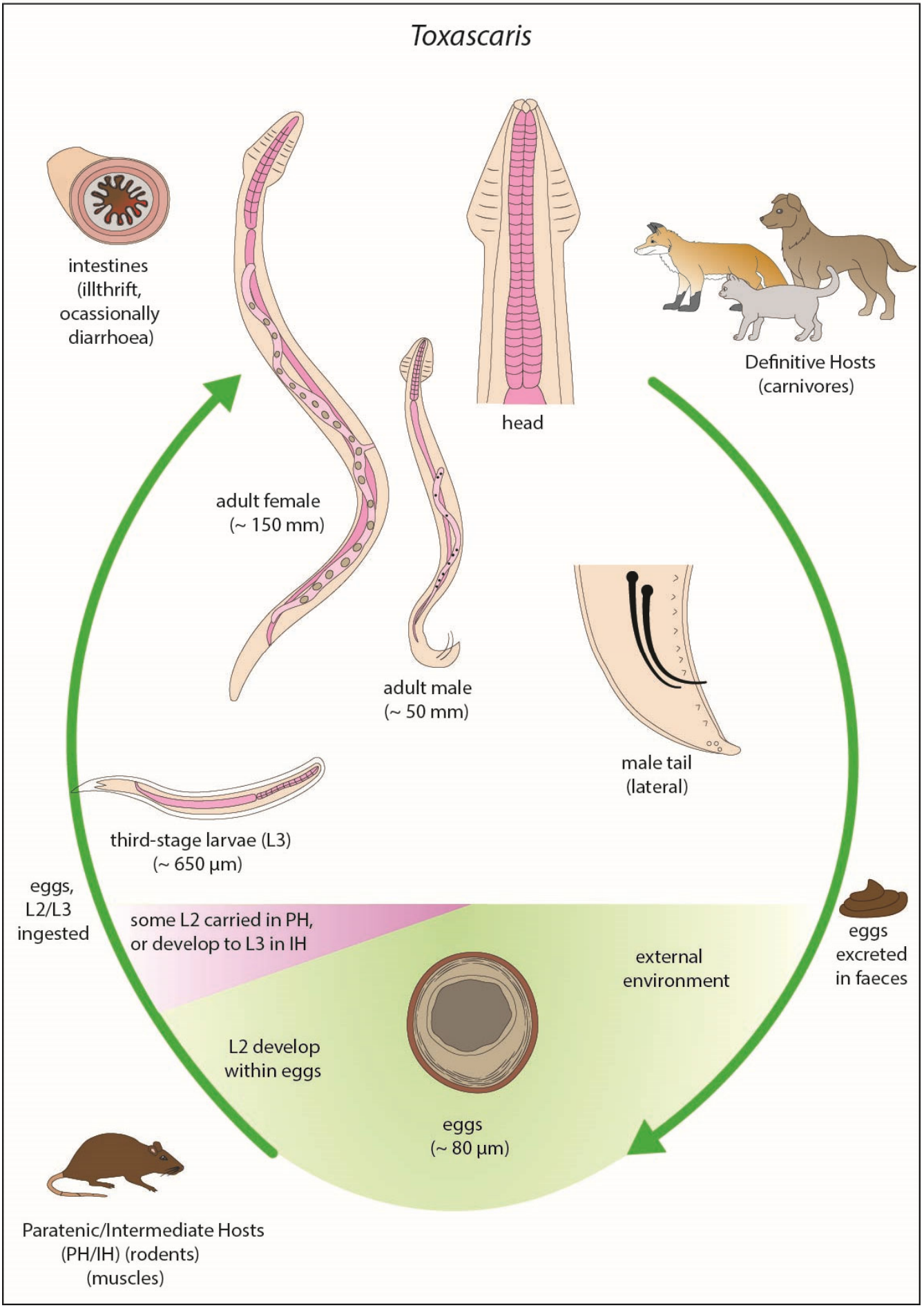
Pathogenesis: Most infections in cats and dogs remain asymptomatic even when moderate numbers of worms may be present. Developing larvae remain within the vicinity of the small intestines (no somatic or hepatic-pulmonary migration) and parasites do not feed on host tissues but absorb nutrients from the lumen. Nonetheless, heavy infections may cause local inflammation interfering with digestive processes with mucoid enteritis, malnutrition, mild diarrhoea, distended abdomens (pot-bellied appearance), dull coat, anorexia, malaise and unthriftiness. Large tangles of worms may sometimes cause intestinal obstruction leading to intussusception and even death. Aberrant migration of worms into the stomach may also cause irritation of the mucosa and vomiting. The pathogenesis of infections is frequently complicated by concomitant infections by *Toxocara* spp. but transplacental and transmammary transmission does not occur and the prolonged prepatent period of ~8 weeks in dogs and ~13 weeks in cats makes it unlikely to observe infections in animals < 2-3 months of age. Felids exhibit some age resistance with infections being more pronounced in kittens than in adult cats, but no age resistance is observed in canids and parasites may be found in puppies and adult dogs. Humans may occasionally become infected with larvae which wander throughout the body causing traumatic damage and inflammation (condition known as visceral larval migrans) but they are unable to complete their development.

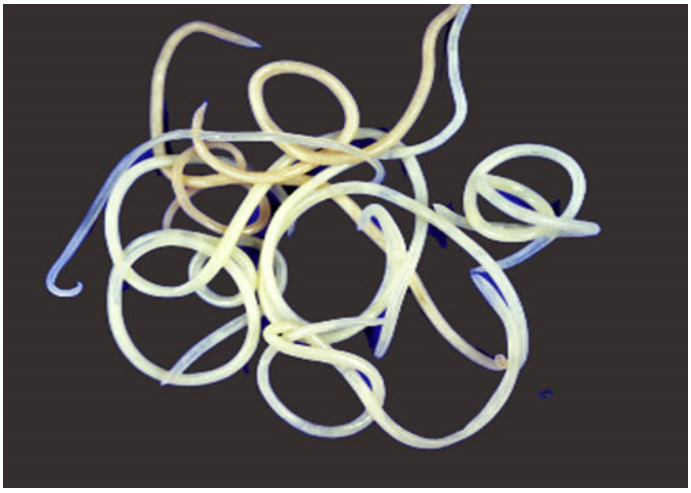
Developmental cycle and mode of transmission: *Toxascaris* spp. are unusual in that their life-cycles may be direct (involving faecal-oral transmission) or indirect (involving predator-prey transmission), the infective stages are usually larvated eggs containing

L2, and parasite development takes place exclusively within the small intestines. Gravid female worms lay unembryonated eggs in the intestines and they are excreted with host faeces into the external environment. The eggs embryonate over several days depending on environmental conditions (3-5 days at 25-30°C, 6-10 days at 17-22°C) producing L1 which moult within the eggshell to form ensheathed L2. The eggs are very resistant to harsh conditions and disinfectants and may survive for several years. Carnivorous definitive hosts become infected when they ingest larvated eggs with contaminated food or water (direct cycle), or by eating encysted larvae in the tissues of small prey animals (indirect cycle). Ingested eggs hatch in the duodenum releasing the infective L2 which moult to L3 and penetrate the mucosa undergoing local migration and histotrophic development to L4 before re-emerging into the lumen 9-14 days later (some larvae have also been observed to develop directly in the lumen). The L4 moult to subadult stages (often referred to as L5) which mature to sexually reproductive adults in the intestines. If larvated eggs are ingested by some small vertebrate animals (rodents, lagomorphs), they may hatch releasing L2 which penetrate the gut wall, migrate via the mesenteries to the musculature over 6-7 days, and then encyst over 9-29 days. Reports differ as to what larval stage becomes encysted: many consider them to still be L2 (which makes the animals paratenic (transport) hosts in which parasites do not further develop); while some consider them to have moulted to L3 (which makes the animals intermediate hosts as they support parasite development). The encysted larvae have been shown experimentally to survive for up to 5 months in mice. Once they are consumed by carnivorous final hosts, the encysted larvae resume development in the intestines eventually maturing to adult worms. The prepatent period (time from infection to first egg excretion) ranges from 42-74 days, and adult worms are thought to live for up to 1.5 years.

Differential diagnosis: Infections are not diagnosed on the basis of symptomatology as most are subclinical and even when clinical signs are present they are vague and nonspecific. Patent infections are conventionally diagnosed by the microscopic detection of characteristic worm eggs in faecal samples, usually following their concentration by sedimentation in water and floatation in saturated sugar or salt solutions. Large white adult worms may also be detected occasionally in vomitus or faecal samples. On necropsy, adult worms may be detected in the small intestinal lumen on dissection. The worms have a characteristic appearance with long narrow spear-like cervical alae (as opposed to the short wide arrowhead-like cervical alae of *Toxocara* spp.). Molecular biological techniques have been used to characterize parasite species by the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (ribosomal RNA) or mitochondrial genomes. Parasites were also detected by DNA analyses in puma coprolites dated back to the Pleistocene in South America.

Treatment and control: A wide range of anthelmintic drugs has proven effective in the treatment of infections in cats and dogs, particularly the benzimidazoles (oxibendazole, mebendazole, fenbendazole) and prebenzimidazoles (febantel), but also including macrocyclic lactones (selamectin, milbemycin, moxidectin, ivermectin), imidazothiazoles (levamisole), tetrahydropyrimidines (pyrantel), isoquinolines (praziquantel), depsipeptides (emodepside), isothiocyanates (nitroscanate) and diethylenediamines (piperazine). Treated animals may be promptly re-infected if returned to the same contaminated facilities. Veterinary authorities recommend regular treatment of kittens and puppies monthly until 6 months of age and then selectively as needed. A range of preventive measures may be used to reduce parasite transmission, mostly involving improved sanitation and hygiene (removing faeces, disinfecting pens/cages using steam or bleaches, avoiding grassy shaded runs, providing clean food and water) but also involving animal control (avoid over-crowding, quarantine and isolation, excluding rodents, preventing hunting/foraging).

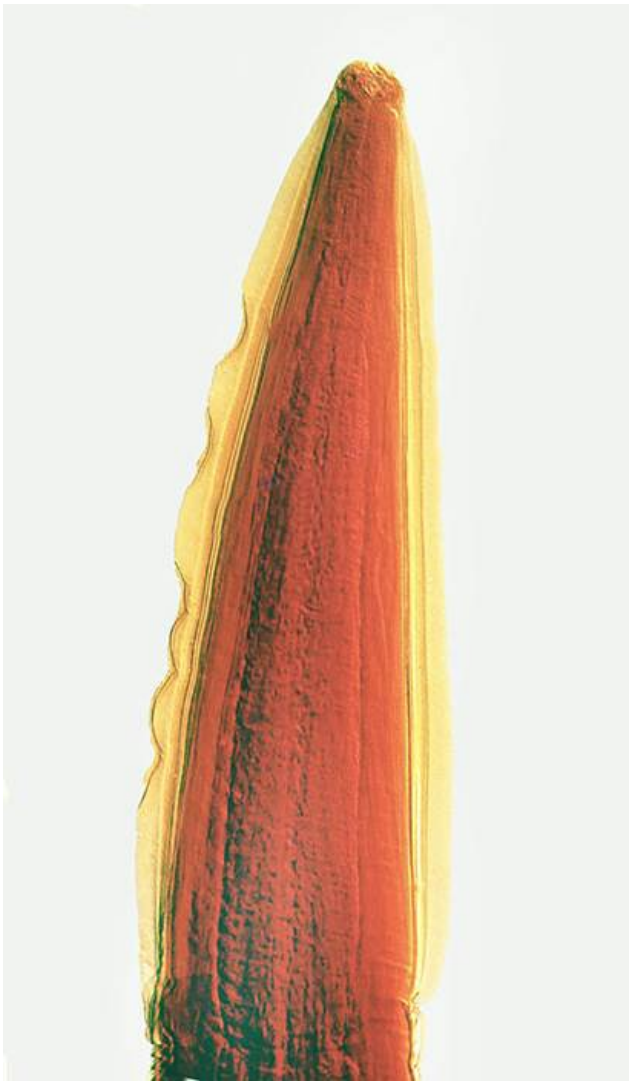

Toxascaris
intestines
(illthrift,
ocassionally
diarrhoea)
adult female
(~ 150 mm)
head
Definitive Hosts
(carnivores)
adult male
(~ 50 mm)
male tail
(lateral)
third-stage larvae (L3)
(~ 650 µm)
eggs,
L2/L3
ingested
some L2 carried in PH,
or develop to L3 in IH
external
environment
eggs
excreted
in faeces
L2 develop
within eggs
eggs
(~ 80 µm)
Paratenic/Intermediate Hosts
(PH/IH) (rodents)
(muscles)



Toxascaris adult worms



Toxascaris worm eggs



Toxascaris adult worm, head

Toxocara
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Ascaridomorpha which includes ascaridoid nematodes (roundworms) characterised by their large size, three prominent anterior lips and the absence of a bursa. They occur in the small intestines of many animals (including humans) and most have simple direct life-cycles involving faecal-oral transmission. Female worms produce numerous eggs which are excreted with host faeces and undergo embryonation to contain infective larvae. When ingested, larvae hatch from the eggs and develop into adult worms in the gut. The larvae of ascaridoid species undergo hepato-pulmonary migration before forming adults, whereas those of heterakoid species do not. Two major ascaridoid families are recognised: ascarids in terrestrial mammals; and anisakids in marine mammals. Infections by *Toxocara* spp. are unusual in that larvae may also be taken up by paratenic (transport) hosts (usually rodents and birds), L3 may undergo somatic migration and arrested development (hypobiosis) in definitive host tissues, and infections can be transmitted vertically (transplacental and transmammary). Infections may cause pulmonary and enteric diseases in dogs, and sometimes cats, while the accidental ingestion of larvae by humans may result in visceral and ocular larva migrans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Ascaridomorpha (large roundworms, mouth surrounded by three large lips, numerous caudal papillae)
Superfamily:	Ascaridoidea (ascarids, eggs thick-shelled, direct cycle but larvae undertake hepato-pulmonary migration)
Family:	Ascarididae (large pale roundworms, in terrestrial mammals)
Genus:	*Toxocara* (parasitic in small intestines of dogs/cats/bovids)
Species:	various species cause enteric diseases in dogs, cats and cattle, and larval migrans in humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but

some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Ascaridomorpha is characterised by large roundworms with poorly developed buccal cavity with 3 large lips sometimes separated by interlabia, an undivided oesophagus, numerous caudal papillae, nonbursate males often with pre-anal suckers, and females with complex ovejectors. Five superfamilies (conventionally assigned to the order Ascaridida) are recognised as parasites in vertebrates: Ascaridoidea (cylindrical oesophagus often terminated by swelling without bulb, coelomyarian, eggs thick-shelled); Heterakoidea (oesophagus cylindrical or with claviform corpus, short isthmus and valved bulb, coelomyarian, pre-anal sucker, eggs thick-shelled); Seuratoidea (lips absent, oesophagus short, platymyarian, eggs with delicate shells or hatch *in utero*); Cosmocercoidea (oesophagus with cylindrical corpus, elongate isthmus and valved bulb, platymyarian, eggs with delicate shells or hatch *in utero*); and Subuluroidea (well-developed buccal capsule without lips, coelomyarian, pre-anal sucker, eggs thick-shelled). Adult worms of the superfamily Ascaridoidea inhabit the gastrointestinal tract of vertebrate hosts and generally consume food ingested by the host. They may have simple monoxenous life cycles involving faecal-oral transmission, or more complicated heteroxenous life-cycles involving larval development in vertebrate intermediate hosts and sometimes larval transport in invertebrate paratenic hosts. Female worms produce unembryonated eggs which are passed in host faeces into the external environment where they embryonate to first-stage larvae (L1) which grow and moult to infective L2 or L3. Aquatic species produce thin-shelled eggs which hatch in water releasing sheathed L2 that are taken up by suitable hosts, while terrestrial species produce thick-shelled eggs which hatch releasing L3 when ingested by suitable hosts. Ascaridoid larval stages then undertake unique journeys: most involving pulmonary or somatic migration in their definitive hosts before maturing in the gut, sometimes including vertical transmission (transplacental and/or transmammary); many migrating into the tissues of intermediate hosts, sometimes involving larval migrans or encapsulation in ‘unsuitable’ hosts; and a few undergoing precocious development in invertebrate hosts.

Five ascaridoid families are recognised: Ascarididae (lips often with toothed ridge, oesophagus with or without ventriculus, parasites of mammals, birds, reptiles, amphibians, fishes); Anisakidae (lips with tongue-like prolongations with cuticular thickenings, oesophagus with ventriculus with suture-like depressions, parasites of mammals, birds, reptiles and fishes); Crossophoridae (lips semicircular with toothed combs, fimbriated collar, long oesophagus without ventriculus, parasites of hyracoids); Heterocheilidae (lips with tongue-like prolongations with cuticular thickenings, cylindrical oesophagus without ventriculus, parasites of sirenians); and Acanthocheilidae (lips small with teeth or toothed ridges, oesophagus with ventriculus, parasites of elasmobranchs). The family Ascarididae contains 4 subfamilies: Ascaridinae (oesophagus simple, gubernaculum absent, lips hexagonal with anterior region offset from posterior, parasites of terrestrial mammals); Toxocarinae (oesophagus with globular ventriculus without appendices, gubernaculum absent, parasites of terrestrial or marine mammals or birds); Angusticaecinae (oesophagus simple, gubernaculum absent, lips quadrangular and not divided into anterior and posterior regions, parasites of reptiles and amphibians); and Multicaecinae (oesophagus with globular ventriculus usually with appendices, gubernaculum present, parasites of crocodilians or rarely fish). Ascaridid genera of medical and veterinary significance are compared in the following table.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Toxocarinae						
Toxocara	26	carnivores, ruminants, rodents	small intestines	3-30 cm long, 3 lips, long thin cervical alae, oesophageal ventriculus present, males with terminal digitiform appendage, larvae undergo somatic migration, hypobiosis	64-91 µm, spherical, thick-shelled	faecal-oral, ingestion of PH, transplacental, transmammary
Ascaridinae						
Ascaris (roundworm)	2 (+ 150 *nomen dubium*)	primates, suids	small intestines	15-50 cm long, 3 small lips, striated cuticle, males with curved tail, simple spicules, females opisthodelphic, larvae undergo hepato-pulmonary migration	50-87 x 35-60 µm, ovoid, thick-shelled	faecal-oral
Parascaris	3	equids	small intestines	10-50 cm long, 3 large lips each with transverse groove, cuticle striated, males abursate, simple spicules, larvae undergo hepato-pulmonary migration	90-120 µm, spherical, thick-shelled	faecal-oral
Toxascaris	2	carnivores	small intestines	2-15 cm long, 3 lips, long thin cervical alae, oesophageal ventriculus absent, males lack terminal digitiform appendage, larvae do not undergo hepato-pulmonary migration	70-85 x 60-75 µm, ovoid, thick-shelled	faecal-oral (sometimes ingestion of infected PH)

The subfamily Toxocarinae contains 3 genera of large roundworms with well-defined lips and an oesophagus with a globular ventriculus without appendices: namely, *Paradujardinia, Porrocaecum* and *Toxocara* (syn. *Belascaris*, *Neoascaris*). The genus *Toxocara* contains the arrow-headed ascaridoids (cervical alae present) which form rough-shelled (pitted) eggs. Adult worms lack intestinal caeca and interlabia, and some 26 species are found as endoparasites in the intestines of terrestrial mammals. Larval stages migrate extensively (tracheal and/or somatic routes) in host tissues and they may undergo developmental arrest (hypobiosis), notably resuming development in pregnant and lactating hosts thus facilitating transplacental and transmammary vertical transmission. Parasites usually have direct cycles with the faecal-oral transmission of embryonated eggs, but some species also have indirect cycles with the predator-prey transmission of infective larvae encysted with the tissues of invertebrate and vertebrate paratenic (transport) hosts. The species *T. canis* is widely distributed in canids worldwide, with infections being more prevalent in puppies due to their immunological immaturity which favours tracheal migration over somatic migration before the development of adults in the gut. Larvae may encyst in the tissues of older animals and resume development in female dogs during pregnancy facilitating transplacental and transmammary transmission. Larvae may also be carried in a wide range of paratenic hosts further contributing to the high incidence of infections. Humans (especially young children) may act as paratenic hosts for several species and the migrating larvae may cause an enigmatic disease known as visceral larval migrans, sometimes ocular larva migrans.

***Toxocara* species**	**Definitive hosts**	**Location [Clinical signs]**	**Paratenic hosts**	**Distribution**
T. alienata	Carnivora: procyonid (South American coati, white-nosed coati, crab-eating raccoon)			South America

T. anakumae	Carnivora: mustelid (Japanese badger)			Asia
T. apodemi	Rodentia: murid (striped field mouse, Korean field mouse)			Asia
T. canarisi	Carnivora: felid (serval)			Africa
T. canis (syn. *T. marginata*, *Ascaris marginata, Belascaris marginata*)	Carnivora: canid (dog, dingo, African wild dog, raccoon dog, wolf, maned wolf, northwestern wolf, dire wolf, Indian wolf, coyote, golden jackal, red fox, American red fox, Japanese red fox, fennec fox, corsac fox, gray fox, crab-eating fox, Iberian fox, Bengal fox, Arctic fox), hyaenid (spotted hyena), felid (cat, wild cat, ocelot, lion, cougar, Bengal tiger, Eurasian lynx, Iberian lynx), viverrid (common genet, small Indian civet), herpestid (slender mongoose, white-tailed mongoose), mustelid (sable, ferret, European polecat, Siberian weasel, Japanese badger), procyonid (raccoon); Didelphimorphia: didelphid (Virginia opossum); Chiroptera: pteropodid (grey-headed flying fox); Diprotodontia: phalangerid (common brushtail possum); Primates: cercopithecid (macaque), hominid (human)	small intestines [larval migrans, pneumonia, enteritis, illthrift, potbelly]	Rodentia: murid (house mouse, wood mouse, yellow-necked mouse, striped field mouse, Ural field mouse, Eurasian harvest mouse, Mongolian gerbil), cricetid (common vole, bank vole); Artiodactyla: suid (pig), bovid (cattle, sheep); Carnivora: canid (fox); Galliformes: phasianid (chicken, Japanese quail); Blattodea: blattid (cockroach *Periplaneta fuliginosa*); Clitellata: megascolecid (earthworm *Pheretima posthuma*)	worldwide
T. cati (syn. *T. mystax, globulus, brachyoptera*?, *Ascaris globulus, leptoptera*)	Carnivora: felid (cat, wild cat, sand cat, fishing cat, Asian wild cat, Asian golden cat, Pallas's cat, African wild cat, jungle cat, jaguar, jaguarundi, leopard cat, bobcat, serval, ocelot, caracal, cougar, leopard, clouded leopard, snow leopard, cheetah, lion, Bengal tiger, Canada lynx, Eurasian lynx, Iberian lynx), canid (dog, red fox, corsac fox), viverrid (common genet, African civet, small Indian civet), herpestid (common dwarf mongoose), mustelid (beech marten, sable, Siberian weasel); Primates: hominid (human)	small intestines [larval migrans, enteritis, illthrift, potbelly]	Rodentia: murid (house mouse, brown rat, Mongolian gerbil); Artiodactyla: bovid (sheep); Carnivora: canid (dog); Galliformes: phasianid (chicken); Clitellata: lumbricid (earthworm); Blattodea: blattid (cockroach)	worldwide
T. cynonycteridis	Chiroptera: pteropodid (fulvous fox bat)			Asia
T. elephantis	Proboscidea: elephantid (Asian elephant)			Asia
T. genettae	Carnivora: viverrid (South African small spotted genet, common genet)			Africa
T. herpestum	Carnivora: herpestid (Egyptian mongoose)			Africa
T. hippopotami	Artiodactyla: hippopotamid (hippopotamus)			Africa
T. indica	Rodentia: murid (greater bandicoot rat)			Asia
T. lyncis	Carnivora: felid (caracal)			Asia
T. mackerrasae	Rodentia: murid (bush rat, rakali)			Australia
T. malaysiensis	Carnivora: felid (cat)	small intestines [enteritis?]		Malaysia, Vietnam, China
T. manzadiensis	Artiodactyla: bovid (African buffalo)			Africa
T. paradoxura	Carnivora: viverrid (Asian palm civet)			Asia
T. pearsei	Chiroptera: natalid (Trinidadian funnel-eared bat), emballonurid (lesser dog-like bat)		Decapoda: alpheid (shrimp *Synalpheus brooksi*)	South America
T. pteropodis	Chiroptera: pteropodid (black flying fox, grey-headed flying fox, spectacled flying fox, small flying fox, little red flying fox, Gedde's fruit bat); Diprotodontia: phalangerid (common brushtail possum);	small intestines		Australia

	Primates: hominid (human)			
T. sprenti	Carnivora: viverrid (small Indian civet)			Asia
T. suricattae	Carnivora: herpestid (meerkat, banded mongoose)			Africa
T. tanuki	Carnivora: canid (raccoon dog, Japanese raccoon dog), procyonid (raccoon)	small intestines		Asia
T. vajrasthirae	Carnivora: mustelid (hog badger)			Eurasia
T. vincenti	Carnivora: viverrid (African civet)			Africa
T. vitulorum (syn. *Neoascaris*)	Artiodactyla: bovid (cattle, Bali cattle, zebu, water buffalo, Asian buffalo, American bison, sheep, goat, impala); Rodentia: murid (mouse); Primates: hominid (human)	small intestines [diarrhoea]		Africa, Americas, Asia, Australia
T. warreni	Artiodactyla: tragulid (water chevrotain)			Asia

Parasite morphology: *Toxocara* spp. form 3 different types of developmental stages: eggs; larvae (4 consecutive stages encoded L1-L4); and adult worms. Eggs are opaque-brown ovoid-subspherical stages measuring 64-91 µm in maximum diameter and they have thick eggshells with a rough pitted surface due to mammillation of the outer protein layer (cf. *Toxascaris* eggs have a smooth surface). Freshly laid eggs are unembryonated and contain a single central morula. The eggs embryonate forming L1 which then moult while still within the eggshell producing ensheathed L2 (several reports have also suggested that L3 may occasionally be formed within eggs). Irrespective, the emergent larvae are elongate and cylindrical measuring 350-530 x 18-30 µm and they have rounded heads, 3 lips (each composed of a dentigerous ridge), a tubular oesophagus, intestines with 2 excretory canals in the middle, and a short tapering tail. L3 recovered from lung tissues measured 0.8-1.0 mm in length while L4 recovered from the intestines measured 1.0-1.5 mm long. Adults are large round cream-yellow worms ranging in length from 3-30 cm depending on species. They have tubular bodies with pointed ends, the anterior end possessing a pair of prominent cervical alae (making them members of the 'arrow-headed' ascaridoids). The alae are striated in appearance and broad (arrowhead-like) diminishing gradually in width (e.g. *T. canis, T. malaysiensis*) or ending abruptly (e.g. *T. cati*). Worms have 3 prominent lips (broad at the base and narrowing anteriorly with dentate margins), a small buccal capsule, a tubular oesophagus with a posterior muscular bulb known as a ventriculus (absent in *Toxascaris*), and short tapering tails. Adults are sexually dimorphic with females being larger than males (*T. mystax* females 40-120 mm, males 30-70 mm; *T. cati* females 60-120 mm, males 30-70 mm; *T. canis* females 50-180 mm, males 40-120 mm; *T. vitulorum* females 220-300 mm, males 150-260 mm). Mature females have straight tails and are didelphic with 2 ovaries and elongate uteri connected to a common vulva located in the anterior third of the body. Mature males have a single tubular testis, 2 curved alate (winged) spicules subequal in length (ranging from 0.75-1.3 mm long) and curved blunt tails with caudal alae and a terminal digitiform appendage (absent in *Toxascaris*).

Site of infection: Adult worms infect the small intestines of their mammalian definitive hosts, living free within the lumen. Earlier developing larval stages undergo extensive migrations through various host tissues (hepato-pulmonary in young and immunocompromised animals, somatic in older immunocompetent animals). Infective larvae may also encyst within the tissues of various paratenic (transport) hosts (including small mammals, birds, insects, crustaceans, earthworms).

Pathogenesis: Infections are common in domestic and wild carnivores and are a significant cause of morbidity (illthrift, growth impairment) and mortality in companion animals. Young animals are particularly susceptible to disease while adults generally develop acquired immunity leading to the expulsion of most of the adult worm population (concomitant or premunitive immunity rather than sterile immunity as larvae and some adults may persist). Clinical disease may occur at 2 different stages of infection: when larvae migrate through host organs causing disseminated microgranulomas; and when adult worms develop and feed in the small intestines causing digestive disorders, mucosal defects, illthrift, obstruction and occasionally perforation. The severity of disease depends on host susceptibility (age, sex and immune status), the routes of larval migration (hepato-pulmonary or somatic migration), the intensity of infection (numbers of parasites, a few worms are well tolerated), and the behaviour of adult worms (aggregations causing intestinal obstructions, and aberrant migrations to the bile ducts or stomach causing obstructive jaundice or vomiting). The route of migration undertaken by larvae is largely determined by the immuno-competency of the host; with hepato-pulmonary migration occurring in young hosts with immature immune systems; and somatic migration occurring in older animals with competent immune systems. Larvae migrating though the lungs cause traumatic damage with focal haemorrhages, hyperaemia, pneumonitis, pulmonary oedema, eosinophilic infiltrates and sometimes pneumonia. Clinical respiratory signs include coughing, dyspnoea, tachypnoea and frothy nasal discharges. Larvae migrating through other body (somatic) tissues often become encapsulated in dense fibrous tissue, particularly in the muscles, heart, liver, lungs, brain and sometimes the eyes. These larvae exhibit arrested development (hypobiosis) remaining viable for extended periods of time, and may re-awaken and resume development during pregnancy, sometimes invading the placenta or mammary glands to facilitate transplacental or transmammary transmission. In humans, both migrating and encysted larvae may die and degenerate provoking intense inflammatory responses that may cause the disease syndrome known as visceral larval migrans (or ocular larval migrans if in the eye). Clinical signs may include neurological conditions (restlessness, seizures, convulsions), vision disorders, hepatitis, pneumonitis, and myositis. Adult worms in

the intestines feed on luminal content (chyme), consuming large amounts of substances (carbohydrates, lipids, amino acids, vitamins and minerals) resulting in metabolic deficiency disorders (hypoglycaemia, hypocalcaemia, hypochromic anaemia, hyperkeratosis, rickets). Worms and their secretions and excretions provoke intense inflammatory responses (mucoid catarrhal enteritis) contributing to the maldigestion, malabsorption and malnutrition syndromes. Clinical signs include intermittent yellow-pasty diarrhoea alternating with constipation, colic, abdominal distention (pot-belly) sensitive to pressure, vomiting, rough and dull coat, anorexia, weight loss, emaciation, and impaired growth (failure to thrive), sometimes with bone deformities. The presence of balls or tangles of worms in the small intestine may lead to blockage, intussusception and sometimes rupture with peritonitis leading to death. Puppies infected *in utero* with *T. canis* can die a few days after birth (from larvae migrating through alveoli), but most clinical signs appear at 2-4 weeks of age with animals developing digestive symptoms, sometimes with nervous convulsions. Infections by *T. cati* in cats usually cause disease after weaning involving digestive and general disorders. Lactogenic transmission of *T. cati* only occurs after acute infection of the queen during late pregnancy. Infections by *T. vitulorum* in cattle may occasionally cause acute disease in neonates but more frequently chronic digestive disorders in calves up to 6-8 months of age.

Zoonotic infections may occur in humans following the ingestion of infective eggs and the release of larvae which wander throughout the body for extended periods (months to years) but are unable to complete their development in nonpermissive (abnormal) hosts. Three types of disease may develop in humans. The most common form is covert toxocariasis, characterised by nonspecific symptoms and signs (not referable to other conditions). Migrating larvae have been implicated in respiratory conditions (coughing, wheezing, asthma, bronchitis, pulmonitis, sometimes with Loeffler syndrome), dermatological disorders (chronic idiopathic urticaria, eczema), lymphadenopathy and myositis (with limb pain), and pseudorheumatic syndrome (arthralgia). The next most frequent form is known as systemic visceral larval migrans (classical or incomplete) where larvae localize in a range of tissues (muscles, liver, lungs, central nervous system, eyes). The larvae often become encapsulated and slowly degenerate triggering hypersensitive immune reactions characterised by eosinophilia, leucocytosis and granuloma formation. Such infections generally occur on young children (< 5 years) and may be associated with geophagia (pica, soil-eating) and onychophagia (nail-biting). Nonspecific signs develop including hepatosplenomegaly, granulomatous hepatitis, upper abdominal discomfort, lymphadenopathy, oedema, pneumonitis, myocarditis, nephritis, vague neurological signs, fever, headache, anorexia, nausea, vomiting, and malaise. The third form of disease is compartmentalized and includes ocular larval migrans and neurological larval migrans. Ocular disease usually develops in children 5-10 years old and may only involve a few larvae with granuloma formation, optic neuritis, keratitis, irititis and hyphoyon. Common symptoms include red eye, uveitis, leukocoria, eye pain, endophthalmitis or papillitis, strabismus, and granular formation in the retina with macular detachment leading to impaired vision and blindness. Neurological disease occurs more frequently in adults with eosinophilic meningoencephalitis and meningitis associated with idiopathic seizures, neuropsychiatric symptoms (sleep and behavioural changes) and encephalopathy which may lead to death.

Developmental cycle and mode of transmission: Infections may be transmitted to definitive hosts directly (horizontally by faecal-oral transmission or vertically by transplacental and/or transmammary transmission) or indirectly (predator-prey transmission involving consumption of larval stages in paratenic (transport) hosts). Gravid female worms lay unembryonated eggs (up to 100,000 per day) which are excreted into the external environment with host faeces. In suitable warm humid conditions, the eggs embryonate in around 6 days to form L1 which subsequently moult around 12-14 days to form infective L2 still contained within the egg. Some sporadic reports have suggested that an extra moult to L3 may also occur in some eggs. Embryonation and larval development may be substantially delayed in suboptimal conditions, but the thick-shelled eggs are very resistant to adverse conditions (most susceptible to desiccation and direct sunlight). The eggs are dispersed from faecal material by water and wind action and their sticky coats allow them to adhere to plants (including vegetables and fruits), invertebrates (earthworms, insects) and small vertebrates (rodents, birds). Larvated eggs may survive in moist soils for up to 4-5 years and they readily contaminate water sources. Definitive hosts become infected when they ingest infective larvae either contained within eggs contaminating food and water, or encysted within the tissues of paratenic hosts. Depending on the parasite species, larvae may also be transmitted vertically across the placenta or in mothers' milk.

The main mode of transmission is direct via the consumption of larvated eggs which hatch in the intestines releasing L2. The larvae then undertake hepato-pulmonary or somatic migration depending on host resistance/susceptibility, age and sex. *T. canis* undergoes standard hepatopulmonary migration in puppies up to 12 weeks of age (as well as in entire (non-neutered) male or immunocompromised dogs). L2 migrate via the circulation to the liver in 1-3 days and then the lungs in 6-7 days where they enter alveoli and move up the trachea to be swallowed. Some studies have suggested that L2 moult to L3 in the lungs whereas other studies report that it occurs later in the gut. Larvae in the intestines moult to L4 in 13 days and then to subadults (often designated L5) in 19-27 days before maturing to adult worms. The prepatent period (time from infection to first egg excretion) ranges from 28-35 days and adult worms are thought to live for up to 4-6 months. Alternatively, *T. canis* larvae rarely enter the pulmonary alveoli in older immunocompetent dogs (> 6 months) but undergo somatic migration by remaining in the circulation to be distributed throughout the body, particularly to the skeletal muscles, heart, kidneys, brain, liver and lungs. Here the larvae become encapsulated in dense fibrous tissue forming cysts containing arrested (hypobiotic) larvae which may remain viable for extended periods (months to years). In male dogs and spayed bitches, the encysted larvae eventually die, but in pregnant bitches, they may awaken and resume their migration and development. Some larvae may complete normal migration in the bitch produce a few adult worms which lead to a small post-parturient rise in egg production. However, other larvae migrate to the placenta and mammary glands where vertical transmission may occur (over 50% of infected bitches transmit infections vertically to puppies). Prenatal (transplacental) transmission occurs when somatic larvae cross the placenta, invade the liver and lungs of the foetus, and remain there until birth

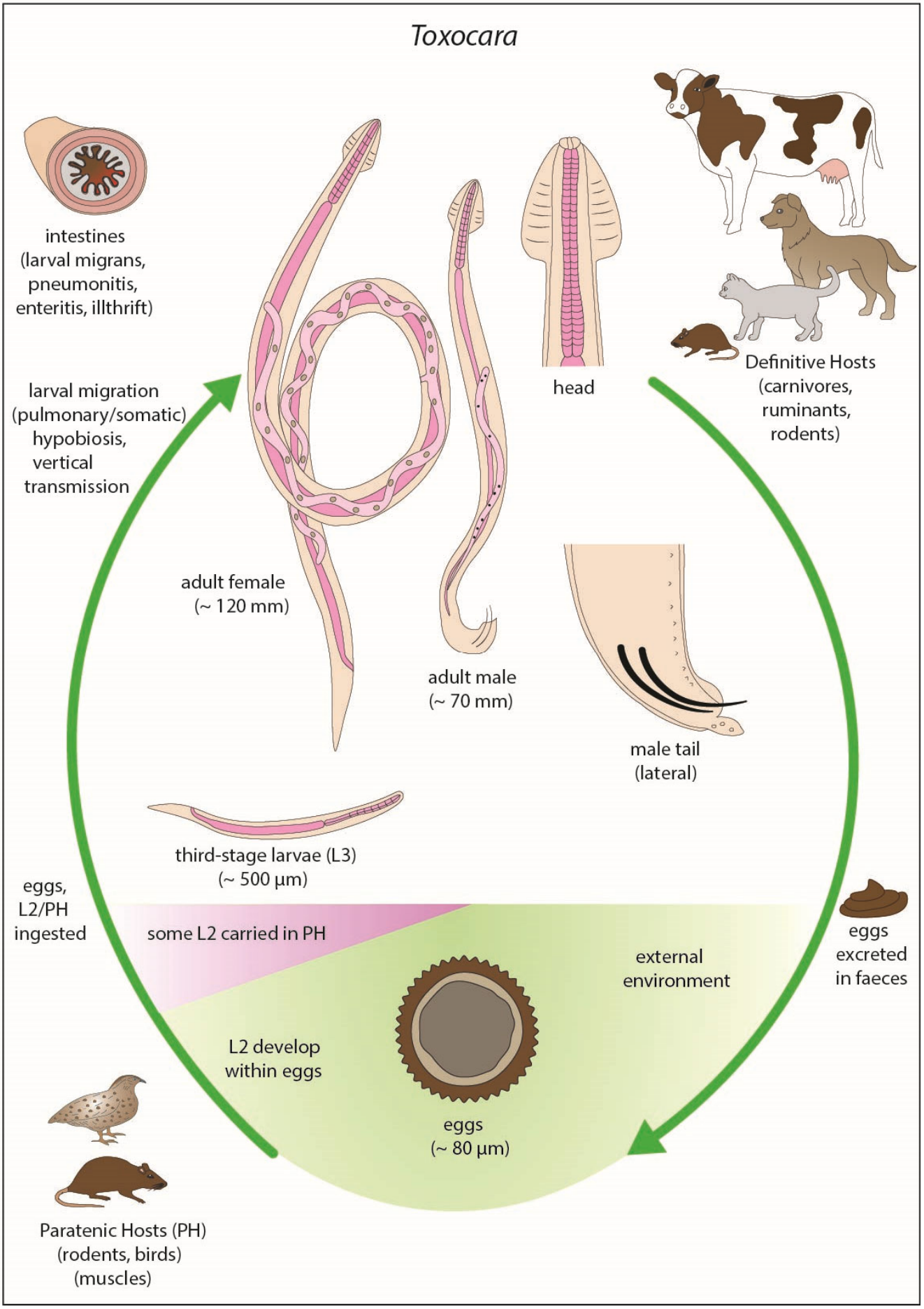
whereupon they complete tracheal migration and develop into adults in the intestines (prepatent period in newborn pups is 12-21 days). Postnatal (lactogenic/transmammary) transmission occurs when somatic larvae are passed in the milk for up to 35 days post-partum to suckling pups where they develop directly into adults in the gut (prepatent period 21-28 days).

Indirect transmission may also occur by paratenesis when prey animals (earthworms, cockroaches, rodents, birds) consume larvated eggs and develop encysted larvae in their tissues (making them paratenic hosts as the larvae do not undergo further development). Final hosts become infected when they consume paratenic hosts via predation or scavenging, with adult worms developing directly in the intestines (prepatent period 28-35 days). Somatic migration is not a feature of *T. cati* infection in the definitive host. Most *T. cati* infections in felids involve the ingestion of larvated eggs with hepato-pulmonary larval migration before adults form in the gut (prepatent period 35-56 days). Some vertical transmission (transmammary but not transplacental) has been reported involving infection of the queen during late pregnancy (rather than reactivation of arrested somatic larvae). A major source of infection for large predatory felids are paratenic hosts (including earthworms, cockroaches, chickens, mice, lambs, dogs). Similarly, most *T. vitulorum* infections in cattle involve egg ingestion and hepato-pulmonary larval migration (prepatent period ranging from 21-70 days) and some vertical transmission (transmammary but not transplacental). Infections in calves over 6 months rarely become patent, but larvae may remain dormant in host tissues and resume development during pregnancy with transmission in milk for 3-4 weeks post-partum. Humans may act as accidental paratenic hosts for several *Toxocara* spp. (*T. canis, T. cati, T. pteropodis, T. vitulorum*) and develop visceral larval migrans. People become infected by ingesting larvated eggs via contaminated food/water, geophagia or practicing poor hygiene after direct contact with soil or pets. Food-borne transmission may occur not only by the consumption of fruit and vegetables contaminated with eggs, but also by the consumption of raw or lightly cooked meat from paratenic hosts carrying encysted larvae (especially raw livers from chickens, ducks, pigs, rabbits). Risk factors include rural residence (dog ownership, poor hygiene), low socio-economic status (poor sanitation, lack of sewers) and favourable environmental conditions (warm humid climate).

Differential diagnosis: Clinical infections are often indicated in young pets on the basis of clinical symptomatology (respiratory signs then diarrhoea, pot-belly) and relevant history (unhygienic conditions, poor nutrition). However, many other conditions may cause similar clinical signs. Developing worms may occasionally be observed in vomitus or faeces, particularly towards the end of the prepatent period. Haematological assessments often demonstrate marked peripheral eosinophilia, while blood biochemistry may reveal transient elevated levels of liver enzymes. Patent infections are conventionally diagnosed by the microscopic detection of characteristic worm eggs in faecal samples, usually following their concentration by sedimentation in water and floatation in saturated sugar or salt solutions. Infections may be diagnosed at post-mortem by the detection of adult worms within the lumen of the small intestines. Larval infections in humans may be suggested by symptomatology (fever, eosinophilia, vision loss, strabismus) and history (pica, nail-biting) but other diseases or conditions cannot be ruled out. Medical imaging techniques may be used to locate suspect lesions, including sonography (hypoechoic lesions), computed tomography (granulomas) and magnetic resonance imaging (cerebral lesions), but are not confirmatory. Examination of cerebrospinal fluid in neurological cases may reveal the presence of eosinophils, and the histopathological examination of tissue biopsies may occasionally detect sections of nematode larvae. Recourse is therefore often made to the indirect demonstration of infections by a variety of immunoserological tests for specific host antibodies (mostly IgG but sometimes IgM or IgE) against larval and adult worm antigens, including skin tests, immunoprecipitation, agglutination, immunofluorescence, enzyme immunoassays and radio-immunoassays. Most tests yielded good specificity but reduced sensitivity possibly due to cross-reactivity with other helminths. Western blotting has been used to confirm results by detecting reactions against specific antigenic bands. Modern molecular biological techniques have been used to detect parasites in environmental and clinical samples and determine phylogenetic relationships by polymerase chain reaction (PCR) amplification, restriction fragment length polymorphism (RFLP) analyses, single strand conformational polymorphism (SSCP) analyses, and sequencing of nuclear genes (5.8S ribosomal RNA, internal transcribed spacers 1 and 2, repetitive DNA) and mitochondrial genes (protein coding regions). DNA cloning and recombination technologies have also been used to explore parasite immuno-evasion mechanisms involved in the long persistence of larvae in host tissues, including cuticular shedding of secreted mucins, cysteine proteases and other proteins unique to hypobiotic stages.

Treatment and control: A broad range of anthelmintic drugs have been used to treat clinical infections in domestic and wild carnivores, including consecutive doses of benzimidazoles (fenbendazole, oxibendazole, flubendazole), probenzimidazoles (febantel), tetrahydropyrimidines (oxantel, pyrantel), macrocyclic lactones (milbemycin, moxidectin, selamectin, eprinomectin), depsipeptides (emodepside), isoquinolines (praziquantel), diethylenediamines (diethylcarbamazine, piperazine), isothiocyanates (nitroscanate) and imidazothiazoles (levamisole). Most drugs were effective against immature and mature worms in the intestines, some (selamectin and moxidectin) were effective against larvae in the circulation, but few were effective against migrating or arrested larvae (other than some reports on levamisole, pyrantel, thiabendazole or febantel in cattle). Repeated treatments should be used to stop infections developing from surviving larvae and to prevent re-infections from contaminated environments or milk from suckling mothers. Several anthelmintics have been found to reduce the burden of vertical and trans-mammary transmission of *T. canis* from dam to pups, including selamectin, fenbendazole and 'off-label' ivermectin. Veterinary authorities recommend treating puppies and kittens at 2 weeks of age, then every 2 weeks until 8 weeks of age, and then monthly until 6 months of age. Nursing bitches and queens should be treated at the same time, and adults should be treated regularly for life every 1-3 months depending on the risk. Post-treatment surgical interventions have also been used to relieve intestinal blockages in heavy infections. Most larval infections in humans resolve spontaneously as the larvae die and degenerate. Some success has been reported in treating infections

with short courses of albendazole, mebendazole or thiabendazole, often with supportive therapy in the form of corticosteroids to suppress intense allergic manifestations and antibiotics to prevent secondary infections. In the case of ocular larval migrans, surgical intervention (vitrectomy) has been used to remove problematic granulomas. Various preventive measures have been applied to domestic and urban situations to reduce parasite transmission, all essentially revolving around improved hygiene (of environment, food/water, animals and people). Environmental contamination may be reduced by the regular removal and disposal of faeces and not using them to fertilise edible crops (note that the tough eggs may survive some biocomposting and sewage treatments), regular cleaning and decontamination of holding facilities (which requires strong disinfectants, flame guns or steam-cleaning), and eliminating moist shaded runs or rest areas which may harbour eggs (by draining, paving or close-crop mowing). Clean water should be provided, giving preference to treated reticulated freshwater sources rather than standing waters. All fruit and vegetables should be thoroughly washed in clean water to remove adherent eggs, and any meat from potential paratenic hosts should be properly cooked to destroy encysted larvae. Animal husbandry practices should include quarantine and isolation procedures when moving or treating animals, particularly in breeding facilities, avoid overcrowding, introduce rodent control, prevent animals from hunting or scavenging, and even hand-rearing or foster-rearing neonates from infected bitches or queens. Improving hygienic practices in human populations often requires intensive education campaigns before people will even adopt simple changes, like hand-washing before eating, preventing children from playing in contaminated soils, covering sandpits in playgrounds, discouraging pica and nail-biting, bathing dogs that roll in soil or faeces, and passing laws requiring the removal of pet faeces from public places.


Toxocara
intestines
(larval migrans,
pneumonitis,
enteritis, illthrift)
larval migration
(pulmonary/somatic)
hypobiosis,
vertical
transmission
adult female
(~ 120 mm)
adult male
(~ 70 mm)
head
Definitive Hosts
(carnivores,
ruminants,
rodents)
male tail
(lateral)
third-stage larvae (L3)
(~ 500 µm)
eggs,
L2/PH
ingested
some L2 carried in PH
external
environment
eggs
excreted
in faeces
L2 develop
within eggs
eggs
(~ 80 µm)
Paratenic Hosts (PH)
(rodents, birds)
(muscles)



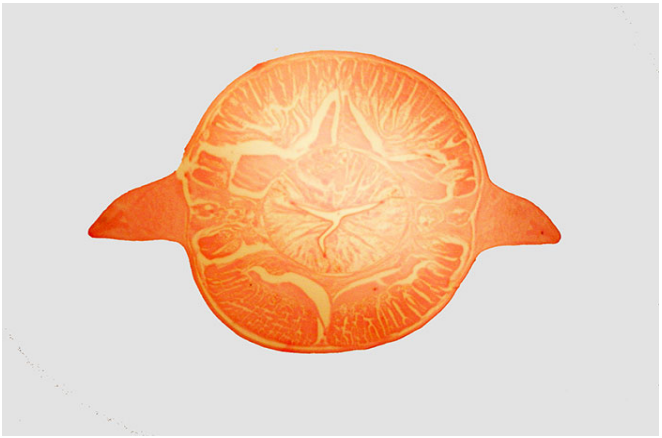
Toxocara adult worms



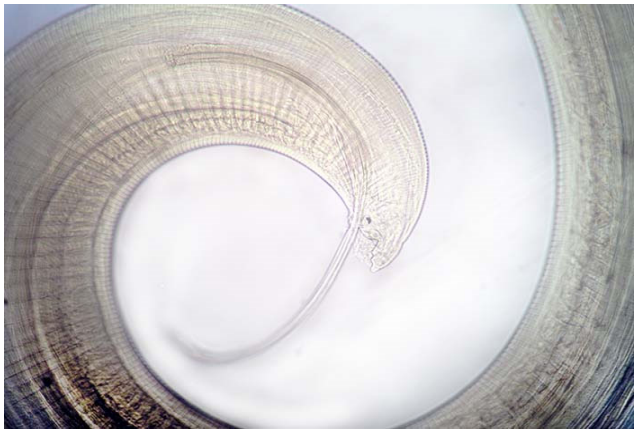
Toxocara adult worms



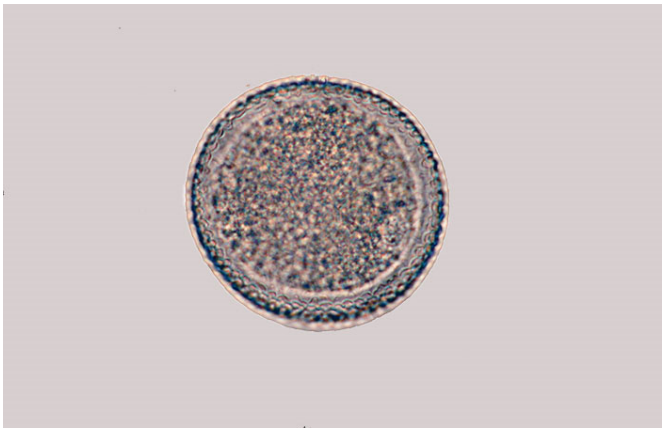
Toxocara adult worm, head



Toxocara adult worm, section through alae



Toxocara adult worms



Toxocara adult worms

Anisakis
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Ascaridomorpha which includes ascaridoid nematodes (roundworms) characterised by their large size, three prominent anterior lips and the absence of a bursa. They occur in the small intestines of many animals (including humans) and most have simple direct life-cycles involving faecal-oral transmission. The larvae of ascaridoid species undergo hepato-pulmonary migration before forming adults, whereas those of heterakoid species do not. Two major ascaridoid families are recognised: ascarids in terrestrial mammals; and anisakids in marine mammals. Adult anisakids are characterised by a post-oesophageal ventriculus and are found in dolphins, whales, predatory teleost fish, sharks and piscivorous birds. Anisakid transmission is unusual in being indirect, involving both intermediate and paratenic hosts. Female worms lay eggs which are passed in host faeces and then ingested by small copepods (intermediate hosts) where they hatch. L3 are passed up the food chain when copepods are eaten by small teleosts (paratenic hosts), which in turn are eaten by larger teleosts before infecting definitive hosts. Infections by larvae may cause enteric disease in humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Ascaridomorpha (large roundworms, mouth surrounded by three large lips, numerous caudal papillae)
Superfamily:	Ascaridoidea (ascarids, eggs thick-shelled, direct cycle but larvae undertake hepato-pulmonary migration)
Family:	Anisakidae (large stout worms, in marine mammals/fishes/birds)
Genus:	*Anisakis* (parasitic in gut of dolphins/whales)
Species:	various species cause enteric disease (anisakiasis) in humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Ascaridomorpha is characterised by large roundworms with poorly developed buccal cavity with 3 large lips sometimes separated by interlabia, an undivided oesophagus, numerous caudal papillae, nonbursate males often with pre-anal suckers, and females with complex ovejectors. Five superfamilies (conventionally assigned to the order Ascaridida) are recognised as parasites in vertebrates: Cosmocercoidea (oesophagus with cylindrical corpus, elongate isthmus and valved bulb, platymyarian, eggs with delicate shells or hatch *in utero*); Seuratoidea (lips absent, oesophagus short, platymyarian, eggs with delicate shells or hatch *in utero*); Heterakoidea (oesophagus cylindrical or with claviform corpus, short isthmus and valved bulb, coelomyarian, pre-anal sucker, eggs thick-shelled); Ascaridoidea (cylindrical oesophagus often terminated by swelling without bulb, coelomyarian, eggs thick-shelled); and Subuluroidea (well-developed buccal capsule without lips, coelomyarian, pre-anal sucker, eggs thick-shelled). Adult worms of the superfamily Ascaridoidea inhabit the gastrointestinal tract of vertebrate hosts and generally consume food ingested by the host. They may have simple monoxenous life cycles involving faecal-oral transmission, or more complicated heteroxenous life-cycles involving larval development in vertebrate intermediate hosts and sometimes larval transport in invertebrate paratenic hosts. Female worms produce unembryonated eggs which are passed in host faeces into the external environment where they embryonate to first-stage larvae (L1) which grow and moult to infective L2 or L3. Aquatic species produce thin-shelled eggs which hatch in water releasing sheathed L2 that are taken up by suitable hosts, while terrestrial species produce thick-shelled eggs which hatch releasing L3 when ingested by suitable hosts. Ascaridoid larval stages then undertake unique journeys: most involving pulmonary or somatic migration in their definitive hosts before maturing in the gut, sometimes including vertical transmission (transplacental and/or transmammary); many migrating into the tissues of intermediate hosts, sometimes involving larval migrans or encapsulation in ‘unsuitable’ hosts; and a few undergoing precocious development in invertebrate hosts.

Five ascaridoid families are recognised: Ascarididae (lips often with toothed ridge, oesophagus with or without ventriculus, parasites of mammals, birds, reptiles, amphibians, fishes); Anisakidae (lips with tongue-like prolongations with cuticular thickenings, oesophagus with ventriculus with suture-like depressions, parasites of mammals, birds, reptiles and fishes); Crossophoridae (lips semicircular with toothed combs, fimbriated collar, long oesophagus without ventriculus, parasites of hyracoids); Heterocheilidae (lips with tongue-like prolongations with cuticular thickenings, cylindrical oesophagus without ventriculus, parasites of sirenians); and Acanthocheilidae (lips small with teeth or toothed ridges, oesophagus with ventriculus, parasites of elasmobranchs). The family Anisakidae contains 3 subfamilies: Anisakinae (cuticular rings without spines, excretory system ribbon-like, parasites of mammals, birds, reptiles or elasmobranch fish); Goeziinae (cuticular rings with posterior spines, parasites of teleost fishes and rarely reptiles); and Raphidascaridinae (cuticular rings without spines, excretory system not ribbon-like, parasites of fish, occasionally birds). The subfamily Anisakinae contains 8 genera: *Anisakis* (syn. *Capsularia*, *Conocephalus*, *Filocapsularia*, *Peritrachelius*, *Stomachus*), *Phocanema*, *Sulcascaris* and *Terranova* classified in the tribe Anisakinea (oesophagus with oblong to cylindrical ventriculus); and *Contracaecum, Duplicaecum, Galeiceps* and *Phocascaris* classified in the tribe Contracaecinea (oesophagus with reduced globular ventriculus).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Anisakis	9-24	marine mammals	stomach, intestines	15-82 mm long, 3 anterior lips, post-oesophageal ventriculus, males abursate, larvae undergo hepato-pulmonary migration	45-66 x-35-55 µm, ovoid, thin-shelled	indirect (L3 in crustacean IH) (sometimes in teleost PH)

The genus *Anisakis* contains anywhere from 9-24 species which form adult worms in the gastrointestinal tracts of marine mammals (seals, dolphins, porpoises, whales), particularly in colder temperate and polar waters. Transmission involves larval stages in aquatic invertebrates and fish acting as intermediate and paratenic hosts. Over 100 fish species have been implicated in transmission cycles as transport hosts harbouring L3, which may also be passed up the food chain from fish-to-fish. Development of larval stages have also been reported in some birds, sea snakes and elasmobranchs. Humans may become accidentally infected when consuming raw or improperly cooked fish with larvae causing eosinophilic granulomas in the alimentary tract (but the larvae are unable to complete their development in humans). Infections have been reported throughout Asia, Oceania, Europe and the Americas, often linked to the consumption of popular local delicacies, such as sushi, sashimi, cod livers or fermented herring.

***Anisakis* species**	**Definitive Hosts (adult worms in stomach, intestines)**	**Intermediate Hosts [plus Paratenic hosts (PH)] (larvae in tissues)**	**Distribution**
A. berlandi (= *A. simplex* sp. C)	Artiodactyla: delphinid (long-finned pilot whale, false killer whale), kogiid (pygmy sperm whale)	[PH: Procellariiformes: procellariid (grey petrel)]	Pacific
A. nascetti	Artiodactyla: ziphiid (strap-toothed beaked whale, Blainville's beaked whale, True's beaked whale, Gray's beaked whale)	[PH: Gadiformes: merlucciid (European hake); Perciformes: trichiurid (black scabbardfish); Cephalopoda: onychoteuthid (greater hooked squid)]	Mediterranean, Southern Atlantic
A. paggiae	Artiodactyla: physeterid (pygmy sperm whale, dwarf sperm whale)	[PH: Beryciformes: berycid (splendid alfonsino)]	Atlantic
A. pegreffii (= *A. simplex* sp. A)	Carnivora: phocid (Mediterranean monk seal); Artiodactyla: cetotheriid (pygmy right whale), delphinid (common bottlenose dolphin, striped dolphin, long-finned pilot whale), physeterid (sperm whale), ziphiid (bottlenose whale, Cuvier's beaked whale)	[PH: Anguilliformes: anguillid (European conger, white-spotted conger); Beloniformes: belonid (garfish); Beryciformes: trachichthyid (silver roughy); Carangiformes: carangid (Cape horse mackerel, Mediterranean horse mackerel, Atlantic horse mackerel, bluejack mackerel); Clupeiformes: engraulid (European anchovy), dussumierid (Whitehead's round herring, sardine); Gadiformes: gadid (blue whiting), merlucciid (European hake, Argentine hake, South African hake), morid (red codling); Istiophoriformes: xiphiid (swordfish); Lophiiformes: lophiid (angler, devil anglerfish); Myctophiformes: myctophid (electric lantern fish, spothead lantern fish); Ophidiiformes: ophidiid	Mediterranean, Atlantic, Pacific

		(kinglip); Perciformes: bramid (Atlantic pomfret), carangid (horse mackerel, Atlantic horse mackerel, Atlantic mackerel), emmelichthyid (Cape bonnetmouth), sciaenid (redlip croaker), trichiurid (black scabbardfish, silver scabbardfish, largehead hairtail); Pleuronectiformes: paralichthyid (cinnamon flounder), scophthalmid (four-spot megrim); Salmoniformes: salmonid (chum salmon); Scombriformes: gempylid (snoek), scombrid (Atlantic bluefin tuna, chub mackerel, Atlantic chub mackerel, Atlantic mackerel); Scorpaeniformes: scorpaenid (red scorpionfish), sebastid (blackbelly rosefish); Stomiiformes: phosichthyid (slender lightfish); Trachiniformes: pinguipedid (blue cod); Zeiformes: zeid (John Dory); Carcharhiniformes: carcharhinid (blue shark); Cephalopoda: ommastrephid (European flying squid, Angola flying squid, lesser flying squid); Procellariiformes: procellariid (grey petrel); Sphenisciformes: spheniscid (little penguin); Primates: hominid (human)]	
A. physeteris (syn. *A. skrjabini, A. oceanica, A. brevispiculata*)	Artiodactyla: balaenopterid (common minke whale, sei whale), delphinid (Risso's dolphin, short-finned pilot whale, melon-headed whale), kogiid (pygmy sperm whale, dwarf sperm whale), phocoenid (Dall's porpoise), physeterid (sperm whale), ziphiid (bottlenose whale, Cuvier's beaked whale); Carnivora: otariid (brown fur seal)	[PH: Beryciformes: berycid (splendid alfonsino), trachichthyid (silver roughy); Carangiformes: carangid (greater amberjack, Chilean jack mackerel, blue jack mackerel, Atlantic horse mackerel), coryphaenid (mahi-mahi); Gadiformes: gadid (Pacific cod, Alaska pollock), merlucciid (European hake, Patagonian grenadier, common Atlantic grenadier, roughsnout grenadier), gadid (blue whiting); Istiophoriformes: xiphiid (swordfish); Lampriformes: trachipterid (ribbonfish); Perciformes: epigonid (black cardinal fish), nototheniid (Patagonian toothfish), trichiurid (black scabbardfish); Pleuronectiformes: paralichthyid (fine flounder); Scombriformes: scombrid (skipjack tuna, chub mackerel); Scorpaeniformes: scorpaenid (red scorpionfish), sebastid (blackbelly rosefish); Spariformes: sparid (silver seabream); Cephalopoda: loliginid (spear squid), ommastrephid (neon flying squid, purpleback flying squid, Japanese flying squid), onychoteuthid (boreal clubhook squid); Primates: hominid (human)]	Mediterranean, Atlantic, Pacific
A. schupakovi	Carnivora: phocid (Caspian seal)	[PH: Acipenseriformes: acipenserid (sterlet, starry sturgeon, Russian sturgeon, beluga sturgeon); Clupeiformes: clupeid (Caspian shad, Caspian marine shad, Caspian andromous shad, Saposhnikovi shad, anchovy sprat, Black Sea sprat, Southern Caspian sprat, Caspian tyulka); Cypriniformes: cyprinid (common carp, common rudd, ziege, common roach, Caspian roach, tench, Danube bleak, asp, Caspian barbel, vimba bream); Esociformes: esocid (northern pike); Gadiformes: gadid (blue whiting); Gobiiformes: gobiid (monkey goby, bighead goby, round goby, stellate tadpole-goby, Caspian goby); Mugiliformes: mugilid (golden grey mullet, leaping mullet); Perciformes: percid (European perch, estuarine perch, zander); Salmoniformes: salmonid (salmon); Serpentes: colubrid (dice snake); Suliformes: phalacrocoracid (great cormorant)]	Caspian Sea, Black Sea

A. simplex (whaleworm, herring worm) (syn. *A. marina, A. ivanizkii, A. kukenthalii, A. kogiae, Ascaris*)	Artiodactyla: balaenid (bowhead whale); balaenopterid (common minke whale, sei whale, blue whale, little piked whale, fin whale, humpback whale), delphinid (short-beaked common dolphin, long-beaked common dolphin, common bottlenose dolphin, white-beaked dolphin, dusky dolphin, pantropical spotted dolphin, rough-toothed dolphin, striped dolphin, hourglass dolphin, northern right whale dolphin, Commerson's dolphin, Risso's dolphin, Frasier's dolphin, Atlantic white-sided dolphin, Pacific white-sided dolphin, killer whale, false killer whale, North Atlantic pilot whale, short-finned pilot whale, long-finned pilot whale, melon-headed whale), eschrichtiid (gray whale), kogiid (pygmy sperm whale, dwarf sperm whale), monodontid (beluga whale, narwhal), physeterid (sperm whale), phocoenid (porpoise, harbour porpoise, Burmeister's porpoise, Dall's porpoise, finless porpoise), platanistid (South Asian river dolphin), pontoporiid (La Plata dolphin); ziphiid (Baird's beaked whale, Blainville's beaked whale, Sowerby's beaked whale, Cuvier's beaked whale, True's beaked whale, giant bottlenose whale, northern bottlenose whale); Carnivora: odobenid (walrus), otariid (Steller sea lion, South American sea lion, California sea lion, northern fur seal, brown fur seal, South American fur seal), phocid (common seal, Mediterranean monk seal, grey seal, leopard seal, ringed seal, hooded seal, bearded seal, ribbon seal, harp seal, spotted seal, northern elephant seal, southern elephant seal)	Malacostraca: crangonid (brown shrimp, *Crangon crangon*), euphausiid (krill, *Euphasia nana, pacifica, similis, vallentini*, *Meganyctiphanes norvegica, Nyctiphanes australis, couchii, Thysanoessa inermis, longicauda, longiceps, longipes, raschii*), gammarid (krill, *Gondogeneia antarctica*; amphipod, *Eurymera monticosa*), lysianassid (amphipod, *Waldeckia obesa*), mysid (opossum-shrimp, *Mesodopsis slabberi*), pandalid (caridean prawn, *Pandalus borealis*, *kessleri*), pontageneiid (amphipod, *Bovallia gigantea, Pontogeneiella brevicornis*); Hexanauplia: acartiid (copepod, *Acartia tonsa*), balanid (barnacle, *Balanus*), oithonid (copepod, *Oithona similis*); Polychaeta: polynoid (scaleworm, *Lepidonotus squamata*); Sagittoidea: sagittid (arrow-worm, *Sagitta elegans*) [PH: Acipenseriformes: acipenserid (white sturgeon); Anguilliformes: anguillid (European eel), congrid (European conger), moraenesocid (daggertooth pike conger), ophichthid (snake eel); Argentiniformes: alepocephalid (Agassiz' slickhead), argentinid (great silver smelt); Atheriniformes: atherinid (sand smelt); Aulopiformes: bathysaurid (deepsea lizardfish), synodontid (slender lizardfish, snakefish); Batrachoidiformes: batrachoidid (banded toadfish); Beloniformes: belonid (needlefish, garfish), scomberesocid (Atlantic saury); Beryciformes: trachichthyid (silver roughy); Carcharhiniformes: carcharhinid (blue shark, spadenose shark), scyliorhinid (small spotted catshark); Carangiformes: carangid (cleftbelly trevally, bigeye trevally, Malabar trevally, double-spotted queenfish, African pompano, Japanese scad, torpedo scad, Japanese amberjack, Mediterranean horse mackerel, Atlantic horse mackerel, Japanese horse mackerel, Chilean jack mackerel, blue jack mackerel, Pacific jack mackerel, bigeye scad), echeneid (live sharksucker), menid (moonfish), rachycentrid (cobia); Clupeiformes: clupeid (blueback herring, allis shad, American shad, Twaite shad, alewife, Atlantic herring, Baltic herring, Pacific herring, Chosa herring, Japanese scaled sardine, European pilchard, Japanese pilchard, round sardinella, European spart), engraulid (anchovy, Japanese grenadier anchovy, Argentine anchoita, Japanese anchovy); Cypriniformes: cyprinid (big-scaled redfin); Gadiformes: gadid (polar cod, poor cod, Pacific cod, Atlantic cod, blue whiting, southern blue whiting, navaga, saithe, Norway pout, pouting, haddock, merling, walleye pollock, European pollock, Alaska pollock), lotid (cusk, five-beard rockling, Arctic rockling, common ling, blue ling), macrourid (common Atlantic grenadier, roughsnout grenadier, rock grenadier, ridge-scaled rattail), merlucciid (hoki, blue grenadier, southern hake, silver hake, shallow-water Cape hake, South Pacific hake, North Pacific hake, Argentine hake, European hake), morid (North Atlantic codling), muraenolepid (small-eye moray cod), phycid (hake,	Atlantic, Pacific, Arctic

		white hake, longfin hake, red hake, greater forkbeard); Gasterosteiformes: gasterosteid (three-spined stickleback, nine-spined stickleback); Gobiiformes: gobiid (common goby, sand goby, painted goby, black goby, two-spotted goby), odontobutid (dark sleeper); Istiophoriformes: xiphiid (swordfish); Labriformes: labrid (goldsinny wrasse, Ballan wrasse); Lamniformes: lamnid (salmon shark); Lophiiformes: lophiid (angler, blackmouth angler, black-bellied angler, American angler); Mugiliformes: mugilid (mullet); Myctophiformes: myctophid (lanternfish, small lanternfish, fragile lanternfish, transparent lanternfish, blackhead lanternfish, metallic lanternfish, pearly lanternfish, multi-spotted lanternfish, Warming's lanternfish, Nichol's lanternfish, Reinhart's lanternfish, electron sub-Antarctic lanternfish, belted lanternfish, flaccid lanternfish, Bermuda lanternfish, large-finned lanternfish, noble lampfish, patchwork lampfish); Myliobatiformes: dasybatid (pale-edged stingray); Ophidiiformes: ophidiid (goatsbeard brotula, pink cuskeel); Osmeriformes: osmerid (capelin, European smelt, surf smelt, Arctic rainbow smelt); Perciformes: anarhichadid (Atlantic wolffish), bramid (Pacific pomfret), centropomid (snook), channichthyid (blackfin icefish), epigonid (black cardinal fish), haemulid (saddle grunt), lateolabrid (Japanese sea bass), leiognathid (ponyfish), lutjanid (crimson snapper, bigeye snapper, emperor red snapper), malacanthid (gold tilefish, Argentine tilefish), mullid (deepwater goatfish, sulphur goatfish, red mullet, sur mullet), nemipterid (golden threadfin bream), nototheniid (Patagonian toothfish, dusky rockcod, humped rockcod, yellow-belly rockcod, marbled rockcod, Antarctic cod, emerald rockcod, striped rockcod), percid (zander), pholid (rock gunnel), priacanthid (red bigeye, purple-spotted bigeye, Japanese bigeye), sciaenid (meagre, yellow drum, large yellow croaker, redlip croaker, sin croaker), serranid (areolate grouper, yellow grouper), siganid (mottled spinefoot), sparid (bogue, threadfin porgy, common pandora, red seabream, goldlined seabream, black seabream), terapontid (large-scaled terapon, Jarbau terapon), trichiurid (black scabbardfish, silver scabbardfish, largehead hairtail), zoarcid (glacial eelpout, Arctic eelpout, viviparous eelpout, longear eelpout); Petromyzontiformes: petromyzontid (European river lamprey, sea lamprey); Pleuronectiformes: cynoglossid (tongue sole), paralichthyid (large-tooth flounder, bastard halibut), pleuronectid (stone, flounder, arrowtooth flounder, Kamchatka flounder, sohachi, righteye flounder, flathead flounder, yellow-tail flounder, yellow-striped flounder, winter flounder, European flounder, American plaice, Atlantic halibut, Pacific halibut, Greenland halibut, common dab, dusky sole), psettodid (Indian halibut), scophthalmid (megrim, fourspot megrim, windowpane flounder); Rajiformes: arhynchobatid (spinytail skate), rajid (Arctic skate, ocellate spot skate, thorny skate); Salmoniformes: salmonid (sakhalin taimen,	

		davatchan, pink salmon, chum salmon, coho salmon, masu salmon, sockeye salmon, Atlantic salmon, white-spotted char, rainbow trout, brown trout, brook trout, Dolly Varden trout); Scombriformes: gempylid (snoek), scombrid (Atlantic mackerel, blue mackerel, narrow-barred Spanish mackerel, Japanese Spanish mackerel, chub mackerel, Atlantic chub mackerel, Atlantic bonito, Indian mackerel, bullet tuna, skipjack tuna, mackerel tuna, yellowfin tuna, Atlantic bluefin tuna), sphyraenid (pickhandle barracuda, Japanese barracuda), stromateid (American butterfish); Scorpaeniformes: agonid (dragon poacher), cottid (Altlantic hookear sculpin, longhorn sculpin, great sculpin, shorthorn sculpin), cyclopterid (lumpfish), hemitripterid (sea raven), hexagrammid (green ling, Okhotsk atka mackerel), platycephalid (crocodile flathead, bartail flathead), scorpaenid (plaintail turkeyfish, red scorpionfish, false stonefish), sebastid (Norway haddock, blackbelly rosefish, canary rockfish, silvergrey rockfish, white-edged rockfish, Korean rockfish, Akodai rockfish, Bocaccio rockfish, Steindachner's rockfish, deepwater redfish, Acadian redfish, Norway redfish, golden redfish, osaga), triglid (red gunard, grey gunnard); Siluriformes: ariid (giant catfish); Squaliformes: etmopterid (velvet-belly lanternshark), squalid (spiny dogfish); Stomiiformes: sternoptychid (Mueller's pearlside); Tetraodontiformes: tetraodontid (yellowfin puffer, lunartail puffer, Japanese puffer); Trachichthyiformes: trachichthyid (orange roughy); Trachiniformes: ammodytid (northern sand lance), trachinid (greater weaver); Zeiformes: zeid (John Dory); Cephalopoda: eledonid (curled octopus), gonatid (arrow squid), loliginid (spear squid, long-finned squid, little squid, European squid), myopsid (squid), octopodid (common octopus), oegopsid (commander squid), ommastrephid (Humboldt squid, Argentine shortfin squid, southern shortfin squid, New Zealand arrow squid, red flying squid, purpleback flying squid, lesser flying squid, Japanese flying squid, European flying squid), onychoteuthid (boreal clubhook squid), sepiid (common cuttlefish, golden cuttlefish); Charadriiformes: alcid (Atlantic puffin, thick-billed murre), larid (glaucous gull); Procellariiformes: procellariid (northern fulmar); Testudines: cheloniid (loggerhead sea turtle); Carnivora: mustelid (Eurasian otter); Rodentia: murid (brown rat); Primates: hominid (human)]	
A. typica	Artiodactyla: delphinid (short-beaked common dolphin, dusky dolphin, striped dolphin, common bottlenose dolphin, Fraser's dolphin, pantropical spotted dolphin, spinner dolphin, Atlantic white-sided dolphin, hourglass dolphin, tucuxi, rough-toothed dolphin, short-finned pilot whale, long-finned pilot whale, melon-headed whale, pygmy killer	[PH: Aulopiformes: synodontid (brushtooth lizardfish); Carangiformes: carangid (longnose trevally, bumpnose trevally, imposter trevally, mackerel scad, bigeye scad, bluejack mackerel), coryphaenid (mahi-mahi), echeneid (live sharksucker); Clupeiformes: chirocentrid (Dorab wolf-herring), clupeid (giant herring); Gadiformes: merlucciid (European hake), Perciformes: carangid (horse mackerel), lutjanid (ornate snapper), monodactylid (silver moonfish), mullid (bartailed goatfish), nemipterid (Japanese whiptail, threadfin	Mediterranean, Atlantic, North Sea

	whale, false killer whale), kogiid (pygmy sperm whale), phocoenid (common porpoise, Dall's porpoise, harbor porpoise), pontoporid (La Plata dolphin), ziphiid (Sowerby's beaked whale, Cuvier's beaked whale, northern bottlenose whale); Carnivora: phocid (grey seal, harbour seal)	bream), serranid (red grouper, orange-spotted grouper, areolate grouper), trichiurid (largehead hairtail); Pleuronectiformes: paralichthyid (Patagonian flounder, fantail flounder); Scombriformes: scombrid (mackerel tuna, frigate tuna, blackfin tuna, Atlantic bluefin tuna, striped bonito, chub mackerel, bullet mackerel, Indian mackerel, narrow-barred Spanish mackerel), sphyraenid (bigeye barracuda, sawtooth barracuda); Trachiniformes: pinguipedid (sandperch, Namorado sandperch, Brazilian sandperch); Carcharhiniformes: carcharhinid (spinner shark); Serpentes: elapid (blue-lipped sea krait)]	
A. ziphidarum	Artiodactyla: ziphiid (strap-toothed beaked whale, Gervais' beaked whale, Cuvier's beaked whale, Blainville's beaked whale)	[PH: Carangiformes: carangid (bluejack mackerel); Gadiformes: merlucciid (European hake, Atlantic grenadier, roughsnout grenadier); Myctophiformes: myctophid (electric lantern fish, spothead lantern fish); Perciformes: carangid (mackerel), trichiurid (black scabbardfish); Scombriformes: scombrid (chub mackerel); Stomiiformes: phosichthyid (slender lightfish)]	Mediterranean, Southern Atlantic
Species inquirenda			
A. alexandrii	Artiodactyla: delphinid (Chinese white-sided dolphin)		Pacific
A. appendiculata	Procellariiformes: procellariid (short-tailed shearwater)		Australia
A. catodontis	Artiodactyla: physeterid (sperm whale, dwarf sperm whale)		Atlantic
A. delphini	Artiodactyla: platanistid (South Asian river dolphin)		India
A. dussumierii	Artiodactyla: delphinid (long-snouted dolphin, spinner dolphin), physeterid (sperm whale)		Asia
A. goldi	Carnivora: canid (dog)		
A. insignis	Artiodactyla: delphinid (Amazon river dolphin)		South America
A. kuekenthalii	Artiodactyla: monodontid (beluga whale)		Arctic
A. pacificus	Artiodactyla: balaenopterid (common minke whale, sei whale, fin whale), delphinid (killer whale), physeterid (sperm whale); Carnivora: phocid ribbon seal)		cosmopolitan
A. patagonica (syn. *Ascaris*)	Carnivora: otariid (South American sea lion, Steller sea lion), phocid (southern elephant seal)		South America
A. rosmari (syn. *A. bicolor, A. alata*)	Carnivora: odobenid (walrus), phocid (ringed seal)		Arctic
A. salaris		[PH: Gadiformes: gadid (Atlantic cod)]	Atlantic
A. similis (syn. *Ascaris*)	Carnivora: otariid (South American sea lion, California sea lion, South American fur seal, Steller sea lion), phocid (southern elephant seal, northern elephant seal, harbor seal, leopard seal, grey seal)		Southern Ocean, Atlantic, Pacific, Arctic
A. tridentata	Carnivora: otariid (Steller sea		Pacific

	lion)		
A. tursionis	Artiodactyla: delphinid (common bottlenose dolphin)		

Parasite morphology: *Anisakis* spp. form 3 different morphological stages in their developmental cycles: eggs; larvae (4 successive stages designated L1-L4); and adult worms. The eggs are round-oval in shape measuring from 45-66 x 35-55 µm with smooth thin transparent shells and are unembryonated when laid containing a single central morula. The eggs embryonate to form L1 which moult while still within the eggshell to form L2. Emergent L2 are elongate cylindrical stages measuring 220-355 µm in length and they are ensheathed within the L1 cuticle (retained as a protective covering). In crustacean intermediate hosts, the L2 exsheath and grow to 3-6 mm long before moulting to pink-yellow L3 ranging in size from 4-50 x 0.3-2.0 mm. The L3 have a prominent anteroventral boring tooth, an excretory pore located anteriorly, an oesophagus with an anterior muscular portion and a posterior glandular ventriculus (0.15-0.67 mm long) connected to the intestines, and a rounded tail with a terminal spine (mucron). In paratenic hosts, L3 are encapsulated by fibrous connective tissue forming flat cysts (4-5 mm diameter) containing the tightly coiled larvae (watch-spring appearance). L3 dissected from cysts ranged in size from 14-30 x 0.3-0.6 mm and they were bound by a tough cuticle with transverse striations, often appearing wrinkled near the tail. The larvae had rounded heads, an anterior boring tooth, a muscular oesophagus followed by a glandular ventriculus connected to the intestines and ending in a subterminal anus. Four different types of encapsulated larvae have been described from paratenic hosts: type I with an average body size of 28 x 0.5 mm and a long ventriculus, an oblique ventriculus-intestinal junction, and a short rounded tail with a mucron (type often referable to *A. simplex*); type II with an average size of 26 x 0.6 mm and a short ventriculus, horizontal junction, and a long conical tapering tail without a mucron (often referable to *A. physeteris*); type III averaging 29 x 0.8 mm with a short ventriculus and a short rounded tail without a mucron; and type IV averaging 20 x 0.5 mm with a short ventriculus and a short conical pointed tail without a mucron. L4 are transient parasitic stages that range in size from 12-38 x 0.4-1.3 mm and have begun to display developing genitalia. Adults are large white worms measuring 15-82 x 0.4-1.9 mm which possess 3 protruding lips with tongue-like prolongations around the mouth and a single prominent anteroventral boring tooth. The cuticle has fine longitudinal striations, except for the smooth anterior region, but is otherwise devoid of cuticular ornamentations, spicules or spines (characteristic for the subfamilies Anisakinae and Raphidascaridinae). Worms have a distinctive alimentary tract with a glandular ventriculus located between the muscular oesophagus and the intestines (oblong-cylindrical ventriculus in members of the tribe Anisakinea, globular in the tribe Contracaecinea), sometimes with intestinal caeca, but always with a subterminal anus. The excretory system is also unique, being asymmetrical and ribbon-like (also characteristic in the subfamily Anisakinae) with the excretory pore located anteriorly between the subventral lips. Adults worms are sexually dimorphic, with females being slightly longer than males. Mature females are didelphic with 2 ovaries and uteri connected to a small common vulva located in the anterior half of the body. They have conical rounded tails lacking caudal papillae. In contrast, mature males have numerous caudal papillae (1 median, 1 pair proximal, 1 pair double paracloacal, 4 pairs distal) with their patterns of distribution varying between species. Males have 2 stout slightly subequal spicules (0.14–0.32 mm long), an attribute for which the genus was named (*anis* = different, *akis* = spicule).

Site of infection: Adult worms infect the stomach and intestines of their definitive (final) hosts (cetaceans and pinnipeds), often embedded in the mucosa. Developing larval stages (L2, L3) are found in the haemocoel of their crustacean intermediate hosts (euphausiids), while L3 may also be found encapsulated in the body cavities and internal tissues of various paratenic hosts (mostly teleost fish and squid). Humans may also act as accidental paratenic hosts for L3 which attach to the wall of the oesophagus, stomach or intestine, sometimes penetrating to extraintestinal sites (abdominal cavity, mesenteries, pancreas, liver, lung).

Pathogenesis: The effects that adult worms have on their final hosts are largely unknown, although clusters have been found in association with small ulcerative lesions and local inflammation usually in the stomach mucosa. Similarly, the effects that larvae have the fitness of their crustacean intermediate hosts are unknown, but the parasites are usually confined to the haemocoel rather than host tissues. In contrast, encysted larvae are often found in the tissues of their piscine paratenic hosts, causing unsightly lesions in many commercial fish species. Most fish appear healthy externally, but encysted larvae may be detected macroscopically either singly or in clusters in the peritoneum, mesenteries, visceral organs and muscles. The larvae are surrounded by fibrous connective tissue, often with melanomacrophage infiltrates in chronic infections. Infected livers appear red-brown due to local haemorrhages or green due to the destruction of bile ducts. In the stomach, infections may also cause crater syndrome whereby the thickened mucosa develops erosive craters up to 10 mm in diameter containing protruding larvae. Many reports have also observed larval migration into the musculature following host death (particularly for *A. simplex*). An increasing number of cases have been described in humans which act as accidental paratenic hosts when they consume L3 in raw or poorly cooked seafood. The larvae attach or migrate in host tissues within a few days of consumption but they cannot complete further development and die after a short period (2-3 weeks) although lesions may persist for several months. The larvae may cause direct tissue damage and provoke strong allergenic responses. The resultant disease may be acute or chronic in presentation and is known as anisakiosis/anisakiasis (terms often restricted to infections by *A. simplex* s.s.) or anisakidosis (more general term including other anisakids, such as *A. pegreffi, Contracaecum* or *Pseudoterranova* spp.). Larvae attach mostly to the stomach mucosa (sometimes the intestines, rarely the oesophagus), where they burrow down to the muscularis mucosae, rarely penetrating the wall and moving to ectopic extra-intestinal locations (abdominal cavity, mesenteries, omentum, bowel). In the mucosa, larvae may often detach and reattach at adjacent sites causing small petechial haemorrhages. The larvae elicit host inflammatory responses ranging from local inflammation to

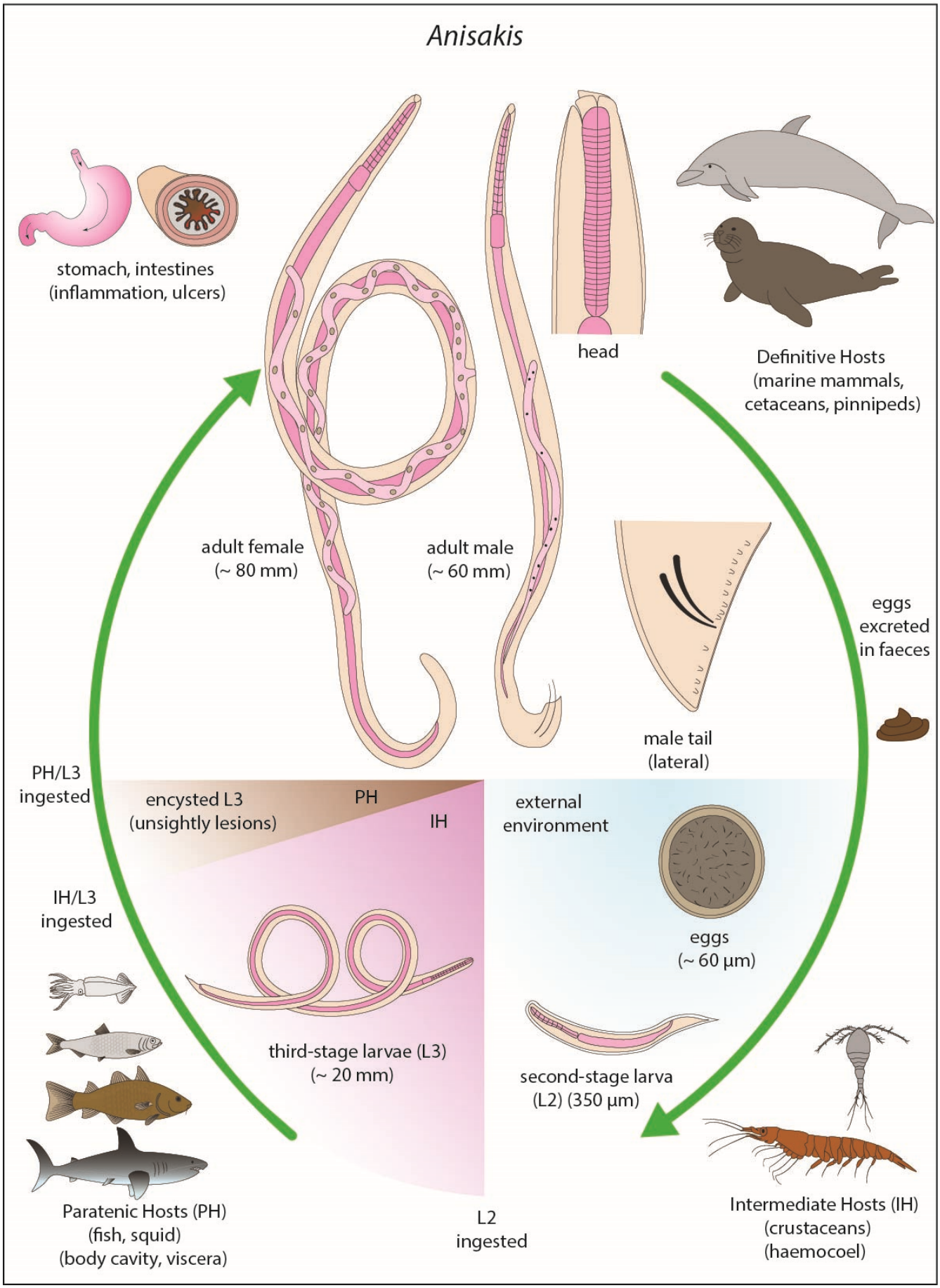
abscess/ulcer formation with necrosis and eosinophilia, to localized granuloma formation with encapsulation, cellular infiltrates (especially eosinophils) and larval degradation, to massive eosinophilic haemorrhagic tumour-like growths (pseudo-neoplasms with larvae at centre), particularly when infections involve the large intestines. Clinical signs vary considerably depending on the individual, the number of larvae (often only one), and the site of infection (gastric, intestinal or extra-intestinal). Initial clinical signs may include the sensation of having something between the teeth, tingling throat, dysphagia, mild cough and nasal congestion. Gastric signs may appear as early as 4-6 hours after infection and are often acute in nature, with epigastric pain (rapid and severe), gastric reflux, nausea and vomiting, sometimes with haematemesis due to ulceration. Intestinal signs may appear 7 days after infection with abdominal pain, colic, diarrhoea (sometimes with faecal occult blood), enteritis, leucocytosis, and sometimes with intestinal obstruction and peritonitis due to inflammation, oedema, granuloma and abscess formation. Lastly, many patients exhibit acute allergic (hypersensitivity) reactions to infection, particularly children and atopic individuals. Larval somatic and secretory products are highly allergenic and have been associated with the production of Th2 cytokines, mastocytosis, IgE antibody production and eosinophilia. Clinical signs may vary from mild to severe: with local irritation, inflammation and ulceration occurring at sites in contact with larvae; general urticaria (occurring in 60–70% of gastric cases); and type I hypersensitivity reactions involving airway hyperactivity (anaphylaxis, asthma, bronchospasms, rhinoconjunctivitis), angioedema with hypotension, and dermatitis.

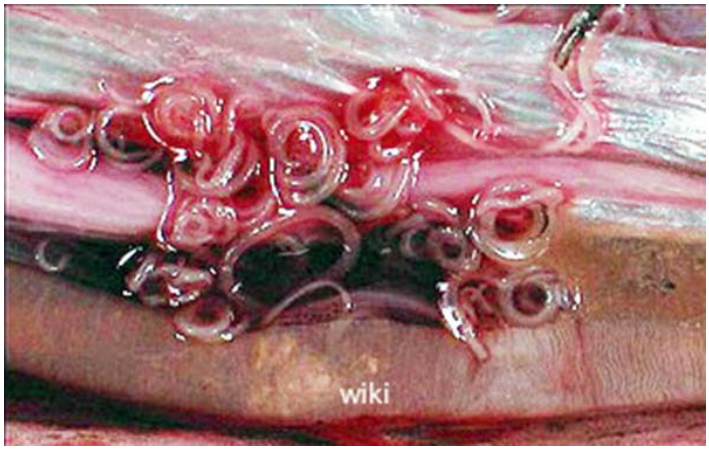
Developmental cycle and mode of transmission: *Anisakis* spp. have indirect heteroxenous life-cycles involving larval development in crustacean intermediate hosts, larval transport in fish or squid paratenic hosts and adult development in piscivorous final hosts (mostly pinnipeds and cetaceans). To date, adult *Anisakis* worms have been detected in 32 species of dolphins (mostly delphinids but including a platanistid and a pontoporiid), 6 species of porpoises (phocoenid), 17 species of toothed whales (ziphiid, physeterid, kogiid, and monodontid), 9 species of baleen whales (balaenopterid, balaenid, cetotheriid, and eschrichtiid), 15 species of seals (phocid), 7 species of sea-lions/fur-seals (otariid) as well as the walrus (odobenid) and dog (canid). Adult worms lay unembryonated eggs in the alimentary tract which are excreted with host faeces. The eggs embryonate in seawater to form L1 which then moult within the egg to form ensheathed L2 (a few miscellaneous reports suggest that L3 may form within some eggs). Eggs are well adapted to cold temperatures, and they embryonate and hatch within 4-8 days at 13-18°C or within 20-27 days at 5-7°C. The released larvae are active stages that swim and drift in seawater surviving for 3-4 weeks at 13-18°C or 6-7 weeks at 5-7°C. The L2 are then ingested by planktonic or pelagic crustaceans which act as intermediate hosts for L3 development. Suitable hosts include euphausiid krill, gammarid, lysianassid and pontageneiid amphipods, crangonid and mysid shrimp, pandalid prawns as well as acartiid and oithonid copepods, balanid barnacles, polynoid polychaetes, and sagittid arrow-worms. Ingested L2 exsheath and penetrate into the haemocoel where they moult and grow to larger L3 which may survive for as long as their hosts. Infections are more prevalent in regions of higher salinity as the juvenile stages of euphausiids favour such conditions for their development. When infected crustaceans are eaten by small teleost fish and cephalopods, the L3 burrow through the gut wall and encyst in fibrous connective tissue capsules usually on the serosa of visceral organs, but occasionally in the muscles or beneath the skin. These hosts act as paratenic (transport) hosts as the L3 are carried in the tissues without undergoing further development. Encysted L3 may also ascend the food chain and establish in larger teleost fish and some elasmobranchs when they consume smaller infected fish. A wide range of paratenic hosts have been reported from 97 families in 35 orders of teleost fish, including many commercially important marine and anadromous species such as herring, mackerel, cod, and salmon, 7 families of squid, 2 families of octopus, 5 families of sharks, and 3 families of rays/skates. Infections by L3 have also been detected occasionally in 2 families of sea-snakes, 1 family of sea turtles, 5 families of sea-birds, 1 family of otters, accidentally in 1 primates (humans) and experimentally in rodents (rats). Final hosts (marine mammals) become infected when they consume infected paratenic hosts. Ingested L3 infect the stomach mucosa where they moult to L4 and then subadults (often called L5) which grow to sexually mature adult worms. Little is known about the prepatent or patent periods of infections in the final hosts (cetaceans or pinnipeds). Humans become infected by the consumption of L3 in fish or cephalopods when eaten raw or semi-raw (lightly cooked, smoked, salted, pickled or fermented) in traditional culinary dishes, such as sushi, sashimi, ceviche, tuna tartare, pickled herring or anchovies, salted or smoked herring, tiradito, gravlax, Chinese kuai, Fijian kokoda, Micronesian kelaguen, or fish tripe.

Differential diagnosis: Most infections by adult worms have been detected incidentally during post-mortem examinations of whales, dolphins or seals following their death in captivity or following boat-strike, strandings or hunting. Infections in crustacean hosts may be detected by their dissection and microscopic examination of the haemocoel for developing larvae, but their identity is difficult to establish. Infections in fish hosts are more frequently detected during processing or food preparation by the discovery of encapsulated coiled larvae in the viscera and muscles (larvae of several species often migrate post-mortem from viscera to muscles). Microscopic studies conducted on larvae recovered from a range of fish species have identified at least 4 major morpho-types (I-IV). Molecular biological studies have used polymerase chain reaction (PCR) amplification, restriction fragment length polymorphism (RFLP) analyses and sequencing of nuclear genes (18S, 5.8 S and 28S ribosomal RNA, internal transcribed spacers 1 and 2) and mitochondrial genes (cytochrome oxidase 2, small subunit ribosomal RNA) to identify a clade of 6 species referable to larval type I (*A. simplex* s.s., *A. berlandi* (= *A. simplex* C), *A. nasceti, A. pegreffi, A. typica, A. ziphidarum*) and another clade of 3 species referable to larval type II (*A. brevispiculata, A. paggiae, A. physeteris*). In humans, infections are difficult to diagnose by symptomatology due to their nonspecific clinical manifestations, even when there is a solid history of the consumption of raw or undercooked fish within the last few days. Many other conditions present with similar clinical signs, such as ulcers, tumours, cholecystitis, appendicitis, peritonitis, Crohn's colitis, diverticulitis, intestinal intussusception, obstruction, various food allergies, and other gastrointestinal infections (viral, bacterial, protozoal and helminth). On occasion, larvae may be coughed up or excreted in

faeces, but most infections are detected by invasive techniques such as endoscopy (gastroscopy, colonoscopy), laparoscopy or explorative surgery. Medical imaging technologies may help focus explorations by revealing mucosal thickenings, luminal constrictions and/or inflammatory foci by radiography, ultrasonography or computed tomography. A range of immunodiagnostic tests have been developed to detect specific antibody-antigen interactions by immuno-diffusion, immuno-electrophoresis, intradermal skin-prick tests, immuno-fluorescence, haemagglutination, enzyme immunoassays, Western blots and radioallergosorbent tests. Most tests demonstrated good sensitivity but reduced specificity due to antigenic cross-reactivity with other helminths, but some improvements have been achieved using defined antigens, monoclonal antibody reagents and specifically testing for IgE antibodies in cases involving hypersensitivity reactions.

Treatment and control: Given that most anisakid infections in their normal hosts (marine mammals, crustaceans, fish and cephalopods) are cryptic and asymptomatic, little information is available about possible treatments. Infections in humans are accidental and frequently transient, many involving just a few larvae that live for several weeks before succumbing to host responses, although lesions and symptoms may persist for months. Most human infections resolve spontaneously without treatment, but the anthelmintic albendazole has been used to kill larvae, often in combination with supportive therapy to reduce inflammatory and allergic reactions. Accessible larvae may also be removed by endoscopy or laparoscopy, or by surgery usually conducted when intestinal obstructions occur. Many countries have developed education campaigns to warn consumers about the dangers of eating not only raw seafood but also improperly processed dishes (many marinating, brining, salting, pickling, fermenting and smoking techniques may not kill encysted larvae). Larvae are rendered nonviable when cooked at 60°C or above for more than one minute, or by freezing at -35°C or below for 16 hours, at -20°C for at least 24-48 hours, or at -10°C for over 7 days. Some success has also been reported treating seafood with high hydrostatic pressures to kill parasites and increase the shelf-life of produce. While stringent food inspection may be used in fish processing plants, it is advisable to remove the viscera of fish shortly after capture to remove sources of infection and to prevent their post-mortem migration from the viscera to the muscles.


Anisakis
stomach, intestines
(inflammation, ulcers)
head
Definitive Hosts
(marine mammals,
cetaceans, pinnipeds)
adult female
(~ 80 mm)
adult male
(~ 60 mm)
male tail
(lateral)
eggs
excreted
in faeces
PH/L3
ingested
encysted L3
(unsightly lesions)
PH
IH
external
environment
IH/L3
ingested
eggs
(~ 60 µm)
third-stage larvae (L3)
(~ 20 mm)
second-stage larva
(L2) (350 µm)
Paratenic Hosts (PH)
(fish, squid)
(body cavity, viscera)
L2
ingested
Intermediate Hosts (IH)
(crustaceans)
(haemocoel)



Anisakis larvae in herring

Heterakis
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Ascaridomorpha which includes ascaridoid nematodes (roundworms) characterised by their large size, three prominent anterior lips and the absence of a bursa. They occur in the small intestines of many animals (including humans) and most have simple direct life-cycles involving faecal-oral transmission. Female worms produce numerous eggs which are excreted with host faeces and undergo embryonation to contain infective larvae. When ingested, larvae hatch from the eggs and develop into adult worms in the gut. The larvae of ascaridoid species undergo hepato-pulmonary migration before forming adults, whereas those of heterakoid species do not. Heterakoid worms have a large sucker anterior to the cloaca in males, and two major families are recognised: heterakids having an oesophagus with a rounded terminal bulb; and ascaridiids having one without. Adult heterakids have lateral alae and eggs/L3 may be transported by earthworms (paratenic hosts). Infections by *Heterakis* spp. are common in poultry but are generally asymptomatic, although they can act as a vector for the protozoan *Histomonas meleagridis*, causing blackhead disease.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Ascaridomorpha (large roundworms, mouth surrounded by three large lips, numerous caudal papillae)
Superfamily:	Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by ingestion of eggs)
Family:	Heterakidae (worms with lateral alae, oesophagus with rounded terminal bulb)
Genus:	*Heterakis* (usually parasitic in caeca of birds)
Species:	various species cause asymptomatic infections in poultry

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Ascaridomorpha is characterised by large roundworms with poorly developed buccal cavity with 3 large lips, an undivided oesophagus, numerous caudal papillae, nonbursate males often with pre-anal suckers, and females with complex ovejectors. Five superfamilies (conventionally assigned to the order Ascaridida) are recognised as parasites in vertebrates: Ascaridoidea (cylindrical oesophagus often terminated by swelling without bulb, coelomyarian, eggs thick-shelled); Heterakoidea (oesophagus cylindrical or with claviform corpus, short isthmus and valved bulb, coelomyarian, pre-anal sucker, eggs thick-shelled); Cosmocercoidea (oesophagus with cylindrical corpus, elongate isthmus and valved bulb, platymyarian, eggs with delicate shells or hatch *in utero*); Seuratoidea (lips absent, oesophagus short, platymyarian, eggs with delicate shells or hatch *in utero*); and Subuluroidea (well-developed buccal capsule without lips, coelomyarian, pre-anal sucker, eggs thick-shelled).

The superfamily Heterakoidea contains worms with prominent pre-anal suckers surrounded by cuticularized rings. Adult worms are parasitic in the gastrointestinal tracts of vertebrates (birds, reptiles, amphibians, mammals) and have direct monoxenous life-cycles where hosts become infected by ingesting larvated eggs and the released larvae do not undertake hepatopulmonary migration. The superfamily contains 4 families: Heterakidae (rounded lips not connected by lateral lobes, short stout oesophagus with rounded trivalved terminal bulb, lateral alae present); Ascaridiidae (large stout lips, slender club-shaped oesophagus without posterior bulb, anterior cuticular flange absent); Aspidoderidae (square lips connected by lateral lobes, long narrow oesophagus with small trivalved terminal bulb, anterior cuticle thickened to form cephalic cap); and Kiwinematidae (shallow rounded lips without distinct margins, oesophagus with trivalved terminal bulb, lateral alae present). Representative genera of significance to animal health and production are tabulated below.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Heterakidae (worms with lateral alae, oesophagus with rounded terminal bulb)						
Heterakis (caecal worm)	51	birds (esp. galliform), rodents	intestines	4-23 mm long, lateral alae, fine longitudinal striations, 3 anterior lips, oesophageal bulb, abursate males with precloacal sucker, larvae do not undertake hepato-pulmonary migration	63-80 x 35-50 µm, ellipsoidal, thick-shelled	direct (faecal-oral) (sometimes eggs/L3 in earthworm PH)
Ascaridiidae (slender club-shaped oesophagus without rounded terminal bulb)						
Ascaridia	45	birds (esp. galliform), reptiles, fish	intestines	3-12 cm long, poorly developed cuticular alae, 3 large trilobed anterior lips, no oesophageal bulb, abursate males with precloacal sucker, larvae do not undertake hepato-pulmonary migration,	80-90 x 45-50 µm, ovoid, thick-shelled	direct (faecal-oral) (sometimes eggs/L3 in earthworm PH)

The family Heterakidae contains 3 subfamilies: Heterakinae (lips not offset from body, caudal alae supported by 3-4 stout papillae or by long thin papillae, head with interlabia or homologues, caudal alae broad supported by long narrow papillae, few sessile papillae present on tail, parasites of birds, rarely mammals); Meteterakinae (lips not offset from body, caudal alae supported by 3-4 pairs of large fleshy papillae, numerous small sessile papillae present on tail, parasites of amphibians, reptiles and mammals); and Spinicaudinae (lips offset from body, caudal alae when present either not supported by papillae or supported by many short stout papillae, parasites of amphibians and reptiles). The subfamily Heterakinae contains 6 genera: *Heterakis* (syn. *Raillietakis*, *Ganguleterakis*, *Inglisakis*), *Gireterakis, Haroldakis, Musserakis, Neohaterakis, Odontoterakis* and *Pseudaspidodera.* The genus *Heterakis* contains some 50 species of small worms with 3 lips without cordons or labial grooves, a complex oesophagus and males with caudal alae, suckers and unequal spicules. Most species are parasitic in the caeca of ground-feeding (mostly grain-eating) birds, particularly Galliformes, although a few species infect mammals. The species *H. gallinarum* is commonly found in domestic and wild poultry around the world. Infections are more prevalent in tropical and subtropical regions than in temperate regions as eggs are unable to develop to the infectious stage at temperatures under 15°C. A variety of invertebrates (earthworms, insects) have also been found to act as paratenic (transport) hosts where larvae may hatch from ingested eggs but they do not undergo further development.

***Heterakis* species**	**Definitive hosts [plus Paratenic hosts (PH)]**	**Location [Clinical signs]**	**Distribution**
Avian hosts			
H. alata (now *Odontoterakis*)	Tinamiformes: tinamid (yellow-legged tinamou, undulated tinamou, red-winged tinamou); Gruiformes: psophiid (dark-winged trumpeter)	intestines	South America
H. arctica	Anseriformes: anatid (greater snowgoose)		Greenland
H. arquata (= *Odontoterakis*)	Gruiformes: psophiid (dark-winged trumpeter); Tinamiformes: tinamid (unspecified tinamou species)	intestines	South America
H. bancrofti (now *Odontoterakis*)	Galliformes: megapodid (Australian brush turkey); Columbiformes: columbid (wonga pigeon)	caecum	Australia
H. beramporia (syn. *H. putaustralis*)	Galliformes: phasianid (chicken, common pheasant, red junglefowl); Anseriformes: anatid (domestic duck, mallard)	caecum [nodule formation]	Asia, Australia
H. bosia	Galliformes: phasianid (Temminck's tragopan, satyr tragopan)		Asia
H. brasiliana sp. dubia	Tinamiformes: tinamid (unspecified tinamou species)		South America
H. brevispeculum	Galliformes: phasianid (chicken), numidid (helmeted guineafowl); Anseriformes: anatid (duck, goose)	caecum, occasionally intestines	worldwide
H. caudebrevis	Galliformes: phasianid (chicken)	caecum	Asia
H. chenonettae sp. inq.	Anseriformes: anatid (Australian wood duck)	caecum	Australia
H. crypturi (now *Odontoterakis*)	Tinamiformes: tinamid (variegated tinamou); Gruiformes: psophiid (dark-winged trumpeter)	intestines	South America
H. dispar (syn. *H. caudata, circumvallata,*	Galliformes: phasianid (chicken, chukar partridge, rock partridge, grey partridge, red-legged partridge, see-see partridge, Barbary partridge, hazel grouse,	caecum, occasionally intestines	worldwide

hyperborea, monticelliana, stylosa, tenuicauda, H. d. brevispiculatus)	common quail, black francolin), numidid (vulturine guineafowl); Anseriformes: anatid (mallard, muscovy, Australian shelduck, domestic goose, greylag goose, greater white-fronted goose, snow goose, swan goose); Strigiformes: strigid (Eurasian pygmy owl)		
H. fariai (now *Odonterakis*)	Galliformes: phasianid (silver pheasant, spot-winged wood quail)		Asia, South America
H. gallinarum (syn. *H. gallinae, papillosa, parisi, pedioecetes, vesicularis*) (poultry caecal worm)	Galliformes: phasianid (chicken, red junglefowl, Indian red junglefowl, grey junglefowl, Indian peafowl, green peafowl, turkey, black francolin, common pheasant, golden pheasant, silver pheasant, Lady Amherst's pheasant, Mrs Hume's pheasant, Reeve's pheasant, Koklass pheasant, copper pheasant, scintillating copper pheasant, green pheasant, Shikoku green pheasant, Japanese green pheasant, Bianchi's pheasant, Korean pheasant, blue-eared pheasant, brown-eared pheasant, chukar partridge, rock partridge, grey partridge, red-legged partridge, Barbary partridge, Daurian partridge, Chinese bamboo partridge, mountain bamboo partridge, hazel grouse, black grouse, common quail, Japanese quail, northern bobwhite quail, willow ptarmigan, rock ptarmigan, western capercaillie, Altai snowcock, Caucasian snowcock, Himalayan snowcock, Sclater's monal, Cabot's tragopan, Temminck's tragopan), numidid (helmeted guinea fowl); Anseriformes: anatid (domestic duck, mallard, muscovy, domestic goose, greylag goose, Eurasian wigeon); Columbiformes: columbid (pigeon); Coraciiformes: mergid (European bee-eater); Cuculiformes: cuculid (lesser coucal); Gruiformes: psophiid (grey-winged trumpeter), rallid (Eurasian coot, common moorhen); Otidiformes: otidid (Houbara bustard, great bustard, little bustard); Passeriformes: corvid (Cayenne jay); Psittaciformes: cacatuid (Major Mitchell's cockatoo); Strigiformes: strigid (tawny owl); Tinamiformes: tinamid (red-winged tinamou, spotted nothura); Carnivora: felid (cat) [PH: Clitellata: lumbricid (*Allolobophora caliginosa, Eisenia foetida, Helodrilus gieseleri, Lumbricus terrestris*); Diptera: muscid (unspecified house fly); Orthoptera (unspecified grasshopper); Crustacea: porcellionid (*Porcellio scaber*)]	caecum, occasionally intestines [vector for *Histomonas meleagridis*]	worldwide
H. hamulus	Galliformes: phasianid (green peafowl, Indian peafowl)		Europe
H. hefeiensis	Galliformes: phasianid (chicken)		Asia
H. indica (syn. *H. linganensis*)	Galliformes: phasianid (chicken, red junglefowl); Anseriformes: anatid (domestic duck)	caecum	Asia
H. interlabiata	Galliformes: phasianid (long-billed partridge)		Africa
H. isolonche (syn *H. bonasae, hastata, lanei, neoplastica, tragopanis, variabilis*) (caecal worm)	Galliformes: phasianid (chicken, prairie chicken, ruffed grouse, turkey, common pheasant, blood pheasant, golden pheasant, blue-eared pheasant, brown-eared pheasant, copper pheasant, Bianchi's pheasant, Lady Amherst's pheasant, northern bobwhite quail, California quail, grey partridge, Himalayan monal, Temminck's tragopan, satyr tragopan); Anseriformes: anatid (domestic duck); Otidiformes: otidid (great bustard); Strigiformes: strigid (Eurasian scops owl)	caecum, occasionally intestines [typhlitis, diarrhoea]	worldwide
H. kotdwarensis	Galliformes: phasianid (chicken)		India

H. kumaoni	Galliformes: phasianid (Indian red junglefowl)		Asia
H. kurilensis	Charadriiformes: alcid (crested auklet, whiskered auklet)		Russia
H. longecaudata (*longicaudata*)	Galliformes: phasianid (chicken, silver pheasant)	caecum	Russia
H. longespiculum	Galliformes: phasianid (crested partridge)		India
H. macroura (syn. *H. altaica*)	Galliformes: phasianid (chukar partridge, grey partridge, rock partridge, Altai snowcock, Caspian snowcock, Caucasian snowcock, Himalayan snowcock, Tibetan snowcock); Anseriformes: anatid (domestic duck, goose)	caecum, intestines	Asia
H. maculosa	Columbiformes: columbid (pigeon, rock dove)		
H. meleagris	Galliformes: phasianid (chicken, turkey)		Asia
H. multidentata (syn. *Odontoterakis*) (now *Haroldakis*)	Tinamiformes: tinamid (variegated tinamou)	caecum, large intestines	South America
H. multipapillata (syn. *Gangulererakis*)	Columbiformes: columbid (pin-tailed green pigeon)		Asia
H. nainitalensis	Galliformes: phasianid (Indian red junglefowl)		
H. nattereri	Tinamiformes: tinamid (solitary tinamou, grey tinamou); Galliformes: cracid (red-billed curassow)	caecum	Americas
H. oscari	Galliformes: cracid (red-billed curassow)	intestine	South America
H. parva	Galliformes: phasianid (chicken, red junglefowl, common pheasant, silver pheasant); Anseriformes: anatid (goose)	caecum	Asia
H. pavonis	Galliformes: phasianid (chicken, peafowl, ring-necked pheasant, green pheasant, copper pheasant); Pelecaniformes: ardeid (black-crowned night heron)		Asia
H. perspicillum	Galliformes: phasianid (chicken)		
H. psophiae	Gruiformes: psophiid (dark-winged trumpeter)	intestines	South America
H. pusilla	Galliformes: phasianid (Ceylon junglefowl, red junglefowl)		Africa
H. rimula	Cuculiformes: cuculid (greater coucal)		Asia
H. silindae	Galliformes: phasianid (red-necked spurfowl, red-necked francolin, hazel grouse)		Africa
H. sinica	Galliformes: phasianid (Temminck's tragopan)		Asia
H. skrjabini (now *Odontoterakis*)	Gruiformes: psophiid (grey-winged trumpeter)		South America
H. spiculatus (incl. *H. inglisi* ex: Vicente *et al.,* 1993)	Tinamiformes: tinamid (yellow-legged tinamou, variegated tinamou, small-billed tinamou, spotted nothura)		Americas
H. valvata (now *Odontoterakis*)	Tinamiformes: tinamid (yellow-legged tinamou, Tataupa tinamou, spotted nothura)	intestines	South America
H. vexans	Galliformes: phasianid (Taiwan partridge)		Taiwan
H. vulvolabiata	Galliformes: phasianid (Taiwan partridge)		Taiwan
H. yamadori	Galliformes: phasianid (chicken, green pheasant, northern green pheasant, copper pheasant, scintillating copper pheasant, Chinese bamboo partridge), numidid (helmeted guineafowl); Pelecaniformes: ardeid (black-crowned night heron)		Asia
H. yani	Galliformes: phasianid (chicken); Anseriformes: anatid (domestic duck)	caecum	Asia
Reptilian/amphibian/piscine hosts			
H. bufonis	Anura: bufonid (Asian common toad)		Asia
H. foveolata	Pleuronectiformes: pleuronectid (European plaice)		Europe
H. govindi (now *Meteterakis*)	Anura: bufonid (Asian common toad); Sauria: varanid (Bengal monitor)	large intestine	Asia
Mammalian hosts			
H. balamukensis	Peramelemorphia: peramelid (common echymipera)		Papua New Guinea
H. dahomensis	Rodentia: cricetid (Gambian pouched rat)		Africa
H. equispiculis sp. inq.	Rodentia: murid (black rat)		India
H. fieldingi	Rodentia: murid (rakali)	caecum, colon	Australia

H. girardi (now *Gireterakis*)	Rodentia: hystricid (Sunda porcupine, Malayan porcupine, crested porcupine)	intestine	Asia
H. inglisi (ex: Gupta & Trivedi, 1982)	Chiroptera: vespertilionid (greater Asiatic yellow bat)		Asia
H. macrospiculum (now *Mammalakis*)	Rodentia: spalacid (mole-rat)		Russia
H. oweni	Peramelemorphia: peramelid (northern brown bandicoot)	large intestines	Australia, Papua New Guinea
H. sirawii	Rodentia: murid (New Guinean rat)		New Guinea
H. spalacis (now *Mammalakis*)	Rodentia: spalacid (lesser mole-rat, greater mole-rat)		Russia
H. spalaxi (now *Mammalakis*)	Rodentia: spalacid (lesser mole-rat, greater mole-rat)		Russia
H. spumosa (syn. *Ganguleterakis, H. rattui*)	Rodentia: murid (house mouse, Algerian mouse, striped field mouse, typical striped grass mouse, small Japanese field mouse, large Japanese field mouse, Himalayan field mouse, Korean field mouse, Natal multimammate mouse, brown rat, black rat, dusky field rat, roof rat, bush rat, Polynesian rat, Australian swamp rat, African grass rat, soft-spined Atlantic spiny rat, rakali, Indian gerbil), cricetid (grey red-backed vole, Japanese red-backed vole, Japanese grass vole, Smith's vole), talpid (Kobe mole); Peramelemorphia: peramelid (northern brown bandicoot); Gruiformes: rallid (slaty-legged crake) [PH: Clitellata: megascolecid (*Pheretima hilgendofi*), lumbricid (*Eisenia foetida*)]	caecum, upper colon	worldwide
H. verrucosa sp. inq.	Rodentia: dasyproctid (agouti)		South America
H. yamagutii (syn. *H. pandei*)	Rodentia: murid (Indian desert jird, black rat)		India

Parasite morphology: *Heterakis* spp. form 3 different morphological stages in their developmental cycles: eggs; larvae (4 successive stages encoded L1-L4); and adult worms. The eggs measure 63-80 x 35-50 µm and are oval-ellipsoidal in shape but have sides that are almost parallel (convex in *Ascaridia* spp.). They are bound by thick smooth eggshells (roughened outer surface for *H. spumosa*) with a small clear lenticular body at one pole. Eggs are unembryonated when laid and contain a single central morula. Following embryonation, the eggs contain coiled first-stage larvae (L1) which moult within the egg to form ensheathed L2 (although a few studies suggest another moult to L3 may occur in some eggs). Infective were cylindrical with an anterior boring tooth and lateral alae. Those recovered from dissected eggs measured 231-274 µm while those recovered from earthworms measured 365-387 µm. L3 and L4 are transient parasitic stages and little is known about their morphological characteristics. Adults are robust cylindrical white worms varying in length from 4-23 mm depending on maturity and species. They have sharply pointed tails and are bound by a tough cuticle with fine longitudinal striations and large lateral alae extending along the body. They have anterior mouths with triangular apertures but without cephalic cordons (present in some other genera). The mouth is surrounded by 3 well-defined round lips (one dorsal and two subventral), each with 2 papillae and thickened radial margins. The lips are not offset from the body and they have interlabia, but lack labial grooves and are not connected by lateral lobes. The mouth opens into a complex oesophagus with a small neck (some species with hinged rods) and a long muscular body with a prominent rounded terminal bulb (lacking in members of the ascaridiid family) with 3 well-marked dentate valves. Adult worms are sexually dimorphic, with females being larger than males (8-23 mm cf. 4-18 mm). Mature females are didelphic with 2 ovaries and uteri in an amphidelphic configuration (opposed) and connected to a common vulva opening close to the midbody. Females have narrow straight tails but do not have any special ejaculatory apparatus (ovejectors) but use powerful uterine muscles to pass developing eggs. Mature males are characterised by the possession of a large precloacal sucker (38-150 µm in diameter) surrounded by a chitinous ring, and pointed bent tails with 2 well developed broad caudal alae supported by 12 pairs of caudal papillae. They do not possess a gubernaculum but have 2 equal or unequal spicules ranging in length 0.3-2.8 mm. The spicules of *Heterakis* spp. of poultry fall into several types: *H. gallinarum* type (unequal with a long slender right spicule and a short alate left spicule); *H. dispar* type (with short subequal spicules); *H. isolonche* type (with long equal asymmetrical spicules), and *H. brevispeculum* type (with short equal barbed spicules).

Site of infection: Most species are parasitic in ground-feeding (mostly grain-eating) birds, especially Galliformes, but a few species infect mammals (mostly rodents). Larval stages develop in the large intestines (often near crypts), while adult worms live in the lumen of the caecum of birds (near the tips or blind ends) or the upper colon of rodents. Larvated eggs and freed L2 may also be carried in the alimentary tract or tissues of invertebrate paratenic hosts (notably earthworms).

Pathogenesis: Most infections remain asymptomatic or subclinical, rarely causing morbidity and mortality. Developing larvae and adult worms feed on intestinal content, and only occasionally have larval stages been observed to invade the mucosa for short periods of time (without undergoing histotrophic development). Nonetheless, parasites have been associated with clinical disease predominantly in young chickens and pheasant chicks. Adult birds are more resistant to infection than young birds, and experimental studies have shown that previous exposure confers hosts with some protective immunity. Infections in young birds may cause petechial haemorrhages, inflammation with caecal mucosal thickening, catarrhal or haemorrhagic typhlitis, congestion, and nodule formation, resulting in vague clinical signs including mild diarrhoea (sometimes green), anaemia, decreased appetite, poor growth and weakness. Infections have occasionally been detected in association with neoplastic-like smooth muscle tumours (fibroids or leiomyomas) in the caecal submucosa. Some studies have reported reduced egg production in layers but no differences were observed in weight gains by infected and control birds. In contrast, more severe disease has been recorded in pheasant infected by *H. gallinarum* or *H. isolonche* due to significant inflammation, diffuse or verrucous typhlitis, ulceration, nodule formation, granulomata and fibrous hyperplastic caecal tissues resulting in diarrhoea, progressive emaciation, and high mortalities (up to 50% without treatment)

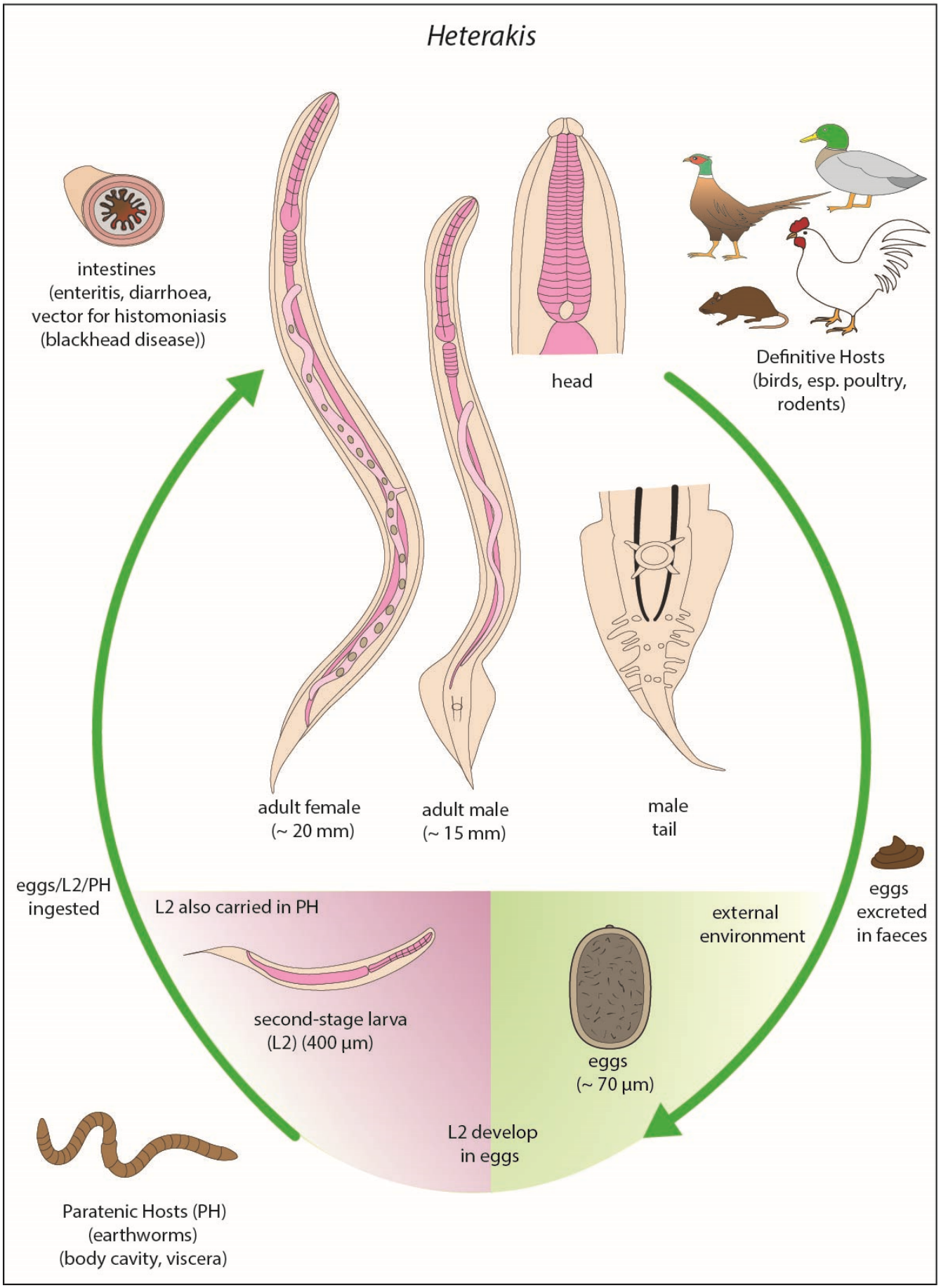
H. gallinarum may also act as a vector for the transmission of the protozoans *Histomonas meleagridis*, the causal agent of infectious enterohepatitis (blackhead disease) and *Histomonas wenrichi.* Protozoal trophozoites multiply in the worm ovary and penetrate oocytes thus infecting worm eggs and their developing larvae. The protozoa are then transmitted to birds when worm eggs/larvae are ingested (direct or via paratenic hosts), resulting in blackhead disease (usually in turkeys, sometimes chickens) with anorexia, lethargy, listlessness, feather loss, caecal inflammation with cheesy exudates, necrotic livers and high mortality (90%) unless treated.

Developmental cycle and mode of transmission: *Heterakis* spp. have direct monoxenous life-cycles that involve the faecal-oral transmission of infective larvae, sometimes within invertebrate paratenic hosts. Gravid female worms lay numerous unembryonated eggs which are excreted into the external environment with host faeces. In warm moist conditions, the eggs embryonate to form L1 which then moult within the egg to form infective L2 in 7-14 days (longer in cooler conditions). The larvated eggs are highly resistant to extremes of temperature and remain infective for long periods (*H. gallinarum* eggs may survive in soil for 1.0-4.5 years, even under snow for 6 months, while *H. spumosa* eggs may survive in faeces at ambient temperature for 120 days). They survive best in well-grassed or densely-vegetated areas with ample moisture and shade, but are susceptible to desiccation in hot dry conditions. Infections are more prevalent in tropical and subtropical regions than in temperate regions as the eggs are unable to develop to the infectious stage at temperatures under 15°C. In addition to egg dispersal by water and wind action, they have also been shown to be mechanically dispersed by various soil invertebrates, including earthworms, grasshoppers, fly larvae and sow bugs. Several earthworm species have also been shown to act as paratenic (transport) hosts when ingested eggs hatch releasing L2 which invade host tissues and remain infective for at least a year without undergoing further development. Final hosts become infected when they ingest infective larvated eggs from the environment or by consuming infective eggs or larvae within paratenic hosts. Following ingestion, eggs hatch in the stomach and small intestines releasing larvae which colonize the caecum in birds or the colon in mammals. The larvae of heterakoid species do not undergo any hepato-pulmonary migration before forming adults (unlike those of ascaridoid species). *Heterakis* larvae develop directly in the lumen into adults, although some may invade the caecal mucosa or caecal glands for 2-5 days before returning to the lumen. The infective larvae moult to L3 in 3-7 days, L4 in 9-10 days, and to preadults (L5) in 14-16 days. The prepatent period (time from infection to first egg excretion) ranges from 21-36 days in birds and 26-47 days in rodents. Adult worms are thought to live for 100-312 days after first producing eggs.

Differential diagnosis: Even when infections cause clinical signs, they are vague and nonspecific and may be attributed to many other conditions. Patent infections are conventionally diagnosed by the microscopic detection of worm eggs in faecal samples, either direct in wet mounts or smears, but usually following their concentration by sedimentation in water and floatation in high specific gravity sugar or salt solutions. The intensity of infection may also be determined by counting worm eggs in faecal aliquots in volumetric McMaster or Whitlock chambers and calculating the number of eggs per gram of faeces. *Heterakis* eggs are similar in morphology to those of *Ascaridia*, both being thick-shelled and ellipsoidal, but those of *Heterakis* are slightly smaller and have nearly parallel sides rather than convex sides. Infections may also be diagnosed by the post-mortem detection of adult worms and lesions in the caeca (usually granulomas with necrotic centres, or leiomyomas with haemosiderosis). Parasites may also be detected in mucosal scrapings, squash preparations or caecal digests. Molecular biological techniques have been used to characterize parasites from environmental and clinical samples following the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (ribosomal RNA and internal transcribed spacers 1 and 2) and the complete mitochondrial genome for several species.

Treatment and control: Clinical infections in young birds (especially chickens and pheasant chicks) have been successfully treated with a range of old and new anthelmintic drugs, including heterocyclic thiazines (phenothiazine, now discontinued), monothiophosphates (coumaphos), benzimidazoles (mebendazole, flubendazole, albendazole, fenbendazole, cambendazole), prebenzimidazoles (febantel), imidazothiazoles (levamisole, tetramisole), diethylenediamines (piperazine) and macrocyclic lactones (ivermectin). Studies on alternative therapies found that extracts of white wormwood, *Artemisia herba-alba*, significantly reduced

worm burdens and fecundity in *H. gallinarum* infections, and other plant extracts (aloe, garlic, root bark) and even bee products (propolis) demonstrated some modest anthelmintic effects. Various preventive strategies have been used in the poultry industries to limit parasite transmission by reducing faecal contamination of the environment and minimizing the exposure of susceptible birds to potential sources of infection. Improved sanitation and hygiene have involved the regular removal of litter from poultry houses, not using faecal material as fertilizer on grazing areas, raising birds on hard substrates (wood slats, wire mesh, hardware cloth, concrete), cleaning cages/yards frequently, providing clean food and water, and treating soil areas with insecticides to reduce paratenic host populations. Appropriate bird management has involved separating young birds from adults, not raising chickens and turkeys together (axiomatic amongst poultry producers), avoid overcrowding, instituting quarantine and isolation procedures, and prevent wild birds from entering facilities.


Heterakis
intestines
(enteritis, diarrhoea,
vector for histomoniasis
(blackhead disease))
head
Definitive Hosts
(birds, esp. poultry,
rodents)
adult female
(~ 20 mm)
adult male
(~ 15 mm)
male
tail
eggs/L2/PH
ingested
L2 also carried in PH
external
environment
eggs
excreted
in faeces
second-stage larva
(L2) (400 µm)
eggs
(~ 70 µm)
L2 develop
in eggs
Paratenic Hosts (PH)
(earthworms)
(body cavity, viscera)



Heterakis adult worm, head



Heterakis worm eggs

Ascaridia
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Ascaridomorpha which includes ascaridoid nematodes (roundworms) characterised by their large size, three prominent anterior lips and the absence of a bursa. They occur in the small intestines of many animals (including humans) and most have simple direct life-cycles involving faecal-oral transmission. Female worms produce numerous eggs which are excreted with host faeces and undergo embryonation to contain infective larvae. When ingested, larvae hatch from the eggs and develop into adult worms in the gut. The larvae of ascaridoid species undergo hepato-pulmonary migration before forming adults, whereas those of heterakoid species do not. Heterakoid worms have a large sucker anterior to the cloaca in males, and two major families are recognised: heterakids having an oesophagus with a rounded terminal bulb, and ascaridiids having one without. Ascaridiid eggs/L3 may be transported by earthworms (paratenic hosts) to birds, and several *Ascaridia* spp. may cause anaemia and/or diarrhoea in poultry.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Ascaridomorpha (large roundworms, mouth surrounded by three large lips, numerous caudal papillae)
Superfamily:	Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by ingestion of eggs)
Family:	Ascaridiidae (slender club-shaped oesophagus without rounded terminal bulb)
Genus:	*Ascaridia* (parasitic in small intestines of birds)
Species:	various species cause anaemia/diarrhoea in poultry

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Ascaridomorpha is characterised by large roundworms with poorly developed buccal cavity with 3 large lips, an undivided oesophagus, numerous caudal papillae, nonbursate males often with pre-anal suckers, and females with complex ovejectors. Five superfamilies (conventionally assigned to the order Ascaridida) are recognised as parasites in vertebrates: Ascaridoidea (cylindrical oesophagus often terminated by swelling without bulb, coelomyarian, eggs thick-shelled); Heterakoidea (oesophagus cylindrical or with claviform corpus, short isthmus and valved bulb, coelomyarian, pre-anal sucker, eggs thick-shelled); Cosmocercoidea (oesophagus with cylindrical corpus, elongate isthmus and valved bulb, platymyarian, eggs with delicate shells or hatch *in utero*); Seuratoidea (lips absent, oesophagus short, platymyarian, eggs with delicate shells or hatch *in utero*); and Subuluroidea (well-developed buccal capsule without lips, coelomyarian, pre-anal sucker, eggs thick-shelled).

The superfamily Heterakoidea contains worms with prominent pre-anal suckers surrounded by cuticularized rings. Adult worms are parasitic in the gastrointestinal tracts of vertebrates (birds, reptiles, amphibians, mammals) and have direct monoxenous life-cycles where hosts become infected by ingesting larvated eggs and the released larvae do not undertake hepatopulmonary migration. The superfamily contains 4 families: Ascaridiidae (large stout lips, slender club-shaped oesophagus without posterior bulb, anterior cuticular flange absent); Heterakidae (rounded lips not connected by lateral lobes, short stout oesophagus with rounded trivalved terminal bulb, lateral alae present); Aspidoderidae (square lips connected by lateral lobes, long narrow oesophagus with small trivalved terminal bulb, anterior cuticle thickened to form cephalic cap); and Kiwinematidae (shallow rounded lips without distinct margins, oesophagus with trivalved terminal bulb, lateral alae present). Representative genera of significance to animal health and production are tabulated below.

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Ascaridiidae (slender club-shaped oesophagus without rounded terminal bulb)						

Ascaridia	45	birds (esp. galliform), reptiles, fish	intestines	15-120 mm long, poorly developed cuticular alae, 3 large trilobed anterior lips, no oesophageal bulb, abursate males with precloacal sucker, larvae do not undertake hepato-pulmonary migration,	55-99 x 40-57 µm, ovoid, thick-shelled	direct (faecal-oral) (sometimes eggs/L3 in earthworm PH)
Heterakidae (worms with lateral alae, oesophagus with rounded terminal bulb)						
Heterakis (caecal worm)	51	birds (esp. galliform), rodents	intestines	4-23 mm long, lateral alae, fine longitudinal striations, 3 anterior lips, oesophageal bulb, abursate males with precloacal sucker, larvae do not undertake hepato-pulmonary migration	63-80 x 35-50 µm, ellipsoidal, thick-shelled	direct (faecal-oral) (sometimes eggs/L3 in earthworm PH)

The family Ascaridiidae is monotypic containing a single genus *Ascaridia* (syn. *Cotylascaris*) of large roundworms which are commonly found in the intestines of birds, especially Galliformes. Around 40 species have been described, some in association with significant diseases in domestic poultry and aviary birds. The parasites have direct monoxenous life-cycles involving faecal-oral transmission of eggs shed into the environment. Infections are more prevalent in tropical and subtropical regions than in temperate regions as eggs are unable to develop to the infectious stage at temperatures under 15°C. Several species are also thought to utilize invertebrates (earthworms) as paratenic (transport) hosts containing larvae hatched from ingested eggs (the larvae do not undergo further development in these hosts).

***Ascaridia* species**	**Definitive Hosts [plus Paratenic Hosts (PH)]**	**Location [Clinical signs]**	**Distribution**
Avian hosts			
A. aegyptiaca	Pelecaniformes: ardeid (little egret)		Europe
A. alectoris	Galliformes: phasianid (chicken, rock partridge)		Europe
A. bonasae	Galliformes: phasianid (ruffed grouse)		North America
A. calcarata	Galliformes: numidid (helmeted guineafowl)		Africa
A. centropusi	Cuculiformes: cuculid (greater coucal)		India
A. columbae	Columbiformes: columbid (domestic pigeon, thick-billed green pigeon, pin-tailed green pigeon, hill pigeon, rock dove, mourning dove, white-winged dove, Eurasian collared dove, Oriental turtle dove, Barbary dove); Galliformes: phasianid (chicken, Caucasian chukar partridge, common pheasant); Anseriformes: anatid (goose); Phoenicopteriformes: phoenicopterid (flamingo); Accipitriformes: accipitrid (cinereous vulture); Dasyuromorphia: thylacinid (Tasmanian tiger, extinct)	small intestines	worldwide
A. cristata	Gruiformes: gruid (grey-crowned crane, black-crowned crane, Sarus crane)		Africa, Asia
A. cuculina	Cuculiformes: cuculid (common cuckoo)		Russia
A. cylindrica	Galliformes: phasianid (black grouse, hazel grouse, western capercaillie, willow ptarmigan)		Russia
A. dissimilis	Galliformes: phasianid (chicken, wild turkey, domestic turkey, chukar, Caucasian chukar); Anseriformes: anatid (goose)	small intestines	worldwide
A. dolichocerca	Accipitriformes: accipitrid (Papuan harrier)		New Guinea
A. fasciata	Columbiformes: columbid (African green pigeon, coastal green-tailed pigeon)		Africa
A. francolina	Galliformes: phasianid (double-spurred spurfowl, Ahanta spurfowl)		Africa
A. galli (syn. *A. anseris, brasiliensis, compar, compressa, granulosa, hamia, lineata, magalhaesi, perspicillum, sinensis, styphlocerca*)	Galliformes: phasianid (chicken, red junglefowl, Indian peafowl, green peafowl, greater prairie chicken, domestic turkey, wild turkey, ocellated turkey, common pheasant, blood pheasant, silver pheasant, grey peacock-pheasant, grey partridge, red-legged partridge, rock partridge, eastern rock partridge, central rock partridge, chukar partridge, Caucasian chukar, Barbary partridge, Daurian partridge, hazel grouse, black grouse, Caucasian black grouse, ruffed grouse, sharp-tailed grouse, Siberian grouse, Caucasian grouse, common	small intestines, sometimes large intestines, stomach [anaemia, diarrhoea]	worldwide

	quail, northern bobwhite quail, Japanese quail, willow ptarmigan, rock ptarmigan, black-billed capercaillie, western capercaillie, black francolin, Himalayan snowcock, Temminck's tragopan), numidid (helmeted guineafowl); Anseriformes: anatid (domestic goose, greylag goose, domestic duck, mallard, muscovy, mottled duck, muscovy duck, common pochard, northern pintail, common scoter); Columbiformes: columbid (pigeon, rock dove, spotted dove, Eurasian collared-dove, ruddy quail-dove, Luzon bleeding-heart dove); Cuculiformes: cuculid (lesser coucal); Passeriformes: emberizid (yellowhammer), passerid (house sparrow), turdid (varied thrush, American robin); Pelecaniformes: ardeid (eastern cattle egret, Indian pond heron); Psittaciformes: psittacid (Alexandrine parrot); Accipitriformes: accipitrid (common buzzard); Strigiformes: strigid (Eurasian eagle-owl); Carnivora: felid (cat) [PH: Clitellata: lumbricid (earthworms, *Allolobophora calliginosa, chlorotica, Eisenia foetida, Nicodrilus calliginosus, roseus*)]		
A. geei	Galliformes: phasianid (chicken); Columbiformes: columbid (Oriental turtle dove)		Asia
A. hermaphrodita (syn. *A. pseudohermaphrodita, truncata*)	Psittaciformes: psittacid (white-eyed parakeet, white-eared parakeet, sun parakeet, scaly-headed parrot, yellow-crowned amazon, vinaceous-breasted amazon, hyacinth macaw), psittaculid (budgerigar); Columbiformes: columbid (Inca dove)		Americas, Australia
A. magnipapilla	Galliformes: phasianid (black grouse, western capercaillie)	small intestines	Russia
A. nepalensis	Galliformes: phasianid (Himalayan monal)		Asia
A. nicobarensis	Psittaciformes: psittacid (long-tailed parakeet)		Africa
A. numidae	Galliformes: numidid (vulturine guineafowl, helmeted guineafowl, crested guineafowl, plumed guineafowl); phasianid (rock partridge)	small intestines	Africa
A. ornata	Psittaciformes: psittacid (orange-winged amazon)		South America
A. orthocerca	Rheiformes: rheid (greater rhea)		South America
A. pagoti	Columbiformes: columbid (Madagascan green pigeon)		Madagascar
A. petrensa	Galliformes: phasianid (chukar partridge)		Eurasia
A. pintoi	Tinamiformes: tinamid (red-winged tinamou)		South America
A. platycerci	Psittaciformes: psittaculid (yellow-collared lovebird, rosy-faced lovebird, Fischer's lovebird, scarlet-chested parrot, red-rumped parrot, princess parrot, Australian king parrot, Australian ringneck parrot, rose-ringed parakeet, eastern rosella, budgerigar), cacatuid (yellow-crested cockatoo)		Australia
A. pterophora	Gruiformes: gruid (whooping crane)		North America
A. razia	Columbiformes: columbid (pigeon)		India
A. sergiomeirai	Psittaciformes: psittacid (white-eyed parakeet, scaly-breasted parrot); Galliformes: cracid (black-fronted piping guan)		South America
A. serrata	Galliformes: cracid (black-fronted piping guan, Trinidad piping guan)		South America
A. skrjabini	Galliformes: phasianid (Himalayan snowcock, Tibetan snowcock)		Asia
A. sprenti	Psittaciformes: psittaculid (eastern bluebonnet, red-winged parrot, red-rumped parrot, elegant parrot, turquoise parrot, scarlet-chested parrot, princess parrot, regent parrot, Australian ringneck parrot, Bourke's parrot)	small intestines	Australia
A. stroma	Gruiformes: gruid (common crane, blue crane, Demoiselle crane, Eurasian crane, Sarus crane)		Africa, Eurasia
A. struthionis	Struthioniformes: struthionid (common ostrich)		Africa
A. subequalis	Cuculiformes: cuculid (cuckoo)		Europe
A. trilabium	Cuculiformes: cuculid (greater coucal)		Asia
A. triloba	Pelecaniformes: threskiornithid (Madagascan ibis)		Madagascar
A. zelandica	Cuculiformes: cuculid (shining cuckoo)		New Zealand
Reptilian hosts			

A. francolina	Sauria: agamid (Oriental garden lizard)		Asia
A. frenatusi	Sauria: gekkonid (common house gecko)		Asia
A. japalurae	Sauria: agamid (Swinhoe's japalura)		Asia
Piscine hosts			
A. alatae	Siluriformes: clariid (walking catfish)		Asia
A. barbi	Cypriniformes: cyprinid (Niger barb)		Africa
A. ganpatii	Synbranchiformes: mastacembelid (zigzag eel)		Asia
A. seenghali	Siluriformes: bagrid (Gangetic mystus)		India

Parasite morphology: *Ascaridia* spp. form 3 morphologically-different stages during their development: eggs; larvae (4 sequential stages designated L1-L4); and adult worms. The ovoid-ellipsoidal eggs measuring 55-99 x 40-57 µm have convex sides and thick albuminous smooth eggshells. They are laid unembryonated containing a central single-celled morula. Excreted eggs embryonate to form first stage larvae (L1) which moult within the eggshell to form infective larvae. It is unsure as to how many moults occur within the egg, with many studies reporting one moult to form infective L2, and other studies reporting 2 moults to form infective L3. Newly hatched larvae measured 0.3-1.0 mm long and had simple mouths without lips, intestines with granular contents and tapering tails. Larvae recovered from the intestinal mucosa of their hosts (probably L3, and sometimes referred to as static or arrested larvae) were similar in morphology and considered small measuring up to 1mm in length. Larvae recovered later from the host gut content (probably L4, as sexual differentiation had begun) were larger measuring 1.6-3.0 mm long but growing rapidly to 6 mm over 1-2 weeks. These larvae had mouths with developing lips, a conspicuous nerve ring and oesophagus, and developing males had preanal swellings (the beginnings of the preanal sucker) on their sickle-shaped tails. Adults are large stout worms measuring 15-120 mm in length with cylindrical semitransparent creamy-white bodies tapering at both ends. They are bound by a tough cuticle with transverse striations and 2 small poorly-developed lateral alae (absent in a few species) but lack an anterior cuticular flange. They have an anterior triangular mouth surrounded by 3 large stout denticulate lips without interlabia, but with 2 conspicuous papillae (sensory organs) on the dorsal lip and one on each of the subventral lips. The oesophagus is slender and club-shaped but lacks a posterior bulb and the tail is conically pointed. Adult worms exhibit distinct sexual dimorphism, with female worms being considerably longer and more robust than males (20-120 mm cf. 15-80 mm). Mature females are didelphic with 2 ovaries and 2 uteri in an amphidelphic configuration (opposed) connected to a short vagina terminating in a midbody vulva. Females have a subterminal anus and straight blunt tails, sometimes ending in a caudal spine. Mature males have a conspicuous round-oval preanal sucker (0.2-0.3 x 0.15-0.2 mm) with a chitinous rim. They have curved pointed tails with 2 narrow smooth membranous caudal alae supported by 9-10 pairs of relatively large caudal papillae arranged longitudinally in various configurations (usually comprising 2-3 pairs pre-anal, 1-2 pairs adanal, 3-5 pairs postanal and 3 pairs subterminal). Males lack a gubernaculum but have 2 equal or subequal spicules ranging in length from 1-4 mm and usually expanded proximally.

Site of infection: Adult worms are found mainly in the small intestines (duodenum, jejunum) of their avian hosts, although adults of several species may occasionally migrate erratically up to the oesophagus, crop, or gizzard, out to the body cavity or liver, or down through the large intestines and cloaca (sometimes passed in host faeces) and entering the oviduct (sometimes infecting host eggs). Earlier larval stages develop within the intestinal mucosa but do not undertake any extra-intestinal migrations. Larvated eggs and freed larvae have also been detected in the intestines of invertebrate paratenic (transport) hosts (earthworms).

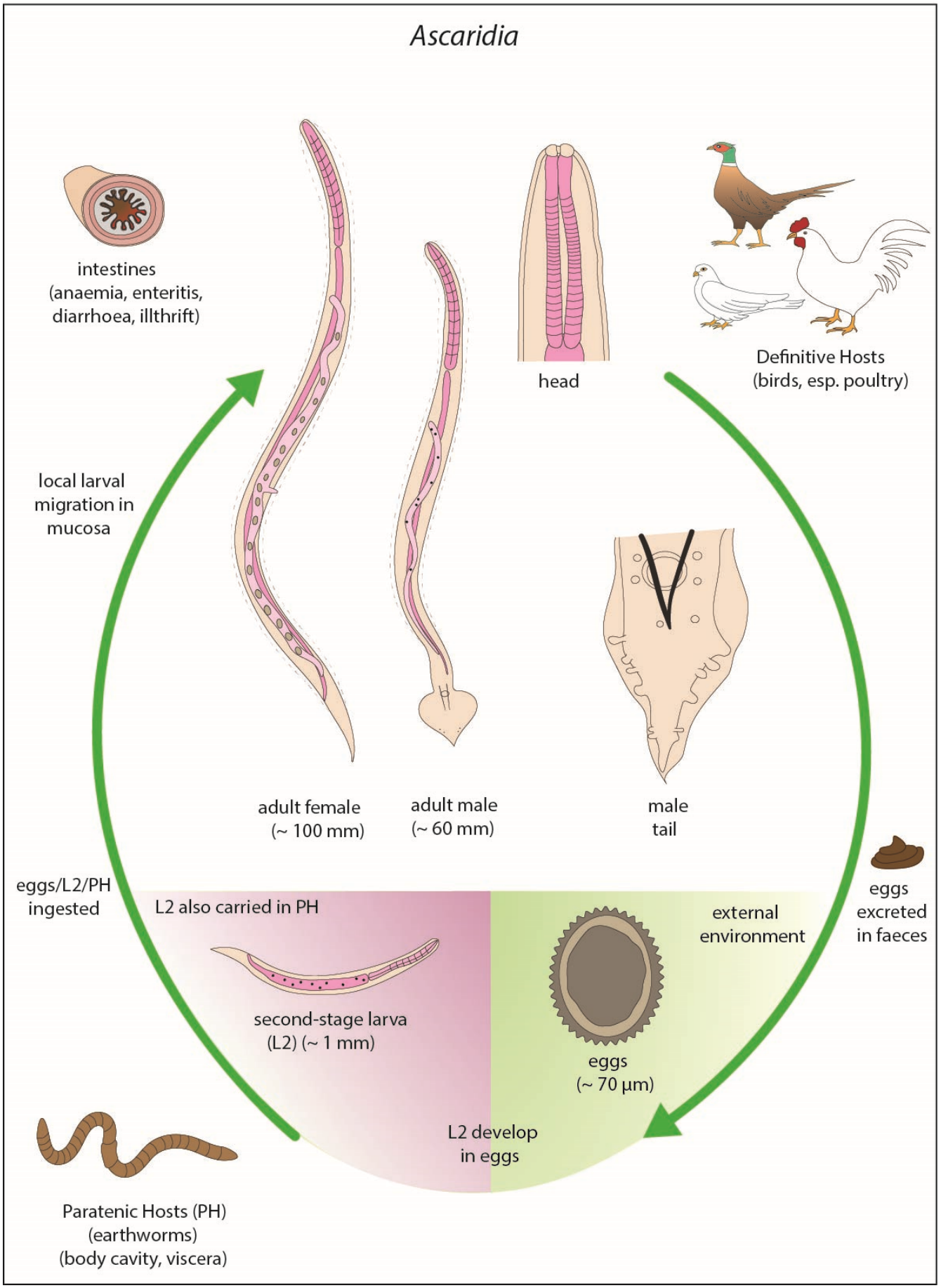
Pathogenesis: Most infections are light and remain subclinical, but heavy infections by *A. galli* in poultry are a major cause of ill-thrift with poor growth, weight depression and reduced egg production. Clinical disease (ascaridiosis) is more common in young birds (< 3 months old) as older animals acquire protective immune responses, but nonetheless may still act as asymptomatic carriers (larvae may sequester in mucosal tissues). Disease usually begins during the prepatent period when larvae invade the intestinal mucosa causing traumatic damage with petechial haemorrhages and provoking catarrhal (sometimes haemorrhagic) enteritis. The subsequent development of large adult worms in the lumen may cause pressure atrophy of villi with epithelial necrosis and villous adhesions. Aggregates or tangles of worms may cause intestinal blockages and aberrant migrations may cause lesions higher or lower in the alimentary tract and sometimes in the liver (fatty degeneration, coagulation necrosis, cellular infiltrations) and lungs (haemorrhages, haemosiderosis). Adult worms consume intestinal content and rob their hosts of proteins, carbohydrates, minerals (calcium, phosphorus) and vitamins (A, B1) contributing to hypoglycaemia, malnutrition, delayed growth and even rickets. It is also thought that parasite secretions/excretions may act as toxins causing metabolic disturbances and thymus atrophy. Clinical signs include intermittent diarrhoea, dehydration, enteritis, anaemia, anorexia, unthriftiness, stunted growth, loss of condition, weight loss, cachexia, emaciation, pica, adynamia, lethargy, listlessness, drooping wings, ruffled feathers, paresis and sudden death. In heavy infections, adult worms infect the oviducts of hens resulting in the production of misshapen eggs with thin soft shells, sometimes containing worms. Disease is worse in birds subject to stress, such as overcrowding, malnourishment (mineral and protein deficiencies), thirst, thermal discomfort, and some concomitant infections by other pathogens (including viruses, bacteria, protozoa and helminths).

Developmental cycle and mode of transmission: *Ascaridia* spp. have direct monoxenous life-cycles involving the faecal-oral transmission of eggs containing infective larvae, sometimes transported in invertebrate paratenic hosts. Female worms in the

intestines of their hosts lay unembryonated eggs which are excreted with faeces into the external environment. The eggs embryonate forming L1 which then moult inside the egg to form infective larvae (some reports state that 1 moult occurs to produce L2, while others say 2 moults occur to form L3). The time taken for larval development depends on prevailing conditions, generally taking 7-20 days in warm moist conditions, but longer in cooler conditions with little development occurring at temperatures under 15°C. The larvated eggs are highly resistant to desiccation and can persist in soil for months. Earthworms may also act as paratenic (transport) hosts carrying larvated eggs or released larvae in their intestines (but not in extraintestinal tissues). New final hosts become infected when they ingest eggs with infective larvae in contaminated food or water or by consuming infected earthworms. Ingested eggs hatch in the proventriculus or duodenum releasing infective larvae which do not undergo extensive somatic or hepato-pulmonary migration (while larvae may sometimes be found in the liver or lungs, experimental studies indicate they fail to develop further). Instead, many infective larvae undergo local transient histotrophic development (sometimes called tissue-phase or mucosa-phase) when they penetrate the mucosal lining. This phase is terminated when the larvae moult to the next stage (L3 or L4 depending on what stage was infective). It generally lasts for 3-16 days, but has been found to be extended up to 54 days or longer in heavily-infected or resistant hosts. It has been suggested that some larvae may arrest their development within the mucosa in response to developing host immune responses (explaining why older birds may carry latent infections). Eventually, the larvae emerge into the lumen of the small intestines where they complete their development to adults in 30-50 days. Other experimental studies have also demonstrated that some infective larvae may develop into adults without leaving the lumen, moulting to L4 in 6-9 days and to subadults (often referred to as L5) in 14-19 days. The prepatent period (time from infection to first egg excretion) is therefore quire variable, ranging from 28-70 days depending on the age of the birds and the site of adult development. Female worms are prolific egg layers and they have been found to live for over 1 year. Infections are more prevalent in poultry enterprises where birds are free-ranging or kept on deep litter, rather than confined to battery cages.

Differential diagnosis: Clinical infections may be indicated in susceptible birds exhibiting vague signs of illthrift, but other causative agents cannot be excluded. Occasionally, large worms may be excreted in host faeces or be found within thin-walled misshapen eggs. Infections are generally diagnosed, however, by the microscopic detection of worm eggs in faecal samples, either in wet mounts or smears but usually following their concentration by sedimentation in water and floatation in saturated sugar or heavy metal salt solutions (with high specific gravities). *Ascaridia* eggs are remarkably similar in appearance to those of *Heterakis,* both being thick-shelled and ellipsoidal, but those of *Ascaridia* are slightly larger and have convex sides rather than nearly parallel sides. Infections may also be detected at post-mortem by the detection of parasites (larvae and adult worms) in the intestinal contents, mucosal scrapings, squash preparations or tissue digests, particularly in areas with acute enteritis and sometimes chronic distention. Molecular biological techniques have been applied to the characterization of parasite species following the polymerase chain reaction (PCR) amplification of random amplified polymorphic DNA (RAPD) or restriction fragment length polymorphism (RFLP) analyses or sequencing of mitochondrial genes (particularly cytochrome c oxidase subunit 3, NADH dehydrogenase subunits 1 and 4).

Treatment and control: Clinical infections in poultry have been treated using a range of anthelmintic drugs, including tetrahydropyrimidines (pyrantel), benzimidazoles (mebendazole, flubendazole, albendazole, fenbendazole), imidazothiazoles (levamisole, tetramisole), diethylenediamines (piperazine) and macrocyclic lactones (ivermectin), with most drugs being effective against both immature and mature stages. Continuous in-feed medication with the aminoglycoside antibiotic hygromycin B has also been widely used to suppress infections in poultry. Most anthelmintics have little residual activity and are not long-lasting so birds require regular treatment as they may be readily re-infected. Control programmes must therefore also adopt preventive strategies designed to reduce parasite transmission, either by reducing contamination of the environment by infective stages or limiting their uptake by new susceptible hosts. Appropriate sanitary and hygienic practices include frequent litter removal, not using faeces as fertiliser in grazing areas, providing clean food and water, preventing the faecal contamination of feeding and watering devices (raising them off the ground), improving drainage, using insecticides to reduce potential paratenic host populations, raising birds on elevated platforms or hard surfaces, and regular cleaning of holding facilities and runs. While worm eggs are resistant to desiccation, they are susceptible to detergents and various plant extracts (such as bishkatali, neem, or papaya extracts impregnated into the litter). Bird management practices should avoid overcrowding and other stressors, use quarantine and isolation procedures particularly for new stock, separate cohorts especially young chickens from adults, exclude wild and feral birds from poultry facilities, and regularly rotate poultry runs, yards, pastures and sheds.

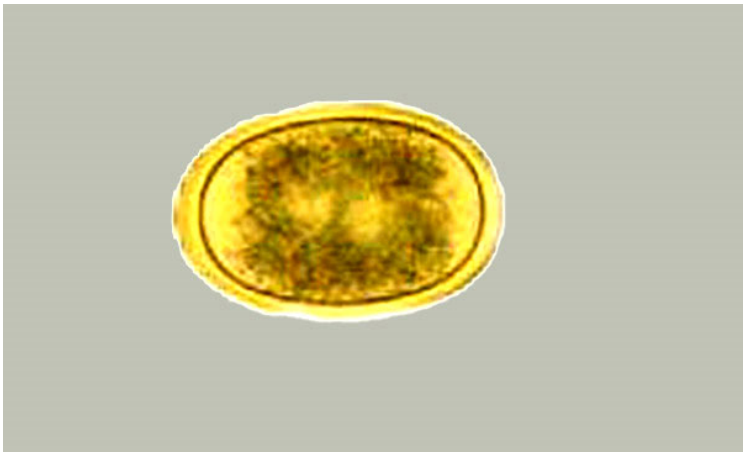

Ascaridia
intestines
(anaemia, enteritis,
diarrhoea, illthrift)
head
Definitive Hosts
(birds, esp. poultry)
local larval
migration in
mucosa
adult female
(~ 100 mm)
adult male
(~ 60 mm)
male
tail
eggs/L2/PH
ingested
L2 also carried in PH
external
environment
eggs
excreted
in faeces
second-stage larva
(L2) (~ 1 mm)
eggs
(~ 70 µm)
L2 develop
in eggs
Paratenic Hosts (PH)
(earthworms)
(body cavity, viscera)



Ascaridia adult worms



Ascaridia adult worms



Ascaridia worm egg



Ascaridia larva

Oxyuris
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Oxyuridomorpha which includes the oxyuroids (pinworms) characterised by their small tapering shape, pointed tails, oesophagus with a terminal bulb, and the males are non-bursate with a single spicule. They have simple direct life-cycles involving faecal-oral transmission of eggs containing infective larvae. The eggs may be passed in faeces or oviposited around the anus (perineum) where they are subsequently dislodged. Pinworms are common in the large intestines of many mammals, birds, reptiles, amphibians and some insects. Infections by *Oxyuris equi* causes perianal pruritus (itching) and restlessness in horses.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Oxyuridomorpha (small pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily:	Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Family:	Oxyuridae (direct cycle, females deposit sticky eggs around anus, infection by ingestion of egg)
Genus:	*Oxyuris* (parasitic in large intestines of horses)
Species:	*O. equi* (causes perianal pruritus in horses)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Oxyuridomorpha comprises the pinworms, unique microphagous nematodes with pointed tails, an oesophagus with a terminal bulb and the males having only a single spicule. Pinworms are conventionally classified in the order Oxyurida, the only major nematode group with adult representatives in either vertebrates or invertebrates. Two superfamilies are recognised: Oxyuroidea (parasites of the posterior gut of vertebrates (including mammals, birds and some reptiles) and Thelastomatoidea (parasites of invertebrates, especially herbivorous arthropods with a fermentation chamber (such as cockroaches, diplopods, orthopterans)). Members of the superfamily Oxyuroidea are distinguished by small nonbursate males with reduced numbers of caudal papillae and females with complex ovejectors producing thin-shelled eggs flattened on one side. The parasites have monoxenous transmission cycles whereby unembryonated eggs are passed into the environment with host faeces or gravid females migrate to the anus and deposit eggs in the perianal region. Three families are recognised: Oxyuridae (amphids non-pedunculate, genital cone without sclerotized supporting structure, male tail irregular, often bluntly truncate with or without dorsal point, sometimes with large digitiform papillae extending into caudal alae, parasitic in mammals and rarely birds); Pharyngodonidae (amphids pedunculate, genital cone supported by V-shaped sclerotized structure, parasitic in lower cold-blooded vertebrates, and a few in archaic mammals); and Heteroxynematidae (amphids non-pedunculate, genital cone without sclerotized supporting structure, male tail regular, conical or flattened dorsoventrally, parasitic in mammals and birds).

The family Oxyuridae contains 25 genera classified into 3 subfamilies: Oxyurinae (short oesophagus, male tail short with broad alae supported by long narrow papillae, single spicule, *Austroxyuris*, *Paraustroxyuris*, *Macropoxyuris* and *Potoroxyuris* in Australian marsupials, *Auchenacantha* in Dermoptera, *Citellina* in sciurids, *Hoplodontophorus* in hyracoids, *Oxyuris* in perissodactyls and *Skrjabinema* in artiodactyls); Syphaciinae (male gubernaculum with hook, area rugosa with parallel transverse grooves, well-developed caudal appendix, 5 tribes: Syphaciini (*Syphacia* (incl. subgenera *Syphacia*, *Seuratoxyuris*, *Cricetoxyuris*, *Segienamsyphacia, Rumbaisyphacia*), *Syphatineria* (incl. subgenera *Syphatineria*, *Africanoxys*, *Quentenora*, *Orientoxys*), *Sypharista* (incl. subgenera *Sypharista*, *Petauxyuris*, *Quentinema*), *Syphabulea*); Hilgertini (*Hilgertia*, *Heteromyoxyuris*, *Rauschtineria*); Passulurini (*Passalurus*); Acanthyoxyurini (*Acanthoxyurus*, *Idiuoxyuris*, *Petronema, Zenkoxyuris*); and Protozoophagini

(*Protozoophaga*, *Helminthoxys*, *Wellcomia*); parasitic in rodents and lagomorphs); and Enterobiinae (sexual dimorphism of lateral alae (single-crested in males, double-crested in females), uterine tube with dividing diaphragm, *Enterobius* (incl. subgenera *Enterobius*, *Colobenterobius*), *Trypanoxyuris* (incl. subgenera *Trypanoxyuris*, *Hapaloxyuris*, *Paraoxyuronema*, *Rodentoxyuris*), *Lemuricola* (incl. subgenera *Lemuricola*, *Protenterobius*, *Madoxyuris*), *Xeroxyuris* in primates and sciurids). Representative pinworm genera of medical and veterinary significance are tabulated below:

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Family: Oxyuridae						
Subfamily: Oxyurinae						
Oxyuris (pinworm)	21	mammals, birds, reptiles	caecum, large intestines	1-16 cm long, oesophagus with terminal globular bulb, pin-tailed, eggs oviposited around anus	85-95 x 40-45 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Subfamily: Syphaciinae						
Passalurus (pinworm)	3	lagomorphs, rodents	large intestines	3-11 mm long, circular cuticular striations, oesophagus with terminal bulb, eggs passed in faeces	93-105 x 43-45 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Syphacia	88	rodents	large intestines	1-6 mm long, small cervical alae, oesophagus with terminal globular bulb, eggs oviposited around anus	72-153 x 25-55 µm, reniform, thin-shelled	ingestion of larvated eggs
Subfamily: Enterobiinae						
Enterobius pinworms	27	primates, rodents	large intestines	1-15 mm long, lateral alae, oesophagus with terminal bulb, slender pointed tails, eggs oviposited around anus	50-60 x 20-30 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Family: Heteroxynematidae						
Subfamily: Heteroxynematinae						
Aspiculuris	23	rodents	large intestines	2-5 mm long, prominent cervical alae, oesophagus with terminal oval bulb, eggs passed in faeces	70-98 x 29-50 µm, spindle-shaped, thin-shelled	ingestion of larvated eggs

The genus *Oxyuris* comprises pinworms whose buccal cavities have complex armature, non-pedunculate anterior amphids, oesophagi with posterior bulbs, males with irregular genital cones without sclerotized supporting structures, and females with long tapering pin-tails. Over 20 species have been described from the large intestines (caecum and colon) of vertebrates (mammals, birds, reptiles). They have direct monoxenous life-cycles whereby female worms migrate to the anus and attach eggs to the peri-anal skin which subsequently drop off to contaminate the environment. Few species have been associated with clinical disease, although *O. equi* commonly found in horses worldwide may cause intense peri-anal pruritus with loss of condition.

***Oxyuris* species**	**Definitive hosts**	**Location [Clinical signs]**	**Distribution**
O. acutissima	Rodentia: sciurid (red squirrel)		Eurasia
O. alata	Carnivora: mustelid (European badger)		Europe
O. ambiguus (= *Passalurus*)	Lagomorpha: leporid (rabbit)		worldwide
O. armata	Sauria: lacertid (common wall lizard)		Europe
O. bicristata (syn. *Trypanoxyuris*) (= *Rodentoxyuris*)	Rodentia: sciurid (fox squirrel, New World flying squirrel)		North America
O. caudata	Pterocliformes: pteroclid (Namaqua sandgrouse)		Africa
O. equi (syn. *O. curvula*) (equine pinworm)	Perissodactyla: equid (horse, Przewalski's horse, Polish konik horse, donkey, mule, onager, plains zebra, Grant's zebra), giraffid (Angolan giraffe); Primates: hominid (human)	caecum, colon [perianal pruritus]	worldwide
O. flagellum	Hyracoidea: procaviid (rock hyrax)		Europe
O. inflata	Testudines: testudinid (Greek tortoise); Pterocliformes: pteroclid (banded sand-grouse)		Europe
O. karamoja	Perissodactyla: rhinocerotid (white rhinoceros,		Africa

	black rhinoceros)		
O. lobata	Testudines: testudinid (tent tortoise)		Africa
O. lunata	Testudines: testudinid (tent tortoise)		Africa
O. magnavulvaris (= *Thelandros*)	Urodela: plethodontid (green salamander, black salamander)	large intestines	North America
O. megaloon	Sauria: gekkonid (Leschenault's leaf gecko)		Asia
O. obvelata	Rodentia: murid (black rat)		
O. opisthogonima	Testudines: testudinid (tent tortoise)		Africa
O. paradoxa	Carnivora: mustelid (European polecat)		Europe
O. parallela (syn. *O. polyoon, Enterobius*) (now *Xeroxyuris*)	Rodentia: sciurid (Cape ground squirrel)		Africa
O. perarmata	Testudines: testudinid (tent tortoise)		Africa
O. praeputialis	Anura: bufonid (toad)		
O. pugio	Hyracoidea: procaviid (rock hyrax)		Europe
O. semilanceolata	Rodentia: murid (mouse)		
O. sumatrensis	Diplopoda: platyrhacid (millipede)		
O. tenuicauda	Perissodactyla: equid (Crawshay's zebra)		Africa

Parasite morphology: *Oxyuris* spp. form 3 different types of developmental stages: namely, eggs, larvae (4 consecutive stages encoded L1-L4); and adult worms. Eggs are ovoid but asymmetrical having one flattened side thus forming a D-shape. They range in size from 85-95 x 40-45 µm and have a white-yellow thin eggshell with a pseudo-operculum at one pole. When laid the eggs are partly embryonated containing a central gastrula stage. Larval development continues within the eggshell with the formation of first-stage larvae (L1) which moult twice to form infective L3. Following infection, eggs hatch releasing L3 which grow rapidly to 3-11 mm in length. L4 developing in host tissues measure from 5-10 mm long and have a large modified buccal capsule used to grasp mucosal tissue, an oesophagus with a well-developed posterior portion, and long tapering tails. Adults are large white-grey pinworms with stout cylindrical bodies (measuring from 1-16 cm in length) being thickened anteriorly and distinctly tapering posteriorly (pin-tailed). Worms are bound by a semi-transparent cuticle often with coarse transverse striations, and they have an anterior hexagonal mouth with 2 lateral lips, each with 2 sucker-like papillae. They also have non-pedunculate anterior amphids, a small buccal capsule armed with 3 bristle-like teeth at bottom, a short double bulbed oesophagus with a corpus, isthmus and posterior bulb with a valvular apparatus, and a subterminal anus/cloaca. Adult worms are sexually dimorphic, with males being much smaller than females (10-30 mm cf. 24-160 mm). Mature males have a truncated tail, often irregular in shape, with a pair of broad caudal alae supported by a pair of long narrow pedunculate papillae. The genital cone lacks sclerotized supporting structures and they do not have a gubernaculum but possess a single needle-shaped spicule 120-200 µm long. Mature females are didelphic with 2 ovaries and uteri connected to a common vulva opening anterior to the midbody. Females have thin tapering pointed pin-tails, either short (around a third of body length) or long (up to 3 times the body length in mature worms).

Site of infection: Adult worms live free within the large intestines of their hosts, with female worms often congregating in the rectum near the anus. Earlier larval stages undergo transient histotrophic development in the mucosa and crypts of the caecal and colon. There are no free-living larval stages, except for those that develop inside eggs in the external environment.

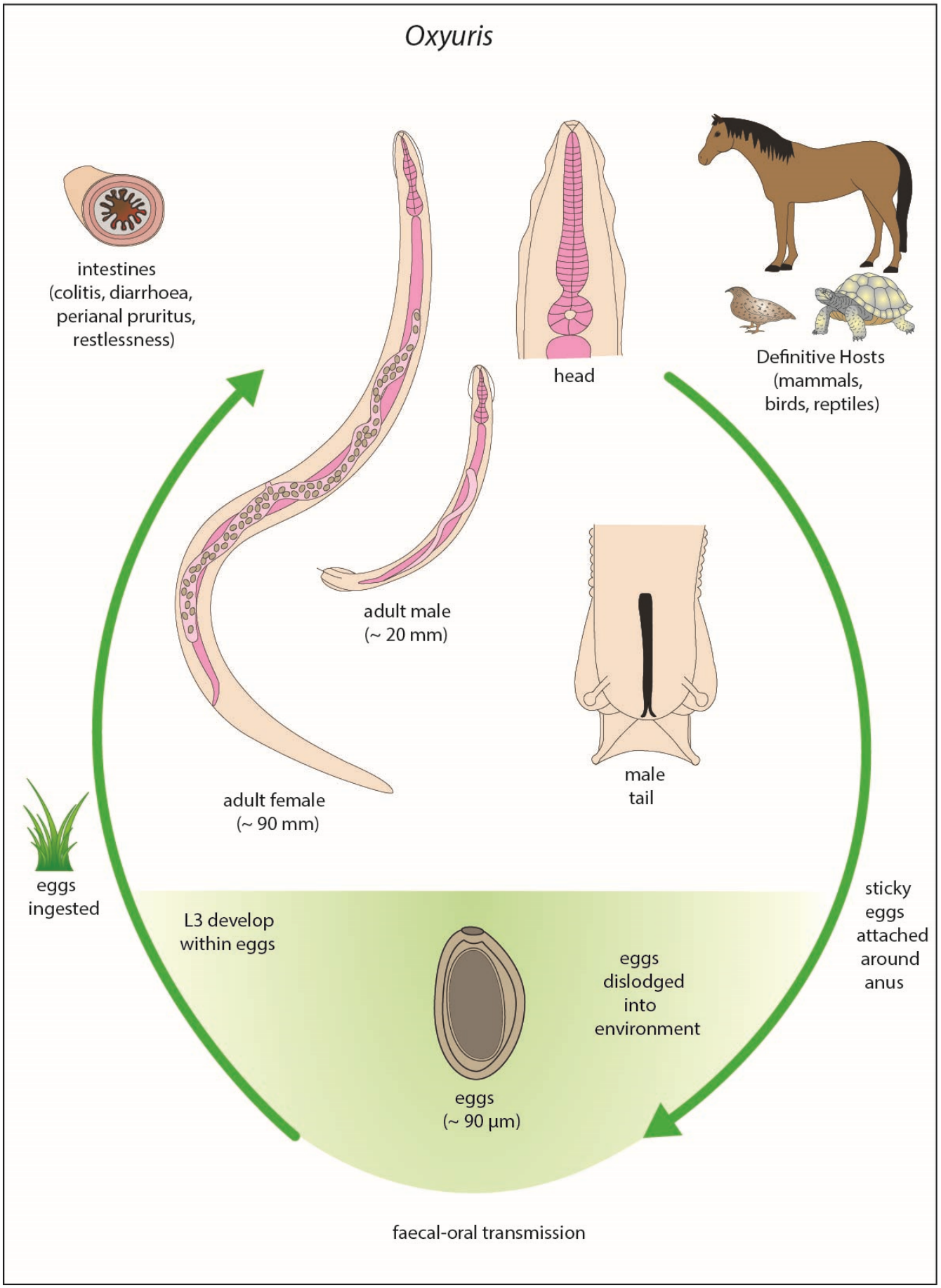
Pathogenesis: Most infections remain subclinical even though developing larvae feed on the gut mucosal lining and adult worms feed on gut content. Even in heavy infections, developing larvae only occasionally cause caecal and colonic inflammation, sometimes with mucosal erosion and ulceration leading to mild diarrhoea and secondary bacterial colonisation. Most of the pathogenesis associated with infections occurs when gravid female worms migrate out of the anus and deposit eggs on the perianal skin. Worm movement over mucosal surfaces may cause irritation resulting in catarrhal colitis and proctitis (becoming hyperplastic in chronic infections). In addition, the gelatinous cement-like substance used to attach eggs to the skin causes irritation and intense anal pruritus. Hosts become very restless and attempt to relieve the itch by rubbing their hindquarters and tails against solid substrates and objects (such as trees, fence posts and stable walls) often causing hair loss, bare patches of skin with erythematous and haemorrhagic dermatitis, and broken skin with scales and crusts (condition known as rat-tail in horses). Hosts are predisposed to secondary bacterial infections through wounds resulting in further irritation and restlessness. Hosts are distracted from feeding and may develop anorexia, dull coats and progressively lose body condition. Infections in horses occur in weaned foals, yearlings and adults, and there appears to be little immunity to re-infection, with heavy burdens sometimes developing with age. Most infections occur in stabled horses rather than those at pasture due to the heavier contamination of the local environment by worm eggs dropping from horses (rather than via faecal contamination).

Developmental cycle and mode of transmission: These pinworms have direct monoxenous life-cycles involving the shedding of worm eggs from the perianal skin of their hosts and their subsequent oral ingestion following embryonation and larval development. Gravid female worms migrate to the rectum and emerge headfirst through the anus laying eggs in clumps in a grey

viscous/gelatinous sticky substance that hardens on contact with air to form white-yellow streaks or crusts. Females are prolific and may produce up to 50,000 eggs, but they shrink as they oviposit and eventually pass out of the anus and die. The worms and their secretions cause intense pruritus which the host attempts to relieve by rubbing against substrates which causes the eggs to dislodge from the skin to contaminate the surrounding environment. In suitable warm moist conditions, the eggs embryonate and moult twice to enclose infective L3 within 3-7 days. Worm eggs are susceptible to desiccation but can survive in moist conditions for periods ranging from 9-10 weeks up to 6 months. Hosts become infected when they ingest larvated eggs in contaminated feed and water. Ingested eggs hatch in the small intestines releasing L3 which move to the large intestines and invade mucosa and crypts in the caecum and colon. They do not undertake any somatic or hepato-pulmonary migration, but do undergo transient histotrophic development in the mucosa for 3-11 days. They then moult to L4 which re-enter the lumen and migrate to the dorsal colon intermittently attaching and feeding on the mucosa. L4 moult to subadults (sometimes designated L5) in 45-60 days and the developing adults feed on intestinal content as they mature over 2-3 months. Fertilised female worms congregate in the rectum where they may live for up to 6 months periodically emerging from the anus to deposit eggs before becoming exhausted and dying. The prepatent period (time from infection to first deposition of eggs) ranges from 120-156 days in horses.

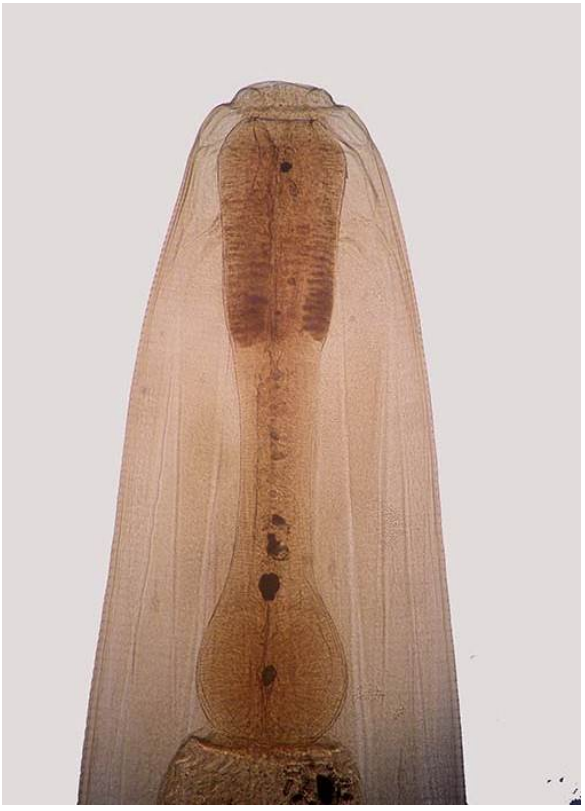
Differential diagnosis: Clinical infections are strongly indicated in equids exhibiting clinical signs of perianal pruritus, dermatitis and hair loss (development of rat-tail). Visual examination of affected areas often reveals white-yellow-grey streaks or crusts, and large white long-tailed female worms may be found in or on faeces, having become dislodged during defaecation. Infections are best confirmed by the microscopic detection of the characteristic D-shaped worm eggs. However, the eggs are rarely passed in faeces so most coprological techniques are not appropriate. Instead, the eggs may be captured on transparent adhesive sticky-tape first applied to the perineum and then stuck onto a glass slide for microscopy. Adult worms may also be detected at post-mortem by dissection of the large intestines and examination of the contents. Molecular biological techniques have been used mostly to examine parasite phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear genes (ribosomal RNA and internal transcribed spacers) and the complete mitochondrial genome (but particularly cytochrome oxidase 1 and cytochrome b genes).

Treatment and control: A range of anthelmintic drugs have been used to treat clinical infections, including benzimidazoles (thiabendazole, cambendazole, parbendazole, oxibendazole, mebendazole, fenbendazole, albendazole, oxfendazole), macrocyclic lactones (ivermectin, moxidectin, abamectin), diethylenediamines (piperazine), tetrahydropyrimidines (pyrantel) and organophosphonates (dichlorvos, trichlorfon), with most being effective against adult or larval pinworms but not eggs. Few anthelmintics have any long-lasting residual activity so repeated treatments are required to prevent re-infections. Various strategies should also be adopted to reduce parasite transmission, primarily by improving hygienic practices. Given that worm eggs are adherent to the host perineum and are then dislodged, maintaining good body hygiene by regular grooming or washing affected areas helps reduce environmental contamination, particularly when soiled litter and bedding are removed and disposed of in nongrazing areas. Holding facilities should be regularly cleansed, not only floors but also potential rubbing spots (walls, doors, rails and posts). Clean food and water should be provided in elevated feed boxes and water troughs that cannot be easily contaminated. Several attempts at biological control have reported variable success using nematophagous fungi (*Pochonia, Duddingtonia, Manacrosporium*) whose mycelial masses entrap worm eggs in soiled litter.


Oxyuris
intestines
(colitis, diarrhoea,
perianal pruritus,
restlessness)
head
Definitive Hosts
(mammals,
birds, reptiles)
adult male
(~ 20 mm)
adult female
(~ 90 mm)
male
tail
eggs
ingested
L3 develop
within eggs
eggs
(~ 90 µm)
eggs
dislodged
into
environment
sticky
eggs
attached
around
anus
faecal-oral transmission



Oxyuris adult worm



Oxyuris adult worm, head

Enterobius
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Oxyuridomorpha which includes the oxyuroids (pinworms) characterised by their small tapering shape, pointed tails, oesophagus with a terminal bulb, and the males are non-bursate with a single spicule. They have simple direct life-cycles involving faecal-oral transmission of eggs containing infective larvae. The eggs may be passed in faeces or oviposited around the anus (perineum) where they are subsequently dislodged. Pinworms are common in the large intestines of many mammals, birds, reptiles, amphibians and some insects. Infections by *Enterobius vermicularis* cause perianal pruritus (itching), insomnia and irritability in humans, especially children.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Oxyuridomorpha (small pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily:	Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Family:	Oxyuridae (direct cycle, females deposit sticky eggs around anus, infection by ingestion of egg)
Genus:	*Enterobius* (parasitic in large intestines of mammals)
Species:	*E. vermicularis* (causes perianal pruritus (enterobiasis) in humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
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Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
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Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
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Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
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Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Oxyuridomorpha comprises the pinworms, unique microphagous nematodes with pointed tails, an oesophagus with a terminal bulb and the males having only a single spicule. Pinworms are conventionally classified in the order Oxyurida, the only major nematode group with adult representatives in either vertebrates or invertebrates. Two superfamilies are recognised: Oxyuroidea (parasites of the posterior gut of vertebrates (including mammals, birds and some reptiles) and Thelastomatoidea (parasites of invertebrates, especially herbivorous arthropods with a fermentation chamber (such as cockroaches, diplopods, orthopterans)). Members of the superfamily Oxyuroidea are distinguished by small nonbursate males with reduced numbers of caudal papillae and females with complex ovejectors producing thin-shelled eggs flattened on one side. The parasites have monoxenous transmission cycles whereby unembryonated eggs are passed into the environment with host faeces or gravid females migrate to the anus and deposit eggs in the perianal region. Three families are recognised: Oxyuridae (amphids non-pedunculate, genital cone without sclerotized supporting structure, male tail irregular, often bluntly truncate with or without dorsal point, sometimes with large digitiform papillae extending into caudal alae, parasitic in mammals and rarely birds); Pharyngodonidae (amphids pedunculate, genital cone supported by V-shaped sclerotized structure, parasitic in lower cold-blooded vertebrates, and a few in archaic mammals); and Heteroxynematidae (amphids non-pedunculate, genital cone without sclerotized supporting structure, male tail regular, conical or flattened dorsoventrally, parasitic in mammals and birds).

The family Oxyuridae contains 25 genera classified into 3 subfamilies: Oxyurinae (short oesophagus, male tail short with broad alae supported by long narrow papillae, single spicule, *Austroxyuris*, *Paraustroxyuris*, *Macropoxyuris* and *Potoroxyuris* in Australian marsupials, *Auchenacantha* in Dermoptera, *Citellina* in sciurids, *Hoplodontophorus* in hyracoids, *Oxyuris* in perissodactyls and *Skrjabinema* in artiodactyls); Syphaciinae (male gubernaculum with hook, area rugosa with parallel transverse grooves, well-developed caudal appendix, 5 tribes: Syphaciini (*Syphacia* (incl. subgenera *Syphacia*, *Seuratoxyuris*, *Cricetoxyuris*, *Segienamsyphacia, Rumbaisyphacia*), *Syphatineria* (incl. subgenera *Syphatineria*, *Africanoxys*, *Quentenora*, *Orientoxys*), *Sypharista* (incl. subgenera *Sypharista*, *Petauxyuris*, *Quentinema*), *Syphabulea*); Hilgertini (*Hilgertia*, *Heteromyoxyuris*, *Rauschtineria*); Passulurini (*Passalurus*); Acanthyoxyurini (*Acanthoxyurus*, *Idiuoxyuris*, *Petronema, Zenkoxyuris*); and Protozoophagini

(*Protozoophaga*, *Helminthoxys*, *Wellcomia*); parasitic in rodents and lagomorphs); and Enterobiinae (sexual dimorphism of lateral alae (single-crested in males, double-crested in females), uterine tube with dividing diaphragm, *Enterobius* (incl. subgenera *Enterobius*, *Colobenterobius*), *Trypanoxyuris* (incl. subgenera *Trypanoxyuris*, *Hapaloxyuris*, *Paraoxyuronema*, *Rodentoxyuris*), *Lemuricola* (incl. subgenera *Lemuricola*, *Protenterobius*, *Madoxyuris*), *Xeroxyuris* in primates and sciurids). Representative pinworm genera of medical and veterinary significance are tabulated below:

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Family: Oxyuridae						
Subfamily: Enterobiinae						
Enterobius pinworms	27	primates, rodents	large intestines	1-15 mm long, lateral alae, oesophagus with terminal bulb, slender pointed tails, eggs oviposited around anus	50-60 x 20-30 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Subfamily: Oxyurinae						
Oxyuris (pinworm)	21	mammals, birds, reptiles	caecum, large intestines	1-16 cm long, oesophagus with terminal globular bulb, pin-tailed, eggs oviposited around anus	85-95 x 40-45 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Subfamily: Syphaciinae						
Passalurus (pinworm)	3	lagomorphs, rodents	large intestines	3-11 mm long, circular cuticular striations, oesophagus with terminal bulb, eggs passed in faeces	93-105 x 43-45 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Syphacia	88	rodents	large intestines	1-6 mm long, small cervical alae, oesophagus with terminal globular bulb, eggs oviposited around anus	72-153 x 25-55 µm, reniform, thin-shelled	ingestion of larvated eggs
Family: Heteroxynematidae						
Subfamily: Heteroxynematinae						
Aspiculuris	23	rodents	large intestines	2-5 mm long, prominent cervical alae, oesophagus with terminal oval bulb, eggs passed in faeces	70-98 x 29-50 µm, spindle-shaped, thin-shelled	ingestion of larvated eggs

Pinworms belonging to the subfamily Enterobiinae have buccal apertures surrounded by 3 prominent lips, each partly covering a corresponding oesophageal tooth (triangular with a small sharp denticle). Adults worms have symmetrical lateral alae (longitudinal expansions of the cuticle running the length of the body) which exhibit sexual dimorphism (single-crested in males, double-crested in females). Some 50 pinworm species have been described from primates around the world, including several *Enterobius* spp. The genus *Enterobius* contains worms with simple buccal cavities and simple cephalic vesicles, cuticular thickenings (corresponding to cuticularized rings) not extending laterally, caudal appendix atrophied or absent, area rugosa without ventral crest, and a cuticular vagina directed posteriorly. Two subgenera are recognised: *E.* (*Enterobius*) (oesophageal teeth without superstructures, cuticularized rings joined with a small square sheet bearing 2 leaf-shaped ventral extensions, lateral alae arise immediately behind cephalic vesicle, female lateral alae with 2 longitudinal parallel crests, males with a short spicule) parasitic in cercopithecid, pongid and hominid primates; and *E.* (*Colobenterobius*) (oesophageal teeth with projections, cuticularized rings connected with a small square without leaf-shaped ventral extensions, lateral alae start behind level of oesophageal bulb, female lateral alae with single crest, males with a long spicule) parasitic in colobid primates. The species *E. vermicularis* is the most common worm found in humans worldwide, particularly in temperate regions. They are commonly found as group infections in children, in families and in institutions (where contact between individuals is high and hygiene may be low). They are estimated to infect from 400-1,000 million people worldwide, but few countries consider them to be of public health significance due to their low pathogenicity. Infections are more irritating than debilitating, causing embarrassment, low morbidity and rarely mortality. However, individual families often spend considerable time and money trying to rid themselves of infections. The species *E. gregorii* is generally indistinguishable from *E. vermicularis* and is considered by some to be a junior synonym, although male worms have smaller spicules. Numerous pinworm species have been described from a range of mammals, birds, reptiles, amphibians, insects and millipedes, but they appear to be highly host-specific. Curiously, dogs and cats do not become infected with pinworms so companion animals should never be considered as sources of human infection. Whilst *Enterobius* spp. are commonly known as pinworms (or seatworms), in some countries they are paradoxically called threadworms (a common name generally applied to *Strongyloides* spp.). This may cause great confusion when considering treatment options because the drugs used to treat these worms are different.

***Enterobius* species**	**Definitive hosts**	**Location [Clinical signs]**	**Distribution**
Subgenus *Enterobius*			
E. (*E.*) *anthropopitheci*	Primates: hominid (chimpanzee, bonobo)	large intestines	Japan, Africa

(chimpanzee pinworm)		[diarrhoea?]	
E. atelis (= *Trypanoxyuris*)	Primates: atelid (black-handed spider monkey)		Asia
E. (*E.*) *bipapillatus*	Primates: cercopithecid (African green monkey, grivet, rhesus macaque)		
E. (*E.*) *brevicauda*	Primates: cercopithecid (chacma baboon)		Africa
E. (*E.*) *buckleyi*	Primates: hominid (Bornean orangutan, Sumatran orangutan)	large intestines [diarrhoea?]	Asia
E. callithricis (= *Trypanoxyuris*)	Primates: callitrichid (common marmoset)		South America
E. (*E.*) *chabaudi*	Primates: cercopithecid (northern plains gray langur)		India
E. duplicidens (= *Paraoxyuronema*)	Primates: atelid (gray woolly monkey)		South America
E. (*E.*) *foecundus sp. inq.*	Primates: hominid (orangutan)		Asia
E. (*E.*) *gregorii* (now considered to be a synonym of *E. vermicularis*)	Primates: hominid (human, chimpanzee)	large intestines [perianal pruritus, insomnia, irritability, occasionally diarrhoea]	Europe, Africa, Asia
E. interlabiata	Primates: aotid (northern night monkey)		South America
E. lagothricis (= *Trypanoxyuris*)	Primates: atelid (gray woolly monkey)		South America
E. lemuris (= *Lemuricola*)	Primates: lemurid (black lemur, white-headed lemur)		Madagascar
E. (*E.*) *lerouxi*	Primates: hominid (western gorilla)		Africa
E. (*E.*) *macaci*	Primates: cercopithecid (rhesus macaque, Japanese macaque, Assam macaque, Taiwan rock macaque, crab-eating macaque, southern pig-tail macaque)	large intestines	Asia, North America
E. microon (= *Trypanoxyuris*)	Primates: aotid (three-striped night monkey)		South America
E. nycticebi (syn. *Lemuricola*)	Primates: cercopithecid (stump-tailed macaque), lorisid (pygmy slow loris)		Asia
E. parallela (syn. *E. polyoon*, *Oxyuris*) (now *Xeroxyuris*)	Rodentia: sciurid (Cape ground squirrel)		Africa
E. sciuri	Rodentia: sciurid (red squirrel, Abert's squirrel)		North America
E. (*E.*) *shriveri*	Primates: cercopithecid (rhesus macaque, southern pig-tail macaque, crab-eating macaque, African green monkey)	large intestines	Asia, North America
E. (*E.*) *simiae sp. inq.*	Primates: hominid (Sumatran orangutan)		Asia
E. (*E.*) *vermicularis* (human pinworm or seatworm) (syn. *Oxyuris*)	Primates: hominid (human, chimpanzee, orangutan), atelid (white-bellied spider monkey), cercopithecid (Arabian sacred baboon, mantled guereza, chacma baboon, crab-eating macaque?); [PH?: Diptera: muscid (house fly, *Musca domestica*)]	large intestines [perianal pruritus, insomnia, irritability, occasionally diarrhoea]	worldwide, esp. temperate zones
E. (*E.*) *yagoi*	Rodentia: murid (gray leaf-eared mouse)		South America
Subgenus *Colobenterobius*			
E. (*C.*) *colobis*	Primates: cercopithecid (ashy red colobus, Thollon's red colobus)	large intestine	Africa
E. (*C.*) *emodensis*	Primates: cercopithecid (Himalayan langur)		Asia
E. (*C.*) *entellus*	Primates: cercopithecid (northern plains gray langur)		Asia
E. (*C.*) *guerezae*	Primates: cercopithecid (mantled guereza)		Africa
E. (*C.*) *inglisi*	Primates: cercopithecid (*Colobus* sp.)		Africa
E. (*C.*) *longispiculum*	Primates: cercopithecid (dusky leaf monkey)		Asia
E. (*C.*) *paraguerezae*	Primates: cercopithecid (mantled guereza)		Africa
E. (*C.*) *pesteri*	Primates: cercopithecid (*Colobus* sp.)		Africa
E. (*C.*) *pitheci*	Primates: cercopithecid (capped langur)		Asia
E. (*C.*) *presbytis*	Primates: cercopithecid (Phayre's leaf monkey)		Asia
E. (*C.*) *pygatrichus*	Primates: cercopithecid (golden snub-nosed monkey)		Asia

E. (*C.*) *serratus*	Primates: cercopithecid (proboscis monkey)		Asia
E. (*C.*) *zakiri*	Primates: cercopithecid (northern plains gray langur)		Asia

Parasite morphology: These worms form three developmental stages: eggs, larvae and adults. The eggs are translucent, elongate-oval in shape, measure 50-60 µm in length by 20-30 µm in width, and are characteristically asymmetric about the long axis being distinctly flattened on one side (forming a D-shape). The eggs are bound by three distinct membranes (inner lipoidal embryonic membrane, middle hyaline chitinous layer and outer albuminous layer) and larvae develop rapidly within the eggs. Mature larvae freed from eggs are long and thin (measuring up to 140-150 µm in length) and are presumed to be third-stage larvae (L3) as they are infective. Adult worms appear as small white elongate spindle-shaped tubes with pointed tails (hence the name, pinworm). They have three lips surrounding the anterior mouth, a large oesophageal bulb, and a conspicuous anterior cuticular inflation (swollen head). Male worms are 1-5 x 0.2-0.6 mm in size, have a single spicule (100-140 µm long in *E. vermicularis*, 68-80 µm in *E. gregorii*), and their posterior ends are strongly curved ventrally and have 4 pairs of caudal papillae (1st and 4th pairs pedunculated and surrounded by cuticular thickenings). Female worms measure 8-15 x 0.3-0.6 mm in size, have a single-crested lateral ala (double-crested in *E. anthropopitheci*), pronounced slender pointed tails and bifurcate reproductive tracts with numerous characteristic eggs developing within the uteri. Adult worms of *E. anthropopitheci* are somewhat smaller (males 1-2 mm, females 3-5 mm).

Site of infection: Adult worms tend to congregate in the ileocaecal region of the gut where they attach to the mucosa, but they may wander throughout the intestines from the stomach to the rectum. Fertilised female worms migrate out through the anus and deposit eggs of the perianal skin.

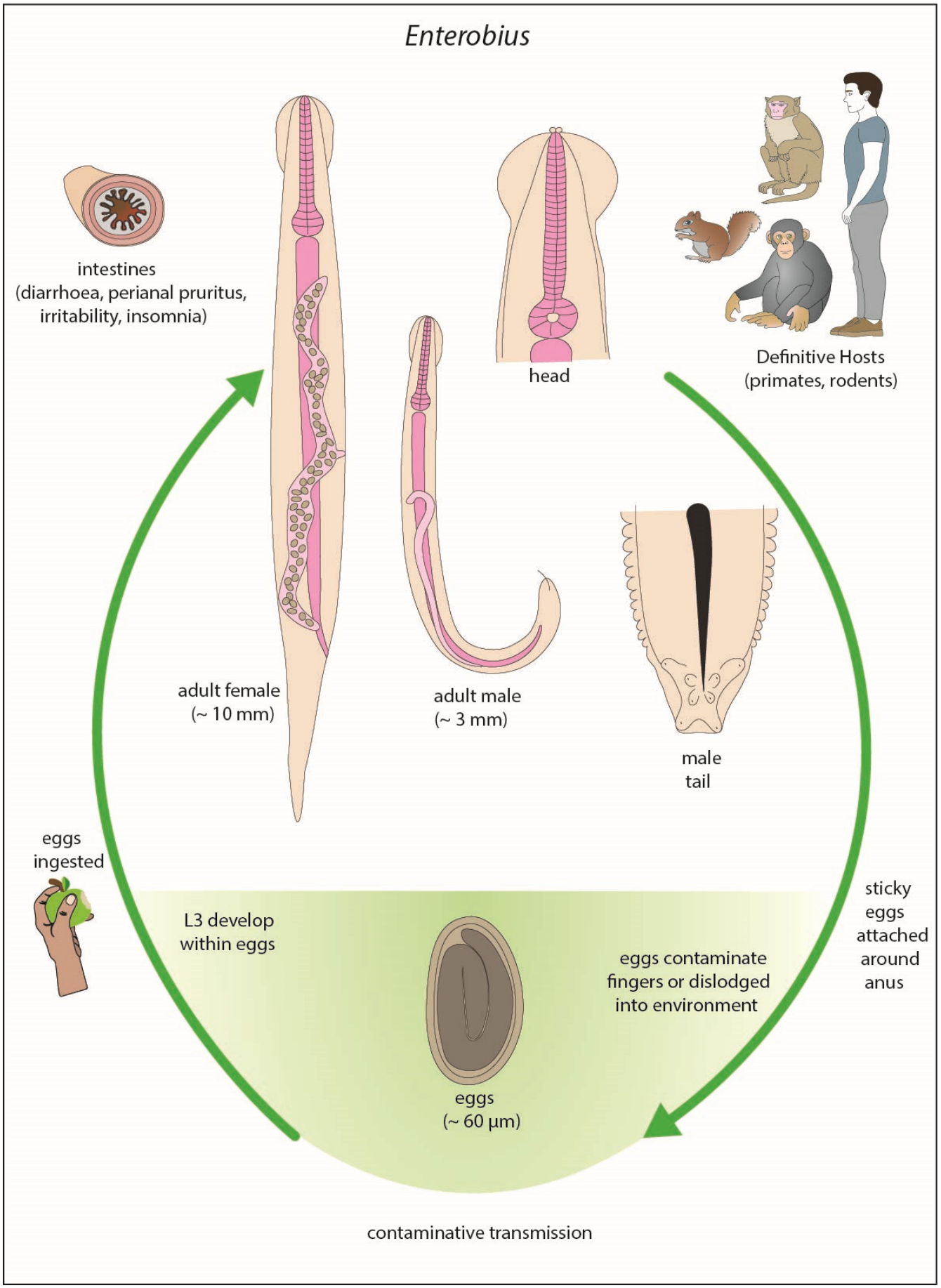
Pathogenesis: While many infections remain asymptomatic, worm burdens may increase with time resulting in damage to the intestines by adult worms and/or damage to the perineum resulting from egg deposition. Adult worms attach to the mucosa and feed on intestinal content, bacteria and possibly epithelial cells, causing minute ulcerations which may lead to mild catarrhal inflammation with diarrhoea, eosinophilia and bacterial infection. More commonly, however, infections are characterised by intense perianal itching (*pruritus ani*) caused by host sensations and reactions to female worms depositing sticky eggs on the skin (particularly overnight). Patients vigorously scratch themselves attempting to relieve the itching, but in doing so, often cause skin damage, excoriation, eczema, bleeding, bacterial dermatitis and folliculitis. Heavy infections in children may cause restlessness, irritability, hyperactivity, anorexia, weight loss, insomnia, nightmares, tooth grinding, incontinence (bed-wetting), perianal pain, nausea and vomiting. Occasionally, wandering worms have been associated with appendicitis, vaginitis, and rarely, extra-intestinal granulomas in ectopic sites. Risk factors for pinworm infection include finger sucking and poor hygiene often prominent in crowded group situations (such as nurseries, day-care centres, orphanages, hospitals and other institutionalized healthcare facilities). Infected families may suffer much shame and embarrassment (sometimes exaggerated into a syndrome known as pinworm neurosis) and they make huge efforts to rid themselves of infections.

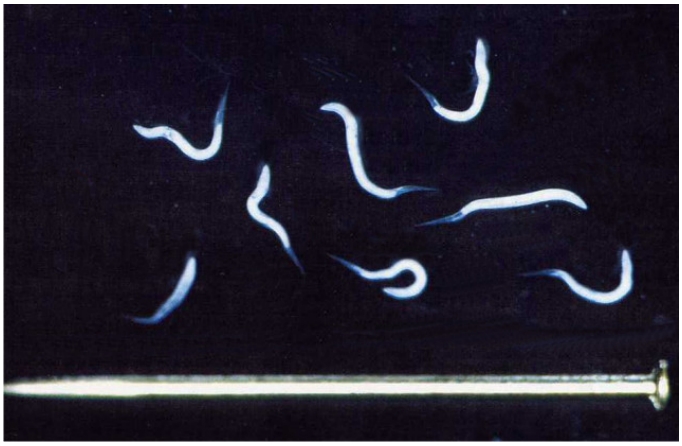
Developmental cycle and mode of transmission: Pinworms have direct life-cycles involving the oral ingestion of eggs containing infective larvae. The eggs, however, are usually not excreted with faecal material, but are attached to the perianal skin. Such transmission is therefore not strictly faecal-oral, but rather contaminative, involving the transfer of eggs to the mouth via host behaviours or inanimate objects. Infections are most prevalent in children, people in institutionalized settings and homosexuals. Gravid females migrate out through the anus onto the perineum, particularly during the night, and leave trails of eggs (up to 10,000) as they crawl about (up to 12 cm per hour). The female worms die after oviposition, whereas the males die soon after copulation. Freshly laid eggs are non-infectious but they rapidly embryonate to contain infective larvae (presumably L3) within 6 hours upon exposure to atmospheric oxygen at body temperature. The eggs are dislodged by host scratching and contaminate hands, bedding, clothing, toys, and furniture. They are very light and easily disseminated with house dust by the slightest of air currents. The embryonated eggs are resistant to putrefaction and disinfectants and may remain viable in cool moist conditions for up to 20 days but will succumb to desiccation in dry conditions within one day. Eggs may also be spread by passive carriage by flies, cockroaches and on the fur of pets. Following ingestion by human hosts (sometimes following inhalation), the eggs hatch in the small intestine and the larvae migrate to the large intestine and mature to adults over 2-6 weeks. Studies have shown worm development to involve haplodiploidy, whereby female worms are diploid and develop from fertilised eggs, whereas male worms are haploid and develop parthenogenetically (in this case, involving a unique process called arrhenotoky as the progeny are male rather than female). After copulation, gravid females migrate down the intestines and emerge from the anus to begin egg laying. Occasionally, eggs trapped in perianal folds may hatch and the larvae may enter the intestines directly via the anus (process called retro-infection). Infrequently, larvae may enter the vulva and infect the vagina of women. The prepatent period (time from infection to first production of eggs) ranges from 15-35 days and the parasite may complete its whole life-cycle in 2-13 weeks, with infections often becoming progressively heavier due to continual parasite uptake through auto-infection (both re-infection and retro-infection).

Differential diagnosis: Worm eggs are rarely found in faeces so conventional coprological examination techniques are not used. Instead, infections are best diagnosed by the macroscopic detection of adult worms or the microscopic detection of eggs on the

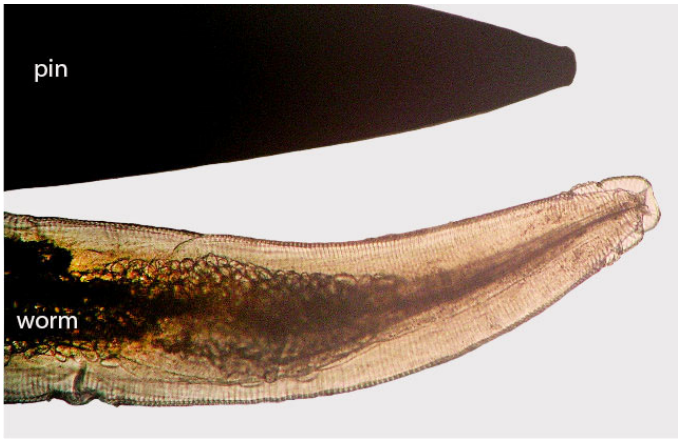
perineum. Motile worms may be seen on perianal skin glistening under bright light when close visual examinations are conducted during the night or early in the morning. Adult worms may sometimes be observed on the surface of fresh stool samples. Alternatively, sticky-tape may be quickly applied to the perianal skin first thing in the morning and then stuck onto a glass slide for microscopic examination of adherent eggs (aptly-named perianal sticky-tape test). Parents of infected children should be trained to collect appropriate samples to respect patient rights and privacy (especially involving minors) and alleviate any shame or embarrassment. Endoscopy (colonoscopy) has been used to detect infections by adult worms in large bowel compartments. More recently, molecular biological techniques using polymerase chain reactions (PCR) to amplify specific parasite gene sequences (mitochondrial cytochrome oxidase gene and nuclear ribosomal RNA genes) have been applied to the genetic characterization of various isolates from humans and chimpanzees from different geographic locations (the studies have confirmed their separate identities).

Treatment and control: Anthelmintic treatment for pinworm infections is readily available from most pharmacies. The drug of choice is mebendazole, although albendazole, levamisole, pyrantel and ivermectin are also effective. Piperazine has been used for many years but requires a longer course of treatment. Treatment should be repeated after about 10 days to kill any newly-acquired worms. It is advisable to institute whole group treatment where appropriate, so that other group, cohort or family members do not continue to act as sources of infection. To avoid constant re-infection, it is imperative that strict personal hygienic precautions are introduced, particularly frequent hand-washing and keeping fingernails clipped short. Household decontamination is difficult as infective eggs can survive for many days in cool moist house dust and for a few days on toys or furniture. Nonetheless, clothes, bed linen and towels should be laundered in hot water, dusty areas should be well vacuumed and potentially contaminated surfaces should be cleaned. While the eggs are very resistant to many disinfectants, they are susceptible to desiccation in dry sunny conditions. Infections are more prevalent in regions with temperate and cooler climates where there is reduced sun exposure and people wear heavier clothing which is laundered infrequently.

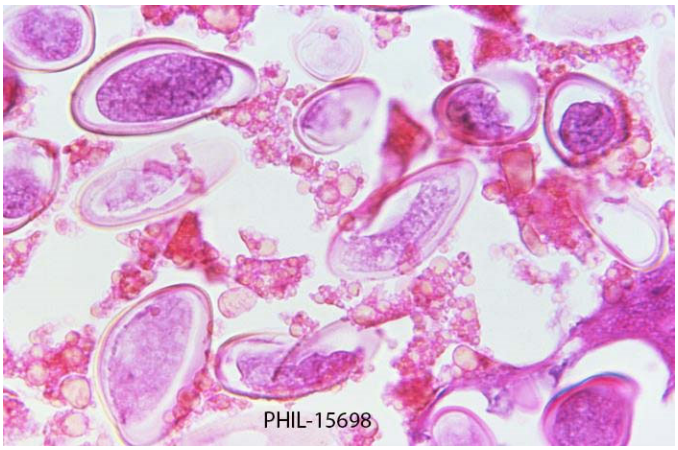

Enterobius
intestines
(diarrhoea, perianal pruritus, irritability, insomnia)
head
Definitive Hosts
(primates, rodents)
adult female
(~ 10 mm)
adult male
(~ 3 mm)
male
tail
eggs
ingested
L3 develop
within eggs
eggs
(~ 60 µm)
eggs contaminate
fingers or dislodged
into environment
sticky
eggs
attached
around
anus
contaminative transmission



Enterobius adult worms



Enterobius adult worm



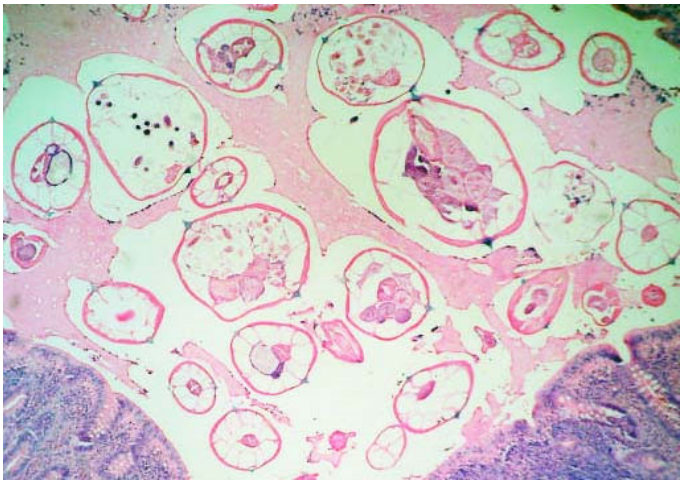
Enterobius worm eggs



Enterobius worm egg



Enterobius larva



Enterobius sections of worms in caecum

Passalurus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Oxyuridomorpha which includes the oxyuroids (pinworms) characterised by their small tapering shape, pointed tails, oesophagus with a terminal bulb, and the males are non-bursate with a single spicule. They have simple direct life-cycles involving faecal-oral transmission of eggs containing infective larvae. The eggs, however, are oviposited around the anus (perineum) where they are subsequently dislodged and ingested by their hosts. Pinworms are common in the large intestines of many mammals, birds, reptiles, amphibians and some insects. Infections by *Passalurus ambiguus* in rabbits are generally asymptomatic, but their presence in rabbit colonies can be problematic.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Oxyuridomorpha (small pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily:	Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Family:	Oxyuridae (direct cycle, females deposit sticky eggs around anus, infection by ingestion of egg)
Genus:	*Passalurus* (parasitic in large intestines of rabbits)
Species:	*P. ambiguus* (causes subclinical infections in rabbits)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
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Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Oxyuridomorpha comprises the pinworms, unique microphagous nematodes with pointed tails, an oesophagus with a terminal bulb and the males having only a single spicule. Pinworms are conventionally classified in the order Oxyurida, the only major nematode group with adult representatives in either vertebrates or invertebrates. Two superfamilies are recognised: Oxyuroidea (parasites of the posterior gut of vertebrates (including mammals, birds and some reptiles) and Thelastomatoidea (parasites of invertebrates, especially herbivorous arthropods with a fermentation chamber (such as cockroaches, diplopods, orthopterans)). Members of the superfamily Oxyuroidea are distinguished by small nonbursate males with reduced numbers of caudal papillae and females with complex ovejectors producing thin-shelled eggs flattened on one side. The parasites have monoxenous transmission cycles whereby unembryonated eggs are passed into the environment with host faeces or gravid females migrate to the anus and deposit eggs in the perianal region. Three families are recognised: Oxyuridae (amphids non-pedunculate, genital cone without sclerotized supporting structure, male tail irregular, often bluntly truncate with or without dorsal point, sometimes with large digitiform papillae extending into caudal alae, parasitic in mammals and rarely birds); Pharyngodonidae (amphids pedunculate, genital cone supported by V-shaped sclerotized structure, parasitic in lower cold-blooded vertebrates, and a few in archaic mammals); and Heteroxynematidae (amphids non-pedunculate, genital cone without sclerotized supporting structure, male tail regular, conical or flattened dorsoventrally, parasitic in mammals and birds).

The family Oxyuridae contains 25 genera classified into 3 subfamilies: Oxyurinae (short oesophagus, male tail short with broad alae supported by long narrow papillae, single spicule, *Austroxyuris*, *Paraustroxyuris*, *Macropoxyuris* and *Potoroxyuris* in Australian marsupials, *Auchenacantha* in Dermoptera, *Citellina* in sciurids, *Hoplodontophorus* in hyracoids, *Oxyuris* in perissodactyls and *Skrjabinema* in artiodactyls); Syphaciinae (male gubernaculum with hook, area rugosa with parallel transverse grooves, well-developed caudal appendix, 5 tribes: Syphaciini (*Syphacia* (incl. subgenera *Syphacia*, *Seuratoxyuris*, *Cricetoxyuris*, *Segienamsyphacia, Rumbaisyphacia*), *Syphatineria* (incl. subgenera *Syphatineria*, *Africanoxys*, *Quentenora*, *Orientoxys*), *Sypharista* (incl. subgenera *Sypharista*, *Petauxyuris*, *Quentinema*), *Syphabulea*); Hilgertini (*Hilgertia*, *Heteromyoxyuris*, *Rauschtineria*); Passulurini (*Passalurus*); Acanthyoxyurini (*Acanthoxyurus*, *Idiuoxyuris*, *Petronema, Zenkoxyuris*); and Protozoophagini

(*Protozoophaga*, *Helminthoxys*, *Wellcomia*); parasitic in rodents and lagomorphs); and Enterobiinae (sexual dimorphism of lateral alae (single-crested in males, double-crested in females), uterine tube with dividing diaphragm, *Enterobius* (incl. subgenera *Enterobius*, *Colobenterobius*), *Trypanoxyuris* (incl. subgenera *Trypanoxyuris*, *Hapaloxyuris*, *Paraoxyuronema*, *Rodentoxyuris*), *Lemuricola* (incl. subgenera *Lemuricola*, *Protenterobius*, *Madoxyuris*), *Xeroxyuris* in primates and sciurids). Representative pinworm genera of medical and veterinary significance are tabulated below:

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Family: Oxyuridae						
Subfamily: Syphaciinae						
Passalurus (pinworm)	3	lagomorphs, rodents	large intestines	3-11 mm long, circular cuticular striations, oesophagus with terminal bulb, eggs passed in faeces	93-105 x 43-45 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Syphacia	88	rodents	large intestines	1-6 mm long, small cervical alae, oesophagus with terminal globular bulb, eggs oviposited around anus	72-153 x 25-55 µm, reniform, thin-shelled	ingestion of larvated eggs
Subfamily: Oxyurinae						
Oxyuris (pinworm)	21	mammals, birds, reptiles	caecum, large intestines	1-16 cm long, oesophagus with terminal globular bulb, pin-tailed, eggs oviposited around anus	85-95 x 40-45 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Subfamily: Enterobiinae						
Enterobius pinworms	27	primates, rodents	large intestines	1-15 mm long, lateral alae, oesophagus with terminal bulb, slender pointed tails, eggs oviposited around anus	50-60 x 20-30 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Family: Heteroxynematidae						
Subfamily: Heteroxynematinae						
Aspiculuris	23	rodents	large intestines	2-5 mm long, prominent cervical alae, oesophagus with terminal oval bulb, eggs passed in faeces	70-98 x 29-50 µm, spindle-shaped, thin-shelled	ingestion of larvated eggs

The genus *Passalurus* contains only a few species of structurally-simple pinworms which are parasitic in the caecum and large intestines of leporid lagomorphs, and sometimes sciurid rodents. The parasites have direct monoxenous life-cycles involving the excretion of eggs into the external environment where they embryonate and are ingested when hosts feed (including auto-infection via coprophagy). Most infections in leporids are benign, even when high worm burdens develop, but their presence may compromise the microbiological integrity required of laboratory animal colonies.

***Passalurus* species**	**Definitive hosts**	**Location [Clinical signs]**	**Distribution**
P. abditus	Rodentia: sciurid (rock squirrel)		North America
P. ambiguus (syn. *Oxyuris ambigua*) (rabbit pinworm)	Lagomorpha: leporid (European rabbit, desert cottontail, antelope jackrabbit, black-tailed jackrabbit, European hare, Granada hare, Cape hare, mountain hare); Rodentia: sciurid (red squirrel); Carnivora: felid (cat); Primates: hominid (human)	caecum, colon	worldwide
P. nonannulatus	Lagomorpha: leporid (European rabbit, volcano rabbit, eastern cottontail, snowshoe hare)		North America

Parasite morphology: *Passalurus* spp. form 3 different types of developmental stages: eggs; larvae (4 successive stages designated L1-L4); and adult worms. The eggs are elongate measuring 93-105 x 43-45 µm and are asymmetrical being flattened on one side (forming a D-shape). They are thin-walled and have a pseudo-operculum at one pole. The eggs are laid unembryonated containing a single central gastrula stage but they quickly embryonate to form first-stage larvae (L1). Two larval moults occur within the egg resulting in the formation of infective L3 that measure up to 400 µm long. L4 are transient parasitic stages measuring 700-800 µm long and they have begun to develop genitalia. Adults are elongate cylindrical worms measuring from 3-11 mm in length and they are slightly thicker anteriorly. They are bound by a white semitransparent cuticle and have an anterior triangular mouth surrounded by 3 simple inconspicuous lips, 4 cephalic papillae arranged in a square and 2 lateral amphidia. They lack a distinct buccal capsule but have a unique club-shaped oesophagus with a well-developed posterior bulb with a tri-radiate valvular apparatus. Adult worms are sexually dimorphic, with females being larger than males (5-11 mm cf. 3-5 mm). Mature females have 2 ovaries and uteri

connected to a ventral ovejector apparatus and an anterior vulva surrounded by protruding lips. They are further characterised by having a long narrow tail (pin-tail) with prominent annular thickenings (up to 40 circular striations). Mature males have finely-pointed tails ending in a long spike, 2 caudal alae supported by a pair of papillae, 4 pairs of papillae surrounding the cloaca, and a single short spicule, often protruding (gubernaculum absent).

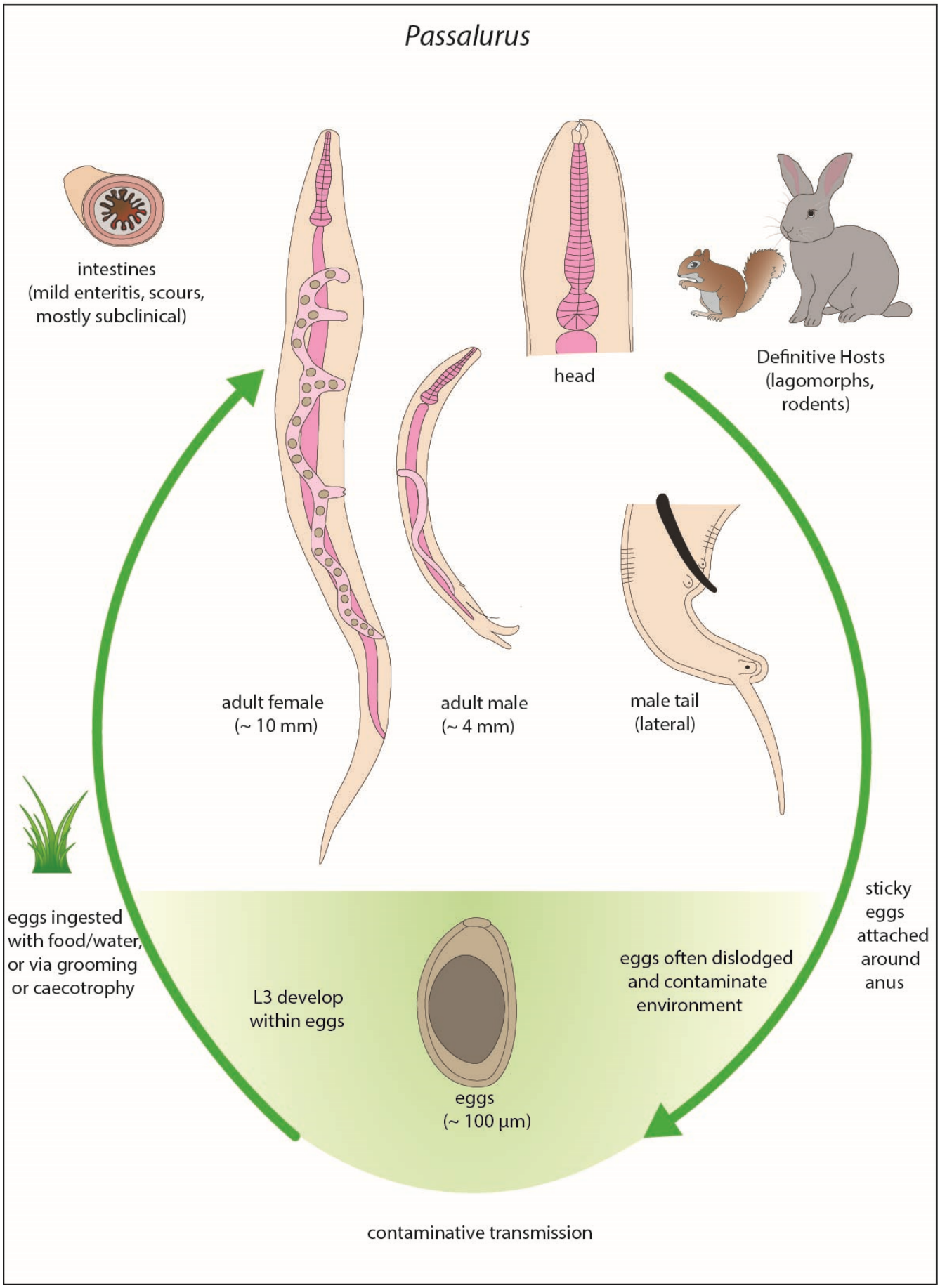
Site of infection: Adult worms live in the lumen of the caecum and colon of lagomorphs, while earlier larval stages develop in the mucosa of the small intestine and the caecum. The only stages contaminating the external environment are worm eggs, in which the first 3 larval stages develop.

Pathogenesis: Infections are generally considered to be benign, remaining asymptomatic or subclinical even when large worm burdens (>1,000) may be present. Some early workers mooted that this nematode may be a nonpathogenic commensal, a few even suggesting a symbiotic relationship with respect to plant digestion. However, *Passalurus* spp. are endoparasites living at the expense of the host. The early larval stages develop in the intestinal mucosa causing local inflammation, and the adult worms move about in the lumen feeding on intestinal content. The pathological consequences of infection are minimal, and clinical signs are infrequently reported. The detection of mucus threads in faeces may indicate intestinal infections, but should be differentiated from mucoid enteritis. Infections have been associated with a scouring syndrome observed around weaning, sometimes with anorexia and loss of body condition, but rarely with mortality. The movement of worms along the colon and the production of inflammatory metabolites is thought to overexcite local nerves leading to a pruritus and an itchy-scratchy syndrome (particularly of the perineum). Large worm populations are thought to sometimes cause intestinal stasis, caecal impaction, abdominal colicky pain, bloat (gas production) and rectal prolapse. On rare occasions, infections have been linked with intestinal granulomas, appendicitis and lymphadenitis. Normally, infections do not present problems in rabbit production, except when their presence compromises the microbiological and immunological integrity of laboratory animals required to be free of spurious infection (e.g. germ-free or specific-pathogen-free colonies).

Developmental cycle and mode of transmission: The parasites have direct monoxenous life-cycles usually involving the faecal-oral transmission of worm eggs contaminating food sources, but possibly also including their transmission via grooming or caecotrophy (coprophagy of soft pellets). Gravid female worms lay unembryonated eggs in the intestines where they undergo rapid development and are embryonated when excreted with faeces, often being contained in the mucus coating of faeces. Early studies suggested that female worms may also migrate to the anus and deposit eggs on the perianal skin, but subsequent studies indicated that oviposition outside the host was unusual for *Passalurus* spp. as any emergent worms quickly desiccated and died. In the external environment, L1 within the worm eggs moulted twice over 7-8 days to form infective L3 still contained within the eggshell. The eggs become very resistant to desiccation as they undergo larval development and may survive for months in mild conditions. Final hosts become infected when they ingest eggs containing infective L3 in contaminated food and water. Auto-infection also occurs during the unique process of caecotrophy exhibited by lagomorphs (night-time coprophagy of soft pellets rich in endosymbiotic microbes) or possibly during grooming of perianal areas. Ingested eggs hatch in the gut releasing L3 which burrow into the mucous layer and glandular crypts of the small intestine, caecum and colon where they moult twice over several days. Young adults emerge into the lumen by 11 days after infection where they slowly mature, mate and begin egg production. The prepatent period (time from infection to first excretion of eggs) ranges from 56-64 days, and adult worms were found to live for up to 106 days.

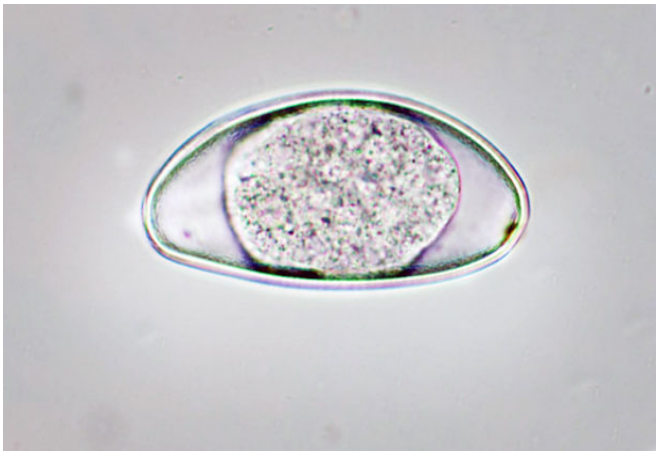
Differential diagnosis: Infections rarely cause any clinical signs, so diagnosis is based on the direct detection of parasites. Live adult worms can occasionally be detected by macroscopic (visual) examination of freshly excreted faeces, where they may be observed writhing slowly on the surface of faecal pellets. More conventionally, worm eggs are detected by the microscopic examination of faecal samples, usually following their concentration by faecal floatation, but sometimes following their recovery by sticky-tape impression smears taken around the anus. Infections may also be detected at post-mortem by examination of the large intestinal mucosa and contents. Molecular biological techniques have been used to characterize parasites and infer phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear genes (18S ribosomal RNA) and mitochondrial genes (cytochrome oxidase 1, cytochrome b).

Treatment and control: When chemotherapy is deemed necessary to treat atypical clinical infections or to rear worm-free laboratory animals, various anthelmintic drugs have proven useful, including benzimidazoles (fenbendazole, thiabendazole, mebendazole, oxibendazole) and diethylenediamines (piperazine). These drugs were effective against larval stages and adult worms but not against eggs, so multiple or sustained treatments were required (e.g. medications in feed or water). Several studies noted that the macrocyclic lactone, ivermectin, was not effective. Preventive control measures may be instituted in breeding and rearing facilities to break transmission cycles: mostly by reducing environmental contamination by worm eggs (regular removal of faeces and bedding, cleaning and disinfection of hutches, runs and hides) as well as limiting opportunities for their uptake (provision of clean food and water, avoid overcrowding, segregation of cohorts, quarantine and isolation procedures, and raising animals in cages).


Passalurus
intestines
(mild enteritis, scours,
mostly subclinical)
head
Definitive Hosts
(lagomorphs,
rodents)
adult female
(~ 10 mm)
adult male
(~ 4 mm)
male tail
(lateral)
eggs ingested
with food/water,
or via grooming
or caecotrophy
L3 develop
within eggs
eggs
(~ 100 µm)
eggs often dislodged
and contaminate
environment
sticky
eggs
attached
around
anus
contaminative transmission



Passalurus adult worm



Passalurus worm egg

Syphacia
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Oxyuridomorpha which includes the oxyuroids (pinworms) characterised by their small tapering shape, pointed tails, oesophagus with a terminal bulb, and the males are non-bursate with a single spicule. They have simple direct life-cycles involving faecal-oral transmission of eggs containing infective larvae. The eggs may be passed in faeces or oviposited around the anus (perineum) where they are subsequently dislodged. Pinworms are common in the large intestines of many mammals, birds, reptiles, amphibians and some insects. Infections by *Syphacia* in rodents are generally asymptomatic, but their presence in laboratory colonies can be problematic.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Oxyuridomorpha (small pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily:	Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Family:	Oxyuridae (direct cycle, females deposit sticky eggs around anus, infection by ingestion of egg)
Genus:	*Syphacia* (parasitic in large intestines of rodents)
Species:	*S. obvelata* (causes subclinical infections in mice)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
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Subfamily: Enterobiinae						
Enterobius pinworms	27	primates, rodents	large intestines	1-15 mm long, lateral alae, oesophagus with terminal bulb, slender pointed tails, eggs oviposited around anus	50-60 x 20-30 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Family: Heteroxynematidae						
Subfamily: Heteroxynematinae						
Aspiculuris	23	rodents	large intestines	2-5 mm long, prominent cervical alae, oesophagus with terminal oval bulb, eggs passed in faeces	70-98 x 29-50 µm, spindle-shaped, thin-shelled	ingestion of larvated eggs

The genus *Syphacia* contains pinworms with cuticularized cephalic plates around the mouth (round, quadrangular, oval, or laterally-elongated) in both sexes, lateral amphids, cephalic papillae not arranged in a square, cervical alae often present, ventral excretory pores and males with 2-4 ventral cuticular swellings. Over 80 species have been classified in 5 subgenera: *S.* (*Syphacia*) (oval cephalic plate, deirids not seen, accessory piece of gubernaculum without ornamentations); *S.* (*Seuratoxyuris*) (buccal ornamentation, deirids apparent, accessory piece of gubernaculum with ornamentations, short conical tail); *S.* (*Cricetoxyuris*) (quadrangular cephalic plate, well-developed lateral alae); *S.* (*Segienamsyphacia*) (oral aperture hexagonal in female); and *S.* (*Rumbaisyphacia*) (oral aperture not hexagonal, anterior margin of pharynx setiferous). *Syphacia* spp. are common pinworms found in the intestines of murid, cricetid and sciurid rodents and some lagomorphs throughout the world, often becoming nuisances in pet stores and laboratory animal colonies.

***Syphacia* species**	**Definitive hosts**	**Location [Clinical signs]**	**Distribution**
S. (*Syphacia*) *abertoni*	Rodentia: murid (common rock rat)	caecum	Australia
S. agraria	Rodentia: murid (striped field mouse, small Japanese field mouse, large Japanese field mouse, Himalayan field mouse, Korean field mouse), cricetid (tundra vole)		Asia
S. (*Syphacia*) *alata*	Rodentia: cricetid (hairy-tailed bolo mouse, Cana rice rat, black-footed pygmy rice rat)		South America
S. (*Syphacia*) *arctica*	Rodentia: cricetid (northern collared lemming)		Europe
S. arvicolae	Rodentia: cricetid (common vole, narrow-headed vole, tundra vole, European water vole)		Eurasia
S. (*Syphacia*) *australasiensis*	Rodentia: murid (Cape York rat)		Australasia
S. bonnei	Primates: atelid (Venezuelan red howler)		South America

S. (*Syphacia*) *boodjamullensis*	Rodentia: murid (common rock rat)	caecum	Australia
S. (*Cricetoxyuris*) *brachyuromyos*	Rodentia: nesomyid (Betsileo short-tailed rat)		Madagascar
S. (*Syphacia*) *brevicaudata*	Rodentia: murid (desert mouse)		Australasia
S. carlitosi	Rodentia: cricetid (Azara's grass mouse)		South America
S. caudibandata	Lagomorpha: leporid (common hare)		Asia
S. (*Syphacia*) *carnarvonensis*	Rodentia: murid (little native mouse)		Australia
S. cepapi	Rodentia: sciurid (Smith's bush squirrel)		Americas
S. citelli	Rodentia: sciurid (Wyoming ground squirrel, Richardson's ground squirrel, Townsend's ground squirrel)		North America
S. (*Syphacia*) *coccymyos*	Rodentia: murid (Rummler's brush mouse)		Asia
S. (*Syphacia*) *coli*	Rodentia: sciurid (Palawan flying squirrel), murid (Polynesian rat)		Asia
S. (*Seuratoxyuris*) *criteci*	Rodentia: cricetid (large vesper mouse, terraced rice rat, golden hamster), caviid (rock cavy)		Eurasia, Americas
S. (*Syphacia*) *critesi*	Rodentia: sciurid (Northern Palawan tree squirrel, Palawan flying squirrel)		Asia
S. (*Syphacia*) *darwini*	Rodentia: murid (Papua grassland mosaic-tailed rat)		Australia
S. (*Syphacia*) *emileromani*	Rodentia: murid (small Japanese field mouse, large Japanese field mouse, Korean field mouse, wood mouse)		Asia
S. eutamii	Rodentia: sciurid (yellow pine chipmunk, panamint chipmunk, Palmer's chipmunk)	caecum, large intestine	Americas
S. (Seuratoxyuris) evaginata	Rodentia: cricetid (marsh rice rat)		Asia
S. (*Syphacia*) *frederici*	Rodentia: murid (striped field mouse, small Japanese field mouse, large Japanese field mouse, Korean field mouse, wood mouse, yellow-necked mouse, herb field mouse, eastern broad-toothed field mouse), cricetid (tundra vole), dipodid (northern birch mouse)		Asia
S. funambuli	Rodentia: sciurid (northern palm squirrel)		Asia
S. guptae	Perciformes: trichiurid (smallhead hairtail)		Asia
S. (*Syphacia*) *helidonensis*	Rodentia: murid (eastern chestnut mouse)		Australia
S. hodarae	Rodentia: cricetid (small vesper mouse)	caecum, rectum	South America
S. (*Syphacia*) *insignis*	Rodentia: sciurid (three-striped ground squirrel)		Asia
S. (*Syphacia*) *kinsellai*	Rodentia: cricetid (black-footed pygmy rice rat)	caecum	Asia
S. (*Rumbaisyphacia*) *kumis*	Rodentia: murid (Sulawesi soft-furred rat)		Indonesia
S. laguri	Rodentia: cricetid (steppe lemming)		Eurasia
S. lahorea	Rodentia: sciurid (northern palm squirrel)		India
S. (*Syphacia*) *longaecauda*	Rodentia: murid (mountain mosaic-tailed rat)		New Guinea
S. (*Syphacia*) *lophuromyos*	Rodentia: murid (rusty-bellied brush-furred rat)		Africa
S. (*Syphacia*) *lorentzimyos*	Rodentia: murid (New Guinean jumping mouse)		New Guinea
S. (*Syphacia*) *magnispicula*	Rodentia: sciurid (Northern Palawan tree squirrel, Palawan flying squirrel)		Asia
S. (*Syphacia*) *mamelontenuis*	Rodentia: murid (New Guinean jumping mouse)		New Guinea
S. (*Syphacia*) *maxomyos*	Rodentia: murid (Whitehead's spiny rat, Musschenbroek's spiny rat)		Indonesia
S. (Seuratoxyuris) megadeiros	Rodentia: cricetid (Alfaria's rice rat, broad-footed climbing mouse)		South America
S. (*Syphacia*) *megaloon*	Rodentia: murid (mouse)		
S. (*Cricetoxyuris*) *mesocriceti*	Rodentia: cricetid (Chinese striped hamster, golden hamster, grey dwarf hamster)	caecum	Asia, North America
S. microtus	Rodentia: cricetid (common vole)		Eurasia

S. (*Syphacia*) *millardiae*	Rodentia: murid (soft-furred rat)		India
S. minuta	Rodentia: murid (eastern spiny mouse)		Asia
S. (*Syphacia*) *montana*	Rodentia: murid (yellow-necked mouse, Korean field mouse, wood mouse, Eurasian harvest mouse, yellow-spotted brush-furred rat), cricetid (muskrat, common vole, bank vole, field vole, reed vole, tundra vole, narrow-headed vole, Sikkim mountain vole, European pine vole, Hokkaido red-backed vole, Anderson's red-backed vole, grey red-backed vole, northern red-backed vole, Japanese grass vole, Smith's vole, Maximowicz's vole, wood lemming, Chinese striped hamster), dipodid (Mongolian five-toed jerboa, northern birch mouse), sciurid (red squirrel); Lagomorpha: ochotonid (Daurian pika); Carnivora: canid (red fox)		Eurasia
S. (*Syphacia*) *muris* (rat pinworm) (syn. *S. baylisi*, *ratti*)	Rodentia: murid (brown rat, black rat, white rat, yellow-tailed rat, rice field rat, lesser rice field rat, dusky field rat, pale field rat, bush rat, Polynesian rat, Alexandrine rat, Asian house rat, Indian house rat, African grass rat, Nile rat, small white-toothed rat, red spiny rat, Natal multimammate mouse, house mouse, lesser short-tailed gerbil); cricetid (northern red-backed vole, Maximowicz's vole): Eulipotyphla: soricid (giant musk shrew); Primates: hominid (human)	caecum, colon	worldwide
S. myopsi	Aulopiformes: synodontid (bluntnose lizardfish)		Atlantic
S. (*Syphacia*) *nigeriana*	Rodentia: cricetid (common vole, field vole, tundra vole, southwestern water vole, Mediterranean pine vole, Lusitanian pine vole, European water vole, European snow vole, Cabrera's vole, Gunther's vole), murid (Stella wood mouse		Eurasia, Africa
S. (*Syphacia*) *niobe*	Rodentia: murid (moss-forest rat)		Indonesia
S. (*Syphacia*) *obvelata* (mouse pinworm)	Rodentia: murid (house mouse, Ryukyu mouse, Cook's mouse, white mouse, striped field mouse, Korean field mouse, Eurasian harvest mouse, yellow-necked mouse, wood mouse, Algerian mouse, brown rat, black rat, white rat, Turkestan rat, Philippine black rat, Alexandrine rat, soft-furred rat, lesser bandicoot rat, midday jird, Shaw's jird, Tamarisk jird, Indian desert jird, Libyan jird, Mongolian gerbil, North African gerbil, lesser Egyptian gerbil, greater Egyptian gerbil, great gerbil, fat-tailed gerbil, Indian gerbil, lesser Egyptian jerboa, greater Egyptian jerboa, jerboa), sciurid (squirrel, ground squirrel, long-tailed ground squirrel, Daurian ground squirrel, flying squirrel, Siberian chipmunk), caviid (guinea pig), cricetid (muskrat, big-eared rat, common vole, bank vole, reed vole, Muisk vole, meadow vole, field vole, tundra vole, narrow-headed vole, grey red-backed vole, northern red-backed vole, large-eared vole, Mediterranean pine vole, Mogollon vole, Maximowicz's vole, Brandt's vole, wood lemming, Arctic lemming, Siberian brown lemming, Chinese striped hamster, winter white dwarf hamster); Eulipotyphla: soricid (common shrew, lesser white-toothed shrew, greater white-toothed shrew, Eurasian water shrew, Eurasian pygmy shrew, alpine shrew); Primates: hominid (human)	caecum, colon	worldwide
S. oceanica (syn. *Syphatineria*)	Rodentia: sciurid (Northern Palawan tree squirrel)		Asia
S. (*Syphacia*) *odilbainae*	Rodentia: murid (short-tailed cane mouse)		Asia
S. (*Syphacia*) *ohtaorum*	Rodentia: murid (Ryukyu mouse, Taiwan field mouse)		Asia
S. (*Cricetoxyuris*) *okuensis*	Rodentia: murid (Mount Oku rat)		Asia
S. oryzomyos	Rodentia: cricetid (marsh rice rat)		Americas
S. oschanensis	Rodentia: murid (Turkestan rat)	caecum	Russia
S. (Seuratoxyuris) pahangi	Rodentia: murid (Indo-Malayan pencil-tailed tree mouse, Chinese white-bellied rat)		Asia

S. pallaryi (syn. *Syphatineria*)	Rodentia: sciurid (Barbary ground squirrel)		Africa
S. (*Syphacia*) *paruromyos*	Rodentia: murid (Sulawesi giant rat)		Indonesia
S. paraxeri	Rodentia: sciurid (red bush squirrel)		Africa
S. pearsei (= *Syphatineria* (*Africanoxys*))	Rodentia: sciurid (red-legged sun squirrel, Gambian sun squirrel)	caecum	Africa
S. pennanti	Rodentia: sciurid (northern palm squirrel)		Asia
S. (Seuratoxyuris) peromysci (syn. *S. samorodini*)	Rodentia: cricetid (cotton mouse, white-footed mouse, deer mouse, Oldfield mouse, Florida mouse)		North America
S. (Seuratoxyuris) petrusewiczi	Rodentia: cricetid (common vole, bank vole, grey red-backed vole, northern red-backed vole, Japanese red-backed vole, Chinese striped hamster), murid (Eurasian harvest mouse)		Eurasia
S. (Seuratoxyuris) phyllotios	Rodentia: cricetid (Darwin's leaf-eared mouse)		South America
S. (*Syphacia*) *pseudomyos*	Rodentia: murid (sandy inland mouse)		Australia
S. quentini	Rodentia: cricetid (dusky rice rat)	caecum	South America
S. (*Cricetoxyuris*) *ramirohitra*	Rodentia: murid (gregarious short-tailed rat)		Asia
S. (Seuratoxyuris) rauschi	Rodentia: cricetid (northern red-backed vole)		Eurasia
S. (*Syphacia*) *rifaii*	Rodentia: murid (hill rat)		Indonesia
S. sarawakensis	Rodentia: sciurid (gray-cheeked flying squirrel)		Indonesia
S. sciuri	Rodentia: sciurid (Indian palm squirrel)		Asia
S. (*Syphacia*) *semiadii*	Rodentia: murid (spiny Boki Mekot rat)		Indonesia
S. sigmodoni (*sigmodontis*?)	Rodentia: cricetid (hispid cotton rat)		Americas
S. srtolana	Rodentia: cricetid (grey-red-backed vole)		Eurasia
S. srivastavi	Artiodactyla: suid (pig)	stomach	India
S. (*Syphacia*) *stroma*	Rodentia: murid (mouse, striped field mouse, alpine field mouse, Ural field mouse, eastern broad-toothed field mouse, wood mouse, yellow-necked mouse, Eurasian harvest mouse, yellow-spotted brush-furred rat, gerbil), cricetid (bank vole, field vole, reed vole, tundra vole, Maximowicz's vole, grey red-backed vole, northern red-backed vole, European water vole); Passeriformes: sturnid (common starling)		Eurasia
S. (Syphacia) sulawesiensis	Rodentia: murid (yellow-tailed rat)		Asia
S. (*Syphacia*) *taeromyos*	Rodentia: murid (Celebes rat)		Indonesia
S. thompsoni	Rodentia: sciurid (northern flying squirrel, southern flying squirrel, fox squirrel, red squirrel, American red squirrel, Caucasian squirrel)		North America
S. tineri	Rodentia: murid (brown rat)		India
S. toschevi	Rodentia: sciurid (red squirrel)		Eurasia
S. transafricana (= *Syphatineria*)	Rodentia: sciurid (striped ground squirrel, unstriped ground squirrel)		Africa
S. ungula	Rodentia: sciurid (red squirrel)		Europe
S. vandenbrueli	Rodentia: murid (Eurasian harvest mouse)		Eurasia
S. (*Syphacia*) *venteli*	Rodentia: cricetid (scaly-footed water rat), murid (Costa Rican dusky rat		South America
S. (*Segienamsyphacia*) *yuniae*	Rodentia: murid (Sulawesi soft-furred rat)		Indonesia

Parasite morphology: *Syphacia* spp. form 3 different types of morphological developmental stages: eggs; larvae (4 consecutive stages designated L1-L4); and adult worms. The eggs are asymmetrically ellipsoidal being flattened on one side and convex on the

other (variously described as reniform, crescentic, banana- or D-shaped). Collectively, the eggs range in size from 72-153 x 25-55 µm, with considerable variation between species (e.g. *S. muris* eggs measure 72-82 x 25-36 µm while *S. obvelata* eggs measure 118-153 x 33-55 µm). They are bound by thin double-walled eggshells with a small opercular cap near one end and they generally contain a developed larva (some *S. muris* eggs may contain a central morula). Little information is available on larval morphology as development from L1 to L3 occurs within the egg and L4 are transient endoparasitic stages in the host. L3 mechanically freed from eggs measured 140-220 µm in length. Adults are small white cylindrical pinworms measuring 1.1-6.0 mm long with narrow tapering tails containing irregular ridges. They are bound by a tough cuticle with transverse annulations (sometimes with interspersed longitudinal ridges), small cervical alae (prominent in male *S. obvelata* but inconspicuous in females, present in *S. muris* females but absent in males) and long lateral alae (absent on *S. obvelata* males) annulated in continuity with the body cuticle. The head is bulb-like and often inflated forming cephalic vesicles (absent in *S. muris*). The anterior end contains a cuticularized cephalic plate or cap (usually round but sometimes oval, square or laterally elongated) with a central mouth surrounded by 3 fleshy lips (without labial papillae), 4 cephalic papillae (not arranged in a square) and 2 lateral amphids. They have a small buccal cavity and a tripartite oesophagus with a prominent posterior globular/subglobular bulb with a triradiate valve-like apparatus. Adult worms are sexually dimorphic, with females being larger than males (e.g. 2.8-4.0 cf. 1.2-1.3 mm for *S. muris*, 3.4-6.0 cf. 1.1-1.6 mm for *S. obvelata*). Mature females have large uteri filled with eggs (often obscuring internal anatomy), a muscular ovejector and an anterior vulva that is either slit-like and guarded by 2 fleshy lips or tetraradiate and guarded by 4 lips. Mature males have a single testis connected to the posterior intestines and opening into a common cloaca. They have long pointed curved tails (without caudal alae), a gubernaculum (sometimes with an accessory hook) and a single long prominent spicule (absent in *Aspiculuris*). Males also have 2-4 conspicuous ventral cuticular protuberances (called mamelons) which are not regularly spaced between species (more posterior in *S. muris* than *S. obvelata*) and have different numbers of transverse striae (8-9 in *S. muris*, 10-12 in *S. obvelata*).

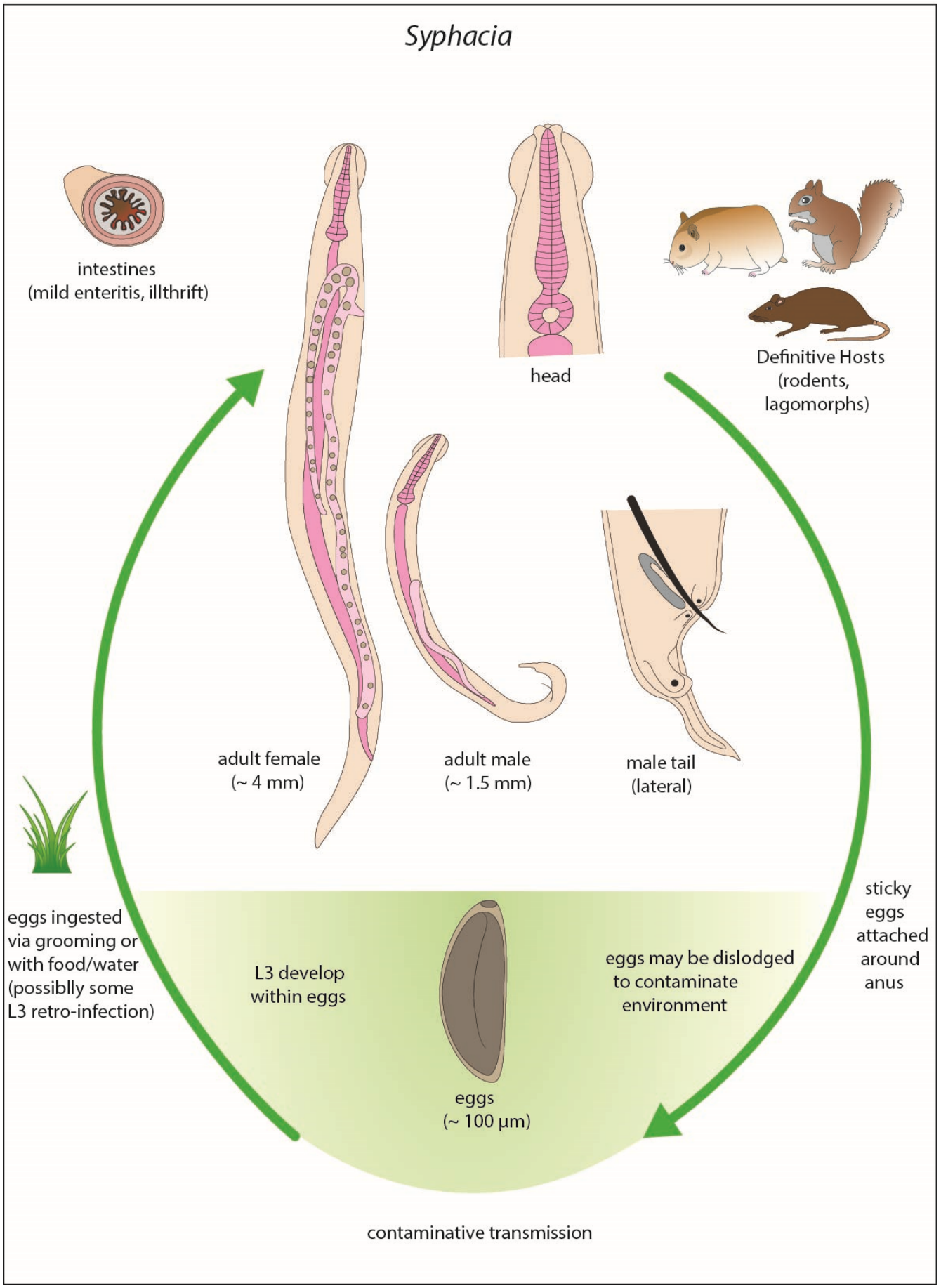
Site of infection: Endoparasitic stages (developing larvae and adult worms) mainly infect the caecum, and sometimes the colon, of their rodent hosts. Infective larvae develop within worm eggs contaminating the external environment.

Pathogenesis: Most infections remain asymptomatic as the parasites do not invade host tissues but feed in the lumen on intestinal content. Heavy infections have sometimes been associated with various inflammatory conditions (perianal irritation, mucoid enteritis) or intestinal perturbations (intestinal impaction, intussusception, rectal prolapse) contributing to unthriftiness (dull coat, depressed growth, loss of condition). The highest worm burdens are found in weaning animals, especially males. Mice develop an age resistance to infection around 4-9 weeks of age with immune expulsion of worms and the acquisition of protection against re-infection (apparently involving strong Th2 cellular responses). Some immunocompromised strains of mice are unable to clear parasites and develop chronic infections, but often without causing disease.

Developmental cycle and mode of transmission: *Syphacia* spp. have direct monoxenous life-cycles involving the ingestion of worm eggs containing infective larvae. Gravid females migrate from the caecum through the colon to the rectum and anus to deposit some 250-550 eggs in small groups or clumps on the perianal area before dying. Migrating adult worms are sometimes found in mucus covering faecal pellets. Eggs develop infective larvae within 5-20 hours of deposition and those dislodged into the external environment may survive for weeks in moderate conditions of temperature and humidity. Some parasite species also demonstrate distinct daily patterns of egg deposition: e.g. most *S. muris* eggs are laid during the daytime (circadian rhythm) when their nocturnally-active hosts are resting and grooming in burrows or nests. Rodents become infected when they ingest infective eggs either directly from the perianal region whilst grooming or less directly when they contaminate bedding, food or water. There are also some reports of auto-infection occurring by retro-infection when hatched larvae migrate through the anus into the colon. Ingested eggs hatch in small intestine releasing L3 which migrate to the caecum and develop within the lumen (larvae do not undergo local histotrophic development nor any somatic or extra-intestinal migration). L3 moult twice over 2-4 days to subadults (often called L5) which then mature over several days to adults. Fertilized females have been found as early as 5 days after infection, and migrating gravid females as early as 6-9 days. The prepatent period (time from infection to first egg deposition) ranges from 8-11 days for *S. muris* and 11-15 days form *S. obvelata.*

Differential diagnosis: Infections rarely produce any clinical signs although perianal irritation may be indicative. Worm eggs are usually detected by microscopic examination of sticky-tape impression smears collected from perianal regions. The eggs are characteristic in size and shape, having a distinctive asymmetrical D-shape (rather than being spindle-shaped like *Aspiculuris* eggs). Worm eggs have also been detected occasionally in anal swabs and faecal floats. Infections may also be diagnosed at post-mortem by the microscopic detection of adult worms in samples of caecal content placed in saline (pinworms usually migrate out of contents into saline over a short period) or by examination of fixed and stained histological sections. *Syphacia* spp. are more commonly found in the caecum while *Aspiculuris* spp. generally occur in the colon. A range of molecular biological techniques have been applied to the characterization of pinworm species by restriction fragment length polymorphism (RFLP) analyses, random amplified polymorphic DNA (RAPD) analyses and the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (ribosomal RNA and internal transcribed spacers) and mitochondrial genes (cytochrome c oxidase subunit 1).

Treatment and control: A wide range of chemicals have been used to treat pinworm infections in laboratory rodents, most as oral medications administered via food or water. Conventional anthelmintics, such as benzimidazoles (thiabendazole, fenbendazole), diethylenediamines (piperazine), organophosphonates (dichlorvos, trichlorfon, haloxon) and heterocyclic thiazines (phenothiazine), were effective against adult worms and larval stages but not eggs. Earlier studies reported some anthelmintic effects using cyanine dyes (pyrvinium), triarylmethane dyes (gentian violet, crystal violet), fluorides (sodium fluoride), iodides (stilbazium iodide), substituted dihydroxybenzene (hexylresorcinol) and halogenated hydrocarbons (carbon tetrachloride, tetrachloroethylene), while more recent studies showed that several antibiotics (terramycin, aureomycin, bacitracin, puromycin) reduced worm burdens. Regular or sustained treatments were required to prevent rapid re-infection in addition to thorough cleaning of animal holding facilities. Worm eggs have been found on cages, equipment, ventilation ducts and even dust in laboratory animal colonies, and the eggs are highly resistant to cold, desiccation and many disinfectants, but are susceptible to heat. Preventive strategies should therefore not only include the removal and disposal of host faeces and soiled bedding, but also the sterilization of cages and rooms preferably using steam-cleaning devices. Care should be taken to prevent the contamination of food and water supplies, and routine surveillance, quarantine and isolation procedures should also be implemented to detect and manage infections in rodent colonies, as they can be difficult to eradicate once entrenched.


Syphacia
intestines
(mild enteritis, illthrift)
head
Definitive Hosts
(rodents,
lagomorphs)
adult female
(~ 4 mm)
adult male
(~ 1.5 mm)
male tail
(lateral)
eggs ingested
via grooming or
with food/water
(possiblly some
L3 retro-infection)
L3 develop
within eggs
eggs
(~ 100 µm)
eggs may be dislodged
to contaminate
environment
sticky
eggs
attached
around
anus
contaminative transmission



Syphacia adult worm



Syphacia worm eggs



Syphacia adult worm, male tail



Syphacia adult worm, head

Aspiculuris
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Oxyuridomorpha which includes the oxyuroids (pinworms) characterised by their small tapering shape, pointed tails, oesophagus with a terminal bulb, and the males are non-bursate with a single spicule. They have simple direct life-cycles involving faecal-oral transmission of eggs containing infective larvae. The eggs may be passed in faeces or oviposited around the anus (perineum) where they are subsequently dislodged. Pinworms are common in the large intestines of many mammals, birds, reptiles, amphibians and some insects. While *Aspiculuris tetraptera* usually causes subclinical infections in mice, the parasites may still pose problems for the production of 'germ-free' laboratory animals.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Oxyuridomorpha (small pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily:	Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Family:	Heteroxynematidae (direct cycle, females deposit eggs in faeces, infection by ingestion of egg/larva)
Genus:	*Aspiculuris* (parasitic in large intestines of rodents)
Species:	*A. tetraptera* (causes subclinical infections in mice)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The infraorder Oxyuridomorpha comprises the pinworms, unique microphagous nematodes with pointed tails, an oesophagus with a terminal bulb and the males having only a single spicule. Pinworms are conventionally classified in the order Oxyurida, the only major nematode group with adult representatives in either vertebrates or invertebrates. Two superfamilies are recognised: Oxyuroidea (parasites of the posterior gut of vertebrates (including mammals, birds and some reptiles) and Thelastomatoidea (parasites of invertebrates, especially herbivorous arthropods with a fermentation chamber (such as cockroaches, diplopods, orthopterans)). Members of the superfamily Oxyuroidea are distinguished by small nonbursate males with reduced numbers of caudal papillae and females with complex ovejectors producing thin-shelled eggs flattened on one side. The parasites have monoxenous transmission cycles whereby unembryonated eggs are passed into the environment with host faeces or gravid females migrate to the anus and deposit eggs in the perianal region. Three families are recognised: Oxyuridae (amphids non-pedunculate, genital cone without sclerotized supporting structure, male tail irregular, often bluntly truncate with or without dorsal point, sometimes with large digitiform papillae extending into caudal alae, parasitic in mammals and rarely birds); Pharyngodonidae (amphids pedunculate, genital cone supported by V-shaped sclerotized structure, parasitic in lower cold-blooded vertebrates, and a few in archaic mammals); and Heteroxynematidae (amphids non-pedunculate, genital cone without sclerotized supporting structure, male tail regular, conical or flattened dorsoventrally, parasitic in mammals and birds).

The family Heteroxynematidae contains 2 subfamilies: Labiostominae (anal papillae grouped around anus, ovejector with glandular ring, thick-shelled egg with operculum, complex pharyngeal and buccal structures with lamellar extensions, parasites of lagomorphs); and Heteroxynematinae (last pair of male post-anal papillae near caudal extremity, glandular part of ovejector not ring-like, egg without operculum, simple pharyngeal and buccal structures, parasites of birds and rodents). The subfamily Heteroxynematinae contains 9 genera: *Aspiculuris* (*Aspicularis*), *Dentostomella, Dermatopallarya, Eudromoxyura, Fastigiuris, Heteroxynema, Rauschoxyuris,* and *Syphaciella.* Pinworm genera of medical and veterinary significance are tabulated below:

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Family: Heteroxynematidae						
Subfamily: Heteroxynematinae						
Aspiculuris	23	rodents	large intestines	2-5 mm long, prominent cervical alae, oesophagus with terminal oval bulb, eggs passed in faeces	70-98 x 29-50 µm, spindle-shaped, thin-shelled	ingestion of larvated eggs
Family: Oxyuridae						
Subfamily: Oxyurinae						
Oxyuris (pinworm)	21	mammals, birds, reptiles	caecum, large intestines	1-16 cm long, oesophagus with terminal globular bulb, pin-tailed, eggs oviposited around anus	85-95 x 40-45 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Subfamily: Syphaciinae						
Passalurus (pinworm)	3	lagomorphs, rodents	large intestines	3-11 mm long, circular cuticular striations, oesophagus with terminal bulb, eggs passed in faeces	93-105 x 43-45 µm, D-shaped, thin-shelled	ingestion of larvated eggs
Syphacia	86	rodents	large intestines	1-6 mm long, small cervical alae, oesophagus with terminal globular bulb, eggs oviposited around anus	72-153 x 25-55 µm, reniform, thin-shelled	ingestion of larvated eggs
Subfamily: Enterobiinae						
Enterobius pinworms	27	primates, rodents	large intestines	1-15 mm long, lateral alae, oesophagus with terminal bulb, slender pointed tails, eggs oviposited around anus	50-60 x 20-30 µm, D-shaped, thin-shelled	ingestion of larvated eggs

The genus *Aspiculuris* contains over 20 species reported from the large intestines of cricetid and murid rodents. Male worms are characterised by having 3 pairs of alae along their tails (precloacal, postcloacal and caudal). While earlier studies allocated some 9 species to 5 different subgenera: *A.* (*Aspiculuris*) (with cephalic bulb, cervical alae with sickle-shaped margins and not continuous with lateral alae), *A.* (*Paraspiculuris*) (with cephalic bulb, cervical alae with sickle-shaped margins and continuous with lateral alae), *A.* (*Pseudaspiculuris*) (with cephalic bulb, cervical alae without sickle-shaped margins and continuous with lateral alae), *A.* (*Anaspiculuris*) (with cephalic bulb, cervical alae with sickle-shaped margins, without lateral alae), *A.* (*Subaspiculuris*) (without cephalic bulb, cervical alae with sickle-shaped margins, without lateral alae), most workers now recognize 2 species groups: one group of 14 species with arrow-headed cervical alae; and another group of 6 species with spear-headed cervical alae. All species have direct monoxenous life-cycles involving the faecal-oral transmission of larvated eggs. The species *A. tetraptera* (commonly known as the mouse pinworm) has a worldwide distribution but rarely causes disease, although persistent infections can become a nuisance in pet stores and laboratory animal colonies.

***Aspiculuris* species**	**Definitive hosts**	**Location [Clinical signs]**	**Distribution**
A. ackerti (now *Lamotheoxyuris*)	Rodentia: cricetid (bushy-tailed woodrat, white-throated woodrat)	caecum, intestines	North America
A. africana	Rodentia: murid (Cairo spiny mouse)	intestines	Africa
A. (*Anaspiculuris*) *americana*	Rodentia: cricetid (cotton mouse, Florida mouse, white-footed mouse, deer mouse, rock mouse)	intestines	North America
A. arianica sp. inq.	Rodentia: sciurid (long-tailed marmot)	intestines	Asia
A. artigasi	Rodentia: murid (house mouse)	intestines	South America
A. aserbaidjanica	Rodentia: murid (wood mouse), cricetid (common vole, European snow vole)	intestines	Europe, Africa
A. (*Pseudaspiculuris*) *asiatica*	Rodentia: cricetid (social vole), murid (great gerbil, jird)	intestines	Asia
A. (*Paraspiculurus*) *bengalensis*	Rodentia: murid (house mouse)	intestines	India
A. (*Subaspiculurus*) *caviellae*	Rodentia: caviid (guinea pig)	intestines	India
A. (*Aspiculuris*) *dinnicki*	Rodentia: cricetid (bank vole, grey red-backed vole, northern red-backed vole, social vole, European water vole, European snow vole, Caucasian snow vole, Robert's snow vole), sciurid (red squirrel)	intestines	Eurasia

A. huascaensis	Rodentia: murid (house mouse)	caecum	North America
A. indicus	Rodentia: murid (house mouse, black rat)	intestines	Asia
A. (*Aspiculuris*) *kazakstanica*	Rodentia: murid (wood mouse), cricetid (social vole)	intestines	Europe, Africa
A. (*Aspiculuris*) *lahorica*	Rodentia: murid (house mouse)	large intestines	Pakistan
A. mexicana	Rodentia: cricetid (tarabundí vole, Mexican harvest mice)	colon	North America
A. (*Paraspiculurus*) *pakistanica*	Rodentia: murid (black rat)	caecum, large intestines	Pakistan
A. (*Paraspiculurus*) *ratti*	Rodentia: murid (black rat)	intestines	India
A. rysavyi	Rodentia: cricetid (silver mountain vole)	intestines	Eurasia
A. (*Aspiculuris*) *schulzi*	Rodentia: murid (wood mouse), cricetid (northern red-backed vole, social vole)	intestines	Europe
A. shikoloveta	Rodentia: murid (Namaqua rock rat)	intestines	Africa
A. tianjinensis	Rodentia: cricetid (gray-sided vole)	intestines	China
A. (*Aspiculuris*) *tetraptera* (syn. *Aspicularis*) (mouse pinworm)	Rodentia: murid (house mouse, Algerian mouse, white mouse, wood mouse, yellow-necked mouse, eastern broad-toothed field mouse, Natal multimammate mouse, brown rat, black rat, white rat, Mongolian gerbil, great gerbil, Libyan jird), cricetid (common vole, bank vole, social vole, European bank vole, European water vole, European snow vole, Robert's snow vole, northern red-backed vole, Mediterranean pine vole, European hamster, Turkish hamster, Chinese striped hamster, grey dwarf hamster), nesomyid (Gambian pouched rat); sciurid (red squirrel)	caecum, colon	worldwide
A. tschertkovi	Rodentia: murid (Korean field mouse), cricetid (European hamster, northern red-backed vole, Chinese striped hamster, grey dwarf hamster)	intestines	Eurasia
A. versterae	Rodentia: murid (Natal multimammate mouse)	caecum	Africa
A. witenbergi	Rodentia: murid (North Agrican gerbil, bushy-tailed jird)		North Africa

Parasite morphology: *Aspiculuris* spp. form 3 different types of morphological stages: eggs; larvae (4 successive stages encoded L1-L4); and adult worms. The eggs are spindle-shaped and slightly asymmetric longitudinally measuring 70-98 x 29-50 µm (although a few species form smaller eggs, e.g. *A. huascaensis* 54-69 x 18-30 µm). The eggs are not operculated and are bound by smooth thin shells containing a central morula or first-stage larvae (L1) when excreted in faeces. Little is known about larval morphology as development to L3 occurs within the eggs and L4 are transient parasitic stages. Adults are small white cylindrical worms measuring 2.6-4.7 mm long and bound by a tough cuticle with poorly-marked but elaborately-wrinkled cuticular annulations. The head is bulb-like being inflated to form cephalic vesicles and both sexes possess well-developed cervical alae. Indeed, 2 species groups are recognised on the basis of their morphology: group 1 having arrow-headed alae (*A. americana, A. arianica, A. aserbaidjanica, A. dinnicki, A. huascaensis, A. kazakstanica, A. lahorica, A. mexicana, A. pakistanica, A. rysavyi, A. schulzi, A. tetraptera, A. tianjinensis, A. tschertkovi, A. versterae*); and group 2 having spear-headed (lanceolate) alae (*A. ackerti, A. africana, A. asiatica, A. ratti, A. shikoloveta, A. witenbergi*). Both sexes also have smooth lateral alae running the length of the body, but not continuous with the cervical alae. The mouth is anterior and contains a cuticularized cephalic plate or cap (usually round but sometimes oval, square or laterally elongated) with 3 poorly-developed lips (each with 2 indistinct labial papillae), 4 cephalic papillae (arranged in a square) and 2 lateral amphids. The oesophagus is bipartite and club-shaped with a long cylindrical anterior muscular part and a stout oval-clavate glandular posterior bulb with serrated ridges (but not valved). Adult worms are sexually dimorphic, with females being slightly larger than males (2.6-4.7 x 0.2-0.3 mm cf. 2.0-4.0 x 0.1-0.2 mm). Mature females are didelphic with 2 ovaries and uteri arranged in a prodelphic configuration (parallel) and connected to muscular ovejector opening into an anterior vulva with a single anterior lip. Females have tapering conical tails 400-600 µm long with transverse striations. Mature males are monorchid having a single testis connected to the posterior intestines to open at a common cloaca. They are readily identified as they possess 3 pairs of alae (precloacal, postcloacal, caudal) around their short conical tails (100-170 µm) but lack mamelons, a gubernaculum and a spicule.

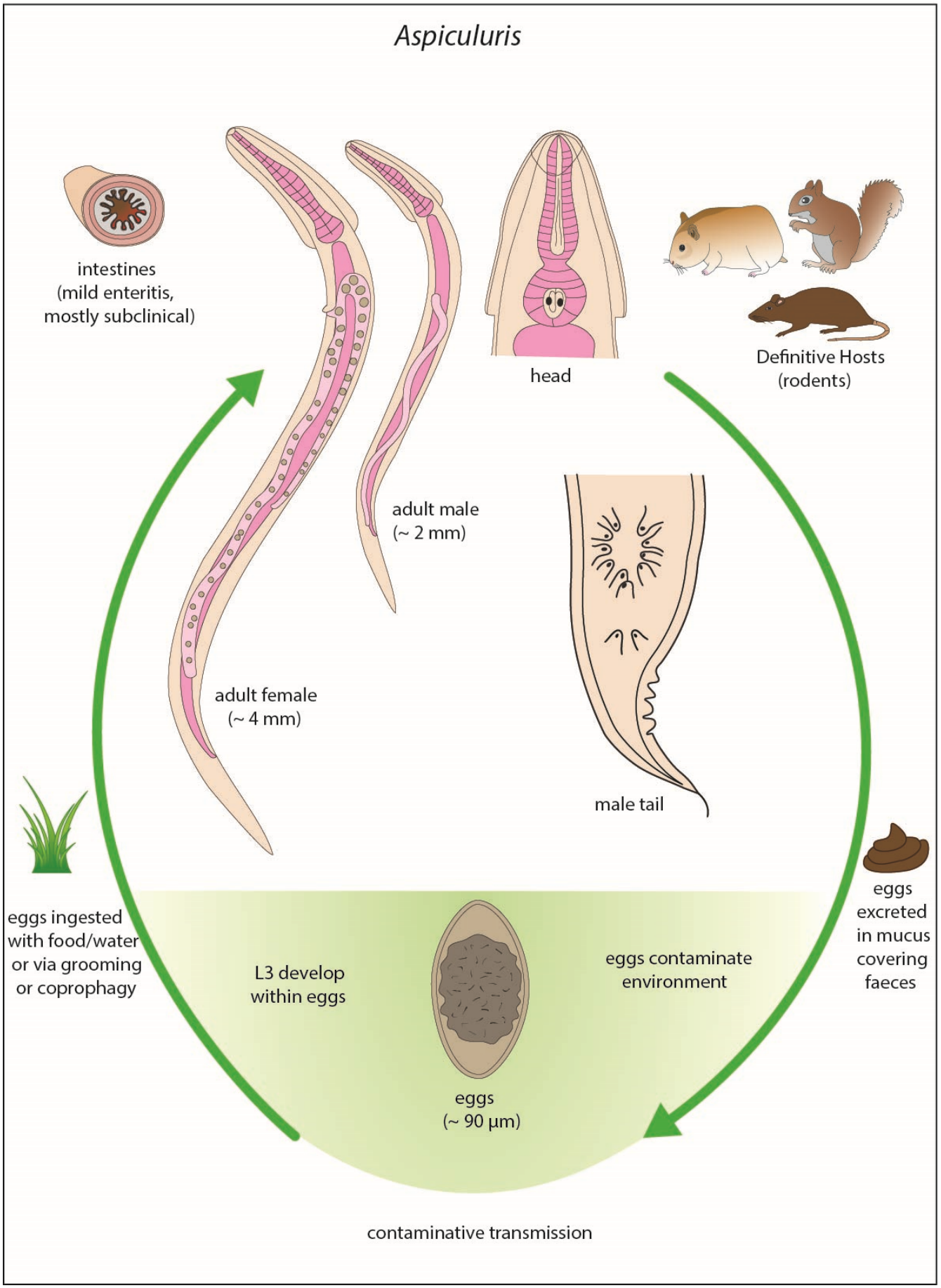
Site of infection: Adult worms live in the lumen of the large intestines (mainly the colon, sometimes the caecum) of their rodent hosts, occasionally extending into the small intestines. Earlier larval stages undergo transient development in intestinal crypts before returning to the lumen to mature.

Pathogenesis: Most infections are asymptomatic and even heavy worm burdens rarely cause mild clinical signs of enteritis. Adult worms reside in the lumen and feed on intestinal contents, and while larvae may enter the crypts for brief periods, they are not considered to be invasive and cause little damage. Mice are most susceptible to infection at 5-6 weeks of age and they subsequently develop an age-related resistance with immune expulsion of parasites and protection against re-infection. Female mice become resistant during their first oestrous, while males gradually developed resistance as they aged. Most parasite species were relatively specific for particular hosts, although a few species apparently had broader host specificity but infections did not thrive in all hosts (e.g. only a few under-developed worms of *A. tetraptera* established experimentally in gerbils and rats).

Developmental cycle and mode of transmission: *Aspiculuris* spp. have simple direct monoxenous life-cycles involving the faecal-oral transmission of infective eggs. Gravid female worms move to lower colon to lay eggs which are excreted in the mucus layer covering faecal pellets. Egg production was often discontinuous or intermittent, and did not show any distinct diurnal rhythm although reports suggested more eggs were deposited at night. In the external environment, larvae developed inside the eggs to form infective L3 in 5-8 days at 24-27°C. The eggs are quite resistant to desiccation and may survive for several weeks, but they are sensitive to high temperatures. Rodents become infected by ingesting eggs contaminating food or by coprophagy. Ingested eggs hatch in the large intestines releasing L3 which moult to L4 and enter colonic crypts where they remain for 4-5 days (larvae do not undertake any somatic or extra-intestinal migration). The larvae return to the lumen and migrate anteriorly to the proximal colon over 1-3 weeks where they moult to subadults (sometimes called L5) which subsequently mature. The prepatent period (time from infection to first egg excretion) ranges from 21-35 days and adult worms have been found to live for 45-50 days.

Differential diagnosis: Infections are conventionally diagnosed by the microscopic detection of worm eggs in faecal samples following their concentration by floatation (sticky-tape impression smears are ineffective as these pinworms do not attach eggs to perianal regions). The worm eggs are characteristic in size and shape, being spindle-shaped rather than D-shaped like *Syphacia* eggs. Infections may also be diagnosed at post-mortem by the detection of adult worms in the colon. Molecular biological techniques have been used to characterize parasite species following the polymerase chain reaction (PCR) amplification of nuclear genes (18S ribosomal RNA) and mitochondrial genes (cytochrome oxidase subunit I).

Treatment and control: A wide range of drug treatments have been tested against pinworm infections in laboratory mice, mostly as oral medications administered via food or water. Conventional anthelmintics, such as benzimidazoles (thiabendazole, fenbendazole), diethylenediamines (piperazine), organophosphonates (dichlorvos, trichlorfon, haloxon) and heterocyclic thiazines (phenothiazine), were effective against adult worms and larval stages but not eggs. Earlier studies reported some anthelmintic effects using cyanine dyes (pyrvinium), triarylmethane dyes (gentian violet, crystal violet), fluorides (sodium fluoride), iodides (stilbazium iodide), substituted dihydroxybenzene (hexylresorcinol) and halogenated hydrocarbons (carbon tetrachloride, tetrachloroethylene). Recent studies also found that several antibiotics (terramycin, aureomycin, bacitracin, puromycin) apparently reduced worm burdens. It should be noted that repeated or sustained treatments were required to prevent re-infection in addition to thorough cleaning of holding facilities. Worm eggs have been found on cages, equipment, ventilation ducts and even dust in laboratory animal colonies, and the eggs are highly resistant to cold, dessication and many disinfectants, but are susceptible to heat. Preventive strategies should therefore not only include the removal and disposal of host faeces and soiled bedding, but also the sterilization of cages and rooms preferably using steam-cleaning devices. Routine surveillance, quarantine and isolation procedures should also be implemented to detect and manage infections in rodent colonies, as they can be difficult to eradicate once established.


Aspiculuris
intestines
(mild enteritis,
mostly subclinical)
adult male
(~ 2 mm)
adult female
(~ 4 mm)
head
male tail
Definitive Hosts
(rodents)
eggs ingested
with food/water
or via grooming
or coprophagy
L3 develop
within eggs
eggs
(~ 90 µm)
eggs contaminate
environment
eggs
excreted
in mucus
covering
faeces
contaminative transmission



Aspiculuris adult worm, head



Aspiculuris worm egg

Habronema/Draschia
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised; including habronematoids (with pseudolabia and median lips) containing the habronematids which live in the stomachs of horses and are transmitted by muscid flies in which L3 develop. Gastric infections by *Habronema* and *Draschia* spp. are generally asymptomatic, but the larvae may cause granulomatous skin lesions (summer sores).

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Habronematoidea (unique head structures with small pseudolabia and median lips)
Family:	Habronematidae (pharynx with dorsal and ventral tooth, indirect cycle involving ingestion of fly)
Genus:	*Habronema* (parasitic in stomach of horses)
Genus:	*Draschia* (parasitic in stomach of horses)
Species:	various species may cause gastritis in horses, while larvae may cause nodular dermatitis

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Habronematoidea contains medium-sized worms with unique head structures comprising small pseudolabia and median lips infecting the alimentary tracts of vertebrates and utilizing terrestrial or aquatic insects and crustaceans as intermediate hosts for larval development. Four families are recognised: Habronematidae (large pseudolabia covering median lips, no cephalic papillae on pseudolabia, 8 papillae on median lips, divided oesophagus, female tail not modified as attachment organ, sexual dimorphism not marked, female body not coiled, globular or inflated, parasites of birds and mammals); Tetrameridae (median lips not extending over pseudolabia, no cephalic papillae on pseudolabia, divided oesophagus, female tail not modified as attachment organ, sexual dimorphism marked, female body spirally coiled or globular or with slender extremity with distal end inflated, parasites of mammals and birds); Hedruridae (median lips extending over pseudolabia, cephalic papillae on pseudolabia, undivided oesophagus, female tail modified as attachment organ, parasites of amphibians, reptiles and fish); and Cystidicolidae (small pseudolabia often reduced to appendix, median lips not extending over pseudolabia, 4 papillae at bases of pseudolabia,

divided oesophagus, female tail not modified as attachment organ, sexual dimorphism not marked, female body not coiled, globular or inflated, parasites of fishes).

The family Habronematidae contains 3 subfamilies: Habronematinae (posterior border of pseudolabia without ornamentation, not forming attachment organ, parasites of mammals); Parabronematinae (posterior border of pseudolabia with ornamentation forming attachment organ consisting of cordons, parasites of mammals); and Histiocephalinae (posterior border of pseudolabia with ornamentation forming attachment organ consisting of simple or denticulate leaf-like structures, parasites of birds). The subfamily Habronematinae contains 9 genera (*Chitwoodspirura*, *Cyrnea* (syn. *Seurocyrnea*, *Skrjabinochiona*, *Chenospirura* p.p., *Metacyrnea*), *Draschia*, *Excisa*, *Gendrespirura* (syn. *Chenospirura* p.p., *Cheniellospirura*, *Sinicaspirura*), *Habronema* (incl. subgenera *Habronema*, *Aviabronema*), *Odontospirura* (syn. *Vaznema*), *Procyrnea* (syn. *Aviabronema?*, *Ruschiella*, *Draschearia*), and *Sicarius*) which are differentiated primarily on the basis of differences in adult morphology (esp. cephalic structures), larval morphology (anatomy and ornamentation), modes of transmission, host occurrence/specificity and geographic distribution. Genera of veterinary and medical significance are tabulated below:

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs/Larvae	Transmission
Family: Habronematidae (pharynx with dorsal and ventral tooth, indirect cycle involving ingestion of fly)						
Habronema	32	perissodactyls, birds	stomach	8-35 mm long, cylindrical buccal capsule, 2 large lateral pseudolabia, 2 median lips, bipartite oesophagus, oviparous, some viviparous	eggs, 40-80 x 10-20 µm, elongate, thin-shelled	indirect (L3 in muscid flies)
Draschia	1	perissodactyls	stomach	7-15 mm long, funnel-shaped buccal capsule, 2 large lateral pseudolabia, 2 median lips, bipartite oesophagus, viviparous	larvae (L1) 330-350 µm, anterior tooth	indirect (L3 in muscid flies)
Family: Tetrameridae (extravagant sexual dimorphism, females swollen, coloured bright red)						
Tetrameres	57	birds	proventriculus	3-10 mm, globular body divided into 4 by longitudinal grooves, lateral pseudolabia, 2 median trilobed lips, bipartite oesophagus, oviparous	eggs, 33-62 x 18-30 µm, oval, thick-shelled, operculate	indirect (L3 in crustaceans, amphipods, insects, earthworms)

Members of the genus *Habronema* have pseudolabia with convex anterior borders and some 32 species have been described from the stomachs of perissodactyls and occasionally from the proventriculus, ventriculus and intestines of birds (mostly non-passerines). Some authors recognize 2 *Habronema* subgenera: namely, *H.* (*Habronema*) (vulva on ventral axis or displaced dorsally, single lateral alae, parasitic in mammals); and *H.* (*Aviabronema*) (vulva on ventral axis, body with or without lateral alae, parasitic in birds); while other authors have synonymized *H.* (*Aviabronema*) with the genus *Procyrnea.* Worms belonging to the genus *Draschia* have pseudolabia with concave anterior borders and the sole species *D. megastoma* is commonly found in perissodactyls. Worms of both genera have indirect life-cycles involving larval development in dipteran flies which deposit infective stages on the mucous membranes of the final hosts where they are ingested. In equids, adult worms develop in the gastric mucosa often causing chronic catarrhal gastritis, sometimes with nodule or tumour formation, while larvae may also cause conjunctival and cutaneous lesions (summer sores).

Parasite species	Definitive Hosts	Location [Clinical signs]	Intermediate Hosts	Distribution
Draschia				
D. megastoma (syn. *Habronema*)	Perissodactyla: equid (horse, donkey, plains zebra, mountain zebra), rhinocerotid (southern black rhinoceros); Lagomorpha: leporid (European rabbit)	stomach [gastritis, nodules, skin lesions (summer sores), conjunctivitis]	Diptera: muscid (*Musca domestica, humilis, sorbens, tempestiva, vicinina, Muscina stabulans, terraereginae, Stomoxys calcitrans, Fannia* spp.)	worldwide
Habronema				
H. (A.) aegotheles	Caprimulgiformes: aegothelid (Australian owlet-nightjar)			Australia
H. (A.) ameerae (= *Procyrnea*)	Falconiformes: falconid (Himalayan kestrel)	proventriculus		India

H. (A.) americanum	Accipitriformes: accipitrid (broad-winged hawk)			North America
H. (A.) asymmetricum	Accipitriformes: accipitrid (pale harrier)			Africa
H. avicedae	Accipitriformes: accipitrid (Indian black-crested baza)			Asia
H. bialatum	Galliformes: phasianid (northern bobwhite quail)			North America
H. (A.) buckleyi	Otidiformes: otidid (northern black korhaan)			Africa
H. bulbosum	Galliformes: phasianid (Indian peafowl)			Asia
H. casuarii	Casuariiformes: casuariid (double-wattled cassowary)			Australasia
H. (A.) chabaudi (= *Procyrnea*)	Falconiformes: falconid (laggar falcon)	proventriculus		India
H. (A.) circi (= *Cyrnea leptoptera*)	Accipitriformes: accipitrid (hen harrier)			Asia
H. (H.) clarki	Perissodactyla: equid (donkey); Rodentia: caviid (capybara, lesser capybara)			South America
H. (A.) colaptes (= *Procyrnea*)	Piciformes: picid (northern flicker)			North America
H. (A.) daleri	Columbiformes: columbid (southern green pigeon)	gizzard		India
H. (A.) diesingi	Galliformes: numidid (vulturine guineafowl)			Africa
H. (A.) dolichocolpos	Accipitriformes: accipitrid (Madagascar cuckoo-hawk, Madagascar harrier-hawk)			Madagascar
H. euplocami	Galliformes: phasianid (kalij pheasant, peacock-pheasant)			Asia
H. (A.) ficheuri (= *Procyrnea*)	Strigiformes: strigid (long-eared owl)			Holarctic
H. hamospiculatum (syn. *H. congolense*, *manidis, zschokkei*) (= *Gendrespirura*)	Pholidota: manid (tree pangolin)			Africa
H. (A.) hrishii	Accipitriformes: accipitrid (black kite)			Eurasia
H. (A.) imbricatum (= *Cyrnea*)	Strigiformes: strigid (oriental scops owl, spotted owlet); Falconiformes: falconid (peregrine falcon)			Holarctic
H. (A.) incertum	Galliformes: phasianid (Gambel's quail)	proventriculus		North America
H. indicum	Coraciiformes: coraciid (Indian roller)			India
H. hyperabadensis	Passeriformes: sturnid (common hill myna)	gizzard		India
H. khalili	Perissodactyla: rhinocerotid (black rhinoceros)			Africa
H. (A.) leptoptera (= *Procyrnea*)	Accipitriformes: accipitrid (Eurasian sparrowhawk); Falconiformes: falconid (Eurasian hobby)			Eurasia
H. longistoma	Perissodactyla: equid (Grant's zebra)	stomach		Africa
H. (A.) longispiculum	Strigiformes: strigid (great grey owl)			Holarctic
H. (A.) longistriata (= *Procyrnea*)	Piciformes: picid (Campo flicker)			South America
H. malani	Perissodactyla: equid (Burchell's zebra, Hartmann's mountain zebra)			Africa
H. (A.) magnilabiatum	Accipitriformes: accipitrid (Himalayan grey-headed fishing			Asia

	eagle)			
H. (A.) magnipapillatum	Accipitriformes: accipitrid (white-eyed buzzard)	proventriculus		India
H. (A.) mansoni (= *Procyrnea*)	Accipitriformes: accipitrid (red-tailed hawk, pallid harrier, common buzzard); Falconiformes: falconid (American kestrel, American peregrine falcon)	proventriculus		North America, Asia
H. (H.) microstoma (syn. *H. majus*) (incl. subspp. *microstoma*, *congolense*)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, plains zebra)	stomach [gastritis, skin lesions (summer sores), conjunctivitis]	Diptera: muscid (house fly, *Musca domestica,* stable fly, *Stomoxys calcitrans,* buffalo fly, *Haematobia exigua,* horn fly, *Lyperosia irritans*), sarcophagid (flesh fly, *Sarcophaga melanura*)	worldwide
H. (A.) monoptera	Accipitriformes: accipitrid (Asian tawny eagle)	proventriculus		India
H. (A.) murrayi (= *Procyrnea*)	Strigiformes: tytonid (barn owl)			Africa
H. (H.) muscae	Perissodactyla: equid (horse, Przewalski's horse, donkey, onager, mountain zebra); Artiodactyla: bovid (cattle, goat)	stomach [skin lesions, conjunctivitis]	Diptera: muscid (*Musca domestica, humilis, lusoria, terraereginae, ventrosa, Pseudopyrellia* (*Neomyia*)), sarcophagid (*Sarcophaga*)	worldwide
H. numidae (= *Cyrnea*)	Galliformes: numidid (helmeted guineafowl)			Africa
H. (A.) seurati (= *Cyrnea*)	Falconiformes: falconid (Eurasian hobby, red-footed falcon)			Eurasia
H. (A.) singhi	Accipitriformes: accipitrid (common pariah kite)	proventriculus		India
H. (A.) skrjabini	Carnivora: felid (spotted wild cat)			Asia
H. (A.) spinosa (= *Procyrnea*)	Strigiformes: strigid (Eurasian eagle-owl); Falconiformes: falconid (common kestrel, lesser kestrel)			North America
H. (A.) suraiyae (= *Procyrnea*)	Falconiformes: falconid (red-necked falcon)	proventriculus		India
H. tomasi	Perissodactyla: equid (Burchell's zebra)			Africa
H. (A.) tulostoma (= *Procyrnea*)	Accipitriformes: accipitrid (Egyptian vulture)			Africa
H. tyosenense	Perissodactyla: equid (horse)	stomach		Asia
H. (A.) uncinipenis (= *Procyrnea*)	Rheiformes: rheid (greater rhea)			South America
H. unilateralis (= *Procyrnea*)	Piciformes: ramphastid (red-billed toucan, spot-billed toucan)			South America
H. (A.) urophasiana (= *Procyrnea*)	Galliformes: phasianid (greater sage-grouse)	gizzard		North America
H. (A.) waheedae	Accipitriformes: accipitrid (Brahminy kite)	proventriculus		India
H. (H.) zebrae	Perissodactyla: equid (mountain zebra)			Africa

Parasite morphology: *Draschia* and *Habronema* spp. form 3 distinct morphological stages in their developmental cycles: eggs; larvae (4 successive stages designated L1-L4); and adult worms. The thin-shelled eggs are oval, sometimes elongated and cigar-

shaped, measuring 40-80 x 10-20 µm, and are larvated when laid. L1 have cylindrical ridged bodies measuring 330-350 µm long with an anterior spine-like tooth. Two types of L2 have been observed, robust sausage-shaped stages measuring 400-500 µm, and elongate slender stages measuring up to 990 µm, many stages apparently enclosed in a sheath of host origin. Infective L3 range in size from 1.5-4.0 mm and have a conspicuous cephalic cone with a hexagonal mouth surrounded by large bilobed dorsal and ventral lips and smaller lateral lips, 4 cephalic papillae and 2 lateral amphids. The cuticle is deeply ridged, transversely and longitudinally, and the tail is conical and studded with small papillae appearing as spiny knobs. Adults are small white-yellow worms measuring from 7-15 mm in length for *Draschia* and from 8-35 mm for *Habronema*. Their bodies are cylindrical with curved conical tails and tapering anterior ends (*Draschia* has a transverse groove or cephalic collar at the anterior end). They have large thick-walled buccal capsules (cylindrical in *Habronema* and funnel-shaped in *Draschia*) with narrow pseudolabia and 2 median lips (ventral and dorsal) with sensory papillae. The buccal capsule may be unarmed (e.g. *D. megastoma, H. muscae*) or armed with teeth (e.g. *H. majus* with 2 teeth). The pseudolabia have convex anterior borders in *Habronema* and concave anterior borders in *Draschia.* The lips may be unlobed (e.g. *D. megastoma*), bilobed (e.g. *H. microstoma*) or trilobed (e.g. *H. muscae*). Worms have one (*Habronema*) or two (*Draschia*) lateral cervical alae, and a bipartite oesophagus (with a short anterior muscular section and a longer posterior glandular section). Adults are sexually dimorphic, with females being slightly larger than males (10-15 cf. 7-10 mm for *Draschia,* 12-35 cf. 8-22 mm for *Habronema*). Mature females are didelphic with 2 ovaries and uteri connected to a short vagina and an ovoid ovejector opening into a common anterior vulva. The body is not spirally twisted nor globular and the caudal extremity is not inflated (in contrast to *Tetrameres*). Mature males have spirally twisted tails with well-developed caudal alae, pedunculate caudal papillae and 2 elongate curved spicules unequal in length (left spicule larger).

Site of infection: Adult *D. megastoma* worms burrow into the gastric mucosa of equids, usually near the junction of the oesophageal and glandular regions. In mammals, adult *Habronema* worms live in the mucus covering the glandular portion (fundus) of the stomach, with their heads attached to the mucosa. In birds, adult *Habronema* worms infect the proventriculus, ventriculus and/or intestines. Larval stages entering the gut complete their development within the lumen, while those entering cutaneous or mucocutaneous tissues are unable to complete their development but nonetheless may cause lesions. Worm eggs release larvae that are taken up by insect intermediate hosts where they form infective larval stages in the haemocoel before invading the mouthparts.

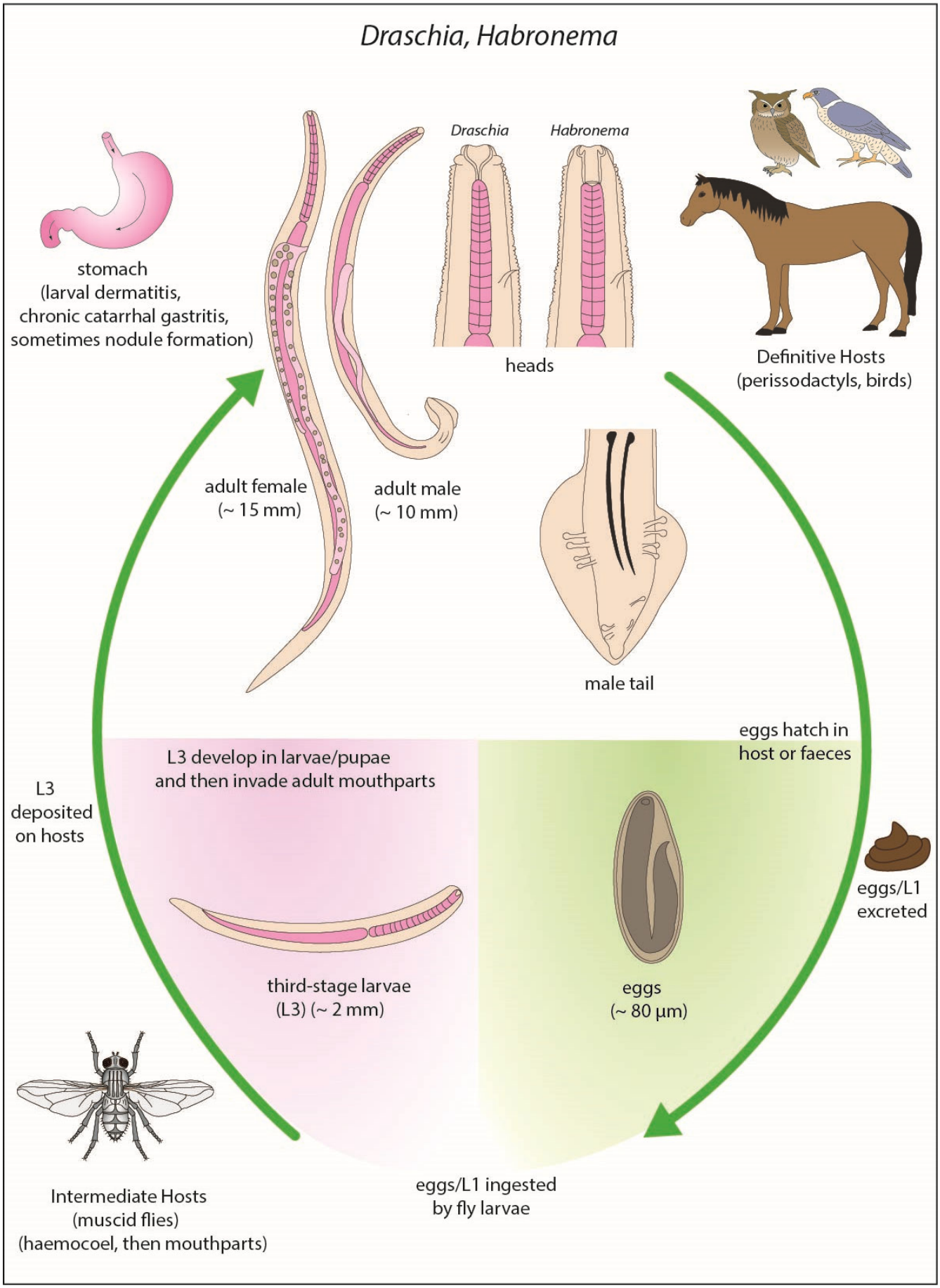
Pathogenesis: Most infections are asymptomatic, although heavy infections by some species may cause gastric signs while larvae infecting superficial tissues may cause cutaneous or conjunctival lesions. Larvae deposited on moist membranes around the muzzle are swallowed thereby reaching the stomach in order to complete their development to adult worms. Most species cause traumatic damage to the gastric mucosa and elicit host inflammatory responses resulting in chronic congestion and mild catarrhal gastritis associated with the secretion of thick tenacious mucus. Some species (e.g. *H. muscae*) have also been associated with petechial haemorrhages and gastric ulcer formation. The species *D. megastoma* is the most pathogenic, however, as worms live in colonies in the fundic submucosa causing large fibrous tumour-like lesions (2-10 cm diameter). The granulomatous nodules have 1-2 central openings and are filled with worms embedded in necrotic and caseous exudate. The nodules project into the lumen but are well tolerated and usually do not produce clinical signs. Infected animals may develop digestive disorders during autumn and winter, with capricious appetite, pica, polydipsia, constipation alternating with diarrhoea, and colic due to pyloric obstruction and severe indigestion. Infections may occasionally cause suppurative gastritis, pyloric stenosis or obstruction, adhesions with adjacent organs and even gastric perforation with subsequent peritonitis, particularly when abscesses are formed due to secondary pyogenic bacterial infections. Different types of disease may arise when larvae invade moist membranes separate from the alimentary tract where they are unable to complete their development to adults but nonetheless may cause severe inflammatory reactions and lesions before they succumb to host immune responses. Larvae deposited on broken skin or open wounds may cause proliferative lesions consistent with nodular granulomatous ulcerative dermatitis. The lesions appear as red-brown cauliflower-like masses (up to 5-15 cm in diameter) that protrude above the surface of the skin and haemorrhage easily (condition known variously as summer sores, jack sores, swamp cancer, bursati, or granular dermatitis). The lesions are intensely pruritic and painful and hosts attempt to relieve the itch by biting, scratching and rubbing thereby causing the wounds to bleed or fester. Summer sores occur mainly due to infection with *D. megastoma* larvae, although some *Habronema* spp. may cause similar lesions which are less severe and transient. The sores are often found on body parts prone to superficial injuries (head, withers, inner lower limbs, coronet above the hoof) and secondary bacterial infections may worsen lesions. As the larvae gradually die, the lesions become fibrous and inactive, but often do not heal until cooler weather commences and fly activity ceases. Larvae deposited around the eyes may burrow in the conjunctivae causing ulcerative weeping lesions at the medial canthus, the nictitating membrane or the eyelid. The lesions become progressively nodular with granulomatous masses (3-4 mm in diameter) causing local irritation, ulceration, conjunctivitis, keratitis, lacrimation with epiphora, photophobia, and squinting. Invading larvae may occasionally be carried to the lungs either via the bloodstream or by migration down the airways. Infections may result in pulmonary granulomas or purulent bronchitis, but they are rarely severe enough to cause clinical signs (cough or nasal discharge). Several instances have also been reported where larvae have invaded the prepuce and glans penis of stallions causing dysuria. In contrast to mammalian infections, those in birds have not been associated with any significant pathological changes, morbidity or mortality.

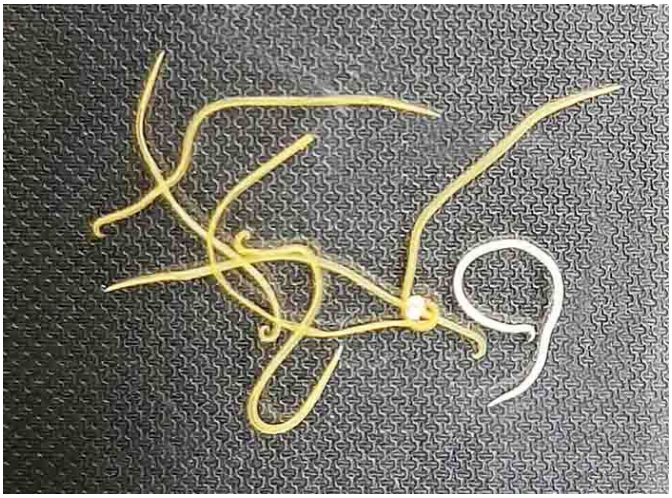
Developmental cycle and mode of transmission: The parasites have indirect heteroxenous life-cycles involving the development of infective larvae in dipteran intermediate hosts which are transmitted to vertebrate definitive hosts in which adult worms form. Gravid female worms lay embryonated eggs in the stomach which hatch in transit through the intestines or immediately after their

excretion in faeces. Several reports have suggested that some species (e.g. *D. megastoma, H. microstoma*) may even be viviparous and give birth to live larvae rather than eggs. L1 survive for some time in faecal material (6-7 days at 25-30°C, 28 days at 5°C) and they are active, exhibiting positive hydrotropism and thermotropism. Embryonated eggs and free L1 are ingested by dung-inhabiting dipteran larvae (biting and non-biting muscid flies) which act as intermediate hosts supporting the development of infective L3. Transmission occurs primarily during the warmer months of the year when flies are active and breeding on pastures. The L1 penetrate the gut of the fly larvae, enter the haemocoel and invade tissues (Malpighian tubules or fat bodies) where they moult to L2 after 3-4 days. These stages encapsulate in the tissues during the fly pupal stage and their further development to L3 is synchronised to coincide with the emergence of the adult fly from the pupa. L3 form over several days (faster at higher temperatures) and migrate to the head of the fly invading the labium within 1-2 weeks. Infective L3 break out of the mouthparts when flies feed on suitable definitive hosts, thus becoming deposited on moist membranes or secretions around the mouth, nostrils, conjunctiva, genitalia, broken skin or open wounds. Infective L3 are very susceptible to dessication and die within a few minutes if deposited on dry substrates. Final hosts may also be infected by ingesting infected flies (live or dead) in feed or water. Larvae that are able to access the alimentary tract are swallowed and develop directly to adults in the stomach (they do not undertake any local, somatic or extra-intestinal migrations). The prepatent period (time from infection to first excretion of eggs/larvae) is around 8 weeks. Larvae that are deposited at sites without access to the gut (e.g. skin, eyes, genitals) may invade local tissues but are unable to develop into adults.

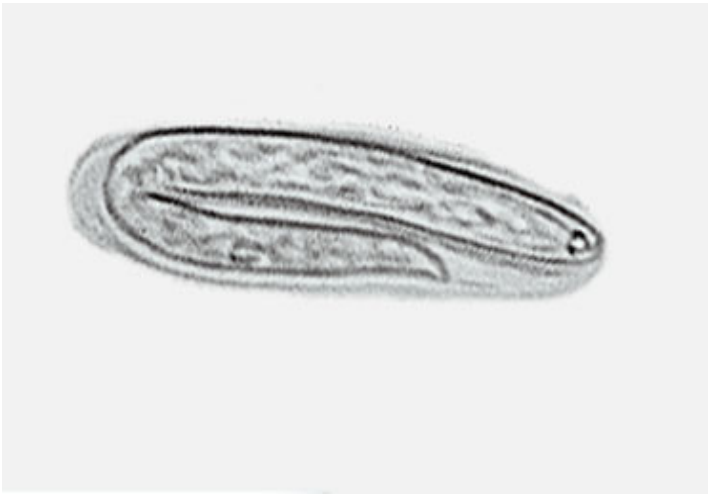
Differential diagnosis: Clinical infections often present with characteristic cutaneous and/or conjunctival lesions during the warm fly season (summer sores) or vague gastric signs (usually involving colic) during cooler non-fly seasons. In either case, other aetiological agents need to be discounted. Scrapings and biopsies of proliferative skin lesions and lachrymal fluid may be examined for parasite larvae, but they are usually difficult to find and identify. Infections are conventionally diagnosed by the microscopic detection of worm eggs and/or larvae in faecal samples, usually following egg concentration by floatation or larval recovery by Baermann filtration, although neither technique is highly sensitive. Worm eggs have sometimes been detected by gastric lavage collected by stomach tube. Infections may be diagnosed at post-mortem by the detection of nodular lesions containing adult worms in samples recovered from the stomach mucosa. Histological examination of sections of cutaneous, ocular or pulmonary tissues may sometimes reveal larval stages. Modern molecular biological techniques have been used to characterize parasites from definitive and intermediate hosts (horses and flies, respectively) by polymerase chain reaction (PCR) amplification of nuclear gene sequences (ribosomal RNA and internal transcribed spacer regions).

Treatment and control: A small range of anthelmintic drugs have been used to successfully treat clinical infections, including the macrocyclic lactones (ivermectin, moxidectin), organophosphonates (dichlorvos), diethylenediamines (diethylcarbamazine) and benzimidazoles (oxibendazole, oxfendazole, cambendazole). Ivermectin is most effective against both larval and adult worms, although repeated treatments are required to prevent re-infection. Ocular disease has responded reasonably well to treatment with various concoctions of topical ophthalmic antibiotics, anthelmintics and corticosteroids (involving combinations of nitrofurazone, trichlorphon, ivermectin, diethylcarbamazine, echothiophate iodide and dexamethasone). Most infections occur in horses kept outdoors on pastures (where dung-inhabiting fly vectors abound, albeit seasonally) rather than in horses stabled indoors (where the insect vectors rarely venture). It is difficult to implement effective preventive strategies in extensive outdoor operations, but some initiatives have helped reduce infection rates by minimizing environmental contamination (regular collection and disposal of faeces), managing fly populations (regular application of insecticides to livestock and fixtures) and limiting opportunities for transmission (timely treatment of skin lesions/wounds so they do not attract flies). Similar strategies may be used around stables to safeguard against infections.


Draschia, Habronema
stomach
(larval dermatitis,
chronic catarrhal gastritis,
sometimes nodule formation)
Draschia
Habronema
heads
Definitive Hosts
(perissodactyls, birds)
adult female
(~ 15 mm)
adult male
(~ 10 mm)
male tail
eggs hatch in
host or faeces
L3 develop in larvae/pupae
and then invade adult mouthparts
L3
deposited
on hosts
eggs/L1
excreted
third-stage larvae
(L3) (~ 2 mm)
eggs
(~ 80 µm)
Intermediate Hosts
(muscid flies)
(haemocoel, then mouthparts)
eggs/L1 ingested
by fly larvae



Habronema adult worms



Habronema worm egg



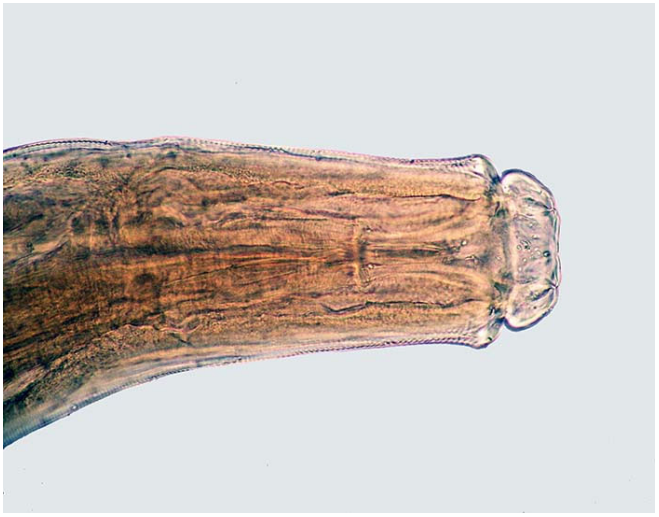
Habronema adult worm, male tail



Habronema adult worm, head



Draschia adult worm, male tail



Draschia adult worm, head

Tetrameres
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including habronematoids (with pseudolabia and median lips) containing the tetramerids which are found in the proventriculus of birds and are transmitted by aquatic crustaceans, amphipods, beetles, cockroaches, grasshoppers or earthworms in which L3 develop. Infections by *Tetrameres* spp. may cause anaemia in domestic and wild birds.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Spiruroidea (two trilobed lips, oesophagus never with bulb, coiled tail in males, two unequal spicules)
Family:	Tetrameridae (extravagant sexual dimorphism, females swollen, coloured bright red)
Genus:	*Tetrameres* (parasitic in proventriculus of birds)
Species:	various species cause anaemia in birds

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Habronematoidea contains medium-sized worms with unique head structures comprising small pseudolabia and median lips infecting the alimentary tracts of vertebrates and utilizing terrestrial or aquatic insects and crustaceans as intermediate hosts for larval development. Four families are recognised: Habronematidae (large pseudolabia covering median lips, no cephalic papillae on pseudolabia, 8 papillae on median lips, divided oesophagus, female tail not modified as attachment organ, sexual dimorphism not marked, female body not coiled, globular or inflated, parasites of birds and mammals); Tetrameridae (median lips not extending over pseudolabia, no cephalic papillae on pseudolabia, divided oesophagus, female tail not modified as attachment organ, sexual dimorphism marked, female body spirally coiled or globular or with slender extremity with distal end inflated, parasites of mammals and birds); Hedruridae (median lips extending over pseudolabia, cephalic papillae on pseudolabia, undivided oesophagus, female tail modified as attachment organ, parasites of amphibians, reptiles and fish); and Cystidicolidae (small pseudolabia often reduced to appendix, median lips not extending over pseudolabia, 4 papillae at bases of pseudolabia, divided oesophagus, female tail not modified as attachment organ, sexual dimorphism not marked, female body not coiled, globular or inflated, parasites of fishes).

The family Tetrameridae contains 3 subfamilies: Tetramerinae (body spirally coiled or globular, parasites of the proventriculus (rarely gizzard) of birds); Geopetitiinae (female body with long posterior constriction (in form of elongate peduncle) followed by terminal swelling, parasites of the gizzard of birds); and Crassicaudinae (female body with short posterior constriction (in form of simple narrowing) followed by terminal swelling, parasites of the tissues of whales). The subfamily Tetramerinae contains 3 genera (*Microhadjelia*, *Tetrameres* and *Microtetrameres*) which are differentiated primarily on the basis of adult anatomy, larval characteristics, modes of transmission, tissue tropism, host specificity and geographic distribution. Genera of veterinary and medical significance are tabulated below:

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs/Larvae	Transmission
Family: Tetrameridae (extravagant sexual dimorphism, females swollen, coloured bright red)						
Tetrameres	57	birds	proventriculus	3-10 mm, globular body divided into 4 by longitudinal grooves, lateral pseudolabia, 2 median trilobed lips, bipartite oesophagus, oviparous	eggs, 33-62 x 18-30 µm, oval, thick-shelled, operculate	indirect (L3 in crustaceans, amphipods, insects, earthworms)
Family: Habronematidae (pharynx with dorsal and ventral tooth, indirect cycle involving ingestion of fly)						
Habronema	32	perissodactyls, birds	stomach	8-35 mm long, cylindrical buccal capsule, 2 large lateral pseudolabia, 2 median lips, bipartite oesophagus, oviparous, some viviparous	eggs, 40-80 x 10-20 µm, elongate, thin-shelled	indirect (L3 in muscid flies)
Draschia	1	perissodactyls	stomach	7-15 mm long, funnel-shaped buccal capsule, 2 large lateral pseudolabia, 2 median lips, bipartite oesophagus, viviparous	larvae (L1) 330-350 µm, anterior tooth	indirect (L3 in muscid flies)

The genus *Tetrameres* contains peculiar non-vermiform worms noted for their marked sexual dimorphism with the body of female worms being globular or spirally-twisted and grossly swollen between the head and tail (commonly known as globular stomach worms). Female worms parasitize the proventricular glands of birds while male worms occur on the mucosal surface. Early studies recognised 2 subgenera: namely *T.* (*Tetrameres*) (body of female globular, male with spines on lateral fields); and *T.* (*Microtetrameres*) (body of female twisted in tight spiral, male without spines on lateral fields). Subsequent studies, however, considered *T.* (*Microtetrameres*) to be a separate genus and recognised 3 *Tetrameres* subgenera; *T.* (*Tetrameres*) (lacking anterior cuticular specializations, body bearing longitudinal rows of cuticular spines); *T.* (*Gynaecophila*) (lacking anterior cuticular specializations, lacking body spines or bearing only a few poorly-developed spines); and *T.* (*Petrowimeres*) (bearing anterior cuticular specializations variously described as 'cordons', flanges or lateral alae, evident as ridges, wing-like structures, funnel-shaped processes or cleft spines). Some 57 species have been described from a wide range of bird species around the world, some in association with clinical disease, especially in young birds.

***Tetrameres* species**	**Definitive hosts**	**Location [Clinical signs]**	**Intermediate hosts**	**Distribution**
T. accipiter	Accipitriformes: accipitrid (sharp-shinned hawk, red-tailed hawk)			Americas
T. (*G.*) *aegypii*	Accipitriformes: accipitrid (cinereous vulture)			Eurasia
T. (*T.*) *americana* (syn. *Tropisurus*) (globular roundworm, stomach worm)	Galliformes: phasianid (chicken, red junglefowl, turkey, northern bobwhite quail, ruffed grouse); Columbiformes: columbid (pigeon)	proventriculus [anaemia]	Blattodea: ectobiid (cockroach, *Blattella germanica*); Orthoptera: acridid (grasshopper, *Locusta migratoria, Melanoplus femurrubrum, differentialis, Scyllina cyanipes*)	Africa, North America
T. anatis	Anseriformes: anatid (mallard)			
T. (*P.*) *anseranas*	Anseriformes: anseranatid (magpie goose)			Australia
T. (*G.*) *aspicula*	Ciconiiformes: threskiornithid (white-faced ibis)	proventriculus		South America
T. (G.) aspinosa	Pelecaniformes: ardeid (snowy egret)			North

				America
T. (P.) australis	Anseriformes: anatid (black swan)			Australia
T. (P.) biziurae	Anseriformes: anatid (musk duck)			Australia
T. (T.) butorides	Ciconiiformes: ardeid (green heron)			Central America
T. cardinalis	Passeriformes: cardinalid (northern cardinal)		Orthoptera: acridid (locust, *Locusta migratoria*)	North America
T. (T.) cladorhynchi	Charadriiformes: recurvirostrid (banded stilt)			Australia
T. (P.) columbicola	Columbiformes: columbid (rock dove, mourning dove, white-winged dove)			Europe
T. (T.) confusa	Galliformes: phasianid (chicken); Passeriformes: cinclid (brown dipper)	proventriculus [anaemia]	Orthoptera: acridid (grasshoppers, *Eutryxalis filata*, *Orphulella punctata*)	South America, Asia
T. (G.) daceloni	Coraciiformes: alcedinid (kookaburra)			Australia
T. (T.) dubia (syn. *T. coloradensis*, *scolopacidis*)	Charadriiformes: scolopacid (common snipe, black turnstone, dunlin, sharp-tailed sandpiper, green sandpiper, wood sandpiper, western sandpiper, long-billed dowitcher, bar-tailed godwit, red-necked stint, red-necked phalarope, ruff, Eurasian woodcock)			Australasia
T. (T.) elyi	Pelecaniformes: ardeid (great egret); Accipitriformes: accipitrid (red-shouldered hawk)	proventriculus		North America
T. (P.) fissispina (syn. *Tropisurus, Tropidocerca, Spiroptera pulicis, T. crami*)	Anseriformes: anatid (domestic duck, mallard, muscovy duck, mandarin duck, wood duck, falcated duck, ring-necked duck, long-tailed duck, mottled duck, marbled duck, tufted duck, ferruginous duck, harlequin duck, ruddy duck, white-headed duck, black-bellied whistling duck, American black duck, Pacific black duck, Indian spot-billed duck, ruddy shelduck, Australian shelduck, northern pintail, northern shoveler, Eurasian teal, Baikal teal, cinnamon teal, blue-winged teal, Eurasian wigeon, American wigeon, common pochard, red-crested pochard, Baer's pochard, common scoter, velvet scoter, surf scoter, common eider, common merganser, red-breasted merganser, smew, garganey, gadwall, common goldeneye, lesser scaup, greater scaup, canvasback, redhead, bufflehead, greylag goose, bar-headed goose, greater white-fronted goose, lesser white-fronted goose, snow goose, magpie goose, Canada goose, tundra swan, whooper swan, black-necked swan, mute swan); Charadriiformes: larid (common gull, lesser black-headed gull, black-headed gull, European herring gull); scolopacid (common snipe, Eurasian woodcock); Columbiformes:	proventriculus [anaemia]	Branchiopoda:daphniid (water flea, *Daphnia pulex*); Malacostraca: gammarid (amphipod, *Gammarus fasciatus, pulex, lacustris, locusta, maeoticus*), hyalellid (amphipod, *Hyalella azteca* (syn. *knickerbockeri*)), idoteid (isopod, *Idotea balthica*); Ostracoda: cypridid (*Heterocypris incongruens*); Insecta: baetid (mayfly larvae, *Cloeon dipterum*), ceratopogonid (midge larvae, *Culicoides*), chironomid (midge larvae, *Cricotopus, Polipedius, Prodadius, Tendipes salinarum*) [plus PH: Clupeiformes: clupeid (Caspian marine shad); Cypriniformes: cyprinid (common roach, common rudd); Gobiiformes: gobiid (monkey goby, round goby), eleotrid (bigmouth sleeper); Perciformes: percid	worldwide

	columbid (common wood pigeon, rock dove, stock dove); Falconiformes: falconid (merlin, red-footed falcon); Galliformes: phasianid (chicken, turkey, chukar, rock partridge, grey partridge, Lady Amherst's pheasant, willow ptarmigan), numidid (helmeted guineafowl); Gruiformes: gruid (crane), rallid (corn crake, sora crake, common moorhen, water rail, Eurasian coot); Pelecaniformes: ardeid (grey heron, great egret, black-crowned night heron), threskiornithid (glossy ibis); Podicipediformes: podicipedid (western grebe, horned grebe, great crested grebe, red-necked grebe, black-necked grebe, little grebe); Strigiformes: strigid (tawny owl)		(zander); Primates: hominid (human)	
T. (T.) flehartyi	Ciconiiformes: ardeid (little blue heron, Louisiana heron, reddish egret, great blue heron, snowy egret, American bittern)	proventriculus		North America
T. (P.) galericulata	Anseriformes: anatid (wood duck, mandarin duck)			Eurasia
T. (G.) globosa (syn. *T. monospicules, pavlovskii, tetrica*)	Gruiformes: rallid (American coot, Eurasian coot, common moorhen, American purple gallinule, sora, Baillon's crake			Holarctic
T. (T.) greeni	Pelecaniformes: pelecanid (Australian pelican)			Australia
T. (G.) gubanovi	Podicipediformes: podicipedid (great crested grebe, red-necked grebe, black-headed grebe, pied-billed grebe, little grebe, Australasian grebe)			cosmopolitan
T. (G.) gynaecophila	Pelecaniformes: threskiornithid (Eurasian spoonbill)			Eurasia
T. (P.) lhuillieri	Galliformes: phasianid (chukar, rock partridge, grey partridge, see-see partridge, Barbary partridge, Daurian partridge, common quail, ring-necked pheasant); Columbiformes: columbid (stock pigeon)			cosmopolitan
T. (T.) megaphasmidiata	Charadriiformes: charadriid (two-banded plover), scolopacid (white-rumped sandpiper)			South America
T. (T.) micropensis	Pelecaniformes: threskiornithid (roseate spoonbill), ardeid (yellow-crowned night heron)			Americas
T. (T.) microspinosa (syn. *T. ardamericanus*, *inerme*)	Pelecaniformes: ardeid (great egret, great blue heron, American bittern, yellow-crowned night heron), pelecanid (brown pelican); Suliformes: phalacrocoracid (double-crested cormorant, neotropic cormorant); Accipitriformes: accipitrid (osprey); Strigiformes: strigid (barred owl)	proventriculus		cosmopolitan
T. minima	Passeriformes: passerid (house sparrow)			Europe
T. (P.) mohtedai	Galliformes: phasianid (chicken, red	proventriculus	Orthoptera: acridid	India

	junglefowl); Anseriformes: anatid (domestic duck, mallard)	[anaemia]	(grasshopper, *Oxya nitudula*); Lepidoptera: tineid (moth, *Setomorpha rutella*); Coleoptera: scarabaeid (dung beetle, *Liatongus cinctus*), hydrophilinid (beetle, *Sphaeridium quinquemaculatus*); Malacostraca: percellionid (woodlouse, *Porcellio laevis*)	
T. (T.) nouveli	Charadriiformes: charadriid (lesser sand plover, Kentish plover), recurvirostrid (black-winged stilt, pied stilt, red-necked avocet)			Australasia
T. numida	Galliformes: numidid (helmeted guineafowl)			Africa
T. occinea	Phoenicopteriformes: phoenicopterid (American flamingo)			Americas
T. (G.) oxylabiata	Galliformes: phasianid (hazel grouse)			Europe
T. (T.) paraaraliensis	Charadriiformes: charadriid (white-faced plover, little ringed plover, northern lapwing, American golden plover, Eurasian dotterel)			Asia
T. paradisea	Gruiformes: gruid (Stanley's crane, sandhill crane, hooded crane)	proventriculus		Africa, North America
T. (T.) paradoxa (syn. *T. certa, robusta, sobolevi, strigiphila*)	Accipitriformes: accipitrid (crested goshawk, swallow-tailed kite, marsh harrier, European honey buzzard); Procellariiformes: diomedeid (wandering albatross, shy albatross); Strigiformes: strigid (Florida barred owl)			Holarctic
T. (G.) pattersoni	Galliformes: phasianid (northern bobwhite quail)		Orthoptera: acridid (grasshopper, *Chortophaga viridifasciata, Melanoplus femurrubrum*)	North America
T. paucispina (syn. *T. quiscali*)	Passeriformes: icterid (scarlet-headed blackbird, greater Antillean grackle, common grackle, Cuban blackbird), cardinalid (northern cardinal)			Americas
T. (G.) pjandzhi	Anseriformes: anatid (mallard)			
T. (T.) prozeskyi	Bucerotiformes: bucerotid (red-billed hornbill, southern yellow-billed thornbill)			Africa
T. (P.) ryjikovi	Anseriformes: anatid (mallard, wood duck, falcated duck, blue-winged teal, Eurasian teal, Baikal teal, Eurasian wigeon, northern pintail, northern shoveler, common pochard, Baer's pochard, greater scaup, canvasback, common goldeneye, garganey, gadwall)	proventriculus		Eurasia
T. (T.) salina	Phoenicopteriformes: phoenicopterid (Chilean flamingo)			South America
T. (G.) shaanxiensis	Accipitriformes: accipitrid (cinereous vulture)			Eurasia
T. (T.) skrjabini	Charadriiformes: larid (common gull, glaucous gull, little gull, slaty-backed gull, European herring gull, Sabine's			Eurasia

	gull, gull-billed tern, sandwich tern)			
T. (P.) somateriae	Anseriformes: anatid (common eider, surf scoter, velvet scoter)			North America
T. spiculigerum	Suliformes: anhingid (American darter)			North America
T. (P.) spinosa (syn. *T. nettatus*, *pavonis*)	Anseriformes: anatid (mallard, tufted duck, ferruginous duck, long-tailed duck, ring-necked duck, ruddy duck, ruddy shelduck, northern pintail, common goldeneye, cinnamon teal, Eurasian wigeon, common pochard, red-crested pochard, bufflehead, velvet scoter, surf scoter, gadwall, greater scaup, lesser scaup, redhead, canvasback, bufflehead, tundra swan, whooper swan); Charadriiformes: larid (lesser black-backed gull), recurvirostrid (black-winged stilt), scolopacid (common redshank); Galliformes: phasianid (Indian peafowl)			Asia
T. (T.) spirospiculum	Ciconiiformes: threskiornithid (buff-necked ibis)	proventriculus		South America
T. (P.) sponsae	Anseriformes: anatid (wood duck)	proventriculus		North America
T. (*P.) striata*	Anseriformes: anatid (mallard, mottled duck, blue-winged teal)			North America
T. (T.) tarapungae	Charadriiformes: larid (red-billed gull)			New Zealand
T. timopheevoi	Galliformes: phasianid (chukar)			Eurasia
T. (*G.*) *tinamicola*	Tinamiformes: tinamid (elegant crested tinamou, pale elegant tinamou)	proventriculus		South America
T. (G.) wetzeli	Sphenisciformes: spheniscid (southern rock-hopper penguin, gentoo penguin)			South America, Antarctica
T. (G.) williamsi	Pelecaniformes: threskiornithid (American white ibis); Gruiformes: gruid (whooping crane)	proventriculus		North America
T. (P.) zakharowi	Anseriformes: anatid (greater white-fronted goose, lesser white-fronted goose, greylag goose, bean goose, brant, tundra swan)			Eurasia
Species inquirenda				
T. (G.) alii sp. inq.	Passeriformes: hirundinid (brown-throated martin)			India
T. araliensis (syn. *T. limicollis*) *sp. inq.*	Charadriiformes: recurvirostrid (pied avocet), charadriid (little ringed plover)			Eurasia
T. (G.) ardeae sp. inq.	Pelecaniformes: ardeid (grey heron)			Eurasia
T. asiatica sp. inq.	Anseriformes: anatid (common goldeneye, smew); Gruiformes: rallid (Eurasian coot)			Eurasia
T. avicula sp. inq.	Galliformes: phasianid (chicken)			Europe
T. calidris sp. inq.	Charadriiformes: scolopacid (red knot)			Australia
T. coccinea sp. inq.	Phoenicopteriformes: phoenicopterid (greater flamingo); Pelecaniformes: ardeid (cattle egret), threskiornithid (Eurasian spoonbill)			Africa

T. cochleare (*cochleariae*) *sp. inq.*	Pelecaniformes: ardeid (cattle egret, black-crowned night heron, boat-billed heron)			South America
T. (T.) cordoniferens sp. inq.	Anseriformes: anatid (lesser whistling duck)			India
T. cubana sp. inq.	Ciconiiformes: phoenicopterid (American flamingo)			Americas
T. cygni sp. inq.	Anseriformes: anatid (Bewick's swan, tundra swan, snow goose, Canada goose, mallard, blue-winged teal, lesser scaup, American wigeon)			Eurasia, Americas
T. (G.) deccani sp. inq.	Pelecaniformes: threskiornithid (Indian white ibis)			India
T. diomedeae sp. inq.	Procellariformes: diomedeid (wandering albatross, yellow-nosed albatross)			Australia
T. (G.) fermini sp. inq.	Ciconiiformes: ardeid (green heron)			Central America
T. gigas sp. inq.	Anseriformes: anatid (mallard)			South America
T. (T.) hagenbecki sp. inq.	Anseriformes: anatid (domestic duck); Galliformes: phasianid (chicken); Ciconiiformes: ciconiid (greater adjutant); Gruiformes: gruid (sarus crane)			Asia
T. (P. indiana sp. inq.	Anseriformes: anatid (ruddy shelduck)			India
T. lobibycis sp. inq.	Charadriiformes: larid (silver gull)			Australia
T. (G.) manoji sp. inq.	Psittaciformes: psittacid (plum-headed parakeet)			India
T. (G.) minutes sp. inq.	Ciconiiformes: ardeid (Indian pond heron)			India
T. numenii sp. inq.	Charadriiformes: scolopacid (Eskimo curlew, Eurasian curlew, common sandpiper)			Russia
T. (T.) phaenicopterus sp. inq.	Columbiformes: columbid (yellow-footed green pigeon)			India
T. (P.) plectropteri sp. inq.	Anseriformes: anatid (spur-winged goose)			Africa
T. schigini sp. inq.	Ciconiiformes: ardeid (purple heron)			Russia
T. scolopacis sp. inq.	Charadriiformes: scolopacid (Eurasian woodcock)			Asia
T. (G.) singhi sp. inq.	Ciconiiformes: ciconiid (white stork); Pelecaniformes: ardeid (great egret)			Africa
T. unispina sp. inq.	Passeriformes: corvid (American crow, carrion crow)			Americas
T. uxoria sp. inq.	Charadriiformes: scolopacid (common sandpiper, curlew sandpiper, Terek sandpiper, long-billed dowitcher)			Eurasia
T. vietnamensis sp. inq.	Galliformes: phasianid (silver pheasant)			Asia
Re-assigned species				
T. centuri (now *Microtetrameres*)	Passeriformes: icterid (eastern meadowlark, western meadowlark), fringillid (canary)		Orthoptera: acridid (grasshopper, *Melanoplus*)	North America
T. cloacitectus (now *Microtetrameres*)	Accipitriformes: accipitrid (Himalayan buzzard)			Asia
T. corax (now *Microtetrameres*)	Passeriformes: corvid (Eurasian magpie, large-billed crow)		Orthoptera: acridid (grasshopper,	Eurasia, North America

			Melanoplus)	
T. cruzi (now *Microtetrameres*)	Piciformes: picid (yellow-fronted woodpecker), bucconid (Guianian puffbird)			Africa
T. helix (now *Microtetrameres*)	Columbiformes: columbid (pigeon)		Orthoptera: acridid (grasshopper, *Melanoplus bivittatus*, *femurrubrum*); Blattodea: blattid (cockroach, *Blattella germanica*)	
T. inermis (now *Microtetrameres*)	Passeriformes: leiothrichid (red-billed leiothrix, Chinese hwamei), muscicapid (Siberian rubythroat), ploceid (orange weaver)		Orthoptera: acridid (grasshopper, *Locusta migratoria, Tylotropidius patagiatus*)	Africa, Asia
T. inflata *(syn. T. haemochrous*) (now *Microtetrameres*)	Falconiformes: falconid (peregrine falcon)			
T. oriolus-orientalis (now *Microtetrameres*)	Passeriformes: leiothrichid (red-billed leiothrix, Chinese hwamei); muscicapid (Siberian rubythroat)			Asia
T. spiralis (now *Microtetrameres*)	Pelecaniformes: ardeid (cattle egret)			Egypt

Parasite morphology: *Tetrameres* spp. form 3 distinct types of morphological stages during their development: eggs; larvae (4 consecutive stages encoded L1-L4); and adult worms. Each of these stages is quite unique (even peculiar) compared to other nematodes. The eggs are small and ovoid, sometimes elongated, measuring 33-62 x 18-30 µm. They have thick smooth eggshells with polar swellings and delicate circular grooves forming opercula, sometimes adorned with polar ornamentations or tufts of short filaments. The eggs are embryonated when laid and larvated when excreted with faeces. L1 are short stout cylindrical stages measuring 150-220 x 9-13 µm with several circles of tiny spines around the head, a left cephalic hook and rasp, a rhabditiform oesophagus, and a rounded tail with a few subterminal spines. L2 are larger transient stages found within invertebrate intermediate hosts, while infective L3 are larger still (measuring 1.5-4.0 mm long) and most species have crenulated cuticles (with deep transverse striations) and rounded tails often equipped with rugosities, bristles or protuberances. L4 are transient stages parasitic within birds and they have just begun to show genital formation (especially in females where the uteri grow around the intestines). Adult worms are characterised by their extreme sexual dimorphism, with pale white males being cylindrical (filiform) and bright red females being almost spherical (sometimes fusiform). Both sexes have mouths with median lips (dorsal and ventral) and lateral pseudolabia (without cephalic papillae), and an elongate bipartite oesophagus. Species belonging to the subgenera *T.* (*Tetrameres*) and *T.* (*Gynaecophila*) have anterior ends lacking specialised cuticular features, whereas those of the subgenus *T.* (*Petrowimeres*) have anterior specializations (variously described as cordons, flanges, alae, ridges, wings, processes or spines. Mature female worms have a peculiar non-vermiform appearance with bulbous globular bodies, sometimes spirally-twisted, but grossly swollen between the tapering cephalic and caudal extremities (hence their common name as globular stomach worms). Females range in size from 3.5-10.2 mm long but they are 3.0-6.0 mm wide (midbody diameter). They have 4 deep longitudinal grooves (furrows) on their surface cuticle (hence their generic name as 'tetra'-'meres'). The body is occupied by expanded uteri containing enormous numbers of eggs and the vulva opens posteriorly near the subterminal anus. In contrast, mature male worms appear vermiform, having slender thread-like bodies measuring 3.0-8.3 mm long by 116-133 µm wide. Males belonging to the subgenus *T.* (*Tetrameres*) have cuticles bearing longitudinal rows of spines, whereas those of the subgenus *T.* (*Gynaecophila*) lack spines. Males have 2 unequal slender spicules (left spicule longer) and the tail often has caudal papillae transformed into spines.

Site of infection: Developing larvae and adult worms infect the glandular stomach (proventriculus) of their avian definitive hosts. The bulbous female worms become embedded in proventricular glands while the small filiform males remain on the mucosal surface. Infective larvae develop in the haemocoel and tissues of intermediate hosts (crustaceans and insects) which have consumed worm eggs.

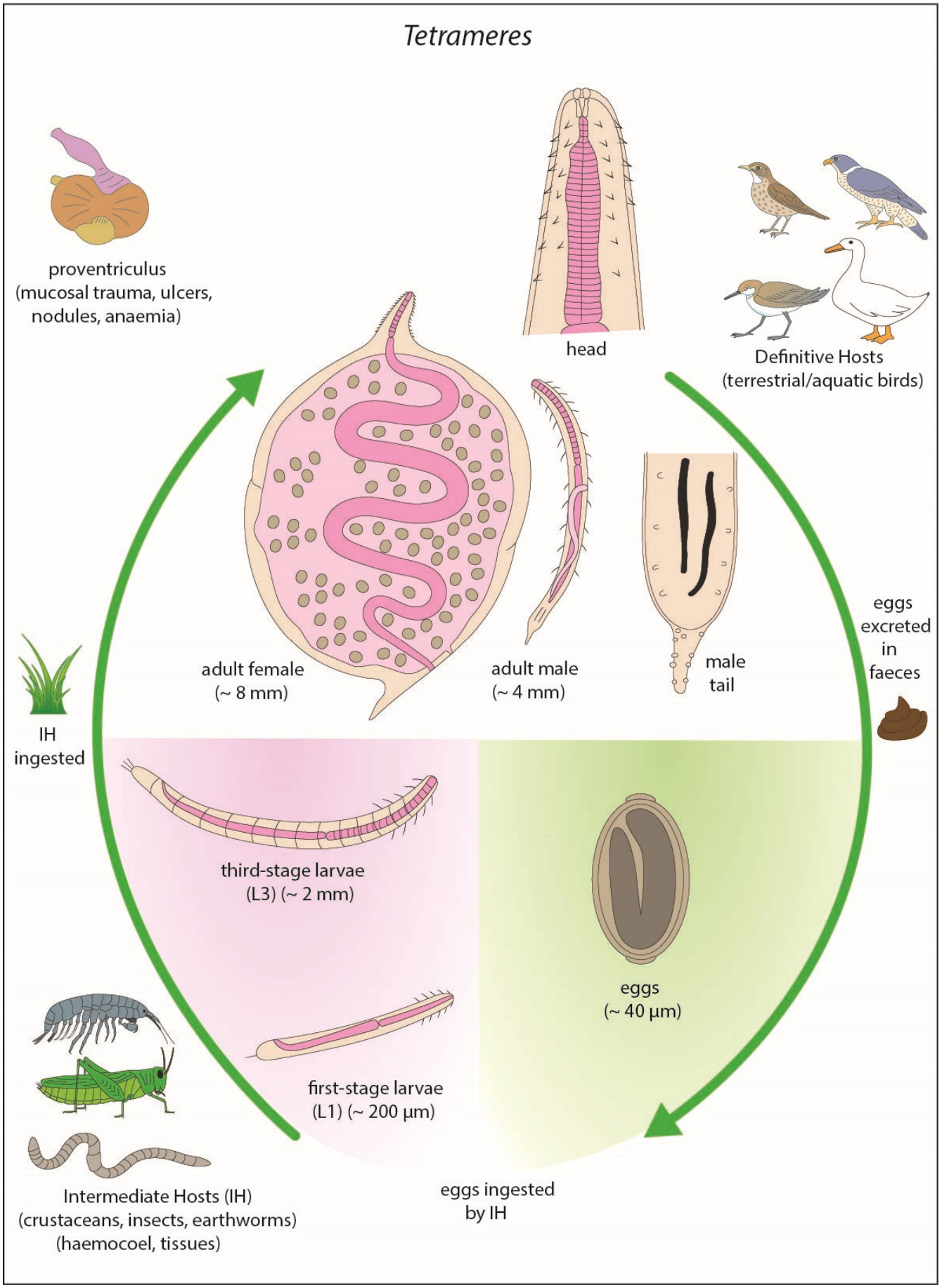
Pathogenesis: Light infections in birds are usually subclinical, but heavy infections can cause morbidity and mortality, particularly in poultry, game birds and waterfowl. Worms develop in the proventricular glands and may cause local traumatic damage, sometimes ulceration, while female worms feed on host blood and may cause anaemia. Most damage occurs, however, when females embedded in the gut wall grow and form large nodules (0.5-2.0 cm in diameter) which act as space-occupying lesions leading to glandular atrophy, proliferative proventriculitis with necrosis and sloughing of the mucosa, and progressive thickening of the gut wall. The lumen fills with thick slimy mucus and sloughed tissues, sometimes becoming partially or even completely occluded. This prevents food passage with undigested material accumulating in the proventriculus which becomes flaccid and

enlarged, sometimes perforating leading to peritonitis. Birds exhibit a range of clinical signs, including anaemia, vomiting, green faeces (due to excess bile), weight loss, weakness and emaciation, with some birds actually dying of starvation. Infections also weaken the immune system, making birds susceptible to other concomitant infections.

Developmental cycle and mode of transmission: *Tetrameres* spp. have indirect heteroxenous life-cycles involving the development of adult worms in vertebrate definitive hosts (terrestrial and aquatic birds) and the development of infective larvae in invertebrate intermediate hosts (terrestrial insects and aquatic crustaceans). Even though female worms are embedded in the proventricular glands of birds, their posterior vulvae and tails are directed towards the lumen so freshly-laid eggs can be carried into the stomach and voided with host faeces. Worm eggs are susceptible to dessication but may survive for several weeks in the external environment in the presence of moisture. The eggs are ingested by various invertebrates which act as intermediate hosts supporting larval development, notably terrestrial insects (grasshoppers, cockroaches), isopods, and earthworms, as well as aquatic crustaceans (amphipods, cladocerans). Ingested eggs hatch in the gut releasing L1 which penetrate the gut into the haemocoel and moult twice to form L3. These larvae remain free in the haemocoel for several days and then gradually encapsulate within host tissues (mostly muscles) becoming infective around 7 weeks. Final hosts become infected when they consume invertebrates containing infective L3 which invade the gastric glands, moult to L4 in 1-2 days and then to subadults (sometimes referred to as L5) in 1-2 weeks. Adult worms mature over 3 weeks and mate, the males then leaving the glands and die, while the female become embedded in fibrous capsules deep within the glands and feed on host blood. The prepatent period (time from infection to first excretion of eggs) ranges from 42-56 days.

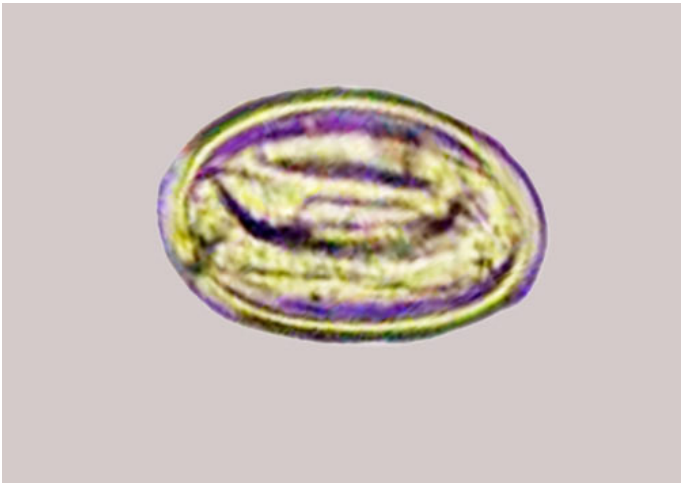
Differential diagnosis: Infections are rarely indicated by clinical signs as they are relatively nonspecific (anaemia, digestive disorders) and often slow in onset. Infections are conventionally diagnosed by the microscopic detection of worm eggs in faecal samples, either in wet mounts, smears or concentrates (floats). The eggs are unique in morphology, often being cigar-shaped and bearing polar adornments. Infections may also be diagnosed at post-mortem by the visual detection of discoloured lesions (red spots) below the proventricular mucosa. Adult worms may be recovered from lesions by dissection (teasing or squeezing with forceps). Molecular biological techniques have recently been applied to phylogenetic analyses of adult worms following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit ribosomal RNA).

Treatment and control: A range of broad spectrum anthelmintics have been used to treat clinical infections in birds, including benzimidazoles (albendazole, fenbendazole, flubendazole, mebendazole, oxfendazole), imidazothiazoles (levamisole), diethylenediamines (piperazine) and macrocyclic lactones (ivermectin). Repeated or sustained treatment is generally required to eliminate deeply embedded worms and to prevent re-infection, with most medications added to food or water in the poultry industry. Clinical infections usually do not develop in birds confined to indoor areas (poultry sheds, aviaries) but they can become problematic when birds have outdoor access where they can encounter invertebrate intermediate hosts. In these situations, attempts should be made to reduce contamination by worm eggs through improved sanitation and hygiene (regular removal of faeces, litter, bedding) and to minimise transmission through insects and crustaceans (provision of clean food and treated water, prevention of foraging, and judicious use of arthropodicidal chemicals in the environment, around holding facilities or on birds).

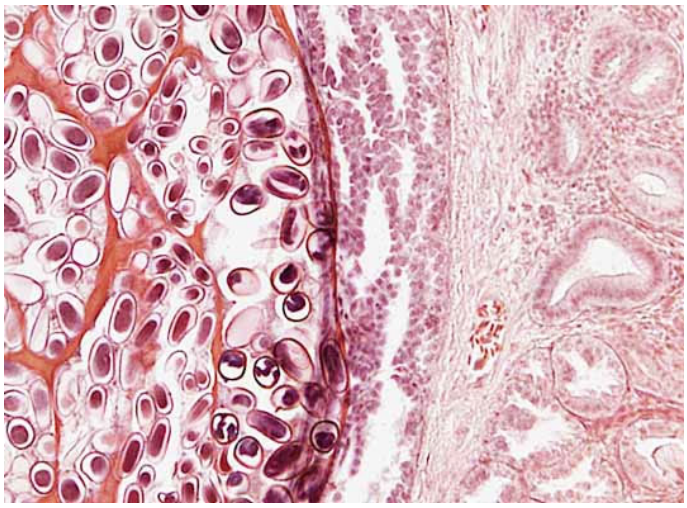

Tetrameres
proventriculus
(mucosal trauma, ulcers,
nodules, anaemia)
head
Definitive Hosts
(terrestrial/aquatic birds)
adult female
(~ 8 mm)
adult male
(~ 4 mm)
male
tail
eggs
excreted
in
faeces
IH
ingested
third-stage larvae
(L3) (~ 2 mm)
eggs
(~ 40 µm)
first-stage larvae
(L1) (~ 200 µm)
Intermediate Hosts (IH)
(crustaceans, insects, earthworms)
(haemocoel, tissues)
eggs ingested
by IH



Tetrameres adult worms



Tetrameres worm egg



Tetrameres nodule

Gongylonema
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including spiruroids (with prominent lips) containing the gongylonematids which have an unusually broad host range living in the oesophagus and stomach of mammals and the crop of birds. Infections are transmitted by coprophagous beetles and cockroaches in which L3 develop. Adult *Gongylonema* spp. are generally asymptomatic in their definitive hosts, although some species may cause regurgitation in birds.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Spiruroidea (two trilobed lips, oesophagus never with bulb, coiled tail in males, two unequal spicules)
Family:	Gongylonematidae (anterior cuticle covered with large bosses or irregular scutes arranged in rows)
Genus:	*Gongylonema* (parasitic in oesophagus/forestomach of cattle/sheep, crop of birds)
Species:	various species cause regurgitation in birds

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Spiruroidea comprises worms with simple non-ornamented heads infecting the stomach (sometimes oesophagus) of mammals and birds and using arthropods as intermediate hosts for the development of distinctive larvae with conspicuous buccal capsules with a left cephalic hook and a rasp of tiny spines. Four families are recognised: Gongylonematidae (body covered with large verruciform thickenings, pseudolabia absent, oral opening octagonal with median lobes, parasites of birds and mammals); Spiruridae (body without verruciform thickenings, reduced pseudolabia, oral opening elongated with lateral elevations, buccal cavity without teeth, parasites of mammals, rarely birds); Spirocercidae (body without verruciform thickenings, reduced pseudolabia, oral opening hexagonal, buccal cavity with teeth, parasites of mammals, rarely birds); and Hartertiidae (body without verruciform thickenings, large pseudolabia subdivided into lobes, parasites of birds). The family Gongylonematidae contains 2 genera: *Gongylonema* (syn. *Gongylomene, Misonunus, Myzomimus*) with worms having few-many verruciform thickenings (parasites of mammals, marsupials and birds); and *Progongylonema* with worms lacking verruciform thickenings (parasites from mucosa under the tongue of corvid birds) [the latter is considered by some to be a special subgenus of *Gongylonema*].

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Family: Gongylonematidae (anterior cuticle covered with large bosses or irregular scutes arranged in rows)						
Gongylonema	46	mammals, birds	oesophagus, stomach	2-15 cm long, numerous anterior bosses, 2 prominent trilobed lips, bipartite oesophagus	40-70 x 22-35 µm, ovoid, thick-shelled	indirect (L3 in insect IH)
Family: Spirocercidae (stout pink-red worm, well-developed buccal capsule, with 6 rudimentary lips)						
Subfamily: Spirocercinae (weakly-developed lips)						
Spirocerca	5	carnivores	stomach, aorta	3-8 cm long, body pink-red, buccal capsule with thick wall, 2 prominent trilobed lips, bipartite oesophagus	22-38 x 8-15 µm, elongate, thick-shelled	indirect (L3 in insect IH) [sometimes rodent, bird, reptile PH]
Cylicospirura (red worm)	10	mammals	stomach	20-30 mm long, buccal capsule with 6 longitudinal ribs ending in bifid knobs, 6 teeth, bipartite oesophagus	30-40 x 15-25 µm, elongate, thick-shelled	indirect (L3 in insect IH)
Cyathospirura (red worm)	5	mammals	stomach	6-12 mm long, buccal capsule with 6 longitudinal ribs ending in single knob, 8 teeth, bipartite oesophagus	29-38 x 13-22 µm, ovoid, thick-shelled	indirect (L3 in insect IH)
Subfamily: Ascaropsinae (buccal cavity with rugose or annular thickenings)						
Ascarops (thick stomach worm)	10	artiodactyls, rodents	stomach	10-25 mm long, oblique annuli in buccal capsule, 2 prominent trilobed lips, bipartite oesophagus	34-51 x 20-26 µm, oval, thick-shelled	indirect (L3 in insect IH) [sometimes amphibian or avian PH]
Physocephalus (thick stomach worm)	10	artiodactyls, rodents	stomach	6-22 mm long, transverse annuli in buccal capsule, 2 prominent trilobed lips, bipartite oesophagus	31-39 x 15-17 µm, ellipsoidal, thick-shelled	indirect (L3 in insect IH) [sometimes amphibian or avian PH]

The genus *Gongylonema* contains 2 subgenera: *G.* (*Gongylonema*) (numerous verruciform thickenings, spicules differ in length, gubernaculum present, parasites of mammals and birds); and *G.* (*Gongylonemoides*) (few verruciform thickenings, spicules similar in length, gubernaculum absent, parasites of American marsupials). Some 33 species infect mammals and 13 species infect birds. They have indirect life-cycles involving larval development in insect intermediate hosts (especially beetles). Infections are common in a range of animals, including poultry and domestic ruminants, but they rarely cause clinical signs, other than some instances of regurgitation in birds.

***Gongylonema* species**	**Definitive hosts**	**Location [Clinical signs]**	**Vectors (IH)**	**Distribution**
G. aegypti	Rodentia: murid (mouse)			
G. aequispicularis	Artiodactyla: cervid (roe deer)			
G. alecturae	Galliformes: megapodid (Australian brush turkey); Diprotodontia: macropodid (agile wallaby, eastern grey kangaroo)	oesophagus, stomach		Australia
G. archboldi	Rodentia: cricetid (cotton rat, cotton mouse, Oldfield mouse, Florida mouse, golden mouse)	stomach		North America
G. baylisi	Artiodactyla: tayassuid (collared peccary)			South America
G. beveridgei	Rodentia: murid (bush rat)			Australia
G. brevispiculum	Rodentia: murid (lesser Egyptian gerbil, greater Egyptian gerbil, North African gerbil, Libyan jird,			Africa

	Shaw's jird, fat sand rat)			
G. capucinus	Primates: cebid (white-faced capuchin)			India
G. caucasica	Galliformes: phasianid (chicken)			Russia
G. congolense	Anseriformes: anatid (duck, muscovy duck); Galliformes: phasianid (chicken, wild fowl)		Orthoptera: acridid (*Locusta migratoria*)	Africa
G. crami	Galliformes: phasianid (chicken)	crop [regurgitation]	Blattodea: (unspecified cockroach): Coleoptera (unspecified beetle)	worldwide, except S. America
G. dipodomysi	Rodentia: heteromyid (Merriam's kangaroo rat)			North America
G. dupuisi	Rodentia: murid (multimammate mouse)		Dermaptera: anisolabidid (*Anisolabis annulipes*)	Africa
G. falconis	Falconiformes: falconid (Eurasian hobby)			Russia
G. fotedari	Rodentia: murid (lesser bandicoot rat)			India
G. freitasi	Galliformes: phasianid (chicken)			South America
G. graberi	Galliformes: phasianid (chicken)			Europe
G. ingluvicola (gullet worm)	Galliformes: phasianid (chicken, turkey, partridge, ring-necked pheasant, mountain quail, northern bobwhite quail); Anseriformes: anatid (domestic duck); Columbiformes: columbid (pigeon)	crop, oesophagus, proventriculus [regurgitation]	Dictyoptera: ectobiid (*Blatella germanica*); Coleoptera: scarabaeid (*Copris minutus*)	worldwide
G. ivaschkini	Lagomorpha: leporid (European rabbit)		Coleoptera: tenebrionid (*Blaps fausti*)	Central Asia
G. longispiculum (incl. subspp. *longispiculum, spalacis*)	Rodentia: sciurid (little ground squirrel, European ground squirrel, Caucasian mountain ground squirrel), spalacid (greater mole-rat), cricetid (muskrat); Didelphimorphia: didelphid (Virginia opossum)			Holarctic
G. macrogubernaculum	Primates: cercopithecid (Japanese macaque)			Asia
G. madeleinensis	Rodentia: murid (Guinea multimammate mouse)			Africa
G. (*Gongylonemoides*) *marsupialis*	Didelphimorphia: didelphid (big-eared opossum, gray four-eyed opossum)	oesophagus		South America
G. mesasiatica	Galliformes: phasianid (ring-necked pheasant)			Europe
G. metopidiusi (syn. *G. indicus*?)	Charadriiformes: jacanid (bronze-winged jacana)			India
G. mexicanum	Didelphimorphia: didelphid (common opossum)			Americas
G. minima	Rodentia: murid (Persian jird)			Middle-East
G. monnigi (rumen gullet worm)	Artiodactyla: bovid (sheep, goat)	rumen, reticulum, omasum		Africa
G. mucronatum	Eulipotyphla: erinaceid (North African hedgehog, southern white-breasted hedgehog)	oesophagus	Orthoptera: acridid (*Locusta migratoria*)	Africa
G. musculi	Rodentia: murid (mouse)			Europe
G. mysciphilia	Rodentia: cricetid (deer mouse)			North America
G. neoplasticum (syn. *G. orientale, problematicum, Spiroptera carcinoma, neoplasticum*)	Rodentia: murid (mouse, yellow-necked mouse, wood mouse, striped field mouse, large Japanese field mouse, brown rat, black rat, Polynesian rat,	oesophagus, stomach [regurgitation]	Blattodea: blattid (*Blatta orientalis, Periplaneta americana*); Coleoptera: tenebrionid (beetle, *Adesmia biseriata, gebleri,*	Eurasia

	Philippine black rat, Asian house rat, Libyan jird, Persian jird, Mongolian gerbil), cricetid (social vole, bank vole, European water vole, Major's pine vole, European hamster, Turkish hamster), caviid (guinea pig); Eulipotyphla: erinaceid (European hedgehog); Lagomorpha: leporid (European rabbit)		*Blaps deplanata, fausti, oblonga, Pisterotarsa gigantea, Trigonoscelis, Tenebrio molitor*)	
G. nepalensis	Artiodactyla: bovid (water buffalo)			Asia
G. nitsulescui	Eulipotyphla: erinaceid (northern white-breasted hedgehog)			Europe
G. pacoi (*now Progongylonema*)	Passeriformes: corvid (Eurasian jay, western jackdaw, azure-winged magpie, Eurasian magpie)	tongue		Europe
G. peromysci	Rodentia: cricetid (deer mouse)			North America
G. phasianella	Galliformes: phasianid (sharp-tailed grouse)			Europe
G. pithyusensis	Rodentia: glirid (garden dormouse)			Europe
G. pulchrum (syn. *G. confusum, contortum, filiforme, hominis, labiale, microgubernaculum, ransomi, scutatum, spirale, subtile, ursi*) (gullet worm)	Artiodactyla: bovid (cattle, African buffalo, sheep, argali, goat, mouflon, impala, goitered gazelle, Maxwell's duiker), cervid (roe deer, chital, fallow deer, red deer, sika deer, white-tailed deer), camelid (camel, dromedary, llama), suid (pig, wild boar, Sardinian wild boar); Perissodactyla: equid (horse, donkey, onager); Lagomorpha: leporid (rabbit, cape hare); Rodentia: murid (brown rat), caviid (guinea pig), hystricid (Indian crested porcupine), echimyid (coypu), sciurid (Sherman's fox squirrel); Eulipotyphla: erinaceid (four-toed hedgehog), soricid (lesser white-toothed shrew); Didelphimorphia: didelphid (common opossum); Carnivora: canid (dog), felid (cat), mephitid (skunk), ursid (American black bear); Galliformes: phasianid (chicken); Anura: bufonid (European green toad); Primates: callitrichid (common marmoset), cercopithecid (Japanese macaque), hominid (human)	oesophagus, mouth, tongue, stomach	Blattodea: blattid (cockroach, *Blattella germanica*); Coleoptera: scarabaeid (beetle, *Amphimallon, Aphodius elegans, fimetarius, fossor, granarius, haroldianus, lugens, lunifer, luridus, macovski, melanostictus, moestus, pusillus, rectus, satellitius, sordidus, sublimatus, tianshanicus, urostigma, Caccobius jessoensis, schreberi, Chironitis hungaricus, Copris acutidens, hispanus, lunaris, ochus, Gymnopleurus aciculatus, mopsus, Liatongus phanaeoides, Oniticellus fulvus, pallens, pallipes, Onitis humerosus, Onthophagus amyntas, bivertex, catta, deflexicollis, fracticornis, gibbulus, koshantschikovi, lemur, leucostigma, nuchicornis, pugargus, quadridentatus, ruficapillis, similis, speculifer, tracticornis, verticicornis, Oryctes nasicornis, Pentodon, Scarabaeus sacer, Sisphyus schaefferi*), dermestid (*Dermestes*), geotrupid (beetle, *Geotrupes impressus*), tenebrionid (*Blaps*	worldwide

			deplanata, oblonga, Cyphogenia gibba, Pisterotarsa gigantea, Tenebrio molitor); Orthoptera: acridid (grasshopper, *Calliptamus barbarus, italicus*), gryllid (*Gryllus bimaculatus*), tettigonid (bush cricket, *Semenoviana tameriana, Tettigonia*)	
G. rodhaini	Artiodactyla: giraffid (okapi)			Africa
G. saimirisi	Primates: cebid (Guianan squirrel monkey)			South America
G. sciurus	Rodentia: sciurid (red squirrel)			Russia
G. soricis	Eulipotyphla: soricid (common shrew, greater white-toothed shrew, greater red musk shrew, Fraser's musk shrew)	oesophagus	Dictyoptera: blattid (*Periplaneta orientalis*)	Africa
G. spalacis	Rodentia: spalacid (lesser mole rat), cricetid (muskrat)			Russia
G. sumani	Galliformes: phasianid (chicken)			India
G. thapari	Galliformes: phasianid (grey junglefowl)			India
G. verrucosum (rumen gullet worm)	Artiodactyla: bovid (sheep, goat, Siberian ibex, cattle, zebu), cervid (white-tailed deer)	rumen, reticulum, omasum	Blattodea: (unspecified cockroach); Coleoptera (unspecified beetle)	Asia, Africa, Americas

Parasite morphology: *Gongylonema* spp. form 3 different types of developmental stages: eggs; larvae (4 successive stages named L1-L4); and adult worms. The thick-shelled eggs are ovoid measuring 40-70 x 22-35 μm and are fully embryonated when laid. L1 are coiled up within the eggs but when freed they are elongate cylindrical stages measuring 100-300 x 6-13 μm and have rounded heads, conspicuous buccal capsules with a left cephalic hook and a rasp of tiny spines, rhabditoid oesophagus, and rounded tails sometimes bearing a circle of small spines. L2 are larger transient stages found in intermediate hosts, while L3 are larger still (measuring 1.0-4.2 mm long) and already possess most cephalic features of adults as well as lateral alae and rounded tapering tails, often with terminal spines or tubercles. L4 are transient parasitic stages that develop in definitive hosts and they possess developing genitalia. Adults are elongate white worms with slender cylindrical bodies measuring from 20-150 mm in length by 150-300 μm in width. The adults are embedded in the mucosa in an undulating, spiral, zipper or zig-zag fashion (hence the occasional common name of zig-zag worm) usually with their anterior and/or posterior ends protruding into the lumen. *Gongylonema* worms are readily identified by occurrence of large swollen verruciform (round-oval) thickenings or protrusions (often called plaques or bosses) that cover the cuticle, few to many in number, and arranged in several longitudinal irregular rows anteriorly which reduce in thickness posteriorly. Two subgenera are recognised: *G.* (*Gongylonema*) with numerous verruciform thickenings; and *G.* (*Gongylonemoides*) with few verruciform thickenings. The cuticles of both subgenera have transverse striations and 2 well-developed cervical alae, festooned in some species (e.g. *G. verrucosum*). The head is rounded with an octagonal mouth surrounded by small inconspicuous lips and some species possess a raised peribuccal rectangular shield (e.g. *G. ingluvicola*). The bipartite oesophagus has an anterior muscular and a posterior glandular portion, the excretory system has lateral canals, and the long tapering tail often displays terminal processes. Adult worms are sexually dimorphic, with females being larger than males (32-55 cf. 17-20 mm long for most species although *G. pulchrum* females may measure up to 150 mm and males up to 62 mm). Mature females are didelphic with 2 ovaries and uteri connected to a common vulva opening posteriorly near the anus. Mature males have 2 unequal narrow caudal alae giving the tail an asymmetric appearance, several pedunculate papillae around the cloaca, a gubernaculum may be present (subgenus *G.* (*Gongylonema*)) or absent (subgenus *G.* (*Gongylonemoides*)), and they contain 2 spicules, either unequal (subgenus *G.* (*Gongylonema*)) or equal (subgenus *G.* (*Gongylonemoides*)), but quite variable in length depending on species (ranging from 4-180 μm).

Site of infection: Developing larvae and adult worms occur primarily in the subepithelial tissue or submucosa of the oesophagus of their final hosts, but sometimes extending up to the tongue and mouth or down to the stomach(s) of mammals or the crop and proventriculus of birds. Infective larvae develop in the haemocoel and internal tissues of insect intermediate hosts, often becoming encapsulated in the musculature.

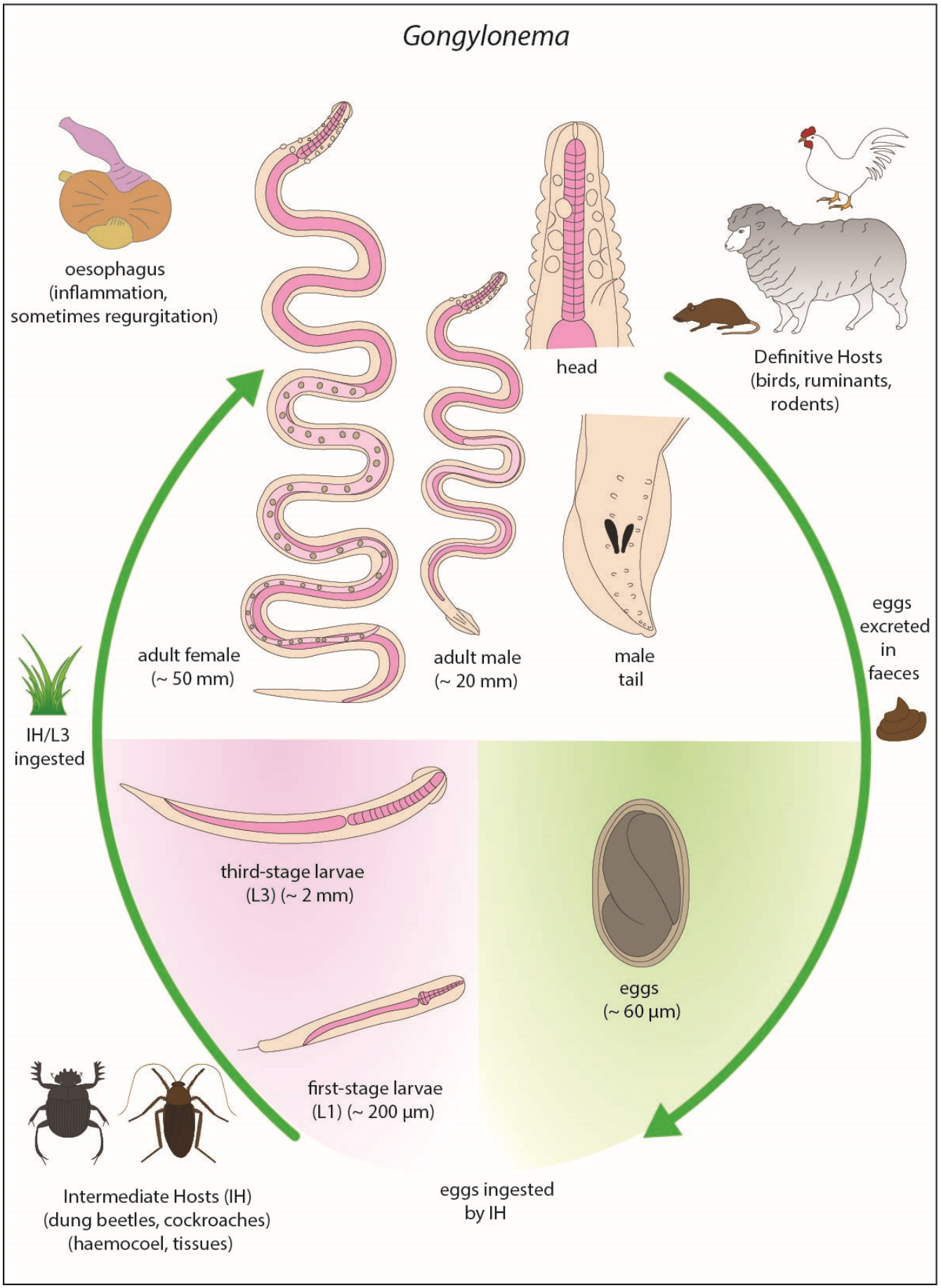
Pathogenesis: Despite the size and location of *Gongylonema* worms in their definitive hosts, infections are generally nonpathogenic and seldom cause clinical signs. Larvae and adults embedded in the mucosa of the upper digestive tract may cause some traumatic

damage and inflammation (oesophagitis) with progressive epithelial cornification, but they rarely cause functional problems as their elasticity and zig-zag configuration allows them to expand and contract along with oesophageal peristalsis. Inflammatory changes in birds may sometimes cause oesophageal sensitivity and dysphagia with occasional regurgitation. Infections by *G. neoplasticum* in rats were initially thought to cause gastric tumours, but the lesions are now considered to be non-malignant and associated with vitamin A-deficiency. Incidental infections in humans are generally noticed when young adult worms migrate beneath mucocutaneous membranes causing discomfort (foreign body sensation) in the buccal, oral or gingival regions. Symptoms take around 6 weeks to develop and may continue for months. Patients often report pulling worms from their gums, tongue, lips and inner cheeks after protracted discomfort.

Developmental cycle and mode of transmission: *Gongylonema* spp. have indirect heteroxenous life-cycles with cyclic transmission between vertebrate definitive hosts (in which adult worms develop) and invertebrate intermediate hosts (in which infective larvae develop). Female worms lay embryonated eggs which pass posteriad and are shed in host faeces into the external environment where they may survive for up to 4 months in favourable warm moist conditions. The eggs are eaten by coprophagous insects (dung beetles, cockroaches) which act as intermediate hosts as they support further larval development. Ingested eggs hatch in the gut of the insects releasing L1 which migrate into the haemocoel within 1-2 days, and then moult twice to form L3 which encapsulate with host tissues (especially the muscles) by 29-32 days. L3 survive for several months (overwinter) in insect tissues, and experimental studies have also shown that L3 dissected from insects may survive for several days in favourable moist conditions. Final hosts become infected when they consume infective L3, usually contained within insects eaten during grazing or foraging, but the possibility of freed L3 being ingested in contaminated food or water cannot be entirely dismissed. All subsequent larval and worm development occurs within the upper digestive tract (larvae do not undertake any somatic or hepatopulmonary migration). L3 migrate upward from the stomach to the oesophagus where they moult to L4 by 11 days and then to subadult stages (often referred to as L5) by 36 days after infection. The worms mature over several weeks and the prepatent period (time from infection to first excretion of eggs) ranges from 56–85 days. Humans become infected accidentally by the ingestion of infected insects or contaminated food and water. Larvae infect the upper oesophagus and migrate into the buccal cavity where some may moult to subadults, but they do not mature nor produce eggs (humans are dead-end hosts).

Differential diagnosis: Infections are generally detected incidentally at post-mortem when adult worms are discovered in the oesophageal mucosa upon dissection. Worm eggs may be detected in faecal samples following their concentration by floatation techniques, but the eggs are similar in morphology to those of some strongyles and spirurids. Infections in humans may be misdiagnosed on clinical grounds as delusional parasitosis, but are convincingly confirmed when motile young worms are detected beneath the buccal mucosa by either the patient or the doctor. Molecular biological techniques have been applied to the characterization of parasites from birds and mammals (including humans) following the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (ribosomal RNA) and mitochondrial genes (cytochrome oxidase I).

Treatment and control: No specific chemotherapeutic treatment has been recommended as many conventional and modern anthelmintics were found to be relatively ineffective. Some infections responded well to treatment with imidazothiazoles (levamisole), benzimidazoles (mebendazole, albendazole, fenbendazole), and macrocyclic lactones (ivermectin), but drug levels needed to be sustained by repeated systemic administration. Infections in humans are generally treated by surgical extraction of worms from submucosal buccal tissues, often guided by endoscopy and followed by albendazole prophylaxis. Control strategies designed to prevent infections generally consist of reducing contamination of the environment with worm eggs (through improved sanitation, faecal collection and disposal) and preventing transmission to and from insect intermediate hosts (using insecticides to control vector populations). While these strategies may be practicable in domestic or intensive-farming enterprises (generally those involving indoor holding facilities), they are unsuited to farming practices involving extensive pastures and rangelands, and should be contra-indicated in natural situations involving wildlife (the indiscriminate use of insecticides against coprophagous insects may have serious environmental consequences). Human populations in endemic regions should also be advised of the risks of accidentally or purposefully ingesting insects, especially dung beetles.


Gongylonema
oesophagus
(inflammation,
sometimes regurgitation)
head
Definitive Hosts
(birds, ruminants,
rodents)
adult female
(~ 50 mm)
adult male
(~ 20 mm)
male
tail
eggs
excreted
in
faeces
IH/L3
ingested
third-stage larvae
(L3) (~ 2 mm)
eggs
(~ 60 µm)
first-stage larvae
(L1) (~ 200 µm)
Intermediate Hosts (IH)
(dung beetles, cockroaches)
(haemocoel, tissues)
eggs ingested
by IH



Gongylonema adult worms



Gongylonema worm eggs

Spirocerca
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including spiruroids (with prominent lips) containing the spirocercids found in the stomach and aorta of dogs and transmitted by coprophagous beetles in which L3 develop. Small mammals (esp. rodents), birds and reptiles may also act as paratenic hosts for L3. Infections by *Spirocerca lupi* in dogs have been associated with vomiting, anorexia, haemothorax and sudden death.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Spiruroidea (two trilobed lips, oesophagus never with bulb, coiled tail in males, two unequal spicules)
Family:	Spirocercidae (stout pink-red worm, well-developed buccal capsule, with 6 rudimentary lips)
Genus:	*Spirocerca* (parasitic in oesophagus/aorta of dogs)
Species:	*S. lupi* (causes vomiting and haemothorax in dogs)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Spiruroidea comprises worms with simple non-ornamented heads infecting the stomach (sometimes oesophagus) of mammals and birds and using arthropods as intermediate hosts for the development of distinctive larvae with conspicuous buccal capsules with a left cephalic hook and a rasp of tiny spines. Four families are recognised: Gongylonematidae (body covered with large verruciform thickenings, pseudolabia absent, oral opening octagonal with median lobes, parasites of birds and mammals); Spiruridae (body without verruciform thickenings, reduced pseudolabia, oral opening elongated with lateral elevations, buccal cavity without teeth, parasites of mammals, rarely birds); Spirocercidae (body without verruciform thickenings, reduced pseudolabia, oral opening hexagonal, buccal cavity with teeth, parasites of mammals, rarely birds); and Hartertiidae (body without verruciform thickenings, large pseudolabia subdivided into lobes, parasites of birds). The family Spirocercidae contains 3 subfamilies: Spirocercinae (lips poorly developed, not prominently raised above oral opening, pharynx without rugose or annular thickenings, parasites of mammals and birds); Ascaropsinae (lips poorly developed, not prominently raised above oral opening, pharynx with rugose or annular thickenings, parasites of mammals); and Mastophorinae (lips highly-developed forming 6 denticulate labial lobes over oral opening, parasites of rodents). The subfamily Spirocercinae contains 8 genera (*Cyathospirura,*

Cylicospirura (syn. *Petrowospirura*), *Didelphonema, Mazzia, Paraspiralatus, Spiralatus*, *Spirocerca* and *Vigisospirura*) which are differentiated primarily on the basis of differences in adult morphology (cephalic, cuticular and genital structures), larval morphology (anatomy and ornamentation), host occurrence/specificity, geographic distribution and transmission patterns (predation, parateny). Genera of veterinary and medical significance are tabulated below:

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Family: Spirocercidae (stout pink-red worm, well-developed buccal capsule, with 6 rudimentary lips)						
Subfamily: Spirocercinae (weakly-developed lips)						
Spirocerca	5	carnivores	stomach, aorta	3-8 cm long, body pink-red, buccal capsule with thick wall, 2 prominent trilobed lips, bipartite oesophagus	22-38 x 8-15 µm, elongate, thick-shelled	indirect (L3 in insect IH) [sometimes rodent, bird, reptile PH]
Cylicospirura (red worm)	10	mammals	stomach	20-30 mm long, buccal capsule with 6 longitudinal ribs ending in bifid knobs, 6 teeth, bipartite oesophagus	30-40 x 15-25 µm, elongate, thick-shelled	indirect (L3 in insect IH)
Cyathospirura (red worm)	5	mammals	stomach	6-12 mm long, buccal capsule with 6 longitudinal ribs ending in single knob, 8 teeth, bipartite oesophagus	29-38 x 13-22 µm, ovoid, thick-shelled	indirect (L3 in insect IH)
Subfamily: Ascaropsinae (buccal cavity with rugose or annular thickenings)						
Ascarops (thick stomach worm)	10	artiodactyls, rodents	stomach	10-25 mm long, oblique annuli in buccal capsule, 2 prominent trilobed lips, bipartite oesophagus	34-51 x 20-26 µm, oval, thick-shelled	indirect (L3 in insect IH) [sometimes amphibian or avian PH]
Physocephalus (thick stomach worm)	10	artiodactyls, rodents	stomach	6-22 mm long, transverse annuli in buccal capsule, 2 prominent trilobed lips, bipartite oesophagus	31-39 x 15-17 µm, ellipsoidal, thick-shelled	indirect (L3 in insect IH) [sometimes amphibian or avian PH]
Family: Gongylonematidae (anterior cuticle covered with large bosses or irregular scutes arranged in rows)						
Gongylonema	46	mammals, birds	oesophagus, stomach	2-15 cm long, numerous anterior bosses, 2 prominent trilobed lips, bipartite oesophagus	40-70 x 22-35 µm, ovoid, thick-shelled	indirect (L3 in insect IH)

The genus *Spirocerca* contains several species of oesophageal worms with well-developed buccal capsules without median lobes or teeth but with 2 prominent trilobed lips. They are parasitic in carnivores (particularly canids) and have indirect heteroxenous life-cycles involving larval stages in intermediate hosts (mainly dung beetles) as well as in paratenic (transport) hosts (reptiles, amphibians, birds and small mammals). Infections have been found throughout the world, particularly in warmer regions where conditions are more suitable for their insect intermediate hosts.

***Spirocerca* species**	**Hosts**	**Location [Clinical signs]**	**Intermediate hosts [plus Paratenic hosts]**	**Distribution**
S. arctica	Carnivora: canid (dog, wolf, Arctic fox), mustelid (wolverine)			Northern Hemisphere
S. lupi (syn. *S. sanguinolenta*)	Carnivora: canid (dog, wolf, maned wolf, red fox, gray fox, Iberian fox, culpeo fox, coyote, golden jackal, black-headed jackal), felid (cat, jungle cat, African wild cat,	oesophagus, stomach, aorta [vomiting, weight loss, haemothorax]	Coleoptera: scarabaeid (dung beetle, *Akis goryi, Canthon depressipennis, pilarius, Catharsius pithecius, Chironitis hungaricus, Copris hispana, lunaris, Euoniticellus pallipes, Geotrupes blackburnii, douei, Gymnopleurus aciculatus, koenigi, mopsus, sinnatus, sturmi, Hister lularius, maindronii, Hybosorus lutarius, orientalis, Oniticellus pallens, pallipes, Onitis bonasus, dama, gazella, mopsus, philemon,*	worldwide, esp. tropics

	South African wild cat, bobcat, tiger, ocelot, Iberian lynx), ailurid (red panda), viverrid (common genet), mustelid (beech marten, European pine marten, stoat, least weasel, ferret)		*Onthophagus amyntas, deflexicollis, quadridentatus, Orthophagus hecate, pennsylvanicus, sylvanicus, Phanaeus vindex, Scarabaeus sacer, variolosus*), carabid (ground beetle, *Scarites indus*), tenebrionid (darkling beetle, *Pisterotarsa gigantea*); Blattodea: blattid (cockroach, *Periplaneta americana*); Odonata: aeshnid (dragonfly, *Anax parthenope*) [plus PH: Rodentia: murid (mouse, brown rat), caviid (guinea pig), glirid (forest dormouse); Lagomorpha: leporid (rabbit); Eulipotyphla: erinaceid (North African hedgehog, European hedgehog, Amur hedgehog, southern white-breasted hedgehog, northern white-breasted hedgehog), soricid (common shrew, Asian gray shrew, Asian house shrew, Eurasian pygmy shrew, bicoloured shrew), talpid (Caucasian mole, Roman mole); Carnivora: mustelid (steppe polecat), felid (cat); Chiroptera: vespertilionid (serotine bat, greater mouse-eared bat, common noctule, Kuhl's pipistrelle), rhinolophid (greater horseshoe bat, Mehely's horseshoe bat; Artiodactyla: bovid (buffalo, goat); Perissodactyla: equid (donkey); Primates: cercopithecid (rhesus macaque), hominid (human); Sauria: agamid (oriental garden lizard, Caucasian agama), lacertid (rapid racerunner, sand lizard), gekkonid (house gecko), anguid (European glass lizard), varanid (desert monitor); Serpentes: colubrid (large whip snake, spotted desert racer, grass snake, diadem snake), boid (dwarf sand boa), elapid (central Asian cobra), lamprophiid (arrow snake), viperid (blunt-nosed viper); Anura: bufonid (Asian common toad, European green toad), ranid (marsh frog); Anseriformes: anatid (duck); Accipitriformes: accipitrid (Eurasian sparrowhawk, common buzzard); Bucerotiformes: upupid (Eurasian hoopoe); Coraciiformes: coraciid (European roller); Falconiformes: falconid (Eurasian hobby); Galliformes: phasianid (chicken, double-spurred spurfowl); Passeriformes: corvid (carrion crow, alpine chough), laniid (brown shrike), meropid (European bee-eater), motacillid (white wagtail), muscicapid (northern wheatear), turdid (red-throated thrush, mistle thrush); Strigiformes: strigid (little owl, tawny owl), tytonid (barn owl)]	
S. melesi	Carnivora: mustelid (European badger)			Europe
S. vigisiana	Carnivora: canid (wolf, red fox, corsac fox), felid (Pallas's cat)			Eurasia
S. vulpis	Carnivora: canid (red fox)	stomach		Europe

Parasite morphology: *Spirocerca* spp. form 3 morphologically different stages during their developmental cycles: namely, eggs; larvae (4 consecutive stages encoded L1-L4); and adult worms. The thin-walled eggs are small (measuring 22-38 x 8-15 µm), oval-elliptical in shape (but with parallel sides) and embryonated when laid. L1 are short cylindrical stages measuring 110-124 µm, with

2 anterior cuticular rods converging at the tip, and tapering trifid tails (middle point longest). L2 are transient developmental stages which moult to form infective L3 ranging in length from 0.8-2.3 mm with heads containing 2 pointed flaps (also present on *Physocephalus* and *Ascarops*), thick-walled buccal cavities, and short tails with up to 5 spinous processes. Adults are stout pink-red worms with cylindrical coiled bodies measuring 30-80 mm long. The rounded head has 2 pointed flaps (dorsal and ventral) and a hexagonal mouth opening. The buccal capsule is well-developed and thick-walled, without median lobes or teeth but with 6 poorly-developed rudimentary lips (or 2 trilobed lips) not prominently raised above oral opening. The pharynx is short and lacks rugose or annular thickenings (present in the genera *Physocephalus* and *Ascarops* in the subfamily Ascaropsinae). Adult worms are sexually dimorphic, with females being larger than males (50-80 cf. 30-55 mm long). Mature females are didelphic with 2 ovaries and large uteri connected to a common anterior vulva. Mature males have spirally coiled tails with caudal alae, pre- and post-cloacal papillae, a rudimentary gubernaculum, and 2 elongate unequal spicules (left spicule 2.4 -2.8 mm long, right spicule 0.5-0.8 mm long).

Site of infection: Adult worms infect the walls of the oesophagus (usually the terminal portion) as well as the stomach (gastric cardial region) and the aorta (dorsal thoracic portion). Earlier developing larval stages undertake extensive migrations in the walls of blood vessels (particularly abdominal arteries), although some may undergo aberrant migration into a wide range of organs. Infective L3 develop in the haemocoel and tissues of invertebrate intermediate hosts (coprophagous beetles), but may also be carried in the tissues of various vertebrate paratenic hosts (mammals, birds, reptiles, amphibians).

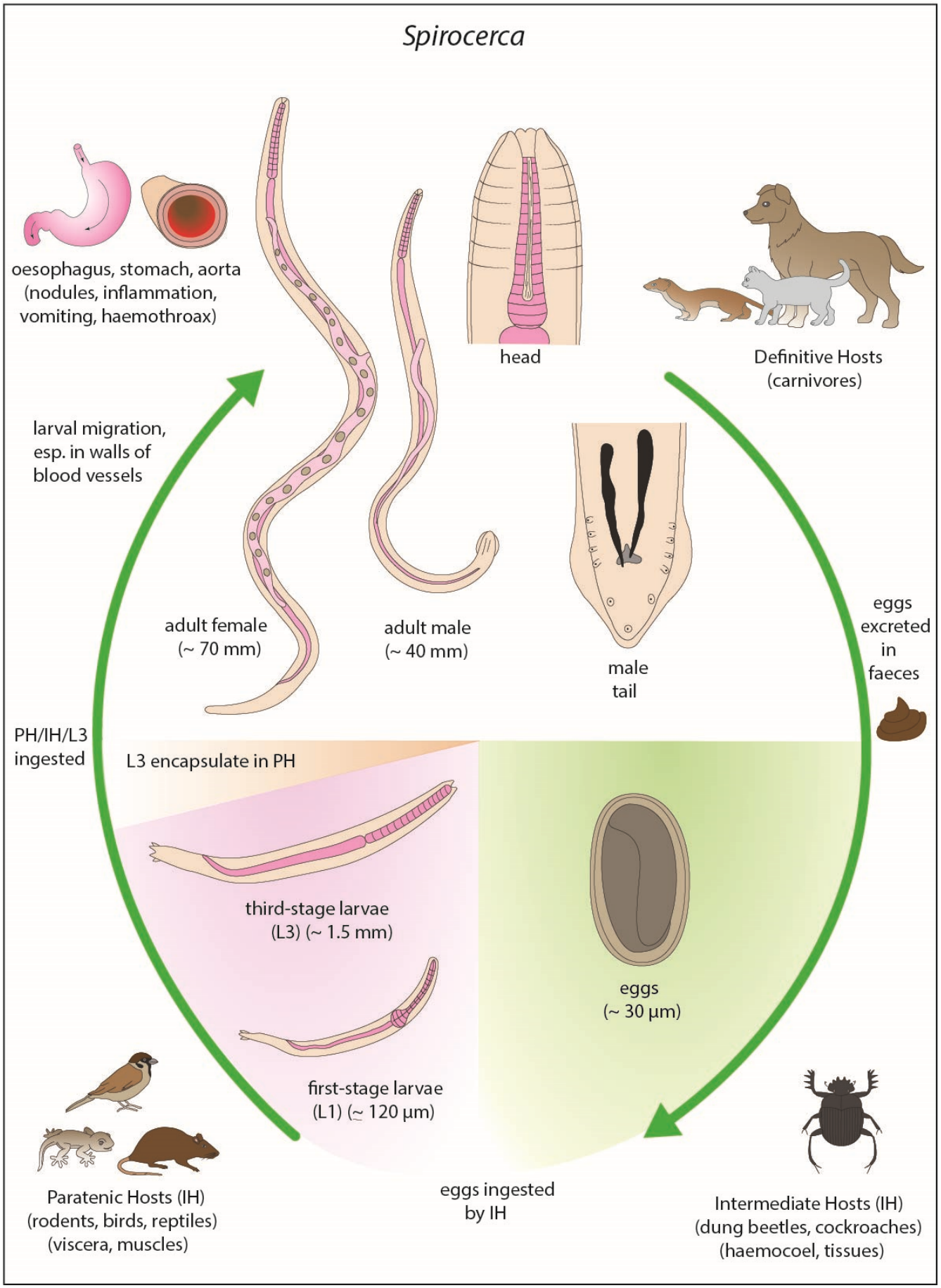
Pathogenesis: Many infections remain subclinical as only a few parasites are involved, although canids seem to tolerate heavier infections and may not develop clinical signs even when extensive lesions are present. The migratory behaviour of larvae in the walls of blood vessels followed by nodular formation by adult worms in the upper digestive tract can cause a variety of clinical signs depending on the organs involved, the susceptibility of the hosts, the numbers of parasites, and the stage of infection (prepatent or patent). Ectopic lesions may also arise due to aberrant migration of the parasites, and chronic infections by *S. lupi* may result in tumour-like lesions (neoplasia). Infective larvae penetrate the stomach wall and begin migration in the walls of coronary, gastric, gastroepiploic and celiac arteries to the upper abdominal and lower thoracic aorta. En route, they may cause small haemorrhages, inflammation (mediastinitis, endocarditis, pleuritis, peripheral lymphadenopathy, interstitial nephritis) and necrosis (including salivary gland necrosis and sialosis). Hosts may experience discomfort leading to dysphagia, vomiting and inappetence. Once within the walls of the aorta, migrating larvae may cause progressive lesions involving eosinophilic infiltrates, intimal roughening, elastic degeneration, thrombosis, muscle fibrosis, mineralization or metaplastic ossification, all contributing to permanent scarring and aneurysms (the rupture of which may result in haemothorax and sudden death). Larvae then migrate from the aortic wall to the oesophagus via the mediastinum, sometimes causing pleuritis and pyothorax presenting with dyspnoea, coughing and retching. In the oesophagus, larvae develop into adult worms in granulomatous nodules containing pleomorphic fibroblasts and several worms entwined together and feeding on host blood. Most nodules develop a fistula (opening) to the lumen for the passage of eggs but some nodules do not. Nodules may also develop in the stomach and aorta, and occasionally in other locations (mediastinum, intestines, rectum, lumbar fascia, diaphragm, trachea, lung, thymus, heart, kidney, urinary bladder, subcutis and interdigital tissue). The nodules range in size from 5-40 mm in diameter and act as space-occupying inflammatory lesions compressing local tissues and associated nerves, blood vessels and lymphatics, thus causing a wide range of clinical signs, including difficulty in swallowing, odynophagia (repeated attempts to swallow), hypersalivation with drooling (due to vagal interference), regurgitation, vomiting, and sometimes gastro-oesophageal intussusception, oesophageal obstruction or perforation, ulceration, chronic haemorrhagic anaemia, melena, haematemesis, pale mucous membranes, submandibular swelling, coughing, dyspnoea, lethargy, depression, decreased appetite or anorexia leading to weight loss and chronic wasting. Ectopic infections have also been associated with a range of secondary lesions (pyothorax, haemothorax, haemopericardium, secondary megaoesophagus, pleural effusion, lung lobe atelectasis, pyaemic nephritis), congestive heart failure (due to aorticopulmonary shunting, anterior vena cava syndrome), neurological signs (paresis, paraplegia, hyporeflexia), hypertrophic pulmonary osteoarthropathy of long bones, and hypertrophic osteopathy with spondylitis or spondylosis of thoracic vertebrae causing bone deformations leading to gait abnormalities and lameness. Chronic infections by *S. lupi* have also been associated with tumour formation (cauliflower-like oesophageal sarcoma, osteosarcoma, fibrosarcoma) in a small proportion of infected dogs. The tumours are often highly invasive and may produce metastases in the lungs and other tissues. They are thought to arise by malignant transformation of granulomas due to a combination of host, parasite and environmental factors.

Developmental cycle and mode of transmission: *Spirocerca* spp. have indirect heteroxenous life-cycles involving predator-prey transmission whereby carnivores become infected by ingesting larval stages in invertebrate intermediate hosts or vertebrate paratenic hosts. Female worms in nodules lay embryonated eggs that pass through small fistula to the lumen of the oesophagus where they are excreted with host faeces, sometimes vomitus. Egg production is often intermittent, but profuse (> 1 million eggs per day in heavy infections). The eggs are ingested by coprophagous insects (dung beetles) which act as intermediate hosts supporting further parasite development. Ingested eggs hatch in the beetle gut releasing L1 which penetrate to the haemocoel and undergo 2 moults within 2 months to form infective L3 within delicate capsules. These larvae are quite robust and can be transferred to a wide range of beetle-eating vertebrates (small mammals, birds, reptiles, amphibians) which act as paratenic (transport) hosts as the L3 do not develop further but encapsulate in various organs and tissues (especially visceral organs, mesenteries, muscles and subcutaneous tissues). L3 may even ascend the food chain being transferred from one paratenic host to another, re-encapsulating each time. Final hosts become infected when they consume infective L3 contained within intermediate or paratenic hosts. The L3 are released in the

stomach and invade the mucosa beginning an extensive migration in the walls of blood vessels (predominantly abdominal arteries) to reach the aorta within 3 weeks. They moult to L4 in 4-5 weeks and then migrate directly from the aorta via the mediastinum to the oesophagus in 12-14 weeks. Here they moult to subadults (often referred to as L5) which provoke the development of granulomatous nodules in which they mature to adults by 20 weeks. The prepatent period (time from infection to first excretion of eggs) ranges from 112-170 days, and the patent period (duration of egg excretion) may last up to 2 years.

Differential diagnosis: Clinical infections may present with a wide spectrum of signs, none of which are pathognomic. Chronic infections often involve recurrent regurgitation with weight loss and weakness, and haematological examinations often reveal anaemia and leucocytosis. Infections are usually diagnosed by the microscopic detection of worm eggs in faecal samples, mainly following their concentration by sedimentation in water and floatation in saturated sugar or heavy metal salt solutions with high specific gravities. The eggs are relatively characteristic in morphology (small, thin-walled, ellipsoidal with flat sides, and embryonated) but are similar to those of other spirurids. Egg excretion is intermittent so repeat samples may be required to rule out false negatives. The numbers of eggs excreted also does not correlate well with the intensity of infection as some nodules remain blind and do not develop fistula to release eggs. Modern imaging techniques (radiography, computed tomography, ultrasonography) may help reveal nodules or dense masses (tumours) in internal organs (especially terminal oesophagus) as well as irregularities (undulations) of the aortic wall and spondylitis of bones. Endoscopy may also be performed to determine the location and extent of nodules and tumours, and to collect biopsy samples. Infections may be diagnosed at post-mortem by the detection of granulomatous masses containing worms in the oesophagus, stomach, trachea, lungs and mediastinum. Immunofluorescence tests developed to detect specific host antibodies against parasite antigens have recorded good sensitivity and specificity in canids. Modern molecular biological techniques have recently been used to explore parasite DNA variation between species from different hosts from different geographic locations following the polymerase chain reaction (PCR) amplification of nuclear (small subunit (18S) ribosomal RNA, internal transcribed spacer 1) and mitochondrial genes (cytochrome c oxidase subunit 1).

Treatment and control: A wide range of drugs have been used in attempts to treat clinical infections in canids, but parasites are generally detected late in the course of infection when they are encapsulated in granulomatous nodules, and sometimes when tumour formation has already commenced. Variable success has been reported using several anthelmintics, including benzimidazole-methylcarbamates (albendazole), imidazothiazoles (levamisole), diethylenediamines (diethylcarbamazine), macrocyclic lactones (ivermectin, doramectin, milbemycin, moxidectin) and even disphenol sodium (now discontinued in many countries). Supportive therapy is often provided for several weeks in the form of anti-inflammatories, phenobarbital for excessive salivation, and feeding animals whilst upright to prevent regurgitation due to megaoesophagus. If neoplasia is suspected, anti-cancer drugs and/or surgical interventions should be considered. Treatment with doxorubicin and/or carboplatin has improved survival in dogs, especially those with osteosarcomas rather than fibrosarcomas. A range of preventive strategies may be implemented in peri-domestic situations where interventions can be used to reduce environmental contamination by worm eggs and to limit their transmission to intermediate, paratenic and definitive hosts. Animal holding facilities should be regularly cleaned and disinfected, and sanitary processes used to dispose of faeces and vomitus. Insecticides may be used to reduce beetle populations, rodent control measures should be implemented, and wild animals should be excluded. Animals should be provided with clean food and water and not be fed uncooked viscera from potential paratenic hosts (e.g. chickens or wild birds). They should be prevented from scavenging, hunting and roaming outdoors. Regrettably, most of these strategies are not feasible in situations involving free-ranging animals or wildlife, and the indiscriminate use of insecticides against coprophagous beetles should be discouraged in natural ecosystems.


Spirocerca
oesophagus, stomach, aorta
(nodules, inflammation,
vomiting, haemothroax)
head
Definitive Hosts
(carnivores)
larval migration,
esp. in walls of
blood vessels
adult female
(~ 70 mm)
adult male
(~ 40 mm)
male
tail
eggs
excreted
in
faeces
PH/IH/L3
ingested
L3 encapsulate in PH
third-stage larvae
(L3) (~ 1.5 mm)
eggs
(~ 30 µm)
first-stage larvae
(L1) (~ 120 µm)
Paratenic Hosts (IH)
(rodents, birds, reptiles)
(viscera, muscles)
eggs ingested
by IH
Intermediate Hosts (IH)
(dung beetles, cockroaches)
(haemocoel, tissues)



Spirocerca adult worm



Spirocerca worm egg



Spirocerca adult worm, head

Cylicospirura/Cyathospirura
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including spiruroids (with prominent lips) containing spirocercids found in the stomachs of wild carnivores and thought to be transmitted by coprophagous beetles. Infections by *Cylicospirura* and *Cyathospirura spp.* have been associated with nodular lesions in cats, dingoes, foxes and carnivorous marsupials.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Spiruroidea (two trilobed lips, oesophagus never with bulb, coiled tail in males, two unequal spicules)
Family:	Spirocercidae (stout pink-red worm, well-developed buccal capsule, with 6 rudimentary lips)
Genus:	*Cylicospirura* (parasitic in stomach of cats/foxes/dasyurids)
Genus:	*Cyathospirura* (parasitic in stomach of cats/foxes/dasyurids)
Species:	various species cause subclinical infections in carnivores

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Spiruroidea comprises worms with simple non-ornamented heads infecting the stomach (sometimes oesophagus) of mammals and birds and using arthropods as intermediate hosts for the development of distinctive larvae with conspicuous buccal capsules with a left cephalic hook and a rasp of tiny spines. Four families are recognised: Gongylonematidae (body covered with large verruciform thickenings, pseudolabia absent, oral opening octagonal with median lobes, parasites of birds and mammals); Spiruridae (body without verruciform thickenings, reduced pseudolabia, oral opening elongated with lateral elevations, buccal cavity without teeth, parasites of mammals, rarely birds); Spirocercidae (body without verruciform thickenings, reduced pseudolabia, oral opening hexagonal, buccal cavity with teeth, parasites of mammals, rarely birds); and Hartertiidae (body without verruciform thickenings, large pseudolabia subdivided into lobes, parasites of birds). The family Spirocercidae contains 3 subfamilies: Spirocercinae (lips poorly developed, not prominently raised above oral opening, pharynx without rugose or annular thickenings, parasites of mammals and birds); Ascaropsinae (lips poorly developed, not prominently raised above oral opening, pharynx with rugose or annular thickenings, parasites of mammals); and Mastophorinae (lips highly-developed forming 6

denticulate labial lobes, separate over oral opening, parasites of rodents). The subfamily Spirocercinae contains 8 genera (*Cyathospirura, Cylicospirura* (syn. *Petrowospirura*), *Didelphonema, Mazzia, Paraspiralatus, Spiralatus*, *Spirocerca* and *Vigisospirura*) which are differentiated primarily on the basis of differences in adult morphology (cephalic, cuticular and genital structures), larval morphology (anatomy and ornamentation), host occurrence/specificity, geographic distribution and transmission patterns (predation, parateny). Genera of veterinary and medical significance are tabulated below:

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Family: Spirocercidae (stout pink-red worm, well-developed buccal capsule, with 6 rudimentary lips)						
Subfamily: Spirocercinae (weakly-developed lips)						
Cylicospirura (red worm)	10	mammals	stomach	20-30 mm long, buccal capsule with 6 longitudinal ribs ending in bifid knobs, 6 teeth, bipartite oesophagus	30-40 x 15-25 µm, elongate, thick-shelled	indirect (L3 in insect IH)
Cyathospirura (red worm)	5	mammals	stomach	6-12 mm long, buccal capsule with 6 longitudinal ribs ending in single knob, 8 teeth, bipartite oesophagus	29-38 x 13-22 µm, ovoid, thick-shelled	indirect (L3 in insect IH)
Spirocerca	5	carnivores	stomach, aorta	3-8 cm long, body pink-red, buccal capsule with thick wall, 2 prominent trilobed lips, bipartite oesophagus	22-38 x 8-15 µm, elongate, thick-shelled	indirect (L3 in insect IH) [sometimes rodent, bird, reptile PH]
Subfamily: Ascaropsinae (buccal cavity with rugose or annular thickenings)						
Ascarops (thick stomach worm)	10	artiodactyls, rodents	stomach	10-25 mm long, oblique annuli in buccal capsule, 2 prominent trilobed lips, bipartite oesophagus	34-51 x 20-26 µm, oval, thick-shelled	indirect (L3 in insect IH) [sometimes amphibian or avian PH]
Physocephalus (thick stomach worm)	10	artiodactyls, rodents	stomach	6-22 mm long, transverse annuli in buccal capsule, 2 prominent trilobed lips, bipartite oesophagus	31-39 x 15-17 µm, ellipsoidal, thick-shelled	indirect (L3 in insect IH) [sometimes amphibian or avian PH]
Family: Gongylonematidae (anterior cuticle covered with large bosses or irregular scutes arranged in 8 rows)						
Gongylonema	46	mammals, birds	oesophagus, stomach	2-15 cm long, numerous anterior bosses, 2 prominent trilobed lips, bipartite oesophagus	40-70 x 22-35 µm, ovoid, thick-shelled	indirect (L3 in insect IH)

The genus *Cyathospirura* comprises worms whose buccal cavities have 8 teeth and 2 lobes (one ventral and one dorsal) while those of the genus *Cylicospirura* have 6 teeth but lack median lobes. Early studies recognised 3 *Cylicospirura* subgenera: namely, *C.* (*Cylicospirura*) (females with median vulva, males with 6 pairs of pedunculate caudal papillae (4 precloacal and 2 postcloacal) and 4 pairs of sessile papillae near tail tip, caudal end of male without spines, parasites of carnivores); *C.* (*Gastronodus*) (females with anterior vulva, males with 9-10 pairs of pedunculate caudal papillae (6-7 precloacal and 3 postcloacal) and 3 pairs of sessile papillae near tail tip, caudal end of male with 1 pair of spines, parasites of insectivores); and *C.* (*Skrjabinocercina*) (females with vulva near anus, males with 6 pairs of pedunculate caudal papillae (4 precloacal and 2 postcloacal) and 2 pairs of sessile papillae (one precloacal and one near tail tip), parasites of rodents). More recent studies, however, have elevated the latter 2 subgenera to the rank of genus, and reclassified the genus *Petrowospirura* as a subgenus of *Cylicospirura* (females with anterior vulva, males with 6 pairs of pedunculate caudal papillae (4 precloacal and 2 postcloacal), parasites of felids). Worms of both genera infect the stomach walls of carnivores (particularly canids and felids) and they are commonly found in wild animals around the world and only occasionally in domestic pets. The life-cycles of most species are not known, but are thought to involve arthropods as intermediate hosts, and possibly small vertebrates as paratenic hosts.

Parasite species	Definitive Hosts	Location [Clinical signs]	Intermediate hosts [plus Paratenic Hosts (PH)]	Distribution
Cylicospirura				
C. C. advena	Carnivora: felid (cat)	stomach		New Zealand
C. P. barusi	Carnivora: felid (cat)	stomach		India

C. crocutae	Carnivora: hyaenid (spotted hyena)			Africa
C. felineus	Carnivora: felid (cat, wildcat, bobcat, Canada lynx, leopard cat, tiger), canid (dog, Arctic fox, red fox)	stomach		worldwide
C. C. heydoni (syn. *Spirocerca*)	Dasyuromorphia: dasyurid (tiger quoll, eastern quoll, northern quoll, New Guinean quoll); Peramelemorphia: peramelid (northern brown bandicoot); Diprotodontia: macropodid (red-necked wallaby, red-bellied pademelon); Carnivora: felid (cat)	stomach, intestines, peritoneal cavity		Australasia
C. P. lyncis	Carnivora: felid (Eurasian lynx, Pallas's cat)	stomach		Russia
C. pardalis	Carnivora: felid (leopard)	oesophagus		Africa
C. petrowi (ex Matschulsky, 1952) (= *Skrjabinocercina*)	Rodentia: dipodid (Mongolian five-toed jerboa)			Russia
C. P. petrowi (ex Sadykhov, 1957)	Carnivora: felid (jungle cat)	stomach		Eurasia
C. skrjabini	Carnivora: canid (red fox, Arctic fox)	stomach		Eurasia
C. G. stresseni (= *Gastronodus*)	Eulipotyphla: soricid (Asian house shrew)	stomach		Asia
C. subaequalis (syn. *Spiroptera*)	Carnivora: felid (cougar, jaguarundi, cat, jungle cat, African wild cat, lynx, Canada lynx, leopard cat, leopard, Bengal tiger, lion), viverrid small Indian civet), canid (red fox), hyaenid (spotted hyena)	stomach		worldwide
Cyathospirura				
C. chabaudi	Carnivora: canid (dog)	stomach	[PH: Sauria: gekkonid (yellow-belly gecko)]	India
C. chevreuxi	Carnivora: felid (African wild cat, ocelot)			Africa
C. grimaldiae	Carnivora: canid (Atlas fox)			Africa
C. nouveli	Carnivora: viverrid (genet)			Africa
C. seurati (*seurata*) (syn. *C. dasyuridis*)	Carnivora: canid (fennec fox, red fox, dog, dingo), felid (cat), viverrid (common genet), mustelid (beech marten); Dasyuromorphia: dasyurid (eastern quoll, tiger quoll, New Guinean quoll, Tasmanian devil); Rodentia: murid (black rat), cricetid (Gambian pouched rat), glirid (garden dormouse)	stomach		worldwide

Parasite morphology: Members of the genera *Cylicospirura* and *Cyathospirura* each form 3 different morphological stages during their developmental cycles: namely, eggs, larvae, and adult worms. The eggs are small thick-shelled oval-elliptical stages measuring 29-38 x 13-25 µm and are fully embryonated when laid. Larvae moult through 4 consecutive stages (designated L1 to L4) before forming adult worms. L1 are formed within worm eggs, L2 appear transiently within invertebrate intermediate hosts, L3 become encysted within the same intermediate hosts and are possibly transferred to small vertebrate paratenic hosts, while L4 appear transiently in definitive hosts prior to moulting to subadult worms. Few detailed studies have been conducted on the development of these larval stages, so their morphometrics are relatively unknown. The L3 of some species have been described as elongate cylindrical stages measuring 1.4-1.5 mm long with weakly developed genital primordia and tapering tails terminating in groups of spines. Adults are bright red cylindrical worms measuring 6-30 mm in length with rounded heads, sometimes with small lateral alae, and short rounded tails without spines. They have thick-walled buccal capsules with rudimentary non-protruding lips and longitudinal supporting ribs terminating anteriorly in tooth-like structures with rounded knobs or pointed bifid or trifid projections. *Cyathospirura* spp. have 2 median lobes (one ventral and one dorsal) and 8 buccal teeth, while *Cylicospirura* spp. lack median lobes and have 6 buccal teeth (2 lateral and 4 submedian). Both genera possess a short pharynx without rugose or annular thickenings (which are present in the genera *Physocephalus* and *Ascarops* in the sister subfamily Ascaropsinae). Adult worms are sexually dimorphic, with females being larger than males (30 cf. 22 mm long). Mature female worms are didelphic with 2 ovaries and uteri

connected to a common vulva located near the oesophageal-intestinal junction. Mature males possess a single testis connected to a posterior cloaca, narrow caudal alae bearing 6 pairs of pedunculate papillae (4 precloacal and 2 postcloacal) and 4 pairs of sessile papillae, a gubernaculum and 2 dissimilar spicules (left spicule 2 mm long, right spicule 0.5 mm long).

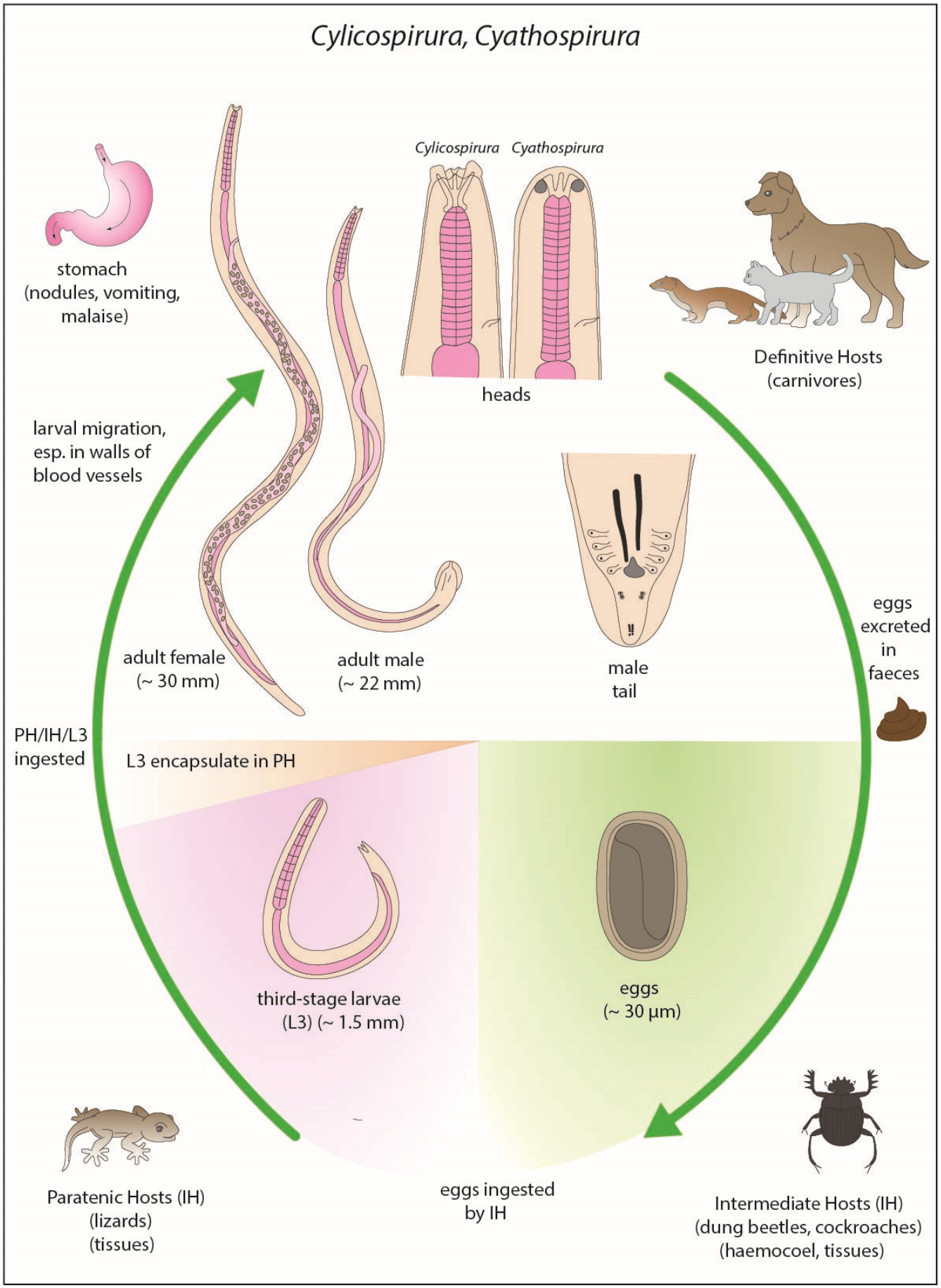
Site of infection: Adult worms infect the stomach (sometimes oesophagus) of their vertebrate hosts, often being found in fibrous nodules in the mucosa, but sometimes free in the lumen. Larval stages are thought to develop in invertebrate intermediate hosts, and encapsulated L3 have been found in the internal organs of lizards presumably acting as paratenic hosts.

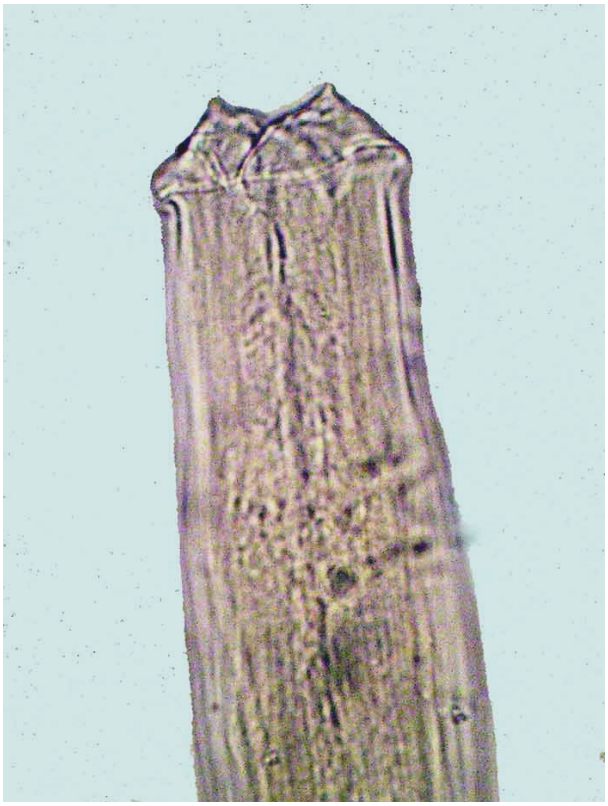
Pathogenesis: Most infections remain subclinical as either few parasites are involved or they are not highly invasive. Some species form adult worms which stay within the stomach lumen while those of other species are found coiled together within granulomatous tumour-like nodules deep in the mucosa or submucosa of the stomach, particularly along the greater curvature. The nodules ranged in size from 4-30 mm in diameter and contained up to 45 worms. Most nodules have a small central orifice from which the posterior ends of some worms protrude. Other small nodules were observed to be filled with firm yellowish caseous material. Infections have been associated with general malaise in cats, with intermittent vomiting, anorexia and weight loss, and occasionally with purulent cysts and melena, and rarely with gut perforation and septicaemia. The unique fibrous stromal reaction involved in nodule formation may cause a condition known as verminous alimentary sclerosing fibroplasia, which may be misdiagnosed as sclerosing mast cell tumours or extraneous osteosarcomas, but *Cylicospirura* nodules have not been shown to progress to neoplasms (unlike those of *Spirocerca lupi).*

Developmental cycle and mode of transmission: While detailed life-cycle studies are lacking, these worms, like other spirocercid nematodes, are thought to have indirect heteroxenous cycles involving larval development in invertebrate intermediate hosts, and possibly larval transport in small vertebrate paratenic hosts. Gravid female worms lay embryonated eggs in the stomach of their vertebrate hosts, either directly into the lumen or through the central orifice in mucosal nodules. The eggs pass posteriad and are excreted with host faeces. It is then thought that the eggs are ingested by terrestrial insects (such as cockroaches, ground beetles and crickets) which act as intermediate hosts supporting further parasite development. Typically, eggs hatch in the arthropods releasing L1 which invade tissues and develop through 2 moults to infective L3. Paratenic transport hosts may now be involved in some cycles, as studies have found L3 encapsulated in the gut tissues of insectivorous lizards were infective to dogs resulting in the development of adult worms in 24 days. It has been speculated that a range of paratenic hosts (e.g. lizards, snakes, frogs and even small mammals such as rodents) may be involved in various cycles. The final hosts (carnivorous eutherian and metatherian mammals) become infected when they consume infective L3 contained within the tissues of intermediate or paratenic hosts . Ingested L3 do not undertake any somatic or extra-intestinal migration but develop through 2 moults to adult worms directly within the gut. The prepatent period (time from infection to first egg excretion) has been variously reported to range from 75-156 days.

Differential diagnosis: Infections are most often diagnosed by the detection of worm eggs in faecal samples, usually following their concentration by floatation in sugar or salt solutions with high specific gravities. Gastroscopy has been used to detect suspect nodular lesions in the stomach mucosa, sometimes with slender red worms extending through the central orifice. Infections may also be diagnosed at post-mortem by the detection of adult worms in the stomach lumen or mucosa. More recently, molecular biological techniques have been used to characterize parasite species by polymerase chain reaction (PCR) amplification and sequencing of mitochondrial genes (cytochrome c oxidase subunit 1).

Treatment and control: Broad-spectrum anthelmintics have been used with some success to treat infections mainly in felids, but those species in which adult worms are contained within large fibrous nodules were more resistant to treatment. Therapeutic courses of benzimidazoles (fenbendazole) and macrocyclic lactones (selamectin) were most effective, particularly when dosages were maintained by repeated or sustained applications. Various preventive strategies may be applied in peri-domestic situations (involving indoor holding facilities) to reduce contamination and transmission rates by improving sanitation and hygiene (regular removal of faeces, cleaning cages, providing clean food and water) and limiting contact with potential intermediate and paratenic hosts (reducing insect vector populations using chemicals and/or barriers, and preventing final hosts from scavenging and hunting).


Cylicospirura, Cyathospirura
stomach
(nodules, vomiting,
malaise)
Cylicospirura
Cyathospirura
heads
Definitive Hosts
(carnivores)
larval migration,
esp. in walls of
blood vessels
adult female
(~ 30 mm)
adult male
(~ 22 mm)
male
tail
eggs
excreted
in
faeces
PH/IH/L3
ingested
L3 encapsulate in PH
third-stage larvae
(L3) (~ 1.5 mm)
eggs
(~ 30 µm)
Paratenic Hosts (IH)
(lizards)
(tissues)
eggs ingested
by IH
Intermediate Hosts (IH)
(dung beetles, cockroaches)
(haemocoel, tissues)



Cylicospirura adult worm, head



Cylicospirura wsorm eggs

Ascarops/Physocephalus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including spiruroids (with prominent lips) containing spirocercids found in the stomach of pigs and transmitted by coprophagous beetles in which L3 develop. Amphibians and birds may act as paratenic hosts for L3. Infections by *Ascarops* and *Physocephalus* spp. have been associated with inappetence in pigs.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Spiruroidea (two trilobed lips, oesophagus never with bulb, coiled tail in males, two unequal spicules)
Family:	Spirocercidae (stout pink-red worm, well-developed buccal capsule, with six rudimentary lips)
Genus:	*Ascarops* (parasitic in stomach of pigs)
Genus:	*Physocephalus* (parasitic in stomach of pigs)
Species:	various species cause inappetence in pigs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Spiruroidea comprises worms with simple non-ornamented heads infecting the stomach (sometimes oesophagus) of mammals and birds and using arthropods as intermediate hosts for the development of distinctive larvae with conspicuous buccal capsules with a left cephalic hook and a rasp of tiny spines. Four families are recognised: Gongylonematidae (body covered with large verruciform thickenings, pseudolabia absent, oral opening octagonal with median lobes, parasites of birds and mammals); Spiruridae (body without verruciform thickenings, reduced pseudolabia, oral opening elongated with lateral elevations, buccal cavity without teeth, parasites of mammals, rarely birds); Spirocercidae (body without verruciform thickenings, reduced pseudolabia, oral opening hexagonal, buccal cavity with teeth, parasites of mammals, rarely birds); and Hartertiidae (body without verruciform thickenings, large pseudolabia subdivided into lobes, parasites of birds). The family Spirocercidae contains 3 subfamilies: Spirocercinae (lips poorly developed, not prominently raised above oral opening, pharynx without rugose or annular thickenings, parasites of mammals and birds); Ascaropsinae (lips poorly developed, not prominently raised above oral opening, pharynx with rugose or annular thickenings, parasites of mammals); and Mastophorinae (lips highly-developed forming 6

denticulate labial lobes, separate over oral opening, parasites of rodents). The subfamily Ascaropsinae contains 10 genera (*Ascarops* (syn. *Arduenna*), *Leiuris* (syn. *Spirocercella*), *Physocephalus* (syn. *Pereiraia*, *Physocephaloides*), *Pygarginema*, *Simondsia*, *Spirobakerus*, *Spirosprattus*, *Streptopharagus*, *Tejeria*, and *Texicospirura*) which are differentiated primarily on the basis of differences in adult morphology (cephalic, cuticular and genital structures), larval morphology (anatomy and ornamentation), host occurrence/specificity, geographic distribution and transmission patterns (predation, parateny). Genera of veterinary and medical significance are tabulated below:

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Family: Spirocercidae (stout pink-red worm, well-developed buccal capsule, with 6 rudimentary lips)						
Subfamily: Ascaropsinae (buccal cavity with rugose or annular thickenings)						
Ascarops (thick stomach worm)	10	artiodactyls, rodents	stomach	10-25 mm long, oblique annuli in buccal capsule, 2 prominent trilobed lips, bipartite oesophagus	34-51 x 20-26 µm, oval, thick-shelled	indirect (L3 in insect IH) [sometimes amphibian or avian PH]
Physocephalus (thick stomach worm)	10	artiodactyls, rodents	stomach	6-22 mm long, transverse annuli in buccal capsule, 2 prominent trilobed lips, bipartite oesophagus	31-39 x 15-17 µm, ellipsoidal, thick-shelled	indirect (L3 in insect IH) [sometimes amphibian or avian PH]
Subfamily: Spirocercinae (weakly-developed lips)						
Spirocerca	5	carnivores	stomach, aorta	3-8 cm long, body pink-red, buccal capsule with thick wall, 2 prominent trilobed lips, bipartite oesophagus	22-38 x 8-15 µm, elongate, thick-shelled	indirect (L3 in insect IH) [sometimes rodent, bird, reptile PH]
Cylicospirura (red worm)	10	mammals	stomach	20-30 mm long, buccal capsule with 6 longitudinal ribs ending in bifid knobs, 6 teeth, bipartite oesophagus	30-40 x 15-25 µm, elongate, thick-shelled	indirect (L3 in insect IH)
Cyathospirura (red worm)	5	mammals	stomach	6-12 mm long, buccal capsule with 6 longitudinal ribs ending in single knob, 8 teeth, bipartite oesophagus	29-38 x 13-22 µm, ovoid, thick-shelled	indirect (L3 in insect IH)
Family: Gongylonematidae (anterior cuticle covered with large bosses or irregular scutes arranged in 8 rows)						
Gongylonema	46	mammals, birds	oesophagus, stomach	2-15 cm long, numerous anterior bosses, 2 prominent trilobed lips, bipartite oesophagus	40-70 x 22-35 µm, ovoid, thick-shelled	indirect (L3 in insect IH)

The genus *Ascarops* contains worms with poorly-developed flat lips, buccal cavities with 6 teeth or 6 groups of teeth, and a straight pharynx with spiral wall thickenings, while those of the genus *Physocephalus* have 6 large lips joined to form 2 lateral masses elevated above the anterior extremity, unarmed buccal cavities and elongated oesophagus. Some 18 species have been described from the stomachs of mammals, and the parasites have indirect life-cycles with larval development occurring in invertebrate intermediate hosts and sometimes being transported in small mammalian paratenic hosts. In particular, 2 species (*Ascarops strongylina* and *Physocephalus sexalatus*) commonly infect pigs around the world, sometimes causing catarrhal gastritis.

Parasite species	Definitive Hosts	Location [Clinical signs]	Intermediate Hosts [and Paratenic Hosts (PH)]	Distribution
Ascarops				
A. africana (syn. *Arduenna*)	Rodentia: murid (four-striped grass mouse), glirid (hazel dormouse); Serpentes: lamprophiid (striped house snake)			Africa
A. dentata	Artiodactyla: suid (pig, wild boar, Indian boar): Eulipotyphla: erinaceid	stomach [inappetence]		Asia

	(four-toed hedgehog)			
A. joliveti	unknown		Coleoptera: tenebrionid (darkling beetle, *Hegeter tristis*)	Canary Islands
A. kutassi	Rodentia: sciurid (little ground squirrel, Asia Minor ground squirrel)			Eurasia
A. minuta	Chiroptera: vespertilionid (West European pond bat)			Europe
A. mogera	Eulipotyphla: talpid (Japanese mole, Kobe mole, Sado mole)			Asia
A. scaptochiri	Rodentia: cricetid (Chinese striped hamster)			China
A. strongylina (thick stomach worm)	Artiodactyla: suid (pig, wild boar, Sardinian wild boar, Indian boar, warthog), bovid (cattle), camelid (camel); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig), murid (black rat), spalacid (trans-Baikal zokor); Psittaciformes: cacatuid (sulphur-crested cockatoo)	stomach, small intestines [inappetence]	Coleoptera: scarabaeinid (dung beetle, *Caccobius*, *Canthon*, *Copris lunaris, Ceratophius*, *Cotinis, Dyscinetus, Oniticellus pallens, pallipes*, *Onitis philemon, ramellosus, Onthophagus catta, cervus, deflexicollis, falsus, gazella, gibbulus, mopsus, nuchicomis, quadridentatus, ramosellus, Phanaeus vindex, Phyllophaga*, *Potosia hungarica, Scarabaeus*), aphodiid (beetle, *Aphodius castaneus, granarius, moestus, rufus, sticticus*), geotrupid (dor beetle, *Anoplotrupes stercorosus, Geotrupes mutator, pyrenacius, stercorarius, vernalis, Gymnopleurus mopsus, pervus, Trypocopris vernalis*), histerid (clown beetle, *Hister corax*, *maindronii*), hybosorid (scavenger beetle, *Hybosorus orientalis*), passalid (leather beetle, *Passalus cornutus*), trogid (*Trox granulatus*); Odonata: aeshnid (dragonfly, *Anax parthenope*) [plus PH: Rodentia: murid (mouse, wood mouse), caviid (guinea pig), glirid (edible dormouse), sciurid (Indian palm squirrel, ground squirrel); Eulipotyphla: erinaceid (four-toed hedgehog, southern white-breasted hedgehog, northern white-breasted hedgehog), soricid (common shrew, lesser white-toothed shrew, Eurasian pygmy shrew), talpid (European mole); Chiroptera: vespertilionid (common noctule, lesser noctule, common pipistrelle, western barbastelle, parti-coloured bat, serotine bat, Bechstein's bat, Daubenton's bat, Natterer's bat, lesser mouse-eared bat, greater mouse-eared bat, brown long-eared bat, whiskered bat, pond bat), rhinolophid (greater horseshoe bat, lesser horseshoe bat); Serpentes: colubrid (Asiatic water snake, pond snake, large whip snake, slender whip snake, smooth snake, grass snake, checkered keelback), lamprophiid (Montpellier snake), viperid (common European adder); Sauria: anguid (sheltopusik, slow worm, European	worldwide

			glass lizard), gekkonid (Mediterranean house gecko), lacertid (sand lizard, Macedonian lizard, common wall lizard, European green lizard, viviparous lizard); Anura: bufonid (European green toad), ranid (moor frog)]	
A. talpa	Eulipotyphla: talpid (Formosan mole)	small intestines		Taiwan
A. tuvensis	Rodentia: sciurid (suslik)			Eurasia
Physocephalus				
P. dromedarii	Artiodactyla: camelid (dromedary)	abomasum	Coleoptera: scarabaeinid (rainbow scarab, *Phanaeus vindex*, dung beetle, *Scarabaeus cristatus*)	Middle-East
P. ellobii *sp. inq.*	Rodentia: heterocephalid (mole rat)		[PH: Coraciiformes: meropid (olive bee-eater)]	Africa
P. gracilis	Pilosa: bradypodid (pale-throated sloth)			South America
P. lassancei	Artiodactyla: cervid (brown brocket, red brocket deer)	abomasum		South America
P. mediospiralis	Rodentia: dasyproctid (agouti), cuniculid (paca)			South America
P. meridionalis	Perissodactyla: tapirid (South American tapir); Rodentia: cuniculid (lowland paca, lappe), dasyproctid (agouti, Azara's agouti)	stomach		South America
P. nitidulans	Perissodactyla: tapirid (South American tapir)	stomach		South America
P. quadrialatus	Rodentia: cricetid (grey dwarf hamster, Turkish hamster)			Eurasia
P. raphiceri	Artiodactyla: bovid (steenbuck)	abomasum		Africa
P. sexalatus	Artiodactyla: suid (pig, wild boar, Sardinian wild boar, warthog), tayassuid (white-lipped peccary, collared peccary), bovid (cattle), camelid (dromedary, Bactrian camel), cervid (roe deer, red brocket deer); Perissodactyla: tapirid (tapir), equid (horse, donkey); Lagomorpha: leporid (rabbit, hare); Diprotodontia: macropodid (Matschie's tree-kangaroo, rufous hare-wallaby, whiptail wallaby, allied rock wallaby, unadorned rock wallaby, red-legged pademelon)	stomach [inappetence]	Coleoptera: scarabaeid (dung beetle, *Amphimallon solstitialis, Aphodius*, *Ataenius cognatus, Ateuchus*, *Boreocanthon*, *Canthon laevis, Catharsuis, Ceratophius*, *Chironitis hungarica, Copris hispanus, lunaris*, *Deltochilum*, *Dichotomius*, *Gymnopleurus aciculatus, mopsus, parvus, sinnatus, sturmi, Melanocanthon*, *Oniticellus pallens, pallipes, Onthophagus bedeli, catta, centricornis, cervus, deflexicollis, gibbulus, hecate, nebulosus, quadridentatus, speculifer, Pentodon idiota, Phanaeus carnifex, vindex, Pinotus*, *Scarabaeus sacer, variolosus*), geotrupid (dung beetle, *Geotrupes douei, stercorarius, Trypocopris vernalis*), passalid (leather beetle, *Passalus cornutus*), silphid (carrion beetle, *Oiceoptoma*), tenebrionid (darkling beetle, *Pisterotarsa gigantea*), trogid (*Trox*); Blattodea: polyphagid (cockroach, *Polyphaga sausserae*); Dermoptera: labidurid (earwig, *Labidura riparia*); Diplopoda: glomerid	worldwide

			(pill millipede, *Glomeris*); Decapoda: penaeid (white shrimp, *Litopenaeus setiferus*) [plus PH: Rodentia: murid (mouse, wood mouse, rat), cricetid (hispid cotton rat); Chiroptera: vespertilionid (little brown bat, common pipistrelle, Kuhl's pipistrelle, Nathusius's pipistrelle, barbastelle bat, northern bat, serotine bat, Bechstein's bat, Daubenton's bat, Natterer's bat, lesser mouse-eared bat, greater mouse-eared bat, brown long-eared bat, whiskered bat, pond bat, common noctule, lesser noctule), rhinolophid (greater horseshoe bat, lesser horseshoe bat); Cingulata: dasypodid (nine-banded armadillo), Eulipotyphla: erinaceid (four-toed hedgehog, European hedgehog, southern white-breasted hedgehog, northern white-breasted hedgehog, long-eared hedgehog), soricid (common shrew, lesser white-toothed shrew), talpid (European mole); Pilosa: bradypodid (three-toed sloth); Sauria: agamid (secret toadhead agama, steppe agama, Caucasian agama), anguid (slow worm, European glass lizard), gekkonid (Caspian bent-toed gecko, frog-eyed gecko), lacertid (sand lizard, Macedonian lizard, viviparous lizard), varanid (desert monitor); Serpentes: boid (dwarf sand boa), colubrid (cat snake, diadem snake, large whip snake, slender whip snake, spotted desert racer, smooth snake, steppe rat snake, grass snake, dice snake, Aesculapian snake), elapid (central Asian cobra), lamprophiid (arrow snake), viperid (common European viper), blunt-nosed viper; Anura: bufonid (European green toad); Accipitriformes: accipitrid (Eurasian sparrowhawk, red-tailed hawk); Charadriiformes: scolopacid (upland sandpiper, long-billed curlew); Cichliformes: cichlid (Pantano cichlid); Galliformes: numidid (helmeted guineafowl); Passeriformes: corvid (Eurasian magpie), laniid (loggerhead shrike); Strigiformes: strigid (eastern screech owl); Cichliformes: cichlid (Pantano cichlid); Siluriformes: heptapterid (pale catfish)]	
P. torresi	Rodentia: dasyproctid (agouti)	stomach		South America

Parasite morphology: *Ascarops* and *Physocephalus* nematodes form 3 different type of morphological stages during their development: eggs; larvae (4 consecutive stages designated L1 to L4); and adult worms. The eggs are small, oval-elliptical in shape but slightly flattened at the poles, thick-shelled and embryonated when laid. *Ascarops* eggs range in size from 34-51 x 20-26 µm, while *Physocephalus* eggs are slightly smaller measuring 31-39 x 15-17 µm. First-stage larvae (L1) freed from eggs were elongate

and cylindrical measuring around 150 μm in length, and they have rounded heads (sometimes with delicate spines), a prominent cephalic hook and tapering tails terminating in a conical knob (sometimes with tiny pointed processes). L2 are transient stages formed within intermediate hosts, while L3 are long-lasting stages often coiled up within membranous capsules. L3 freed from cysts range in length from 1.9-2.3 mm and have a cylindrical pharynx and tails terminating in a smooth knob-like process (*Ascarops*) or numerous digitiform processes (*Physocephalus*). L4 are transient parasitic stages that are beginning to develop adult mouthparts and genital primordia. Adults are small red-brown worms with cylindrical bodies measuring 6-25 mm in length. They often possess cervical, lateral and caudal alae, the former 2 being separated by an anterior cuticular inflation in the genus *Physocephalus* resulting in an arrowhead appearance. The anterior mouth has poorly-developed flat lips (*Ascarops*) or 2 trilobed lateral lips projecting upwards (*Physocephalus*). Both genera have well-developed thick-walled buccal capsules without median lobes but with prominent annuli (transverse in *Physocephalus*, oblique in *Ascarops*). The buccal capsule is unarmed (*Physocephalus*) or armed with 6 teeth or 6 groups of teeth (*Ascarops*). The oesophagus is bulbous and elongated (*Physocephalus*) or straight with spiral wall thickenings (*Ascarops*). Adult worms are sexually dimorphic, with females being larger than males (15-25 cf. 10-15 mm long for *Ascarops*, 13-22 cf. 6-13 mm long for *Physocephalus*). Mature females are didelphic with 2 ovaries and uteri connected to a midbody vulva and their tails have poorly-developed caudal alae. Mature males have curved twisted tails with well-developed caudal alae, characteristically asymmetrical (right side wider than left), 4 pairs of long pedunculate papillae (3 pairs precloacal, 1 pair adcloacal), and 2 unequal dissimilar spicules (long thin left spicule, short thick blunt right spicule).

Site of infection: Adult worms infect the stomachs (rarely the small intestines) of their definitive hosts, usually residing on top of the epithelium under a layer of mucus. Infective L3 develop in the body cavities of insect intermediate hosts, and they may also encapsulate in the mesenteries and viscera of small vertebrate paratenic hosts.

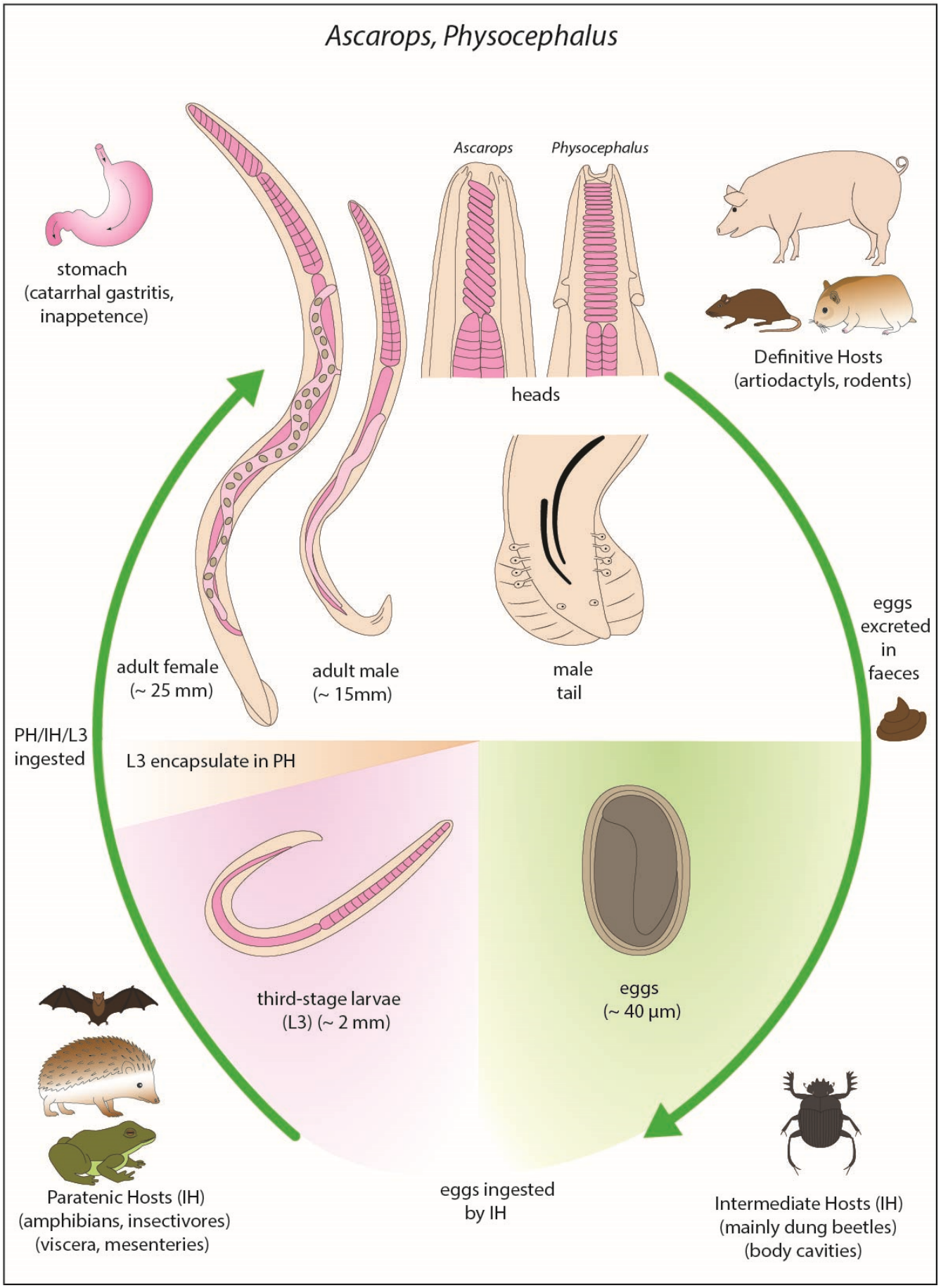
Pathogenesis: Infections by these stomach worms are relatively non-pathogenic as the parasites do not invade tissues but live in the lumen of the stomach. Heavy infections in young animals may cause a mild catarrhal gastritis with reddening and oedema of the mucosa but rarely resulting in clinical signs other than softening of the faeces and inappetence. Adult worms are found in animals over the age of 4 months, and the intensity of infection may increase with host age due to repeated exposure. Rare reports have been made where adult worms were detected in association with small haemorrhages and gastric ulcerations in pigs with anaemia, bloody diarrhoea and weight loss, but the animals were also infected with other nematodes considered to be more pathogenic (notably *Hyostrongylus* and *Gnathostoma*).

Developmental cycle and mode of transmission: *Ascarops* and *Physocephalus* spp. have indirect heteroxenous life-cycles involving the development of adult worms in vertebrate definitive hosts, larval development in invertebrate intermediate hosts, and sometimes larval carriage in vertebrate paratenic hosts. Gravid females lay embryonated eggs in the stomach which are excreted with host faeces. The eggs survive well in the external environment, particularly in moist areas, and they have been shown to be dispersed in manure used to fertilise pastures and in wastewater used for irrigation. The eggs are ingested by variety of coprophagous insects (especially dung beetles, but also including other terrestrial beetles, cockroaches, earwigs, millipedes, dragonflies) which act as intermediate hosts supporting further larval development. Ingested eggs hatch in the gut within 1-3 days releasing L1 which migrate to the haemocoel, moult to L2 in 16-19 days and again to L3 in 25-31 days before encapsulating in host tissues. Infective L3 may be transferred to a range of insect-eating animals (rodents, bats, insectivores, birds, lizards, snakes, amphibians, fish, shrimp) which act as paratenic transport hosts because the larvae do not undergo any further development but re-encapsulate within host tissues. Final (definitive) hosts become infected by ingesting L3 contained within intermediate or paratenic hosts. Ingested L3 are released within the stomach and migrate to the pyloric region within 5-9 days (they do not undertake any somatic or extraintestinal migration). They moult to L4 in 4-5 days and then subadults (sometimes referred to as L5) within 20 days before maturing to adult worms by 25-31 days. The prepatent period (time from infection to first egg excretion) ranges from 42-50 days, and adult worms are thought to live for 10-11 months.

Differential diagnosis: Infections are diagnosed by the direct detection of parasites, either by the antemortem detection of worm eggs in faecal samples, or by the postmortem detection of adult worms on the stomach lining. The worm eggs are small, thick-shelled and contain active larvae, but they are not very buoyant so are best concentrated by floatation in heavy metal salt solutions with high specific gravities. Adult worms are usually visible due to their bright red colouration but they may be obscured by mucus. Molecular biological techniques have been used to examine parasite phylogenetic relationships and identify larvae following the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (ribosomal RNA and internal transcribed spacers).

Treatment and control: There is little information on specific drug treatments for these stomach worms as they are not considered to be serious pathogens in livestock production. However, several broad spectrum anthelmintics regularly used for other helminth parasites are thought to be effective against adult stomach worms, including tetrahydropyrimidines (pyrantel), organophosphonates (dichlorvos) and macrocylic lactones (ivermectin, doramectin). It has been recommended that regular chemoprophylaxis be used in intensive farming situations, with drenches give twice a year (around weaning in spring and confinement in autumn). Most infections are found in wild or feral pigs, or farmed pigs which are free-range or have some access to open pastures where they can contact potential intermediate and paratenic hosts. Various preventive strategies may be

implemented in intensive farm situations to reduce pasture contamination and limit transmission, but such strategies are not practical in extensive farming situations or in natural systems involving wildlife. Where possible, sanitary practices should be used to remove and dispose of faeces. Animals should have access to clean food and water, and manure should not be used to fertilise pastures and wastewater should not be used for irrigation. Pasture rotation with other livestock or crops may be used but care should be taken that other parasites with broad host specificities do not become more widespread. Holding facilities should be regularly cleaned and disinfected, and coprophagous insects should be excluded (using chemicals and/or barriers). Livestock should be prevented from foraging in open areas and they should not be fed with offal or tissues from terrestrial or aquatic animals which may act as paratenic hosts.


Ascarops, Physocephalus
stomach
(catarrhal gastritis,
inappetence)
Ascarops
Physocephalus
heads
Definitive Hosts
(artiodactyls, rodents)
adult female
(~ 25 mm)
adult male
(~ 15mm)
male
tail
eggs
excreted
in
faeces
PH/IH/L3
ingested
L3 encapsulate in PH
third-stage larvae
(L3) (~ 2 mm)
eggs
(~ 40 µm)
Paratenic Hosts (IH)
(amphibians, insectivores)
(viscera, mesenteries)
eggs ingested
by IH
Intermediate Hosts (IH)
(mainly dung beetles)
(body cavities)



Ascarops adult worm, head



Physocephalus adult worm, head



Ascarops worm egg

Acuaria/Cosmocephalus/Dispharynx/Echinuria/Streptocara
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including acuarioids (with cephalic cordons) found in the oesophagus, proventriculus and gizzards of birds and are transmitted by water fleas, isopods, grasshoppers and beetles in which L3 develop. Numerous genera (*Acuaria, Cosmocephalus, Dispharynx, Echinuria, Streptocara*) have been associated with oesophagitis, proventriculitis and emaciation predominantly in waterfowl.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Family:	Acuariidae (cephalic cordons, grooved cuticular structures)
Genus:	*Acuaria* (parasitic in gizzard of birds)
Genus:	*Cosmocephalus* (parasitic in oesophagus of birds)
Genus:	*Dispharynx* (parasitic in proventriculus of birds)
Genus:	*Echinuria* (parasitic in oesophagus of birds)
Genus:	*Streptocara* (parasitic in gizzard of birds)
Species:	various species cause inflammation and emaciation in birds

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but

some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Acuarioidea comprises medium-sized worms with 2 triangular pseudolabia and elaborate cephalic ornamentation consisting of grooved cuticular elevations (in the form of cordons, collarettes or ptilina) infecting the stomach of birds (rarely mammals) and using arthropods (aquatic crustaceans or terrestrial insects) as intermediate hosts for larval development, and sometimes fish and amphibians as paratenic hosts for larval transport. A single family (Acuariidae) is recognised with over 300 species classified in 40 genera in 3 subfamilies: Acuariinae with 4 cordons extending beyond the pseudolabia and males with 4 pairs of precloacal papillae (*Acuaria, Antechiniella, Aviculariella, Chandleronema, Cheilospirura, Chevreuxia, Chordatortilis, Chordocephalus, Cosmocephalus, Decorataria* (sometimes included in *Syncuaria*), *Desportesius, Dispharynx* (sometimes included in *Synhimantus*), *Echinuria* (syn. *Hamannia*), *Parachordatortilis, Paracuaria, Pectinospirura, Pelecanema, Pseudoavicularielle,*

Sexansocara, Skrjabinocara, Skrjabinocerca, Skrjabinoclava, Stammerinema, Syncuaria (sometimes included in *Echinuria*), *Synhimantus, Voguracuaria, Willmottia,* and *Xenocordon*); Seuratiinae with cephalic collarettes limited to the bases of the pseudolabia and males with 4 pairs of precloacal papillae (*Deliria, Ingliseria, Navonia, Proyseria, Pseudohaplonema, Rusguniella, Seuratia, Stegophorus, Streptocara* and *Tikusnema*); and Schistorophinae with 4 ptilina arising from the sublabia in the form of horns, lappets, blades or leaf-like structures, and males with 5 or more pairs of precloacal papillae (*Ancyracanthopsis, Molinacuaria, Quasithelazia* (sometimes included in *Schistorophus*), *Schistorophus, Sciadiocara,* and *Viktorocara*). Recent molecular phylogenetic studies have shown the family Acuariidae to be monophyletic with 2 major clades: one formed by members of the subfamily Schistorophinae (with ptilina), and the other composed of members of the subfamilies Acuariinae (with cordons) and Seuratiinae (with collarettes alternatively interpreted as cordons restricted to the cephalic region).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission
Subfamily: Acuariinae (cordons extend longitudinally)						
Acuaria	70	mainly passerine birds	gizzard	8-30 mm long, cordons long, vulva median	40-65 x 27-50 µm, ovoid, thick-shelled	indirect (L3 in insect IH)
Cosmocephalus	9	fish-eating birds	oesophagus, proventriculus	9-22 mm long, cordons looped, vulva median	31-40 x 18-22 µm, ovoid, thick-shelled	indirect (L3 in amphipod IH) [fish PH]
Dispharynx	15	passerine, galliform birds, some birds of prey	oesophagus, proventriculus	3-10 mm long, cordons curved, vulva posterior	22-42 x 17-26 µm, ovoid, thick-shelled	indirect (L3 in isopod IH)
Echinuria	16	water birds	proventriculus	4-21 mm long, cordons displaced ventrally, vulva posterior	28-37 x 17-23 µm, ovoid, thick-shelled	indirect (L3 in crustacean IH)
Subfamily: Seuratiinae (cordons forming collarette)						
Streptocara	8	water birds	gizzard	3-11 mm long, collarette serrated	32-65 x 18-50 µm, ovoid, thick-shelled	indirect (L3 in amphipod IH) [fish PH]

Many genera have been described from the upper digestive tracts of a wide range of passerine and non-passerine birds around the world, sometimes in association with inappetence, wasting and sometimes anaemia and death. Representative genera include *Acuaria* (cordons long, rectilinear and extending longitudinally (not recurrent or anastomosing), spicules equal or subequal, no tuft of spines on tail of female, vulva median), *Cosmocephalus* (cordons recurrent anteriorly and anastomose laterally, composed of inner row of plates (giving scalloped appearance) and an outer longitudinal ridge, female tail with terminal projection, vulva median), *Dispharynx* (cordons with descending arms forming several curves (not anastomosing), vulva posterior), *Echinuria* (cordons anastomose but not recurrent, 2 pairs of longitudinal rows of cuticular spines, vulva posterior), and *Streptocara* (circular cephalic collarette (sometimes described as cordons), limited to bases of paired pseudolabia, posterior border generally serrated or divided into several teeth, female tail short and rounded, vulva median-posterior).

Parasite species	Definitive hosts	Location [Clinical signs]	Intermediate hosts [plus Paratenic hosts (PH)]	Distribution
Subfamily Acuariinae				
Acuaria				
A. alii	Passeriformes: motacillid (grey wagtail), muscicapid (black redstart), sturnid (common mynah, common starling)			Eurasia
A. anthuris (syn. *A. corvicola, depressa*, *nebraskensis*, *scutata*)	Coraciiformes: coraciid (European roller); Passeriformes: alaudid (horned lark), campephagid (long-tailed minivet), cinclid (brown dipper, white-throated dipper), corvid (Eurasian magpie, Oriental magpie, black-billed magpie, red-billed blue magpie, blue jay, Eurasian jay, American crow, Cuban crow, house crow, large-	gizzard	Coleoptera: tenebrionid (darkling beetle, *Adesmia biseriata, Pisterotarsa gigantea*); Orthoptera: acridid (grasshopper, *Calliptamus italicus, Chorthippus longicornis, Locusta migratoria, Melanoplus femurrubrum*), gryllid (unidentified crickets); Malacostraca: gammarid	worldwide

	billed crow, hooded crow, fish crow, carrion crow, eastern carrion crow, rook, common raven, Chihuahuan raven, rufous treepie, Indian treepie, red-billed chough), motacillid (pipit), muscicapid (blue whistling thrush), oriolid (Indian golden oriole), passerid (sparrow), sturnid (common mynah, crested mynah, great mynah, common starling, black-collared starling, red-billed starling, vinous-breasted starling, rosy starling), vaganid (large wood shrike)		(amphipod, *Gammarus lacustris*)	
A. brevispicula	Passeriformes: muscicapid (bluethroat), sturnid (common mynah)			Europe
A. brumpti (syn. *A. attenuata*, *dollfusi, muscicapae*, *papillifera*, *paragalliardi*)	Passeriformes: acrocephalid (great reed warbler, icterine warbler), alaudid (crested lark, horned lark, calandra lark), corvid (hooded crow, rook, Eurasian jay), emberizid (red-headed bunting), hirundinid (common house martin, sand martin, barn swallow), laniid (brown shrike), motacillid (white wagtail, tree pipit), muscicapid (spotted flycatcher), phylloscopid (greenish warbler), sturnid (rosy starling), sylviid (common whitethroat, lesser whitethroat), turdid (common nightingale, thrush nightingale)			worldwide
A. caeruleus	Passeriformes: muscicapid (blue whistling thrush)			Eurasia
A. cettiae	Passeriformes: cettid (Manchurian bush warbler)			Asia
A. cincli	Passeriformes: cinclid (brown dipper)			Asia
A. cissae	Passeriformes: corvid (red-billed blue magpie)			Asia
A. coloradensis	Passeriformes: hirundinid (violet-green swallow)			North America
A. colluricinclae	Passeriformes: pachycephalid (western shrikethrush)			Australia
A. copsychusi	Passeriformes: muscicapid (Oriental magpie-robin)	gizzard		India
A. cordata	Passeriformes: alaudid (horned lark), corvid (common raven), dicrurid (black drongo, hair-crested drongo), laniid (red-backed shrike, great grey shrike, lesser grey shrike, long-tailed shrike, brown shrike), motacillid (water pipit, white wagtail, grey wagtail), muscicapid (black redstart), phylloscopid (dusky warbler), sturnid (rosy starling), turdid (common blackbird)			Eurasia
A. cordonspinosa	Passeriformes: vireonid (white-eyed vireo)	gizzard		Cuba

A. crami	Passeriformes: dicrurid (fork-tailed drongo)			Africa
A. crypsirinae	Passeriformes: corvid (grey treepie)			Asia
A. dicrura	Passeriformes: dicrurid (greater racket-tailed drongo), motacillid (white wagtail)			Africa
A. europaea	Piciformes: picid (Syrian woodpecker); Passeriformes: oriolid (Eurasian golden oriole)	gizzard		Europe
A. excubitori	Passeriformes: laniid (great grey shrike)	gizzard		India
A. flindersi	Falconiformes: falconid (brown falcon)			Australia
A. galliardi	Passeriformes: muscicapid (flycatcher)			Europe
A. gracilis	Passeriformes: corvid (Eurasian jay), motacillid (olive-backed pipit), oriolid (Eurasian golden oriole)			Eurasia
A. gruveli	Galliformes: phasianid (double-spurred spurfowl, grey partridge, Barbary partridge, chukar, red-legged partridge, Daurian partridge, common quail, Japanese quail, ring-necked pheasant, black grouse, Himalayan snowcock); Passeriformes: corvid (Eurasian jay); Strigiformes: strigid (Eurasian eagle-owl)	gizzard	Orthoptera: acridid (grasshopper, *Tylotropidus patagiatus*)	Africa, Eurasia
A. hamulosa (syn. *A. pavonis, Cheilospirura*)	Galliformes: phasianid (chicken, red junglefowl, Burmese peafowl, Indian peafowl, turkey, chukar, rock partridge, ring-necked pheasant, common quail), numidid (helmeted guineafowl); Anseriformes: anatid (domestic duck); Columbiformes: columbid (rock dove); Passeriformes: corvid (large-billed crow), pycnonotid (light-vented bulbul), sturnid (white-shouldered starling); Pelecaniformes: ardeid (whistling heron, yellow-crowned night heron)	gizzard [weight loss, anaemia]	Orthoptera: acridid (grasshopper, *Aeolopus tamulus, Melanoplus differentialis, femurrubrum, Oxya chinensis, nitidula, sinensis, Paroxya clavuliger, Prumna* (*Primnoa*) *ussriensis*), pyrgomorphid (*Atractomorpha ambigua*), tettigoniid (*Conocephalus sallator, Decticus verrucivorous, Gampsocleis sadahovi, Phaenoreptereus falcata, Stilpnochlora couloniana*); Malacostraca: talitrid (amphipod, *Orchestia platensis*); Coleoptera: curculionid (flower beetle, *Oxydema fisiforme, Sitophilus oryzae*), dermestid (skin beetle, *Dermestes ater*), hydrophilid (water scavenger beetle, *Dactylosternum abdominale*), mycetophagid (fungus beetle, *Litargus balteatus, Typhaea stercorea*), nitidulid (sap beetle, *Carpophilus dimidiatus*), scarabaeid (dung beetle, *Scarabaeus sacer*), tenebrionid (darkling beetle, *Adesmia biseriata, Epitragus*	worldwide

			diremptus, Palorus ratzeburgi, Tenebroides nana, Tenturia gigas, Tribolium castaneum); Blattodea: blattid (cockroach); Diptera: ulidiid (picture-winged fly, *Euxestus*), Dermaptera: anisolabidid (earwig, *Carcinophora americana, Euborellia annulipes*), forficulid (*Doru taeniata*), labidurid (*Labidura bidens, reporia*), spongiphorid (*Marava unidentata*); Diplopoda: spirobolellid (millipede, *Microspirobolus*)	
A. kinsellai	Passeriformes: dicrurid (black drongo)			Asia
A. kungi	Passeriformes: muscicapid (Indian robin)			India
A. lanii	Passeriformes: laniid (long-tailed shrike)			Asia
A. lina	Passeriformes: icterid (western meadowlark), motacillid (grey wagtail)			North America
A. longicaudata	Passeriformes: corvid (large-billed crow, collared crow, Oriental magpie)			Asia
A. lophurae (syn. *Cheilospirura*)	Galliformes: phasianid (silver pheasant, ring-necked pheasant)			Asia
A. lucknowensis	Passeriformes: corvid (common green magpie)	gizzard		India
A. magpii	Passeriformes: corvid (blue magpie)	gizzard		India
A. mamillaris	Passeriformes: corvid (cayenne jay)	gizzard		South America
A. martinagliai	Passeriformes: ploceid (South African weaver)			Africa
A. mayori	Passeriformes: corvid (purplish jay, plush-chested jay), thraupid (double-collared seedeater, saffron finch), tyrannid (Nutting's fly catcher)			Americas
A. microecae	Passeriformes: petroicid (jacky winter)			Australia
A. microspinosa	Pelecaniformes: ardeid (yellow-crowned night heron)			Americas
A. minor	Passeriformes: icterid (western meadowlark)			North America
A. minuta	Passeriformes: icterid (common grackle)			North America
A. mirafrae	Passeriformes: alaudid (Horsfield's bush lark)			Australia
A. muelleri	Bucerotiformes: upupid (hoopoe); Passeriformes: passerid (sparrow)			Europe, Africa
A. ornata	Passeriformes: corvid (rook), sturnid (common starling, white-throated dipper)			Asia
A. paraguayensis	Passeriformes: tyrannid (sibilant sirystes)			South America
A. parorioli	Passeriformes: oriolid (Eurasian golden oriole)			Eurasia

A. pattoni	Passeriformes: icterid (western meadowlark)			North America
A. petterae	Passeriformes: artamid (pied butcherbird, black-faced woodswallow), campephagid (varied triller), cinclosomatid (cinnamon quail-thrush), meliphagid (red wattlebird, singing honeyeater, yellow-fronted honeyeater, spiny-cheeked honeyeater), monarchid (restless flycatcher), oreoicid (crested bellbird), petroicid (southern scrub robin)			Australia
A. phalacrocoracis	Suliformes: phalacrocoracid (European shag)	stomach		Russia
A. pseudicettiae	Passeriformes: hirundinid (common house martin)			Asia
A. ptilopachydis	Galliformes: phasianid (stone partridge)			Africa
A. quadriloba	Piciformes: picid (black woodpecker, European green woodpecker)	oesophagus		Europe, North America
A. quiscali	Passeriformes: corvid (Florida scrub jay), icterid (common grackle, great Antillean grackle); Piciformes: picid (hairy woodpecker)			North America
A. raillieti	Pelecaniformes: pelecanid (pelican)			
A. rectovaginata	Falconiformes: falconid (European kestrel)	stomach		Africa
A. resticula	Cuculiformes: cuculid (groove-billed ani)			Americas
A. rotundata	Passeriformes: laniid (lesser grey shrike)	oesophagus		Asia
A. sagittata	Pelecaniformes: ardeid (purple heron, black-crowned night heron); Ciconiiformes: ciconiid (black stork)	stomach		Europe
A. semei	Otidiformes: otidid (kori bustard)			Africa
A. sialia	Passeriformes: turdid (western bluebird)			North America
A. singhi	Passeriformes: sturnid (Brahminy starling)	gizzard		India
A. skrjabini (syn. *A. buttnerae*)	Passeriformes: alaudid (greater short-toed lark), corvid (Eurasian magpie), estrildid (long-tailed finch, plum-headed finch, red-throated parrotfinch, red-cheeked cordon-bleu, orange-cheeked waxbill, tricoloured munia), passerid (house sparrow, Spanish sparrow, Eurasian tree sparrow, Japanese tree sparrow), prunellid (alpine accentor), sturnid (white-cheeked starling, gray starling), thraupid (Cuban grassquit)	oesophagus, gizzard		Eurasia, Australasia
A. spinosa	Galliformes: phasianid (greater prairie chicken, sharp-tailed grouse)			North America
A. sturni	Passeriformes: sturnid (common starling, Caucasian starling, rosy			North America

	starling)			
A. subula	Passeriformes: acrocephalid (thrush warbler), alaudid (red-capped lark, horned lark), bombycillid (Bohemian waxwing), campephagid (black-winged cuckooshrike), corvid (Eurasian jay, spotted nutcracker, Eurasian magpie, grey treepie), dicrurid (black drongo), emberizid (Ortolan bunting, pine bunting), fringillid (hawfinch), hirundinid (sand martin), laniid (brown shrike, great grey shrike, lesser grey shrike), motacillid (white wagtail, citrine wagtail), muscicapid (blue-and-white flycatcher, spotted flycatcher, European pied flycatcher, Siberian rubythroat, European robin, pied bush chat, western black-eared wheatear, Isabelline wheatear, northern wheatear, variable wheatear), passerid (house sparrow, Eurasian tree sparrow), sittid (Eurasian nuthatch), sturnid (common starling, white-cheeked starling), sylviid (great reed warbler, Blyth's reed warbler, Eurasian reed warbler, icterine warbler, willow warbler, common chiffchaff), turdid (scaly thrush); Apodiformes: apodid (white-throated needletail); Columbiformes: columbid (oriental turtle dove); Coraciiformes: coraciid (European roller); Piciformes: picid (white-backed woodpecker, black woodpecker, grey-headed woodpecker)	gizzard		Palearctic
A. sygmoidea	Accipitriformes: accipitrid (crested goshawk)			South America
A. tenuis	Galliformes: phasianid (chukar); Passeriformes: cinclid (brown dipper), muscicapid (whinchat)			Eurasia
A. triaenucha	Pelecaniformes: ardeid (American bittern)			North America
A. tuberculata	Coraciiformes: alcedinid (kookaburra)			Africa?
A. tyranna	Passeriformes: tyrannid (eastern kingbird)			North America
A. upupa	Bucerotiformes: upupid (Eurasian hoopoe)	gizzard		India
A. vanelli	Charadriiformes: charadriid (northern lapwing)			India
A. wangi	Passeriformes: thamnophilid (white-cheeked antbird, spotted antbird)			South America
Cosmocephalus				
C. aduncus	Charadriiformes: larid (great black-backed gull, Audouin's			Eurasia

	gull); Podicipediformes: podicipedid (great crested grebe)			
C. asturis	Pelecaniformes: ardeid (cattle egret)			
C. capellae	Anseriformes: anatid (northern shoveler, garganey); Charadriiformes: charadriid (northern lapwing), scolopacid (common snipe, broad-billed sandpiper, marsh sandpiper, red-necked phalarope, common redshank, spotted redshank)			Holarctic
C. faridi	Pelecaniformes: pelecanid (great white pelican)			Africa
C. imperialis	Charadriiformes: alcid (common murre)			Russia
C. jaenschi	Suliformes: phalacrocoracid (great cormorant)			Australia
C. obvelatus (syn. *C. alatus, argentinensis, diesingii, firlottei, papillosus, tanakai*)	Charadriiformes: alcid (common murre), larid (common gull, ring-billed gull, slender-billed gull, slaty-backed gull, black-headed gull, lesser black-headed gull, great black-backed gull, brown-backed gull, kelp gull, European herring gull, Mediterranean gull, Caspian gull, Vega gull, Audouin's gull, common tern, little tern, sandwich tern, gull-billed tern, black skimmer, black-legged kittihawk), scolopacid (sanderling, western willet, marbled godwit, Wilson's phalarope, lesser yellowlegs), stercocoriid (pomarine jaeger); Anseriformes: anatid (common eider); Ciconiiformes: ciconiid (wood stork); Gaviiformes: gaviid (common loon, black-throated loon, Pacific loon); Passeriformes: bombycillid (cedar waxwing); Pelecaniformes: ardeid (great egret, great blue heron), pelecanid (American white pelican, brown pelican), threskiornithid (roseate spoonbill); Podicipediformes: podicipedid (western grebe, horned grebe, great crested grebe, red-necked grebe, black-necked grebe); Sphenisciformes: spheniscid (southern rockhopper penguin, Magellanic penguin)	oesophagus, proventriculus	Amphipoda: gammarid (*Crangonyx laurentianus, Gammarus fasciatus*), hyalellid (*Hyalella azteca*); Malacostraca: mysid (opossum shrimp, *Neomysis americana*) [plus PH: Anguilliformes: anguillid (European eel); Atheriniformes: atherinid (bigscale sand smelt); Carangiformes: carangid (Atlantic horse mackerel); Clupeiformes: clupeid (twaite shad, Atlantic herring, European sprat), engraulid (European anchovy); Cypriniformes: cyprinid (goldfish, spottail shiner, creek chub, Danube bleak); Cyprinodontiformes: fundulid (mummichog); Gadiformes: merluccid (European hake); Gasterosteiformes: gasterosteid (three-spined stickleback, four-spined stickleback, nine-spined stickleback); Gobiiformes: gobiid (common goby, sand goby, monkey goby, round goby, grass goby); Labriformes: labrid (goldsinny wrasse); Mugiliformes: mugilid (so-iuy mullet); Osmeriformes: osmerid (rainbow smelt, European smelt); Perciformes: percid (ruffe, zander), sparid (two-banded seabream), zoarcid (viviparous eelpout); Pleuronectiformes: pleuronectid (European flounder), soleid (common sole); Salmoniformes:	worldwide

			salmonid (rainbow trout); Scorpaeniformes: cottid (shorthorn sculpin); Syngnathiformes: syngnathid (lesser pipefish); Trachiniformes: ammodytid (great sand eel); Sauria: lacterid (sand lizard); Serpentes: colubrid (dice snake)]	
C. pelecani	Pelecaniformes: pelecanid (Australian pelican)			Australia
C. podicipis	Podicipediformes: podicipedid (great crested grebe, black-necked grebe)			Asia
Dispharynx				
D. aduncus	Charadriiformes: larid (common gull, yellow-legged gull)			Europe
D. aegyptica (syn. *Acuaria*)	Pelecaniformes: ardeid (cattle egret)			Africa
D. affinis	Strigiformes: strigid (barn owl)			Americas
D. buteonis	Accipitriformes: accipitrid (roadside hawk)			South America
D. capitata	Accipitriformes: accipitrid (greater spotted eagle, tiny hawk)			Europe, Americas
D. emberizae	Passeriformes: sturnid (common mynah)			Asia
D. karachii	Accipitriformes: accipitrid (black kite)			India
D. laplantei	Passeriformes: corvid (Eurasian jay)			Eurasia
D. magnilabiata	Pelecaniformes: threskiornithid (roseate spoonbill)			South America
D. malvyae	Accipitriformes: accipitrid (black kite)			Africa
D. mathevossianae	Falconiformes: falconid (Eurasian kestrel)			Eurasia
D. nasuta (syn. *A. spiralis, D. spiralis*)	Galliformes: phasianid (chicken, greater prairie chicken, red junglefowl, turkey, peacock, Indian peafowl, ruffed grouse, hazel grouse, dusky grouse, sharp-tailed grouse, common quail, northern bobwhite quail, California quail, chukar, rock partridge, grey partridge, Barbary partridge, golden pheasant, ring-necked pheasant, Bianchi's pheasant), numidid (helmeted guineafowl), cracid (plain chachalaca); Accipitriformes: accipitrid (black kite, swallow-tailed kite, American kestrel); Anseriformes: anatid (garganey); Charadriiformes: charadriid (northern lapwing, killdeer, European golden plover), jacanid (African jacana), larid (slender-billed gull, Mediterranean gull, black-headed gull, common tern, sandwich tern, gull-billed tern); Columbiformes: columbid (pigeon, rock dove, common	proventriculus oesophagus, [weight loss, anaemia]	Malacostraca: armadillid (woodlouse, *Armadillidium vulgare, Cubaris*), porcellionid (woodlouse, *Porcellio fedtschencoi, laevis, scaber, Porcellionides pruinosus*), trachelipodid (woodlouse, *Hemilepistus pectinatus, reductus*)	worldwide

	ground dove, white-winged dove, mourning dove, Luzon bleeding-heart dove); Coraciiformes: coraciid (European roller); Cuculiformes: cuculid (smooth-billed ani); Falconiformes: falconid (kestrel hawk, Eurasian hobby); Gruiformes: gruid (whooping crane, sandhill crane); Passeriformes: acrocephalid (great reed warbler, Eurasian reed warbler), alaudid (Eurasian skylark), cardinalid (northern cardinal, rose-breasted grosbeak, black-faced grosbeak), corvid (blue jay, Florida scrub jay, Eurasian magpie, American crow, Cuban crow, carrion crow, fish crow, rook), emberizid (common reed bunting, red-headed bunting, yellow hammer), icterid (red-winged blackbird, common grackle, boat-tailed grackle, greater Antillean grackle, brown-headed cowbird), mimid (northern mockingbird, gray catbird), motacillid (tree pipit), oriolid (Eurasian golden oriole), parulid (prairie warbler, Blackburnian warbler, Tennessee warbler, grey-crowned yellowthroat), passerellid (eastern towhee), passerid (sparrow), polioptilid (trilling gnatwren), sturnid (common mynah, common starling, Caucasian starling, golden-breasted starling), thraupid (blue-gray tanager), troglodytid (Carolina wren), turdid (common blackbird, clay-coloured robin, American robin, red-throated thrush, eastern bluebird), tyrannid (least flycatcher); Piciformes: picid (red-bellied woodpecker, red-headed woodpecker, yellow-shafted flicker, yellow-bellied sapsucker, northern flicker); Psittaciformes: psittaculid (princess parrot, Alexandra's parrot); Rheiformes: rheid (greater rhea); Strigiformes: strigid (little owl, eastern screech owl, Eurasian scops owl)			
D. noctuae	Strigiformes: strigid (little owl)			Europe
D. pipilonis	Passeriformes: passerellid (red-eyed towhee)			North America
D. stonae	Passeriformes: troglodytid (Carolina wren)			North America
Echinuria				
E. australis	Anseriformes: anatid (Pacific black duck)			New Zealand
E. borealis	Anseriformes: anatid (long-tailed			Holarctic

	duck, surf scoter, common eider, king eider, ruddy shelduck)			
E. cincli	Passeriformes: cinclid (brown dipper)			Asia
E. gilsoni	Charadriiformes: scolopacid (ruff)	oesophagus		Africa
E. heterobrachiata	Charadriiformes: larid (little gull, slender-billed gull), scolopacid (western sandpiper)			North America
E. hypognatha	Anseriformes: anatid (common scoter, surf scoter)			North America
E. jugadornata	Anseriformes: anatid (duck)			
E. minor	Anseriformes: anatid (knob-billed duck)			Africa
E. pamirica (syn. *E. leiperi*)	Anseriformes: anatid (common shelduck, ruddy shelduck)			Eurasia
E. parva	Anseriformes: anatid (bufflehead, Canada goose)			North America
E. phoenicopteri	Phoenicoptiformes: phoenicopterid (greater flamingo)			Africa
E. skrjabiniana	Anseriformes: anatid (mute swan)	proventriculus		Asia
E. skrjabiniensis	Charadriiformes: scolopacid (dunlin, curlew sandpiper, white-rumped sandpiper, Baird's sandpiper, sanderling, little stint, Wilson's phalarope), recurvirostrid (pied avocet)			Eurasia, Americas
E. singhi	Anseriformes: anatid (common pochard)	proventriculus		India
E. squamata (syn. *Acuaria*)	Suliformes: phalacrocoracid (great cormorant)			Australia
E. uncinata (syn. *A. uncinata, E. querquedulae*)	Anseriformes: anatid (domestic duck, mallard, muscovy duck, ring-necked duck, falcated duck, spectacled duck, white-eyed duck, mottled duck, white-winged duck, yellow-billed duck, blue duck, tufted duck, harlequin duck, ruddy duck, American black duck, African black duck, Pacific black duck, Philippine duck, comb duck, wood duck, Hartlaub's duck, Mandarin duck, black-bellied whistling duck, white-faced whistling duck, fulvous whistling duck, West Indian whistling duck, gadwall, garganey, redhead, lesser scaup, greater scaup, common pochard, red-crested pochard, rosy-billed pochard, common shelduck, ruddy shelduck, canvasback, bufflehead, common eider, king eider, northern shoveler, northern pintail, white-cheeked pintail, yellow-billed pintail, ringed teal, blue-winged teal, cape teal, chestnut teal, cinnamon teal, silver teal, Eurasian teal, Eurasian wigeon, American wigeon, Chiloe wigeon, brant, common merganser, cotton pygmy goose, African pygmy goose, domestic	proventriculus, oesophagus [weight loss, anaemia]	Cladocera: daphniid (*Ceriodaphnia, Daphnia magna, pulex*, *Simocephalus vetulus*); Amphipoda: gammarid (*Gammarus*); Isopoda: asellid (*Asellus aquaticus*); Ostracoda: cypridid (*Heterocypris incongruens*); Branchiopoda: lynceid (*Lynceus brachyurus*)	Africa, Asia, Americas

	goose, greylag goose, red-breasted goose, greater white-fronted goose, bar-headed goose, snow goose, swan goose, barnacle goose, Canada goose, Hawaiian goose, Orinoco goose, Egyptian goose, emperor goose, brant, smew, black swan, trumpeter swan, black-necked swan, whooper swan, mute swan); Charadriiformes: larid (Pallas's gull), scolopacid (sanderling, semipalmated sandpiper, Baird's sandpiper, willet, ruff, marbled godwit, Wilson's phalarope, horned grebe, great crested grebe, red-necked grebe, black-necked grebe, little grebe)			
Subfamily Seuratiinae				
Streptocara				
S. californica (syn. *S. dogieli*)	Anseriformes: anatid (mallard, long-tailed duck, velvet scoter, surf scoter, white-winged scoter, greater scaup, common eider, canvasback, Burrow's goldeneye, common merganser, red-breasted merganser)			Eurasia, North America
S. cirrohamata (= *Ingliseria*)	Suliformes: phalacrocoracid (Kerguelen shag, Auckland shag)			sub-Antarctic islands
S. crassicauda (syn. *S. pectinifera*)	Anseriformes: anatid (domestic duck, mallard, muscovy duck, mottled duck, ruddy duck, ring-necked duck, long-tailed duck, tufted duck, harlequin duck, fulvous whistling duck, plumed whistling duck, common shelduck, ruddy shelduck, blue-winged teal, cinnamon teal, European teal, Baikal teal, lesser scaup, greater scaup, red-crested pochard, ferruginous pochard, northern shoveler, northern pintail, gadwall, garganey, canvasback, European wigeon, American wigeon, common eider, king eider, redhead, bufflehead, common goldeneye, Barrow's goldeneye, common merganser, red-breasted merganser, hooded merganser, common scoter, surf scoter, velvet scoter, white-winged scoter, black scoter, smew, greylag goose, Japanese goose, Hawaiian goose, swan goose, tundra swan, whooper swan, trumpeter swan); Charadriiformes: alcid (pigeon guillemot, common murre, razorbill, horned puffin), charadriid (Kentish plover, snowy plover, northern lapwing), haematopodid (Eurasian	gizzard	Malacostraca: gammarid (amphipod, *Gammarus lacustris, locusta, maeoticus, pulex, triacanthus, Rivulogammarus pulex*), hyalellid (amphipod, *Hyalella azteca*) [plus PH: Clupeiformes: clupeid (Brashnikow herring); Cypriniformes: cyprinid (crucian carp, lake minnow, common rudd, common roach, Albanian roach, common minnow), nemacheilid (stone loach); Gobiiformes: gobiid (monkey goby, round goby, grass goby); Salmoniformes: salmonid (brown trout); Serpentes: colubrid (dice snake)	worldwide

	oystercatcher), larid (common tern, gull-billed tern, sandwich tern, Caspian tern, slender-billed gull, little gull, black-headed gull, Thayer's gull, European herring gull), recurvirostrid (pied avocet, American avocet), scolopacid (common sandpiper, spotted sandpiper, wood sandpiper, Terek sandpiper, ruff, common greenshank, common redshank, ruddy turnstone); Ciconiiformes: ciconiid (great bittern); Falconiformes: falconid (peregrine falcon); Galliformes: phasianid (chicken, red junglefowl, chukar, see-see partridge, ring-necked pheasant, black grouse, sharp-tailed grouse), numidid (helmeted guineafowl); Gaviiformes: gaviid (common loon, black-throated loon, red-throated loon, Arctic loon); Gruiformes: rallid (Eurasian coot); Passeriformes: sturnid (common starling); Pelecaniformes: phalacrocoracid (great cormorant), Podicipediformes: podicipedid (western grebe, horned grebe, great crested grebe, red-necked grebe, black-necked grebe, little grebe, hoary-headed grebe, Australasian grebe); Procellariiformes: procellariid (Manx shearwater)			
S. formosensis (syn. *S. somateriae*)	Anseriformes: anatid (mallard, muscovy, ring-necked duck, long-tailed duck, tufted duck, ferruginous duck, bufflehead, greater scaup, common goldeneye, Barrow's goldeneye, common merganser, red-breasted merganser, hooded merganser, common eider, velvet scoter, surf scoter, white-winged scoter, black scoter); Gaviiformes: gaviid (common loon)			Eurasia
S. formosus	Gaviiformes: gaviid (common loon)			Asia
S. incognita	Anseriformes: anatid (mallard, ruddy duck, Barrow's goldeneye, swan goose, Japanese goose); Phoenicopteriformes: phoenicopterid (Chilean flamingo)	gizzard	water flea	Americas
S. indica	Galliformes: phasianid (chicken)			India
S. penihamata	Strigiformes: strigid (variable screech-owl, western barn owl, black-banded owl)	stomach		Americas
S. recta	Gaviiformes: gaviid (red-throated loon, black-throated loon); Podicipediformes: podicipedid			Holarctic, Australia

	(horned grebe, little grebe, great crested grebe, black-necked grebe, Japanese black-necked grebe, hoary-headed grebe, Australasian grebe)			
S. triaenucha (= *Synhimantus*)	Pelecaniformes: ardeid (great blue heron, American bittern)			Americas
S. tridentata (= *Paracuaria*)	Charadriiformes: larid (European herring gull)			Europe

Parasite morphology: Acuariid nematodes form 3 different types of morphological stages during their development: namely, eggs, larvae (4 consecutive stages encoded L1 to L4), and adult worms. The eggs are bound by smooth thick shells and are oval-elliptical in shape ranging in size from 22-65 x 17-50 μm but varying according to genus (e.g. *Echinuria* 28-37 x 17-23 μm, *Dispharynx* 22-42 x 17-26 μm, *Cosmocephalus* 31-40 x 18-22 μm, *Acuaria*, 40-65 x 27-50 μm, *Streptocara* 32-65 x 18-50 μm). The eggs are fully embryonated when laid and contain a first stage larva (L1). Freed L1 are elongate and cylindrical, measuring 165-260 μm long, with rounded heads containing an indistinct subterminal cephalic hook, a rhabditoid oesophagus, and long conical tails, sometimes terminating in a delicate mucron. L2 are transient stages formed in intermediate hosts, while L3 are persistent stages found in their haemocoels or coiled up in their tissues. L3 vary in size from 0.5-3.7 mm depending on the parasite species and their maturity. They have well-developed buccal capsules, 2 triangular pseudolabia, lateral alae, a bipartite oesophagus, and short conical tails that are unarmed or ornamented with cuticular processes (spines or tubercles). L4 are transient parasitic stages in birds and they have begun to develop characteristic anterior ornamentations and genital primordia. Adults are small-medium white worms with stout cylindrical filiform bodies measuring from 3-30 mm long. They are bound by tough cuticles with fine or well-developed transverse striations and some species have lateral alae (e.g. *Cosmocephalus*) and others have 2 rows of cuticular spines (e.g. *Echinuria*). The mouth opening is flattened laterally and has 2 large pseudolabia involving the whole cephalic surface. The worms, however, are easily recognised by the possession of anterior cuticular ornamentations in the form of longitudinal elevations (called cordons). In the subfamily Seuratiinae, the cordons are restricted to the cephalic region forming a collarette just posterior to the pseudolabia. The collarette may be interrupted dorsally and ventrally, or laterally, or take the form of continuous serrated ring (e.g. *Streptocara*). In the subfamily Acuariinae, the cordons are expanded on the cervical region but extending longitudinally down the body, sometimes up to 2/3rd the body length. They arise at the mouth between the 2 pseudolabia and extend posteriorly as 4 sublateral structures which may be straight (e.g. *Acuaria*), curved/sinuous (e.g. *Dispharynx*), recurrent (e.g. *Cosmocephalus*) or anastomosing (e.g. *Echinuria*). Each cordon forms a longitudinal canal (gutter) bound either by a single row of cuticular plates and an outer longitudinal ridge (e.g. *Cosmocephalus*) or 2 rows of rectangular plates (e.g. *Acuaria, Echinuria*) or one lamellar row and one mosaic (mamillated) row (e.g. *Dispharynx*). The buccal cavity is well-developed and often cylindrical and the oesophagus is clearly divided into an anterior muscular and a posterior glandular section. Adult worms are sexually dimorphic, with males being smaller than females (*Acuaria* 8-19 cf. 9-30 mm, *Cosmocephalus* 9-14 cf. 11-22 mm, *Dispharynx* 3-7 cf. 3-10 mm, *Echinuria* 4-13 cf. 10-21 mm, *Streptocara* 3-8 cf. 8-11 mm). Mature females are didelphic with 2 ovaries and uteri connecting to a common vulva located around the median or posterior body. They may have short rounded tails (in the case of *Streptocara*) but usually have long conical tails, sometimes with a terminal projection (in the case of *Cosmocephalus*). Female worms are oviparous and lay embryonated eggs that contain fully developed L1. Mature males have coiled tails with caudal alae varying in length and width (and a precloacal ridge in *Cosmocephalus*), 9-10 pairs of caudal papillae, and 2 spicules, often dissimilar (left spicule being long and slender, right spicule being short and curved).

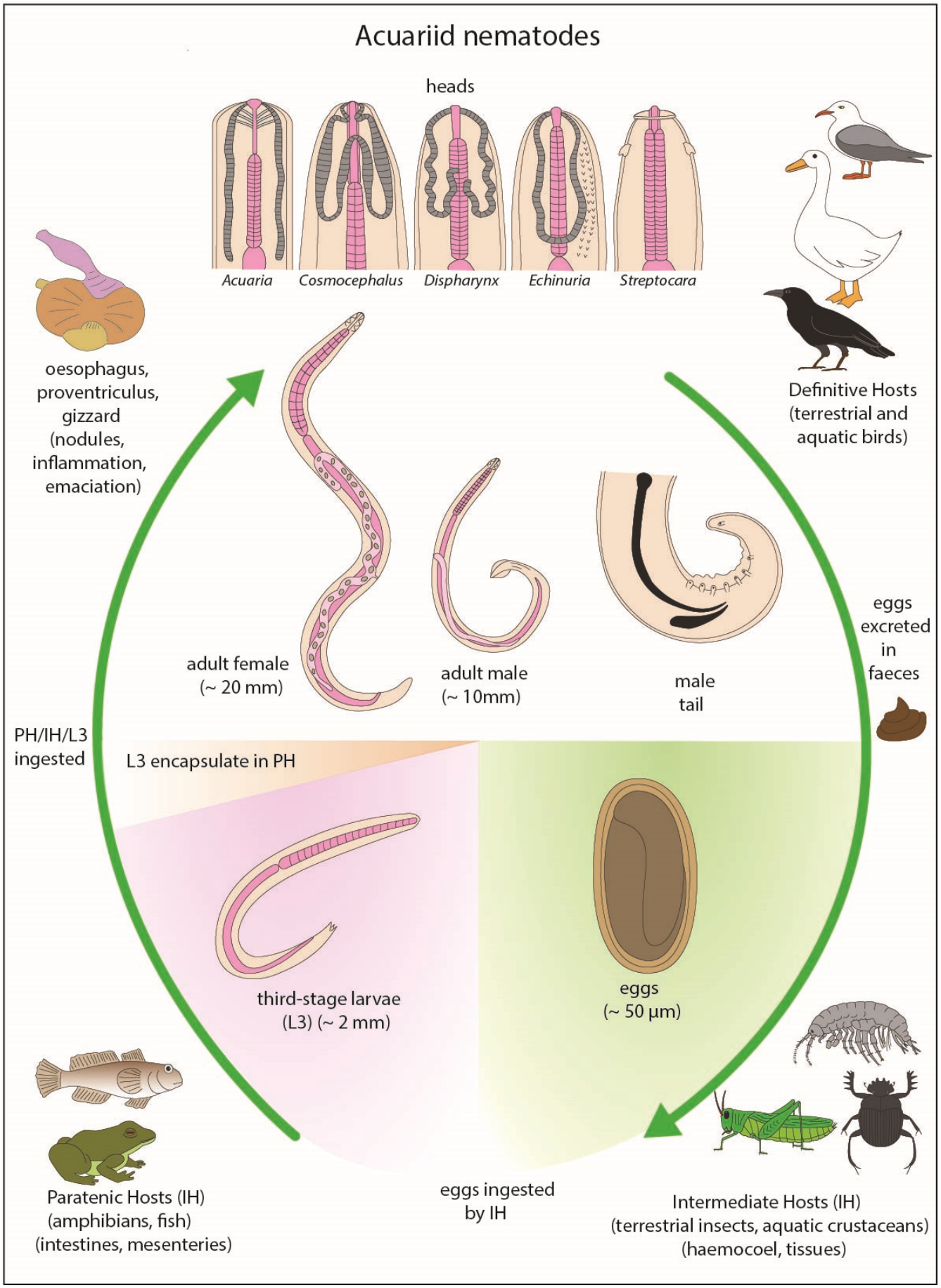
Site of infection: Adult worms infect the upper alimentary tract of their avian definitive hosts, with many species being found in the gizzard (*Acuaria, Streptocara*), some in the proventriculus (*Dispharynx*) and oesophagus (*Cosmocephalus*), and a few extending from the oesophagus to the small intestines (*Echinuria*). Larval stages develop in the haemocoel or tissues of invertebrate intermediate hosts (aquatic and terrestrial arthropods), and are sometimes carried in the tissues of small vertebrate paratenic hosts (amphibians, fish).

Pathogenesis: Most infections are light and remain subclinical, but heavy infections may cause morbidity and mortality in both wild and domestic birds. The severity of disease depends on parasite virulence (some species very pathogenic), host susceptibility (young birds most susceptible), the intensity of infection (numbers of parasites) and the stage of infection (with chronic disease development often following seasonal breeding). Adult worms feed on host tissues and blood and are found tunnelling or with their heads embedded in the mucosa, those in the gizzard being found under the koilin (tough keratinized layer) but sometimes penetrating to muscle layers. The parasites cause local tissue trauma, petechial haemorrhages, catarrhal inflammation, mucosal hypertrophy and thickening, oedema and nodule formation (soft yellow-red nodules). Worms become almost covered by proliferative tissue, the organ lumen becomes significantly narrowed, and lesions are predisposed to secondary bacterial infections, abscess formation, and sometimes granulomas. The keratinized layer of the gizzard may be progressively destroyed, sometimes resulting in organ rupture. Numerous parasite species have been associated with oesophagitis, proventriculitis and emaciation, especially in waterfowl. Clinical signs include listless, weakness, dysphagia, diarrhoea, dyspnoea, anaemia, untidy plumage, awkward gait, inability to fly, anorexia, reduced growth, weight loss, emaciation and death.

Developmental cycle and mode of transmission: Acuariid worms have indirect heteroxenous life-cycles involving the formation of adult worms in avian definitive hosts and larval development in invertebrate intermediate hosts. Infections have become well adapted to hosts occupying aquatic or terrestrial habitats, with parasites in sea and wetland birds (ducks, gulls, petrels, waders, herons, grebes, fishers, pelicans) developing in aquatic crustaceans (cladocerans, amphipods, ostracods, fiddler crabs), and those in terrestrial birds (mostly insectivorous passerines, birds of prey, some galliforms) developing in terrestrial arthropods (grasshoppers, beetles, diplopods, isopods, weevils, earwigs). Parasite species vary considerably in their host range and specificity, but many appear to stenoxenous and infect numerous closely-related host species. Gravid female worms lay embryonated eggs which are excreted with host faeces into the external environment where they may survive for 2-3 months (most susceptible to dessication and solar radiation). Eggs ingested by invertebrate intermediate hosts hatch in the gut releasing L1 which invade the haemocoel and moult twice to form L3 within 9-40 days. Infective L3 may remain free in the haemocoel or encapsulate in host tissues where they may survive for long periods (facilitating over-wintering in some arthropods). Studies have also shown that the L3 of some species may be transferred to small arthropod-eating vertebrates (fish, frogs) where they re-encapsulate in the intestines or mesenteries without further development. These vertebrates thus act as paratenic (transport) hosts, particularly for parasites infecting fish- or frog-eating final hosts. Birds therefore become infected when they consume L3 contained within intermediate or paratenic hosts. Ingested L3 do not undertake any somatic or extra-intestinal migration, but develop directly in the alimentary tract through 2 moults to adult worms, often in the proventriculus before moving to the oesophagus or gizzard. The prepatent period (time from infection to first egg excretion) generally ranged from 30-50 days, although that for some *Streptocara* spp. was as short as 9 days. Adult worms are thought to have short lifespans, living only for several months or seasons.

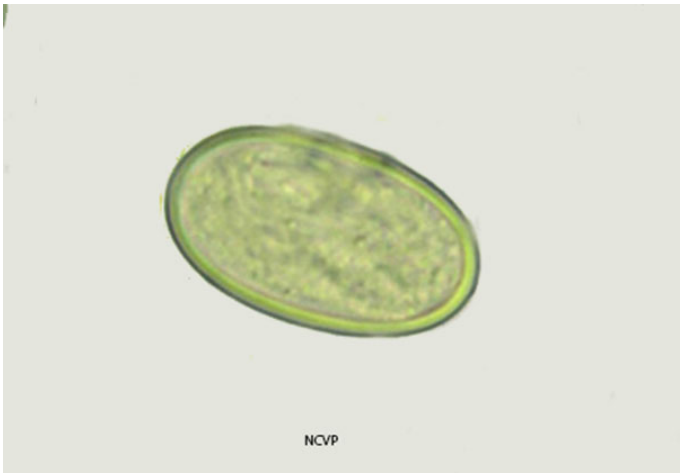
Differential diagnosis: Infections do not present with any distinctive clinical signs, but generally involve malaise and emaciation. The diagnosis of infections therefore relies on the direct detection of parasites, either worm eggs in faecal samples collected antemortem, or adult worms in tissue samples taken at necropsy. Eggs are best concentrated from faecal samples by floatation in heavy metal salt solutions with high specific gravities, but their identification by morphometrics is difficult as many acuariid genera and species produce eggs similar in size and appearance. Adult worms are best detected by close visual examination of the mucosal surface after rinsing off excess mucus and teasing apart nodular lesions. Modern molecular biological techniques have recently been used to explore parasite phylogenetic relationships by polymerase chain reaction (PCR) amplification and sequencing nuclear genes (predominantly 28S ribosomal RNA).

Treatment and control: While few detailed chemotherapeutic studies have been conducted, clinical infections by several species in domestic birds have responded reasonably well to treatment with several anthelmintics, including benzimidazoles (mebendazole) and macrocyclic lactones (ivermectin, moxidectin), but there are frequent reports of poor responses to other conventional anthelmintics. Preventive measures in farmed and aviary birds have included improved sanitation (removal and disposal of faeces), better hygiene (regular cleaning of holding facilities, providing clean food and water), vector control (using exclusion screens, barriers and possibly some surface insecticides) and bird management (preventing foraging, grazing or access to open pastures or pools). Note that the indiscriminate use of insecticides in the general environment is not encouraged, and may even be illegal, due to many concerns about their toxic impacts on ecosystem health.


Acuariid nematodes
heads
Acuaria
Cosmocephalus
Dispharynx
Echinuria
Streptocara
oesophagus, proventriculus, gizzard (nodules, inflammation, emaciation)
Definitive Hosts (terrestrial and aquatic birds)
adult female (~ 20 mm)
adult male (~ 10mm)
male tail
eggs excreted in faeces
PH/IH/L3 ingested
L3 encapsulate in PH
third-stage larvae (L3) (~ 2 mm)
eggs (~ 50 µm)
Paratenic Hosts (IH) (amphibians, fish) (intestines, mesenteries)
eggs ingested by IH
Intermediate Hosts (IH) (terrestrial insects, aquatic crustaceans) (haemocoel, tissues)



Acuaria adult worm



Dispharynx worm egg



Cosmocephalus adult worm, head



Dispharynx adult worm, head

Thelazia
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including both oviparous and viviparous thelazioids (lacking lips). The latter are found around the eyes of mammals and are transmitted by muscid flies feeding on ocular secretions (containing L1 released by female worms). Infections by *Thelazia* spp. have been associated with eye conditions ranging from conjunctivitis to corneal opacities mainly in cattle and horses.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Family:	Thelaziidae (hexagonal mouth, lacking lips, conspicuous transverse anterior striations, live on surface of eye)
Genus:	*Thelazia* (parasitic in conjunctiva of cattle/horses)
Species:	various species cause eye conditions in cattle/horses

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Thelazioidea comprises medium-sized worms with hexagonal or subspherical mouths without pseudolabia infecting the eyes or lungs of mammals, the eyes of birds or the intestines of fish, and using arthropods as intermediate hosts for larval development. Three families are recognised: Thelaziidae (buccal capsule well-developed, pharynx not elongated, parasites of eyes of birds and mammals); Rhabdochonidae (buccal capsule well-developed, pharynx cylindrical and elongated, parasites of intestines or organs of fish, sometimes other vertebrates); and Pneumospiruridae (buccal capsule small or absent, 6 lips sometimes well-developed or atrophied, cuticle with sheath, gubernaculum often double, parasites of lungs of mammals). The family Thelaziidae (or eyeworms) have hexagonal mouths and conspicuous transverse anterior striations. Two subfamilies are recognised: Oxyspirurinae (inner surface of buccal capsule often armed with teeth, oesophagus divided, vulva near anus, tail pointed in both sexes); and Thelaziinae (inner surface of buccal capsule without teeth, oesophagus not divided, vulva in anterior half of body, tail rounded in both sexes). The subfamily Thelaziinae contains 4 genera: *Ceratospira, Hempelia, Thelazia* and *Thelazo.* The genus *Thelazia* includes 3 subgenera: *T.* (*Thelazia*) (female tail short, gubernaculum absent, eggs thin-shelled, viviparous, parasites of

mammals); *T.* (*Thelaziella*) (female tail long, gubernaculum present, eggs thick-shelled, viviparous, parasites of birds); and *T.* (*Annulofilaria*) (male without caudal alae, parasites of birds).

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs/larvae	Transmission
Subfamily: Thelaziinae						
Thelazia (eyeworms)	43	mammals, birds	eyes	14-21 mm long, cuticle with anterior striations, males with coiled tails, 2 dissimilar spicules, ovoviviparous	larvae (L1) 220-280 µm sheathed	indirect (L1 in dipteran IH, esp. muscids)
Subfamily: Oxyspirurinae						
Oxyspirura (eyeworms)	81	birds	eyes	9-20 mm long, smooth cuticle, males with coiled tails, 2 spicules, some with lateral alae, oviparous	eggs 55-60 x 40-45 µm, ellipsoidal, thin-shelled	indirect (L3 in insect IH, esp. cockroaches)

Some 43 *Thelazia* spp. have been described from the eyes of numerous species of mammals and birds around the world. While 4 subgenera have been named, most authors have synonymized them into 2 subgenera: *T.* (*Thelazia*) syn. *T.* (*Pericyema*) (female tail short, male gubernaculum absent, ovoviviparous, thin-shelled eggs *in utero*, parasites of mammals); and *T.* (*Thelaziella*) syn. *T.* (*Isothela*) (female tail long, male gubernaculum present, oviparous, thick-shelled eggs, parasites of birds). Infections are transmitted by muscid flies which feed on ocular secretions ingesting parasite eggs and supporting larval development. Several species cause clinical disease in domestic livestock, mostly ungulates, producing mild to severe conjunctivitis and blepharitis. Zoonotic transmission to humans has also been reported for several species.

***Thelazia* species**	**Definitive hosts**	**Location [Clinical signs]**	**Intermediate hosts**	**Distribution**
T. anadorhynchi	Psittaciformes: psittacid (hyacinth macaw)	eyes		South America
T. annamensis	Galliformes: phasianid (Burmese peacock-pheasant); Passeriformes: muscicapid (hill blue flycatcher)	conjunctiva, orbit, nasal cavity		Asia
T. (*Thelaziella*) *anolabiata* (syn. *T.* (*Isothela*) *lutzi*)	Galliformes: cracid (Belem curassow, bare-faced curassow, Chaco chachalaca, rusty-margined guan); Passeriformes: cotingid (Andean cock-of-the-rock); Piciformes: ramphastid (black-necked aracari); Psittaciformes: psittacid (hyacinth macaw)	eyes		South America
T. anadorhynchi	Psittaciformes: psittacid (hyacinth macaw)			South America
T. (*Thelaziella*) *aquilina*	Accipitriformes: accipitrid (bicoloured hawk, great black hawk); Falconiformes: falconid (yellow-headed caracara, southern crested caracara)			South America
T. balayi	Artiodactyla: bovid (black-fronted duiker)			Africa
T. bubalis	Artiodactyla: bovid (water buffalo)			India
T. buteonis	Galliformes: cracid (blue-throated piping-guan); Accipitriformes: accipitrid (Swainson's hawk)	orbit		Americas
T. californiensis (California eyeworm)	Carnivora: canid (dog, coyote), felid (cat), ursid (American black bear); Artiodactyla: bovid (sheep), cervid (mule deer); Lagomorpha: leporid (European rabbit, jackrabbit); Primates: hominid (human)	eye, conjunctival sac, lachrymal duct [lacrimation, conjunctivitis]	Diptera: fannid (canyon fly, *Fannia benjamini, canicularis*), muscid (face fly, *Musca autumnalis*)	North America
T. (*Thelazia*) *callipaeda* (Oriental eyeworm) (syn. *T.* (*Pericyema*))	Carnivora: canid (dog, raccoon dog, wolf, American red fox), felid (cat, wildcat); Lagomorpha: leporid (European rabbit), Artiodactyla: bovid (sheep), cervid (deer); Primates: hominid (human)	eye, conjunctival sac, lachrymal duct [lacrimation, conjunctivitis]	Diptera: drosophilid (vinegar fly, *Phortica* (= *Amiota*) *variegata*, *okadai*)	Eurasia
T. campanulata	Accipitriformes: accipitrid (roadside hawk,			Asia,

	gray-headed kite, Pallas's fish eagle); Tinamiformes: tinamid (Brazilian tinamou)			Americas
T. cheni (syn. *Annulofilaria*)	Accipitriformes: accipitrid (northern goshawk)			Asia
T. cholodkowskii	Caprimulgiformes: caprimulgid (European nightjar); Strigiformes: strigid (tropical screech-owl)			South America
T. chungkingensis	Galliformes: cracid (Alagoas curassow); Passeriformes: dicrurid (Indian hair-crested drongo)	eyes		South America, Asia
T. cuculina	Cuculiformes: cuculid (large hawk-cuckoo)			Asia
T. dacelonis	Coraciiformes: alcedinid (blue-winged kookaburra); Tinamiformes: tinamid (grey tinamou); Trogoniformes: trogonid (black-tailed trogon)			South America, Australia
T. dentifera	Piciformes: picid (Burmese black-naped green woodpecker)	conjunctiva		Asia
T. depressa	Carnivora: herpestid (mongoose); Accipitriformes: accipitrid (hooded vulture, red-headed vulture)	orbit		Africa, Asia
T. digiticauda	Caraciiformes: alcedinid (ruddy kingfisher)			Asia
T. digitata	Galliformes: cracid (red-throated piping guan); Piciformes: picid (ringed woodpecker, red-stained woodpecker), ramphastid (Toco toucan); Trogoniformes: trogonid (black-tailed trogon)			Holarctic
T. dollfusi	Pelecaniformes: threskiornithid (crested wood ibis)			Africa
T. erschowi	Artiodactyla: suid (pig)			Russia
T. gulosa (syn. *T. alfortensis*) (cattle eyeworm)	Artiodactyla: bovid (cattle, yak, European bison, sheep); Primates: hominid (human)	eye, conjunctival sac, lachrymal duct [lacrimation, conjunctivitis, photophobia]	Diptera: muscid (face fly, *Musca autumnalis, amica, domestica, larvipara, osiris, vitripennis*)	worldwide
T. iheringi	Rodentia: dasyproctid (agouti, Azara's agouti)			South America
T. (*Thelaziella*) *kaimurensis*	Caprimulgiformes: caprimulgid (nightjar)			Americas
T. lacrymalis (equine eyeworm)	Perissodactyla: equid (horse); Artiodactyla: bovid (cattle, yak)	eye, conjunctival sac, lachrymal duct [lacrimation, conjunctivitis, photophobia]	Diptera: muscid (*Musca autumnalis, osiris*)	Eurasia, Americas
T. leesei (eyeworm)	Artiodactyla: camelid (Bactrian camel, dromedary)	conjunctival sac [conjunctivitis]	Diptera: muscid (*Musca lucidulus*)	Africa, Asia, Russia
T. longicauda	Strigiformes: strigid (Asian barred owlet)	conjunctiva		Asia
T. (*Thelaziella*) *lutzi* (syn. *T.* (*Isothela*))	Galliformes: cracid (rusty-margined guan)	eye		South America
T. nyctardeae	Pelecaniformes: ardeid (black-crowned night heron, grey heron)			Eurasia, Africa
T. (*Thelaziella*) *orissae*	Accipitriformes: accipitrid (crested honey buzzard)			Eurasia
T. papillosa	Perissodactyla: equid (horse)			South America
T. philippinensis	Piciformes: picid (woodpecker)			Philippines
T. pittae	Accipitriformes: accipitrid (black-and-white hawk-eagle); Passeriformes: pittid (Papuan pitta)			Central America, Australia
T. platyptera	Accipitriformes: accipitrid (broad-winged hawk)			Eurasia
T. (*Thelazia*)	Artiodactyla: bovid (cattle, zebu, European	eye, conjunctival	Diptera: muscid	Eurasia,

rhodesii (cattle eyeworm)	bison, water buffalo, sheep, goat, roan antelope, Kafue lechwe, Cape bushbuck, greater kudu), camelid (dromedary, vicuna), cervid (red deer, moose); Perissodactyla: equid (horse)	sac, lachrymal duct [lacrimation, conjunctivitis, photophobia]	(*Musca autumnalis, convexifrons, crassirostris, domestica, herveia, larvipara, sorbens*)	Africa
T. sicki	Strigiformes: strigid (scops owl)			South America, Indo-China
T. skrjabini (cattle eyeworm)	Artiodactyla: bovid (cattle, yak, sheep), cervid (white-tailed deer)	eye, conjunctival sac, lachrymal duct [lacrimation, conjunctivitis, photophobia]	Diptera: muscid (face flies, *Musca amica, autumnalis, corvina, herveia, larvipara, osiris, viscinia, vitripennis*)	Eurasia, North America
T. (*Thelaziella*) *spizaeti*	Accipitriformes: accipitrid (ornate hawk-eagle); Piciformes: ramphistid (black-necked aracari)			South America
T. (*Thelaziella*) *stereura*	Accipitriformes: accipitrid (Pallas's fish eagle)			Asia
T. tonkinensis	Passeriformes: cotingid (Amazonian umbrellabird)			South America
T. travassosfreitasi	Rodentia: dasyproctid (Azara's agouti)			South America
T. ugandensis	Accipitriformes: accipitrid (hooded vulture)			Africa

Parasite morphology: *Thelazia* spp. form 3 different types of morphological stages during their development: eggs (produced *in utero*); larvae (4 consecutive stages encoded L1-L4); and adult worms. Gravid females contain numerous ovoid eggs measuring around 60 x 55 µm which have thin shells (in members of the subgenus *T.* (*Thelazia*)) or thick shells (subgenus *T.* (*Thelaziella*)). The eggs embryonate *in utero* but there is continuing debate about whether the worms are oviparous (releasing eggs) or ovoviviparous (releasing larvae), as no true hatching event seems to occur *in utero* or *ex utero*. The embryonated eggs transform within the uterus becoming coiled first-stage larvae (L1) still encased (encysted or ensheathed) in the shell membrane. When laid, the surrounding membrane becomes loose and often expanded at one end allowing the L1 to move about inside, sometimes even becoming reflexed. L1 are elongate cylindrical stages measuring from 220-280 µm, and the surrounding shell of some species develops conspicuous transverse folds or striations. Early L1 often have enlarged heads, sometimes with a central notch, while later L1 have grown substantially in width becoming stout with a central longitudinal oesophagus and intestines. The surrounding shell (sheath) is usually shed after ingestion of the L1 by dipteran intermediate hosts. L2 are transient developmental stages in the intermediate hosts, while L3 are long-lasting encapsulated stages. Freed L3 are elongate cylindrical stages ranging in length from 2-5 mm and surrounded by tough cuticles with prominent transverse striations. They have a short buccal cavity, a muscular oesophagus and a short bluntly tapered or rounded tail. L4 are transient parasitic stages in final hosts and they have begun to show oral structures similar to adults as well as genital primordia. Adults are small yellow-white worms with thin cylindrical filiform bodies 4-21 mm long and characterised by the possession of numerous prominent transverse striations of the anterior cuticle. They have hexagonal mouths, lacking lips but surrounded by 2 lateral amphids and 4 submedian cephalic papillae. In some species, the anterior edge of the mouth was thickened and recurved, sometimes forming up to 6 festoons. The buccal cavity is thick-walled, deep, cup-shaped and unarmed (lacking teeth). The cylindrical oesophagus appears undivided and the tail is rounded in both sexes. Adult worms are sexually dimorphic, with males being smaller than females (4-12 cf. 8-21 mm). Mature males have recurved coiled tails with variable numbers (5-33 pairs) of precloacal papillae and 2-3 pairs postcloacal papillae and 2 asymmetrical spicules (long slender left spicule, short stout right spicule). Members of the subgenus *T.* (*Thelazia*) lack a gubernaculum (present in the subgenus *T.* (*Thelaziella*)), and some species have small narrow caudal alae. Mature females are didelphic with 2 ovaries and 2 uteri directed posteriorly but connected to a common anterior vulva. Members of the subgenus *T.* (*Thelazia*) have short conical tails (long in the subgenus *T.* (*Thelaziella*)), but neither possessed caudal alae.

Site of infection: Adult eye-worms occur in the orbits of birds and mammals, being found on the cornea, under the eyelids, conjunctiva, nictitating membrane, in the lachrymal glands and ducts, and occasionally in the vitreous cavity of the eyeball itself. Larval stages develop in the haemocoel and internal organs of dipteran intermediate hosts, before migrating to their mouthparts.

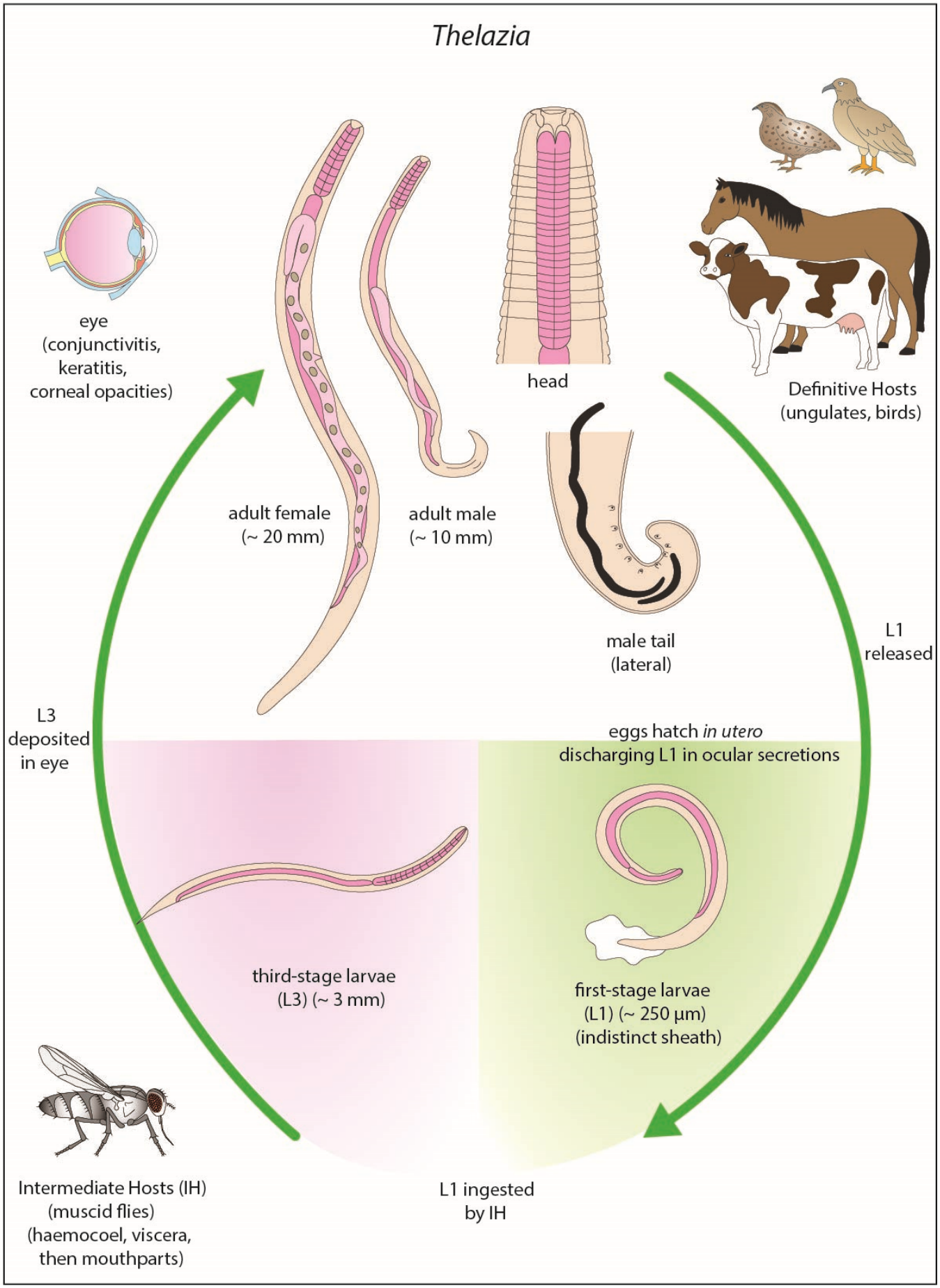
Pathogenesis: Many infections remain asymptomatic, even when eye-worms are observed in the eye, but heavy and chronic infections may cause ocular disease. It is thought that active young adult worms are most pathogenic, while older adult worms are better tolerated by hosts (effectively making some of them asymptomatic carriers). Eye-worms are secretophagous consuming ocular/lachrymal secretions and their movement causes local irritation and inflammation, initially stimulating excessive lachrymation followed by catarrhal and/or petechial conjunctivitis, then chronic follicular conjunctivitis, blepharitis, lachrymal duct

inflammation with necrotic exudates and obstruction, and keratitis (potentially leading to corneal opacities and ulceration, and occasionally perforation and permanent fibrosis). Clinical signs may develop after a short 3-5 day incubation period with mild to severe conjunctivitis with lymphoid hyperplasia and seromucoid exudates, congestion, localized oedema, epiphora with excessive lachrymation and ocular secretions, photophobia and periorbital pruritus. Clinical signs may progressively worsen over 1-2 weeks resulting in ophthalmia, even panophthalmia, purulent discharges, corneal ulcers and opacities, and sometimes subconjunctival cysts. Infected animals may become listless, distressed, anorexic and lose condition (weight loss, reduced milk production), but many infections resolve spontaneously in about 2 months, although some corneal opacities may remain. Eye-worm infections are also thought to predispose hosts to secondary infections, especially infectious keratoconjunctivitis (pink-eye) caused by *Moraxella* bacteria. Humans may also become infected as aberrant hosts, developing mild to severe symptoms (including lachrymation, epiphora, conjunctivitis, keratitis, and corneal ulcers).

Developmental cycle and mode of transmission: *Thelazia* spp. have indirect heteroxenous life-cycles involving the formation of adult worms in vertebrate definitive hosts (birds and mammals) and the development of larvae in invertebrate intermediate hosts (dipteran insects). Female worms produce thin-shelled eggs which hatch *in utero* discharging sheathed L1 into ocular secretions. The L1 are ingested by various dipteran species (face flies, vinegar flies, canyon flies) which do not bite or suck blood but are secretophagous and cluster around the eye to feed on ocular secretions. Ingested L1 exsheath in the gut and invade the haemocoel and internal organs (fat bodies, testes, ovarian follicles) where they moult twice to form L3 in thin-walled capsules over 15-30 days. Encapsulated L3 may survive over winter in the pupal stages of flies. When adult flies feed on final hosts, infective L3 migrate to the mouthparts and emerge from the labellum to be mechanically deposited in the eye. They develop through 2 moults to form adult worms in ocular tissues (mostly the conjunctival sac) and do not undertake any extra-ocular migration. The prepatent period (time from infection to first release of L1) ranges from 20-25 days in cattle and 21-42 days in horses, and adult worms may live longer than 1 year. The intensity of infection may increase with advancing host age, reaching maximum levels in 2-3 year old animals, due primarily to repeated exposure as the parasites appear to elicit little protective immunity. While infections may be detected throughout the year, clinical disease outbreaks are often seasonal and coincident with warm summers when flies are most abundant and active.

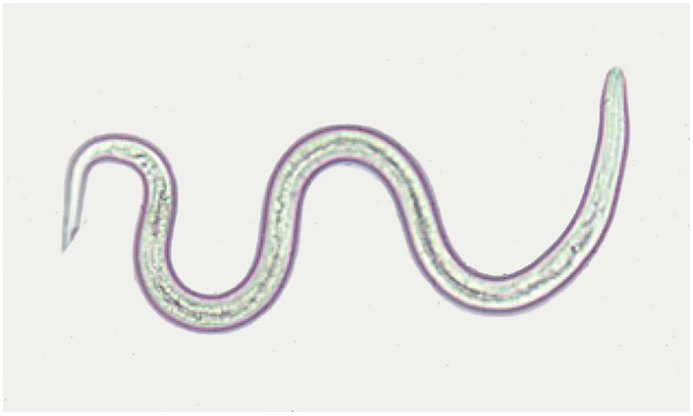
Differential diagnosis: The occurrence of conjunctivitis in livestock coincident with the fly season is generally indicative of infection, but other conditions need to be discounted (especially pink-eye). Physical examination of the eyes (using topical anaesthetics to allow manipulation of the third eyelid) may reveal worms in the conjunctival sac, but some species are more invasive and are less likely to be observed. Worms may even be found incidentally on periorbital skin or hair during surgery or upon necropsy. On occasion, larvae have been detected in lachrymal fluids on microscopic examination, but they need to be differentiated from *Onchocerca* microfilariae and *Draschia* or *Habronema* infective larvae. Molecular biological techniques have been used to examine parasite phylogenetic relationship by polymerase chain reaction (PCR) amplification and sequencing of nuclear (ribosomal RNA) and mitochondrial genes (cytochrome c oxidase subunit I), but they are not used for routine diagnosis.

Treatment and control: The location of the parasites in the superficial structures of the eye (an immunologically privileged location) makes treatment of eye-worms difficult. For many years, treatment was based on mechanical removal of worms under local anaesthesia, often combined with topical applications (eye washes, ointments) of antiseptics, antibiotics, steroidal anti-inflammatories and cicatrizants (healing promoters). Nowadays, modern anthelmintic drugs may be applied topically or systemically to treat infections in livestock and companion animals, including the macrocyclic lactones (ivermectin, doramectin, milbemycin, moxidectin, eprinomectin), imidazothiazoles (levamisole, tetramisole), isoquinolines (praziquantel) and some benzimidazoles (fenbendazole). The regular use of some anthelmintics (especially the macrocyclic lactones) may also help reduce fly populations as drug residues excreted in faeces appear to suppress the development of muscid flies in dung. Clinical infections often occur seasonally during warm months when flies are active, so various preventive strategies may be adopted to interrupt transmission between fly vectors and final hosts, either by reducing fly populations (restricting breeding areas, removing organic waste), protecting animals from face flies (indoor housing, eye shields/covers, chemical repellents/insecticides (impregnated ear-tags, pour-on formulations, spraying holding facilities), or stock/pasture management (animals on dry open pastures have fewer face flies than those on shaded moist pastures).


Thelazia
eye
(conjunctivitis,
keratitis,
corneal opacities)
adult female
(~ 20 mm)
adult male
(~ 10 mm)
head
male tail
(lateral)
Definitive Hosts
(ungulates, birds)
L1
released
L3
deposited
in eye
eggs hatch in utero
discharging L1 in ocular secretions
third-stage larvae
(L3) (~ 3 mm)
first-stage larvae
(L1) (~ 250 µm)
(indistinct sheath)
Intermediate Hosts (IH)
(muscid flies)
(haemocoel, viscera,
then mouthparts)
L1 ingested
by IH



Thelazia larvated egg



Thelazia larva



Thelazia adult worm in eye

Oxyspirura
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including both oviparous and viviparous thelazioids (lacking lips). The former are found in the eyes of birds and are transmitted by cockroaches in which L3 develop from ingested eggs. Infections by *Oxyspirura mansoni* have been associated with ophthalmitis in poultry worldwide.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Family:	Thelaziidae (hexagonal mouth, lacking lips, conspicuous transverse anterior striations, live on surface of eye)
Genus:	*Oxyspirura* (parasitic in eyes of birds)
Species:	various species cause ophthalmitis in poultry

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Thelazioidea comprises medium-sized worms with hexagonal or subspherical mouths without pseudolabia infecting the eyes or lungs of mammals, the eyes of birds or the intestines of fish, and using insects as intermediate hosts for larval development. Three families are recognised: Thelaziidae (buccal capsule well-developed, pharynx not elongated, parasites of eyes of birds and mammals); Rhabdochonidae (buccal capsule well-developed, pharynx cylindrical and elongated, parasites of intestines or organs of fish, sometimes other vertebrates); and Pneumospiruridae (buccal capsule small or absent, 6 lips sometimes well-developed or atrophied, cuticle with sheath, gubernaculum often double, parasites of lungs of mammals). The family Thelaziidae (or eyeworms) have hexagonal mouths and conspicuous transverse anterior striations. Two subfamilies are recognised: Oxyspirurinae (inner surface of buccal capsule often armed with teeth, oesophagus divided, vulva near anus, tail pointed in both sexes); and Thelaziinae (inner surface of buccal capsule without teeth, oesophagus not divided, vulva in anterior half of body, tail rounded in both sexes). The subfamily Oxyspirurinae is monotypic and only contains a single genus, *Oxyspirura.*

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs/larvae	Transmission
Subfamily: Oxyspirurinae						
Oxyspirura (eyeworms)	81	birds	eyes	9-20 mm long, smooth cuticle, males with coiled tails, 2 spicules, some with lateral alae, oviparous	eggs 55-60 x 40-45 µm, ellipsoidal, thin-shelled	indirect (L3 in insect IH, esp. cockroaches)
Subfamily: Thelaziinae						
Thelazia (eyeworms)	43	mammals, birds	eyes	14-21 mm long, cuticle with anterior striations, males with coiled tails, 2 dissimilar spicules, ovoviviparous	larvae (L1) 220-280 µm sheathed	indirect (L1 in dipteran IH, esp. muscids)

The genus *Oxyspirura* contains over 80 species of eyeworms described from some 40 families of birds around the world. Female worms are oviparous and their eggs are taken up by insect vectors in which infective larvae develop. Over the years, 6 subgenera have been recognised: *O.* (*Molinospirura*) (buccal capsule undivided, spicules similar but subequal, ovejector dilated, oral opening surrounded by sclerotized ring); *O.* (*Cramispirura*) (buccal capsule undivided, spicules similar but subequal, ovejector not dilated, oral opening without sclerotized ring); *O.* (*Barusispirura*) (buccal capsule undivided, spicules dissimilar and unequal, lateral alae present, gubernaculum absent); *O.* (*Hamulofilaria*) (= *O.* (*Skrjabinispirura*)) (buccal capsule undivided, spicules dissimilar and unequal, lateral alae absent, gubernaculum present or absent); *O.* (*Caballeroispirura*) (buccal capsule divided into anterior and posterior chambers, spicules dissimilar and unequal, lateral alae present, gubernaculum present); and *O.* (*Oxyspirura*) (= *O.* (*Yorkeispirura*)) (buccal capsule divided into anterior and posterior chambers, spicules dissimilar and unequal, lateral alae absent, gubernaculum present or absent). Infections by various species have been associated with clinical disease (primarily conjunctivitis) in poultry and game birds and numerous wild passerine birds.

***Oxyspirura* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Intermediate Hosts**	**Distribution**
O. acuticauda	Passeriformes: sturnid (bank myna)	eye		India
O. alauda	Passeriformes: alaudid (oriental skylark), pycnonotid (red-vented bulbul)	eye		Asia
O. alii	Passeriformes: vangid (common woodshrike)	eye		Asia
O. (*Cramispirura*) *altensis*	Cariamiformes: cariamid (red-legged seriema); Accipitriformes: accipitrid (savanna hawk)	eye		South America
O. anacanthura	Cuculiformes: cuculid (smooth-billed ani, greater ani, guira cuckoo); Piciformes: ramphastid (yellow-ridged toucan, channel-billed toucan)	eye		South America
O. asiatica	Accipitriformes: accipitrid (Eurasian sparrowhawk)	eye		Eurasia
O. basiri	Cuculiformes: cuculid (Jacobin cuckoo)	eye		Asia
O. baskakowi	Passeriformes: muscicapid (European woodland flycatcher, common nightingale), sylviid (lesser whitethroat)	eye		Eurasia
O. bosei (syn. *Chandlerella*)	Passeriformes: corvid (Eurasian magpie)	eye		Eurasia
O. (*O.*) *brasiliensis*	Cuculiformes: cuculid (greater ani); Passeriformes: ploceid (cinnamon weaver, village weaver)	eye		South America, Africa
O. (*O.*) *brevisubulata*	Caprimulgiformes: caprimulgid (pauraque), Strigiformes: strigid (variable screech owl), tytonid (barn owl)	eye		Americas
O. buccosulcata	Passeriformes: sturnid (Brahminy starling, chestnut-tailed starling, pied myna)	eye		India
O. (*Cramispirura*) *buckleyi*	Passeriformes: motacillid (white wagtail)	eye		Eurasia
O. cameroni	Passeriformes: tityrid (black-tailed tityra)	eye		South America

O. (*Molinospirura*) *cassici*	Passeriformes: icterid (red-rumped cacique)	eye		South America
O. cephaloptera	Coraciiformes: momotid (blue-crowned motmot); Passeriformes: icterid (orange-backed troupial)	eyes		South America
O. chabaudi	Passeriformes: motacillid (white wagtail), ploceid (village weaver, red-billed quelea)	eye		Eurasia, Africa
O. chauvancyi	Passeriformes: thamnophilid (northern slaty antshrike)	eye		South America
O. chrysomma	Passeriformes: paradoxornithid (yellow-eyed babbler)	eye		Asia
O. cisticola	Passeriformes: cisticolid (streaked fantail warbler)	eye		Eurasia
O. congolensis	Passeriformes: muscicapid (spotted flycatcher)	eye		North America
O. crami	Otidiformes: otidid (black-bellied bustard)	eye		Africa
O. (*O.*) *crassa*	Strigiformes: strigid (great horned owl)	eye		Americas
O. cruzi	Tinamiformes: tinamid (red-winged tinamou)	eye		South America
O. dendropicosi	Piciformes: picid (cardinal woodpecker)	eye		Africa
O. dicruri	Passeriformes: dicrurid (fork-tailed drongo)	eye		India
O. dicruricola	Passeriformes: dicrurid (fork-tailed drongo)	eye		India
O. dukhunensis	Piciformes: picid (yellow-crowned woodpecker)	eye		India
O. egretta	Pelecaniformes: ardeid (little egret)	eye		Asia
O. elani	Accipitriformes: accipitrid (black-winged kite)	eye		Africa
O. eremopterixa	Passeriformes: alaudid (ashy-crowned sparrow-lark)	eye		Asia
O. fulica	Gruiformes: rallid (Eurasian coot)	eye		Eurasia
O. grandipapillata	Passeriformes: dicrurid (fork-tailed drongo)	eye		India
O. gubernaculata	Passeriformes: motacillid (grey wagtail)	eye		India
O. hexapapillata	Passeriformes: meropid (olive bee-eater)	orbit		India
O. hispanica	Otidiformes: otidid (great bustard)	eye		Europe
O. hyderabadensis	Passeriformes: dicrurid (black drongo)	eye		India
O. (*Cramispirura*) *indica*	Passeriformes: muscicapid (white-rumped shama)	eye		India
O. laharpurensis	Passeriformes: sturnid (common myna)	eye		India
O. leiperi	Passeriformes: leiothrichid (jungle babbler)	eye		Asia
O. lerouxi	Passeriformes: turdid (Indian blackbird)	eye		India
O. lobipluvia	Charadriiformes: charadriid (yellow-wattled lapwing)	eye		India
O. malabarica	Passeriformes: sturnid (chestnut-tailed starling)	eye		India
O. (*Yorkeispirura*) *mansoni* (syn. *O. parvorum*, *Filaria mansoni, Spiroptera mansoni, Microfilaria seguini*) (Manson's eyeworm, tropical fowl worm)	Accipitriformes: accipitrid (northern harrier); Anseriformes: anatid (domestic duck, whistling duck); Columbiformes: columbid (pigeon); Cuculiformes: cuculid (common hawk-cuckoo); Galliformes: phasianid (chicken, red junglefowl, red spurfowl, turkey, ring-necked pheasant, Chinese bamboo partridge, peafowl), numidid (guinea fowl); Passeriformes: icterid (bobolink, red-winged blackbird), laniid (loggerhead shrike), corvid (blue jay, Florida scrub jay); Piciformes: megalaimid (great barbet, black-browed barbet), picid (golden-cheeked woodpecker)	eye, conjunctiva, lachrymal glands [opthalmitis]	Blattodea: blaberid (cockroach, *Pycnoscelus surinamensis*)	worldwide, except Europe
O. mehransis	Pelecaniformes: ardeid (cattle egret)	intestine?		India
O. meropsicola	Coraciiformes: meropid (green bee-eater)	eye		India
O. mirzai	Passeriformes: leiothrichid (jungle babbler)	eye		India
O. myzomelae	Passeriformes: meliphagid (unspecified	eye		Asia

	honeyeater)			
O. (*Yorkeispirura*) *navali*	Accipitriformes: accipitrid (red-tailed hawk)	eye		North America
O. nigerica	Passeriformes: ploceid (weaver, cinnamon weaver, village weaver)	eye		Africa
O. (*Yorkeispirura*) *octopapillata*	Caprimulgiformes: caprimulgid (pauraque); Falconiformes: falconid (northern crested caracara)	eye		Americas
O. opthalmica	Charadriiformes: turnicid (Indian bustard-quail)	eye		India
O. orientalis	Passeriformes: dicrurid (fork-tailed drongo)	eye		India
O. papillosa	Accipitriformes: accipitrid (harpy eagle); Falconiformes: falconid (gray crane hawk)	eye		South America
O. peipingensis (syn. *O. cochlearispiculata*, *lalagea, streparae, yehi*)	Bucerotiformes: upupid (oriental hoopoe); Passeriformes: artamid (black currawong), campephagid (black-headed cuckooshrike), corvid (red-billed chough), emberizid (red-headed bunting), laniid (brown shrike, great grey shrike, lesser grey shrike), leiothrichid (common babbler), ploceid (cinnamon weaver, village weaver, red-billed quelea), sturnid (pied myna), turdid (Naumann's thrush)	eye		Eurasia, Africa
O. petrowi (syn. *O. kaitingensis*, *lumsdeni, matogrosensis, otocompsa*)	Caprimulgiformes: caprimulgid (little nightjar); Coraciiformes: meropid (blue-cheeked bee-eater), momotid (blue-crowned motmot); Galliformes: phasianid (greater prairie chicken, lesser prairie chicken, greater prairie chicken, chukar, Daurian partridge, hazel grouse, black grouse, ruffed grouse, sharp-tailed grouse, greater sage-grouse, ring-necked pheasant, northern bobwhite, scaled quail, harlequin quail); Passeriformes: cardinalid (northern cardinal), corvid (alpine chough, Eurasian magpie, plush-crested jay, purplish jay), hirundid (tree swallow), icterid (common grackle, boat-tailed grackle, purple grackle, eastern meadow lark, red-winged blackbird, brown-headed cowbird), laniid (lesser grey shrike, red-backed shrike, long-tailed shrike, tiger shrike, Turkestan shrike), leiothrichid (white-browed laughing thrush, Chinese hwanei), meropid (blue-cheeked bee-eater), motacillid (water pipit), parulid (common yellowthroat),), ploceid (cinnamon weaver, village weaver, red-billed quelea), pycnonotid (red-whiskered bulbul), turdid (American robin), tyrannid (eastern kingbird, great crested flycatcher), vireonid (white-eyed vireo); Pelecaniformes: ardeid (green heron, cattle egret)	eye	Orthoptera: acridid (grasshopper, *Hippiscus ocelote, Melanoplus differentialis, femurrubrum, ponderosus, Opeia obscura*, *Trimerotropis pallidipenni*s), gryllid (cricket, *Acheta domesticus, Gryllus texensis), romaleid (*plains lubber grasshopper, *Brachystola magna*); *Blattodea: blattid (cockroach, Periplaneta americana), ectobiid (w*ood cockroach, *Parcoblatta)* [plus rare cutaneous larval infection in Primates: hominid (human)]	worldwide
O. pici	Passeriformes: corvid (carrion crow, western jackdaw, Eurasian magpie, red-billed chough, alpine chough)	eye		Holarctic
O. (*Cramispirura*) *popovi*	Caprimulgiformes: caprimulgid (little nightjar); Galliformes: phasianid (prairie chicken, common pheasant, ruffed grouse, sharp-tailed grouse); Passeriformes: artamid (butcherbird), icterid (streak-backed oriole, meadowlark), laniid (lesser grey shrike, Turkestan shrike), motacillid (wagtail),	eye		Eurasia

	muscicapid (blue rock thrush, oriental magpie-robin, nightingale), oriolid (oriole), passerellid (seaside sparrow), turdid (thrush); Piciformes: picid (hairy woodpecker)			
O. (*Cramispirura*) *prinia*	Passeriformes: cisticolid (ashy prinia)	eye		India
O. (*Yorkeispirura*) *pusillae*	Passeriformes: cardinalid (northern cardinal), corvid (Florida scrub jay), icterid (purple grackle), mimid (brown thrasher), parulid (common yellowthroat), sittid (brown-headed nuthatch), troglodytid (Carolina wren), turdid (eastern bluebird), tyrannid (great crested flycatcher); Piciformes: picid (red-bellied woodpecker, red-headed woodpecker, hairy woodpecker)	eye		Americas
O. (*Cramispirura*) *rhipidurae*	Passeriformes: rhipidurid (white-throated fantail)	eye		Asia
O. rodriguesi	Passeriformes: icterid (Cuban blackbird)	eye		India
O. rustica	Passeriformes: dicrurid (fork-tailed drongo)	eye		India
O. (*O.*) *rysavyi*	Passeriformes: oriolid (Eurasian golden oriole)	eye		Eurasia
O. schulzi	Cuculiformes: cuculid (Asian koel); Galliformes: phasianid (chukar, grey partridge, Daurian partridge, hazel grouse, black grouse, common quail, western capercaillie); Gruiformes: rallid (Eurasian coot); Passeriformes: corvid (long-billed crow)	eye		Holarctic
O. siamensis	Cuculiformes: cuculid (greater coucal)	eye		India
O. singhi	Passeriformes: motacillid (Richard's pipit)	eye		Eurasia
O. solitaria	Coraciiformes: meropid (green bee-eater)	eye		India
O. stereura	Accipitriformes: accipitrid (spotted eagle)	eye, auditory meatus		Europe
O. sturnia	Cuculiformes: cuculid (sirkeer cuckoo); Galliformes: phasianid (grey francolin); Passeriformes: sturnid (pied myna, bank myna)	eye		India
O. suraiyai	Passeriformes: timalid (Indian scimitar babbler)	eye		India
O. sygmoidea	Passeriformes: corvid (carrion crow, rook, Eurasian magpie, Eurasian jay); Piciformes: ramphastid (Toco toucan, Cuvier's toucan)	eye		Europe, South America
O. (*Yorkeispirura*) *tanasijtschuki*	Passeriformes: icterid (unspecified species)	eye		Russia
O. thanhhoaensis	Passeriformes: leiothrichid (white-crested laughingthrush), muscicapid (blue whistling thrush)	conjunctiva		
O. (*O.*) *toroi*	Galliformes: phasianid (northern bobwhite)	eye		North America
O. (*Yorkeispirura*) *tsingchengensis*	Passeriformes: pycnonotid (black bulbul)	eye		Asia
O. turcottei	Galliformes: phasianid (wild turkey)	eye		North America
O. turdi	Passeriformes: turdid (mistle thrush)	eye		Eurasia
O. (*Yorkeispirura*) *turnicis*	Charadriiformes: turnicid (barred button-quail, common Indian bustard-quail)	eye		Asia
O. wellsi	Passeriformes: ploceid (black-winged red bishop)	eye		Africa
O. youngi	Primates: cercopithecid (Patas monkey)	eye		Russia (zoo)
Species inquirenda				
O. acanthochaerae	Passeriformes: meliphagid (spiny-cheeked	eye		Australia

sp. inq.	honeyeater)			
O. bancrofti sp. inq.	Passeriformes: meliphagid (little friarbird)	eye		Australia
O. brevipenis sp. inq.	Cariamiformes: cariamid (red-legged seriema)	eye		South America
O. conjunctivalis sp. inq.	Primates: lemurid (lemur)	eye		Russia (zoo)
O. heteroclita sp. inq.	Galliformes: cracid (nocturnal curassow), phasianid (Siamese fireback)	eye		Asia
O. podjapolskoi sp. inq.	Charadriiformes: scolopacid (wood sandpiper)	eye		Russia
O. wittei sp. inq.	Passeriformes: corvid (Eurasian magpie)	eye		Africa

Parasite morphology: *Oxyspirura* spp. form 3 different morphological stages in their developmental cycles: eggs; larvae (4 stages designated L1 to L4); and adult worms. The eggs are smooth-shelled, ovoid measuring 55-60 x 40-45 µm, and embryonated when laid. First-stage larvae (L1) freed from eggs have elongate cylindrical bodies measuring 145-235 µm but lack any distinct internal organs. L2 are larger, measuring 625-770 µm, and have a well-developed oesophagus and intestines. L3 are larger still, measuring up to 7.0-8.5 mm, and they have developed 6 lobes around the mouth and distinct cells surrounding the anterior end of the oesophagus. L4 have grown to 10-12 mm in length and the intestines have been laterally displaced by genital primordia, but males have not yet formed spicules and females have only formed incomplete ovaries. Adults are slender white worms measuring 9-20 mm in length with smooth cuticles usually lacking lateral alae (present only in members of the subgenus *O.* (*Barusispirura*)). They have simple mouth openings (surrounded by a sclerotized ring in the subgenus *O.* (*Molinospirura*)), globular buccal capsules (only divided into anterior and posterior chambers in the subgenera *O.* (*Oxyspirura*) and *O.* (*Caballeroispirura*)), tubular intestines, and pointed tails. Adults are sexually dimorphic, with male worms being smaller than females (9-16 cf. 12-20 mm). Mature males have ventrally curved tails, a gubernaculum present only in the subgenus *O.* (*Caballeroispirura*) and sometimes in the subgenera *O.* (*Oxyspirura*) and *O.* (*Hamulofilaria*), and 2 unequal spicules which similar in the subgenera *O.* (*Molinospirura*) and *O.* (*Cramispirura*), but dissimilar in the subgenera *O.* (*Oxyspirura*), *O.* (*Barusispirura*), *O.* (*Hamulofilaria*), and *O.* (*Caballeroispirura*) (right spicule short and stubby, left spicule long and slender). Mature female worms are didelphic with 2 large ovaries and uteri (often filled with eggs) connected via an ovejector (sometimes dilated) to a common vulva located in the posterior half of the body.

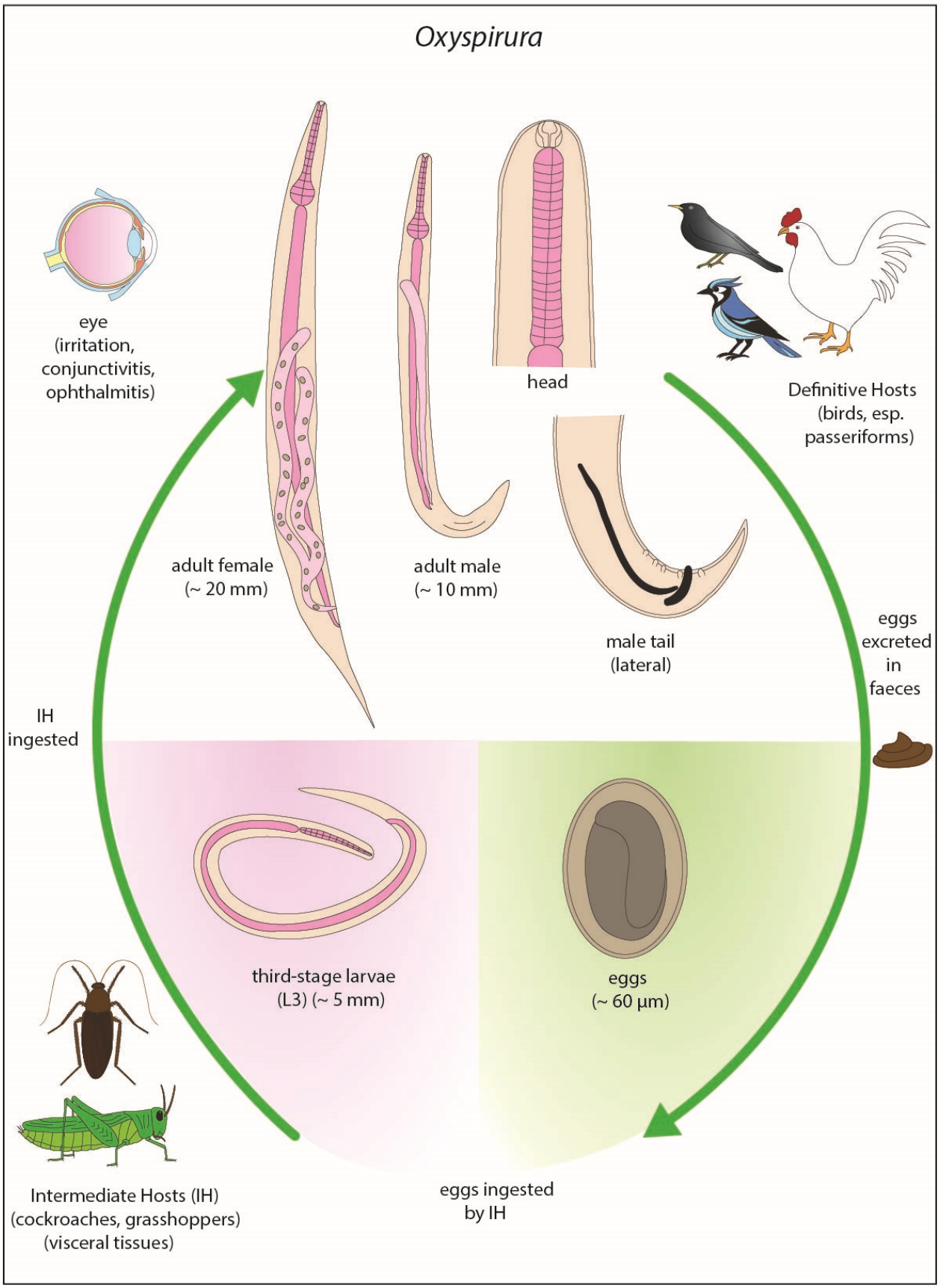
Site of infection: Adult eye-worms infect the eyes of their avian hosts, being found around the orbit on the corneal surface under the nictitating membrane, and in conjunctival sacs, nasolacrimal ducts, and sometimes nasal sinuses. Larval stages develop in capsules in the tissues of invertebrate intermediate hosts (insects, especially cockroaches).

Pathogenesis: Infections are mostly benign and have not been associated with disease in domestic or wild birds (somewhat counter-intuitively when relatively large worms are found in such small eyes). In poultry flocks, a few individual birds tend to be infected, rather than large numbers of birds. Nonetheless, clinical disease may occur in heavy and/or chronic infections. The worms are secretophagous and consume ocular secretions and their movements cause local irritation, exacerbated as birds attempt to relieve the discomfort by scratching. The resultant inflammation produces watery inflamed eyes with excessive lachrymation, conjunctivitis and ophthalmitis. The nictitating membrane may become swollen and flicker constantly, or the eyelids may become stuck together with thick viscous material which may also occlude the nasal passages. Birds become restless and exhibit photophobia. In severe cases, ulceration and erosion of the eyeball may destroy sight completely. Chronic infections are also thought to predispose to secondary bacterial infections.

Developmental cycle and mode of transmission: *Oxyspirura* spp. have indirect heteroxenous life-cycles whereby infections in birds are transmitted via insect intermediate hosts. Gravid female worms lay embryonated eggs in lachrymal secretions which pass through the lachrymal duct to the oral cavity and are swallowed and excreted in host faeces. The eggs survive in moist environments for short periods and are ingested by insects (cockroaches, grasshoppers) which act as intermediate hosts supporting larval development. Ingested eggs hatch in the insect gut releasing the L1 which penetrate the gut wall and enter the haemocoel around 10-14 days. The larvae become encysted in 17-18 days within insect tissues, mainly fat bodies but also Malpighian tubules and intestines, where they moult twice to form L3 by 42-52 days. Birds become infected when they eat insects containing infective L3 which are released in the gut and migrate along the oesophagus, pharynx and mouth to the lachrymal duct and then the eyes (this migration has been observed to be very fast and may occur within 20 minutes). The larvae moult to L4 after 3-5 days and then to subadults (sometimes referred to as L5) around 15-19 days. They mature to sexually reproductive adult worms in several weeks and the prepatent period (time from infection to first excretion of eggs) ranges from 21-48 days for most species, but can be extended up to 86 days in other species.

Differential diagnosis: Infections in birds may be suggested by clinical ocular signs (lachrymation, conjunctivitis), but most diagnoses are made by the direct detection of adult worms under the nictitating membrane or in the conjunctival sac during observation or handling. In the absence of visible adult worms, lachrymal secretions and faecal samples may be examined microscopically for eggs/larvae, although detection rates are often low. Molecular biological techniques have been used to examine parasite phylogeny by polymerase chain reaction (PCR) amplification of nuclear gene sequences (internal transcribed spacer region 2 of ribosomal RNA).

Treatment and control: Infections have conventionally been treated by the physical removal of eye-worms using fine forceps under local anaesthesia, and then the topical application of antiseptics, antibiotics, and sometimes steroidal anti-inflammatory drugs. Although few detailed chemotherapeutic studies have been conducted, several anthelmintic drugs have proven effective when applied topically or orally, including imidazothiazoles (levamisole, tetramisole) and macrocyclic lactones (ivermectin). Preventive strategies appropriate to poultry and aviary industries involve breaking transmission cycles through improved sanitation and hygiene (removal of faeces/litter, cleaning cages, providing dry bedding) and controlling insect vector populations (using exclusion barriers/screens, insect repellents, insecticides), However, care should be taken to only use approved products in poultry facilities.


Oxyspirura
eye
(irritation,
conjunctivitis,
ophthalmitis)
adult female
(~ 20 mm)
adult male
(~ 10 mm)
head
male tail
(lateral)
Definitive Hosts
(birds, esp.
passeriforms)
eggs
excreted
in
faeces
IH
ingested
third-stage larvae
(L3) (~ 5 mm)
eggs
(~ 60 µm)
Intermediate Hosts (IH)
(cockroaches, grasshoppers)
(visceral tissues)
eggs ingested
by IH



Oxyspirura adult worms in eye of bird



Oxyspirura worm eggs



Oxyspirura adult worm, head

Physaloptera
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including physalopteroids (with pseudolabia and teeth) found in the stomachs of cats and dogs, and transmitted by beetles, cockroaches and crickets in which L3 develop. Small mammals (esp. rodents), birds and reptiles may also act as paratenic hosts for L3. Infections by *Physaloptera* spp. have been associated with vomiting and anorexia in cats.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Physalopteroidea (stomach worms in mammals, insect IH)
Family:	Physalopteridae (two large lateral pseudolabia, armed with teeth, lips with basal collar, caudal alae on males)
Genus:	*Physaloptera* (parasitic in stomach of cats)
Species:	various species cause vomiting and anorexia in cats

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Physalopteroidea contains moderately large worms with an anterior collarette and large pseudolabia infecting the alimentary tract of vertebrates and using insects as intermediate hosts for larval development. The single family Physalopteridae is recognised with 3 subfamilies: Physalopterinae (caudal papillae distinct from cuticular ornamentation, caudal alae united on ventral surface, bursa ornamented, parasites of terrestrial vertebrates); Proleptinae (caudal papillae distinct from cuticular ornamentation, caudal alae fading into lateral borders, small area rugosa, parasites of elasmobranchs and marine fishes); and Thubunaeinae (collarette absent, caudal papillae similar to cuticular ornamentation, parasites of reptiles and amphibians). The subfamily Physalopterinae contains 9 genera: *Abbreviata, Kreisiella, Paraphysaloptera, Pentadenoptera* (syn. *Physalopteriata*), *Physaloptera, Pseudabbreviata, Pseudophysaloptera, Skrjabinoptera,* and *Turgida.*

Genus	No. spp.	Definitive Hosts	Location	Adult worms	Eggs	Transmission

Physaloptera	135	carnivores, birds, reptiles	stomach, intestines	10-60 mm long, collar, buccal capsule with pseudolabia and teeth, bipartite oesophagus, tail with prepuce-like cuticular extension	44-58 x 29-42 µm, ovoid, thick-shelled	indirect (L3 in insect IH) [sometimes rodent, reptile PH]

The genus *Physaloptera* is characterised by stomach worms possessing a cephalic collarette, large dentate pseudolabia (each with 3 internal teeth), 4 pairs of pedunculate papillae, a prepuce-like cuticular extension on the tail and female worms having two to several uteri. Some workers proposed 2 subgenera: *P.* (*Physaloptera*) (male with closed prepuce-like sheath on posterior end); and *P.* (*Chlamydonema*) (male and female with open prepuce-like sheath at distal end). Other workers recognised several species groups according to female uterus type: namely, didelphic, tridelphic, tetradelphic and polydelphic with 2, 3, 4 or > 4 uteri/uterine branches, respectively. Regrettably, many early descriptions did not include enough detail for species to be classified to subgenus or species group. To date, some 135 *Physaloptera* species have been described from a range of vertebrate definitive hosts; mostly terrestrial reptiles, birds of prey, marsupials, rodents, insectivores, carnivores, and primates (including some reports in humans). The parasites have indirect life-cycles with larvae developing in invertebrate intermediate hosts (esp. insects such as beetles, cockroaches, and crickets) and sometimes being transported by vertebrate paratenic hosts (small rodents, birds, and reptiles).

***Physaloptera* species**	**Definitive Hosts**	**Location [Clinical signs]**	**Intermediate Hosts [plus Paratenic Hosts (PH)]**	**Distribution**
Group Didelphys				
P. abjecta	Serpentes: colubrid (coachwhip, prairie kingsnake)	stomach		North America
P. acuticauda	Accipitriformes: accipitrid (bicoloured hawk, red-tailed hawk, broad-winged hawk, grey-headed hawk, hen harrier); Falconiformes: falconid (peregrine falcon, laughing falcon)	stomach, oesophagus		Holarctic
P. agkistrodontis	Serpentes: viperid (sharp-nosed pitviper)			Asia
P. alata (incl. subspp. *alata*, *chevreuxi*)	Accipitriformes: accipitrid (Eurasian sparrowhawk, besra, shikra, roadside hawk, kestrel hawk, crested goshawk, hen harrier, Montagu's harrier, short-toed snake eagle, booted eagle, common buzzard, European honey buzzard); Falconiformes: falconid (saker falcon, laughing falcon, peregrine falcon, Eleonore's falcon, common kestrel, Eurasian hobby); Galliformes: phasianid (jungle bushquail)	stomach, intestines		Eurasia
P. anomala	Carnivora: felid (jaguar)	stomach		South America
P. apivori	Accipitriformes: accipitrid (European honey buzzard)			Europe
P. bainae	Sauria: teiid (Argentine black-and-white tegu)	stomach		South America
P. banfieldi	Peramelemorphia: peramelid (northern brown bandicoot); Rodentia: murid (fawn-footed mosaic-tailed rat)			Australia
P. bedfordi	Chiroptera: rhinolophid (Geoffroy's horseshoe bat)			Africa
P. bispiculata	Carnivora: felid (cat, wildcat), mustelid (honey badger); Rodentia: cricetid (South American water rat, hispid cotton rat); Lagomorpha:	stomach		Africa, Americas

	ochotonid (American pika)			
P. bonnei	Sauria: teiid (tegu (sapakara))	stomach		South America
P. brachycerca	Accipitriformes: accipitrid (lizard buzzard)	stomach		Africa
P. brevivaginata	Chiroptera: miniopterid (common bentwing bat), vespertilionid (greater mouse-eared bat, lesser mouse-eared bat, grey long-eared bat, Kuhl's pipistrelle)	stomach		Europe
P. canis	Carnivora: canid (black-backed jackal), felid (Southern African wildcat), viverrid (common genet, Cape genet)			Africa
P. cerdocyona	Carnivora: canid (crab-eating fox)	subcutis		Africa
P. chamaeleontis	Sauria: chamaeleonid (slender chameleon)	stomach		Africa
P. P. clausa	Carnivora: canid (culpeo, gray fox, South American gray fox); Eulipotyphla: erinaceid (north African hedgehog, European hedgehog, northern white-breasted hedgehog, southern white-breasted hedgehog, long-eared hedgehog, desert hedgehog)	stomach	[PH: Sauria: lacertid (sand lizard, European green lizard); Rodentia: dipodid (southern birch mouse)]	South America, Africa
P. crosi	Accipitriformes: accipitrid (Bonnelli's eagle); Coraciiformes: coraciid (European roller); Strigiformes: strigid (Eurasian eagle-owl)	stomach		Eurasia
P. cruzsilvai	Accipitriformes: accipitrid (white-bellied sea-eagle)			Asia
P. galinieri	Accipitriformes: accipitrid (unspecified eagle)	stomach, oesophagus		Eurasia
P. getula	Rodentia: cricetid (South American water rat), murid (mouse, black rat, Polynesian rat)	stomach		Americas, Asia, Africa
P. herthameyerae	Didelphimorphia: didelphid (agile gracile opossum)	stomach		South America
P. hispida	Rodentia: cricteid (hispid cotton rat, marsh rice rat, cotton mouse, Oldfield mouse, Florida mouse), murid (brown rat)	stomach	Blattodea: blattid (cockroach, *Blatella germanica*); Coleoptera: carabid (ground beetle, *Harpalus*); Dermaptera: forficulid (earwig, *Forficula auricularia*)	Americas
P. immerpaini	Eulipotyphla: erinaceid (Southern African hedgehog)			Africa
P. limbata	Eulipotyphla: talpid (eastern mole, prairie mole, Missouri valley mole, hairy-tailed mole), soricid (northern short-tailed shrew); Rodentia: geomyid (plains pocket gopher)	stomach, intestines		North America
P. liophis	Serpentes: colubrid (military ground snake)	stomach		South America
P. longissima	Serpentes: colubrid (unspecified snakes)			Australia
P. losseni	Accipitriformes: accipitrid (white-collared kite)	pharyngeal cavity		South America
P. lumsdeni	Primates: galagid (bush baby)			Africa
P. lutzi	Sauria: teiid (giant ameiva, Brazilian whiptail lizard), tropidurid (neotropical ground lizard, Amazon			South America

	lava lizard)			
P. malayensis	Carnivora: felid (junglecat, bushcat, tiger), hyaenid (striped hyena)	stomach, intestines		Malaysia
P. masoodi	Primates: lorisid (slender loris)	stomach		Eurasia
P. massino	Rodentia: dipodid (Gobi jerboa, Mongolian five-toed jerboa), murid (mouse), sciurid (Siberian chipmunk, Tarbagan marmot, long-tailed ground squirrel, Sherman's fox squirrel); Lagomorpha: ochotonid (Daurian pika)			Africa, Europe
P. maxillaris	Carnivora: mephitid (striped skunk, hooded skunk, Molina's hog-nosed skunk), canid (gray fox); Pelecaniformes: pelecanid (brown pelican)	stomach	Orthoptera: gryllid (fall field cricket); Blattodea: blattid (unspecified cockroach) [plus PH: Anura: ranid (northern leopard frog); Serpentes: colubrid (common garter snake)]	Americas
P. mexicana	Accipitriformes: accipitrid (buzzard)			North America
P. mirandai	Didelphimorphia: didelphid (brown four-eyed opossum)			South America
P. monodens	Serpentes: boid (boa constrictor)	stomach, intestines		South America
P. murisbrasiliensis	Rodentia: cricetid (web-footed marsh rat, hispid cotton rat), murid (Polynesian rat), sciurid (Brazilian squirrel)	stomach, small intestines		cosmopolitan
P. myotis	Chiroptera: miniopterid (common bentwing bat), rhinolophid (greater horseshoe bat, lesser horseshoe bat), vespertilionid (common noctule, lesser mouse-eared bat, greater mouse-eared bat, serotine bat, Bechstein's bat, Daubenton's bat, Nathusius's pipistrelle)			Eurasia
P. ngoci	Eulipotyphla: erinaceid (short-tailed gymnure); Rodentia: murid (mouse, rat)			Asia
P. obtusissima	Sauria: iguanid (Mexican spiny-tailed iguana); Serpentes: colubrid (indigo snake)	stomach		Americas
P. papillotruncata	Pilosa: choloepodid (Linnaeus's two-toed sloth), myrmecophagid (collared anteater)	stomach		South America
P. phrynosoma	Sauria: phrymnosomatid (Texas horned lizard, regal horned lizard)	stomach		Americas
P. (C.) praeputialis (syn. *P. (C.) felineus*)	Carnivora: felid (cat, sand cat, fishing cat, Pallas's cat, wildcat, South African wildcat, bobcat, lynx, Canada lynx, Iberian lynx, leopard cat, cougar, leopard, clouded leopard, ocelot, jaguarundi), canid (dog, wolf, maned wolf, red fox, corsac fox, Iberian fox), viverrid (common genet)	stomach [vomiting, anorexia]	Orthoptera: anostostomatid (king cricket), gryllid (Jamacian field cricket, *Acheta assimilis,* trilling cricket, *Gryllus*, striped cricket, *Miogryllus*), rhaphidophorid (camel cricket, *Ceuthophilus*); Dictyoptera: blattid (American cockroach, *Periplaneta americana*, Australian cockroach, *P. australasiae*); ectobiid (German cockroach, *Blatella germanica*)	worldwide

			[plus PH: Anura: bufonid (European green toad); Sauria: agamid (steppe agama), sphaerodactylid (frog-eyed gecko), varanid (desert monitor); Serpentes: colubrid (diadem snake, spotted desert racer), lamprophiid (arrow snake), viperid (painted carpet viper, lebetine viper); Eulipotyphla: erinaceid (long-eared hedgehog); Rodentia: murid (mouse)]	
P. pseudopraeputialis	Carnivora: felid (cat)	stomach		Philippines
P. rapacis	Accipitriformes: accipitrid (steppe eagle)			Africa
P. rara (syn. *P. felidis*) (oesophageal worm)	Carnivora: canid (dog, coyote, wolf, red fox, gray fox), felid (cat, bobcat, cougar, ocelot), mustelid (badger), procyonid (raccoon), ursid (American black bear, Florida black bear)	stomach, intestines [vomiting, anorexia]	Coleoptera: carabid (ground beetle, *Harpalus*), tenebrionid (flour beetle, *Tribolium confusum*); Blattodea: ectobiid (German cockroach, *Blatella germanica*), Orthoptera: gryllid (Jamacian field cricket, *Acheta assimilis*), acridid (red-legged grasshopper, *Melanoplus femurrubrum*) [plus PH: Serpentes: viperid (prairie rattlesnake); Rodentia: murid (mouse); Anura: ranid (northern leopard frog)]	North America, Egypt
P. reevesi	Accipitriformes: accipitrid (Eurasian sparrowhawk, crested goshawk)			Eurasia
P. retusa	Sauria: anguid (southern alligator lizard, Mexican alligator lizard, snake lizard), crotaphytid (long-nosed leopard lizard), iguanid (Lutz's tree iguana), liolaemid (Lutz's tree iguana), phrynosomatid (western fence-lizard, eastern fence-lizard, common side-blotched lizard, torquate lizard, rosebelly lizard, bluebelly lizard, zebra-tailed lizard, canyon lizard, cleft lizard, plateau spiny lizard, crevice spiny lizard, blue spiny lizard, desert spiny lizard, granite spiny lizard, Mexican emerald spiny lizard, Boccourt's spiny lizard, Yarrow's spiny lizard, plateau lizard, sage brush lizard, mesquite lizard), scincid (western skink, Paraguay mabuya), teiid (giant ameiva, rainbow ameiva, canyon spotted whiptail, rainbow whiptail, Brazilian whiptail, Spix's whiptail), tropidurid (Amazon lava lizard); Serpentes: colubrid (hog-nosed	stomach, intestines	[PH: Anura: bufonid (granular toad, leaf litter toad)]	Americas

	snake)			
P. semilanceolata	Carnivora: procyonid (white-nosed coati)	stomach		South America
P. seurati	Eulipotyphla: erinaceid (Algerian hedgehog, desert hedgehog)	stomach		Africa
P. sibirica	Carnivora: canid (wolf, red fox, corsac fox), felid (lynx), mustelid (European badger, mountain weasel, Siberian weasel)		[PH: Rodentia: glirid (garden dormouse)]	Eurasia
P. spinicauda	Rodentia: sciurid (Nelson's antelope squirrel)			North America
P. squamatae	Sauria: dactyloid (brown anole), leiocephalid (northern curly-tailed lizard), phrynosomatid (Florida scrub lizard), scincid (little brown skink), teiid (Caribbean ameiva); Serpentes: viperid (eastern copperhead, Texas copperhead)			Americas
P. subalata	Accipitriformes: accipitrid (bicoloured hawk, crane hawk)	stomach		South America
P. tacapensis	Rodentia: ctenodactylid (common gundi)	stomach		Eurasia
P. terdentata	Carnivora: felid (cougar, tiger)	stomach		South America
P. thalacomys	Peramelemorphia: peramelid (eastern barred bandicoot), thylacomyid (lesser bilby)			Australia
P. tupinambae	Sauria: teiid (Argentine black-and-white tegu)	stomach		South America
Group Tridelphys				
P. cebi	Primates: cercopithecid (hamadryas baboon, crab-eating macaque)	stomach		South America
P. coelebs	Afrosoricida: tenrecid (tenrec)			Madagascar
Group Tetradelphys				
P. bluntschlii	Afrosoricida: tenrecid (tenrec)	stomach		Madagascar
P. colubri	Serpentes: colubrid (smooth snake)	intestines		Australia
P. ericuli	Afrosoricida: tenrecid (spiny tenrec)			Madagascar
P. (C.) lagothricis	Primates: atelid (spider monkey)			Africa
P. magnipapilla	Pilosa: myrmecophagid (collared anteater)	stomach		South America
P. singhi	Primates (unspecified South American monkey)			South America
P. simplicidens	Sauria: scincid (sleepy lizard)			Australia
P. tumefaciens	Primates: cercopithecid (stump-tailed monkey, crab-eating macaque)	stomach		Asia
Group Polydelphys				
P. capensis	Rodentia: sciurid (Cape ground squirrel)	stomach		Africa
P. dilatata	Carnivora: felid (cougar, margay); Primates: atelid (brown woolly monkey), callitrichid (golden lion tamarin, marmoset), pitheciid (black bearded saki, titi monkey)	intestines, stomach		South America
P. torresi	Didelphimorphia: didelphid (common opossum); Lagomorpha: cuniculid (lowland paca); Rodentia: dasyproctid (agouti), cricetid (rice rat)	stomach		South America
P. turgida (syn. *Turgida*)	Didelphimorphia: didelphid (Virginia opossum, big-eared opossum, brown four-eyed	stomach	Blattodea: blattid (German cockroach, *Blatella germanica*); Orthoptera:	Americas

	opossum, bare-tailed woolly opossum); Carnivora: mustelid (American badger); Primates: cercopithecid (gelada)		gryllid (field cricket, *Acheta pennsylvanicus*)	
Group undetermined				
P. accipiteri	Accipitriformes: accipitrid (shikra)			India
P. ackerti	Didelphimorphia: didelphid (Virginia opossum)	stomach		North America
P. aduensis	Rodentia: murid (Peters's striped mouse)			Africa
P. (C.) agarwali	Carnivora: felid (tiger)			
P. amphibia	Anura: ranid (fanged river frog)	stomach		Eurasia
P. anadonta	Eulipotyphla: erinaceid (long-eared hedgehog)	stomach		Eurasia
P. bedfordi	Chiroptera: rhinolophid (Geoffroy's horseshoe bat)			Africa
P. bellicosa	Sauria: chamaeleonid (southwestern Madagascar chameleon)			Madagascar
P. bilabiata	Passeriformes: laniid (lesser grey shrike)	intestines		Eurasia
P. brevispiculum	Carnivora: felid (cat, wildcat, rusty spotted cat, African wildcat, leopard cat), mustelid (honey badger), viverrid (small Indian civet)	stomach	Dermaptera: labidurid (earwig, *Labidura riparia*) [plus PH: Sauria: agamid (Indian spiny-tailed lizard), gekkonid (yellow-belly gecko); Anura: bufonid (Indian marbled toad); Rodentia: sciurid (Indian palm squirrel)]	Africa, Asia
P. buteonis	Accipitriformes: accipitrid (red-tailed hawk)			North America
P. cahuidei	Carnivora: mephitid (Molina's hog-nosed skunk)			South America
P. calunensis	Rodentia: cricteid (small vesper mouse)	stomach		South America
P. cesticillata	Carnivora: canid (fennec fox)	stomach		Egypt
P. circularis	Rodentia: murid (black rat)	stomach		Africa
P. citilli (*citelli*)	Rodentia: sciurid (European ground squirrel)	stomach		Eurasia
P. confusa	Serpentes: elapid (tiger snake)		[PH: Anura: hylid (Australian green tree frog, Peron's tree frog), limnodynatsid (pobblebonk, spotted grass frog), pelodryadid (golden bell frog)	Australia
P. crassa	Passeriformes: alaudid (Eurasian skylark)	intestines		Eurasia
P. dentata	Sauria: agamid (steppe agama, secret toadhead agama); Serpentes: viperid (common European viper)	intestines, mouth		Russia
P. digitata	Carnivora: felid (cougar)	stomach		South America
P. dispar	Eulipotyphla: erinaceid (African hedgehog, North African hedgehog)	stomach		Africa
P. dogieli	Rodentia: murid (Libyan jird, Persian jird, Tristam's jird), sciurid (long-tailed ground squirrel)			Eurasia
P. elegantissima	Carnivora: mustelid (honey badger)	stomach		Africa
P. galvaoi	Rodentia: cricetid (terraced rice rat)	stomach		South America

P. georginapedreirae	Serpentes: elapid (coral snake)			
P. goytaca	Rodentia: cricteid (goytaca)	stomach		South America
P. guiarti	Carnivora: phocid (Weddell seal)	stomach		Antarctica
P. incurva	Eulipotyphla: erinaceid (southern African hedgehog)	stomach, intestines		Africa
P. inermis	Rodentia: sciurid (Prevost's squirrel)	stomach		Eurasia
P. inflata	Accipitriformes: accipitrid (Harris's hawk)	stomach, oesophagus		Central America
P. lagarda	Sauria: teiid (red tegu)			South America
P. longispicula	Rodentia: echimyid (common punare)	stomach		South America
P. massimo	Rodentia: sciurid (fox squirrel, thirteen-lined ground squirrel)			North America
P. megalostoma	Accipitriformes: accipitrid (Eurasian sparrowhawk)	proventriculus		Eurasia
P. mephites	Carnivora: mephitid (skunk)			South America
P. mydai	Carnivora: mephitid (stink badger)	stomach		Asia
P. nasilionis	Macroscelidea: macroscelidid (elephant shrew)	connective tissue		Africa
P. pacitae	Carnivora: felid (cat)	stomach		Philippines
P. papuensis	Peramelemorphia: peramelid (spiny bandicoot)			Australasia
P. parvicollaris	Peramelemorphia: peramelid (long-nosed bandicoot)			Australia
P. peragale	Peramelemorphia: thylacomyid (lesser bilby)			Australia
P. peramelis	Peramelemorphia: peramelid (northern brown bandicoot, long-nosed bandicoot), thylacomyid (lesser bilby)			Australia
P. pyramidalis	Pilosa: choloepodid (Linnaeus's two-toed sloth)			South America
P. quadridentata	Accipitriformes: accipitrid (broad-winged hawk)			North America
P. rauschi	Carnivora: mustelid (American badger)			North America
P. ruwenzorii	Rodentia: murid (Abyssinian grass rat, Natal multimammate mouse)	intestines		Africa
P. sarcophili	Dasyuromorphia: dasyurid (northern quoll, tiger quoll, Tasmanian devil)			Australia
P. sciuri	Rodentia: sciurid (Mentawai squirrel)	stomach, intestines		Asia
P. sonsinoi	Sauria: agamid (desert agama)	stomach		Europe
P. spiralis	Sauria: amphisbaenid (worm lizard)	stomach		South America
P. tadorna	Anseriformes: anatid (common shelduck)			Eurasia
P. tigrinae	Anura: ranid (Indian bullfrog)			India
P. torquata	Carnivora: mustelid (American badger, wolverine); Rodentia: cricteid (hispid cotton rat)	stomach		America
P. transfuga	Carnivora: canid (dog), felid (cat); Primates: hominid (human)		Coleoptera (unspecified beetle)	
P. troughtoni	Rodentia: murid (bush rat)			Australia
P. truncata	Galliformes: phasianid (junglefowl)	stomach		South America
P. upembae	Gruiformes: rallid (African			Africa

	swamphen)			
P. variegata	Serpentes: colubrid (eastern racer, eastern hognose snake); Sauria: anguid (eastern glass lizard)			North America
P. versicoli	Sauria: agamid (oriental garden lizard)			Asia
P. vigisiana	Galliformes: phasianid (chicken)			Russia
P. visakhapatnamensis	Rodentia: sciurid (Indian palm squirrel)			Asia
P. zigodontomis	Rodentia: cricetid (cane mouse)			Asia
Species inquirenda				
P. brevicauda sp. inq.	Galliformes: phasianid (red-billed spurfowl)	intestines		Africa
P. hieracideae sp. inq.	Falconiformes: falconid (brown hawk)			Australia
P. malleus sp. inq.	Passeriformes: corvid (hooded crow, Eurasian magpie)			Eurasia
P. papilloradiata sp. inq.	Carnivora: canid (wolf)	pectoral cavity		Eurasia
P. spirula sp. inq.	Hyracoidea: procaviid (rock hyrax, Cape hyrax)	large intestines		Eurasia
Re-assigned species				
P. abbreviata (now *Abbreviata*)	Sauria: agamid (sand lizard), anguid (European glass lizard), lacertid (ocellated lizard, European green lizard, Iberian emerald lizard, Iberian wall lizard); Serpentes: colubrid (water snake)	stomach		North Africa, Europe
P. africana (now *Abbreviata*)	Rodentia: murid (striped mouse, white-nosed rat, Pretoria rat), octodontid (cane rat), sciurid (gray-footed squirrel)			Africa
P. aloisii-sabaudiae (now *Abbreviata*)	Sauria: agamid (black-necked agama)	intestines		Africa
P. amaniensis (now *Abbreviata*)	Sauria: agamid (dragon lizard)			Africa
P. antarctica (syn. *P. alba*) (now *Abbreviata*)	Serpentes: pythonid (diamond python), elapid (death adder); Sauria: scincid (western blue-tongued lizard, eastern blue-tongued lizard), varanid (lace monitor)	stomach, oesophagus		Australia
P. bancrofti (syn. *P. natricus, physignathi*) (now *Abbreviata*)	Sauria: agamid (Australian water dragon), gekkonid (broad-tailed gecko); Serpentes: colubrid (Bismarck keelback)			Australia, New Zealand
P. britanica (now *Abbreviata*)	Sauria: agamid (unspecified agamid)	intestines		Africa
P. bulbosa (now *Cyrnea*)	Galliformes: phasianid (green peafowl)	stomach		Asia
P. calotisi (now *Abbreviata*)	Sauria: agamid (oriental garden lizard)			Asia
P. capensis (now *Abbreviata*)	Rodentia: sciurid (Cape ground squirrel)			Africa
P. caucasica (syn. *P. mordens*) (now *Abbreviata*)	Primates: cercopithecid (hamadryas baboon, yellow baboon, chacma baboon, Barbary macaque, rhesus macaque), hominid (orangutan, human)	stomach, oesophagus, intestines	Blattodea: blattid (German cockroach, *Blatella germanica*); Coleoptera (unspecified beetle); Orthoptera: acridid (desert locust, *Schistocerca gregaria*)	Africa
P. constricta (now *Spiroxys*)	Serpentes: colubrid (common water snake)	stomach		North America

P. contorta (now *Spiroxys*)	Testudines: emydid (pond slider, chicken turtle, eastern box turtle), kinosternid (eastern mud turtle)	stomach		North America
P. funambuli (now *Abbreviata*)	Rodentia: sciurid (northern palm squirrel)			Asia
P. gemina (now *Abbreviata*)	Carnivora: felid (cat)	stomach, intestines		Egypt
P. gracilis (now *Abbreviata*)	Sauria: lacertid (unspecified lizard)			Africa
P. guptae (now *Abbreviata*)	Sauria: agamid (oriental garden lizard)			Asia
P. kotlani (syn. *P. soricina, riukiuana*) (now *Pseudophysaloptera formosana*)	Eulipotyphla: soricid (common shrew, alpine shrew, bicoloured shrew, Eurasian pygmy shrew, Asian house shrew, Laxmann's shrew, moonrat); Rodentia: sciurid (squirrel, long-tailed ground squirrel, tropical ground squirrel)	stomach		Eurasia
P. indica (now *Abbreviata*)	Sauria: agamid (oriental garden lizard)			Asia
P. johnsoni (now *Abbreviata*)	Sauria: varanid (monitor lizard)			Asia
P. joyeuxi (now *Abbreviata*)	Artiodactyla: suid (warthog)			Africa
P. kherai (now *Abbreviata*)	Sauria: varanid (yellow monitor)			Asia
P. leptosoma (now *Abbreviata*)	Sauria: agamid (North African spiny-tailed lizard, Moroccan spiny-tailed lizard), varanid (desert monitor)	stomach, oesophagus		Africa
P. mucronata (now *Ascaris*)	Crocodilia: alligatorid (American alligator)			North America
P. multipapillata (now *Abbreviata*)	Primates: cercopithecid (hamadryas baboon)			Africa
P. musculi (now *Abbreviata*)	Rodentia: murid (mouse)			Sri Lanka
P. numidica (now *Abbreviata*)	Rodentia: murid (North African gerbil)	stomach		Africa
P. ortleppi (now *Abbreviata*)	Sauria: chamaeleonid (flap-necked chameleon)			Africa
P. ovata (now *Cyrnea*)	Accipitriformes: accipitrid (black sparrowhawk)	ventriculus		Africa
P. pallaryi (now *Abbreviata*)	Sauria: agamid (Bibron's agama)	stomach, intestines		Africa
P. paradoxa (syn. *P. affinis, algeriensis*) (now *Abbreviata*)	Sauria: varanid (white-throated monitor, rock monitor, gray monitor); Serpentes: colubrid (whipsnake), psammophiid (hissing sand snake), viperid (horned viper)	stomach, intestines		Africa
P. poicilometra (now *Abbreviata*)	Primates: cercopithecid (blue monkey, mangabey, guenon)	stomach		Africa
P. polydentata (now *Abbreviata*)	Sauria: gekkonid (tropical house gecko)			Africa
P. ranae (now *Abbreviata*)			[larvae: Anura: ranid (American bullfrog, southern leopard frog, northern leopard frog), bufonid (Woodhouse's toad)]	Americas
P. rotundata (now *Habronema*)	Otidiformes: otidid (MacQueen's bustard)	intestines		Asia
P. saginata	Caprimulgiformes: caprimulgid			

(now *Spiroptera*)	(goatsucker); Passeriformes: corvid (crow)			
P. striata (now *Cyrnea*)	Ciconiiformes: ciconiid (white-stork); Serpentes: colubrid (dice snake)	stomach		Eurasia
P. tasmani (now *Abbreviata*)	Sauria: chamaeleonid (chameleon)			Africa
P. tenuicollis (now *Ascaris*)	Accipitriformes: pandionid (osprey)	intestine		Europe
P. terrapenis (now *Abbreviata*)	Testudines: chelydrid (common snapping turtle), emydid (western box turtle, western painted turtle, Blanding's turtle)			North America
P. thaparus (now *Abbreviata*)	Sauria: agamid (oriental garden lizard)			Asia
P. vandenbrandeni (now *Abbreviata*)	Carnivora: felid (wildcat)			Africa
P. varani (syn. *P. quadrovaria*) (now *Abbreviata*)	Sauria: varanid (yellow monitor, Bengal monitor, Indian monitor, Nile monitor), phrynosomatid (eastern fence lizard); Serpentes: colubrid (big-eye rat snake)	stomach, intestines		Asia, North America

Parasite morphology: *Physaloptera* spp. form 3 different types of morphological stages during their development: namely, eggs; larvae; and adult worms. The eggs range in size from 42-58 x 29-42 μm and are oval-elliptical in shape with slightly flattened sides. They are bound by a thick smooth shell thickened at the poles and are embryonated when laid. The parasites form 4 successive larval stages, usually encoded L1 to L4. The eggs contain coiled L1 which measure 150-250 μm in length and have conical heads with a subterminal left hook and 1-2 pairs of median scales, a bipartite oesophagus (with a posterior bulb), long sac-like intestines, and conical tails. L2 have elongate cylindrical bodies up to 1.2 mm long, laterally flattened mouths with cephalic and labial papillae, small buccal capsules, a divided oesophagus, and conical tails. L3 range in length from 1.5-4.2 mm and have adult cephalic characteristics (2 massive pseudolabia, each with an external tooth and 3 internal teeth), flattened mouths with labial papillae no longer identifiable, a divided oesophagus and conical tails. L4 are transient parasitic stages that have begun to develop sexual characteristics in the form of genital primordia. Adults are pink robust worms with cylindrical bodies ranging from 10-60 mm in length and are bound by thick cuticles with fine transverse striations. Most species possess an anterior cuticular recess appearing as a cervical collarette, broad caudal alae, and a preputial-like sheath extending posteriorly (closed distally in males of the subgenus *P.* (*Physaloptera*), but open in both males and females of the subgenus *P.* (*Chlamydonema*)). The anterior mouth is laterally flattened and possesses 2 large triangular lateral pseudolabia, each armed with 3 flattened internolateral teeth and a single conical externolateral tooth. The buccal capsule is atrophied and not well-developed or absent, and the bipartite oesophagus has a short anterior muscular and a long posterior glandular section. Adults worms are sexually dimorphic, with males being smaller than females (10-45 cf. 15-60 mm). Mature males have coiled tails with a specialised ventral cuticular patch of tubercles (area rugosa), well-developed caudal papillae (4 cloacal pairs), 2 caudal alae which join ventrally (forming an ornamental caudal bursa), and 2 well-developed subequal spicules (left spicule longer). Mature female worms have a single vulva opening anterior to the midbody but connected to 2 or more uteri/uterine branches (didelphic with 2, tridelphic with 3, tetradelphic with 4, polydelphic with > 4). Gravid females produce embryonated eggs containing fully developed larvae.

Site of infection: Adult worms infect the stomachs of their final hosts (mammals, birds, reptiles) where they are found attached to the mucosal wall. Infective larvae develop within the gut wall of invertebrate intermediate hosts (insects), and they may also be carried in the tissues of small vertebrate paratenic hosts.

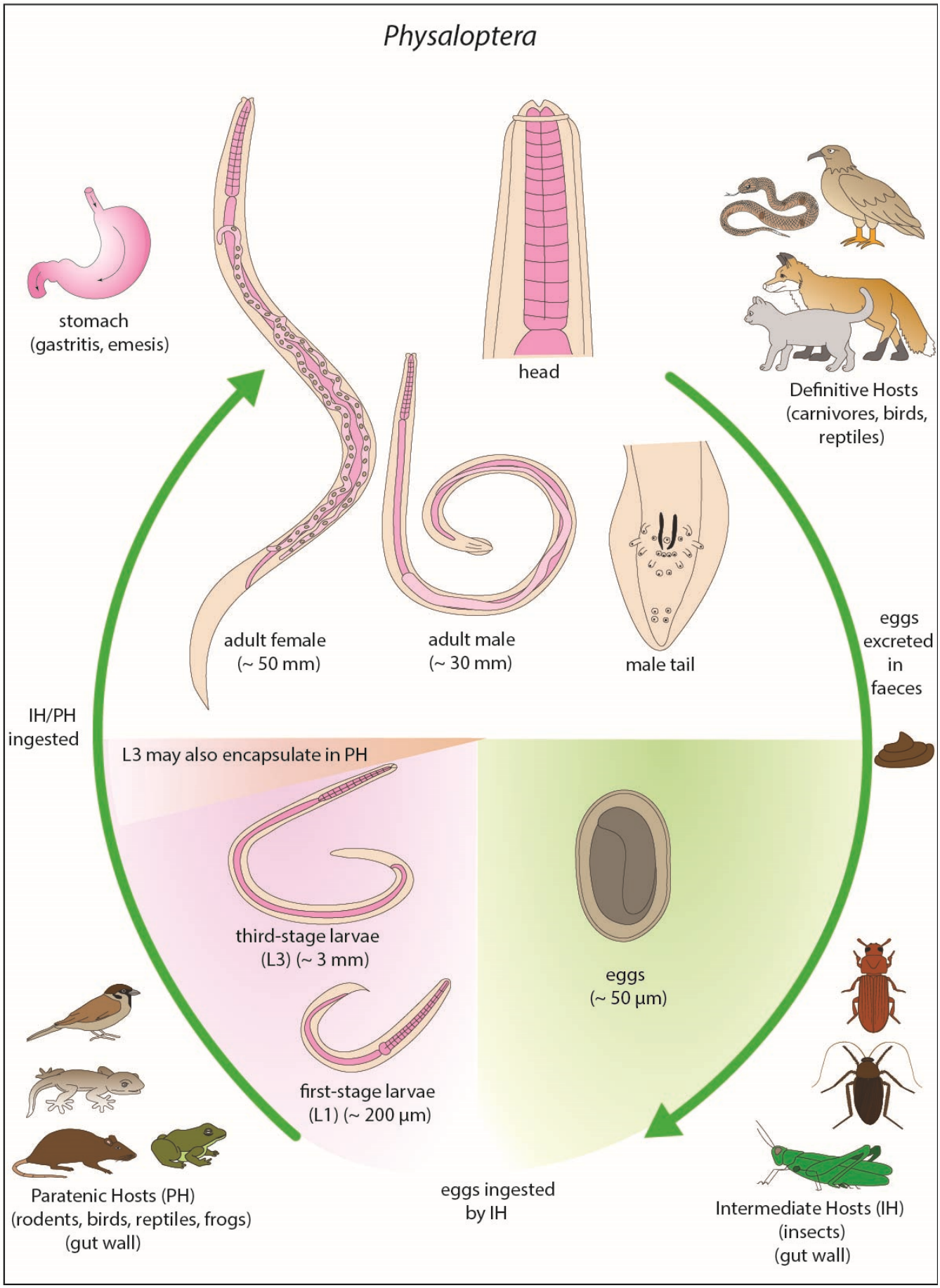
Pathogenesis: While light infections often remain subclinical, heavier infections may cause disease typified by gastritis and emesis (vomiting). Worms attach to the stomach wall using their anterior collarettes and sublabial teeth but do not appear to feed on host tissues, but rather on stomach content. Nevertheless, they frequently detach to move to new locations leaving behind small erosive lesions which continue to haemorrhage and may ulcerate. The mucosa becomes inflamed (catarrhal gastritis with mucus production), hosts may vomit stomach content, and the faeces may appear dark in colour due to the presence of blood (melena). Continued blood loss in heavy infections may result in anaemia and animals may become anorexic and progressively lose body weight and condition.

Developmental cycle and mode of transmission: *Physaloptera* spp. have indirect heteroxenous life-cycles involving adult worm formation in predatory or scavenging vertebrates (definitive hosts), larval development in coprophagous insects (intermediate hosts),

and often larval carriage in small insectivorous vertebrates (paratenic hosts). Embryonated eggs laid by gravid females in the stomach are excreted with host faeces (sometimes vomitus) into the external environment where may survive for short periods in moist conditions. The eggs are ingested by a range of insects (cockroaches, beetles, grasshoppers, crickets, earwigs) which act as intermediate hosts supporting larval development. Ingested eggs hatch in the gut releasing L1 which penetrate the gut wall inducing the formation of local syncytia (hypertrophied multinucleate epithelial cells) which eventually become encapsulated by loose fibrous connective tissue. Enclosed L1 moult twice to form L3 by 30-35 days and the growing capsules often become pedunculate and bulge into the haemocoel. Larvae do not undergo arrested development in the insect intermediate hosts but continue growing and reach an advanced stage of sexual development. Infective L3 may also re-encapsulate in the gut wall of a range of vertebrate paratenic hosts (rodents, birds, reptiles, amphibians) which have consumed infected insects. Final hosts become infected when they ingest infective L3 contained within the tissues of intermediate or paratenic hosts. Ingested L3 develop directly in the gut without undertaking any local or somatic migration. They moult twice to form subadults (sometimes termed L5) which then mature to adult worms. The prepatent period (time from infection to the first excretion of eggs) varies considerably depending on parasite species, ranging from 56-70 days in those with rapid development, from 73-90 days in those with moderate development, and from 131-156 days in those with slow development.

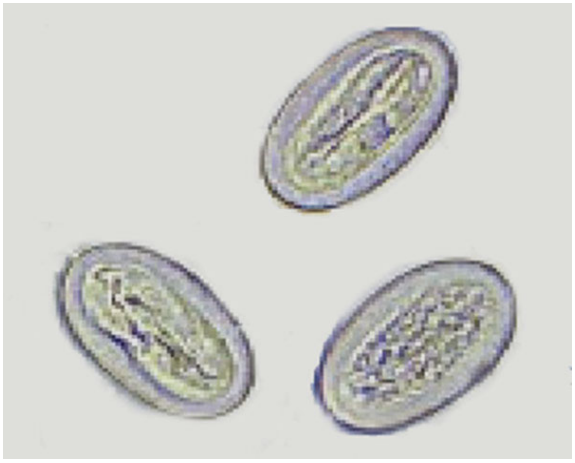
Differential diagnosis: Clinical infections may be suggested in hosts exhibiting signs of gastritis involving vomiting, melena and anaemia, but differential diagnosis requires the direct detection of parasites. Immature worms may be found in vomitus of puppies or kittens, but mature worms are usually firmly attached to the mucosa. Endoscopic examination (gastroscopy) has been used to detect stomach worms *in situ*. Worm eggs may be detected by coprological examination of faecal samples, but the characteristic eggs (thick-shelled, elliptical, embryonated) are not very buoyant and are best detected by sedimentation rather than floatation. Adult worms may also be detected at post-mortem by dissection of the stomach mucosa. Modern molecular biological techniques have been used to examine parasite phylogenetic relationships following polymerase chain reaction (PCR) amplification of nuclear gene sequences (small subunit ribosomal RNA).

Treatment and control: Infections have been successfully treated using a range of anthelmintic drugs, including benzimidazoles (fenbendazole), tetrahydropyrimidines (pyrantel) and macrocyclic lactones (ivermectin). Infections responded best to sustained treatment over 5 days or repeated treatment over several weeks. Few preventive strategies are practicable in natural situations involving wildlife, but commonsense measures may be taken to limit transmission in domestic or peridomestic situations. Efforts should be made to routinely remove potential sources of contamination (faeces and vomitus), decontaminate animal holding facilities (regular cleaning and disinfection), reduce insect populations (using barriers and insecticides), exclude potential paratenic hosts (close-mesh screens and fencing) and prevent parasite uptake by final hosts (prevent hunting and scavenging, and providing clean food and water).

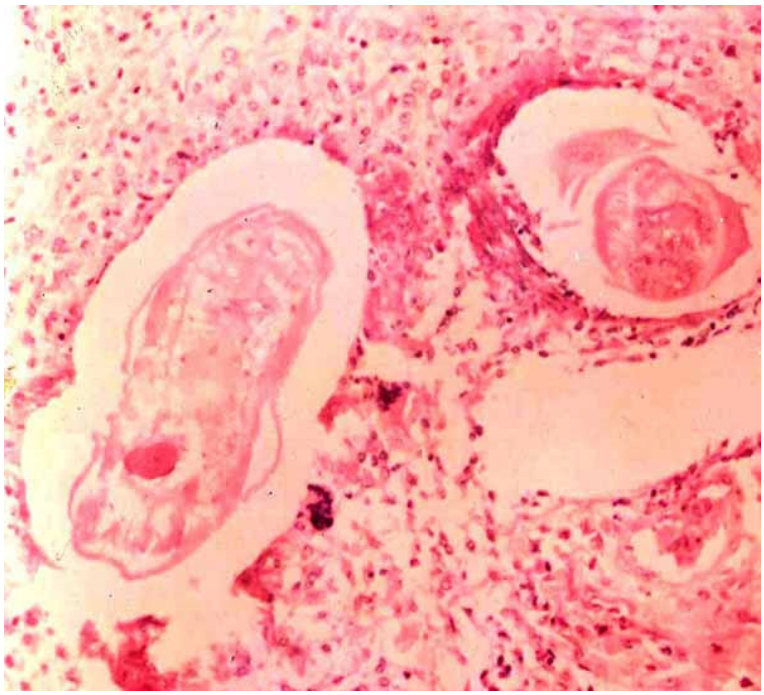

Physaloptera
stomach
(gastritis, emesis)
adult female
(~ 50 mm)
head
adult male
(~ 30 mm)
male tail
Definitive Hosts
(carnivores, birds,
reptiles)
eggs
excreted
in
faeces
IH/PH
ingested
L3 may also encapsulate in PH
third-stage larvae
(L3) (~ 3 mm)
first-stage larvae
(L1) (~ 200 µm)
eggs
(~ 50 µm)
Paratenic Hosts (PH)
(rodents, birds, reptiles, frogs)
(gut wall)
eggs ingested
by IH
Intermediate Hosts (IH)
(insects)
(gut wall)



Physaloptera adult worm



Physaloptera worm eggs



Physaloptera lesion

Gnathostoma
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Gnathostomatomorpha which includes the gnathostomatoids with enlarged head bulbs covered with hooks and indirect life-cycles. Gnathostomids are found in the stomachs of carnivores and are transmitted through copepods (acting as first intermediate hosts) and then small mammals, birds, reptiles, fish and amphibians (which act as second intermediate hosts or paratenic hosts). Infections by *Gnathostoma* spp. may cause cutaneous lesions and acute abdominal signs, perforation and peritonitis in their definitive hosts.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily:	Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Family:	Gnathostomidae (swollen anterior head bulb, covered with rows of hooks, two lateral lips, four cervical sacs)
Genus:	*Gnathostoma* (parasitic in stomach of cats/pigs)
Species:	various species cause gut lesions in carnivores

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Gnathostomatoidea is characterised by worms with large complex pseudolabia and 4 cervical sacs and infects the alimentary tracts of vertebrates and using invertebrates as intermediate hosts for larval development and vertebrates as paratenic hosts for larval transport. Only one family (Gnathostomatidae) is recognised with 4 subfamilies: Gnathostominae (cephalic bulb present, parasites of mammals, reptiles or fish); Metaleptinae (cephalic bulb absent, pseudolabia with small teeth, *Metalepus* in sharks); Spiroxyinae (cephalic bulb absent, pseudolabia without posterior appendages, *Spiroxys* in snakes, tortoises, amphibians); and Ancyracanthinae (cephalic bulb absent, pseudolabia with long ramified appendages, *Ancyracanthus* in fishes and chelonians). The subfamily Gnathostominae contains 3 genera: *Tanqua* (cephalic bulb divided into 2 or 4 lobes with transverse cuticular ridges with sharp posteriorly-projecting edges but without hooks, parasites of aquatic reptiles); *Echinocephalus* (cephalic bulb undivided and armed with transverse rows of recurved hooks, body unarmed, parasites of fishes); and *Gnathostoma* (cephalic bulb undivided and armed with transverse rows of recurved hooks, body partially or wholly armed with posteriorly-directed spines, parasites of mammals).

Genus	No.	Definitive	Location	Adult worms	Eggs	Transmission

	spp.	Hosts				
Gnathostoma	18	carnivores	stomach	10-55 mm long, bulbous head with 2 lateral pseudolabia covered with spines extending to anterior body	62-79 x 36-42 µm ellipsoidal, thick-shelled, polar cap	indirect (L3 in copepodid intermediate hosts) [small vertebrates acting as second intermediate hosts or paratenic hosts]

Gnathostoma spp. are heteroxenous (multi-host) parasites with adult stages occurring in the gut of vertebrate hosts and larval stages developing in copepods (first intermediate hosts) and then ascending the food chain in a range of small vertebrates (second intermediate hosts or paratenic hosts). Some 18 species have been described in the genus *Gnathostoma,* most infecting the stomach (sometimes oesophagus and rarely kidneys) of carnivores. Several species have been associated with clinical disease in domestic animals, mainly *G. spinigerum* in cats and dogs and *G. hispidum* in pigs. The larval stages, however, have a broad host range and may infect many different species of small vertebrates (fish, amphibians, reptiles, birds and mammals) as paratenic hosts. The larvae may undertake extensive migrations through cutaneous tissues or visceral organs causing traumatic damage and inflammation. Several species are zoonotic (*G. spinigerum, G. hispidum*, *G. doloresi*, *G. nipponicum,* and *G.binucleatum*) as larvae infect humans as accidental hosts when they eat or handle raw or undercooked meat or drink water containing infected copepods.

***Gnathostoma* species**	**Definitive hosts [DH]**	**Location [Clinical signs]**	**First Intermediate Hosts [IH-1] Second Intermediate Hosts [IH-2] Paratenic Hosts [PH]**	**Distribution**
G. accipitris	Accipitriformes: accipitrid (imperial eagle)			Africa
G. americanum	Carnivora: felid (oncilla, Geoffroy's cat)	stomach		South America
G. binucleatum	Carnivora: canid (dog), felid (cat, ocelot), procyonid (Mexican raccoon)	stomach	IH-1: Copepoda: cyclopid (water flea, *Cyclops bicuspidatus, Eucyclops agilis, macrurus, prasinus, Macrocyclops albidus, Mesocyclops edax, leuckarti, tenuis*) [plus IH-2/PH: Characiformes: erythrinid (trahira); Cichliformes: cichlid (three spot cichlid, fenestrated cichlid, Mayan cichlid, blue tilapia, Mozambique tilapia, Nile tilapia, bay snook); Gobiiformes: eleotrid (bigmouth sleeper, spotted sleeper, Pacific sleeper, Pacific fat sleeper); Mugiliformes" mugilid (white mullet); Perciformes: centropomid (fat snook), haemulid (long-spined grunt); Siluriformes: ariid (dark sea catfish, Congo Sea catfish); Pelecaniformes: ardeid (great egret), pelecanid (American white pelican); Testudines: emydid (pond slider), kinosternid (Mexican mud turtle); Primates: hominid (human)]	Americas
G. doloresi	Artiodactyla: suid (pig, wild boar, Japanese boar)	stomach [inappetence]	IH-1: Copepoda: cyclopid (*Apocyclops royi, Cyclops strenuus, vicinus, Eucyclops serrulatus, Mesocyclops leuckarti, Thermocyclops hyalinus, taihokuensis*) [plus IH-2/PH: Urodela: hynobiid (spotted salamander, amber-coloured salamander); Anura: ranid (tiger frog); Serpentes: colubrid (loo-choo big-tooth snake, Japanese forest rat snake, Japanese striped snake, Pryer's keelback, tiger keelback), viperid (elegant pit viper, Okinawa habu, Hime habu, Siberian pit viper); Perciformes: centrarchid	Asia, Australasia

			(bluegill); Salmoniformes: salmonid (masu salmon); Rodentia: murid (mouse, rat); Peramelemorphia: peramelid (northern brown bandicoot); Primates; hominid (human)]	
G. gracile	Osteoglossiformes: arapaimid (pirarucu)	intestines		South America
G. hispidum	Artiodactyla: suid (pig, wild boar), Carnivora: felid (cat)	stomach [inappetence]	IH-1: Copepoda: cyclopid (*Acanthocyclops virides, Apocyclops royi, Cyclops strenuus, varicans, vicinus, Eucyclops serratus, Macrocyclops albidis, Mesocyclops leuckarti, Thermocyclops hyalinus, oithonides, taihokuensis*) [plus IH-2/PH: Anabantiformes: anabantid (climbing gourami), channid (striped snakehead, northern snakehead); Anguilliformes: anguillid (Japanese eel); Cypriniformes: cobitid (pond loach), cyprinid (common carp, predatory carp, goldfish, common bleak, Danube bleak, spotted steed, three-lips, common roach); Cyprinodontiformes: poeciliid (mosquitofish, guppy); Gobiiformes: odontobutid (dark sleeper); Perciformes: percid (European perch, zander), sinipercid (mandarin fish); Siluriformes: bagrid (yellow catfish), silurid (Amur catfish, wels catfish); Synbranchiformes: synbranchid (Asian swamp eel); Anura: dicroglossid (rice field frog), ranid (dark-spotted frog, Indian bullfrog); Serpentes: colubrid (Chinese garter snake, checkered keelback), viperid (short-tailed pit viper); Accipitriformes: accipitrid (northern goshawk); Anseriformes: anatid (duck, smew); Columbiformes: columbid (spotted dove); Falconiformes: falconid (peregrine falcon); Galliformes: phasianid (chicken); Passeriformes: sturnid (crested myna); Rodentia: caviid (guinea pig), murid (brown rat, black rat, mouse, southwestern Asian house mouse, Mongolian gerbil); Eulipotyphla: soricid (Asian house shrew); Lagomorpha: ochotonid (Daurian pika); Primates: cercopithecid (rhesus macaque), hominid (human)]	Asia, Australia, Central America
G. lamothei	Carnivora: procyonid (Mexican raccoon)	stomach		Americas
G. malaysiae	Rodentia: murid (red spiny rat)	stomach	[plus IH-2/PH: Synbranchiformes: synbranchid (Asian swamp eel); Primates: hominid (human)]	Asia
G. minutum	Serpentes: viperid (rhinoceros viper)	connective tissue		Africa
G. miyazakii	Carnivora: mustelid (North American river otter)	kidney		North America
G. nipponicum	Carnivora: mustelid (Japanese mink, American mink, weasel, Japanese weasel, Siberian weasel, ferret)	oesophagus	IH-1: Copepoda: cyclopid (*Acanthocyclops vernalis, Cyclops vicinus, Eucyclops serrulatus, Macrocyclops fuscus, Thermocyclops hyalinus*) [plus IH-2/PH: Urodela: hydnobiid (clouded	Japan, Korea

			salamander); Anura: ranid (black-spotted frog, American bullfrog); Beloniformes: adrianichthyid (Japanese rice fish); Cypriniformes: cyprinid (big-scaled redfin); Cyprinodontiformes: cobitid (pond loach); Perciformes: centrarchid (largemouth bass); Salmoniformes: salmonid (masu salmon); Siluriformes: silurid (Amur catfish); Serpentes: colubrid (Japanese striped snake, tiger keelback); Rodentia: murid (mouse, brown rat); Primates: hominid (human)]	
G. occipitri	Accipitriformes: accipitrid (unspecified eagle)	subcutis		Russia
G. pelecani	Pelecaniformes: pelecanid (great white pelican)	subcutis, respiratory sacs		Eurasia
G. procyonis (syn. *G. 'neoprocyonis'*)	Carnivora: felid (cougar), procyonid (raccoon); Didelphimorphia: didelphid (common opossum)	stomach	IH-1: Copepoda: cyclopid (*Cyclops bicuspidatus, vernalis, Macrocyclops albidis*) [plus IH-2/PH Amiiformes: amiid (bowfin); Testudines: emydid (common box turtle, pond slider); Serpentes: viperid (water moccasin), colubrid (common kingsnake, common water snake); Testudines: emydid (false map turtle, yellow-bellied slider, common box turtle), kinosternid (eastern mud turtle); Crocodilia: alligatorid (American alligator); Pelecaniformes: threskiornithid (American white ibis); Primates: hominid (human)]	North America
G. socialis	Carnivora: mustelid (American mink)	stomach		Americas
G. spinigerum (syn. *Filaria radula*)	Carnivora: felid (cat, wildcat, Asian golden cat, lion, leopard, tiger), canid (dog, golden jackal), herpestid (Indian grey mongoose), mustelid (mink, ferret), procyonid (raccoon); Didelphimorphia: didelphid (common opossum)	stomach [acute abdominal signs, gut perforation, peritonitis]	IH-1: Copepoda: cyclopid (*Cyclops strenuus, varicans, vicinus, Eucyclops agilis, serrulatus, Mesocyclops leuckarti, Thermocyclops*) [plus IH-2/PH: Decapoda: cambarid (crayfish, *Procambarus clarkii*), parathelphusid (freshwater crab, *Paratelphusa sexpunctatum*), potamid (freshwater crab, *Potamon dehaani, smithanus*), varunid (mitten crab, *Eriocheir japonicus*); Gastropoda: ampullariid (snail, *Pila ampullacea, Pomacea canaliculata*); Anguilliformes: anguillid (Japanese eel); Anabantiformes: anabantid (climbing perch), channid (snakehead murrel, striped snakehead, northern snakehead, spotted snakedhead, blotched snakehead, forest snakehead, giant snakehead, Assamese snakehead, dalug), osphronemid (banded gourami, moonlight gourami, snakeskin gourami, three-spot gourami); Beloniformes: belonid (freshwater garfish); Characiiformes: erythrinid (trahira); Cypriniformes: cyprinid (common carp, predatory carp, Crucian carp, spotted steed, three-lips, slender rasbora); Cyprinodontiformes: cobitid (pond loach), poeciliid (eastern mosquitofish); Gobiiformes: gobiid (tank goby, javelin goby), eleotoid (dark sleeper), oxudercid	Asia, Americas, Africa, Australia

			(yellowfin goby); Osteoglossiformes: notopterid (Asian knifefish); Perciformes: nandid (Gangetic leaf-fish), sinipercid (mandarin fish), terapontid (silver perch, ayungin); Siluriformes: ariid (engraved catfish), bagrid (yellowhead catfish, yellow catfish, pla kayeng), clariid (walking catfish, Hong Kong catfish, broadhead catfish), heteropneostid (Asian stinging catfish), silurid (butter catfish, padbah catfish, Amur catfish, helicopter catfish, pla deng, pla neua on); Synbranchiformes: mastacembelid (spiny eel), synbranchid (Asian swamp eel, Gangetic swamp eel, Bengal eel); Anura: bufonid (common toad, Asian common toad), dicroglossid (Chinese edible frog, Indian bullfrog, rice field frog), hylid (European tree frog), microhylid (banded bullfrog), ranid (common green frog, dark-spotted frog, American bullfrog); Urodela: hynobiid (spotted salamander), salamandrid (Japanese newt); Serpentes: acrochordid (elephant trunk snake), colubrid (checkered keelback, tiger keelback, grass snake, cateye snake, oriental odd-tooth snake, Japanese striped snake), cylindrophiid (red-tailed pipe snake), elapid (Asian cobra, king cobra, banded krait), homalopsid (bockadam snake), pythonid (reticulated python), viperid (green pit viper, Russell's viper); Sauria: agamid (oriental garden lizard, common butterfly lizard), gekkonid (Tokay gecko, Schlegel's Japanese gecko), lacertid (Japanese grass lizard), scincid (Herbert's writhing skink), varanid (Bengal monitor, Asian water monitor, clouded monitor); Testudines: geoemydid (Chinese three-keeled pond turtle), geomyid (snail-eating turtle); Accipitriformes: accipitrid (black kite, black-eared kite, northern goshawk, Eurasian sparrowhawk, pied harrier), pandionid (osprey); Anseriformes: anatid (domestic duck, Eurasian teal, red-breasted merganser); Charadriiformes: jacanid (pheasant-tailed jacana), scoilopacid (Eurasian woodcock); Coraciiformes: alcedinid (common kingfisher); Galliformes: phasianid (chicken, common quail); Gruiformes: rallid (Indian water rail); Passeriformes: corvid (carrion crow, large-billed crow, oriental magpie, Australian raven); Pelecaniformes: ardeid (grey heron, striated heron, great blue heron, cattle egret, eastern great egret, little egret, intermediate egret, black-crowned night heron, bittern), pelecanid (American white pelican, brown pelican, spot-billed pelican); Podicipediformes: podicipedid (little grebe); Strigiformes: strigid (Ural owl); Rodentia: caviid (guinea pig), cricetid (golden hamster), murid (greater bandicoot rat, black rat, brown rat, white rat, Polynesian rat, white mouse, southwestern Asian house mouse), sciurid (Pallas's squirrel);	

			Scandentia: tupaiid (common treeshrew); Dasyuromorphia: dasyurid (northern quoll); Didelphimorphia: didelphid (common opossum, Virginia opossum); Lagomorpha: leporid (rabbit); Artiodactyla: suid (pig); Carnivora: herpestid (Javan mongoose), mustelid (Siberian weasel); Primates: cercopithecid (crab-eating macaque, stump-tailed monkey, silver leaf monkey), hylobatid (lar gibbon), hominid (human)]	
G. turgidum (syn. *G. brasiliense, didelphis*, *oligomucronatum*)	Didelphimorphia: didelphid (common opossum, white-eared opossum, Virginia opossum, lutrine opossum, gray four-eyed opossum); Carnivora: ursid (American black bear)	stomach, liver	[IH-2/PH: Cichliformes: cichlid (Nile tilapia); Primates: hominid (human)]	Americas
G. vietnamicum	Carnivora: mustelid (Asian small-clawed otter)	kidney	IH-1: Copepoda: cyclopid (*Mesocyclops leuckarti*) [plus IH-2/PH: Synbranchiformes: synbranchid (Asian swamp eel)]	Asia

Parasite morphology: *Gnathostoma* spp. form 3 different types of morphological stages during their development: eggs; larvae (moulting through 4 stages, designated L1-L4); and adult worms. Eggs are ovoid-ellipsoidal in shape measuring 62-79 x 36-42 µm in size and vary in colour from yellow-brown to green due to bile staining. They are bound by thick shells with a finely pitted surface and conspicuous polar swellings at one or both ends and a distinctive mucoid cap (plug or protrusion) at one pole. When laid, they are unembryonated and contain a central morula, either unsegmented or cleaved at the 2-4 cell (blastomere) stage. First-stage larvae (L1) have elongated bodies measuring 180-360 µm in length with rounded heads armed with small solid spine-like structures. They are coiled up within eggs apparently within a delicate smooth transparent sheath. L2 have cylindrical bodies ranging from 400-625 µm in length and they have retained the L1 cuticle (exuvium) as a transparent sheath with a smooth cuticle and no visible striations. The larvae have bulbous heads with 3-4 rows of cephalic spines (hooklets), cervical sacs and glands, 2 lateral trilobed lips, a cylindrical oesophagus, tubular intestines, and rounded tails. L3 have elongate red-white bodies measuring 2-4 mm in length (some species measure up to 12.5 mm) and usually coiled up within tissue cysts. The larvae have inflated heads with 3-4 transverse rows of cephalic spines, bodies with incomplete coverings of small spines and they contain tubular alimentary tracts and undifferentiated genital primordia. L4 are transient parasitic stages that have developed most adult features, particularly head and body armature, but the genitalia are still immature. Adults have thick elongate tapering bodies measuring from 10-55 mm in length and ranging from red-beige in colour (sometimes red anteriorly and yellow-grey posteriorly). They have characteristic bulbous heads (cephalic bulb) armed with 8-12 transverse rows of recurved cuticular spines (also called hooks or hooklets) and spinose bodies partly or wholly armed with flat leaf-like posteriorly-directed spines (sometimes absent on hindbody). The cephalic bulb is connected to 4 muscular cervical sacs and 4 ballonets which are used to inflate and deflate the bulb. The anterior mouth has 2 well-developed lateral pseudolabia leading to an elongate undivided oesophagus and tubular intestines, the latter being one cell thick, each cell having 2-6 nuclei depending on the species. Adult worms are sexually dimorphic, with males being smaller than females (10-40 cf. 10-55 mm in length). Mature males have rounded tails with 2 cuticular dilations, 8 peri-cloacal caudal papillae, and 2 long blunt unequal spicules. Mature females have curved tails and are didelphic with 2 ovaries and 2 uteri connected to a distinct vagina and a common vulva opening in near the midbody. Gravid females are oviparous and produce partially embryonated eggs.

Site of infection: Adult worms usually infect the wall of the stomach of their definitive hosts (carnivorous mammals, birds, some reptiles), although some species may also infect the oesophagus, intestines, kidneys or urinary bladder. Larval stages develop in the body cavities of aquatic copepods (first intermediate hosts), and infective larvae may be carried in the tissues of numerous small copepod-eating vertebrates (acting as second intermediate and/or paratenic hosts). Humans are accidental hosts for larval stages which do not mature to adult worms but migrate throughout the body before dying.

Pathogenesis: Many infections are clinically inapparent while others have been associated with a wide variety of conditions ranging from vague abdominal signs to specific cutaneous lesions to gastritis with anorexia, illthrift and sometimes life-threatening peritonitis. The severity of disease depends on many factors, including parasite species (some species are more invasive and virulent), host susceptibility (especially young animals, although infections may accumulate with age due to repeated exposure and

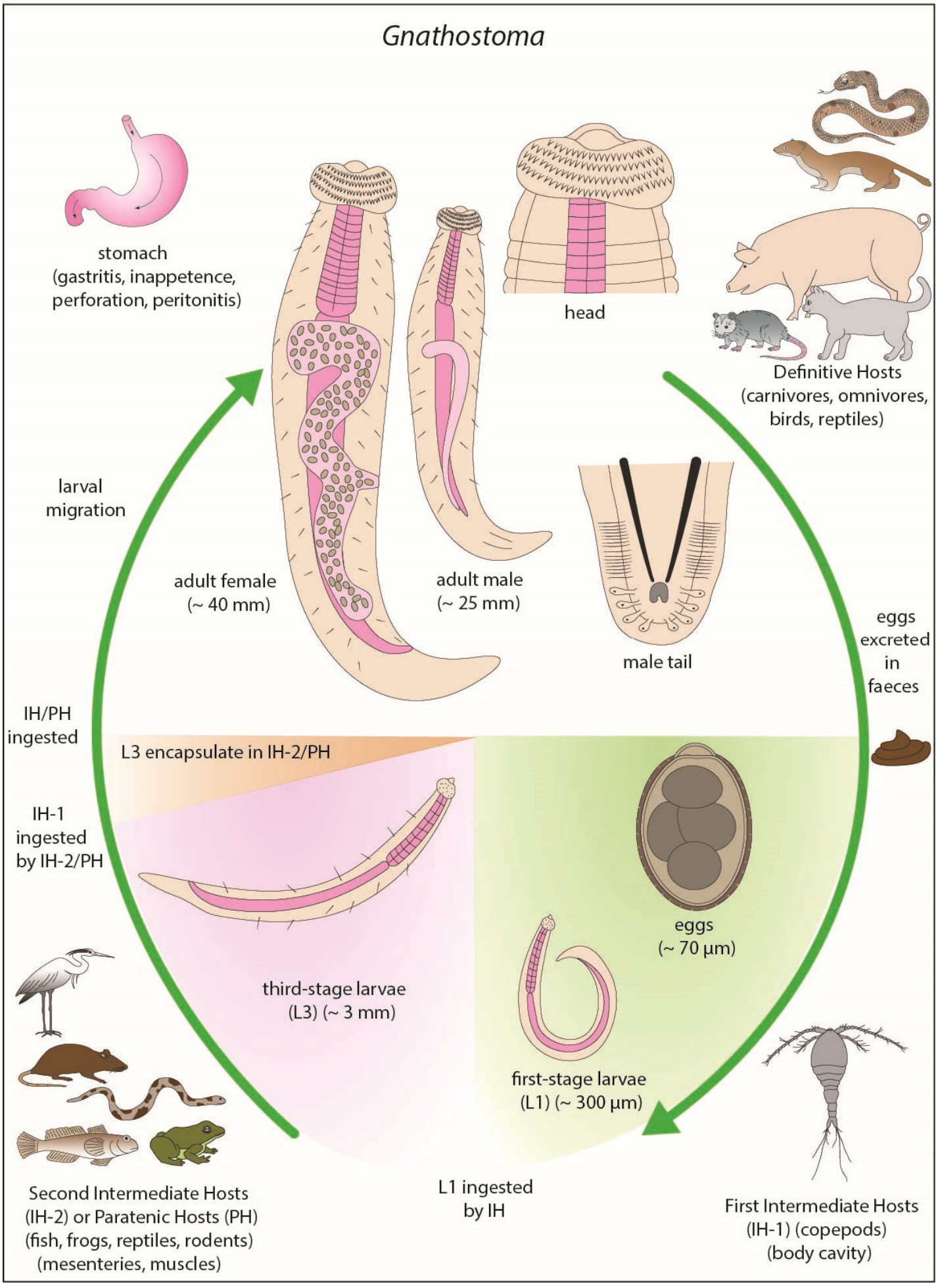
little protective immunity), the site of infection (damage to vital organs more problematic than superficial locations), the intensity of infection (numbers of parasites) and the stage of infection (prepatent period involving larval migration, or patent period involving adult worms). Parasites use their fluid-filled muscular sacs to expand and contract the cephalic bulb armed with rows of recurved hooks thus facilitating their invasion and migration in host tissues. Both larvae and adult worms may cause disease at different stages of infection. Larvae are aggressive migrators and may cause acute clinical signs or more chronic cutaneous and/or visceral lesions. They may infect a wide variety of tissues and organs causing trauma by mechanical and chemical disruption and provoking inflammation with leucocytosis (marked eosinophilia). Larval migration may last for several weeks to several years. In contrast, adult worms remain in the gastric mucosa where they become deeply embedded forming conical fibrous nodules, which sometimes ulcerate or even perforate resulting in peritonitis. Clinical signs may first become evident within 1-2 days as infective larvae penetrate the gut wall and migrate to the liver and other abdominal organs. This stage may last for 2-3 weeks and involve tissue trauma, microlesions, petechial haemorrhages, and the development of sinuous necrotic tracts in the liver and other organs. Signs may include burning abdominal pain (especially epigastric) with fever, nausea, vomiting, salivation, diarrhoea, anorexia, malaise, and urticaria accompanied by marked eosinophilia, all of which gradually subside. Most infections then progress to the development of cutaneous lesions, usually within 3-4 weeks but sometimes delayed for many months. Dermatological manifestations are caused by larvae migrating through subcutaneous tissues resulting in the condition variously known as cutaneous gnathostomiasis, cutaneous larval migrans, creeping eruption (regional variants include Yangtze River oedema, Consular disease or Shanghai rheumatism in China, tuao chid in Japan, paniculitis nodular migratoria eosinofilica in central America, and Woodbury bug in Australia). Lesions are characterised by recurrent or intermittent migratory (wandering) swellings, usually on the trunk and upper limbs, and larvae have been observed to move at 1 cm/hr. The swellings typically last 1-2 weeks and recurrent episodes become less intense and shorter in duration although they can persist for many years if left untreated. The non-pitting oedematous swellings vary in size and are often pruritic, sometimes painful and/or erythematous with a continuous non-linear track appearing beneath the skin due to subcutaneous haemorrhages and localised panniculitis, and occasionally with nodule, pseudofuruncle (boil-like) or abscess formation. Migration of larvae into the viscera may cause a more serious form of disease, known as visceral gnathostomiasis or visceral larval migrans. A wide range of organs may be involved resulting in clinical manifestations unique to that organ system. Larvae migrating through the lungs may cause pleuritic chest pain, cough, haemoptysis, pneumonitis with lobar consolidation, pleural effusions, and hydropneumothorax. Larvae frequently migrate to the eye causing pain, conjunctival erythema, lachrymation, uveitis, ophthalmitis, increased intraocular pressure, ocular haemorrhages and lesions, retinal detachment, diminished vision and sometimes blindness. Occasionally, larvae migrate to the ears causing mastoiditis and sensorineal hearing loss. Invasion of the genitourinary system is uncommon but may result in haematuria with adnexal masses, cervicitis and vaginal bleeding in females and balanitis and haematospermia in males. More often, larvae migrate along nerves to the central nervous system causing serious neurological signs including radiculitis, myelitis, cranial nerve palsies, subarachnoid haemorrhages, eosinophilic meningitis, myeloencephalitis, muscle stiffness and weakness, paresis/paralysis, loss of bladder/intestinal control, headaches, seizures, coma and even death. Adult worms live in tunnels in gastric nodules which appear as thick-walled fibrous growths up to 40 mm in diameter on the stomach wall. The nodules are often cavitated and contain several worms and yellow-green fluid and sometimes purulent material. The gastric mucosa is reddened, swollen and oedematous (catarrhal, haemorrhagic or nodular gastritis) and often covered with easily removable pseudomembranes. The nodules usually open into the stomach, and they sometimes ulcerate and may even perforate the gut wall leading to purulent peritonitis and death. Clinical signs include abdominal sensitivity and intermittent pain (sometimes mimicking acute appendicitis or intestinal obstruction), vomiting, constipation alternating with diarrhoea, excessive thirst, inappetence, and loss of condition with weight loss and growth retardation. Heavy infections in pigs may lead to production losses due primarily to gastritis with inappetence and weight loss, while heavy infections in dogs and cats often cause acute abdominal signs, and sometimes gastric perforation and fatal peritonitis. Humans are accidental hosts in which larvae may migrate throughout the body without maturing to adult worms but eventually dying or spontaneously leaving through the skin. Larvae have been found in association with lesions and disease in the alimentary, respiratory, lymphatic, muscular, cutaneous, genitourinary and nervous systems of human patients around the world.

Developmental cycle and mode of transmission: *Gnathostoma* spp. have indirect heteroxenous life-cycles involving adult stages developing in carnivores (definitive hosts), larval stages developing in copepods (intermediate hosts) and then transported in small vertebrate (paratenic hosts), often ascending the food chain. Gravid female worms in gastric nodules lay unembryonated eggs which pass to the lumen of the stomach and are excreted with host faeces. Eggs deposited in freshwater bodies embryonate and hatch in 7-14 days depending on the prevailing temperature. Most reports state that eggs hatch to release L1 although a few studies indicate they may be L2. The freed larvae are ingested by cyclopoid copepods which act as first intermediate hosts supporting further parasite development. Ingested larvae shed their sheaths and penetrate the intestinal wall to the haemocoel (body cavity) where they moult to form early-stage L3 within 10 days. Many reports indicate that these early-stage L3 are not directly infective to final hosts but require further maturation in small copepod-eating vertebrates, but several experimental studies have infected final hosts by feeding them copepods containing L3. Nevertheless, a variety of aquatic, amphibious or terrestrial vertebrates (freshwater fishes, amphibians, reptiles, birds and mammals) that have consumed infected copepods may act as second intermediate hosts in which further larval development occurs (even if it is limited to L3 maturation). Ingested early-stage L3 penetrate the gut wall of these vertebrate hosts and migrate to the muscles and mesenteries in 6-7 days where they encapsulate and develop to advanced- or late-stage L3. Advanced L3 may also ascend the food chain via predation and scavenging as they are able to re-encapsulate in tissues of numerous paratenic (transport) hosts (including fish, frogs, snakes, lizards, turtles, birds, mammals). Definitive hosts become infected when they consume L3 either in first intermediate hosts (copepods), in second intermediate hosts (small copepod-eating vertebrates), or in paratenic hosts (small predatory vertebrates). Ingested L3 penetrate the stomach wall and migrate to the liver then

the muscles and connective tissues over several weeks (prolonged to several months in some species) before returning to the stomach. Larvae moult twice during these migrations forming L4 and then subadults (sometimes called L5) which embed themselves in the stomach mucosa where they mature to adult worms and form nodules over 2-6 months. The prepatent period (time from infection to first excretion of eggs) can be as short as 2 months for some species but is often longer at 5-6 months, and adult worms may live for over 1 year. Humans are non-permissive hosts in which larval migration may occur without developing to sexually-mature adult worms. Humans usually become infected with L3 by eating raw or undercooked meat (fish, frogs, poultry, pork), such as koi pla and som phac in Thailand, sushi and sashimi in Japan, and ceviche in Latin America. Some infections have also been reported in people handling raw meat when larvae penetrate through the skin, and a few infections have been linked to people drinking water contaminated by infected copepods. Several instances of prenatal infection have also been reported in newborn babies.

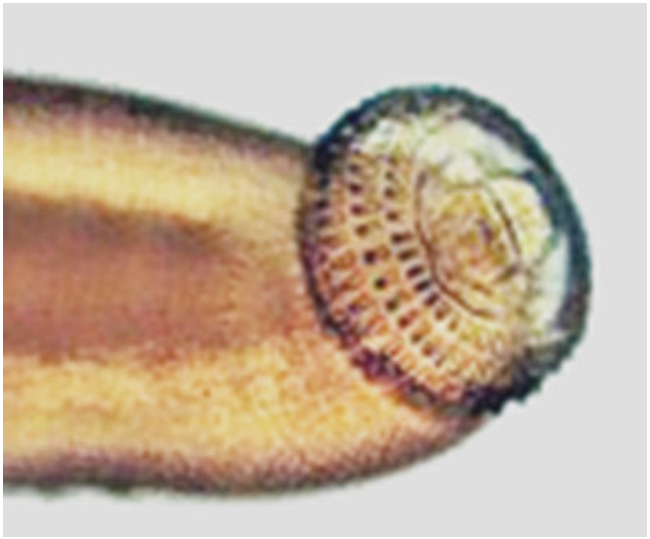
Differential diagnosis: Infections in animals are rarely diagnosed on the basis of clinical symptomatology as they have been associated with a wide range of nonspecific clinical signs either caused by larvae migrating through tissues and organs or by adult worms developing in the stomach. In contrast, infections in humans are often indicated by intermittent migratory cutaneous swellings in association with a history of travel to endemic areas and the consumption of undercooked foods. Patent infections are conventionally diagnosed by the detection of characteristic eggs in faecal samples, usually following their concentration by sedimentation and/or floatation techniques (but remember that worms do not mature in humans so infections do not become patent). Haematological examinations often reveal leucocytosis (especially eosinophilia) during larval migration, and eosinophils may also be detected in cerebrospinal fluid (which may be bloody or xanthochromic). Medical imaging techniques have been used to assist diagnoses by locating migratory or space-occupying lesions in superficial tissues by ultrasonography or deeper tissues by radiography, computed tomography (CT) and magnetic resonance imaging (MRI). Endoscopy (gastroscopy) has also been used to reveal nodular masses in the stomach wall. Infections may also be diagnosed by the recovery and identification of parasites: either larvae in biopsy samples (some larvae may also emerge spontaneously from the skin, particularly after anthelmintic treatment); or adult worms in surgical or necropsy samples. A range of immunodiagnostic techniques have been evaluated with variable success. Skin tests using intradermal injections of parasite antigens have generally yielded poor results lacking both sensitivity and specificity. Several immunoserological tests have been developed to detect host antibodies in serum samples (sometimes in cerebrospinal fluids), including fluorescent antibody tests, radio-immunoassays and enzyme-linked immunosorbent assays, but some cross-reactivity with other nematodes was observed despite using partially purified antigens and monoclonal antibody reagents. More recently, Western blots have been used to detect parasite antigens in clinical samples with good sensitivity and specificity observed for a small number of parasite species. Molecular biological techniques have been successfully used to characterize larvae and adult worms from a range of piscine and carnivorous hosts following the polymerase chain reaction (PCR) amplification of nuclear (ribosomal RNA and internal transcribed spacers) and mitochondrial genes (cytochrome c oxidase subunit I).

Treatment and control: Infections by adult worms have responded reasonably well to treatment with conventional anthelmintics, including benzimidazoles (albendazole), imidazothiazoles (levamisole), isoquinolines (praziquantel) and macrocyclic lactones (ivermectin, doramectin), but repeated treatments are required to avoid relapses from developing larvae. Many veterinary authorities also recommend chemoprophylactic treatment of livestock at least twice a year (at weaning and before confinement). Anthelmintic treatment has been shown to reduce the severity of cutaneous migratory swellings and dermatitis induced by larvae, but treatment was not effective against neurological infections (drugs unable to access blood-brain barrier). There was also some evidence to suggest that treatment may exacerbate cutaneous and/or neurological symptoms, and that supportive treatment with anti-inflammatory corticosteroids may help alleviate symptoms. In some instances, albendazole treatment was shown to result in the emergence of larvae from the skin. Cutaneous infections in humans have also been treated by the surgical removal of the larvae, sometimes simply by needle manipulation and extraction, but often by deeper excision. Various preventive strategies may be applied in domestic or agricultural situations to curb transmission between hosts, but such interventions are not suitable for broader use in natural ecosystems involving wildlife. The parasites utilize a broad range of definitive, intermediate and paratenic hosts involved in complex predator-prey relationships in the food chain. Improved sanitary practices may reduce environmental contamination by worm eggs, particularly when faeces are not allowed to pollute water sources but are regularly collected and treated. Manure should not be used as fertiliser and wastewater should not be used for irrigation. Animal holding facilities should be kept clean, and drinking water supplies should be treated, even if only by coarse filtration to remove copepods. Wildlife should be excluded from holding facilities and livestock and companion animals should be prevented from hunting and scavenging. Several public education campaigns have been used in endemic regions to help prevent infections in humans, primarily by reducing the risks of food-borne transmission by improved food preparation and hygiene. Cooks should be alerted to the risks of handling raw meat products (from which larvae may emerge) and people should avoid the consumption of raw or undercooked fish, poultry and pork (potentially containing infective larvae). Experimental studies have shown that larvae may survive treatment with lime juice for up to 5 days, pickling in vinegar for up to 6 hours, and salting in soy sauce for up to 12 hours, but they do not survive cooking temperatures > 63°C or freezing at -20°C for 3-5 days or at -4°C for 4 weeks. Nonetheless, it is very difficult to change traditional culinary practices, particularly those promoted as healthy and fresh alternatives to processed foods.

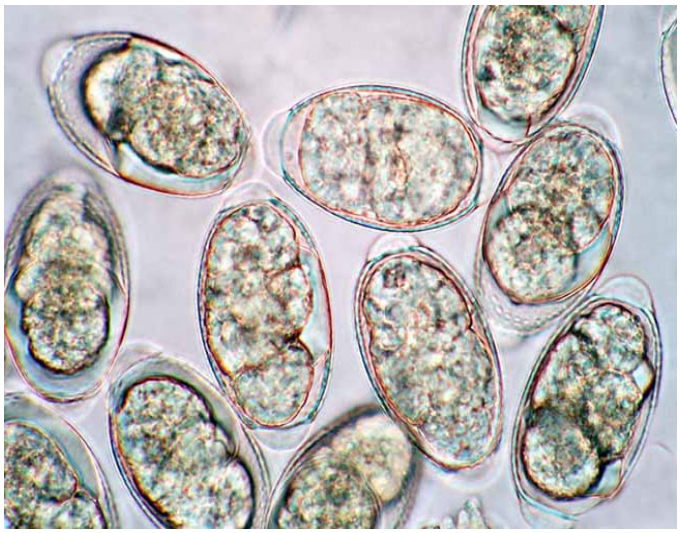

Gnathostoma
stomach
(gastritis, inappetence,
perforation, peritonitis)
head
Definitive Hosts
(carnivores, omnivores,
birds, reptiles)
larval
migration
adult female
(~ 40 mm)
adult male
(~ 25 mm)
male tail
eggs
excreted
in
faeces
IH/PH
ingested
L3 encapsulate in IH-2/PH
IH-1
ingested
by IH-2/PH
eggs
(~ 70 µm)
third-stage larvae
(L3) (~ 3 mm)
first-stage larvae
(L1) (~ 300 µm)
Second Intermediate Hosts
(IH-2) or Paratenic Hosts (PH)
(fish, frogs, reptiles, rodents)
(mesenteries, muscles)
L1 ingested
by IH
First Intermediate Hosts
(IH-1) (copepods)
(body cavity)



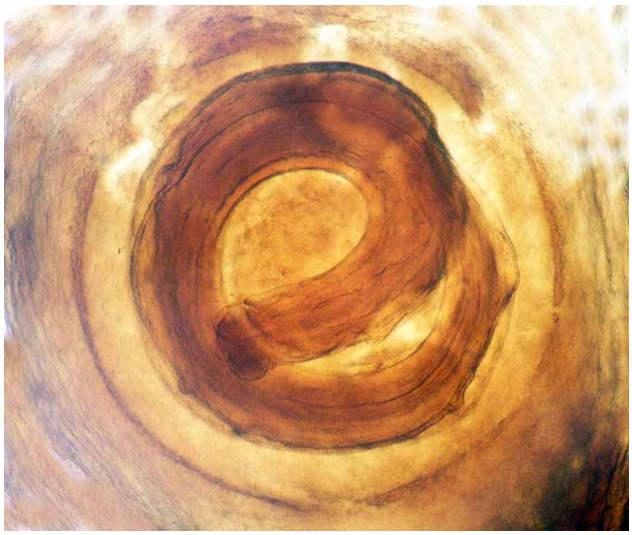
Gnathostoma adult worm



Gnathostoma adult worm, head



Gnathostoma worm eggs



Gnathostoma larva, mouse tissue

Parafilaria
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including filarioids (without lips) living in subcutaneous, intermuscular, vascular or lymphatic systems of mammals. Two main families include the oviparous filariids (lay eggs) and the ovoviviparous onchocercids (eggs hatch internally releasing pre-larvae called microfilariae). Infections by the filariid genus *Parafilaria* are transmitted by muscid and horn flies and cause bleeding lesions on the skin of cattle and horses.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Filarioidea (tissue-dwelling filarial parasites, lack lips)
Family:	Filariidae (numerous anterior papillae and cuticular ridges, lay eggs with L1 already fully formed)
Genus:	*Parafilaria* (parasitic in connective tissues of horses/cattle)
Species:	various species cause skin bleeding lesions in horses/cattle

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Filarioidea contains long thread-like nematodes which are predominantly tissue-dwelling parasites infecting the body cavities, subcutis, intermuscular tissues, blood vessels or lymphatic systems of terrestrial hosts. These worms are known colloquially as 'filariae', 'filarids' or 'filarioids' [Note: take care with terminology as the cognate family Filariidae (esp. genus *Filaria*) are known colloquially as 'filariids', and the unrelated metastrongyle (lungworm) family Filaroididae (genus *Filaroides*) are known colloquially as 'filaroids']. Adult filariae have a cylindroid pharynx with an anterior muscular portion and a posterior glandular portion. Males often have spirally coiled tails, well-developed alae and dissimilar spicules. Females of most species are ovoviviparous (eggs hatch within body of parent) releasing pre-larval stages known as microfilariae (sometimes sheathed). Filariae have indirect life-cycles whereby microfilariae are taken up by blood-sucking or tissue-feeding invertebrates (arthropods, esp. mosquitoes) which act as intermediate hosts for the development of infective L3 larvae. Ten families are recognised: Filariidae and Onchocercidae infecting mammals, birds, reptiles and amphibians; Setariidae infecting mammals; Aproctidae infecting birds; and Creagrocercidae, Drilonematidae, Homungellidae, Mesidionematidae, Scolecophilidae and Ungellidae infecting terrestrial annelids. Examples of filarioid genera covered in this resource are compared in the following table.

Genus	Definitive hosts	Adults (location)	Microfilariae (location)	Periodicity	Vectors	*Wolbachia* symbiotes
Family Filariidae						
Parafilaria (4 spp.)	ungulates	2-7 cm (subcutis)	40-58 x 23-33 µm larvated eggs (skin)	diurnal	flies	absent
Stephanofilaria (7 spp.)	ungulates	0.2-1.4 cm (subcutis)	45-195 µm sheathed (skin)	-	flies	absent
Family Onchocercidae						
Onchocerca (35 spp.)	primates, carnivores, ungulates, rodents	1.5-80 cm (subcutis, ligaments)	105-440 µm unsheathed (skin)	-	flies, midges	present
Mansonella (29 spp.)	primates, carnivores, ungulates, rodents	3-8 cm (subcutis, serosa)	170-300 µm unsheathed (blood/skin)	-	midges, flies, mosquitoes	present
Dirofilaria (34 spp.)	primates, carnivores, ungulates, rodents, lagomorphs, marsupials	4-31 cm (blood vessels)	180-385 µm unsheathed (blood)	-	mosquitoes, flies	present
Dipetalonema, Acanthocheilonema (57 spp.)	primates, carnivores, ungulates, rodents, cingulates, marsupials	1-7 cm (subcutis, serosa)	85-300 µm unsheathed (blood)	-	flies, fleas, lice, ticks	absent
Wuchereria (2 spp.)	primates	2.5-10 cm (lymphatics)	210-320 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Brugia (10 spp.)	primates, carnivores, rodents	1-9 cm (lymphatics)	170-380 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Loa (3 spp.)	primates, ungulates, rodents	2-7 cm (subcutis, eye)	250-300 µm sheathed (blood)	diurnal	flies	absent
Family Setariidae						
Setaria (42 spp.)	primates, ungulates, rodents, lagomorphs	4-19 cm (body cavities)	140-310 µm sheathed (blood)	-	mosquitoes	absent

Members of the family Filariidae form adult worms bearing numerous anterior papillae and cuticular ridges which live under the surface of the skin near where they deposit eggs/larvae (unlike onchocercids which live deeper in tissues or cavities). Five filariid genera are recognised in 2 subfamilies: namely, Filariinae (syn. Pseudofilariinae) containing those which produce larvated eggs (*Parafilaria* of horses and cattle, *Suifilaria* of swine, *Pseudofilaria* of African antelopes, and *Filaria* (syn. *Hyracofilaria*) of carnivores and rodents); and Stephanofilariinae which produce microfilariae (*Stephanofilaria* of ruminants). *Parafilaria* infections in domestic animals (cattle and horses) induce bloody cutaneous lesions (referred to as 'summer bleeding') which attract dipteran (muscid) intermediate hosts.

***Parafilaria* species**	**Definitive Hosts (DH)**	**Location**	**Vectors/Intermediate Hosts (IH)**	**Distribution**
P. antipinni	Artiodactyla: cervid (red deer), bovid (saiga antelope)	subcutaneous tissues		Eurasia
P. bassoni	Artiodactyla: bovid (springbok,	subcutaneous		Africa

	African buffalo)	tissues, eyes		
P. bovicola (syn. *P. sahaii*)	Artiodactyla: bovid (cattle, buffalo)	subcutaneous and intermuscular connective tissues	Diptera: muscid (face flies) (*Musca autumnalis*, *fasciata, lusoria, vitripennis, xanthomelis*)	Africa, Europe, India, Asia
P. multipapillosa	Perissodactyla: equid (horse, donkey, mule); Artiodactyla: bovid (cattle)	subcutaneous and intermuscular connective tissues	Diptera: muscid (horn flies) (*Haematobia atripalpis*)	North Africa, Europe, South America, Asia

Parasite morphology: *Parafilaria* spp. form 3 different developmental stages: adult worms (sexually dimorphic), eggs (larvated) and larvae (moulting through 4 stages designated L1-4). Worms are slender and white in colour, measuring from 20-70 mm in length by 0.4-0.5 mm in width. They are covered by a tough flexible cuticle which possesses anterior ornamentations in the form of numerous irregular transverse rugosities (wrinkles, ridges) or elliptical papilliform thickenings. They have a small mouth lacking lips, a short oesophagus and a tubular digestive system extending to the anus. Mature worms are sexually dimorphic with female worms being larger than males (40-70 x 0.42-0.44 mm cf. 20-40 x 0.26-0.28 mm). Males usually have short blunt slightly-coiled tails with caudal alae, large pedunculated precloacal and postcloacal papillae, a gubernaculum and 2 unequal spicules (one 500-750 µm long and the other 130-150 µm). Females have large ovaries and their uteri terminate in a vulva located very close to mouth (anterior to the nerve ring). Gravid females produce and lay thin-walled ellipsoidal eggs 40-58 x 23-33 µm. The eggs are embryonated when laid and contain a fully developed pre-larvae (microfilariae). Freed microfilariae are unsheathed, measure 215-230 x 10 µm and have attenuated tails. They moult twice growing in size to form infective third-stage larvae (L3) measuring 1.6-4.3 mm with a short muscular oesophagus.

Site of infection: Adult *Parafilaria* worms infect subcutaneous and intermuscular connective tissues in their definitive hosts, mostly upper body parts and dorsal surfaces, especially the forequarters. Microfilariae hatch from eggs released onto the skin and are taken up by dipteran intermediate hosts in which larval development occurs in the body cavity and/or fat bodies.

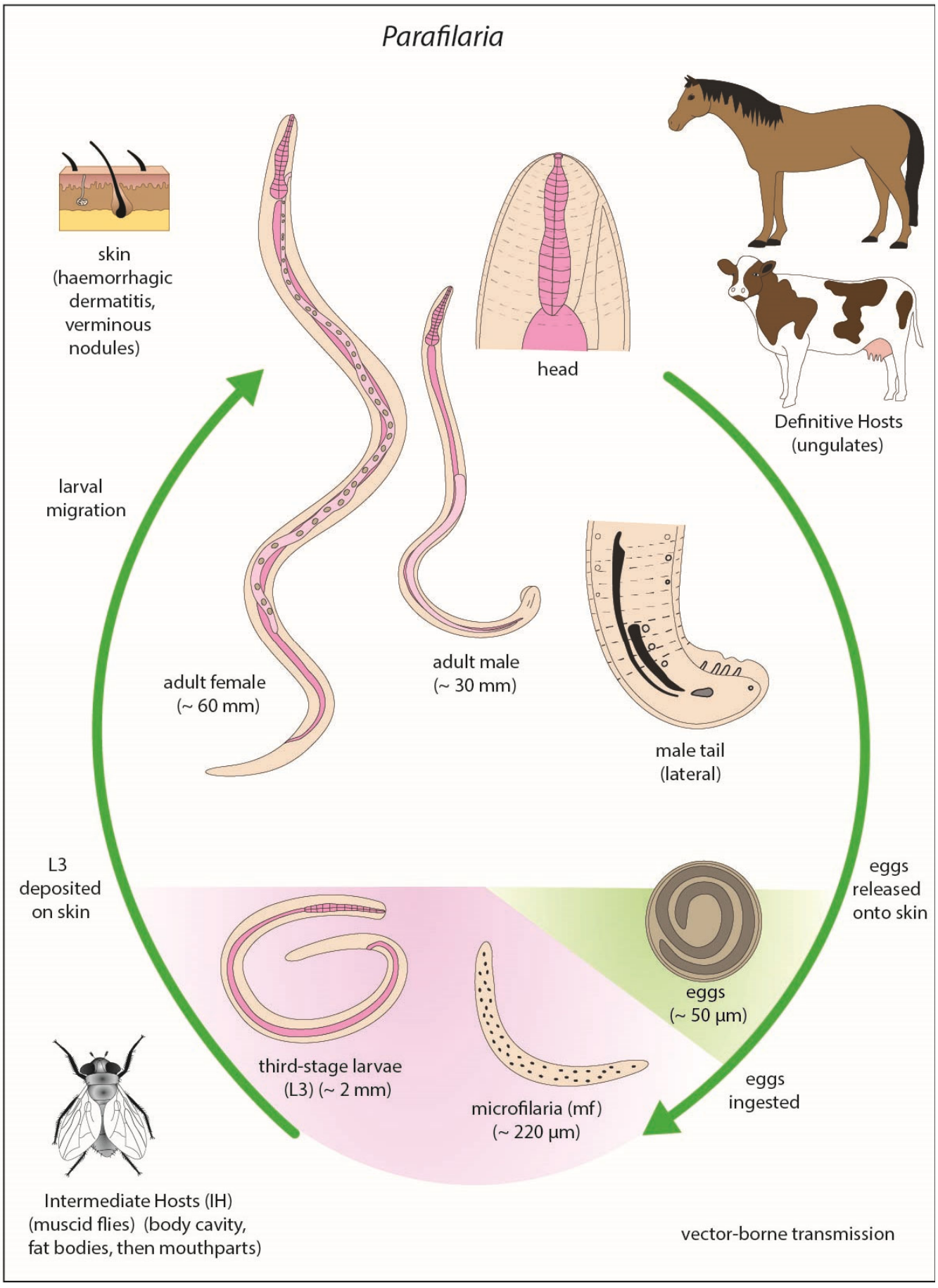
Pathogenesis: *Parafilaria* infections are not highly pathogenic for livestock, but subcutaneous lesions may result in haemorrhagic dermatitis (known as summer bleeding, summer sores, bloody sweat, verminous nodules or parafilariasis) which predispose to secondary bacterial infections. The lesions may interfere with harnessing working animals and economic losses may be incurred following slaughter due to carcase trimming, rejection or condemnation as well as hide degradation. Carcases may contain numerous pea-sized nodules that are usually superficial but may involve underlying musculature resulting in irregular oedematous green-yellow lesions (resembling bruising). The lesions are caused by gravid female worms which penetrate the skin to lay larvated eggs. The perforated nodules bleed through a small pore which may ooze for several hours running in streaks on hairs before clotting and drying to brown crusts and mats. Although bleeding is transient, it may be profuse before resolving and occasionally nodules suppurate and become exudative. Further haemorrhagic nodules develop as the worms moves to different site. The bleeding spots attract flies which feed on exudates and they often demonstrate diurnal periodicity as sunlight appears necessary for lesions to bleed. The lesions are also markedly seasonal, occurring in spring and summer and disappearing during the winter leaving distinctive scars.

Developmental cycle and mode of transmission: These filariid worms have indirect life-cycles where adults develop in mammalian definitive hosts and larval developmental stages occur in blood-feeding dipteran intermediate hosts. Female worms in subcutaneous nodules pierce the skin causing transient focal haemorrhages into which they lay larvated eggs. The bleeding spots attract flies which feed on host blood and parasite eggs. Ingested eggs hatch almost immediately in suitable intermediate hosts releasing their contained microfilariae. Larval development has been observed in the body cavity and/or fat body of various muscid flies, notably face flies (*Musca* spp.) and horn flies (*Haematobia* spp.). Infective third-state larvae (L3) develop within 10-15 days and move to the fly mouthparts where they infect new mammalian hosts when feeding on skin wounds, lachrymal secretions (tears) or other exudates. Larvae penetrate to subcutaneous tissues and migrate to various body parts (especially the neck, shoulders, rump and loins) where they complete development to adults in 5-7 months. Nodules and bleeding spots then develop shortly thereafter and the prepatent period (time from infection to first eggs shed) ranges from 7-12 months. Infections are most pronounced during summer and their prevalence and intensity varies considerably by region but depends largely on the distribution and abundance of suitable fly vectors. Infections have been found in wild and domesticated animals, in free-range animals (especially in African savannas) and penned animals (notably European herds turned out to pasture in spring after winter housing).

Differential diagnosis: Infections may be suspected by the occurrence of characteristic nodules and bleeding spots, although similar traumatic lesions may be caused by thorns, wire, ticks or biting insects. Diagnosis may be confirmed by the microscopic

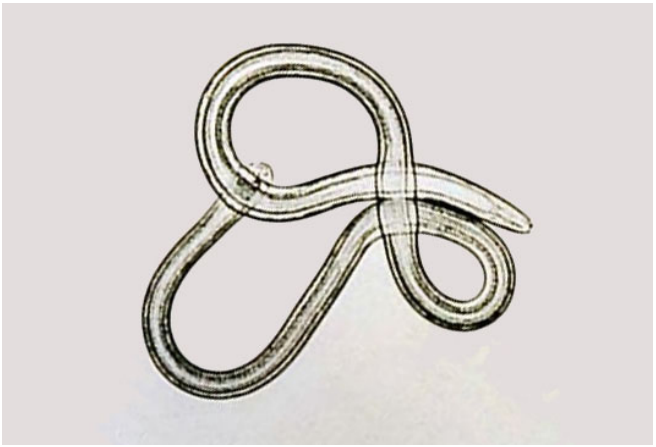
examination of fresh or dried blood mixed with water for the presence of characteristic larvated eggs or microfilariae, before or after sedimentation by mild centrifugation. Nodules may be biopsied, incubated in warm saline and examined for adult worms but the recovery rate is very low due to their sparse distribution, migrating behaviour and cryptic colouration (same as host tissues). Carcase lesions may be differentiated from bruising by the occurrence of numerous eosinophils in impression smears, and some maintain that affected tissues have a disagreeable metallic smell. More recently, an enzyme immunoassay has been developed to detect host antibodies against *P. bovicola,* but the long persistence of many antibodies makes it difficult to discriminate between recent infection and previous exposure.

Treatment and control: The long life-cycle of the parasite presents a challenge to effective treatment and control. While many conventional anthelmintic drugs have proven ineffective, several macrocyclic lactones, including the avermectins (doramectin, eprinomectin, ivermectin) and milbemycin (moxidectin), as well as the broad spectrum halogenated monophenol (nitroxynil) have been found to kill adult worms, but they do not completely eliminate migrating larvae so new nodules may appear following treatment. Animals are usually treated 70–90 days prior to slaughter to allow sufficient time for lesions to resolve, but should not exceed 120 days as new nodules may form. The control of fly vectors is a sensible precaution to reduce infections, but muscid flies are difficult to manage as they are ubiquitous, able to feed on many other hosts or substrates (such as manure or other organic wastes), and may rapidly develop resistance to a range of insecticides. Nevertheless, improved sanitation in livestock facilities by removing manure can help to reduce fly populations and the use of long-lasting residual pyrethroid insecticides (in dips or impregnated eartags) has effectively reduced the prevalence and transmission of infections in several countries.


Parafilaria
skin
(haemorrhagic
dermatitis,
verminous
nodules)
head
Definitive Hosts
(ungulates)
larval
migration
adult female
(~ 60 mm)
adult male
(~ 30 mm)
male tail
(lateral)
L3
deposited
on skin
eggs
released
onto skin
eggs
(~ 50 µm)
third-stage larvae
(L3) (~ 2 mm)
microfilaria (mf)
(~ 220 µm)
eggs
ingested
Intermediate Hosts (IH)
(muscid flies) (body cavity,
fat bodies, then mouthparts)
vector-borne transmission



Parafilaria adult worm



Parafilaria adult worm



Parafilaria larvated egg



Parafilaria larvae

Stephanofilaria
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including filarioids (without lips) living in subcutaneous, intermuscular, vascular or lymphatic systems of mammals. Two main families include the oviparous filariids (lay eggs) and the ovoviviparous onchocercids (eggs hatch internally releasing pre-larvae called microfilariae). Infections by the filariid genus *Stephanofilaria* are transmitted by horn flies and cause exudative, sometime haemorrhagic, dermatitis in cattle.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Filarioidea (tissue-dwelling filarial parasites, lack lips)
Family:	Filariidae (numerous anterior papillae and cuticular ridges, produce larvated eggs or microfilariae)
Genus:	*Stephanofilaria* (parasitic in skin of cattle)
Species:	various species cause dermatitis in cattle

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Filarioidea contains long thread-like nematodes which are predominantly tissue-dwelling parasites infecting the body cavities, subcutis, intermuscular tissues, blood vessels or lymphatic systems of terrestrial hosts. These worms are known colloquially as 'filariae', 'filarids' or 'filarioids' [Note: take care with terminology as the cognate family Filariidae (esp. genus *Filaria*) are known colloquially as 'filariids', and the unrelated metastrongyle (lungworm) family Filaroididae (genus *Filaroides*) are known colloquially as 'filaroids']. Adult filariae have a cylindroid pharynx with an anterior muscular portion and a posterior glandular portion. Males often have spirally-coiled tails, well-developed alae and dissimilar spicules. Females of most species are ovoviviparous (eggs hatch within body of parent) releasing pre-larval stages known as microfilariae (sometimes sheathed). Filariae have indirect life-cycles whereby microfilariae are taken up by blood-sucking or tissue-feeding invertebrates (arthropods, esp. mosquitoes) which act as intermediate hosts for the development of infective L3 larvae. Ten families are recognised: Filariidae and Onchocercidae infecting mammals, birds, reptiles and amphibians; Setariidae infecting mammals; Aproctidae infecting birds; and Creagrocercidae, Drilonematidae, Homungellidae, Mesidionematidae, Scolecophilidae and Ungellidae infecting terrestrial annelids. Examples of filarioid genera covered in this resource are compared in the following table.

Genus	Definitive hosts	Adults (location)	Microfilariae (location)	Periodicity	Vectors	*Wolbachia* symbiotes
Family Filariidae						
Stephanofilaria (7 spp.)	ungulates	0.2-1.4 cm (subcutis)	45-195 µm sheathed (skin)	-	flies	absent
Parafilaria (4 spp.)	ungulates	2-7 cm (subcutis)	40-58 x 23-33 µm larvated eggs (skin)	diurnal	flies	absent
Family Onchocercidae						
Onchocerca (35 spp.)	primates, carnivores, ungulates, rodents	1.5-80 cm (subcutis, ligaments)	105-440 µm unsheathed (skin)	-	flies, midges	present
Mansonella (29 spp.)	primates, carnivores, ungulates, rodents	3-8 cm (subcutis, serosa)	170-300 µm unsheathed (blood/skin)	-	midges, flies, mosquitoes	present
Dirofilaria (34 spp.)	primates, carnivores, ungulates, rodents, lagomorphs, marsupials	4-31 cm (blood vessels)	180-385 µm unsheathed (blood)	-	mosquitoes, flies	present
Dipetalonema, Acanthocheilonema (57 spp.)	primates, carnivores, ungulates, rodents, cingulates, marsupials	1-7 cm (subcutis, serosa)	85-300 µm unsheathed (blood)	-	flies, fleas, lice, ticks	absent
Wuchereria (2 spp.)	primates	2.5-10 cm (lymphatics)	210-320 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Brugia (10 spp.)	primates, carnivores, rodents	1-9 cm (lymphatics)	170-380 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Loa (3 spp.)	primates, ungulates, rodents	2-7 cm (subcutis, eye)	250-300 µm sheathed (blood)	diurnal	flies	absent
Family Setariidae						
Setaria (42 spp.)	primates, ungulates, rodents, lagomorphs	4-19 cm (body cavities)	140-310 µm sheathed (blood)	-	mosquitoes	absent

Members of the family Filariidae form adult worms bearing numerous anterior papillae and cuticular ridges which live under the surface of the skin near where they deposit eggs/larvae (unlike onchocercids which live deeper in tissues or cavities). Five filariid genera are recognised in 2 subfamilies: namely, Filariinae (syn. Pseudofilariinae) containing those which produce larvated eggs (*Parafilaria* of horses and cattle, *Suifilaria* of swine, *Pseudofilaria* of African antelopes, and *Filaria* (syn. *Hyracofilaria*) of carnivores and rodents) and Stephanofilariinae which produce microfilariae (*Stephanofilaria* of ruminants). *Stephanofilaria* infections in ruminants produce an exudative/haemorrhagic dermatitis which attracts dipteran (muscid) intermediate hosts.

Stephanofilaria spp.	Definitive Hosts (DH)	Location	Vectors/Intermediate Hosts (IH)	Distribution
S. andamani sp. inq.	Artiodactyla: bovid (water buffalo)	adults in skin		Andaman Islands
S. boomkeri	Artiodactyla: suid (pig)	adults in skin, eggs containing		Africa

		microfilariae in tissues		
S. dedoesi (syn. *S. assamensis, S. kaeli, S. okinawaensis, S. rono*) (cascado, humpsore, Calcutta sores, Dum Dum sores, filarial sore, krian sore)	Artiodactyla: bovid (cattle, buffalo, goat); Proboscidea: elephantid (Indian elephant); Perissodactyla: rhinocerotid (Indian rhinoceros)	adults in skin, microfilariae in tissues	Diptera: muscid (*Musca conducens, Haematobia atripalpis, H.* (*Liperosia*) *irritans, H.* (*L.*) *titillans*)	Asia, India, southern Russia
S. dinniki	Perissodactyla: rhinocerotid (black rhinoceros)	adults in skin, microfilariae in tissues		Africa
S. jaheeri	Artiodactyla: bovid (cattle, buffalo, nilgai)	adults in skin		Asia
S. srivastavai sp. inq.	Proboscidea: elephantid (Indian elephant)	adults in skin		India
S. stilesi	Artiodactyla: bovid (cattle, goat)	skin (midventral line), eggs cont. mf	Diptera: muscid (horn fly) (*Haematobia* (*Liperosia*) *irritans, H.* (*L.*) *titillans*)	Americas, Eurasia, Australia
S. thelazioides	Artiodactyla: hippopotamid (hippopotamus)	adults in skin, microfilariae in tissues		Africa
S. zaheeri (ear sore)	Artiodactyla: bovid (cattle, buffalo, nilgai)	adults in skin (ears), eggs containing microfilariae in tissues	Diptera: muscid (*Musca autumnalis, M. planiceps*)	India, Asia

Parasite morphology: These filariid parasites form 3 different stages in their developmental cycles: eggs (releasing microfilariae), larvae (four stages designated L1-4) and adult worms. Female worms are ovoviviparous and produce thin-shelled ovoid eggs measuring 60-70 µm *in utero* which embryonate internally to contain elongate microfilariae (they are less well developed than typical nematode first-stage larvae (L1) so are considered advanced embryos or pre-larvae). The microfilariae vary in size depending on species: most being small ranging from 45-60 µm in length (e.g. *S. stilesi*), although some are larger measuring 100-120 µm (e.g. *S. kaeli*) or 160-195 µm (e.g. *S. assamensis*). Most have a blunt anterior end with a digitiform process, long conical tail and are usually surrounded by a highly-specialised semi-rigid fluid-filled vitelline membrane (sheath) that is elongate-oval in shape (enclosed microfilariae cannot migrate). Microfilariae mature and moult twice to form infective third-stage larvae (L3) ranging in size from 0.6-1.3 x 0.04-0.05 mm with narrow ends, the head bearing a single ventral lateral spine or small crown-like projections with numerous spines, a short undivided oesophagus, a rounded tail with delicate ventro-terminal serrations, and genital primordia mid-body. In the definitive host, infective L3 grow in the dermis to 0.9-1.2 mm long, moult and grow to L4 measuring 1.7-2.2 mm long which subsequently moult to form adults. Mature worms are small and slender, measuring from 2-14 x 0.1-0.2 mm, and covered with a tough flexible cuticle with numerous anterior transverse striations/thickenings. The head possesses a characteristic protruding cuticular ring with numerous small denticles or spines around the mouth (4-24 cephalic spines, 14-19 peribuccal spines). The digestive system is tubular, the oesophagus is bipartite with an anterior muscular and a posterior glandular section, and female worms lack an anus. Worms are sexually dimorphic whereby females are larger than males (6-14 mm cf. 2-6 mm). Males have slightly curved tails with a gubernaculum and 2 elongate spicules that are unequal in size (right spicule smaller). Females have larger ovaries and their uteri terminate in a parabuccal vulva (located anterior to the nerve ring).

Site of infection: Adult *Stephanofilaria* worms infect the dermis of their mammalian definitive hosts, often being located just beneath the epidermis particularly along the mid-ventral line between the navel and brisket, and sometimes around the hump and ears. Microfilariae may be found in skin lesions and in surrounding dermal papillae. Larvae develop in the haemocoel of their dipteran intermediate hosts and infective L3 move to the fly mouthparts.

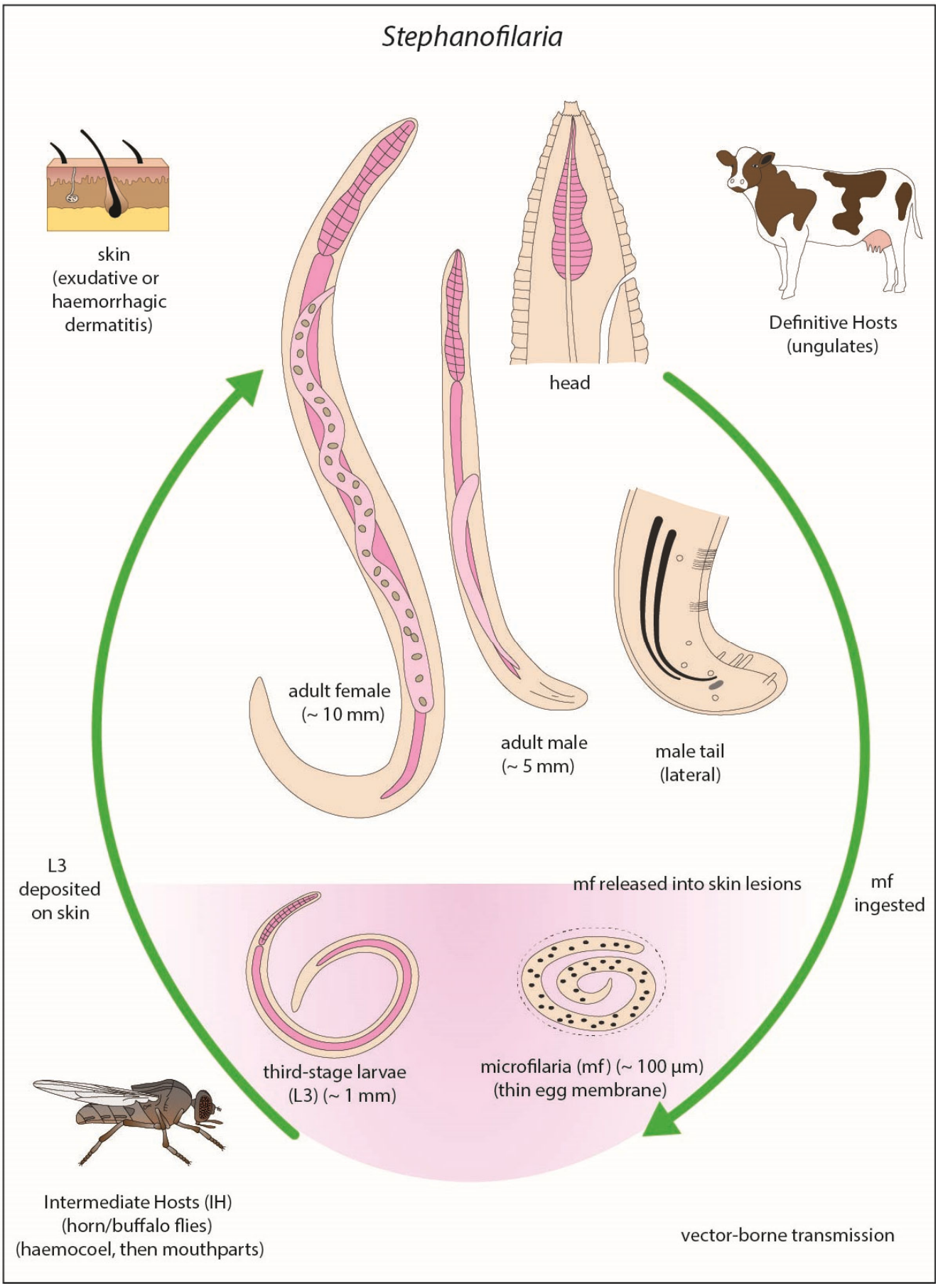
Pathogenesis: *Stephanofilaria* infections are not highly pathogenic, but worms in the skin damage hair follicles and glands and may cause unsightly dermatitis. The disease is called stephanofilariasis, known variously as filarial sores, cascado sores, hump sores, Calcutta sores, Dum Dum sores, krian sores or ear sores. Infections cause a circumscribed haemorrhagic and/or exudative dermatitis, often along the belly but with repeated exposure, lesions may spread to the teats, scrotum, flanks neck and ears. Active lesions may be raw and bloody or covered with a serous exudate, and may persist for as long as 1-3 years. Lesions begin as small papules but later coalesce to become 3-15 cm in diameter. The epidermis demonstrates hyperkeratosis and parakeratosis and

affected areas become intensely inflamed, pruritic (itchy) and show partial hair loss (alopecia). As exudates dry, they form thick flaky or crumbly scabs that often split to expose blood-tinged fluids. Lesions are highly attractive to flies and secondary bacterial infections mat ensue. Severe infections may cause significant stress to animals which may undertake erratic behaviours in relieve the intense irritation (laying, rocking, sliding, rubbing, rolling, etc). Infections in dairy cattle may hamper manual or mechanical milking, as well as compromise milk hygiene. Chronic lesions may heal over after several months to years but they often leave a dry thickened scar devoid of hair. At slaughter, hides may be so damaged that they are downgraded or rejected. Infections of cattle by *S. stilesi* were found to be more prevalent on yearlings and mature animals, though this may probably reflect horn fly vector preferences for older animals.

Developmental cycle and mode of transmission: Like other filarioid parasites, *Stephanofilaria* spp. have indirect heteroxenous life-cycles involving vector-borne transmission between adult worms in mammalian definitive hosts and larval stages in blood-feeding dipteran intermediate hosts. Gravid females living in dermal beds release microfilariae into tissues and bleeding lesions where they are taken up by flies which are attracted to wounds and feed on host exudates. Suitable intermediate hosts include the horn fly or buffalo fly *Haematobia irritans*, particularly in Europe, America and Australia, but numerous other muscid flies (stable flies, face flies, house flies) act as intermediate hosts elsewhere. Most of these flies flourish in rangelands or irrigated pastures where manure and other organic waste is abundant, but are scarcer in well-maintained intensive production systems (feed-lots and barns) where manure is frequently disturbed, removed or scattered. Ingested microfilariae penetrate to the body cavity (haemocoel), sometimes the fat body, of the fly and moult to L2 within 4-10 days and again to L3 within 15-25 days. The infective L3 migrate to the head and proboscis and are deposited on the skin of new definitive hosts when the flies feed again. Transmission appears to be mechanical and contaminative rather than inoculative. The larvae develop, moult and grow in the dermis of the mammalian host and form adults which mature and mate. The ovoviviparous female worms produce eggs which hatch internally releasing microfilariae. The prepatent period (time from infection to first shedding of microfilariae) is around 6-8 weeks. It is not known how long adult worms survive in hosts nor how long they continue producing microfilariae. The incidence of infection is partly seasonal (spring and autumn) and attuned to periods of peak fly activity (e.g. horn flies prefer temperatures ranging from 22-28°C and seek shade under hosts when temperatures become too warm). In endemic areas, infections may afflict most animals in a herd.

Differential diagnosis: Infections are usually detected on the basis of symptomatology, involving the detection of characteristic wounds and animal rubbing/scratching behaviors, and confirmed by the microscopic detection of worms, worm fragments or microfilariae in skin scrapings after maceration and incubation in warm isotonic saline. Nonetheless, the detection of parasites is often difficult due to their scattered distribution, cryptic appearance and possible confusion with microfilariae of other filarioid nematodes (e.g. *Onchocerca*, *Setaria* and *Pelodera* spp.). Histological sections of skin biopsies may reveal sections of adult worms in hair follicles with microfilariae and eosinophils present in the dermis.

Treatment and control: Few countries have approved anthelmintic products for the treatment of stephanofilariasis, but several studies have shown that macrocyclic lactones, including the avermectins (ivermectin, eprinomectin) and milbemycin (moxidectin), were effective against infections in livestock, including lactating cattle. Other studies suggest that the injectable imidazothiazole (levamisole) may help control infections, though multiple applications appeared necessary. Several preventive strategies have been designed to minimise transmission by reducing vector (fly) populations. The topical application of organophosphates (trichlorfon) and long-lasting residual pyrethroids (in dips or impregnated eartags) have been found to reduce populations of biting horn flies in several endemic regions, but had little impact on other non-biting muscid flies breeding in manure and other organic wastes. In Asia, it was noticed that many infections required a pre-existing wound for infection to take place, so simple wound prevention and treatment with ointments containing insecticides was recommended to reduce the risk of disease. In regions where horn flies are endemic (such as Europe, America and Australia), it was found that keeping livestock indoors during the peak fly season reduced the incidence of infections (horn flies do not attack stock indoors). In regions where the main vectors are non-biting flies (such as face flies and house flies), population numbers may be reduced by improving environmental hygiene and sanitation (cleaning stalls, manure and waste removal).


Stephanofilaria
skin
(exudative or
haemorrhagic
dermatitis)
head
Definitive Hosts
(ungulates)
adult female
(~ 10 mm)
adult male
(~ 5 mm)
male tail
(lateral)
L3
deposited
on skin
mf released into skin lesions
mf
ingested
third-stage larvae
(L3) (~ 1 mm)
microfilaria (mf) (~ 100 µm)
(thin egg membrane)
Intermediate Hosts (IH)
(horn/buffalo flies)
(haemocoel, then mouthparts)
vector-borne transmission



Stephanofilaria adult worm



Stephanofilaria lesion on cow

Onchocerca
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including filarioids (without lips) living in subcutaneous, intermuscular, vascular or lymphatic systems of mammals. Two main families include the oviparous filariids (lay eggs) and the ovoviviparous onchocercids (eggs hatch internally releasing pre-larvae called microfilariae). Infections by the onchocercid genus *Onchocerca* are transmitted by biting midges or black flies (in which L3 develop). Various species cause nodule formation in the connective tissues of domestic and wild animals, while *O. volvulus* causes severe disease in humans, involving the skin (cutaneous nodules, dermatitis, elephantiasis) and eyes (river blindness).

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Filarioidea (tissue-dwelling filarial parasites, lack lips)
Family:	Onchocercidae (adults loose in tissues or in nodules, viviparous (live birth of microfilariae))
Genus:	*Onchocerca* (parasitic in connective tissues of humans/cattle/horses)
Species:	*O. volvulus* (causes skin lesions, nodules and river blindness in humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species,

including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Filarioidea contains long thread-like nematodes which are predominantly tissue-dwelling parasites infecting the body cavities, subcutis, intermuscular tissues, blood vessels or lymphatic systems of terrestrial hosts. These worms are known colloquially as ‘filariae’, ‘filarids’ or ‘filarioids’ [Note: take care with terminology as the cognate family Filariidae (esp. genus *Filaria*) are known colloquially as ‘filariids’, and the unrelated metastrongyle (lungworm) family Filaroididae (genus *Filaroides*) are known colloquially as ‘filaroids’]. Adult filariae have a cylindroid pharynx with an anterior muscular portion and a posterior glandular portion. Males often have spirally-coiled tails, well-developed alae and dissimilar spicules. Females of most species are ovoviviparous (eggs hatch within body of parent) releasing pre-larval stages known as microfilariae (sometimes sheathed). Filariae have indirect life-cycles whereby microfilariae are taken up by blood-sucking or tissue-feeding invertebrates (arthropods, esp. mosquitoes) which act as intermediate hosts for the development of infective L3 larvae. Ten families are

recognised: Filariidae and Onchocercidae infecting mammals, birds, reptiles and amphibians; Setariidae infecting mammals; Aproctidae infecting birds; and Creagrocercidae, Drilonematidae, Homungellidae, Mesidionematidae, Scolecophilidae and Ungellidae infecting terrestrial annelids. Examples of filarioid genera covered in this resource are compared in the following table.

Genus	Definitive hosts	Adults (location)	Microfilariae (location)	Periodicity	Vectors	*Wolbachia* symbiotes
Family Onchocercidae						
Onchocerca (35 spp.)	primates, carnivores, ungulates, rodents	1.5-80 cm (subcutis, ligaments)	105-440 µm unsheathed (skin)	-	flies, midges	present
Mansonella (29 spp.)	primates, carnivores, ungulates, rodents	3-8 cm (subcutis, serosa)	170-300 µm unsheathed (blood/skin)	-	midges, flies, mosquitoes	present
Dirofilaria (34 spp.)	primates, carnivores, ungulates, rodents, lagomorphs, marsupials	4-31 cm (blood vessels)	180-385 µm unsheathed (blood)	-	mosquitoes, flies	present
Dipetalonema, Acanthocheilonema (57 spp.)	primates, carnivores, ungulates, rodents, cingulates, marsupials	1-7 cm (subcutis, serosa)	85-300 µm unsheathed (blood)	-	flies, fleas, lice, ticks	absent
Wuchereria (2 spp.)	primates	2.5-10 cm (lymphatics)	210-320 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Brugia (10 spp.)	primates, carnivores, rodents	1-9 cm (lymphatics)	170-380 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Loa (3 spp.)	primates, ungulates, rodents	2-7 cm (subcutis, eye)	250-300 µm sheathed (blood)	diurnal	flies	absent
Family Filariidae						
Parafilaria (4 spp.)	ungulates	2-7 cm (subcutis)	40-58 x 23-33 µm larvated eggs (skin)	diurnal	flies	absent
Stephanofilaria (7 spp.)	ungulates	0.2-1.4 cm (subcutis)	45-195 µm sheathed (skin)	-	flies	absent
Family Setariidae						
Setaria (42 spp.)	primates, ungulates, rodents, lagomorphs	4-19 cm (body cavities)	140-310 µm sheathed (blood)	-	mosquitoes	absent

Members of the family Onchocercidae form adult worms that live loose in body cavities or in tissue nodules. Female worms release microfilariae which disperse into the blood or dermal connective tissues (unlike filariids which live in the skin close to where they deposit eggs or larvae). Some 88 onchocercid genera are divided into 7 subfamilies: Onchocercinae and Dirofilariinae (syn. Loainae) mostly in mammals but some in birds and reptiles, Waltonellinae and Icosiellinae in amphibians, Oswaldofilariinae in reptiles, Splendidofilariinae and Lemdaninae in birds, reptiles and mammals (former subfamily Setariinae in large mammals recently elevated to family status as Setariidae). Members of the subfamily Onchocercinae are characterised as forming males with markedly dissimilar spicules and long tails lacking caudal alae (while members of the subfamily Dirofilariinae form males with highly developed caudal alae). Some 43 genera occur in the subfamily Onchocercinae: namely, *Acanthocheilonema, Ackertia*, *Agamofilaria*, *Andersonfilaria*, *Bisbalia*, *Breinlia* (incl. *Johnstonema*), *Brugia*, *Cercopithifilaria*, *Chabfilaria*, *Cherylia*, *Courduriella*, *Cruorifilaria*, *Cystofilaria*, *Deraiophoronema*, *Dessetfilaria*, *Dipetalonema*, *Elaeophora* (syn. *Cordophilus*, *Alcefilaria*), *Filarissima*, *Fuscicorpa*, *Josefilaria*, *Litomosa*, *Litomosoides* (syn. *Vestibulosetariam Finlaynema*), *Mansonella*,

Microfilaria, *Migonella*, *Molossinema*, *Monanema*, *Onchocerca* (syn. *Wehrdikmansia*, *Acanthospiculum*), *Paramadochotera*, *Paraochoterenella*, *Paraprocta*, *Paulianfilaria*, *Pseudolitomosa*, *Rumenfilaria*, *Sandnema, Serofilaria*, *Skrjabinofilaria* (syn. *Cortiamosoides*), *Sprattia, Strianema*, *Wuchereria* and *Yatesia* in mammals, *Struthiofilaria* in birds, and *Macdonaldius* (syn. *Saurofilaria*) in reptiles. Three groups of human filariasis are distinguished on the basis of their tissue tropism: cutaneous dermal filariasis (onchocerciasis in Africa, Asia, Central and South America, loiasis in Africa, *streptocerca* mansonelliasis in Africa); lymphatic filariasis (wuchereriasis in Africa and Asia, brugiasis in South Asia); and serous filariasis (*perstans* mansonelliasis in Africa, Central and South America, *ozzardi* mansonelliasis in Central and South America).

The genus *Onchocerca* comprises worms have simple mouths often lacking lips and almost no buccal capsule but with surrounding circlets of papillae. They have a flexible cuticle often with distinctive transverse striations and regular spiral thickenings (ridges or annulations) often interrupted in lateral fields, although some species have smooth cuticles. Female worms form nodules in subcutaneous tissues, ligaments and aponeuroses of large mammals and they produce vermiform embryos (microfilariae) which disperse and accumulate in dermal connective tissues, resulting in microfiladerma (while those of other filariae (e.g. *Wuchereria, Brugia, Dirofilaria, Acanthocheilonema*, *Setaria*) circulate in blood). *Onchocerca* spp. are transmitted by biting midges or black flies (in which infective L3 develop). There are some 36 *Onchocerca* species infecting humans and animals (predominantly ungulates) around the world. The species *O. volvulus* infects humans throughout central Africa, Central America and northern South America. It is thought to have originated in Africa and was taken to Central America by the slave trade. It is estimated that some 30 million people in Africa suffer from onchocerciasis, up to 1 million being blind. *O. volvulus* infections have also been recorded in higher primates, chimpanzees and gorillas. There appear to be two lineages of *Onchocerca* spp. in Africa: one more primitive lineage found in forested regions and another more derived lineage found in savannah regions. Onchocercal infections are common in cattle, horses, donkeys, camels, deer, antelopes and pigs, mainly in the tropics but also in temperate zones. Eight species have been described in cattle and four in horses. *Onchocerca* spp. are transmitted by dipteran vectors, predominantly black flies (*Simulium, Prosimulium*) but some species utilizing midges (*Culicoides*). Vector distribution, abundance and competence therefore influences the distribution of *Onchocerca* spp. infections. The primary vectors of *O. volvulus* are *S. damnosum, S. neavei* and *S. woodi* in Africa, *S. ochraceum, S. metallicum, S. callidum* in Mexico, *S. exiguum* in Colombia and Ecuador, *S. metallicum* and *S. exiguum* in Venezuela, and *S. guianense* and *S. oyapockense* in Brazil. Another 40 black fly species have been implicated in the transmission of *Onchocerca* spp. to domestic animals, and several *Culicoides* spp. have been found to transmit *O. reticulata, O. cervicalis* and *O. raillieti* to equids, *O. gibsoni, O. gutturosa* and *O. armillata* to cattle and sheep, *O. cebei* to buffalo, and *O. fasciata* to camels. Other filarial worms infect humans causing severe disease and disfigurement, most being restricted to tropical regions and involving mosquitoes or other flies as vectors.

***Onchocerca* spp.**	**Definitive Hosts (DH)**	**Location**	**Vectors/Intermediate Hosts (IH)**	**Distribution**
O. alcis	Artiodactyla: cervid (moose)			North America
O. armillata	Artiodactyla: bovid (zebu, cattle, buffalo, goat, sheep, four-horned antelope), camelid (camel); Perissodactyla: equid (horse, donkey)	thoracic aorta	Diptera: ceratopogonid (*Culicoides*); simuliid (*Simulium*)	Africa, India, Middle East
O. beaveri	Artiodactyla: bovid (blue duiker)	ligaments		Africa
O. boehmi (now *Elaeophora*)	Perissodactyla: equid (horse)	metacarpal region		Europe
O. caprae	Artiodactyla: bovid (goat)			
O. cebei (syn. *O. sweetae*)	Artiodactyla: bovid (water buffalo, cattle)	abdomen, thorax, brisket	Diptera: ceratopogonid (*Culicoides*)	Far East, Australia
O. cervicalis (equine neck threadworms)	Perissodactyla: equid (horse, donkey); Primates: hominid (human)	ligamentum nuchae	Diptera: ceratopogonid (*Culicoides variipennis, victoriae, parotti, robersti, nubeculosus*); simuliid (*Simulium pictipes*)	Europe, North America, Australia
O. cervipedis (legworm)	Artiodactyla: cervid (mule deer, black-tailed deer, white-tailed deer, moose, caribou)	subcutaneous tissues, tibio-tarsal joint	Diptera: simuliid (*Prosimulium impostor, Simulium decorum, venustum*)	North America
O. denkei	Artiodactyla: bovid (cattle)	subcutaneous connective tissues		Africa
O. dewittei (incl. ssp. *dewittei* and	Artiodactyla: suid (boar, Japanese boar); Primates: hominid (human)	subcutaneous connective tissues	Diptera: simuliid (*Simulium bidentatum, bovis, damnosum, hargreavesi, vorax, aokii, arakawae,*	Malaysia, Japan

japonica)			*japonicum, quinquestriatum, rulibasis*)	
O. dukei	Artiodactyla: bovid (cattle)	intermuscular connective tissues	Diptera: simuliid (*Simulium bovis*)	Africa
O. eberhardi	Artiodactyla: cervid (sika deer)	carpal ligament		Japan
O. fasciata	Artiodactyla: camelid (camel, dromedary)	connective tissues, ligamentum nuchae	Diptera: ceratopogonid (*Culicoides*)	Arabia, Australia, Asia
O. flexuosa	Artiodactyla: cervid (roe deer, fallow deer, red deer), bovid (goat)	subcutaneous tissues	Diptera: simuliid (*Simulium ornatum, argyreatum, Prosimulium nigripes, Boophthora erythrocephala, Wilhelmia equina*)	Europe
O. garmsi	Artiodactyla: cervid (red deer)	subcutaneous tissues	Diptera: simuliid (*Simulium*)	Europe
O. gibsoni	Artiodactyla: bovid (cattle, zebu, buffalo, sheep), camelid (camel)	connective tissues, esp. brisket	Diptera: ceratopogonid (*Culicoides buckleyi, marksi, orientalis, oxystoma, pungens, shortii, Forcipomyia townsvillensis*), simuliid (*Simulium*)	Africa, Asia, Australasia
O. gutturosa (syn. *O. lienalis*)	Artiodactyla: bovid (cattle, European bison, American bison, buffalo, sheep), camelid (camel); Perissodactyla: equid (horse, donkey); Carnivora: canid (dog); Primates: hominid (human)	connective tissue, ligamentum nuchae, femurotibial ligaments, gastro-splenic ligament	Diptera: simuliid (*Simulium arakawae, bidentatum, daisense, decorum, erythrocephalum, galeratum, jenningsi, kyushuense, ornatum, pictipes, reptans, tuberosum, variegata, vittatum, Boophthora sericata*), ceratopogonid (*Culicoides variipennis, nubeculosus*)	Europe, Africa, Americas, Australia, Asia
O. hamoni	Artiodactyla: bovid (kob, reedbok)	subcutaneous nodules		Africa
O. indica	Artiodactyla: bovid (cattle, buffalo)			
O. jakutensis (syn. *O. tubingensis*)	Artiodactyla: cervid (red deer); Macroscelidea: macroscelidid (four-toed elephant shrew); Primates: hominid (human)	subcutaneous tissues	Diptera: simuliid (*Simulium*)	Europe
O. katangensis (syn. *Katanga*?)	Macroscelidea: macroscelidid (four-toed elephant shrew)			Africa
O. lerouxi	Artiodactyla: bovid (black-fronted duiker)	intermuscular connective tissue		Africa
O. lupi	Carnivora: canid (dog, wolf, steppe wolf), felid (cat); Primates: hominid (human)	sclera of eyes	Diptera: simuliid (*Simulium tribulatum*)	Europe, Middle-East, North America
O. ochengi (syn. *O. dermata*)	Artiodactyla: bovid (cattle, zebu)	connective tissue, scrotum, udder	Diptera: simuliid (*Simulium damnosum, hargreavesi, ornatum, sanctipauli, sirbanum, squamosum, wellmanni*)	West and Central Africa
O. pandei	Artiodactyla: bovid (buffalo)			
O. raillieti	Perissodactyla: equid (horse, donkey)	cervical ligament, intermuscular connective tissue	Diptera: ceratopogonid (*Culicoides kingi?*)	Africa
O. ramachandrini	Artiodactyla: suid (warthog)	subcutaneous tissue (feet), tibia-tarsal ligaments	Diptera: simuliid (*Simulium damnosum, squamosum*)	West Africa
O. reticulata (Kasen summer mange, equine dhobie itch)	Perissodactyla: equid (horse, donkey, mule)	connective tissues, flexor tendons, suspensory ligaments of fetlock	Diptera: ceratopogonid (*Culicoides nubeculosus, obsoletus*)	worldwide
O. schulzkeyi	Artiodactyla: bovid (roan antelope)	dermal nodules		Africa
O. skrjabini	Artiodactyla: cervid (roe	subcutaneous	Diptera: simuliid (*Simulium arakawae,*	Western

(syn *O. tarsicola*)	deer, Japanese serow, red deer, sika deer, reindeer)	tissue, tarsal/carpal joints	*bidentatum, daisense, japonicum, oitanum, ornatum, aokii, Prosimulium nigripes, tomosvaryi, Odagmia ornato, Twinnia japonensis*)	Europe, Japan
O. sonini	Artiodactyla: bovid (black-fronted duiker)	tendon		Africa
O. stilesi	Artiodactyla: bovid (cattle)	connective tissues stifle joints		North America
O. suzukii	Artiodactyla: bovid (cattle), cervid (Japanese serow)	subcutaneous tissues	Diptera: simuliid (*Simulium bidentatum, japonicum, Prosimulium* sp.)	Japan
O. synceri	Artiodactyla: bovid (African buffalo)	subcutaneous tissue		Africa
O. takaokai	Artiodactyla: suid (Japanese wild boar)	skin		Japan
O. volvulus (river blindness, 'craw craw')	Primates: atelid (Geoffroy's spider monkey), cercopithecid (sooty mangabey), hominid (human, gorilla, chimpanzee, bonobo); Artiodactyla: bovid (cattle), camelid (dromedary); Rodentia: murid (mouise)	subcutaneous tissues, skin nodules, dermatitis, pachyderma, ocular complications	Diptera: simuliid (*S. albivirgulatum, amazonicum-sanguineum* complex, *callidum, damnosum, dieguerense, ethiopiense, exiguum, gonzalezi, guianense, haematopotum, hargreavesi, horacioi, incrustatum, kilibanum, konkourense, leonense, limbatum, mengense, metallicum, neavei, ochraceum, oyapockense, pintoi, quadrivittatum, rasyani, sanctipauli, sirbanum, soubrense, squamosum, thyolense, veracruzanum, woodi, yahense, yarzabali*)	Africa, Central and South America

Parasite morphology: Filarial worms form adults (sometimes called macrofilariae) and pre-larvae (microfilariae) in vertebrates, while three larval developmental stages occur in the arthropod vectors. Adult worms are long and slender and have simple mouths with two surrounding circles of four papillae (they lack lips and buccal capsules). They are filariform with a long oesophagus not divided conspicuously. They have a flexible cuticle with distinctive transversal (cross) striations and regularly-spaced spiral thickenings (ridges or annulations) which are often interrupted in lateral fields. Differences in cuticular characters have been used to identify three groups of *Onchocerca* spp.: one group comprising species with ridges ~25 µm apart and 2-3 intervening striations (e.g. *O. volvulus, O. reticulata, O. gibsoni, O. ochengi*); a second group with ridges ~50 µm apart and 4-5 intervening striations (e.g. *O. cervicalis, O. gutturosa*); and a third group with smooth cuticles (e.g. *O. raillieti, O. cervipedis, O. jakutensis*). The size of mature worms varies according to species, but all exhibit marked sexual dimorphism with female worms being much larger (250-800 x 0.2-0.6 mm) than males (15-270 x 0.1-0.3 mm). In females, the vulva is located at the anterior end of the worm but posterior to the nerve ring. In males, the tail is curved ventrally, bears caudal papillae arranged in several groups (4-6 pairs precloacal/pericloacal/adanal, 6-8 pairs postcloacal/postanal/terminal), two unequal and dissimilar spicules and some species have small caudal alae. Differences in the dispositions of caudal papillae have been noted between (and sometimes within) several *Onchocerca* spp., with variations from a basic (primitive) plan (of 4+6) exhibited by *O. raillieti* including precloacal papillae grouping towards the cloaca (*O. volvulus*), and terminal papillae grouping towards the cloaca (*O. reticulata, O. armillata*), being modified into cuticular points (*O. gutturosa, O. ochengi, O. dukei, O. skrjabini*) or being reduced in number (*O. jakutensis*). Gravid females are ovoviviparous and produce eggs which hatch internally releasing motile pre-larvae known as microfilariae (sometimes reported as first-stage (L1) larvae although they are not as developed as those of other nematodes). Microfilariae are elongate, measuring from 105-440 µm long by 5-9 µm wide depending on the species, and have rounded heads (some species with ventral cephalic hooks), a thread-like oesophagus, nerve ring, excretory vesicle, median sac-like inner body (Innenkorper) and a series of posterior nuclei forming the genital primordia. The microfilariae of various filarial worms can be differentiated on the basis of their morphology, those of *Onchocerca* being unsheathed with pointed attenuated tails possessing nuclei which do not extend to the posterior tip (compared to those of *Wuchereria*, *Brugia* and *Loa* which are ensheathed retaining their thin flexible 'egg-shell' membrane). In the invertebrate vectors, microfilariae ingested during feeding undergo further development to become infective third-stage (L3) larvae which vary in size depending on the species (ranging from 380-1,030 µm in length). The infective larvae generally have trapezoidal heads, short buccal capsules and a long glandular oesophagus.

Site of infection: Adult worms live in the connective tissues and/or ligaments in their definitive (vertebrate) hosts, where they become encapsulated forming distinctive nodules containing tangled pairs or groups of worms. Differences in the anatomical locations of the worms have been used to identify five groups of *Onchocerca* spp.: one comprising species that induce encapsulation of adults within fibrous nodules (e.g. *O. volvulus, O. fasciata, O. gibsoni, O. dukei, O. cervipedis, O. flexuosa*); one whose adults live in the connective tissues of the gastro-splenic and cervical ligaments (*O. gutturosa, O. cervicalis*); one in the subcutaneous

connective tissues (*O. reticulata, O. raillieti, O. tarsicola, O. dewittei*); one intradermal (*O. ochengi, O. cebei*); and one in the aorta (*O. armillata*). Live microfilariae are released directly into adjacent host tissues (or blood for other filarial worms). In the intermediate (invertebrate) hosts, infective larvae have been recovered from the head, thorax and/or abdomen of the dipteran vectors.

Pathogenesis: *Onchocerca* causes the disease onchocerciasis which has four principal manifestations: subcutaneous nodule formation, dermatitis, lymphadenopathy and blindness. Adult worms coil up and become surrounded by fibrous nodules (onchocercomas) often containing a single female and a single male worm. They become embedded in intensely eosinophilic material (proteins, immune complexes, inflammatory debris, etc.) consistent with Splendore-Hoeppli reactions surrounding other micro-organisms (including fungi, bacteria and parasites). In humans, *O. volvulus* nodules usually develop over bony prominences (especially the pelvis in Africa and the head in Mexico). The most pathogenic effects, however, are caused by the death and degeneration of numerous microfilariae into host tissues (live microfilariae elicit little inflammation). Early-stage infections are often associated with intense pruritus (itching) progressing to papular rashes (known as craw-craw in Africa). Over time (months to years), inflammatory responses manifest as chronic papular dermatitis characterised by large papules and hyper-pigmented thickened skin. Affected skin may also exhibit asymmetric lichenization ('sowda' in Africa), spotty depigmentation ('leopard' skin), thickened wrinkled pachyderma ('crocodile' or 'elephant' skin) or purplish depigmentation ('mal morado' in Mexico). The World Health Organization has adopted a staged classification scheme for recording acute papular onchodermatitis (APOD), chronic papular onchodermatitis (CPOD), lichenified onchodermatitis (LOD), atrophy (ATR) and depigmentation (DPM). In addition to dermatitis, infections by microfilariae cause intradermal oedema with enlargement and inflammation of draining lymph nodes (lymphadenopathy), particularly in the groin or axilla, with progressive loss of elastic fibres causing hernias or hanging groin. Infections have also been associated occasionally with an unusual form of epilepsy (Nodding disease) in young children in Africa. Ocular infections by microfilariae may result in compromised sight (reduced vision to total blindness) due to anterior (corneal) lesions causing punctate opacities and sclerosing keratitis, or posterior (retinal) lesions resulting in marked sclerosis (hardening) of choroidal vessels, retinochoroiditis and atrophy of the optic nerve. Infections have also been associated with increased intraocular pressure leading to secondary cataracts and glaucoma. People are afflicted more in savannah than forest regions, and the common name 'river blindness' actually indicates an association between the distribution of infections and suitable habitats for the insect vector. Immunological studies have indicated that host resistance to infection and disease wanes when cellular responses are impaired or down-regulated leading to persistent chronic conditions. Infections in animals by other *Onchocerca* spp. usually do not result in severe diseases; infections in cattle may lead to blemished hides and devaluation of carcasses due to nodules, and infections in horses have been associated with fistulous withers (verminous granulomatous nodules in ligaments), cutaneous lesions (hypersensitivity reactions (scaliness, pruritus, alopecia) of ventral body, head and neck), periodic ophthalmia (with corneal vascularization) and lameness (due to parasitic suspensory desmitis, flexor tendonitis or navicular syndrome).

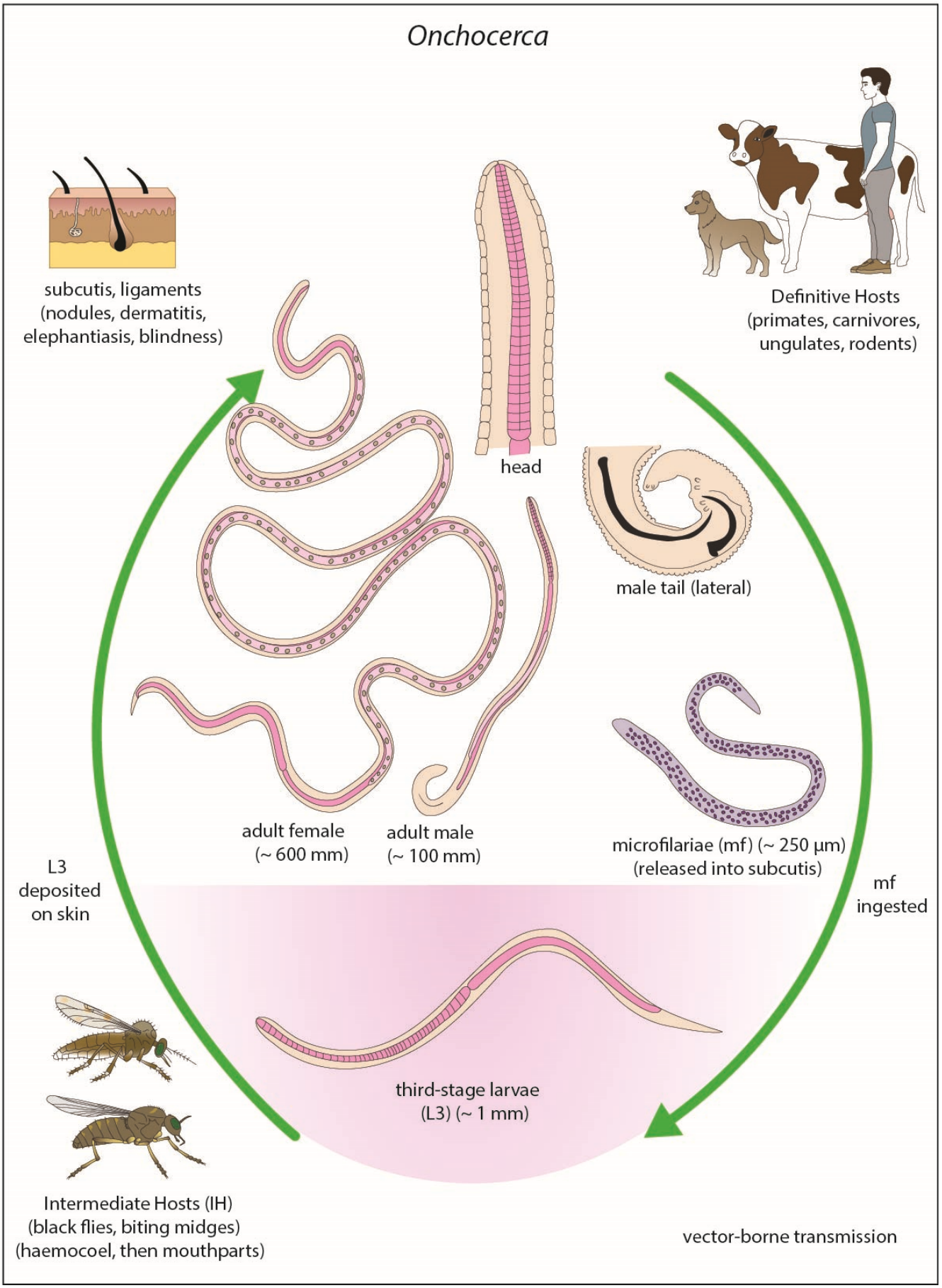
The recent discovery of unique endosymbiotic rickettsial α-proteobacteria (*Wolbachia* supergroups C, D and F) in many filarial nematodes, including most *Onchocerca* spp. except *O. flexuosa*, has interesting implications for both worm biology and pathogenicity. The bacteria are present in all worm developmental stages; they occur in syncytial hypodermal cord cells and also undergo transovarian transmission to developing embryos. They are considered to be essential for the normal development and longevity of many filarial worms, with various biochemical benefits shown for each of the symbiotic partners (mutualism). This dependency has been exploited by using antibiotics to eliminate the bacteria, with subsequent detrimental effects on worm vitality. On the down-side, while microfilariae are well known to induce intense inflammatory reactions, especially upon their death, there is now evidence to suggest that the consequential release of endosymbiotic bacteria may exacerbate that inflammation (bacterial surface proteins have been shown to trigger innate immune responses and Th1 pro-inflammatory responses).

Developmental cycle and mode of transmission: All filarial worms have indirect life-cycles, involving vector-borne transmission using dipteran (simuliid or ceratopogonid) intermediate hosts. *O. volvulus* infections are transmitted by small black flies (sometimes called buffalo gnats) of the genus *Simulium*. Larval black flies only live in clear fast-running streams and adult flies live in adjacent areas with high humidity and abundant streamside vegetation. The adult flies are pool-feeders with coarse mouthparts that rasp and tear host tissues. They feed on a variety of mammals and birds, and their painful bites cause considerable annoyance. Microfilariae ingested during feeding enter the gut and migrate to the thoracic flight muscles of the fly progressing to first-stage (L1) larvae. The larvae moult to second-stage (L2) larvae which migrate to the proboscis and moult into infective third-stage (L3) larvae. Larval development in flies takes around 7-12 days depending mostly on prevailing temperatures. Infective larvae are not injected into definitive hosts when flies feed, but break out of the proboscis when it is bent during feeding and are deposited on the skin where they wriggle and invade the puncture wound. They move to subcutaneous tissues and moult twice developing into mature worms over 1-3 months before mating. Immature adults may be attracted to existing nodules and settle on their surface as satellite nodules, or juvenile female worms may provoke encapsulation and form new separate nodules. The large females remain within nodules their entire lives, but the small males may move from nodule to nodule (re-insemination appears necessary to maintain annual cyclic phases of reproduction, each phase lasting 2.0-4.5 months). The prepatent period (time from infection to first microfilariae release) may be as long as 16 months for some species and the patent period (duration of microfilariae release) may vary considerably with intermittent production occurring over years. Adult worms may live up to 9-16 years and produce billions of microfilariae, with estimates of peak numbers released over 3-4 weeks ranging from 700-1,500 per day. The microfilariae migrate to the skin and eyes and may remain viable for up to 6-24 months. Many studies have demonstrated differences in the temporal and spatial distribution

of microfilariae; many species exhibit a daily periodicity or tissue tropism which is attuned to the feeding habits of the vector species; e.g. microfilariae of *Onchocerca* in Africa normally concentrate in the lower body to maximize transmission to low-biting *Simulium damnosum* but infections in Guatemala concentrate in the upper body where the vector is the high-biting *Simulium ochraceum*. In animals, microfilariae accumulate in different regions of the body (e.g. dorsal midline for *O. gutturosa*, ventral midline and legs for *O. gibsoni*, ventral abdomen for *O. cervicalis*, etc.) which are predilection biting sites for their specific black fly or midge vectors.

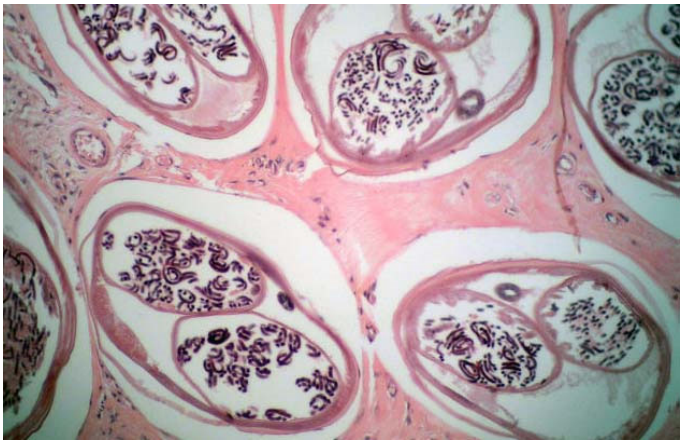
Differential diagnosis: The diagnosis of early-stage infections on the basis of the appearance of a pruritic rash is not distinctive enough as other conditions may cause similar conditions. Infections are generally diagnosed after they have become patent and worms have formed characteristic palpable nodules under the skin. Portions of worms can be obtained by biopsy to confirm diagnosis. Infections can also be detected by examining skin-snip biopsies for active microfilariae after incubation in saline for 30 mins. In heavy infections, microfilariae can occasionally be found in blood and urine. The morphological characteristics of microfilariae are distinctive enough to differentiate all human filarial worms, but it is recommended that multiple samples be collected from different body sites at different times of the day to account for any species-specific differences in tissue tropism and periodicity. *Onchocerca* microfilariae are rarely found in blood whereas those of other filarial worms are commonly found in peripheral blood samples (from which they can be concentrated using Knott's technique to lyse erythrocytes or by filtration using 3-5 μm pore-sized polycarbonate filters). A variety of immunoserological tests (enzyme immunoassays, immunoblots, immunoprecipitation assays) have been developed in attempts to detect specific host antibodies or parasite antigens, especially during early-stage infections, but most tests have lacked sensitivity and specificity. Various molecular biological techniques are currently under development to detect parasite DNA in skin biopsies, blood samples and vector pools using polymerase chain reactions (PCR) to amplify specific sequences (tandemly repeated DNA units (O-150 family), major sperm protein (msp) genes and internal transcribed spacer (ITS) regions of ribosomal DNA).

Treatment and control: A common therapeutic practice in endemic regions is that of nodulectomy, that is, the surgical removal of detectable nodules from superficial aspects to stop microfilariae production and curb attendant pathology. Some nodules, however, may by non-palpable or the adults may be freely migrating. Chemotherapy is therefore warranted, and a major advance was made with the development of ivermectin which is well tolerated in humans and animals. Single doses were found to eliminate microfilariae from the skin, and to suppress their release from adults for over a year. Multiple doses were also found to slowly kill adults. Ivermectin treatment, however, is contraindicated in patients infected with *Loa loa*, as severe reactions may occur. Other microfilaricidal drugs include diethylcarbamazine (DEC), mebendazole, flubendazole and benzimidazole derivatives, but they have little or no effect on adult *Onchocerca* worms. DEC treatment may also precipitate serious dermal, systemic or ocular complications caused by dying microfilariae, although such side-effects can be ameliorated by the use of anti-inflammatory drugs. Skin-patch tests can also be used to monitor for possible Mazzotti reactions before DEC treatment. Suramin does have an effect on adult worms, but it must be administered systemically and it is nephrotoxic. More recently, the antibiotic doxycycline has been used to treat filariae-infected individuals to eliminate *Wolbachia* endosymbiotic bacteria with resultant reductions in adult worm fecundity and survival. Preventive measures involve vector control and avoiding black fly bites. Residual insecticides can be used around dwellings to reduce adult fly numbers, but better results are obtained using larvicides to treat rivers and streams where black flies breed. Unfortunately, there are recurring problems with the development of insecticide resistance in black fly populations.

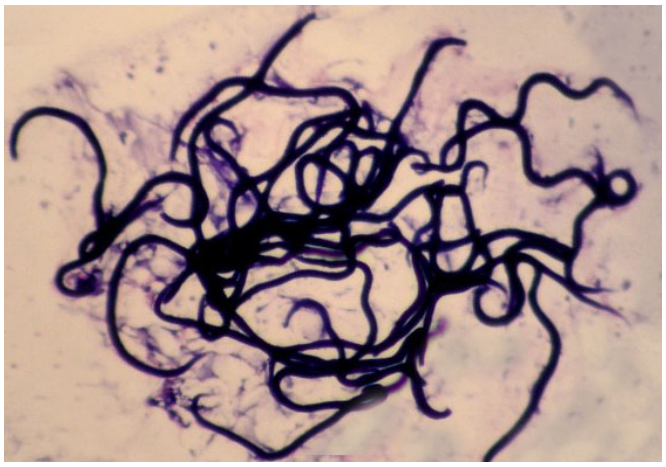

Onchocerca
subcutis, ligaments
(nodules, dermatitis,
elephantiasis, blindness)
Definitive Hosts
(primates, carnivores,
ungulates, rodents)
head
male tail (lateral)
adult female
(~ 600 mm)
adult male
(~ 100 mm)
microfilariae (mf) (~ 250 µm)
(released into subcutis)
L3
deposited
on skin
mf
ingested
third-stage larvae
(L3) (~ 1 mm)
Intermediate Hosts (IH)
(black flies, biting midges)
(haemocoel, then mouthparts)
vector-borne transmission



Onchocerca nodule



Onchocerca nodule



Onchocerca microfilariae



Onchocerca microfilaria

Wuchereria
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including filarioids (without lips) living in subcutaneous, intermuscular, vascular or lymphatic systems of mammals. Two main families include the oviparous filariids (lay eggs) and the ovoviviparous onchocercids (eggs hatch internally releasing pre-larvae called microfilariae). Infections by the onchocercid genus *Wuchereria* are transmitted by mosquitoes and cause lymphatic (Bancroftian) filariasis in humans, involving severe lymphoedema (elephantiasis) of the appendages.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Filarioidea (tissue-dwelling filarial parasites, lack lips)
Family:	Onchocercidae (adults loose in tissues or in nodules, viviparous (live birth of microfilariae))
Genus:	*Wuchereria* (parasitic in lymphatics of humans, mosquito IH)
Species:	*W. bancrofti* (causes lymphatic filariasis (elephantiasis) in humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Filarioidea contains long thread-like nematodes which are predominantly tissue-dwelling parasites infecting the body cavities, subcutis, intermuscular tissues, blood vessels or lymphatic systems of terrestrial hosts. These worms are known colloquially as ‘filariae’, ‘filarids’ or ‘filarioids’ [Note: take care with terminology as the cognate family Filariidae (esp. genus *Filaria*) are known colloquially as ‘filariids’, and the unrelated metastrongyle (lungworm) family Filaroididae (genus *Filaroides*) are known colloquially as ‘filaroids’]. Adult filariae have a cylindroid pharynx with an anterior muscular portion and a posterior glandular portion. Males often have spirally-coiled tails, well-developed alae and dissimilar spicules. Females of most species are ovoviviparous (eggs hatch within body of parent) releasing pre-larval stages known as microfilariae (sometimes sheathed). Filariae have indirect life-cycles whereby microfilariae are taken up by blood-sucking or tissue-feeding invertebrates (arthropods, esp. mosquitoes) which act as intermediate hosts for the development of infective L3 larvae. Ten families are recognised: Filariidae and Onchocercidae infecting mammals, birds, reptiles and amphibians; Setariidae infecting mammals;

Aproctidae infecting birds; and Creagrocercidae, Drilonematidae, Homungellidae, Mesidionematidae, Scolecophilidae and Ungellidae infecting terrestrial annelids. Examples of filarioid genera covered in this resource are compared in the following table.

Genus	Definitive hosts	Adults (location)	Microfilariae (location)	Periodicity	Vectors	*Wolbachia* symbiotes
Family Onchocercidae						
Wuchereria (2 spp.)	primates	2.5-10 cm (lymphatics)	210-320 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Onchocerca (35 spp.)	primates, carnivores, ungulates, rodents	1.5-80 cm (subcutis, ligaments)	105-440 µm unsheathed (skin)	-	flies, midges	present
Mansonella (29 spp.)	primates, carnivores, ungulates, rodents	3-8 cm (subcutis, serosa)	170-300 µm unsheathed (blood/skin)	-	midges, flies, mosquitoes	present
Dirofilaria (34 spp.)	primates, carnivores, ungulates, rodents, lagomorphs, marsupials	4-31 cm (blood vessels)	180-385 µm unsheathed (blood)	-	mosquitoes, flies	present
Dipetalonema, Acanthocheilonema (57 spp.)	primates, carnivores, ungulates, rodents, cingulates, marsupials	1-7 cm (subcutis, serosa)	85-300 µm unsheathed (blood)	-	flies, fleas, lice, ticks	absent
Brugia (10 spp.)	primates, carnivores, rodents	1-9 cm (lymphatics)	170-380 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Loa (3 spp.)	primates, ungulates, rodents	2-7 cm (subcutis, eye)	250-300 µm sheathed (blood)	diurnal	flies	absent
Family Filariidae						
Parafilaria (4 spp.)	ungulates	2-7 cm (subcutis)	40-58 x 23-33 µm larvated eggs (skin)	diurnal	flies	absent
Stephanofilaria (7 spp.)	ungulates	0.2-1.4 cm (subcutis)	45-195 µm sheathed (skin)	-	flies	absent
Family Setariidae						
Setaria (42 spp.)	primates, ungulates, rodents, lagomorphs	4-19 cm (body cavities)	140-310 µm sheathed (blood)	-	mosquitoes	absent

Members of the family Onchocercidae form adult worms that live loose in body cavities or in tissue nodules. Female worms release microfilariae which disperse into the blood or dermal connective tissues (unlike filariids which live in the skin close to where they deposit eggs or larvae). Some 88 onchocercid genera are divided into 7 subfamilies: Onchocercinae and Dirofilariinae (syn. Loainae) mostly in mammals but some in birds and reptiles, Waltonellinae and Icosiellinae in amphibians, Oswaldofilariinae in reptiles, Splendidofilariinae and Lemdaninae in birds, reptiles and mammals (former subfamily Setariinae in large mammals recently elevated to family status as Setariidae). Members of the subfamily Onchocercinae are characterised as forming males with markedly dissimilar spicules and long tails lacking caudal alae (while members of the subfamily Dirofilariinae form males with highly developed caudal alae). Some 43 genera occur in the subfamily Onchocercinae: namely, *Acanthocheilonema, Ackertia*, *Agamofilaria*, *Andersonfilaria*, *Bisbalia*, *Breinlia* (incl. *Johnstonema*), *Brugia*, *Cercopithifilaria*, *Chabfilaria*, *Cherylia*, *Courduriella*, *Cruorifilaria*, *Cystofilaria*, *Deraiophoronema*, *Dessetfilaria*, *Dipetalonema*, *Elaeophora* (syn. *Cordophilus*, *Alcefilaria*), *Filarissima*, *Fuscicorpa*, *Josefilaria*, *Litomosa*, *Litomosoides* (syn. *Vestibulosetariam Finlaynema*), *Mansonella*, *Microfilaria*, *Migonella*, *Molossinema*, *Monanema*, *Onchocerca* (syn. *Wehrdikmansia*, *Acanthospiculum*), *Paramadochotera*,

Paraochoterenella, *Paraprocta*, *Paulianfilaria*, *Pseudolitomosa*, *Rumenfilaria*, *Sandnema, Serofilaria*, *Skrjabinofilaria* (syn. *Cortiamosoides*), *Sprattia, Strianema*, *Wuchereria* and *Yatesia* in mammals, *Struthiofilaria* in birds, and *Macdonaldius* (syn. *Saurofilaria*) in reptiles. Three groups of human filariasis are distinguished on the basis of their tissue tropism: cutaneous dermal filariasis (onchocerciasis in Africa, Asia, Central and South America, loiasis in Africa, *streptocerca* mansonelliasis in Africa); lymphatic filariasis (wuchereriasis in Africa and Asia, brugiasis in South Asia); and serous filariasis (*perstans* mansonelliasis in Africa, Central and South America, *ozzardi* mansonelliasis in Central and South America). It is estimated that 1 billion people in tropical and subtropical countries are exposed to filarial infections and at least 200 million are infected (predominantly *Wuchereria bancrofti, Brugia malayi* and *Onchocerca volvulus*). In humans, species of *Wuchereria* and *Brugia* are responsible for causing lymphatic filariasis (known regionally as Bancroftian and Brugian (Malayan or Timorian) filariasis), involving inflammation of the lymphatics (lymphangitis) and blockage of lymph flow, frequently leading to massive swellings (elephantiasis) of the groin, genitalia (common in Bancroftian filariasis) and lower limbs (common in Brugian filariasis). *W. bancrofti* causes Bancroftian filariasis, which represents the majority (> 90%) of lymphatic filariasis cases.

The genus *Wuchereria* is characterised by the formation of elongate thread-like worms with a defined head and mouth bearing 2 circles of papillae. The genus has been considered to be monotypic containing only one species, *W. bancrofti*, which infects the lymphatic vessels of humans (and rarely langur monkeys), although some also recognize the species *W. kalimantani* in leaf monkeys. Other species reported in early studies have mostly been transferred to the genus *Brugia*, or are considered *species inquirenda* as only microfilariae were found. Female *W. bancrofti* are ovoviviparous and release sheathed microfilariae into the blood which are taken up by mosquito vectors in which infective larvae develop. Different strains demonstrate variable periodicity in microfilaraemia (nocturnal or diurnal) attuned to differences in oxygen tension between venous and arterial blood during the sleeping/waking habits of the host, thus favouring night- or day-biting mosquito species in different geographic regions. *W. bancrofti* is common in tropical regions (found in some 76 countries bounded roughly by latitudes 30-41°N and 28-30°S), notably where climatic requirements are suitable for mosquito intermediate hosts, in and around temporary pools or standing water.

***Wuchereria* species**	**Definitive Hosts (DH)**	**Location**	**Vectors/Intermediate Hosts (IH)**	**Distribution**
W. bancrofti (syn. *Filaria, W. pacifica, W. philippinensis, W. vauceli, W. kalimantani*?) (Bancroftian filariasis, elephantiasis)	Primates: hominid (human), cercopithecid (silvered leaf monkey, gray langur)	lymphatics, mf in blood (sheathed, variable periodicity)	Diptera: culicid (*Aedes aegypti, aquasalis, bellator, cooki, darlingi, futunae, kochi, niveus, poecilius, polynesiensis, pseudoscutellaris, rotumae, samoanus, scapularis, scutellaris, tabu, togoi, tongae, tutuilae, upolensis, vigilax, Anopheles aconitus, anthropophagus, arabiensis, balabacensis, bancroftii, barbirirostris, bwambae, candidiensis, dirus, donaldi, farauti, flavirostris, fluviatilis, funestus, gambiae, jamesi, koliensis, kweiyangensis, letifer, leucosphyrus, maculatus, melas, merus, minimus, nigerrimus, nili, pauliani, philippinensis, punctulatus, sinensis, stephensi, subpictus, vagus, wellcomei, whartoni, Culex annulirostris, antennatus, bitaeniorhynchus, fatigans, modestus, pallens, pipiens, quinquefasciatus, sitiens, tritaeniorhynchus, vishnui, Coquiollettidia juxtamansonia, Mansonia pseudotitillans, titillans, uniformis, Ochlerotatus fijiensis, harinasutai, niveus, oceanicus, poicilius, samoanus, scapularis, togoi, vigilax, Psorophora jamaicensis*); Hemiptera: cimicid (*Cimex lectularis*)	South-East Asia, spread to Pacific Islands, China, Japan, India, Africa and then Central and South America, Caribbean, (no longer found in Australia or North America)
W. kalimantani	Primates: cercopithecid (silvered leaf monkey)	lymphatics, testes, mf in blood (sheathed, nocturnally periodic)	Diptera: culicid (*Aedes balabacensis, togoi*)	Borneo
W. lewisi sp. inq.	Primates: hominid (human)	adult not detected, mf in blood	mosquito?	Brazil

Parasite morphology: *Wuchereria* spp. form 3 morphologically distinct developmental stages: microfilariae, larvae and adult worms. Gravid female worms do not lay eggs but are ovoviviparous and release advanced embryos or pre-larvae (known as microfilariae). These stages are elongate, measuring 210-320 x 6-10 µm, and are ensheathed (enclosed within a transparent egg membrane). They have a striated cuticle, rounded anterior end, short cephalic region, neck-like constriction and pointed tail (tapers to a delicate rounded tip). Microfilariae have nuclear columns loosely dispersed along the body but not inside the tip of tail (no terminal nuclei like *Brugia* and *Loa*). These pre-larvae undergo a series of moults to form sausage-shaped first-stage larvae (L1) measuring up to 300 µm long, elongate second-stage larvae (L2) measuring up to 600 µm long, and then elongate third-stage larvae (L3) measuring 1,000-2,000 x 18-23 µm. The infective L3 have truncated trapezoidal heads, circular oral openings lined with papillae on the outer edge, a glandular oesophagus and blunt tails with three bulbous caudal papillae (two latero-ventral and one dorso-terminal). They moult to form fourth-stage larvae (L4) and then adults (L5), both stages marked by the transformation of the truncated conic head to a rounded appearance. Adults worms are long and thread-like in appearance, measuring 25-100 x 0.1-0.4 mm. They are covered by a translucent white smooth cuticle with very fine transverse striations and have slightly swollen heads with a rounded oral opening bearing 2 circles of distinct papillae. Mature worms are sexually dimorphic, with females being larger than males (80-100 mm cf. 25-40 mm) and having rounded tails rather than curved tails. Both sexes live coiled together in host lymphatic tissues. Males have conspicuous unequal copulatory spicules and a cloaca ringed with sensillae. Females are ovoviviparous and produce embryonated eggs which hatch internally freeing microfilariae which are released from the anterior vulva (located just posterior to the nerve ring).

Site of infection: Adult *Wuchereria* worms occur in humans in tightly coiled nodular masses in major lymphatic ducts, mostly in afferent lymph vessels, usually in the lower limbs or groin region in men or the upper limbs and breasts in women. Mature worms also occur sometimes in lymphatic vessels in the peritoneal cavity or subcutaneous tissues. Gravid female worms release microfilariae which pass through the lymphatic ducts and reach the peripheral blood stream where they circulate. Some microfilariae exhibit nocturnal or diurnal periodicity and sequester in deep capillaries (esp. in the lungs) during the day or night, respectively. Larval development occurs in the thoracic (flight) muscles of mosquito vectors and infective L3 stages migrate through the body cavity (haemocoel) to reach the proboscis.

Pathogenesis: *W. bancrofti* has been associated with a wide variety of clinical manifestations, ranging from asymptomatic subclinical infections to acute lymphatic inflammation to chronic granulomatous reactions, lymphoedema and the extensive disfiguring enlargements of extremities (elephantiasis) typically associated with Bancroftian filariasis. Pathological changes occur due to a combination of direct effects (live parasites in lymph vessels), indirect effects (metabolites released from dying parasites and their endosymbiotic *Wolbachia* bacteria), host inflammatory and immune responses, and secondary infections (bacterial and fungal). Live parasites often elicit few host reactions, but significant inflammation occurs when worms die (posing a serious complication to drug therapy). Symptomatic infection has been associated with recurrent incidences of fever, malaise, lymphadenitis (enlargement of lymph nodes) and lymphangitis (inflammation of lymphatic system) typically affecting the lower extremities (sometimes with genital or breast involvement). Lymphatic filariasis is debilitating, but not typically fatal, and the progression of disease may be divided into 3 phases: incubation; acute; and chronic.

The incubation phase may last for up to a year as worms mature and start producing microfilariae. Around two-thirds of infections remain asymptomatic while others have mild vague symptoms, often involving fever. Some patients recover spontaneously and are unaware of having been infected. The incubation phase has been associated with immuno-tolerance or hypo-responsiveness due to suppressed Th1 responses. *In utero* exposure to worm antigens has even been associated with tolerance to post-partum infection. Nonetheless, even asymptomatic infections may cause subclinical pathology with damage to the lymphatics, notably lymphangiectasia (dilatation of lymph vessel walls) with alternating areas of fibrosis and hyperplasia, and the kidneys, with haematuria, proteinuria and glomerulonephritis (possibly associated with increased immune complexes in the circulation). In endemic areas, asymptomatic individuals remain amicrofilaraemic for extended periods, being known as ‘endemic normals’ with no symptoms and no microfilariae although they test positive to worm antigens. Over time, however, this tolerance might break down and patients may become symptomatic

The acute (or inflammatory) phase commences after female worms have matured and produced microfilariae. Worms and their metabolites, as well as antigens from endosymbiotic *Wolbachia* bacteria, provoke intense inflammatory responses in the lymphatic system, especially in the lower body. Patients experience periodic attacks of lymphangitis and lymphadenitis as well as exhibiting chills, fever, toxaemia, skin infections, painful lymph nodes, localized swellings in arms and legs, tender skin covering lymphoedematous extremities, and sometimes orchitis (inflammation of testes) and epididymitis (inflammation of spermatic cord). These symptoms may persist for 5-7 days and then subside, but often recur at frequent intervals. The parasites cause significant lymphatic damage with concomitant immune dysfunction, which predisposes the host to secondary infections; particularly 2 distinct syndromes: ADLA and AFL. Acute dermatolymphangioadenitis (ADLA) is characterised by diffuse plaque-like inflammatory lesions (with classic signs of fever, redness, swelling and warmth) when skin on the limbs becomes secondarily infected by bacteria (*Staphylococcus* or *Streptococcus*) or fungi, with symptoms lasting up to two weeks. ADLA is often accompanied by pain, fever, chills, inflammation of the lymph vessels and nodes, and potentially oedema. Recurrent episodes can lead to permanent damage, and has been linked to chronic lymphoedema and elephantiasis. Acute filarial adenolymphangitis (AFL) is rarer and characterised by less severe lymphatic inflammation (often an isolated nodule or cord), regional pain, hydrocele and oedema, generally resolving

within a week. These symptoms are due to a granulomatous responses (involving macrophages, eosinophils, neutrophils and lymphocytes) resulting in granuloma formation, fibrosis and temporary lymphatic obstruction. Only dead or dying worms elicit these responses, so this syndrome can paradoxically be triggered as a side effect to the treatment of infections.

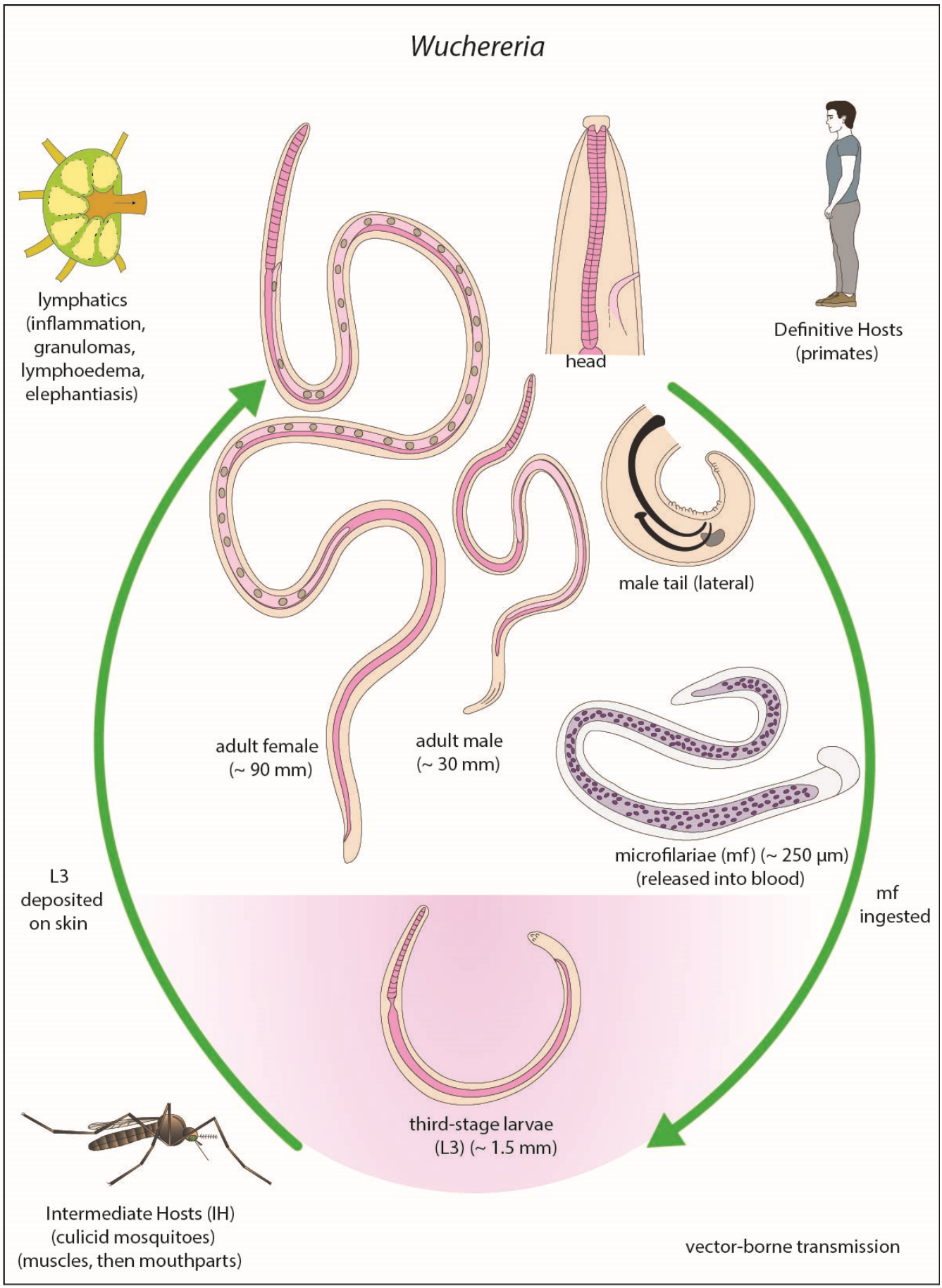
The chronic (or obstructive) phase occurs well after patency (formation of adults and microfilariae), although afflicted patients are usually amicrofilaraemic. The host lymphatic system becomes progressively damaged over the course of several years, the damage often exacerbated by secondary bacterial and fungal infections. Chronic disease has been associated with heavy infections, recurrent ADLA episodes, and hyper-immunoresponsiveness. If not treated, chronic infections can result in permanent tissue damage with significant cellular and fibrous infiltration producing lymph varices, lymphoedema (fluid retention and tissue swelling), hydrocoele (grossly swollen scrota), epididymitis (inflammation of the spermatic cord), orchitis (inflammation of the testes), elephantiasis (especially of the limbs and scrotum in men, and the limbs, vulva and breasts in women), and sometimes chyluria (lymph passed in urine). Worms and host inflammatory responses cause significant changes (remodeling) to lymph vessels with damage to walls and valves affecting lymph pressure, transport and drainage leading to backflow, blockages and consequently lymphoedema. The movement of interstitial fluid may also be reduced across lymphatic epithelia, exacerbating lymphoedema, and weakened lymphatic vessels may rupture releasing chyle (lymph) into surrounding tissues. In swollen tissues, the accumulation of protein-rich lymph recruits keratinocytes, fibroblasts and adipocytes, with hyperkeratosis and hyperplasia leading to further thickening. Lymphocytes accumulate underneath the epidermis contributing to the extensive inflammation. The overlying skin becomes fibrotic, granulomatous, thickened, hardened, verrucous, cracked, ulcerated and highly susceptible to secondary infections. Elephantiasis is grossly disfiguring and a major cause of morbidity and disability in endemic regions, with negative social stigma and spiraling health costs. Although only some 10% of infected people develop elephantiasis after many years of continual filarial reinfection, the condition is nonetheless seen in an estimated 40 million people (90% due to *W. bancrofti*). It is most prevalent in those older than 40 years of age, and is rarely seen in people < 25 years old. On rare occasions, a condition known as tropical pulmonary eosinophilia may develop when microfilariae migrate to the lungs and invoke hypersensitivity responses with paroxysmal cough, wheeze, interstitial fibrosis, cellular infiltrates, reduced pulmonary function and weight loss.

The recent discovery of unique endosymbiotic rickettsial α-proteobacteria (*Wolbachia*) in many filarial nematodes, including *Wuchereria*, has interesting implications for both disease progression and treatment. In addition to worm antigens, metabolites (endotoxins and lipopolysaccharides) released from live and dying bacteria have been shown to contribute to host pathology by provoking inflammatory responses, fibrosis, extravasation, lymphatic endothelial cell hyperplasia and lymphoedema. This presents a problem for chemotherapy as parasites killed by anthelmintic drugs break down releasing their bacterial symbionts. Several studies have shown that concomitant treatment with the antibiotic doxycycline leads to reductions in plasma lymphangiogenesis factors with reduced lymph vessel dilation. Further studies are required to assess the interdependent relationships between filarial worms and their symbiotic (mutualistic) bacteria.

Developmental cycle and mode of transmission: *Wuchereria* has a heteroxenous indirect life-cycle involving cyclic transmission between mammals (definitive hosts) harboring adult parasites and haematophagous mosquito vectors (intermediate hosts) harboring larval stages. Adult worms in humans produce thousands of ensheathed microfilariae which are released into the lymph but enter the blood stream via the thoracic duct. Once in the circulation, the microfilariae display circardian periodicity with peaks in concentration in peripheral blood at certain times of the day whereas they sequester within deep capillaries (especially in the lungs) at other times. Three major subtypes of *W. bancrofti* have been detected: nocturnally periodic, nocturnally subperiodic and diurnally subperiodic strains. The nocturnally periodic strain (microfilariae at highest concentrations in peripheral blood between hours of 10 pm and 2 am) is transmitted by night-biting mosquitoes, principally *Culex* spp. which flourish in the poor drainage systems of overcrowded tropical towns in Asia, East Africa and the Americas, *Anopheles* spp. in rural areas, particularly sub-Saharan Africa, and *Mansonia* spp. in West Africa. The nocturnally subperiodic strain (microfilariae present in peripheral blood at all times but with peak concentration around midnight) was once common in Thailand and the Andaman and Nicobar Islands of India where the mosquito *Ochlerotatus* (*Aedes*) *niveus* and related species served as vectors. The diurnally subperiodic strain (microfilariae present in peripheral blood at all times but with peak concentrations between noon and 8 pm) are transmitted by day-biting mosquitoes, principally *Aedes polynesiensis* which breeds in rural brush areas of the Pacific islands (Fiji, Samoa, Philippines, Tahiti). Microfilariae ingested by mosquitoes exsheath in the intestines in 2-6 hours and then invade the thoracic muscles in 4-17 hours where they develop to sausage-shaped L1 in 5-6 days, moult to elongate L2 in 8-10 days and then to L3 in 11-14 days. Infective L3 migrate through the haemocoel to the proboscis where they are deposited onto the skin of the mammalian host when the mosquito feeds (contaminative rather than inoculative transmission). This form of transmission is considered relatively inefficient so a large number of infective mosquito bites are thought necessary to establish infection. The larvae invade the skin often through the feeding puncture site and migrate to the lymphatic system (varices of lymphatic glands of the groin and epididymis of males and labial and mammary glands of females). They moult twice and mature to thread-like adult worms over at least 6-8 months. Mature adults live intertwined and nest together in major lymphatic ducts (preferentially in the intrascrotal lymphatics and inguinal, axillary and epitrochlear lymph nodes). After mating, gravid female worms may produce up to 10,000 microfilariae each day for up to 10 years. Microfilariae are released into the lymph and make their way to the bloodstream via the thoracic duct (lymphatic drainage duct). The prepatent period (time from infection to first release of microfilariae) ranges from 8-12 months.

Differential diagnosis: Despite the characteristic gross deformities (elephantiasis) associated with long-standing chronic *W. bancrofti* infections, early infections are difficult to diagnose because of the long incubation period (up to 12 months), the absence of clinical symptoms during this period, the absence of microfilariae in many patients (esp. 'endemic normals') and, when present, their variable occurrence due to their nocturnal or diurnal periodicity. Blood samples collected from patients around midnight in the tropics/subtropics (nocturnal periodicity) and around 4 pm in the Pacific (diurnal subperiodicity) may be examined microscopically for the presence of characteristic sheathed microfilariae (with no terminal nuclei). Blood samples may be examined as thick or thin smears or following concentration by filtration through polycarbonate membranes (5 uμ pore size) or by centrifugation of lysates (saponin, formalin or hypotonic saline lysis). Smears may be stained with Giemsa, Delafield's haematoxylin or Field's rapid stain, while concentrates may be coloured with methylene blue or cresyl blue. Medical imaging techniques have been used to examine infected tissues for worms. In particular, high-frequency ultrasound revealed nests with live adult worms performing a signature 'filarial dance' (rapid threshing). Dead and calcified worms may be detected upon X-ray examination. A range of immunological tests have been developed to detect host antibodies against infection, including intradermal tests, immunochromatography and enzyme immunoassays, but their diagnostic sensitivities and specificities were poor. More recently, similar technologies have been adapted to detect parasite antigens in host blood samples, especially enzyme immunoassays and rapid immunochromatographic card tests using monoclonal or polyclonal antibodies. Molecular biological techniques have also been used to detect adult and larval DNA in samples following amplification by single, nested, multiplex, restriction fragment, reverse transcriptase, real-time polymerase chain reaction (PCR) or loop-mediated isothermal amplification (LAMP) of specific gene sequences (18S and 5.8S ribosomal RNA and internal transcribed spacer regions, repetitive sequences (SspI, pWb12, pWb-35, long DNA repeat (LDR), abundant larval transcript-2) or genes encoding surface proteins (e.g. Gp29).

Treatment and control: Infections by adult *Wuchereria* worms and microfilariae have been successfully treated using several anthelmintic drugs: notably the diethylenediamine diethylcarbamazine (DEC), the macrocyclic lactone ivermectin, and the benzimidazole-methylcarbamate albendazole or combinations thereof. These drugs quickly kill microfilariae but generally slowly kill macrofilariae (adult worms), so repeated treatments are required, particularly in endemic areas where re-infections are common. Patient compliance to treatment may waver as various side effects arise; including pruritus, nausea, fever, dizziness, headache, muscle and joint pain. Mass treatments have been used to great effect in several countries where drugs are given on a monthly, semi-annual or annual basis, sometimes in combination with DEC-fortified salt (although this is contraindicated in areas where onchocerciasis or loiasis are present due to worsening of eye or brain lesions). A novel strategy recently adopted has been to also treat patients with antibiotics to destroy the endosymbiotic *Wolbachia* bacteria within the worms. These bacteria are present in all life stages, are transferred from mother to offspring and appear to be essential to healthy growth and development of the parasite. Treatment with tetracyclines (tetracycline, doxycycline) and ansamycin (rifamycin) have been shown to inhibit the motility, viability and release of microfilariae and impede their development. The reduced survival and/or fecundity of the worms may substantially reduce transmission rates. Nonetheless, treatment with anthelmintics and/or antibiotics may have unintended consequences as much of the disease pathology is caused by host reactions to dead and dying worms and bacteria. Patients should be carefully monitored for worsening of their conditions. Despite the apparent efficacy of drug treatments, patients with established hydrocoele and elephantiasis require major interventions. These conditions cause severe disfigurement and in societies with many stigmas attached, so patients often hide their afflictions. Many are also poverty-stricken and simply cannot afford to be treated. It has been shown that recurrent secondary bacterial infections are associated with the development and worsening of elephantiasis, so patient management must include improved hygiene, regular washing and disinfection, careful inspections to detect and treat lesions, and appropriate exercise and physiotherapy to help slow, and sometimes reverse, the onset of elephantiasis. Elastic pressure bandages may be used to combat lymphoedematous swellings of affected limbs. However, incapacitating deformities usually require radical surgery to remove granulomatous, fibrous and calcified tissues, but such options are not always applicable in advanced cases. Most preventive strategies are designed to interrupt transmission patterns by reducing mosquito vector populations or avoiding mosquito bites. Various chemical insecticides have been used to kill adult mosquitoes (aerial spraying or fogging machines) or larval/pupal stages (aquatic larvicides, oils, solvents or even polystyrene beads), despite emergent problems with insecticide resistance. Mosquito breeding sites may be eliminated through improved hygiene and sanitation to reduce standing or polluted water bodies. Protection against mosquito bite has been found to be most effective using repellents (sprays, lotions), physical barriers (window screens, impregnated bed nets or long-sleeved clothing) and by curbing outdoor activities during peak mosquito feeding times. Public education campaigns, coupled with mass chemotherapy, has helped reduce the incidence of lymphatic filariasis in many countries.


Wuchereria
lymphatics
(inflammation,
granulomas,
lymphoedema,
elephantiasis)
head
Definitive Hosts
(primates)
male tail (lateral)
adult female
(~ 90 mm)
adult male
(~ 30 mm)
microfilariae (mf) (~ 250 µm)
(released into blood)
L3
deposited
on skin
mf
ingested
third-stage larvae
(L3) (~ 1.5 mm)
Intermediate Hosts (IH)
(culicid mosquitoes)
(muscles, then mouthparts)
vector-borne transmission



Wuchereria adult worms



Wuchereria sections of worms in lymph node



Wuchereria microfilaria

Brugia
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including filarioids (without lips) living in subcutaneous, intermuscular, vascular or lymphatic systems of mammals. Two main families include the oviparous filariids (lay eggs) and the ovoviviparous onchocercids (eggs hatch internally releasing pre-larvae called microfilariae). Infections by the onchocercid genus *Brugia* are transmitted by mosquitoes and cause lymphatic (Malayan/Timorian) filariasis in humans, involving severe lymphoedema (elephantiasis) of the appendages.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Filarioidea (tissue-dwelling filarial parasites, lack lips)
Family:	Onchocercidae (adults loose in tissues or in nodules, viviparous (live birth of microfilariae))
Genus:	*Brugia* (parasitic in lymphatics of humans/cats, mosquito IH)
Species:	various species cause lymphatic Malayan/Timorian filariasis in humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Filarioidea contains long thread-like nematodes which are predominantly tissue-dwelling parasites infecting the body cavities, subcutis, intermuscular tissues, blood vessels or lymphatic systems of terrestrial hosts. These worms are known colloquially as ‘filariae’, ‘filarids’ or ‘filarioids’ [Note: take care with terminology as the cognate family Filariidae (esp. genus *Filaria*) are known colloquially as ‘filariids’, and the unrelated metastrongyle (lungworm) family Filaroididae (genus *Filaroides*) are known colloquially as ‘filaroids’]. Adult filariae have a cylindroid pharynx with an anterior muscular portion and a posterior glandular portion. Males often have spirally-coiled tails, well-developed alae and dissimilar spicules. Females of most species are ovoviviparous (eggs hatch within body of parent) releasing pre-larval stages known as microfilariae (sometimes sheathed). Filariae have indirect life-cycles whereby microfilariae are taken up by blood-sucking or tissue-feeding invertebrates (arthropods, esp. mosquitoes) which act as intermediate hosts for the development of infective L3 larvae. Ten families are recognised: Filariidae and Onchocercidae infecting mammals, birds, reptiles and amphibians; Setariidae infecting mammals;

Aproctidae infecting birds; and Creagrocercidae, Drilonematidae, Homungellidae, Mesidionematidae, Scolecophilidae and Ungellidae infecting terrestrial annelids. Examples of filarioid genera covered in this resource are compared in the following table.

Genus	Definitive hosts	Adults (location)	Microfilariae (location)	Periodicity	Vectors	*Wolbachia* symbiotes
Family Onchocercidae						
Brugia (10 spp.)	primates, carnivores, rodents	1-9 cm (lymphatics)	170-380 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Wuchereria (2 spp.)	primates	2.5-10 cm (lymphatics)	210-320 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Onchocerca (35 spp.)	primates, carnivores, ungulates, rodents	1.5-80 cm (subcutis, ligaments)	105-440 µm unsheathed (skin)	-	flies, midges	present
Mansonella (29 spp.)	primates, carnivores, ungulates, rodents	3-8 cm (subcutis, serosa)	170-300 µm unsheathed (blood/skin)	-	midges, flies, mosquitoes	present
Dirofilaria (34 spp.)	primates, carnivores, ungulates, rodents, lagomorphs, marsupials	4-31 cm (blood vessels)	180-385 µm unsheathed (blood)	-	mosquitoes, flies	present
Dipetalonema, Acanthocheilonema (57 spp.)	primates, carnivores, ungulates, rodents, cingulates, marsupials	1-7 cm (subcutis, serosa)	85-300 µm unsheathed (blood)	-	flies, fleas, lice, ticks	absent
Loa (3 spp.)	primates, ungulates, rodents	2-7 cm (subcutis, eye)	250-300 µm sheathed (blood)	diurnal	flies	absent
Family Filariidae						
Parafilaria (4 spp.)	ungulates	2-7 cm (subcutis)	40-58 x 23-33 µm larvated eggs (skin)	diurnal	flies	absent
Stephanofilaria (7 spp.)	ungulates	0.2-1.4 cm (subcutis)	45-195 µm sheathed (skin)	-	flies	absent
Family Setariidae						
Setaria (42 spp.)	primates, ungulates, rodents, lagomorphs	4-19 cm (body cavities)	140-310 µm sheathed (blood)	-	mosquitoes	absent

Members of the family Onchocercidae form adult worms that live loose in body cavities or in tissue nodules. Female worms release microfilariae which disperse into the blood or dermal connective tissues (unlike filariids which live in the skin close to where they deposit eggs or larvae). Some 88 onchocercid genera are divided into 7 subfamilies: Onchocercinae and Dirofilariinae (syn. Loainae) mostly in mammals but some in birds and reptiles, Waltonellinae and Icosiellinae in amphibians, Oswaldofilariinae in reptiles, Splendidofilariinae and Lemdaninae in birds, reptiles and mammals (former subfamily Setariinae in large mammals recently elevated to family status as Setariidae). Members of the subfamily Onchocercinae are characterised as forming males with markedly dissimilar spicules and long tails lacking caudal alae (while members of the subfamily Dirofilariinae form males with highly developed caudal alae). Some 43 genera occur in the subfamily Onchocercinae: namely, *Acanthocheilonema, Ackertia*, *Agamofilaria*, *Andersonfilaria*, *Bisbalia*, *Breinlia* (incl. *Johnstonema*), *Brugia*, *Cercopithifilaria*, *Chabfilaria*, *Cherylia*, *Courduriella*, *Cruorifilaria*, *Cystofilaria*, *Deraiophoronema*, *Dessetfilaria*, *Dipetalonema*, *Elaeophora* (syn. *Cordophilus*, *Alcefilaria*), *Filarissima*, *Fuscicorpa*, *Josefilaria*, *Litomosa*, *Litomosoides* (syn. *Vestibulosetariam Finlaynema*), *Mansonella*, *Microfilaria*, *Migonella*, *Molossinema*, *Monanema*, *Onchocerca* (syn. *Wehrdikmansia*, *Acanthospiculum*), *Paramadochotera*,

Paraochoterenella, *Paraprocta*, *Paulianfilaria*, *Pseudolitomosa*, *Rumenfilaria*, *Sandnema, Serofilaria*, *Skrjabinofilaria* (syn. *Cortiamosoides*), *Sprattia, Strianema*, *Wuchereria* and *Yatesia* in mammals, *Struthiofilaria* in birds, and *Macdonaldius* (syn. *Saurofilaria*) in reptiles. Three groups of human filariasis are distinguished on the basis of their tissue tropism: cutaneous dermal filariasis (onchocerciasis in Africa, Asia, Central and South America, loiasis in Africa, *streptocerca* mansonelliasis in Africa); lymphatic filariasis (wuchereriasis in Africa and Asia, brugiasis in South Asia); and serous filariasis (*perstans* mansonelliasis in Africa, Central and South America, *ozzardi* mansonelliasis in Central and South America). It is estimated that 1 billion people in tropical and subtropical countries are exposed to filarial infections and at least 200 million are infected (predominantly *Wuchereria bancrofti, Brugia malayi* and *Onchocerca volvulus*). In humans, species of *Wuchereria* and *Brugia* are responsible for causing lymphatic filariasis (known regionally as Bancroftian and Brugian (Malayan or Timorian) filariasis), involving inflammation of the lymphatics (lymphangitis) and blockage of lymph flow, frequently leading to massive swellings (elephantiasis) of the groin, genitalia (common in Bancroftian filariasis) and lower limbs (common in Brugian filariasis).

The genus *Brugia* is characterised by the formation of elongate thread-like adult worms with transversely striated cuticles and round mouths bearing 2 circles of papillae. Female *Brugia* worms are ovoviviparous and release sheathed microfilariae into the blood which are taken up by mosquito vectors in which infective larvae develop. Different strains demonstrate variable periodicity in microfilaraemia (nocturnally periodic or subperiodic) attuned to differences in oxygen tension between venous and arterial blood during the sleeping/waking habits of the host, and thus their availability to day- or night-biting mosquito species. Some 10 *Brugia* spp. have been described in the lymphatic systems of a small range of mammals (primates, carnivores and lagomorphs) mainly in South-East Asia, but also in the Americas. In particular, the species *B. timori* causes Timorian filariasis in humans in Indonesia, and *B. malayi* causes Malayan filariasis in humans throughout Asia (South-East Asia, Philippines, Sri Lanka, India, East Indies, China, Japan and Korea). Recent molecular studies have identified 2 major *Brugia* clades: *malayi-timori-buckleyi* (parasites of primates and lagomorphs in Asia) and *pahangi-beaveri* (parasites of carnivores in Asia and America).

***Brugia* species**	**Definitive Hosts (DH)**	**Location**	**Vectors/Intermediate Hosts (IH)**	**Distribution**
Subgenus *Brugia*				
B. beaveri (syn. *Onchocerca*)	Carnivora: felid (cat, bobcat), mustelid (American mink), procyonid (raccoon); Rodentia: murid (Mongolian gerbil); Primates: hominid (human)	lymph nodes, subcutis	Diptera: culicid (*Aedes aegypti*)	North America
B. ceylonensis	Carnivora: canid (dog), felid (cat); Primates: hominid (human)	lymph nodes	Diptera: culicid (*Aedes aegypti, Anopheles stephensi, Mansonoides annulifera, uniformis*)	Sri Lanka
B. guyanensis	Carnivora: procyonid (South American coati); Primates: hominid (human)			South America
B. lepori	Lagomorpha: leporid (eastern cottontail, swamp rabbit)	abdominal lymphatics, subcutis		North America
B. malayi (incl 2 strains differing in periodicity) (Malayan filariasis, elephantiasis)	Carnivora: canid (dog), felid (cat, flat-headed cat, leopard cat), mustelid (European polecat), viverrid (small-toothed palm civet, Asian palm civet, Malayan civet); Rodentia: murid (jird, southern multimammate mouse, Natal multimammate mouse, Mongolian gerbil); Pholidota: manid (Sunda pangolin); Primates: callitrichid (common marmoset), lorisid (Sunda slow loris), cercopithecid (crab-eating macaque, rhesus macaque, silvered leaf monkey, gray langur), hominid (human)	lymph nodes and vessels, mf in blood (sheathed, nocturnally periodic or subperiodic)	Diptera: culicid (*Aedes aegypti, kiangensis, kwaiangensis, togoi, Anopheles anthropophagus, barbirirostris, barbirostris, campestris, donaldi, kweiyangensis, lesteri, nigerrimus, quadrimaculatus, sinensis, Armigeres subalbatus, Coquillettidia crassipes, Culex erythrothorax, quinquefasciatus, tarsalis, tritaeniorhynchus, Mansonia annulata, annulifera, bonneae, dives, indiana, longipalpis, uniformis, Ochlerotatus oceanicus, togoi*), Hemiptera: cimicid (*Cimex hemipterus, C. lectularius*)	South and East Asia (esp. Malaya/Timor)
B. pahangi	Carnivora: canid (dog), felid (cat, leopard cat, flat-headed cat, wild cat, lion, tiger), viverrid (Asian palm civet, small-toothed palm civet, large Indian	lymph nodes and vessels (sometimes heart, lungs,	Diptera: culicid (*Aedes aegypti, Anopheles barbirirostris, crucians, dirus, gambiae, quadrimaculatus, stephensi,*	South-East Asia

	civet, binturong), mustelid (European polecat); Rodentia: murid (brown rat, moon rat, wood rat, mouse, jird, Natal multimammate mouse, Mongolian gerbil), sciurid (black giant squirrel), cricetid (golden hamster); Eulipotyphla: erinaceid (moonrat); Pholidota: manid (Sunda pangolin); Primates: callitrichid (common marmoset, white-lipped tamarin), lorisid (Sunda slow loris), cercopithecid (dusky leaf monkey), hominid (human)	testes), microfilariae in blood	*Armigeres obturbans, subalbatus, Culex pipiens, quinquefasciatus, Mansonia annulatus, longipalpis, uniformis, Psorophora confinnis*)	
B. patei (syn. *Wuchereria*)	Carnivora: felid (cat), viverrid (genet), canid (dog)	lymphatics, microfilariae in blood (sheathed)	Diptera: culicid (*Aedes pembaensis, togoi, Anopheles gambiae, Mansonia africanus, uniformis*)	Africa
B. timori (Timorian filariasis, elephantiasis)	Primates: hominid (human), cercopithecid (silvery lutung); Rodentia: murid (Mongolian gerbil); Carnivora: felid (cat)	lymph nodes and vessels, microfilariae in blood (nocturnally periodic)	Diptera: culicid (*Aedes togoi, Anopheles barbirostris*)	Indonesia
B. tupaiae	Scandentia: tupaiid (common tree shrew, large tree shrew)	lymphatics	Diptera: culicid (*Aedes aegypti, albopictus, togoi, Armigeres subalbatus*)	South-East Asia
Subgenus *Brugiella*				
B. buckleyi	Lagomorpha: leporid (Indian hare); Carnivora: mustelid (Asian small-clawed otter)	heart and blood vessels		Sri Lanka

Parasite morphology: The filarial nematode *Brugia* forms 3 different stages in its developmental cycle: adult worms, pre-larvae (microfilariae) and several larval stages (L1-4). Microfilariae are elongate and variable in size depending on species, ranging from 170-380 µm in length by 3-7 µm in width (*B. timori* 265-380 µm long, *B. tupaiae* 283-322 µm, *B. beaveri* 200-325 µm, *B. ceylonensis* 220-275 µm, *B. pahangi* 186-260 µm, *B. malayi* 175-230 µm). They are often coiled or dorsally flexed and are enclosed by a delicate sheath (eggshell membrane) that is usually smooth and translucent, but sometimes granular (e.g. *B. pahangi*). These pre-larval stages have striated cuticles, rounded heads and tapering pointed tails, with a small rounded mouth, pharyngeal thread, cephalic space (sometimes with spines and tooth e.g. *B. malayi*), band-like nerve ring, sac-like innenkorper, excretory cell and pore, and nuclear column (genital primordia)). The nuclear column is tightly packed with nuclei extending to the tip of the tail (not in a continuous row) and 2 conspicuous terminal nuclei isolated at the tip (unlike *Wuchereria* microfilariae which lack terminal nuclei). Different species exhibit variations in the sizes and locations of microfilarial internal structures, especially in the cephalic space (larger in *B. timori*) and innenkorper (longer in *B. pahangi*). Microfilariae exsheath and develop into short sausage-shaped first-stage larvae (L1) measuring 140-150 x 15-20 µm in which the nerve rings and innenkorper become obscure. They moult into elongate second-stage larvae (L2) measuring 400-450 x 25-30 µm with bluntly rounded heads and posterior ventrally-curved spikes. These in turn moult into third stage larvae (L3) measuring 1.0-1.9 mm x 22-30 µm with 2 anterior circles of 4 cephalic papillae, transversely striated cuticles, a glandular oesophagus, and tails with 3 rounded papillae (less prominent in *Brugia* than *Wuchereria*). Adult worms are white, delicate and thread-like in shape ranging from 10-90 mm in length (but usually shorter than *Wuchereria*). They are covered by a smooth, transversely striated cuticle, have a bulbous head with well-defined papillae, long cephalic spaces, a buccal ring, an oesophagus clearly divided into 2 parts (thin anterior muscular, thicker posterior glandular) and the posterior end is ventrally curved. They have longitudinal muscles and move with a conspicuous threshing (S-shaped) motion. Mature worms are sexually dimorphic and live coiled up in pairs, with females being larger than males (40-90 mm x 130-300 µm cf. 10-30 mm x 70-80 µm). The exception is *B. buckleyi* which grows to almost twice that length. Males have a gubernaculum and 2 dissimilar unequal copulatory spicules (left spicule thinner with shorter distal section) and they have ~ 11 caudal papillae (fewer than *Wuchereria*). Female worms have long reproductive organs with the ovary located posteriorly and connected through oviducts and uteri to the vulva located anteriorly (but posterior to the nerve ring). Gravid females are ovoviviparous, producing embryonated eggs which hatch internally releasing microfilariae.

Site of infection: Adult *Brugia* worms live coiled together in pairs in the lymphatic vessels, and sometimes the lymph nodes, of their mammalian (definitive) hosts, typically in the extremities of the legs and arms. The exception is *B. buckleyi* which infects in the heart and coronary circulation. Microfilariae are released into the lymph and make their way to the blood stream via the thoracic duct. They occur in the peripheral circulation at peak concentrations mostly at night (exhibiting nocturnal periodicity or

subperiodicity). Larval stages develop in the thoracic muscles of their mosquito (intermediate) hosts and infective L3 migrate through the haemocoel to the proboscis.

Pathogenesis: *Brugia* infections in domestic and wild animals are usually inapparent and worms are mostly detected serendipitously at post-mortem. Two-thirds of infections in humans are asymptomatic or subclinical, nonetheless, pathological changes still occur due to the combined effects of live worms and host responses to dead and dying worms, microfilariae and their bacterial endosymbionts. In particular, persistent inflammation causes progressive damage to lymph vessels which may eventually result in acute or chronic disease, characterised by lymphoedema (tissue swelling) and elephantiasis. *Brugia* spp. cause lymphatic filariasis in humans, often called Brugian filariasis, with regional variants known as Malayan and Timorian filariasis. These conditions are similar to Bancroftian filariasis caused by *Wuchereria bancrofti*, but genital involvement, hydrocoele and chyluria are rare. The incubation period (time from infection to disease presentation) varies considerably as worms take months to mature (3-6 months for *B. malayi* and 6-12 months for *B. timori*) and adult worms are able to evade the host immune system for several years causing little immunopathology. Adult worms cause lymph vessel dilatation which compromises lymph transportation and immune surveillance, thus rendering the host more susceptible to secondary bacterial and fungal infections. When worms die, they release potent immuno-stimulatory ligands not only from the worms themselves but also from their endosymbiotic *Wolbachia* bacteria. This results in significant inflammation of lymph nodes (lymphadenitis) and the lymphatic system (lymphangitis) with immune cell infiltration, fibrosis, endothelial cell hyperplasia, vessel obstruction, lymph retention and lymphoedema (swelling). The earliest sign is often lymph varicose, and lymph (chyle) is released into surrounding tissues if vessels rupture. Chyluria (cloudy urine due to the presence of chyle) may also develop. Acute presentation involves episodic attacks of fever and chills, inflamed lymph nodes and localised swellings. Infections usually progress from asymptomatic microfilaraemia to acute adenolymphangitis (ADL) characterised by fever and lymphoedema associated with lymphadenitis as a result of secondary bacterial infection. Lymphadenitis may involve supraclavicular, axillary, epitrochlear, antecubital, abdominal, pelvic, inguinal and cervical lymph nodes, which become swollen, tender and painful. Lymphangitis may initially appear as a focal oedema but which continues to spread distally, commonly affecting the scrotum and/or limbs. Chronic infections and/or repeated episodes of ADL can lead to marked lymphoedema with elephantiasis evident as gross swelling and thickening of the tissues and overlying skin, particularly of the limbs, scrotum or breasts. Chronic oedema eventually results in irreversible changes to the skin, such as fibrosis, sclerosis, scarring, verrucous dermatitis and cellular infiltration. Elephantiasis caused by *B. malayi* and *B. timori* usually involves the legs below the knees and involvement of the genitals is uncommon. Elephantiasis of the arms below the elbows may sometimes occur in *B. malayi* infections. The lymphatic system normally performs immune surveillance for foreign material, but this function becomes compromised as lymph pools and is no longer or improperly screened. Patients become susceptible to secondary opportunistic infections by bacteria and fungi, which further exacerbates skin lesions. It has been estimated that some 40 million people worldwide develop elephantiasis (~10% due to Brugian filariasis) which typically causes high morbidity but low mortality. While infections may be acquired in childhood, symptoms generally do not appear until adolescence or early adulthood. Patients become increasingly are unable to provide for themselves or their families and may be ostracized by local communities.

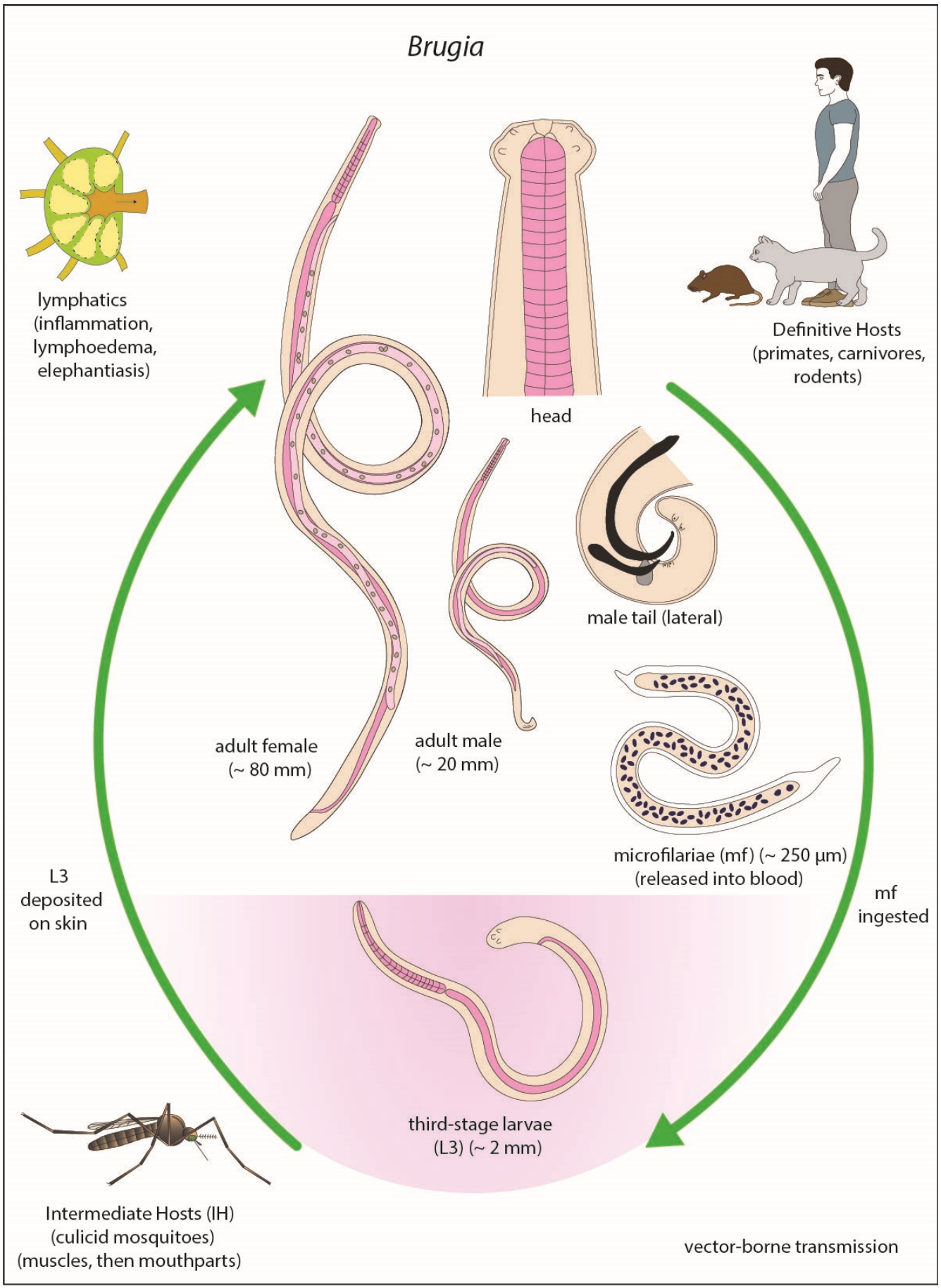
The discovery of unique endosymbiotic rickettsial α-proteobacteria (*Wolbachia*) in many filarial nematodes, including *Brugia* spp., presents a conundrum for disease progression and management. The bacteria are present in all worm developmental stages and they are passed from mother to offspring. They are considered to be mutualistic symbiotes essential for worm development and longevity. However, when worms die, the bacterial symbionts break down releasing surface proteins that have been shown to trigger innate immune responses and Th1 pro-inflammatory responses. The bacteria therefore contribute to disease development. This presents a problem for treatment as chemotherapy should include both anthelmintics to kill worms and antibiotics to kill bacteria, but avoiding heroic doses so the host is not overwhelmed by inflammatory molecules.

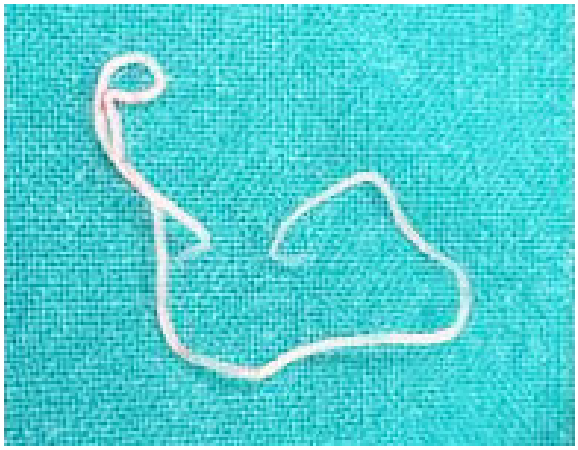
Developmental cycle and mode of transmission: Like other filarial worms, *Brugia* spp. have indirect heteroxenous life-cycles involving sequential development of adult stages in mammalian (definitive) hosts and larval stages in haematophagous mosquito vectors (intermediate hosts). Gravid female worms produce thousands of sheathed microfilariae which make their way from the lymph to the bloodstream via the thoracic duct. The concentration of microfilariae in the peripheral circulation may exhibit circadian (daily) variation with a periodicity attuned to the wake/sleep cycles of their mammalian hosts and the feeding behaviours of their mosquito vectors. *B. timori* is nocturnally periodic (microfilariae at highest concentration between 10 pm and 2 am) and is transmitted by night-biting mosquitoes (*Aedes, Anopheles*) breeding in moist areas of Indonesia. Two strains of *B. malayi* are recognized: a nocturnally periodic strain (microfilariae at highest concentration between 10 pm and 2 am) which is transmitted between humans and domesticated carnivores by mosquitoes (*Aedes*, *Anopheles* and *Mansonia* spp.) that breed in rural areas in open swamps or coastal rice-growing areas throughout Asia and that usually bite during night (anthropophilic vectors are mostly *Anopheles* mosquitoes); and a nocturnally subperiodic strain (microfilaraemic all the time but with higher numbers between noon and 8 pm) transmitted between humans and forest-dwelling animals by zoophilic vectors (*Mansonia* mosquitoes) breeding in swamp-forest areas in Malaysia, Indonesia and Philippines and biting mostly by night but sometimes in the shade by day. Other *Brugia* spp. are mosquito-borne but little is known about the periodicity of their microfilaraemias. Ingested microfilariae exsheath in the mosquito gut and migrate to the thoracic (flight) muscles, and sometimes the fat bodies, where they moult to second-stage larvae (L2) in 4-5 days and then third-stage larvae (L3) in 6-8 days. Infective L3 larvae move through the body cavity (haemocoel) to the proboscis by 9-21 days. When mosquitoes feed on mammalian blood, the infective larvae are released onto the skin and enter through the bite site or other adjacent wounds. This contaminative (rather than inoculative) form of transmission is considered to be

relatively inefficient, and it has been estimated that hundreds of mosquito bites are required to establish infection. Infective larvae migrate to the lymphatic system where they moult to fourth-stage larvae (L4) in 6-9 days and then to immature adults (L5) in 18-40 days. Sexually mature adult worms develop over 2-3 months in animals but 3-12 months in humans. The prepatent period (time from infection to first release of microfilariae) ranges from 55-120 days, and gravid females may produce thousands of microfilariae per day and live for up to 5-15 years.

Differential diagnosis: Infections may be suspected on the basis of clinical symptomatology, such as swelling of limbs, but other conditions may present with similar symptoms, such as Milroy disease or Hodgkin lymphoma. It is usual for provisional diagnoses to be confirmed by microscopically examining blood samples for the presence of characteristic microfilariae. Peripheral blood is best collected around 9 pm to midnight to account daily variations due to nocturnal periodicity or subperiodicity. Microfilariae may be observed directly in thick or thin blood smears or following concentration by filtration through polycarbonate membranes (5 µm pore size) or by centrifugation of lysates (formalin, saponin or hypotonic saline lysis). Smears are best stained with Giemsa, Delafield's haematoxylin or Field's rapid stain, while concentrates may be counter-stained with cresyl blue or methylene blue. *Brugia* microfilariae are sheathed, often kinked, have an elongate cephalic space, crowded nuclear column and a pointed tail with 2 terminal nuclei. Despite the ease and versatility of blood examination techniques, they may exhibit low diagnostic sensitivity due to the absence of microfilariae during the long incubation period after infection and the persistence of asymptomatic amicrofilaraemic infections. Modern medical imaging techniques have been applied to the detection of adult worms and pathological changes in host tissues. Ultrasonography may reveal living adult worms performing a signature 'filarial dance' (*Brugia* spp. may be distinguished from *Wuchereria bancrofti* by differences in the amplitudes of worm movements, as the latter are larger in size when fully mature). X-ray examination may reveal dead and calcified worms in tissues. Lymphoscintigraphy (injection of radiolabeled albumin or dextran into tissues) has also been used to examine the extent of lymphatic dilatation, obstruction or other abnormalities in affected limbs. Several immunological tests have been developed to detect host antibodies or parasite antigens in blood samples, involving enzyme immunoassays and immunochromatographic tests, respectively. More recently, molecular biological techniques have been used to detect parasite DNA in samples from mammals and mosquitoes by polymerase chain reaction (PCR) amplification of nuclear genes encoding small subunit ribosomal RNA, internal transcribed spacer regions 1 and 2, trans-spliced leading Exon I, small heat-shock protein, and HhaI repetitive region.

Treatment and control: The drug of choice for the treatment of Brugian filariasis is the anthelmintic diethylenediamine diethylcarbamazine (DEC), which is effective against both adult worms and microfilariae, thus ameliorating disease and curtailing transmission. Adverse side-effects are rare so chemotherapy has been widely employed in mass drug administration programs in endemic areas, sometimes using DEC-fortified table salt. However, caution is advised in some regions as DEC may worsen onchocercal eye disease and can cause serious side-effects in patients with loiasis. Alternatively, the macrocyclic lactone ivermectin and the benzimidazole-methylcarbamate albendazole have been shown to be effective, but less so against microfilariae so they are often used in combination with DEC. Another treatment strategy recently adopted has been to target the endosymbiotic bacteria (*Wolbachia*) inside the worms. The bacteria appear to have a mutualistic symbiotic relationship essential for the growth and development of most filarial worms. Treatment with the antibiotics tetracycline, doxycycline or rifamycin has been associated with reduced survival and fecundity of adult worms, with substantial decreases in the numbers of microfilariae produced. A complicating side-effect of such treatment is that material released from dead and dying bacteria has been shown to contribute to host inflammatory responses and disease development. In patients with significant lymphoedema and elephantiasis, the management of secondary bacterial and fungal infections has proven critical for preventing acute adenolymphangitis (ADL), reducing skin inflammation and generally improving their quality of life. This involves strict hygiene with regular (daily) washing with soap and water and treating all local injuries with antibiotics (topical or systemic). Swelling may be alleviated by keeping limbs elevated, wearing stocking or compression bandages and using proper footwear. Radical surgery may be required in advanced cases to remove excessive granulomatous, fibrous or calcified tissue but, regrettably, surgical options are not always suitable. At present, there are no vaccines available to prevent infections, but various strategies have been adopted in endemic countries to break transmission cycles either by vector population control or preventing mosquito bites. Insecticides sprayed on and around houses may substantially reduce adult mosquito numbers, although there are growing concerns about the emergence of insecticide resistance. Aquatic breeding sites may be treated with chemicals (larvicides, solvents, oils or even polystyrene beads) or eliminated by improved sanitation or non-flooding irrigation in agriculture. A variety of procedures may be adopted to protect humans against mosquito bites, particularly the use of long-life or residual insect repellents (sprays, lotions), physical barriers (impregnated bed nets, window screens), wearing clothing to cover exposed skin and curbing outdoor activities during peak mosquito feeding times. Few options are available, however, for preventing infections in domestic animals and wildlife which may act as reservoirs of infection in rural or wilderness areas. Nonetheless, the incidence of lymphatic filariasis has been substantially reduced in many countries with pervasive public education campaigns coupled with regular mass chemotherapy.

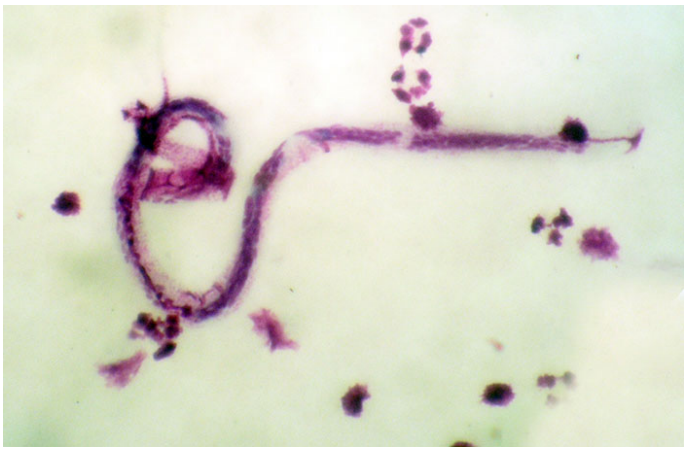

Brugia
lymphatics
(inflammation,
lymphoedema,
elephantiasis)
head
Definitive Hosts
(primates, carnivores,
rodents)
male tail (lateral)
adult female
(~ 80 mm)
adult male
(~ 20 mm)
microfilariae (mf) (~ 250 µm)
(released into blood)
L3
deposited
on skin
mf
ingested
third-stage larvae
(L3) (~ 2 mm)
Intermediate Hosts (IH)
(culicid mosquitoes)
(muscles, then mouthparts)
vector-borne transmission



Brugia adult worm



Brugia microfilaria



Brugia microfilaria

Mansonella
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including filarioids (without lips) living in subcutaneous, intermuscular, vascular or lymphatic systems of mammals. Two main families include the oviparous filariids (lay eggs) and the ovoviviparous onchocercids (eggs hatch internally releasing pre-larvae called microfilariae). Infections by the onchocercid genus *Mansonella* are transmitted by sand flies and black flies and cause skin lesions in humans in Central America.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Filarioidea (tissue-dwelling filarial parasites, lack lips)
Family:	Onchocercidae (adults loose in tissues or in nodules, viviparous (live birth of microfilariae))
Genus:	*Mansonella* (parasitic in body cavities of humans)
Species:	various species cause skin lesions in humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Filarioidea contains long thread-like nematodes which are predominantly tissue-dwelling parasites infecting the body cavities, subcutis, intermuscular tissues, blood vessels or lymphatic systems of terrestrial hosts. These worms are known colloquially as 'filariae', 'filarids' or 'filarioids' [Note: take care with terminology as the cognate family Filariidae (esp. genus *Filaria*) are known colloquially as 'filariids', and the unrelated metastrongyle (lungworm) family Filaroididae (genus *Filaroides*) are known colloquially as 'filaroids']. Adult filariae have a cylindroid pharynx with an anterior muscular portion and a posterior glandular portion. Males often have spirally-coiled tails, well-developed alae and dissimilar spicules. Females of most species are ovoviviparous (eggs hatch within body of parent) releasing pre-larval stages known as microfilariae (sometimes sheathed). Filariae have indirect life-cycles whereby microfilariae are taken up by blood-sucking or tissue-feeding invertebrates (arthropods, esp. mosquitoes) which act as intermediate hosts for the development of infective L3 larvae. Ten families are recognised: Filariidae and Onchocercidae infecting mammals, birds, reptiles and amphibians; Setariidae infecting mammals; Aproctidae infecting birds; and Creagrocercidae, Drilonematidae, Homungellidae, Mesidionematidae, Scolecophilidae and Ungellidae infecting terrestrial annelids. Examples of filarioid genera covered in this resource are compared in the following table.

Genus	Definitive hosts	Adults (location)	Microfilariae (location)	Periodicity	Vectors	*Wolbachia* symbiotes
Family Onchocercidae						
Mansonella (29 spp.)	primates, carnivores, ungulates, rodents	3-8 cm (subcutis, serosa)	170-300 µm unsheathed (blood/skin)	-	midges, flies, mosquitoes	present
Onchocerca (35 spp.)	primates, carnivores, ungulates, rodents	1.5-80 cm (subcutis, ligaments)	105-440 µm unsheathed (skin)	-	flies, midges	present
Dirofilaria (34 spp.)	primates, carnivores, ungulates, rodents, lagomorphs, marsupials	4-31 cm (blood vessels)	180-385 µm unsheathed (blood)	-	mosquitoes, flies	present
Dipetalonema, Acanthocheilonema (57 spp.)	primates, carnivores, ungulates, rodents, cingulates, marsupials	1-7 cm (subcutis, serosa)	85-300 µm unsheathed (blood)	-	flies, fleas, lice, ticks	absent
Wuchereria (2 spp.)	primates	2.5-10 cm (lymphatics)	210-320 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Brugia (10 spp.)	primates, carnivores, rodents	1-9 cm (lymphatics)	170-380 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Loa (3 spp.)	primates, ungulates, rodents	2-7 cm (subcutis, eye)	250-300 µm sheathed (blood)	diurnal	flies	absent
Family Filariidae						
Parafilaria (4 spp.)	ungulates	2-7 cm (subcutis)	40-58 x 23-33 µm larvated eggs (skin)	diurnal	flies	absent
Stephanofilaria (7 spp.)	ungulates	0.2-1.4 cm (subcutis)	45-195 µm sheathed (skin)	-	flies	absent
Family Setariidae						
Setaria (42 spp.)	primates, ungulates, rodents, lagomorphs	4-19 cm (body cavities)	140-310 µm sheathed (blood)	-	mosquitoes	absent

Members of the family Onchocercidae form adult worms that live loose in body cavities or in tissue nodules. Female worms release microfilariae which disperse into the blood or dermal connective tissues (unlike filariids which live in the skin close to where they deposit eggs or larvae). Some 88 onchocercid genera are divided into 7 subfamilies: Onchocercinae and Dirofilariinae (syn. Loainae) mostly in mammals but some in birds and reptiles, Waltonellinae and Icosiellinae in amphibians, Oswaldofilariinae in reptiles, Splendidofilariinae and Lemdaninae in birds, reptiles and mammals (former subfamily Setariinae in large mammals recently elevated to family status as Setariidae). Members of the subfamily Onchocercinae are characterised as forming males with markedly dissimilar spicules and long tails lacking caudal alae (while members of the subfamily Dirofilariinae form males with highly developed caudal alae). Some 43 genera occur in the subfamily Onchocercinae: namely, *Acanthocheilonema, Ackertia*, *Agamofilaria*, *Andersonfilaria*, *Bisbalia*, *Breinlia* (incl. *Johnstonema*), *Brugia*, *Cercopithifilaria*, *Chabfilaria*, *Cherylia*, *Courduriella*, *Cruorifilaria*, *Cystofilaria*, *Deraiophoronema*, *Dessetfilaria*, *Dipetalonema*, *Elaeophora* (syn. *Cordophilus*, *Alcefilaria*), *Filarissima*, *Fuscicorpa*, *Josefilaria*, *Litomosa*, *Litomosoides* (syn. *Vestibulosetariam Finlaynema*), *Mansonella*, *Microfilaria*, *Migonella*, *Molossinema*, *Monanema*, *Onchocerca* (syn. *Wehrdikmansia*, *Acanthospiculum*), *Paramadochotera*, *Paraochoterenella*, *Paraprocta*, *Paulianfilaria*, *Pseudolitomosa*, *Rumenfilaria*, *Sandnema, Serofilaria*, *Skrjabinofilaria* (syn. *Cortiamosoides*), *Sprattia, Strianema*, *Wuchereria* and *Yatesia* in mammals, *Struthiofilaria* in birds, and *Macdonaldius* (syn.

Saurofilaria) in reptiles. Three groups of human filariasis are distinguished on the basis of their tissue tropism: cutaneous dermal filariasis (onchocerciasis in Africa, Asia, Central and South America, loiasis in Africa, *streptocerca* mansonelliasis in Africa); lymphatic filariasis (wuchereriasis in Africa and Asia, brugiasis in South Asia); and serous filariasis (*perstans* mansonelliasis in Africa, Central and South America, *ozzardi* mansonelliasis in Central and South America).

Members of the genus *Mansonella* form worms in subcutaneous tissues and sometimes the body cavities of mammals (mainly primates, but also including carnivores, insectivores, rodents and ungulates). Worms have a small pore-like mouth with almost no buccal capsule and a slender thread-like oesophagus. Females have 4 caudal lappets and are ovoviviparous releasing unsheathed microfilariae into the blood or skin where they are taken up by dipteran intermediate hosts (midges, black flies or mosquitoes). Around 30 *Mansonella* spp. are recognised in 7 subgenera: *M.* (*Mansonella*) (with non-striated cuticle, annular swellings, vulva anterior to oesophageal-intestinal junction, short vagina, male tail without lappets, right spicule with heel, microfilariae without terminal nuclei, parasitic in rodents, carnivores and primates); *M.* (*Cutifilaria*) (with non-striated cuticle, without annular swellings, area rugosa with transverse bands of pointed rugosities, vulva posterior to oesophageal-intestinal junction, short vagina, male tail without lappets, right spicule with distal spoon-like portion, microfilariae with terminal nuclei, parasitic in cervids); *M.* (*Esslingeria*) (with non-striated cuticle, some with annular swellings, vulva anterior to oesophageal-intestinal junction, long vagina, male tail without lappets, right spicule without heel, microfilariae with terminal nuclei, parasites in rodents and primates); *M.* (*Filyamagutia*) (with non-striated cuticle, annular swellings, vulva anterior to oesophageal-intestinal junction, long tubular vagina, microfilariae without terminal nuclei, parasitic in carnivores); *M.* (*Pseudolitomosa*) (with non-striated cuticle, without annular swellings, vulva level to oesophageal-intestinal junction, long vagina, male tail with lappets, right spicule with heel, parasitic in rodents); *M.* (*Tetrapetalonema*) (with striated cuticle, some with annular swellings, vulva anterior to oesophageal-intestinal junction, globular vagina, male tail with lappets, right spicule without heel, microfilariae with terminal nuclei, parasitic in primates); and *M.* (*Tupainema*) (with non-striated cuticle, with annular swellings, vulva at level of oesophageal-intestinal junction, globular vagina, male tail with lappets, right spicule without heel, microfilariae without terminal nuclei, parasitic in tree shrews). Another subgenus (viz. *M.* (*Sandnema*) containing 2 species) has recently been elevated to generic status. Infections by *Mansonella* spp. occur primarily in tropical regions where warm climatic conditions are conducive to the survival of the invertebrate intermediate hosts. Nonetheless, most species differ in their geographical distribution and tissue tropism. Infections in humans usually involve 3 species: *M.* (*E.*) *perstans* and *M.* (*E.*) *streptocerca* in Africa (the former translocated to the Americas during the slave trade era) and *M.* (*M.*) *ozzardi* in the New World (South and Central America). It is currently conservatively estimated that over 114 million people are infected.

***Mansonella* species**	**Definitive Hosts (DH)**	**Location**	**Vectors/Intermediate Hosts (IH)**	**Distribution**
Subgenus: *Mansonella*				
M. interstitium (syn. *Dipetalonema, Tetrapetalonema*)	Rodentia: sciurid (eastern gray squirrel)	subcutaneous tissues		North America
M. llewellyni (syn. *Dipetalonema, Tetrapetalonema*)	Carnivora: procyonid (raccoon)	subcutaneous tissues and fascia, microfilariae in blood	Diptera: ceratopogonid (*Culicoides hollensis*)	North America
M. ozzardi (syn. *Dipetalonema, Filaria, F. demarquayi, F. juncea, F. tucumana*)	Primates: cercopithecid (patas monkey), hominid (human)	subcutaneous tissues, peritoneal cavity, visceral adipose tissue, microfilariae in blood (unsheathed, nonperiodic)	Diptera: ceratopogonid (*Culicoides barbosai, furens, paraensis, phlebotomus, Leptoconops becquaerti*), simuliid (*Simulium amazonicum, argentiscutum, exiguum, oyapockense, sanguineum*)	Central and South America, Caribbean
Subgenus: *Cutifilaria*				
M. perforata	Artiodactyla: cervid (sika deer)			Japan
M. wenki (syn. *Cutifilaria*)	Artiodactyla: cervid (red deer)			Europe
Subgenus: *Esslingeria*				
M. gorillae (syn. *Dipetalonema, Microfilaria*)	Primates: hominid (gorilla)			Africa
M. leopoldi (syn. *Dipetalonema, Microfilaria, Tetrapetalonema*)	Primates: hominid (gorilla)			Africa

M. longicapita	Rodentia: caviid (capybara)			South America
M. lopeensis	Primates: hominid (gorilla)			Africa
M. perstans (syn. *Dipetalonema, D. semiclarum, Filaria, Acanthocheilonema, Tetrapetalonema*)	Primates: hominid (human, gorilla, chimpanzee)	pleural and abdominal cavities, pericardial, perirenal and retroperitoneal tissues, skin lesions, serous cavity filariasis, microfilariae in blood (unsheathed)	Diptera: ceratopogonid (*Culicoides austeni, grahami*?, *inornatipennis*)	sub-Saharan Africa, Central and South America, Caribbean
M. rodhaini (syn. *Dipetalonema, Microfilaria, Monnigofilaria, Tetrapetalonema*)	Primates: hominid (human, bonobo, chimpanzee)			Africa
M. rotundicapita	Rodentia: caviid (capybara)	dermal and subcutaneous tissues		South America
M. streptocerca (syn. *Agamofilaria, Dipetalonema, Acanthocheilonema, Moennigofilaria, Tetrapetalonema*)	Primates: hominid (human, bonobo, gorilla, chimpanzee)	subcutaneous tissues, microfilariae in skin/blood (unsheathed, nonperiodic)	Diptera: ceratopogonid: (*Culicoides austeni, grahami, milnei*)	Central Africa
M. vanhoofi (syn. *Dipetalonema, Acanthocheilonema, Tetrapetalonema*)	Primates: hominid (bonobo, gorilla), cercopithecid (baboon)	subcutaneous tissue		Africa
Subgenus: *Filyamagutia*				
M. akitensis (syn. *Tetrapetalonema*)	Carnivora: ursid (Japanese black bear)	adipose tissue, mesentery, serous membrane		Japan
Subgenus: *Pseudolitomosa*				
M. musasabi (syn. *Pseudolitomosa*)	Rodentia: sciurid (Japanese giant flying squirrel)	abdominal cavity		Japan
Subgenus: *Tetrapetalonema*				
M. atelensis (syn. *Tetrapetalonema*) (incl. subspp. *atelensis*, *amazonae*)	Primates: atelid (Geoffroy's spider monkey, Columbian black spider monkey), cebid (wedge-capped capuchin)	subcapsular region		South America
M. barbascalensis (syn. *Dipetalonema, Tetrapetalonema*)	Primates: aotid (three-striped night monkey, Spix's night monkey)			South America
M. colombiensis (syn. *Tetrapetalonema*)	Primates: cebid (common squirrel monkey, tufted capuchin)	ns	Diptera: culicid (*Aedes aegypti*)	South America
M. mariae	Primates: cebid (common squirrel monkey)		Diptera: culicid (*Aedes aegypti*)	South America
M. marmosetae (syn. *Dipetalonema, Tetrapetalonema*)	Primates: callitrichid (Geoffroy's tamarin, cotton-top tamarin, brown-mantled tamarin), cebid (Central American squirrel monkey, black-capped squirrel monkey, common squirrel monkey, Columbian white-faced capuchin), atelid (red-faced spider monkey, howler monkey, Columbian black spider monkey, Geoffroy's spider monkey), aotid (three-striped night monkey,	intermuscular connective tissue, microfilariae in blood	Diptera: ceratopogonid: (*Culicoides furens, hollensis*)	South and Central America

	Panamanian night monkey)			
M. mystaxi (syn. *Tetrapetalonema*)	Primates: callitrichid (moustached tamarin)			South America
M. obtusa (syn. *Microfilaria, Dipetalonema, Tetrapetalonema*)	Primates: cebid (Colombian white-faced capuchin, Humboldt's white-fronted capuchin, Central American squirrel monkey)			South and Central America
M. panamensis (syn. *Microfilaria, Tetrapetalonema*)	Primates: cebid (Colombian white-faced capuchin, red-backed squirrel monkey, tufted capuchin), aotid (Panamanian night monkey, three-striped night monkey, Nancy Ma's night monkey)	subcutaneous tissue		South America
M. parvum (syn. *Tetrapetalonema*)	Primates: cebid (Colombian white-faced capuchin, black-crowned Central American squirrel monkey)			South and Central America
M. peruviana	Primates: cebid (common squirrel monkey)			South America
M. saimiri (syn. *Tetrapetalonema*)	Primates: cebid (common squirrel monkey)			South America
M. tamarinae (syn. *Dipetalonema, Tetrapetalonema*)	Primates: callitrichid (black-mantled tamarin)			South America
M. zakii sp. inq. (syn. *Parlitomosa, Dipetalonema, Tetrapetalonema*)	Primates: callitrichid (golden lion tamarin)			Egypt (ex. Brazil)
Subgenus: *Tupainema*				
M. dunni (syn. *Dipetalonema, Tetrapetalonema*)	Scandentia: tupaiid (common treeshrew, large treeshrew)	subcutaneous tissue		Malaysia

Another subgenus, *Mansonella* (*Sandnema*), has recently been promoted to generic status on the basis of morphotypic differences; in that worms possess a tubular buccal capsule, the vulva is at the level of the oesophageal-intestinal junction, the vagina is long and surrounded by muscle fibres, the area rugosa has transverse bands of short longitudinal cuticular crests, the 2 spicules are unequal but both are divided into handle and lamina regions, and the microfilariae have nuclei in the tip of the tail.

***Sandnema* species**	**Definitive Hosts (DH)**	**Location**	**Vectors/Intermediate Hosts (IH)**	**Distribution**
S. digitatum (syn. *Mansonella, Dirofilaria, Tetrapetalonema, Dipetalonema, Moennigofilaria*)	Artiodactyla: bovid (cattle); Primates: hylobatid (hoolock gibbon, Lar gibbon, northern white-cheeked gibbon), cercopithecid (dusky leaf monkey, stump-tailed macaque)	abdominal cavity		Asia
S. sunci (syn. *Mansonella, Dipetalonema, Tetrapetalonema, Moennigofilaria*)	Eulipotyphla: soricid (Asian house shrew)	subcutaneous tissue		Asia

Parasite morphology: *Mansonella* species form 3 different morphological stages in their developmental cycles: adult worms, pre-larvae (microfilariae) and 4 sequential larval stages (designated L1-4). Gravid female worms produce elongate sinuous microfilariae generally ranging in size from 170-240 x 4-7 µm. Microfilariae of some species may contract and expand significantly, ranging up to 300 µm long (e.g. *M. marmosetae*), but they are usually smaller than microfilariae produced by other filarial worms (such as *Wuchereria* or *Loa*). All *Mansonella* microfilariae are unsheathed and have curled attenuated tails with a blunt, pointed or knob-like tip with or without terminal nuclei (*M. ozzardi* has a pointed button-hook tail without terminal nuclei, *M. streptocerca* has a curved shepherd's crook tail with a single row of terminal nuclei, and *M. perstans* has a rounded tail with a nuclear column terminating in a single large nucleus). Microfilariae develop into sausage-shaped first-stage larvae (L1) measuring around 230 x 23 µm, which moult

to elongate second-stage larvae (L2) measuring up to 370 x 23 μm, and then to longer third-stage larvae (L3) measuring around 570 x 19 μm. L3 grow to infective stages measuring up to 600-900 μm in length characteristically with a long glandular oesophagus and a broad posterior with a long tail ending in 4 small terminal papilla-like swellings. They moult twice to form long thin thread-like adult worms measuring 30-80 mm long by 45-120 μm wide. Adults are covered with a tough white cuticle, some species having cuticular striations and some having annular cuticular swelling. They have small pore-like mouths without buccal capsules, and a long thread-like oesophagus and intestinal tract separated from the body wall by a fluid-filled pseudocoelom. Most worms have hair-like setae (mechanoreceptors), rostral amphids and caudal phasmids (chemoreceptors). Mature adults exhibit sexual dimorphism, with female worms being larger than males (50-80 mm x 80-120 μm cf. 30-55 mm by 45-60 μm). Males have a gubernaculum, 2 unequal spicules (the right spicule sometimes bearing a distal heel) and the tail is often coiled (e.g. *M perstans*) or bent like a shepherd's crook (e.g. *M. streptocerca*), often bearing 4 caudal lappets. The female tail is short, half -coiled curving ventrad, and bears 4 caudal lappets (2 lateral and a bifurcated axial point). Gravid females are ovoviviparous and produce embryonated eggs in the uterus which hatch internally releasing live microfilariae which pass out through the anterior vulva (located posterior to the nerve ring but near the oesophageal-intestinal junction).

Site of infection: Adult *Mansonella* worms live in the dermis, subcutaneous tissues or serous body cavities (peritoneal, pleural and pericardial) of their mammalian definitive hosts. Different parasite species exhibit tissue tropism for particular predilection sites of infection: *M. streptocerca* infecting the dermis, *M. ozzardi* forming nodules in subcutaneous tissues, and *M. perstans* developing in deep connective tissues in the mesenteries in serous body cavities. Microfilariae are found in the peripheral blood (*M. perstans, M. ozzardi*) or in dermal tissues (*M. streptocerca*). Adults and/or microfilariae have also occasionally been detected in pleural effusions, ascitic fluid, cerebrospinal fluid, bone marrow and other body organs. Larval stages develop mainly in the thoracic (flight) muscles of their dipteran vectors (intermediate hosts).

Pathogenesis: Studies on *Mansonella* infections are often confounded by high rates of co-infections with other filarial parasites, especially *Onchocerca* spp., and other microbial diseases, including malaria, tuberculosis and human immunodeficiency virus (HIV). Although it has been suggested that *Mansonella* infections may interfere with homeostatic mechanisms and immune function, they are usually asymptomatic or produce a benign self-limiting illness. Infections may produce a variety of nonspecific clinical symptoms that become evident on the death of adult worms and microfilariae; including transient angioedematous swellings of the arms, face or other body parts (not unlike the Calabar swellings of loiasis), upper abdominal pain, arthralgias, urticaria, pruritus, eosinophilia, fever, headache, extreme exhaustion, and neurologic or psychologic symptoms. Infections have occasionally been associated with pericarditis, hepatitis and hepatomegaly, pulmonary symptoms, lymphadenopathy, skin lesions and elephantitis. In Africa, *M. perstans* may invade the conjunctiva of the eye resulting in periorbital oedema (known as Kampala or Ugandan eye worm), but rarely progressing to blindness. *M. perstans* is considered mildly pathogenic in man and apes, with subcutaneous lesions, angioedema, and periorbital oedema generally more common in Africa, and arthralgia more prevalent in South America. *M. streptocerca* infections in Africa commonly cause chronic pruritic dermatitis, hypopigmented macules and skin thickening over the thorax and shoulders, occasionally with abscess or granuloma formation. *M. ozzardi* is generally considered asymptomatic, but chronic infections have been associated with skin nodules, lymphadenopathy, arthralgia, fever and eosinophilia in humans in the New World and West Indies. Infections occur more frequently and heavily in males than in females, and the incidence increases with age with little evidence of host resistance or protective immunity.

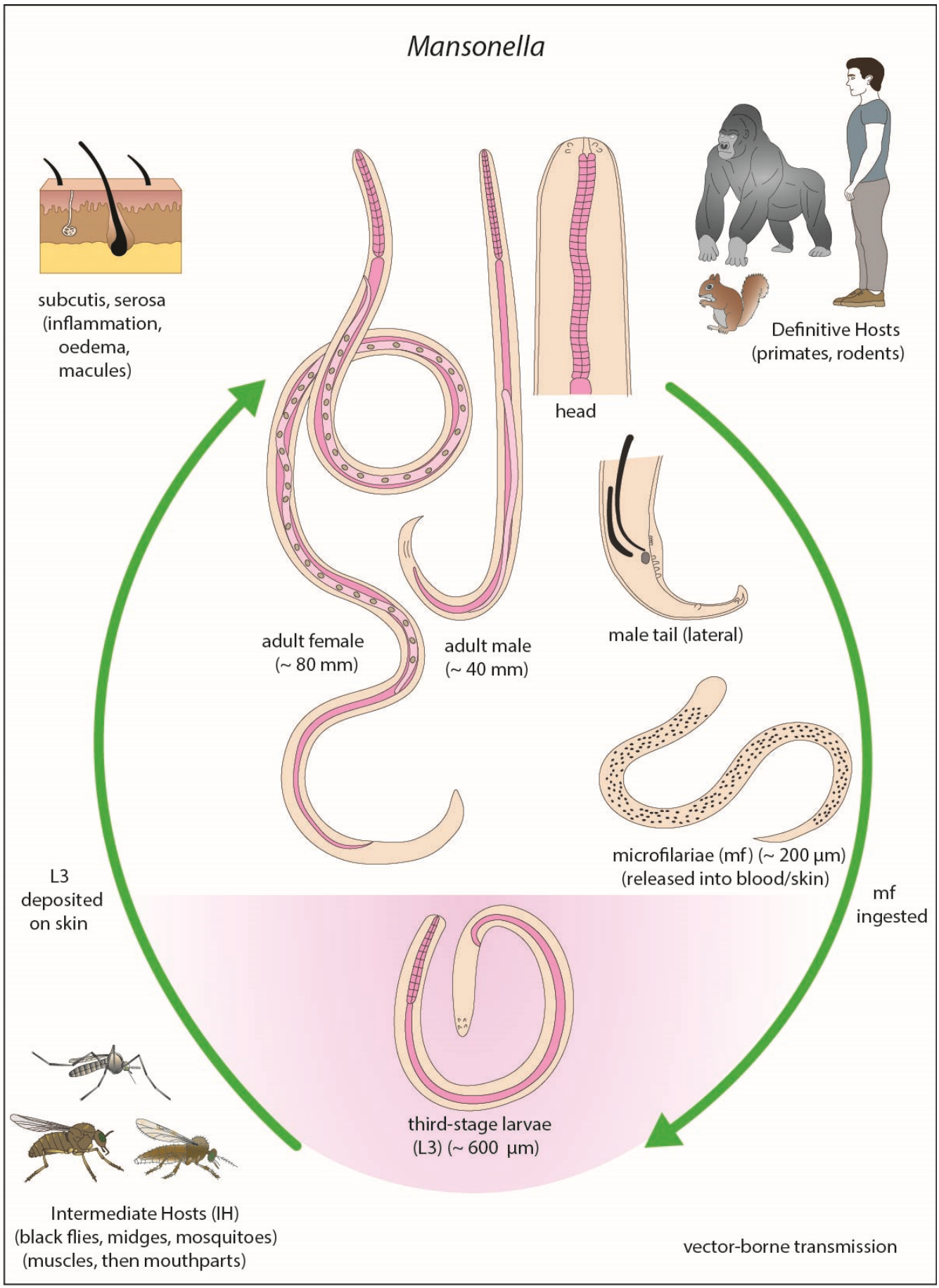
The occurrence of endosymbiotic bacteria (*Wolbachia*) within worms has contradictory implications for disease development and management. The bacteria are considered to be mutualistic symbionts crucial for worm survival and reproduction. However, surface proteins from freed bacteria provoke strong innate immune responses in humans, thus contributing to the chronic inflammatory disease produced by material released from dead and dying worms. Treating patients with antibiotics to kill the bacteria may therefore reduce worm burdens and fecundity, but it may also exacerbate host inflammation.

Developmental cycle and mode of transmission: *Mansonella* spp. have indirect heteroxenous life-cycles with adult worms forming in vertebrate definitive hosts (mammals) and larval stages developing in invertebrate intermediate hosts (dipteran vectors). Female worms release live young (microfilariae) into the tissues of their mammalian hosts which make their way to the bloodstream or accumulate in dermal tissues. Most *Mansonella* spp. do not exhibit any periodicity in microfilaraemia, although some studies suggest that *M. perstans* may sometimes be nocturnally subperiodic (microfilariae always present but peak in concentration at night). All species utilize blood-sucking or tissue-feeding dipteran insects as intermediate hosts, notably ceratopogonids (biting midges) in the Americas and Africa, simuliids (black flies) and culicids (mosquitoes) in South America. Female insects require blood meals for egg maturation, and they often bite around dawn and dusk. They breed in organically-enriched sites such as stream, swamps, and sometimes dung. They often have flight ranges limited to a few hundred metres, but can move further in windy conditions. Ingested microfilariae migrate from the midgut through the haemocoel to the thoracic flight muscles where they undergo a series of moults (first moult in 3-7 days, second moult in 6-9 days) to form L3 larvae that move to the insect mouthparts in 10-14 days. These infective larvae are transmitted to mammalian hosts when the midges, mosquitoes or blackflies feed on blood or tissues. Transmission is contaminative rather than inoculative as the larvae escape the insect proboscis by stretching and bursting the terminal membrane of the labrum and are deposited on mammalian skin. The larvae penetrate the skin, usually though bites sites or adjacent wounds, and then moult twice while migrating to their predilection sites of infection where they mature into adult worms

and mate. Gravid females are ovoviviparous and birth live microfilariae which accumulate in dermal tissues or make their way to the bloodstream. The incubation or prepatent period (time from infection to first microfilarial release) ranges from 5-8 months, but can extend up to 2 years in some individuals.

Differential diagnosis: While most infections remain asymptomatic, some may be suspected on the basis of transient swellings and allergic reactions, but these symptoms are nonspecific and may be caused by other conditions. Infections are conventionally diagnosed by the microscopic detection of characteristic microfilariae (small, unsheathed, bent tails with or without terminal nuclei) in blood samples (thick or thin smears, filtrates, sediments or lysates) or in skin tissues (skin snips or punch biopsies incubated in saline or media). Microfilariae may be stained with Giemsa, haematoxylin, cresyl blue or methylene blue. A small range of immunological tests have been developed to detect host antibodies against parasite antigens, including complement fixation, bentonite flocculation, haemagglutination and intradermal tests, but there have been problems with poor sensitivity and cross-reactions with other filarial worms. More recently, an enzyme immunoassay has been used to detect filarial antigens in blood samples. Molecular biological techniques have also been used to detect parasite DNA in clinical samples following single, nested or multiplex polymerase chain reaction (PCR) amplification of nuclear gene sequences (5S and 28S ribosomal RNA, internal transcribed spacer regions 1 and 2, and major sperm protein (MSP)).

Treatment and control: *Mansonella* infections have proven difficult to treat and while various anthelmintic drugs have been shown to reduce worm growth and fecundity (decreased microfilarial counts), they have not cured infections. An extended course of treatment with the benzimidazole-methylcarbamates mebendazole or albendazole were most effective in the treatment of symptomatic infections, while treatment with the diethylenediamine diethylcarbamazine (DEC) or the macrocyclic lactone ivermectin were less effective. Combination therapies using DEC with mebendazole or ivermectin with albendazole were found to significantly reduce microfilaraemia, but they sometimes produced undesirable side-effects, including abdominal pain, headache, nausea and vomiting. The tetracycline antibiotic doxycycline was recently found to be partially effective in the treatment of *M. perstans* infections, by targeting the endosymbiotic *Wolbachia* bacteria regarded to be vital for worm growth and development. It has been noted that patients undergoing chemotherapy should be carefully monitored for allergic responses arising from the death of too many worms and/or bacteria suddenly releasing potent inflammatory immunogens. In cases where worm nodules are superficial or localized in accessible areas, recourse may be made to their surgical excision. The prevention of infections is based around vector control, better sanitation, protective barriers and public education. Insecticides may be used against adult midges, mosquitoes and blackflies, especially those chemicals with long-lasting residual activity around homes and workplaces. Larvicides may also be used to target aquatic developmental stages, but this approach is confined to small accessible water bodies in semi-rural situations rather than wilderness areas. Careful monitoring of insecticidal efficacy should also be conducted to address mounting concerns about the emergence and spread of resistance in insects. Where possible, environmental interventions may be made to eliminate insect breeding sites, such as draining temporary standing waters, puddles and ditches, using non-flooding irrigation practices, covering tanks and ponds, and improving sewerage systems and waste management. An alternative approach to vector population control is to minimise contact with vectors, by using chemical repellents (sprays, lotions), physical barriers (bed nets, protective clothing), or changing behaviour patterns (avoid waterways, limit outdoor activities at dusk and dawn). Many infections occur in poor rural areas so proactive public education campaigns should aim to inform residents of risks as well as to provide treatment opportunities.


Mansonella
subcutis, serosa
(inflammation,
oedema,
macules)
Definitive Hosts
(primates, rodents)
head
adult female
(~ 80 mm)
adult male
(~ 40 mm)
male tail (lateral)
microfilariae (mf) (~ 200 µm)
(released into blood/skin)
L3
deposited
on skin
mf
ingested
third-stage larvae
(L3) (~ 600 µm)
Intermediate Hosts (IH)
(black flies, midges, mosquitoes)
(muscles, then mouthparts)
vector-borne transmission



Mansonella microfilaria

Dipetalonema, Acanthocheilonema
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including filarioids (without lips) living in subcutaneous, intermuscular, vascular or lymphatic systems of mammals. Two main families include the oviparous filariids (lay eggs) and the ovoviviparous onchocercids (eggs hatch internally releasing pre-larvae called microfilariae). Infections by the onchocercid genera *Dipetalonema* and *Acanthocheilonema* are transmitted by fleas and ticks (in which L3 develop). Various species live in the subcutaneous tissues in wild and companion animals, but usually not in association with clinical disease.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Filarioidea (tissue-dwelling filarial parasites, lack lips)
Family:	Onchocercidae (adults loose in tissues or in nodules, viviparous (live birth of microfilariae))
Genus:	*Dipetalonema, Acanthocheilonema* (parasitic in connective tissues of dogs/camelids/humans)
Species:	various species cause subclinical infections in dogs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Filarioidea contains long thread-like nematodes which are predominantly tissue-dwelling parasites infecting the body cavities, subcutis, intermuscular tissues, blood vessels or lymphatic systems of terrestrial hosts. These worms are known colloquially as 'filariae', 'filarids' or 'filarioids' [Note: take care with terminology as the cognate family Filariidae (esp. genus *Filaria*) are known colloquially as 'filariids', and the unrelated metastrongyle (lungworm) family Filaroididae (genus *Filaroides*) are known colloquially as 'filaroids']. Adult filariae have a cylindroid pharynx with an anterior muscular portion and a posterior glandular portion. Males often have spirally-coiled tails, well-developed alae and dissimilar spicules. Females of most species are ovoviviparous (eggs hatch within body of parent) releasing pre-larval stages known as microfilariae (sometimes sheathed). Filariae have indirect life-cycles whereby microfilariae are taken up by blood-sucking or tissue-feeding invertebrates (arthropods, esp. mosquitoes) which act as intermediate hosts for the development of infective L3 larvae. Ten families are recognised: Filariidae and Onchocercidae infecting mammals, birds, reptiles and amphibians; Setariidae infecting mammals;

Aproctidae infecting birds; and Creagrocercidae, Drilonematidae, Homungellidae, Mesidionematidae, Scolecophilidae and Ungellidae infecting terrestrial annelids. Examples of filarioid genera covered in this resource are compared in the following table.

Genus	Definitive hosts	Adults (location)	Microfilariae (location)	Periodicity	Vectors	*Wolbachia* symbiotes
Family Onchocercidae						
Dipetalonema, Acanthocheilonema (57 spp.)	primates, carnivores, ungulates, rodents, cingulates, marsupials	1-7 cm (subcutis, serosa)	85-300 µm unsheathed (blood)	-	flies, fleas, lice, ticks	absent
Dirofilaria (34 spp.)	primates, carnivores, ungulates, rodents, lagomorphs, marsupials	4-31 cm (blood vessels)	180-385 µm unsheathed (blood)	-	mosquitoes, flies	present
Onchocerca (35 spp.)	primates, carnivores, ungulates, rodents	1.5-80 cm (subcutis, ligaments)	105-440 µm unsheathed (skin)	-	flies, midges	present
Mansonella (29 spp.)	primates, carnivores, ungulates, rodents	3-8 cm (subcutis, serosa)	170-300 µm unsheathed (blood/skin)	-	midges, flies, mosquitoes	present
Wuchereria (2 spp.)	primates	2.5-10 cm (lymphatics)	210-320 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Brugia (10 spp.)	primates, carnivores, rodents	1-9 cm (lymphatics)	170-380 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Loa (3 spp.)	primates, ungulates, rodents	2-7 cm (subcutis, eye)	250-300 µm sheathed (blood)	diurnal	flies	absent
Family Filariidae						
Parafilaria (4 spp.)	ungulates	2-7 cm (subcutis)	40-58 x 23-33 µm larvated eggs (skin)	diurnal	flies	absent
Stephanofilaria (7 spp.)	ungulates	0.2-1.4 cm (subcutis)	45-195 µm sheathed (skin)	-	flies	absent
Family Setariidae						
Setaria (42 spp.)	primates, ungulates, rodents, lagomorphs	4-19 cm (body cavities)	140-310 µm sheathed (blood)	-	mosquitoes	absent

Members of the family Onchocercidae form adult worms that live loose in body cavities or in tissue nodules. Female worms release microfilariae which disperse into the blood or dermal connective tissues (unlike filariids which live in the skin close to where they deposit eggs or larvae). Some 88 onchocercid genera are divided into 7 subfamilies: Onchocercinae and Dirofilariinae (syn. Loainae) mostly in mammals but some in birds and reptiles, Waltonellinae and Icosiellinae in amphibians, Oswaldofilariinae in reptiles, Splendidofilariinae and Lemdaninae in birds, reptiles and mammals (former subfamily Setariinae in large mammals recently elevated to family status as Setariidae). Members of the subfamily Onchocercinae are characterised as forming males with markedly dissimilar spicules and long tails lacking caudal alae (while members of the subfamily Dirofilariinae form males with highly developed caudal alae). Some 43 genera occur in the subfamily Onchocercinae: namely, *Acanthocheilonema, Ackertia*, *Agamofilaria*, *Andersonfilaria*, *Bisbalia*, *Breinlia* (incl. *Johnstonema*), *Brugia*, *Cercopithifilaria*, *Chabfilaria*, *Cherylia*, *Courduriella*, *Cruorifilaria*, *Cystofilaria*, *Deraiophoronema*, *Dessetfilaria*, *Dipetalonema*, *Elaeophora* (syn. *Cordophilus*, *Alcefilaria*), *Filarissima*, *Fuscicorpa*, *Josefilaria*, *Litomosa*, *Litomosoides* (syn. *Vestibulosetariam Finlaynema*), *Mansonella*, *Microfilaria*, *Migonella*, *Molossinema*, *Monanema*, *Onchocerca* (syn. *Wehrdikmansia*, *Acanthospiculum*), *Paramadochotera*,

Paraochoterenella, *Paraprocta*, *Paulianfilaria*, *Pseudolitomosa*, *Rumenfilaria*, *Sandnema, Serofilaria*, *Skrjabinofilaria* (syn. *Cortiamosoides*), *Sprattia, Strianema*, *Wuchereria* and *Yatesia* in mammals, *Struthiofilaria* in birds, and *Macdonaldius* (syn. *Saurofilaria*) in reptiles.

Adult *Dipetalonema* worms are long and slender with a thick transparent cuticle and a slightly bulbous head bearing 4 pairs of papillae and conspicuous amphids and a tail with 3-4 conical petals. Gravid females release unsheathed microfilaria into the blood and/or skin where they are taken up by a variety of haematophagous arthropod intermediate hosts (mosquitoes, flies, fleas, lice and ticks) in which larval stages develop mostly in the fat body. Many *Dipetalonema* spp. have previously been described, but almost half have been reassigned to other genera (notably *Breinlia* and *Sprattia* in Australian marsupials; *Skrjabinofilaria* in American marsupials; *Ackertia, Filarissima* and *Monanema* in rodents; *Macdonaldius* in American reptiles) and the remainder placed in several *Dipetalonema* subgenera (*D.* (*Orihelia*) and *D*. (*Dasypafilaria*) in cingulates; *D.* (*Molinema*) in rodents; *D.* (*Loxodontofilaria*) in African ungulates; *D.* (*Chenofilaria*) in Asiatic pholidotids and Australian marsupials; *D.* (*Dipetalonema*) and *D.* (*Yatesia* syn. *Alafilaria*) in primates and rodents; and *D.* (*Acanthocheilonema*) in insectivores, carnivores, pinnipeds and some rodents). Various authorities have elevated many of these subgenera to generic status causing considerable taxonomic confusion; which hopefully will be unravelled in the future by careful molecular and ultrastructural studies. Notwithstanding, most authorities now recognize *Acanthocheilonema* (syn. *Skrjabinaria*, *Monnigofilaria*, *Hepaticofilaria*) as a separate genus from *Dipetalonema*. In particular, the species *Acanthocheilonema reconditum* commonly found in dogs is often still reported under its older name *Dipetalonema reconditum* in many veterinary texts. While this species rarely causes clinical infections, its microfilariae may sometimes be confused with those of canine heartworm (*Dirofilaria immitis*). Another species in rodents, *Acanthocheilonema viteae* (previously *Dipetalonema viteae*), has often been used as a model to study human filarial infections.

Parasite species	Definitive Hosts (DH)	Location	Intermediate Hosts/Vectors (IH)	Distribution
***Dipetalonema* (*Dipetalonema*)** **[**cephalic extremity laterally expanded, oesophagus divided, gubernaculum present, microfilaria sheathed, parasitic in American primates]				
D. D. caudispina (syn. *D.* (*Alafilaria*))	Primates: atelid (Geoffroy's spider monkey, Guiana spider monkey, southern muriqui, brown woolly monkey, Venezuelan red howler), cebid (white-fronted capuchin, black-capped squirrel monkey, common squirrel monkey), aotid (Spix's night monkey), callitrichid (golden lion tamarin)	abdominal and thoracic cavities	Diptera: ceratopogonid (*Culicoides hollensis*)	South America
D. D. freitasi	Primates: cebid (white-faced capuchin)			South America
D. D. gracile	Primates: atelid (Geoffroy's spider monkey, Guiana spider monkey, black-headed spider monkey, Peruvian spider monkey, brown woolly monkey, southern muriqui), callitrichid (common marmoset, moustached tamarin, pied tamarin, black mantled tamarin, black lion tamarin, golden lion tamarin), cebid (black-capped capuchin, Azarae's capuchin, white-faced capuchin, Humboldt's white-fronted capuchin, gracile capuchin, wedge-capped capuchin, common squirrel monkey, Central American squirrel monkey), aotid (gray-bellied night monkey)	abdominal cavity, microfilariae in blood	Diptera: culicid (*Aedes aegypti*), ceratopogonid (*Culicoides hollensis*)	Americas
D. D. graciliformis	Primates: callitrichid (red-handed tamarin, moustached tamarin)			South America
D. D. robini	Primates: cebid (common squirrel monkey, black-capped squirrel monkey)		Diptera: culicid (*Aedes aegypti*)	South America
D. D. yatesi	Primates: atelid (Peruvian spider monkey)			South America
***Dipetalonema* (*Orihelia*)** [cephalic shield laterally elongated, tail with 2 lappets, oesophagus divided, gubernaculum present, microfilaria sheathed, parasitic				

in cingulates]				
D. O. anticlava (syn. *Acanthocheilonema, A. tatusi*)	Cingulata: chlamyphorid (screaming hairy armadillo, six-banded armadillo, southern three-banded armadillo), dasypodid (southern long-nosed armadillo)	peritoneum		South America
***Dipetalonema* (*Molinema*)** [cephalic extremity flat or concave in lateral view, oesophagus divided, gubernaculum absent, microfilaria unsheathed, parasitic in rodents]				
D. M. arbuta	Rodentia: erethizontid (North American porcupine); Primates: hominid (human)	peritoneal cavity	Diptera: culicid (*Aedes aegypti, canadensis, cinereus, euedes, excrucians, fitchii, stimulans, vexans, Taeniorhynchus perturbans*)	North America
D. M. bifida	Rodentia: echimyid (Atlantic bamboo rat)	body cavity		South America
D. M. dessatae	Rodentia: echimyid (Guyenne spiny rat)	abdominal cavity	Diptera: culicid (*Anopheles stephensi*)	South America
D. M. diacantha (syn. *Filaria, Acanthocheilonema*)	Rodentia: erethizontid (Rothschild's porcupine, Brazilian porcupine, Paraguayan hairy dwarf porcupine), echimyid (red-crested tree-rat)	body cavity		South America
D. M. proechimyis	Rodentia: echimyid (Guyenne spiny rat)	body cavity		South America
D. M. raposoensis	Rodentia: echimyid (Tome's spiny rat)	body cavity		Central America
D. M. sprenti	Rodentia: castorid (North American beaver); Primates: hominid (human)	peritoneal, pleural and pericardial cavities	Diptera: culicid (*Aedes abserratus, intrudens*)	North America
D. M. travassosi	Rodentia: echimyid (coypu)	body cavity		South America
M. algardneri	Rodentia: echimyid (Napo spiny rat)	body cavity		South America
M. barbarae	Rodentia: echimyid (Guyenne spiny rat)	body cavity		South America
M. peruviensis	Rodentia: echimyid (Steere's spiny rat)	body cavity		South America
M. nattereri	Rodentia: echimyid (Brazilian spiny tree rat)	body cavity		South America
***Dipetalonema* (*Loxodontofilaria*)** [oesophagus undivided, gubernaculum absent, microfilariae unsheathed, parasitic in African ungulates]				
D. L. asiatica	Proboscidea: elephantid (Indian elephant)	unknown		Burma
D. L. caprini	Artiodactyla: bovid (Japanese serow)			Japan
D. L. faini	Artiodactyla: bovid (black-fronted duiker)	abdomen		Africa
D. L. gossi	Proboscidea: elephantid (African bush elephant)	portal veins		Africa
D. L. hippopotami	Artiodactyla: hippopotamid (hippopotamus)	abdominal cavity		Africa
D. L. loxodontis	Proboscidea: elephantid (African elephant)			Africa
D. L. okapiae sp. inq.	Artiodactyla: giraffid (okapi)			Africa
D. L. ruandae	Artiodactyla: bovid (cattle)	oesophageal connective tissue		Africa
***Dipetalonema* (*Chenofilaria*)** [body slightly expanded laterally behind cephalic extremity, oesophagus divided or undivided, gubernaculum absent, microfilaria unsheathed, parasitic in Asiatic pholidotids and Australian marsupials]				

D. C. filaria (syn. *D. fausti, Acanthocheilonema*)	Pholidota: manid (Chinese pangolin)	cystic pockets of intrahepatic portal system		China
D. C. johnstoni (syn. *Breinlia*, *D. lutreoli*) (now possibly *Cercopithifilaria*?)	Rodentia: murid (bush rat, Australian swamp rat, giant white-tailed rat); Peramelemorphia: peramelid (eastern barred bandicoot, long-nosed bandicoot, northern brown bandicoot, southern brown bandicoot); Diprotodontia: pseudocheirid (greater glider); Dasyuromorphia: dasyurid (Tasmanian devil)	subcutaneous and intermuscular connective tissues, mf in skin, lymphatics, occasionally in blood (unsheathed)	Ixodida: ixodid (*Ixodes trichosura, facialis, holocyclus, tasmani*)	Australia
D. C. japonica	Carnivora: ursid (Japanese black bear)	subcutaneous tissue		Japan
D. C. pearsoni (now possibly *Cercopithifilaria*?)	Peramelemorphia: peramelid (northern brown bandicoot)	subcutaneous connective tissue		Australia
***Dipetalonema* (*Dasypafilaria*)** [cephalic shield laterally elongated, tail with 2 lappets, oesophagus divided, gubernaculum absent, sheathed microfilariae, parasitic in armadillo]				
D. D. averyi	Cingulata: dasypodid (nine-banded armadillo)	omentum		North America
***Dipetalonema* (*Yatesia* = *Alafilaria*)** [cephalic shield rectangular, divided oesophagus, gubernaculum absent, microfilaria unsheathed, parasitic in capybara]				
D. Y. hydrochoerus	Rodentia: caviid (capybara)	skeletal muscle fascia	Ixodida: ixodid (*Amblyomma americanum, cajennense*)	South America
Acanthocheilonema, sometimes reported as ***Dipetalonema* (*Acanthocheilonema*)** [cephalic extremity flat or convex in lateral view, oesophagus divided, gubernaculum absent, microfilaria unsheathed, parasitic in insectivores, carnivores, pinnipeds and some rodents]				
A. didelphis (syn. *Dipetalonema, Cercopithifilaria*)	Didelphimorphia: didelphid (common opossum, Virginia opossum)	subcutaneous and perioesophageal tissues		Americas
A. delicata	Carnivora: mustelid (Japanese badger)	subcutaneous tissues		Japan
A. dracunculoides (syn. *Dipetalonema*)	Carnivora: canid (dog, red fox), hyaenid (spotted hyaena, aardwolf)	peritoneal cavity, microfilariae in blood (unsheathed)	Diptera: hippoboscid (*Hippobosca longipennis*); Ixodida: ixodid (*Rhipicephalus sanguineus*)	Eurasia, Africa
A. finlayi (syn. *Dipetalonema, Ackertia*)	Rodentia: chinchillid (northern viscacha)	peritoneal cavity		South America
A. mansonbahri (syn. *Dipetalonema*)	Rodentia: petetid (East African springhare)	subcutaneous tissue and fascia	Siphonaptera: pulicid (*Delopsylla crassipes, Ctenocephalides felis, Xenopsylla cheopis*)	Africa
A. mephitis (syn. *Dipetalonema*)	Carnivora: mephitid (striped skunk)			North America
A. odendhali (syn. *Dipetalonema*)	Carnivora: phocid (harbour seal), otariid (California sea lion, northern fur seal)	intermuscular fascia		North America
A. pachycephalum (syn. *Dipetalonema*)	Carnivora: mustelid (African striped weasel)			Africa
A. pricei (syn. *Dipetalonema, Skrjabinofilaria*)	Didelphimorphia: didelphid (big-eared opossum, Virginia opossum)	subcutaneous tissues		Americas
A. procyonis	Carnivora: procyonid (raccoon)	subcutaneous tissues		North America
A. reconditum (syn. *Dipetalonema*)	Carnivora: canid (dog, red fox, jackal), hyaenid (hyaena); Artiodactyla: bovid (blackbuck)	subcutaneous connective tissue, body cavity,	Siphonaptera: pulicid (*Ctenocephalides canis*, *felis, Pulex irritans,*	Africa, Europe, Americas

		microfilariae in blood subcutaneous tissues, body cavity, kidneys	*simulans, Echidnophaga gallinacea*); Phthiraptera: boopid (*Heterodoxus spiniger*), haematopinid (*Haematopinus*), lonognathid (*Linognathus setosus*); Ixodida: ixodid (*Rhipicephalus sanguineus*); Diptera: culicid (*Culex*)	
A. sabanicolae	Cingulata: dasypodid (Llanos long-nosed armadillo)	subcutaneous tissue		South America
A. setariosa (syn. *Dipetalonema setariosum*)	Rodentia: murid (Libyan jird); Carnivora: herpestid (mongoose)	pleural cavity		North and East Africa
A. spirocauda (seal heartworm) (syn. *Dipetalonema*)	Carnivora: phocid (hooded seal, harp seal, bearded seal, ringed seal, common seal, ribbon seal, spotted seal, harbour seal), odobenid (walrus)	heart (right ventricle), pulmonary arteries	Phthiraptera: echinophthiriid (*Echinophthirius horridus*)	Northern Hemisphere
A. viteae (syn. *Dipetalonema*)	Rodentia: murid (wood mouse, brown spiny mouse, southern multimammate mouse, Natal multimammate mouse, striped field mouse, Libyan jird, Shaw's jird, Mongolian gerbil, soft-furred rat), cricetid (golden hamster, Campbell's dwarf hamster), dipodid (greater Egyptian jerboa)	subcutaneous tissues, fascia, body cavities	Ixodida: argasid (*Ornithodoros moubata, O. tartakovskyi*)	Asia, Africa
A. weissi (syn. *Dipetalonema*)	Macroscelidea: macroscelid (North African elephant-shrew)	peritoneum, subcutaneous tissues	Ixodida: argasid (*Ornithodoros erraticus*)	North Africa
Other reports				
D. boltoni (now *Breinlia*)	Diprotodontia: macropodid (agile wallaby)	peritoneal cavity		Australia
D. capilliforme (syn. *Breinlia*) (now *Sprattia*)	Dasyuromorphia: dasyurid (northern quoll)	hepatic venous spaces, mesenteric and portal veins		Australia
D. cephalophi (now *Cercopithifilaria*)	Artiodactyla: bovid (bay duiker)	subcutaneous tissue		Africa
D. dasyuri (now *Breinlia*)	Dasyuromorphia: dasyurid (eastern quoll, tiger quoll)	peritoneal cavity		Australia
D. degraaffi (now *Cercopithifilaria*)	Primates: cercopithecid (Chacma baboon)	subcutaneous tissue		Africa
D. dendrolagi (syn. *Breinlia*)	Diprotodontia: macropodid (grizzled tree-kangaroo)	peritoneal cavity		New Guinea
D. dentonensis (now *Breinlia*)	Diprotodontia: macropodid (eastern grey kangaroo, red kangaroo)	subcutaneous connective tissue		Australia
D. dermicola	Artiodactyla: bovid (cattle)	skin		Africa
D. evansi (syn. *D. cameli*) (now *Deraiophoronema*)	Artiodactyla: camelid (camel, dromedary); Perissodactyla: equid (horse)	pulmonary and testicular arteries, lymph spaces and nodes, microfilariae in blood (sheathed)	Diptera: culicid (*Aedes caspius*)	North Africa, Eastern Russia, Asia, Australia
D. freitaslenti (syn. *Bostrichodera, Deraiophoronema*)	Pilosa: myrmecophagid (giant anteater)	mesentery		South America
D. gabonensis (now *Cercopithifilaria*)	Rodentia: hystricid (African brush-tailed porcupine)	subcutaneous tissue		Africa

D. grassi sp. inq. (syn. *Acanthocheilonema*) (now *Cercopithifilaria*)	Carnivora: canid (dog)	subcutaneous tissues	Ixodida: ixodid (*Rhipicephalus sanguineus*)	Southern Europe, Africa
D. herpestis	Carnivora: herpestid (mongoose)	peritoneal cavity		India
D. interstitium	Rodentia: sciurid (Sherman's fox squirrel, eastern gray squirrel)	subcutaneous tissue		North America
D. kenyensis (now *Cercopithifilaria*)	Primates: cercopithecid (olive baboon)	subcutaneous tissue		Africa
D. laemmleri	Rodentia: sciurid (Hodgson's giant flying squirrel)			India
D. macropi (now *Breinlia*)	Diprotodontia: macropodid (quokka)	peritoneal cavity		Australia
D. marmosetae (now *Mansonella* (*Tetrapetalonema*))	Primates: callitrichid (white-footed tamarin)			South America
D. mundayi (now *Breinlia*)	Diprotodontia: macropodid (red-necked wallaby)	pericardium		Australia
D. petteri sp. inq.	Primates: lemurid (black lemur)			Madagascar
D. pseudocheiri (now *Breinlia*)	Diprotodontia: pseudocheirid (common ringtail possum)	peritoneal cavity		Australia
D. rarum	Diprotodontia: macropodid (bridled nail-tail wallaby)	subcutaneous tissues		Australia
D. robertsi (syn. *D. australiense, D. tenue, Breinlia tenuis*)	Diprotodontia: macropodid (common wallaroo, eastern grey kangaroo, red kangaroo)	peritoneal cavity		Australia
D. rugosicauda (syn. *D.* (*Orihelia*), *Wehrdikmansia*) (now *Cercopithifilaria*)	Artiodactyla: cervid (roe deer)	microfilariae in subcutis (sheathed)	Ixodida: ixodid (*Ixodes ricinus*)	Europe, America
D. schneideri (now *Elaeophora*)	Artiodactyla: cervid (mule deer, black-tailed deer, elk/wapiti, moose, sika deer), bovid (sheep, goat)	arteries, cornea (migrating larvae may cause neurological signs), microfilariae in skin and capillary beds	Diptera: tabanid (*Hybomitra aatos, laticornis, osburni, phaenops, procyon, rupestris, tetrica, Tabanus abditus, eurycerus, gilanus, lineola, monsensis, nigrovittatus, punctifer, subsimilis, stoni, Silvius quadrivittatus*)	North America
D. spelaea (syn. *D. australe, Filaria, F. australis, Setaria, Acanthocheilonema*) (now *Breinlia*)	Diprotodontia: macropodid (brush-tailed rock-wallaby, Bennett's tree-kangaroo?)	peritoneal cavity		Australia
D. spiralis (syn. *D. spirale, Deraiophoronema*) (now *Bostrichodera*)	Pilosa: choloepodid (Linnaeus's two-toed sloth)			South America
D. thylogali (syn. *Breinlia*)	Diprotodontia: macropodid (red-legged pademelon, Tasmanian pademelon)	peritoneal and pleural cavities		Australia
D. trichosuri (syn. *Filaria, Acanthocheilonema australe*)	Diprotodontia: phalangerid (common brushtail possum)	peritoneal cavity		Australia

(now *Breinlia*)				
D. venacavincola (now *Sprattia*)	Diprotodontia: phalangerid (short-eared possum)	vena cava and hepatic veins, microfilariae in blood (sheathed)		Australia
Species assigned to *Johnstonema* (now considered to be a subgenus in the genus *Breinlia*)				
J. andersoni (now *Breinlia*)	Diprotodontia: macropodid (red kangaroo, eastern grey kangaroo, common wallaroo, swamp wallaby)	subcutaneous connective tissue		Australia
J. annulipapillatum (syn. *Dipetalonema*) (now *Breinlia*)	Diprotodontia: macropodid (black-striped wallaby, bridled nail-tail wallaby, swamp wallaby)	subcutaneous tissue, knee joint, body cavity?		Australia
J. woerlei (now *Breinlia*)	Diprotodontia: macropodid (short-eared rock-wallaby)	heart		Australia

Parasite morphology: These filarial worms produce 3 different morphological stages in their developmental cycles: adult worms; pre-larvae (microfilariae); and 4 consecutive larval stages (termed L1-4). Female worms produce and release unsheathed microfilariae which make their way into the vertebrate host circulation. The microfilariae are elongate and range considerably in size (85-300 x 4-6 µm) depending on species: most being moderate ranging from 250-300 µm in length (e.g. *Acanthocheilonema reconditum, A. mansonbahri, A. spirocauda, Dipetalonema dracunculoides, D. schneideri*); several being smaller ranging from 170-205 µm (e.g. *A. viteae*); and a few being comparatively tiny ranging from 85-130 µm (e.g. *D. gracile*). Microfilariae have a blunt-to-conical conical anterior end, most bearing a cephalic hook, and they often have attenuated pointed tails (e.g. *A. mansonbahri*), sometimes blunt (e.g. *D. schneideri*), often hooked (e.g. *A. reconditum*), sometimes straight (e.g. *D. dracunculoides*). [In comparison, *Dirofilaria* microfilariae are slightly larger (260-330 µm) and have straight, pointed filamentous tails.] *Dipetalonema* and *Acanthocheilonema* spp. form 3 larval stages in their arthropod vectors: first-stage larvae (L1) measuring 350-400 µm in length; second-stage-larvae (L2) 400-700 µm; and third-stage larvae (L3) growing up to 5.9 mm in length and distinguished by tails with a terminal cone-shaped structure flanked by 2 small dorsoventral projections. Adult worms are slender and elongate measuring up to 40 mm in length and are surrounded by a thick white-to-transparent cuticle, sometimes with striations. Adults have a slightly bulbous head bearing 4 pairs of papillae and conspicuous amphids, a small buccal capsule (buccal ring), an oesophagus with a well-developed glandular portion, and tails with 10 pairs of caudal papillae and 3 caudal lappets. Mature worms are sexually dimorphic, with female worms being larger than males (e.g. *A. reconditum* females 20-36 mm x 70-205 µm, males 9-17 mm x 70-133 µm; *A. dracunculoides* females 30-60 mm x 100-370 µm, males 13-31 mm x 100-310 µm; *A. sabanicolae* females 25-31 mm x 61-78 µm, males 11-15 mm x 42-44 µm; *A. vitae* females 49-72 mm x 230-350 µm, male 38-41 mm x 150-170 µm). Males have a long spiral tail with caudal alae and less than 5 large pedunculate precloacal papillae (cf. *Dirofilaria* which have short tails with 5 or more large pedunculate precloacal papillae). Mature males have 2 unequal dissimilar copulatory spicules: in *Acanthocheilonema* the right spicule is stout and curved and the left spicule has a slender and pointed distal third, while in *Dipetalonema* the right spicule is long and slender and the long left spicule has a slender distal half. Female worms have 2 ovaries with oviducts and uteri terminating in a common vagina opening into a vulva (located anteriorly around the oesophageal level but posterior to the nerve ring). Gravid females are ovoviviparous and release live young (microfilaria).

Site of infection: Adult worms live in the subcutaneous tissues or body cavities of their mammalian (definitive) hosts and their unsheathed microfilariae are found in peripheral blood. Larval developmental stages occur mainly in the fat body and sometimes the muscles of their arthropod (intermediate) hosts).

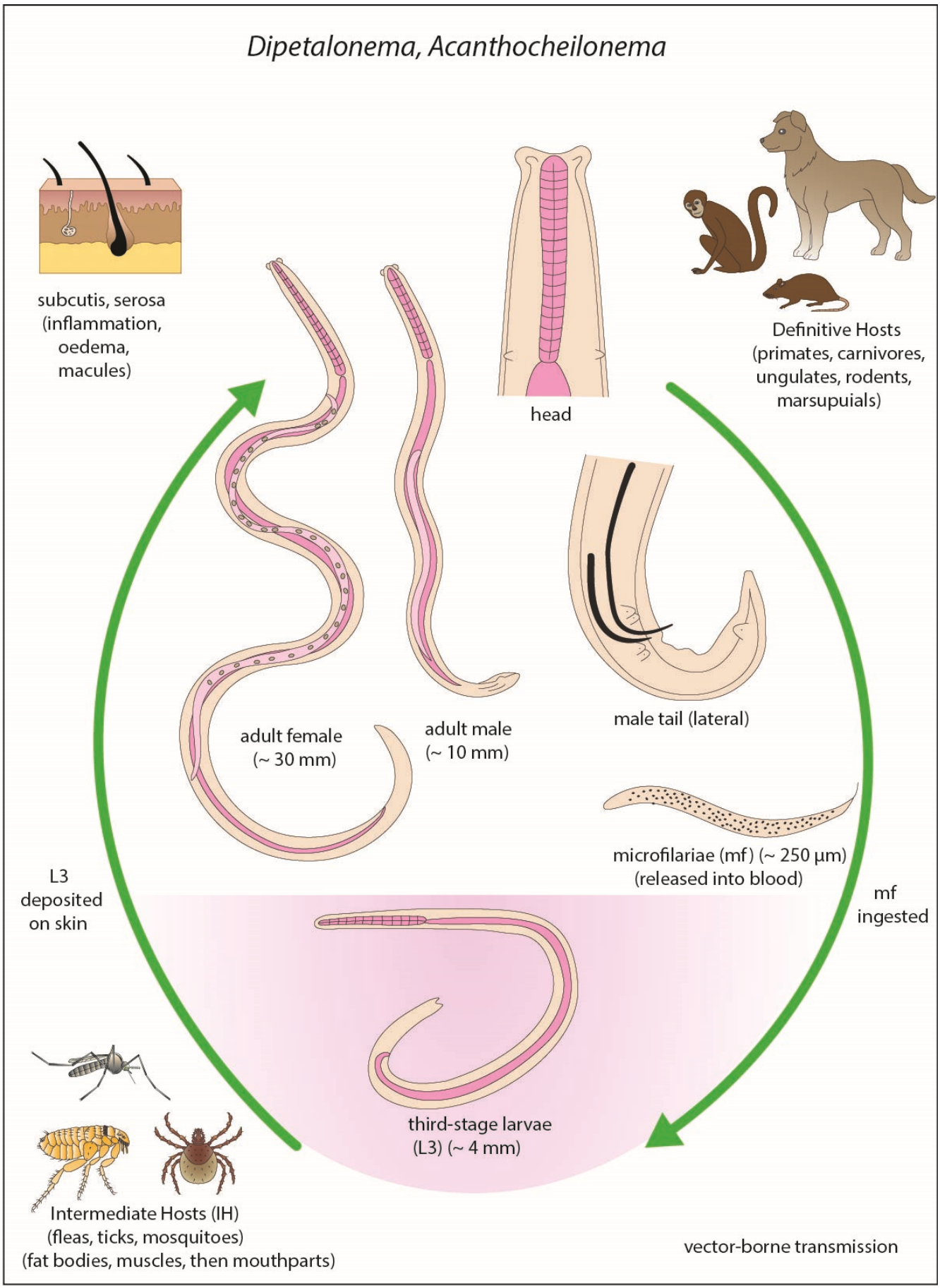
Pathogenesis: Infections are generally asymptomatic and rarely cause clinical disease. However, heavy infections by adult *A. reconditum* have been associated with subcutaneous nodule formation, pruritus, alopecia and dermal abrasions in dogs, adult *D. evansi* with arteriosclerosis, cardiac insufficiency and emaciation in camels, adult *D. johnstoni* with skin and ocular lesions in Australian marsupials, and migrating larvae of *D. schneideri* may cause neurological signs, allergic responses, vascular lesions, dermatitis, ischaemia necrosis and blindness in deer. It is often difficult to determine the pathogenicity of *Dipetalonema* and *Acanthocheilonema* infections as concurrent infections with other parasites generally occur. To date, no endosymbiotic *Wolbachia* bacteria have been found in these filarial worms, but molecular studies have detected *Wolbachia*-like sequences in their genomes suggesting prior acquisition and subsequent loss.

Developmental cycle and mode of transmission: *Dipetalonema* and *Acanthocheilonema* spp. have indirect heteroxenous life-cycles involving the development of adult worms in mammalian definitive hosts and larval stages in arthropod intermediate hosts. Transmission occurs when the arthropods feed on mammalian blood: vectors becoming infected when they ingest microfilariae with their blood meals; and mammals becoming infected when infective larvae are introduced during vector feeding. Unlike other filarial worms, a broad range of haematophagous vectors may act as intermediate hosts, including insects (flies, mosquitoes, fleas, lice) and acari (ticks). Ingested microfilariae penetrate the gut and invade the fat body, sometimes the muscles, where they moult twice over

7-10 days to form third-stage larvae (L3) which are found in the haemocoel 15-20 days after infection. Larval development took longer in ticks and in vectors held at lower ambient temperatures (e.g. 54-67 days at 20°C). Mammals become infected when the relatively large L3 escape from the vector mouthparts during feeding and invade the bite site (contaminative transmission rather than inoculative salivary transmission). The larvae moult twice and form adults in the subcutaneous tissues and/or body cavities where they mature and mate. The prepatent period (time from infection to first detection of microfilariae) ranges from 45-126 days depending on species. Adult worms of *A. viteae* were found to live for up to 2 years, but it was noted that frequent matings were required to maintain continuous fertility.

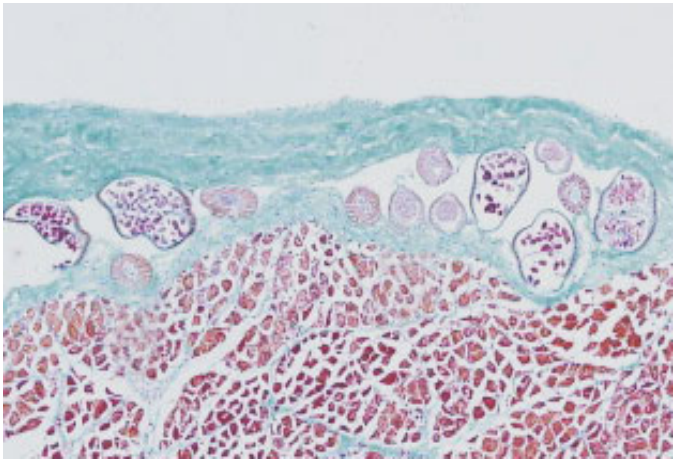
Differential diagnosis: Most infections are diagnosed serendipitously when unsheathed microfilariae are detected microscopically in blood samples, either in wet preparations coloured with methylene blue or cresyl blue, fixed thick or thin blood smears stained with Giemsa or haematoxylin, or in concentrates obtained by membrane filtration (5 µm pore size) or centrifugation (following saponin or formalin erythrolysis). The microfilariae are distinguished from those of other filarial worms by their moderate size, curved bodies with blunt heads and often hooked tails and by their progressive movement in wet preparations (in contrast, *Dirofilaria immitis* microfilariae have larger straight bodies with tapered heads and pointed tails and they exhibit nonprogressive (stationary) movement in wet preparations). Nonetheless, microscopic differentiation of microfilariae can sometimes be difficult due to morphological variation, especially in mixed infections. Occasionally, adult worms, or fragments thereof, may be detected in biopsies of skin nodules or incidentally during surgery or necropsy. No immunoserological tests have been developed to specifically detect *Dipetalonema/Acanthocheilonema* infections, even though little cross-reactivity was observed in tests for *Dirofilaria immitis* in dogs. More recently, molecular biological techniques have been used to detect parasite DNA in clinical samples following the polymerase chain reaction (PCR) amplification of specific gene sequences, notably internal transcribed spacer (ITS) regions of ribosomal RNA.

Treatment and control: A range of anthelmintic drugs have been used to treat the small number of symptomatic infections detected in mammalian hosts, mostly carnivores with cutaneous manifestations due to adult worms or herbivores with neurological complications due to migrating larvae. Treatment with diethylenediamine (diethylcarbamazine), macrocyclic lactones (ivermectin, doramectin, selamectin, moxidectin) and benzimidazole-methylcarbamates (mebendazole) have been found to be effective against microfilariae. While it is not known whether such treatment killed adult worms, in many cases they were effectively sterilized and no longer produced microfilariae. The prevention of infections centres around vector control, with various insecticides and acaricides used to reduce vector populations, improved sanitation and environmental hygiene used to eliminate breeding sites, and physical and chemical barriers used to protect hosts from vector bites.


Dipetalonema, Acanthocheilonema
subcutis, serosa
(inflammation,
oedema,
macules)
head
Definitive Hosts
(primates, carnivores,
ungulates, rodents,
marsupuials)
adult female
(~ 30 mm)
adult male
(~ 10 mm)
male tail (lateral)
microfilariae (mf) (~ 250 µm)
(released into blood)
L3
deposited
on skin
mf
ingested
third-stage larvae
(L3) (~ 4 mm)
Intermediate Hosts (IH)
(fleas, ticks, mosquitoes)
(fat bodies, muscles, then mouthparts)
vector-borne transmission



Dipetalonema adult worms



Dipetalonema in section through skin



Dipetalonema microfilaria

Dirofilaria
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including filarioids (without lips) living in subcutaneous, intermuscular, vascular or lymphatic systems of mammals. Two main families include the oviparous filariids (lay eggs) and the ovoviviparous onchocercids (eggs hatch internally releasing pre-larvae called microfilariae). Infections by the onchocercid genus *Dirofilaria* are transmitted by mosquitoes (in which L3 develop). One species (*D. immitis*) causes canine heartworm disease involving circulatory obstruction progressing to congestive heart failure, while another (*D. repens*) causes cutaneous disease with nodules formed in the skin and muscles of carnivores.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Filarioidea (tissue-dwelling filarial parasites, lack lips)
Family:	Onchocercidae (adults loose in tissues or in nodules, viviparous (live birth of microfilariae))
Genus:	*Dirofilaria* (parasitic in heart of dogs/cats/humans)
Species:	*D. immitis* (cause heartworm disease in dogs)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine species but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Filarioidea contains long thread-like nematodes which are predominantly tissue-dwelling parasites infecting the body cavities, subcutis, intermuscular tissues, blood vessels or lymphatic systems of terrestrial hosts. These worms are known colloquially as ‘filariae’, ‘filarids’ or ‘filarioids’ [Note: take care with terminology as the cognate family Filariidae (esp. genus *Filaria*) are known colloquially as ‘filariids’, and the unrelated metastrongyle (lungworm) family Filaroididae (genus *Filaroides*) are known colloquially as ‘filaroids’]. Adult filariae have a cylindroid pharynx with an anterior muscular portion and a posterior glandular portion. Males often have spirally-coiled tails, well-developed alae and dissimilar spicules. Females of most species are ovoviviparous (eggs hatch within body of parent) releasing pre-larval stages known as microfilariae (sometimes sheathed). Filariae have indirect life-cycles whereby microfilariae are taken up by blood-sucking or tissue-feeding invertebrates (arthropods, esp. mosquitoes) which act as intermediate hosts for the development of infective L3 larvae. Ten families are recognised: Filariidae and Onchocercidae infecting mammals, birds and amphibians; Setariidae infecting mammals; Aproctidae

infecting birds; and Creagrocercidae, Drilonematidae, Homungellidae, Mesidionematidae, Scolecophilidae and Ungellidae infecting terrestrial annelids. Examples of filarioid genera covered in this resource are compared in the following table.

Genus	Definitive hosts	Adults (location)	Microfilariae (location)	Periodicity	Vectors	*Wolbachia* symbiotes
Family Onchocercidae						
Dirofilaria (34 spp.)	primates, carnivores, ungulates, rodents, lagomorphs, marsupials	4-31 cm (blood vessels)	180-385 µm unsheathed (blood)	-	mosquitoes, flies	present
Dipetalonema, Acanthocheilonema (57 spp.)	primates, carnivores, ungulates, rodents, cingulates, marsupials	1-7 cm (subcutis, serosa)	85-300 µm unsheathed (blood)	-	flies, fleas, lice, ticks	absent
Onchocerca (35 spp.)	primates, carnivores, ungulates, rodents	1.5-80 cm (subcutis, ligaments)	105-440 µm unsheathed (skin)	-	flies, midges	present
Mansonella (29 spp.)	primates, carnivores, ungulates, rodents	3-8 cm (subcutis, serosa)	170-300 µm unsheathed (blood/skin)	-	midges, flies, mosquitoes	present
Wuchereria (2 spp.)	primates	2.5-10 cm (lymphatics)	210-320 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Brugia (10 spp.)	primates, carnivores, rodents	1-9 cm (lymphatics)	170-380 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Loa (3 spp.)	primates, ungulates, rodents	2-7 cm (subcutis, eye)	250-300 µm sheathed (blood)	diurnal	flies	absent
Family Filariidae						
Parafilaria (4 spp.)	ungulates	2-7 cm (subcutis)	40-58 x 23-33 µm larvated eggs (skin)	diurnal	flies	absent
Stephanofilaria (7 spp.)	ungulates	0.2-1.4 cm (subcutis)	45-195 µm sheathed (skin)	-	flies	absent
Family Setariidae						
Setaria (42 spp.)	primates, ungulates, rodents, lagomorphs	4-19 cm (body cavities)	140-310 µm sheathed (blood)	-	mosquitoes	absent

Members of the family Onchocercidae form adult worms that live loose in body cavities or in tissue nodules. Female worms release microfilariae which disperse into the blood or dermal connective tissues (unlike filariids which live in the skin close to where they deposit eggs or larvae). Some 88 onchocercid genera are divided into 7 subfamilies: Onchocercinae and Dirofilariinae (syn. Loainae) mostly in mammals but some in birds and reptiles, Waltonellinae and Icosiellinae in amphibians, Oswaldofilariinae in reptiles, Splendidofilariinae and Lemdaninae in birds, reptiles and mammals (former subfamily Setariinae in large mammals recently elevated to family status as Setariidae). Members of the subfamily Dirofilariinae are characterised as forming males with highly developed caudal alae (while members of the subfamily Onchocercinae form males with markedly dissimilar spicules and long tails lacking caudal alae). Some 16 genera are recognised in the subfamily Dirofilariinae: namely, *Bostrichodera*, *Dirofilaria*, *Dirofilariaeformia*, *Edesonfilaria*, *Eulimdana*, *Foleyellides*, *Heimnema*, *Loa* (syn. *Paraloa*), *Loaina, Macacanema*, *Madochotera*, *Ochoterenella*, *Skrjabinodera* and *Tawila* in mammals, *Pelecitus* (syn. *Spirofilaria*, *Eulimdana*) in birds, and *Foleyella* (syn. *Foleyellides*) in saurians.

The genus *Dirofilaria* is characterised by the formation of long tubular adult worms in the circulatory system or connective tissues of mammalian hosts. Mature female worms produce unsheathed microfilariae which undergo further larval development primarily in mosquito vectors. Some 34 *Dirofilaria* spp. have been described predominantly from carnivores and primates and allocated to 2 subgenera: *D.* (*Dirofilaria*) comprising long thin worms with smooth cuticles that infect the lungs, heart and blood-vessels; and *D.* (*Nochtiella*) being represented by shorter stout worms with cuticular ornamentations (longitudinal ridges with transverse striations) that infect subcutaneous and conjunctival tissues. Various *Dirofilaria* spp. are zoonotic and may infect humans, usually as accidental hosts, causing either subcutaneous or ocular dirofilariasis. The most common species infecting humans are *D. repens* mainly in Eurasia and *D. immitis* (syn. *D. lousianensis*, *D. magalhaesi*, *D. ochmanni*?) in the Americas. Other species occasionally infecting humans are *D. honkongensis* and *D. magnilarvatum* in Asia, and *D. tenuis*, *D. ursi*, *D. striata* and *D. spectans* in North America. The species *D. immitis* is quite notorious as the cause of canine heartworm disease and is transmitted by more than 70 different mosquito species. *D. immitis* has a world-wide distribution but it is found mainly in tropical and subtropical regions (roughly bounded by latitudes 43-48°N and 34°S). The geographical distribution of heartworm has expanded in recent years presumably due to greater translocations of infected dogs, anthropogenic changes favouring vector survival (e.g. irrigation, deforestation, global warming, increased urbanization), and paradoxically, adaptation of parasites to develop at lower temperatures.

***Dirofilaria* species**	**Definitive Hosts (DH)**	**Location**	**Vectors/Intermediate Hosts (IH)**	**Distribution**
Subgenus *Dirofilaria*				
D. ailure	Carnivora: ailurid (red panda)	heart		Asia
D. fausti (possible syn. of *D. immitis*)	Carnivora: otariid (California sea lion)	heart		North America
D. freitasi	Primates: bradypodid (pale-throated sloth)	abdominal cavity		South America
D. immitis (canine heartworm)	Carnivora: canid (dog, dingo, African wild dog, raccoon dog, golden jackal, wolf, Great Plains wolf, Northwestern wolf, red wolf, Florida black wolf, maned wolf, Gregory's wolf, Japanese wolf, coyote, dhole, crab-eating fox, gray fox, island fox, Bengal fox, red fox, American red fox, Iberian fox), felid (cat, bobcat, black-footed cat, Asian golden cat, tiger, lion, jaguar, jaguarundi, black panther, leopard, clouded leopard, snow leopard, ocelot), ursid (brown bear, Asian black bear, Florida black bear, polar bear), mustelid (wolverine, otter, giant otter, North American river otter, Eurasian otter, Japanese weasel, European polecat, ferret, American mink), ailurid (red panda), procyonid (white-nosed coati, raccoon), phocid (hooded seal, ringed seal, harbour seal), otariid (California sea lion, Stellar sea lion); Rodentia: cricetid (musk rat), castorid (American beaver); Lagomorpha: leporid (European rabbit, Japanese hare); Artiodactyla: cervid (sika deer); Perissodactyla: equid (horse); Primates: hylobatid (Lar gibbon), cercopithecid (rhesus macaque), hominid (human, orangutan); Sphenisciformes: spheniscid (Humboldt penguin)	heart (right ventricle, right atrium), lungs (pulmonary artery), vena cava, subcutaneous, intraocular tissues, abdominal cavity, microfilariae in blood (unsheathed, nonperiodic), exercise intolerance, chronic congestive heart failure, pulmonary emboli	Diptera: culicid (*Aedes aegypti, albopictus, canadensis, cantator, caspius, cinereus, detritus, echinus, edgari, excricians, fijiensis, gaumensis, geniculatus, infirmatus, koreicus, longitubus, melanimon, pandani, polynesiensis, pseudoscutellaris, punctor, rotumae, samoanus, scapularis, sierrensis, solicitans, stictius, stimulans, taeniorhynchus, togoi, triseriatus, trivittatus, vexans, Anopheles algeriensis, bradleyi, campestris, crucians, earlei, freeborni, hyracanus, lesteri, maculipennis, plumbeus, punctipennis, nigerrimus, quadrimaculatus, superpictus, walkeri, Armigeres malayi, Coquilletidia* (*Culex*) *richiardi, Culex annulirostris, declarator, erythrothorax, fatigans, modestus, nigripalpus, pipiens, quinquefasciatus, restuans, salinarius, saltanensis, sitiens, tarsalis, territans, theileri, torrentum, tritaeniorhynchus, Culiseta incidens, inornata,*	Americas, Europe, Indo-China, Asia, Australia

			Mansonia annulata, bonneae, dives, indiana, titillans, uniformis, Psorophora columbiae, ferox, Wyeomyia bourrouli); reports of development in Phthiraptera: pulicid (*Ctenocephalides felis*) now attributed to *Acanthocheilonema reconditum*)	
D. indica (possible syn. of *D. immitis*)	Carnivora: canid (dog)	heart		India
D. louisianensis (possible syn. of *D. immitis*)	Primates: hominid (human)	heart		North America
D. lutrae	Carnivora: mustelid (North American river otter)	subcutaneous tissue, heart		North America
D. magalhaesi (possible syn. of *D. immitis*)	Primates: hominid (human)	heart		South America
D. nasuae (possible syn. of *D. immitis*)	Carnivora: procyonid (coati)	heart		South America
D. pongoi (possible syn. of *D. immitis*)	Primates: hylobatid (northern grey gibbon), hominid (orangutan)	heart		Asia
D. spectans	Carnivora: mustelid (tayra, giant otter, neotropical otter); Primates: hominid (human)	heart, pulmonary artery		Americas
D. spirocauda (syn. *Skrjabinaria*) (possible syn. of *D. immitis*)	Carnivora: phocid (hooded seal, harbour seal)	heart		
Subgenus *Nochtiella*				
D. acutiuscula (possible syn. of *D. repens p.p.*)	Carnivora: canid (Azara's fox), felid (Canada lynx); Rodentia: caviid (capybara); Artiodactyla: tayassuid (white-lipped peccary, collared peccary)	stomach wall, subcutaneous tissue, heart		South and North America
D. bonnei	Rodentia: murid (black rat)	body cavity		Asia, South America
D. cancrivori	Carnivora: procyonid (crab-eating raccoon)	subcutaneous tissue		South America
D. corynodes (syn. *D. aethiops*, *D. schoutedeni*)	Primates: cercopithecid (white-eyelid mangabey, sooty mangabey, mona monkey, Campbell's mona monkey, moustached monkey, grivet, greater spot-nosed monkey, patas monkey, black-and-white colobus, western red colobus, king colobus, rhesus macaque, steel-grey monkey)	subcutaneous and intermuscular connective tissues, mf in blood (nocturnal periodicity)	Diptera: culicid (*Aedes aegypti, pembaensis, Anopheles maculipennis*)	Africa, Asia
D. genettae (syn. *D. andersoni*)	Carnivora: felid (cat), viverrid (Cape genet), herpestid (banded mongoose)	connective tissue		Africa
D. hongkongensis	Carnivora: canid (dog); Primates: hominid (human)	subcutaneous and subconjunctival tissues		Hong Kong
D. incrassata (possible syn. of *D.*	Pilosa: brachypodid (brown-throated sloth, pale-throated sloth),	pleura, peritoneum		South and Central

macrodemos p.p.)	choloepodid (Hoffman's two-toed sloth); Carnivora: procyonid (white-nosed coati, South American coati			America
D. linstowi	Primates: cercopithecid (Toque macaque, gray langur, purple-faced leaf monkey)	subcutaneous tissues		Sri Lanka
D. macacae	Primates: cercopithecid (Assam macaque, northern pig-tailed macaque, stump-tailed monkey, iris monkey)	subcutaneous tissues		Indochina
D. macrodemos	Pilosa: brachypodid (brown-throated three-toed sloth, pale-throated sloth)	subserosa		South America
D. magnilarvatum	Primates: hylobatid (silvery gibbon), cercopithecid (iris monkey, rhesus macaque, silvered leaf monkey, dusky leaf monkey, Sumatran surili), hominid (human)	subcutaneous tissues, large microfilariae in blood (nonperiodic)	Diptera: culicid (*Mansonia longipalpis*, *uniformis*)	Asia
D. minor	Carnivora: felid (leopard cat)	subcutaneous tissues		Asia
D. pagumae	Carnivora: viverrid (masked palm civet)	subcutaneous tissues		Indochina
D. panamensis	Pilosa: choloepodid (Hoffman's two-toed sloth)	subserosa		South America
D. repens (syn. *D. conjunctivae, Loa extraocularis*)	Carnivora: canid (dog, wolf, golden jackal, red fox, crab-eating fox, Bengal fox, Azara's fox), felid (cat, wildcat, Asian golden cat, fishing cat, Canada lynx, lion), viverrid (Cape genet), procyonid (South American coati), mustelid (giant otter); Primates: hominid (human)	subcutaneous, subconjunctival and intermuscular tissues, cutaneous dirofilariosis (skin nodules, pruritus)	Diptera: culicid (*Aedes aegypti, albopictus, caspius, detritus, fasciata, geniculatus, mariae, pembaensis, vexans, Anopheles atroparvus, claviger, daciae, maculipennis, petragnanii, sinensis, stephensi, Armigeres obturbans, Culex pipiens, Mansonia africanus, annulifera, uniformis*); tabanid (*Haematopota variegata*); Phthiraptera: pulicid (*Ctenocephalides canis*)	Eurasia, Africa, North America
D. sachsi	Artiodactyla: bovid (hartebeest, blue wildebeest)	subcutaneous and intermuscular connective tissue		Africa
D. striata	Carnivora: felid (Florida panther, long-tailed tiger cat, ocelot, bobcat, margay, cougar, tiger), canid (dog); Artiodactyla: tayassuid (white-lipped peccary); Primates: hominid (human)	subcutaneous and intermuscular connective tissues; microfilariae in blood	Diptera: culicid (*Anopheles quadrimaculatus*)	Americas
D. subdermata (syn. *D. hystrix*, *D. spinosa*, *D. subcutanea*)	Rodentia: erethizontid (North American porcupine); Carnivora: mustelid (polecat)	peritoneal and subcutaneous tissues		North America, Africa
D. sudanensis (syn. *D. granulosa*)	Carnivora: felid (lion, leopard), hyaenid (hyaena)	subcutaneous tissue		Africa, Asia
D. tawila	Primates: cercopithecid (western red colobus)	subcutaneous tissues		Africa
D. tenuis	Carnivora: procyonid (raccoon); Primates: hominid (human)	subcutaneous, submucosal and intermuscular tissues, microfilariae in blood, nodules, ophthalmic	Diptera: culicid (*Aedes taeniorhynchus, sollicitans, Anopheles quadrimaculatus, Psorophora confinnis*)	North America

		dirofilariasis		
D. ursi (syn. *D. desportesi*)	Carnivora: ursid (American black bear, Japanese black bear, Asian black bear, brown bear, Kamchatka brown bear), felid (tiger); Primates: hominid (human)	subcutaneous, perirenal and peritracheal tissues, abdominal cavity, microfilariae in blood	Diptera: simuliid (*Simulium venustum*)	Asia, North America
Species inquirenda				
D. ochmanni (syn. *Microfilaria*)	Carnivora: canid (dog, red fox); Primates: hominid (human)	no adults described, mf in blood		Africa
D. timidi (syn. *Brugia*)	Lagomorpha: leporid (mountain hare)	abdominal cavity		Siberia
Species transferred to other genera				
D. digitata (syn. *Dipetalonema*, *Dirofilariaeformia*) (now *Sandnema*)	Artiodactyla: bovid (cattle); Primates: hylobatid (hoolock gibbon, Lar gibbon, northern white-cheeked gibbon), cercopithecid (dusky leaf monkey, stump-tailed macaque)	abdominal cavity		Indochina
D. kuelzii (syn. *D. asymmetrica*) (now *Skrjabinodera*)	Artiodactyla: bovid (duiker, bay duiker, Maxwell's duiker)	subcutaneous and intermuscular connective tissue		Africa
D. pauliani (now *Paulianfilaria*)	Primates: lepilemurid (weasel sportive lemur), indriid (Verreaux's sifaka)	pleural cavity		Madagascar
D. roemeri (syn. *Filaria, F. websteri, Acanthocheilonema, Dirofilaria, D. websteri, Agamofilaria tabanicola*) (now *Pelecitus*)	Diprotodontia: macropodid (agile wallaby, antilopine wallaby, black-striped wallaby, whiptail wallaby, western grey kangaroo, eastern grey kangaroo, common wallaroo, red-necked wallaby, red kangaroo, bridled nailtail wallaby, swamp wallaby)	subcutaneous and intermuscular connective tissues, limb joints, mf in blood (loose sheath)	Diptera: tabanid (*Dasybasis acutipalpis, circumdata, dubiosa, hebes, moretonensis, neobasalis, oculata, Mesomyia fuliginosa, Scaptia testaceomaculata, Tabanus australicus, pallipennis, particaecus, parvicallus, strangmenii, townsvilli*)	Australia
D. scapiceps (syn. *Loaina*) (now *Pelecitus*)	Lagomorpha: leporid (European rabbit, cottontail rabbit, eastern cottontail, marsh rabbit, snowshoe hare, Cape hare, prairie hare)	limb joints, mf in blood (loose sheath)	Diptera: culicid (*Aedes aegypti, canadensis, euedes, excrucians, provocans, punctor, stimulans, vexans, Mansonia perturbans*)	Africa, Europe, North America
D. uniformis (now *Loaina*)	Lagomorpha: leporid (European rabbit, eastern cottontail, marsh rabbit)	subcutaneous tissue, microfilariae in blood (sheathed)	Diptera: culicid (*Anopheles quadrimaculatus*)	North America

Parasite morphology: *Dirofilaria* spp. form 3 different morphotypic stages in their developmental cycles: adult worms; pre-larvae (microfilariae); and 4 sequential larval stages (designated L1-4). Female worms are ovoviviparous and do not lay eggs but produce live microfilariae in their mammalian (definitive) hosts. Even though microfilariae are often called first-stage larvae (L1), they are not as well developed as typical nematode L1 and may also be referred to as advanced embryos or pre-larvae. Microfilariae occur in the blood and are tubular in shape and elongate in size ranging from 180-385 x 3.0-8.3 µm depending on species; e.g. *D. repens* 207-385 µm, *D. immitis* 180-340 µm, *D. corynodes* 250-290 µm, *D. ursi* 185-290 µm, *D. tenuis* 220-250 µm, and *D. striata* 230-240 µm. They are typically unsheathed, as opposed to those of other onchocercid filarial worms, such as *Wuchereria, Brugia,* and *Loa,* whose microfilariae are ensheathed by vitelline eggshell membranes. *Dirofilaria* microfilariae have straight bodies with pointed tapering heads and pointed filamentous tails (compared to *Dipetalonema* and *Acanthocheilonema* microfilariae which have curved bodies with hooked tails). The internal nuclear column (formed by the primordia or anlage of developing organs) also does not extend to the end of the tail inside *Dirofilaria* microfilariae (unlike that of other filarial taxa). In insect (intermediate) hosts, microfilariae mature to L1 and then moult twice to form infective third-stage larvae (L3) measuring from 0.7-1.3 mm in length and possessing a cigar-shaped tail with one terminal and 2 subventral papillae. At this stage, different sexes may be discerned by the position of genital primordia, especially spicule primordia in males. Following transmission back to definitive hosts, infective L3 moult to fourth-stage larvae (L4) measuring from 30-110 mm long and then to sub-adults (effectively L5). Adult worms may grow

up to 310 mm in length and 2 subgenera are recognised primarily on the basis of their girth and cuticle morphology: *D.* (*Dirofilaria*) comprising long thin worms (< 0.1 mm in diameter) with smooth cuticles; and *D.* (*Nochtiella*) containing shorter stout worms (0.2-0.5 mm diameter) with cuticles adorned with longitudinal ridges and transverse striations). Worms of both subgenera have a rounded head, a small buccal cavity without lips, a mouth surrounded by 8 small inconspicuous cephalic papillae and 2 lateral amphids, an oesophagus indistinctly divided into anterior and posterior regions, and a short tail (straight in females, spirally-coiled in males). Adult worms are sexually dimorphic in many characters, especially in size with females being larger than males (e.g. *D. immitis* females 210-310 x 1.0-1.3 mm, males 110-200 x 0.6-0.9 mm; *D. repens* females 84-170 x 0.4-0.7 mm, males 39-70 x 0.3-0.5 mm; *D. tenuis* females 80-130 x 0.3-0.4 mm, males 40-50 x 0.2-0.3 mm; *D. ursi* females 180-230 x 0.6-0.8 mm, males 63-93 x 0.3-0.6 mm). In addition to their short spirally-coiled tails, males also have prominent caudal alae, 5 or more large pedunculate precloacal papillae (compared to less than 5 in *Dipetalonema* males), and 2 unequal dissimilar spicules (long left spicule with a cylindrical handle and a membranous lamina, and a short blunt right spicule). Female worms have 2 ovaries each with an oviduct and uterus terminating in a common vagina that opens into an anterior vulva (located postoesophageal). Gravid females produce and release unsheathed microfilariae.

Site of infection: Adult *Dirofilaria* worms are tissue-dwelling parasites that live in the circulatory system or connective tissues of their vertebrate hosts. Mature *D. immitis* worms normally reside in cardiopulmonary arteries of carnivores, but may be found in the right ventricle, right atrium and caudal vena cava of the heart (hence the common name of heartworm), and occasionally in femoral or hepatic arteries. Other species (e.g. *D. repens* and *D. tenuis*) are commonly found in subcutaneous connective tissues of their carnivorous hosts. Microfilariae accumulate in the peripheral blood and are transmitted to blood-feeding dipteran insects where larval development occurs mainly in the Malpighian tubules, and sometimes the fat bodies.

Pathogenesis: Many *Dirofilaria* infections are asymptomatic or subclinical and go unnoticed by their hosts. They are often sporadic and hosts remain amicrofilaraemic. However, infections by some *Dirofilaria* spp. may cause severe disease particularly in carnivores (notably canids, and sometimes felids, otariids and mustelids). Disease severity has been associated with high parasite burdens, long-term chronic infections, and aggressive host immune responses. Foci of clinical infections (hotspots) may arise due to a combination of host, parasite, and environmental factors (especially abundant hosts and competent vectors in favourable climatic conditions). In dogs, heartworm disease primarily involves the cardio-pulmonary system with mild-severe symptoms reflecting pulmonary hypertension and congestive heart failure. Clinical signs include inappetence, loss of condition, weight loss, cough (sporadic progressing to persistent), haemoptysis (coughing blood), dyspnoea (breathing difficulty), tiredness, exercise intolerance, jugular venous distention, cardiac arrhythmias, right-side murmurs and crackles upon auscultation, syncope (collapse), hepatomegaly and ascites. Pathological changes are not due to worm blockages but to a combination of host inflammatory and immune responses. While adult worms have been found to release toxic excretory/secretory metabolites, including vasoactive substances that cause blood vessel constriction, blood flow becomes restricted due mainly to thickening of the arterial walls due to endothelial (intima) proliferation, inflammation (arteritis) and fibrosis, often exacerbated by infiltrates of host immune cells (leucocytes, esp. eosinophils releasing destructive enzymes). Platelets may also be activated leading to disseminated intravascular coagulation. Dead and dying worms may cause granulomatous and villous inflammation and thrombosis. Thickened arteries become constricted, narrow, and occluded with reduced elasticity and turbulent blood flow. This results in pulmonary hypertension which eventually causes compensatory right heart enlargement (right ventricular dilatation and hypertrophy), cardiac insufficiency and possibly congestive heart failure. Thromboembolisms further contribute to the pulmonary hypertension. The liver may become enlarged due to chronic venous congestion (consistent with right-sided heart failure). In some instances, the presence of worms in the right atrium and venae cavae may cause caval syndrome characterised by inflow obstruction to the right heart, tricuspid insufficiency, hypertension, ascites, and haemolytic anaemia (the latter due to the lysis of fragile erythrocytes when passing through the mesh of tangled worms and fibrin deposits). Dogs present with dyspnoea, tachypnoea, cardiac thrill with heart murmur, jaundice, and haemoglobinuria. Heartworm infections may also lead to renal disease with glomerulonephritis and proteinuria occurring due to immune complex (antigen-antibody) formation. Occasionally, broncho-arterial fistulas may develop when weakened arteries rupture into the airways leading to marked haemoptysis especially after exercise. Rare ectopic infections may also result from aberrant migration of worms into the eye, brain, liver, peritoneal cavity, or skin. Infections are more prevalent and severe in dogs > 2 years of age, in larger breeds of dogs, and in dogs housed outdoors. While cats are atypical hosts and more resistant to *D. immitis* infections than dogs, they have comparatively smaller pulmonary trees so even a small number of worms can cause pulmonary manifestations. Clinical signs include peracute respiratory distress, tachypnoea, coughing, haemoptysis, vomiting unrelated to eating, seizures, collapse, and sudden death. Pathological changes are generally insufficient to cause persistent pulmonary hypertension or congestive heart failure. Instead, immature worms may produce an acute inflammatory reaction known as heartworm-associated respiratory disease, often misdiagnosed as allergic bronchitis or asthma. Degenerating worms have also been associated with symptoms similar to acute respiratory distress syndrome, involving pulmonary inflammation, oedema and thromboembolism contributing to respiratory failure. Infections in cats rarely cause caval syndrome, but even a few worms may cause tricuspid valve regurgitation with cardiac thrill and heart murmur. Ectopic infections have been detected in cats in systemic arteries in the central nervous system or body cavity. Several *Dirofilaria* spp. have been detected in humans: mostly *D. immitis* and sometimes *D. tenuis*, *D. ursi*, *D. striata* and *D. spectans* in the Americas; *D. repens* in Eurasia; and *D. hongkongensis* and *D. magnilarvatum* in Asia. Infections in humans appear to be accidental as worms do not mature or produce microfilariae. However, migrating and/or degenerating worms may cause pulmonary or subcutaneous lesions. *Dirofilaria immitis* and *D. repens* may cause nodular pulmonary granulomas resulting in chest pain, fever, cough, haemoptysis, and dyspnoea. *Dirofilara repens, D. tenuis* and

other zoonotic species may cause wandering lesions and pruritic dermatitis in subcutaneous tissues, and occasionally in submucosal breast tissues, which eventually encapsulate into granulomatous nodules. Ectopic infections have been detected infrequently in humans in the conjunctiva, meninges, liver, testicles and mesenteric adipose tissue.

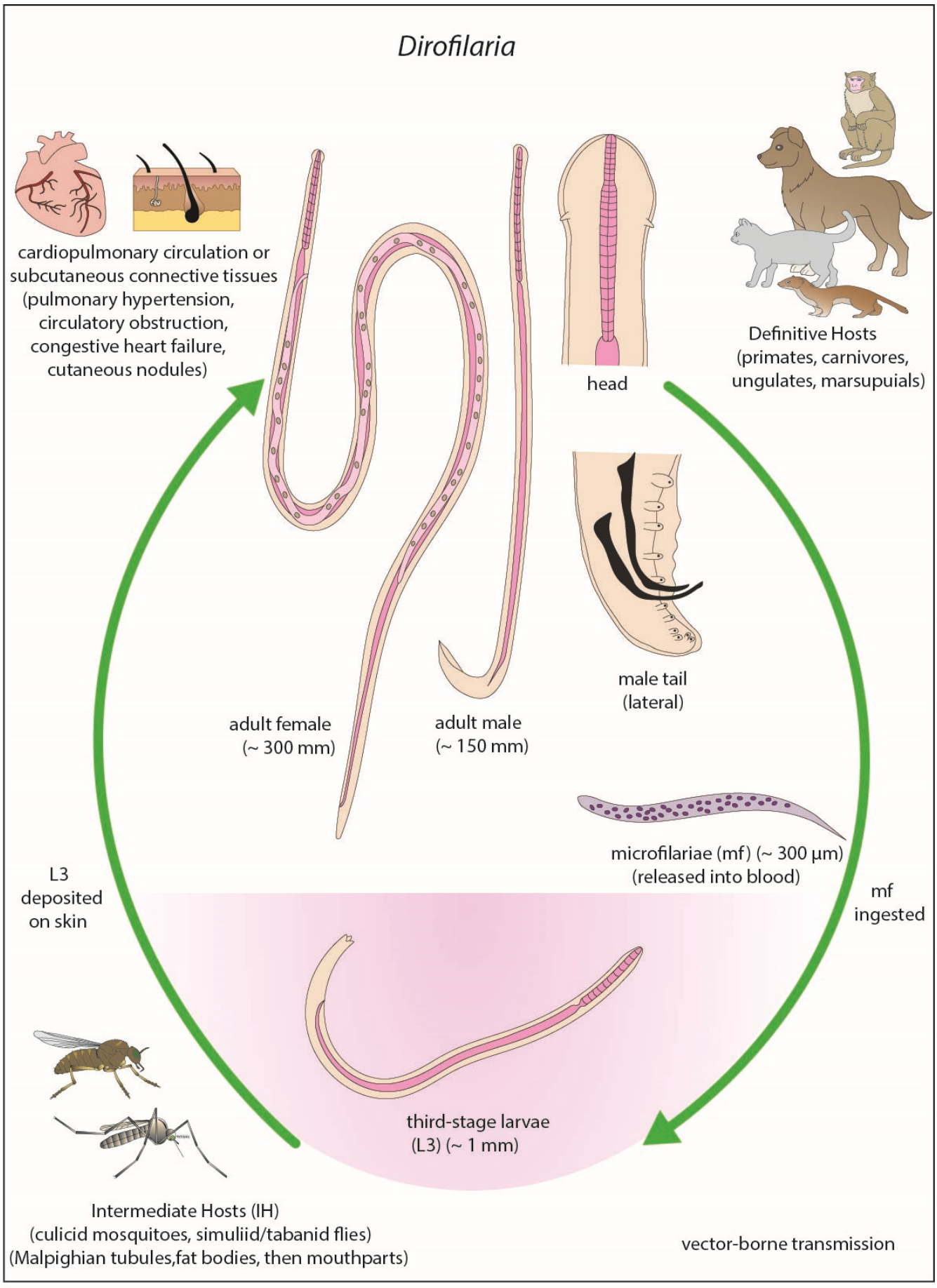
The recent detection of the rickettsial α-proteobacteria *Wolbachia pipientis* as intracellular endosymbionts in *D. immitis* provides somewhat of a conundrum between disease causation and treatment. The bacteria are present in all parasite stages and are considered to be essential for their normal development and survival (mutualistic symbiosis). Heartworm parasites cause significant inflammation in their vertebrate hosts in the form of proliferative pulmonary endarteritis, particularly when worms are dying and degenerating. Surface proteins from exposed (extracellular) bacteria have been shown to up-regulate host inflammatory responses, thus contributing to disease. Killing worms with anthelmintics and killing bacteria with antibiotics may have the unintended consequences of exposing the host to a flood of pro-inflammatory disease-causing substances, albeit transiently.

Developmental cycle and mode of transmission: *Dirofilaria* spp. exhibit indirect heteroxenous life-cycles with adult worms forming in vertebrates (carnivores and primates acting as definitive hosts) and larval stages developing in invertebrates (insects acting as intermediate hosts). Cyclic transmission between hosts is vector-borne and associated with haematophagous feeding behaviours. Mature female worms release microfilariae which accumulate in the peripheral circulation and are ingested by blood-feeding dipteran insects. Most *Dirofilaria* spp. are transmitted by mosquitoes, notably female mosquitoes which require protein-rich blood meals for reproductive purposes. *Dirofilaria immitis* infections may utilize more than 70 species of culicid mosquitoes as intermediate hosts (including *Aedes, Anopheles, Armigeres, Coquilletidia, Culex, Culiseta, Mansonia, Psorophora, Wyeomyia* spp.), but most infections are transmitted by a few major vectors which vary according to their geographic distribution (including *Ae. albopictus, Ae. canadensis, Ae. caspius, Ae. notoscriprus, Ae. trivittatus, Ae. vexans, An. annulipes, An. maculipennis, An. punctipennis, An. quadrimaculatus, An. walkeri, Cx. annulirostris, Cx. pipiens, Cx. quinquefasciatus, Cx. theileri* and *Cq. richiardii*). A few *Dirofilaria* spp. do not use mosquito vectors, instead *D. ursi* is transmitted by simuliid flies and *D. roemeri* by tabanid flies. In all cases, ingested microfilariae migrate from the insect midgut through the haemocoel to the Malpighian tubules, except *D. corynodes* and *D. roemeri* which invade the fat body (in contrast, *Brugia* and *Wuchereria* larvae develop in the thoracic flight muscles of mosquitoes). The microfilariae form sausage-shaped first-stage larvae (L1) in 3-5 days, which then moult to form second-stage larvae (L2) in 7-10 days and then third-stage larvae (L3) in 11-16 days which migrate through the haemocoel to the mosquito's proboscis. Larval development takes longer when ambient temperatures are cooler, with the prepatent period in mosquitoes (time from infection to generation of infective L3) being extended up to 30 days at temperatures around 20°C, and even being arrested at temperatures lower than 15°C. Transmission occurs during blood-feeding when infective L3 exit the insect's labial sheath and are deposited on the skin of the mammalian host where they invade the puncture wound (contaminative transmission rather than inoculative salivary transmission). The larvae move into adjacent tissues and moult into fourth-stage larvae (L4) within a week. The L4 moult into young adults in submuscular membranes or subcutaneous tissues over 6-8 weeks and then migrate to their final predilection sites (arteries and/or connective tissues depending on species). Young *D. immitis* adults penetrate the vasculature and migrate to pulmonary arteries and the right heart 10-16 weeks after infection and reach maturity in another 8 weeks. Young *D. repens* and *D. tenuis* worms migrate primarily to subcutaneous connective tissues where they mature over several months. Following mating, female worms produce and release microfilariae which accumulate in the bloodstream. The prepatent period (time from infection to first release of microfilariae) ranges from 6-9 months and adult worms may live for up to 10 years while microfilariae may remain in the circulation for up to 2 years.

Differential diagnosis: Heartworm infections may be suspected on the basis of symptomatology involving signs of pulmonary or subcutaneous disease, particularly coughing and exercise intolerance in dogs infected with *D. immitis*, or pruritic dermatitis in humans infected with *D. repens*. Nonetheless, clinicians should pay careful attention to relevant patient history (geographic location, potential exposure, prophylaxis) as many other disease conditions may cause similar signs. Most clinical parameters (haematological and biochemical) are non-specific, so infections are generally confirmed by the microscopic detection of microfilariae in peripheral blood samples, either in wet mounts, fixed thick or thin smears, or concentrates obtained by membrane filtration (5 µm pore size), haematocrit tube centrifugation (microfilariae band immediately above buffy coat) or sedimentation (following haemolytic treatment with formalin (Knott's method), saponin or hypotonic saline). Permanent mounts may be stained with Giemsa, Delafield's haematoxylin or Field's rapid stain, while live organisms may be stained supravitally with cresyl blue or methylene blue. Some laboratories also stain microfilariae for alkaline phosphatase activity (*D. immitis* shows activity at the anal and excretory pores, *D. repens* only shows activity at the anal pore, while *Acanthocheilonema reconditum* shows diffusely distributed activity). *D. immitis* microfilariae are distinguished from those of other filarial worms by their large straight bodies with tapered heads and pointed tails and they exhibit nonprogressive (stationary) movement in wet preparations (in contrast, those of *Dipetalonema/Acanthocheilonema* have medium curved bodies with blunt heads and hooked tails and by their progressive movement in wet preparations). Caution is advised when interpreting the results of microfilarial examinations as quantitative studies have shown that the degree of microfilaraemia (number of circulating microfilariae) bears little relationship to the intensity of infection (number of adult worms). Indeed, many hosts have occult infections (adults present but no circulating microfilariae) for a variety of reasons: such as only one worm being present; all worms being the same sex; young worms not yet producing microfilariae; old worms no longer producing microfilariae; host immune responses rapidly clearing microfilariae; previous drug treatment(s) eliminating microfilariae or sterilizing adult worms; or worms infecting ectopic sites. On occasion, adult worms or fragments thereof may be examined after their collection by biopsy of subcutaneous or pulmonary lesions or during necropsy.

Worms may be identified by their characteristic morphotypic features, especially with respect to size, cuticular features, lateral chords and somatic muscle development. Over the last several decades, recourse has been made to the immunological detection of either host antibodies or parasite antigens in blood samples. Several generations of antibody tests were developed, most based on enzyme immunoassays, but many demonstrated poor diagnostic sensitivity and specificity due to antigenic cross-reactivity, the absence of antibodies in the first 6-8 weeks of infection or the persistence of antibodies for years after infections have been eradicated. Several generations of antigen tests were then developed using polyclonal or monoclonal immunoreagents in enzyme immunoassays or immunochromatographic tests. These antigen tests demonstrated a good threshold of detection (able to detect one worm) and little cross-reactivity with other nematodes (especially tests using monoclonal reagents). However, false negative results may occur as many tests use glycoprotein antigens from the reproductive tracts of female worms and therefore will only detect mature infections (> 6 months). False positive results may also occur occasionally when antigens persist in the circulation although adult worms are dead. Modern medical imaging techniques, including X-ray (radiography), ultrasound (sonography, echocardiography), computed tomography (CT) scans and magnetic resonance imaging (MRI), have been used to detect characteristic pathological changes to pulmonary arteries (increased size, tortuosity, 'coin' lesions) or to the heart (right-sided cardiomegaly), and sometimes to reveal worms themselves in arteries (the worm cuticle is hyperechogenic and may be visualized as parallel lines). More recently, molecular biological techniques have been used to detect parasite DNA in fresh, frozen, or fixed blood/tissue samples following polymerase chain reaction (PCR) amplification of specific nuclear gene sequences (ribosomal RNA, internal transcribed spacer regions, cuticular antigens with multiple tandem repeats) and mitochondrial gene sequences (12S mtRNA, cytochrome c oxidase 1).

Treatment and control: Existing heartworm infections can be treated chemotherapeutically, but different anthelmintic drugs are used to kill adult worms and developing larvae. Animals should be tested before treatment to determine their infection status, so the correct treatment is used. Animals should also be hospitalized during and shortly after adulticide treatment as the risk of pulmonary embolisms due to fragments of dying worms is high and supportive therapy may be required to manage shock, including intravenous corticosteroids, balanced electrolyte solutions, bronchodilators, and oxygen therapy. The drug of choice for killing adult *D. immitis* worms > 4 months old is the organoarsenical melarsomine, but it does not act on microfilariae. Previously, another organoarsenical thiacetarsamide was used but it was not well tolerated and caused hepato-renal toxicity. Treatment should involve multiple graded doses, so worms are eliminated in stages, rather than single heroic doses which often causes complications. Side-effects to adulticide treatment include rapid onset of pulmonary oedema (managed with dimercaprol), hypersensitivity (managed with corticosteroids or non-steroidal anti-inflammatory drugs), but mostly pulmonary thromboembolisms usually occurring 5-21 days after treatment (minimised using anti-thrombotic and anti-inflammatory drugs). Some degree of pulmonary thromboembolism will occur as worms are destroyed so supportive therapy should be continued for several weeks after adulticide treatment. Animals should not be exercised during this recovery period and cage rest may be warranted for boisterous animals. In some instances, pre-treatment with drugs active against developing larvae may be used prior to adulticide treatment to ensure infections do not re-establish (the risk of delaying adulticide treatment should be considered on a case-by-case basis). The most commonly used pre-treatment drugs are macrocyclic lactones (e.g. milbemycin) which are active against L3, L4, sub-adult worms as well as microfilariae. A complication of such therapy in microfilaraemic dogs is an anaphylactic reaction to antigens released from microfilariae, especially in small dog breeds with heavy parasite loads. Dogs have also been pre-treated with tetracycline antibiotics (doxycycline) which act against the endosymbiotic *Wolbachia*-bacteria and cause worm sterility. However, bacterial surface proteins have been implicated in pro-inflammatory host responses and may contribute to heartworm disease pathogenesis. Nevertheless, heartworm-positive dogs pretreated with macrocyclic lactones and doxycycline prior to melarsomine treatment had less pulmonary pathology associated with worm death. An alternative soft-kill approach using monthly macrocyclic lactones (ivermectin) with antibiotics (doxycycline) to slowly kill worms over 9-12 months was trialled, but it was not as effective as melarsomine treatment and has mostly been discontinued. In dogs in which caval syndrome has developed, recourse is made to the surgical removal of worms occluding the vena cava and/or the right atrium. In humans, surgical removal of subcutaneous nodules and even lung granulomas is the preferred option. The prevention of infections is based around chemoprophylaxis, vector control and protective barriers. Anthelmintic drugs that are active against developing larvae include the macrocyclic lactones (ivermectin, milbemycin, moxidectin and selamectin) and the diethylenediamine (diethylcarbamazine, DEC). The former are available as topical, oral or injectable formulations, usually applied monthly (injectables yearly), while DEC is available orally but must be given daily or on alternate days (missing a dose temporarily voids protection). DEC is currently being phased out due to the strict treatment regimen and adverse side effects, notably hypovolaemic shock and death. Dogs should be tested for infections before beginning chemoprophylaxis and treated with adulticides if infected. In endemic areas, puppies should commence preventive medication no later than 8 weeks of age. Various strategies are available for controlling insect vector populations, including the use of insecticides to kill adult mosquitoes, the elimination of mosquito breeding sites, and using protective screens, clothing or insect repellents to avoid mosquito bites. Public education campaigns have done much to raise public awareness and protect pets at risk.


Dirofilaria
cardiopulmonary circulation or subcutaneous connective tissues (pulmonary hypertension, circulatory obstruction, congestive heart failure, cutaneous nodules)
Definitive Hosts (primates, carnivores, ungulates, marsupuials)
head
male tail (lateral)
adult female (~ 300 mm)
adult male (~ 150 mm)
microfilariae (mf) (~ 300 µm) (released into blood)
L3 deposited on skin
mf ingested
third-stage larvae (L3) (~ 1 mm)
Intermediate Hosts (IH) (culicid mosquitoes, simuliid/tabanid flies) (Malpighian tubules,fat bodies, then mouthparts)
vector-borne transmission



Dirofilaria adult worms



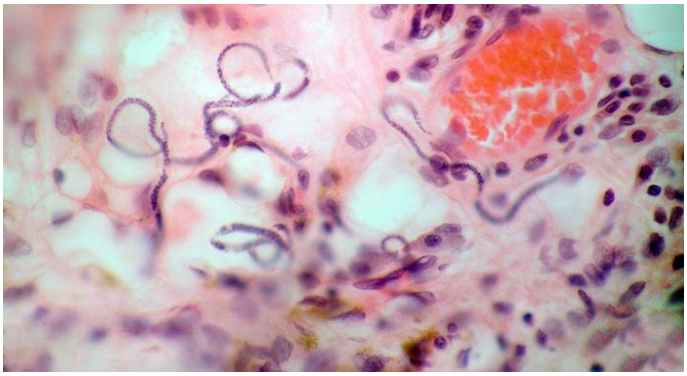
Dirofilaria adult worms



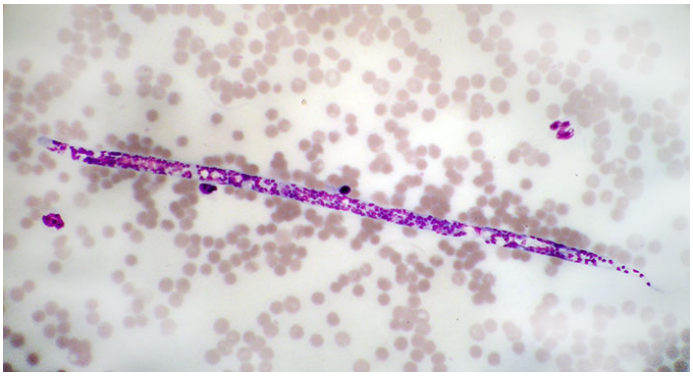
Dirofilaria adult worm, head



Dirofilaria adult worm, male tail



Dirofilaria microfilariae in skin



Dirofilaria microfilaria in blood

Loa
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including filarioids (without lips) living in subcutaneous, intermuscular, vascular or lymphatic systems of mammals. Two main families include the oviparous filariids (lay eggs) and the ovoviviparous onchocercids (eggs hatch internally releasing pre-larvae called microfilariae). Infections by the onchocercid genus *Loa* are transmitted by tabanid flies and cause subcutaneous Calabar swellings in humans in Africa.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Filarioidea (tissue-dwelling filarial parasites, lack lips)
Family:	Onchocercidae (adults loose in tissues or in nodules, viviparous (live birth of microfilariae))
Genus:	*Loa* (parasitic in subcutaneous tissues of humans, fly IH)
Species:	*Loa loa* (causes Calabar swellings in humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Filarioidea contains long thread-like nematodes which are predominantly tissue-dwelling parasites infecting the body cavities, subcutis, intermuscular tissues, blood vessels or lymphatic systems of terrestrial hosts. These worms are known colloquially as 'filariae', 'filarids' or 'filarioids' [Note: take care with terminology as the cognate family Filariidae (esp. genus *Filaria*) are known colloquially as 'filariids', and the unrelated metastrongyle (lungworm) family Filaroididae (genus *Filaroides*) are known colloquially as 'filaroids']. Adult filariae have a cylindroid pharynx with an anterior muscular portion and a posterior glandular portion. Males often have spirally-coiled tails, well-developed alae and dissimilar spicules. Females of most species are ovoviviparous (eggs hatch within body of parent) releasing pre-larval stages known as microfilariae (sometimes sheathed). Filariae have indirect life-cycles whereby microfilariae are taken up by blood-sucking or tissue-feeding invertebrates (arthropods, esp. mosquitoes) which act as intermediate hosts for the development of infective L3 larvae. Ten families are recognised: Filariidae and Onchocercidae infecting mammals, birds, reptiles and amphibians; Setariidae infecting mammals; Aproctidae infecting birds; and Creagrocercidae, Drilonematidae, Homungellidae, Mesidionematidae, Scolecophilidae and Ungellidae infecting terrestrial annelids. Examples of filarioid genera covered in this resource are compared in the following table.

Genus	Definitive hosts	Adults (location)	Microfilariae (location)	Periodicity	Vectors	*Wolbachia* symbiotes
Family Onchocercidae						
Loa (3 spp.)	primates, ungulates, rodents	2-7 cm (subcutis, eye)	250-300 µm sheathed (blood)	diurnal	flies	absent
Onchocerca (35 spp.)	primates, carnivores, ungulates, rodents	1.5-80 cm (subcutis, ligaments)	105-440 µm unsheathed (skin)	-	flies, midges	present
Mansonella (29 spp.)	primates, carnivores, ungulates, rodents	3-8 cm (subcutis, serosa)	170-300 µm unsheathed (blood/skin)	-	midges, flies, mosquitoes	present
Dirofilaria (34 spp.)	primates, carnivores, ungulates, rodents, lagomorphs, marsupials	4-31 cm (blood vessels)	180-385 µm unsheathed (blood)	-	mosquitoes, flies	present
Dipetalonema, Acanthocheilonema (57 spp.)	primates, carnivores, ungulates, rodents, cingulates, marsupials	1-7 cm (subcutis, serosa)	85-300 µm unsheathed (blood)	-	flies, fleas, lice, ticks	absent
Wuchereria (2 spp.)	primates	2.5-10 cm (lymphatics)	210-320 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Brugia (10 spp.)	primates, carnivores, rodents	1-9 cm (lymphatics)	170-380 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Family Filariidae						
Parafilaria (4 spp.)	ungulates	2-7 cm (subcutis)	40-58 x 23-33 µm larvated eggs (skin)	diurnal	flies	absent
Stephanofilaria (7 spp.)	ungulates	0.2-1.4 cm (subcutis)	45-195 µm sheathed (skin)	-	flies	absent
Family Setariidae						
Setaria (42 spp.)	primates, ungulates, rodents, lagomorphs	4-19 cm (body cavities)	140-310 µm sheathed (blood)	-	mosquitoes	absent

Members of the family Onchocercidae form adult worms that live loose in body cavities or in tissue nodules. Female worms release microfilariae which disperse into the blood or dermal connective tissues (unlike filariids which live in the skin close to where they deposit eggs or larvae). Some 88 onchocercid genera are divided into 7 subfamilies: Onchocercinae and Dirofilariinae (syn. Loainae) mostly in mammals but some in birds and reptiles, Waltonellinae and Icosiellinae in amphibians, Oswaldofilariinae in reptiles, Splendidofilariinae and Lemdaninae in birds, reptiles and mammals (former subfamily Setariinae in large mammals recently elevated to family status as Setariidae). Members of the subfamily Dirofilariinae are characterised as forming males with highly developed caudal alae (while members of the subfamily Onchocercinae form males with markedly dissimilar spicules and long tails lacking caudal alae). Some 16 genera are recognised in the subfamily Dirofilariinae: namely, *Bostrichodera*, *Dirofilaria*, *Dirofilariaeformia*, *Edesonfilaria*, *Eulimdana*, *Foleyellides*, *Heimnema*, *Loa* (syn. *Paraloa*), *Loaina, Macacanema*, *Madochotera*, *Ochoterenella*, *Skrjabinodera* and *Tawila* in mammals, *Pelecitus* (syn. *Spirofilaria*, *Eulimdana*) in birds, and *Foleyella* (syn. *Foleyellides*) in saurians. Three groups of human filariasis are distinguished on the basis of their tissue tropism: cutaneous dermal filariasis (loiasis in Africa, onchocerciasis in Africa, Asia, Central and South America, *streptocerca* mansonelliasis in Africa); lymphatic filariasis (wuchereriasis in Africa and Asia, brugiasis in South Asia); and serous filariasis (*perstans* mansonelliasis in Africa, Central and South America, *ozzardi* mansonelliasis in Central and South America).

The genus *Loa* forms thread-like worms in subcutaneous and deep connective tissues predominantly in primates. Adult worms have cuticular coverings with irregular bosses (protrusions) and delicate transverse striations, simple heads lacking lips but with 8 cephalic papillae, and blunt tails. Mature female worms are ovoviviparous releasing sheathed microfilariae into the blood where they are taken up by day-biting tabanid flies (*Chrysops* spp. known variously as mango flies, horse flies, or deer flies). The species *L. loa* is endemic in humans and monkeys in equatorial rainforests of West and central Africa and it is estimated that up to 20 million people may be infected.

***Loa* species**	**Definitive Hosts (DH)**	**Location**	**Clinical signs**	**Vectors/Intermediate Hosts (IH)**	**Distribution**
L. loa (African eye worm) (includes human and monkey strains)	Human strain Primates: hominid (human, gorilla), cercopithecid (grey-cheeked mangabey, mandrill, olive baboon, patas monkey); Perissodactyla: equid (horse); Rodentia: murid (jird, Mongolian gerbil, mouse) Monkey strain Primates: cercopithecid (greater spot-nosed monkey, drill, mona monkey)	subcutaneous tissues, subconjunctiva, mf in blood (sheathed, human strain diurnally periodic, monkey strain nocturnally periodic)	skin (Calabar) swellings, allergic reactions	Diptera: tabanid human strain (*Chrysops dimidiata, silacea, atlanticus, distinctipennis, longicornis, zahrai*), monkey strain (*Chrysops centurionis, langi*)	tropical West and Central Africa
L. papionis (or *L. loa papionis*)	Primates: cercopithecid (yellow baboon)	larger worms in tissues, mf in blood (sheathed, nocturnally periodic)	simian loiasis	Diptera: tabanid (*Chrysops centurionis, langi*)	Africa
L. inquirenda	Primates: hominid (human)	subconjunctiva, neck			India

Parasite morphology: Filarial nematodes belonging to the genus *Loa* form 3 distinct morphological stages in their developmental cycles: adult worms, microfilariae and larvae (moulting through 4 stages). Gravid females produce embryonated eggs which hatch internally releasing live microfilariae (considered to be pre-larvae as they are not as developed as typical first-stage nematode larvae). Microfilariae are elongate and slender, measuring 250-300 x 6-8 µm. They are ensheathed in an eggshell-like membrane and have a tapering tail hooked or coiled within the sheath. The body contains a densely packed nuclear column which extends to the tip of the tail. Microfilariae exsheath and develop into first-stage larvae (L1) which undergo a series of 4 moults to eventually form sub-adult worms. Developing larvae vary in size, measuring from 1.1-5.3 mm in length depending on their stage of maturation in the moult cycle. Infective third-stage larvae (L3) grow to 1.3-2.6 mm long and the tip of the tail has a digitiform process with 2 ventrolateral papillae and 2 subterminal papillae. Fourth-stage larvae (L4) begin to show sexual differentiation in their genital primordia and the larvae vary in size according to gender, with developing female worms being larger than males (5.3 mm cf. 4.4 mm). Adult worms are sexually dimorphic, with females being larger than males (40-70 x 0.4-0.5 mm cf. 20-35 x 0.3-0.4 mm). They have long slender thread-like bodies with prominent bosses (protrusions) of cuticular material scattered in irregular patterns as well as delicate transverse striations, a short undivided oesophagus, simple heads with 8 cephalic papillae and blunt tails. Males have 2 uneven dissimilar spicules (around 120 and 90 µm long), 3 caudal lappets and often asymmetrical arrangements of 3 pairs of pre-anal and 5 pairs of post-anal papillae. Female worms are ovoviviparous and give birth to live microfilariae through an anteriorly-located vulva (posterior to nerve ring).

Site of infection: Adult male and female *Loa* worms live and migrate in subcutaneous connective tissues in their mammalian definitive hosts, particularly on the back, chest, axilla, groin, and scalp. Migrating worms may sometimes traverse the subconjunctiva of eye, and on rare occasions, they may infiltrate into deeper connective tissues, lymph nodes and the anterior chamber of the eye, causing serious complications. Microfilariae are found in predominantly in the bloodstream, although they have sometimes been isolated from cerebrospinal fluid, urine, sputum, and saliva. Larval stages develop in the thoracic muscles and fat body of their invertebrate intermediate hosts, and then migrate to the mouthparts.

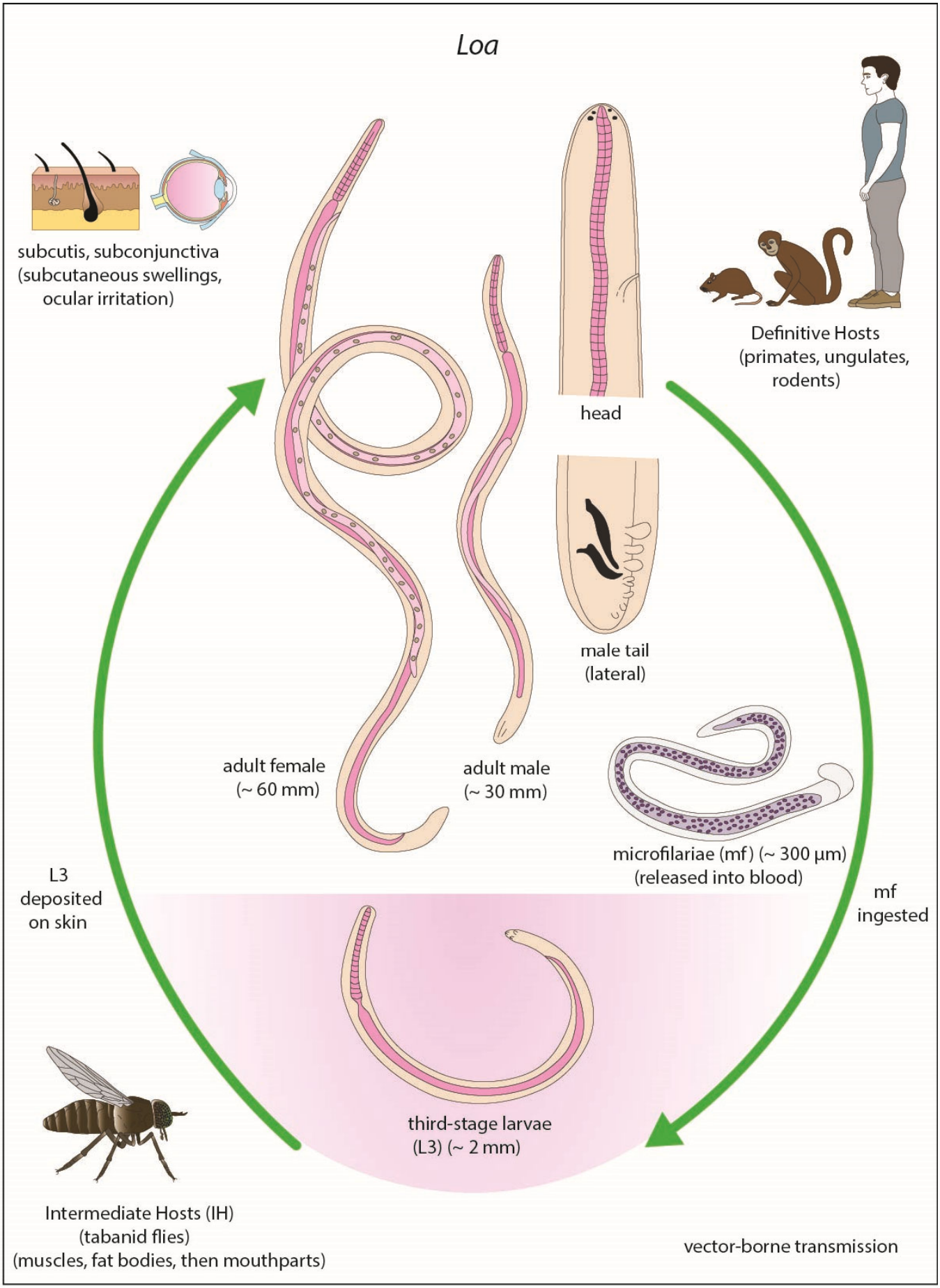
Pathogenesis: *L. loa* infections are frequently asymptomatic, but some may cause a mild disease (loiasis) in which symptoms may appear within a few months of infection, but often not for more than a decade. Many cases are therefore latent or occult, and the absence of circulating microfilariae appears to be due to their destruction by the host immune system and/or their possible sequestration within tissues. The pathogenesis of infections also varies according to exposure, with residents indigenous to endemic areas often having high blood microfilarial counts without symptoms, and non-indigenous people often having low or no microfilarial counts but with massive hypersensitivity responses, involving peripheral eosinophilia, hypergammaglobulinaema (esp. IgE) and systemic symptoms. Most symptoms are caused by the extensive migrations of worms in subcutaneous tissues, sometimes moving at rates up to 1.5 cm/min, resulting in 3 principal manifestations: cutaneous; ocular; and cerebral signs. While many worm migrations may go unnoticed, others may trigger localized inflammatory (hypersensitive) responses resulting in transient angioedematous swellings on the body (known as Calabar swellings). The swellings develop rapidly and last from 1-3 days, usually accompanied by localized pain, urticaria and pruritus. They can be found anywhere on the body, usually involving the face and limbs, and those near joints make movement difficult and painful. Occasionally, developing larvae or young adult worms may migrate across the surface of the eye under the conjunctiva (condition commonly known as eyeworm) resulting in inflammatory swelling of the orbit, congestion, itching, pain, photophobia and psychosomatic manifestations. Subconjunctival migration may take anywhere from 15 min to a full day to be completed. Rarely, worms may invade the interior of the eye, causing severe inflammation, ocular irritation and occasionally leading to blindness. Ectopic infections of deeper tissues may also sometimes occur leading to severe complications, including endomyocardial fibrosis, pleural effusion, nephropathy, neurological problems (ranging from headache to loss of sensation and motor deficiencies) and sometimes fatal encephalitis. Infection can also induce fatigue and sudden bouts of popular or vesicular rash. Loiasis is confined to sub-Saharan Africa (it was introduced into the Caribbean during the slave trade era, but did not persist) and those most at risk reside or work near rainforests, savannahs and areas near streams or rivers. The prevalence of infection increases with age, and Calabar swellings occur more frequently in women than men, with greater recurrences. This mild disease was neglected for many years in favour of more severe infectious diseases, but this changed when mass eradication programs for onchocerciasis were conducted in regions endemic for *Loa*. It was found that ivermectin drug treatment led to severe neurological complications (termed serious adverse events, SAEs), such as encephalitis and coma, in patients with concomitant *Loa* infections (esp. those with heavy microfilaraemias). It is estimated that some 30 million people live in areas where both infections co-exist.

Developmental cycle and mode of transmission: All filarial worms have indirect heteroxenous life-cycles involving vector-borne transmission. Gravid *Loa* worms produce microfilariae which demonstrate a circadian (daily) rhythm to their concentration in host blood. Microfilariae in humans exhibit diurnal periodicity, whereby they occur in peripheral blood during daylight hours (5 am to 7 pm, but peak concentrations from 10 am to 2 pm) and are sequestered in capillaries of the skin, lungs and other organs at night (Note: some workers have reported a variant *Loa* strain in monkeys which apparently demonstrates a nocturnal periodicity). Nonetheless, the characteristic diurnal periodicity of loiasis distinguishes it from Bancroftian and Brugian filariasis which are nocturnally periodic. The occurrence of *Loa* microfilariae in blood during the day corresponds well to the peak feeding times (9 am to 4 pm) of the tabanid fly vectors, *Chrysops* spp. (known as deer flies, mango flies or mangrove flies). Female flies require a blood meal for egg production and they use specialized scissor-like mouthparts to cut the skin, thus inflicting painful bites which often cause allergic reactions in humans. They breed in swamps, muddy ponds and slow-moving waters impeded by rotting vegetation. The main vectors for human infections are *C. silacea, C. dimidiata* and *C. distinctipennis* which are found in tropical rainforests and gallery forests of West and Central Africa, particularly during rainy seasons. In contrast, the nocturnal variant strain found in monkeys is transmitted mainly by *C. centurionis* and *C. langi* which feed on animals in the forest canopy at night. Ingested microfilariae exsheath in the gut and migrate through the haemocoel to the thoracic cavity (infected tissues become disorganized and syncytial). Here they moult to second-stage larvae (L2) in 3-5 days, to third-stage larvae (L3) in 6-9 days and then migrate to the mouthparts by 9-14 days. Infective L3 larvae emerge from the proboscis when the labium is bent (kinked) during feeding. Transmission is contaminative (rather than inoculative) as the larvae are deposited onto the host skin and invade the bite wound into subcutaneous tissues. They moult to fourth-stage larvae (L4) in 18-30 days and then to sub-adult stages around 50 days. Developing worms migrate extensively through the connective tissues and become sexually mature over several months. Female worms are ovoviviparous and may produce thousands of microfilariae per day. The prepatent period (time from infection to first appearance of microfilariae) may be as short as 4-5 months, but is often extended to 12 months. Adult worms have been found to live as long as 15-17 years in infected patients.

Differential diagnosis: Infections may be suspected on the basis of clinical manifestations (e.g. Calabar swellings or wandering eyeworm) in patients with a history of residency or travel to endemic areas, but similar swelling may arise due to other conditions (such as hereditary angioedema (HAE) due to C1 esterase inhibitor deficiency) and other worms may undertake subconjunctival migration (e.g. *Dirofilaria repens, Thelazia californiensis*). In some cases, worms may be surgically removed from the subconjunctiva, or from accessible subcutaneous locations, and examined microscopically for distinctive features (size, cuticular protrusions, transverse striations, simple heads with 8 cephalic papillae, and blunt tails). Generally, infections are confirmed by the microscopic examination of blood samples for microfilariae, taking care to differentiate those of *Loa* from other filarial worms often found in the same geographic locations (such as *Onchocerca volvulus* and *Wuchereria bancrofti*). It is recommended that blood be collected around 1 pm as the microfilaraemia associated with loiasis exhibits diurnal periodicity. Microfilariae may be found in thick or thin blood smears stained with Giemsa or haematoxylin, or in concentrates obtained by membrane filtration (3-5 μm pore size) or by centrifugation after haemolysis (treatment with formalin, saponin or hypotonic saline). *Loa* microfilariae are identified by

their large faintly-staining sheath and tapering tail with nuclei extending to the tip. It should be remembered, however, that infections undergo a long incubation period before becoming microfilaraemic (months to years) and some infections remain amicrofilaraemic with or without symptoms. A range of immunological tests have been developed to detect host antibodies against infection, including class-specific fluorescent or enzyme immunoassays, but many have demonstrated poor sensitivity, cannot differentiate recent infection from previous exposure and sometimes cross-react with other filarial infections. Studies are currently examining immunological techniques to detect parasite antigens in blood samples, and promising results have been obtained with enzyme immunoassays and luciferase immunoprecipitation assays. Molecular biological techniques have also been used to detect parasite DNA in both occult and regular loiasis following the polymerase chain reaction (PCR) amplification of specific gene sequences, particularly the repeat 3 region of a 15 kDa polyprotein allergen (15r3).

Treatment and control: Infections may be treated with filaricidal anthelmintics, including diethylenediamine (diethylcarbamazine (DEC)), macrocyclic lactones (ivermectin) and benzimidazole-methylcarbamate (albendazole and mebendazole). Chemotherapy was found to significantly reduce microfilariaemia, but only DEC was effective against adult worms, with some minor side-effects (headache, rash, fever). Mass treatments for onchocerciasis with single or combination anthelmintics had been undertaken in many endemic areas, but it quickly became evident that treatment of patients with high *Loa* microfilarial counts caused serious adverse events (SAEs), including shock, encephalitis and retinal haemorrhage coincident with massive antigen release from dying microfilariae. While such events may be ameliorated through the concurrent application of steroids and other anti-inflammatory drugs, treatment programs were curtailed or closely monitored in areas where both loiasis and onchocerciasis occurred. *Loa* is one of the few filarial worms that does not have endosymbiotic *Wolbachia* bacteria, so it is not susceptible to treatment with tetracycline antibiotics. In eyeworm cases, worms may often be surgically removed after local anaesthesia, but it is chemotherapy is still required to treat microfilariae or any remaining adults. Surgery may also be used to extract worms from subcutaneous tissues when infections are superficial, easily accessible and are not threaded through joints. The prevention of infections relies on avoiding vector bites rather than on vector control. Deer flies are active during the day and rarely enter buildings (houses, barns), so the use of residual insecticides on dwellings and impregnated bed nets has limited efficacy. Flies also breed in wet and wild locations not particularly suited to intervention strategies (physical, chemical or biological). Instead, people should practise personal protection to avoid fly bites through the use of personal repellents (esp. DEET), impregnated clothing (esp. permethrin) and wearing long-sleeved shirts and long pants when working outdoors.


Loa
subcutis, subconjunctiva
(subcutaneous swellings,
ocular irritation)
Definitive Hosts
(primates, ungulates,
rodents)
head
male tail
(lateral)
adult female
(~ 60 mm)
adult male
(~ 30 mm)
microfilariae (mf) (~ 300 µm)
(released into blood)
L3
deposited
on skin
mf
ingested
third-stage larvae
(L3) (~ 2 mm)
Intermediate Hosts (IH)
(tabanid flies)
(muscles, fat bodies, then mouthparts)
vector-borne transmission



Loa adult worm



Loa microfilaria

Setaria
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including filarioids (without lips) living in subcutaneous, intermuscular, vascular or lymphatic systems of mammals. Two main families include the oviparous filariids (lay eggs) and the ovoviviparous onchocercids (eggs hatch internally releasing pre-larvae called microfilariae). Infections by the onchocercid genus *Setaria* are transmitted by mosquitoes and cause asymptomatic infections of the body cavities of cattle and deer, but neurological signs when ectopic.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Filarioidea (tissue-dwelling filarial parasites, lack lips)
Family:	Onchocercidae (adults loose in tissues or in nodules, viviparous (live birth of microfilariae))
Genus:	*Setaria* (parasitic in peritoneum/eye/scrotum of sheep/cattle/horses, mosquito IH)
Species:	various species cause neurological signs in cattle

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Ten spirurinid superfamilies are recognised: Gnathostomatoidea and Physalopteroidea (buccal cavity weakly cuticularized, 2 large lateral pseudolabia); Habronematoidea and Acuarioidea (buccal cavity well cuticularized, 2 large lateral pseudolabia); Filarioidea, Rictularioidea, Aproctoidea and Diplotriaenoidea (buccal cavity well cuticularized, without pseudolabia); Thelazioidea (long cylindrical buccal cavity well cuticularized, body without caudal alae); and Spiruroidea (short buccal cavity well cuticularized, body with caudal alae).

The superfamily Filarioidea contains long thread-like nematodes which are predominantly tissue-dwelling parasites infecting the body cavities, subcutis, intermuscular tissues, blood vessels or lymphatic systems of terrestrial hosts. These worms are known colloquially as ‘filariae’, ‘filarids’ or ‘filarioids’ [Note: take care with terminology as the cognate family Filariidae (esp. genus *Filaria*) are known colloquially as ‘filariids’, and the unrelated metastrongyle (lungworm) family Filaroididae (genus *Filaroides*) are known colloquially as ‘filaroids’]. Adult filariae have a cylindroid pharynx with an anterior muscular portion and a posterior glandular portion. Males often have spirally-coiled tails, well-developed alae and dissimilar spicules. Females of most species are ovoviviparous (eggs hatch within body of parent) releasing pre-larval stages known as microfilariae (sometimes sheathed). Filariae have indirect life-cycles whereby microfilariae are taken up by blood-sucking or tissue-feeding invertebrates (arthropods, esp. mosquitoes) which act as intermediate hosts for the development of infective L3 larvae. Ten families are recognised: Filariidae and Onchocercidae infecting mammals, birds, reptiles and amphibians; Setariidae infecting mammals;

Aproctidae infecting birds; and Creagrocercidae, Drilonematidae, Homungellidae, Mesidionematidae, Scolecophilidae and Ungellidae infecting terrestrial annelids. Examples of filarioid genera covered in this resource are compared in the following table.

Genus	Definitive hosts	Adults (location)	Microfilariae (location)	Periodicity	Vectors	*Wolbachia* symbiotes
Family Setariidae						
Setaria (42 spp.)	primates, ungulates, rodents, lagomorphs	4-19 cm (body cavities)	140-310 µm sheathed (blood)	-	mosquitoes	absent
Family Filariidae						
Parafilaria (4 spp.)	ungulates	2-7 cm (subcutis)	40-58 x 23-33 µm larvated eggs (skin)	diurnal	flies	absent
Stephanofilaria (7 spp.)	ungulates	0.2-1.4 cm (subcutis)	45-195 µm sheathed (skin)	-	flies	absent
Family Onchocercidae						
Onchocerca (35 spp.)	primates, carnivores, ungulates, rodents	1.5-80 cm (subcutis, ligaments)	105-440 µm unsheathed (skin)	-	flies, midges	present
Mansonella (29 spp.)	primates, carnivores, ungulates, rodents	3-8 cm (subcutis, serosa)	170-300 µm unsheathed (blood/skin)	-	midges, flies, mosquitoes	present
Dirofilaria (34 spp.)	primates, carnivores, ungulates, rodents, lagomorphs, marsupials	4-31 cm (blood vessels)	180-385 µm unsheathed (blood)	-	mosquitoes, flies	present
Dipetalonema, Acanthocheilonema (57 spp.)	primates, carnivores, ungulates, rodents, cingulates, marsupials	1-7 cm (subcutis, serosa)	85-300 µm unsheathed (blood)	-	flies, fleas, lice, ticks	absent
Wuchereria (2 spp.)	primates	2.5-10 cm (lymphatics)	210-320 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Brugia (10 spp.)	primates, carnivores, rodents	1-9 cm (lymphatics)	170-380 µm sheathed (blood)	nocturnal, subperiodic	mosquitoes	present
Loa (3 spp.)	primates, ungulates, rodents	2-7 cm (subcutis, eye)	250-300 µm sheathed (blood)	diurnal	flies	absent

Members of the family Setariidae (formerly classified as the subfamily Setariinae in the family Onchocercidae) typically form medium to large worms in the abdominal cavities of mammals. Three genera are recognised: *Chabfilaria* in edentates, *Setaria* (syn. *Hyraconema*, *Artionema*) in ungulates and hyracoids, and *Papillosetaria* in ungulates. Adult worms have complex cephalic structures (spines, ridges or shield-like thickenings), sclerotized buccal capsules with thin peribuccal rings, and tails with conspicuous conical lappets. Females have a complex vagina and an anterior vulva through which they birth sheathed microfilariae which are transmitted by mosquitoes. Over 40 *Setaria* spp. have been described throughout the world from domestic and wild artiodactyls (mostly bovids and cervids) and perissodactyls (mainly equids). Heavy infections by larvae may cause cerebrospinal filariasis with neurological disorders, resulting in considerable economic losses to some livestock industries.

***Setaria* species**	**Definitive Hosts (DH)**	**Location**	**Vectors/Intermediate Hosts (IH)**	**Distribution**

S. africana	Perissodactyla: rhinocerotid (black rhinoceros); Artiodactyla: bovid (African buffalo, great eland, greater kudu, harnessed bushbuck, common duiker, grey duiker)			Africa
S. bernardi	Artiodactyla: suid (pig)			?
S. bicoronata	Artiodactyla: bovid (Soemmering's gazelle, waterbuck, lechwe, southern reedbuck, African buffalo)			Africa
S. bidentata (syn. *Artionema*)	Artiodactyla: cervid (red brocket)			South America
S. boulengeri	Artiodactyla: bovid (waterbuck, lechwe, Bohor reedbuck, mountain reedbuck)			Africa
S. capreoli	Artiodactyla: cervid (moose, roe deer)			North America
S. castroi	Artiodactyla: suid (desert warthog, bushpig)	peritoneal cavity		Africa
S. cervi (syn. *S. altaica*, *indica*)	Artiodactyla: bovid (cattle, zebu, yak, Asian buffalo, water buffalo, sheep, goat, blackbuck), cervid (moose, roe deer, wapiti, chital, fallow deer, red deer, sika deer, sambar deer, Indian muntjac, black-tailed deer, white-tailed deer, reindeer); Perissodactyla: equid (horse); Rodentia: murid (brown rat)	abdominal and thoracic cavities, mf in blood (sheathed), (larvae may cause neurological signs in aberrant hosts)	Diptera: muscid (*Haematobia stimulans, Haematobosca stimulans, Stomoxys calcitrans*), hippoboscid (*Hippobosca maculata*), tabanid (*Tabanus brunnipenis*), culicid (*Aedes aegypti, albopictus, scatophagoides, Anopheles peditaeniatus, stephensi, subpictus, Armigeres obturbans, Culex fatigans, vishnui, fuscanus*); Ixodida: ixodid (*Boophilus microplus, Haemaphysalis bispinosa*)	Eurasia
S. congolensis	Artiodactyla: suid (warthog, desert warthog)	peritoneum, pleural cavity	mosquito	Africa
S. cornuta	Artiodactyla: bovid (red forest duiker, black-fronted duiker, bushbuck, suni)			Africa
S. digitata (kumri)	Artiodactyla: bovid (cattle, zebu, gayal, buffalo, sheep, goat), cervid (Reeve's muntjac); Perissodactyla: equid (horse); Rodentia: murid (southern multimammate mouse); Lagomorpha: leporid (European rabbit); Primates: cercopithecid (rhesus macaque)	peritoneum, pleural cavity, (larvae may cause neurological or ocular signs in aberrant hosts)	Diptera: culicid (*Aedes togoi, vittatus*, *Armigeres obturbans, Anopheles sinensis, nigerrimus, Culex tritaeniorhynchus*)	Asia, Mauritius
S. dipetalonematoides	Artiodactyla: bovid (duiker)			Africa
S. dubosti	Artiodactyla: bovid (duiker, Peter's duiker)			Africa
S. effilaria	Artiodactyla: tragulid (Java mouse-deer)			Asia
S. equina (syn. *S. lymphatica*) (abdominal worm)	Perissodactyla: equid (horse, Przewalski's horse, donkey, mule, onager, quagga, plains zebra); Artiodactyla: bovid (cattle), camelid (dromedary): Primates: hominid (human)	peritoneum, pleural cavity, (ectopic infections may cause neurological	Diptera: muscid (*Haematobia stimulans*), culicid (*Aedes aegypti, pembaensis, communis, maculatus*)	worldwide

		signs)		
S. gagarini	Artiodactyla: bovid (European bison)			Europe
S. gaillardi	Artiodactyla: bovid (oribi, common duiker)			Africa
S. graberi	Artiodactyla: bovid (southern reedbuck, Bohor reedbuck)	abdominal cavity		Africa
S. hornbyi	Artiodactyla: bovid (roan antelope, sable antelope, common eland, waterbuck, lechwe, steenbok, southern reedbuck, common duiker)			Africa
S. javensis	Artiodactyla: tragulid (mouse-deer)		Diptera: culicid (*Aedes togoi*)	Malaysia
S. kabarga	Artiodactyla: moschid (Siberian musk deer)			Europe
S. labiatopapillosa	Artiodactyla: bovid (cattle, zebu, American bison, European bison, water buffalo, African buffalo, yak, goat, sheep, argali, Cyprus mouflon, alpine ibex, nilgai, southern reedbuck, Cape bushbuck), cervid (moose, roe deer, red deer, sambar deer, Indian muntjac, sika deer), camelid (camel), suid (pig); Perissodactyla: equid (horse); Primates: hominid (human)	peritoneum, pleural cavity (ectopic infections may cause neurological or ocular signs)	Diptera: culicid (*Aedes aegypti, albopictus, caspius, togoi, vexans, Anopheles claviger, hyrcanus, maculopennis, Armigeres obturbans, Culex nilgiricus, Mansonia*?), muscid (*Haematobia stimulans*)	worldwide
S. lamyfortensis	Artiodactyla: bovid (Bohor reedbuck)			Africa
S. longicauda	Artiodactyla: bovid (kob)			Africa
S. loveridgei (syn. *S. hyracis*)	Hyracoidea: procaviid (tree hyrax, yellow-spotted rock hyrax)			Africa
S. machadoi	Artiodactyla: bovid (duiker)			Africa
S. marshalli	Artiodactyla: bovid (cattle, water buffalo); Perissodactyla: equid (horse)	peritoneal cavity, mf in blood, parasites in foetuses, prenatal infection?		Asia
S. pillersi	Artiodactyla: bovid (kob, southern reedbuck, Cape bushbuck)			Africa
S. poultoni	Artiodactyla: bovid (hartebeest, tiang)			Africa
S. rodhaini	Artiodactyla: suid (red river hog)			Africa
S. saegeri	Artiodactyla: bovid (common duiker)			Africa
S. sandersoni	Artiodactyla: bovid (bay duiker)			Africa
S. scalprum	Artiodactyla: bovid (impala, red forest duiker, common duiker, bushbuck, oribi, steenbok, southern reedbuck)			Africa
S. shohoi	Artiodactyla: suid bushpig)			Africa
S. southwelli	Artiodactyla: bovid (duiker)			Africa
S. thomasi	Artiodactyla: suid (pig)	peritoneal cavity		South-East Asia
S. thwaitei	Artiodactyla: bovid (roan antelope, waterbuck, bluebuck)			Africa
S. transcaucasica	Artiodactyla: cervid (moose, roe deer, white-tailed deer)			Eurasia
S. transversata	Artiodactyla: bovid (blue duiker, yellow-backed duiker, bushbuck)			Africa
S. tundra (syn. *S. hartwichi*)	Artiodactyla: cervid (reindeer, roe deer, white-tailed deer, moose)		Diptera: culicid (*Aedes vexans*)	Holarctic
S. yehi	Artiodactyla: cervid (moose, mule			Eurasia

	deer, white-tailed deer, reindeer, woodland caribou, barren-ground caribou)			
S. yorkei	Artiodactyla: bovid (impala, bushbuck)			Africa

Parasite morphology: *Setaria* spp. form 3 distinct morphological stages: adult worms, live young (microfilariae) and a series of larval developmental stages (designated L1-4). Mature female worms in mammalian definitive hosts produce and release microfilariae (pre-larvae) that range in size from 140-310 x 5-8 µm depending on species. The microfilariae are sheathed and surrounded closely by vitelline eggshell membranes with some free space observed anteriorly and posteriorly. They have rounded heads and straight tapering tails and the nuclear column formed by the primordia of internal organs does not extend to the tip of the tail. In dipteran intermediate hosts, the microfilariae exsheath and moult twice to form infective third-stage larvae (L3) measuring from 1.5-2.6 mm in length and characterised by tails with a terminal papilla and 2 small lateral subterminal papillae. Back in the definitive host, the larvae moult twice to form thin slender adult worms measuring up to 190 mm long. Adults are covered by a tough flexible cuticle with a milky translucent appearance. They have elaborate heads, sometimes with spines, and a chitinous cuticular ring surrounding the mouth forming 4 lip-like structures. They have a tubular digestive system with a well-sclerotized buccal capsule (thin peribuccal ring present) and an oesophagus with a well-developed glandular portion. Adults have tapering curved tails with conspicuous conical lappets. Mature worms demonstrate marked sexual dimorphism, with females being larger than males (measuring 60-190 x 1.0-1.2 mm cf. 40-80 x 0.4-0.6 mm). Males have 2 unequal dissimilar copulatory spicules (left spicule 370-660 µm long, right spicule 120-210 µm long sometimes ending in a claw). Females may have a spiny knob or a few large conical projections on the tail, 2 large ovaries with oviducts and uteri opening into an anterior vulva with a muscular ovejector. Mature female worms are ovoviviparous and produce embryonated eggs which develop internally to release sheathed microfilariae. Different *Setaria* spp. are distinguished primarily on the basis of morphotypic differences in the peribuccal crown (projections, lips, mouth shape) and tail (size, shape, appendages).

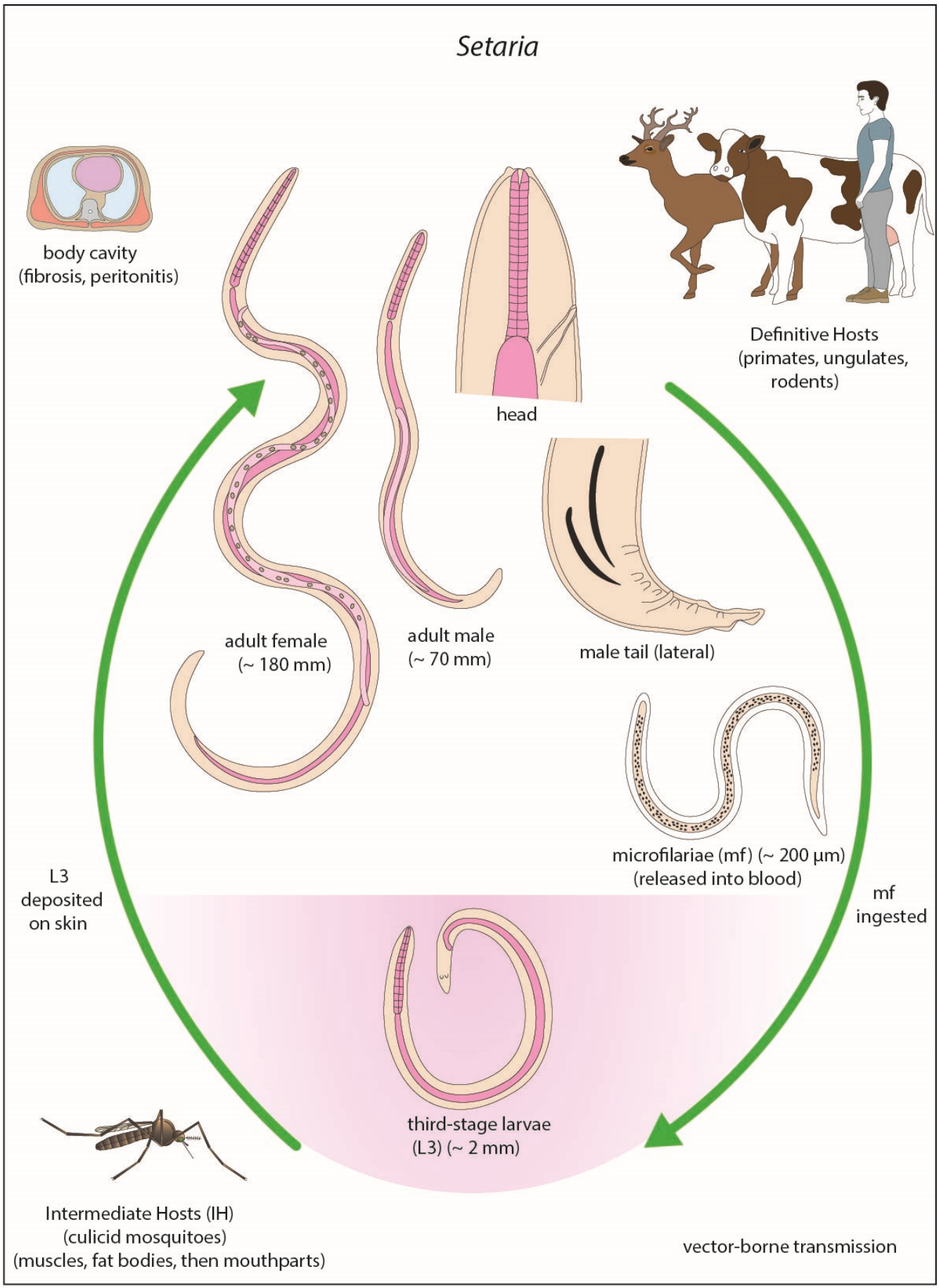
Site of infection: Adult *Setaria* worms commonly infect the abdominal (peritoneal) cavity of domesticated and wild mammals, mainly artiodactyls and perissodactyls, and microfilariae occur in the peripheral circulation. Occasionally, pre-adult larval stages (L4) or sub-adults (L5) may invade the central nervous system or eyes of their hosts, or localize under the serosal surfaces of internal organs (liver, spleen, lungs, heart). Larval development (L1-3) occurs in the thoracic muscles or fat bodies of their dipteran insect vectors.

Pathogenesis: Infections are mostly asymptomatic as the adult worms cause little damage in the body cavities of their mammalian hosts, although they may cause focal fibrosis and occasionally mild focal peritonitis. Infections by microfilariae has been associated with systemic clinical signs in horses, involving fever, depression, stiff gait and poor body condition. Immature developmental stages may sometimes invade the central nervous system of unusual (atypical?) susceptible hosts (mainly horses, sheep and goats, particularly the young) causing traumatic damage to nerve tracts and the neuropil (especially in the spinal cord), resulting in neurological manifestations (verminous meningoencephalomyelitis) including muscular weakness, ataxia, conscious proprioceptive deficits, uncoordinated movements of the hindlimbs or all four limbs, atonic tail and bladder, paralysis and death. Disease may appear overnight and rapidly worsen within days to become life-threatening. Occasionally, infections by larvae or adult worms may cause ocular setariasis (commonly known as eye worm) in horses and donkeys, with clinical signs including excessive lacrimation, photophobia, blepharospasm, corneal opacities and blindness.

Developmental cycle and mode of transmission: Like other filarial worms, *Setaria* spp. have indirect life-cycles involving transmission between vertebrate definitive hosts (mammals) and invertebrate intermediate hosts (haematophagous insects). Adult female worms release microfilariae which move from the host abdominal cavity into the bloodstream where they are taken up by blood-feeding dipteran insects. Some *Setaria* spp. exhibit nocturnal subperiodicity (with maximum microfilaraemia observed at night) while other species do not demonstrate any periodicity. The former apparently utilize blood-sucking culicid mosquitoes as intermediate hosts, while the latter often use pool-feeding muscid or tabanid flies. Ingested microfilariae exsheath in the insect gut and migrate through the haemocoel to the thoracic muscles (sometimes the fat body). Here they transform to sausage-shaped first-stage larvae (L1) in 5 days, moult to second-stage larvae (L2) in 5-12 days and then to third-stage larvae (L3) in 10-15 days. L3 migrate to the haemocoel where they develop into infective stages over several days before moving to the insect mouthparts. When the insect next feeds, infective L3 are expelled from the labium and are deposited on the skin of the mammalian host where they penetrate the puncture wound (contaminative transmission rather than inoculative salivary transmission). Infective larvae migrate to the peritoneal cavity where they moult and complete development to adult worms over several months. After mating, female worms birth live microfilariae which accumulate in the host circulation. The prepatent period (time between infection and first release of microfilariae) ranges from 5-8 months depending on the host and worm species. Adult worms may live for several years and continue to produce microfilariae. Transplacental transmission has also been reported in several pregnant animals.

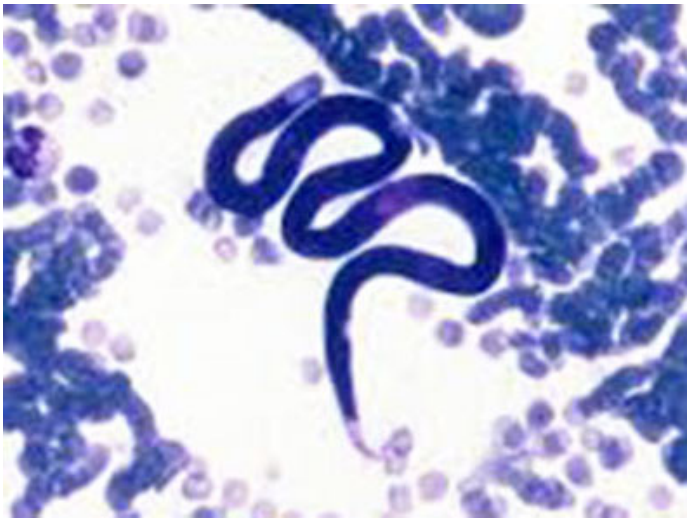
Differential diagnosis: Infections are conventionally diagnosed by the microscopic detection of microfilariae in blood samples, either wet mounts, thick or thin blood smears or concentrates following membrane filtration (5 µm pore size) or centrifugation of lysates (after formalin or saponin haemolytic treatment). Microfilariae may be visualized in wet mounts or concentrates using methylene blue or cresyl blue supravital stains or permanent mounts may be stained with Giemsa, Delafield's haematoxylin, or Field's rapid stain. Many infections are detected as incidental gross or histopathological findings during surgery or following necropsy, particularly migrating larvae in nervous tissues. Ocular eyeworm infections may sometimes be diagnosed by the detection of parasites in the anterior chamber and aqueous humor of the eye.

Treatment and control: Several anthelmintic drugs have been found to be reasonably effective against *Setaria* microfilariae, including the macrocyclic lactones (ivermectin, moxidectin) and the diethylenediamine (diethylcarbamazine), but they were not effective against adult worms. Some hosts required supportive therapy with anti-inflammatory agents to minimise adverse reactions to material suddenly released from many dying parasites. There have been reports of the successful surgical removal of worms from the anterior chamber of equids, but various complications have also been reported, such as corneal oedema, phthisis bulbi (shrunken nonfunctional eye), and scarring and prolapse of the iris. Various preventive measures have been used to break transmission cycles, mainly in cattle, through the use of insecticides to control vector populations, environmental management to eliminate vector breeding sites, and protecting hosts against vector bites through the use of insect repellents (topical applications or impregnated tags) and indoor housing (with screens).


Setaria
body cavity
(fibrosis, peritonitis)
Definitive Hosts
(primates, ungulates,
rodents)
head
adult female
(~ 180 mm)
adult male
(~ 70 mm)
male tail (lateral)
microfilariae (mf) (~ 200 µm)
(released into blood)
L3
deposited
on skin
mf
ingested
third-stage larvae
(L3) (~ 2 mm)
Intermediate Hosts (IH)
(culicid mosquitoes)
(muscles, fat bodies, then mouthparts)
vector-borne transmission



Setaria adult worms



Setaria microfilaria

Camallanus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. The latter contains the infraorder Spiruromorpha: an enigmatic clade linked by molecular characters, but all having indirect life-cycles involving one or more intermediate hosts, the first invariably being an arthropod. Most possess two trilobed lips (sometimes greatly reduced), a bipartite oesophagus (anterior muscular, posterior glandular) and non-bursate males with coiled tails and two dissimilar spicules. Several superfamilies are recognised: including camallanoids with well-developed buccal capsules (many containing two sclerotized valves) found in the intestines of fishes, amphibians and reptiles. Infections by *Camallanus* spp. are commonly found in the intestines of freshwater ornamental fish, red worms sometimes protruding from the anus.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
Infraorder:	Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily:	Camallanoidea (conspicuous phasmids, L1 with dorsal prominence/tooth, ovoviviparous, L1-L3 in copepod)
Family:	Camallanidae (buccal capsule well-developed, with pair sclerotized valves, male with caudal alae)
Genus:	*Camallanus* (parasitic in intestines of fish)
Species:	various species cause enteritis in fish

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate

classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha ('rod-shaped' buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha ('jaw-mouthed' due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Two camallaninid superfamilies are recognised: Camallanoidea (buccal cavity well-developed, tiny internal labial papillae, gut parasites); and Dracunculoidea (buccal cavity weakly-developed, prominent internal labial papillae, tissue parasites).

The superfamily Camallanoidea contains small red nematodes with large buccal capsules (often orange in colour). They are gastrointestinal parasites of predaceous lower vertebrates (fish, amphibians and reptiles) usually within aquatic habitats (freshwater, estuarine or marine). Female worms are viviparous and birth live larvae (L1) which are released into the water column. Most species have indirect heteroxenous life-cycles involving larval development in crustacean intermediate hosts (copepods), although some species may utilize paratenic hosts (usually planktivorous fish) and a few species have been found to have direct homoxenous cycles with final hosts ingesting free-living larvae. Numerous genera have been described in the single family Camallinidae, principally on the basis of morphological differences in the prominent buccal capsule. However, it was recently noticed that buccal capsule morphology varied within several species, with male and female worms of the same species having different buccal structures. This led to several taxonomic revisions whereby many genera were synonymized and others were demoted to subgeneric status. At present, 12 genera are currently recognised in 3 subfamilies: Procamallaninae with rounded buccal capsules (*Batrachocomallanus*, *Malayocamallanus*, *Onchocamallanus*, *Platocamallanus*, *Procamallanus* (syn. *Indocamallanus*) (incl. subgenera *Denticamallanus, Isospiculus*, *Monospiculus*, *Procamallanus* (syn. *Spirocotyle*), *Punctocamallanus*, *Spirocamallanoides*, *Spirocamallanus*)); Camallaninae with buccal capsules divided by lateral valves into large anterior chamber and minute posterior chamber (*Camallanides, Camallanus* (incl subgenera *Camallanus, Zeylanema*) *Neocamallanus* (syn. *Neozeylanema*), *Neoparacamallanus,*

Oncophora (syn. *Piscilania*), *Serpinema*); and Paracamallaninae with buccal capsules divided by lateral valves into anterior and posterior chambers almost equal in depth (*Paracamallanus* (incl subgenera *Paracamallanus*, *Dentocamallanus*)). The genus *Camallanus* is characterised by the possession of buccal capsules divided into 2 chambers by a pair of sclerotized valves (the second chamber being very small). The dorsoventral margins of the buccal capsule also have 3 posteriorly-directed rods (tridents) on each side. Over 110 species have been described, mostly in predatory fish, but some in amphibians and reptiles (esp. turtles). Many species are euryxenous and have a broad host range, although a few species appear to be stenoxenous or oioxenous and restricted to a few closely-related host species. Infections frequently occur in freshwater ornamental fish and are clearly evident when red adult worms protrude from the anus of their hosts.

***Camallanus* species**	**Definitive Hosts**	**Location**	**Intermediate Hosts [Paratenic Hosts (PH)]**	**Distribution**
C. acaudatus	Osteoglossiformes: osteoglossid (silver arowana)	intestines		South America
C. alatae	Anura: dicroglossid (Indian bullfrog)			India
C. alii	Cypriniformes: cyprinid (mud carp)	intestines		Asia
C. amazonicus (syn. *Serpinema*)	Testudines: kinosternid (scorpion mud turtle), podocnemidid (Arrau turtle)	intestines		South America
C. anabantis (*anabantus*) (syn. *Zeylanema*)	Anabantiformes: anabantid (climbing perch), channid (dwarf snakehead, spotted snakehead), osphronemid (Howong betta, three-spot gourami); Cypriniformes: cyprinid (filament barb, slender rasbora); Siluriformes: clariid (walking catfish); Synbranchiformes: mastacembelid (zig-zag eel)	intestines, caeca	Copepoda: cyclopid (*Mesocyclops leuckarti*)	Asia
C. ancylodirus	Cypriniformes: catostomatid (quillback); Perciformes: centrarchid (green sunfish, bluegill); Gadiformes: lotid (burbot)			North America
C. aotea	Perciformes: emmelichthyid (bigscale rubyfish); Scombriformes: scombrid (yellowfin tuna, bigeye tuna)			worldwide
C. atridentus	Anabantiformes: channid (spotted snakehead)			India
C. atropusi	Carangiformes: carangid (cleftbelly trevally)	intestines		Indo-Pacific
C. aurangabadensis	Anabantiformes: channid (striped snakehead)	intestines		India
C. bahli (syn. *Neozeylanema*)	Anabantiformes: anabantid (climbing perch)			Asia
C. barilii	Cypriniformes: cyprinid (trout barb)			India
C. barragi (syn. *Zeylanema*)	Synbranchiformes: mastacembelid (zig-zag eel)			
C. baylisi	Anura: bufonid (European green toad), dicroglossid (Indian bullfrog)			Eurasia
C. beveridgei	Testudines: chelid (northern snapping turtle)	intestines		Australia
C. bispiculus	Clupeiformes: chirocentrid (dorab wolf-herring); Anguilliformes: anguillid (European eel)	intestines		Indo-Pacific
C. boomkeri	Anabantiformes: channid (Ceylon snakehead)	swim bladder		Asia
C. bufonis	Anura: bufonid (toad)			
C. cancelai (*cancilai*)	Beloniformes: belonid (freshwater garfish)			Asia
C. carangis (syn. *C. paracarangis*)	Carangiformes: carangid (yellowtail scad, trevally); Scorpaeniformes: platycephalid (fringe-eye flathead); Perciformes: serranid (honeycomb grouper), leiognathid (toothpony, pony-fish), priacanthid (glasseye), trichiurid (largehead hairtail), terapontid (spiny-cheeked grunter), nemipterid (fork-tailed threadfin bream), mullid (yellow-striped goatfish, white-saddle goatfish); Scombriformes: scombrid (chub mackerel); Siluriformes: ariid (veined catfish)	intestines		Indo-Pacific

C. ceylonensis (syn. *Neoparacamallanus*)	Siluriformes: silurid (helicopter catfish)			Asia
C. charsaddiensis	Anabantiformes: channid (dwarf snakehead)			Asia
C. chauhani	Perciformes: trichiurid (smallhead hairtail)	intestines		Indo-Pacific
C. chiralensis (syn. *Zeylanema*)	Anabantiformes: channid (spotted snakehead)	intestines		India
C. chelonius (syn. *Serpinema, C. nithoggi*)	Testudines: pelomedusid (serrated hinged terrapin), chelid (broad-shelled river turtle, saw-shelled turtle, Krefft's turtle)	intestines		Africa, Australia
C. chorinemi	Carangiformes: carangid (double-spotted queenfish, barred queenfish); Clupeiformes: chirocentrid (dorab wolf-herring)			Indo-Pacific
C. cinereusis	Anguilliformes: muraenesocid (daggertooth pike conger)			worldwide
C. corderoi	Osmeriformes: galaxiid (peladilla, puye, tollo, common galaxias); Atheriniformes: atherinopsid (Chilean silverside, Patagonian freshwater pejerrey); Characiformes: characid (pocha); Salmoniformes: salmonid (rainbow trout, brown trout, brook trout); Perciformes: percichthyid (largemouth perch, Creole perch)			Americas
C. cotti (syn. *C. fotedari*)	Cyprinodontiformes: poeciliid (rainbow fish, shortfin molly, green swordtail, southern platyfish), nothobranchiid (blue lyretail); Cypriniformes: cyprinid (predatory carp, zebrafish, yellowcheek, Mongolian redfin, sharpbelly, minnow, white Amur bream, barbel chub, pale chub, common snow trout), nemacheilid (Kashmiri kobertrulling); Gobiiformes: oxudercid (scribbled goby, Hawaiin freshwater goby, Naniha goby), eleotrid (Hawaiin sleeper); Siluriformes: sisorid (devil catfish), bagrid (Korean bullhead); Scorpaeniformes: cottid (utsusemi); Anabantiformes: osphronemid (paradise fish, paradise gourami), channid (northern snakehead); Salmoniformes: salmonid (masu salmon); Perciformes: percid (European perch), polynemid (Indian threadfin); Centrarchiformes: percichthyid (mandarin fish); Myliobatiformes: potamotrygonid (freshwater stingray)	intestines	Copepoda: cyclopid (*Macrocylops albidus, Cyclops*)	Eurasia, Africa
C. ctenopomae	Perciformes: anabantid (tailspot ctenopoma)			Africa
C. cynophylectis	Anura: dicroglossid (skittering frog)			India
C. dimitrovi	Anura: alytid (painted frog)			Europe
C. dollfusi	Perciformes: trichiurid (ribbonfish, largehead hairtail); Pleuronectiformes: soleid (elongated sole)	intestines		Indo-Pacific
C. emydidius	Testudines: emydid (black-bellied slider)	intestines		South America
C. equispiculus (syn. *Neoparacamallanus*)	Siluriformes: heteropneustid (Asian stinging catfish)			Asia
C. farooqii	Perciformes: sciaenid (sin croaker), haemulid (saddle grunt); Carangiformes: carangid (giant queenfish, double-spotted queenfish, needle-scaled queenfish)			Indo-Pacific
C. fernandoi	Anabantiformes: channid (spotted snakehead, snakehead murrel)			India
C. gibsonia	Anabantiformes: channid (snakehead murrel)			India
C. gomtii	Anabantiformes: channid (spotted snakehead)			India
C. guptae	Siluriformes: ariid (veined catfish);	intestines		Indo-Pacific

	Perciformes: trichiurid (smallhead hairtail)			
C. guttatii	Scombriformes: scombrid (Indo-Pacific king mackerel)			Indo-Pacific
C. hampalae	Cypriniformes: cyprinid (hampala barb)			Asia
C. hypophthalmichthys	Cypriniformes: cyprinid (bighead carp, silver carp, black carp)	intestines	Copepoda: cyclopid (*Mesocyclops leuckarti*)	Asia
C. indicus	Anura: dicroglossid (skittering frog); Carangiformes: carangid (barred queenfish)			Indo-Pacific
C. inglisi	Anura: dicroglossid (Indian bullfrog)			India
C. intermedius (syn. *Serpinema*)	Testudines: geomydid (Chinese pond turtle)			Asia
C. intestinalus	Anabantiformes: channid (spotted snakehead, snakehead murrel)			Asia
C. jadhavae	Anabantiformes: channid (spotted snakehead)	intestines		India
C. jiyuensis	Gobiiformes: oxudercid (shokihaze goby)	intestines		China
C. jodhpurensis	Anura: dicroglossid (skittering frog)			India
C. jullundurense	Synbranchiformes: mastacembelid (zig-zag eel)			Asia
C. kaapstaadi	Anura: pipid (African clawed frog, Lake Victoria clawed frog, DeWitte's clawed frog, Marsabit clawed frog, Fraser's plantanna, Muller's plantanna)			Africa
C. kachugae (syn. *Serpinema*)	Testudines: geomydid (brown roofed turtle), kinosternid (scorpion mud turtle)			Asia, South America
C. karachiensis	Scombriformes: scombrid (Indian mackerel)			Asia
C. khalili	Cypriniformes: cyprinid (common snowtrout); Osteoglossiformes: notopterid (bronze featherback)			India
C. kherai	Anabantiformes: channid (spotted snakehead)			India
C. kirandensis	Rhinopristiformes: pristid (saw fish); Cypriniformes: cyprinid (barbel, rednose labeo, Nile carp)			Africa
C. kollerensis	Anabantiformes: channid (spotted snakehead), anabantid (climbing perch)			India
C. kulasirii (syn. *Zeylanema*)	Anabantiformes: channid (spotted snakehead)			India
C. kumaoni	Cypriniformes: cyprinid (korang, stoneroller)			India
C. lacustris (syn. *Echinorhynchus*)	Cypriniformes: cyprinid (common carp, sabre carp, common roach, common bream, white bream, vimba bream, common bleak, common dace, common minnow, Marmara chub, tench, rudd, zope, asp, ide); Perciformes: percid (European perch, ruffe, Eurasian ruffe, zander, Volga zander, common zingel); Anguilliformes: anguillid (European eel); Cichliformes: cichlid (bay snook, firemouth cichlid, blackgullet cichlid); Salmoniformes: salmonid (masu salmon, Atlantic salmon, grayling, rainbow trout, brown trout, Arctic char, European cisco, common whitefish, northern whitefish, Siberian taimen, beloribitsa); Scorpaeniformes: cottid (European bullhead, alpine bullhead, fourhorn sculpin); Esociformes: esocid (northern pike); Gasterosteiformes: gasterosteid (three-spined stickleback, nine-spine stickleback); Gobiiformes: gobiid (bighead goby, sand goby, tubenose goby); Gadiformes: lotid (burbot); Osmeriformes: osmerid (European smelt); Siluriformes: silurid (Wels catfish); Pleuronectiformes: pleuronectid (European	intestines	Copepoda: cyclopid (*Megacyclops viridis, Macrocyclops albidus, Acanthocyclops vernalis, Mesocyclops leuckarti, Eucyclops serrulatus, Cyclops strenuus, quadricornis*), canthocamptid (*Canthocamptus staphylinus*) [plus PH: nonpredatory cyprinids, cobitids]	worldwide

	flounder), scophthalmid (turbot); Acipenseriformes: acipenserid (dwarf sturgeon); Serpentes: colubrid (dice snake)			
C. lissemysus (syn. *Serpinema*)	Testudines: trionychid (Indian flapshell turtle)			India
C. longicaudatus	Cypriniformes: cyprinid (Assuan labeo)			Africa
C. longitridentatus (syn. *Neoparacamallanus*)	Siluriformes: clariid (walking catfish)	intestines		Asia
C. luchnowensis	Anabantiformes: channid (striped snakehead)			India
C. macrocephalus	Anura: pipid (Marsabit clawed frog)			Africa
C. maculatus	Cyprinodontiformes: poeciliid (southern platyfish)			South America
C. magathi (syn. *Serpinema, C. parvus*)	Testudines: kinosternid (Mexican mud turtle)	intestines		Americas
C. magna (*magnus*) (syn. *Zeylanema, Paracamallanus*)	Synbranchiformes: mastacembelid (barred spiny eel, zig-zag eel)			Asia
C. magnavaginus (syn. *C. cinereusis*)	Anguilliformes: muraenesocid (daggertooth pike conger)			Asia
C. magnorugosus	Testudines: emydid (ornate slider)			North America
C. marinus	Carangiformes: carangid (yellowtail scad, white-tipped mackerel scad, oxeye scad); Scombriformes: nomeid (cubehead), scombrid (narrow-barred Spanish mackerel); Scorpaeniformes: platycephalid (fringe-eye flathead); Perciformes: leiognathid (toothpony), trichiurid (largehead hairtail)	intestines		Indo-Pacific
C. mastacembeli (syn. *Zeylanema*)	Synbranchiformes: mastacembelid (zig-zag eel)			Asia
C. melanocephalus	Scombriformes: scombrid (bluefin tuna, bullet tuna, Atlantic bonito, Atlantic chub mackerel)			Atlantic
C. microcephalus (syn. *Serpinema*)	Testudines: geomydid (Caspian turtle), emydid (pond slider, painted turtle, map turtle, Blanding's turtle), chelydrid (snapping turtle)	stomach, intestines		North America, Europe
C. monospiculatus (syn. *Serpinema*)	Testudines: chelid (common toad-headed turtle, tuberculate toad-headed turtle, Geoffroy's toad-headed turtle)			South America
C. moraveci	Cyprinodontiformes: poeciliid (millionfish); Cichliformes: cichlid (freshwater angelfish)			South America
C. mujibia (syn. *Zeylanema*)	Anura: dicroglossid (skittering frog)			Asia
C. multilineatus	Cypriniformes: catostomid (highfin carpsucker)			Asia
C. multiruga	Anura: ranid (West African frog)	intestines		Africa
C. mustelus	Carcharhiniformes: triakid (smooth-hound)			Pacific
C. myopsi	Aulopiformes: synodontid (bluntnose lizardfish)			Atlantic
C. nandai	Anabantiformes: nanid (Gangetic leaf-fish)			Asia
C. nigrescens	Anura: dicroglossid (green pond frog)	intestines		Europe
C. nigriscens	Testudines: geomydid (Indian roofed turtle)			India
C. nodulosus	Anura: dicroglossid (skittering frog)			Asia
C. octorugatus (syn. *Serpinema*)	Testudines: geoemydid (Amboina box turtle)	intestines		Asia
C. ophichthyi	Anguilliformes: ophichthid (rice paddy eel)	intestines		Asia
C. ophiocephali (*ophicepahli*) (syn. *Neocamallanus, C. adamsi*)	Anabantiformes: channid (snakehead murrel, striped snakehead, spotted snakehead, bullseye snakehead); Siluriformes: silurid (helicopter catfish)	intestines	Copepoda: cyclopid (*Mesocyclops leuckarti, Thermocyclops*	India

			crassus)	
C. oxycephalus	Perciformes: moronid (white bass), percid (yellow perch, common logperch, walleye, scaly sand darter, Iowa darter), centrarchid (small-mouth bass, large-mouth bass, rock bass, spotted bass, redbreast sunfish, green sunfish, long-ear sunfish, red-ear sunfish, red-spotted sunfish, spotted sunfish, pumpkinseed, warmouth, bluegill, black crappie), sciaenid (freshwater drum); Cypriniformes: cyprinid (spotfin shiner, emerald shiner, golden shiner), catostomid (quillback); Cyprinodontiformes: fundulid (banded killifish); Osmeriformes: osmerid (rainbow smelt); Clupeiformes: clupeid (alewife); Amiiformes: amiid (bowfin); Characiformes: characid (Mexican tetra); Cichliformes: cichlid (Texas cichlid); Esociformes: esocid (northern pike); Siluriformes: ictalurid (blue catfish); Gadiformes: lotid (burbot); Salmoniformes: salmonid (coho salmon, sock-eye salmon)	intestines	Copepoda: cyclopid (*Cyclops bicuspidatus, vernalis*) [plus PH: Cypriniformes: cyprinid (spotfin shiner, emerald shiner); Osmeriformes: osmerid (rainbow smelt); Perciformes: sciaenid (freshwater drum); Clupeiformes: clupeid (alewife)]	North America
C. oxygasterae	Cypriniformes: cyprinid (large razorbelly minnow)			North America, India
C. papillifer	Acipenseriformes: acipenserid (European sera sturgeon)			Europe
C. patani	Synbranchiformes: mastacembelid (zig-zag eel)			Asia
C. pearsei (syn. *Zeylanema*)	Anabantiformes: anabantid (climbing perch), channid (dwarf snakehead, striped snakehead); Cypriniformes: cyprinid (slender rasbora)			Asia
C. pentkotai	Clupeiformes: chirocentrid (dorab wolf-herring); Perciformes: sparid (gold-lined seabream), mullid (ubakan); Aulopiformes: synodontid (bluntnose lizardfish);	intestines		Indo-Pacific
C. pernandoi	Anabantiformes: channid (spotted snakehead)			Asia
C. polyodontis	Acipenseriformes: polyodontid (American paddlefish)			North America
C. polypteri	Siluriformes: clariid (mudfish), mochokid (wahrindi); Polypteriformes: polypterid (Nile bichir)			Africa
C. prashadi	Anura: dicroglossid (Indian bullfrog)	intestines		India
C. praveeni	Cypriniformes: cyprinid (ticto barb)	ovary		India
C. psettodi	Pleuronectiformes: psettodid (Indian halibut)			India
C. puriensis	Siluriformes: ariid (veined catfish)	intestines		Asia
C. qadrii	Perciformes: sciaenid (black-spotted croaker)			Indo-Pacific
C. ranae	Anura: dicroglossid (skittering frog, Indian bullfrog)			Asia
C. salmonae	Salmoniformes: salmonid (salmon)			India
C. satyapali	Cypriniformes: cyprinid (vagra baril)			India
C. sauridai	Synbranchiformes: mastacembelid (zig-zag eel)	intestines		India
C. scabrae	Testudines: dermatemydid (hickatee)			South America
C. siluranae	Anura: pipid (western clawed frog)			Africa
C. spinosa (syn. *Zeylanema*)	Anabantiformes: osphronemid (spotted betta)	intestines		Malaya
C. sprenti	Testudines: chelid (saw-shelled turtle, Krefft's turtle)	intestines		Australia
C. surmai (syn. *C. goaensis*)	Scombriformes: scombrid (Indo-Pacific king mackerel)			Indo-Pacific
C. sweeti	Anabantiformes: channid (spotted snakehead,	intestines	Copepoda: cyclopid	Asia

(syn. *Paracamallanus*)	dwarf snakehead), anabantid (climbing perch)		(*Mesocyclops leuckarti, hyalinus*) [plus PH: Cypriniformes: cobitid (spotted loach), cyprinid (redside barb, twospot barb); Cyprinodontiformes: poeciliid (gambusia)]	
C. testudineusi	Anabantiformes: anabantid (climbing perch)			Asia
C. thapar	Anura: dicroglossid (Indian bullfrog)			Asia
C. thaparus	Anabantiformes: channid (snakehead murrel)			Asia
C. therapsi	Centrarchiformes: terapontid (large-scaled terapon)	intestines		Indo-Pacific
C. tholukodensis	Siluriformes: bagrid (Gangetic mystus)			India
C. tigrinis	Anura: dicroglossid (Indian bullfrog)			Asia
C. trichiuris (*trichiurusi*)	Perciformes: trichiurid (largehead hairtail, smallhead hairtail); Siluriformes: ariid (veined catfish)	intestines		Indo-Pacific
C. tridentatus (syn. *Cucullanus*)	Osteoglossiformes: osteoglossid (silver arowana), arapinnid (pirarucu); Perciformes: percichthyid (large-mouth perch, creole perch); Salmoniformes: salmonid (rainbow trout, brook trout)			Americas
C. trispinosus (syn. *Serpinema trisponosum*)	Testudines: emydid (red-eared slider, pond slider, painted turtle), chelydrid (snapping turtle)	stomach, intestines	[plus PH: Gastropoda: lymnaeid (*Lymnaea stagnalis*)]	North America
C. truncatus (syn. *Cucullanus*)	Perciformes: percid (common perch, yellow perch, European perch, ruffe, striped ruffe, Eurasian ruffe, European chub, ide, zander, Volga zander, zingel); Cypriniformes: cyprinid (sabre carp, common bream, gudgeon, white-finned gudgeon, asp); Gadiformes: lotid (burbot); Salmoniformes: salmonid (European whitefish); Scorpaeniformes: cottid (European bullhead); Esociformes: esocid (northern pike); Siluriformes: bagrid (mystus), silurid (wels catfish); Osmeriformes: osmerid (European smelt); Pleuronectiformes: pleuronectid (flounder); Salmoniformes: salmonid (Atlantic salmon, Arctic char, brown trout); Anguilliformes: anguillid (European eel)		Copepoda: cyclopid (*Mesocyclops leuckarti, Acanthocyclops viridis, Macrocyclops albidus, Cyclops strenuus, Megacyclops viridis*) [plus PH: amphibians, fish]	Eurasia
C. tuckeri	Testudines: chelid (northern red-faced turtle, sandstone snake-necked turtle)	intestines		Australia
C. undulatus (syn. *Serpinema, C. viviparus*)	Testudines: geoemydid (Chinese pond turtle)	intestines		Asia
C. unispiculus	Synbranchiformes: mastacembelid (zig-zag eel): Anura: dicroglossid (skittering frog)			Asia
C. vachaii	Siluriformes: schilbeid (schilbid catfish)			Asia
C. varanasiensis	Siluriformes: bagrid (rita)			Asia
C. viastimili	Anura: dicroglossid (skittering frog)			Asia
C. waelhreow	Testudines: chelid (eastern short-necked turtle, broad-shelled river turtle, Krefft's turtle)	intestines		Australia
C. xenentodoni (syn. *C. cancelai*)	Beloniformes: belonid (freshwater garfish); Synbranchiformes: mastacembelid (lesser spiny eel)		Copepoda: cyclopid (*Mesocyclops crassus, leuckarti*)	Asia
C. xenopodis (syn. *Procamallanus, Spirocamallanus*)	Anura: pipid (African clawed toad, Marsabit clawed frog)	stomach	Copepoda: cyclopid (*Thermocyclops infrequens, Mesocyclops leuckarti*)	Africa

C. yehi	Anabantiformes: channid (striped snakehead)	intestines		Asia
C. zacconis	Cypriniformes: cyprinid (dark chub); Anguilliformes: anguillid (Japanese eel)		Copepoda: cyclopid (*Mesocyclops leuckarti*)	China

In addition to commonly accepted synonyms (given in the Table above), several recent review papers have endeavoured to synonymize many *Camallanus* spp. on the basis of their pleomorphic structural features and similar host ranges and distributions; in particular; *C. anabantis* (= *testudineusi, unisiculus, bahli, jullundurense*); *C. atroposi* (= *dollfusi, chauhani, guptae, ophichthyi, pentkotai, puriensis, therapsi, trichiuris/trichiurusi*); *C. aurangabadensis* (= *ophiocephali*); *C. chorinemi* (= *ophichthyi, indicus*); *C. cotti* (= *fotedari, jiyuensis, incognitus, moraveci, zacconis*); *C. lacustris* (= *wolgensis, Cucullanus alatus, anguillae, armatus, cernuae, coronatus, elegans, lucii, luciopercae, papillosus, percae, tincae, viviparus*); *C. microcephalus* (= *confusus, testudinis, seurati, Cucullanus dumerilii*); *C. nodulosus* (= *inglisi, thapari*); *C. sweeti* (= *testudineusi, ophiocephali*); and *C. trispinosus* (= *americanus, chelydrae, cyathocephalus, elegans, floridianae, magnarugosus, microcephalus, pipientis, scabrae, troosti*), but further studies are warranted due to imperfect or inconsistent descriptions.

Parasite morphology: Camallanid nematodes form 2 different types of stages in their developmental cycles: larvae; and adult worms. Gravid females are ovoviviparous and produce eggs which hatch *in utero* releasing first-stage larvae (L1). The larvae are elongate and slender, measuring from 260-650 µm in length depending on species, and have rounded heads with a small dorsal cuticular tooth and attenuated tails. Infective third-stage larvae (L3) are usually orange in colour and elongate, measuring from 420-910 µm in length depending on species, but stouter. They have tapering tails armed with a few terminal spines (mucrons) and already have well-developed buccal cavities characteristic of camallanids. Adult worms are small (measuring from 2-16 mm in length) but are readily recognizable by their red body colour (often discoloured to white in fixed samples) and their prominent orange-brown buccal capsules (often discoloured to yellow in fixed samples). The buccal capsules of camallanid worms may be rounded without valves (subfamily Procamallaninae) or segmented with 2 sclerotized valves (subfamily Camallininae). The interior of the capsule may be smooth, ridged or granular, and the capsule margins may be clear or supported by posteriorly-directed rod(s) and sometimes lateral tridents. The mouths of *Camallanus* spp. appear slit-like due to the presence of 2 valves and the larger anterior chamber of the buccal capsule is ridged or granular and supported by a pair of tridents. Adult worms possess a bipartite oesophagus (with a short anterior muscular and a longer posterior glandular section) connected to the tubular intestines and rectum terminating in a posterior subterminal anus. Worms are covered by a thin flexible cuticle often with fine transverse striations and they have conspicuous anterior and posterior papillae. Adult worms are sexually dimorphic, female worms being larger than males. Mature males have coiled tails rolled ventrally and they have small caudal alae, 2 dissimilar unequal spicules (no gubernaculum) and a single anterior testis (often twisted or reflexed). Mature females have a single ovary, a posterior uterus and a vulva opening near the middle of the body, sometimes with elevated vulvar lips. In gravid females, the uterus is filled with small eggs (30-40 µm in diameter) which hatch internally releasing L1 (coiled *in utero* but over 260 µm long).

Site of infection: Adult camallanid worms infect the gastrointestinal tracts of their vertebrate definitive hosts, some infecting the stomach, some the small intestines and some the large intestines. Many species in small freshwater fish may often be seen protruding from the anus of their hosts. Larval stages develop in the haemocoel of copepodid intermediate hosts. Various species have also been found to infect paratenic hosts (amphibians and planktivorous fish), being found as L3 in the gut or sometimes encapsulated as L3 or L4 in host tissues (usually the mesenteries).

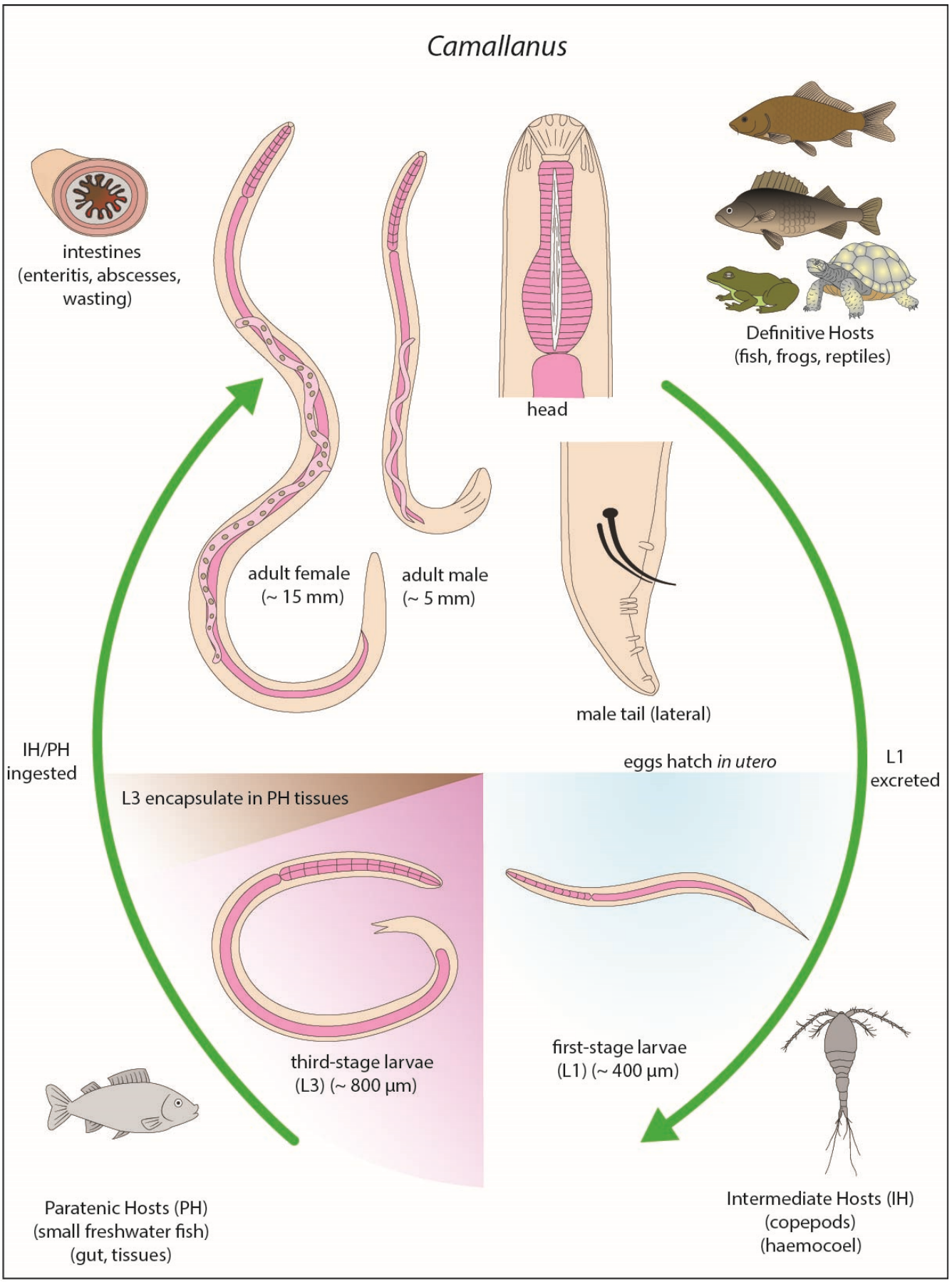
Pathogenesis: Even though adult worms penetrate the intestinal mucosa and feed on host tissues and fluids (incl. blood), most infections remain asymptomatic as only a few worms are involved. Heavy infections, however, may cause significant intestinal irritation and inflammation, haemorrhage, ulceration and abscess formation resulting in reduced appetite, anorexia, abdominal bloating, weight loss and wasting, diarrhoea (sometimes with melena) and secondary bacterial infections. Clinical infections have been recorded in fish and turtles, especially those living in crowded and confined situations such as aquaria and breeding ponds.

Developmental cycle and mode of transmission: These nematodes have indirect heteroxenous life-cycles involving the cyclic transmission of adult worms in aquatic or amphibious vertebrates (definitive hosts) and larval stages in aquatic invertebrates (intermediate hosts). Female worms produce eggs which hatch *in utero* releasing L1 which are either passed into water with host faeces or when gravid females protrude from the anus and rupture on contact with water. The larvae swim around in the water column or wriggle around while attached to submerged substrates by their tails. Their vigorous activity attracts copepodid crustaceans which devour them and act as intermediate hosts for larval development. L1 survival in water is related to temperature with many surviving up to 10 weeks at 5°C but only for 4 weeks at 20°C, although their infectivity for copepods was lost after 1-2 weeks. When infective L1 are ingested by suitable copepods, they penetrate the gut wall and invade the haemocoel where they moult into L2 in 3-4 days and then to L3 in 6-7 days. Infective L3 lay coiled and dormant in the haemocoel until the copepod is eaten by a suitable (permissive) definitive host (lower predaceous vertebrate). The L3 infect the gut mucosa and moult to L4 in 9-10 days and then to adults in 17-91 days (males develop first). After mating, female worms produce eggs which hatch *in utero* releasing

L1 to complete the cycle. In some species, L3 may apparently move up the food chain using paratenic hosts. When eaten by an unsuitable (non-permissive) host (such as planktivorous fishes), L3 may persist in the gut or become encapsulated in tissues (usually mesenteries), only occasionally growing to L4. When these paratenic (transport) hosts are eaten by predatory definitive hosts, the larvae infect the gut mucosa and develop into adults. An exception to this indirect transmission was found for a few species (such as *C. cotti*) which appear to also be capable of direct transmission when definitive hosts ingest free-living L1 directly from the water column (without copepods being involved).

Differential diagnosis: Few infections cause clinical disease and even when present, clinical signs are relatively non-specific. Infections are generally diagnosed ante-mortem by the detection of red thread-like worms emerging from the anus of the host in heavy infections, or serendipitously upon post-mortem. Coprological techniques do not facilitate diagnosis as the worms release larvae (and not eggs) which are relatively fragile in the chemicals and conditions used for faecal concentrations.

Treatment and control: Clinical infections in fishes have been successfully treated with anthelmintics; including benzimidazole-methylcarbamates (fenbendazole) and imidazothiazoles (levamisole). Infections in aquaria and intensive culture facilities have been associated with over-crowding, poor water quality, and using live crustaceans as food sources. Strategies designed to break transmission cycles should redress these conditions, but remembering that some parasite species can undergo direct transmission (effectively fish-to-fish).

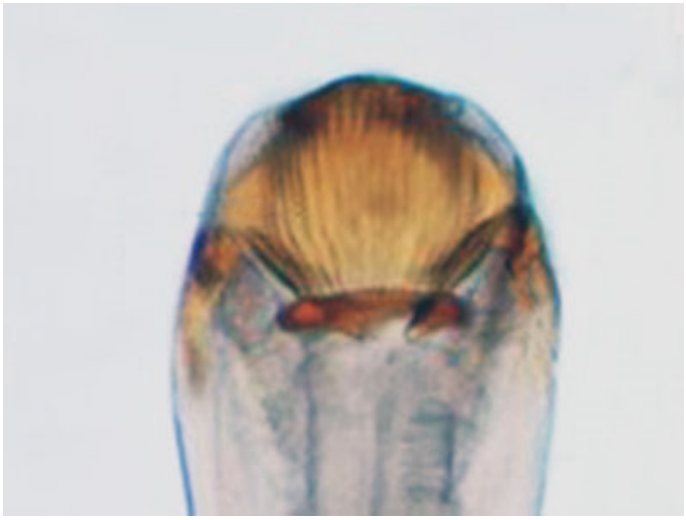

Camallanus
intestines
(enteritis, abscesses,
wasting)
adult female
(~ 15 mm)
adult male
(~ 5 mm)
head
male tail (lateral)
Definitive Hosts
(fish, frogs, reptiles)
IH/PH
ingested
L3 encapsulate in PH tissues
third-stage larvae
(L3) (~ 800 µm)
eggs hatch *in utero*
L1
excreted
first-stage larvae
(L1) (~ 400 µm)
Paratenic Hosts (PH)
(small freshwater fish)
(gut, tissues)
Intermediate Hosts (IH)
(copepods)
(haemocoel)



Camallanus adult worm removed from fish vent



Camallanus adult worms



Camallanus adult worm, head

Dracunculus
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Many phasmidian parasites of vertebrates are grouped in the chromadorian order Rhabditida; including tylenchinids, rhabditinids and spirurinids. On molecular evidence, the latter is considered to contain the superfamily Dracunculoidea *incertae sedis*. These non-bursate worms have conspicuous phasmids (broad cavities and prominent pores) and indirect life-cycles involving crustacean (copepod) intermediate hosts in which L3 develop. Dracunculids have weakly-developed buccal capsules and the elongate adult females are found in the tissues of reptiles and mammals. Subcutaneous infections of humans by the guinea worm *Dracunculus medinensis* cause painful fiery blisters through which larvae are released into cooling waters to infect copepods. Infections have been described throughout human history; the iconic 'staff-with-serpent' adopted as the official symbol of medicine may even depict the traditional means of worm removal by winding it onto a stick. It is one of the few parasitic nematodes currently brought close to extinction due to effective environmental control measures.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Chromadorea (spiral amphids, three oesophageal glands, usually annulated bodies, free-living and parasitic)
Order:	Rhabditida (Secernentea, Phasmidea) (secretors, with phasmids, bipartite oesophagus, single testis)
Suborder:	Spirurina (mostly parasitic in vertebrate hosts)
	Incertae sedis
Superfamily:	Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Family:	Dracunculidae (buccal capsule reduced, female highly enlarged, filled with L1, copepod IH)
Genus:	*Dracunculus* (parasitic in subcutaneous tissues of humans)
Species:	*D. medinensis* (causes dracunculiasis in humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

Molecular phylogenetic studies have grouped a variety of superfamilies into the infraorder Spiruromorpha whose members are parasites of vertebrates with indirect life-cycles involving larval development within invertebrate intermediate hosts. Most members were previously classified within the order Spirurida: either within the suborder Camallanina (worms with conspicuous phasmids, uninucleate oesophageal glands, larvae without cephalic hooks, usually with copepodid intermediate hosts); or the suborder Spirurina (worms with inconspicuous phasmids, multinucleate oesophageal glands, larvae with cephalic hooks or spines, usually with non-copepodid intermediate hosts). Two camallaninid superfamilies are recognised: Camallanoidea (buccal cavity well-developed, tiny internal labial papillae, gut parasites); and Dracunculoidea (buccal cavity weakly-developed, prominent internal labial papillae, tissue parasites). Five dracunculoidid families are recognised: Anguillicolidae, Guyanemidae and Philometridae in fishes; Micropleuridae in reptiles; and Dracunculidae in mammals, reptiles and birds.

The family Dracunculidae contains worms with marked sexual dimorphism: small males with pointed tails sometimes with narrow caudal alae; and large females with reproductive organs that atrophy in mature worms so that the body becomes filled with first-stage larvae (L1). Two genera are recognised: *Dracunculus* (syn. *Ophiodracunculus*, *Chelonidracunculus*, *Pesteria*) in mammals and reptiles; and *Avioserpens* (syn. *Oshimaia*, *Petroviprocta*) in marine birds. The genus *Dracunculus* contains around 14 species of worms with weakly-developed buccal capsules, triangular mouths with quadrangular sclerotized plates, thick peribuccal rings, 2 circlets of cephalic papillae and conspicuous phasmids. Adult males are small and non-bursate, while adult females are highly enlarged and ovoviviparous (releasing embryos rather than eggs). They all have indirect life-cycles involving the development of infective (L3) larvae in freshwater copepodid hosts. Infections of humans by *D. medinensis* have been recorded many times in history, being described as ‘little snakes’ by Greek and Roman scholars, ‘fiery serpents’ in Biblical texts (Numbers 21:4-8), and colloquially named Medina-worms, guinea-worms or dragon-worms. Infections occurred throughout semi-desert areas of sub-Saharan Africa, India, the Middle-East and Brazil, mainly in rural areas where water was drawn from wells or shallow ponds during the rainy season. However, the amazing successes of preventive campaigns fostered by the World Health Organization

(WHO) have significantly reduced the global prevalence of infections (from 15 million in 1980 to 4 million in 1986, 60,000 in 1997, 1,785 in 2010 and 25 in 2016) and led to its eradication in over 20 countries (as of 2016, small foci persisting only in Chad, Ethiopia and South Sudan). This parasite is facing imminent extinction due to deliberate human intervention. It must be remembered that infections by *D. medinensis* have also been found occasionally in dogs, cats, cattle, horses and other mammals, so some animals may act as reservoirs for zoonotic infection. The species *D. insignis* has been found in raccoons, muskrats, mink, weasels and other carnivores (sometimes humans) in North America, and other species in opossums, otters, snakes and turtles from several continents (Americas, Africa, India, Asia, Australia). The larval stages of all *Dracunculus* spp. use aquatic copepods as intermediate hosts (vectors) and some may even survive in tadpoles/frogs and freshwater fish which subsequently act as paratenic (transport) hosts.

***Dracunculus* species**	**Definitive hosts (DH)**	**Location**	**Intermediate hosts (IH)**	**Distribution**
D. alii	Serpentes: colubrid (checkered keelback snake)	body cavity, mesenteries		India
D. brasiliensis	Serpentes: boid (anaconda), colubrid (brown-banded water snake)	connective tissue, body cavity		Brazil
D. coluberensis	Serpentes: colubrid (trinket snake)	lung		India
D. dahomensis	Serpentes: pythonid (African rock python)	connective tissue		Africa
D. doi	Serpentes: boid (Madagascar boa), pythonid (royal python)	peritoneal mesentery	Copepoda: cyclopid (*Cyclops strenuus*)	Madagascar
D. fuelleborni	Didelphimorphia: didelphid (opossum)	subcutaneous tissue		Americas
D. globocephalus	Testudines: chelydrid (common snapping turtle)	mesenteries, body cavity	Copepoda: cyclopid (*Cyclops bicuspidatus*)	North America
D. houdemeri	Serpentes: colubrid (checkered keelback snake)	cutaneous connective tissue		Vietnam
D. insignis (North American guinea worm)	Carnivora: mustelid (American mink, fisher, river otter, badger, weasel, ferret, American marten, European polecat), procyonid (raccoon), mephitid (striped skunk), canid (coyote, gray fox, dog), felid (cat); Didelphimorphia: didelphid (opossum); Rodentia: cricetid (muskrat); Primates: cercopithecid (rhesus macaque), hominid (human)	subcutaneous tissues	Copepoda: cyclopid (*Cyclops bicuspidatus, vernalis, Cryptocyclops linjanticus, Mesocyclops aequatorialis, leukarti, Thermocyclops emini*) [tadpoles/frogs and freshwater fish may act as paratenic hosts]	North America
D. lutrae	Carnivora: mustelid (river otter)	subcutaneous tissue	Copepoda: cyclopid (*Cyclops*)	North America
D. medinensis (Guinea worm, Medina worm, fiery dragon, fiery serpent) (syn. *D. graecorum, D. aethiopicus*)	Primates: hominid (human); Carnivora: canid (dog, golden jackal), felid (cat, leopard), mustelid (ferret); Artiodactyla: bovid (cattle, chinkara); Perissodactyla: equid (horse); Rodentia; cricetid (muskrat) Serpentes: elapid (cobra)	subcutaneous connective tissue	Copepoda: cyclopid (*Cyclops atter, bisetosus, coronatus* (*fuscus*)*, decipiens, fimbriatus, hyalinus, inopinus, iranicus, karvei, magnus, microspinulous, nigerianus, oithonoides, quadricornis, rylovi, tinctus, varicans, vermifer, vernalis, Eucyclops, Macrocyclops, Mesocyclops aequatorialis, aspericornis, hyalinus, kieferi, leukarti, Metacyclops margaretae, Thermocyclops crassus, emini, incisus, inopinus, kieferi, neglectus, nigerianus, oblongatus, spinosus, vermifer*) [tadpoles/frogs may act as paratenic hosts]	Africa, India, Middle East, South America (range considerably reduced due to control programs)
D. mulbus	Serpentes: pythonid (Papuan	connective tissue,		Australia

	python, water python)	body cavity		
D. oesophagea (syn. *D. ricci*)	Serpentes: colubrid (viperine water snake, ringed snake, grass snake)	body cavity	Copepoda: cyclopid (*Macrocyclops fuscus*)	Eurasia
D. ophidensis	Serpentes: colubrid (blackbelly garter snake)	subcutaneous tissue	Copepoda: cyclopid (*Cyclops viridis*) [tadpoles may act as paratenic hosts]	North America

Parasite morphology: Guinea-worms develop through four larval stages prior to the formation of large adult worms; eggs are not produced. First-stage larvae (L1) appear as thin white tubular stages measuring 490-737 by 18-24 µm in size and having a rhabditiform pharynx, long pointed tail, striated cuticle with lateral ridges and a dorsal tooth. The third-stage larvae (L3) are elongate measuring from 240-608 by 12-23 µm in size, and they have a filariform pharynx, intestines containing transparent and brown globules and a genital primordium consisting of 6-8 cells. Adult worms exhibit marked sexual dimorphism: males measuring from 12-40 mm in length with unequal spicules (490-750 µm) and an accessory organ (gubernaculum) in most species; while creamy-white females may grow up to exceptional lengths of 500-1,200 mm by 0.9-2.0 mm in width. In young females, the vulva is located around the midbody but it becomes atrophied and non-functional in adults, as does the intestine due to the high internal pressure generated by the gravid uterus. Mature females are ovoviviparous and contain thousands of developing embryos. The mouth is a triangular opening surrounded by a quadrangular sclerotized plate (lips are absent) with two circlets of cephalic papillae. Although the worms are very long and thin, they differ from filarial worms morphologically (e.g. females only have one uterus rather than 2 like filariae), biologically (aquatic copepodid intermediate hosts rather than terrestrial arthropods) and genetically (phylogenetic studies based on 18S ribosomal DNA sequences group them separately).

Site of infection: Infective larvae (L3) ingested by definitive hosts penetrate the gut and invade subcutaneous connective tissues, migrating mainly to the axillary and inguinal regions. Maturing female worms of *D. medinensis* migrate from deep connective tissues to peripheral subsurface locations, particularly in the extremities of limbs (legs and arms) although they can occur elsewhere. The adults of other *Dracunculus* spp. also develop in subcutaneous locations in their mammalian hosts as well as in the internal tissues and body cavities of their reptilian hosts. Larval stages (L1-3) develop in the haemocoel of their copepodid intermediate hosts.

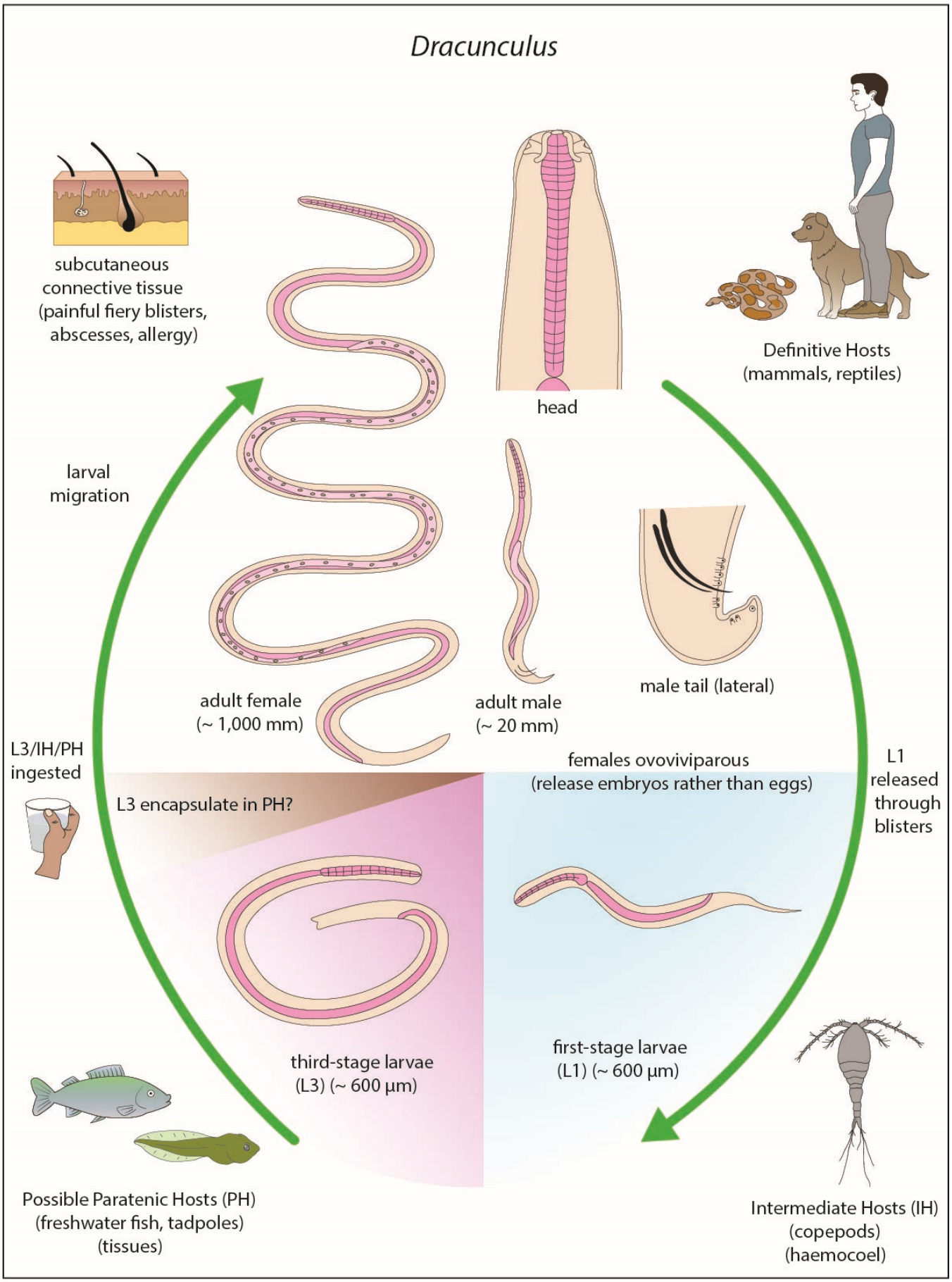
Pathogenesis: Despite their eventual enormous size, infections by guinea-worms usually do not produce any clinical signs until the mature female worms migrate to the skin and provoke the formation of a papule then a blister. Migration may sometimes produce vague allergic reactions, including nausea, dizziness, fainting, diarrhoea, rash, asthma, local oedema and eosinophilia. Infections then cause disease known variously as subcutaneous filariasis, Guinea worm disease, dracunculosis or dracunculiasis. Infections generally produce two types of lesions: subcutaneous or deep abscesses around dead worms (involving many inflammatory cell types) that tend to calcify; or cutaneous papules that rapidly blister and then rupture to form cup-shaped ulcers through which females release live larvae. Skin lesions may involve local erythema, urticaria, inflammation, ulceration and intense burning pain (fiery serpent of biblical times). In the majority of infections, blisters form on the lower extremities and only occasionally involve other body parts, such as the genitalia, buttocks, torso, upper extremities and head. Patients seek to relieve symptoms by immersing the affected region in cool water. Lesions are initiated by secreted irritants and the deposition of larvae in the tissues and the induction of hypersensitivity reactions which ultimately produce ulcers through which larvae, and parts of the adult worm, emerge (a unique means for tissue-dwelling parasites to seek egress from their hosts). In uncomplicated cases, lesions may only last for several weeks until the worm is completely expelled. However, many cases involve secondary bacterial infection of the worm track with persistence of the lesion, chronic ulceration and possible sequelae, involving abscessation, disseminated infections, phlegma of limbs, contractures of tendons, fibrous ankylosis or arthritis in the joints, or even tetanus.

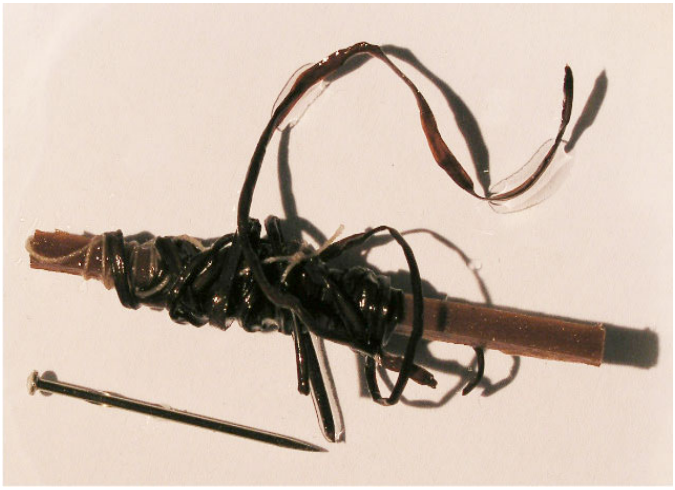
Developmental cycle and mode of transmission: The parasites have a unique indirect life-cycle, involving cyclopoid copepods (water fleas) as intermediate hosts. When adult female worms in the skin mature and become gravid, the high internal pressure causes the body wall to burst forcing through a loop of the uterus. Larvae released into the tissues provoke a violent allergic reaction causing skin blisters which eventually rupture (particularly on contact with water) releasing larvae from the tissues as well as from the exposed and protruding anterior portion of the worm from which the gravid uterus may prolapse. Muscular contractions of the body wall (instigated by cool water) force thousands of larvae out in periodic spurts (up to half a million per day). As exposed portions of the uterus empty, they disintegrate and adjacent portions move into the ulcer. Release of larvae can continue over several weeks if the lesion is repeatedly immersed in water, although the remnants of the female worms die within 2-6 weeks of penetrating the skin. Liberated larvae are infective for less than a week and they actively move about in water attracting copepodid crustaceans which ingest them. Copepods range in size from 0.5-2.0 mm and breed best in standing waters such as ponds, pools, cisterns and open wells, so infections are common in remote rural areas reliant on such water supplies. The larvae penetrate into the haemocoel of the copepods, especially dorsal to the gut, and develop into infective third-stage larvae (L3) over 12-20 days (at 25°C). Humans become infected by swallowing infected copepods with drinking water. Larvae of several *Dracunculus* spp. (especially those

infecting wildlife) have also been found to survive in tadpoles, frogs and even some freshwater fish, which apparently act as paratenic (transport) hosts. When infected copepods (or infected paratenic hosts) are ingested by definitive hosts, the infective larvae penetrate the intestinal wall and migrate for about 3 months through connective tissues where male and female worms develop and mate. The males remain in the tissues and become encapsulated and die in a few months, while the fertilised females migrate to subcutaneous sites and grow to essentially become non-feeding bags full of larvae. Gravid females begin to emerge from the skin around 10-14 months after infection.

Differential diagnosis: Local itching, urticaria and a burning pain at the site of a small blister are usually the first clear symptoms of dracunculiasis. Infections become obvious once part of the female worm emerges. Milky clouds of larvae can also be seen under low magnification when the lesion is placed in water. X-ray imaging techniques have been used to detect calcified worms. Immunoserological tests (enzyme immunoassays) have been developed to detect host antibodies formed against parasite antigens, but given the persistence of circulating antibodies it can be difficult to discriminate between recent and previous exposure. Molecular tests have been developed to differentiate *Dracunculus* spp. by using polymerase chain reactions (PCR) to amplify specific parasite gene sequences (small subunit (18S) ribosomal RNA).

Treatment and control: Wet compresses may be applied to blistered lesions to relieve pain associated with the emergence of worms (although this may trigger larval release). Occlusive bandages may be used to maintain hygiene, together with topic antiseptics and/or antibiotics to prevent secondary infections and reduce inflammation. The traditional means of curing infections involves the slow extraction of worms by winding them onto a stick a few centimetres a day for several weeks, combined with sterile dressings and acriflavine cream. Excessive force should not be used to avoid breaking the worm which may result in complicated lesions and intense inflammatory reactions. Surgical removal may be successful when worms are restricted to superficial sites, but can be difficult when worms are threaded through tendons or deep fascia. Chemotherapy with conventional anthelmintics has not proven effective, but various compounds, such as albendazole, mebendazole, niridazole, thiabendazole and metronidazole, appear to act as anti-inflammatory agents, thus allowing worms to be extracted more easily. Preventive measures involve breaking the cycle of transmission by reducing contamination of water supplies and eliminating copepod hosts. Public education programmes have been developed to discourage infected persons from entering ponds or wells to collect drinking water or to bath. Local water supplies can be treated with copper sulphate or temephos which kills copepods for several weeks. Improving water supplies by the installation of bores, pumps and reticulated (piped) systems, instead of step-wells, helps reduce contamination by both parasites and copepods. Drinking water can also be purified by chlorination, boiling or filtering through fine-meshed cloth (< 0.15 mm). The World Health Organization has accredited the global decline in the prevalence of infections to the adoption of many of these simple preventive measures.


Dracunculus
subcutaneous connective tissue (painful fiery blisters, abscesses, allergy)
head
Definitive Hosts (mammals, reptiles)
larval migration
adult female (~ 1,000 mm)
adult male (~ 20 mm)
male tail (lateral)
L3/IH/PH ingested
L3 encapsulate in PH?
females ovoviviparous (release embryos rather than eggs)
L1 released through blisters
third-stage larvae (L3) (~ 600 µm)
first-stage larvae (L1) (~ 600 µm)
Possible Paratenic Hosts (PH) (freshwater fish, tadpoles) (tissues)
Intermediate Hosts (IH) (copepods) (haemocoel)



Dracunculus adult worm



Dracunculus adult worm



Dracunculus larvae



Dracunculus copepod vector

Trichuris
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most aphasmid nematodes are free-living, although some are parasitic on plants and animals. They possess a non-muscular stichosome oesophagus (slender thin-walled tube) and their life-cycles involve infective L1 (rather than L3) which have a buccal stylet (very common for plant parasites). The males lack a bursa and have only one spicule when present. Three major families of animal parasites are grouped together in the dorylaimian order Trichinellida: trichurids in the caecum/colon of mammals, capillarids in the gut/lungs of mammals/birds, and trichinellids in the intestines and muscles of mammals. Trichurids are known as whipworms because they have a short broad posterior end and a very long narrow whip-like anterior end embedded in the intestinal mucosa. They have simple direct life-cycles involving the faecal-oral transmission of eggs containing infective L1. Eggs excreted with host faeces contaminate soil, food and water supplies and have a characteristic barrel-shape with mucoid polar plugs at each end. Heavy infections by *Trichuris* spp. in humans and domestic animals may cause diarrhoea, anaemia, malnutrition, and occasionally rectal prolapse.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass:	Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)
Order:	Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily:	Trichinelloidea (oesophagus with short muscular anterior portion and long glandular posterior portion)
Family:	Trichuridae (whipworms, sudden transition in width, slender anteriorly, barrel-shaped eggs with polar plugs)
Genus:	*Trichuris* (parasitic in caeca of mammals)
Species:	various species cause trichuriasis in humans and animals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Trichinelloidea is characterised by worms having a distinctive oesophagus consisting of a short anterior muscular section and a long posterior glandular section (stichosome) encircled by 1-3 rows of unicellular glands (stichocytes). Adult worms generally have long narrow anterior necks (containing only the stichosome) and stouter posterior bodies (containing the reproductive organs). Female worms produce thick-shelled eggs with bipolar mucoid plugs giving them a lemon- or barrel-shape. Most genera pass unembryonated eggs, but those of some groups (Trichinellidae, Trichosomoididae) embryonate *in utero.* The first-stage larvae (L1) have an oral stylet, similar to their presumed soil-dwelling dorylaimid ancestors. Unlike other parasitic nematodes, the L1 of trichinelloids (rather than L3) is used to infect their final hosts, sometimes after a brief period in an invertebrate intermediate host (such as earthworms) to become infective. Adults worms are endoparasites in most classes of vertebrates, generally occurring within the intestinal mucosa but some infecting epithelia of the urinary, respiratory or integumentary systems. An increasing number of genera have been recognised but their higher classification is confounded as some authorities distinguish 6 families while others have demoted several to subfamily status. The former ranking has been retained in this resource to better help the reader differentiate genera on the basis of recognised apomorphic characters, although future studies may reveal different phylogenetic relationships. The 6 trichinelloid families include: Trichuridae (syn. Trichuroididae), Trichinellidae, Anatrichosomatidae and Trichosomoididae primarily in mammals; Capillariidae in birds, mammals and fish; and Cystoopside in fish and reptiles.

The family Trichuridae contains the whipworms which show a sudden transition in width with the thin anterior portion embedded in the large intestinal epithelia of mammals. Mature worms have 1-3 stichosomes composed of 40-200 stichocytes, male worms have a single spicule and a cirrus with spines or tubercles, and females are oviparous producing distinctive lemon-shaped eggs with mucoid polar plugs. Some 6 genera are recognised: *Trichuris* (syn. *Buckleyuris, Mastigodes, Rudolphia, Salamia, Trichocephalos, Trichocephalus p.p.*), *Capillostrongyloides, Liniscus, Orthothomix, Sclerotrichum* and *Tenoranema.* Infections are transmitted directly when eggs containing infective first-stage larvae (L1) are ingested with contaminated food or water. The genus

Trichuris contains over 110 spp., some of which have been associated with clinical disease in ruminants, marsupials, rodents and primates. The species *T. trichiura* is found in human populations throughout the world, mainly in tropical and subtropical regions. It is estimated that around 10% of the world population (800 million people) may be infected. Parasites are very prevalent in regions where human excrement (nightsoil) is used to fertilise vegetable gardens. Infections are typically over-dispersed, where a few individuals harbour most of the worms. Other whipworm species occur in a range of domestic and wild animals: including *T. ovis*, *T. skrjabini*, *T. discolor* and *T. globulosa* in ruminants; *T. vulpis*, *T. campanula* and *T. serrata* in dogs and cats; *T. suis* in pigs; and *T. muris* in rodents. Zoonotic transmission of *T. vulpis* and *T. suis* to humans has occasionally been reported. Whipworms are more prevalent in animals kept under intensive husbandry situations where hygiene may be poor; such as overcrowded kennels, pens and paddocks.

***Trichuris* species**	**Definitive Hosts [adults in large intestines]**	**Clinical signs**	**Distribution**
T. alcocki	Artiodactyla: cervid (Eld's deer)		India
T. antidorchi	Artiodactyla: bovid (springbok, blesbok)		Africa
T. arvicolae	Rodentia: cricetid (common vole, bank vole, field vole, water vole, southwestern water vole)		Europe, North America
T. baeri	Artiodactyla: giraffid (okapi)		Africa
T. bainae	Rodentia: cricetid (rat-headed rice rat)		South America
T. barbertonensis	Artiodactyla: bovid (cattle, African buffalo, goat, steenbok, impala)		Africa
T. barusi	Rodentia: murid (black rat, Indian gerbil, Indian desert jird)		Asia
T. baskakovi (syn. T. *baskokowi*)	Artiodactyla: cervid (reindeer), bovid (cattle)		Russia
T. bradleyi	Rodentia: octodontid (common degu)		South America
T. buckleyi (now *Buckleyuris*)	Artiodactyla: bovid (steinbok)		Africa
T. bursacaudata	Rodentia: ctenomyid (Talas tuco-tuco)		South America
T. busuluk	Eulipotyphla: talpid (European mole)		Europe
T. cameli	Artiodactyla: camelid (bactrian camel)		Asia
T. campanula	Carnivora: felid (cat)	mostly subclinical	Caribbean
T. capreoli	Artiodactyla: cervid (roe deer, red deer, fallow deer), bovid (mouflon); Rodentia: murid (yellow-necked mouse), cricetid (common vole, European pine vole)	mostly subclinical	worldwide
T. carlieri	Rodentia: murid (fringe-tailed gerbil)		Africa
T. cervicaprae	Artiodactyla: bovid (goat, chamois, blackbuck)		Eurasia
T. chiliensis	Rodentia: cricetid (long-haired grass mouse)		South America
T. citelli	Rodentia: sciurid (California ground squirrel)		North America
T. citellorum	Rodentia: sciurid (long-tailed ground squirrel)		Russia
T. colobae	Primates: cercopithecid (colobus monkey)		Africa
T. contorta	Rodentia: bathyergid (mole-rat)		Africa
T. cutcasheni	Rodentia: sciurid (Caucasian squirrel)		Eurasia
T. cynocephalus	Primates: cercopithecid (Hamadryas baboon)		Africa
T. cyrenaica	Carnivora: canid (red fox, fennec fox)		Europe
T. deseirani	Artiodactyla: bovid (cattle)		Europe
T. didelphis	Didelphimorphia: didelphid (white-eared opossum, Virginnia opossum)		Americas
T. dipodomis	Rodentia: heteromyid (Merriam's kangaroo-rat, chisel-toothed kangaroo-rat, Ord's kangaroo-rat)		North America
T. discolor	Artiodactyla: bovid (cattle, zebu, water buffalo, yak, nilgai, sheep, mountain sheep, bighorn sheep, goat, mouflon, Cyprus mouflon, chamois, Japanese serow), cervid (moose), giraffid (okapi); Rodentia: murid Indian gerbil)	mostly subclinical, sometimes watery diarrhoea	Eurasia, Africa, North America, Australia
T. diversicolor	Artiodactyla: bovid (cattle)		
T. dolichotis	Rodentia: caviid (Patagonian mara)		South America
T. dzejrani	Artiodactyla: bovid (cattle, goitered gazelle)		Russia
T. elatoris	Rodentia: heteromyid (Texas kangaroo-rat, Merriam's kangaroo-rat, Ord's kangaroo-rat)		North America
T. erschovi	Artiodactyla: bovid (cattle)		Russia
T. felis	Carnivora: felid (cat)		Europe

T. feliui	Eulipotyphla: talpid (European mole)		Europe
T. fossor	Rodentia: cricetid (Zacatecan deer mouse), geomyid (Botta's pocket gopher, northern pocket gopher)		Americas
T. fulvi	Rodentia: ctenomyid (tawny tuco-tuco)		South America
T. gazellae	Artiodactyla: bovid (goat)		
T. georgicus	Artiodactyla: bovid (goat, mouflon, sheep)		Africa, Europe
T. gerbillis	Rodentia: murid (North African gerbil, greater Egyptian gerbil, Libyan jird, Shaw's jird, fat sand rat)		Africa
T. germani	Rodentia: murid (large tree mouse, Champion's tree mouse, chesnut tree mouse, gray-bellied tree mouse)		Papua New Guniea
T. giraffae (syn. *Trichocephalus*)	Artiodactyla: giraffid (reticulated giraffe, northern giraffe, okapi)		Africa
T. globulosa	Artiodactyla: bovid (cattle, yak, Indian yak, nilgai, buffalo, goat, sheep, Cyprus mouflon, mouflon, chamois, impala, Dorcas gazelle, Cuvier's gazelle, Soemmering's gazelle, Sharpe's grysbok, roan antelope, sable, waterbuck), camelid (bactrian camel, dromedary), giraffid (reticulated giraffe, Angolan giraffe), cervid (roe deer, red deer, fallow deer, reindeer)	mostly subclinical, sometimes watery diarrhoea	worldwide
T. gracilis	Rodentia: caviid (Brazilian guinea pig), dasyproctid (agouti, red-rumped agouti)		South America
T. guevarai	Artiodactyla: cervid (red deer)		Eurasia
T. gundii	Rodentia: ctenodactylid (gundi)		Africa
T. hyracis	Hyracoidea: procaviid (southern tree hyrax)		Africa
T. hystricis	Rodentia: hystricid (crested porcupine)		Africa
T. indicus	Artiodactyla: bovid (cattle)		Russia
T. infundibulus (*infundibulum*)	Rodentia: hystricid (African crested porcupine); Artiodactyla: bovid (goat, mouflon, sheep)		Africa, Europe
T. laevitestis	Rodentia: cricetid (Azara's grass mouse, hairy-tailed bolo mouse, Argentine swamp rat)		South America
T. landak	Rodentia: hystricid (Sunda porcupine)		Asia
T. lani	Artiodactyla: camelid (dromedary), bovid (sheep), cervid (fallow deer, sika deer, moose)		Asia
T. lenkorani	Rodentia: hystricid (Indian crested porcupine)		Asia
T. leporis (syn. *T. unguiculatus*, *T. sylvilagi*, *T. tineri*)	Lagomorpha: leporid (snowshoe hare, Cape hare, European hare, mountain hare, Tolai hare, European rabbit, volcano rabbit, eastern cottontail), sciurid (Richardson's ground squirrel)	mostly subclinical	North America, Eurasia
T. longispiculus	Artiodactyla: cervid (reindeer, sika deer, roe deer, moose), bovid (sheep, urial, mouflon, long-tailed goral)		Russia
T. madisonensis	Rodentia: sciurid (eastern chipmunk)		North America
T. marsupialis	Didelphimorphia: didelphid (Virginia opossum)		North America
T. massino	Artiodactyla: cervid (reindeer)		Russia
T. mastomysi	Rodentia: murid (Natal multimammate mouse)		Africa
T. media	Artiodactyla: bovid (zebu)		Russia
T. mettami	Rodentia: hystricid (crested porcupine)		Asia
T. minuta	Didelphimorphia: didelphid (water opossum, big-eared opossum, common opossum, Viginia opossum, Linnaeus's mouse opossum); Cingulata: dasypatid (nine-banded armadillo)		Americas
T. muris	Rodentia: murid (house mouse, wood mouse, yellow-necked mouse, typical striped grass mouse, Natal multimammate mouse, African pygmy mouse, Algerian mouse, striped field mouse, Jackson's soft-furred mouse, black rat, Philippine black rat, brown rat, African grass rat, rusty-bellied brush-furred rat, water rat, eastern wood rat, mid-day jird), glirid (woodland dormouse), nesomyid (Gambian pouched rat), hystricid (African brush-tailed porcupine), cricetid (common vole, reed vole, narrow-headed vole, Maximowicz's vole, Muisk vole, European snow vole, Tundra vole, European water vole, European pine vole, bank vole, grey red-backed vole, northern red-	mostly subclinical	worldwide

	backed vole, field vole, root vole, yellow steppe lemming, Chinese striped hamster, gray hamster), sciurid (long-tailed ground squirrel); Eulipotyphla: soricid (Indian musk shrew)		
T. myocastoris	Rodentia: echimyid (coypu)		South America
T. navonae	Rodentia: cricetid (Montane grass mouse, blackish grass mouse)		South America
T. neomi	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
T. neotomae	Rodentia: cricetid (dusky-footed woodrat)		North America
T. nodosus (syn. *Trichocephalus*)	Rodentia: murid (mouse)		Europe
T. nutria	Rodentia: echimyid (coypu)		South America
T. odocoileus	Artiodactyla: cervid (white-tailed deer)		North America
T. opaca	Rodentia: cricetid (muskrat, meadow vole), erethizontid (bristle-spined rat)	intestines	Americas
T. oreamnos	Artiodactyla: bovid (mountain goat, Rocky Mountain goat)		North America
T. ovis	Artiodactyla: bovid (cattle, American bison, sheep, bighorn sheep, argali, tahr, mouflon, Cyprus mouflon, Afghan urial, chamois, goat, mountain goat, blackbuck, alpine ibex), cervid (sika deer, roe deer, red deer, maral, Iberian red deer, fallow deer, marsh deer, black-tailed deer, boreal woodland caribou, reindeer, moose), camelid (bactrian camel, dromedary), suid (pig), giraffid (reticulated giraffe)	mostly subclinical, sometimes watery diarrhoea, often with blood	worldwide
T. palaeformis	Primates: cercopithecid (green monkey)		Africa
T. pampeana	Rodentia: ctenomyid (Azara's tuco-tuco, Talas tuco-tuco)		South America
T. pardinasi	Rodentia: cricetid (Buenos Aires leaf-eared mouse, yellow-rumped leaf-eared mouse)		South America
T. parvispicularis	Rodentia: thryonomyid (greater cane rat)		Africa
T. parvispiculum	Artiodactyla: bovid (cattle, sheep, goat)		Africa, Australia
T. pedetei	Rodentia: pedetid (South African springhare)		Africa
T. peramelis	Peramelemorphia: peramelid (northern brown bandicoot, long-nosed bandicoot)		Australia
T. perognathi	Rodentia: heteromyid (pocket mouse, California pocket mouse)		North America
T. peromysci	Rodentia: cricetid (California mouse)		North America
T. petteri	Rodentia: murid (Jackson's soft-furred mouse)		Africa
T. procaviae	Hyracoidea: procaviid (rock hyrax)		Africa, Middle-East
T. raoi	Artiodactyla: camelid (camel)		India
T. rhinopiptheroxella	Primates: cercopithecid (Sichuan snub-nosed monkey)		Asia
T. rhinopithecus	Primates: cercopithecid (Yunnan snub-nosed monkey)		Asia
T. rhombomydis (syn. *T. rhombomidis*)	Rodentia: cricetid (gray hamster), murid (midday jird, great gerbil)		Russia
T. robusti	Rodentia: ctenomyid (tawny tuco-tuco)		South America
T. rupicaprae	Artiodactyla: bovid (chamois)		Europe
T. schumakovitschi	Artiodactyla: bovid (Rocky Mountain bighorn sheep, mountain goat)		North America
T. serrata	Carnivora: felid (cat, wildcat), canid (dog)	mostly subclinical	Americas
T. skrjabini	Artiodactyla: bovid (sheep, mouflon, chamois, goat, ibex, cattle), camelid (camel, dromedary), giraffid (okapi), cervid (red deer, fallow deer)	mostly subclinical	Eurasia, Africa, North America, Australia
T. spalacis	Rodentia: spalacid (lesser mole-rat), murid (great gerbil)		Africa, Russia
T. spiricollis	Artiodactyla: giraffid (reticulated giraffe)		Africa
T. suis	Artiodactyla: suid (pig, wild boar, Japanese boar, Sardinian wild boar); Rodentia: cricetid (muskrat), castorid (American beaver); Primates: hominid (human)	mostly subclinical, sometimes watery diarrhoea, often with blood, anaemia	worldwide
T. surka	Rodentia: sciurid (long-tailed marmot)		Asia

T. sylvilagi	Lagomorpha: leporid (rabbit, black-tailed jackrabbit, Japanese hare, Cape hare, European hare)		worldwide
T. syrca	Rodentia: sciurid (Tarbagan marmot)		China
T. tarandi	Artiodactyla: cervid (reindeer)		Russia
T. tenuis	Artiodactyla: camelid (dromedary, llama, vicuna), bovid (goat)	mostly subclinical, sometimes diarrhoea	worldwide
T. thrichomysi	Rodentia: echimyid (common punare)		South America
T. travassosi	Rodentia: cricetid (black-footed pygmy rice rat)		South America
T. trichiura (syn. *Trichocephalus trichiuris, T. dispar*) [human whipworm]	Primates: hominid (human, eastern gorilla, eastern chimpanzee), cercopithecid (grivet, Skye's monkey, Campbell's mona monkey, blue monkey, king colobus, western red colobus, Japanese macaque, southern pig-tailed macaque, crab-eating macaque, togue, baboon, yellow baboon, chacma baboon, Guinea baboon, northern plain gray langur, purple-faced leaf monkey), cebid (patas monkey); Artiodactyla: bovid (sheep), suid (pig); Gadiformes: gadid (Alaska pollock) [plus carriage by Diptera: calliphorid (oriental latrine fly), muscid (house fly)]	mostly subclinical, sometimes watery diarrhoea, often with blood, anaemia, illthrift, finger clubbing, tenesmus, rectal prolapse	worldwide, esp. tropics
T. ursinus	Primates: cercopithecid (chacma baboon)		Africa
T. vondwei	Artiodactyla: bovid (goat, sheep, mouflon)		Africa, Europe
T. vulpis [dog whipworm]	Carnivora: canid (dog, golden jackal, coyote, wolf, maned wolf, racoon dog, swift fox, red fox, Japanese red fox, Iberian fox), felid (cat), mustelid (European polecat); Primates: hominid (human)	mostly subclinical, sometimes watery diarrhoea, often with blood, anaemia	worldwide

Parasite morphology: Whipworms form 3 different developmental stages; eggs, larvae and adults. The eggs are usually yellow-brown (bile-stained), barrel- to lemon-shaped and measure 50-93 µm in length by 22-42 µm in width. They have smooth outer shells and distinctive mucoid bipolar opercular plugs (one at each end). Eggs are typically unembryonated in faecal samples and develop infective larvae in the external environment. The elongate larval stages measure from 115-155 µm in length and have a rounded cephalic end with a sharp protrusible stylet. Adult worms have elongated tubular bodies with a long thin (0.1-0.2 mm wide) anterior end (up to 2/3rds of body length) that suddenly becomes thicker (up to 0.5 mm wide) at the posterior end (hence the common name whipworm). The thin anterior portion contains the stichosome oesophagus and the thicker posterior portion contains the intestines and reproductive organs (both sexes have a single gonad). The mouth is a simple opening without lips but provisioned with a minute spear (stylet) protruding from the small buccal capsule. The moniliform oesophagus is thin, tubular, capillary-like and surrounded by a single row of 40-200 glandular stichocytes (whole structure referred to as stichosome pharynx). Adult female worms measure from 30-80 mm in length and the uterus (containing many lemon-shaped eggs) ends in a ventral midbody vulva, sometimes with a protruding spiny ridge. Adult male worms are smaller measuring 23-60 mm in length and they have a tightly coiled posterior end with a single spicule 8.5-11.0 mm long surrounded by a spiny protrusible sheath (sometimes called a cirrus). *Trichuris* spp. have conventionally been differentiated on the basis of host occurrence, egg and worm morphometrics, and spicule, cloacal and uterine structure. *T. trichiura* from humans and *T. suis* from pigs are remarkably similar in appearance (despite some reports of differences in the sizes of eggs, infective larvae, spicules and the presence/absence of caudal papillae), but recent molecular characterization studies have confirmed their separate classification.

Site of infection: Juvenile worms develop in glands of the caecal and colonic mucosa where they moult and grow. Adult worms have their anterior ends embedded in tunnels in the mucosa with their posterior ends dangling into the lumen.

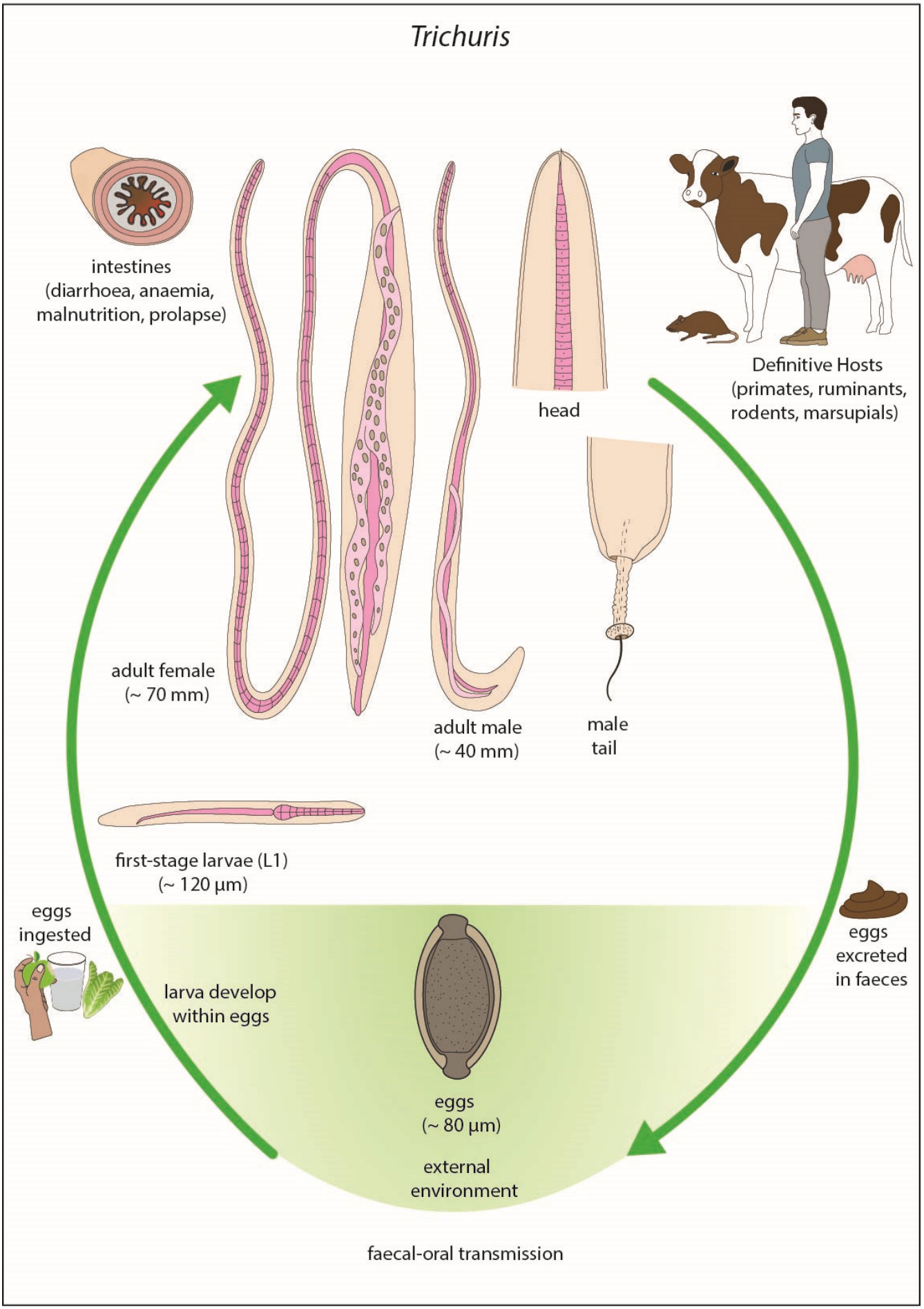
Pathogenesis: Infections may cause trichuriasis (whipworm disease), one of the most important geohelminthiases (soil-transmitted helminthiases) widespread in tropical regions. Small worm burdens (< 100) rarely cause disease, while heavier infections may produce a variety of conditions, ranging from local enteric disturbances to systemic conditions and occasionally death. Infections tend to be over-dispersed in host populations, with a few hosts harbouring heavy infections (especially small children). The anterior ends of the adult worms are embedded in the gut mucosa where they are constantly probing back and forth feeding on fluids, digested tissues and possibly blood. Worms may also release cytolytic enzymes to assist in tissue digestion. Collectively, this may cause significant mechanical and chemical trauma to the mucosa with chronic haemorrhage leading to dysentery and anaemia. Heavy infections may cause haemorrhagic colitis and/or diphtheritic inflammation of the caecal mucosa, both associated with epithelial desquamination, necrosis, excess mucus production, congestion and submucosal oedema. This may result in intermittent watery diarrhoea often with fresh blood and mucus, dehydration, anaemia and anorexia. Pathogenesis has been related to host inflammatory responses, involving markedly reduced cell-mediated responses and elevated IgE responses, characteristic of local

tissue anaphylactic responses. Whipworm infections are more common in children due to their poor hygiene practices, particularly in impoverished rural regions where toilet facilities are sparse. Persistent infections have been associated with malnutrition, growth retardation, and reduced cognitive function in children. Chronic infections may also cause finger (and occasionally toe) clubbing evident as odd thickening of the ends of the digits. Heavy infections may produce tenesmus (urgency) causing the host to strain and possibly suffer rectal prolapse (recto-rectal intussusception). Infections in pigs and dogs may be pathogenic causing severe typhlitis whereas infections in ruminants and other animals are usually subclinical but may cause problems when animals are stressed (e.g. in feedlots or under drought conditions).

Developmental cycle and mode of transmission: Whipworms have a direct developmental cycle whereby embryonated eggs are directly infective to the definitive host. Infections are transmitted by the faecal-oral route, involving the ingestion of eggs with contaminated food, water or soil. Fertilised female worms produce numerous eggs (sporadic production from none up to 3,000-10,000 per day) which are excreted with host faecal material. The eggs embryonate in around 10 days and develop infective larvae in about 3 weeks in moist shady soil (or in as little as 2 weeks in warm conditions or up to 4 months in cold conditions). Eggs are dispersed in the environment by anthropogenic activities as well as by wind, water and insects (house flies can act as mechanical vectors). The eggs are resistant to environmental conditions and may remain viable under suitable conditions for up to 4-5 years. They may contaminate soil, water and foodstuffs that are consumed by definitive hosts. When ingested, infective larvae emerge from the eggs in the small intestines and enter the crypts of Lieberkuhn where they penetrate basal cells and tunnel within the epithelium back towards the lumen. They continue to invade the mucosa as they move to the lower intestines where they complete moulting and form adults. Patent infections may develop in 5-12 weeks and can persist for 1-4 years. Infections may also accumulate in hosts as they are constantly re-infected from their heavily-contaminated environments.

Differential diagnosis: Infections may be indicated by clinical history and symptomatology but are routinely confirmed by the microscopic detection of characteristic eggs by coprological examination of faecal samples, usually following concentration by centrifugation in saturated heavy metal salt or sugar solutions (preferable to use high specific gravity solutions as whipworm eggs are relatively dense). Because eggs may be shed intermittently, repeat samples should be examined. In individuals with rectal prolapse, worms can be seen macroscopically attached to the mucosa. Colon endoscopy has also been used to reveal the presence of worms. Several immunoserological tests (enzyme immunoassays, Western blots) have been developed in research laboratories to detect specific host antibodies or parasite antigens, but they have demonstrated variable cross-reactions with other helminths and cannot reliably differentiate between recent or previous infection. Molecular biological techniques have recently been developed to discriminate species by polymerase chain reaction (PCR) amplification of specific gene sequences (small subunit (SSU) ribosomal RNA and internal transcribed spacer regions (ITS1, ITS2)).

Treatment and control: Whipworms are resistant to many anthelmintic treatments due to their relative inaccessibility in the host mucosa. Nonetheless, several groups of nematocidal drugs are effective against whipworms, with some notable exceptions. Benzimidazoles (mebendazole, albendazole, flubendazole, fenbendazole) have proven effective in various hosts (although thiabendazole produces unpleasant side-effects) and tetrahydropyrimidines (oxantel, pyrantel) and depsipeptides (emodepside) also have good activity. These drugs may not be effective against immature stages so repeat treatments may be required. Domestic animals have been successfully treated using macrocyclic lactones (avermectins, milbemycins) and imidazothiazoles (levamisole by injection), but infections in some hosts (mostly camelids) appear to be refractory. Other conventional de-wormers, such as diethylenediamines (piperazine) and diphenylethers (nitroscanate), are not effective against whipworm. Any eggs contaminating the environment may still be viable for several years so patients may quickly become re-infected, therefore so regular de-worming treatments may be mandated. It is difficult to decontaminate environmental sources as the eggs are very resistant to most chemical disinfectants. Some success has been reported using strong bleach solutions, steam-cleaning and/or flame guns to decontaminate concrete holding facilities. Alternatively, stock at risk may be translocated to cleaner surroundings. It is essential to reduce exposure by maintaining high standards of hygiene and sanitation with sewage containment or regular removal of faeces. Prevention of infections is best achieved by prohibiting the use of excrement (night-soil) as fertiliser (or ensuring it is processed by suitable microbial biocomposting prior to use) and thoroughly washing vegetables, salads and fruits with clean water prior to consumption. Control measures include education programmes to improve personal hygiene and sanitary conditions, and regular deworming campaigns.

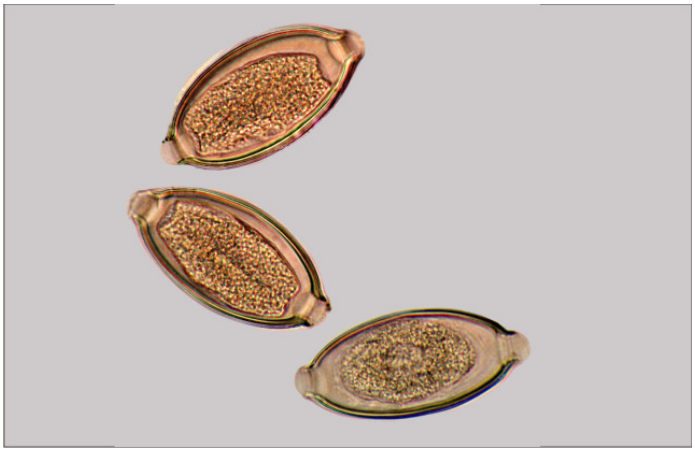

Trichuris
intestines
(diarrhoea, anaemia,
malnutrition, prolapse)
head
Definitive Hosts
(primates, ruminants,
rodents, marsupials)
adult female
(~ 70 mm)
adult male
(~ 40 mm)
male
tail
first-stage larvae (L1)
(~ 120 µm)
eggs
ingested
larva develop
within eggs
eggs
excreted
in faeces
eggs
(~ 80 µm)
external
environment
faecal-oral transmission



Trichuris adult worms



Trichuris adult worms



Trichuris worm eggs



Trichuris sections of worms in colon

Capillaria
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most aphasmid nematodes are free-living, although some are parasitic on plants and animals. They possess a non-muscular stichosome oesophagus (slender thin-walled tube) and their life-cycles involve infective L1 (rather than L3) which have a buccal stylet (very common for plant parasites). The males lack a bursa and have only one spicule when present. Three major families of animal parasites are grouped together in the dorylaimian order Trichinellida: trichurids in the caecum/colon of mammals, capillarids in the gut/lungs of mammals/birds, and trichinellids in the intestines and muscles of mammals. Capillarids are small uniformly-slender hairworms frequently embedded in host tissues. Many species have simple direct life-cycles involving the faecal-oral transmission of eggs, whereas other species have indirect cycles using earthworms as paratenic or intermediate hosts for L1. Eggs have a characteristic barrel-shape with mucoid polar plugs at each end. Capillarids have recently been divided between different genera, but most texts provide both old and new names to facilitate comprehension. Infections in birds and fish have been associated with unthriftiness, sometimes involving anaemia and diarrhoea, while infections in mammals range from asymptomatic to causing severe enteric, respiratory, urinary and hepatic diseases.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass:	Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)
Order:	Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily:	Trichinelloidea (oesophagus with short muscular anterior portion and long glandular posterior portion)
Family:	Capillariidae (gradual transition in width, in gut/respiratory tract of mammals/birds, eggs with polar plugs)
Genus:	*Capillaria* (parasitic in tissues of mammals/birds)
Species:	various species cause enteric, respiratory, hepatic, urinary diseases in mammals, birds and fish

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a

terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Trichinelloidea is characterised by worms having a distinctive oesophagus consisting of a short anterior muscular section and a long posterior glandular section (stichosome) encircled by 1-3 rows of unicellular glands (stichocytes). Adult worms generally have long narrow anterior necks (containing only the stichosome) and stouter posterior bodies (containing the reproductive organs). Female worms produce thick-shelled eggs with bipolar mucoid plugs giving them a lemon- or barrel-shape. Most genera pass unembryonated eggs, but those of some groups (Trichinellidae, Trichosomoididae) embryonate *in utero.* The first-stage larvae (L1) have an oral stylet, similar to their presumed soil-dwelling dorylaimid ancestors. Unlike other parasitic nematodes, the L1 of trichinelloids (rather than L3) is used to infect their final hosts, sometimes after a brief period in an invertebrate intermediate host (such as earthworms) to become infective. Adults worms are endoparasites in most classes of vertebrates, generally occurring within the intestinal mucosa but some infecting epithelia of the urinary, respiratory or integumentary systems. An increasing number of genera have been recognised but their higher classification is confounded as some authorities distinguish 6 families while others have demoted several to subfamily status. The former ranking has been retained in this resource to better help the reader differentiate genera on the basis of recognised apomorphic characters, although future studies may reveal different phylogenetic relationships. The 6 trichinelloid families include: Capillariidae in birds, mammals and fish; Trichuridae (syn. Trichuroididae), Trichinellidae, Anatrichosomatidae and Trichosomoididae primarily in mammals; and Cystoopside in fish and reptiles.

The family Capillariidae contains small slender worms (often called hair-worms) which show a gradual transition in width with the anterior end being narrowest. Mature worms have 1-3 stichosomes composed of 20-60 stichocytes. The entire adult worm is embedded in the intestinal, urinary or respiratory mucosa, sometimes the liver, spleen or skin, of hosts belonging to all vertebrate groups (birds, mammals, reptiles, amphibians, fish). Many capillariid taxa have been described primarily on the basis of parasite morphology and host occurrence, with over 400 species assigned to over 35 genera. Several attempts have been made to revise their

classification, but no consensus has yet been achieved and comparative molecular phylogenetic studies are in their infancy. Some authorities attempt to list all species in the single genus *Capillaria sensu latu* (in the broadest sense), but most continue to list both old and new names under various synonyms; including *Aonchotheca* (with 3 subgenera *Aonchotheca, Avesaonchotheca/Avescapillaria, Armocapillaria*), *Baruscapillaria*, *Brevithominx*, *Calodium* (syn. *Hepaticola*), *Capillaria sensu stricto* (syn. *Trichosoma*, *Trichosomum, Thominx*, *Orthothominx, Nematoideum p.p.*) (with 6 subgenera *Capillaria, Capillaroides, Hepatocapillaria, Neocapillaria, Procapillaria, Tridentocapillaria*), *Capillostrongyloides, Crocodylocapillaria, Echinocoleus, Eucoleus* (syn. *Ritaklossia*), *Freitascapillaria, Gessyella, Hepatospina*, *Liniscus, Lobocapillaria, Ornithocapillaria*, *Paracapillaria* (with 3 subgenera *Paracapillaria, Crossicapillaria, Ophidocapillaria*), *Paracapillaroides, Paratrichosoma, Pearsonema, Pseudocapillaria* (with 4 subgenera *Pseudocapillaria*, *Ichthyocapillaria, Indocapillaria, Discocapillaria*), *Pseudocapillaroides, Pterothominx* (syn. *Armocapillaria*), *Schulmanela* (with 4 subgenera *Schulmanela, Piscicapillaria, Lomakinela*, *Amphibiocapillaria*), *Skrjabinocapillaria,* and *Tenoranema*. Some other *Capillaria* species parasitic in fish are now included in the genus *Huffmanela* in the family Trichosomoididae. Female capillariid worms produce distinctive eggs with bipolar mucoid plugs which are excreted with host faeces or urine, with the exception of those species living in internal organs which are only liberated only after infected tissues are eaten by carnivores or scavengers which then excrete intact eggs. In the external environment, most eggs embryonate to contain a small first-stage larva (L1) with a well-defined stylet. The eggs of most species are directly infective to the final host, whereas those of some other species must first be ingested by intermediate hosts (mostly earthworms, but some fish) where they hatch releasing the L1 which becomes infective after some modest growth. Many species infect the digestive tracts of birds and some species have been associated with clinical disease involving catarrhal or fibrinous enteritis and mild anaemia. Other species infect the intestines or airways of mammals, some causing gastroenteric or respiratory perturbances. To date, 4 species are known to infect humans: most cases involving *Aonchotheca philippinensis* infecting the intestines after being acquired by eating undercooked fish; and some sporadic cases involving *Calodium hepaticum* infecting the liver, *Eucoleus aerophilus* infecting the respiratory tract, and *Pearsonema plica* infecting the urinary tract, after the accidental consumption of eggs.

Parasite species	**Definitive Hosts [plus Intermediate Hosts (IH) as applicable]**	**Site of infection (clinical signs)**	**Distribution**
Aonchotheca (male tail with caudal lateral alae and membranous bursa supported by lateral projections, spicule with nonspiny sheath, parasites of digestive tracts of mammals, birds and amphibia)			
A. (*Avesaonchotheca*) *alpina* (syn. *Pterothominx*)	Galliformes: phasianid (black grouse, western capercaillie)		Europe
A. annulosa (*annulosum*) (syn. *Trichosoma*, *Capillaria*)	Rodentia: murid (brown rat, black rat, house mouse, wood mouse, Korean field mouse, yellow-necked mouse), cricetid (bank vole, Lusitanian pine vole); Eulipotyphla: erinaceid (Algerian hedgehog)	intestines	Eurasia, Africa
A. armeniaca	Rodentia: sciurid (European ground squirrel, long-tailed ground squirrel)		Europe
A. baylisi	Rodentia: murid (rusty-bellied brush-furred rat)		Africa
A. bilobata (syn. *C. bisonis, megrelica*)	Artiodactyla: bovid (cattle, zebu, European bison, sheep, mouflon, goat), cervid (roe deer)	intestines	Europe
A. bovis (syn. *A. brevipes*)	Artiodactyla: bovid (cattle, water buffalo, yak, muskox, American bison, European bison, sheep, bighorn sheep, mouflon, chamois, Barbary sheep, argali, goat, ibex, Himalayan goral, East Caucasian tur, Japanese serow), antilocaprid (pronghorn), cervid (roe deer, fallow deer, red deer, sika deer, Pere Danid's deer, water deer, white-tailed deer, chital, Javan rusa, reindeer, moose), giraffid (okapi), camelid (dromedary)	intestines	worldwide
A. brochieri	Primates: hominid (bonobo)	intestines	Africa
A. brosseti	Chiroptera: rhinolophid (Lander's horseshoe bat)		Africa
A. buccalis	Anura: bufonid (common toad, Japanese common toad), dicroglossid (large-headed frog)		Asia
A. (*Avesaonchotheca*) *bursata* (syn. *Pterothominx*)	Galliformes: phasianid (chicken, turkey, ring-necked pheasant, chukar partridge, grey partridge, hazel grouse, western capercaillie, black-billed capercaillie), numidid (helmeted guineafowl); Columbiformes: columbid (pigeon); Anseriformes: anatid (greylag goose) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]	small intestine (bloody diarrhoea)	worldwide
A. caprae	Artiodactyla: bovid (goat)		India
A. (*Avesaonchotheca*)	Galliformes: phasianid (chicken, turkey, ring-necked pheasant,	small	worldwide

caudinflata (syn. *Pterothominx*)	golden pheasant, green pheasant, grey partridge, chukar partridge, rock partridge, red-legged partridge, common quail, northern bobwhite quail, willow ptarmigan, rock ptarmigan, black grouse, hazel grouse, red grouse, Caucasian grouse, western capercaillie, black-billed capercaillie), numidid (helmeted guineafowl, vulturine guineafowl); Anseriformes: anatid (greylag goose, mallard, muscovy duck); Columbiformes: columbid (pigeon, rock dove, European collared dove, Eurasian collared dove, Oriental turtle dove); Tinamiformes: tinamid (Chilean tinamou); Passeriformes: passerid (sparrow), emberizid (common reed bunting), sturnid (common starling), turdid (American robin, redwing, common blackbird, song thrush, mistle thrush, fieldfare), muscicapid (European robin), corvid (Eurasian jay), lariid (red-backed shrike), sittid (Eurasian nuthatch), thraupid (red-crested cardinal bird); Otidiformes: otidid (little bustard); Bucerotiformes: bucertid (northern red-billed hornbill, western red-billed hornbill); Falconiformes: falconid (common kestrel) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]	intestine (bloody diarrhoea)	
A. chabaudi	Chiroptera: rhinolophid (forest horseshoe bat)		Africa
A. corneti	Eulipotyphla: soricid (hero shrew)		Africa
A. crociduri	Eulipotyphla: soricid (Dsinezumi shrew)		Africa
A. cubana	Chiroptera: molossid (Bonda mastiff bat, velvety free-tailed bat)		South America
A. dessetae	Lagomorpha: ochotonid (Royle's pika)		Nepal
A. europaea	Eulipotyphla: soricid (greater white-toothed shrew, lesser white-toothed shrew), talpid (Spanish mole)		Europe, Africa
A. euryali	Chiroptera: rhinolophid (Mediterranean horseshoe bat)		Europe
A. (*Avesaonchotheca*) *exile* (*exilis*) (syn. *Pterothominx*)	Passeriformes: sturnid (common starling), turdid (song thrush, mistle thrush, red-throated thrush, Swainson's thrush, common blackbird, eastern bluebird, redwing, American robin, ring ouzel), alaudid (Eurasian skylark), fringillid (European greenfinch, brambling), corvid (rook, Eurasian jay, alpine chough), emberizid (common reed bunting), passerid (house sparrow); Galliformes: phasianid (ring-necked pheasant); Anseriformes: anatid (wood duck); Coraciiformes: coraciid (European roller)		Europe
A. forresteri	Rodentia: cricetid (marsh rice rat)	stomach	North America
A. gabonensis	Chiroptera: rhinolophid (forest horseshoe bat)		Africa
A. gastrosuis	Artiodactyla: suid (pig)	stomach	Europe
A. italica	Chiroptera: vespertilionid (brown long-eared bat, Bechstein's bat, long-fingered bat, pond bat, Daubenton's bat, Natterer's bat, lesser noctule, common pipistrelle)		Eurasia
A. kashmirensis	Chiroptera: vespertilionid (wall-roosting mouse-eared bat)	stomach	India
A. landauae	Chiroptera: rhinolophid (Lander's horseshoe bat)		Africa
A. legerae	Rodentia: glirid (garden dormouse)	intestines	Europe
A. (*Avesaonchotheca*) *longifilla* (*longifila*) (syn. *Pterothominx*)	Passeriformes: prunellid (dunnock, alpine accentor), alaudid (Eurasian skylark), corvid (alpine chough, black-chested jay), sittid (Eurasian nuthatch), muscicapid (Siberian rubythroat), leiothrichid (white-eared sibia), thraupid (red-crested cardinal bird), zosteropid (Taiwan yuhina); Galliformes: phasianid (common quail); Bucerotiformes: bucerotid (northern red-billed hornbill, western red-billed hornbill); Anseriformes: anatid (wood duck, bar-headed goose)		Europe, Africa
A. martinezi	Chiroptera: natalid (Mexican greater funnel-eared bat)		North America
A. mergelica	Artiodactyla: bovid (sheep)		Europe
A. minuta	Eulipotyphla: soricid (common shrew, Laxmann's shrew, Eurasian pygmy shrew)		Eurasia
A. moraveci	Chiroptera: vespertilionid (lesser mouse-eared bat, greater mouse-eared bat, long-fingered bat)	stomach	Europe
A. murissylvatici	Rodentia: murid (house mouse, striped field mouse, yellow-necked	intestines	Eurasia

(syn. *Trichosomum*)	mouse, Korean field mouse, small Japanese field mouse, wood mouse, brown rat, black rat), cricetid (common vole, field vole, bank vole, tundra vole, social vole, grey red-backed vole, northern red-backed vole, Hokkaido red-backed vole, Baluchistan vole, Sikkim Mountain vole, grey dwarf hamster, Turkish hamster)		
A. musimon	Artiodactyla: bovid (mouflon)		Europe
A. mustelorum	Carnivora: mustelid (European badger, American mink, least weasel)		Europe, North America
A. myoxinitelae	Rodentia: glirid (garden dormouse)	intestines	Europe
A. nycticeiusi	Chiroptera: vespertilionid (Kuhl's pipistrelle)	intestines	India
A. okapi	Artiodactyla: giraffid (okapi)		Africa
A. palmata	Chiroptera: vespertilionid (big brown bat, little brown bat, evening bat, tricolored bat, southeastern myotis)		North America
A. papuensis	Artiodactyla: suid (pig)	intestines	New Guinea
A. paranalis	Carnivora: mustelid (beech marten)		Europe
A. parca	Chiroptera: phyllostomid (Pallas's long-tongued bat)		Americas
A. petrovi	Eulipotyphla: soricid (bicolored shrew, common shrew, Eurasian pygmy shrew, Eurasian water shrew, Mediterranean water shrew)		Eurasia
A. philippinensis (*Capillaria, Calodium, Paracapillaria, P.* (*Crossicapillaria*))	Primates: hominid (human), cercopithecid (rhesus macaque, crab-eating macaque, Formosan rock macaque); Rodentia: murid (mouse, brown rat, Natal multimammate mouse, Mongolian gerbil); Gruiformes: rallid (white-breasted waterhen, common waterhen); Pelecaniformes: ardeid (Chinese pond heron, western cattle egret, yellow bittern, black-crowned night heron); Charadriiformes: rostratulid (greater painted-snipe); Columbiformes: columbid (pigeon);; Galliformes: phasianid (chicken); Anseriformes: anatid (mallard) [plus L1 in IH: Perciformes: ambassid (flag-tailed glassfish, Commerson's glassy); Gobiiformes: oxudercid (large snout goby, stream goby), eleotrid (dusky sleeper, tropical carp-gudgeon, apagon); Anabantiformes: osphronemid (croaking gourami); Cyprinodontiformes: poeciliid (rainbow fish, eastern mosquitofish, guppy), aplocheilid (blue panchax); Cypriniformes: cyprinid (common carp, mirror carp, Java barb, red-tailed rasbora, blackline rasbora)] [plus embryonated auto-infective eggs]	intestines (wasting disease, intractable diarrhoea)	Eurasia
A. phyllonycteris	Chiroptera: phyllostomid (Cuban flower bat)		Americas
A. plathyspicula	Artiodactyla: suid (boar)	urinary bladder	Russia
A. praeputialis	Rodentia: murid (bush rat)	preputial gland	Australia
A. putorii	Carnivora: canid (coyote, dog, raccoon dog, red fox), mustelid (American marten, beech marten, European pine marten, Japanese marten, European polecat, American mink, European mink, Eurasian otter, fisher, sable, stoat, Japanese weasel, Siberian weasel, least weasel, ferret, European badger), felid (cat), memphitid (striped skunk), procyonid (raccoon), ursid (American black bear) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]	stomach, small intestines (anorexia, bloody vomitus)	Europe, New Zealand
A. ransomia (syn. *Baruscapillaria*)	Rodentia: cricetid (muskrat)	intestines	Americas
A. rara	Chiroptera: rhinolophid (greater horseshoe bat)		Eurasia
A. rhinolophi	Chiroptera: rhinolophid (Chinese rufous horseshoe bat)		Asia
A. riukiuensis	Artiodactyla: suid (wild boar)		Asia
A. romana	Chiroptera: vespertilionid (Bechstein's bat, pond bat, Daubenton's bat, greater mouse-eared bat, whiskered bat, lesser noctule, common pipistrelle, Mediterranean horseshoe bat, greater horseshoe bat)		Europe
A. soricis	Eulipotyphla: talpid (Kobe mole, Sado mole), soricid (Eurasian pygmy shrew, Shinto shrew, long-clawed shrew)	stomach	Asia

A. speciosa	Chiroptera: vespertilionid (northern bat, serotine bat, Bechstein's bat, pond bat, Daubenton's bat, Natterer's bat, greater mouse-eared bat, whiskered bat, common noctule, parti-colored bat), miniopterid (common bentwing bat), rhinolophid (Mediterranean horseshoe bat, greater horseshoe bat, lesser horseshoe bat)		Eurasia, Africa, North America
A. tamiasstriati	Rodentia: sciurid (North American chipmunk)	intestines	North America
A. viguerasi	Chiroptera: phyllostomid (Waterhouse's leaf-nosed bat)	intestines	Cuba
A. vietnamensis	Chiroptera: vespertilionid (lesser Asiatic yellow bat)	stomach, intestines	Asia
A. wioletti	Rodentia: cricetid (European water vole)	stomach	Europe
Baruscapillaria (male tail without caudal lateral alae, with well-developed membranous bursa supported by lateral lobes, spicule with nonspiny sheath, parasites of digestive tract of birds and mammals)			
B. angusta	Passeriformes: fringillid (common chaffinch), passerid (house sparrow)		Europe
B. anseris	Anseriformes: anatid (mallard, northern pintail, long-tailed duck, common merganser, greater white-fronted goose, snow goose, bean goose, Egyptian goose)		Europe
B. appendiculata	Atheriniformes: atheropsid (pike silverside); Cypriniformes: cyprinid (common carp)		Europe
B. belopolskaiae	Charadriiformes: scolopacid (common snipe), recurvirostrid (black-winged stilt)		Eurasia
B. calliopsis	Passeriformes: muscicapid (Siberian rubythroat)		Russia
B. carbonis (syn. *Trichosoma, Capillaria*)	Charadriiformes: larid (common gull, slender-billed gull, European herring gull, common tern, black tern, gull-billed tern), charadriid (European golden plover, grey plover); Pelecaniformes: pelecanid (great white pelican, Dalmatian pelican), ardeid (great egret, little egret, grey heron, purple heron, squacco heron, black-crowned night heron), threskiornithid (glossy ibis); Podicipediformes: podicipedid (red-necked grebe, black-necked grebe); Gaviiformes: gaviid (black-throated loon, Pacific loon); Siluriformes: phalacrocoracid (double-crested cormorant, great cormorant, pygmy cormorant); Serpentes: viperid (Russell's viper)		Eurasia
B. cincli	Passeriformes: cinclid (white-throated dipper)		Eurasia
B. conspecta	Rodentia: murid (bush rat, Cape York rat, Australian water rat); Diprotodontia: hypsiprymnodontid (musky rat-kangaroo)	intestines	Australia
B. corvorum (syn. *Pseudocapillaria*)	Passeriformes: corvid (western jackdaw, common raven, carrion crow, hooded crow, large-billed crow, rook, Eurasian jay, blue jay, Eurasian magpie, spotted nutcracker, alpine chough), motacillid (white wagtail), turdid (common blackbird, song thrush, mistle thrush), sturnid (rosy starling), emberizid (yellowhammer), passerid (house sparrow, Eurasian tree sparrow) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]		Eurasia, North America
B. cylindrica	Accipitriformes: accipitrid (common buzzard); Falconiformes: falconid (American kestrel); Strigiformes: strigid (tawny owl)		Palearctic
B. emberizae	Passeriformes: emberizid (bunting, grey bunting); motacillid (tree pipit), sturnid (bed-cheeked starling)		Eurasia
B. grallinae	Passeriformes: monarchid (magpie-lark)		Australia
B. herodiae	Pelecaniformes: ardeid (grey heron, great egret, great blue heron)		cosmopolitan
B. inflexa	Passeriformes: turdid (blue rock thrush, song thrush), sturnid (common starling)		Europe
B. kutori (syn. *Aonchotheca*)	Eulipotyphla: soricid (common shrew, tundra shrew, alpine shrew, Tien Shan shrew, Laxmann's shrew, Eurasian water shrew, Eurasian pygmy shrew)		Eurasia
B. longevaginata	Passeriformes: alaudid (Eurasian skylark)		Eurasia
B. multicellularis	Rodentia: murid (brown rat)	intestines	Asia
B. obsignata (syn. *C. columbae*, *droummondi, dujardini, gigantotecta*)	Columbiformes: columbid (pigeon, common wood pigeon, white-winged dove, mourning dove, stock dove, Eurasian collared dove, European turtle dove); Galliformes: phasianid (chicken, turkey, common quail, northern bobwhite quail, ring-necked pheasant, grey partridge, red-legged partridge, black grouse, western	intestines (diarrhoea, emaciation)	worldwide

	capercaillie, Congo peafowl), numidid (helmeted guineafowl); Anseriformes: anatid (mallard, American black duck, garganey, nene, common pochard, Cape teal, yellow-billed pintail, greylag goose, snow goose, black swan, black-necked swan); Piciformes: ramphastid (Toco toucan); Podicipediformes: podicipedid (great crested grebe, western grebe, horned grebe, red-necked grebe, black-necked grebe); Bucerotiformes: bucerotid (Malabar pied hornbill); Pelecaniformes: ardeid (great blue heron, snowy egret), pelecanid (grey pelican); Cuculiformes: cuculid (greater coucal); Charadriiformes: recurvirostrid (black-necked stilt); Passeriformes: fringillid (European greenfinch), sturnid (great myna, common starling), turdid (American robin, varied thrush), passerid (house sparrow)		
B. ovopunctata	Passeriformes: turdid (oriental magpie-robin, song thrush, red-throated thrush, mistle thrush, grey-cheeked thrush, wood thrush, thrush nightingale, common blackbird, redwing, American robin, fieldfare), sturnid (rosy starling, common starling), muscicapid (European robin, white-capped redstart), motacillid (meadow pipit), passerid (rock sparrow), prunellid (alpine accentor), icterid (common grackle, red-winged blackbird), alaudid (Eurasian skylark), corvid (rook, Eurasian jay)		Eurasia
B. pachykeramota	Carnivora: felid (cheetah)		Africa
B. phalacrocoraxi	Siluriformes: phalacrocoracid (pygmy cormorant)		Eurasia
B. pitti	Passeriformes: pittid (hooded pitta), muscicapid (white-vented shama, oriental magpie-robin); Columbiformes: columbid (common emerald dove)	intestines	Asia
B. podicipitis	Podicipediformes: podicipedid (horned grebe, little grebe, pied-billed grebe, great crested grebe, red-necked grebe, black-necked grebe); Charadriiformes: larid (black-headed gull); Anseriformes: anatid (mallard, northern pintail, long-tailed duck, Indian spot-billed duck, tufted duck, greater scaup, garganey, northern shoveler, common pochard, Eurasian teal, Eurasian wigeon, greylag goose, bean goose, greater white-fronted goose, smew, common merganser)		Eurasia
B. prashadi	Rodentia: murid (brown rat)	urinary bladder	India
B. quiscali	Passeriformes: turdid (varied thrush, American robin)		North America
B. rauschi	Eulipotyphla: soricid (cinereous shrew, vagrant shrew)	intestines	North America
B. resecta	Passeriformes: corvid (common raven, rook, western jackdaw, carrion crow, hooded crow, Eurasian magpie, Eurasian jay, blue jay, alpine chough, spotted nutcracker), motacillid (white wagtail), turdid (common blackbird, song thrush, fieldfare); Galliformes: phasianid (chicken)		Palearctic
B. rudolphii	Suliformes: phalacrocoracid (great cormorant)	intestines	Europe
B. ryzhikovi	Podicipediformes: podicipedid (little grebe, red-necked grebe, black-necked grebe)		Europe
B. saurotherae	Cuculiformes: cuculid (lizard-cuckoo)	intestines	Cuba
B. spiculata (*spiculatus*)	Suliformes: phalacrocoracid (double-breasted cormorant, neotropical cormorant)		Americas
B. tiaras	Galliformes: phasianid (grey partridge)		Europe
B. traverae	Rodentia: murid (Pacific rat, black rat)	intestines	Asia
Calodium (syn. *Hepaticola*) (male tail rounded with caudal lateral alae, spicule with nonspiny sheath, parasites of internal organs of mammals)			
C. alatum	Carnivora: mustelid (ferret)		Europe
C. cholidicola (syn. *Hepaticola*)	Eulipotyphla: soricid (common shrew)		Europe
C. hepaticum (*hepatica*) (syn. *Capillaria, Eucoleus, Hepaticola, H. anthropopitheci,*	Carnivora: canid (dog, coyote, wolf, maned wolf), felid (cat), castorid (Eurasian beaver), memphitid (skunk), mustelid (weasel, stoat); Didelphimorphia: didelphid (opossum); Rodentia: murid (brown rat, black rat, ricefield rat, Annandale's rat, Bartel's spiny rat, Kaiser's rock rat, African grass rat, African marsh rat, long-	liver (often subclinical, sometimes hepatitis)	worldwide

Trichocephalus, Trichosoma)	tailed giant rat, giant white-tailed rat, Edward's swamp rat, Edward's long-tailed giant rat, Hellwald's rat, Hoffman's rat, Malayan field rat, Musschenbroek's spiny rat, Pacific rat, South African viel rat, Plains rat, white-bellied rat, yellow-breasted rat, bush rat, opossum rat, greater bandicoot rat, lesser bandicoot rat, fawn-footed mosaic-tailed rat, house mouse, Florida mouse, striped field mouse, typical striped grass mouse, white-footed mouse, yellow-necked mouse, eastern broad-toothed field mouse, small Japanese field mouse, large Japanese field mouse, Korean field mouse, Ethiopian white-footed mouse, Jackson's soft-furred mouse, Natal multimammate mouse, wood mouse, Campana field mouse, savanna gerbil), dipodid (woodland jumping mouse), cricetid (cotton mouse, white-footed mouse, deer mouse, hispid cotton rat, muskrat, marsh rice rat, tundra vole, Venezuelan vole mouse, European water vole, European snow vole, common red-backed vole, southern red-backed vole, northern red-backed vole, grey red-backed vole, bank vole, field vole, common vole, meadow vole, Major's pine vole, tundra vole, social vole, southern bog lemming, grey dwarf hamster), sciurid (woodchuck, eastern chipmunk, American red squirrel, Caucasian squirrel, Brazilian squirrel, Franklin's ground squirrel, Richardson's ground squirrel, groundhog), geomyid (northern pocket gopher), nesomyid (Emin's pouched rat, Gambian pouched rat), echimyid (coypu), erethizontid (North American porcupine), caviid (guinea pig, Brazilian guinea pig); Hyracoidea: procaviid (hyrax); Diprotodontia: phalangerid (common brushtail possum); Eulipotyphla: soricid (Asian house shrew), erinaceid (European hedgehog); Lagomorpha: leporid (rabbit, European hare, mountain hare); Artiodactyla: bovid (Kirk's dik-dik), antilocaprid (pronghorn), tayassuid (peccary); Perissodactyla: equid (horse); Primates: atelid (Geoffrey's spider monkey), cercopithecid (grivet), hominid (mountain gorilla, chimpanzee, human) [plus IH: Diptera: calliophorid (latrine fly)]		
C. soricicola (syn. *Hepaticola*)	Eulipotyphla: soricid (common shrew, greater white-toothed shrew, lesser white-toothed shrew, bicolored shrew, Laxmann's shrew, Tien Shan shrew, Eurasian pygmy shrew, Eurasian water shrew, Mediterranean water shrew), talpid (European mole)		Europe, Africa
C. splenaecum	Eulipotyphla: soricid (greater white-toothed shrew)		Europe
Capillaria s.s. (syn. *Trichosoma, Trichosomum, Thominx, Orthothominx*) (male tail without membranous bursa or pseudobursa but rounded with 2 lateral lobes, spicule with spiny sheath, parasites of digestive tract of fish, amphibia, reptiles, birds and mammals)			
C. acanthopagri	Perciformes: sparid (blackhead seabream)	intestines	Asia
C. alainchabaudi	Rodentia: cricteid (Argentine swamp rat)	intestines	South America
C. anatis (syn. *C. tumida, collare, collaris, semiteres, uruguayensis, Trichosoma brevicolle, dubium, longicolle, retusum, Thominx*)	Anseriformes: anatid (mallard, mandarin duck, Muscovy duck, wood duck, mottled duck, falcated duck, Baikal duck, American black duck, tufted duck, bronze-winged duck, ring-necked duck, long-tailed duck, ferruginous duck, European sea duck, ruddy duck, white-headed duck, Australian shelduck, velvet scoter, common scoter, surf scoter, merganser, red-breasted merganser, hooded merganser, canvasback, common pochard, red-crested pochard, bufflehead, common goldeneye, spectacled eider, common eider, greater scaup, lesser scaup, New Zealand scaup, garganey, gadwall, northern shoveler, northern pintail, ringed teal, chesnut teal, cinnamon teal, Eurasian teal, Cape teal, Eurasian wigeon, American wigeon, Chiloe wigeon, smew, greylag goose, snow goose, bean goose, red-breasted goose, greater white-fronted goose, lesser white-fronted goose, Canada goose, Egyptian goose, goosander, black swan, whooper swan, mute swan); Charadriiformes: charadriid (Kentish plover), larid (black tern, little tern, sandwich tern, Caspian tern, European herring gull, black-headed gull, lesser black-headed gull, slender-billed gull, little gull), recurvirostrid (black-necked stilt, American avoset),	crop, oesophagus, intestines, caeca (bloody diarrhoea)	worldwide

	scolopacid (solitary snipe); Gruiformes: rallid (Eurasian coot); Phoenicopteriformes: phoenicopterid (American flamingo); Podicipediformes: podicipedid (red-necked grebe); Galliformes: phasianid (chicken, Indian peafowl, turkey, golden pheasant, ring-necked pheasant, red-legged partridge, grey partridge, hazel grouse, black grouse, Japanese quail, spot-winged wood quail, willow ptarmigan, rock ptarmigan), numidid (helmeted guineafowl) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]		
C. appendigera	Perciformes: lutjanid (gold-banded jobfish)	intestines	Australia
C. aramidesi	Gruiformes: rallid (grey-necked wood rail)	caeca	South America
C. ariusi (syn. *Thominx*)	Siluriformes: ariid (catfish)		Eurasia
C. blarinae	Eulipotyphla: soricid (northern short-tailed shrew)	oesophagus	North America
C. bohmi (syn. *Thominx*)	Carnivora: canid (red fox, wolf)		Europe
C. bombinatoris (syn. *Trichosoma*)	Anura: bombinatorid (European fire-bellied toad)		Europe
C. brasiliana	Pelecaniformes: ardeid (black-crowned night heron)	intestines	South America
C. bursata (syn. *Piscicapillaria*)	Carcharhiniformes: sphyrnid (great hammerhead, scalloped hammerhead)		Australia
C. (*Neocapillaria*) *carioca*	Tetraodontiformes: tetraodontid (checkered puffer fish)	intestines	Pacific
C. catenata (syn. *Thominx*, *Capillaria, Capillaroides, Capillostrongyloides*)	Salmoniformes: salmonid (cutthroat trout, sockeye salmon); Perciformes: centrarchid (rock bass, largemouth bass, green sunfish, pumpkinseed, bluegill, black crappie), percid (yellow perch, walleye)	intestine	North America
C. cecumitis (syn. *Thominx*)	Charadriiformes: scolopacid (red knot, dunlin, willet)		Eurasia
C. chandleri	Rodentia: sciurid (Franklin's ground squirrel)	intestines	North America
C. (*Hepatocapillaria*) *cichlasomae*	Cichliformes: cichlid (Mayan cichlid)	liver	South America
C. (*Neocapillaria*) *cooperi* (syn. *Pseudocapillaria*)	Callionymiformes: callionymid (crook-spined dragonet); Tetraodontiformes: monacanthid (horseshoe leatherjacket)		Australasia
C. (*Hepatocapillaria*) *cyprinodonticola* (syn. *Schulmanela*)	Cyprinodontiformes: goodeid (goldbreast splitfin, Balsas splitfin), poeciliid (common molly, sailfin molly, shortfin molly, porthole livebearer), cyprinodontid (sheepshead minnow, gold-spotted killifish), fundulid (Gulf killifish); Characiformes: characid (Mexican tetra); Cichliformes: cichlid (convict cichlid)	liver	worldwide
C. dicruri (syn. *Thominx*)	Passeriformes: dicrurid (hair-crested drongo)		Asia
C. (*Tridentocapillaria*) *eurycerca* (*eurycercus*) (syn. *Echinocoleus*)	Piciformes: picid (grey-headed woodpecker)		Europe
C. fulicae (syn. *Thominx*)	Gruiformes: rallid (American coot, Eurasian coot, American purple gallinule, common moorhen), gruid (whooping crane)		Eurasia, North America
C. (*Procapillaria*) *gracilis* (*gracile*) (syn. *Thominx, C. kabatai*)	Gadiformes: gadid (Atlantic cod, poor cod, haddock, merling, whiting-pout), phycid (red hake, Boston hake), macrourid (roughhead grenadier, marlin-spike grenadier), merluciid (offshore hake, silver hake, European hake, shallow-water Cape hake, deep-water Cape hake), lotid (common ling, shore rockling, four beard rockling); Pleuronectiformes: pleuronectid (European flounder, American plaice, Atlantic halibut); Scorpaeniformes: cottid (longhorn sculpin), agonid (hooknose), scorpaenid (red scorpionfish); Callionymiformes: callionymid (common dragonet); Perciformes: anarhichadid (Atlantic wolffish), percid (greenside darter); Carangiformes: carangid (Florida pompano);	intestines	Palearctic

	Trachiniformes: trachinid (weever fish) [plus L1 in IH: Oligochaeta: lumbricid (earthworms): Diptera: chironomid (lake fly)]		
C. (*Neocapillaria*) *hakofugu*	Tetraodontiformes: ostraciid (blue-spotted boxfish)	rectum	Asia
C. (*Tridentocapillaria*) *hirundinis*	Apodiformes: apodid (common swift); Caprimulgiformes: capramulgid (European nightjar); Passeriformes: hirundinid (common house martin, sand martin), muscicapid (spotted flycatcher)	intestines	Eurasia
C. indica (syn. *Pseudocapillaria*)	Anabantiformes: channid (dwarf snakehead)	intestines	Asia
C. (*Tridentocapillaria*) *javanensis*	Piciformes: picid (common flameback, buff-necked woodpecker), megalaimid (golden-whiskered barbet)	intestines	Asia
C. longistriata	Piciformes: picid (northern flicker, pileated woodpecker)	intestines	North America
C. madnesi	Passeriformes: corvid (large-billed crow)	stomach, intestines	Asia
C. manica	Passeriformes: fringillid (common chaffinch)	intestines	Europe
C. (*Procapillaria*) *margolisi* (syn. *Pseudocapillaria (Discocapillaria)*)	Pleuronectoformes: pleuronectid (Pacific halibut); Scorpaeniformes: cottid (cabezon); Cypriniformes: cyprinid (mola carplet, rosy barb, pool barb)	caeca	Asia
C. michiganensis	Rodentia: cricetid (muskrat)	intestines	North America
C. (*Procapillaria*) *navoneae*	Anguilliformes: congrid (Argentine conger)	intestines	South America
C. nyrocinarum	Anseriformes: anatid (mallard, garganey, tufted duck, greater scaup, common goldeneye, long-tailed duck, white-winged scoter, velvet scoter, common scoter, surf scoter, common eider, king eider, mute swan); Charadriiformes: scolopacid (Eurasian whimbrel)	intestines, caeca	
C. orectolobi (syn. *Piscicapillaria*)	Orectolobiformes: orectolobid (ornate wobbegong)		Australia
C. ornamentata	Dasyuromorphia: dasyurid (agile antechinus, dusky antechinus)	nasal sinus	Australia
C. (*Tridentocapillaria*) *parusi*	Passeriformes: parid (green-backed tit), sittid (Eurasian nuthatch)	intestines	Eurasia
C. patzcuarensis	Cypriniformes: cyprinid (Patzauaro chub, common carp); Cyprinodontiformes: goodeid (blackfin goodea); Atheriniformes: atherinopsid (slender silverside, pike silverside)	intestines	South America
C. phasianina (syn. *Thominx*)	Galliformes: phasianid (chicken, Indian peafowl, turkey, golden pheasant, blood pheasant, ring-necked pheasant, grey partridge, chukar partridge, Himalayan snowcock, Tibetan snowcock, Temminck's tragopan), numidid (helmeted guineafowl): Passeriformes: corvid (Eurasian jay)	intestines, caeca	Eurasia
C. (*Neocapillaria*) *phoxini*	Cypriniformes: cyprinid (Amur minnow)		Asia
C. platyrrhinorum (syn. *Thominx*)	Primates: cebid (capuchin monkey)	intestines	Americas
C. plectropomi	Perciformes: serranid (coral trout)	intestines	New Caledonia
C. (*Neocapillaria*) *pterophylli*	Cichliformes: cichlid (Jack Dempsey, Altum angelfish, freshwater angelfish, blue discus, red discus, uaru); Cypriniformes: cyprinid (tiger barb, White Cloud Mountain minnow); Anabantiformes: osphronemid (dwarf gourami)	intestines	Americas, Asia
C. recondita	Anura: hylodid (Gaudichaud's frog)	intestines	South America
C. recurvirostrae	Charadriiformes: recurvirostrid (American avocet)	intestines	Americas
C. rhinobati (syn. *Piscicapillaria*)	Rajiformes: rhinobatid (shovelnose ray)		Asia
C. rigidula	Passeriformes: prunellid (dunnock, alpine collaris), passerid (Spanish sparrow)	intestines	Eurasia
C. (*Procapillaria*)	Rajiformes: rajid (thorny skate)	intestines	Atlantic

schmidtii			
C. serpentina (syn. *Amphibiocapillaria*)	Testudines: chelydrid (common snapping turtle), emydid (painted turtle, Cuban slider), kinosternid (common musk turtle)	intestines	Americas
C. similis (syn. *Thominx*)	Passeriformes: fringillid (common chaffinch), corvid (Eurasian jay), muscicapid (common redstart, Guidenstadt's redstart), sturnid (common starling), turdid (common blackbird, song thrush, Neumann's thrush, song thrush, mistle thrush, fieldfare); Anseriformes: anatid (red-crested pochard)		Eurasia
C. skrjabini	Anseriformes: anatid (mute swan)	caeca	Russia
C. spinulosa (*spinulosum*) (syn. *Thominx*)	Anseriformes: anatid (mallard, ring-necked duck, ferruginous duck, falcated duck, mottled duck, tufted duck, American black duck, long-tailed duck, gadwall, velvet scoter, common scoter, greater scaup, common goldeneye, garganey, Eurasian wigeon, common pochard, red-crested pochard, northern shoveler, northern pintail, dunbird, Eurasian teal, Baikal teal, whooper swan, mute swan); Gruiformes: rallid (Eurasian coot)	caeca	Palearctic
C. spirale (syn. *Thominx*)	Pelecaniformes: threskiornithid (Eurasian spoonbill)		Eurasia
C. talpae (syn. *Nematoideum talpae*) (*sp. inq.*?)	Eulipotyphla: talpid (European mole, Caucasian mole, Spanish mole, Roman mole)		Europe
C. tenuissima (syn. *Thominx*)	Strigiformes: strigid (boreal owl, short-eared owl, long-eared owl, little owl, Eurasian eagle-owl, Eurasian pygmy owl, Ural owl, barred owl, great horned owl, barn owl, snowy owl, oriental scops owl, tawny owl); Accipitriformes: accipitrid (Eurasian sparrowhawk, common buzzard, rough-legged buzzard) [plus IH: Salmoniformes: salmonid (grayling)]	gizzard, intestines	Palearctic
C. totani (syn. *Pterothominx*)	Charadriiformes: scolopacid (common sandpiper, Terek sandpiper), charadriid (common ringed plover)	caeca	Europe
C. (*Tridentocapillaria*) *tridens* (syn. *Thominx, C. pirangae*)	Passeriformes: passerid (house sparrow, Eurasian tree sparrow), passerellid (eastern towhee), parid (great tit, green-backed tit), parulid (yellow-throated warbler, hooded warbler, blackburnian warbler, black and white warbler), sturnid (spotless starling, rosy starling), cardinalid (scarlet tanager, summer tanager), leiothricid (Taiwan barwing, Steere's liocichla), emberizid (red-headed bunting), laniid (long-tailed shrike), icterid (red-winged blackbird), turdid (common nightingale), pellorneid (grey-cheeked fulvetta), cinclid (brown dipper), sylviid (garden warbler, vinous-throated parrotbill), timaliid (streak-breasted scimitar babbler), vireonid (white-eyed vireo), pycnonotid (collared finchbill), muscicapid (spotted flycatcher), corvid (large-billed crow, Sumatran treepie, spotted nutcracker), zosteropid (warbling white-eye); Piciformes: picid (northern flicker, maroon woodpecker, red-bellied woodpecker); Caprimulgiformes: caprimulgid (large-tailed nightjar); Coraciiformes: coraciid (European roller); Galliformes: phasianid (turkey)	oesophagus, stomach, intestines, mesentery, body cavity	Americas, Eurasia
C. uruguaynensis	Galliformes: phasianid (chicken)	intestines, caeca	South America
C. vazi	Galliformes: odontophorid (spot-winged wood quail)	intestine	South America
C. venusta	Piciformes:picid (northern flicker), ramphastid (black-necked aracari, toco toucan, channel-billed toucan)		South America
C. (*Neocapillaria*) *wickinsi*	Pleuronectiformes: pleuronectid (European plaice)	intestines, rectum	North Sea
Capillostrongyloides (male tail with membranous bursa-like structure supported by subventral lobes, spicule with nonspiny sheath, parasites of stomach of freshwater fish)			
C. ancistri	Siluriformes: loricariid (bushy mouth catfish)	intestines	South America
C. congiopodi	Scorpaeniformes: congiopodid (horsefish)	gall bladder	South America
C. fritschi	Siluriformes: bagrid (bayad, semutundu), malapterurid (electric		Africa

	catfish)		
C. minima	Characiformes: anostomid (banded leporinus)		South America
C. morae	Gadiformes: morid (common mora)	stomach	Europe
C. norvegica	Gadiformes: gadid (four-bearded rockling)	stomach	Atlantic
C. physiculi	Gadiformes: morid (southern bastard codling)		Australia
C. sentiosa	Characiformes: characid (Mexican tetra), erythrinid (wolf fish)		Americas
C. tandani	Siluriformes: plotosid (eel-tailed catfish)		Australia
C. tasmanica	Gadiformes: macrourid (javelinfish), merlucciid (blue grenadier)	stomach	Australasia
C. zederi	Characiformes: erythrinid (wolf fish)		Americas
Crocodylocapillaria (male tail without caudal alae, without pseudobursa, with 2 posterior lobes, spicule with spinose sheath, parasites of digestive tract of crocodiles)			
C. longiovata	Crocodilia: crocodylid (freshwater crocodile, New Guinea crocodile, saltwater crocodile)	stomach	Australasia
Echinocoleus (male tail with small membranous bursa-like structure supported by 2 lobular projections, spicule with spiny sheath, parasites of digestive tract of birds and mammals)			
E. auritae	Didelphimorphia: didelphid (common opossum, gray four-eyed opossum)		Americas
E. confusus (syn. *Capillaria, Thominx*)	Gruiformes: rallid (wood rail)	oesophagus	South America
E. cyanopicae	Passeriformes: corvid (azure-winged magpie, Eurasian magpie)		Asia
E. ellisi (syn. *Thominx*)	Anseriformes: anatid (black swan)		Australia
E. hydrochoeri (syn. *Capillaria, Eucoleus*)	Rodentia: caviid (capybara)	stomach, intestines	South America
Eucoleus (syn. *Ritaklossia*) (male tail with rudimentary pseudobursa formed by 2 tiny lobes connected by dorsal cuticular membrane, slender spicule with long spiny sheath, parasites of digestive and respiratory tracts of birds and mammals)			
E. aerophilus (*aerophila*) (syn. *Thominx, Capillaria*) (tracheal worm)	Carnivora: canid (dog, wolf, coyote, red fox, Arctic fox, gray fox, kit fox, crab-eating fox, golden jackal, raccoon dog), felid (cat, Iriomote cat, Eurasian lynx, Iberian lynx, bobcat, wildcat, leopard cat, Florida panther), mustelid (American pine marten, European pine marten, beech marten, Japanese marten, European badger, European polecat, sable, Eurasian otter, stoat, least weasel, ferret), herpestid (Egyptian mongoose), procyonid (raccoon), ursid (American black bear, brown bear); Didelphimorphia: didelphid (Virginia opossum); Eulipotyphla: erinaceid (European hedgehog); Primates: hominid (human) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]	trachea, bronchi, nasal passages (nasal discharge, wheezing cough, sneezing)	worldwide
E. annulatus (*annulata*)	Columbiformes: columbid (pigeon); Galliformes: phasianid (chicken, turkey, jungle fowl, ring-necked pheasant, ruffed grouse, black grouse, northern bobwhite quail, golden pheasant, Reeve's pheasant, grey partridge, willow ptarmigan, western capercaillie, black-billed capercaillie, Himalayan snowcock), numidid (helmeted guineafowl, crested guineafowl); Anseriformes: anatid (mallard, northern shoveler) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]	oesophagus, crop (inappetence)	worldwide
E. bacillatus (*bacillata*)	Rodentia: murid (mouse, wood mouse, yellow-necked mouse, Algerian mouse, black rat, brown rat, ricefield rat), cricetid (common vole, Major's pine vole, southwestern water vole, European water vole, bank vole)	oesophagus	Europe
E. baskakowi	Rodentia: sciurid (Caucasian Mountain ground squirrel)	trachea, oesophagus	Europe
E. bernardi	Eulipotyphla: soricid (Eurasian water shrew, Mediterranean water shrew)		Europe
E. boehemi	Carnivora: canid (wolf, red fox, dog)	sinuses, nasal passages	Eurasia
E. breviductus	Dasyuromorphia: dasyurid (eastern quoll, northern quoll, spotted-tailed quoll, kowari, agile antechinus, fawn antechinus, brown	tongue, stomach,	Australia

	antechinus, yellow-footed antechinus, dusky antechinus, sandstone antechinus, white-footed dunnart)	intestines	
E. buckenbourensis	Peramelemorphia: peramelid (long-nosed bandicoot)	lips	Australia
E. cairinae	Anseriformes: anatid (muscovy duck)	oesophagus	South America
E. contortus (*contorta*) (syn. *Thominx, Capillaria*) (syn. *C. oesphagealis, C. laricola*, *C. venteli, E. lophortygis, E. thomascameroni, E. spirale*)	Anseriformes: anatid (mallard, wood duck, ring-necked duck, mandarin duck, mottled duck, falcated duck, tufted duck, ruddy duck, marbled duck, ferruginous duck, long-tailed duck, American black duck, northern pintail, northern shoveler, common eider, Eurasian teal, Baikal teal, blue-winged teal, green-winged teal, cinnamon teal, Eurasian wigeon, garganey, gadwall, lesser scaup, greater scaup, canvasback, redhead, common pochard, red-crested pochard, bufflehead, common goldeneye, common shelduck, greylag goose, smew); Galliformes: phasianid (chicken, turkey, red-legged partridge, Barbary partridge, ring-necked pheasant, bobwhite quail, western capercaillie); Accipitriformes: accipitrid (bald eagle, common buzzard, eastern buzzard, red-tailed hawk, red-shouldered hawk, northern goshawk); Strigiformes: strigid (tawny owl); Charadriiformes: scolopacid (dunlin, common snipe, common redshank, spotted redshank, ruff, green sandpiper, Terek sandpiper, ruddy turnstone, red knot, Temminck's stint, black-tailed godwit, European woodcock), charadriid (common ringed plover, little ringed plover, European golden plover, white-tailed lapwing, northern lapwing, common sandpiper, Eurasian dotterel), recurvirostrid (black-necked stilt, pied avocet), alcid (little auk, black guillemot, thick-billed murre), larid (black-legged kittiwake, European herring gull, common gull, little gull, silver gull, slender-billed gull, Pallas's gull, great black-backed gull, black-headed gull, black-tailed gull, lesser black-backed gull, great black-backed gull, slaty-backed gull, glaucous gull, Caspian gull, Mediterranean gull, common tern, white-winged tern, black tern, gull-billed tern, little tern, royal tern, sandwich tern, Arctic tern, Aleutian tern, Caspian tern); Podicipediformes: podicipedid (horned grebe, great crested grebe, red-necked grebe, black-necked grebe, little grebe); Pelecaniformes: pelecanid (brown pelican), ardeid (black-crowned night heron, Eurasian bittern), threskiornithid (American white ibis, Eurasian spoonbill, roseate spoonbill, glossy ibis); Siluriformes: phalacrocoracid (double-breasted cormorant, neotropical cormorant, great cormorant); Gruiformes: rallid (common crane, corn crake, spotted crake, Eurasian coot, common moorhen, water rail); Passeriformes: corvid (blue jay, Eurasian jay, Eurasian magpie, carrion crow, American crow, carrion crow, rook, western jackdaw), passerid (fox sparrow, rock sparrow), sturnid (common starling, spotless starling), turdid (common blackbird, song thrush, fieldfare), acrocephalid (sedge warbler), alaudid (Eurasian skylark, crested lark), muscicapid (European robin, blue throat, northern wheatear, black redstart), oridid (Eurasian golden oriole), prunellid (dunnock) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]	oesophagus, crop (anaemia, inappetence)	worldwide
E. corvicola	Passeriformes: corvid (hooded crow)		Europe
E. didelphis	Didelphimorphia: didelphid (Virginia opossum)		North America
E. dispar (syn. *Thominx*)	Accipitriformes: accipitrid (common buzzard, long-legged buzzard, northern goshawk, Eurasian sparrowhawk, black kite); Falconiformes: falconid (saker falcon, merlin, peregrine falcon, Eurasian hobby, common kestrel); Strigiformes: strigid (barred owl, boreal owl, short-eared owl, long-eared owl); Galliformes: phasianid (chukar partridge, grey partridge, Barbary partridge, common quail, ring-necked pheasant, western capercaillie, Altai snowcock, Himalayan snowcock); Anseriformes: anatid (mallard); Passeriformes: acrocephalid (sedge warbler), corvid (carrion crow, hooded crow, rook, Eurasian jay, Eurasian magpie), sturnid		Eurasia, North America

	(common starling)		
E. dubia (*dubius*)	Chiroptera: vespertilionid (Brandt's bat)		Asia
E. eberthi	Didelphimorphia: didelphid (grey four-eyed opossum)		Americas
E. fluminensis	Didelphimorphia: didelphid (common opossum, big-eared opossum)		Americas
E. fluvidus	Peramelemorphia: peramelid (long-nosed bandicoot, eastern barred bandicoot)	tongue, oesophagus, stomach	Australia
E. frugilegi	Passeriformes: corvid (carrion crow, rook) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]	oesophagus	Europe
E. garfiai	Artiodactyla: suid (pig) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]	tongue	Europe
E. gastricus (*gastrica*) (syn. *Thominx, Capillaria, C. muris, Hepaticola, H. cancerogena*)	Rodentia: cricetid (common vole, Gunther's vole, European water vole, muskrat, marsh rice rat), murid (brown rat, black rat, Pacific rat, bush rat, Australian swamp rat, Cape York rat, dusky field rat, house mouse, Natal multimammate mouse, striped field mouse, yellow-necked mouse, wood mouse, alpine field mouse, yellow-necked mouse), spalacid (lesser mole-rat); Dasyuromorphia: dasyurid (dusky antechinus)	stomach, oesophagus	Eurasia, Americas, Australia
E. lemmi	Rodentia: cricetid (northern red-backed vole, muskrat)	stomach	Eurasia
E. longiductus	Peramelemorphia: peramelid (long-nosed bandicoot, eastern barred bandicoot, southern brown bandicoot, northern brown bandicoot); Dasyuromorphia: dasyurid (agile antechinus, fawn antechinus, dusky antechinus, northern quoll)	lips, tongue, oesophagus, stomach	Australia
E. marii (syn. *Thominx, Capillaria*)	Eulipotyphla: talpid (Russian desman)		Russia
E. medjerdae	Rodentia: murid (mouse)		Europe
E. obtusiuscula	Charadriiformes: scolopacid (common sandpiper, little stint, Temminck's stint, common snipe, great snipe, ruff, grey-tailed tattler, wandering tattler, common sandpiper, wood sandpiper, marsh sandpiper, common redshank), charadriid (common ringed plover, little ringed plover, lesser sand plover, grey plover, northern lapwing, white-tailed lapwing, Eurasian dotterel), recurvirostrid (black-winged stilt), haematopodid (Eurasian oystercatcher); Anseriformes: anatid (garganey); Gruiformes: gruid (common crane, blue crane, black-crowned crane, whooping crane, great gray crane)		Eurasia, Africa
E. oesophagicola (syn. *Thominx*)	Eulipotyphla: soricid (common shrew, bicolored shrew, lesser white-toothed shrew, Eurasian pygmy shrew, Eurasian water shrew, Mediterranean water shrew, northern short-tailed shrew, vagrant shrew), talpid (European mole)	oesophagus, stomach	Eurasia, North America
E. parvulus	Peramelemorphia: peramelid (southern brown bandicoot, northern brown bandicoot, eastern barred bandicoot, long-nosed bandicoot)	stomach, intestines	Australia
E. penidoi	Tinamiformes: tinamid (spotted nothura)	oesophagus, oral cavity	South America
E. perforans (syn. *Thominx*)	Galliformes: phasianid (turkey, chukar partridge, grey partridge, ring-necked pheasant, western capercaillie), numidid (vulturine guineafowl, helmeted guineafowl); Anseriformes: anatid (mallard, northern pintail); Gruiformes: pallid (common moorhen)	oesophagus, crop	worldwide
E. perplexus	Peramelemorphia: peramelid (long-nosed bandicoot)	lips	Australia
E. plumosus	Rodentia: murid (bush rat, swamp rat, house mouse)	intestines	Australia
E. posterus	Peramelemorphia: peramelid (long-nosed bandicoot)	lips, scrotum	Australia
E. procyonis	Carnivora: procyonid (raccoon), memphitid (striped skunk)		North America
E. pseudoplumosus	Peramelemorphia: peramelid (southern brown bandicoot, northern brown bandicoot, eastern barred bandicoot, long-nosed bandicoot); Dasyuromorphia: dasyurid (agile antechinus, brown antechinus, dusky antechinus, white-footed dunnart)	stomach, intestines	Australia
E. raillieti	Anseriformes: anatid (mallard)		Europe

(syn. *Thominx, Capillaria*)			
E. rickardi	Dasyuromorphia: dasyurid (brown antechinus, dusky antechinus, agile antechinus, white-footed dunnart)	stomach, intestines	Australia
E. schvalovoj	Carnivora: mustelid (Eurasian otter)		Europe
E. strumosus	Galliformes: phasianid (chicken)		Europe
E. suppereri	Accipitriformes: accipitrid (common buzzard)		Eurasia
E. tenuis	Eulipotyphla: erinaceid (southern white-breasted hedgehog, northern white-breasted hedgehog, European hedgehog)		Europe
E. trilobus	Charadriiformes: charadriid (grey-headed lapwing, grey plover)		Europe
E. tringae	Charadriiformes: scolopacid (spotted redshank)		Asia
E. trophimenkovi	Carnivora: mustelid (European pine marten)		Europe
E. urotrichi (syn. *Thominx*)	Eulipotyphla: talpid (Japanese shrew mole)		Asia
E. vanelli (syn. *Thominx, Capillaria*)	Charadriiformes: charadriid (killdeer, northern lapwing, grey-headed lapwing)		Holarctic
Freitascapillaria (male tail laterally expanded, spicule absent, nonspiny sheath, parasites of digestive tract of freshwater fish)			
F. laticauda	Scorpaeniformes: cottid (blue ridge sculpin)	intestines	North America
F. maxillosa (syn. *Capillaria maxillosa, Pseudocapillaria nuda*)	Characiformes: characid (dorado)	stomach, pyloric caeca	South America
Gessyella (male tail with caudal lateral alae, eggs enclosed in special capsules, parasites of digestive tract of fish)			
G. latridopsis	Perciformes: latrid (bastard trumpeter)		Australia
Liniscus (male tail with membranous pseudobursa supported by 2 short projections, long thin spicule with nonspiny sheath, parasites of urinary tract of small mammals)			
L. capillaris	Eulipotyphla: soricid (common shrew, Laxmann's shrew), talpid (European mole, Spanish mole)		Eurasia
L. diazae	Rodentia: cricteid (red hocicudo, Azara's akodont)	urinary bladder	South America
L. himizu	Eulipotyphla: talpid (Japanese shrew mole)	urinary bladder	Asia
L. hokkaidensis	Eulipotyphla: soricid (Eurasian pygmy shrew, Shinto shrew, long-clawed shrew)	urinary bladder	Asia
L. incrassatus (*incrassata*) (syn. *L. exilis, Trichosoma, T. capillare, Capillaria, C. linstowi, sunci, urinicola*)	Eulipotyphla: soricid (common shrew, bicolored shrew, greater white-toothed shrew, lesser white-toothed shrew, Radde's shrew, Mediterranean water shrew, Eurasian water shrew, Eurasian pygmy shrew, Radde's shrew, Tien Shan shrew, Asian house shrew), talpid (European mole, Caucasian mole, Roman mole)	intestine, urinary bladder	Eurasia
L. maseri	Eulipotyphla: soricid (Pacific shrew, marsh shrew, Trowbridge's shrew, vagrant shrew), talpid (American shrew mole)	urinary bladder	North America
L. papillosus (*papillosa, papillosum*) (syn. *Trichosoma*, *T. schmidtii, Capillaria, Calodium, Aonchotheca*)	Rodentia: murid (brown rat, black rat), cricetid (common vole, grey dwarf hamster)	urinary bladder	Eurasia
Lobocapillaria (male tail rounded with 2 large elongate lateral caudal lobes, flat grooved spicule with long nonspiny sheath, parasites of digestive tract of fish)			
L. austropacifica	Perciformes: sphyraenid (obtuse barracuda)	gall bladder	Australia
L. sphyraeni (syn. *Capillaria, Pseudocapillaria*)	Scombriformes: sphyraenid (blackfin barracuda)	gall bladder	Atlantic
Paracapillaria (male tail with membranous bursa-like structure supported by rays, spicule with undivided nonspiny sheath, parasites of digestive tract of fish, amphibia and reptiles)			
P. (*Paracapillaria*) *argentinensis*	Trachiniformes: pinguipedid (Brazilian sandperch)	stomach	South America
P. bufonis (syn. *Amphibiocapillaria*)	Anura: bufonid (Japanese common toad), ranid (dark-spotted frog)	intestines	Asia
P. colubra	Serpentes: colubrid (southern black racer)	oviducts	North

			America
P. (*Ophidiocapillaria*) *congolensis*	Serpentes: colubrid (ornate water snake)		Africa
P. (*Paracapillaria*) *epinepheli*	Perciformes: serranid (red grouper)		Atlantic
P. (*Paracapillaria*) *gibsoni* (syn. *Pseudocapillaria* (*Ichthyocapillaria*))	Pleuronectiformes: pleuronectid (European flounder); Perciformes: sillaganid (Gangetic whiting)	stomach	Eurasia
P. (*Paracapillaria*) *helenae*	Perciformes: stichaeid (Japanese warbonnet)		Asia
P. heterodontis	Serpentes: viperid (cottonmouth), colubrid (banded water snake)		North America
P. (*Ophidiocapillaria*) *huffmani*	Serpentes: colubrid (diamondback water snake)	urinary bladder	North America
P. (*Ophidiocapillaria*) *kuntzi*	Serpentes: colubrid (Japanese striped snake, tiger keelback, greater green snake)	intestines	Asia
P. (*Ophidiocapillaria*) *longispicula* (*longispiculum*) (syn. *Trichosoma, Capillaria*)	Serpentes: pythonid (amethystine python, carpet python, Indian python, Burmese python)		Asia, Australia
P. (*Ophidiocapillaria*) *madagascariensis*	Serpentes: lamprophiid (Madagascar weater snake)		Madagascar
P. (*Paracapillaria*) *malayensis*	Anura: bufonid (Asian common toad)	intestines	Asia
P. mingazzinii	Serpentes: colubrid (viperine ater snake)		Asia
P. (*Ophidiocapillaria*) *modiglianii* (syn. *Trichosoma*)	Serpentes: viperid (Sumatran pit viper)		Asia
P. (*Ophidiocapillaria*) *murinae*	Serpentes: boid (green anaconda)		South America
P. (*Ophidiocapillaria*) *najae*	Serpentes: elapid (Indian cobra)		India
P. (*Paracapillaria*) *parophrysi*	Pleuronectiformes: pleuronectid (Pacific halibut, English sole)		Atlantic, Pacific
P. (*Paracapillaria*) *piscicola*	Characiformes: characid (characin, dorado, golden dorado, dientudo jorobado), erythrinid (wolf fish), acestrorhynchid (red-tailed freshwater barracuda), anostomid (head stander, three-point leporinus)		South America
P. (*Paracapillaria*) *plectroplites*	Perciformes: terapontid (silver perch), percichthyid (bluenose cod, golden perch, Estuary perch)		Australia
P. ptyasi	Serpentes: colubrid (oriental ratsnake); Anura: ranid (Gunther's frog)		Asia
P. (*Paracapillaria*) *rhamdiae*	Siluriformes: heptapterid (pale catfish)	stomach	Americas
P. (*Paracapillaria*) *sesokoensis*	Syngnathiformes: fistulariid (red cornetfish)		Americas
P. (*Ophidiocapillaria*) *sonsinoi*	Serpentes: colubrid (southern black racer, green whip snake, viperine water snake, eastern water snake, northern water snake, plain-bellied water snake, banded water snake, grass snake, blackbelly garter snake, oriental rat snake), viperid (horned viper)		Europe, Africa
P. (*Paracapillaria*) *spratti*	Anura: microhylid (rubber frog, burrowing Papuan frog)	intestines	New Guinea
P. (*Paracapillaria*) *teixeirafreitasi*	Perciformes: eleotrid (bigmouth sleeper, Pacific sleeper, finescale sleeper)	intestines	Americas
P. viperae	Serpentes: viperid (horned viper)		Europe
P. (*Paracapillaria*) *xenentodoni*	Beloniformes: belonid (freshwater garfish)		Asia
Paracapillaroides (male tail without caudal alae, with membranous pseudobursa with 2 projections, short spicule with sheath divided into spiny proximal portion and nonspined distal portion, parasites of digestive tract of fish)			
P. acanthocotylus	Perciformes: latrid (castaneta)	stomach	South America

P. agonostomi	Mugiliformes: mugilid (mountain mullet)	stomach	Americas
Paratrichosoma (male tail without spicules or sheath, parasites of crocodiles)			
P. crocodilus (*crocodylus*)	Crocodila: crocodylid (freshwater crocodile, saltwater crocodile, American crocodile, New Guinea crocodile)		Australasia, Americas
P. recurvum	Crocodila: crocodylid (American crocodile, Morelet's crocodile)		Americas
Pearsonema (male tail with small membranous pseudobursa supported by 2 long projections, long thin spicule with nonspiny sheath, parasites of urinary tract of carnivorous mammals)			
P. feliscati	Carnivora: felid (cat, wildcat, African wildcat, Tsushima cat, ocelot), herpestid (Egyptian mongoose)	urinary system	Asia, Africa, Americas
P. linsi (syn. *Pseudocapillaria*)	Rodentia: caviid (capybara); Carnivora: mustelid (greater grison)		Americas
P. mucronata	Carnivora: mustelid (European otter, beech marten, stoat, least weasel, ferret, American mink) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]		Europe
P. pearsoni (syn. *Pseudocapillaria*)	Carnivora: procyonid (crab-eating raccoon)		South America
P. plica (syn. *Calodium*) (bladder hairworm)	Carnivora: canid (dog, wolf, coyote, red fox, American red fox, gray fox, Arctic fox, raccoon dog), felid (wildcat, bobcat, leopard, serval), mustelid (fisher, American pine marten, European pine marten, Japanese marten, beech marten, European badger, North American river otter), memphitid (striped skunk), procyonid (raccoon); Eulipotyphla: soricid (common shrew); Primates: hominid (human) [plus L1 in IH: Oligochaeta: lumbricid (earthworms)]	bladder, sometimes kidney (cystitis)	worldwide
Pseudocapillaria (male tail with 2 large round lobes, spicule with nonspiny sheath, parasites of digestive tract of fish, reptiles, birds and mammals)			
P. (*Ichthyocapillaria*) *adriatica*	Perciformes: sparid (bogue)		Atlantic
P. (*Pseudocapillaria*) *amarali*	Serpentes: colubrid (military ground snake)		South America
P. (*Pseudocapillaria*) *americana*	Rodentia: geomyid (Plains pocket gopher), sciurid (southern flying squirrel, eastern gray squirrel), cricetid (white-footed mouse, North American deermouse)	intestines	North America
P. (*Pseudocapillaria*) *bainae*	Blenniformes: blennid (tompot blenny)		Atlantic
P. (*Pseudocapillaria*) *carangi*	Carangiformes: carangid (shrimp scad, razorbelly scad, yellowtail scad, round scad, torpedo scad, bigeye scad, black-banded trevally, white trevally, cleftbelly trevally, longfin trevally, Malabar trevally, Atlantic horse mackerel)		Atlantic
P. (*Pseudocapillaria*) *catostomi* (syn. *Hepaticola bakeri, Skrjabinocapillaria bakeri*)	Gadiformes: lotid (burbot); Cypriniformes: catostomatid (white sucker), cyprinid (common carp); Salmoniformes: salmonid (cut-throat trout)		Holarctic
P. (*Pseudocapillaria*) *cesarpintoi* (syn. *Paracapillaria* (*Ophidiocapillaria*))	Serpentes: colubrid (military ground snake, yellow-bellied water snake)		South America
P. (*Ichthyocapillaria delamurei*	Carnivora: phocid (Caspian seal)		Russia
P. (*Pseudocapillaria*) *echenei*	Carangiformes: echeneid (live sharksucker)		New Caledonia
P. (*Pseudocapillaria*) *falconis*	Accipitriformes: accipitrid (white-tailed eagle, bald eagle, steppe eagle, lesser spotted eagle, tawny eagle, northern goshawk, Eurasian sparrowhawk, red kite, common European kite, black kite, red-tailed hawk, red-shouldered hawk, western marsh harrier, hen harrier, Montagu's harrier, common buzzard, Himalayan buzzard, rough-legged buzzard), pandionid (osprey); Falconiformes: falconid (common kestrel, American kestrel, red-footed falcon); Strigiformes: strigid (boreal owl, Ural owl, short-eared owl, long-eared owl, little owl, Eurasian eagle-owl, Eurasian pygmy owl, northern hawk-owl, great horned owl, tawny owl,		worldwide

	spotted owl, barred owl, northern saw-whet owl)		
P. (*Pseudocapillaria*) *gobionina*	Gobiiformes: gobiid (monkey goby)	intestines	Caspian Sea
P. (*Pseudocapillaria*) *lepidocephali*	Cypriniformes: cobitid (Guntea loach)		Asia
P. (*Pseudocapillaria*) *magalhaesi*	Perciformes: sciaenid (Atlantic croaker)		Atlantic
P. (*Ichthyocapillaria*) *maricaensis*	Sauria: liolaemid (Lutz's tree iguana)		South America
P. (*Pseudocapillaria*) *mergi*	Pelecaniformes: threskiornithid (roseate spoonbill), ardeid (little blue heron, grey heron), pelecanid (American white pelican, brown pelican); Charadriiformes: recurvirostrid (black-necked stilt); Podicipediformes: podicipedid (little grebe); Gaviiformes: gaviid (black-throated loon, red-throated loon, common loon); Ciconiiformes: ciconiid (wood stork); Passeriformes: turdid (red-throated thrush); Anseriformes: anatid (tufted duck, long-tailed duck, canvasback, common goldeneye, common merganser, scaly-sided merganser, red-breasted merganser, common eider, Eurasian teal, velvet scoter, smew, whooper swan)		Palearctic
P. (*Pseudocapillaria*) *microspicula*	Pleuronectiformes: pleuronectid (starry flounder)		Atlantic
P. moraveci	Gobiiformes: gobiid (rock goby)	stomach	Europe
P. (*Ichthyocapillaria*) *nannupensis*	Siluriformes: plotosid (freshwater cobbler)	intestines	Australia
P. novaecaledoniensis	Perciformes: lutjanid (ornate jobfish)	gut	New Caledonia
P. (*Ichthyocapillaria*) *ophisterni*	Synbranchiformes: synbranchid (obscure swamp eel)	intestines	Asia
P. parablennii	Blenniformes: blennid (tompot blenny)	intestines	Europe
P. (*Ichthyocapillaria*) *pearsei*	Rodentia: sciurid (red-cheeked rope squirrel), murid (Tullberg's soft-furred mouse)		Africa
P. (*Pseudocapillaria*) *petiti*	Anura: bufonid (cane toad)		South America
P. (*Pseudocapillaria*) *picorum*	Piciformes: picid (northern flicker, great spotted woodpecker, black woodpecker, grey-headed woodpecker, European green woodpecker)		Palearctic
P. (*Pseudocapillaria*) *pusilla*	Chiroptera: phyllostomid (orange nectar bat, little yellow-shouldered bat)	intestines	South America
P. (*Ichthyocapillaria*) *salvelini*	Salmoniformes: salmonid (pink salmon, Atlantic salmon, Adriatic salmon, coho salmon, masu salmon, chinook salmon, grayling, Arctic grayling, Arctic char, Russian char, white-spotted char, white char, Dolly Varden trout, lake trout, rainbow trout, brown trout, brook trout, marble trout, Biwa trout, sharp-snouted lenok, blunt-snouted lenok, vendace, lake whitefish, broad whitefish, humpback whitefish, common whitefish, round whitefish, neiva, beloribitsa); Gadiformes: gadid (burbot); Scorpaeniformes: cottid (slimy sculpin, prickly sculpin, Anadyr sculpin, szanaga sculpin), cottocomephorid (stone sculpin, bighead sculpin); Cypriniformes: cyprinid (grass carp); Osmeriformes: osmerid (European smelt, rainbow smelt); Siluriformes: silurid (Amur catfish); Esociformes: esocid (northern pike)		Palearctic
P. (*Pseudocapillaria*) *tomentosa* (syn. *P. brevispicula*)	Cypriniformes: cyprinid (common bream, white bream, blue bream, white-eye bream, vimba bream, goldfish, tench, common nase, common carp, grass carp, black carp, Crucian carp, sabre carp, predatory carp, common minnow, gudgeon, common chub, bleak, ide, rudd, ziege, asp, tench, pike asp, common dace, common roach, dwarf Altai osman, common barbel, Aral barbel, Bulatmai barbel, Tyberian barbel, tiger barb, common minnow, Amur bitterling, Sattar snowtrout, eastern shiner, golden shiner, creek chub, sharpray, naked osman, false osman, gudgeon, white-finned gudgeon, sharpbelly, moramec, redfin, Pacific redfin, big-scaled redfin, stone moroko, rovella), alburnid (spirlin), cobitid (European weather loach, spined loach), nemacheilid (stone loach,	intestines (anaemia, emaciation)	worldwide

	Tibetan stone loach), catostomid (longnose sucker, white sucker); Cyprinodontiformes: poeciliid (guppy), goodeid (bulldog goodeid, blackfin goodea); Siluriformes: silurid (Wels catfish); Scorpaeniformes: cottid (European bullhead); Gadiformes: lotid (burbot); Osmeriformes: osmerid (European smelt); Atheriniformes: atherinopsid (slender silverside, pike silverside); Gobiiformes: gobiid (tubenose goby, Kessler's goby, double-spotted goby, Caspian bighead goby); Anguilliformes: anguillid (European eel); Blenniformes: blennid (freshwater blenny); Salmoniformes: salmonid (lake whitefish, brown trout); Esociformes: esocid (northern pike); Perciformes: centrarchid (green sunfish, blue gill, pumpkinseed), percid (Volga pikeperch) [plus L1 in IH: Oligochaeta: lumbricid (earthworms), naidid (tubificids)]		
P. (*Pseudocapillaria*) *yucatanensis*	Siluriformes: heptapterid (pale catfish)	intestines	South America
P. (*Pseudocapillaria*) *xochimilcensis* (syn. *Paracapillaria*)	Serpentes: colubrid (blackbelly garter snake)		North America
Pseudocapillaroides (male tail rounded with 2 small lobes, spicule with nonspiny sheath, parasites of skin of amphibians)			
P. xenopi (syn. *C. xenopodis*)	Anura: pipid (African clawed frog)	skin (lesions, wasting)	Africa
Pterothominx (syn. *Armocapillaria*) (male tail with caudal lateral alae and large membranous bursa-like structure supported by lateral projections, spicule with sheath covered in minute spines or sclerotized protuberances, parasites of digestive tracts of birds and mammals)			
P. angrensis	Chiroptera: molossid (black mastiff bat)	small intestines	South America
P. blomei	Galliformes: phasianid (hazel grouse, black grouse, grey partridge, ring-necked pheasant, western capercaillie, black-billed capercaillie)		Eurasia
P. brevidelphis	Chiroptera: vespertilionid (black myotis)		South America
P. erinacei (syn. *Aonchotheca*)	Eulipotyphla: erinaceid (North African hedgehog, southern white-breasted hedgehog, European hedgehog); Carnivora: mustelid (European badger); Rodentia: cricetid (Mediterranean water shrew)		Europe, Africa
P. meleagridis (syn. *Thominx, Capillaria*)	Galliformes: phasianid (turkey, ring-necked pheasant)		Europe
P. meleagrisgallopavo	Galliformes: phasianid (turkey, ring-necked pheasant)		Europe
P. moraveci	Psittaciformes: psittaculid (Australian ringneck parrot)	intestines	Australia
P. moschiferi (syn. *Aonchotheca, Armocapillaria*)	Artiodactyla: moschid (Siberian musk deer)		Russia
P. neopulchra (syn. *Thominx*)	Chiroptera: miniopterid (common bentwing bat), vespertilionid (brown long-eared bat, grey long-eared bat, Bechstein's bat, greater mouse-eared bat, lesser mouse-eared bat, long-fingered bat, pond bat, Natterer's bat, Daubenton's bat, common noctule, lesser noctule, Nathusius's pipistrelle)		Eurasia
P. pulchra (syn. *Aonchotheca*)	Chiroptera: miniopterid (common bentwing bat), molossid (Mexican free-tailed bat, big free-tailed bat, broad-eared bat)	stomach	Asia, Americas
P. sadovskoi (syn. *Thominx, Capillaria, Armocapillaria*)	Rodentia: murid (brown rat, yellow-necked mouse, wood mouse), cricetid (bank vole, grey red-backed vole, northern red-backed vole), sciurid (red squirrel, Siberian chipmunk)		Eurasia
P. wavilovoi	Galliformes: phasianid (chicken, black grouse, hazel grouse, ring-necked pheasant), western capercaillie; Columbiformes: columbid (pigeon); Otidiformes: otidid (little bustard)		Eurasia
Schulmanela (male tail with small membranous bursa-like structure supported by rays, spicule with transverse grooves, spiny sheath, parasites of digestive tract of fish and amphibia)			
S. (*Piscicapillaria*) *baylisi*	Carcharhiniformes: scyliorhinid (small spotted catshark, nursehound)		Atlantic
S. (*Amphibiocapillaria*)	Urodela: salamandrid (Corsican brook salamander)		Europe

combesi			
S. (*Amphibiocapillaria*) *costacruzi*	Anura: ranid (Perez's frog, edible frog)		Americas
S. (*Piscicapillaria*) *freemani*	Rajiformes: arhynchobatid (sandpaper skate), rajid (longnose skate, Pacific starry skate)	intestines	Pacific
S. (*Amphibiocapillaria*) *freitaslenti*	Sauria: tropidurid (Amazon lava lizard)		South America
S. (*Piscicapillaria*) *hathawayi*	Squaliformes: squalid (spiny dogfish)		Pacific
S. (*Amphibiocapillaria*) *inequalis* (probable syn. of *S. tritonispunctati*)	Urodela: ambystomatid (woodland salamander, grotto salamander, mole salamander, dusky salamander, seal salamander, Allegheny Mountain dusky salamander, blackbelly salamander, eastern newt), plethodontid (spotted tail salamander, shovelnose salamander)		North America
S. (*Schulmanela*) *petrushchewskii* (syn. *Thominx*, *Capillaria*, *Hepaticola*) (syn. *Hepatospina acerinae*)	Perciformes: percid (European perch, ruffe, zander, schraetzer), centrarchid (pumpkinseed); Cypriniformes: cyprinid (common carp, gibel carp, grass carp, Crucian carp, goldfish, common barbel, round-scaled barbel, Aral barbel, common bream, silver bream, white bream, vimba bream, white-eye bream, spirlin, common roach, common chub, common minnow, stone moroko, Amur bitterling, rudd, ide, souffia, tench, gudgeon), cobitid (spiny loach, spined loach), nemacheilid (stone loach); Salmoniformes: salmonid (rainbow trout, brown trout, grayling, common whitefish, beloribitsa); Siluriformes: silurid (wels catfish), ictalurid (brown bullhead); Anguilliformes: anguillid (European eel); Gasterosteiformes: gasterosteid (three-spined stickleback); Cichliformes: cichlid (blue tilapia) [plus L1 in IH: Oligochaeta: lumbricid (earthworms), naidid (tubificids)]	liver	Europe
S. (*Amphibiocapillaria*) *tenua* (probable syn. of *S. tritonispunctati*)	Urodela: salamandrid (eastern newt); Anura: ranid (Pickerel frog)		North America
S. (*Amphibiocapillaria*) *texensis*	Urodela: plethodontid (Texas blind salamander)	intestines	North America
S. (*Amphibiocapillaria*) *tritoniscristati* (syn. *Trichosomum tritonis cristati, T. tritonis p.p., Capillaria fagei, C. hepatophila*)	Urodela: salamandrid (northern crested newt, smooth newt, palmate newt)	liver	Europe
S. (*Amphibiocapillaria*) *tritonispunctati* (syn. *Capillaria, C. brevicollis, brachyauchenia, Trichosomum tritonis punctati, T. tritonis p.p., Trichosoma filiforme*)	Urodela: salamandrid (eastern newt, northern crested newt, southern banded newt, alpine newt, smooth newt, Caucasian salamander, Japanese firebelly newt, Japanese clawed salamander, sword-tail newt), hynobiid (Mitsjama salamander, amber-coloured salamander, Tokyo salamander), ambystomatid (marbled salamander), cryptobranchid (Japanese giant salamander), plethodontid (northern dusky salamander, seal salamander, Allegheny Mountain dusky salamander, blackbelly salamander, spotted-tail salamander, spring salamander, shovelnose salamander, northern slimy salamander, red salamander, grotto salamander) [plus Malacostraca: odontodactylid (mantis shrimp)]	intestines	Eurasia, North America
S. (Piscicapillaria) tuberculata (syn. *Piscicapillaria* (*Lomakinela*))	Acipenseriformes: acipenserid (Russian sturgeon, bastard sturgeon, starry sturgeon, beluga, sterlet, European sea sturgeon)	intestines	Eurasia
Skrjabinocapillaria (male tail with caudal lateral alae, spicule absent, nonspiny sheath, parasites of digestive tract of bats)			
S. chandigarhensis	Chiroptera: vespertilionid (Dormer's pipistrelle)		India
S. eubursata	Chiroptera: vespertilionid (serotine bat, Bechstein's bat, Daubenton's bat, Geoffroy's bat, little brown bat, whiskered bat, Natterer's bat, common noctule, lesser noctule, brown long-eared bat, lesser mouse-eared bat, parti-colored bat), rhinolophid (lesser		Eurasia

	horseshoe bat)		
S. giganteus	Cypriniformes: cyprinid (Amur minnow)		Russia
Tenoranema (male tail with caudal lateral alae ventrally bent, small membranous caudal bursa, spicule with nonspiny sheath, parasites of digestive tract of terrestrial mammals)			
T. alcoveri	Rodentia: glirid (garden dormouse)	intestines	Europe
T. magnifica (syn. *Aonchotheca*)	Chiroptera: molossid (black mastiff bat)		South America
T. rivarolai	Chiroptera: molossid (broad-eared bat)	small intestines	South America
Capillaria sensu latu			
C. africana (syn. *Skrjabinocapillaria*)	Eulipotyphla: soricid (smoky white-toothed shrew)		Africa
C. alaudae	Passeriformes: alaudid (greater short-toed lark)		Europe
C. anthracocerosi	Bucerotiformes: bucerotid (Palawan hornbill)	intestines	Asia
C. avellari	Ciconiiformes: ciconiid (wood stork)		America
C. baicalensis	Salmoniformes: salmonid (sharp-snouted lenok)		Atlantic
C. bonnevillei	Rodentia: heteromyid (Ord's kangaroo rat)		North America
S. caballeroi (syn. *Skrjabinocapillaria*)	Carnivora: herpestid (Javan mongoose)	gut	Caribbean
C. cadovulvata	Galliformes: phasianid (grey partridge)	caeca	Europe
C. chauhani	Ciconiiformes: ciconiid (painted stork)		India
C. coeca	Eulipotyphla: talpid (blind mole)		Europe
C. combologiodes	Galliformes: phasianid (turkey)	crop	Europe
C. coregoni	Salmoniformes: salmonid (brown trout)		North America
C. crossostomae	Cypriniformes: balitorid (river loach)		Asia
C. dessatae	Lagomorpha: ochotonid (Royle's pika)		Asia
C. diesingi	Chiroptera: vespertilionid (greater mouse-eared bat, lesser mouse-eared bat, Bechstein's bat)		Eurasia
C. euproctus	Carnivora: felid (bobcat)		North America
C. exigua	Eulipotyphla: soricid (common shrew, bicolored shrew, greater white-toothed shrew, lesser white-toothed shrew, Mediterranean water shrew, Eurasian water shrew, Eurasian pygmy shrew), erinaceid (northern white-breasted hedgehog, southern white-breasted hedgehog, European hedgehog)		Eurasia
C. falconis-nisi	Strigiformes: strigid (great horned owl)		North America
C. fudingensis	Scombriformes: stromateid (silver pomfret)		Asia
C. fujianensis	Anura: bufonid (Asian common toad)	intestines	Asia
C. fuzhouensis	Cypriniformes: cyprinid (silver carp)		Asia
C. gallinae	Galliformes: phasianid (chicken, ring-necked pheasant); Columbiformes: columbid (pigeon)		Asia
C. honghuensis	Synbranchiformes: mastacembelid (Asian spiny eel)		Asia
C. jaenschi	Siluriformes: phalacrocoracid (great cormorant)	intestines	Australia
C. khalili	Rajiformes: rajid (thorny skate)		Atlantic
C. konstantini	Eulipotyphla: soricid (Eurasian water shrew, Mediterranean water shrew)		Eurasia
C. lepidopodis (*sp. inq.*)	Perciformes: trichiurid (silver scabbardfish)		Atlantic
C. leucisci	Cypriniformes: cyprinid (asp)		Europe
C. lewaschoffi	Cypriniformes: cyprinid (ziege)		Europe
C. limicolae	Charadriiformes: scolopacid (common sandpiper, common redshank, Terek sandpiper, ruddy turnstone, dunlin, little stint, common snipe, pin-tailed snipe, little curlew, ruff, Eurasian woodcock), charadriid (common ringed plover, American golden plover, grey plover), recurvirostrid (pied avocet, red-necked avocet)		Palearctic
C. liuyangensis	Passeriformes: leiothrichid (Chinese hwamei, red-billed leiothrix)		Asis
C. longicauda	Didelphimorphia: didelphid (Virginia opossum, gray four-eyed opossum)		Americas

C. longipes	Artiodactyla: bovid (sheep, goat)	small intestines	worldwide
C. magnova	Chiroptera: miniopterid (greater long-fingered bat)		Africa
C. merluccii	Gadiformes: merlucciid (shallow-water Cape hake, deep-water Cape hake)	rectum	Africa
C. miniopterae	Chiroptera: miniopterid (common bentwing bat))		cosmopolitan
C. mogurndae	Gobiiformes: eleotrid (Japanese freshwater goby)		Asia
C. montevidensis	Galliformes: phasianid (chicken)		Europe
C. murismusculi	Rodentia: murid (brown rat)		Europe
C. murisnitedula	Rodentia: glirid (forest dormouse)		Europe
C. myotisi	Chiroptera: vespertilionid (greater mouse-eared bat)		
C. namibiensis	Gadiformes: merlucciid (shallow-water Cape hake, deep-water Cape hake)		Africa
C. ohbayashii	Eulipotyphla: soricid (Asian house shrew, Himalayan shrew, Himalayan water shrew, Hodgsen's brown-toothed shrew)		Asia
C. ovis	Artiodactyla: bovid (sheep)		
C. ovoreticulata	Eulipotyphla: erinaceid (European hedgehog)		Europe
C. pipistrelli	Chiroptera: vespertilionid (Japanese pipistrelle, Java pipistrelle, long-fingered bat, bird-like noctule), rhinolophid (greater horseshoe bat)	intestines	Eurasia
C. piscatori	Serpentes: colubrid (checkered keelback)		Asia
C. plagiaticia	Psittaciformes: nestorid (kea)	intestines	New Zealand
C. pseudorasborae	Cypriniformes: cyprinid (stone moroko)		Asia
C. pudendotecta	Anseriformes: anatid (swan)		Asia
C. ranae	Anura: ranid (Gunther's frog)		Asia
C. rangiferi	Artiodactyla: cervid (reindeer)		Europe
C. retusa	Galliformes: phasianid (chicken); Passeriformes: corvid (Eurasian jay)		Eurasia
C. sibirica	Rodentia: sciurid (long-tailed ground squirrel, Siberian chipmunk)		Asia
C. sinipercae	Perciformes: sinipercid (Chinese perch)		Asia
C. spinosa	Pleuronectiformes: cynoglossid (Nigerian tongue sole)		Africa
C. splenacea	Eulipotyphla: soricid (greater white-toothed shrew, Eurasian water shrew)		Eurasia
C. strigis	Strigiformes: strigid (tawny owl)		Palearctic
C. pigolkini (syn. *C. suis*)	Artiodactyla: suid (pig)		
C. tavernae	Rodentia: murid (rat)	intestines	Europe
C. vespertilionis	Chiroptera: vespertilionid (greater noctule bat, common noctule, parti-coloured bat)		Eurasia
C. yamagutii	Siluriformes: bagrid (bayad)		Africa

Parasite morphology: All capillariids form 3 different morphological stages in their developmental cycles: eggs; larvae; and adult worms. Gravid female worms produce unembryonated (uncleaved) ellipsoidal eggs measuring from 36-81 x 14-43 µm depending on species (e.g. those of *Calodium hepaticum* measure 48-66 x 28-37 µm, *Aonchotheca philippinensis* 35-45 x 20-25 µm, and *Eucoleus aerophilus* 80-98 x 30-40 µm). The eggs have a characteristic lemon- or barrel-shape with 2 mucoid polar plugs (less conspicuous than those of *Trichuris* spp.) and are surrounded by a thick wall with radial striations and a pitted (*C. hepaticum*) or smooth (*A. philippinensis*) surface. A few species, including *A. philippinensis,* have also been found to form thin-shelled eggs which embryonate and hatch *in utero* or within the host gut lumen releasing larvae which may be autoinfective. There are 4 larval stages (designated L1-4) which undergo successive moults before forming adults. First-stage larvae (L1) are elongate, measuring 0.14-0.25 mm in length, are bluntly rounded at both ends with a small buccal stylet and possess conspicuous genital primordia. L2 measure from 0.16-0.55 mm in length and have an elongate oesophagus ringed by stichocytes. L3 are longer (0.20-1.56 mm) and the anterior genital column is well-developed while the posterior genitalia are still developing. L4 measure up to 3.6 mm in length and their sexual differentiation is well progressed, although the male spicule is not as sclerotized as in adult worms and is usually sheathed. Adults appear as white slender hair-like worms ranging in size from 4-100 mm in length by 10-400 µm in cross-sectional diameter depending on species (their length can be difficult to determine as adults are frequently embedded in host tissues). They are surrounded by a tough flexible cuticle with longitudinal bacillary bands (rows of specialised glandular and nonglandular hyodermal cells) and they exhibit a gradual transition in width becoming thicker posteriorly. They possess a characteristic non-muscular stichosome oesophagus evident as a slender thin-walled tube with 1-3 rows of 20-60 stichocytes. Adults worms are sexually dimorphic with females being larger than males. For most species, females measure 23-80 mm x 29-105 µm while males measure 15-39 mm x 23-62 µm, although those of *Calodium hepaticum* in rodents and other mammals can be larger (females 52-104 mm x 100-400 µm, males 15-37 mm x 40-100 µm), those of *Pseudocapillaria tomentosa* in ornamental fish being smaller (females 7-12

mm, males 4-7 mm), and those of *A. philippinensis* being tiny (females 2.3-5.3 mm x 29-47 μm, males 1.5-3.9 mm x 23-28 μm). Mature females possess a single ovary connected to a coiled uterus which opens into a conspicuous vulva located anteriorly near the oesophageal-intestinal junction. The uterus may contain a few to many developing ova often arranged in elongate strands. Adult males have blunted rounded tails, some with caudal lateral alae, and many with a pair of papillae located near the cloacal aperture. Males are non-bursate but many species have a membranous pseudobursa or a primitive bursa-like structure with a pair of subventral lobes often supported by lateral projections (rays). Males of most capillarid species have a single prominent elongate sclerotized spicule (sometimes up to 500 μm long) with an eversible sheath (up to 400 μm long) often covered with small spines.

Site of infection: Adult worms of most capillariid species infect the intestinal, urinary or respiratory epithelia of their vertebrate definitive hosts where they become embedded in the mucosa. Infections in the alimentary tract have been recorded along the entire length from the oesophagus to the rectum, but are most common in the small and large intestines (e.g. *A. philippinensis* larval and adult worms infect the small intestine). Infections in the respiratory tract are found in the nasal passages and upper airways mostly of avian hosts, while infections in the urinary system may occur in the bladder, and rarely the kidneys, of rodents and insectivores. Female worms produce unembryonated eggs which are excreted with host faeces or urine. Eggs embryonate in the external environment to contain first-stage larvae (L1) which are infective to new definitive hosts. Alternatively, the eggs of some species only become infective when ingested by oligochaetes (sometimes fish) in which L1 are released into tissues (these hosts are known variously as intermediate hosts or paratenic (transport) hosts as the larvae do not moult or develop further but may exhibit modest growth). A notable variation occurs for a few species which infect the internal organs of their definitive hosts, particularly the liver, but also including the spleen and skin (e.g. *C. hepaticum* larvae migrate from the intestines to the liver where they mature into adults in the hepatic parenchyma). In these cases, eggs released by female worms become tissue-bound and only make their way to the external environment when ingested by predators or scavengers and subsequently voided intact without undergoing further development in these hosts.

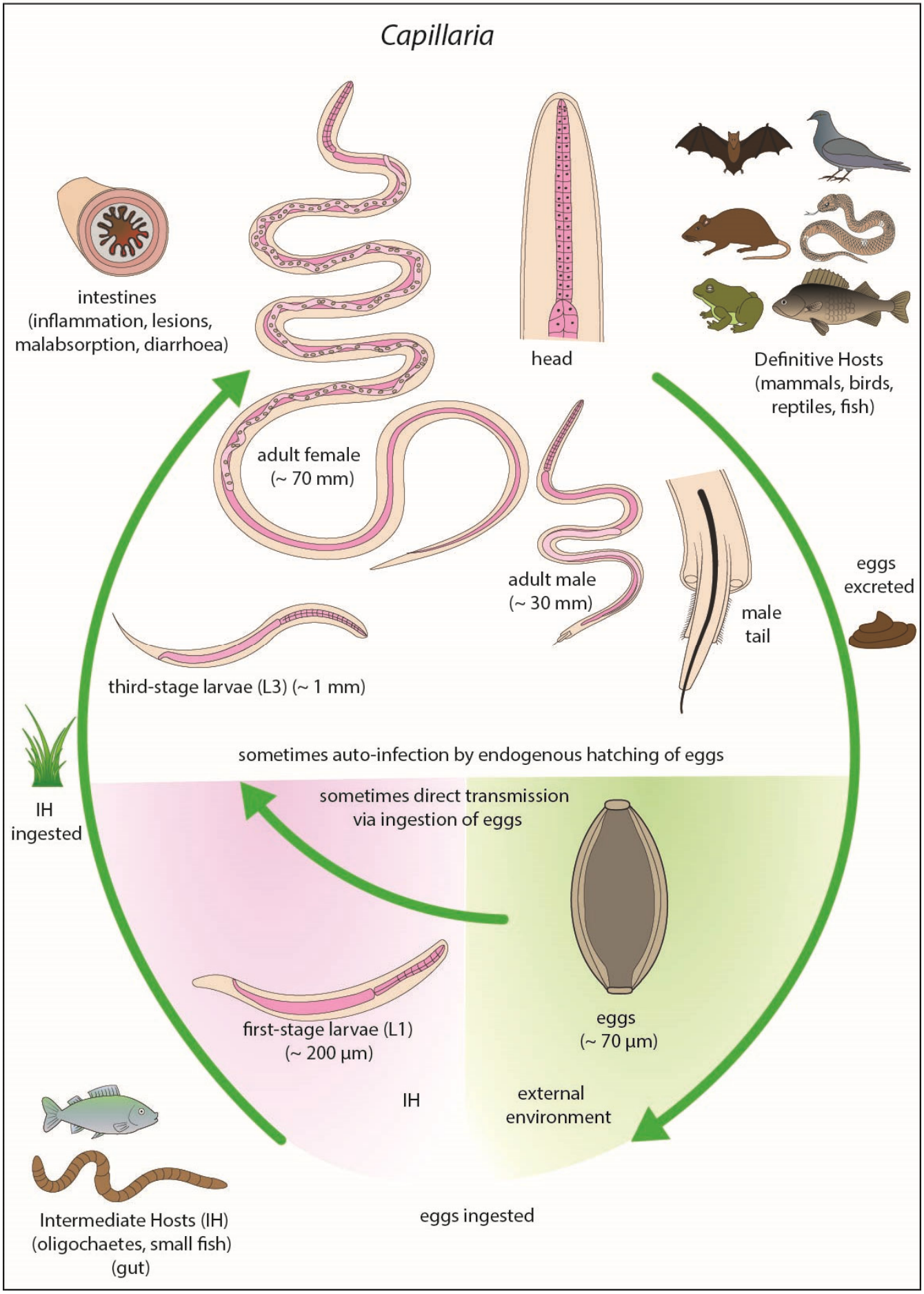
Pathogenesis: While larval and adult worms cause tissue trauma and inflammation in their Definitive hosts due to their burrowing and feeding activities, the clinical consequences depend on the intensity of infection (worm burden) and tissue tropism (site of infection). Most infections are mild and remain asymptomatic, but heavier infections result in greater cumulative damage which may manifest in clinical disease. Infections in the digestive tract disrupt the mucosa leading to structural and functional deficits, usually involving villous atrophy, localized inflammation with cellular infiltrates, ulcerative and degenerative lesions and malabsorption with loss of fluids, protein and electrolytes. Malabsorption of sugars and fats also appears to be exacerbated by proteolytic substances released by worms. The onset of symptoms is often benign with vague abdominal pains and borborygmi but may progress to episodic or persistent diarrhoea with bulky or watery faeces, steatorrhea, nausea, vomiting, hypotension, oedema, anorexia, malaise, poor growth and wasting. Shifts in clinical parameters include hypoproteinemia and low serum levels of potassium, sodium, calcium and carotene, but eosinophilia is not a feature. Heavy worm burdens in mammals may cause protracted malabsorption and cachexia which can prove fatal within 4-6 months if left untreated (death may occur from pneumonia, cerebral oedema, hypokalaemia and heart failure). Infections by *A. philippinensis* in humans are progressive and eventually cause disease as female worms may switch from being oviparous to larviparous, resulting in auto- and hyper-infections. Gastrointestinal infections in birds have also been associated with severe oesophagitis or enteritis resulting in poor growth, wasting and death (e.g. *A. bursata, A. caudinflata, B. obsignata, C. anatis, E. annulatus, E. contortus*). Heavy infections in the gut of fishes may cause severe debilitating disease involving cellulitis, hepatomegaly, anaemia, lethargy, emaciation and death, particularly in farmed cyprinids or aquarium fish infected with *P. tomentosa.* Infections of the respiratory tract may cause rhinitis, tracheitis, bronchitis and pulmonary capillariasis in birds, particularly young birds infected with *E. aerophilus.* Animals may produce purulent expectorates, mucoid or bloody sputum with dyspnoea, sneezing, coughing, fever, pneumonia, eosinophilia, anorexia, fatigue and secondary bacterial infections. Infections of the urinary tract have only occasionally been associated with clinical disease, with *P. plica* sometimes causing cystitis in companion animals. Those species that infect internal organs cause more invasive tissue damage and provoke stronger host inflammatory responses. *C. hepaticum* adult worms become enclosed in syncytial (multinucleate) masses in the liver parenchyma where they feed on host cell cytoplasm, Female worms move along sinuous tracts depositing numerous clusters of eggs before dying after several months. The dead worms and egg masses become encapsulated in fibrotic connective tissues with granuloma formation, leucocytic infiltrates, periportal inflammation and eventual mineralization and calcification of the parasites within the lesions. Clinical signs are similar to those found in toxocariaisis (visceral larval migrans) and include chronic fever, hepatomegaly, splenomegaly, anorexia and weight loss. Changes in clinical parameters include hyperglobulinaemia (esp. IgE), leucocytosis with pronounced eosinophilia, and elevated plasma levels of liver enzymes (alanine and aspartate aminotransferases and sometimes glutamic dehydrogenase). Several mortalities have been attributed to hepatic failure with severe granulomatous hepatitis, hepatocyte lysis and cirrhosis. Most clinical infections in humans occur in children less than 8 years old who exhibit poor personal hygiene and/or consume soil (pica). Clinical signs are uncommon in larger mammals but infections in smaller (rodent-sized) animals may include matted fur, lethargy, hepatomegaly and splenomegaly.

Developmental cycle and mode of transmission: Capillariid species have been found to undergo either of 2 types of transmission: one type being homoxenous and direct involving the faecal-oral transmission of eggs (sometimes including the passage of eggs through paratenic hosts e.g. *C. hepaticum*); and the other type being heteroxenous and indirect involving the consumption of infective larvae in intermediate hosts (such as oligochaetes and fish). Several species have been found to be able to undergo both

homoxenous and heteroxenous transmission. In all cases, the infective stages are first-stage larvae (L1) located either within embryonated eggs or within the tissues of intermediate hosts (rather than L3 like most other parasitic nematodes). Direct transmission occurs when gravid female worms deposit eggs in mucosal tissues where they are subsequently excreted with host faeces or urine. Eggs deposited in respiratory epithelia are coughed up, swallowed and excreted with faeces. Eggs deposited in internal organs (e.g. *C. hepaticum* in the liver) remain tissue-bound until the organ is eaten by a predator or scavenger which then excretes the eggs essentially unchanged in their faeces (thus acting as a paratenic host). Voided eggs are typically uncleaved and not infective but must embryonate in the external environment to produce infective L1. Depending on species and prevailing environmental conditions, eggs embryonate in 5-42 days given adequate moisture and oxygen. Development takes longer at lower temperatures and may be arrested below 10°C. Embryonated eggs containing infective L1 may remain viable for over a year. When ingested by susceptible definitive hosts, the eggs hatch in the intestines releasing the L1 which invade the mucosa, migrate to their predilection sites and moult 4 times over 12-16 days to form adult worms. The prepatent period (time from infection to first egg production) ranges from 16-30 days and female worms remain fecund before dying after several months. Indirect transmission occurs when embryonated eggs are ingested by suitable intermediate hosts, especially oligochaetes such as earthworms and tubificids (cf. *E. annulatus, E. contortus*), or small fish species (*A. philippinensis*). The eggs hatch releasing their L1 which invade intestinal tissues and undergo modest growth over several weeks but do not moult or develop further. Infections are acquired by final hosts when they eat infected intermediate hosts releasing the infective L1 which migrate to their predilection sites and develop into adult worms over several weeks. Infections by *A. philippinensis* are acquired by humans when they eat raw fish too small to eviscerate and are so eaten whole, often as a traditional delicacy. *A. philippinensis* is also unusual in that adult worms that are normally oviparous producing thick-shelled unembryonated eggs may start producing thin-shelled embryonated eggs which may hatch endogenously soon after release, and sometimes even hatching *in uteri* making the worms larviparous (birthing live larvae). The larvae may infect the same individual host (process of auto-infection) resulting in the rapid amplification of worm numbers (hyper-infections). Unless treated, many people may develop progressively worsening disease which often proves fatal.

Differential diagnosis: Infections are difficult to diagnose on clinical grounds, as many infections are asymptomatic and when present, symptoms are relatively nonspecific and may be referable to other disease conditions. Even liver infections presenting with the classical triad of hepatomegaly, eosinophilia and fever may be due to acute viral hepatitis, granulomatous hepatitis or hepatic cancer. Definitive diagnosis is dependent on the microscopic detection of characteristic unembryonated eggs (sometimes larvae) in faeces, urine, sputum, nasal or tracheal lavage, either in wet mounts, dried smears or concentrates following centrifugal floatation in saturated sugar or heavy metal salt solutions (taking care not to mis-identify *Trichuris* eggs). Adult worms have sometimes been observed upon endoscopy (gastroduodenoscopy, sometimes colonoscopy) and worm fragments and/or egg masses may be detected histologically in biopsy or necropsy samples of intestinal or pulmonary mucosa or hepatic parenchyma. Several serological tests have been developed to detect host antibodies against infections, including immunoprecipitation, haemagglutination, fluorescent-antibody tests and enzyme immunoassays, but it was difficult to differentiate active infections from prior exposure. Molecular biological techniques have also recently been used to detect parasite DNA in clinical samples following the polymerase chain reaction (PCR) amplification of nuclear or mitochondrial gene sequences (ribosomal RNA and cytochrome c oxidase subunit 1, respectively).

Treatment and control: Several anthelminthic drugs have been used to successfully treat infections, notably the benzimidazoles (albendazole, mebendazole and thiabendazole) which were effective against all parasite developmental stages but produced several side-effects including fever, dizziness, nausea and hair loss. Other anthelmintics were less effective in that they mainly suppressed egg production, including the imidazothiazoles (levamisole), halogenated monophenols (disophenol), other benzimidazoles (fenbendazole), macrocyclic lactones (ivermectin) and tetrahydropyrimidines (pyrantel and oxantel), all of which also produced various side-effects, such as skin rash, diarrhoea, nausea, and vomiting. Infections in fish responded well to treatment with ivermectin, but the drug proved toxic to various fish species. Bath treatments in levamisole and fenbendazole were also used but found to be ineffective for some hosts (such as golden shiners) or caused sterility in others (such as zebrafish). Chemotherapy was more effective in mammals and birds when complemented with supportive therapies such as anti-diarrhoeal and anti-inflammatory agents, fluid and electrolyte replacements and high protein diets. Timely diagnosis and treatment have proven critical for many infections, particularly *A. philippinensis* infections in humans which worsens in left untreated due to repeated auto-infection. Various control strategies have been devised to break transmission cycles by reducing faecal contamination of food and water sources (improved sanitation, enhanced hygiene), educating people against geophagia (soil-eating), restricting access of potential paratenic hosts to carcases (especially by rodent control in fauna parks), preventing hosts from foraging for earthworms (notably in poultry units and aviaries), eliminating oligochaetes as food sources (particularly in aquaculture), and advocating cooking fish properly prior to consumption (hard to achieve in communities with strong culinary traditions). Health-education campaigns proved invaluable in curbing epidemics in the Philippines associated with poor hygiene and inadequate food preparation.

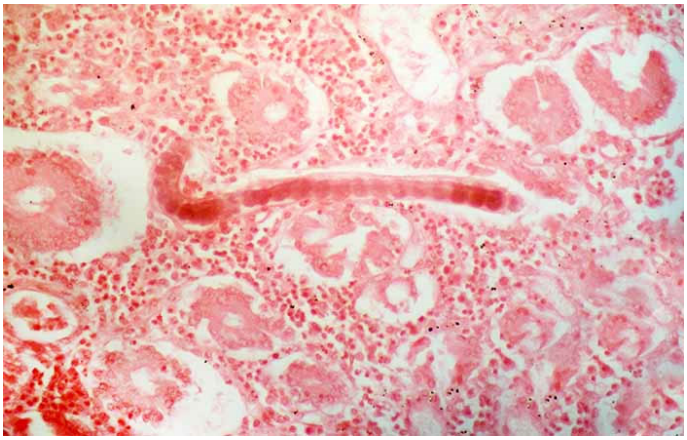

Capillaria
intestines
(inflammation, lesions,
malabsorption, diarrhoea)
head
Definitive Hosts
(mammals, birds,
reptiles, fish)
adult female
(~ 70 mm)
adult male
(~ 30 mm)
male
tail
eggs
excreted
third-stage larvae (L3) (~ 1 mm)
IH
ingested
sometimes auto-infection by endogenous hatching of eggs
sometimes direct transmission
via ingestion of eggs
eggs
(~ 70 µm)
first-stage larvae (L1)
(~ 200 µm)
IH
external
environment
Intermediate Hosts (IH)
(oligochaetes, small fish)
(gut)
eggs ingested



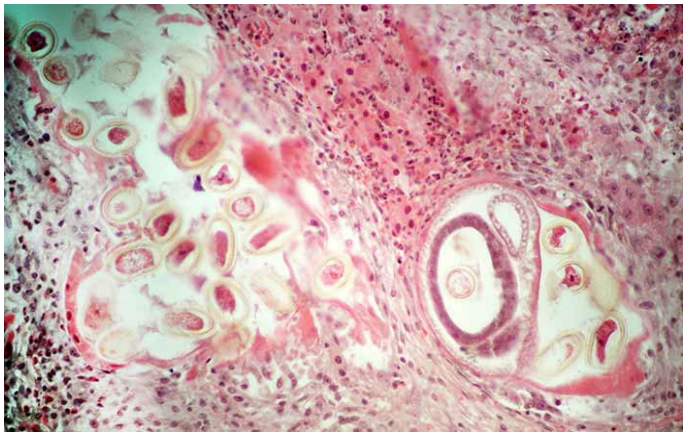
Capillaria adult worm



Capillaria worm egg



Capillaria larva in intestinal section



Capillaria in liver section

Trichinella
(helminth: nematode)

Overview

Nematodes are triploblastic pseudocoelomate unsegmented worms that undergo protostomial embryonic cleavage and grow by cuticular moulting (ecdysis). Two groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most aphasmid nematodes are free-living, although some are parasitic on plants or animals. They possess a non-muscular stichosome oesophagus (slender thin-walled tube) and their life-cycles involve infective L1 (rather than L3) which have a buccal stylet (very common for plant parasites). The males lack a bursa and have only one spicule when present. Three major families of animal parasites are grouped together in the dorylaimian order Trichinellida: trichurids in the caecum/colon of mammals, capillarids in the gut/lungs of mammals/birds, and trichinellids in the intestines and muscles of mammals. Trichinellids have unusual indirect life-cycles where viviparous females release L1 which encyst in striated muscle cells of the same host until they are ingested by carnivorous/omnivorous hosts where adults develop rapidly (2-6 days) in the small intestines. Infections ascend through the food chain via predation or carrion-feeding in domestic and sylvatic cycles. Several *Trichinella* spp. have been associated with enteric and muscular diseases in human populations around the world, and trichinoscopy is routinely used as a means of detecting L1 during meat inspection in many countries.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Nematoda (unsegmented, pseudocoelomate roundworms, tubular digestive tract, dioecious)
Class:	Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass:	Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)
Order:	Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily:	Trichinelloidea (oesophagus with short muscular anterior portion and long glandular posterior portion)
Family:	Trichinellidae (males with pseudobursa, no spicules, viviparous, juveniles in skeletal muscle cells)
Genus:	*Trichinella* (parasitic in small intestines/muscles of mammals, direct (carnivorism))
Species:	*T. spiralis* (causes trichinellosis in mammals)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods, all with jointed limbs). Nematodes (roundworms) are unsegmented tubular worms with a fluid-filled body cavity (pseudocoelom) that acts as a hydrostatic skeleton. They have longitudinal muscles and typically exhibit a sideways thrashing motion. They have well developed digestive tracts with various partitions: the foregut comprising the mouth (often with lips and papillae), buccal capsule (sometimes with ridges, rods, plates, spears, stylets or teeth) and oesophagus (glandular, muscular or both); the midgut (nonmuscular absorptive section); and hindgut (rectum) emptying through a subterminal anus (cloaca in males). Most nematodes are dioecious and form separate sexes. Male worms have a single testis (sometimes 2), an elongate vas deferens often equipped with a seminal vesicle and ejaculatory duct (glandular and/or muscular), 1-2 copulatory spicules (sometimes with an accessory gubernaculum), and bursate species with elaborate posterior claspers. Female worms are usually didelphic (some monodelphic or polydelphic) with 2 ovaries, 2 oviducts usually with spermatheca, 2 uteri opening into a common vagina and a vulva often equipped with a muscular ovejector. Female worms are oviparous or viviparous and produce numerous eggs or larvae, respectively. Larval stages undergo several moults (L1-L4) before maturing into adult worms. Some nematodes have direct life-cycles where eggs or larvae infect definitive hosts (per os or per cutaneous), but many have indirect cycles where larvae first develop in invertebrate intermediate hosts before infecting definitive hosts (by ingestion, injection or deposition). Many nematode species are free-living in terrestrial and aquatic habitats, while some species from diverse groups have become plant or animal parasites. Two nematode groups identified by the presence/absence of sensory phasmids have partly been ratified by molecular studies recognising three subclasses: Enoplia and Dorylaimia (both without phasmids) and Chromadoria (most with phasmids). Most Enoplia are free-living marine organisms but some are found in freshwater, and on land as plant parasites. The Dorylaimia comprise numerous freshwater and terrestrial species, including major groups of plant and animal parasites. The Chromadoria is represented by many marine groups as well as a terrestrial group of plant and animal parasites. The taxonomic ranks of many nematode assemblages vary considerably depending

on which classification system has been followed. Molecular phylogenetic studies, however, have supported the separate classification of most groups, particularly at the level of superfamily. Collectively, species from at least 16 superfamilies are considered to pose serious threats to human and animal health as infectious diseases.

CLASSIFICATION* OF SUPERFAMILIES OF PARASITIC NEMATODES
Class: Enoplea (Aphasmidea, Adenophorea) (gland-bearers, cylindrical oesophagus, no phasmids, setae, two testes)
Subclass: Dorylaimia (five or more oesophageal glands, buccal stylet (odontostyle), free-living or parasitic)[clade I(2)]
Order: Trichinellida (Trichocephalida, Trichurida) (single spicule, stichosome oesophagus, L1 with buccal stylet)
Superfamily: Trichinelloidea (oesophagus with short anterior muscular and long posterior glandular portions)
Class: Chromadorea (spiral amphids, 3 oesophageal glands, usually annulated bodies, free-living and parasitic)
Order: Rhabditida (Secernentea, Phasmidea) (secretors, phasmids present, amphids anterior, bulbous oesophagus)
Suborder: Rhabditina (free-living or parasitic in invertebrates/lower vertebrates)[clade V(9)]
Infraorder: Rhabditomorpha (‘rod-shaped’ buccal cavity)
Superfamily: Rhabditoidea (open tube stoma, excretory system with lateral canals)
Superfamily: Strongyloidea (bursate males, prominent buccal capsules, parasites of mammals, birds, reptiles)
Suborder: Spirurina (animal parasites, many use invertebrate intermediate hosts (IH))[clade III(8)]
Incertae sedis Superfamily: Dracunculoidea (elongate parasites of vertebrate tissues, freshwater crustacean IH)
Infraorder: Ascaridomorpha (large roundworms, three large lips, numerous caudal papillae)
Superfamily: Ascaridoidea (ascarids, eggs thick-shelled, larvae may undertake hepato-pulmonary migration)
Superfamily: Heterakoidea (preanal sucker anterior to cloaca in males, direct cycle, infection by egg ingestion)
Infraorder: Gnathostomatomorpha (‘jaw-mouthed’ due to unique bulbous armed heads)
Superfamily: Gnathostomatoidea (first IH copepod, often use paratenic hosts)
Infraorder: Oxyuridomorpha (pinworms, pointed tails, oesophagus with terminal bulb, males with single spicule)
Superfamily: Oxyuroidea (common in mammals, birds, reptiles, amphibians)
Infraorder: Spiruromorpha (enigmatic clade linked by molecular characters, indirect cycles with IHs)
Superfamily: Acuarioidea (small parasites mostly of birds, with cephalic cordons, ptilina or serrated shields)
Superfamily: Camallanoidea (conspicuous phasmids, L1 with dorsal tooth, ovoviviparous, L1-L3 in copepod)
Superfamily: Filarioidea (tissue-dwelling filarial parasites, lack lips, infect tissues/vessels, arthropod IH)
Superfamily: Habronematoidea (unique head structures with small pseudolabia and median lips)
Superfamily: Physalopteroidea (stomach worms in mammals, insect IH)
Superfamily: Spiruroidea (pseudolabia, bipartite oesophagus, infect birds (crop/gizzard), arthropod IHs
Superfamily: Thelazioidea (eye-worms of birds and mammals, transmitted by insects)
Suborder: Tylenchina (fungal, plant and animal parasites)[clade IV(10,11,12)]
Infraorder: Panagrolaimomorpha (free-living or parasitic (insects, reptiles, amphibians, mammals))
Superfamily: Strongyloidoidea (dauer stages, lip region without processes, striated cuticle)

*Contemporary genotypic classification schemes recognize strong monophyletic clades at the level of superfamily and infraorder, while previous phenotypic classification schemes had ranked many as separate orders.

The superfamily Trichinelloidea is characterised by worms with a distinctive oesophagus consisting of a short anterior muscular section and a long posterior glandular section (stichosome) encircled by 1-3 rows of unicellular glands (stichocytes). Adult worms usually have long narrow anterior necks (containing only the stichosome) and stouter posterior bodies (containing the reproductive organs). Female worms produce thick-shelled eggs with bipolar mucoid plugs giving them a lemon- or barrel-shape. Most genera pass unembryonated eggs, but those of some groups (Trichinellidae, Trichosomoididae) embryonate *in utero.* The first-stage larvae (L1) have an oral stylet, similar to their presumed soil-dwelling dorylaimid ancestors. Unlike other parasitic nematodes, the L1 of trichinelloids (rather than L3) is used to infect their final hosts, sometimes after a brief period in an invertebrate intermediate host (such as earthworms) to become infective. Adults worms are endoparasites in most classes of vertebrates, generally occurring within the intestinal mucosa but some infecting epithelia of the urinary, respiratory or integumentary systems. An increasing number of genera have been recognised but their higher classification is confounded as some authorities distinguish 6 families while others have demoted several to subfamily status. The former ranking has been retained in this resource to better help the reader differentiate genera on the basis of recognised apomorphic characters, although future studies may reveal different phylogenetic relationships. The 6 trichinelloid families include: Trichinellidae, Trichuridae, Anatrichosomatidae and Trichosomoididae primarily in mammals; Capillariidae in birds, mammals and fish; and Cystoopsidae in fish and reptiles.

The family Trichinellidae is monotypic with the single genus *Trichinella* (syn *Trichina*) containing some 9 species infecting almost all vertebrate classes (mammals, birds, reptiles, fish). Contemporary molecular characterization studies have also recognised a growing number of genotypes (encoded T1-T12), most of which conform to named species, but some (T6, T8, T9) possibly representing cryptic species. *Trichinella* spp. have unusual developmental cycles which can be completed within the same host. Adult worms rapidly develop embedded in the intestinal mucosa, and the ovoviviparous females release first-stage larvae (L1) into lymph and blood capillaries; these larvae are then disseminated to skeletal muscle cells which they enter and remain as L1 (they are arrested in terms of development, but still move). The larvae of some *Trichinella* spp. in mammals (such as *T. spiralis*)

transform the host muscle cells into nurse cells which become encapsulated in collagen, while those of other species in birds, reptiles and some mammals (such as *T. pseudospiralis*) do not cause modification of the muscle cell nor become encapsulated. The larvae are transmitted to carnivores when they feed on infected prey or carrion, infections being maintained in domestic and/or sylvatic cycles involving livestock and/or wildlife. The species *T. spiralis* infects pigs and rats as its primary hosts, but infections have also been found in more than 100 mammalian species, including humans. *T. spiralis* has a cosmopolitan distribution, but is absent from Australasia, the United Kingdom and Denmark. Infections are most prevalent in developing countries, particularly those where undercooked pork products are consumed. It is estimated that some 11 million people may be infected worldwide, with 10,000 clinical cases of the disease (known as trichinellosis or trichinosis) occurring annually.

***Trichinella* species [and genotype]**	**Definitive Hosts [adults in small intestines] [larvae in muscles]**	**Clinical signs**	**Distribution**
Capsule forming (or 'encapsulated')			
T. spiralis [T1] (trichina or muscle worm) [domestic/sylvatic] (syn. *T. affinis, T. canis, T. circumflexa, T. pseudalius, Pseudalius trichina*)	Carnivora: canid (dog, wolf, coyote, golden jackal, red fox, Arctic fox, gray fox, blue fox, raccoon dog, Japanese raccoon dog), hyaenid (spotted hyena), felid (cat, bobcat, lion, cougar, Eurasian lynx, Canada lynx, European wildcat), viverrid (civet cat, common genet), procyonid (raccoon), mustelid (wolverine, Eurasian otter, American marten, American mink, European pine marten, fisher, stoat, sable, European badger, Asian badger, steppe polecat, European polecat, long-tailed weasel, least weasel), herpestid (Javan mongoose), memphitid (striped skunk), myocastorid (coypu), ursid (Asian black bear, Japanese black bear, American black bear, brown bear, polar bear); Cingulata: chlamyphorid (big hairy armadillo); Artiodactyla: suid (pig, boar, desert warthog), bovid (cattle, sheep, goat), cervid (roe deer, reindeer), phocid (bearded seal, ringed seal), odobenid (walrus), monodontid (beluga whale); Perissodactyla: equid (horse); Rodentia: murid (brown rat, black rat, mouse, striped field mouse, yellow-necked mouse, wood mouse, lesser bandicoot rat, Mongolian gerbil, golden hamster), caviid (guinea pig, montane guinea pig), cricetid (common vole, bank vole, muskrat, white-footed mouse, deer mouse, Oldfield mouse, hispid cotton rat), sciurid (American red squirrel, Columbian ground squirrel); Didelphimorphia: didelphid (common opossum, Virginia opossum); Eulipotyphla: talpid (European mole), soricid (white-toothed shrew, vagrant shrew), erinaceid (European hedgehog, northern white-breasted hedgehog); Primates: hominid (human); Urodela: ambystomid (axolotl); Cypriniformes: cyprinid (common bleak, common carp); Perciformes: percid (ruffe, European perch); Accipitriformes: accipitrid (common buzzard); Falconiformes: falconid (American kestrel); Galliformes: phasianid (chicken); Struthioniformes: struthionid (ostrich); Testudines: emydid (European pond turtle); Anura: ranid (edible frog) [plus carriage in Coleoptera: clerid (checkered beetle); Diptera: tabanid (horsefly), sarcophagid (fleshflies); Hymenoptera: vespid (umbrella wasp); Siphonaptera: pulicid (oriental rat flea)]	diarrhoea, myositis, eosinophilia	Eurasia, North America
T. nativa [T2] [sylvatic]	Carnivora: canid (dog, wolf, red fox, Arctic fox, corsac fox, blue fox, golden jackal, raccoon dog), felid (cat, leopard cat, lynx, Eurasian lynx, Siberian tiger, Far Eastern forest cat), mustelid (wolverine, stoat, American marten, European pine marten, European badger, European polecat), ursid (polar bear, brown bear), phocid (grey seal), obodenid (walrus), procyonid (raccoon); Rodentia: murid (mouse, brown rat), caviid (guinea pig), cricetid (deer mouse); Artiodactyla: cervid (reindeer), suid (pig, boar); Perissodactyl: equid (horse); Primates: hominid (human)	diarrhoea, myositis, eosinophilia	Holarctic
T. britovi [T3] (syn. *Bessonoviella britovi*) [sylvatic, rarely domestic]	Carnivora: canid (dog, wolf, golden jackal, raccoon dog, Japanese raccoon dog, red fox), felid (cat, European wildcat, Eurasian lynx), mustelid (beech marten, European pine marten, stoat, least weasel, European polecat, badger), viverrid (European genet, African palm civet, true civet), ursid (brown bear, Marsican brown bear, Asian black bear, Japanese black bear); Artiodactyla: bovid (goat,	diarrhoea, myositis, eosinophilia	Palearctic (Eurasia, Africa)

	sheep), cervid (fallow deer), suid (pig, boar); Perissodactyla: equid (horse); Rodentia: murid (mouse, field mouse, brown rat, black rat), caviid (guinea pig), echimyid (coypu), cricetid (bank vole, European snow vole), glirid (garden dormouse), sciurid (red squirrel), histricid (crested porcupine); Eulipotyphla: soricid (common shrew, Eurasian pygmy shrew, greater white-toothed shrew, lesser white-toothed shrew), erinaceid (European hedgehog), talpid (European mole); Primates: hominid (human)		
T. murrelli [T5] [sylvatic]	Carnivora: canid (dog, coyote, red fox, American red fox), felid (bobcat, cat), mustelid (American mink), procyonid (raccoon), ursid (American black bear); Artiodactyla: suid (pig, boar, bushpig, warthog); Perissodactyla: equid (horse); Rodentia: murid (mouse), cricetid (deer mouse); Primates: hominid (human)	diarrhoea, myositis, eosinophilia	Nearctic
Trichinella T6 (related to *T. nativa*) [sylvatic]	Carnivora: canid (gray wolf, red fox, gray fox), felid (cougar, bobcat), mustelid (wolverine, fisher), ursid (grizzly bear, brown bear, American black bear): Rodentia: murid (mouse); Artiodactyla: suid (pig, boar); Primates: hominid (human)		North America
T. nelsoni [T7] [sylvatic]	Carnivora: hyaenid (striped hyena, spotted hyena), canid (dog, wolf, red fox, bat-eared fox, side-striped jackal, black-backed jackal,), felid (cat, lion, leopard, cheetah, serval cat), ursid (Marsican brown bear), herpestid (common slender mongoose); Rodentia: murid (mouse, brown rat, black rat, hamster, Natal multimammate mouse), caviid (guinea pig); Lagomorpha: leporid (rabbit); Artiodactyla: suid (pig, boar, bushpig, desert warthog); Perissodactyla: equid (horse); Primates: cercopithecid (grivet, dogface baboon), hominid (human)	diarrhoea, myositis, eosinophilia	equatorial Africa
Trichinella T8 (related to *T. britovi*) [sylvatic]	Carnivora: hyaenid (spotted hyena), felid (lion, leopard); Rodentia: murid (mouse)		South Africa
Trichinella T9 (related to *T. murrelli*) [sylvatic]	Carnivora: ursid (Asian black bear, brown bear), canid (raccoon dog, red fox), procyonid (raccoon); Rodentia: murid (mouse)		Japan
T. patagoniensis [T12] [sylvatic]	Carnivora: felid (cougar); Artiodactyla: suid (pig); Rodentia: murid (mouse, rat)		South America
Non-capsule forming (or 'non-encapsulated')			
T. pseudospiralis [T4] [sylvatic, domestic]	Carnivora: felid (cat, oncilla), canid (raccoon dog, red fox, corsac fox), procyonid (raccoon), felid (lynx); Artiodactyla: bovid (sheep), cervid (fallow deer, moose), suid (pig, boar); Rodentia: murid (mouse, brown rat, lesser bandicoot rat), caviid (guinea pig), cricetid (deer mouse), echimyid (coypu); Dasyuromorphia: dasyurid (tiger quoll, eastern quoll, Tasmanian devil); Diprotodontia: phalangerid (common brushtail possum); Primates: hominid (human); Cathartiformes: cathartid (black vulture); Accipitriformes: accipitrid (Cooper's hawk, tawny eagle, common buzzard, western marsh harrier); Galliformes: phasianid (chicken); Falconiformes: falconid (brown falcon, American kestrel); Strigiformes: strigid (little owl, great horned owl, tawny owl), tytonid (Australian masked owl); Anseriformes: anatid (mallard, greylag goose); Passeriformes: corvid (rook, crow), turdid (common blackbird); Charadriiformes: stercocoracid (pomarine jaeger); Struthioniformes: struthionid (ostrich); Cypriniformes: cyprinid (common bleak, common carp); Perciformes: percid (ruffe, European perch) [plus carriage in Coleoptera: clerid (checkered beetle); Diptera: tabanid (horse fly); Hymenoptera: vespid (umbrella wasp)]		Nearctic, Oceania
T. papuae [T10] (syn. *Bessonoviella papuae*) [sylvatic]	Crocodilia: crocodylid (saltwater crocodile), alligatorid (caiman); Serpentes: pythonid (Indian python); Testudines: pelomedusid (African helmeted turtle); Rodentia: murid (mouse); Carnivora: canid (red fox); Artiodactyla: suid (pig); Primates: hominid (human)		Papua New Guinea
T. zimbabwensis [T11] [sylvatic]	Crocodilia: crocodylid (Nile crocodile); Sauria: varanid (Nile monitor lizard); Carnivora: hyaenid (spotted hyena), canid (red fox), felid (lion, leopard), viverrid (small spotted genet); Rodentia:		Africa

	murid (mouse, rat, hamster); Artiodactyla: suid (pig, boar); Primates: cercopithecid (baboon, vervet monkey)		

Parasite morphology: *Trichinella* spp. form several different morphological stages in their developmental cycles: adult worms (male and female) and larvae (4 sequential stages, designated L1-L4). Female worms are ovoviviparous and birth live young in the form of first-stage larvae (L1). Newborn larvae are elongate and tubular, measuring from 80-160 µm in length by 7-9 µm in diameter, and have a thicker anterior end bearing a sword-like stylet at the oral cavity. They invade striated muscle cells where they grow to 800-1,000 µm in length but coil up inside ellipsoidal cysts measuring from 250-500 µm in length. The larvae of most *Trichinella* spp. in mammals (e.g., *T. spiralis*) are found in enlarged host cells (called nurse cells) encapsulated by a thick collagen capsule, whereas those of other species in birds, reptiles and some mammals (e.g., *T. pseudospiralis*) remain non-encapsulated (although a very thin collagen capsule may be detected by electron microscopy). The coiled larvae show precocious development of genital primordia, meaning males and females can be differentiated. When ingested by suitable hosts, the larvae undergo 4 moults to form adult worms which mature rapidly (1-6 days) but have short lifespans (up to 4 weeks). Adult worms are slender and tubular, measuring from 1-4 mm in length, being enclosed by a whitish cuticle that may be translucent or opaque (matte) in appearance. They have a small head with a simple mouth, an elongate non-muscular oesophagus (stichosome) encircled by a chain of single glandular cells (stichocytes), a thin-walled intestine, and a muscular rectum opening into a terminal anus. Mature worms are sexually dimorphic, with female worms being larger than males (2-4 mm by 60-90 µm in diameter compared to 1-2 mm by 40-60 µm). Males do not have spicules but have curved tails with 2 large conical projections (variously named pseudobursae, caudal alae, or copulatory appendages), a single posterior testis connected to the seminal vesicle and terminating at the anal aperture to form a cloaca. Females have blunted rounded tails and contain a single ovary, seminal receptacle, uterus and vagina opening into an anterior vulva. In gravid females, the uterus carries developing eggs and hatching larvae. The eggs are subspherical, measuring 30-40 µm in diameter and are surrounded by a delicate vitelline membrane (no true eggshell). They embryonate *in utero* and first-stage larvae escape from the surrounding membrane and are released through the vulva.

Site of infection: Adult worms infect the small intestines of their hosts where they embed themselves in the mucosa between villi. Gravid females release L1 which move through the lymphatics and circulation to invade striated (skeletal) muscles, particularly those of the diaphragm, jaw (masseter), tongue, eyes, arms, and legs.

Pathogenesis: The clinical consequences of infection are dose-related, in that light infections are often asymptomatic, whereas heavier infections may result in disease (known as trichinellosis or trichinosis) caused by damage to host tissues by adult and larval parasites as well as host hypersensitivity responses to worm excretory-secretory (ES) products. Clinical presentation varies over time with 3 phases recognised: an early enteric phase; an intermittent vascular phase; and an extended muscular phase. In most clinical infections, symptoms peak over 2-4 weeks and then gradually subside 6-8 weeks after infection. Heavy infections, however, may cause severe symptoms which persist for months or progressively worsen leading to death. The enteric phase is caused when ingested larvae invade the intestinal mucosa (within hours) where they become embedded and rapidly mature into adults (within days) producing more larvae. All stages cause tissue trauma and microscopic lesions in the intestines during the first week of infection, but only heavy infections produce symptoms, including catarrhal enteritis, loose stools or diarrhoea, abdominal pain, anorexia, nausea and/or vomiting. Pathological changes include villous atrophy, goblet cell and crypt hyperplasia, and cellular immune responses consistent with type I hypersensitivity (thought to be associated with subsequent worm expulsion). Most symptoms subside after 5-10 days, but diarrhoea, with or without abdominal pain, may last for several weeks. The vascular (parenteral) phase occurs when newborn larvae enter intestinal lymphatics or mesenteric venules and are carried to other tissues. Larval migration may last up to 3 weeks and wandering larvae damage blood vessels with local necrosis producing fever, chills, headache, weakness, profuse perspiration, tachycardia, facial oedema (e.g., periorbital), and retinal, conjunctival or subungual splinter haemorrhages, with eosinophilia, leucocytosis and hyperglobulinaemia. This acute stage develops into the muscular phase when migrating larvae invade skeletal muscle cells in the second or third week, particularly active muscles (such as those of the diaphragm, jaws, tongue, larynx, and/or eyes). The larvae cause structural and functional deficits when they penetrate muscle cells, coil up and encyst, and induce nurse cell formation with subsequent collagen encapsulation around 20 days later (even the non-encapsulated species can have a very thin collagen capsule). The muscle cells infected with encapsulated species are called nurse cells because they transform from contractile cells into turgid metabolically-active cells with few cytoskeletal elements surrounded by small blood vessels providing nutrients and removing wastes. Heavy infections reduce muscle contractibility and cause myositis (often in extraocular muscles progressing to masseters, neck muscles, limb and lumbar muscles), myalgia, weakness, fatigue, muscle degeneration and fibrosis, sometimes myocytosis (muscle breakdown), dyspnoea, cough, hoarseness, dysphagia, constipation, hepatomegaly, occasionally macular or petechial rash, pruritus, aching joints with eosinophilia, hypoalbuminaemia, proteinuria and haematuria (but rarely renal dysfunction). Many symptoms are generalised or resemble those occurring due to rheumatism, pneumonia, encephalitis, meningitis, pleurisy, myocarditis, peritonitis, nephritis, and conjunctivitis. Symptoms may progressively disappear 6-8 weeks after infection, although some may persist for months, including hypocalcaemia, hypomagnesaemia, fatigue and myalgia (esp. legs). Other symptoms may progress to cause serious cardiovascular, respiratory, neurological, psychiatric or allergic disorders, and mortalities have been attributed to heart failure (myocarditis), respiratory congestion (pneumonia), peritonitis (bacteraemia and sepsis due to tissue invasion by enteric flora) or cerebral involvement (encephalitis, eosinophilic meningitis). Survivors often enter a convalescent phase during which most of the intramuscular cysts (e.g., nurse-cell-parasite complexes)

become calcified over time (6-18 months), although live larvae have been detected in some people decades after infection. Survivors also appear to acquire some protective immunity to re-infection and disease. Different *Trichinella* spp. vary in their pathogenicity to humans: *T. spiralis* being the most pathogenic (apparently due to its high reproductive capacity and immuno-reactivity); *T. nelsoni, T. britovi* and *T. murrelli* being moderately pathogenic (low to medium reproductive capacities and immuno-reactivities); and *T. nativa, T. pseudospiralis* and *T. papuae* being more benign (lower reproductive capacities and slower development).

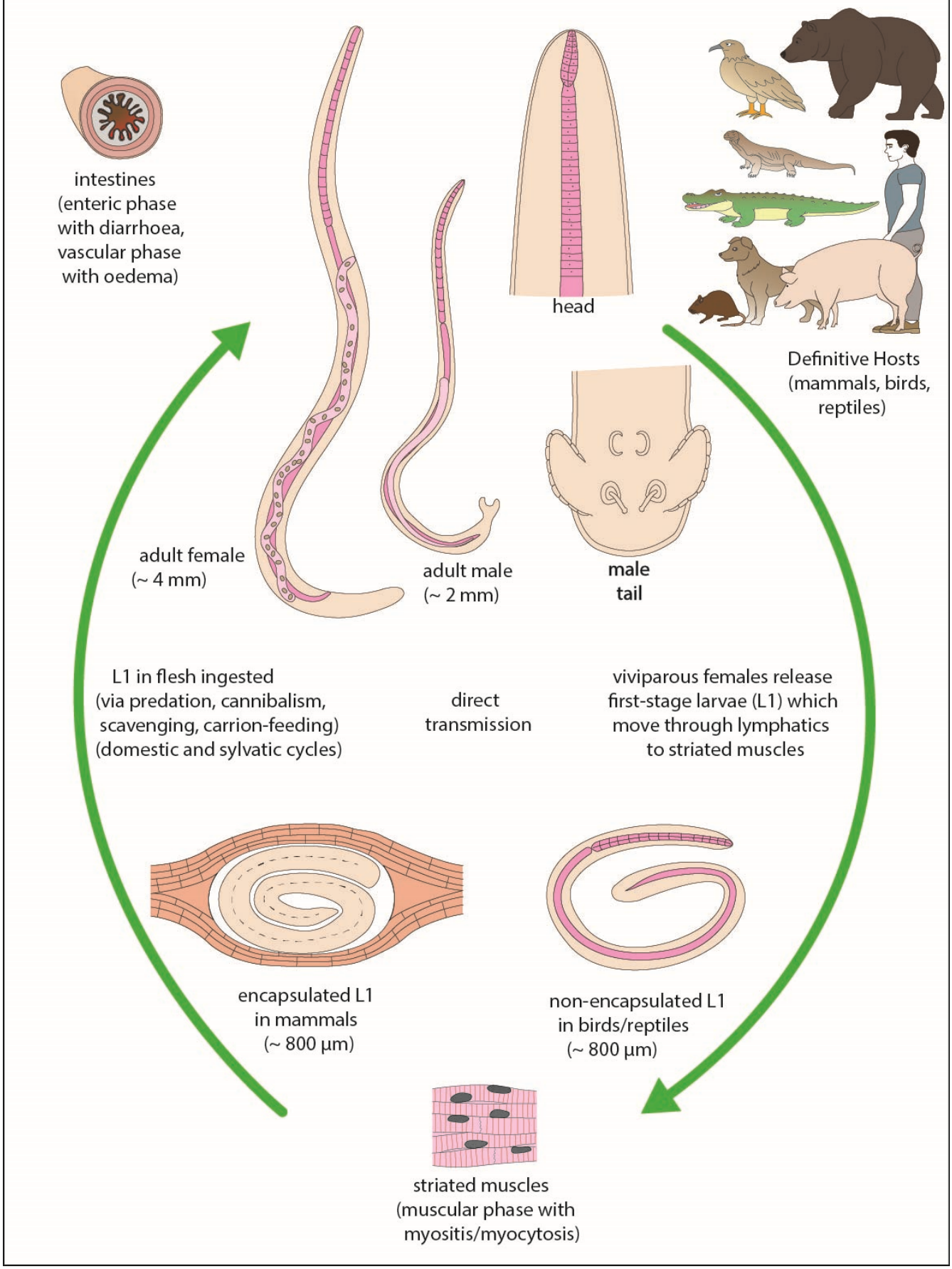
Developmental cycle and mode of transmission: *Trichinella* spp. have unusual life-cycles whereby infectious stages are not voided by the definitive host but become encysted in the muscles of the same host as first-stage larvae (the infectious stages of most other nematodes are third-stage larvae which develop in the external environment or in separate intermediate hosts). When muscle cysts are ingested by carnivores, they are digested in the small intestines releasing the L1 which penetrate the mucosa within several hours. The larvae embed themselves in the mucosa between villous folds and undergo 4 rapid moults developing into mature (dioecious) adults worms within days (1-3 days). After mating, male worms die and pass out of the host while female worms burrow deeper into the mucosa and submucosa, sometimes into lymph ducts and lymph nodes. Gravid females are ovoviviparous, and produce and release motile L1 by day 6. Females may produce up to 1,500 larvae over 5-10 days before dying around day 30. The L1 enter local lymphatics and blood capillaries and are spread throughout the body via the circulation. Larvae invade striated muscle cells, especially very active muscles (like the diaphragm, jaws, tongue, larynx, eyes). The larvae grow in size, coil up by day 17 and remain within cells. Some species (e.g., *T. spiralis*) cause the infected muscle cell to transform into a nurse cell (myofilaments disappear, smooth endoplasmic reticulum increases, nuclei enlarge to form a complex around the larva). The larvae derive nutrients from the sarcoplasm as well as from a growing network of capillaries surrounding the parasite-nurse cell complex. By day 21, the coiled larvae begin to become encased in a collagen capsule laid down by surrounding fibroblasts, this process of encapsulation takes up to 3 months. The capsule is thick and double-walled in encapsulated species (e.g., *T. spiralis*, but remains thin and membranous for non-encapsulated species (e.g., *T. pseudospiralis*). The larvae are infective after 8 weeks but may remain viable in developmental arrest for years, although most cysts eventually calcify within 6-18 months. Transmission occurs when infected raw flesh is eaten by carnivorous or omnivorous animals via predation, cannibalism, scavenging or carrion-feeding in sylvatic or domestic cycles. Zoonotic transmission to humans occurs when people eat raw or undercooked meat of infected animals, particularly pigs and wild boar, but also including other game animals, such as walrus and bear. All *Trichinella* species have sylvatic cycles in wildlife, either by ingestion of infected prey or fresh, frozen or decomposing carcases. The larval cysts of different *Trichinella* spp. show variable resistance to being frozen in host tissues: those of species found in cold Arctic regions (*T. nativa* and *T. britovi*) may survive extended periods (weeks), while those of species found in more temperate regions (*T. spiralis, T. nelson, T. murrelli, T. pseudospiralis* and *T. papuae*) do not survive long (hours or days). Human activities often contribute to sylvatic cycles or lead to the development of domestic cycles: e.g. hunting wildlife for food, baiting traps with meat, leaving carcases for scavengers, or feeding scraps to domestic or companion animals, including meat animals (pigs, crocodiles), fur animals, pets or working animals (especially sled dogs). In particular, urban cycles become established amongst pigs, rats and humans when high risk farming practices facilitate transmission through feeding offal and pork scraps back to pigs, disposing of waste in open garbage dumps and housing animals in facilities that are not vermin-proof. Infections in humans have been recorded around the world, with Europe and North America reporting some 150,000-300,000 infections per year, but only ~ 150 of these are clinical cases. Infections are rarer in tropical regions usually due to the lower consumption of pork, or meat in general, due to greater vegetable/fruit consumption, fish diets, or religious bans on eating pork.

Differential diagnosis: Although several clinical symptoms may be indicative of trichinellosis (e.g. myalgia, periorbital oedema, fever), they are relatively nonspecific and might be attributable to other disease conditions. Blood tests may reveal eosinophilia, leucocytosis and elevated levels of muscle enzymes (creatine kinase and lactate dehydrogenase) during infection, but these are similarly nonspecific. Infections are unequivocally diagnosed by the microscopic detection of parasite larvae in muscle biopsy samples (usually deltoid or gastrocnemius muscle) or necropsy samples (usually diaphragm), either in squash (glass compression) preparations (trichinoscopy) or following enzyme-acid (pepsin-HCl) digestion. Several immunoserological tests have been developed to detect host serum antibodies against infections, including intradermal, flocculation and agglutination tests and enzyme immunoassays), but they do not detect early infections as circulating antibodies only appeared 3-4 weeks after infection. Various molecular characterization studies have been used to demonstrate differences between *Trichinella* spp., including Western blots of parasite antigens and allozyme electrophoresis (ACO, ACP, ADA, ALAT, ALDO, EST, G6PD, GLDH, GOT, GPD, LDH, ME, 6PGD, PGM, SOD, TPI). More recently, molecular biological techniques have been used to detect parasite DNA in clinical samples (as restriction fragment length polymorphisms (RFLP), single strand conformational polymorphisms (SSCP), random amplified polymorphic DNA (RAPD) or partial gene sequences) following polymerase chain reaction (PCR) amplification of repetitive DNA (pPRA, pBP2, pT1.6), nuclear genes (small subunit ribosomal RNA, expansion segment V of ribosomal DNA repeat, internal transcribed spacer regions 1 and 2) and mitochondrial genes (cytochrome c oxidase subunit 1, large subunit ribosomal RNA).

Treatment and control: Several anthelmintic drugs have been found to be effective against adult worms in the gut if applied early enough in infection, but they were less effective against encysted larval stages in the muscles. The benzimidazole-methylcarbamates (mebendazole, albendazole and flubendazole) are the drugs of choice, but not in pregnant women or young children due to adverse side effects, including bone marrow suppression. The tetrahydropyrimidine pyrantel has been used in children and pregnant women. The anthelmintic drugs are often given together with analgesics to relieve symptoms, antipyretics to reduce fever, and steroid

therapy to reduce inflammation, particularly in cases involving the heart or central nervous system. Bed rest is advised to avoid exertion antagonizing muscular symptoms. Several strategies have been developed to prevent infections by breaking transmission cycles where possible. Strict regulations have been implemented governing the production of livestock for meat, especially pigs, with mandatory testing at slaughter (trichinoscopy) and certification of *Trichinella*-free producers. Many countries have reported great success in controlling zoonotic infections in humans by banning the feeding of offal and scraps to pigs, prohibiting the consumption of wild boar, and advocating the thorough cooking of pork products. Larvae in muscle cysts are killed when pork is cooked to a core temperature of 71°C for at least one minute or 59°C for at least 10 minutes. It is recommended that thermometers be used to monitor roasting or microwave cooking of meat. Drying and curing meats have also been shown to be relatively effective, but they do not always kill larvae found in game meats. Freezing may be used to kill encapsulated larvae in pork when frozen at -15°C for at least 3 weeks or at -20°C for at least 3 days, but cooking is recommended for game meats which may be infected with non-encapsulated parasite species that have a high tolerance to freezing. Gamma-irradiation has also been used to sterilize meats in sealed packaged foods. It is critical that carcases be disposed of properly (preferably by burning or burying), that unprocessed meat scraps are not dumped in garbage tips or fed to farmed or wild carnivores, and that farms undertake rodent control. Compliance with government regulations or recommendations is high in regions where intensive husbandry practices are used (indoor piggeries), but lower in regions where animals are kept in pig-sties or are free-ranging. Epidemiological investigations have shown that non-compliance has resulted in several outbreaks traced back to pigs and even horses fed pork scraps, and fur animals, sled dogs and crocodiles fed carcases of the same animal species or other game animal species. Public education campaigns should be implemented in communities consuming pork products and the posting of warning signs in endemic wilderness areas should continue to warn hunters of the risks involved in eating wild game.

Trichinella

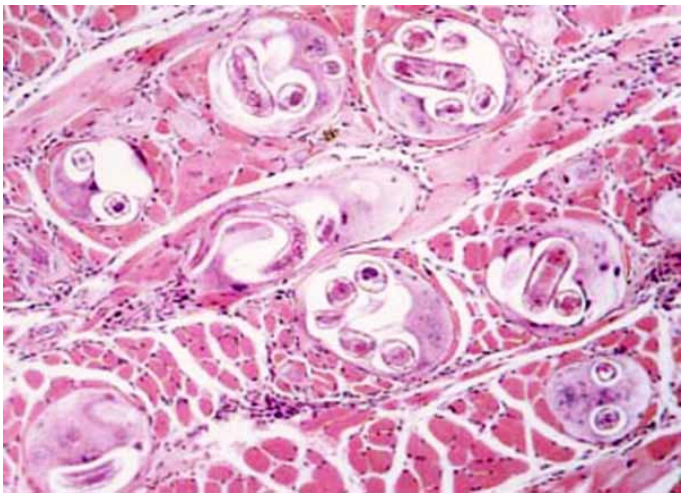




Trichinella adult worm



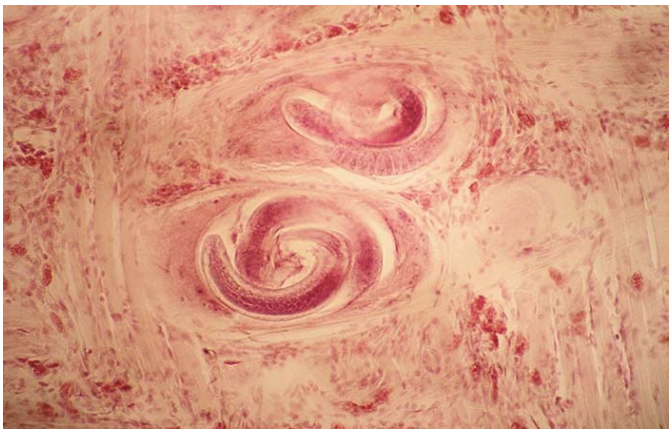
Trichinella in gut section



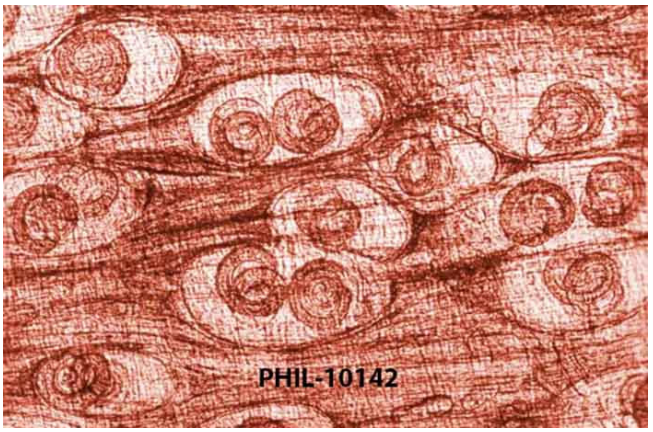
Trichinella larvae in muscles



Trichinella larvae in muscles



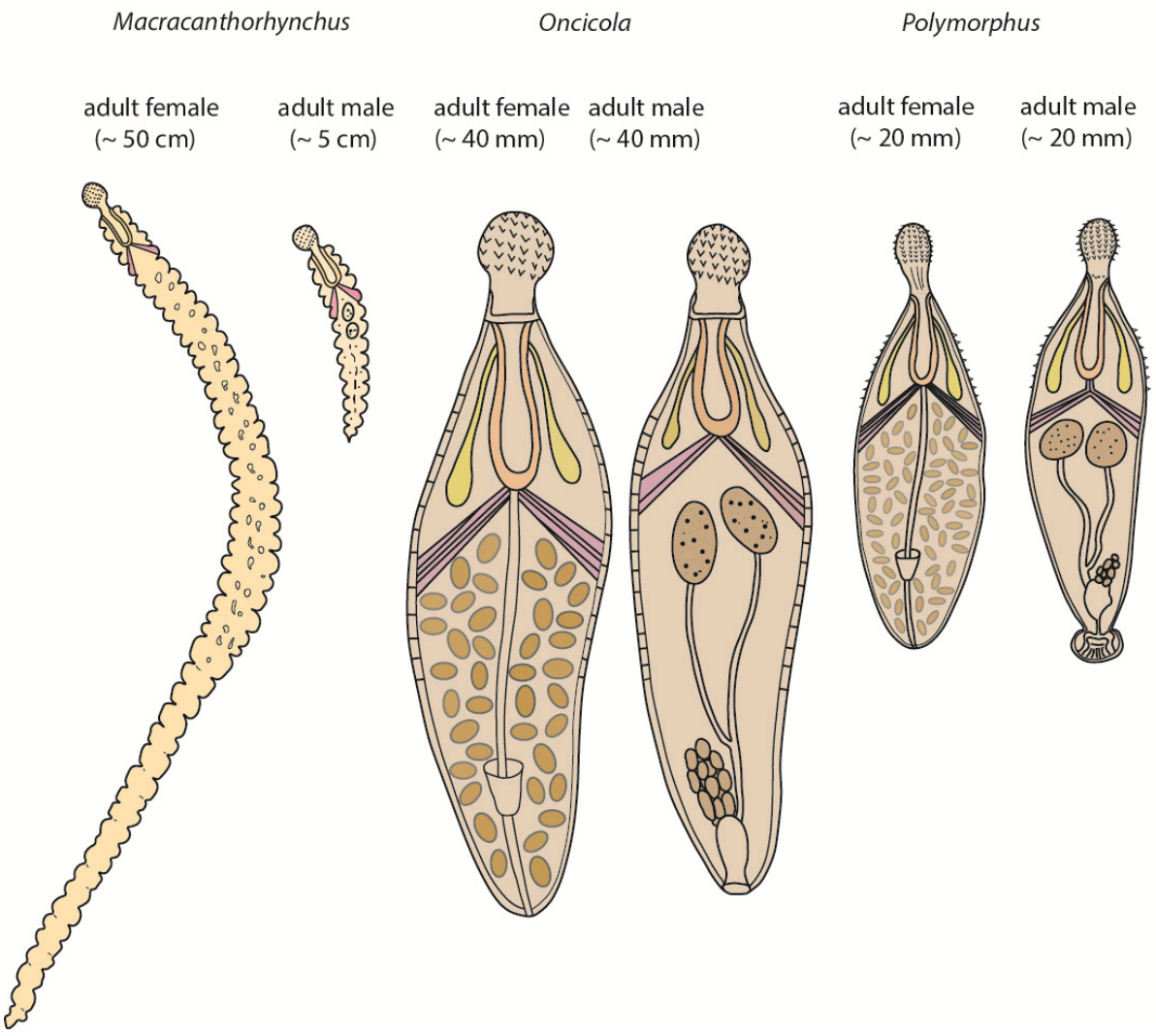
Trichinella larvae in muscles



Trichinella larvae in muscles

Acanthocephala
(thorny-headed worms)

Acanthocephala



Macracanthorhynchus
(acanthocephalan)

Overview

Acanthocephalans have pseudocoelomate unsegmented tubular bodies and are commonly called thorny-headed worms due to the possession of a retractable anterior proboscis armed with rows of hooks for attachment. They undergo protostomial embryonic development but do not moult during growth. They are classified within the Lophotrochozoa but do not have jawed mouthparts or digestive tracts, instead they absorb nutrients through their eutelic syncytial cuticles. All species are parasites in the intestinal tracts of vertebrates and they have indirect life-cycles, involving aquatic or terrestrial arthropods as intermediate hosts. Female worms produce mature eggs that float freely in the body cavity and are passed through a unique uterine bell into the uterus to be voided with host faeces. The eggs have thick shells comprised of 4-5 membranes and contain a larval stage (acanthor) armed with hooks and spines which is infective to an invertebrate intermediate host. When ingested by arthropods, the acanthor migrates to the haemocoel and develops into an acanthella which matures into an infective cystacanth. When the arthropod is ingested by the vertebrate host, the cystacanth attaches and matures in the intestinal tract. Infections by *Macracanthorhynchus hirudineus* are transmitted by coprophagous beetles to pigs and have been associated with mild enteric disease.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Clade:	Syndermata (eutelic syncytial epidermis)
Phylum:	Acanthocephala (thorny-headed worms, pseudocoelomate, retractable proboscis with hooks, indirect cycles, eggs with acanthor, acanthella develops in arthropod IH (or PH))
Class:	Archiacanthocephala (oval thick-shelled eggs, body wall lacunar canals dorsal & ventral (or just dorsal))
Order:	Oligacanthorhynchida (proboscis subspherical, short rows of several hooks, protonephridial organs present)
Family:	Oligacanthorhynchidae (single family)
Genus:	*Macracanthorhynchus* (parasitic in small intestines of pigs)
Species:	*M. hirudineus* (causes enteritis in pigs)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. In addition to the parasitic flatworms (platyhelminths), other metazoan worm-like groups live as endoparasites in vertebrate hosts. Acanthocephalans have pseudocoelomate unsegmented round-flattened bodies and are commonly called thorny-headed or spiny-headed worms due to the possession of an anterior spherical-cylindrical invaginable proboscis bearing rows of recurved hooks used for attachment. They undergo protostomial embryonic development but do not moult during growth, thus belonging to the Lophotrochozoa (embryos with spiral mosaic cleavage) rather than the Ecdysozoa. On the basis of molecular evidence, they are classified within the clade Gnathifera even though they do not have complex cuticular jaws. They lack digestive tracts and absorb nutrients across their eutelic (constant number of nuclei) syncytial (multinucleate) epidermis, and have been grouped together with the Rotifera into the clade Syndermata.

Over 1,400 species of acanthocephalans have been described worldwide as endoparasites with adult stages living in the intestinal tracts of a wide range of fish, amphibians, reptiles, birds and mammals. They have indirect life-cycles with arthropods always acting as intermediate hosts for larval stages. Female worms pass thick-shelled eggs containing an acanthor armed with hooks and spines. When ingested by aquatic crustaceans or terrestrial insects, the acanthor migrates to the haemocoel and forms an acanthella which matures into an infective cystacanth. When the arthropod is ingested by the vertebrate host, the cystacanth attaches and matures into an adult in the intestinal tract. Within the phylum Acanthocephala, four classes are recognized: Archiacanthocephala with terrestrial cycles involving mammals/birds and insects; Palaeacanthocephala with aquatic cycles in fish/birds/seals and crustaceans; Eoacanthocephala with aquatic cycles in fish/amphibia/reptiles and crustaceans; and Polyacanthocephala with aquatic cycles in fish/crocodiles and crustaceans.

Order	Environment	Definitive hosts	Intermediate hosts	Characters

Class: Archiacanthocephala (proboscis hooks in concentric circular rows, trunk lacking spines)				
Oligacanthorhynchida	terrestrial	birds, mammals	insects	subspherical proboscis
Gigantorhynchida	terrestrial	birds, mammals	insects, millipedes, crustaceans	conical proboscis, truncated, bipartite
Moniliformida	terrestrial	birds, mammals	insects	cylindrical proboscis
Apororhynchida	terrestrial	birds	unknown	globular proboscis
Class: Palaeacanthocephala (proboscis hooks in alternating longitudinal rows, trunk with or without spines)				
Echinorhynchida	aquatic	fish, amphibians, reptiles	crustaceans	variable proboscis (globular, cylindrical, claviform)
Polymorphida	aquatic, terrestrial	birds, mammals, amphibians, reptiles	crustaceans	variable proboscis (bulbous, spherical, oval, cylindrical)
Heteramorphida	aquatic, terrestrial	shore birds	unknown	spindle-shaped proboscis
Class: Eoacanthocephala (proboscis hooks in radial rows, trunk with or without spines)				
Gyracanthocephala	aquatic	fish	crustaceans	small spheroid proboscis
Neoechinorhynchida	aquatic	fish, amphibians, reptiles	crustaceans	variable proboscis (globular-cylindrical)
Class: Polyacanthocephala (proboscis hooks in longitudinal rows, trunk with spines)				
Polactorhynchida	aquatic	fish, crocodiles	crustaceans	long claviform proboscis

The class Archiacanthocephala contains 4 orders of terrestrial acanthocephalans whose body walls contain dorsal (and sometimes ventral) lacunar canals, usually 8 uninucleate cement glands, few elongated or branched subcuticular (tegumental) nuclei, and ligament sacs inside the pseudocoel. Worms in the order Oligacanthorhynchida possess a subspherical proboscis with short rows of several hooks and they have protonephridial organs. The order contains a single family Oligacanthorhynchidae with 13 genera (*Macracanthorhynchus, Cucullanorhynchus, Echinopardalis, Heptamegacanthus, Multisentis, Neoncicola, Nephridiacanthus, Oligacanthorhynchus, Oncicola, Pachysentis, Paraprosthenorchis, Prosthenorchis, Tchadorhynchus*). The genus *Macracanthorhynchus* contains 5 species parasitizing domestic and wild animals which become infected by consuming larval stages in intermediate hosts (insects, particularly beetles) or sometimes small vertebrate paratenic hosts (amphibians, lizards).

***Macracanthorhynchus* species**	**Definitive hosts, DH (adults in intestines)**	**Intermediate hosts, IH (larval acanthellae then cystacanths in tissues) [plus paratenic hosts, PH]**	**Distribution**
M. aegypticus	Eulipotyphla: erinaceid (hedgehog)		Africa
M. catulinus	Carnivora: canid (dog, red fox), mustelid (weasel, stoat); Rodentia: murid (spiny mouse, gerbil)	Coleoptera: tenebrionid (soil beetles, *Adesmia*, *Dissonomus, Pachyscelis, Stalagmoptera, Tentyria, Trigonoscelis*) [plus PHs, Sauria: anguid (European legless lizard), agamid (Caucasian agama, spiny-tailed lizard), gekkonid (Mediterranean house gecko), scincid (Berber skink), lacertid (trans-Caucasian racerunner, Caspian green lizard); Serpentes: colubrid (black whipsnake), elapid (Caspian cobra), viperid (blunt-nosed viper); Anura: ranid (marsh frog); Rodentia: sciurid (Tarbagan marmot); Carnivora: mustelid (badger, least weasel, steppe polecat)]	Eurasia
M. erinacei	Eulipotyphla: erinaceid (hedgehog)		Africa
M. hirudinaceus (syn. *M. gigas, Echinorhynchus gigas, E. hirudinaceus, Gigantorhynchus gigas, G. hirudinaceus, Hormorhynchus gigas, H. hirudinaceus, Taenia haeruca, T.*	Artiodactyla: suid (pig); Carnivora: canid (dog); Primates: hominid (human)	Coleoptera (mainly larval grubs but also adult beetles): scarabaeid (cockchafers, rose chafer, vine chafer, shining leaf chafer, flower chafer, May bugs, June beetle, dung beetles, scarab beetles, Japanese beetle, rhinoceros beetle), carabid (ground beetles), hydrophilid (water beetles); Diptera: empidid (dance fly); Blattodea: ectobiid (wood	worldwide

hirudinaceus) (giant thorny-headed worm)		cockroach), blattid (cockroach)	
M. ingens (syn. *Echinorhynchus, Prosthenorchis*)	Carnivora: procyonid (raccoon, ring-tailed cat), canid (dog, grey fox), mephitid (striped skunk), mustelid (American mink), ursid (American black bear); Eulipotyphla: talpid (hairy-tailed mole); Primates: hominid (human); Artiodactyla: suid (pig); Strigiformes: strigid (barred owl); Charadriiformes: larid (western gull)	Coleoptera (mainly larval grubs but also adult beetles): scarabaeid (May bugs, scarab beetles, rhinoceros beetle); Blattodea: ectobiid (wood cockroach); Diplopoda: spirobolid (large millipedes) [plus PHs, Serpentes: colubrid (eastern kingsnake, green water snake, banded water snake, eastern racer, common garter snake), viperid (cottonmouth); Anura: ranid (northern leopard frog); Cingulata: dasypodid (nine-banded armadillo)]	North America, Eurasia

Parasite morphology: Acanthocephalan worms form three different developmental stages: eggs; larvae (acanthor, acanthella and cystacanth); and adults. The eggs are oval (measuring 90-110 x 50-65 µm), dark brown in colour, embryonated (containing the first larval stage known as an acanthor), and thick-shelled (surrounded by 3 embryonic envelopes). Acanthors released in the intermediate host are spindle-shaped with anterior hooks and spines. They penetrate to the body cavity where they encapsulate and moult into second stage larvae (acanthella) which are the main growing stages. They increase in size from mm to cm and come to resemble miniature adult worms, albeit immature in that they do not yet possess mature reproductive organs. They form encysted infective stages (cystacanths), essentially resting juveniles containing an inverted proboscis. When ingested by a definitive host, they excyst, evert their proboscis and attach to the gut wall to develop further. Adult worms have elongated curved sac-like bodies, some species measuring up to 1 m in length by 3-9 mm wide. They have 3 main body regions (proboscis, neck and trunk) and are usually flattened bilaterally (although specimens pretreated with water before fixation may become turgid and cylindrical). Most worms are cream in colour but may occasionally be pigmented (yellow-brown to pink) depending on host gut content. Adults do not contain alimentary tracts, the body cavity being bound by syncytial body walls with prominent transverse wrinkles and minute crypts greatly increasing their surface area for the exchange of gases, nutrients and wastes by diffusion. Much of the tegument comprises radial fibers with a fluid-filled lacunar system continuous with the tubular muscles of the body wall. Worms possess an excretory system consisting of protonephridial organs and flame cells. A distinctive feature of these thorny-headed or spiny-headed worms is the possession of a retractable (invertible) cylindrical proboscis or rostellum armed with several rows of recurved spiny hooks. The bulk of the trunk contains the proboscis receptacle, retractor muscles and associated lemnisci (elongate hydraulic sacs thought to act a reservoirs for lacunar fluid). Mature worms are dioecious, with females being larger than males (10-65 cm long compared to 2-15 cm). Males possess two testes, each with a vas deferens, cement glands and a common ejaculatory duct and Safftigen's pouch terminating in a small eversible copulatory bursa. During copulation, sperm ejected into the vagina escape into the body cavity via the genital duct and the male then plugs the vagina using the cement glands to prevent further copulation. Females contain a unique funnel-shaped uterine bell that receives and delivers developing shelled embryos to the uterus (only mature eggs are delivered, while immature eggs are returned to the pseudocoelom for further maturation).

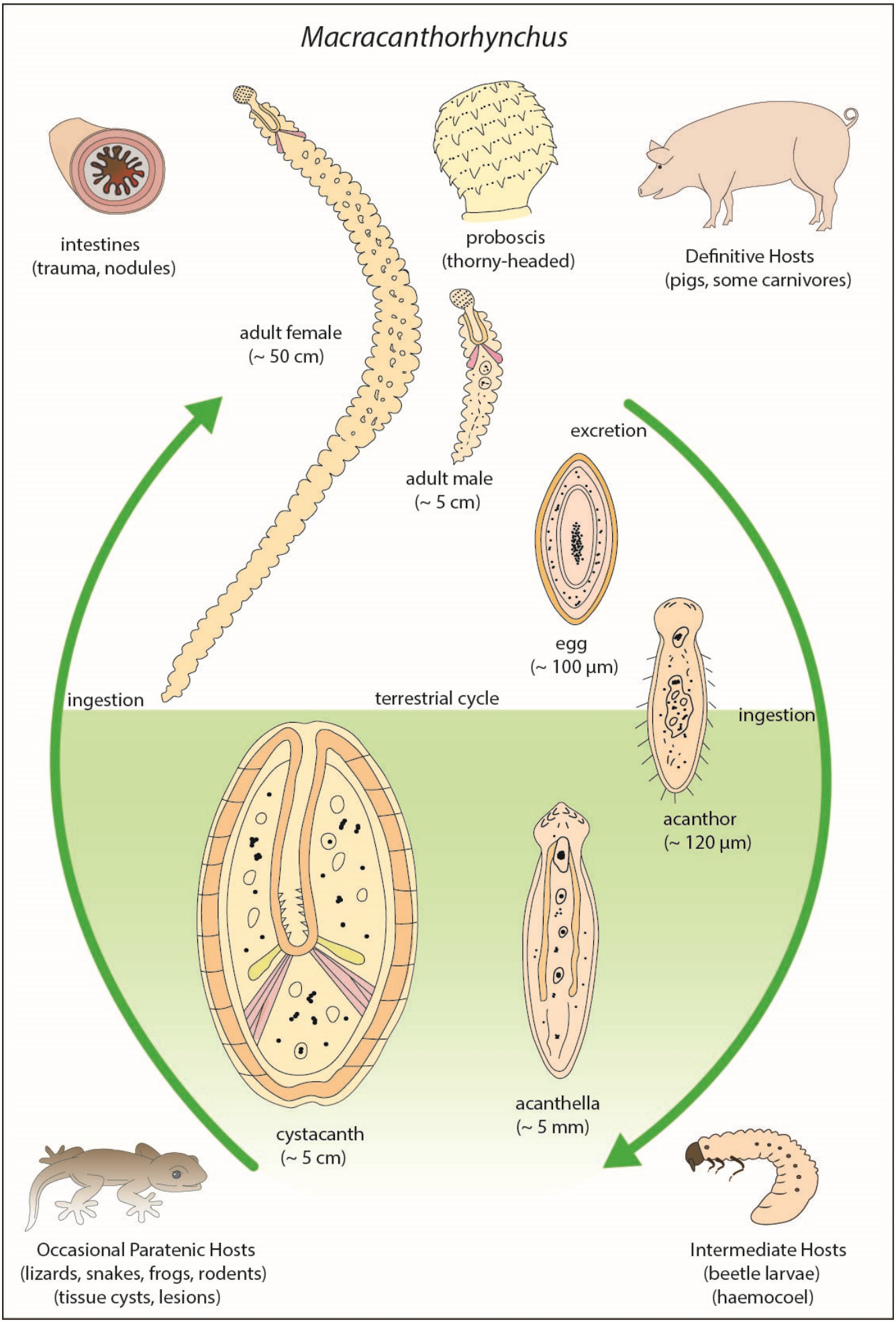
Site of infection: Adult worms infect the small intestines of their definitive hosts (suids, rodents and carnivores) while larval stages (acanthella and cystacanths) form in the haemocoel (body cavity) of their intermediate hosts (insects) or encyst within the internal tissues of paratenic hosts (amphibians, reptiles and carnivores).

Pathogenesis: Adult acanthocephalans do not feed on host tissues but absorb nutrients across their body walls. However, adult worms insert their armed proboscis deeply into the wall of the intestine and they also move occasionally to attach to new sites. Intestinal bacteria usually infect attachment sites forming inflammatory granulomatous nodules (sometimes called blackberry spots). These lesions may become haemorrhagic with blood and protein loss. Recently vacated sites appeared as deep infected ulcers while old healed sites appear as firm fibrous nodules. Nonetheless, light infections by only a few parasites often remain subclinical, while heavy infections by many parasites may result in significant unthriftiness due to blood loss, impaired nutrition and escalating inflammation (cumulative effects of many localized lesions leading to enteritis and gastritis). Clinical signs of diarrhoea, emaciation, abdominal pain and poor weight gain have been described in pigs infected with *M. hirudinaceus*. On occasion, the long parasite proboscis may perforate the thin intestinal wall and if not sealed off by host inflammatory reactions, such perforations may lead to peritonitis and death. Infected pigs become listless, unthrifty and may experience severe pain if the gut wall is perforated. Most human cases have involved mild infections of the gastrointestinal tract, although one case reported an ectopic infection of a patient's eye.

Developmental cycle and mode of transmission: Acanthocephalans have indirect life cycles involving cyclic transmission between definitive hosts (vertebrates infected with adult stages), intermediate hosts (invertebrates infected with larval stages) and sometimes paratenic hosts (vertebrates infected with larval stages) or post-cyclic hosts (vertebrates infected with adult stages). Mature female worms lay embryonated eggs which are voided into the environment with host faeces. The eggs do not hatch until they are ingested by an appropriate arthropod intermediate host (including beetles, esp. larval grubs, cockroaches, flies and millipedes). They then release the enclosed acanthor which burrows into the host body cavity (haemocoel) where they encapsulate and grow through an acanthella stage to a resting infective cystacanth in 6-12 weeks. These stages do not develop further until infected intermediate hosts are ingested by suitable definitive hosts, whereupon they excyst, evert their armed proboscis and attach to the gut wall to feed, grow and develop into sexually mature adult worms over 8-12 weeks. If the cystacanths of some species are ingested by inappropriate hosts (non-definitive hosts), they may bore through the gut wall into the body cavity and then re-encyst (thus utilizing these hosts as paratenic hosts). *M. ingens* and *M. catulinus* have been found to use amphibians, snakes, lizards, rodents and armadillos as paratenic hosts, but *M. hirudinaceus* does not. Post-cyclic transmission may also occur when adults in definitive hosts are ingested by predators in which they may survive. In definitive hosts, adult worms mature, mate and females begin egg production (individual females may lay up to 250,000 eggs per day for several months). The prepatent period (time from infection until egg production) is around 2-3 months and worms may live for up to 1 year. Infections in pigs are most prevalent in areas where animals are kept under poor hygienic conditions and beetles have access to pig faeces. Infections in humans generally occur in areas where insects are eaten for dietary or medicinal reasons.

Differential diagnosis: Infections can be difficult to detect by ante-mortem coprological examination because the parasite eggs are heavy and do not float reliably in most conventional salt solutions. Sedimentation techniques should therefore be used. Adult worms can be detected on post-mortem examination of gut samples, and darkened nodular lesions are often visible through the serosal surface.

Treatment and control: Anthelmintic chemotherapy with levamisole, ivermectin or doramectin has proven effective against clinical infections in pigs, dogs and humans. The drugs fenbendazole, niclosamide and loperamide have also been used with some success against infections in pigs, but earlier treatments with carbon tetrachloride, tetrachlorethylene and nicotine sulphate were only partly effective. Many infections in livestock, however, appear to be self-limiting and do not persist so chemoprophylaxis is not widely used except in high-risk situations. Parasite control in piggeries is best afforded by improving housing hygiene, regular removal of faeces, proper effluent treatment and disposal, limiting exposure to contaminated lots or pastures, insect-proofing feed storage areas and restricting access of beetles (the usual intermediate hosts) to pigs and pig faeces.


Macracanthorhynchus
intestines
(trauma, nodules)
proboscis
(thorny-headed)
Definitive Hosts
(pigs, some carnivores)
adult female
(~ 50 cm)
adult male
(~ 5 cm)
excretion
egg
(~ 100 µm)
ingestion
terrestrial cycle
ingestion
acanthor
(~ 120 µm)
acanthella
(~ 5 mm)
cystacanth
(~ 5 cm)
Occasional Paratenic Hosts
(lizards, snakes, frogs, rodents)
(tissue cysts, lesions)
Intermediate Hosts
(beetle larvae)
(haemocoel)



Macracanthorhynchus adult worms



Macracanthorhynchus anterior proboscis

Oncicola
(acanthocephalan)

Overview

Acanthocephalans have pseudocoelomate unsegmented tubular bodies and are commonly called thorny-headed worms due to the possession of a retractable anterior proboscis armed with rows of hooks for attachment. They undergo protostomial embryonic development but do not moult during growth. They are classified within the Lophotrochozoa but do not have jawed mouthparts or digestive tracts, instead they absorb nutrients through their eutelic syncytial cuticles. All species are parasites in the intestinal tracts of vertebrates and they have indirect life-cycles, involving aquatic or terrestrial arthropods as intermediate hosts. Female worms produce mature eggs that float freely in the body cavity and are passed through a unique uterine bell into the uterus to be voided with host faeces. The eggs have thick shells comprised of 4-5 membranes and contain a larval stage (acanthor) armed with hooks and spines which is infective to an invertebrate intermediate host. When ingested by arthropods, the acanthor migrates to the haemocoel and develops into an acanthella which matures into an infective cystacanth. When the arthropod is ingested by the vertebrate host, the cystacanth attaches and matures in the intestinal tract. The species *Oncicola pomatostomi* apparently uses small birds as paratenic hosts for cystacanths, and infections are predominantly found in cats.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Clade:	Syndermata (eutelic syncytial epidermis)
Phylum:	Acanthocephala (thorny-headed worms, pseudocoelomate, retractable proboscis with hooks, indirect cycles, eggs with acanthor, acanthella develops in arthropod IH (or PH))
Class:	Archiacanthocephala (oval thick-shelled eggs, body wall lacunar canals dorsal & ventral (or just dorsal))
Order:	Oligacanthorhynchida (proboscis subspherical, short rows of several hooks, protonephridial organs present)
Family:	Oligacanthorhynchidae (single family)
Genus:	*Oncicola* (parasitic in small intestines of cats/foxes/dingoes)
Species:	various species cause enteritis in companion animals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. In addition to the parasitic flatworms (platyhelminths), other metazoan worm-like groups live as endoparasites in vertebrate hosts. Acanthocephalans have pseudocoelomate unsegmented round-flattened bodies and are commonly called thorny-headed or spiny-headed worms due to the possession of an anterior spherical-cylindrical invaginable proboscis bearing rows of recurved hooks used for attachment. They undergo protostomial embryonic development but do not moult during growth, thus belonging to the Lophotrochozoa (embryos with spiral mosaic cleavage) rather than the Ecdysozoa. On the basis of molecular evidence, they are classified within the clade Gnathifera even though they do not have complex cuticular jaws. They lack digestive tracts and absorb nutrients across their eutelic (constant number of nuclei) syncytial (multinucleate) epidermis, and have been grouped together with the Rotifera into the clade Syndermata.

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Order	Environment	Definitive hosts	Intermediate hosts	Characters

Class: Archiacanthocephala (proboscis hooks in concentric circular rows, trunk lacking spines)				
Oligacanthorhynchida	terrestrial	birds, mammals	insects	subspherical proboscis
Gigantorhynchida	terrestrial	birds, mammals	insects, millipedes, crustaceans	conical proboscis, truncated, bipartite
Moniliformida	terrestrial	birds, mammals	insects	cylindrical proboscis
Apororhynchida	terrestrial	birds	unknown	globular proboscis
Class: Palaeacanthocephala (proboscis hooks in alternating longitudinal rows, trunk with or without spines)				
Echinorhynchida	aquatic	fish, amphibians, reptiles	crustaceans	variable proboscis (globular, cylindrical, claviform)
Polymorphida	aquatic, terrestrial	birds, mammals, amphibians, reptiles	crustaceans	variable proboscis (bulbous, spherical, oval, cylindrical)
Heteramorphida	aquatic, terrestrial	shore birds	unknown	spindle-shaped proboscis
Class: Eoacanthocephala (proboscis hooks in radial rows, trunk with or without spines)				
Gyracanthocephala	aquatic	fish	crustaceans	small spheroid proboscis
Neoechinorhynchida	aquatic	fish, amphibians, reptiles	crustaceans	variable proboscis (globular-cylindrical)
Class: Polyacanthocephala (proboscis hooks in longitudinal rows, trunk with spines)				
Polactorhynchida	aquatic	fish, crocodiles	crustaceans	long claviform proboscis

The class Archiacanthocephala contains 4 orders of terrestrial acanthocephalans whose body walls contain dorsal (and sometimes ventral) lacunar canals, usually 8 uninucleate cement glands, few elongated or branched subcuticular (tegumental) nuclei, and with ligament sacs inside the pseudocoel. Worms in the order Oligacanthorhynchida possess a subspherical proboscis with short rows of several hooks and they have protonephridial organs. The order contains a single family Oligacanthorhynchidae with 13 genera (*Oncicola, Cucullanorhynchus, Echinopardalis, Heptamegacanthus, Macracanthorhynchus, Multisentis, Neoncicola, Nephridiacanthus, Oligacanthorhynchus, Pachysentis, Paraprosthenorchis, Prosthenorchis, Tchadorhynchus*). The genus *Oncicola* contain over 20 species parasitizing domestic and wild animals which become infected by consuming larval stages in intermediate hosts (insects, particularly beetles) or sometimes small vertebrate paratenic hosts (birds, amphibians, lizards).

***Oncicola* species**	**Definitive hosts [adults in intestines]**	**Intermediate hosts, IH; (larval acanthellae then cystacanths in tissues) [plus paratenic hosts, PH]**	**Distribution**
O. angolense	Carnivora: canid (jackal)		Africa
O. atrata	Carnivora: herpestid (Egyptian mongoose), felid (cat), canid (fox)		Middle East
O. bursata	Carnivora: felid (Asian golden cat)		Indonesia
O. campanulata (syn. *Echinorhynchus, E. ovatus)*)	Carnivora: felid (ocelot, Geoffroy's cat, jaguar, puma, tiger cat), mustelid (honey badger)		Americas, Asia
O. canis (syn. *Echinorhynchus*) (canine thorny-headed worm)	Carnivora: canid (dog, coyote, red fox, side-striped jackal), felid (cat, bobcat, ocelot)	Coleoptera: scarabaeid (dung beetles); [plus PHs Cingulata: dasypodid (nine-banded armadillo), Galliformes: phasianid (turkey)]	Americas
O. chibigouzouensis	Carnivora: felid (ocelot)		Brazil
O. decrescens	Carnivora: felid (margay)		Americas
O. dimorpha	Carnivora: felid (leopard)		Asia
O. fraterna	Carnivora: felid (leopard)		Asia
O. gigas	Carnivora: felid (black panther, leopard)		Asia
O. macrurae	Carnivora: felid (margay, bobcat), mephitid (eastern spotted skunk)		North America
O. malayana	Carnivora: felid (panther)		Indochina
O. martini	Carnivora: felid (Geoffroy's cat)		Paraguay
O. magalhaesi	Carnivora: felid (puma)		Brazil
O. michaelseni	Carnivora: felid (leopard)		Asia
O. micracantha	Carnivora: mephitid (Molina's hog-nosed skunk)		Brazil
O. paracampanulata	Carnivora: felid (jaguarundi)		Brazil

O. pardalis	Carnivora: felid (cat, ocelot, cougar, Geoffroy's cat, jaguar, tiger cat), mustelid (honey badger)		Americas, Asia
O. pomatostomi (syn. *Echinorhynchus*, *Oligacanthorhynchus*)	Carnivora: felid (cat), canid (fox, dingo)	arthropod IH: [plus PHs: Passeriformes: acanthizid (southern whiteface, chestnut-rumped heathwren, redthroat, spotted scrubwren), climacterid (white-throated treecreeper, brown treecreeper), cinclosomatid (cinnamon quail-thrush, chestnut quail-thrush), pachycephalid (Gilbert's whistler), pomatostomid (chestnut-crowned babbler, white-browed babbler, grey-crowned babbler, red-breasted babbler); Galliformes: phasianid (king quail); Gruiformes: rallid (buff-banded rail); Charadriiformes: pedionomid (plains-wanderer)]	Australia, Philippines, Borneo, Malaya
O. schacheri	Carnivora: canid (fox), mustelid (badger)		Europe
O. skrjabini	Carnivora: canid (wolf)		Asia
O. travassosi	Carnivora: felid (cat)		Middle East
O. venezuelensis	Carnivora: felid (ocelot)		Venezuela
Reassigned species			
O. confusa (now *Prosthenorchis*)	Primates: cebid (capuchin monkey)		Brazil
O. freitasi (now *Prosthenorchis*)	Primates: cebid (capuchin monkey)		Brazil
O. juxtatesticularis (now *Prosthenorchis*)	Primates: callitrichid (white-headed marmoset)		Brazil
O. luehei (now *Prosthenorchis*)	Carnivora: procyonid (ring-tailed coati); Didelphimorphia: didelphid (American opossum)		South and Central America
O. machadoi (now *Prosthenorchis*)	Primates: cebid (tufted capuchin)		Brazil
O. oncicola (now *Prosthenorchis*)	Carnivora: felid (jaguar, jaguarundi, margay, Geoffroy's cat)	arthropod IH: [plus PHs: Galliformes: phasianid (chicken), odontophorid (bobwhite quail); Columbiformes: columbid (white-tipped dove); Cingulata: chlamyphorid (armadillo)]	Americas
O. sigmoides (now *Prosthenorchis*)	Carnivora: mustelid (grison); Primates: callitrichid (common marmoset, lion tamarin, black tamarin), cebid (squirrel monkey)		South America
O. spirula (now *Prosthenorchis*)	Primates: cebid (tufted capuchin, squirrel monkey), callitrichid (golden lion tamarin)	Blattodea: blaberid (South American cockroach, Madeira cockroach), ectobiid (German cockroach), blattid (Oriental cockroach)	South America

Parasite morphology: Acanthocephalan worms form three different developmental stages: eggs; larvae (acanthor, acanthella, cystacanth) and adults. The eggs are oval in shape, measuring 60-75 x 40-50 μm, brown in colour, thick-shelled and embryonated.

Eggs hatch in intermediate hosts to release the first larval stage (acanthor) which is membrane-bound and spindle-shaped with an anterior spined invagination (aclid organ). Acanthors moult to form second stage larvae (acanthellae) which are the main growing developmental stages that ultimately form encysted infective stages (cystacanths). These stages come to resemble miniature adult worms which contain all tissues and structures except mature reproductive organs. Adult worms are white-grey in colour, elongate measuring from 1-5 cm long, the body tapering posteriorly and possessing a subspherical anterior proboscis armed with 12 longitudinal rows of 3 hooks. In larval stages, the proboscis is invaginated (retracted) within the body (in a proboscis receptacle) while in adults, it is everted and used to attach to host tissues. Worms do not possess a digestive tract and nutrients are taken up through the body wall. Mature worms are dioecious, with females being slightly larger than males. Mature males have two testes lying on either side of the genital ligament, each with a vas deferens bearing diverticula, cement glands and an ejaculatory duct terminating in a copulatory bursa. During copulation, sperm ejected into the vagina escape into the pseudocoelom via the genital duct and the male then plugs the vagina using the cement glands to prevent further copulation. Ovaries dehisce (break down) in cystacanth or adult female stages to form ovarian balls that float freely in the body cavity. Fertilized eggs are brought to the uterus through a unique funnel-shaped uterine bell while immature eggs are returned to the body cavity for further maturation.

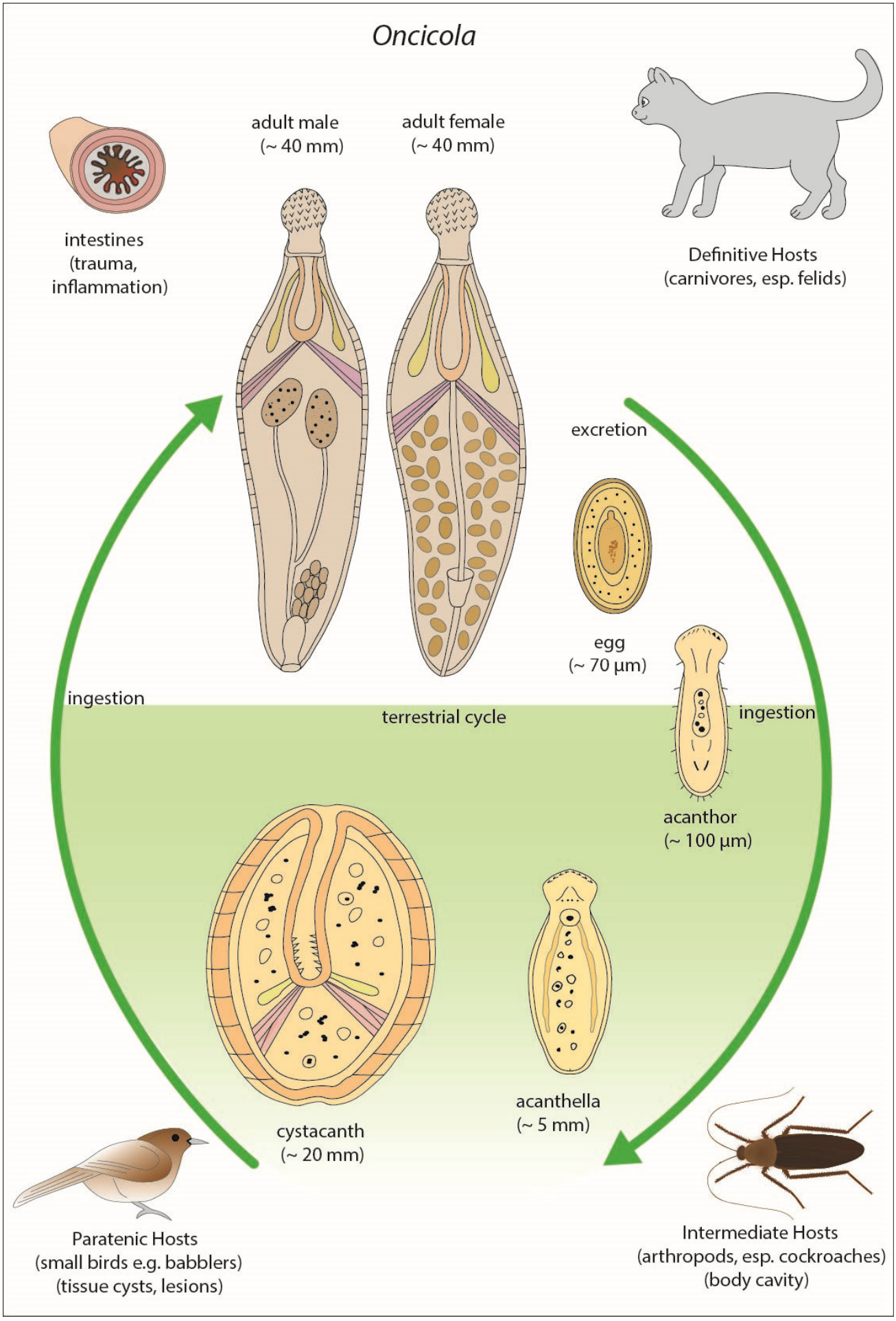
Site of infection: Adult *Oncicola* spp. infect the small intestines of their definitive hosts (carnivores and primates) while larval stages (acanthellae and cystacanths) occur in the body cavity of their intermediate hosts (beetles and cockroaches) and the internal tissues (esp. subcutis) of their paratenic hosts (mostly birds).

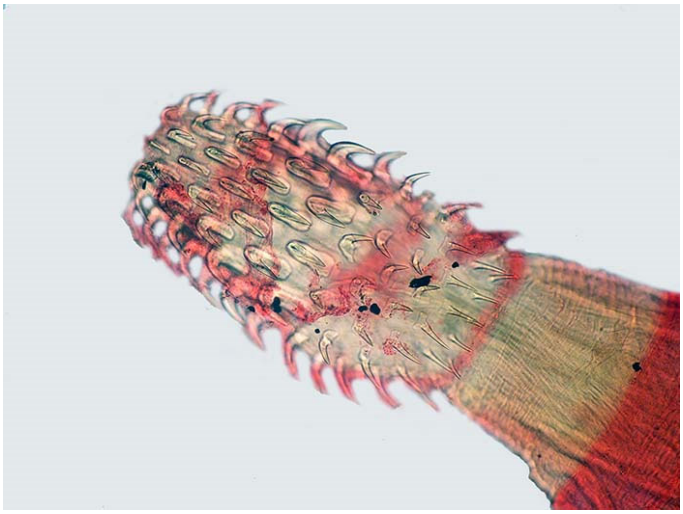
Pathogenesis: Adult worms absorb nutrients through their body walls and do not feed on host tissues. However, they embed their armed proboscis in the intestinal mucosa causing trauma, focal lesions and inflammation. Nevertheless, few clinical signs have been associated with infections, except for occasional peritonitis when the parasite proboscis penetrates through to the peritoneum. Concomitant infections with other gut parasites have been shown to contribute to enteric signs including diarrhoea, anorexia and weight loss.

Developmental cycle and mode of transmission: Although the life-cycles of most *Oncicola* spp. are not known, studies on several species have shown them to have indirect life-cycles involving cyclic transmission between vertebrate definitive hosts (infected by adult stages), arthropod intermediate hosts and avian paratenic hosts (harbouring larval cystacanths). Mature female worms lay eggs which are passed in the faeces of the definitive hosts (carnivores and primates). The eggs are ingested by intermediate hosts (arthropods including beetles and cockroaches) wherein they hatch releasing the enclosed acanthor stages. These larvae penetrate to the body cavity (haemocoel) and form the main growing stages (acanthellae) before becoming infective as cystacanths after 6-12 weeks. When infected arthropods are ingested by definitive hosts, the cystacanths evert their proboscis, attach to the gut wall and mature into adult worms over several months. If the arthropods are ingested by paratenic (non-definitive) hosts, the cystacanths may migrate through host tissues, re-encyst and await ingestion by carnivorous definitive hosts. Several *Oncicola* spp. have been found to use wide range of birds as paratenic hosts, especially Passeriformes. Mature female worms can be highly fecund producing thousands of eggs per day but they are thought to only live for several months.

Differential diagnosis: Patent infections may be detected by coprological examination of faecal sediments for characteristic acanthocephalan eggs which are relatively heavy and do not float well except in high specific gravity salt or sugar solutions. Most infections, however, have been detected incidentally during post-mortem examination of definitive hosts (adults found in gut samples) or paratenic hosts (cystacanths found in bird tissues).

Treatment and control: Infections in carnivores (mostly dogs and cats) have been successfully treated with fenbendazole, ivermectin, doramectin or selamectin, while infections in captive primates (tamarins) responded well to treatment with albendazole. It is important to identify infected animals to institute appropriate quarantine and hygienic measures so that contact with intermediate and paratenic hosts can be reduced.


Oncicola
adult male
(~ 40 mm)
adult female
(~ 40 mm)
intestines
(trauma,
inflammation)
Definitive Hosts
(carnivores, esp. felids)
excretion
egg
(~ 70 µm)
ingestion
terrestrial cycle
ingestion
acanthor
(~ 100 µm)
cystacanth
(~ 20 mm)
acanthella
(~ 5 mm)
Paratenic Hosts
(small birds e.g. babblers)
(tissue cysts, lesions)
Intermediate Hosts
(arthropods, esp. cockroaches)
(body cavity)



Oncicola proboscis

Polymorphus
(acanthocephalan)

Overview

Acanthocephalans have pseudocoelomate unsegmented tubular bodies and are commonly called thorny-headed worms due to the possession of a retractable anterior proboscis armed with rows of hooks for attachment. They undergo protostomial embryonic development but do not moult during growth. They are classified within the Lophotrochozoa but do not have jawed mouthparts or digestive tracts, instead they absorb nutrients through their eutelic syncytial cuticles. All species are parasites in the intestinal tracts of vertebrates and they have indirect life-cycles, involving aquatic or terrestrial arthropods as intermediate hosts. Female worms produce mature eggs that float freely in the body cavity and are passed through a unique uterine bell into the uterus to be voided with host faeces. The eggs have thick shells comprised of 4-5 membranes and contain a larval stage (acanthor) armed with hooks and spines which is infective to an invertebrate intermediate host. When ingested by arthropods, the acanthor migrates to the haemocoel and develops into an acanthella which matures into an infective cystacanth. When the arthropod is ingested by the vertebrate host, the cystacanth attaches and matures in the intestinal tract. Infections by *Polymorphus* spp. are transmitted by freshwater crustaceans to aquatic birds and have been associated with enteric disease.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Clade:	Syndermata (eutelic syncytial epidermis)
Phylum:	Acanthocephala (thorny-headed worms, pseudocoelomate, retractable proboscis with hooks, indirect cycles, eggs with acanthor, acanthella develops in arthropod IH (or PH))
Class:	Palaeacanthocephala (elongate eggs, sometimes with polar thickenings, body wall lacunar canals lateral)
Order:	Polymorphida (trunk may show pseudosegmentation, proboscis swollen/bulbous/cylindrical, with numerous hooks in alternating rows)
Family:	Polymorphidae (marked sexual dimorphism, spinose trunk, proboscis bulbous)
Genus:	*Polymorphus* (parasitic in small intestines of birds and mammals)
Species:	various species cause enteritis in ducks

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. In addition to the parasitic flatworms (platyhelminths), other metazoan worm-like groups live as endoparasites in vertebrate hosts. Acanthocephalans have pseudocoelomate unsegmented round-flattened bodies and are commonly called thorny-headed or spiny-headed worms due to the possession of an anterior spherical-cylindrical invaginable proboscis bearing rows of recurved hooks used for attachment. They undergo protostomial embryonic development but do not moult during growth, thus belonging to the Lophotrochozoa (embryos with spiral mosaic cleavage) rather than the Ecdysozoa. On the basis of molecular evidence, they are classified within the clade Gnathifera even though they do not have complex cuticular jaws. They lack digestive tracts and absorb nutrients across their eutelic (constant number of nuclei) syncytial (multinucleate) epidermis, and have been grouped together with the Rotifera into the clade Syndermata.

Over 1,400 species of acanthocephalans have been described worldwide as endoparasites with adult stages living in the intestinal tracts of a wide range of fish, amphibians, reptiles, birds and mammals. They have indirect life-cycles with arthropods always acting as intermediate hosts for larval stages. Female worms pass thick-shelled eggs containing an acanthor armed with hooks and spines. When ingested by aquatic crustaceans or terrestrial insects, the acanthor migrates to the haemocoel and forms an acanthella which matures into an infective cystacanth. When the arthropod is ingested by the vertebrate host, the cystacanth attaches and matures into an adult in the intestinal tract. Within the phylum Acanthocephala, four classes are recognized: Archiacanthocephala with terrestrial cycles involving mammals/birds and insects; Palaeacanthocephala with aquatic cycles in fish/birds/seals and crustaceans; Eoacanthocephala with aquatic cycles in fish/amphibia/reptiles and crustaceans; and Polyacanthocephala with aquatic cycles in fish/crocodiles and crustaceans.

Order	Environment	Definitive hosts	Intermediate hosts	Characters
Class: Archiacanthocephala (proboscis hooks in concentric circular rows, trunk lacking spines)				
Oligacanthorhynchida	terrestrial	birds, mammals	insects	subspherical proboscis
Gigantorhynchida	terrestrial	birds, mammals	insects, millipedes, crustaceans	conical proboscis, truncated, bipartite
Moniliformida	terrestrial	birds, mammals	insects	cylindrical proboscis
Apororhynchida	terrestrial	birds	unknown	globular proboscis
Class: Palaeacanthocephala (proboscis hooks in alternating longitudinal rows, trunk with or without spines)				
Echinorhynchida	aquatic	fish, amphibians, reptiles	crustaceans	variable proboscis (globular, cylindrical, claviform)
Polymorphida	aquatic, terrestrial	birds, mammals, amphibians, reptiles	crustaceans	variable proboscis (bulbous, spherical, oval, cylindrical)
Heteramorphida	aquatic, terrestrial	shore birds	unknown	spindle-shaped proboscis
Class: Eoacanthocephala (proboscis hooks in radial rows, trunk with or without spines)				
Gyracanthocephala	aquatic	fish	crustaceans	small spheroid proboscis
Neoechinorhynchida	aquatic	fish, amphibians, reptiles	crustaceans	variable proboscis (globular-cylindrical)
Class: Polyacanthocephala (proboscis hooks in longitudinal rows, trunk with spines)				
Polactorhynchida	aquatic	fish, crocodiles	crustaceans	long claviform proboscis

The largest and most diversified class Palaeacanthocephala contains 2 orders of aquatic acanthocephalans whose body walls contain lateral lacunar canals, 2-8 multinucleate cement glands, numerous tegumental nuclei, the ligament sacs break down in reproductive females and they lack protonephridia. Worms in the order Polymorphida have a wrinkled trunk and a bulbous-cylindrical proboscis with numerous hooks in alternating rows. The order contains 3 families (Centrorhynchidae, Plagiorhynchidae, Polymorphidae) which infect all classes of vertebrates. The family Polymorphidae contains worms with a spinose trunk and usually a bulbous proboscis bulbous and a distinct neck. The family contains 15 genera (*Andracantha*, *Ardeirhynchus, Arhythmorhynchus*, *Bolbosoma*, *Corynosoma*, *Diplospinifer*, *Filicollis*, *Hexaglandula*, *Ibirhynchus, Neoandracantha, Polymorphus*, *Profilicollis* (syn. *Falsifilicollis, Parafilicollis*), *Pseudocorynosoma, Southwellina*, *Tenuisoma*). The genus *Polymorphus* contains around 30 species parasitizing domestic and wild birds and mammals which become infected by consuming larval stages in intermediate hosts (aquatic crustaceans, especially amphipods). Another 10 species formerly classified within the genus have recently been transferred to the genus *Profilicollis* based on morphological and molecular differences and the use of decapod crustaceans as intermediate hosts. The genera are cosmopolitan in distribution, and several species cause significant problems in farmed waterfowl (ducks and geese).

Polymorphid species	Definitive hosts, DH (adults in gut)	Intermediate hosts, IH (larval acanthellae then cystacanths in tissues) [plus paratenic hosts, PH]	Distribution
Polymorphus (when known, IHs are amphipods)			
P. actuganensis	Anseriformes: anatid (puddle ducks)	Amphipoda: gammarid (*Gammarus bergi, G. lacustris*)	Russia
P. acutis	Anseriformes: anatid (duck); Podicipediformes: podicipedid (grebe); Charadriiformes: larid (gull), scolopacid (godwit); Gruiformes: rallid (coot)		North America, Russia
P. ariusis (syn. *Hexaglandula*)	Suliformes: bagrid (catfish)		India
P. boschadis (syn. *P. magnus, P. minutus, Echinorhynchus minutus, E. anatis, E. collaris*)	Anseriformes: anatid (duck, mallard, white-winged scoter, swan, mute swan, merganser, goose); Podicipediformes: podicipedid (grebe); Galliformes: phasianid (chicken); Gruiformes: rallid (moorhen, rail, coot); Accipitriformes: accipitrid (eagle); Charadriiformes: larid (gull, tern), alcid (murre, guillemot, dovekie); Procellariiformes: procellariid (fulmar); Passeriformes: corvid (rook, crow), troglodytid (wren), turdid (thrush), sturnid (starling), motacillid (white	Amphipoda: gammarid (*Gammarus bergi, G. pulex, G. duebeni, G. fassarum, G. lacustris, G. limnaeus, G. maeoticus, G. pulex, G. wilkitzkii*), carinogammarid (*Carinogammarus roeselii*); Decapoda: cambarid (*Cambarus affinis*); astacid (*Potamobius astacus*) [plus PH: Anguilliformes:	worldwide

	wagtail)	anguillid (eel); Atheriniformes: atherinid (silverside); Gobiiformes: gobiid (goby); Pleuronectiformes: pleuronectid (plaice); Scorpaeniformes: cyclopterid (lumpfish); Trachiniformes: trachinid (weever)	
P. brevis (syn. *Arhythmorhynchus*)	Accipitriformes: pandionid (osprey); Pelecaniformes: ardeid (bittern, great blue heron, black-crowned night heron)		North America
P. cetaceum (syn. *P. arctocephali*)	Artiodactyla: delphinid (short-beaked common dolphin, common bottlenose dolphin), pontoporiid (La Plata dolphin); Carnivora: otariid (brown fur seal)		Australasia, South America
P. chongqingensis	Anseriformes: anatid (duck)		China
P. cincli	Passeriformes: cinclid (dipper)		Russia
P. contortus (syn. *Echinorhynchus collurionis*)	Anseriformes: anatid (ducks); Pelecaniformes: ardeid (bittern); Passeriformes: laniid (shrike)	Amphipoda: gammarid (*Gammarus lacustris*), hyalellid (*Hyalella azteca*)	Europe
P. corynoides (syn. *Subcorynosoma*)	Anseriformes: anatid (mallard)		Asia
P. corynosoma (*caryosoma* misspelling) (syn. *Hexaglandula*)	Pelecaniformes: ardeid (heron)		South America
P. crassus	Ciconiiformes: ciconiid (wood ibis)		Nearctic
P. cucullatus	Anseriformes: anatid (hooded merganser)		North America
P. diploinflatus	Anseriformes: anatid (ducks)		Europe, Russia
P. fatimaae	Passeriformes: corvid (house crow)		India
P. fulicai	Gruiformes: rallid (black coot)		India
P. gavii (syn. *Subfilicollis*)	Gaviiformes: gaviid (black-throated loon, common loon)		Russia
P. inermis (syn. *Hexaglandula*)	Pelecaniformes: ardeid (heron)		South America
P. karachiensis (syn. *Hexaglandula*)	Suliformes: bagrid (catfish)		India
P. kostylewi	Anseriformes: anatid (velvet scoter)		Russia
P. marchii (syn. *Corynosoma*)	Anseriformes: anatid (ducks); Gruiformes: rallid (water rail)		Europe, Russia
P. marilis	Anseriformes: anatid (white-winged scoter, lesser scaup); Suliformes: phalacrocoracid (cormorant); Charadriiformes: scolopacid (sandpiper)	Amphipoda: gammarid (*Gammarus lacustris*)	Nearctic
P. mathevossianae	Anseriformes: anatid (ducks)		Russia
P. meyeri	Anseriformes: anatid (tufted duck, mallard)		Europe
P. miniatus (syn. *Echinorhynchus*)	Anseriformes: anatid (duck)		South America
P. mohiuddini	Strigiformes: strigid (brown wood owl)		India
P. mutabilis (syn. *Hexaglandula*)	Pelecaniformes: ardeid (heron, egret), threskiornithid (roseate spoonbill); Coraciiformes: alcedinid (kingfisher); Charadriiformes: larid (tern); Suliformes: phalacrocoracid (cormorant); Gruiformes: aramid (limpkin)		North America, Europe
P. nickoli	Passeriformes: corvid (house crow)		Pakistan
P. obtusus	Suliformes: anhingid (water turkey); Pelecaniformes: arceid (heron); Anseriformes: anatid (duck, merganser)		North America
P. paradoxus	Rodentia: castorid (beaver), cricetid (muskrat)	Amphipoda: gammarid (*Gammarus lacustris*)	North America

P. pauchihamata (syn. *Hexaglandula*)	Charadriiformes: larid (Iceland gull)		Iceland
P. phippsi (syn. *Echinorhynchus borealis, E. mollissimae, Subfilicollis phippsi*))	Anseriformes: anatid (ducks, eider); Podicipediformes: podicipedid (grebe)		Russia
P. piriformis (syn. *Echinorhynchus*)	Passeriformes: turdid (common blackbird)		Europe
P. pupa sp. inq.	Anseriformes: anatid (eider)		Russia
P. sichuanensis	Anseriformes: anatid (duck)		China
P. sindensis	Passeriformes: corvid (house crow)		Pakistan
P. spindulatus	Pelecaniformes: ardeid (black-crowned night heron)		Peru
P. striatus (syn. *Echinorhynchus striatus, E. ardeae*)	Anseriformes: anatid (duck, merganser, swan); Pelecaniformes: ardeid (heron, egret, bittern); Accipitriformes: accipitrid (eagle)		Eurasia
P. strumosoides (syn. *Subcorynosoma*)	Anseriformes: anatid (goldeneye)	Amphipoda: gammarid (*Gammarus pulex*)	Russia
P. swartzi	Anseriformes: anatid (Barrow's goldeneye)		Alaska
P. trochus	Gruiformes: rallid (American coot), Anseriformes: anatid (mallard)	Amphipoda: hyalellid (*Hyalella azteca*)	Nearctic
Profilicollis (IHs are decapod crustaceans)			
Pr. altmani (syn. *Pr. bullocki, kenti, texensis*)	Anseriformes: anatid (eider, scoters, surf scoter, lesser scaup); Charadriiformes: larid (European herring gull, brown-hooded gull, Franklin's gull, grey gull, kelp gull), scolopacid (sanderling, dunlin, whimbrel, willet), alcid (rhinoceros auklet); Rodentia: murid (rats)	Decapoda: hippid (Pacific sand crab, mole crab) [plus PH: Carnivora: mustelid (southern sea otter)]	Americas
Pr. antarcticus	Charadriiformes: chionid (sheathbill), larid (kelp gull)	Decapoda: varunid (hairy-handed crab)	South America, Shetlands, New Zealand
Pr. arcticus	Anseriformes: anatid (eider)		Canada, Russia
Pr. biziurae	Anseriformes: anatid (musk duck)	Decapoda: parastacid (yabby)	Australia
Pr. botulus	Anseriformes: anatid (eider, common goldeneye, Barrow's goldeneye, greater scaup, oldsquaw, seaduck, long-tailed duck)	Decapoda: nephropid (American lobster), portunid (green crab), oregoniid (great spider crab), pagurid (Northern Atlantic hairy hermit crab), varunid (green shore crab)	North America, Eurasia
Pr. chasmagnathi (syn. *Falsifilicollis*)	Gruiformes: rallid (coot); Podicipediformes: podicipedid (grebe); Pelecaniformes: threskiornithid (ibis); Charadriiformes: larid (Olrog's gull), recurvirostrid (white-backed stilt); Rodentia: caviid (guinea pig)	Decapoda: varunid (estuarine crabs)	South America
Pr. formosus	Anseriformes: anatid (duck)	Decapoda: palaemonid (freshwater shrimp)	Taiwan
Pr. major	Anseriformes: anatid (sea ducks, bay ducks)	Decapoda: cancrid (Atlantic rock crab) [plus PH: Carnivora: mustelid (southern sea otter)]	North America
Pr. novaezelandensis	Charadriiformes: haematopodid (South Island pied oystercatcher), scolopacid (bar-tailed godwit)	Decapoda: varunid (hairy-handed crab, tunnelling mud crab), macrophthalmid (stalk-eyed mud crab)	New Zealand
Pr. sphaerocephalus	Charadriiformes: larid (kelp gull, silver gull), haematopodid (oystercatcher);	Decapoda: grapsid (little shore crab, purple mottled shore	Australia, South America

	Pelecaniformes: ardeid (yellow-crowned night heron), threskiornithid (scarlet ibis); Gruiformes: rallid (wood rails)	crab, red-spotted shore crab, mottled shore crab, four-toothed shore crab), portunid (red swimmer crab)	

Parasite morphology: Acanthocephalan worms form three different developmental stages: eggs, larvae (acanthor, acanthella, cystacanth) and adults. The eggs are yellow-brown in colour and elongate spindle-shaped (measuring 100-120 x 12-19 µm) with thick polar prolongations of the middle eggshell membrane. Upon hatching in the intermediate host, the eggs release the first larval stage (acanthor) which is spindle-shaped with anterior hooks. These stages form second stage larvae (acanthellae) which are the main growing stages that increase in size before becoming encysted as resting infective stages (cystacanths). These stages slowly come to resemble small immature adult stages that have not yet developed reproductive organs. Cystacanths possess an armed proboscis that is retracted (inverted) within a proboscis receptacle while adult worms evert the proboscis anteriorly to attach to definitive host tissues. Adults are cream-orange in colour, elongate and cylindrical in shape, measuring up to 3 cm in length and 1-2 mm in width. The trunk usually has a midline constriction and the anterior body wall bears numerous spines. The cylindrical proboscis is highly conspicuous and armed with up to 20 longitudinal rows of 7-10 backward-facing hooks (the numbers of rows and hooks differing between species). They lack an alimentary system and nutrients are taken up through the syncytial tegument. Mature adult worms are dioecious and females are larger (> 2x) than males. Males have 2 testes diagonally arranged in the center of the trunk and several long tubular glands which produce cement to plug the vagina of females after copulation. Females have ovaries which dehisce (break down) to produce ovarian balls and eggs free-floating in the body cavity, and a unique apparatus known as the uterine bell which acts as a sorting device allowing mature fertilized eggs to pass through to the uterus while immature eggs are returned for further maturation. The genera *Polymorphus* and *Profilicollis* (formerly subgenera) are distinguished primarily by the shape of the proboscis (cylindrical with bulbous expansion in *Polymorphus* cf. fully ovoid in *Profilicollis*), length of the neck (long in *Profilicollis*) and whether the fibrillar coat of the egg possesses polar swellings (present in *Polymorphus*).

Site of infection: Adult worms infect the small intestines of their vertebrate definitive hosts (mainly birds) while larval stages occur in the body cavities of their crustacean intermediate hosts (amphipods, decapods).

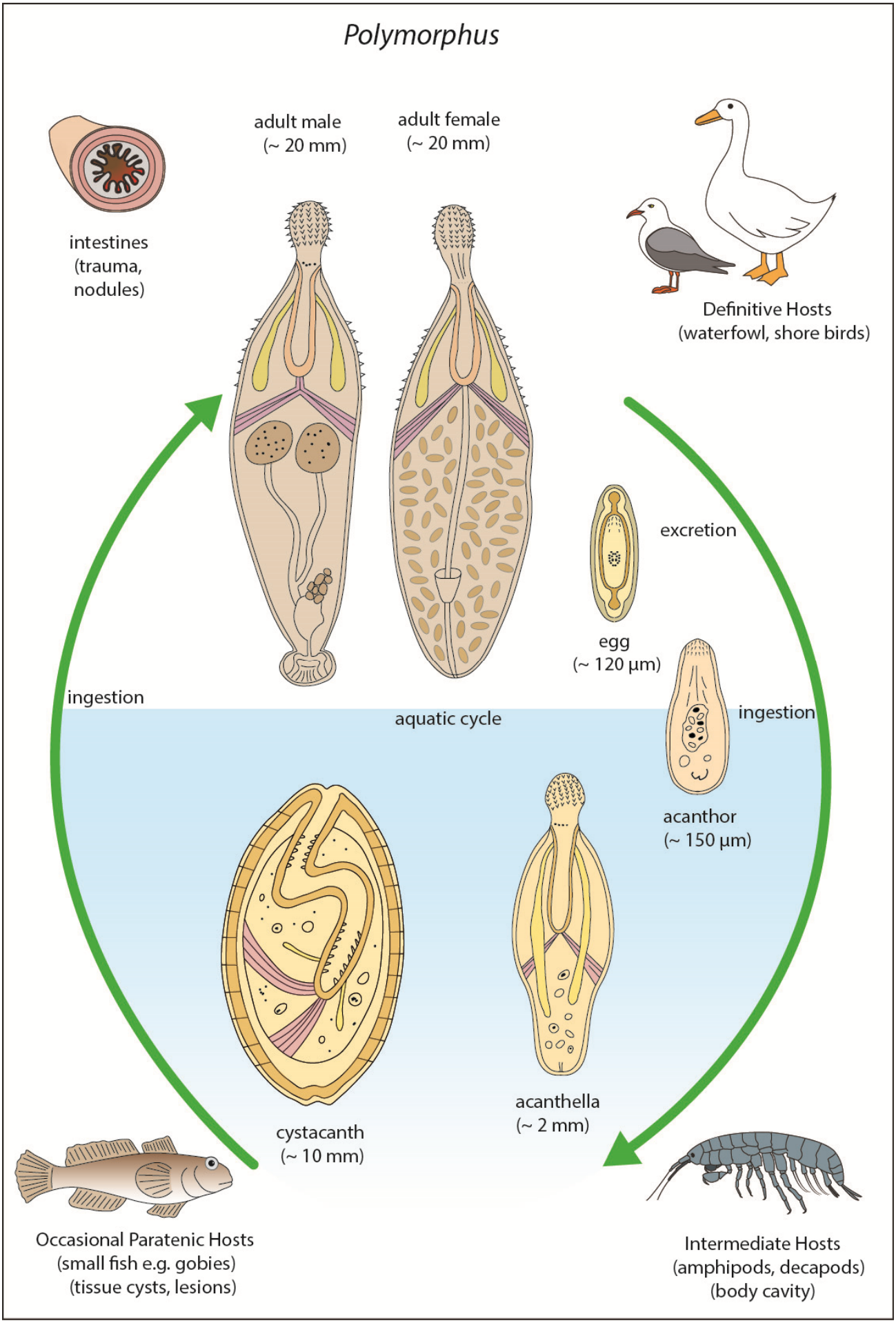
Pathogenesis: Acanthocephalans do not feed on host tissues but adults damage the gut when they attach by inserting their armed proboscis deeply into the intestinal wall, often reaching to the muscularis interna and sometimes perforating the wall. Sites of attachment become inflamed and fibrous connective tissue forms small nodules 2-3 mm in diameter. There are often more nodules than worms as juveniles move between sites and are often found free in the lumen. After mating, females attach permanently and begin egg laying while males pass out of the gut. Most infections are light and subclinical, but heavy infections may cause severe enteritis and even peritonitis contributing to death. Heavy infections have commonly been recorded in shorebirds and waterfowl exhibiting weakness, emaciation and stunting. Episodic clinical infections also appear to occur in sea otters as accidental or paratenic hosts, with significant intestinal inflammation and peritonitis observed in carcasses washed up on North American coasts.

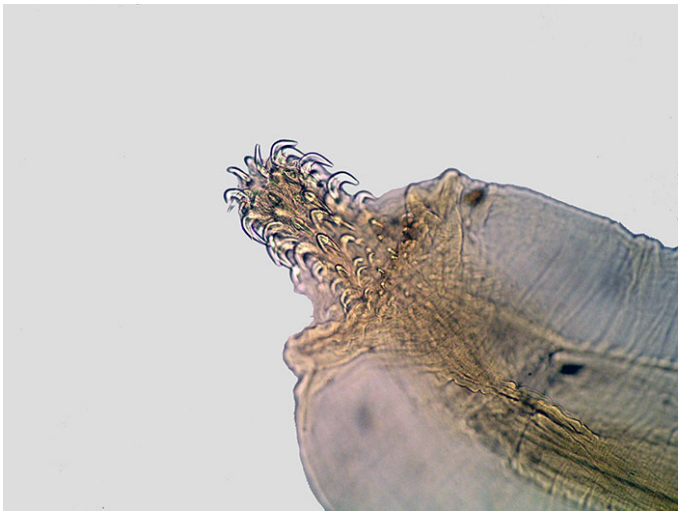
Developmental cycle and mode of transmission: Polymorphid acanthocephalans have indirect life-cycles involving cyclic transmission between definitive hosts (birds infected with adult worms) and aquatic crustaceans as intermediate hosts (mostly amphipods for *Polymorphus* spp. and decapods for *Profilicollis* spp.). Female worms lay eggs which are voided with host faeces. When ingested by crustacean hosts, the eggs hatch releasing larval acanthors which penetrate to the body cavity and grow through an acanthella stage into infective cystacanths over a period of weeks. Some infections in amphipods have also been associated with altered host behaviour, making them more prone to predation by being attracted to light, swimming to the surface and even latching onto aquatic vegetation. When infected crustaceans are eaten by avian definitive hosts, the cystacanths evert their proboscis, attach to the gut wall and grow into sexually mature adults. Following mating, female worms produce numerous embryonated eggs over a period of months thus completing the life-cycle. The duration of the entire cycle is variable as eggs may remain viable for several months in water at 10-17°C, acanthors may take up to 2 weeks to establish, acanthellae grow over 6-8 weeks, cystacanths may remain viable for several months, and adults take up to 3-4 weeks to mature and produce eggs. Epidemiological studies suggest seasonal patterns to infection (with summer peaks), often associated with host behaviour as many waterfowl spend less time on water as they age.

Differential diagnosis: Infections by most polymorphid worms can be diagnosed by coprological examination of bird droppings for characteristic eggs, although egg shedding by some species (e.g. *P. minutus*) can be sporadic generating false negative results. Infections may also be detected at postmortem by finding incriminating nodules and adult worms in gut samples.

Treatment and control: No satisfactory treatment for polymorphid acanthocephalans of waterfowl or shorebirds has been established although some partial successes have been reported using niclosamide, carbon tetrachloride, fenbendazole and loperamide. Some success in reducing worm populations in domesticated stock has also been reported by with-holding food and

starving infected birds for several days. Prevention by controlling intermediate host populations is difficult as amphipod and decapod crustaceans are ubiquitous in aquatic environments.


Polymorphus
adult male
(~ 20 mm)
adult female
(~ 20 mm)
intestines
(trauma,
nodules)
Definitive Hosts
(waterfowl, shore birds)
excretion
egg
(~ 120 µm)
ingestion
aquatic cycle
ingestion
acanthor
(~ 150 µm)
cystacanth
(~ 10 mm)
acanthella
(~ 2 mm)
Occasional Paratenic Hosts
(small fish e.g. gobies)
(tissue cysts, lesions)
Intermediate Hosts
(amphipods, decapods)
(body cavity)

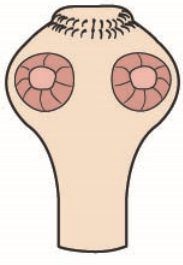


Polymorphus proboscis

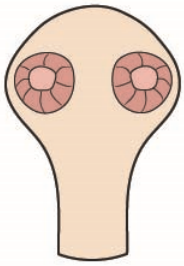
Cestoda
(tapeworms)

Cestode scolices

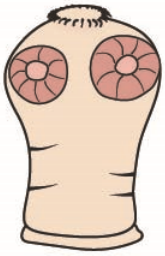
Cyclophyllidea



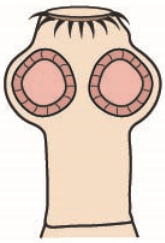
Taenia solium



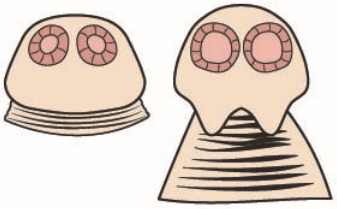
Taenia saginata



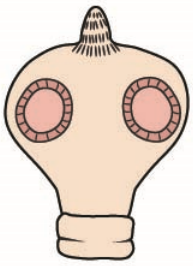
Taenia multiceps



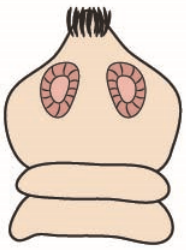
Echinococcus



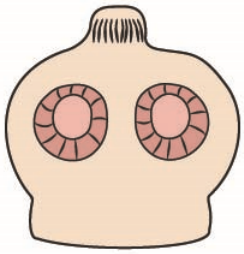
Anoplocephala



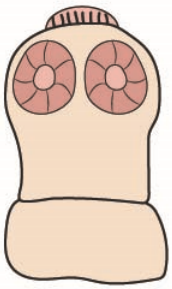
Dipylidium



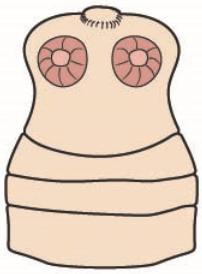
Amoebotaenia



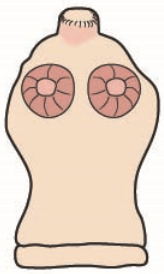
Choanotaenia



Davainea



Raillietina

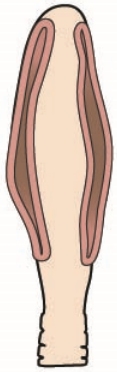


Hymenolepis

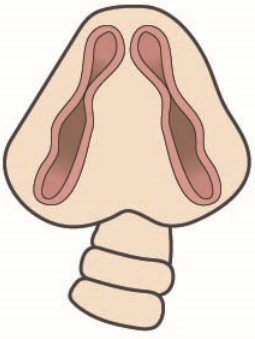
Pseudophyllidea



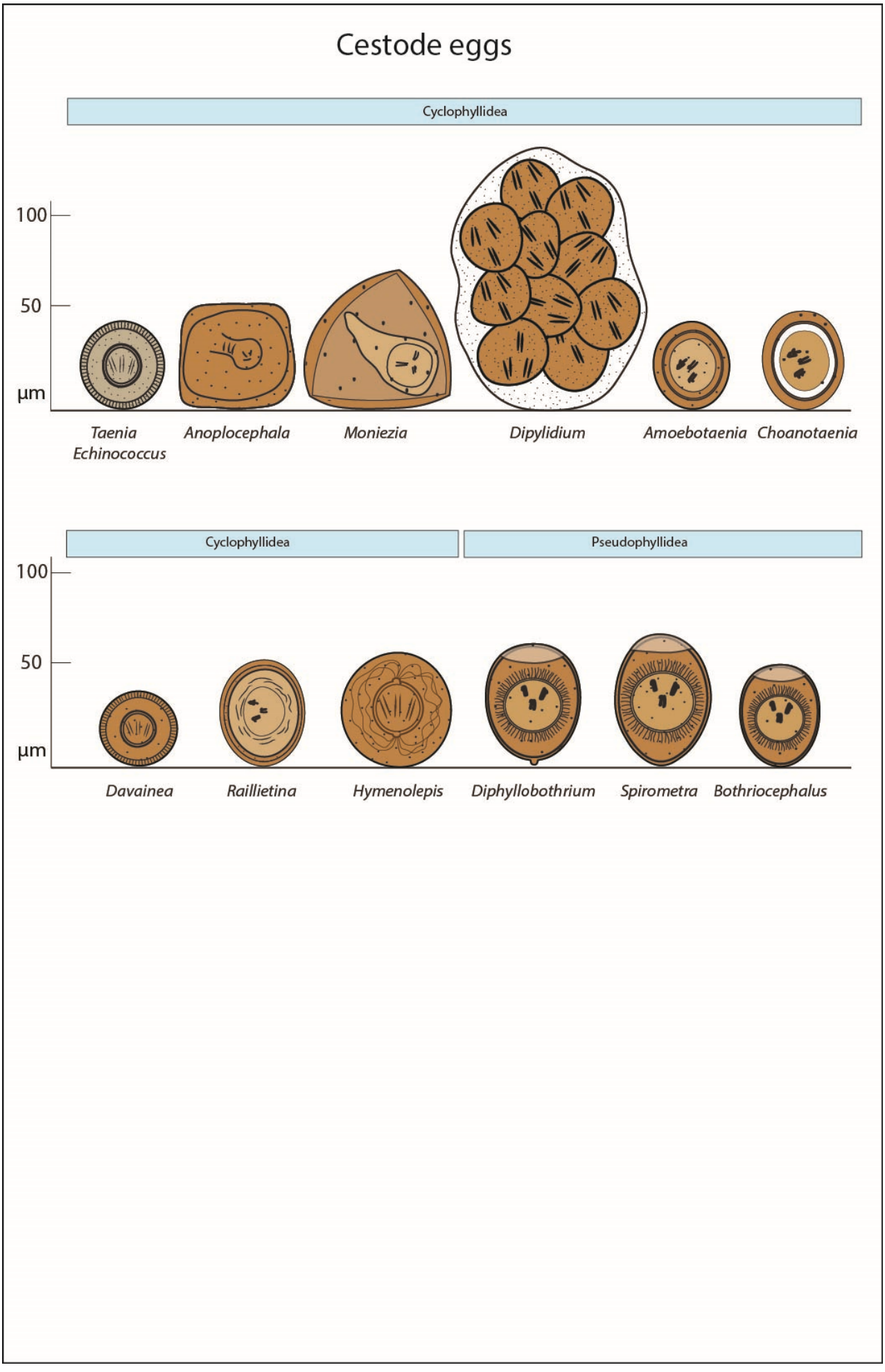
Diphyllobothrium



Spirometra



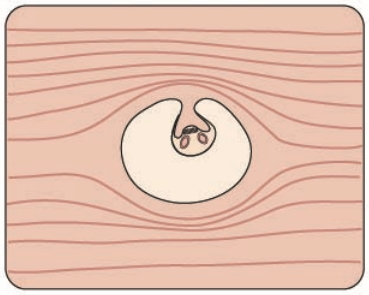
Bothriocephalus


Cestode eggs
Cyclophyllidea
100
50
µm
Taenia
Echinococcus
Anoplocephala
Moniezia
Dipylidium
Amoebotaenia
Choanotaenia
Cyclophyllidea
Pseudophyllidea
100
50
µm
Davainea
Raillietina
Hymenolepis
Diphyllobothrium
Spirometra
Bothriocephalus

Metacestodes

Cyclophyllidea

cysticercus



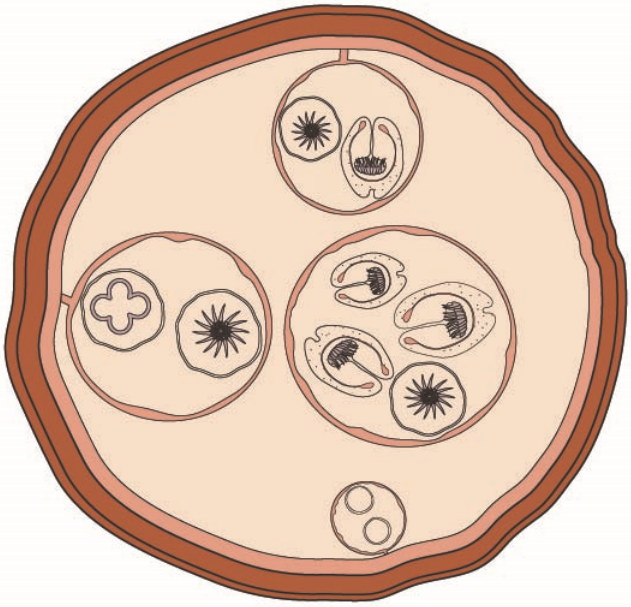
Taenia

cysticercoid



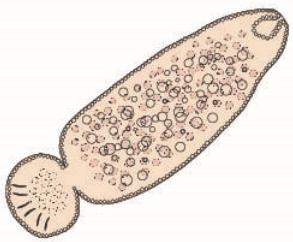
Anoplocephala, Moniezia, Dipylidium, Amoebotaenia, Choanotaenia, Davainea, Raillietina, Hymenolepis

hydatid cyst



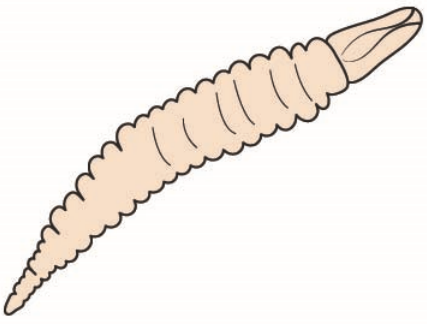
Echinococcus

procercoid



Diphyllobothrium, Spirometra

plerocercoid (spargana)



Diphyllobothrium, Spirometra, Bothriocephalus

Taenia
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Cyclophyllidean tapeworms are usually intestinal parasites of terrestrial vertebrates and have an anterior scolex (hold-fast organ with suckers and sometimes hooks) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). Eucestodes have indirect life-cycles involving oncospheres (hexacanth embryos) released from ingested eggs to form encysted larval stages (metacestodes) in the tissues of intermediate hosts and their transmission to carnivorous definitive hosts. Adult taeniids have an armed rostellum (except *T. saginata*), elongate gravid segments and are rarely pathogenic. *Taenia* spp. form encysted larval stages (cysticerci, coenuri or strobilocerci) causing space-occupying lesions and disease in domestic animals and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)
Family:	Taeniidae (scolex often armed, proglottids with single genital pore, fluid-filled cystic metacestodes)
Genus:	*Taenia* (parasitic in intestines/tissues of carnivores/omnivores)
Species:	*T. saginata* (causes cysticercosis in cattle)
	T. solium (causes cysticercosis in pigs and humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some

with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia, rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Cyclophyllidean cestodes are polyzoic containing from 2 to > 1,000 proglottids demarcated by external segmentation. They possess an anterior scolex with 4 suckers, many with a rostellum (often armed), and they have compact post-ovarian vitellaria. Adult worms are found in terrestrial vertebrate definitive hosts (mammals, birds, reptiles, amphibians) while larval metacestodes occur in vertebrate (mammal, amphibian, bird) or invertebrate (mollusc, acari, insect) intermediate hosts. Over 3,000 species have been described in 400 genera in 16 families: Acoleidae, Amabiliidae, Anoplocephalidae, Catenotaeniidae, Davaineidae, Dioecocestidae, Dilepididae, Dipylidiidae, Gyrporhynchidae, Hymenolepididae, Mesocestoididae, Metadileptidae, Nematotaeniidae, Paruterinidae, Progynotaeniidae, and Taeniidae (all with lateral genital pores, except the Mesocestoididae). Mature taeniid tapeworms have proglottids with unpaired reproductive organs and a single genital pore, and the scolex is often armed with hooks. Taeniids produce round non-operculated eggs with striated shells, the oncospheres are non-ciliated and they form fluid-filled cystic metacestodes (cysticercus, coenurus, strobilocercus, or hydatid cyst). Several genera (*Taenia* (*Multiceps, Taeniarhynchus*), *Hydatigera,*

Echinococcus, Versteria) have been reported predominantly in carnivorous definitive hosts (canids, felids, primates incl. humans) and herbivorous or omnivorous intermediate hosts (artiodactyls, lagomorphs, rodents, primates).

Over 40 *Taenia* spp. are found in carnivores and herbivores throughout the world. Many species appear to have two scientific names because the larval stages in herbivores were often named (as *Cysticercus*, *Strobilocercus* or *Coenurus* spp.) before it was realized they were developmental stages of adult *Taenia* tapeworms in carnivores. Several workers also proposed new generic names for species forming coenuri (*Multiceps*) or strobilocerci (*Hydatigera*) rather than cysticerci (*Taenia sensu stricto*). Molecular phylogenetic studies have provided some support for the latter proposal (recognizing the genus *Hydatigera*) as well as erecting a new genus *Versteria* for the enigmatic *T. mustelae* (and possibly *T. brachyacantha*). Many classifications continue to use the single genus *Taenia sensu lato* (in the broadest sense) with other genera listed as synonyms or subgenera pending further definitive studies. Three *Taenia* spp. form adult tapeworms in humans which thus act as definitive hosts (*T. solium, T. saginata, T. asiatica*), but humans may also be infected by larval (metacestode) stages of other species (mostly *T. solium*, but occasionally *T. crassiceps, T. multiceps, T. serialis* and rarely *T. taeniaeformis*). *T. solium* infections cycle between humans and pigs in many areas where pork products are common, including regions throughout South and Central America, Eastern Europe, South Africa, China and Indonesia. *T. saginata* infections cycle between humans and cattle in most pastoral (beef and dairy) areas throughout the world. *T. asiatica* (Asian taeniid) cycles between humans and pigs or cattle in several South-East Asian countries and was initially thought to be a strain of *T. saginata* but is now considered a separate species. *T. crassiceps* cycles between canids and rodents in countries in the Northern Hemisphere, although infections by larval stages have been recorded in several humans, mostly immunocompromised individuals. Species forming coenuri in domestic animals and rodents develop mainly in canids, while those forming strobilocerci in rodents develop in many small carnivores, such as felids and viverrids. Several other *Taenia* spp. have been described predominantly from adult worms recovered from wild carnivores throughout Africa, North America and Russia: including *T. polyacantha, T. parenchymatosa, T. ovata* and *T. retracta* from foxes and dogs; *T. acinonyxi, T. gonyamai, T. regis, T. ingwei, T. selousi, T. omissa, T. pseudolaticollis* (syn. *T. laticollis*) and *T. rileyi* from lions, cheetahs, leopards, wildcats, cougars and lynx; and *T. mustelae, T. martis, T. taxidiensis* and *T. secunda* from weasels, martens and badgers.

Taeniid species (synonyms) [metacestode synonyms]	**Definitive hosts (DH) [adults in small intestines] {clinical signs}**	**Intermediate hosts (IH) [metacestodes in tissues] {clinical signs}**	**Distribution**
Species forming cysticerci in IH			
T. acinonyxi	Carnivora: felid (leopard, cheetah)	Artiodactyla: bovid (impala, sable antelope, gerenuk, gemsbok, grey duiker, African buffalo), suid (warthog) [cysticercus in muscles]	Africa
T. arctos	Carnivora: ursid (brown bear)		Europe
T. arvicolae sp. inq.	Rodentia: cricetid (common vole)		Europe
T. asiatica (may be a subspecies of *T. saginata*) [syn. *Cysticercus viscerotropica*]	Primates: hominid (human) {occasionally diarrhoea}	Artiodactyla: bovid (cattle), suid (pig) [cysticercus in muscles] {carcase lesions}	Asia, Africa, Europe
T. brachyacantha (now *Versteria*)	Carnivora: mustelid (white-naped weasel)	Rodentia: murid (rats) [cysticercus in liver]	Africa
T. brevicollis sp. inq.	Carnivora: mustelid (stoat)		Eurasia
T. cervi (syn. *Cysticercus cervi*) (incl. *T. krabbei*) [syn. *Cysticercus tarandi*]	Carnivora: canid (wolf, fox, dog)	Artiodactyla: cervid (deer, reindeer) [cysticercus in muscles] {carcase lesions}	worldwide
T. crassiceps (syn. *T. hyperborea*) [syn. *Cysticercus longicollis*]	Carnivora: canid (Arctic fox, red fox, wolf, coyote, dog), felid (wild cat, lynx), mustelid (beech marten)	Rodentia: murid (mice, rats), cricetid (Arctic lemming, brown lemming, collared lemmings, common vole, northern water vole, Tundra vole, social vole, meadow vole, muskrat, hamster), sciurid (marmot, groundhog, chipmunk, squirrel, sousliks); Eulipotyphla: talpid (common mole); Lagomorpha: leporid (hare); rarely Primates: hominid (human) [cysticercus in abdominal cavity, subcutaneous tissues, muscles]	Northern Hemisphere
T. crocutae	Carnivora: hyaenid (spotted hyaena, brown hyaena)	Artiodactyla: bovid (Ugandan kob, impala, Lelwel hartebeest, hartebeest, blue wildebeest, sassaby, topi, roan antelope,	Africa

		sable antelope, lechwe, gemsbok, southern reedbuck, giant eland, kewel, Grant's gazelle, greater kudu, common duiker, African buffalo); occasionally Primates: cercopithecid (baboon) [cysticercus in muscles]	
T. dinniki	Carnivora: hyaenid (spotted hyaena, striped hyaena)	unknown	Africa
T. gonyamai (syn. *T. hlosei*)	Carnivora: felid (lion, cheetah)	Artiodactyla: bovid (hartebeest, blue wildebeest) [cysticercus in muscles, lymph nodes, lungs]	Africa
T. hyaenae (syn. *T. lycaontis*) [syn. *Cysticercus dromedarii*]	Carnivora: hyaenid (hyaena), canid (African wild dogs)	Artiodactyla: camelid (camel), bovid (cattle, zebu, African buffalo, goat, sheep, kob, Lelwel hartebeest, Grant's gazelle, Thomson's gazelle, Soemmerring's gazelle, roan antelope, common duiker, giant eland, kewel) [cysticercus in muscle, liver]	Africa
T. hydatigena (syn. *T. jakhalsi*) (false hydatid worm) [syn. *Cysticercus tenuicollis*]	Carnivora: canid (dog, red fox, wolf, coyote, black-backed jackal, golden jackal), hyaenid (hyaena), felid (cougar, bobcat, lion), ursid (grizzly bear), mustelid (weasel, stoat, polecat)	Artiodactyla: bovid (sheep, mouflon, goat, chamois, cattle, muskox, blue duiker, goitered gazelle), cervid (deer, moose, mule deer, white-tailed deer, Rocky Mountain elk, roe deer, fallow deer, red deer, reindeer), suid (pig); Perissodactyla: equid (horse); Rodentia: castorid (Eurasian beaver), aplodontid (mountain beaver); Carnivora: ursid (black bear), mustelid (beech marten); Primates: cercopithecid (vervet monkey, African red monkey) [cysticercus in peritoneum, liver]	worldwide
T. ingwei	Carnivora: felid (leopard)		Africa
T. ingwei	Carnivora: felid (leopard)		Africa
T. jaipurensis	Carnivora: felid (lion)		Asia
T. madoquae [syn. *Cysticercus madoquae*]	Carnivora: canid (silver-backed jackal, dog)	Artiodactyla: bovid (Gunther's dik-dik) [cysticercus in muscles]	Africa
T. martis (incl. *T. m. martis* and *T. m. americana*)	Carnivora: mustelid (European pine marten, American pine marten, beech marten, European polecat, American mink, stoat, weasel, fisher), procyonid (ringtail cat), felid (wild cat)	Rodentia: cricetid (bank vole, field vole, Siberian brown lemming, taiga vole, muskrat, European pine vole), murid (mouse, striped field mouse) [cysticercus in body cavity]	Europe, North America
T. melesi sp. inq.	Carnivora: mustelid (European badger)		Europe
T. mustelae (syn. *T. parviuncinatus*) (now *Versteria*)	Carnivora: mustelid (stoat, weasel, Siberian weasel, mountain weasel, Steppe polecat, European pine marten, beech marten, sable, mink, ferret), mephitid (skunk)	Rodentia: murid (house mouse, wood mouse, kleinwuhlmaus, brown rat), sciurid (red squirrel, grey squirrel, fox, squirrel, Daurian ground squirrel, Franklin's ground squirrel, white-tailed prairie dog, groundhog, eastern chipmunk, least chipmunk, Alaska marmot, hoary marmot), cricetid (deer mouse, white-footed mouse, muskrat, common vole, social vole, tundra vole, Major's pine vole, snow vole, field vole, meadow vole, singing vole, Schidlovsky's vole, northern water vole, grey red-backed vole, southern red-backed vole, northern red-backed vole, bank vole, northern bog lemming, southern bog lemming, brown lemming, hamster), dipodid (meadow jumping mouse), aplodontid (mountain beaver)	North America, Europe, Mongolia

		[cysticercus in viscera]	
T. olnojinei	Carnivora: hyaenid (spotted hyaena, striped hyaena)	Artiodactyla: bovid (hartebeest, blue wildebeest, topi, Grant's gazelle) [cysticercus in sacral epidural space]	Africa
T. omissa	Carnivora: felid (cougar, oncilla, jaguarundi)	Artiodactyla: cervid (white-tailed deer, mule deer, brocket deer) [cysticercus in lungs, pericardium]	Americas
T. ovis (sheep measles worm) (syn. *T. krabbei, T. rangifer*) (incl. *T. o. ovis, T. o. krabbei*) [syn. *Cysticercus ovis*]	Carnivora: canid (dog, wolf, coyote, Arctic fox, red fox), felid (cougar), ursid (black bear, brown bear) {sometimes diarrhoea}	Artiodactyla: bovid (sheep, mouflon, bighorn sheep, goat, goitered gazelle), antilocaprid (pronghorn), cervid (roe deer, red deer, fallow deer, mule deer, reindeer, caribou, elk, moose) [cysticercus in muscles] {carcase lesions}	worldwide
T. parenchymatosa	Carnivora: canid (dog, Arctic fox)	Artiodactyla: cervid (reindeer, red deer) [cysticercus in viscera]	Russia
T. pencei	Carnivora: procyonid (ring-tailed cat)		North America
T. pisiformis (syn. *T. serrata, T. novella, T. utricularis*) [syn. *Cysticercus pisiformis*]	Carnivora: canid (dog, wolf, red wolf, red fox, Arctic fox, grey fox, golden jackal, black-backed jackal, coyote, African wild dog), felid (bobcat, Canada lynx, wild cat, oncilla, lion, leopard), mustelid (polecat)	Lagomorpha: leporid (rabbit, black-tailed jackrabbit, white-tailed jackrabbit, marsh rabbit, snowshoe hare, Cape hare, European hare, Abyssinian hare, Tolai hare, mountain hare, desert cottontail, eastern cottontail, mountain cottontail, New England cottontail, tapeti); Rodentia: murid (house mouse, yellow-necked mouse, brown rat, black rat), sciurid (fox squirrel), cricetid (bank vole, common vole, muskrat), caviid (guinea pig) [cysticercus in peritoneum, liver) {occasionally hepatitis}	worldwide
T. polyacantha (incl. *T. p. arctica, T. p. polyacantha*)	Carnivora: canid (Arctic fox, red fox, wolf, dog)	Rodentia: cricetid (Siberian brown lemming, Steppe lemming, common vole, Tundra vole, singing vole, narrow-headed vole, bank vole, grey red-backed vole); Lagomorpha: ochotonid (Mongolian pika), leporid (European rabbit) [cysticercus in peritoneal cavity, pleura]	Northern Hemisphere
T. regis (syn. *T. bubesei*)	Carnivora: felid (lion, leopard)	Artiodactyla: bovid (hartebeest, blue wildebeest, topi, beisa, gemsbok, sable antelope, waterbuck, southern reedbuck), suid (desert warthog); Perissodactyla: equid (plains zebra) [cysticercus in body cavity]	Africa
T. saginata (syn. *T. africana, T. bremneri, T. confusa, T. cylindrica, T. hominis, T. mediocanellata, T. philippina, T. tonkinensis, Taeniarhynchus saginatus*) (human beef tapeworm, beef measles worm) [syn. *Cysticercus bovis, C. inermis*]	Primates: hominid (human) {occasionally diarrhoea}	Artiodactyla: bovid (cattle, zebu, topi, kob, beisa, harnessed bushbuck, red-fronted gazelle, dorcas gazelle, Mongolian gazelle), cervid (reindeer) [cysticercus in muscles] {carcase lesions, calcification}	worldwide
T. saigoni	Primates: cercopithecid (crab-eating macaque)		Asia
T. selousi	Carnivora: felid (wildcat)	Rodentia: murid (four-striped grass mouse)	South Africa
T. simbae	Carnivora: felid (lion)	unknown	Africa
T. solium (human pork tapeworm, pork measles worm) [syn. *Cysticercus cellulosae*]	Primates: hominid (human) {occasionally diarrhoea}	Artiodactyla: suid (pig, wild boar, bushpig), camelid (camel); Primates: cercopithecid (vervet monkey, moustached monkey, patas monkey, chacma baboon, rhesus macaque), hylobatid (lar gibbon), hominid (human);	worldwide

		Carnivora: canid (dog, red fox), felid (wildcat), mustelid (polecat), ursid (brown bear), otariid (brown fur seal); Lagomorpha: leporid (mountain hare, European rabbit); Rodentia: sciurid (ground squirrel), murid (mice, black rat), cricetid (golden hamster) [cysticercus in muscles, organs] {lesions, neurological signs}	
T. talicei		Rodentia: ctenomyid (collared tuco-tuco)	South America
T. taxidiensis	Carnivora: mustelid (American badger), canid (coyote)	Rodentia: sciurid (rock squirrel, Wyoming ground squirrel, Franklin's ground squirrel)	North America
Species forming coenuri in IH			
T. (*Multiceps*) *clavifer sp. inq.*		Rodentia: echimyid (coypu)	Europe
T. (*Multiceps*) *endothoracicus* [syn. *Coenurus endothoracicus*]	Carnivora: canid (fox)	Rodentia: murid (rats, mice, gerbils, jirds) [coenurus in muscles, body cavity]	Asia, North Africa
T. (*Multiceps*) *gaigeri* (possible synonym of *T. multiceps*) [syn. *Coenurus gaigeri*]	Carnivora: canid (dog, fox)	Artiodactyla: bovid (goat, sheep) [coenurus in muscle, subcutis] {carcase lesions}	worldwide
T. (*Multiceps*) *multiceps* [syn. *Coenurus cerebralis*]	Carnivora: canid (dog, raccoon dog, Arctic fox, red fox, corsac fox, coyote, black-backed jackal, wolf), felid (cougar)	Artiodactyla: bovid (sheep, mouflon, argali, goat, Caucasian goat, chamois, Pyrenean chamois, cattle, wisent, yak, gemsbok, Siberian ibex, goitered gazelle, roan antelope, saiga antelope), cervid (roe deer, reindeer), camelid (dromedary, Bactrian camel), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (snowshoe hare); occasionally Primates: cercopithecid (gelada), hominid (human) [coenurus in brain, spinal cord, subcutis] {occasionally neurological signs known as gid, sturdy or staggers}	worldwide, except North America, New Zealand
T. (*Multiceps*) *macracantha*	Carnivora: viverrid (genet, Cape genet), herpestid (mongoose), mustelid (striped polecat, weasel), felid (wildcat)	Rodentia: murid (house mouse, wood mouse, African pygmy mouse, African grass rat, red rock rat, Namaqua rock rat, acacia rat, four-striped grass rat, African soft-furred rat) [coenurus in liver]	Europe, Africa
T. (*Multiceps*) *otomys sp. inq.*		Rodentia: murid (South Africa vlei rat)	Africa
T. (*Multiceps*) *serialis* (incl. *T. s. brauni, T. brauni,* syn. *T. laruei, M. glomeratus, M. packi*) [syn. *Coenurus serialis, C. brauni*]	Carnivora: canid (dog, African wild dog, black-backed jackal, red fox)	Lagomorpha: leporid (European rabbit, European hare, snowshoe hare, eastern cottontail); Rodentia: murid (house mouse, typical striped grass mouse, southern multimammate mouse, black rat, thicket rats, Southern African vlei rat, African soft-furred rat, greater Egyptian gerbil), nesomyid (climbing mouse), hystricid (porcupines), spalacid (Rwanda mole-rat); Primates: cercopithecid (blue monkey, purple-faced leaf-monkey), hominid (human) [coenurus in connective tissue, subcutaneous tissue, eyes]	America, Africa, Europe
T. (*Multiceps*) *skrjabini* (possible synonym of *T. multiceps*) [syn. *Coenurus skrjabini*]	Carnivora: canid (dog, fox)	Artiodactyla: bovid (sheep) [coenurus in muscle, subcutis] {carcase lesions}	worldwide
T. (*Multiceps*) *smythi sp. inq.*	Carnivora: canid (wolf)		Europe
T. (*Multiceps*) *twitchelli*	Carnivora: mustelid (wolverine)	Rodentia: erethizontid (North American porcupine), cricetid (muskrat, Siberian brown lemming, meadow vole), sciurid	North America

		(European ground squirrel, American red squirrel) [coenurus in muscles]	
Species forming strobilocerci in IH			
T. (*Hydatigera*) *balaniceps sp. inq.*	Carnivora: canid (wolf)		North America
T. (*Hydatigera*) *kamiyai* (now *Hydatigera*)	Carnivora: felid (European wild cat)		Europe
T. (*Hydatigera*) *krepkogorski* (now *Hydatigera*)	Carnivora: felid (African wild cat, European wild cat, sand cat, jungle cat), canid (red fox)	Rodentia: murid (rats, mice, gerbils); Lagomorpha: leporid (rabbits, hares) [strobilocercus in mesenteries, liver]	Russia, Asia
T. macrocystis [syn. *Cysticercus macrocystis*] (now *Hydatigera*)	Carnivora: felid (oncilla, jaguarundi, margay, Geoffroy's cat, bobcat, Canada lynx)	Lagomorpha: leporid (tapeti, snowshoe hare, jackrabbit, mountain hare); Rodentia: sciurid (red squirrel) [strobilocercus in muscles, mesenteries, liver]	Americas, Russia
T. (*Hydatigera*) *parva* (now *Hydatigera*)	Carnivora: viverrid (common genet)		Africa
T. (*Hydatigera*) *pseudolaticollis* (syn. *T. laticollis*) (now *Hydatigera*)	Carnivora: felid (lynx)		North America
T. (*Hydatigera*) *rileyi* (syn. *T. lyncis*) (now *Hydatigera*)	Carnivora: felid (Eurasian lynx, bobcat, cougar, wildcat)	Rodentia: sciurid (American red squirrel), aplodontid (mountain beaver), cricetid (packrat, marsh rice rat, hispid cotton rat, northern red-backed vole, Tundra vole) [hemistrobilocercus in liver]	Nearctic
T. (*Hydatigera*) *taeniaeformis* (syn. *T. infantis, T. longihamatus, H. himalayotaenia*) [syn. *Strobilocercus fasciolaris, S. crassicollis, Cysticercus fasciolaris*] (now *Hydatigera*)	Carnivora: felid (cat, bobcat, wildcat, lynx, tiger), mustelid (stoat), canid (red fox, coyote-wolf hybrid)	Rodentia: murid (house mouse, spiny mouse, pygmy field mouse, Algerian mouse, brown rat, black rat, African grass rat, lesser Egyptian gerbil), cricetid (muskrat, hispid cotton rat, common vole, field vole, meadow vole, woodland vole, European pine vole, Savi's pine vole, deermouse, yellow-rumped leaf-eared mouse), echimyid (coypu), sciurid (grey squirrel); Lagomorpha: leporid (rabbit); occasionally Strigiformes: strigid (Eurasian eagle-owl); Galliformes: phasianid (common pheasant); rarely Primates: hominid (human) [strobilocercus in liver]	worldwide

Parasite morphology: These tapeworms form three developmental stages: eggs, larvae and adults. The morphological characteristics of the adults are distinctive; all adults having an anterior scolex (holdfast organ), with four muscular acetabulate (saucer-like) suckers, surmounting a long (up to 10 m) ribbon-like strobila (tape) made up of numerous (as many as 2,000) proglottids (segments). *T. solium* tapeworms are usually 1.8-4 m long (some reported up to 8 m) while *T. saginata* tapeworms are usually smaller ranging from 0.3-0.6 m long (some up to 2.5 m). The anterior scolex is small measuring around 1-2 mm in section: that of *T. solium* is spheroidal and armed with two circles of 22-32 rostellar hooks (alternating in size from long 180 µm to short 130 µm), while that of *T. saginata* is cuboidal and un-armed. Adult worms are hermaphroditic with segments containing both male and female reproductive organs. Anterior segments are usually immature and broader than long, middle segments with fully developed genitalia are square, and posterior segments are gravid (filled with eggs) and longer than broad (especially those of *T. saginata* compared to *T. solium*). Gravid proglottids have a prominent uterus with a medial stem and numerous lateral branches on either side (7-13 for *T. solium* and 15-32 for *T. saginata*). Genital pores are marginal, alternating irregularly. Most *Taenia* spp. were assigned to either of two morpho-groups based on the arrangement of genital ducts: those with ducts passing between the lateral excretory canals (e.g. taeniids of humans, dogs and cats, except *T. taeniaeformis*) or those with ducts passing the canals ventrally (e.g. *T. taeniaeformis* and taeniids of viverrids and mustelids). The eggs of most species are similar in morphology; being spherical, 31-48 µm in diameter, surrounded by a thick radially-striated wall, and containing a hexacanth (six-hooked) nonciliated embryo (oncosphere). The larval stages (metacestodes) are lacunate (internal channel forms during development) and they become encysted within intermediate host tissues. Most *Taenia* spp. (e.g. *T. saginata* and *T. solium*) form distinctive pearly-white cysticerci (*singular* cysticercus) which appear as small (8-10 mm in diameter) fluid-filled bladders (hence the common name of bladder-worms), each containing a single invaginated scolex (infective stage). Other taeniids form different larval stages: those belonging to the subgenus

T. (*Multiceps*) (e.g. *T.* (*M.*) *multiceps*) forming larger coenuri (*singular* coenurus) containing clusters of numerous invaginated scoleces on its internal wall; and those belonging to the genus *Hydatigera* (e.g. *H. taeniaeformis*) forming strobilocerci (*singular* strobilocercus) with an invaginated scolex at the end of a long pseudo-segmented neck.

Site of infection: Adult tapeworms lay in the lumen of the small intestines of their definitive hosts, attached to the mucosa only by their scoleces. Larval stages (metacestodes) may develop in a range of tissues and organs in their intermediate hosts, particularly in muscles, visceral organs and sometimes the brain.

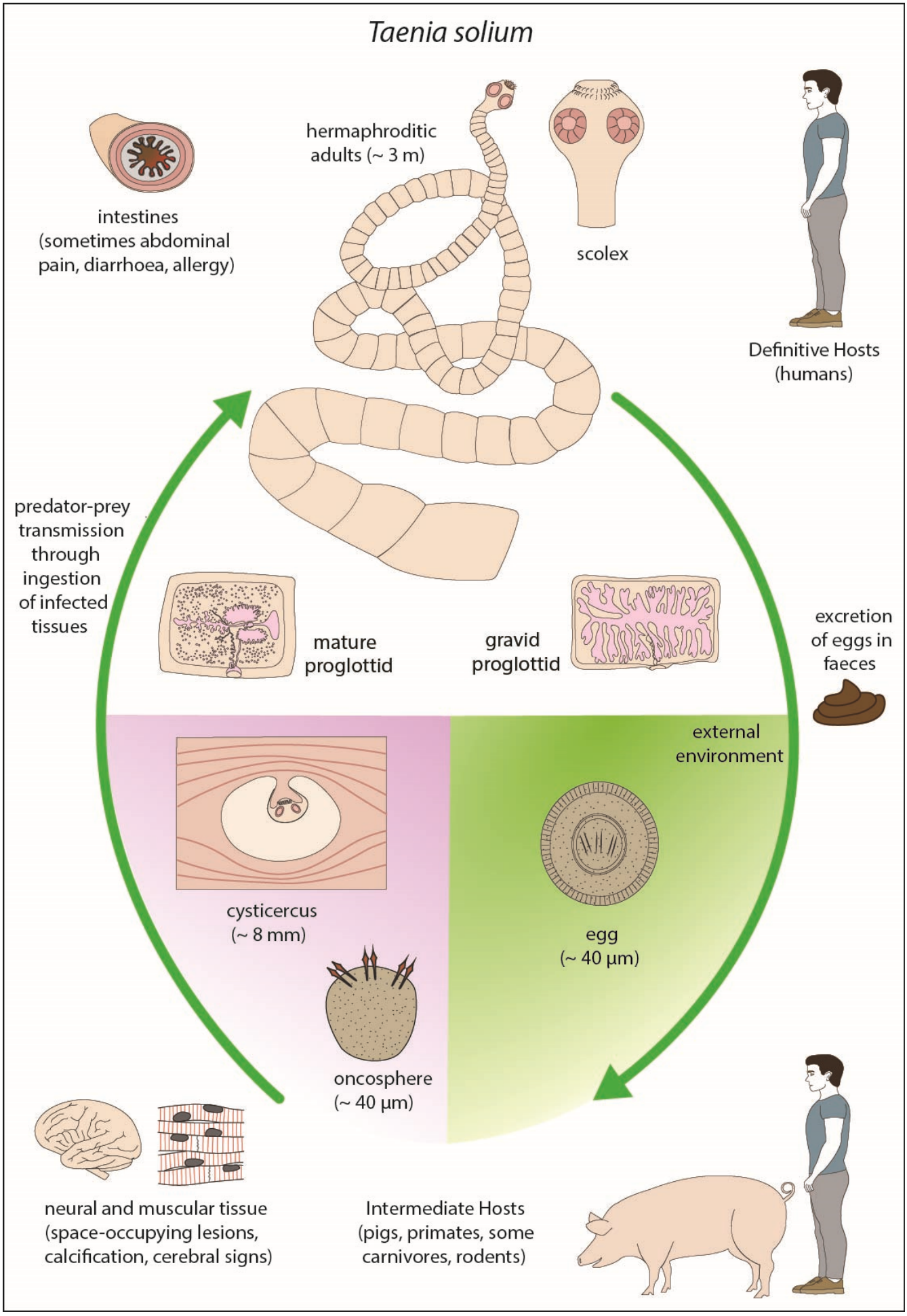
Pathogenesis: Infections in humans by the large adult tapeworms generally involve only 1-2 worms, and often do not result in any distinct symptoms, although there may be vague abdominal pains with mild intermittent diarrhoea or constipation, epigastric pain, nausea and generalized allergic manifestations, including urticaria, anal pruritus and eosinophilia. Infections by the encysted larval stages (cysticerci) do not appear to cause any severe clinical disease in their normal hosts (cattle and pigs) even when present in relatively high numbers. The cysts often occur in skeletal muscles and connective tissues of the skin (reports in the liver appear to be incorrect identifications), and while they may occupy space, they generally do not cause organ enlargement, tissue displacement or untoward pressure on surrounding areas. Degenerating cysticerci tend to calcify and are palpable in the tissues. Heavy infections by live and calcified cysts impart a measly appearance to the flesh and may lead to the condemnation of the carcase. Unfortunately, humans may also be infected with *T. solium* through the process of self-infection when eggs are accidentally ingested (and possibly by retroinfection when eggs carried upwards by reverse peristalsis hatch in the gut). Cysticerci may develop in virtually every organ and tissue of the human body, although they show a particular affinity for the muscles and brain, and less commonly for subcutaneous connective tissue, eye, heart, liver, lungs and coelom. Humans are quite susceptible to pressure necrosis, particularly when cysticerci develop in the brain (neurocysticercosis with cerebral signs, headaches, seizures, epilepsy and coma), eyes (ocular signs, pain, and loss of vision), muscles (myositis, hypertrophy/swelling) or subcutaneous tissues (nodules on the torso and extremities, sometimes painful). Degenerating cysticerci may elicit severe acute, and even fatal, inflammatory responses before their eventual calcification. Similarly, most infections of intermediate hosts by *Taenia* (*Multiceps*) spp. forming coenuri are asymptomatic unless the larval cysts degenerate or become large enough to interfere with vital organs. Coenuri may develop in the brain, eyes, muscles or subcutis causing symptoms ranging from altered neurological status, behavioural changes, irritability, unusual tilting of the head (gid), increased intracranial pressure, hydrocephalus, meningoencephalitis, seizures, paralysis and death. Naive animals are highly susceptible to taeniid infection; heavy infections sometimes causing significant liver damage, and heavy pasture contamination sometimes resulting in focal outbreaks (cysticercosis storms). In contrast, animals in endemic areas may develop premunitive (concomitant) immunity when persistent primary infections provide protection against subsequent re-infection.

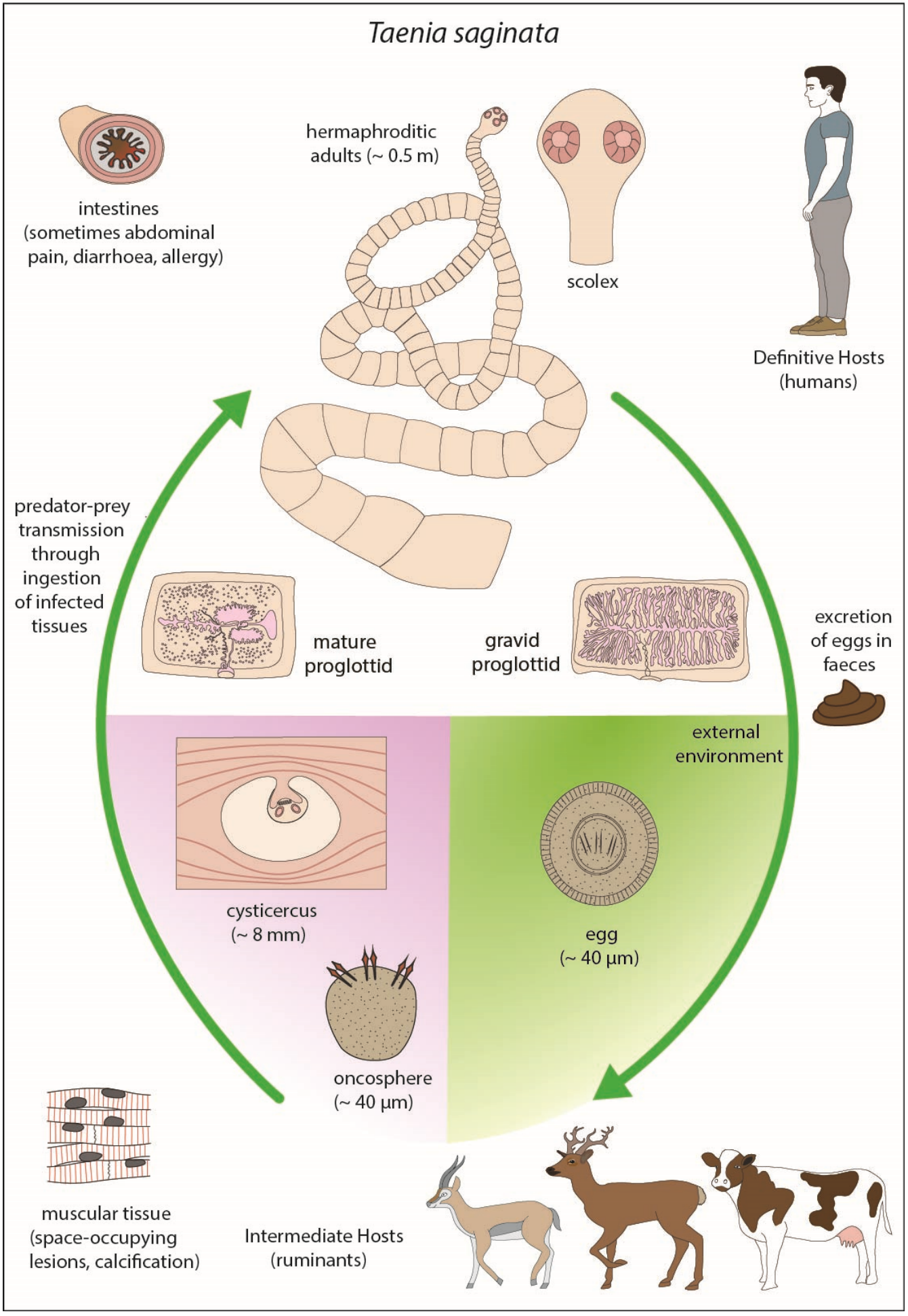
Developmental cycle and mode of transmission: These tapeworms have indirect life-cycles: involving predator-prey transmission where carnivores acquire infections by ingesting larval stages in meat. Adult worms produce thousands of eggs which are released from caudal segments (proglottids) and shed in faeces, or the gravid proglottids themselves break off and are shed as packages of eggs in faeces (sometimes up to 6 segments per day). The eggs are very resistant to desiccation and sewage treatment and can live for weeks on pastures. They are ingested by intermediate hosts with contaminated feed, drinking water, or are physically transferred to the mouth. The eggs hatch releasing the oncospheres which use their hooks and gland secretions to penetrate the gut wall into the circulation where they carried mainly to the skeletal muscles and connective tissues. Over 3 months, they metamorphose into thin-walled cysticerci; each containing a single tiny scolex invaginated into the lumen. Coenuri with several scoleces may take up to 9 months to develop. These encysted larval stages are transmitted to their definitive hosts by carnivory, when infected meat or offal is consumed raw or under-cooked. After ingestion, the outer bladder is digested away releasing the scolex which evaginates, attaches to the small intestinal mucosa and grows into an adult in about 10 weeks. Each segment is hermaphroditic containing both female and male reproductive organs. Cross-fertilization occurs when the segments have matured to a certain point in their development (around the middle of the tapeworm). Mating occurs between adjacent segments when the tapeworm repeatedly folds back on itself. Adult worms may live for as long as 25 years and they will produce billions of eggs in that time. Parasite life-cycles may be inadvertently facilitated by human activities in domestic situations; including poor hygiene and sanitation, intensive husbandry practices with over-crowding, inadequate meat inspection, poor effluent disposal in flood-prone areas and using untreated nightsoil or sewage for fertilizing pastures and crops. In particular, faeces from humans (and canids) may contain taeniid eggs which cause cysticercosis in domestic meat animals (and in humans in the case of *T. solium*). Many sylvatic cycles also occur between wildlife species with natural predator-prey relationships involving carnivores (mainly canids, felids and viverrids) and herbivores/omnivores (particularly suids, ruminants, lagomorphs and rodents).

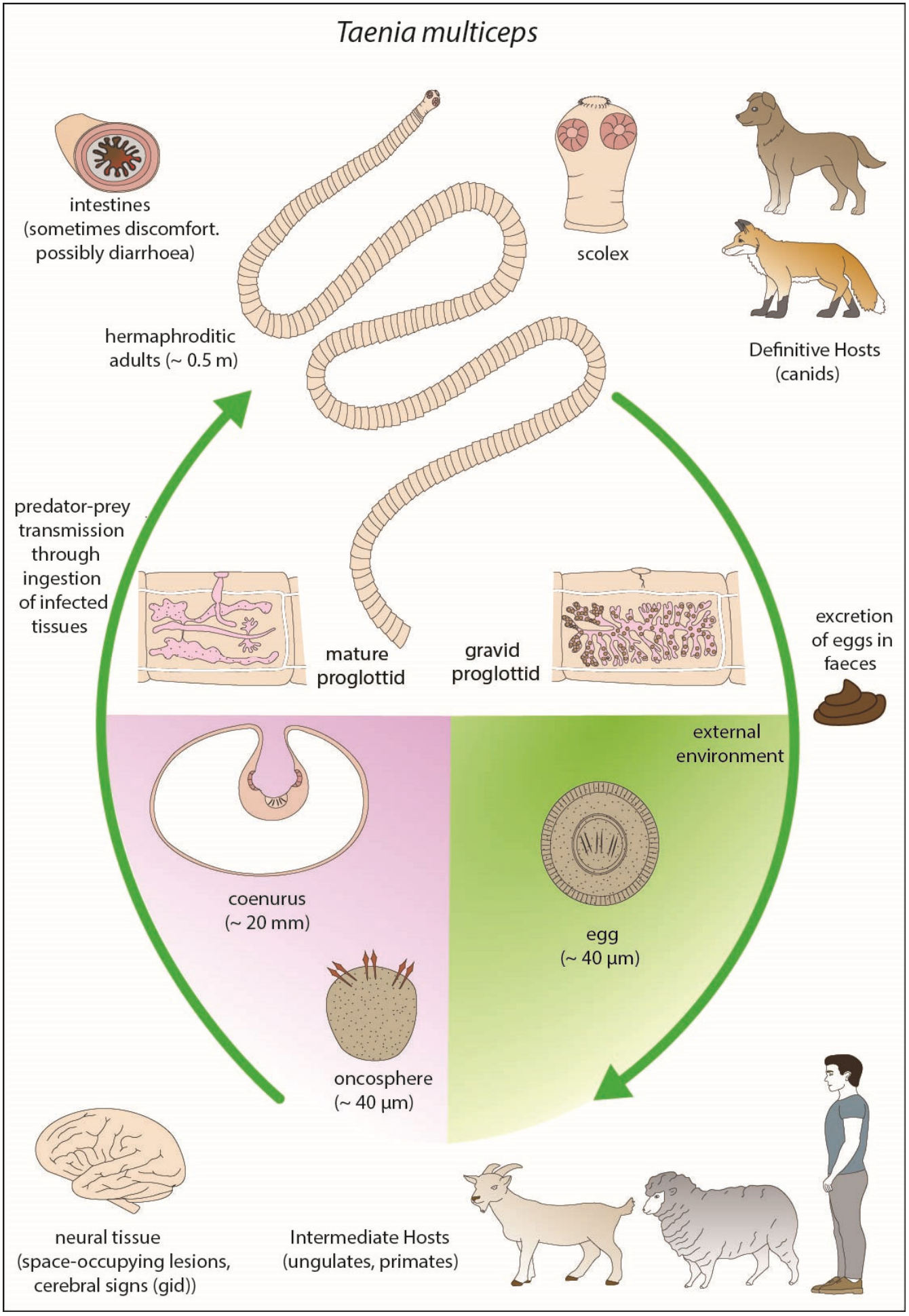
Differential diagnosis: Intestinal infections in humans are diagnosed by the detection of gravid segments or eggs in faecal samples, the latter being detected best after concentration in high specific gravity salt or sugar solutions. The eggs of *T. saginata* and *T. solium* are identical, but the gravid segments of *T. saginata* are more active than those of *T. solium*, the vaginal opening is guarded by a muscular sphincter, and they have more lateral branches of the uterus (although some overlap in numbers may occur). Infections by cysticerci may be suspected on the basis of clinical symptomatology (especially neurocysticercosis), but the metacestodes often can only be visualized and/or felt when in superficial locations. Modern medical imaging techniques (magnetic resonance imaging (MRI), computerized axial tomography (CAT) and ultrasonography) may detect cysticerci in soft tissues, while

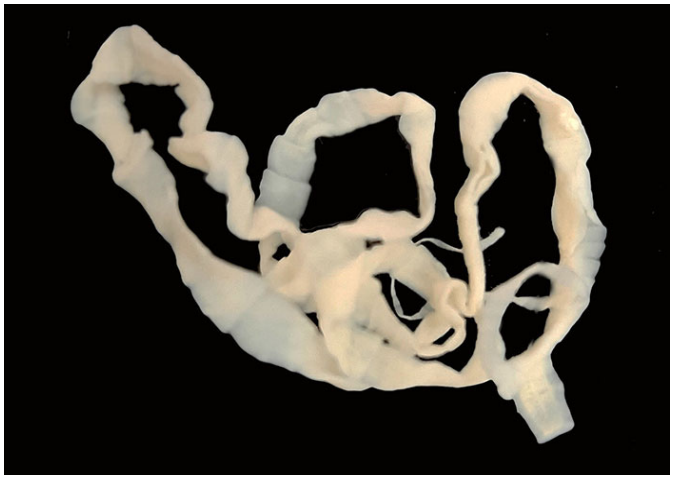
X-rays generally only detect calcified cysticerci. Several immunological tests (enzyme immunoassays, immunoblots) have recently been developed to detect host antibodies or parasite antigens in host samples (serum, cerebrospinal fluid, tissue biopsies/aspirates or faeces); most tests appear to be sensitive and specific although some cross-reactions have been observed with other tapeworm species. Molecular tests are also being developed to characterize parasites, including Southern blot hybridization, restriction fragment length polymorphism (RFLP), single strand conformational polymorphism (SSCP), random amplified polymorphic DNA (RAPD), loop-mediated isothermal amplification (LAMP), multiplex analyses and DNA sequencing, most using polymerase chain reactions (PCR) to amplify specific sequences of nuclear genes (18S and 28S ribosomal RNA (rRNA), internal transcribed spacer (ITS) regions, oncosphere-specific proteins (*Tso31*), cathepsin L-like cysteine peptidase (*clp*), noncoding DNA fragments (HDP1, 2), sequence characterized amplified region (SCAR) markers) or mitochondrial genes (cytochrome c oxidase subunit 1 (*cox1*), cytochrome b (*cob*), ATP synthases (*atp*) and NADH dehydrogenases (*nad*)). In many countries, meat inspection of slaughtered animals is mandatory to screen for various carcase lesions, including larval stages of tapeworms (cysticerci, coenuri). While cysts may be detected in superficial or accessible locations on carcases, usually the masseter muscles, tongue and heart, such screening has low sensitivity.

Treatment and control: Several groups of anthelmintic drugs (isoquinolines, benzimidazoles, salicylanilides, isothiocyanates) may be used to kill adult tapeworms but they are generally not effective against eggs. Single doses of praziquantel or niclosamide can cure infections in definitive hosts, while daily doses of praziquantel given for 1-2 weeks are effective against larval cysticercosis in intermediate hosts. Repeated doses of benzimidazoles (mebendazole, albendazole and fenbendazole) are effective against adult and larval stages. Epsiprantel is poorly absorbed and is most effective against adult stages in the gut. Nitroscanate has been used as a broad spectrum anthelmintic against enteric nematodes and cestodes in dogs. In humans afflicted with neurocysticercosis, surgical intervention may be required to remove cysts from the brain, and treatment of the patient pre- and post-surgery with albendazole or praziquantel has been recommended. The prevention of infections involves breaking the transmission cycle; through stringent meat inspection for ‘measly’ meat, tracing heavy infections back to individual farms, condemnation of infected carcases for human consumption, proper cooking or freezing of meat (pickling meat often does not kill larvae), sanitary disposal of faeces, prohibiting the use of sewage for fertilizing pastures, washing salad vegetables, strict personal hygiene, curbing hunting/scavenging behaviour in dogs, and mounting public awareness and education campaigns. Vaccines developed for *T. ovis, T. saginata* and *T. solium* have proven very effective in clinical trials but they have yet to be released commercially.


Taenia solium
intestines
(sometimes abdominal
pain, diarrhoea, allergy)
hermaphroditic
adults (~ 3 m)
scolex
Definitive Hosts
(humans)
predator-prey
transmission
through
ingestion
of infected
tissues
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
external
environment
cysticercus
(~ 8 mm)
egg
(~ 40 µm)
oncosphere
(~ 40 µm)
neural and muscular tissue
(space-occupying lesions,
calcification, cerebral signs)
Intermediate Hosts
(pigs, primates, some
carnivores, rodents)


Taenia saginata
intestines
(sometimes abdominal
pain, diarrhoea, allergy)
hermaphroditic
adults (~ 0.5 m)
scolex
Definitive Hosts
(humans)
predator-prey
transmission
through
ingestion
of infected
tissues
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
external
environment
cysticercus
(~ 8 mm)
egg
(~ 40 µm)
oncosphere
(~ 40 µm)
muscular tissue
(space-occupying
lesions, calcification)
Intermediate Hosts
(ruminants)

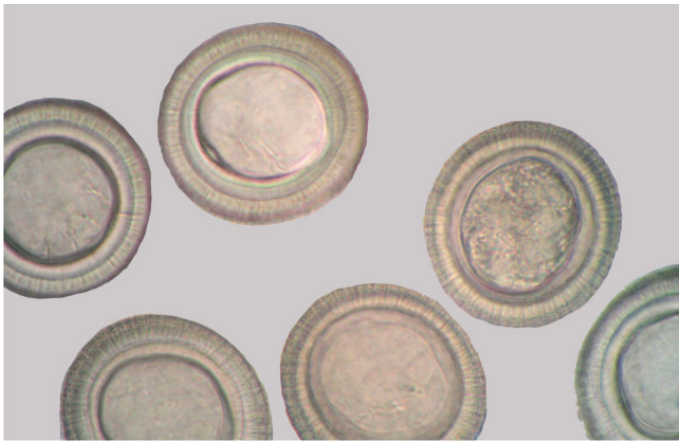

Taenia multiceps
intestines
(sometimes discomfort.
possibly diarrhoea)
scolex
Definitive Hosts
(canids)
hermaphroditic
adults (~ 0.5 m)
predator-prey
transmission
through
ingestion
of infected
tissues
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
external
environment
coenurus
(~ 20 mm)
egg
(~ 40 µm)
oncosphere
(~ 40 µm)
neural tissue
(space-occupying lesions,
cerebral signs (gid))
Intermediate Hosts
(ungulates, primates)



Taenia adult worm



Taenia adult worm segments



Taenia worm eggs



Taenia cysticercus



Taenia saginata scolex



Taenia solium scolex



Taenia saginata segment



Taenia solium segment

Echinococcus
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Cyclophyllidean tapeworms are usually intestinal parasites of terrestrial vertebrates and have an anterior scolex (hold-fast organ with suckers and sometimes hooks) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). Eucestodes have indirect life-cycles involving oncospheres (hexacanth embryos) released from ingested eggs to form encysted larval stages (metacestodes) in the tissues of intermediate hosts and their transmission to carnivorous definitive hosts. Adult taeniids have an armed rostellum (except *T. saginata*), elongate gravid segments and are rarely pathogenic. *Echinococcus* spp. form encysted larval stages (unilocular or multilocular cysts) causing space-occupying lesions and disease (hydatidosis) in wild and domestic animals and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)
Family:	Taeniidae (scolex often armed, proglottids with single genital pore, fluid-filled cystic metacestodes)
Genus:	*Echinococcus* (parasitic in gut/tissues of canids/omnivores)
Species:	*E. granulosus* (causes hydatid disease in mammals)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce

eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Cyclophyllidean cestodes are polyzoic containing from 2 to > 1,000 proglottids demarcated by external segmentation. They possess an anterior scolex with 4 suckers, many with a rostellum (often armed), and they have compact post-ovarian vitellaria. Adult worms are found in terrestrial vertebrate definitive hosts (mammals, birds, reptiles, amphibians) while larval metacestodes occur in vertebrate (mammal, amphibian, bird) or invertebrate (mollusc, acari, insect) intermediate hosts. Over 3,000 species have been described in 400 genera in 16 families: Acoleidae, Amabiliidae, Anoplocephalidae, Catenotaeniidae, Davaineidae, Dioecocestidae, Dilepididae, Dipylidiidae, Gyrporhynchidae, Hymenolepididae, Mesocestoididae, Metadileptidae, Nematotaeniidae, Paruterinidae, Progynotaeniidae, and Taeniidae (all with lateral genital pores, except the Mesocestoididae). Mature taeniid tapeworms have proglottids with unpaired reproductive organs and a single genital pore, and the scolex is often armed with hooks. Taeniids produce round non-operculated eggs with striated shells, the oncospheres are non-ciliated and they form fluid-filled cystic metacestodes (cysticercus, coenurus, strobilocercus, or hydatid cyst). Several genera (*Taenia* (*Multiceps, Taeniarhynchus*), *Hydatigera,*

Echinococcus, Versteria) have been reported predominantly in carnivorous definitive hosts (canids, felids, primates incl. humans) and herbivorous or omnivorous intermediate hosts (artiodactyls, lagomorphs, rodents, primates).

Conventional classification schemes recognize four main *Echinococcus* species: *E. granulosus, E. multilocularis, E. vogeli* and *E. oligarthus,* mostly utilizing canids (and some felids) as definitive hosts and a range of herbivorous mammals as intermediate hosts. *E. granulosus* occurs in most sheep and cattle producing areas around the world, being most prevalent in South America, East Africa, Southeast Asia and China, but being absent in Iceland, Greenland, New Zealand and Tasmania. Canids (dogs, dingoes, wolves, and coyotes) act as definitive hosts for adult worms, while omnivorous/herbivorous mammals (humans, domestic animals and wildlife) serve as intermediate hosts for larval stages (unilocular hydatid cysts). It is estimated that infections may affect around 2-3 million people worldwide, occurring in up to 10% of certain communities in some areas of South America, Africa, and Asia. Infections in domestic animals are prevalent in many rural agricultural zones while the extent of infections in wildlife can only be surmised. Various strains of *E. granulosus* have been identified on the basis of both phenotypic and genotypic differences, with many strains being 'adapted' to particular animals (intermediate host specificity being narrowly stenoxenous rather than strictly oioxenous). This has considerable epidemiological significance for infections in humans; for instance, pig and horse strains in Europe probably do not infect humans, whereas sheep and cattle strains do. More recently, biological and molecular characterization studies have indicated that *E. granulosus sensu lato* (in the broadest sense) may be comprised of several cryptic species: *E. equinus, E. ortleppi, E. canadensis, E. felidis* as well as *E. granulosus sensu stricto* (in the strictest sense). *E. equinus* was already thought to be a subspecies of *E. granulosus* but highly specific for equid intermediate hosts in Europe (most cases in other countries have been traced back to imported European horses). *E. ortleppi* appears to be a cattle genotype/strain found in many countries and transmitted by dogs. *E. canadensis* is composed of several closely-related genotypes (camel, pig and deer strains) found throughout Eurasia and North America and transmitted by wolves and dogs. *E. felidis* was initially thought to be a subspecies of *E. granulosus*, but is now considered to be a separate species in Africa with lions as definitive hosts. A new species, *E. shiquicus,* recently described from China was thought to be closely related to *E. multilocularis* but it forms unilocular minicysts in lagomorphs. *E. multilocularis* commonly cycles between foxes and rodents in Europe and North America, although domestic animals and humans may become infected with larval stages (multilocular hydatid cysts). *E. vogeli* cycles between bush dogs and rodents, and *E. oligarthus* between felids and rodents, in Central and South America, with intermediate hosts (sometimes humans) developing polycystic and unicystic hydatid cysts, respectively.

***Echinococcus* species**	**Definitive hosts [adults in small intestines] {clinical signs}**	**Intermediate hosts [metacestodes in tissues] {clinical signs}**	**Distribution**
Species causing cystic (unilocular) echinococcosis (CE) (*E. granulosus sensu lato*)			
E. granulosus sensu stricto (genotypes G1-3) (dwarf dog tapeworm, hydatid tapeworm) (probable synonyms: *E. cameroni, E. cepanzoi, E. intermedius, E. iraqii, E. longimanubrius, E. lycaontis, E. minimus, E. patagonicus*)	Carnivora: canid (dog, wolf, fox, jackal, dingo, coyote?), hyaenid (hyaena) {occasionally diarrhoea}	Artiodactyla: bovid (sheep, goat, cattle*, buffalo, yak), camelid (camel), suid (pig), cervid (deer?); Diprotodontia: macropodid (wallaby, kangaroo), vombatid (wombat); Lagomorpha: leporid (rabbit, hare); Primates: cercopithecid (macaques, vervets, baboons), lemurid (lemurs), hominid (human) [unilocular hydatid cysts in liver, lungs, organs] *sterile cysts {space-occupying lesions}	Europe, Middle-East, Africa, Americas, Asia, Australia (except Iceland, New Zealand, Tasmania)
E. equinus (*E. granulosus* genotype G4)	Carnivora: canid (dog, fox)	Perissodactyla: equid (horse, donkey, zebra) [unilocular hydatid cysts in liver, lungs, organs]	Europe, Middle-East, Africa
E. ortleppi (*E. granulosus* genotype G5)	Carnivora: canid (dog, jackal)	Artiodactyla: bovid (cattle, buffalo, sheep, goat), suid (pig); Perissodactyla: equid (zebra) [unilocular hydatid cysts in viscera]	Europe, Africa, Asia, South America
*E. canadensis** (*E. granulosus* genotypes G6-10)	Carnivora: canid (dog, wolf)	Artiodactyla: bovid (cattle, sheep, goat), suid (pig), camelid (camel), cervid (moose, elk, reindeer, caribou, mule deer?); rarely Primates: hominid (human) [unilocular hydatid cysts in viscera]	Middle-East, Africa, Asia, Americas, Europe
*Some workers suggested that *E. canadensis* genotypes could be allocated to 3 species: G6/G7 to *E. intermedius*, G8 to *E. borealis*, and G10 to *E. canadensis;* while others regarded the latter two to be conspecific or even a 'Northern biotype' of *E. granulosus,* and the separation of *E. intermedius* (presumed to have pigs and camels as intermediate hosts) to be premature.			

E. felidis (syn. *E. granulosus felidis*)	Carnivora: felid (lion, African wild cat), hyaenid (spotted hyaena), canis (Cape hunting dog, silver-backed jackal)	Artiodactyla: suid (warthog, bushpig), bovid (wildebeest, buffalo, antelope), giraffid (giraffe), hippopotamid (hippopotamus?); Perissodactyla: equid (zebra) [unilocular hydatid cysts in viscera]	Africa
E. shiquicus	Carnivora: canid (Tibetan fox)	Lagomorpha: ochotonid (pika) [unilocular minicysts in liver and lungs]	Tibet
Species causing polycystic echinococcosis (PE)			
E. vogeli	Carnivora: canid (bush-dog, dog, crab-eating fox)	Rodentia: cuniculid (paca), dasyproctid (agouti), echimyid (coypu); Primates: hominid (gorilla, orangutan, human) [unilocular + polycystic hydatid cysts in liver, lungs, organs] {space-occupying lesions}	Central and South America
Species causing unicystic echinococcosis (UE)			
E. oligarthus (syn. *E. cruzi, E. pampeanus*)	Carnivora: felid (cougar, jaguar, ocelot, jaguarundi, puma, pampas cat, Geoffroy's cat, bobcat, cat)	Rodentia: cuniculid (paca), dasyproctid (agouti), murid (gerbil, spiny rat, climbing rat, cotton rat), Didelphimorphia: didelphid (opossum); Lagomorpha: leporid (cottontail); rarely Primates: hominid (human) (unicystic hydatid cysts in viscera, muscles, skin) [space-occupying lesions]	Central and South America
Species causing alveolar (multilocular) echinococcosis (AE)			
E. multilocularis (dwarf fox tapeworm) [syn. *E. russicensis, E. sibiricensis*]	Carnivora: canid (red fox, arctic fox, sand fox, grey fox, Tibetan fox, corsac fox, wolf, coyote, dog, raccoon dog), felid (cat, lynx)	Rodentia: echimyid (coypu), cricetid (common vole, tundra vole, northern red-backed vole, grey red-backed vole, Hokkaido red-backed vole, meadow vole, northern water vole, bank vole, European pine vole, steppe vole, lemming, muskrat, deermouse), soricid (long-tailed shrews), murid (house mouse, brown rat, Mongolian gerbil), echimyid (coypu), sciurid (ground squirrel), spalacid (Chinese zokor); Lagomorpha: leporid (rabbit), ochotonid (plateau pika); Artiodactyla: suid (pig); Perissodactyla: equid (horse); Carnivora: canid (dog); Primates: cercopithecid (crab-eating macaques), atelid (spider monkey), lemurid (ring-tailed lemur), hominid (gorilla, human) [multilocular (alveolar) hydatid cysts in liver, lungs, organs] {space-occupying lesions}	North America, Asia, Europe

Parasite morphology: Tapeworms form three different developmental stages: eggs; larvae; and adults. Adult worms are small (1-7 mm long) and have a scolex and strobila ranging from 3-7 proglottids. The scolex has four lateral suckers and a non-retractable rostellum armed with a double crown of recurved hooks (28-50 in *E. granulosus*, 26-36 in *E. multilocularis*). All adults are hermaphroditic and contain both male and female reproductive organs. While the gonads in anterior segments are immature, they are mature and functional in posterior segments. The caudal segment is gravid and the uterus is filled with eggs. The eggs are typical for most taeniid species and are small and round (30-43 µm in diameter), thick-shelled and contain a hexacanth (6-hooked) non-ciliated embryo (oncosphere). Larval (metacestode) stages are lacunate (internal channel forms during development) and they become encysted in tissues as hydatid cysts (bladder-worms) which produce multiple infective stages known as protoscoleces (scoleces invaginated into their neck portions and already containing suckers and developing hooks) either directly from the inner

germinal layer of the cyst wall, or by forming brood sacs by endogenous (internal) or exogenous (external) budding of the germinal layer (detached sacs freely floating in vesicular fluid known as hydatid sand). *E. granulosus* forms fluid-filled unilocular cysts with endogenous budding to form brood capsules, *E. vogeli* forms fluid-filled polycystic cysts with exogenous budding to form new cysts and endogenous budding to form septae, and *E. multilocularis* forms fluid-free multilocular or alveolar cysts with exogenous budding to form multiple cysts.

Site of infection: The small adult tapeworms attach to the mucosa of the small intestines in dogs, sometimes in their thousands. The larval stages (hydatids) most commonly infect visceral tissues and organs, especially the liver and lungs, in their mammalian intermediate hosts, although cysts may be found in many other locations, including the brain and long bones.

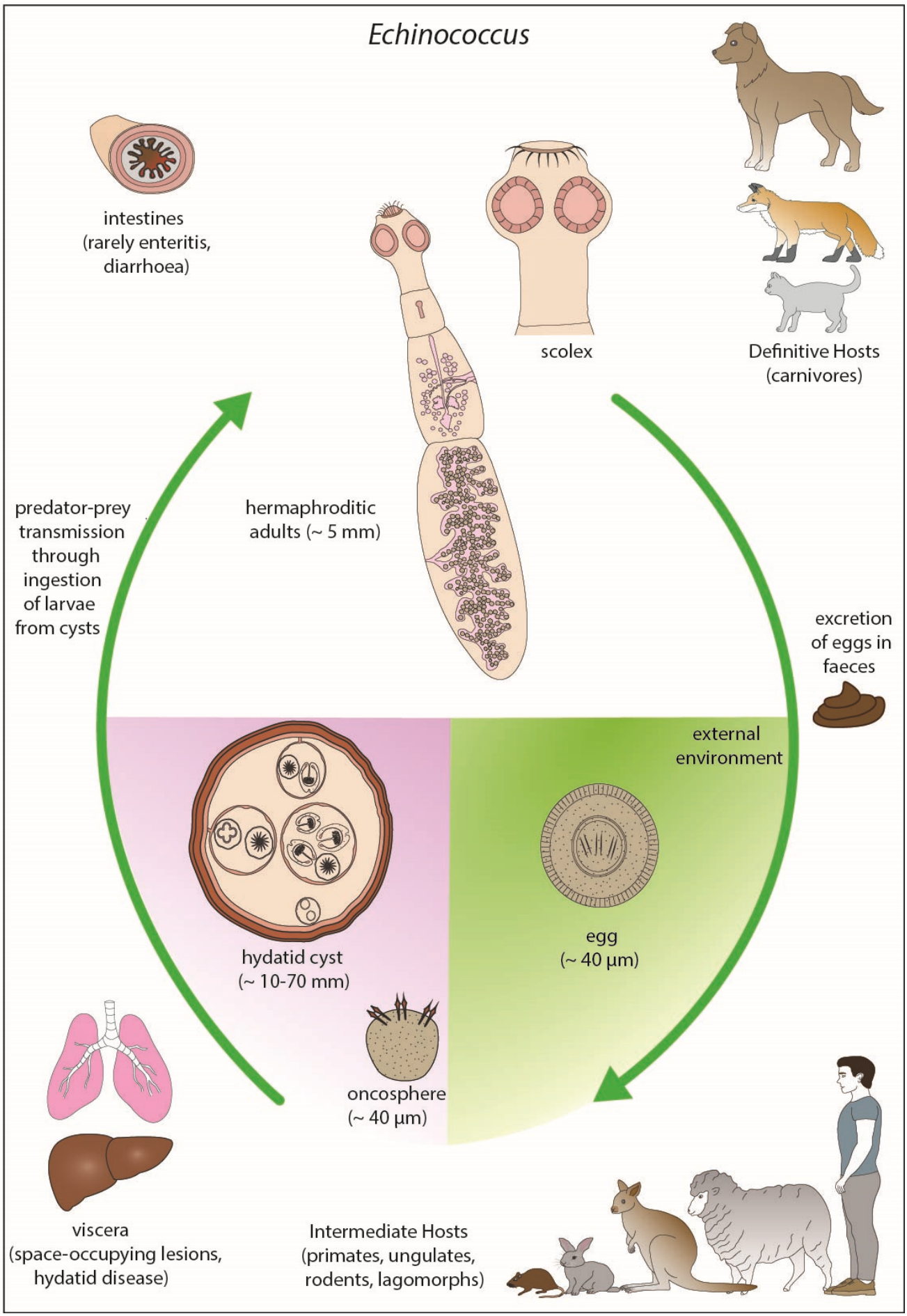
Pathogenesis: The adult stages are considered benign and do not cause disease in their definitive hosts, as the small tapeworms do not invade or feed on host tissues. Large numbers of worms (thousands) have been found in asymptomatic canid hosts, and only rarely have heavy infections been associated with any clinical signs (enteritis, diarrhoea). The larval (metacestode) stages which encyst within visceral tissues in intermediate hosts initially do not cause clinical disease, but they may cause significant pathological changes as the cysts grow and put pressure on surrounding tissues producing chronic space-occupying lesions. *Echinococcus* spp. form different types of cysts, either discrete single-compartment (unilocular) cysts which exhibit expansive growth or budding multi-compartmented (multilocular) cysts which can infiltrate organs and even disseminate to other tissues and organs. *E. granulosus s.l.* causes cystic echinococcosis (CE, also known as unilocular echinococcosis or cystic hydatid disease), *E. multilocularis* causes alveolar echinococcosis (AE, also called multilocular or multivesicular echinococcosis, or alveolar hydatid disease), while *E. vogeli* and *E. oligarthus* cause polycystic echinococcosis (PE, recently called neotropical PE). Because only discrete cysts of *E. oligarthus* have been detected in humans, this disease has also been called unicystic echinococcosis (UE). Cysts may grow around 1 mm per month and are often 1-7 cm in diameter when discovered, but some may eventually measure up to 20-30 cm in diameter with litres of fluid containing thousands of protoscoleces. Cysts in humans develop over many years before symptoms become apparent, while most domestic livestock are slaughtered before cysts become large enough to cause clinical signs (although longer-lived animals such as horses may develop clinical disease). However, CE may cause significant economic losses in agriculture from the condemnation of animal organs at meat inspection, and possibly from reduced meat, milk and fibre production during the course of infection and disease. Organ enlargement may be accompanied by a variety of clinical signs depending on the size and location of the cysts. CE generally involves the liver and lungs, and less frequently the bones, kidneys, spleen, muscles, central nervous system and eyes. Cysts in the liver may cause pressure atrophy, compression, hepatomegaly, cholestatic jaundice, anaemia, portal hypertension, ascites, cirrhosis, abdominal distention, pain, nausea, vomiting and indigestion. Cysts in the lung may cause chronic cough, haemoptysis (coughing up blood), dyspnoea (difficulty breathing), chest pain, pneumothorax and abscess formation (from secondary bacterial infection). Cysts in the brain or spinal cord can provoke acute inflammatory responses and numerous neurological sequelae, including epilepsy, seizures and blindness. Cysts in the bones can destroy internal structure and result in spontaneous fractures. Cysts in the heart can cause pericardial effusion, heart block or other arrhythmias, and sudden death. Infections may also be accompanied by non-specific signs such as anorexia, weight loss and weakness. Cyst rupture has been associated with acute clinical signs (such as peritonitis and pneumothorax), and the sudden release of hydatid fluid may cause severe allergic reactions (such as asthma, pruritus, urticaria and anaphylactic shock). Protoscoleces released from ruptured cysts can regress and form new hydatid cysts throughout the body. Some cysts formed are sterile and never produce brood capsules, while others become sterile after bacterial infection or calcification. AE is less common than CE but is more serious and can be fatal if left untreated. It is characterized by the slow development of a primary tumour-like lesion usually in the liver (often misdiagnosed as hepatocellular carcinoma) and then larval metastases may spread to other organs (such as the spleen, lungs or brain) by dissemination via the blood and lymphatic systems. Clinical signs include weight loss, abdominal pain, general malaise and progressive hepatic failure. Larval stages of *E. multilocularis* may also exhibit incomplete atypical development in humans by forming sheets of thin membranes (with no identifiable cestode structures) which bisect the liver disrupting structure and function. Several hundred cases of PE have been recorded in humans, with multi-chambered interconnected cysts typically developing in the liver (often leading to hepatic insufficiency) and then spreading in the peritoneal and pleural cavities and invading other organs. Only three cases of UE have been reported in humans, two involving discrete cysts behind the eyes and one in the heart.

Developmental cycle and mode of transmission: Tapeworms have an indirect life-cycle involving predator-prey transmission between definitive (carnivorous) and intermediate (herbivorous/omnivorous) mammalian hosts. Mature tapeworms release numerous thick-shelled eggs from gravid segments (proglottids), although occasionally the hindmost segment may break off and be shed as a package of eggs. The eggs are very resistant to external environmental conditions and can survive for several weeks or months on pastures or fomites, unless they are exposed to hot dry conditions. The eggs have a sticky coat and may adhere to animal fur and other objects. Birds and insects (beetles, flies) may also act as mechanical vectors. Herbivores and omnivores become infected by ingesting eggs; either on herbage, in water, or by hand-to-mouth transfer. Following ingestion, the eggs hatch releasing the oncosphere which uses its three pairs of hooks to penetrate the gut, enter the circulation and settle in various organs and tissues (frequently in the liver after being filtered out by portal capillaries). Over many months, they form fluid-filled hydatid cysts (unilocular or multilocular depending on the parasite species) and eventually produce multiple infective protoscoleces (directly from the germinal membrane or via brood sacs formed by endogenous or exogenous budding). This asexual reproduction of the metacestode stage is a unique feature for the genus *Echinococcus*. When mature cysts in offal or carcases are eaten by carnivorous

definitive hosts, the cyst wall is digested away freeing the protoscoleces, which evaginate and attach to the small intestinal mucosa. They mature to adult worms in about 8 weeks and may live for 5-20 months. Various *Echinococcus* species, strains and genotypes have been recognized based on differences in parasite morphology, development, biochemistry, genetics and host specificity. Most appear to be adapted to particular intermediate host species and do not develop well in other host species. Infections are particularly well adapted to pastoral cycles involving farm dogs and domestic livestock (notably sheep and cattle), as well as sylvatic cycles involving wild carnivores (wolves, coyotes, dingoes) and free-ranging herbivores (such as deer, moose and wallabies). Spill-over may occur between sylvatic and pastoral cycles. Infections in human populations occur more frequently in rural areas, particularly where local traditions are conducive to transmission; e.g. feeding dogs offal, eating dog intestines, not burying the dead, and even using dog faeces to tan hides.

Differential diagnosis: Infections in dogs may be diagnosed by the detection of eggs, and occasionally worms, in faecal samples. Eggs, however, are morphologically indistinguishable from those of *Taenia* spp. Purgation with arecoline prior to faecal testing has been discontinued due to safety concerns for both definitive hosts and diagnosticians. Immuno-coprological tests have also been developed to detect parasite antigens in faecal samples. Infections in intermediate hosts are generally diagnosed well after the larvae have encysted. Clinical symptoms of a slow-growing tumour accompanied by eosinophilia are suggestive. Cysts may be visualized by various medical imaging techniques; including X-rays, ultrasound, computerized axial tomography (CAT) scans, and magnetic resonance imaging (MRI). Biopsies (fine needle aspiration of cyst fluid) can be used to assist diagnosis, but there is always the attendant risk of cyst rupture or leakage leading to allergic reactions or further cyst development. Cyst fluid can be examined microscopically for protoscoleces or tested for parasite antigens by enzyme immunoassays or for parasite DNA by polymerase chain reaction (PCR) assays. Several immunological tests (complement fixation, agglutination, enzyme immunoassays, immunoblots, immunochromatography) have been developed to detect host antibodies or parasite antigens (e.g. Em16, Em 18, antigen B) in host serum or faecal samples. Best results were obtained using semi-defined or recombinant antigens, although some cross-reactivity problems were encountered and some people simply do not develop detectable antibody levels. An intradermal (Casoni) test using hydatid fluid has also been used in surveys. Molecular tests are also being developed to characterize parasite DNA by PCR amplification of nuclear (18S ribosomal RNA, internal transcribed spacers (ITS), elongation factor 1-α (*ef1a*)) or mitochondrial (cytochrome c oxidase subunit 1 (*cox1*), cytochrome b (*cob*), large subunit ribosomal RNA (*rrnL*), NADH dehydrogenase subunit 1 (*nad1*)) genes, and by restriction fragment length polymorphism (RFLP), single strand conformational polymorphism (SSCP) or microsatellite analyses.

Treatment and control: Despite some promising indications, the treatment of hydatid disease with conventional anthelmintic drugs has not proven wholly effective, being complicated by the large size and inaccessible location of cysts and their thick, possibly impenetrable, walls. Variable results have been obtained using select isoquinolines (praziquantel) and benzimidazoles (mebendazole), while albendazole and niclosamide have been less effective. The only remaining treatment option is for the surgical removal of cysts, provided they are in favourable sites. Surgeons must take care not to rupture cysts as protoscoleces may spread to new sites to form more cysts. Scolecidal chemicals, such as cetrimide, may also be used during surgery to sterilize excision sites. Where cystectomy is contraindicated, surgeons may use the puncture-aspiration-injection-reaspiration (PAIR) technique to puncture cysts under ultrasound guidance, aspirate cyst fluid, inject scolecides and reaspirate contents. Infections by adult worms in dogs can be successfully treated with praziquantel, and it is advisable to confine dogs and/or use purgatives to facilitate the collection and disposal of infected faeces. Preventing dogs from becoming infected involves eliminating offal and other potentially infected material from their diets, curbing their hunting behaviour, properly disposing of carcases in the field, and culling wild and feral dogs. Several countries have developed highly successful hydatid eradication campaigns based around dog management and treatment. Oncospheres have proven to be highly immunogenic and intermediate hosts may become immune to reinfection after primary exposure. This has prompted studies on vaccine development using defined oncosphere antigens, with considerable success reported using recombinant vaccines to prevent hydatid formation in domestic herbivores. Vaccination trials are continuing as some measure of control may be possible in livestock involved in pastoral cycles, although there will be access problems vaccinating wildlife involved in sylvatic cycles.


Echinococcus
intestines
(rarely enteritis,
diarrhoea)
scolex
Definitive Hosts
(carnivores)
predator-prey
transmission
through
ingestion
of larvae
from cysts
hermaphroditic
adults (~ 5 mm)
excretion
of eggs in
faeces
external
environment
hydatid cyst
(~ 10-70 mm)
egg
(~ 40 µm)
oncosphere
(~ 40 µm)
viscera
(space-occupying lesions,
hydatid disease)
Intermediate Hosts
(primates, ungulates,
rodents, lagomorphs)



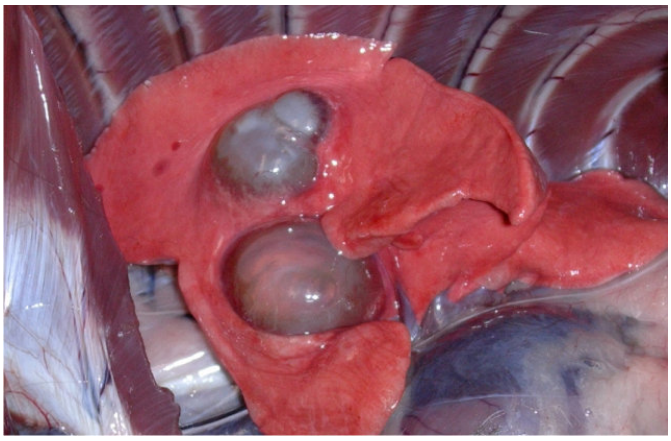
Echinococcus adult worm



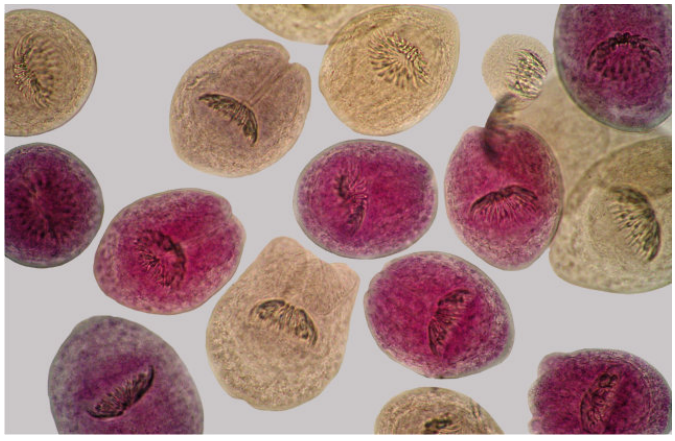
Echinococcus scolex



Echinococcus egg



Echinococcus hydatid cysts in lung of kangaroo



Echinococcus protoscoleces from hydatid cyst

Anoplocephala, Anoplocephaloides, Equinia, Moniezia, Thysaniezia
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Cyclophyllidean tapeworms are usually intestinal parasites of terrestrial vertebrates and have an anterior scolex (hold-fast organ with suckers and sometimes hooks) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). Eucestodes have indirect life-cycles involving oncospheres (hexacanth embryos) released from ingested eggs to form encysted larval stages (metacestodes) in the tissues of intermediate hosts and their transmission to carnivorous definitive hosts. Adult anoplocephalids lack a rostellum and hooks, have broad gravid segments and are parasitic in hoofed mammals, birds and reptiles but are rarely pathogenic. The encysted larval stages (cysticercoids) occur in arthropods, usually oribatid mites which are ingested with pasture or during grooming.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)
Family:	Anoplocephalidae (tapeworms of hoofed animals, scolex unarmed, cysticercoids in arthropods)
Genus:	*Anoplocephala* (parasitic in intestines of herbivores)
Genus:	*Anoplocephaloides* (parasitic in intestines of herbivores)
Genus:	*Equinia* (parasitic in intestines of herbivores)
Genus:	*Moniezia* (parasitic in intestines of herbivores)
Genus:	*Thysaniezia* (parasitic in intestines of herbivores)
Species:	various species cause enteritis in horses and ruminants

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on

the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda ('true' tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
"Tetraphyllidea' relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Cyclophyllidean cestodes are polyzoic containing from 2 to > 1,000 proglottids demarcated by external segmentation. They possess an anterior scolex with 4 suckers, many with a rostellum (often armed), and they have compact post-ovarian vitellaria. Adult worms are found in terrestrial vertebrate definitive hosts (mammals, birds, reptiles, amphibians) while larval metacestodes occur in vertebrate (mammal, amphibian, bird) or invertebrate (mollusc, acari, insect) intermediate hosts. Over 3,000 species have been described in 400 genera in 16 families: Acoleidae, Amabiliidae, Anoplocephalidae, Catenotaeniidae, Davaineidae, Dioecocestidae, Dilepididae, Dipylidiidae, Gyrporhynchidae, Hymenolepididae, Mesocestoididae, Metadileptidae, Nematotaeniidae, Paruterinidae, Progynotaeniidae, and Taeniidae (all with lateral genital pores, except the Mesocestoididae). Anoplocephalid tapeworms are parasitic in the small intestines or bile ducts of herbivorous definitive hosts (mammals, birds, reptiles) and they form larval stages

(cysticerci) in arthropod intermediate hosts (oribatid mites). Mature worms range in size from 0.2-5.0 m in length, the scolex is unarmed and bears 4 suckers, some with lappets. Over 400 species have been described in 55 genera.

Four anoplocephalid subfamilies have been described based on differences in their uterine development: Anoplocephalinae with a tubular or reticular uterus that persists in gravid proglottids (230 species in 32 genera, including *Anoplocephala*, *Anoplocephaloides*, *Andrya*, *Aporina, Bertiella*, *Cittotaenia*, *Ctenotaenia*, *Diandrya, Equinia, Gallegoides*, *Genovia, Hemiparonia*, *Killigrewia*, *Moniezia*, *Monoecocestus, Mosgovoyia*, *Neandrya, Paramoniezia gen. inq.*, *Paronia, Paranoplocephala*, *Parasciurotaenia, Phascolocestus, Phascolotaenia*, *Progamotaenia*, *Pulluterina, Schizorchis, Schizotaenia, Sciurotaenia, Stringopotaenia, Sudarikovina, Triplotaenia, Wallabicestus*); Linstowiinae with a uterus that disintegrates to form capsules around individual eggs (100 species in 13 genera, including *Atriotaenia*, *Cycloskrjabinia*, *Echidnotaenia*, *Gekkotaenia, Linstowia*, *Mathevotaenia*, *Oochoristica*, *Paralinstowia*); Thysanosominae with a paruterine organ receiving eggs from the uterus (30 species in 5 genera, including *Avitellina*, *Stilesia*, *Thysaniezia*, *Thysanosoma*, *Wyominia*); and Inermicapsiferinae with complex egg capsules (25 species in 4 genera, including *Inermicapsifer, Thysanotaenia*). Anoplocephalines primarily infect herbivorous mammals (ruminants, equids, lagomorphs, phalangerids) which accidentally ingest infected oribatid mites while grazing, but they may also infect other mammals (rodents, flying lemurs, primates (including humans)), and birds (especially parrots). Linstowiines infect insectivorous mammals (bats, rodents, marsupials) and reptiles, and form larval stages in Coleoptera (beetles). Thysanosomines infect ruminants and have Psocoptera (barklice) as intermediate hosts, while Inermicapsiferines infect hyraxes in Africa (IH unknown). The genera of greatest veterinary importance are those that parasitise domestic ruminants and equids; particularly *Anoplocephala, Equinia, Moniezia* and *Thysaniezia* species, many of which have cosmopolitan distributions along with their hosts, although some are confined to specific areas of Africa, Asia or North America depending on their host distributions. Many anoplocephaline species have also been found to infect rodents and lagomorphs, notably *Paranoplocephala* and *Anoplocephaloides* spp. in voles, lemmings and rabbits in Holarctic regions.

Parasite species	**Definitive hosts [adults in gut]**	**Intermediate hosts [cysticercoids in body cavity]**	**Distribution**
Subfamily: Anoplocephalinae (uterus persisting in gravid proglottids, eggs with pyriform apparatus)			
Moniezia (2 sets of reproductive organs in each segment, 2 reticular uteri)			
M. amphibia sp. inq	Artiodactyla: hippopotamid (hippopotamus)		Africa
M. babai	Artiodactyla: bovid (goat)		India
M. baeri	Artiodactyla: cervid (reindeer)		Europe, North America
M. benedeni (syn. *M. alba, M. autumnalia, M. conjugens, M. crassicollis, M. denticulata, M. kuznetsovi, M. latifrons, M. neumanni, M. parva, M. pellucida, M. planissima, M. rupicaprae, M. skrjabini, M. translucida, M. triangularis*)	Artiodactyla: bovid (cattle, buffalo, European bison, zebu, sheep, goat, mountain goat, West African dwarf goat, sable antelope, Jackson's hartebeest, greater kudu), cervid (white-tailed deer, mule deer, roe deer, elk), camelid (camel)	Oribatida: achipteriid (*Achipteria coleoptrata*), peloppiid (*Ceratoppia*), ceratozetid (*Ceratozetes, Trichoribates*), galumnid (*Galumna elimata, G. obvia, Pergalumna*), liacurid (*Liacarus coracinus*), scheloribatid (*Liebstadia, Scheloribates laevigatus*), oribatulid (*Oribatula, Zygoribatula*), camisiid (*Platynothrus*), punctoribatid (*Punctoribates*)	worldwide
M. bequaerti	Rodentia: capromyid (Desmarest's hutia)		Central America
M. caprae	Artiodactyla: bovid (goat)		Europe
M. chappuisi	Artiodactyla: bovid (roan antelope)i		Africa
M. devraoi	Artiodactyla: bovid (goat)		India
M. elongata sp. inq.	Artiodactyla: bovid (goat)		India
M. expansa (syn. *M. aishvaryae, M. aurangabadensis, M. bharalae, M. caprai, M. jadhavii, M. jalnaensis, M. mansurae, M. marathwadensis, M. minima, M. murhari, M. osmanabadensis, M. roshanensis, M. shegaonesis, M. shindei, M. sureshi, M. trigonophora, M.*	Artiodactyla: bovid (sheep, goat, West African dwarf goat, cattle, zebu, ibex, common duiker, gazelle, scimitar oryx, steenbok, Sharpe's grysbok, bharal), cervid (red deer, white-tailed deer, roe deer, fallow deer), camelid (camel), suid (pig); rarely Primates: hominid (human)	Oribatida (mites): achipteriid (*Achipteria coleoptrata, A. punctata, Parachipteria*), astegistid (*Furcoribula*), camisiid (*Platynothrus*), carabodoid (*Carabodes minusculus*), cepheid (*Cepheus*), ceratozetid (*Ceratozetes, Pelops planicornis, Trichoribates*	worldwide

waranangarensis) (sheep tapeworm, double-pored ruminant tapeworm)		*trimaculatus*), damaeid (*Notaspis punctatus*), eremaeid (*Eremaeus*), euzetid (*Euzetes*), galumnid (*Galumna elimata, G. obvia, G. nervosus, G. baloghi, Allogalumna, Pergalumna*), haplozetid (*Peloribates, Protoribates lophotrichus*), hermanniellid (*Hermanniella*), liacurid (*Liacarus coracinus, Xenillus*), mochlozetid (*Unguizetes reticulatus*), oribatellid (*Oribatella*), oribotritiid (*Oribotritia loricata*), oribatulid (*Oribatula tibialis, O. cognata, O. friziae, Zygoribatula*), parakalummid (*Neoribates aurantiacus*), peloppiid (*Ceratoppia*), phenopelopid (*Eupelops, Peloptulus, Phenopelops planicornis*), punctoribatid (*Punctoribates punctum*), scheloribatid (*Scheloribates latipes, S. laevigatus, S. perforatus, S. fimbriatus, Protoschelobates seghetti*), scutoverticid (*Scutovertex*), tectocepheid (*Tectocepheus velatus*)	
M. govindae	Artiodactyla: bovid (goat)		India
M. hircusae	Artiodactyla: bovid (goat)		India
M. interproglottina	Artiodactyla: bovid (bharal)		India
M. kalavati	Artiodactyla: bovid (goat)		India
M. lyallpuriensis	Artiodactyla: bovid (goat)		Pakistan
M. madhukarae	Artiodactyla: bovid (goat)		India
M. maharashtrae	Artiodactyla: bovid (goat)		India
M. mathevossianae	Artiodactyla: cervid (reindeer)		Eurasia
M. mettami	Artiodactyla: suid (desert warthog)		Africa
M. mizkewitschi	Artiodactyla: cervid (reindeer)		Eurasia
M. monardi	Artiodactyla: bovid (Ugandan kob, roan antelope, waterbuck)		Africa
M. orientalis	Artiodactyla: bovid (bharal)		India
M. ovisae	Artiodactyla: bovid (bharal)		India
M. pallida	Perissodactyla: equid (horse)		Africa
M. phacochoeri	Artiodactyla: suid (desert warthog, common warthog)		Africa
M. rajalaensis	Artiodactyla: bovid (goat)		India
M. rangiferina sp. inq.	Artiodactyla: cervid (reindeer)		Eurasia
M. rhea	Rheiformes: rheid (greater rhea)		South America
M. rugosa	Primates: atelid (northern muriqui)		South America
M. shivajiraovae	Artiodactyla: bovid (goat)		India
M. sichuanensis	Artiodactyla: cervid (musk deer)		China
M. taimyrica	Artiodactyla: cervid (reindeer)		Eurasia
M. transvaalensis	Rodentia: thryonomyid (greater cane rat)		Africa
Equinia (single set of reproductive organs per segment, arborescent (tree-like) uterus)			
E. mamillana (syn. *Paranoplocephala, Anoplocephala,*	Perissodactyla: equid (horse)	Oribatida (mites): achipteriid (*Achipteria*), ceratozetid (*Ceratozetes*), galumnid	worldwide

Anoplocephaloides)		(*Galumna, Allogalumna*), scheloribatid (*Scheloribates*)	
Anoplocephala (single set of reproductive organs per segment, uterus elongated sac with pocket-like appendages)			
A. diminuta	Perissodactyla: rhinocerotid (Javan rhinoceros)		Asia
A. gigantea (syn. *A. vulgaris*)	Perissodactyla: rhinocerotid (black rhinoceros)		Africa
A. gorillae	Primates: hominid (eastern gorilla)		Africa
A. latissima	Perissodactyla: rhinocerotid (Javan rhinoceros)		Asia
A. magna (syn. *A. plicata*) (equine tapeworm)	Perissodactyla: equid (horse, donkey)	Oribatida (mites): scheloribatid (*Scheloribates*)	worldwide
A. manubriata	Proboscidea: elephantid (Asian elephant)		Asia
A. perfoliata (syn. *A. rhodesiensis*)	Perissodactyla: equid (horse, donkey, zebra, Burchell's zebra)	Oribatida (mites): achipteriid (*Achipteria, Parachipteria*), ceratozetid (*Ceratozetes, Trichoribates*), galumnid (*Galumna, Allogalumna*), scheloribatid (*Scheloribates, Liebstadia, Urubambates*), carabodoid (*Carabodes*), eremaeid (*Eremaeus*), hermanniellid (*Hermanniella*), liacurid (*Liacarus*), oribatulid (*Zygoribatula*), camisiid (*Platynothrus*)	worldwide
Anoplocephaloides (single set of reproductive organs per segment, tubular uterus)			
A. bulmeri	Rodentia: cricetid (southern bog lemming)		North America
A. dentata	Rodentia: cricetid (common vole, European snow vole, Balkan snow vole, European pine vole, Gunther's vole, tundra vole, field vole, singing vole, meadow vole, reed vole, tiaga vole, bank vole), murid (yellow-necked mouse), spalacid (lesser mole-rat)		Eurasia, North America
A. dentatoides	Rodentia: cricetid (gray red-backed vole)		Eurasia
A. kontrimavichusi	Rodentia: cricetid (northern bog lemming)		North America
A. lemmi	Rodentia: cricetid (North American brown lemming, Siberian brown lemming)		North America, Russia
A. troeschi (syn. *Paranoplocephala infrequens*)	Rodentia: cricetid (meadow vole, montane vole), geomyid (plains pocket gopher)		North America
Reassigned species			
A. acanthocirrosa (now *Afrobaeria*)	Rodentia: murid (southern African vlei rat, Dent's vlei rat)		Africa
A. apodemi (now *Hokkaidocephala*)	Rodentia: murid (small Japanese field mouse)		Japan
A. arfaai (now *Gallegoides*)	Rodentia: murid (wood mouse)		Europe
A. baeri (now *Hokkaidocephala*)	Rodentia: murid (small Japanese field mouse)		Japan
A. floresbarroetae (now *Genovia,* formerly *Leporidotaenia*)	Lagomorpha: leporid (tapeti)		Central America
A. indicata (now *Flabelloskrjabinia*)	Perissodactyla: tapirid (Malaysian tapir)		Asia
A. isomydis (now *Afrobaeria*)	Rodentia: murid (Abyssinian grass rat, common rufous-nosed rat, tropical vlei rat)		Africa

A. neofibrinus (now *Microcephaloides*)	Rodentia: cricetid (round-tailed muskrat)		North America
A. pseudowimerosa (now *Genovia,* formerly *Leporidotaenia*)	Lagomorpha: leporid (European rabbit)		Europe
A. rauschi (now *Paranoplocephala*)	Rodentia: cricetid (European snow vole, European pine vole)		Europe
A. romerolagi (now *Leporidotaenia*)	Lagomorpha: leporid (volcano rabbit)		Mexico
A. ryjikovi (formerly *Paranoplocephala*, now *Parasciurotaenia*)	Rodentia: sciurid (gray marmot, Himalayan marmot)		Asia
A. schachmatovae (now *Paranoplocephaloides*)	Rodentia: cricetid (tundra vole)		Eurasia, North America
A. tapirus (now *Flabelloskrjabinia*)	Perissodactyla: tapirid (tapir)		Asia
A. tenoramuraiae (now *Microcephaloides*)	Rodentia: cricetid (European snow vole, European pine vole)		Europe
A. transversaria (now *Marmotocephala*)	Rodentia: sciurid (long-tailed marmot, gray marmot)		Asia
A. variabilis (syn. *Paranoplocephala borealis*) (now *Microcephaloides*)	Rodentia: geomyid (plains pocket gopher, northern pocket gopher), cricetid (meadow vole, singing vole, tundra vole, prairie vole, montane vole, Siberian brown lemming)		North America, Russia
A. wigginsi (now *Marmotocephala*)	Rodentia: sciurid (Arctic ground squirrel)		North America
A. wimerosa (now *Genovia,* formerly *Leporidotaenia*)	Lagomorpha: leporid (European rabbit, mountain hare)		Europe
Paranoplocephala (single set of reproductive organs per segment, reticular uterus, long vagina and cirrus)			
P. batzlii	Rodentia: cricetid (singing vole, insular vole)		Alaska
P. campestris sp. inq.	Rodentia: cricetid (common vole)		Europe
P. communis sp. inq.	Rodentia: cricetid (southern red-backed vole, western harvest mouse, meadow vole, montane vole, long-tailed vole)		North America
P. feodorovi (syn. *Parandrya*)	Rodentia: cricetid (European water vole, field vole, Maximowicz's vole)		Eurasia
P. forcipata sp. inq.	Rodentia: chinchillid (northern viscacha)		South America
P. freemani	Rodentia: cricetid (taiga vole, muskrat)		Alaska
P. jarrelli	Rodentia: cricetid (tundra vole)		Europe, North America
P. kalelai	Rodentia: cricetid (grey red-backed vole, bank vole)		Palearctic
P. kirbyi	Rodentia: cricetid (California vole)		North America
P. macrocephala (syn. *P. translucida*)	Rodentia: geomyid (plains pocket gopher), cricetid (meadow vole)		North America
P. maseri	Rodentia: cricetid (sagebrush vole)		North America
P. microti	Rodentia: cricetid (prairie vole)		North America
P. montana sp. inq.	Rodentia: cricetid (common vole, European snow vole)		Russia
P. omphalodes (syn. *P. caucasica*)	Rodentia: cricetid (common vole, European water vole, tundra vole, insular vole, singing vole, field vole, bank vole, social vole, grey dwarf hamster), murid (southern African vlei rat, bush vlei rat)		Palearctic, Africa

Reassigned species			
P. acanthocirrosa (now *Afrobaeria*	Rodentia: murid (Southern African vlei rat, Dent's vlei rat)		Africa
P. alaskensis (now *Douhtittia nordensikoeldi*)	Rodentia: cricetid (singing vole)		North America
P. alternata (now *Rauschoides*)	Rodentia: cricetid (northern collared lemming, Arctic lemming)		Holarctic
P. aquatica (now *Rodentocestus*)	Rodentia: cricetid (European water vole, muskrat)		Europe
P. arctica (now *Rauschoides*)	Rodentia: cricetid (northern collared lemming)		Nearctic
P. bairdi (syn. *Andrya*) (now *Douhtittia*)	Rodentia: cricetid (eastern heather vole, western heather vole, red tree vole, Sonoma tree vole, white-footed vole)		North America
P. blanchardi (now *Microticola*)	Rodentia: cricetid (common vole, field vole, Skomer vole, European water vole, muskrat)		Palearctic
P. buryatiensis (now *Gulyaevia*)	Rodentia: cricetid (grey red-backed vole, reed vole)		Russia
P. dasymidis (now *Hunkeleriella*)	Rodentia: murid (African marsh rat)		Africa
P. etholeni (now *Microticola*)	Rodentia: cricetid (meadow vole)		Finland
P. fellmani (now *Lemminia*)	Rodentia: cricetid (Norway lemming)		Holarctic
P. genovi (now *Rodentocestus*)	Rodentia: cricetid (muskrat)		Europe
P. gracilis (now *Eurotaenia*)	Rodentia: cricetid (field vole)		Europe
P. gubanovi (now *Lemminia*)	Rodentia: cricetid (wood lemming)		Siberia
P. gundii (now *Afrojoyeuxia*)	Rodentia: ctenodactylid (common gundi)		Africa
P. janickii (now *Tenoraia*)	Rodentia: cricetid (field vole)		Palearctic
P. krebsi (now *Microcephaloides*)	Rodentia: cricetid (northern collared lemming)		Nearctic
P. longivaginata (now *Gulyaevaia*)	Rodentia: cricetid (red vole, grey red-backed vole), sciurid (red squirrel)		Siberia
P. mascomai (now *Microcephaloides*)	Rodentia: cricetid (Cabrera's vole)		Europe
P. neotomae (now *Andrya*)	Rodentia: cricetid (dusky-footed woodrat)		North America
P. neofibrinus (now *Microcephaloides*)	Rodentia: cricetid (round-tailed muskrat)		North America
P. nevoi (now *Microcephaloides*)	Rodentia: spalacid (Middle East blind mole-rat)		Syria
P. nordenskioeldi (now *Douthittia*)	Rodentia: cricetid (northern collared lemming, Arctic lemming)		Holarctic
P. octodonensis (now *Andrya*)	Rodentia: octodontid (common degu)		South America
P. oeconomi (now *Parandrya*)	Rodentia: cricetid (bank vole)		Palearctic
P. nearctica (now *Douthittia*)	Rodentia: cricetid (southern red-backed vole, northern red-backed vole, long-tailed vole)		North America
P. ondatrae (now *Cookiella*)	Rodentia: cricetid (meadow vole, montane vole, muskrat)		North America
P. otomyos (now *Afrobaeria*)	Rodentia: murid (southern African vlei rat)		Africa
P. petuaristae (now *Bertiella*)	Rodentia: sciurid (Japanese giant flying squirrel)		Japan

P. primordialis (now *Douthittia*)	Rodentia: sciurid (American red squirrel), cricetid (meadow vole, long-tailed vole, singing vole, montane vole, tundra vole, water vole, southern red-backed vole, northern red-backed vole, dusky-footed woodrat, western harvest mouse)		Nearctic
P. sciuri (now *Rodentocestus*)	Rodentia: sciurid (northern flying squirrel)		North America
P. serrata (now *Arctocestus*)	Rodentia: cricetid (northern collared lemming, Arctic lemming)		Holarctic
P. threlkeldi (now *Monoecocestus*)	Rodentia: chinchillid (northern viscacha)		South America
P. yoccozi (now *Chionocestus*)	Rodentia: cricetid (European snow vole)		Europe
Subfamily: Thysanosominae (paruterine organ receiving eggs from uterus)			
Stilesia (2 sets of reproductive organs in each segment)			
S. ambajogaensis sp. inq.	Artiodactyla: bovid (cattle, zebu)		India
S. aurangabadensis sp. inq.	Artiodactyla: bovid (bharal)		India
S. daulatabadensis sp. inq. (syn. *S. thapari*)	Artiodactyla: bovid (goat)		India
S. globipunctata (syn. *S. alii, S. caprai, S. dhondagae, S. garhwalensis, S. govinda, S. kotdwarensis, S. mehdii, S. ovipunctata*)	Artiodactyla: bovid (sheep, goat, cattle, zebu, gazelle), camelid (camel)	Oribatida (mites): galumnid (*Galumna, Allogalumna*), scheloribatid (*Scheloribates*), oribatulid (*Zygoribatula*), hygrobatid (*Africacarus*)	Eurasia, Africa
S. hepatica (syn. *S. sjostedti*) (liver tapeworm)	Artiodactyla: bovid (sheep, goat, cattle, Cape bushbuck), cervid (elk, deer, moose) [bile ducts]	Oribatida (mites)	Africa, Asia
S. hircusi sp. inq.	Artiodactyla: bovid (goat)		India
S. marathwadaensis sp. inq.	Artiodactyla: bovid (goat)		India
S. okapi sp. inq.	Artiodactyla: giraffid (okapi)		Africa
S. vittata	Artiodactyla: bovid (sheep, goat), camelid (camel)	Oribatida (mites)	India, Africa
S. wadaensis sp. inq.	Artiodactyla: bovid (goat)		India
S. yavalensis sp. inq.	Artiodactyla: bovid (goat)		India
Thysanosoma (2 sets of reproductive organs per segment, but only single uterus)			
T. actinioides (fringed tapeworm)	Artiodactyla: bovid (sheep, goat, cattle, antelope), cervid (deer, elk) [also bile ducts]	Oribatida (mites)	Americas
T. misrai sp. inq.	Artiodactyla: bovid (goat)		India
Thysaniezia (single set of reproductive organs per segment)			
T. connochaeti	Artiodactyla: bovid (cattle, blue wildebeest)		Africa
T. giardi (Giard's tapeworm) (syn. *Helictometra*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat)	Oribatida (mites): achipteriid (*Achipteria*), scheloribatid (*Scheloribates, Liebstadia*), oribatulid (*Zygoribatula*), ceratozetid (*Trichoribates*), punctoribatid (*Punctoribates*)	Eurasia, Africa, Americas
T. ovilla (syn. *T. aspinosa, T. himalayai, Thysanosoma ovilla*)	Artiodactyla: bovid (cattle, water buffalo, zebu, sheep, goat, dama gazelle, impala, eland, hartebeest), camelid (camel)	Oribatida (mites); Psocoptera: psocid (bark lice)	Africa

Parasite morphology: Anoplocephalid tapeworms form 3 different developmental stages: eggs, larvae (cysticercoids) and adults. Gravid proglottids containing eggs are passed in host faeces: those of anoplocephaline species retain their uteri and the eggs possess a unique pyriform apparatus, while thysanosomine species have eggs grouped together within special paruterine organs. The eggs range from triangular to square in shape, some having a distinctive D-shape (flattened on one side), and they measure from 50-80 µm in diameter. They are surrounded by a heavy hyaline capsule comprising an outer vitelline membrane and a thick albuminous layer. Mature eggs are embryonated and contain a hexacanth (6-hooked) non-ciliated embryophore (oncosphere). In anoplocephaline species, the oncosphere is surrounded by the pyriform apparatus, which is pear-shaped, chitinous, refractile and bears 2 finger-like projections. The larval metacestode stage is an encysted cysticercoid into which the scolex has been retracted. Cysticercoids range in size from 100-180 x 90-140 µm and possess a retracted scolex, 3 pairs of hooks, germinal cells, an excretory

pore and a tail-like cercomer. Adult tapeworms range considerably in size from 0.2-10.0 m in length depending on the species. Most *Anoplocephala* spp. are large measuring from 5 cm to 1 m in length by 1-2 cm in width. *Moniezia* spp. are larger and elongate measuring up to several metres in length. Tapeworms have flat ribbon-shaped white-yellow bodies comprising an anterior scolex (holdfast organ) and posterior tape (strobilia) made up of numerous segments (proglottids). The scolex is circular and bears 4 large muscular suckers, some species also possessing 4 basal flaps called lappets (e.g. *A. perfoliata*). The proglottids are wider than they are long, have lateral genital pores and their posterior borders are lined with interproglottid glands (often linear or rosette arrangements of glandular cell clusters in some species of *Moniezia*). Tapeworms do not possess mouth parts or an intestinal tract but absorb nutrients through their body surface (tegument). Mature worms are hermaphroditic and possess male and female reproductive organs in each proglottid, some genera even having two sets of reproductive organs per segment (e.g. *Moniezia*). Individual sets comprise numerous testes and compact ovaries with 2 lobes which produce eggs that are fertilized and mature in the uteri. Posterior proglottids become sac-like as they mature and become gravid filling with numerous eggs. Anoplocephaline species have a tubular or reticular uterus that persists in gravid proglottids, while thysanosomine species have a special paruterine organ that receives eggs. Gravid segments detach and are passed with host faeces, whereupon eggs are discharged into the environment.

Site of infection: Anoplocephalid genera infect the gastro-intestinal tracts and bile ducts of their definitive hosts, mainly ruminants. Adult *Anoplocephala* occur in the small and large intestines, *Moniezia* and *Thysaniezia* in the small intestines, *Equinia* in the small intestines and occasionally the stomach, and *Stilesia* and *Thysanosoma* in hepatic bile ducts. Different species may exhibit some tissue tropism within these regions, e.g. *A. perfoliata* is found in clusters along the ileocecal junction. The larval metacestodes (cysticercoids) are found in the body cavities of their invertebrate intermediate hosts, mostly oribatid mites.

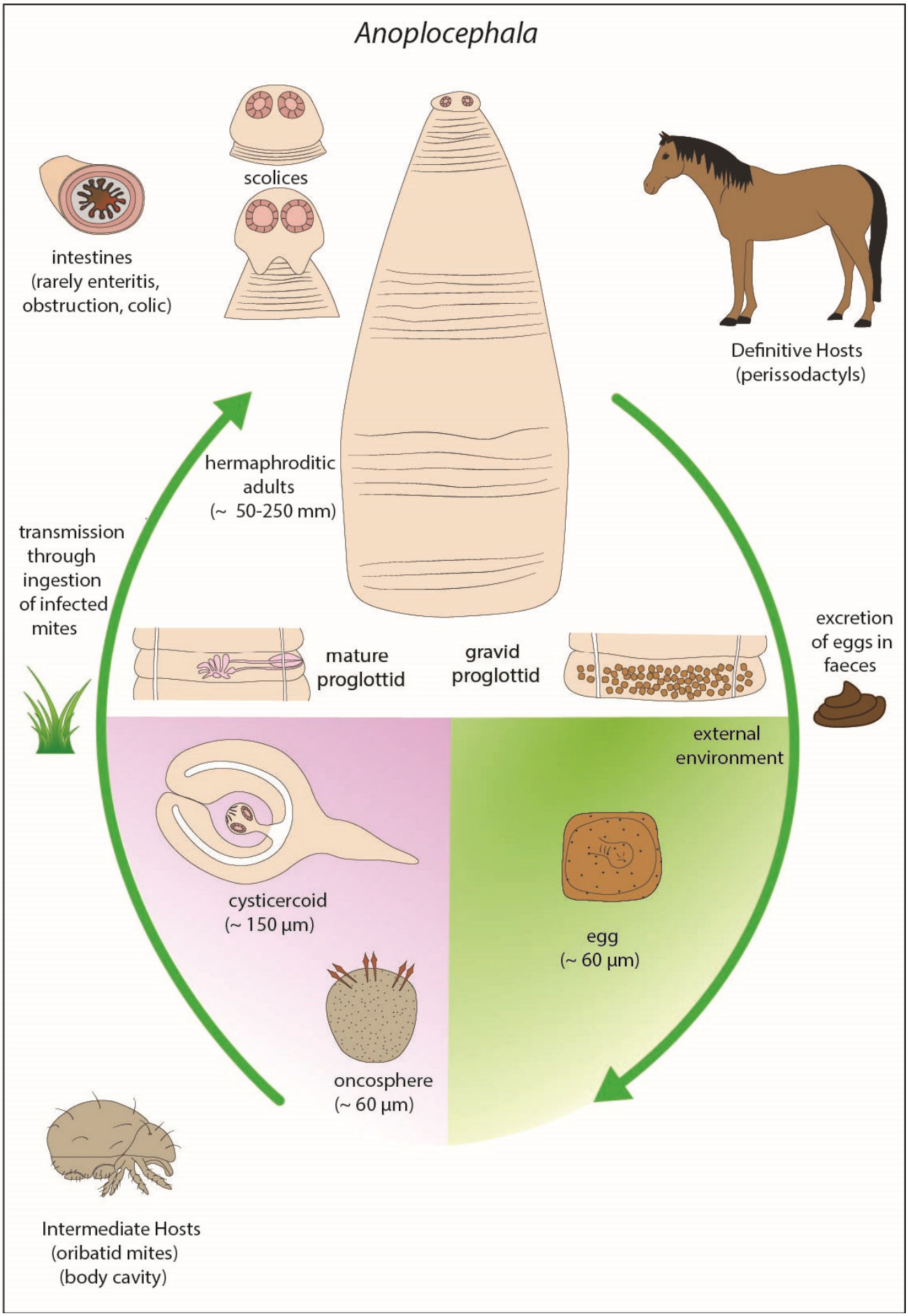
Pathogenesis: These tapeworms occur commonly in domestic livestock, especially ruminants and horses. Infections are rarely associated with clinical disease, even when large numbers of worms may be present. Adult worms attach to mucosal surfaces using their unarmed muscular suckers but do not feed on host tissues (they absorb nutrients across their body walls). Attachment and detachment causes traumatic damage to the mucosa, becoming cumulative as worm numbers increase but often not resulting in overt clinical signs. The exception is the species *Anoplocephala perfoliata* which can be very pathogenic in horses. Chronic infections by large numbers of worms (hundreds) may cause severe enteritis, intestinal obstruction (blockage of ingesta flow in the caecum, terminal ileum or ileocaecal junction), ileocaecal colic (severe abdominal discomfort/pain), reduced gut motility and intussusception (telescoping of the gut, usually of the small intestine into the caecum), caecal perforation leading to peritonitis, and death. At or near attachment sites, there is hyperaemia, erosion and necrotic ulceration of the mucosal epithelium, often with diphtheritic membrane formation and sometimes with focal haemorrhages, villous atrophy, inflammation, epithelial and goblet cell hyperplasia and muscular layer hypertrophy. Large numbers of eosinophils and lymphocytes are present in the tissues with oedema, extensive fibrosis (resulting in mucosal thickening, polyps or raised verrucous granulating masses), and neurological changes (degeneration of neurons and mesenteric ganglia). The risk of colic (spasmodic and acute) increases with higher parasite burdens. Other clinical signs observed have included chronic diarrhoea, fever, increased heart rate, poor growth and unthriftiness. Disease is more severe in young horses but older horses may also show signs. There is also some evidence that heavy infections by *A. magna* in the small intestines of horses may cause enteritis and possibly duodenal rupture. Contradictory results have been observed with respect to *Moniezia* infections in calves and lambs, with some studies finding no ill-effects and others reporting diarrhoea, anaemia, mucosal inflammation, anorexia and reduced weight gain and wool growth.

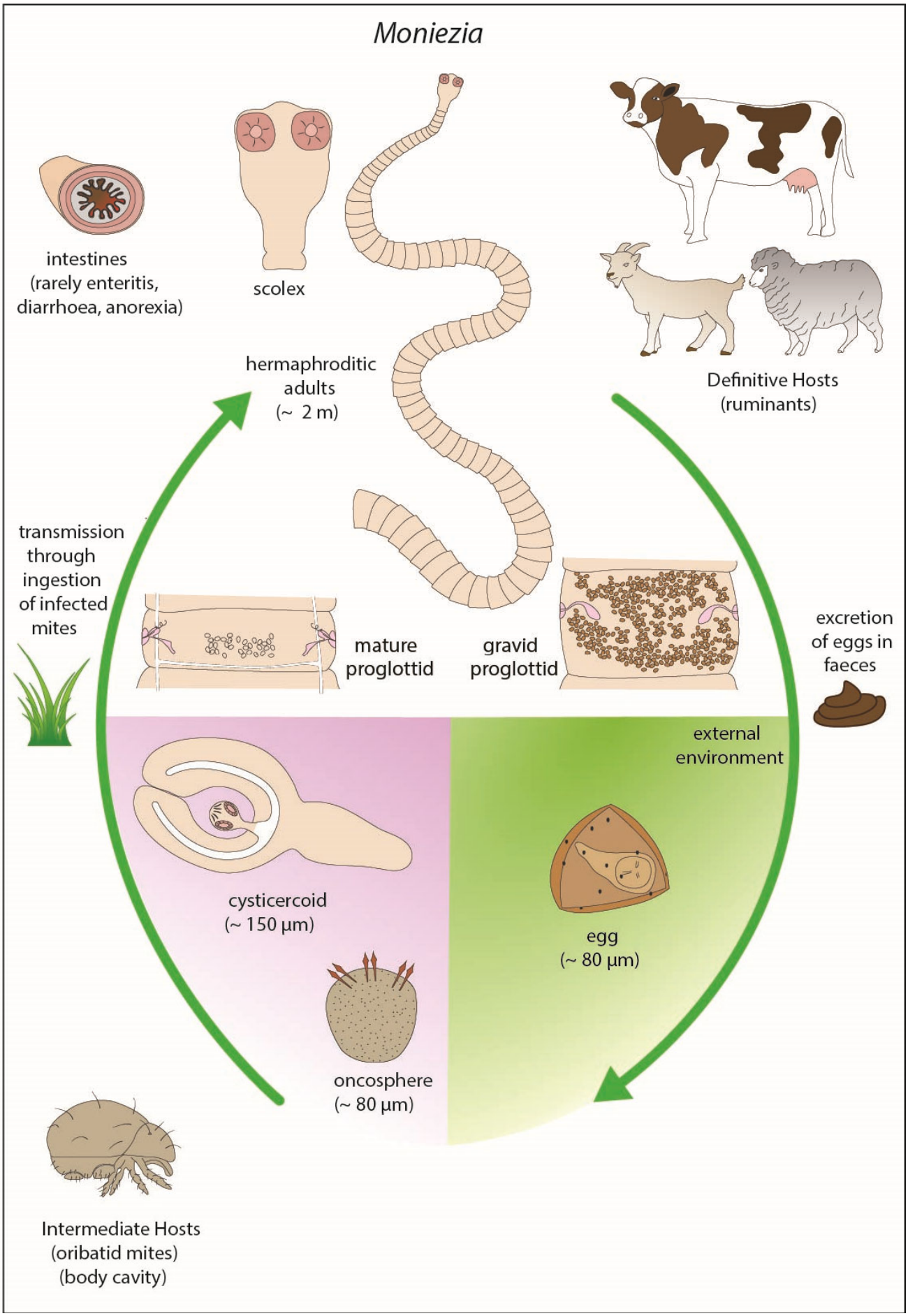
Developmental cycle and mode of transmission: Anoplocephalid species have indirect heteroxenous life-cycles involving cyclic transmission between vertebrate definitive hosts (herbivores infected with adult tapeworms) and invertebrate intermediate hosts (pasture mites infected with larval metacestodes). Parasite species exhibit high host specificity for both definitive and intermediate hosts. Eggs released from gravid proglottids (either in the intestines or in faeces) contaminate pastures and are dispersed by faecal decomposition and rainfall. The embryonated eggs survive for several days although this depends on ambient conditions with eggs surviving up to several months in moist cool environments. The eggs are ingested by pasture-dwelling arthropods, mostly oribatid mites (especially achipteriid, ceratozetid, galumnid, haplozetid, liacurid, oribatulid, phenopelopid and scheloribatid families) for anoplocephaline eggs, psocopterid insects (psocid booklice) for thysanosomine eggs, and coleopteran insects (beetles) for linstowiine eggs. Many infections exhibit seasonal patterns of infection as most of these arthropods feed and breed in particular micro-environments at particular times of the year (pasture mites are more active and prevalent over summer). The eggs hatch within the arthropods releasing the contained embryos (oncospheres) which burrow through the gut using their hooks and glandular secretions. Oncospheres encyst in the body cavity (haemocoel) and develop into cysticercoid stages over 2-4 months. Definitive hosts acquire infections by ingesting infected arthropods on vegetation when grazing. Once ingested, the larval cysticercoid extends its retracted scolex and uses its suckers to attach to mucosa where it develops to a sexually-mature adult over 6-10 weeks (prepatent period). Adult tapeworms are thought to live for several years and progressive maturation of proglottids can ultimately produce thousands of eggs.

Differential diagnosis: Many anoplocephalid tapeworm species do not shed most of their eggs in host faeces but pass gravid proglottids from which eggs are subsequently released. Infections are therefore usually diagnosed in livestock by the detection of motile (writhing) segments (looking like rice grains) in faeces or moving around the anus. Nonetheless, faecal samples may be

examined microscopically for the presence of characteristic eggs, but the standard McMaster chamber floatation technique shows low sensitivity which may be improved by employing centrifugal floatation. Post-mortem examination commonly reveals the presence of species forming large tapeworms in gut samples, but small species may be overlooked by cursory visual examination. Enzyme immunoassays have been developed to detect host antibodies (serum or saliva) against somatic or excretory/secretory (ES) products from *A. perfoliata* in horses, and an immunoassay was recently developed to detect parasite antigens in faecal samples. However, host antibody responses to infection were found to vary greatly as was antigen shedding. Isoenzyme electrophoresis has been used to characterize several *Moniezia* spp., and molecular techniques based on polymerase chain reaction (PCR) amplification of parasite DNA (nuclear genes for ribosomal RNA and internal transcribed spacers, and mitochondrial genes for proteins, rRNA and tRNA) have been used to discriminate equine anoplocephalids.

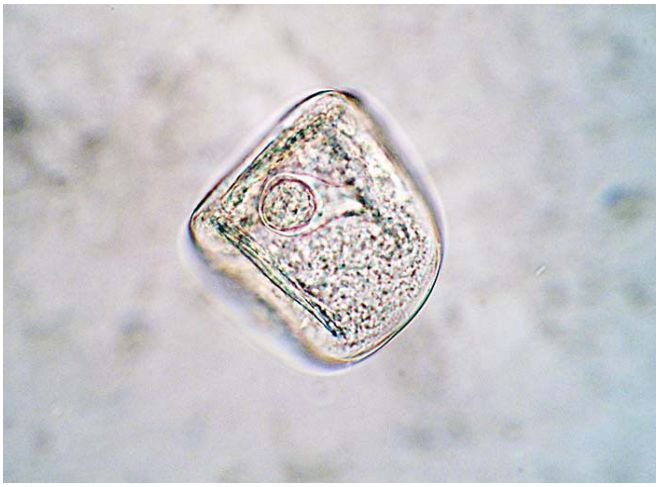
Treatment and control: Infections in livestock have been successfully treated using a range of anthelmintics, including praziquantel, niclosamide, albendazole, fenbendazole, oxfendazole, dichlorophen and sometimes pyrantel or morantel. Other modern anthelmintics commonly used on horses, such as macrocyclic lactones (ivermectin, moxidectin), have no effect. Treatment should be conducted strategically to eliminate tapeworms and reduce pasture contamination when intermediate hosts are most active, usually over summer. Re-infection from contaminated pastures can easily occur so regular preventive treatments may be required (every few months for horses). Environmental management procedures can also be instituted to curb infections by reducing contact between parasite eggs, pasture arthropods and grazing animals. Stabling horses overnight limits contact with arthropods which climb pastures during cooler periods and hide during hotter periods. Grazing management strategies can be instituted so definitive hosts can be rotated between pastures (e.g. periodic swapping of horses and cattle). Other extreme methods of pasture management to reduce contamination and arthropod populations include cropping or ploughing, but such interventions are laborious and costly.


Anoplocephala
scolices
intestines
(rarely enteritis,
obstruction, colic)
Definitive Hosts
(perissodactyls)
hermaphroditic
adults
(~ 50-250 mm)
transmission
through
ingestion
of infected
mites
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
external
environment
cysticercoid
(~ 150 µm)
egg
(~ 60 µm)
oncosphere
(~ 60 µm)
Intermediate Hosts
(oribatid mites)
(body cavity)


Moniezia
intestines
(rarely enteritis,
diarrhoea, anorexia)
scolex
hermaphroditic
adults
(~ 2 m)
Definitive Hosts
(ruminants)
transmission
through
ingestion
of infected
mites
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
external
environment
cysticercoid
(~ 150 µm)
egg
(~ 80 µm)
oncosphere
(~ 80 µm)
Intermediate Hosts
(oribatid mites)
(body cavity)



Anoplocephala adult worms



Anoplocephala worm egg



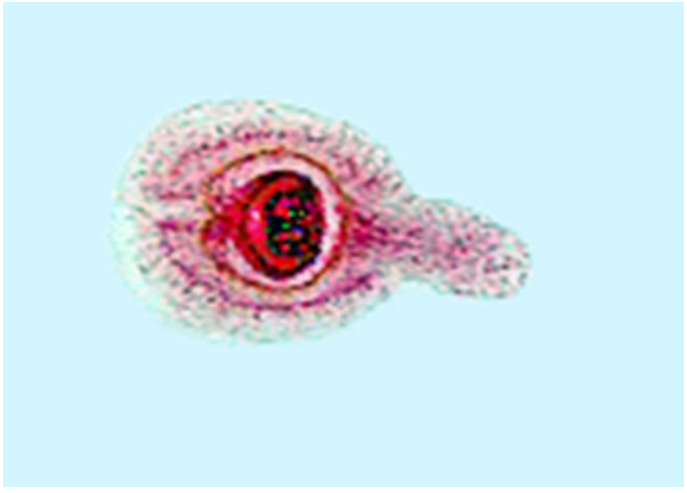
Moniezia adult worm



Moniezia worm egg



Moniezia scolex



Moniezia cysticercoid

Dipylidium
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Cyclophyllidean tapeworms are usually intestinal parasites of terrestrial vertebrates and have an anterior scolex (hold-fast organ with suckers and sometimes hooks) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). Eucestodes have indirect life-cycles involving oncospheres (hexacanth embryos) released from ingested eggs to form encysted larval stages (metacestodes) in the tissues of intermediate hosts and their transmission to carnivorous definitive hosts. Adult dipylidiids have an armed rostellum, elongate gravid segments with two lateral pores and are parasitic in various carnivores (esp. dogs and cats) but are rarely pathogenic. The encysted larval stages (cysticercoids) occur in fleas and lice which are ingested during grooming.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)
Family:	Dipylidiidae (armed scolex, proglottids with paired reproductive organs and two lateral genital pores)
Genus:	*Dipylidium* (parasitic in small intestines of dogs/cats)
Species:	various species cause anal discomfort in dogs/cats

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce

eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Cyclophyllidean cestodes are polyzoic containing from 2 to > 1,000 proglottids demarcated by external segmentation. They possess an anterior scolex with 4 suckers, many with a rostellum (often armed), and they have compact post-ovarian vitellaria. Adult worms are found in terrestrial vertebrate definitive hosts (mammals, birds, reptiles, amphibians) while larval metacestodes occur in vertebrate (mammal, amphibian, bird) or invertebrate (mollusc, acari, insect) intermediate hosts. Over 3,000 species have been described in 400 genera in 16 families: Acoleidae, Amabiliidae, Anoplocephalidae, Catenotaeniidae, Davaineidae, Dioecocestidae, Dilepididae, Dipylidiidae, Gyrporhynchidae, Hymenolepididae, Mesocestoididae, Metadileptidae, Nematotaeniidae, Paruterinidae, Progynotaeniidae, and Taeniidae (all with lateral genital pores, except the Mesocestoididae).

Dipylidiid tapeworms have proglottids with paired reproductive organs and two lateral genital pores (*di* = two, *pylidium* = entrance), and the scolex has 4 suckers and a protrusible rostellum armed with hooks. The tapeworms shed terminal gravid

proglottids containing numerous eggs within uterine capsules (egg balls). Three genera are recognized: *Dipylidium*, *Diplopylidium*, and *Joyeuxiella* (formerly *Joyeuxia*) which all parasitize the small intestines of mammals. Species in all 3 genera utilize arthropods (usually fleas) as intermediate hosts for larval stages (cysticercoid metacestodes), but the latter 2 genera also form encysted cysticercoid stages (monocercus and polycercus, respectively) in second intermediate hosts (usually reptiles, but occasionally amphibians or small mammals). The genus *Dipylidium* is characterized by the possession of a rostellum with rosethorn-shaped hooks, the vagina is situated posterior to the cirrus sac, the genital pore occurs in the middle of the lateral border of the segment, and the 'egg balls' contain up to 30 eggs. The species *D. caninum* commonly infects dogs and cats (and their fleas) around the world, and humans in close contact with pets (especially children) can also be infected. Molecular studies on nuclear and mitochondrial gene sequences have suggested the occurrence of at least two 'host-adapted' genotypes of *D. caninum*: a 'canine' genotype found predominantly in dogs, dog fleas and human fleas; and a 'feline' genotype found mostly in cats, cat fleas and cat lice. However, this apparent host specificity is not absolute as instances of cross-infections have been recorded.

Dipylidiid species	**Definitive hosts [adults in intestines]**	**Intermediate hosts (IH) [cysticercoids in body cavity/tissues]**	**Distribution**
Dipylidium (rosethorn-shaped hooks, egg capsules contain up to 30 eggs)			
D. buencaminoi	Carnivora: canid (dog)		Philippines
D. caninum (flea tapeworm, double-pored tapeworm, cucumber seed tapeworm) (syn. *D. ascalabotidis, canicum, canium, caracidoi, cati, compactum, crassum, cucumerinum, diffusum, gracile, halli, longulum, manthaensis, oerleyi, porimamillanum, sexcoronatum, terensis, walkeri*)	Carnivora: canid (dog, dingo, golden jackal, black-backed jackal, red fox, bat-eared fox, crab-eating fox), hyaenid (striped hyena, aardwolf), felid (cat, African wildcat, Egyptian hunting cat, Charteux cat, fallow cat, jungle cat, fishing cat), viverrid (palm civet, common genet); occasionally Primates: hominid (human)	Siphonaptera: pulicid fleas (*Ctenocephalides canis, C. felis, Pulex irritans*); Phthiraptera: trichodectid lice (*Trichodectes canis, Felicola subrostratus*)	Eurasia, Africa, Americas, Australasia
D. otocyonis	Carnivora: canid (bat-eared fox)		Africa
Reassigned species			
D. latissimum (now *Cittotaenia denticulata*)	Lagomorpha: leporid (rabbit)		Europe
D. leuckarti (now *Neoctenotaenia ctenoides*)	Lagomorpha: leporid (rabbit)		Europe
D. pectinatum (now *Mosgovoyia*)	Lagomorpha: leporid (mountain hare)		Europe
Diplopylidium (clawhammer-shaped ('taenioid') hooks, egg capsules contain single egg, prey animals may act as second IH)			
D. acanthotetra (syn. *D. fabulosum, D. quinquecoronatum, D. trichchesii, D. triseriale*)	Carnivora: felid (cat), viverrid (African civet, common genet), canid (dog)	first IH unknown; second IHs include Serpentes: colubrid (green whip snake, horseshoe whip snake, spotted whip snake, viperine water snake, northern green bush snake), psammophiid (eastern Montpellier snake); Sauria: agamid (roughtail rock agama), scincid (cylindrical skink, ocellated skink), lacertid (sand lizard, common wall lizard), phyllodactylid (common wall gecko), gekkonid (Mediterranean house gecko, northern house gecko); Anura: bufonid (Berber toad)	Europe, Middle East, Africa
D. aurangabadensis	Carnivora: felid (cat)		India
D. avicola	Accipitriformes: accipitrid (Cape griffon)		South Africa
D. genettae	Carnivora: viverrid (common genet, small-		Africa

(syn. *Dipylidium genettae, Dipylidium dongolense*)	spotted genet)		
D. monoophorum	Carnivora: felid (cat), viverrid (Malabar civet, common genet)	first IH unknown; second IHs include Serpentes: colubrid (northern green bush snake)	Africa
D. nolleri (syn *D. monoophoroides*)	Carnivora: felid (cat), canid (dog, sand fox)	first IH unknown; second IHs include Sauria: phyllodactylid (common wall gecko), lacertid (Lebanon lizard), gekkonid (Mediterranean house gecko); Serpentes: colubrid (spotted whip snake), psammophiid (eastern Montpellier snake), viperid (horned desert viper)	Europe, Middle East
D. paurodex	Carnivora: viverrid (rusty-spotted genet)		Africa
D. skrjabini	Carnivora: felid (cat)	first IH unknown; second IHs include Sauria: phyllodactylid (naked-toed gecko)	Europe
D. udgirensis	Carnivora: felid (cat)		India
D. zschokkei	Carnivora: herpestid (yellow mongoose)	first IH unknown; second IHs possibly includes Serpentes: viperid (horned desert viper)	South Africa
Joyeuxiella (rosethorn-shaped hooks, egg capsules contain single egg, prey animals may act as second IH)			
J. echinorhyncoides (syn. *Taenia, Dipylidium*)	Carnivora: canid (dog, fox, bat-eared fox, fennec fox, golden jackal), felid (cat); Rodentia: murid (Indian gerbil)	first IH unknown; second IHs include Sauria: agamid (roughtail rock agama), scincid (cylindrical skink, common skink), phyllodactylid (fan-footed gecko); Serpentes: colubrid (green whip snake, Dahl's whip snake, spotted whip snake, European cat snake); psammophiid (eastern Montpellier snake, hissing sand snake)	Middle East, India
J. fuhrmanni (syn. *Dipylidium fuhrmanni, Joyeuxiella paucitestis*)	Carnivora: felid (cat, serval, African wildcat), viverrid (common genet, rusty-spotted genet)		Africa
J. pasqualei (syn. *Dipylidium chyzeri, D. rossicum, Diplopylidium fortunatum, Joyeuxia aegyptica, J. pasqualeiformis, Joyeuxiella guilhoni, J. domestica*)	Carnivora: felid (cat, serval, European wildcat, African wildcat, South African wildcat), canid (dog, gray wolf, fox, golden jackal), mustelid (common weasel)	first IH unknown; second IHs include Sauria: agamid (roughtail rock agama), lacertid (common wall lizard, European green lizard, Schreiber's fringe-fingered lizard), phyllodactylid (common wall gecko), gekkonid (Mediterranean house gecko, common house gecko); varanid (desert monitor), scincid (snake-eyed skink); Serpentes: colubrid (green whip snake, Dahl's whip snake, European cat snake); Eulipotyphla: soricid (lesser white-toothed shrew)	Europe, Middle East, Africa, India, Asia

Parasite morphology: *Dipylidium* spp. form three distinct developmental stages: eggs (containing oncospheres), larvae (cysticercoids) and adult tapeworms. Definitive hosts excrete gravid proglottids containing uterine packets of 8-30 eggs. The eggs are yellow to brown in colour, oval to spherical in shape and range from 20-60 µm in diameter. Each egg contains a nonciliated hexacanth (6-hooked) embryo (oncosphere) covered by a thin eggshell and a non-striated embryophore (outer cellular covering of embryo). Oncospheres are ovoid measuring around 25 µm in diameter, lacunate (with internal channels) and possess anterior penetration glands. Metacestodes (cysticercoids) develop in intermediate hosts; firstly in insects (fleas, lice), then secondly in reptiles (lizards, snakes). Cysticercoids have oval-elongate contractile bodies (0.1-2.0 mm in length) with a tail-like cercomer and a retracted (not invaginated) scolex with a fully developed rostellum. Adult tapeworms have elongated ribbon-like bodies measuring from 15-80 cm (most 20-40 cm) in length and ranging in colour from white (ivory) to yellowish-pink. The posterior strobila (tape) is composed of numerous (60-175) elliptical segments (proglottids) measuring 0.5-1.0 cm long by 0.1-0.2 cm wide. The anterior scolex is small, muscular, rhomboidal in shape (0.35-0.50 mm in diameter), bearing 4 cup-shaped acetabula (suckers) and surmounted by an apical retractable club-shaped protuberance (rostellum) armed with 30-150 rosethorn-shaped hooks arranged in 1-8 (usually 4-6) rows. *Joyeuxiella* spp. have similar rosethorn-shaped hooks, while *Diplopylidium* spp. have clawhammer-shaped ('taenioid'-like) hooks. Adult dipylidiid worms are hermaphroditic and each segment contains not one but 2 sets of male and female reproductive organs (one set per side) with bilateral genital pores used for reproduction and not egg release (one of the common names for *D. caninum* is the 'double-pored' tapeworm). Female reproductive organs comprise an ovary, oviduct, ootype, seminal receptacle, vitelline gland, vagina and a reticulated net-like uterus. Male reproductive organs consist of numerous testes (up to 200) in the intervascular space, a sperm duct, coiled vas deferens, and cirrus. Fertilized oocytes enter the uterus and develop to preoncospheres. As proglottids mature, the uteri disappear and are replaced by hyaline egg capsules (also known as egg packets, clusters or balls). Mature *Dipylidium* proglottids may contain up to 150 egg capsules (120-200 µm), each containing 15-30 oncospheres with distinctive inner and outer envelopes. In contrast, the egg capsules of *Diplopylidium* and *Joyeuxiella* spp. contain single eggs. Gravid proglottids drop off and are passed in host faeces where they crawl about, expanding and contracting to release egg packets. They resemble cucumber or pumpkin seeds and eventually desiccate and shrivel to resemble rice grains.

Site of infection: Adult *Dipylidium* tapeworms infect the small intestines of their mammalian definitive hosts. Metacestodes (cysticercoids) develop in the body cavities (haemocoel) of their first intermediate hosts (insects) or become encysted within connective tissues of their second intermediate hosts (reptiles).

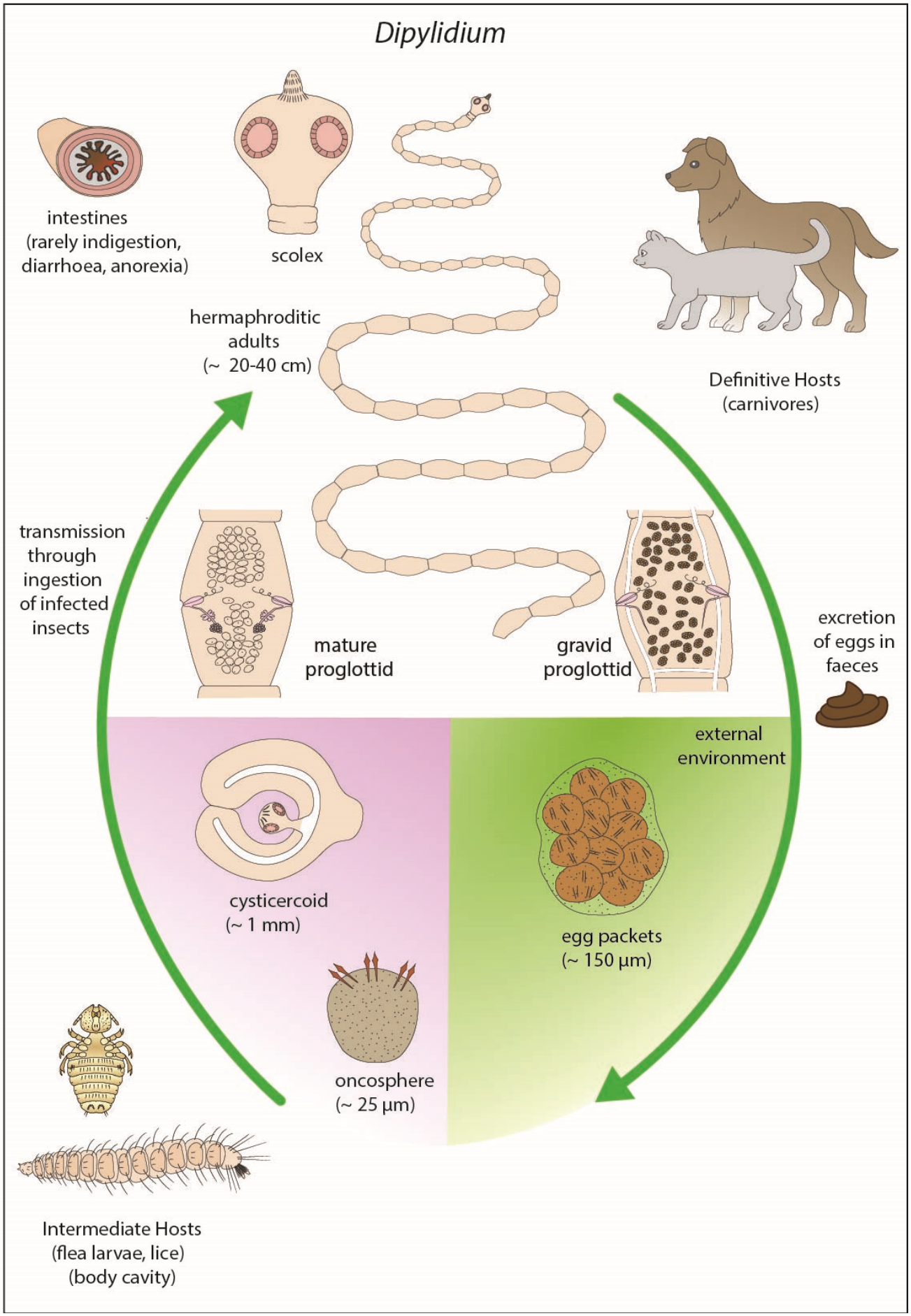
Pathogenesis: Tapeworms do not have digestive tracts and do not feed off host tissues but rather absorb nutrients from the gut lumen. *Dipylidium* spp. generally do not cause clinical disease in their definitive hosts, except in heavily-infected or malnourished individuals which may experience indigestion, abdominal pain, constipation or diarrhoea, and weight loss. Such animals may appear pot-bellied and unthrifty, but rarely do they develop life-threatening intestinal obstructions. Heavy infections in cats and dogs have occasionally been associated with convulsions, epileptiform seizures and haemorrhagic enteritis. More often, infections in companion animals cause anal pruritus when gravid proglottids migrate out onto perianal regions or attach to hairs where they may dry out. Pruritus may be accompanied by fever and eosinophilia due to host inflammatory responses and afflicted animals may itch and scratch by scooting their perineum along the ground. Infections in humans are usually low in intensity, being related to the small number of intermediate hosts and cysticercoids ingested. Most *D. caninum* infections are asymptomatic, but some patients (typically infants or small children in contact with domestic pets) may exhibit indigestion, abdominal pain, nocturnal irritability, anorexia, poor weight gain or weight loss and dysphoria (depression), sometimes with diarrhoea, dizziness, nausea and allergenic (hypersensitivity) manifestations such as urticaria, pruritus ani and eosinophilia. Parents and pet owners frequently express psychological 'disgust' when encountering proglottids writhing in nappies or underwear or crawling over perianal hair or faeces.

Developmental cycle and mode of transmission: Tapeworms have indirect heteroxenous (2 host) life-cycles involving faecal-oral transmission of eggs from definitive hosts to invertebrate intermediate hosts and then predator-prey transmission of larval stages from intermediate hosts back to definitive hosts. Gravid proglottids filled with egg packets are released from posterior end of the adult tapeworm body through a process known as apolysis. The proglottids are motile and emerge from the host's anus or are excreted with faeces where they contract and expand releasing egg capsules. Eggs have been found to survive for several months in desiccated proglottids. Egg capsules are ingested by first intermediate hosts, mainly flea larvae which have mandibulate (chewing) mouthparts (adult fleas have siphon-like (sucking) mouthparts and cannot ingest egg capsules). *D. caninum* develops more effectively in larvae of the cat flea *Ctenocephalides felis* rather than those of the dog flea *C. canis.* Occasionally, chewing lice (*Trichodectes canis, Felicola subrostratus*) have been implicated as additional intermediate hosts. Eggs ingested by flea larvae and lice release their contained oncospheres which then enter the body cavity (haemocoel) using their hooks and penetration glands secreting lytic enzymes. The oncospheres lie dormant until the insect larvae form pupae, at which time they begin transformation into cysticercoids. Pupation generally lasts from 5-24 days before adult fleas or lice hatch and take bloodmeals which stimulates the growth and encystment of tailed cysticercoids in the epithelium of the insect midgut. Metacestode growth rates have been found to vary according to temperature (ambient temperature for stages in insect pupae then host body temperature for stages in feeding adult insects), but development to infective cysticercoids is completed within 3 weeks (usually 13-18 days). Infected fleas may contain 2-82 cysticercoids (average of 10), although some have been found with over 160. Many dipylidiid tapeworms have also been found to utilize second intermediate hosts in the form of reptiles (lizards and snakes) which have ingested infected insects (presumably) and developed encysted cysticercoid stages mainly within connective tissues. Definitive hosts become infected by ingesting

cysticercoids in fleas and lice during grooming (or accidentally when children play with pets) or, in the case of most *Diplopylidium* and *Joyeuxiella* spp., by ingesting cysticercoids in reptile prey animals. The ingested cysticercoids attach to the mucosa of the small intestine of the definitive host and develop into mature adult tapeworms in around a month (prepatent period of 2-4 weeks). Adult tapeworms are not long-lived and generally die within a year. The dynamics (quantity) and kinetics (timing) of transmission and infection intensity depends largely on the population density of intermediate hosts (first and second intermediate hosts, as applicable), the abundance and gregarious nature of definitive hosts and prevailing climatic conditions (all demonstrating different seasonal patterns in different countries).

Differential diagnosis: Infections are usually diagnosed by the direct detection of ivory-coloured barrel-shaped gravid proglottids (either crawling or dried) in faeces, bedding or around the anus. Specimens may deteriorate quickly so fresh samples are required or they may be preserved in 70% alcohol. Dried proglottids resemble uncooked rice grains but upon rehydration they often return to their characteristic cucumber or pumpkin seed appearance. Visual examination may reveal the presence of bilateral genital pores located just behind the middle of each segment which can be confirmed by light microscopy after clearing segments with carboxylene. Squashing gravid proglottids may also reveal the presence of numerous egg capsules containing nonoperculated eggs with nonstriated walls (most other tapeworms do not form egg capsules and their eggs have striated walls or may be operculate). Infections in insect intermediate hosts are diagnosed by the demonstration of cysticercoid stages in haemolymph smears or histological sections, while infections in reptilian intermediate hosts are usually made by the detection of cysticercoid stages in host tissues during dissection or upon histological examination. Serological techniques (enzyme immunoassays) have recently been developed to detect host antibodies in dogs against *D. caninum* antigens derived from mature and gravid proglottids. Molecular biological techniques have also used polymerase chain reactions (PCR) to characterize restriction fragment length polymorphisms (RFLP) or partial sequences for nuclear (28S ribosomal RNA, repeat units D1-3) and mitochondrial genes (cytochrome c oxidase subunit 1).

Treatment and control: Infections by dipylidiid tapeworms may be successfully treated with a range of anthelmintic (deworming) drugs, especially the isoquinolines (praziquantel and epsiprantel), salicylanilides (niclosamide) and substituted isothiocyanate (nitroscanate). The current treatment of choice is praziquantel which is well tolerated in animals and humans, although some people develop skin rashes. It is effective against immature and mature tapeworms and can be administered orally, subcutaneously, transcutaneously or intramuscularly. In comparison, epsiprantel is less effective as it is poorly absorbed in the gut, niclosamide may cause abdominal pain and pruritus, and nitroscanate may have adverse side effects such as lethargy, vomiting, diarrhoea and anorexia. Parasite control options should also include interventions to reduce transmission between intermediate and definitive hosts, such as the hygienic disposal of contaminated faecal material, monitoring the hygiene habits of infants playing with pets, eliminating intermediate host populations (fleas and lice) using regular insecticidal treatments, instituting environmental control by cleaning fomites (bedding, furniture, carpets/rugs, household surfaces, utensils) potentially contaminated with insect larvae/pupae, curbing the hunting behaviour of carnivores for reptilian second intermediate hosts, and above all, educating pet owners and the general public.


Dipylidium
intestines
(rarely indigestion,
diarrhoea, anorexia)
scolex
hermaphroditic
adults
(~ 20-40 cm)
Definitive Hosts
(carnivores)
transmission
through
ingestion
of infected
insects
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
external
environment
cysticercoid
(~ 1 mm)
egg packets
(~ 150 µm)
oncosphere
(~ 25 µm)
Intermediate Hosts
(flea larvae, lice)
(body cavity)



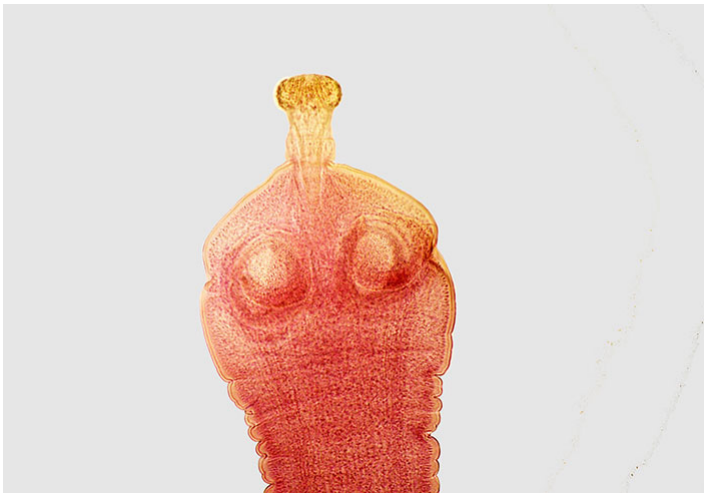
Dipylidium adult worms



Dipylidium adult worms



Dipylidium scolex



Dipylidium scolex extended



Dipylidium egg packet

Amoebotaenia
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Cyclophyllidean tapeworms are usually intestinal parasites of terrestrial vertebrates and have an anterior scolex (hold-fast organ with suckers and sometimes hooks) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). Eucestodes have indirect life-cycles involving oncospheres (hexacanth embryos) released from ingested eggs to form encysted larval stages (metacestodes) in the tissues of intermediate hosts and their transmission to definitive hosts by predation. Adult dilepidids usually have an armed rostellum and are parasitic in poultry but are rarely pathogenic. The encysted larval stages (cysticercoids) of *Amoebotaenia* spp. occur in earthworms which are consumed during foraging.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)
Family:	Dilepididae (tapeworms of dog/cat and fowl, scolex usually armed, genital pores alternate, some with paired genitalia, cysticercoid larva)
Genus:	*Amoebotaenia* (parasitic in small intestines of birds)
Species:	various species cause infections in chickens

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce

eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Cyclophyllidean cestodes are polyzoic containing from 2 to > 1,000 proglottids demarcated by external segmentation. They possess an anterior scolex with 4 suckers, many with a rostellum (often armed), and they have compact post-ovarian vitellaria. Adult worms are found in terrestrial vertebrate definitive hosts (mammals, birds, reptiles, amphibians) while larval metacestodes occur in vertebrate (mammal, amphibian, bird) or invertebrate (mollusc, acari, insect) intermediate hosts. Over 3,000 species have been described in 400 genera in 16 families: Acoleidae, Amabiliidae, Anoplocephalidae, Catenotaeniidae, Davaineidae, Dioecocestidae, Dilepididae, Dipylidiidae, Gyrporhynchidae, Hymenolepididae, Mesocestoididae, Metadileptidae, Nematotaeniidae, Paruterinidae, Progynotaeniidae, and Taeniidae (all with lateral genital pores, except the Mesocestoididae).

Over 120 dilepidid genera have been described as intestinal parasites of birds and some carnivores. Adult tapeworms usually possess an armed scolex and the genital pores alternate in their lateral location on consecutive proglottids. Larval stages (cysticercoids) are formed in invertebrate intermediate hosts which are ingested when the definitive hosts feed. The genus

Amoebotaenia contains over 20 species mostly parasitizing wild and domestic birds throughout the world, including chickens, turkeys, pheasant and quail. Cysticercoid stages have been recorded in a diverse range of insects (flies, locusts, ants, termites) and annelids (earthworms).

***Amoebotaenia* species**	**Definitive host (DH) [adults in small intestines]**	**Intermediate hosts (IH) [cysticercoids in tissues]**	**Distribution**
A. aveeki	Passeriformes: leiothrichid (white-crested laughingthrush)		India
A. awogera	Piciformes: picid (Japanese green woodpecker)		Japan
A. bhonslei	Galliformes: phasianid (chicken)		India
A. bhujangi	Charadriiformes: charadriid (yellow-wattled lapwing)		India
A. brevis (syn. *Nototaenia*)	Charadriiformes: charadriid (European golden plover, black-bellied plover, common ringed plover)		Europe, North America
A. cohni	Galliformes: phasianid (chicken)		India
A. cuneata (syn. *A. sphenoides*)	Columbiformes: columbid (pigeon); Galliformes: phasianid (chicken); Charadriiformes: charadriid (lapwing)	Oligochaeta: lumbricid (*Allolobophora* (*Eisenia*) *foetida, Lumbericus, Allotophora*?), megascolecid (*Pheretima peguana*), ocnerodrilid (*Ocnerodrilus* (*Ilyogenia*) *africana*)	worldwide
A. domesticus	Galliformes: phasianid (chicken)		India
A. fragida	Galliformes: phasianid (chicken)		Egypt
A. fuhrmanni	Charadriiformes: scolopacid (snipe)		China
A. gallusae	Galliformes: phasianid (chicken)		India
A. indiana	Galliformes: phasianid (chicken, grey francolin)		India
A. jadhavae	Galliformes: phasianid (chicken)		India
A. kharati	Galliformes: phasianid (chicken)		India
A. lini	Charadriiformes: scolopacid (Eurasian woodcock)		Asia
A. longisacculus	Galliformes: phasianid (chicken)		Indonesia
A. madrasiensis	Passeriformes: passerid (house sparrow)		India
A. maharashtrii	Galliformes: phasianid (chicken, grey francolin)		India
A. megascolesis	Galliformes: phasianid (chicken, grey francolin)		India
A. minuta	Charadriiformes: charadriid (yellow-wattled lapwing)		India
A. mohekarae	Galliformes: phasianid (chicken)		India
A. oligorchis	Galliformes: phasianid (chicken)		Japan
A. pekinensis	Charadriiformes: charadriid (oriental plover)		China
A. prabhuravii	Galliformes: phasianid (chicken)		India
A. scolopax	Charadriiformes: scolopacid (Eurasian woodcock)		Asia
A. soyagaonensis	Galliformes: phasianid (chicken)		India
A. spinosa	Galliformes: phasianid (chicken)		Indonesia
A. urotrichi	Eulipotyphla: talpid (Japanese shrew mole)		Japan
Reassigned species			
A. lumbrici (now *Paricterotaenia*)	Eulipotyphla: talpid (European mole), soricid (common shrew)		Eurasia

Parasite morphology: *Amoebotaenia* spp. form 3 different stages in their developmental cycles: eggs, larval metacestodes (cysticercoids) and adult tapeworms. Eggs are almost spherical measuring from 35-45 μm in diameter and they contain a nonciliated hexacanth (6 hooked) embryo (oncosphere) surrounded by a non-striated shell (embryophore) and a delicate membrane. Cysticercoids are lacunate (with internal cavity) and possess a retracted (not invaginated) scolex and a tail-like cercomer. Adult tapeworms are small and triangular measuring only 1-4 mm long and usually containing 20-30 proglottids, which are wider than long. They have an anterior scolex with 4 unarmed suckers surmounted by a small retractable rostellum armed with 12-14 hooks in a single row. Adult worms are hermaphroditic and each segment possesses one set of male and female reproductive organs with a common genital pore located laterally at the anterior end of the proglottid margin. Those of consecutive segments alternate sides irregularly. Each proglottid contains 12-20 testes and a sac-like slightly-lobed uterus. Reproductive organs become more mature in

posterior segments which become larger in size (thus contributing to the triangular shape of the worm). Gravid segments are shed from the posterior end of the worm and passed in host faeces.

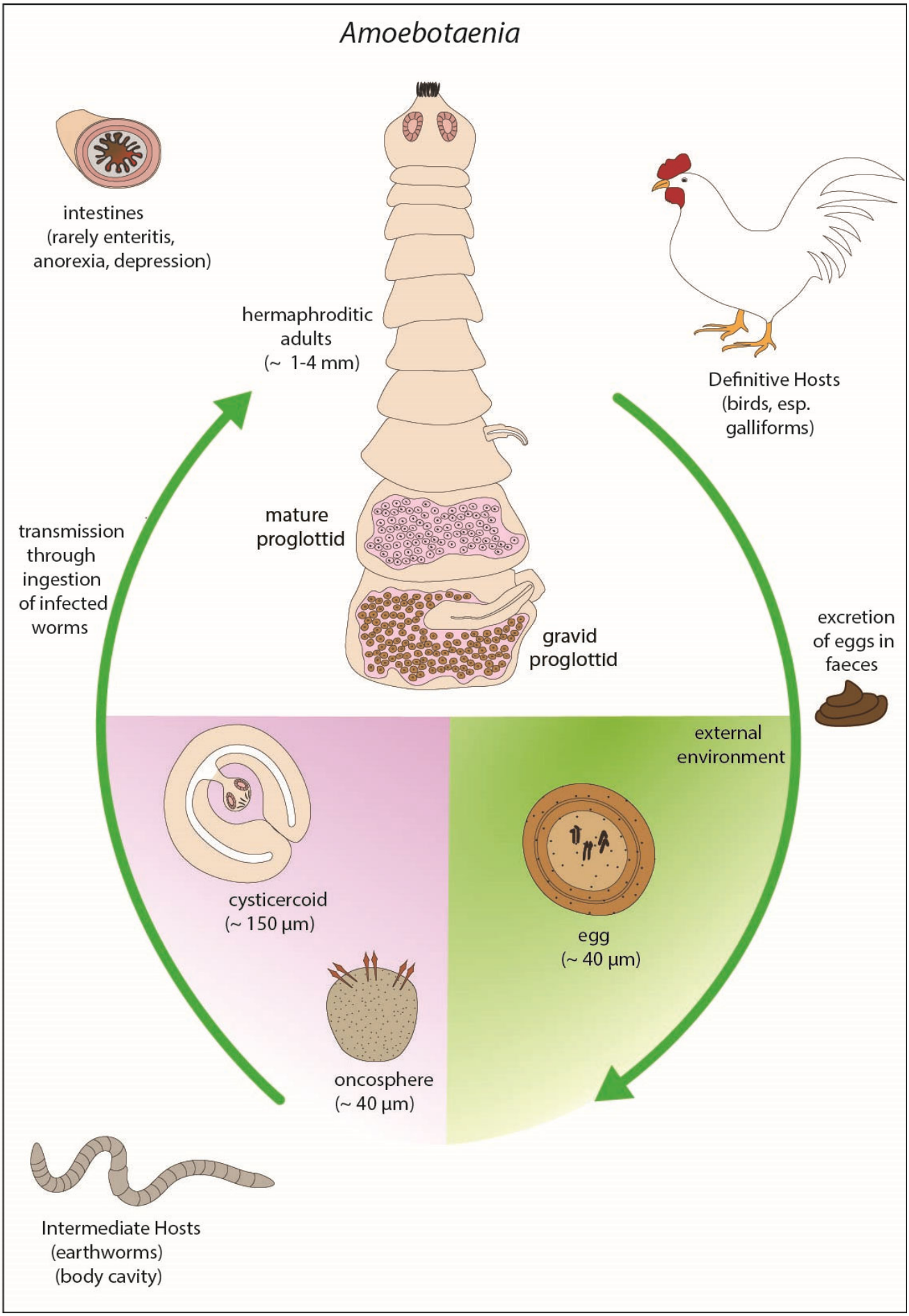
Site of infection: Adult *Amoebotaenia* tapeworms are found in the small intestines of a range of birds, particularly in galliform birds. Larval stages (cysticercoids) develop in the body cavities and tissues of invertebrate intermediate hosts, notably earthworms.

Pathogenesis: Most infections by *Amoebotaenia* are asymptomatic or subclinical as the tapeworms do not feed on host tissues but absorb nutrients from the gut lumen. Nonetheless, this competition for food may result in low feed conversion efficiency and reduced production parameters, including retarded growth, reduced weight gain and decreased egg production. Heavy infections may cause clinical signs, including enteritis (sometimes haemorrhagic), anorexia, weight loss, apathy and depression. Histopathological changes include vacuolation of epithelial cells, catarrhal enteritis, congestion of submucosal glands, granuloma formation, desquamation of villi and villous atrophy. Heavy infections also appear to lower host resistance to other infectious agents.

Developmental cycle and mode of transmission: These dilepidid tapeworms have indirect heteroxenous life-cycles involving cyclic transmission between avian definitive hosts (harbouring adult tapeworms) and annelid intermediate hosts (infected with larval stages). Gravid proglottids containing eggs are shed with bird faeces into the external environment. The proglottids are motile and move into the surrounding vegetation and soil. Earthworms ingest the gravid segments which are digested in the gut thereby releasing the eggs. The eggs then hatch releasing the contained oncospheres which actively migrate through host tissues into the body cavity of the earthworms. Here they develop into infective cysticercoids within 14 days. Birds ingest infected earthworms which become digested releasing the cysticercoids which attach to the gut wall and develop into adult tapeworms. The prepatent period (time between infection and shedding of first eggs) is around 4 weeks, and adult tapeworms live for around a year. Infections in domestic poultry are common in tropical regions, especially where housing and husbandry practices are poor and climatic conditions are favorable for parasite survival. Frequently, poultry become infected after moderate-heavy rainfall which draws earthworms towards the soil surface and facilitates their easier predation by birds. Various seasonal patterns of infection have been reported around the world.

Differential diagnosis: Infections are usually diagnosed by the direct detection of gravid segments in bird faeces, but the dropping must be fresh as the proglottids rapidly migrate out into the surrounding environment. Faecal concentration techniques (sedimentation and/or floatation) rarely detect free *Amoebotaenia* eggs as they remain inside gravid segments. Adult tapeworms may be detected at post-mortem after dissecting the gut and examining the mucosa for attached worms.

Treatment and control: Individual birds or flocks at risk may be treated for infections using broad spectrum anthelmintics effective against cestodes (including benzimidazoles (albendazole, febantel, fenbendazole, mebendazole, oxfendazole), halogenated phenols (hexachlorophene) or halogenated hydrocarbons (butynorate)) or specific cestodicides (niclosamide, praziquantel). Most drugs are available as additives for drinking water or feed, but careful attention should be given to any contra-indications (e.g. niclosamide is toxic for geese, praziquantel plus pyrantel tartrate is toxic for chickens). Some measure of parasite control may also be afforded in domestic flocks or aviaries by improving bird housing conditions (especially by eliminating earthen floors), frequently changing litter and bedding materials, sanitary disposal of faecal material, and restricting bird foraging behaviours for earthworms (particularly after rainfall). Few of these options are available for managing infections in wild bird populations, and any efforts to reduce earthworm populations should be discouraged for ecological reasons.


Amoebotaenia
intestines
(rarely enteritis,
anorexia, depression)
hermaphroditic
adults
(~ 1-4 mm)
Definitive Hosts
(birds, esp.
galliforms)
mature
proglottid
gravid
proglottid
transmission
through
ingestion
of infected
worms
excretion
of eggs in
faeces
external
environment
cysticercoid
(~ 150 µm)
egg
(~ 40 µm)
oncosphere
(~ 40 µm)
Intermediate Hosts
(earthworms)
(body cavity)



Amoebotaenia adult worm

Choanotaenia
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Cyclophyllidean tapeworms are usually intestinal parasites of terrestrial vertebrates and have an anterior scolex (hold-fast organ with suckers and sometimes hooks) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). Eucestodes have indirect life-cycles involving oncospheres (hexacanth embryos) released from ingested eggs to form encysted larval stages (metacestodes) in the tissues of intermediate hosts and their transmission to definitive hosts by predation. Adult dilepidids usually have an armed rostellum and are parasitic in poultry but are rarely pathogenic. The encysted larval stages (cysticercoids) of *Choanotaenia* spp. occur in house flies, beetles and grasshoppers which are consumed during foraging.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)
Family:	Dilepididae (tapeworms of dog/cat and fowl, scolex usually armed, genital pores alternate, some with paired genitalia, cysticercoid larva)
Genus:	*Choanotaenia* (parasitic in small intestines of birds)
Species:	various species cause enteritis in chickens

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some

with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Cyclophyllidean cestodes are polyzoic containing from 2 to > 1,000 proglottids demarcated by external segmentation. They possess an anterior scolex with 4 suckers, many with a rostellum (often armed), and they have compact post-ovarian vitellaria. Adult worms are found in terrestrial vertebrate definitive hosts (mammals, birds, reptiles, amphibians) while larval metacestodes occur in vertebrate (mammal, amphibian, bird) or invertebrate (mollusc, acari, insect) intermediate hosts. Over 3,000 species have been described in 400 genera in 16 families: Acoleidae, Amabiliidae, Anoplocephalidae, Catenotaeniidae, Davaineidae, Dioecocestidae, Dilepididae, Dipylidiidae, Gyrporhynchidae, Hymenolepididae, Mesocestoididae, Metadileptidae, Nematotaeniidae, Paruterinidae, Progynotaeniidae, and Taeniidae (all with lateral genital pores, except the Mesocestoididae).

Over 120 dilepidid genera have been described as intestinal parasites of birds and some carnivores. Adult tapeworms usually possess an armed scolex and the genital pores alternate in their lateral location on consecutive proglottids. Larval stages

(cysticercoids) are formed in invertebrate intermediate hosts which are ingested when the definitive hosts feed. The genus *Choanotaenia* contains over 110 nominal species, most parasitizing wild and domestic birds throughout the world, particularly gallinaceous (chickens, turkeys, pheasant, quail) and passerine birds (finches). Cysticercoid stages have been recorded in a diverse range of insects (flies, locusts, beetles, ants, termites). Several attempts have been made to revise generic identities and it was recently proposed that the genus *Choanotaenia* retain only those species with a single crown of rostellar hooks (most species being parasitic in galliform birds) while others with a double crown of rostellar hooks and atrial tufts of bristle-like spines be transferred to the genus *Spiniglans* (most species being parasitic in passeriform birds). Many other genera and species remain to be revised.

***Choanotaenia* species**	**Definitive host [adults in small intestines]**	**Intermediate hosts [cysticercoids in tissues]**	**Distribution**
C. abassenae	Passeriformes: sturnid (superb starling)		Africa
C. acridotheresi	Passeriformes: sturnid (common myna, bank myna)		India
C. angolensis	Passeriformes: pittid (African pitta)		Africa
C. arctica	Charadriiformes: scolopacid (sandpiper)		Europe
C. arquata	Charadriiformes: scolopacid (Eurasian curlew)		Europe
C. asymetrica	Caprimulgiformes: caprimulgid (nightjar)		South America
C. atopa	Carnivora: felid (cat)		North America
C. aurantina	Charadriiformes: larid (river tern)		Asia
C. aurti	Charadriiformes: burhinid (Eurasian stone-curlew)		India
C. baicalensis	Eulipotyphla: soricid (long-clawed shrew)		Japan
C. barbara	Passeriformes: passerid (Eurasian tree sparrow)		Europe
C. bhattacharai	Anseriformes: anatid (garganey)		India
C. campanulata	Opisthocomiformes: opisthocomitid (hoatzin)		South America
C. cayennensis	Charadriiformes: charadriid (southern lapwing)		Americas, Africa
C. chandleri	Charadriiformes: charadriid (red-wattled lapwing)		Europe
C. cholodkowskyi	Passeriformes: alaudid (Eurasian skylark)		Eurasia
C. cingulifera	Charadriiformes: scolopacid (common redshank)		Europe
C. constricta (syn *Anomotaenia*)	Passeriformes: icterid (white-browed meadowlark), turdid (Eurasian blackbird), corvid (grey crow, Eurasian magpie)		Holarctic
C. crassitestata	Piciformes: ramphastid (lettered aracari)		South America
C. croaxum	Passeriformes: corvid (house crow)		India
C. cylindrocephala	Passeriformes: corvid (western jackdaw)		Europe
C. dispar (syn. *Dictymetra volvulus*)	Charadriiformes: charadriid (yellow-wattled lapwing)		India
C. dogieli	Charadriiformes: scolopacid (great knot)		Eurasia
C. estavarensis	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
C. falsificata	Charadriiformes: burhinid (Eurasian stone curlew)		Egypt
C. fortunata	Ciconiiformes: ciconiid (white stork)		Europe
C. fotedari	Passeriformes: sturnid (common myna)		Asia
C. fuhrmanni	Accipitriformes: accipitrid (cinereous harrier)		South America
C. galbulae	Columbiformes: columbid (laughing dove); Passeriformes: corvid (house crow)		India, Pakistan
C. globulus	Charadriiformes: scolopacid (green sandpiper)		Africa, Europe
C. gondwana	Columbiformes: columbid (laughing dove); Passeriformes: passerid (common sparrow)		India
C. hypoleucia	Charadriiformes: scolopacid (common sandpiper)		India
C. ibanezi	Charadriiformes: scolopacid (whimbrel)		North America
C. infundibulum (syn. *C.*	Galliformes: phasianid (chicken, turkey, pheasant, common quail, Japanese quail,	Diptera: muscid (*Musca domestica, Stomoxys calcitrans*);	worldwide

infundibuliformis)	California quail, rock partridge); Columbiformes: columbid (pigeon, laughing dove); Accipitriformes: accipitrid (black kite, brown hawk)	Coleoptera: geotrupid (*Geotrupes sylvaticus*), carabid (*Amara fallax, Anaferonia constricta, Cratacanthus dubius, Stenocellus debilipes, Stenolophus conjunctus, Calathus, Hyparpalus indicus*), ostomid (*Tenebroides mauritanicus*), tenebrionid (*Alphitophagus bifasciatus, Tribolium castaneum*), staphylinid (*Apocellus sphaericollis*), scarabaeid (*Ataenius cognatus, Aphodius granarius, Geotrupes sylvaticus*), dermestid (*Dermester ater*), anthicid (*Anthicus confucii*); Orthoptera: acridid (*Dicromorpha viridis, Melanoplus femurrubrum, Spathosternum prasiniferum, Hieroglyphus nigrorepletus*), tettigoniid (*Conocephalus pallidus, Hexacentrus munda*)	
C. intermedia	Charadriiformes: scolopacid (giant snipe)		South America
C. intestinalis	Charadriiformes: charadriid (red-wattled lapwing)		India
C. isacantha	Passeriformes: emberizid (bunting)		Europe
C. joyeuxi	Charadriiformes: scolopacid (Eurasian woodcock)		Eurasia, Africa
C. kapurdiensis	Charadriiformes: glareolid (cream-colored courser)		India
C. khadgaonensis	Charadriiformes: charadriid (red-wattled lapwing)		India
C. larimarina	Charadriiformes: larid (great black-backed gull)		Europe
C. littoriae	Strigiformes: strigid (scops owl)		Europe
C. lobipluviae	Charadriiformes: charadriid (yellow-wattled lapwing)		India
C. macrocantha	Charadriiformes: scolopacid (sandpiper)		America
C. macrocephala	Charadriiformes: scolopacid (Eurasian woodcock)		Japan
C. magnicirrosa	Passeriformes: sturnid (common myna)		Myanmar
C. malaconoti	Passeriformes: malaconotid (grey-headed bushshrike)		Africa
C. mancocapaci	Cuculiformes: cuculid (groove-billed ani)		Americas
C. manipurensis	Charadriiformes: charadriid (yellow-wattled lapwing), scolopacid (snipe)		India
C. marchali	Charadriiformes: larid (gull)		Eurasia
C. megacantha	Charadriiformes: scolopacid (common sandpiper)		Palearctic
C. megistacantha	Charadriiformes: burhinid (Senegal thick-knee)		Africa
C. meridionalis	Charadriiformes: larid (kelp gull, brown-hooded gull)		South America
C. microphallos (syn. *Anomotaenia*)	Charadriiformes: charadriid (northern lapwing), scolopacid (long-toed stint)		Europe, North America
C. mollis	Accipitriformes: accipitrid (black kite)		India
C. multitesticularis	Eulipotyphla: soricid (Chinese mole shrew)		Asia
C. musculosa	Passeriformes: fringillid (common chaffinch), sturnid (common starling), muscicapid (European pied flycatcher)		Europe

C. nebraskensis	Rodentia: cricetid (prairie vole), sciurid (western fox squirrel)		North America
C. nilotica	Charadriiformes: glareolid (cream-colored courser)		Europe, Africa
C. orioli	Passeriformes: sturnid (common myna)		India
C. pandei	Passeriformes: pycnonotid (red-vented bulbul)		India
C. paranumenii	Charadriiformes: scolopacid (long-billed curlew)		North America
C. passerellae	Passeriformes: passerellid (fox sparrow)		North America
C. pauciannulata	Caprimulgiformes: caprimulgid (nacunda nighthawk)		South America
C. perisorei	Passeriformes: corvid (Siberian jay)		Eurasia
C. peromysci	Rodentia: cricetid (North American deer mouse)		North America
C. platycephala	Passeriformes: alaudid (Eurasian skylark, crested lark), motacillid (tawny pipit, meadow pipit, water pipit, tree pipit, western yellow wagtail), locustellid (river warbler), muscicapid (common redstart, European stonechat, northern wheatear), sylviid (Eurasian blackcap, lesser whitethroat, western Orphean warbler, barred warbler)		Europe
C. plegadis	Charadriiformes: scolopacid (marsh sandpiper)		Eurasia
C. polyorchis	Falconiformes: falconid (lesser kestrel, common kestrel)		Africa, Europe
C. prinopsia (syn. *Anomotaenia*)	Passeriformes: vangid (straight-crested helmetshrike)		Africa
C. prunellae	Passeriformes: prunellid (alpine accentor)		Japan
C. ratticola	Rodentia: murid (bush rat)		Australia
C. rhynchopis	Charadriiformes: larid (black skimmer)		South America
C. ridibundum	Charadriiformes: larid (black-headed gull)		Europe
C. rostellata	Charadriiformes: recurvirostrid (black-necked stilt)		Americas
C. sciuricola	Rodentia: sciurid (fox squirrel)		North America
C. scolopacina	Charadriiformes: scolopacid (Eurasian woodcock)		Europe
C. scythica	Galliformes: phasianid (pheasant)		Russia
C. shohoi	Galliformes: phasianid (chicken)		China
C. singhii	Charadriiformes: charadriid (red-wattled lapwing)		India
C. skrjabini	Charadriiformes: charadriid (common ringed plover)		Eurasia
C. slesvicensis	Charadriiformes: scolopacid (Eurasian woodcock)		Eurasia
C. sonoti	Passeriformes: sturnid (common myna, jungle myna, Brahminy myna)		India
C. southwelli	Charadriiformes: charadriid (yellow-wattled lapwing)		India
C. spasskii	Eulipotyphla: talpid (large mole)		Eurasia
C. speotytonis	Strigiformes: strigid (western burrowing owl)		North America
C. spermophili (syn. *Prochoanotaenia*)	Rodentia: sciurid (thirteen-lined ground squirrel, Richardson's ground squirrel)		North America
C. srivastavai	Passeriformes: leiothrichid (black-winged babbler)		India
C. stercoraria	Charadriiformes: larid (gull)		Europe
C. strigium	Strigiformes: strigid (Eurasian scops owl)		Europe
C. sylvarum	Galliformes: phasianid (hazel grouse)		Russia
C. tandani	Passeriformes: muscicapid (blue whistling thrush)		India
C. taylori	Passeriformes: malurid (superb fairywren)		Australia

C. tetrastes	Galliformes: phasianid (hazel grouse)		Eurasia
C. thraciensis	Charadriiformes: scolopacid (Eurasian woodcock)		Russia
C. trapezoides	Accipitriformes: accipitrid (great black-hawk)		South America
C. tubirostellata	Eulipotyphla: soricid (Chinese mole shrew)		Asia
C. tugarinovi	Passeriformes: muscicapid (African stonechat)		Africa
C. ululae	Strigiformes: strigid (spotted eagle-owl)		Africa
C. upupae	Bucerotiformes: upupid (African hoopoe)		Africa
Reassigned species			
C. bilateralis (now *Laterochites*)	Podicipediformes: podicipedid (least grebe)		Americas
C. borealis (now *Paricterotaenia*)	Anseriformes: anatid (mallard, common shelduck, long-tailed duck, common scoter)		Eurasia
C. brevis (now *Liga*)	Piciformes: picid (great spotted woodpecker)		Eurasia
C. burhini (now *Onderstpoortia taeniaeformis*)	Charadriiformes: burhinid (Eurasian stone-curlew)		India
C. centuri (now *Liga*)	Piciformes: picid (West Indian woodpecker)		Americans
C. chionis (now *Anomotaenia*)	Charadriiformes: chionid (snowy sheathbill)		Antarctica
C. citrus (now *Anomotaenia*)	Anseriformes: anatid (velvet scoter) Charadriiformes: scolopacid (common sandpiper, ruddy turnstone, common snipe, great snipe, pin-tailed snipe, dunlin, little stint, wandering tattler, black-tailed godwit, jack snipe, ruff, Eurasian woodcock, wood sandpiper, green sandpiper, Terek sandpiper, common redshank), charadriid (southern lapwing, little ringed plover, Oriental plover)	Gastropoda: succineid (*Succinea putris*)	Europe, Africa, Americas
C. coronata (now *Burhinotaenia*)	Charadriiformes: burhinid (Eurasian stone curlew)		Eurasia
C. corvi (now *Spiniglans constricta*)	Passeriformes: corvid (fan-tailed raven)		Africa
C. crassiscolex (now *Molluscotaenia*)	Eulipotyphla: soricid (common shrew, Eurasian water shrew, Eurasian pygmy shrew)	Gastropoda: oxychilid (*Oxychilus cellarius*), discid (*Goniodiscus* (*Discus*) *ruderatus*), gastrodontid (*Zonitoides nitidus*), succineid (*Succinea* putris), vitrinid (*Vitrina pellucida*), cochlicopid (*Cochlicopa lubrica*), bradybaenid (*Eulopa fruticum*), pristilomatid (*Vitrea contracta*), zonitid (*Schistophallus orientalis*), helicid (*Isognomostoma isognomostomos*); Coleoptera: scarabaeoid (*Geotrupes stercorosus*), silphid (*Silpha sinuata*)	Europe
C. crateriformis (now *Liga*)	Piciformes: picid (white-backed woodpecker, great spotted woodpecker, middle spotted woodpecker, black woodpecker, Eurasian wryneck)		Europe
C. decacantha (now *Fuhrmannolepis*)	Charadriiformes: scolopacid (dunlin)		Europe
C. delachauxi (now *Burhinotaenia)*	Charadriiformes: burhinid (stone curlew)		Europe

C. discoidea (now *Anomotaenia)*	Ciconiiformes: ciconiid (white stork)		Europe
C. dodecacantha (now *Paricterotaenia*)	Charadriiformes: larid (little gull)		Eurasia
C. fieldingi (now *Cracticotaenia*)	Passeriformes: artamid (grey butcherbird)		Australia
C. filamentosa (now *Rodentotaenia*)	Eulipotyphla: soricid (Eurasian water shrew), talpid (European mole)		Europe
C. glareoli (now *Kowalewskiella*)	Charadriiformes: scolopacid (wood sandpiper)		Sri Lanka
C. guiarti (now *Panuwa*)	Charadriiformes: charadriid (little ringed plover)		Eurasia
C. hepatica (now *Rodentotaenia*)	Eulipotyphla: soricid (common shrew)		Europe
C. hydrochelidonis (now *Laritaenia*)	Charadriiformes: larid (black-headed gull)		Eurasia
C. iola (now *Sobolevitaenia*)	Passeriformes: turdid (American robin), icterid (western meadowlark, red-winged blackbird)		North America
C. magnihamata (now *Burhinotaenia*)	Charadriiformes: charadriid (yellow-wattled lapwing)		India
C. meliphagidarum (now *Ptilolepis*)	Passeriformes: meliphagid (New Holland honeyeater, white-cheeked honeyeater, white-eared honeyeater, yellow-eared honeysucker)		Australia
C. micracantha (now *Anomotaenia*)	Passeriformes: corvid (western jackdaw)		Eurasia
C. microsoma (now *Spiniglans*)	Passeriformes: emberizid (crested bunting), ploceid (Heuglin's masked weaver)		India
C. mutabilis (now *Cuclincola*)	Pelecaniformes: ardeid (black-crowned night heron)		Europe
C. numenii (now *Dictymetra*)	Charadriiformes: scolopacid (long-billed curlew)		North America
C. parina (now *Monosertum*)	Passeriformes: passerid (Eurasian tree sparrow), parid (great tit)		Europe
C. passerina (now *Icterotaenia*)	Passeriformes: passerid (common sparrow, Eurasian tree sparrow), parid (great tit)		Europe
C. picusi (now *Liga*)	Piciformes: picid (scaly-bellied woodpecker)		India
C. pirinica (now *Spiniglans*)	Passeriformes: corvid (Eurasian magpie)		Russia
C. porosa (now *Paricterotaenia*)	Charadriiformes: larid (black-headed gull, common gull, slender-billed gull); Passeriformes: sturnid (common starling)		Eurasia
C. ransomi (now *Paricterotaenia*)	Charadriiformes: larid (European herring gull, laughing gull, ring-billed gull, Bonaparte's gull, tern, kittiwake); Gaviiformes: gaviid (common loon)		Eurasia
C. ricii (now *Dictymetra*)	Ciconiiformes: ciconiid (Abdim's stork)		Africa
C. scutigerum (now *Monopylidium*)	Eulipotyphla: soricid (common shrew, greater white-toothed shrew)		Europe
C. secunda (now *Anomotaenia*)	Charadriiformes: charadriid (southern lapwing)		Americas
C. sinensis (now *Birovilepis*)	Passeriformes: eurylaimid (long-tailed broadbill)		Indochina
C. soricina (now *Molluscotaenia*)	Eulipotyphla: soricid (common shrew)		Eurasia
C. spinosocapite (now *Sobolevitaenia*)	Passeriformes: sturnid (common starling)		Europe
C. stagnatildis (now *Kowalewskiella*)	Charadriiformes: scolopacid (marsh sandpiper)		Eurasia
C. sternina	Charadriiformes: larid (common tern)		Holarctic

(now *Paricterotaenia*)			
C. triganciensis (now *Fuhrmanolepis slesvicensis*)	Charadriiformes: scolopacid (Eurasian woodcock)		Eurasia
C. tringae (now *Onderstepoortia*)	Charadriiformes: scolopacid (sandpiper)		Africa
C. uncinata (now *Pseudochoanotaenia*)	Charadriiformes: scolopacid (lesser yellowlegs)		Americas
C. unicoronata (now *Sobolevitaenia*)	Passeriformes: turdid (mistle thrush, common blackbird), muscicapid (northern wheatear)		Europe
C. variabilis (now *Anomotaenia*)	Charadriiformes: charadriid (northern lapwing, grey plover), scolopacid (common redshank, curlew sandpiper, dunlin, common snipe, American woodcock)		Holarctic
C. zoniferae (now *Polycerus*)	Charadriiformes: charadriid (banded lapwing)		Australia

Parasite morphology: *Choanotaenia* spp. form 3 different developmental stages: eggs, larvae (metacestodes) and adults. The eggs are ovoid measuring 35-54 µm in diameter and they contain a nonciliated hexacanth (6 hooked) embryo (oncosphere) surrounded by a non-striated shell (embryophore) and a delicate outer membrane with elongate polar processes (filaments which recede as the embryophore develops). Larval metacestodes appear as ovoid encysted stages (cysticercoids) measuring 120-600 µm in diameter. Cysticercoids are lacunate (with internal cavity) and they possess an anterior retracted scolex complete with rostellar hooks and a tail-like cercomer. Adult tapeworms appear as elongate white ribbons measuring from 4-25 cm long by 1-3 mm wide. The strobila (tape) is usually composed of not more than 30 proglottids, which are wider than long. The margins of the worm also have a saw-tooth appearance as the segments are wider posteriorly than anteriorly. The anterior scolex is small (150-500 µm long) and has 4 unarmed suckers (85-120 µm in diameter) surmounted by a large rostellum (130-230 µm long) armed with a single row of 16-22 thorn-shaped hooks (25-30 µm long) with long slender blades. There is still some debate as to the taxonomic classification of *Choanotaenia*-like species with other configurations of rostellar hooks (e.g. species with a double crown of rostellar hooks have recently been transferred to the genus *Spiniglans*). Adult tapeworms lack digestive tracts and each segment has specialized excretory cells known as flame cells (protonephridia). The tapeworms are hermaphroditic and each segment has one set of male and female reproductive organs with a common opening (genital pore) located at the anterior lateral margin. Genital pores of consecutive segments alternate sides irregularly. Proglottids have multiple testes (20-60), a cylindrical cirrus pouch, a lobed ovary and a saccular uterus that eventually form egg capsules each containing only one egg. The hindmost proglottids are gravid, bell-shaped and filled with eggs.

Site of infection: Most *Choanotaenia* spp. are found as adult tapeworms in the small intestines of birds belonging to over 12 orders, particularly Passeriformes and Charadriiformes, but also including domestic poultry. A growing number of species have been found in the intestines of mammalian hosts (shrews, rodents and felids). Larval metacestodes (cysticercoids) have been detected in the body cavities of many insects (flies, locusts, beetles, ants, termites).

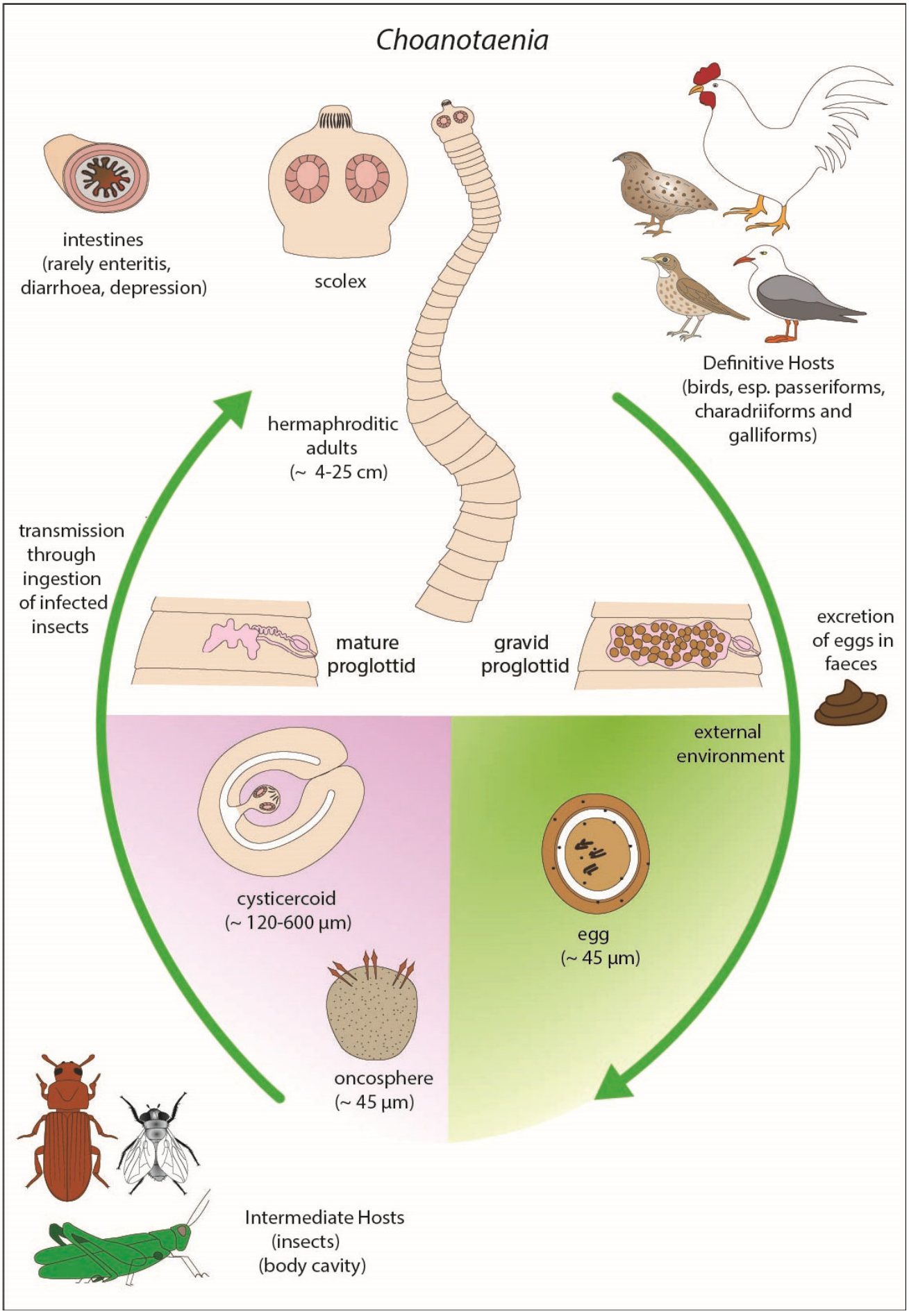
Pathogenesis: Infections by most *Choanotaenia* spp. are not considered to be pathogenic as the tapeworms absorb nutrients from the gut lumen rather than feeding on host tissues. Nevertheless, several species have been associated with subclinical production losses in poultry enterprises by reducing feed conversion efficiency, retarding growth, reducing weight gain and decreasing egg production. Heavy infections by a few species have also been found to cause mild to severe clinical disease typified by enteritis, diarrhoea, weight loss, lethargy, apathy, depression and death, notably in poultry and aviary birds (e.g. finches). Histopathological changes have included catarrhal enteritis, vacuolation of epithelial cells, desquamation and atrophy of villi, inflammation and congestion of submucosal glands, and granuloma formation. Heavy infections are also thought to predispose towards concomitant infections by other infectious agents by lowering host resistance.

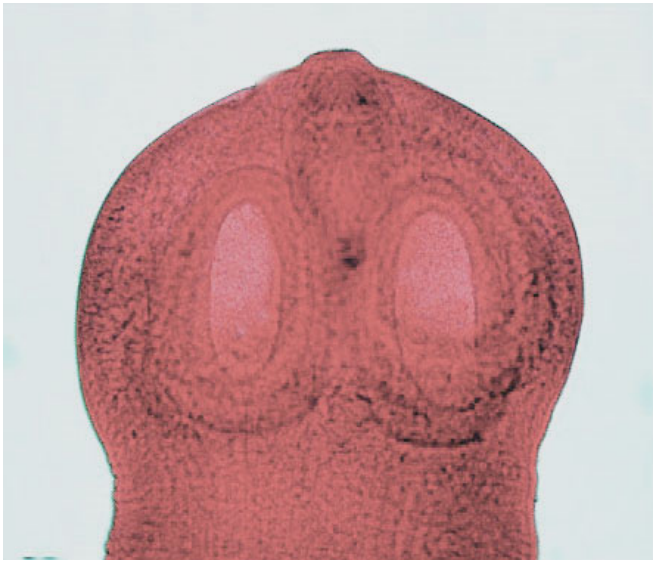
Developmental cycle and mode of transmission: Dilepidid tapeworms have indirect life-cycles alternating between 2 types of hosts; vertebrates acting as definitive hosts (infected by adult stages), and invertebrates (insects) acting as intermediate hosts (infected with larval stages). Mature tapeworms shed gravid proglottids which are passed with host faeces. These segments are highly motile and rapidly migrate from droppings into the surrounding environment. Here they are eaten by insects and digestive processes break down the proglottids releasing the contained eggs. The eggs hatch and the freed oncospheres actively penetrate host tissues to form larval cysticercoid stages in the insect body cavity. A diverse range of insects (flies, beetles, grasshoppers, locusts, ants, termites) have been found to act as intermediate hosts for *Choanotaenia* spp. When infected insects are eaten by birds or insectivorous mammals, the cysticercoids excyst and attach to the gut wall where they develop into adult tapeworms. The prepatent period (= time between infection and shedding of first eggs) is about 2-4 weeks and adult tapeworms generally do not live longer

than one year. Infections are common in many bird species throughout the tropics where climatic conditions are conducive to parasite survival and the abundance of insect populations.

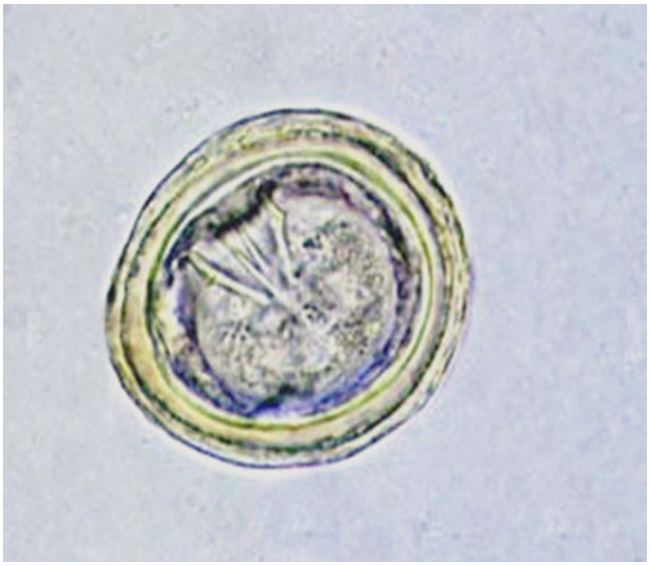
Differential diagnosis: Infections by *Choanotaenia* spp. are conventionally diagnosed by the detection of gravid segments in host faeces, preferably fresh droppings as the motile proglottids migrate out rapidly. Faecal concentration techniques (sedimentation and/or floatation) usually do not recover freed eggs as they remain within excreted segments. Adult tapeworms may be detected upon post-mortem examination of the intestinal mucosa.

Treatment and control: Individual birds or flocks at risk may be treated for infections using specific cestodicides (niclosamide, praziquantel) or broad spectrum anthelmintics proven to be effective against cestodes, notably the benzimidazoles (albendazole, febantel, fenbendazole, mebendazole, oxfendazole). These drugs are often available as additives for drinking water or feed, but careful attention should be given to any contra-indications (e.g. niclosamide is toxic for geese, praziquantel plus pyrantel tartrate is toxic for chickens). Some measure of parasite control may also be afforded in domestic flocks or aviaries by improving bird housing conditions to exclude potential insect intermediate hosts, disposing of faecal material in a sanitary manner, storing feed in insect-proof containers, and reducing insect populations (using barriers, chemicals or biological control options). Obviously, few of these management strategies can be applied to wild bird populations, and the widespread use of insecticides should be discouraged for ecological reasons.


Choanotaenia
intestines
(rarely enteritis,
diarrhoea, depression)
scolex
hermaphroditic
adults
(~ 4-25 cm)
Definitive Hosts
(birds, esp. passeriforms,
charadriiforms and
galliforms)
transmission
through
ingestion
of infected
insects
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
external
environment
cysticercoid
(~ 120-600 µm)
egg
(~ 45 µm)
oncosphere
(~ 45 µm)
Intermediate Hosts
(insects)
(body cavity)



Choanotaenia scolex



Choanotaenia worm egg

Davainea
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Cyclophyllidean tapeworms are usually intestinal parasites of terrestrial vertebrates and have an anterior scolex (hold-fast organ with suckers and sometimes hooks) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). Eucestodes have indirect life-cycles involving oncospheres (hexacanth embryos) released from ingested eggs to form encysted larval stages (metacestodes) in the tissues of intermediate hosts and their transmission to definitive hosts by predation. Adult davaineids usually have an armed rostellum and suckers and are parasitic in birds and mammals, sometimes causing enteric disorders and mortalities. The encysted larval stages (cysticercoids) of *Davainea* spp. occur in snails and slugs which are consumed during foraging.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)
Family:	Davaineidae (tapeworms of birds, large rostellum with hammer-shaped hooks and spiny suckers)
Genus:	*Davainea* (parasitic in small intestines of birds)
Species:	various species cause enteritis in poultry

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce

eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Cyclophyllidean cestodes are polyzoic containing from 2 to > 1,000 proglottids demarcated by external segmentation. They possess an anterior scolex with 4 suckers, many with a rostellum (often armed), and they have compact post-ovarian vitellaria. Adult worms are found in terrestrial vertebrate definitive hosts (mammals, birds, reptiles, amphibians) while larval metacestodes occur in vertebrate (mammal, amphibian, bird) or invertebrate (mollusc, acari, insect) intermediate hosts. Over 3,000 species have been described in 400 genera in 16 families: Acoleidae, Amabiliidae, Anoplocephalidae, Catenotaeniidae, Davaineidae, Dioecocestidae, Dilepididae, Dipylidiidae, Gyrporhynchidae, Hymenolepididae, Mesocestoididae, Metadileptidae, Nematotaeniidae, Paruterinidae, Progynotaeniidae, and Taeniidae (all with lateral genital pores, except the Mesocestoididae).

The family Davaineidae is characterized by adult tapeworms usually possessing a scolex with small numerous hammer-shaped hooks around the suckers as well as on the rostellum. Over 30 davaineid genera have been described: including *Calostaurus, Cotugnia, Davainea, Fernandezia, Fuhrmannetta, Houttuynia, Idiogenes, Ophryocotyle, Otiditaenia, Paroniella, Paspalia,*

Pseudidiogenes, Raillietina and *Skrjabinia.* The family Davaineidae is conventionally divided into 2 subfamilies: the Davaineinae (often including the Ophyryocotylinae) whose adults do not possess a paruterine organ; and the Idiogeninae whose adults have a paruterine organ. Davaineine tapeworms are commonly found in birds (occasionally mammals) and larval stages develop in insects (such as flies and ants) or gastropod molluscs (slugs and snails). Several taxonomic reviews have attempted to reconcile differences between the davaineine genera, particularly *Davainea* and *Raillietina*. Most *Davainea* spp. are small triangular worms with only 4-9 proglottids, the scolex has rostellar hooks in several rows, the 4 suckers are armed, and the segments have genital pores alternating regularly; while *Raillietina* spp. are generally long tapeworms with numerous proglottids, the scolex has rostellar hooks in 1-2 circular rows, the 4 suckers are sometimes armed, and the segments have genital pores which are unilateral or alternate irregularly. Over 100 *Davainea* spp. have been recorded worldwide from 120 different hosts, but almost half have been synonymized with *Raillietina*. Most *Davainea* infections are asymptomatic although several species have previously been associated with production losses in commercial poultry flocks.

***Davainea* species**	**Definitive host [adults in intestines]**	**Intermediate hosts [cysticercoids in tissues]**	**Distribution**
D. alii	Passeriformes: pycnonotid (red-vented bulbul)		India
D. allagea	Psittaciformes: psittaculid (double-eyed fig parrot)		New Guinea
D. ambajogaiensis	Galliformes: phasianid (chicken)		India
D. andrei	Galliformes: phasianid (grey partridge)		Asia
D. aurangabadensis	Galliformes: phasianid (chicken); Charadriiformes: charadriid (red-wattled lapwing)		India
D. baeri	Piciformes: picid (red-rumped green woodpecker)		Asia
D. balasahebae	Galliformes: phasianid (chicken)		India
D. biroi (syn. *Raillietina, Kotlania*)	Psittaciformes: psittacid (orange-breasted fig parrot)		New Guinea
D. brachyrhyncha	Cariamiformes: cariamid (red-legged seriema)		South America
D. calva	Galliformes: phasianid (red grouse)		Europe
D. cantaniana (syn. *D. oligophora*)	Galliformes: phasianid (chicken, common pheasant, turkey), numidid (grey-breasted helmeted guineafowl)		Europe
D. carioca	Galliformes: phasianid (chicken)		South America
D. casuarii	Casuariiformes: casuariid (dwarf cassowary)		New Guinea
D. chauhani	Galliformes: phasianid (blood pheasant, chicken)		India
D. clavulus	Passeriformes: paradisaeid (magnificent riflebird)		Australia
D. columbae	Columbiformes: columbid (common wood pigeon, rock dove, European turtle dove)		Europe
D. difformis sp. inq. (syn. *Taenia, T. brevicollis*)	Cuculiformes: cuculid (common cuckoo)		Eurasia
D. domesticusi	Galliformes: phasianid (chicken)		India
D. exilis	Galliformes: phasianid (chicken)		India
D. fuhrmanni	Galliformes: phasianid (turkey)		North America
D. guivillensis	Galliformes: phasianid (pheasant); Columbiformes: columbid (wood pigeon)		Europe
D. gunjotinesis	Galliformes: phasianid (chicken)		India
D. hewetensis	Galliformes: phasianid (chicken)		India
D. himantopodis	Charadriiformes: recurvirostrid (pied stilt)		India, Australia
D. isomydis	Rodentia: murid (Abyssinian grass rat)		Africa
D. jalnaensis	Galliformes: phasianid (chicken)		India
D. kekhalensis	Galliformes: phasianid (chicken)		India
D. kramerii	Psittaciformes: psittaculid (rose-ringed parakeet)		India
D. lagopodis	Galliformes: phasianid (grouse)		North America
D. macrorchida	Psittaciformes: psittaculid (Edwards's fig-parrot)		New Guinea
D. marchii	Charadriiformes: scolopacid (common		Eurasia

(syn. *Taenia*)	redshank, spotted redshank)		
D. meleagridis	Galliformes: phasianid (turkey)		North America, India
D. minuta	Charadriiformes: scolopacid (common redshank)		India
D. muktabae	Galliformes: phasianid (chicken); Passeriformes: sturnid (common myna)		India
D. musculosa	Passeriformes: sturnid (common starling)		Europe
D. nana	Galliformes: numidid (guineafowl)		India
D. nitini	Passeriformes: pycnonotid (red-vented bulbul)		India
D. osmanabadensis	Galliformes: phasianid (chicken)		India
D. passerae	Passeriformes: passerid (house sparrow)		India
D. paucisegmentata	Galliformes: numidid (guineafowl)		Africa, India
D. polycalcaria	Passeriformes: corvid (Indian jungle crow)		Sri Lanka
D. polychalix	Psittaciformes: psittaculid (coconut lorikeet)		New Guinea
D. pondicerianusi	Galliformes: phasianid (grey francolin)		India
D. proglottina [incl. *D. p.* var. *dublanensis*] (syn. *D. varians, Taenia*)	Galliformes: phasianid (chicken, turkey); Columbiformes: columbid (pigeon)	Gastropoda: limacid (*Limax cinereus, L. agrestis, L. variegatus, Agriolimax, Cepoa, Deroceras panormitanium*), physid (*Physa heterostropha*), arionid (*Arion*)	worldwide
D. retharei	Columbiformes: columbid (Eurasian collared-dove); Galliformes: phasianid (chicken)		India
D. rhyncota	Piciformes: picid (northern flicker)		North America
D. shindei	Galliformes: phasianid (chicken)		India
D. shrigondaensis	Galliformes: phasianid (chicken)		India
D. sphaerocephala	Charadriiformes: scolopacid (Eurasian curlew)		Eurasia
D. spiralis	Columbiformes: columbid (dove)		New Guinea
D. struthionis	Struthioniformes: struthionid (common ostrich, blue-necked ostrich); Rheiformes: rheid (greater rhea)		Africa, South America
D. tauricollis	Rheiformes: rheid (greater rhea)		South America
D. tetraoensis	Galliformes: phasianid (capercaillie)		India
D. uniuterina	Passeriformes: cotingid (Guianan cock-of-the-rock)		South America
Reassigned species			
D.allomyodes (syn. *Raillietina*) (now *Idiogenoides*)	Psittaciformes: psittaculid (Edward's fig-parrot)		New Guinea
D. anatina (now *Raillietina*)	Anseriformes: anatid (mallard)		India
D. aruensis (now *Raillietina*)	Psittaciformes: psittaculid (blue-banded lorikeet)		Indonesia
D. australis (now *Raillietina*)	Casuariiformes: casuariid (emu)		Australia
D. bycanistis (now *Raillietina*)	Bucerotiformes: bucerotid (black-and-white-casqued hornbill)		Africa
D. cacatuinae (now *Raillietina*)	Psittaciformes: cacatuid (sulphur-crested cockatoo)		Australia
D. calcaria (now *Raillietina*)	Musophagiformes: musophagid (great blue turaco)		Africa
D. campanulata (syn. *Raillietina*) (now *Davaineolepis*)	Galliformes: phasianid (partridge)		South America
D. capillaris (now *Raillietina*)	Tinamiformes: tinamid (tinamou)		South America
D. celebensis (now *Raillietina*)	Rodentia: murid (trefoil-toothed giant rat)		Indonesia
D. centropi (now *Raillietina*)	Cuculiformes: cuculid (common coucal)		Sri Lanka
D. ceylonica	Galliformes: phasianid (Indian peafowl)		Sri Lanka

(now *Raillietina*)			
D. circumcinata (now *Raillietina*)	Pelecaniformes: ardeid (little egret)		Egypt
D. clavicirrosa (now *Raillietina*)	Galliformes: phasianid (Clapperton's francolin)		Egypt
D. cohni (now *Raillietina*)	Galliformes: phasianid (chicken)		Africa
D. comitata (now *Raillietina*)	Piciformes: picid (northern flicker)		North America
D. compacta (now *Raillietina*)	Passeriformes: oriolid (Eurasian golden oriole)		Eurasia
D. conopophilae (now *Raillietina*)	Passeriformes: meliphagid (rufous-banded honeyeater)		Australia
D. contorta (now *Dioriraillietina*)	Pholidota: manid (Chinese pangolin)	Hymenoptera: formicid (ants)	Indochina
D. crassula (now *Raillietina*)	Columbiformes: columbid (rock dove)		Eurasia
D. cryptacantha (now *Raillietina*)	Columbiformes: columbid (rock dove)		Egypt
D. crypturi (now *Raillietina*)	Tinamiformes: tinamid (yellow-legged tinamou)		South America
D. cyrtus (now *Raillietina*)	Anseriformes: anatid (duck)		South America
D. debilis (now *Raillietina*)	Ciconiiformes: ciconiid (African openbill)		Africa
D. elongata (syn. *Fuhrmannetta Johnstonia*) (now *Raillietina*)	Tinamiformes: tinamid (tinamou, red-winged tinamou, lesser nothura)		South America
D. emperus (syn. *Ransomia*) (now *Raillietina*)	Bucerotiformes: bucerotid (hornbill)		Africa
D. galeritae (now *Raillietina*)	Passeriformes: alaudid (Maghreb lark)		Africa
D. globirostris (now *Raillietina*)	Galliformes: phasianid (common partridge)		Europe
D. globocephala (now *Raillietina*)	Passeriformes: icterid (red-rumped cacique)		South America
D. goura (now *Raillietina*)	Columbiformes: columbid (Albert's crowned pigeon)		New Guinea
D. gracilis (now *Raillietina*)	Rodentia: murid (eastern spiny mouse), thryonomyid (greater cane rat)		North America, Africa
D. indica (now *Raillietina*)	Galliformes: phasianid (chicken)		India
D. infrequens (now *Raillietina*)	Casuariiformes: casuariid (dwarf cassowary)		New Guinea
D. laticanalis (now *Raillietina*)	Galliformes: phasianid (grey partridge)		South America
D. leptacantha (now *Raillietina*)	Galliformes: cracid (black curassow)		South America
D. longicirrosa (now *Chapmania*)	Accipitriformes: accipitrid (black kite)		Africa
D. longicollis (now *Raillietina*)	Galliformes: phasianid (chicken)		Europe
D. longispina (now *Raillietina*)	Piciformes: picid (chestnut woodpecker)		South America
D. lutzi (now *Raillietina*)	Piciformes: picid (chestnut woodpecker)		South America
D. macrocirrosa (now *Raillietina*)	Musophagiformes: musophagid (red-crested turaco)		Africa
D. macroscolecina (now *Raillietina*)	Psittaciformes: psittaculid (chattering lory)		South America

D. magnicoronata (now *Raillietina*)	Caprimulgiformes: caprimulgid (Nacunda nighthawk)		South America
D. micracantha (now *Raillietina*)	Columbiformes: columbid (European turtle dove)		Europe
D. microscolecina (now *Raillietina*)	Psittaciformes: psittaculid (Eclectus parrot)		Asia
D. multicapsulata (now *Raillietina*)	Galliformes: phasianid (common pheasant)		Europe
D. numida (now *Raillietina*)	Galliformes: numidid (helmeted guineafowl)		Africa
D. oligacantha (now *Raillietina*)	Tinamiformes: tinamid (red-winged tinamou)		South America
D. oligorchida (now *Raillietina*)	Psittaciformes: psittaculid (Eclectus parrot)		Indonesia
D. paradisea (now *Raillietina*)	Passeriformes: paradisaeid (crinkle-collared manucode)		New Guinea
D. parva (syn. *Raillietina* (*Skrjabinia*)) (now *Mathevotaenia*)	Eulipotyphla: erinaceid (hedgehog)		Europe
D. paucitesticulata (now *Raillietina*)	Columbiformes: columbid (Nicobar pigeon)		
D. penelopina (now *Raillietina*)	Galliformes: cracid (dusky-legged guan)		South America
D. penetrans (now *Raillietina*)	Galliformes: phasianid (chicken)		Africa
D. polycalceola (now *Raillietina*)	Rodentia: murid (Muschenbrock's mouse)		Indonesia
D. polyuterina (now *Raillietina*)	Galliformes: phasianid (grey partridge)		Europe
D. psittacea (now *Raillietina*)	Psittaciformes: cacatuid (triton cockatoo)		Indonesia
D. retusa (now *Raillietina*)	Galliformes: phasianid (black grouse)		Russia
D. sphaeroides (now *Raillietina*)	Accipitriformes: accipitrid (common buzzard)		Russia
D. sphecotheridis (now *Raillietina*)	Passeriformes: oriolid (short-billed honeyeater)		Australia
D. tragopani (now *Raillietina*)	Galliformes: phasianid (satyr tragopan)		India
D. trapezoides (now *Raillietina*)	Rodentia: murid (striped mouse, African grass rat)		Africa
D. undulata (now *Raillietina*)	Musophagiformes: musophagid (great blue turaco)		Africa
D. vaganda (now *Raillietina*)	Accipitriformes: accipitrid (African fish eagle)		Africa

Parasite morphology: *Davainea* spp. form 3 different sequential stages in their developmental cycles: eggs, larvae (metacestodes) and adults. Mature eggs are usually grey in colour and ovoid-spherical in shape measuring 28-40 µm in diameter. They each contain a single nonciliated hexacanth (6 hooked) embryo (oncosphere) enclosed within an extraembryonic envelope which is nonstriated and without a distinctive membrane. Cysticercoid larvae are white in colour, mostly ovoid in shape measuring from 120-250 µm in diameter, lacunate (with internal cavity) and contain an anterior scolex (retracted into a small double-walled cavity) and a posterior tail-like cercomer, all enclosed within a wrinkled gelatinous coat. Adult *Davainea* tapeworms are small and triangular in shape, only measuring up to 3 cm long and comprising 4-9 segments (proglottids) ranging from 1.4-2.0 mm in length by 0.4-0.6 mm in width. The worms have a small anterior scolex with 4 suckers and a rostellum approx. 80 µm long. The suckers and rostellum are armed with numerous (60-100) small hammer-shaped hooks, the rostellar hooks occurring in 3-10 rows (cf. those of *Raillietina* spp. in 1-2 rows). Adult worms are hermaphroditic, with anterior proglottids being immature (lacking gonads), middle proglottids being mature (containing both male and female gonads) and posterior proglottids being gravid (containing numerous eggs). The eggs are scattered throughout the parenchyma enclosed singly in egg capsules and are shed individually or in short chains through the single genital pore located at the lateral margin (side alternating regularly in consecutive proglottids).

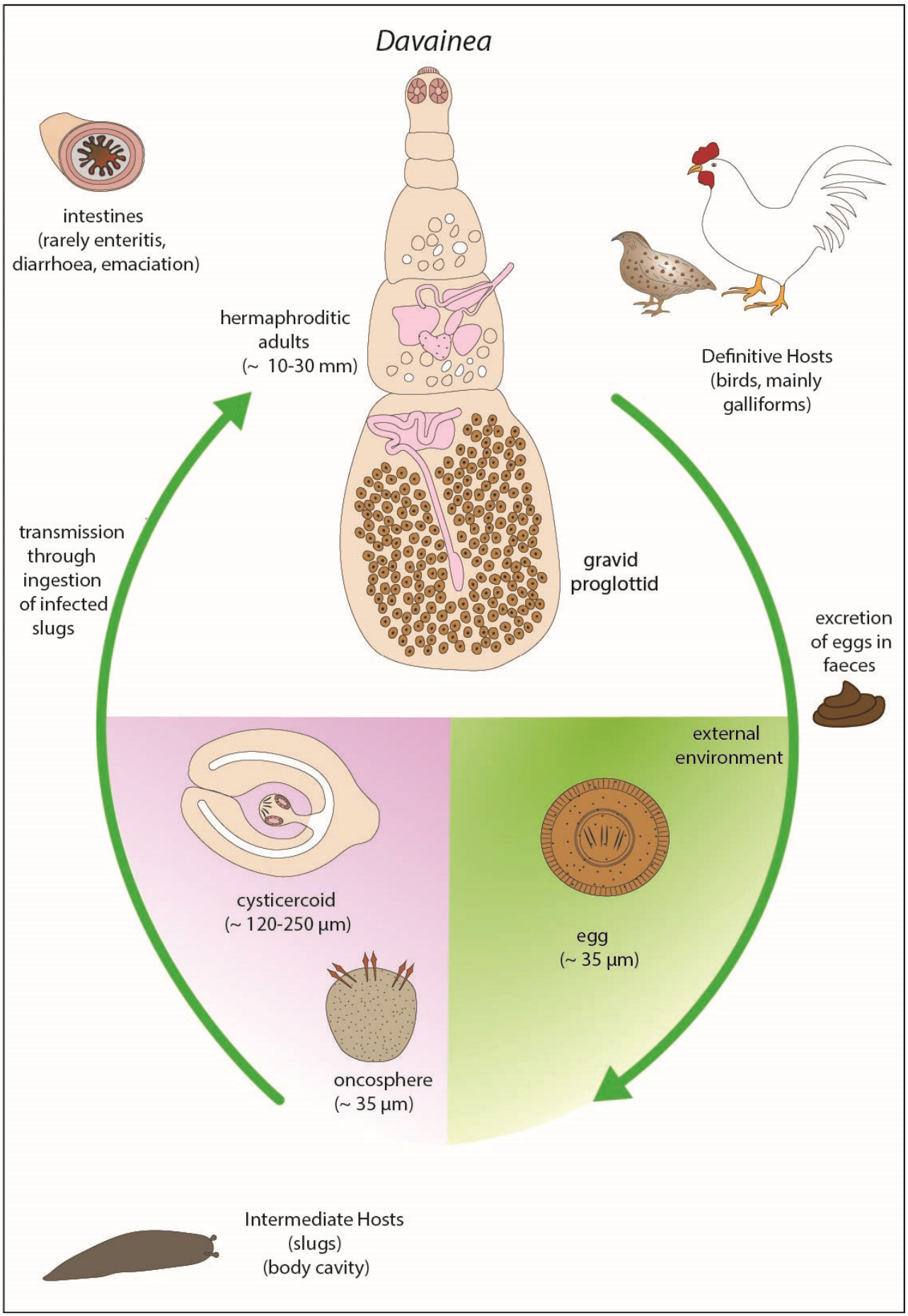
Site of infection: Adult *Davainea* tapeworms infect the small intestines (duodenum) of their avian definitive hosts, mostly galliform birds. Metacestodes (cysticercoids) infect the body cavities of their invertebrate intermediate hosts, presumed to be gastropods (slugs) for most species, although insects (ants) have been implicated for some species.

Pathogenesis: Adult tapeworms lack digestive tracts and do not feed on host tissues but rather absorb nutrients from the gut lumen. Worms attach to the intestinal wall using their armed scoleces and this may cause traumatic damage, inflammation and reduced gut function (poor absorption). While light to mild infections by most species do not cause overt clinical disease, some species have been associated with subclinical production losses in poultry resulting from poor feed conversion efficiencies, retarded growth, reduced weight gain and decreased egg production. In contrast, heavy infections may cause severe disease in birds, particularly when they have ingested large numbers of larval cysticercoids in infected slugs. Birds may experience enteritis, intestinal haemorrhages, bloody diarrhoea, lethargy, dull plumage and ruffled feathers, progressive weight loss, emaciation and eventually difficulty in breathing, leg paralysis and death. Despite its small size, *D. proglottina* is one of the most pathogenic tapeworms of poultry penetrating deeply into the mucosa and causing intense inflammation and mucosal thickening, particularly in chronic cumulative infections. Histopathological changes include vacuolation of epithelial cells, villous atrophy and desquamation, congestion of submucosal glands, granuloma formation and catarrhal enteritis. Heavy infections also lower host resistance to other infectious agents. Infections in poultry are common throughout tropical regions where poor housing and husbandry practices as well as favourable climatic conditions are conducive to parasite survival and transmission.

Developmental cycle and mode of transmission: *Davainea* spp. have indirect heteroxenous (2-host) life-cycles with avian definitive hosts becoming infected when consuming larval stages in invertebrate intermediate hosts. Gravid proglottids containing eggs are passed in bird faeces, often at a rate of one per day. The proglottids migrate out of droppings into adjacent vegetation of soil. The eggs may survive in the external environment for several days in the presence of moisture, but desiccate rapidly. Terrestrial gastropods (slugs) feed on the proglottids and eggs resulting in the release of the contained oncospheres which penetrate the gut wall using their hooks and penetration gland secretions. The oncospheres develop into encysted larvae (cysticercoids) in the body cavity (coelom) of the slugs. Multiple cysticercoids often occur within individual slugs (over 1,500 detected once) and they remain infective for up to 11 months. Foraging birds become infected when they ingest infected slugs and the contained cysticercoids break down releasing the larvae which attach to the gut wall and develop into adult tapeworms. Infections are not multiplicative but cumulative (ingestion of 1 cysticercoid leads to development of 1 tapeworm). Because slugs may harbour multiple cysticercoids, birds often become infected with multiple tapeworms (up to 4,000 recorded in one heavily infected fowl). The time from infection until the first release of gravid proglottids (i.e. the pre-patent period) is around 2-3 weeks, and adult tapeworms have been found to live for up to 3 years.

Differential diagnosis: Infections may be diagnosed ante-mortem in birds by the detection of characteristic gravid proglottids in faecal samples. Motile proglottids may be detected by visual examination while their internal morphology is best revealed by microscopic examination. The detection of egg capsules containing single eggs may be facilitated by dissecting or squashing proglottids or by differential staining. Alternatively, infections may be diagnosed post-mortem by the detection of characteristic adult tapeworms in intestinal mucosal preparations (scrapings, smears or digests). Some urgency is required in examining mucosal preparations as the small tapeworms autolyse rapidly over 24 hours.

Treatment and control: Clinical infections in poultry have been successfully treated using a range of anthelmintics effective against cestodes; including isoquinolines (praziquantel), benzimidazole-methylcarbamates (flubendazole) and halogenated hydrocarbons (butynorate, in conjunction with piperazine or phenothiazine). Treatment is often applied as a feed additive in commercial flocks. Control programmes should also target transmission to and from molluscs, either by minimizing faecal contamination of the environment (hygienic waste disposal and/or effluent treatment), eliminating or reducing slug populations (using physical barriers, molluscicides or manipulating environmental conditions by alternate grazing, soil rotovation or weed control), and by curbing bird foraging behaviours (by providing better housing or clean free-range conditions).


Davainea
intestines
(rarely enteritis,
diarrhoea, emaciation)
hermaphroditic
adults
(~ 10-30 mm)
Definitive Hosts
(birds, mainly
galliformes)
transmission
through
ingestion
of infected
slugs
gravid
proglottid
excretion
of eggs in
faeces
external
environment
cysticercoid
(~ 120-250 µm)
egg
(~ 35 µm)
oncosphere
(~ 35 µm)
Intermediate Hosts
(slugs)
(body cavity)



Davainea adult worm



Davainea adult worm

Raillietina
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Cyclophyllidean tapeworms are usually intestinal parasites of terrestrial vertebrates and have an anterior scolex (hold-fast organ with suckers and sometimes hooks) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). Eucestodes have indirect life-cycles involving oncospheres (hexacanth embryos) released from ingested eggs to form encysted larval stages (metacestodes) in the tissues of intermediate hosts and their transmission to definitive hosts by predation. Adult davaineids usually have an armed rostellum and suckers and are parasitic in birds and mammals, sometimes causing enteric disorders and mortalities. The encysted larval stages (cysticercoids) of *Raillietina* spp. occur in ants and beetles which are consumed during foraging.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)
Family:	Davaineidae (tapeworms of birds, large rostellum with hammer-shaped hooks and spiny suckers)
Genus:	*Raillietina* (parasitic in small intestines of birds)
Species:	various species cause enteritis in poultry

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce

eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Cyclophyllidean cestodes are polyzoic containing from 2 to > 1,000 proglottids demarcated by external segmentation. They possess an anterior scolex with 4 suckers, many with a rostellum (often armed), and they have compact post-ovarian vitellaria. Adult worms are found in terrestrial vertebrate definitive hosts (mammals, birds, reptiles, amphibians) while larval metacestodes occur in vertebrate (mammal, amphibian, bird) or invertebrate (mollusc, acari, insect) intermediate hosts. Over 3,000 species have been described in 400 genera in 16 families: Acoleidae, Amabiliidae, Anoplocephalidae, Catenotaeniidae, Davaineidae, Dioecocestidae, Dilepididae, Dipylidiidae, Gyrporhynchidae, Hymenolepididae, Mesocestoididae, Metadileptidae, Nematotaeniidae, Paruterinidae, Progynotaeniidae, and Taeniidae (all with lateral genital pores, except the Mesocestoididae).

The family Davaineidae is characterized by adult tapeworms usually possessing a scolex with hammer-shaped hooks around the suckers as well as on the rostellum. Some 14 davaineid genera have been described: including *Calostaurus, Cotugnia, Davainea, Fernandezia, Fuhrmannetta, Houttuynia, Idiogenes, Ophryocotyle, Otiditaenia, Paroniella, Paspalia, Pseudidiogenes,*

Raillietina and *Skrjabinia.* The family Davaineidae is conventionally divided into 2 subfamilies: the Davaineinae (often including the Ophyryocotylinae) whose adults do not possess a paruterine organ; and the Idiogeninae whose adults have a paruterine organ. Several taxonomic reviews have attempted to reconcile differences between davaineine genera and many *Raillietina* and *Davainea* spp. have subsequently been synonymized. *Raillietina* spp. are generally long tapeworms with numerous proglottids, the scolex has rostellar hooks in 1-2 circular rows, the 4 suckers are sometimes armed, and the segments have genital pores which are unilateral or alternate irregularly; while *Davainea* spp. are small triangular worms with only 4-9 proglottids, the scolex has rostellar hooks in several rows, the 4 suckers are armed, and the segments have genital pores which alternate regularly. Several newly erected genera have also previously been recorded as subgenera of the genus *Raillietina*, differentiated as follows: *R.* (*Raillietina*) (genital apertures unilateral, several oncospheres per egg capsule); *R.* (*Paroniella*) (genital apertures unilateral, one oncosphere per egg capsule); *R.* (*Fuhrmannetta*) (genital apertures alternating irregularly, several oncospheres per egg capsule) and *R.* (*Skrjabinia*) (genital apertures alternating irregularly, one oncosphere per egg capsule). Adult tapeworms occur in vertebrates (birds and mammals) while larval stages develop in insects (such as flies and ants) or gastropod molluscs (slugs and snails). Over 230 *Raillietina* spp. have been recorded worldwide, with some 200 spp. occurring in birds (wild and domestic) and around 40 spp. in mammals (lagomorphs, rodents and occasionally primates).

***Raillietina* species**	**Definitive host [adults in small intestines]**	**Intermediate hosts [cysticercoids in tissues]**	**Distribution**
Subgenus *Raillietina* (genital apertures unilateral, several oncospheres per egg capsule)			
R. (*R.*) *afghana*	Rodentia: cricetid (Afghan vole)		Afghanistan
R. (*R.*) *africana* (syn. *Davainea*)	Carnivora: herpestid (mongoose); Primates: hominid (human)		Africa
R. (*R.*) *alagea*	Psittaciformes: psittaculid (double-eyed fig-parrot)		New Guinea
R. (*R.*) *alectori*	Galliformes: phasianid (rock partridge)		Middle-East
R. (*s.l.*) *anatina* (syn. *Davainea*)	Anseriformes: anatid (mallard); Columbiformes: columbid (dove, yellow-footed green pigeon)		Eurasia
R. (*R.*) *angusta*	Galliformes: numidid (helmeted guineafowl)		Africa
R. (*R.*) *apivori*	Accipitriformes: accipitrid (European honey buzzard)		Russia
R. (*R.*) *aruensis* (syn. *Davainea*)	Psittaciformes: psittaculid (coconut lorikeet, blue-banded lorikeet, black-capped lory, Edward's fig-parrot, double-eyed fig-parrot)		New Guinea
R. (*R.*) *asiatica* (syn. *Davainea, Ransomia*)	Rodentia: murid (black rat, lesser bandicoot rat, bush rat, striped field mouse, Mayer's brush mouse); Primates: hominid (human)		Asia, Australia
R. (*R.*) *australis* (syn. *Taenia, Davainea, Ransomia, Kotlania*)	Casuariiformes: casuariid (emu)	Hymenoptera: formicid (*Pheidole*)	Australia
R. (*R.*) *baeri*	Rodentia: murid (black rat, Nile rat, Natal multimammate mouse, Jackson's soft-furred mouse)		Africa
R. (*R.*) *baghdadensis*	Columbiformes: columbid (rock dove)		Iraq
R. (*R.*) *bakeri*	Rodentia: murid (cotton rat), sciurid (western fox squirrel)		North America
R. (*R.*) *bembezi*	Strigiformes: strigid (spotted eagle owl)		Africa
R. (*R.*) *beveridgei*	Casuariiformes: casuariid (emu)	Hymenoptera: formicid (*Pheidole*)	Australia
R. (*R.*) *boueti* (syn. *Kotlania*)	Galliformes: phasianid (double-spurred spurfowl)		Africa
R. (*s.l.*) *brevicollis*	Cuculiformes: cuculid (common cuckoo)		Europe
R. (*R.*) *buckleyi* (syn. *Ransomia*)	Columbiformes: columbid (laughing dove)		Africa
R. (*R.*) *bumi*	Strigiformes: strigid (spotted eagle owl)		Africa
R. (*R.*) *bungoensis*	Columbiformes: columbid (rock dove)		Japan
R. (*R.*) *bycanistis* (syn. *Davainea*)	Bucerotiformes: bucerotid (black-casqued hornbill, white-crested hornbill, black-and-white-casqued hornbill)		Africa
R. (*R.*) *cacatuinae* (syn. *Davainea*)	Psittaciformes: cacatuid (sulphur-crested cockatoo)		Australia

R. (*R.*) *calcaria* (syn. *Davainea, Ransomia*)	Musophagiformes: musophagid (great blue turaco); Cuculiformes: cuculid (blue-headed coucal)		Africa
R. (*R.*) *calyptomenae* (syn. *Ransomia*)	Passeriformes: calyptomenid (Whitehead's broadbill)		Indonesia
R. (*R.*) *canabia*	Columbiformes: columbid (rock dove)		Middle-East
R. (*R.*) *capillaris* (syn. *Davainea, Ransomia*)	Tinamiformes: tinamid (tinamou)		South America
R. (*R.*) *cameostrobilata*	Galliformes: phasianid (common pheasant, wild turkey)		Russia
R. (*R.*) *carpophagi*	Columbiformes: columbid (rock dove, green imperial pigeon)		Indochina
R. (*R.*) *casuari* (syn. *Davainea, Ransomia*)	Casuariiformes: casuariid (dwarf cassowary)		New Guinea
R. (*R.*) *celebensis* [incl. *R. c. paucicapsulata*] (syn. *Davainea, Ransomia*)	Rodentia: murid (trefoil-toothed giant rat, brown rat); Primates: hominid (human)		Indonesia, Myanmar
R. (*R.*) *ceylonica* (syn. *Davainea, Ransomia*)	Galliformes: phasianid (Indian peafowl); Columbiformes: columbid (Bengal green pigeon, snow pigeon)		India
R. (*R.*) *chilmei*	Galliformes: phasianid (snow partridge)		Nepal
R. (*R.*) *chiltoni*	Casuariiformes: casuariid (emu)	Hymenoptera: formicid (*Pheidole*)	Australia
R. (*s.l.*) *circumcinata* (syn. *Davainea*)	Pelecaniformes: ardeid (little egret)		Egypt
R. (*R.*) *clairae*	Piciformes: picid (grey-headed woodpecker)		China
R. (*R.*) *clavicirrosa* (syn. *Davainea, Ransomia*)	Galliformes: phasianid (Clapperton's francolin, crested francolin)		Egypt
R. (*R.*) *clerci* (syn. *Davainea, Ransomia*)	Anseriformes: anatid (duck); Columbiformes: columbid (rock dove, European turtle dove, Oriental turtle dove)		Eurasia, Africa, Americas
R. (*R.*) *cohni* (syn. *Davainea, Ransomia*)	Galliformes: phasianid (chicken), numidid (helmeted guineafowl); Pterocliformes: pteroclid (chestnut-bellied sandgrouse, black-bellied sandgrouse)		Africa, India
R. (*R.*) *colinia*	Galliformes: odontophorid (northern bobwhite quail)		North America
R. (*R.*) *columbiella*	Columbiformes: columbid (rock dove)		Africa
R. (*R.*) *comitata* (syn. *Davainea, Ransomia*)	Piciformes: picid (northern flicker, red-headed woodpecker)		North America
R. (*R.*) *congolensis*	Passeriformes: estrildid (orange-winged pytilia)		Africa
R. (*R.*) *coreensis*	Rodentia: murid (small Japanese field mouse, striped field mouse)		Asia
R. (*R.*) *coturnixi*	Galliformes: phasianid (common quail)		Russia
R. (*R.*) *cryptacantha* (syn. *Ransomia, Davainea*)	Columbiformes: columbid (rock dove, European turtle dove, mourning collared-dove, eastern bronze-naped pigeon, laughing dove, ring-necked dove)		Africa
R. (*R.*) *crypturi* (syn. *Davainea, Ransomia*)	Tinamiformes: tinamid (yellow-legged tinamou)		South America
R. (*R.*) *cyrtus* (syn. *Davainea, Ransomia*)	Anseriformes: anatid (duck)		South America
R. (*R.*) *daetensis*	Columbiformes: columbid (green pigeon)		Philippines
R. (*R.*) *dartevellei*	Accipitriformes: accipitrid (palm-nut vulture)		Africa
R. (*R.*) *dattai*	Galliformes: phasianid (chicken)		India
R. (*R.*) *debilis* (syn. *Davainea, Ransomia*)	Ciconiiformes: ciconiid (African openbill)		Africa
R. (*R.*) *delalandei*	Columbiformes: columbid (African green pigeon)		Africa
R. (*R.*) *demerariensis* [incl. *R. d. trinitae, R. d. venezolanensis*]	Rodentia: capromyid (Desmarest's hutia), cuniculid (lowland paca), dasyproctid (red-rumped agouti), echimyid (Guyenne spiny rat),		South and Central America

(syn. *R. brumpti, R. davainei, R. equatoriensis, R. halli, R. luisaleoni, R. leoni, R. quitensis*)	erethizontid (black-tailed hairy dwarf porcupine); Primates: atelid (Guatemalan black howler monkey, Venezuelan red howler monkey), hominid (human)		
R. (*R.*) *deweti*	Galliformes: numidid (guineafowl)		Africa
R. (*R.*) *douceti*	Musophagiformes: musophagid (turaco)		Africa
R. (*R.*) *dromaius*	Casuariiformes: casuariid (emu)	Hymenoptera: formicid (*Pheidole*)	Australia
R. (*R.*) *echinobothrida* (syn. *R. grobbeni, R. sinensis, Johnstonia, Taenia infundibuliformis, T. botrioplites, Ransomia botrioplites, Davainea echinobothrida, D. parechinobothrida*)	Galliformes: phasianid (chicken, red junglefowl, turkey, grey partridge, rock partridge, common pheasant, common quail), numidid (helmeted guineafowl); Anseriformes: anatid (mallard); Columbiformes: columbid (Oriental turtle dove, rock dove, laughing dove); Accipitriformes: accipitrid (Eurasian sparrowhawk)	Hymenoptera: formicid ants (*Monomorium salmonis indicum, Tetramorium caespitum, T. c. jacotti, T. semilaeve, T. simillium, Pheidole bergi, P. fossulata, P. rhombinoda P. vinelandica*)	worldwide
R. (*R.*) *emperus* (syn. *Davainea, Ransomia*)	Bucerotiformes: bucerotid (hornbill); Cuculiformes: cuculid (Senegal coucal)		Africa
R. (*R.*) *ershovi*	Columbiformes: columbid (Oriental turtle dove)		Russia
R. (*R.*) *eupodotidis*	Otidiformes: otidid (white-bellied bustard)		Africa
R. (*R.*) *famosa*	Psittaciformes: psittaculid (eclectus parrot)		Asia
R. (*R.*) *fausti*	Piciformes: picid (grey-headed woodpecker, European green woodpecker)		China
R. (*R.*) *fischthali*	Columbiformes: columbid (green imperial pigeon, white-bellied green pigeon)		Philippines
R. (*R.*) *flabralis*	Bucerotiformes: bucerotid (great hornbill)		Asia
R. (*R.*) *flaccida*	Pterocliformes: pteroclid (black-bellied sandgrouse)		Asia
R. (*R.*) *flaminata*	Columbiformes: columbid (rock dove, western crowned pigeon)		Asia
R. (*s.l.*) *fluxa sp. inq.*	Rodentia: murid (brown rat)		Asia
R. (*R.*) *formosana*	Primates: hominid (human)		Asia
R. (*R.*) *fragilis*	Columbiformes: columbid (pale-capped pigeon)		Asia
R. (*R.*) *francolini*	Galliformes: phasianid (black francolin)		Iraq
R. (*R.*) *frayi*	Columbiformes: columbid (green imperial pigeon, white-bellied green pigeon)		Asia
R. (*R.*) *friedbergeri* (syn. *Davainea, Ransomia*)	Galliformes: phasianid (Indian peafowl, turkey, common pheasant, rock partridge, common quail)		Eurasia
R. (*R.*) *frontina* (syn. *Davainea, Ransomia*)	Piciformes: picid (Syrian woodpecker, great spotted woodpecker, middle spotted woodpecker, green woodpecker, black woodpecker, Campo flicker); Passeriformes: icterid (Baltimore oriole), laniid (great grey shrike)		Eurasia, Americas
R. (*R.*) *fuhrmanni* (syn. *Davainea*) [incl. subspp. *fuhrmanni, idiogenoides, intermedia*]	Columbiformes: columbid (rock dove, Bengal green pigeon, thick-billed green pigeon, African green pigeon, Oriental turtle dove, laughing dove, green spotted wood dove, Namaqua dove); Passeriformes: alaudid (Maghreb lark)		Asia, India, Africa
R. (*R.*) *funebris sp. inq*	Rodentia: murid (brown rat)		Asia
R. (*R.*) *galeritae* (syn. *Davainea, Ransomia*)	Passeriformes: alaudid (Maghreb lark, crested lark), passerid (house sparrow)		Africa, India
R. (*R.*) *galli*	Galliformes: phasianid (chicken)		Japan
R. (*R.*) *garciai*	Passeriformes: icterid (greater Antillean grackle)		Central America
R. (*R.*) *garmi*	Columbiformes: columbid (pigeon)		Eurasia

R. (*R.*) *gendrei*	Columbiformes: columbid (rock dove, thick-billed green pigeon)		Africa
R. (*R.*) *georgiensis*	Galliformes: phasianid (turkey, eastern wild turkey)	Hymenoptera: formicid ant (*Pheidole rinelandica*)	North America
R. (*R.*) *geraldschmidti*	Casuariiformes: casuariid (southern cassowary)		Australia
R. (*R.*) *gevreyi*	Strigiformes: tytonid (African barn owl)		Africa
R. (*R.*) *globirostris* (syn. *Davainea, Ransomia*)	Galliformes: phasianid (grey partridge, common partridge, Barbary partridge, rock partridge, Chukar partridge); Columbiformes: columbid (rock dove)		Eurasia, Africa
R. (*s.l.*) *globocephala* (syn. *Davainea*)	Passeriformes: icterid (red-rumped cacique)		South America
R. (*R.*) *goura* (syn. *Davainea, Ransomia*)	Columbiformes: columbid (crowned pigeon, Albert's crowned pigeon))		New Guinea
R. (*R.*) *gracilis* (syn. *Davainea*)	Rodentia: murid (eastern spiny mouse), thryonomyid (greater cane rat)		North America, Africa
R. (*R.*) *graeca*	Galliformes: phasianid (rock partridge, chukar partridge, Mongolian ring-necked pheasant); Columbiformes: columbid (rock dove)		Russia, India
R. (*R.*) *gvosdevi*	Columbiformes: columbid (European turtle dove)		Russia
R. (*R.*) *idiogenoides*	Columbiformes: columbid (African green pigeon)		Africa
R. (*R.*) *inda*	Columbiformes: columbid (spotted dove)		India
R. (*s.l.*) *infrequens* (syn. *Davainea*)	Casuariiformes: casuariid (dwarf cassowary)		New Guinea
R. (*R.*) *insignis* (syn. *Davainea, Ransomia*)	Columbiformes: columbid (Oceanic pigeon, mountain imperial pigeon, Mauritius blue pigeon)		Africa, Indonesia
R. (*R.*) *interrupta* (syn. *Skrjabinotaurus*)	Columbiformes: columbid (spotted dove, Oriental turtle dove)		Asia
R. (*R.*) *johri*	Psittaciformes: psittaculid (rose-ringed parakeet)		India
R. (*R.*) *joyeuxbaeri*	Columbiformes: columbid (red turtle dove)		Asia
R. (*R.*) *joyeuxi*	Columbiformes: columbid (rock dove)		Europe
R. (*R.*) *kantipura*	Columbiformes: columbid (rock dove)		Nepal
R. (*R.*) *khalili*	Musophagiformes: musophagid (Guinea turaco)		Africa
R. (*R.*) *kirghizica*	Columbiformes: columbid (rock dove)		Russia
R. (*R.*) *klebergi*	Galliformes: odontophorid (northern bobwhite quail)		North America
R. (*R.*) *kordofanensis*	Rodentia: murid (African grass rat)		Africa
R. (*R.*) *korkei* (syn. *R.* (*Fuhrmannetta*))	Columbiformes: columbid (rock dove, European turtle dove, Oriental turtle dove, rock partridge)		India, Russia
R. (*R.*) *kunisakiensis*	Columbiformes: columbid (white-bellied green pigeon)		Japan
R. (*R.*) *lateralis* (syn. *Davainea, Ransomia*)	Dermoptera: cynocephalid (Sunda flying lemur)		Indonesia
R. (*R.*) *leipoae*	Galliformes: megapodiid (mallee fowl)		Australia
R. (*R.*) *leptacantha* (syn. *Davainea, Ransomia*)	Galliformes: cracid (black curassow, bare-faced curassow, black curassow)		South America
R. (*R.*) *leptosoma* (syn. *Davainea, Ransomia*)	Psittaciformes: psittacid (turquoise-fronted amazon, hyacinth macaw, golden-collared macaw, scarlet macaw, red-bellied macaw, blue-winged macaw, red-shouldered macaw, chestnut-fronted macaw, golden parakeet, short-tailed parrot, grey parrot), psittaculid (eastern rosella), cacatuid (galah); Musophagiformes: musophagid (purple-crested		Africa, Asia, Australia, Americas

	turaco)		
R. (*R.*) *loeweni*	Lagomorpha: leporid (black-tailed jackrabbit)	Hymenoptera: formicid ant (*Pheiodole sitarches camptestris, P. bicarinata*)	North America
R. (*s.l.*) *longicollis* (syn. *Davainea*)	Galliformes: phasianid (chicken)		Europe
R. (*R.*) *lutzi* (syn. *Davainea, Ransomia*)	Piciformes: picid (chestnut woodpecker, blond-crested woodpecker)		South America
R. (*R.*) *macracanthos*	Piciformes: picid (European green woodpecker)		Russia
R. (*R.*) *macrocirrosa* (syn. *Davainea, Ransomia*)	Musophagiformes: musophagid (red-crested turaco); Cuculiformes: cuculid (Senegal coucal, blue-headed coucal); Galliformes: phasianid (francolin)		Africa
R. (*R.*) *macrarhyncha*	Columbiformes: columbid (thick-billed green pigeon)		Asia
R. (*R.*) *macroscolecina* (syn. *Davainea, Ransomia*)	Psittaciformes: psittaculid (chattering lory, red-capped parrot)		South America
R. (*R.*) *mahonae*	Rodentia: thryonomyid (greater cane rat)		Africa
R. (*R.*) *malhotracapoori*	Columbiformes: columbid (rock dove)		India
R. (*R.*) *maplestonei*	Psittaciformes: psittacid (parrot)		India
R. (*R.*) *mathevossianae*	Galliformes: phasianid (see-see partridge)		Russia
R. (*R.*) *mehrai*	Columbiformes: columbid (rock dove)	Hymenoptera: formicid ant (*Pheidole rhombinola*)	India
R. (*R.*) *melomyos*	Rodentia: murid (black-tailed mosaic-tailed rat)		New Guinea
R. (*R.*) *michaelseni*	Pterocliformes: pteroclid (variegated sandgrouse)		Africa, India
R. (*R.*) *micracantha* (syn. *Davainea, Ransomia*)	Columbiformes: columbid (rock dove, European turtle dove, laughing dove)		Eurasia
R. (*R.*) *microrhyncha*	Columbiformes: columbid (spotted dove)		Asia
R. (*R.*) *microscolecina* (syn. *Davainea, Kotlania, Ransomia*)	Psittaciformes: psittaculid (Eclectus parrot, great red parrot, violet-necked lory), cacatuid (salmon-crested cockatoo)		Asia
R. (*R.*) *mitchelli*	Casuariiformes: casuariid (emu)	Hymenoptera: formicid (*Pheidole*)	Australia
R. (*R.*) *moldavica*	Piciformes: picid (European green woodpecker, grey-headed woodpecker, Eurasian wryneck)		Europe
R. (*R.*) *multicapsulata* (syn. *Davainea, Ransomia*)	Galliformes: phasianid (common pheasant)		Europe
R. (*R.*) *murium*	Rodentia: murid (brown rat)		Madagascar
R. (*R.*) *nagpurensis*	Columbiformes: columbid (rock dove)		India
R. (*R.*) *namaquensis*	Rodentia: murid (Namaqua rock rat)		Africa
R. (*R.*) *neyrai*	Otidiformes: otidid (red-crested bustard)		Africa
R. (*R.*) *nripendra*	Columbiformes: columbid (rock dove)		Nepal
R. (*R.*) *oitensis*	Accipitriformes: accipitrid (Japanese sparrowhawk)		Japan
R. (*R.*) *oligocapsulata*	Lagomorpha: leporid (tapeti)		South America
R. (*R.*) *oligorchida* (syn. *Davainea, Ransomia*)	Psittaciformes: psittaculid (Eclectus parrot)		Polynesia
R. (*R.*) *ortleppi*	Columbiformes: columbid (pigeon)		Africa
R. (*R.*) *osakensis*	Anseriformes: anatid (duck)		Japan
R. (*R.*) *osipovi*	Pterocliformes: pteroclid (black-bellied sandgrouse)		Russia
R. (*R.*) *palawanensis*	Columbiformes: columbid (common emerald dove)		Philippines
R. (*R.*) *parviuncinata* (syn. *Ransomia*)	Anseriformes: anatid (mallard)		China
R. (*R.*) *passeriformicola*	Passeriformes: sturnid (hill myna)		Philippines
R. (*R.*) *paucicapsulata*	Piciformes: picid (great spotted woodpecker)		Europe
R. (*R.*) *paucitesticulata*	Columbiformes: columbid (spotted dove,		India

(syn. *Davainea, Ransomia*)	Nicobar pigeon)		
R. (*R.*) *penelopina* (syn. *Davainea, Ransomia*)	Galliformes: cracid (dusky-legged guan)		South America
R. (*R.*) *penetrans* [incl. *R. p. nova*] (syn. *Davainea, Ransomia*)	Galliformes: phasianid (chicken, black-gold pheasant, rock partridge, black grouse); Passeriformes: sturnid (common mynah)		Eurasia
R. (*R.*) *peradenica*	Galliformes: phasianid (chicken)		Sri Lanka
R. (*R.*) *permista*	Piciformes: picid (green-backed woodpecker); Charadriiformes: scolopacid (common sandpiper)		Africa
R. (*R.*) *perplexa*	Columbiformes: columbid (rock pigeon, dove)		India
R. (*R.*) *pici*	Piciformes: picid (Japanese green woodpecker, great spotted woodpecker)		Japan, Russia
R. (*R.*) *pintneri* (syn. *Davainea, Ransomia*) [incl. var. *polyorchis*, *polychalix*]	Galliformes: numidid (helmeted guineafowl, Reichenow's guineafowl, tufted helmeted guineafowl, southern crested guineafowl); Psittaciformes: psittaculid (coconut lorikeet, rosella, rock parrot)		Africa, New Guinea
R. (*R.*) *provincialis* (syn. *Davainea, Ransomia*)	Galliformes: phasianid (red-billed francolin)		Africa
R. (*R.*) *pseudocyrtus*	Anseriformes: anatid (mallard)		Asia
R. (*R.*) *psittacea* (syn. *Davainea, Ransomia*)	Psittaciformes: cacatuid (triton cockatoo), psittaculid (eclectus parrot)		Polynesia
R. (*R.*) *quadritesticulata*	Columbiformes: columbid (red-collared dove)		India
R. (*s.l.*) *rothlisbergeri*	Primates: lorisid (Bengal slow loris)		Indonesia
R. (*R.*) *rybickae*	Galliformes: phasianid (chicken)		India
R. (*R.*) *saharanpurensis*	Galliformes: phasianid (chicken)		India
R. (*R.*) *sartica* (syn. *Davainea*) [incl. var. *massilliensis*, *mediterranea*]	Passeriformes: corvid (carrion crow), passerid (house sparrow), emberizid (striolated bunting), phylloscopid (Siberian chiffchaff)		Russia, Europe
R. (*R.*) *selfi*	Lagomorpha: leporid (desert cottontail)		North America
R. (*R.*) *senaariensis* (syn. *Davainea, Ransomia*)	Columbiformes: columbid (speckled pigeon)		Africa
R. (*R.*) *sequens*	Columbiformes: columbid (Philippine collared-dove)		Philippines
R. (*R.*) *shantungensis* (syn. *R. sinensis*)	Galliformes: phasianid (chicken); Rodentia: murid (black rat)		China
R. (*R.*) *sigmodontis*	Rodentia: cricetid (hispid cotton rat)		North America
R. (*R.*) *singhi*	Columbiformes: columbid (rock dove)	Hymenoptera: formicid ant (*Pheidole rhombinoda*)	India
R. (*R.*) *skrjabini*	Galliformes: phasianid (grey partridge, Indian peafowl)		Russia, India
R. (*R.*) *somalensis*	Galliformes: numidid (vulturine guineafowl)		Africa
R. (*R.*) *sonini*	Piciformes: picid (black woodpecker, grey-headed woodpecker, great spotted woodpecker); Passeriformes: muscicapid (common rock thrush), turdid (mistle thrush)		Russia
R. (*s.l.*) *sphaeroides* (syn. *Davainea*)	Accipitriformes: accipitrid (black kite, common buzzard, eastern steppe buzzard)		Russia
R. (*R.*) *spiralis* (syn. *Ransomia*)	Galliformes: phasianid (chicken)		India
R. (*R.*) *steinhardtii*	Galliformes: numidid (helmeted guineafowl, southern crested guineafowl)		Africa
R. (*R.*) *streptopeliae*	Columbiformes: columbid (red turtle dove)		India
R. (*R.*) *taiwanensis*	Columbiformes: columbid (pigeon)		Asia
R. (*R.*) *taylori*	Psittaciformes: psittacid (grey parrot)		Africa
R. (*R.*) *tetragona* [incl. *R. t.* var. *cohni*]	Galliformes: phasianid (chicken, Indian peafowl, green peafowl, turkey, francolin, great	Diptera: muscid fly (*Musca domestica*);	worldwide

(syn. *Davainea, Ransomia*)	argus, ruffed grouse, rock ptarmigan, willow ptarmigan, grey partridge, rock partridge, common quail), numidid (helmeted guinea fowl, southern crested guineafowl); Columbiformes: columbid (rock dove, European turtle dove); Anseriformes: anatid (duck)	Hymenoptera: formicid ants (*Leptothorax, Pheidole rhombinoda, vinelandica, Pachycondyla sennaarensis, Tetramorium simillium, caespitum*); Gastropoda: hygromiid snails (*Helix carthusianella, H. maculosa*)	
R. (*R.*) *tetragonoides* (syn. *Ransomia*)	Galliformes: numidid (helmeted guineafowl)		Africa
R. (*R.*) *thapari* (syn. *Davainea*)	Piciformes: picid (scaly-bellied woodpecker); Galliformes: phasianid (chicken); Passeriformes: pomatostomatid (babbler)		India
R. (*s.l.*) *thryonomysi*	Rodentia: thryonomyid (greater cane rat)		Africa
R. (*R.*) *tokyoensis*	Columbiformes: columbid (rock dove)		Japan
R. (*R.*) *torquata* [incl. *R. t.* var. *rajae*]	Columbiformes: columbid (rock dove)		India, Asia
R. (*R.*) *toyohashiensis*	Galliformes: numidid (helmeted guineafowl)		Japan
R. (*R.*) *trapezoides* (syn. *Davainea, Ransomia*)	Rodentia: murid (typical striped grass mouse, striped mouse, African grass rat)		Africa
R. (*R.*) *trinitatae*	Rodentia: dasyproctid (agouti), echimyid (Guyenne spiny rat)		South America
R. (*R.*) *tunetensis*	Columbiformes: columbid (rock dove, Oriental turtle dove, European turtle dove, pigeon)		Russia, India
R. (*R.*) *turaci*	Musophagiformes: musophagid (Livingstone's turaco)		Africa
R. (*R.*) *turnixae*	Charadriiformes: turnicid (yellow-legged buttonquail)		Asia
R. (*R.*) *undulata* (syn. *Davainea, Ransomia*)	Musophagiformes: musophagid (great blue turaco, purple-crested turaco); Cuculiformes: cuculid (African emerald cuckoo)		Africa
R. (*s.l.*) *vaganda* (syn. *Davainea*)	Accipitriformes: accipitrid (African fish eagle)		Africa
R. (*R.*) *vietnamense*	Columbiformes: columbid (spotted dove)		Asia
R. (*R.*) *vinagoi*	Columbiformes: columbid (African green pigeon)		Africa
R. (*R.*) *vivieni*	Galliformes: phasianid (Japanese quail)		Indochina
R. (*R.*) *vogeli*	Columbiformes: columbid (African green pigeon)		Africa
R. (*s.l.*) *voluta*	Eulipotyphla: erinaceid (four-toed hedgehog)		Africa
R. (R.) volzi (syn. *Davainea, Ransomia*)	Galliformes: phasianid (chicken, Indian peafowl); Columbiformes: columbid (rock dove)		Russia, India
R. (*R.*) *waltairensis*	Columbiformes: columbid (spotted dove)		India
R. (R.) weissi [incl. *R. w.* var. *valiclusa*] (syn. *Ransomia*)	Columbiformes: columbid (rock dove, European turtle dove, Oriental turtle dove, laughing dove, yellow-eyed pigeon)		Russia, Africa, Australia
R. (R.) werneri (syn. *Davainea, Ransomia*)	Coliiformes: coliid (speckled mousebird)		Africa, Europe, India
R. (*R.*) *williamsi*	Galliformes: phasianid (turkey)		North America
R. (*R.*) *zahratis*	Columbiformes: columbid (rock dove)		Middle-East
Subgenus *Paroniella* (genital apertures unilateral, one oncosphere per egg capsule) (some authors have promoted this subgenus to generic status, thus various synonyms exist)			
R. (*P.*) *acanthovagina*	Galliformes: phasianid (chicken)		Malaya
R. (*P.*) *amethiensis*	Passeriformes: nectariniid (purple sunbird)		India
R. (*P.*) *assamensis*	Galliformes: phasianid (chicken)		India
R. (*P.*) *bargetzii*	Piciformes: lybiid (grey-throated barbet)		Africa

R. (*P.*) *barmerensis*	Passeriformes: corvid (house crow)		India
R. (*P.*) *beppuensis*	Passeriformes: corvid (eastern jungle crow)		Japan
R. (*P.*) *blanchardi* (syn. *Davainea*)	Rodentia: murid (Mentawai long-tailed giant rat, noisy rat, Rajah spiny rat), thryonomyid (greater cane rat)		Africa, Indonesia
R. (*P.*) *bomensis*	Piciformes: lybiid (double-toothed barbet)		Africa
R. (*P.*) *bovieni*	Pholidota: manid (Sunda pangolin)		Indonesia
R. (*P.*) *bulbularum*	Passeriformes: pycnonotid (yellow-vented bulbul)		Philippines
R. (*P.*) *capoori*	Galliformes: phasianid (grey francolin)		India
R. (*P.*) *centuri*	Piciformes: picid (red-bellied woodpecker)		North America
R. (*P.*) *cirroflexa*	Piciformes: picid (sooty woodpecker)		Philippines
R. (*P.*) *compacta* (incl. *R. c. polytestis*) (syn. *Davainea*)	Passeriformes: turdid (mistle thrush), oriolid (Eurasian golden oriole, African golden oriole, black-naped oriole), ploceid (orange weaver), parid (Eurasian blue tit)		Eurasia, Africa
R. (*P.*) *conopophilae* (syn. *Davainea*)	Passeriformes: meliphagid (blue-faced honeyeater, rufous-banded honeyeater, garrulous honeyeater, white-throated honeyeater)		Australasia
R. (*P.*) *coronea*	Passeriformes: corvid (Philippine crow, common raven, Australian raven)		Philippines, India
R. (*P.*) *corvina* (syn. *Davainea, D. polycalcarata*)	Passeriformes: corvid (Indian jungle crow, large-billed crow, white-billed crow), icterid (Dumont's grackle), artamid (magpie)		Africa, India, Asia
R. (*P.*) *cruciata* (syn. *Davainea*)	Piciformes: picid (lineated woodpecker, grey-headed woodpecker), corvid (magpie)	Coleoptera: kateretid (*Brachypterus aurantiacus*)	South America, Russia
R. (*P.*) *culiauana*	Passeriformes: oriolid (Philippine oriole)		Philippines
R. (*P.*) *delhiensis*	Galliformes: numidid (helmeted guineafowl)		India
R. (*P.*) *dendrocopina*	Piciformes: picid (Japanese pygmy woodpecker)		Japan
R. (*P.*) *duosyntesticulata*	Piciformes: megalaimid (coppersmith barbet)		India
R. (*P.*) *facile* (syn. *Davainea*)	Galliformes: phasianid (satyr tragopan)		Asia
R. (*P.*) *fecunda*	Anseriformes: anatid (duck)		Asia
R. (*P.*) *filiforme*	Columbiformes: columbid (European turtle dove)		Cuba
R. (*P.*) *fulvia*	Pterocliformes: pteroclid (black-bellied sandgrouse)		Asia
R. (*P.*) *huebscheri*	Pelecaniformes: ardeid (yellow bittern)		China
R. (*P.*) *japonica*	Passeriformes: corvid (large-billed crow)		Japan
R. (*P.*) *karatchvili*	Passeriformes: corvid (Eurasian magpie)		Asia
R. (*P.*) *kashiwarensis*	Galliformes: phasianid (chicken)		Japan
R. (*P.*) *longispina* (syn. *Davainea*)	Piciformes: picid (chestnut woodpecker, blond-crested woodpecker, giant lineated woodpecker)		South America
R. (*P.*) *macassarensis*	Galliformes: phasianid (chicken)		Indonesia
R. (*P.*) *magninumida*	Galliformes: phasianid (chicken, turkey), numidid (helmeted guineafowl)	Coleoptera: cerabycid (*Solenophorus pedicularis*)	Iran, North America
R. (*P.*) *minuta*	Galliformes: phasianid (northern bobwhite quail)		North America
R. (*P.*) *molpastina*	Passeriformes: pycnonotid (Sri Lankan red-vented bulbul)		India
R. (*P.*) *mothensis*	Passeriformes: corvid (large-billed crow)		India
R. (*P.*) *myzomelae*	Passeriformes: meliphagid (Micronesian myzomela)		Indonesia
R. (*P.*) *nedumangadensis*	Columbiformes: columbid (rock dove)		India
R. (*P.*) *ngoci*	Columbiformes: columbid (mountain imperial pigeon)		Indochina

R. (*P.*) *numida* (syn. *Davainea*)	Galliformes: numidid (helmeted guineafowl)		Africa, Americas
R. (*P.*) *paradisea* (syn. *Davainea*)	Passeriformes: paradisaeid (crinkle-collared manucode)		New Guinea
R. (*P.*) *parbata*	Galliformes: phasianid (chicken)		Nepal
R. (*P.*) *perreti*	Passeriformes: pycnonotid (dark-capped bulbul)		Africa
R. (*P.*) *pinsonae*	Piciformes: picid (lesser yellownape, black woodpecker)		Asia
R. (*P.*) *pycnonoti*	Passeriformes: pycnonotid (light-vented bulbul)		China
R. (*P.*) *rangonica*	Galliformes: phasianid (chicken)		India
R. (*P.*) *rangoonica*	Accipitriformes: accipitrid (black kite)		India
R. (*P.*) *retractilis* (syn. *Davainea*)	Lagomorpha: leporid (black-tailed jackrabbit, cottontail rabbit, desert cottontail); Rodentia: murid (black rat)		Africa, North America
R. (*P.*) *reynoldsae*	Passeriformes: corvid (house crow, fan-tailed raven)		Africa, Asia
R. (*P.*) *rhynchota* (syn. *Davainea*)	Piciformes: picid (northern flicker, red-headed woodpecker)		North America
R. (*P.*) *siamensis*	Piciformes: megalaimid (lineated barbet, green-eared barbet)		Asia
R. (*P.*) *singapurensis*	Passeriformes: oriolid (black-naped oriole)		Singapore
R. (*P.*) *southwelli*	Galliformes: phasianid (chicken)		Malaya
R. (*P.*) *sphecotheridis* (syn. *Davainea*)	Passeriformes: oriolid (short-billed honeyeater), dicrurid (drongo)		Australasia
R. (*P.*) *symonsii*	Galliformes: phasianid (Indian peafowl)		India
R. (*P.*) *tenuiformis*	Galliformes: phasianid (chicken)		Africa
R. (*P.*) *tinguiana*	Galliformes: phasianid (chicken)		Philippines
R. (*P.*) *tragopani* (syn. *Davainea*)	Galliformes: phasianid (satyr tragopan)		India
R. (*P.*) *urogalli* (syn. *Davainea*)	Galliformes: phasianid (grey partridge, rock partridge, red-legged partridge, see-see partridge, willow ptarmigan, white-tailed ptarmigan, rock ptarmigan, red grouse, black grouse, western capercaillie, Himalayan snowcock, Altai snowcock, satyr tragopan); Pelecaniformes: ardeid (little bittern)	Hymenoptera: formicid ants	Eurasia
R. (*P.*) *vigintivasus*	Galliformes: phasianid (chicken)		South America
R. (*P.*) *woodlandi*	Galliformes: numidid (helmeted guineafowl)		Africa
R. (*P.*) *yaponensis*	Piciformes: picid (woodpecker)		Africa
Subgenus *Skrjabinia* (genital apertures alternating irregularly, one oncosphere per egg capsule) (some authors have promoted this subgenus to generic status, thus various synonyms exist)			
R. (*S.*) *bodkini*	Charadriiformes: scolopacid (spotted sandpiper)		South America
R. (*S.*) *boehmi*	Galliformes: phasianid (chicken)		Europe
R. (*S.*) *bolivari*	Galliformes: phasianid (common quail, rock partridge, red-legged partridge)		Europe
R. (*S.*) *bonini*	Columbiformes: columbid (common wood pigeon, Oriental turtle dove); Galliformes: phasianid (chicken); Anseriformes: anatid (duck)		Europe
R. (*S.*) *campetherae*	Piciformes: picid (woodpecker)		Africa
R. (*S.*) *caprimulgi*	Caprimulgiformes: caprimulgid (Indian nightjar)		India
R. (*S.*) *caucasica*	Galliformes: phasianid (chicken, turkey)	Hymenoptera: formicid ant (*Tetramorium caespitum*)	Russia
R. (*S.*) *centrocerci*	Galliformes: phasianid (greater sage-grouse)		North America
R. (*S.*) *centropi* (syn. *Davainea*)	Cuculiformes: cuculid (common coucal)		India

R. (*S.*) *cesticillus* (syn. *Davainea, Ransomia mutabilis*)	Galliformes: phasianid (chicken, grey junglefowl, turkey, grey partridge, Daurian partridge, rock partridge, common quail, willow ptarmigan, red grouse, black grouse, hazel grouse, common pheasant, western capercaillie), numidid (helmeted guineafowl), odontophorid (northern bobwhite quail); Anseriformes: anatid (mallard); Otidiformes: otidid (Houbara bustard); Passeriformes: fringillid (canary)	Coleoptera: carabid (*Agonoderus*, *Amara basillaris, fallax, laticollis, muscula, obesa*, *Anaferonia constricta, substriata*, *Anisodactylus*, *Anisotarsus agilis, subvirens*, *Bradycellus*, *Bradytus*, *Calathus opaculus*, *Chalenius tomentosus*, *Cratacanthus dubius*, *Discoderus*, *Harpalus faunus, herbivagus, pennsylvanicus*, *Poecilus*, *Pterostichus permudus, chalcites, constricta, torvus*, *Rhagadus*, *Selenophorus pedicularis*, *Stenocellus*, *Stenolophus*, *Tachys*, *Triplectrus rusticus*, *Zabrus*), ostomid (*Tenebroides mauritanicus*), tenebrionid (*Alphitobius*, *Tenebrio*, *Tribolium confusum*), anthicid (*Anthicus*), scarabaeid (*Aphodius granarius*, *Choeridium histeroides*), histerid (*Carcinops pumilo*, *Epierus pulicarius*), dermestid (*Dermestes*), cantharid (*Podabrus modestus*); Diptera: ichneumonid (*Stenophorus*); Sauria: agamid (*Gonocephalus*)	worldwide
R. (*S.*) *circumvallata* (syn. *R. fedjuschini, R. c. cadarachensis, R. c. siberica, Davainea, Ransomia, Johnstonia*)	Galliformes: phasianid (chicken, turkey, common quail, grey partridge, Barbary partridge, black grouse)		Eurasia
R. (*S.*) *crepidocotyle*	Passeriformes: leiothrichid (black-throated laughingthrush)		Indochina
R. (*S.*) *cryptocotyle* (syn. *Davainea*)	Galliformes: phasianid (common quail)		Africa
R. (*S.*) *daviesi*	Galliformes: phasianid (rock partridge)		India
R. (*S.*) *dendrocopina*	Piciformes: picid (Japanese pygmy woodpecker)		Japan
R. (*S.*) *dhuncheta*	Galliformes: phasianid (Kalij pheasant)		Nepal
R. (*S.*) *fatalis*	Rodentia: murid (lesser bandicoot rat, brown rat)		Asia
R. (*S.*) *hiyodori*	Passeriformes: pycnonotid (brown-eared bulbul)		Japan
R. (*S.*) *indica* (syn. *Davainea*)	Galliformes: phasianid (chicken, chukar partridge)		India, Africa
R. (*S.*) *kakia*	Passeriformes: corvid (house crow)		India

R. (*S.*) *lavieri* (syn. *Davainea*)	Cuculiformes: cuculid (coucal)		Africa
R. (*S.*) *magnicoronata* (syn. *Davainea*)	Caprimulgiformes: caprimulgid (Nacunda nighthawk)		South America
R. (*S.*) *maroteli*	Galliformes: phasianid (turkey)		Europe
R. (*S.*) *metacentropi*	Cuculiformes: cuculid (greater coucal)		Asia
R. (*S.*) *microcotyle* (syn. *Davainea*)	Anseriformes: anatid (mallard)		Europe
R. (*S.*) *oligacantha* (syn. *Davainea*)	Tinamiformes: tinamid (red-winged tinamou)		South America
R. (*S.*) *petrovi* (syn. *Davainea*)	Galliformes: phasianid (chicken)		Europe
R. (*S.*) *polyhamata*	Charadriiformes: scolopacid (Siberian whimbrel)		Japan
R. (*S.*) *polyuterina* (syn. *Davainea*)	Galliformes: phasianid (grey partridge, rock partridge, common quail, black grouse, western capercaillie)		Eurasia, Africa
R. (*S.*) *progenesia*	Galliformes: phasianid (black grouse, grey partridge)		Russia
R. (*S.*) *pterocleti*	Pterocliformes: pteroclid (black-bellied sandgrouse, Pallas's sandgrouse)		Russia
R. (*S.*) *ransomi* (syn. *Davainea*)	Galliformes: phasianid (chicken, turkey)		North America
R. (*S.*) *retusa* (syn. *Davainea*)	Galliformes: phasianid (black grouse, hazel grouse, western capercaillie)		Russia
R. (*S.*) *spinosissima* (syn. *Davainea*)	Passeriformes: turdid (common blackbird, redwing)		Europe
R. (*S.*) *sudanica*	Galliformes: phasianid (chicken)		Africa
R. (*S.*) *variabilis*	Galliformes: phasianid (greater prairie chicken)		North America
Subgenus *Fuhrmannetta* (genital apertures alternating irregularly, several oncospheres per egg capsule) (some authors have promoted this subgenus to generic status, thus various synonyms exist)			
R. (*F.*) *bandicotensis*	Rodentia: murid (greater bandicoot rat)		China
R. (*F.*) *birmanica*	Galliformes: phasianid (chicken); Anseriformes: anatid (duck)		Eurasia
R. (*F.*) *bucerotidarum*	Piciformes: lybiid (double-toothed barbet)		Africa
R. (*F.*) *caballeroi*	Columbiformes: columbid (Zenaida dove, grey-fronted quail-dove)		Central America
R. (*F.*) *crassula* (syn. *Davainea, Johnstonia*)	Columbiformes: columbid (rock dove, European turtle dove, Oriental turtle dove, laughing dove, lemon dove); Galliformes: phasianid (creek partridge, rock partridge, common quail)		Eurasia, Americas
R. (*F.*) *elongata* (syn. *Davainea, Johnstonia*)	Tinamiformes: tinamid (tinamou, red-winged tinamou, lesser nothura)		South America
R. (*F.*) *globocaudata* (syn. *Davainea, Johnstonia*)	Galliformes: phasianid (western capercaillie, hazel grouse, willow grouse)		Eurasia
R. (*F.*) *hertwigi* (syn. *Davainea, Johnstonia*)	Accipitriformes: accipitrid (Bonelli's eagle, red kite)	Sauria: lacertid (common wall lizard)	Eurasia
R. (*F.*) *jurubatensis*	Rodentia: cricetid (Goytaca mouse)		South America
R. (*F.*) *laticanalis* (syn. *Davainea, Johnstonia*)	Galliformes: phasianid (chicken, red junglefowl, common quail, grey partridge)		Europe, South America
R. (*F.*) *leptotrachela* (syn. *Davainea, Johnstonia*)	Pterocliformes: pteroclid (Namagua sandgrouse)		Africa
R. (*F.*) *lophoceri*	Bucerotiformes: bucerotid (red-billed hornbill, yellow-billed hornbill)		Africa
R. (*F.*) *malakartis*	Galliformes: odontophorid (northern bobwhite quail, California quail)		Egypt
R. (*F.*) *nepalis*	Passeriformes: passerid (house sparrow)		Nepal
R. (*F.*) *pluriuncinata*	Galliformes: phasianid (common quail, Barbary		Europe

(syn. *Davainea, Johnstonia*)	partridge)		
R. (*F.*) *pseudoechinobothrida*	Galliformes: phasianid (chicken, turkey, common quail)		Indochina
R. (*F.*) *salmoni* (syn. *R. stilesiella, R. stilesialla, Davainea, Johnstonia*)	Lagomorpha: leporid (eastern cottontail rabbit, black-tailed jackrabbit)		North America
R. (*F.*) *srbuhiae*	Galliformes: phasianid (chukar partridge)		Russia
R. (*F.*) *talourensis*	Galliformes: phasianid (chicken)		India
R. (*F.*) *vandenbrandeni*	Psittaciformes: psittacid (grey parrot)		Africa
Reassigned species			
R. (*R.*) *allomyodes* (syn. Davainea) (now *Idiogenoides*)	Psittaciformes: psittaculid (Edward's fig-parrot); Columbiformes: columbid (pink-necked green pigeon)		New Guinea, South America
R. (*R.*) *alouttae* (syn. *R. multitesticulata*) (now *Buginetta*)	Primates: atelid (Guianan red howler, Venezuelan red howler, Columbian red howler), hominid (human)		South America
R. (*R.*) *anoplocephaloides* (now *Baerfainia*)	Pholidota: manid (tree pangolin)		Africa
R. (*s.l.*) *biroi* (syn. *Kotlani*) (now *Davainea*)	Psittaciformes: psittacid (orange-breasted fig parrot)		New Guinea
R. (*s.l.*) *campanulata* (syn. *Davainea*) (now *Davaineolepis*)	Galliformes: phasianid (partridge)		South America
R. (*S.*) *columbae* (now *Davainea*)	Columbiformes: columbid (rock dove)		Europe
R. contorta (syn. *Paroniella, Davainea*) (now *Dioriraillietina*)	Pholidota: manid (Chinese pangolin)	Hymenoptera: formicid (ants)	Indochina
R. cubensis (syn. *R. loechenesalavezi, R.* (*F.*) *kouridovali, Thysanotaenia*) (now *Inermicapsifer*)	Primates: hominid (human)		Cuba
R. (*P.*) *macropa* (now *Calostaurus*)	Diprotodontia: macropodid (dusky pademelon)		Australia
R. (*R.*) *madagascariensis* (syn. *R. garrisoni, R. siriraji, Davainea, Ransomia, Taenia*) (now *Inermicapsifer*)	Rodentia: murid (brown rat, black rat); Primates: hominid (human)		Africa, Asia
R. (*S.*) *parva* (syn. *Davainea*) (now *Mathevotaenia*)	Eulipotyphla: erinaceid (hedgehog)		Europe
R. (*S.*) *polycalceola* (syn. *Davainea*) (now *Delamuretta*)	Rodentia: murid (Abyssinian grass rat, Musschenbroek's mouse)		Africa, Indonesia
R. (*R.*) *rahmi* (now *Manitaurus*)	Pholidota: manid (tree pangolin)		Africa

Parasite morphology: *Raillietina* spp. form 3 sequential developmental stages: eggs, larvae and adults. Mature worm eggs are oval in shape and vary considerably in size depending on species, most ranging from 25-50 µm long but some forming larger eggs (60-90 x 45-80 µm). Each egg contains a single nonciliated hexacanth (6 hooked) embryo (oncosphere) surrounded by a non-striated shell (embryophore) and a delicate membrane. Cysticercoid larvae are milky white in colour and elliptical in shape measuring 180-450 x 125-325 µm. They are lacunate (with internal cavity), surrounded by a thick cyst wall (18-25 µm) and have a tail-like cercomer and an anterior scolex retracted into an internal bladder. Adult tapeworms have an anterior knob-like everted scolex, a short flattened neck region and an elongate highly-segmented ribbon-like whitish body (strobila) measuring 10-12 cm long (some up to 25 cm) by 1-4 mm wide. The scolex measures up to 300 µm long and has an elongate rostellum (50-150 µm in diameter) armed with several hundred hammer-shaped hooks arranged in 1-2 circular rows. The scolex also has 4 oval suckers (85-200 µm in diameter) often armed with numerous (usually 8-12) hooks (5-15 µm long). Adult worms are hermaphroditic and each segment possesses male and female reproductive organs with a common genital pore located at the margin either unilaterally or alternating irregularly for consecutive segments. The uterus in mature segments breaks down into small capsules containing either 1 or several (6-12) eggs and gravid proglottids detach from the strobila. The location of the genital pores and the structure of egg capsules have been used to

recognize 4 subgenera (some authorities recognize them as separate genera), as follows: *R.* (*Raillietina*) with unilateral genital pores and egg capsules containing several oncospheres; *R.* (*Paroniella*) with unilateral genital pores and egg capsules containing one oncosphere; *R.* (*Fuhrmannetta*) with genital pores alternating irregularly and egg capsules containing several oncospheres; and *R.* (*Skrjabinia*) with genital pores alternating irregularly and egg capsules containing one oncosphere.

Site of infection: *Raillietina* tapeworms occur in the small intestines of vertebrate definitive hosts, predominantly birds, but also some mammals (rodents, lagomorphs, primates, insectivores). Infections in birds are commonly found in the posterior small intestine, but some may extend from the stomach to the cloaca. Larval stages (cysticercoids) develop in the body cavities of invertebrate intermediate hosts; mostly insects (beetles, ants, flies) but sometimes including gastropods (slugs and snails). Several species may also form cysticercoid stages in connective tissues of second intermediate hosts such as lizards.

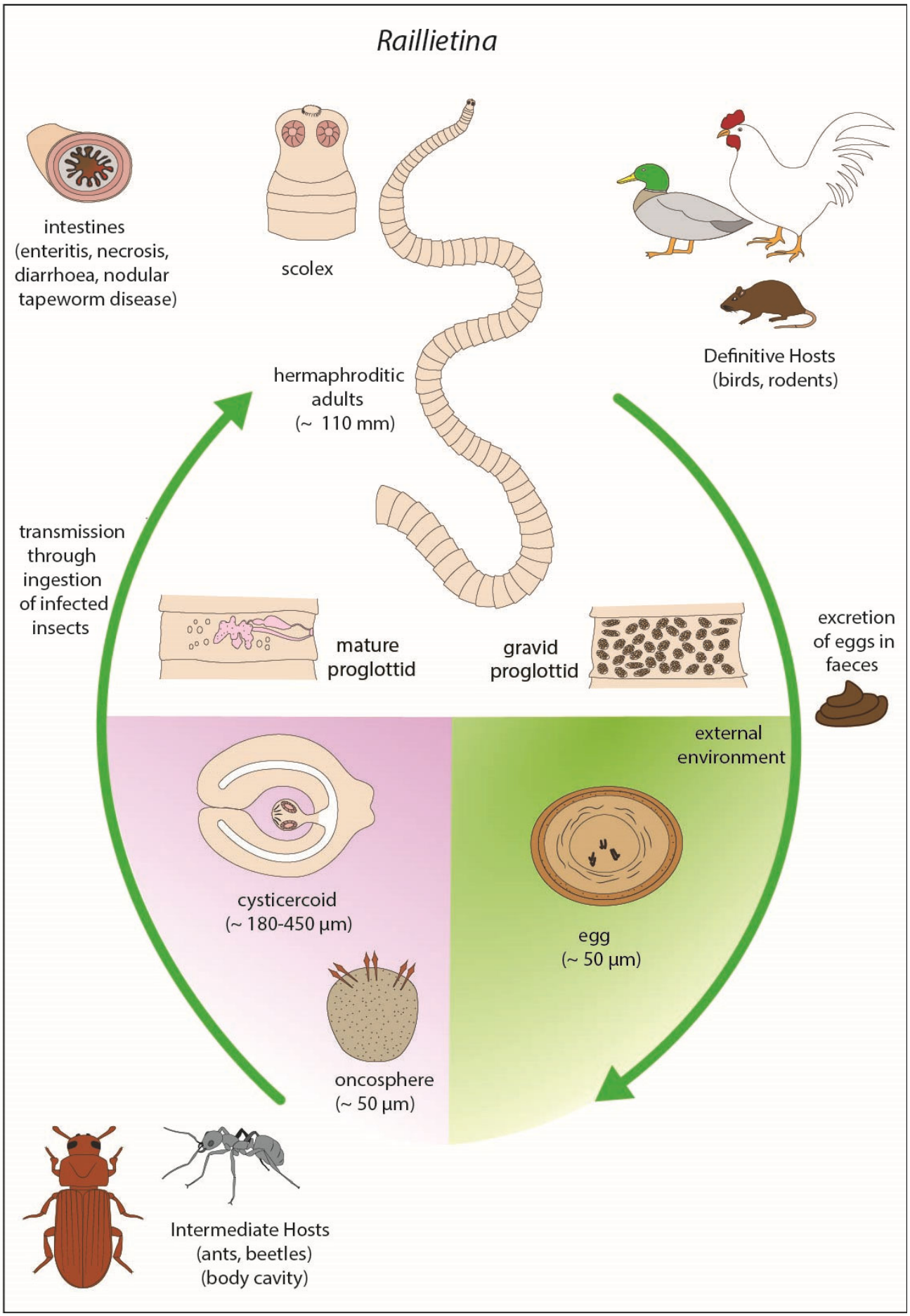
Pathogenesis: Adult tapeworms attach themselves to the intestinal wall using their anterior attachment organs (scolex with suckers and armed rostellum). They can insert their scoleces through mucosal layers with the rostellum buried deeply in the muscularis mucosae, thereby causing traumatic damage and eliciting inflammatory reactions. The worms lack digestive tracts and do not feed on host tissues but absorbing nutrients from partly digested food (chyme) in the gut lumen. Light infections in healthy well-fed birds are mostly asymptomatic, although there is mounting evidence that subclinical infections may reduce production parameters in poultry, including growth retardation, reduced weight gain and decreased egg production. Heavy infections markedly reduce feed conversion efficiencies (parasites compete with host for nutrition) which can result in weight loss and stunted growth in juvenile birds and emaciation in adult birds. Severe infections may lead to the formation of intestinal granuloma/nodular lesions (pinhead to pea-sized) around attachment sites due to leucocytic cellular infiltrates (neutrophils, eosinophils, mononuclear cells) and connective tissue encapsulation. The disruption may be so extensive that not only villi and underlying layers (mucosa, submucosa and muscularis) may be affected but intestinal secretory glands may be replaced or undergo significant proliferative (atrophy, hyperplasia) and degenerative (necrosis, desquamation) changes. The disease caused by the species *R. echinobothrida* has been termed “nodular tapeworm disease” in poultry. Collectively, the pathological changes may result in enteritis and diarrhoea leading to emaciation and death, occasionally involving intestinal obstruction and/or perforation. Petechial haemorrhages at attachment sites may also lead to the presence of blood in faeces. Perturbations in clinical parameters have included reductions in haemoglobin concentrations, haematocrits (packed cell volumes), total serum proteins and total erythrocyte counts as well as increases in total leucocyte counts. Chronic infections are thought to lower host resistance to other infectious agents. Infections in poultry are common in tropical regions where climatic conditions and husbandry practices are more favorable for parasite survival and transmission.

Developmental cycle and mode of transmission: Like all tapeworms, *Raillietina* spp. have indirect heteroxenous life-cycles whereby adult tapeworms infect vertebrate definitive hosts and larval metacestode stages infect invertebrate intermediate hosts. Cyclic transmission between hosts involves faecal-oral transmission to intermediate hosts and predator-prey transmission to definitive hosts. Gravid segments containing egg capsules are passed in faeces into the external environment where they remain viable for extended periods depending on moisture and temperature conditions (survival longer in mild moist conditions). These stages are ingested by a range of invertebrates which may act as intermediate hosts for larval development, particularly insects (ants, beetles, flies) and sometimes gastropod molluscs (slugs, snails). Oncospheres released in the invertebrate gut migrate through tissues to the body cavity where they encyst as larval cysticercoids. In the case of ants, foraging workers collect and transport food to their nests to feed their larvae, which are therefore probably the developmental stages that become infected with cysticercoids. These encysted larvae lay dormant until ingested with the invertebrate host by foraging definitive hosts (birds or insectivorous mammals) whereupon they emerge, attach to the gut wall and develop into adult tapeworms. Segments from adjacent worms cross-fertilize (rarely self-fertilize) and gravid proglottids containing eggs within egg capsules are shed some 13-21 days later (= prepatent period).

Differential diagnosis: Patent infections are diagnosed by the detection of gravid proglottids containing eggs in faecal samples, usually by direct visual examination of droppings or by microscopic examination of faecal smears (sometimes faecal floats). Several staining techniques have been employed to highlight anatomical features, including Ziehl Neelsen (acid-fast), periodic acid-Schiff (PAS), Scheider’s (acetic alum carmine) and Gram’s (crystal violet) stains. Infections may also be detected at necropsy by the detection of adult tapeworms and/or nodules in the small intestinal mucosa. Species may be differentiated on the basis of structural features, notably egg capsule configuration, genital pore position, scolex morphology, rostellar hook arrangements, proglottid morphometrics and genital anatomy. More recently, molecular techniques have been used to characterize different species by polymerase chain reaction (PCR) amplification of specific sequences in nuclear (internal transcribed spacer regions of ribosomal RNA) and mitochondrial (nicotinamide adenine dinucleotide dehydrogenase subunit 1, ND1) genes.

Treatment and control: Clinical infections may be treated with a range of anthelmintics, particularly broad-spectrum drugs exhibiting cestodicidal activity, including isoquinolines (praziquantel), benzimidazole-methylcarbamates (albendazole, fenbendazole, oxfendazole) and salicylanilides (niclosamide). Other treatment options using natural plant extracts are currently being investigated in India. Various strategies have also been developed to control transmission to and from invertebrate

intermediate hosts near poultry enterprises, involving limiting faecal contamination of the environment (by proper waste disposal/treatment), reducing intermediate host populations (using physical barriers, chemical treatments or biological control agents) and preventing bird foraging behaviours (by indoor confinement or providing clean free-range conditions).


Raillietina
intestines
(enteritis, necrosis,
diarrhoea, nodular
tapeworm disease)
scolex
hermaphroditic
adults
(~ 110 mm)
Definitive Hosts
(birds, rodents)
transmission
through
ingestion
of infected
insects
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
external
environment
cysticercoid
(~ 180-450 µm)
egg
(~ 50 µm)
oncosphere
(~ 50 µm)
Intermediate Hosts
(ants, beetles)
(body cavity)



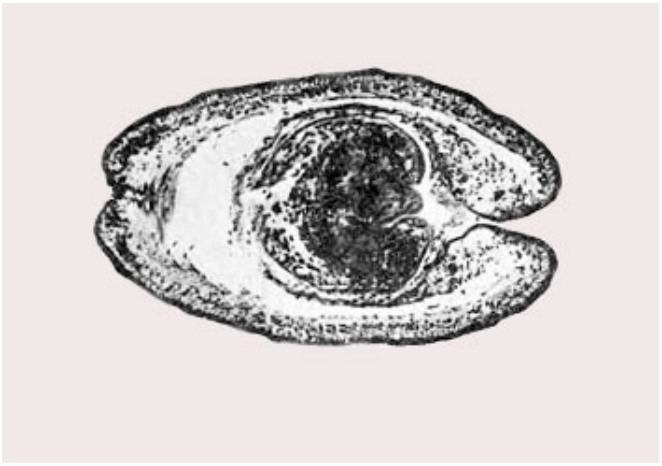
Raillietina scolex



Raillietina segments



Raillietina egg



Raillietina cysticercoid

Hymenolepis
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Cyclophyllidean tapeworms are usually intestinal parasites of terrestrial vertebrates and have an anterior scolex (hold-fast organ with suckers and sometimes hooks) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). Eucestodes have indirect life-cycles involving oncospheres (hexacanth embryos) released from ingested eggs to form encysted larval stages (metacestodes) in the tissues of intermediate hosts and their transmission to definitive hosts by predation. Adult hymenolepids have an armed or unarmed rostellum, slender strobila and are parasitic in birds, rodents and humans, infections often being asymptomatic but sometimes causing enteritis. The encysted larval stages (cysticercoids) of *Hymenolepis* spp. occur in a range of terrestrial insects or aquatic copepods which are consumed during foraging.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Cyclophyllidea (terrestrial species, scolex with four suckers, often bearing hooks, eggs release oncospheres)
Family:	Hymenolepididae (tapeworms of birds/rodents/humans, slender strobilia, 1-4 testes, cysticercoid larva)
Genus:	*Hymenolepis* (parasitic in small intestines of mammals/birds)
Species:	various species cause enteritis in humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce

eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Cyclophyllidean cestodes are polyzoic containing from 2 to > 1,000 proglottids demarcated by external segmentation. They possess an anterior scolex with 4 suckers, many with a rostellum (often armed), and they have compact post-ovarian vitellaria. Adult worms are found in terrestrial vertebrate definitive hosts (mammals, birds, reptiles, amphibians) while larval metacestodes occur in vertebrate (mammal, amphibian, bird) or invertebrate (mollusc, acari, insect) intermediate hosts. Over 3,000 species have been described in 400 genera in 16 families: Acoleidae, Amabiliidae, Anoplocephalidae, Catenotaeniidae, Davaineidae, Dioecocestidae, Dilepididae, Dipylidiidae, Gyrporhynchidae, Hymenolepididae, Mesocestoididae, Metadileptidae, Nematotaeniidae, Paruterinidae, Progynotaeniidae, and Taeniidae (all with lateral genital pores, except the Mesocestoididae).

Members of the family Hymenolepididae are characterized by adult tapeworms having slender proglottids with a small number of testes (1-4), large seminal vesicles and unilateral or irregularly alternating genital pores. Over 900 species have been described in some 130 genera; including *Allohymenolepis*, *Armadolepis*, *Brachylepis*, *Colibrilepis*, *Dollfusilepis*, *Hilmylepis*,

Hsuolepis, *Hymenolepis* (sometimes included in *Rodentolepis*), *Mathevolepis*, *Pararodentolepis, Passerilepis*, *Potorolepis*, *Pseudhymenolepis*, *Rodentolepis*, *Staphylolepis, Triodontolepis* and *Vampirolepis*. Most species infect the intestines of their definitive hosts (over 700 species of birds and 250 species of mammals) and they form larval cysticercoid stages in arthropod intermediate hosts. *Hymenolepis* spp. occur throughout the world in temperate to tropical areas. They are found in mainly in rodents and insectivores, including birds, and several species are able to infect humans when they accidentally ingest infected arthropods (usually flour-beetles). The two species found in humans are *H. nana* and *H. diminuta,* the former often being referred to as the "dwarf tapeworm" of mice and humans (some consider it to belong to the genus *Vampirolepis* as it possesses an armed rostellum), and the latter being predominantly a parasite of rodents (it has also been used extensively as a laboratory model). Some authorities recognize two variants or subspecies of *H. nana*: namely *H. n. nana* which infects humans and *H. n. fraterna* which infect rodents, while others consider the latter to be a separate species in the genus *Rodentolepis* (more recently apparently transferred to the genus *Pararodentolepis*). Species commonly found in poultry include *H. cantaniana* and *H. carioca*.

Hymenolepid species	**Definitive host [adults in intestines] [some forming cercocysts in tissues]**	**Intermediate hosts [cysticercoids in tissues]**	**Distribution**
Hymenolepis spp. (globular scolex, 4 suckers, short retractable rostellum, sometimes armed with hooks)			
H. aciculasinuata	Anseriformes: anatid (mallard)		Europe
H. acirrosa	Bucerotiformes: upupid (African hoopoe)		Africa
H. acridotheridis	Passeriformes: sturnid (jungle myna)		India
H. alaskensis	Charadriiformes: haematopodid (black oystercatcher)		North America
H. almiquil	Eulipotyphla: solenodontid (Cuban solenodon)		Central America
H. alterna	Rodentia: murid (Philippine forest rat)		Philippines
H. ampla	Rodentia: cricetid (bank vole)		Europe
H. angularostris	Anseriformes: anatid (mallard)		Europe
H. aploparaksioides	Charadriiformes: haematopodid (Eurasian oystercatcher)		Europe
H. apodemi	Rodentia: murid (Korean field mouse, Ural field mouse, striped field mouse)		Russia
H. arenariae	Charadriiformes: scolopacid (ruddy turnstone)		Eurasia
H. arguei	Charadriiformes: larid (European herring gull)		Europe
H. armata	Columbiformes: columbid (naked-eyed pigeon)		Asia
H. asketus	Eulipotyphla: soricid (northern short-tailed shrew)		North America
H. barroisii	Eulipotyphla: talpid (European mole)		Europe
H. baschkiriensis	Charadriiformes: larid (common gull)		Holarctic
H. belopolskaiae	Charadriiformes: scolopacid (sanderling)		Russia
H. bennetti	Rodentia: dipodid (woodland jumping mouse)		North America
H. bicauda	Rodentia: murid (small Luzon forest mouse)		Philippines
H. breviannulata	Pelecaniformes: threskiornithid (plumbeous ibis)		South America
H. brevis	Passeriformes: locustellid (river warbler), muscicapid (Oriental magpie-robin)		Eurasia, Africa
H. brustae	Eulipotyphla: soricid (lesser white-toothed shrew)		Eurasia
H. cameroni	Anseriformes: anatid (Indian spot-billed duck)		India
H. capensis	Afrosoricida: chrysochlorid (Cape golden mole)		Africa
H. cebidarum	Primates: pitheciid (black-fronted titi monkey)		South America
H. cerberensis	Eulipotyphla: soricid (pygmy white-toothed shrew)		Europe
H. cervotestis	Charadriiformes: recurvirostrid (American avocet)		North America
H. chenopsis	Anseriformes: anatid (black swan)		Australia
H. cholodkowskyi	Otidiformes: otidid (great bustard, little bustard)		Eurasia
H. christensoni	Chiroptera: vespertilionid (little brown bat)		North America
H. chrysolampidis	Apodiformes: trochilid (ruby-topaz hummingbird)		South America
H. ciconia	Ciconiiformes: ciconiid (white stork)		Europe
H. citelli	Rodentia: geomyid (Botta's pocket gopher, northern pocket gopher, southern pocket gopher)		North America
H. columbae	Columbiformes: columbid (lemon dove, rock dove, European turtle dove)		Eurasia, Africa

H. contracta	Rodentia: murid (house mouse, brown rat, black rat)		worldwide
H. coraciae	Coraciiformes: coraciid (European roller)		Europe
H. crociduri	Eulipotyphla: soricid (African giant shrew)		Africa
H. cryptacantha	Charadriiformes: glareolid (collared pratincole)		Europe
H. diminuta (syn. *H. flavopunctata*, *varesina*) (rat tapeworm, flavopunctate tapeworm)	Rodentia: murid (brown rat, black rat, roof rat, Mozambique thicket rat, tree rat, creek groove-toothed swamp rat, house mouse, wood mouse, African pygmy mouse, Barbary striped grass mouse, plain mouse, Gray's white-footed mouse, Jackson's soft-furred mouse, red-nosed mouse, southern multimammate mouse, Natal multimammate mouse, Shaw's jird, great gerbil), nesomyid (fat mouse), cricetid (bank vole, field vole, Savi's pine vole, hispid cotton rat), sciurid (squirrel), geomyid (northern pocket gopher, plains pocket gopher, Mazama pocket gopher, yellow-faced pocket gopher): Primates: cercopithecid (red-tailed monkey), hominid (human)	Siphonaptera: ceratophyllid (*Nosopsyllus* fleas), pulicid (*Xenopsylla* fleas), Lepidoptera: pyralid (*Asopia farinalis* meal moth, larvae and adults); Dermaptera: anisolabidid (*Anisolabis annulipes* earwigs, larvae and adults); Coleoptera: tenebrionid (*Scaurus striatus* darkling beetle, adults)	worldwide
H. dymecodontis	Eulipotyphla: talpid (True's shrew mole)		Japan
H. ellisi	Pelecaniformes: pelecanid (Australian pelican)		Australia
H. exigua	Galliformes: phasianid (chicken)	Amphipoda: talitrid (*Orchestia*)	Europe
H. exilis	Galliformes: phasianid (chicken)		Europe
H. fallax	Anseriformes: anatid (garganey, common goldeneye, Eurasian wigeon, common pochard, tufted duck, greater scaup, common eider)		Holarctic
H. fanatica	Phoenicoptiformes: phoenicopterid (greater flamingo)		Africa
H. fasciculata (syn. *Taenia fasciata*)	Anseriformes: anatid (greater white-fronted goose, greylag goose, Eurasian wigeon, common pochard)	Copepoda: cyclopid (*Cyclops*), diaptomid (*Diaptomus*)	Eurasia
H. fernandensis	Passeriformes: turdid (common thrush)		Europe
H. filta	Pelecaniformes: ardeid (cattle egret)		Eurasia, Africa
H. fimula	Anseriformes: anatid (common pochard)		Eurasia
H. finta sp. inq.	Strigiformes: strigid (brown fish owl)		Asia
H. flaminata	Otidiformes: otidid (houbara bustard)		Africa
H. floreata	Anseriformes: anatid (northern shoveler)		Holarctic
H. fodientis	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
H. fola	Charadriiformes: rostratulid (greater painted snipe)		India
H. folkertsi	Rodentia: cricetid (Oldfield mouse)		North America
H. fona	Anseriformes: anatid (mute swan)		Eurasia
H. foveata	Anseriformes: anatid (Indian spot-billed duck)		Asia
H. fructifera	Anseriformes: anatid (northern shoveler)		Egypt
H. fructicosa	Anseriformes: anatid (northern shoveler)		Egypt
H. fungosa	Otidiformes: otidid (Houbara bustard)		India
H. furcouterina	Suliformes: anhingid (Oriental darter)		Asia
H. futilis	Pelecaniformes: threskiornithid (Eurasian spoonbill)		Eurasia
H. gallinae	Galliformes: phasianid (chicken)		Europe
H. geomydis	Rodentia: geomyid (plains pocket gopher)		North America
H. glandularis	Charadriiformes: recurvirostrid (black-winged stilt)		Eurasia, Africa
H. graeca	Galliformes: phasianid (rock partridge)		India
H. guadeloupensis	Anseriformes: anatid (mallard)		Central America
H. guschanakoi	Charadriiformes: scolopacid (little stint)		Russia
H. haukisalmii	Rodentia: murid (large Luzon forest rat, Philippine forest rat)		Philippines
H. hibernia	Rodentia: murid (wood mouse)		Europe

H. hipposideri	Chiroptera: hipposiderid (roundleaf bat)		Eurasia
H. ibidis	Pelecaniformes: threskiornithid (yellow-billed spoonbill)		New Zealand
H. importata	Passeriformes: estrildid (Cinderella waxbill)		Africa
H. intermedia	Cuculiformes: cuculid (common cuckoo, Himalayan cuckoo)		Eurasia, Africa
H. intricatus	Eulipotyphla: soricid (vagrant shrew)		North America
H. introversa	Anseriformes: anatid (Eurasian teal, mallard, Indian spot-billed duck, American black duck)		Holarctic
H. iriei	Chiroptera: rhinolophid (greater horseshoe bat)		Eurasia
H. isoodontis	Peramelemorphia: peramelid (southern brown bandicoot)		Australia
H. jasuta	Galliformes: phasianid (common quail)		India
H. jerratta	Charadriiformes: scolopacid (little stint)		India
H. kempi	Suliformes: phalacrocoracid (pygmy cormorant)		Eurasia
H. kenki	Eulipotyphla: soricid (vagrant shrew)		North America
H. kerivoulae	Chiroptera: vespertilionid (painted bat)		Asia
H. lali	Charadriiformes: larid (river tern)		Asia
H. lasionycteridis	Chiroptera: vespertilionid (silver haired bat)		North America
H. limnodromi	Charadriiformes: scolopacid (short-billed dowitcher)		North America
H. lincola	Eulipotyphla: soricid (smoky shrew)		North America
H. linea	Anseriformes: anatid (goose); Galliformes: phasianid (Barbary partridge, rock partridge, common quail, chicken, red grouse, grey partridge); Passeriformes: alaudid (Eurasian skylark)		Europe, Africa
H. lintonella	Podicipediformes: podicipedid (red-necked grebe)		Eurasia
H. liphallos	Anseriformes: anatid (black swan)		Australia
H. lobata	Anseriformes: anatid (white-cheeked pintail)		South America
H. lomeensis	Eulipotyphla: soricid (greater red musk shrew)		Africa
H. longi	Eulipotyphla: soricid (smoky shrew)		North America
H. longiovata	Charadriiformes: scolopacid (little stint)		Europe
H. longocylindrocirrus	Charadriiformes: charadriid (common ringed plover)		Eurasia
H. macrocephala	Anseriformes: anatid (mallard)		Eurasia
H. macrorchida	Psittaciformes: psittaculid (Salvadori's fig parrot)		Indonesia
H. macyi	Eulipotyphla: soricid (vagrant shrew)		North America
H. magna	Chiroptera: rhinolophid (intermediate horseshoe bat)		Asia
H. mahonae	Passeriformes: aegithinid (common iora)		Asia
H. malaccensis	Anseriformes: anatid (lesser whistling duck)		Asia
H. mandabbi	Anseriformes: anatid (tufted duck)		North America
H. mathevossianae	Rodentia: cricetid (Turkish hamster)		Russia
H. megaloon	Rodentia: sciurid (ground squirrel)		Palearctic
H. megalops	Anseriformes: anatid (northern pintail, Brazilian teal, Eurasian teal, mallard, muscovy, Coscoroboa swan, whooper swan, tufted duck, greater scaup, white-headed duck, northern shoveler, Pacific black duck, magpie goose, Australian teal)		Holarctic, Australasia
H. megalorhyncha	Charadriiformes: scolopacid (purple sandpiper)		Holarctic
H. meggitteella	Otidiformes: otidid (Houbara bustard)		Africa
H. meleagris	Galliformes: phasianid (turkey)		Europe
H. micrancistrota	Anseriformes: anatid (black swan, whooper swan, black scoter)		America, Australia
H. microacantha	Rodentia: murid (highveld gerbil)		Africa
H. microcephala	Pelecaniformes: ardeid (grey heron, purple heron, black-crowned night heron), threskiornithid (ibis, glossy ibis); Ciconiiformes: ciconiid (white stork, Marabou stork, Abdim's stork); Charadriiformes:		Africa, Eurasia

	charadriid (Eurasian dotterel)		
H. microsoma	Anseriformes: anatid (Eurasian teal, long-tailed duck, Eurasian wigeon, velvet scoter, greater scaup, black scoter, common eider, king eider); Charadriiformes: larid (glaucous gull)		Holarctic
H. minimedius	Chiroptera: pteropodid (Indian flying fox)		India
H. minor	Charadriiformes: scolopacid (red-necked phalarope, red phalarope)		Holarctic
H. modiglianii	Passeriformes: corvid (slender-billed crow)		Indonesia
H. mogerae	Eulipotyphla: talpid (Kobe mole)		Japan
H. moghensis	Charadriiformes: chionid (stone-curlew)		tropics
H. moniezi	Chiroptera: pteropodid (Indian flying fox)		Asia
H. mujibi	Eulipotyphla: soricid (Asian house shrew)		Asia
H. multistriata	Anseriformes: anatid (common merganser); Podicipediformes: podicipedid (black-necked grebe, red-necked grebe, little grebe)		Eurasia
H. nana (syn. *Rodentolepis*, *Vampirolepis*, *Taenia*) (dwarf tapeworm)	Rodentia: murid (brown rat, black rat, dwarf field mouse, house mouse, garden dormouse); Primates: hominid (human)	Coleoptera: tenebrionid (flour beetles), Siphonaptera: ceratophyllid (*Nosopsyllus* fleas), pulicid (*Xenopsylla* fleas)	worldwide
H. nasuta	Passeriformes: parid (Eurasian blue tit, European crested tit, great tit, coal tit, marsh tit), aegithalid (long-tailed tit)		Eurasia, Africa
H. neomeggittilis	Anseriformes: anatid (northern shoveler)		Eurasia
H. neosouthwelli	Charadriiformes: larid (Caspian tern, brown-headed gull)		Europe
H. nitida	Charadriiformes: scolopacid (common snipe, dunlin, purple sandpiper, Temminck's stint, little stint, long-toed stint, black-tailed godwit), charadriid (European golden plover)		cosmopolitan
H. octacantha	Anseriformes: anatid (northern pintail, Eurasian teal, mallard, gadwall, northern shoveler)		Eurasia
H. odaensis	Chiroptera: miniopterid (eastern bent-wing bat)		Japan
H. ognewi	Rodentia: murid (great gerbil, Tamarisk jird, Midday jird)		Palearctic
H. olivieri	Eulipotyphla: soricid (African giant shrew)		Africa
H. palmarum	Rodentia: sciurid (Indian palm squirrel)		India
H. paradoxus	Charadriiformes: scolopacid (black-tailed godwit)		Asia
H. parvirostellata	Coraciiformes: coraciid (broad-billed roller)		Africa
H. parvissima	Eulipotyphla: soricid (marsh shrew)		North America
H. parvus	Chiroptera: rhinolophid (greater horseshoe bat)		Eurasia
H. pauciproglottis	Eulipotyphla: soricid (vagrant shrew)		North America
H. peipingensis	Eulipotyphla: talpid (mole)		Eurasia
H. pennanti	Rodentia: sciurid (northern palm squirrel)		India
H. petrocinclae	Passeriformes: muscicapid (eastern rock thrush)		Philippines
H. pigmentata	Anseriformes: anatid (greater scaup)		Holarctic
H. pitymi	Rodentia: cricetid (pine vole)		North America
H. poculifera	Gruiformes: rallid (Eurasian coot)		Eurasia
H. polygramma	Passeriformes: parid (great tit)		Eurasia
H. potoroi	Diprotodontia: potoroid (long-nosed potoroo)		Australia
H. procera	Rodentia: cricetid (European water vole), murid (Shaw's jird)		Europe, Egypt
H. pribilofensis	Eulipotyphla: soricid Pribilof Island shrew)		Alaska
H. promopsis	Chiroptera: molossid (mastiff bat)		South America
H. prudhoei	Anseriformes: anatid (upland goose)		Falkland Islands
H. pseudodiminuta	Rodentia: murid (Eurasian field mouse)		Japan
H. pseudoinflata	Gruiformes: rallid (Eurasian coot)		Eurasia
H. pseudosetigera	Anseriformes: anatid (duck)		Iceland
H. pulchra	Eulipotyphla: soricid (Trowbridge's shrew)		North America

H. rashomonensis	Chiroptera: rhinolophid (Japanese greater horseshoe bat), vespertilionid (Natterer's bat)		Japan
H. relicta	Rodentia: murid (house mouse, brown rat)		Europe
H. rhinopomae	Chiroptera: rhinopomatid (greater mouse-tailed bat)		Middle East
H. robertsi	Anseriformes: anatid (Sunda teal, magpie goose)		Australasia
H. rosseteri	Anseriformes: anatid (mallard, northern shoveler)		Holarctic
H. rudolphica	Charadriiformes: glareolid (collared pratincole), scolopacid (jack snipe)		Africa, Europe
H. rustica	Galliformes: phasianid (chicken)		Europe
H. rymzhanovi	Rodentia: spalacid (Siberian zokor)		Russia
H. sacciperum	Anseriformes: anatid (greater scaup)		Holarctic
H. scalopi	Eulipotyphla: talpid (eastern mole)		North America
H. sciurina sp. inq.	Rodentia: sciurid (red squirrel)		Russia
H. scotophii	Chiroptera: vespertilionid (lesser Asiatic yellow bat)		Asia
H. septaria	Bucerotiformes: upupid (hoopoe)		Eurasia, Africa
H. serrula	Eulipotyphla: soricid (smoky shrew)		North America
H. shentsengi	Charadriiformes: rostratulid (greater painted-snipe)		Asia, Africa
H. skrjabini	Rodentia: murid (Persian jird)		Russia
H. skrjabinissima	Charadriiformes: scolopacid (long-toed stint)		Russia
H. smythi	Anseriformes: anatid (common pygmy goose)		India
H. solowiowi	Anseriformes: anatid (northern pintail, common pochard)		Eurasia
H. sphaerophora	Charadriiformes: scolopacid (common snipe, Eurasian curlew, slender-billed curlew, Eurasian woodcock)		cosmopolitan
H. sphenomorphus	Eulipotyphla: soricid (vagrant shrew)		North America
H. spinosa	Charadriiformes: rostratulid (greater painted-snipe)		Asia, Africa
H. steatomidis	Rodentia: murid (African marsh rat, white-bellied brush-furred rat)		Africa
H. stylosa	Passeriformes: corvid (western jackdaw, common raven, Eurasian jay, Eurasian magpie, rook), muscicapid (spotted flycatcher), icterid (Baltimore oriole), sylviid (warbler)		Eurasia, North America
H. subrostellata	Chiroptera: rhinolophid (greater horseshoe bat)		Japan
H. sulcata	Rodentia: glirid (edible dormouse)		Europe
H. suslika	Rodentia: sciurid (European ground squirrel)		Russia
H. tanakpuris	Galliformes: phasianid (rock partridge)		Europe
H. tenuicollis	Anseriformes: anatid (mallard)		Europe
H. tenuis	Charadriiformes: scolopacid (dunlin)		Holarctic
H. trichodroma	Passeriformes: trichodromid (wallcreeper)		Eurasia
H. tokoinsis	Eulipotyphla: soricid (greater red musk shrew)		Africa
H. trichosoma	Anseriformes: anatid (common pochard)		Europe
H. tritesticulata	Anseriformes: anatid (mallard, surf scoter, velvet scoter, common merganser, red-breasted merganser, greater scaup); Gruiformes: rallid (American coot)		Holarctic
H. tsuzurasensis	Chiroptera: rhinolophid (greater horseshoe bat)		Japan
H. tualatinensis	Rodentia: geomyid (Camas pocket gopher)		North America
H. uliginosa	Charadriiformes: scolopacid (jack snipe, Eurasian curlew, whimbrel, ruff); Otidiformes: otidid (houbara bustard)		Eurasia, Africa, Australia
H. uncinata	Eulipotyphla: soricid (greater white-toothed shrew, common shrew)		Europe, Africa
H. uralensis	Charadriiformes: scolopacid (common sandpiper, ruddy turnstone, common redshank)		Palearctic
H. uranomidis	Rodentia: murid (white-bellied brush-furred rat, African grass rat, African marsh rat, typical striped grass mouse, Guinea multimammate		Africa

	mouse)		
H. victoriata	Passeriformes: sturnid (pied myna)		India
H. vilocirrus	Charadriiformes: scolopacid (Hudsonian godwit)		North America
H. vistulae	Anseriformes: anatid (common merganser)		Europe
H. vogeae	Rodentia: murid (common Indian field mouse, Libyan jird)		India, Egypt
H. wardlei	Anseriformes: anatid (Indian spot-billed duck)		India
H. weldensis	Rodentia: geomyid (plains pocket gopher, yellow-faced pocket gopher, Mazama pocket gopher, northern pocket gopher)	Coleoptera: tenebrionid (*Tenebrio molitor* mealworm beetle)	North America

Hymenolepid species	**Definitive host [adults in intestines] [some forming cercocysts in tissues]**	**Intermediate hosts [cysticercoids in tissues]**	**Distribution**
Rodentolepis spp. (armed rostellum, cricetoid-type hooks, three testes aligned in triangle)			
R. asymmetrica (syn. *H. arvicolae*)	Rodentia: cricetid (common vole, European snow vole, field vole)		Eurasia
R. avetjanea	Rodentia: echimyid (coypu)		South America
R. bahli (syn. *Vampirolepis, Hymenolepis*)	Eulipotyphla: soricid (grey musk shrew)		India
R. blarinae (syn. *Vampirolepis, Hymenolepis*)	Eulipotyphla: soricid (northern short-tailed shrew)		North America
R. cercarteti (syn. *Hymenolepis*)	Diprotodontia: burramyid (long-tailed pygmy possum)		Australia
R. crassa (syn. *Hymenolepis, Vampirolepis*)	Rodentia: murid (house mouse, brown rat)		worldwide
R. criceti (syn. *Vampirolepis, Hymenolepis*)	Rodentia: cricetid (European hamster)		Europe
R. erinacei (syn. *Hymenolepis, H. steudeneri, Taenia, Dicranotaenia*)	Eulipotyphla: erinaceid (European hedgehog)		Europe
R. evaginata (syn. *Hymenolepis, Staphylocystis, Dicranotaenia*)	Rodentia: cricetid (muskrat)		Eurasia, North America
R. falculata (syn. *Vampirolepis, Hymenolepis*)	Eulipotyphla: soricid (shrew)		North America
R. fraterna (syn. *Hymenolepis fraterna, H. nana fraterna, Vampirolepis*) (possibly transferred to *Pararodentolepis*)	Rodentia: murid (Abyssinian grass rat, Shaw's jird, striped field mouse, Eurasian harvest mouse, house mouse, wood mouse, spinifex hopping mouse, brown rat, black rat), caviid (montane guinea pig), glirid (garden dormouse), cricetid (field vole)		Africa, Europe, South America, Australia
R. globirostris (syn. *Vampirolepis, Hymenolepis suricattae*)	Carnivora: herpestid (meerkat)		Africa
R. merionis (now *Nomadolepis*)	Rodentia: murid (Tamarisk jird)		Russia
R. microstoma syn. Hymenolepis, Vampirolepis, Taenia, T. brachydera, muris-decumani) (mouse bile duct tapeworm)	Rodentia: nesomyid (montane African climbing mouse), murid (pygmy mouse, southern multimammate mouse, house mouse, Jackson's soft-furred mouse, Shaw's jird, brown rat, black rat), cricetid (field vole)	Coleoptera: tenebrionid (flour beetles, *Tenebrio molitor* mealworm), silvanid (grain beetles)	Africa, Europe

R. muris-variegati (syn. *Vampirolepis, Sphenocanthus*)	Rodentia: murid (African grass rat)		Africa
R. myoxi	Rodentia: glirid (garden dormouse, fat dormouse), murid (black rat), sciurid (Pallas's squirrel, Eurasian red squirrel)		Eurasia
R. octocoronata (syn. *Vampirolepis*)	Rodentia: echimyid (coypu)		Americas
R. srivastavi (syn. *Vampirolepis*)	Rodentia: cricetid (hairy-tailed bolo mouse)		South America
R. straminea (syn. *Vampirolepis*)	Rodentia: cricetid (European hamster), murid (African grass rat, Guinea multimammate mouse, Temminck's mouse, Peter's mouse, white-bellied brush-furred rat), nesomyid (gray climbing mouse)		Europe

Hymenolepid species	**Definitive host [adults in intestines] [some forming cercocysts in tissues]**	**Intermediate hosts [cysticercoids in tissues]**	**Distribution**
Vampirolepis spp. (armed rostellum, fraternoid-type hooks, testes aligned linearly)			
V. acollaris	Chiroptera: rhinolophid (croslet horseshoe bat)		Thailand
V. acuta (syn. *Hymenolepis*)	Chiroptera: miniopterid (common bent-wing bat), vespertilionid (Natterer's bat, brown long-eared bat, parti-coloured bat, common noctule, common pipistrelle, serotine bat), emballonurid (Egyptian tomb bat)		Eurasia, Africa
V. aelleni	Chiroptera: pteropodid (Wahlberg's epauletted fruit bat)		Africa
V. akodontis	Rodentia: cricetid (montane grass mouse)		South America
V. alisahnensis	Eulipotyphla: soricid (lesser white-toothed shrew)		China
V. allahabadensis	Eulipotyphla: soricid (mole)		India
V. antechini (syn. *Hymenolepis*)	Dasyuromorphia: dasyurid (dusky antechinus)		Australia
V. artibei	Chiroptera: phyllostomid (Jamaican fruit bat, Pallas's long-tongued bat)		Cuba
V. australiensis (syn. *Hymenolepis*)	Rodentia: murid (bush rat)		Australia
V. baeri	Chiroptera: vespertilionid (common noctule)		Europe
V. balsaci (syn. *Hymenolepis*)	Chiroptera: vespertilionid (Bechstein's bat, serotine bat)		Eurasia
V. bidentatus	Chiroptera: phyllostomid (Cuban flower bat)		Cuba
V. bihamata	Chiroptera: phyllostomid (white-bellied big-eared bat)		South America
V. brachysoma	Chiroptera: hipposiderid (great roundleaf bat)		Asia
V. brevihamata	Chiroptera: vespertilionid (Ikonnikov's bat)		Japan
V. cercopitheci (syn. *Hymenolepis*)	Primates: cercopithecid (greater spot-nosed monkey)		Africa
V. chalinolobi (syn. *Hymenolepis*)	Chiroptera: vespertilionid (New Zealand long-tailed bat)		New Zealand
V. chiangmaiensis	Chiroptera: rhinolophid (lesser brown horseshoe bat)		Thailand
V. chiropterophila	Chiroptera: molossid (velvety free-tailed bat)		Cuba
V. christensoni	Chiroptera: vespertilionid (little brown bat)		North America
V. coelopis	Chiroptera: hipposiderid (East Asian tailless leaf-nosed bat)		Asia
V. copihamata	Chiroptera: molossid (wrinkle-lipped free-tailed bat)		Asia
V. crassihamata	Chiroptera: molossid (velvety free-tailed bat)		South America
V. curvihamata	Chiroptera: rhinolophid (Marshall's horseshoe bat)		Thailand

V. dasipteri (syn. *Hymenolepis*)	Chiroptera: vespertilionid (southern yellow bat)		South America
V. decipiens (syn. *Hymenolepis*)	Chiroptera: mormoopid (dark brown bat, Parnell's mustached bat), molossid (western bonneted bat, Patagonian bonneted bat, Wagner's bonneted bat, cinnamon dog-faced bat, dwarf dog-faced bat, broad-eared bat), vespertilionid (big brown bat, silver-tipped myotis)		South America
V. elongatus	Chiroptera: mormoopid (ghost-faced bat, Davy's naked-backed bat, Wagner's mustached bat), molossid (black mastiff bat), phyllostomid (Pallas's long-tongued bat, dark fruit-eating bat, flat-faced fruit-eating bat, great fruit-eating bat, Ipanema bat, greater spear-nosed bat, Heller's broad-nosed bat)		Americas
V. ezoensis	Chiroptera: vespertilionid (Japanese northern bat)		Japan
V. formosana	Eulipotyphla: soricid (Chinese mole shrew)		Asia
V. fugiensis	Chiroptera: rhinolophid (greater horseshoe bat)		Japan
V. gertschi (syn. *Hymenolepis*)	Chiroptera: vespertilionid (California myotis)		North America
V. gracilistrobila	Eulipotyphla: soricid (Asian house shrew)		Japan
V. grisea (syn. *Hymenolepis*)	Chiroptera: rhinolophid (greater horseshoe bat), vespertilionid (parti-coloured bat, serotine bat)		Eurasia
V. guarany	Chiroptera*:* phyllostomid (great fruit-eating bat), molossid (black mastiff bat, Patagonian bonneted bat)		South America
V. hakusanensis	Eulipotyphla: soricid (Shinto shrew)		Japan
V. hamanni	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
V. haradai	Chiroptera: miniopterid (western bent-wing bat)		Asia
V. hattorii (syn. *Rodentolepis*)	Chiroptera: rhinolophid (greater horseshoe bat)		Japan
V. hidaensis	Chiroptera: miniopterid (eastern bent-wing bat)		Japan
V. ikesakii	Chiroptera: rhinolophid (little Japanese horseshoe bat)		Japan
V. insula	Chiroptera: vespertilionid (brown long-eared bat, ambliotus bat)		Russia
V. iraqensis	Chiroptera: emballonurid (naked-rumped tomb bat)		Iraq
V. iriomotensis	Chiroptera: rhinolophid (Imaizumi's horseshoe bat)		Japan
V. isensis	Chiroptera: rhinolophid (little Japanese horseshoe bat, greater horseshoe bat)		Japan
V. iwatensis	Chiroptera: rhinolophid (greater horseshoe bat)		Japan
V. jacobsoni (syn. *Hymenolepis*, *Rodentolepis*)	Eulipotyphla: soricid (musk shrew, white-toothed shrew)		Eurasia
V. jakounezumi	Eulipotyphla: soricid (Asian water shrew)		Asia
V. johnsoni (syn. *Rodentolepis*)	Rodentia: cricetid (meadow vole)		North America
V. kagurakoumori (syn. *Hymenolepis*)	Chiroptera: hipposiderid (great roundleaf bat)		Japan
V. kaguyae	Chiroptera: miniopterid (lesser long-fingered bat), vespertilionid (fraternal myotis)		Japan
V. kawasakiensis	Chiroptera: vespertilionid (birdlike noctule)		Japan
V. kengtingensis	Chiroptera: rhinolophid (Formosan woolly horseshoe bat))		Asia
V. kerivoulae	Chiroptera: vespertilionid (painted bat)		Asia
V. khalili	Eulipotyphla: soricid (shrew)		Africa
V. kobayashii	Chiroptera: rhinolophid (Creagh's horseshoe bat)		Japan
V. krishna	Rodentia: cricetid (water vole)		Nepal
V. kulkinae	Chiroptera: vespertilionid (common noctule bat)		Russia
V. lasionycteridis	Chiroptera: vespertilionid (silver-haired bat,		North America

	California myotis, Yuma myotis, long-eared myotis, long-legged myotis, little brown bat, big brown bat)		
V. lineola (syn. *Rodentolepis*) (now *Lineolepis*)	Eulipotyphla: soricid (smoky shrew)		North America
V. longicollaris	Chiroptera: rhinolophid (croslet horseshoe bat)		Thailand
V. longisaccata	Chiroptera: molossid (velvety free-tailed bat)		South America
V. maclaudi (syn. *Hymenolepis*)	Eulipotyphla: soricid (shrew-mouse)		Africa
V. macroscelidarum (syn. *Hymenolepis*)	Eulipotyphla: macroscelidid (short-snouted elephant shrew)		Africa
V. macrostrobilodes (syn. *Hymenolepis*)	Anseriformes: anatid (American black duck)		North America
V. macrotesticulatus (syn. *Rodentolepis*)	Chiroptera: rhinolophid (greater horseshoe bat, little Japanese horseshoe bat)		Japan
V. macroti	Chiroptera: phyllostomid (Waterhouse's leaf-nosed bat)		Central America
V. magnihamata	Eulipotyphla: soricid (Chinese mole shrew)		Asia
V. magniovifera	Eulipotyphla: soricid (Himalayan shrew)		Asia
V. magnirostellata (syn. *Hymenolepis*) (now *Neomylepis*)	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
V. malayensis (syn. *Hymenolepis*)	Chiroptera: rhinolophid (horseshoe bat), vespertilionid (woolly bat, bamboo bat)		Malaysia
V. manidis (syn. *Rodentolepis*)	Pholidota: manid (giant pangolin)		Africa
V. masaldari	Rodentia: murid (black rat)		India
V. mazanensis	Chiroptera: emballonurid (greater sac-winged bat, proboscis bat)		South America
V. mesopotamiana	Chiroptera: hipposiderid (trident bat)		Africa
V. meszarosi	Rodentia: cricetid (Royle's mountain vole)		Asia
V. microscolex	Eulipotyphla: soricid (Asian house shrew)		Asia
V. minatoi	Chiroptera: miniopterid (eastern bent-wing bat)		Japan
V. miniopteri	Chiroptera: miniopterid (little bent-wing bat)		Australia
V. molani	Chiroptera: vespertilionid (Kuhl's pipistrelle)		Iraq
V. molus	Eulipotyphla: soricid (Asian house shrew)		India
V. montana	Eulipotyphla: soricid (Asian house shrew)		Sri Lanka
V. mukooyamai	Chiroptera: vespertilionid (Natterer's bat)		Europe
V. multihamatus	Chiroptera: vespertilionid (Asian particolored bat)		Japan
V. muraiae	Chiroptera: vespertilionid (mouse-eared bat)		China
V. negevi (syn. *Rodentolepis*)	Rodentia: murid (Cairo spiny mouse)		Middle East
V. neomidis (syn. *Hymenolepis*)	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
V. nepalensis	Eulipotyphla: soricid (Himalayan shrew)		Asia
V. novadomensis	Chiroptera: vespertilionid (whiskered bat)		Europe
V. novosibirskiensis (now *Staphylocystis furcata*)	Eulipotyphla: soricid (common shrew, Eurasian pygmy shrew, Laxmann's shrew)		Russia
V. ogaensis	Chiroptera: rhinolophid (greater horseshoe bat)		Japan
V. okinawaensis	Eulipotyphla: soricid (Asian house shrew)		Japan
V. olsoni (syn. *Rodentolepis*)	Eulipotyphla: talpid (Townsend's mole)		North America
V. oregonensis (syn. *Rodentolepis*)	Rodentia: cricetid (muskrat)		Eurasia
V. ozensis	Chiroptera: vespertilionid (brown long-eared bat)		Japan
V. pandoensis	Chiroptera: vespertilionid (Argentine brown bat)		South America
V. parva (syn. *Rodentolepis*) (now *Lineolepis*)	Eulipotyphla: soricid (shrew)		Eurasia

V. pearsei (syn. *Hymenolepis*)	Rodentia: murid (Peter's striped mouse, Temminck's striped mouse, Edward's swamp rat)		Africa
V. petrodromi (syn. *Hymenolepis*)	Eulipotyphla: macroscelidid (four-toed elephant shrew)		Africa
V. phyllostomi (syn. *Hymenolepis*)	Chiroptera: phyllostomid (greater spear-nosed bat), molossid (dwarf bonneted bat)		South America
V. pipistrelli	Chiroptera: vespertilionid (common pipistrelle)		Europe
V. promopsis	Chiroptera: molossid (big crested mastiff bat)		South America
V. rikuchuensis	Chiroptera: vespertilionid (Ikonnikov's bat)		Japan
V. roudabushi (syn. *Hymenolepis*)	Chiroptera: vespertilionid (big brown bat, evening bat, silver-haired bat)		North America
V. rysavyi	Chiroptera: vespertilionid (serotine bat)		Europe
V. sandgroundi	Chiroptera: vespertilionid (banana pipistrelle)		Africa
V. santacruzensis	Chiroptera: molossid (velvety free-tailed bat)		South America
V. schilleri (syn. *Hymenolepis*)	Eulipotyphla: soricid (cinereus shrew)		North America
V. schmidti	Chiroptera: hipposiderid (rufous trident bat)		Africa, Middle-East
V. sessilihamatus	Eulipotyphla: soricid (Asian house shrew)		Asia
V. shirotanii	Chiroptera: rhinolophid (Japanese greater horseshoe bat)		Japan
V. siamensis	Chiroptera: hipposiderid (great roundleaf bat)		Thailand
V. sichuanensis	Chiroptera: rhinolophid (little Japanese horseshoe bat)		
V. sinensis (syn. *Hymenolepis*)	Rodentia: cricetid (Chinese hamster)		Asia
V. skrjabinariana	Chiroptera: vespertilionid (serotine bat)		Russia
V. solisoricis	Eulipotyphla: soricid (Pearson's long-clawed shrew)		Sri Lanka
V. somariensis	Passeriformes: leiothrichid (jungle babbler)		India
V. soriculi	Eulipotyphla: soricid (Taiwanese brown-toothed shrew)		Asia
V. spasskii	Chiroptera: vespertilionid (common noctule)		Russia
V. stefanski	Eulipotyphla: soricid (common shrew)		Russia
V. stenocephala	Chiroptera: vespertilionid (birdlike noctule)		Japan
V. sunci (syn. *Hymenolepis*)	Eulipotyphla: soricid (Asian house shrew)		Asia
V. tadaridae	Chiroptera: molossid (wrinkle-lipped free-tailed bat)		Japan
V. taiwanensis	Chiroptera: miniopterid (eastern bent-wing bat)		Thailand
V. tanegashimensis	Chiroptera: vespertilionid (eastern long-fingered bat)		Japan
V. taruiensis (syn. *Rodentolepis*)	Chiroptera: rhinolophid (little Japanese horseshoe bat)		Japan
V. temmincki	Chiroptera: molossid (dwarf dog-faced bat)		South America
V. tookokuensis	Chiroptera: vespertilionid (birdlike noctule)		Japan
V. uchimakiensis	Chiroptera: vespertilionid (Ikonnikov's bat)		Japan
V. uncinispinosa (syn. *Hymenolepis*)	Rodentia: murid (Guinea multimammate mouse, Peter's striped mouse, Temminck's striped mouse, Edward's swamp rat)		Africa
V. urawaensis	Chiroptera: vespertilionid (Japanese house bat)		Japan
V. versihamata	Chiroptera: rhinolophid (intermediate horseshoe bat)		Thailand
V. virilis (syn. *Hymenolepis*)	Eulipotyphla: soricid (Trowbridge's shrew)		North America
V. wakasensis	Chiroptera: vespertilionid (eastern long-fingered bat)		Japan
V. wislockii	Eulipotyphla: solenodontid (Hispaniolan solenodon)		Central America
V. yakushimaensis	Chiroptera: vespertilionid (Ussuri tube-nosed bat)		Japan
V. yoshiyukiae	Chiroptera: vespertilionid (fraternal myotis)		Japan

Reassigned hymenolepid species	Definitive host [adults in intestines] [some forming cercocysts in tissues]	Intermediate hosts [cysticercoids in tissues]	Distribution
H. abortiva (now *Abortilepis*)	Anseriformes: anatid (mallard, red-breasted merganser, tufted duck, northern shoveler)		Holarctic
H. aduncihami (now *Staphylocystis*)	Eulipotyphla: soricid (Bottego's shrew)		Africa
H. aequabilis (now *Wardium*)	Anseriformes: anatid (common goldeneye, whooper swan, mute swan, greater scaup)		Holarctic
H. alpestris (now *Staphylocystis*)	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
H. ambigua (now *Parvitaenia*)	Otidiformes: otidid (little bustard)		Eurasia
H. amphitricha (now *Limnolepis*)	Charadriiformes: scolopacid (common sandpiper, red knot, common snipe, sanderling, dunlin, purple sandpiper, Temminck's stint, Eurasian woodcock, wood sandpiper, common redshank)		cosmopolitan
H. anatina (now *Drepanidotaenia*)	Anseriformes: anatid (northern pintail, mallard, greylag goose, gadwall, mute swan, tufted duck, northern shoveler); Galliformes: phasianid (grey partridge); Gruiformes: rallid (Eurasian coot)		Holarctic
H. anceps (now *Dicranotaenia*)	Anseriformes: anatid (red-breasted merganser)		Holarctic
H. annandalei (now *Limnolepis*)	Charadriiformes: scolopacid (black-tailed godwit)		Eurasia, Africa, Australasia
H. anthocephalus (now *Cryptocotylepis*)	Eulipotyphla: soricid (northern short-tailed shrew)		North America
H. arcuata (now *Microsomacanthus*)	Anseriformes: anatid (common pochard, greater scaup)		Holarctic
H. ardeae (now *Gryporhynchus*)	Pelecaniformes: ardeid (striated heron, green heron)		Americas
H. bacillaris (now *Staphylocystis*)	Eulipotyphla: soricid (grey musk shrew), talpid (European mole, eastern mole)		Eurasia, North America
H. bauchei (now *Dilepidoides*)	Galliformes: phasianid (chicken)		Europe
H. beringiensis (now *Arostrilepis*)	Rodentia: cricetid (Siberian brown lemming)		Eurasia
H. bettongiae (now *Potorolepis*)	Diprotodontia: potoroid (eastern bettong)		Australia
H. biaculeata (now *Amphipetrovia*)	Anseriformes: anatid (Egyptian goose)		Africa
H. bilateralis (now *Laterorchites*)	Anseriformes: anatid (brant goose)		North America
H. bilharzii (now *Variolepis*)	Passeriformes: dicrurid (black drongo), malaconotid (black-crowned tchagra), muscicapid (rufous-tailed scrub robin)		Eurasia, Africa
H. bisaccata (now *Sobolevicanthus*)	Anseriformes: anatid (Brazilian teal, muscovy duck)		South America
H. bisacculina (now *Parabisaccanthes*)	Anseriformes: anatid (black swan)		Australia
H. brachycephala (now *Monosaccacanthes*)	Charadriiformes: haematopodid (Eurasian oystercatcher), scolopacid (ruff)		Eurasia
H. brasiliensis (now *Variolepis*)	Caprimulgiformes: caprimulgid (chuck-will's-widow, band-tailed nighthawk)		Americas
H. brevicirrosus (now *Microsomacanthus*)	Passeriformes: paradisaeid (twelve-wired bird of paradise)		New Guinea
H. cantaniana (now *Staphylepis*)	Galliformes: phasianid (chicken, turkey, Indian peafowl, ring-necked pheasant), numidid (helmeted guineafowl)	beetles	Europe, Africa, America
H. capellae (now *Limnolepis*)	Charadriiformes: scolopacid (common snipe)		Eurasia
H. capillaris	Gaviiformes: gaviid (black-throated loon,		Arctic

(now *Variolepis*)	common loon); Podicipediformes: podicipedid (horned grebe, great crested grebe, red-necked grebe, black-necked grebe)		
H. capillaroides (now *Variolepis*)	Podicipediformes: podicipedid (least grebe)		Americas
H. caprimulgorum (now *Variolepis*)	Caprimulgiformes: caprimulgid (jungle nightjar, sand-coloured nighthawk, Nacunda nighthawk)		India, Americas
H. carioca (now *Echinolepis*)	Galliformes: phasianid (chicken, turkey, grey partridge)	Coleoptera: carabid (*Anisotarsus agilis*), scarabaeid (*Aphodius granaruis*, *Choeridium histeroides*), histerid (*Carcinops quatuordecimstriata*); Diptera: muscid (*Stomoxys calcitrans*)	worldwide
H. caroli (now *Retinometra*)	Phoenicoptiformes: phoenicopterid (greater flamingo)		Africa
H. charadrii (now *Nadejdolepis*)	Charadriiformes: charadriid (Kentish plover)		Eurasia
H. chionis (now *Limnolepis*)	Charadriiformes: chionid (snowy sheathbill)		Antarctic
H. chrysochloridis (now *Staphylocystis*)	Afrosoricida: chrysochlorid (Cape golden mole)		Africa
H. clandestina (now *Wardium*)	Charadriiformes: haematopodid (Eurasian oystercatcher)		Eurasia
H. clausa (now *Aploparaksis brachyphallos*)	Anseriformes: anatid (lesser whistling duck); Columbiformes: columbid (rock dove)		Eurasia
H. clerci (now *Aploparaksis*)	Passeriformes: muscicapid (pied flycatcher), passerid (Eurasian tree sparrow)		Eurasia
H. collaris (now *Myxolepis*)	Anseriformes: anatid (northern pintail, Eurasian teal, mallard, Indian spot-billed duck, greylag goose, Eurasian wigeon, greater scaup, tufted duck, northern shoveler, Pacific black duck, Australian teal, magpie goose)	Copepoda: cyclopid (*Acanthocyclops bicuspidatus, vernalis, viridis, Cyclops lucidulus, strenuus, Eucyclops agilis, serrulatus, Mesocyclops leuckarti, oithonoides, Diaptomus coeruleus*); Amphipoda: gammarid (*Gammarus pulex*)	Eurasia, Australia
H. columbina (now *Variolepis*)	Columbiformes: columbid (Namaqua dove)		Africa
H. compressa (now *Microsomacanthus*)	Anseriformes: anatid (northern pintail, Brazilian teal, mallard, greylag goose, Eurasian wigeon, common pochard, tufted duck, greater scaup, canvas-back duck, black scoter)		Holarctic
H. conscripta (now *Microsomacanthus*)	Anseriformes: anatid (greylag goose)		Europe
H. coronoidis (now *Variolepis*)	Passeriformes: corvid (Philippine crow)		Philippines
H. coronula (now *Dicranotaenia*)	Anseriformes: anatid (mallard, greylag goose, common goldeneye, long-tailed duck, mandarin duck, Eurasian wigeon, surf scoter, greater scaup, white-headed duck, common shelduck)		Holarctic
H. corvi (now *Dicranotaenia*)	Passeriformes: corvid (American crow)		Americas
H. crenata (now *Passerilepis*)	Piciformes: picid (black woodpecker)		Eurasia
H. creplini (now *Wardium*)	Anseriformes: anatid (greater white-fronted goose, greylag goose, whooper swan		Eurasia

H. curiosa (now *Anatinella*)	Anseriformes: anatid (black swan)		Australia
H. cyrtoides (now *Retinometra*)	Anseriformes: anatid (ruddy duck)		North America
H. dahurica (now *Passerilepis*)	Passeriformes: corvid (Eurasian jackdaw)		Eurasia
H. diaphana (now *Soricinia*)	Eulipotyphla: soricid (common shrew, Eurasian pygmy shrew)		Eurasia
H. diorchis (now *Microsomacanthus*)	Anseriformes: anatid (common eider)		Holarctic
H. dolosa (now *Echinocotyle*)	Passeriformes: viduid (village indigobird, pin-tailed whydah), ploceid (orange weaver), estrildid (bronze mannikin)		Africa
H. ductilis (now *Microsomacanthus*)	Charadriiformes: larid (European herring gull, great black-backed gull)		Holarctic
H. echinocotyle (now *Echinocotyle*)	Anseriformes: anatid (mallard, ruddy shelduck, northern shoveler)		Holarctic
H. elongata (now *Drepanidotaenia*)	Pelecaniformes: threskiornithid (plumbeous ibis)		South America
H. falsata (now *Hispaniolepis*)	Otidiformes: otidid (houbara bustard)		Africa
H. farciminosa (now *Variolepis*)	Passeriformes: sturnid (common myna, common starling, black-collared starling, spotless starling), corvid (Eurasian jay, Eurasian magpie), icterid (Baltimore oriole), turdid (thrush)		Eurasia, North America
H. fausti (now *Dicranotaenia*)	Anseriformes: anatid (mallard)		Europe
H. fedtschenkowii (now *Hispaniolepis*)	Galliformes: phasianid (chicken, Himalayan snowcock)		Eurasia
H. filirostris (now *Microsomacanthus*)	Pelecaniformes: threskiornithid (Eurasian spoonbill)		Eurasia
H. fista (now *Retinometra*)	Anseriformes: anatid (cotton pygmy goose)		Asia
H. flagellata (now *Sobolevicanthus*)	Anseriformes: anatid (white-cheeked pintail)		Americas
H. flamingo (now *Flamingolepis*)	Phoenicoptiformes: phoenicopterid (greater flamingo)		Africa
H. fola (now *Passerilepis*)	Charadriiformes: rostratulid (greater painted-snipe)		Asia, Africa
H. francolini (now *Microsomacanthus*)	Galliformes: phasianid (Chinese francolin)		Asia
H. fryei (now *Dicranotaenia*)	Charadriiformes: larid (glaucous-winged gull)		North America
H. fulleborni (now *Staphylocystis*)	Eulipotyphla: soricid (musk shrew)		Africa
H. furcata (now *Staphylocystis*)	Eulipotyphla: soricid (common shrew, musk shrew, white-toothed shrew, Eurasian pygmy shrew)		Eurasia
H. furcifera (now *Variolepis*)	Podicipediformes: podicipedid (horned grebe, great crested grebe, red-necked grebe, black-necked grebe, little grebe)		Arctic
H. giranensis (now *Retinometra*)	Anseriformes: anatid (mallard)		Europe
H. globocephala (now *Variolepis*)	Passeriformes: zosteropid (silvereye)		Pacific
H. globosa (now *Soricinia*)	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
H. globulosa (now *Armadoskrjabinia*)	Anseriformes: anatid (black swan)		Australia
H. gracilis (now *Sobolevicanthus*)	Anseriformes: anatid (common teal, mallard, greylag goose, gadwall, Eurasian wigeon, common merganser, red-breasted merganser,		Holarctic, Africa

	common pochard, greater scaup, northern shoveler, common shelduck); Otidiformes: otidid (houbara bustard)		
H. groenlandica (now *Aploparaksis*)	Anseriformes: anatid (long-tailed duck)		Holarctic
H. haldemani (now *Branchiopodataenia*)	Charadriiformes: larid (Sabine's gull)		North America
H. hamulacanthos (now *Retinometra*)	Anseriformes: anatid (redhead)		North America
H. hassalli (now *Variolepis*)	Cuculiformes: cuculid (bronze cuckoo)		Europe
H. hemignathi (now *Passerilepis*)	Passeriformes: fringillid (Kauai 'akialoa)		Hawaii
H. himantopodis (now *Wardium*)	Charadriiformes: scolopacid (red knot), charadriid (Wilson's plover), recurvirostrid (black-winged stilt, pied avocet)		cosmopolitan
H. horrida (now *Arostrilepis*)	Rodentia: cricetid (montane water vole, field vole, common vole, European water vole), murid (Shaw's jird, Eurasian harvest mouse, brown rat), geomyid (Botta's pocket gopher, mountain pocket gopher, northern pocket gopher)		Europe, Africa, North America
H. infirma (now *Insectivorolepis*)	Eulipotyphla: soricid (common shrew, Eurasian pygmy shrew)		Europe
H. inhamata (now *Staphylepis*)	Apodiformes: trochilid (swallow-tailed hummingbird)		South America
H. innominata (now *Polycercus*)	Charadriiformes: recurvirostrid (pied avocet)		Eurasia
H. interrupta (now *Passerilepis*)	Charadriiformes: scolopacid (Eurasian woodcock		Eurasia
H. jacutensis (now *Skrjabinacantha*)	Eulipotyphla: soricid (common shrew, Eurasian pygmy shrew)		Europe
H. jaenschi	Pelecaniformes: pelecanid (Australian pelican)		Australia
H. jagerskioldi (now *Microsomacanthus*)	Anseriformes: anatid (mallard, velvet scoter, common eider)		Eurasia
H. japonica (now *Variolepis*)	Podicipediformes: podicipedid (little grebe)		Europe
H. khalili (now *Staphylocystis*)	Eulipotyphla: soricid (common shrew)		Europe
H. kowalewski (now *Wardium*)	Anseriformes: anatid (tufted duck); Gruiformes: rallid (Eurasian coot)		Eurasia
H. krabbeella (now *Sobolevicantha*)	Anseriformes: anatid (Eurasian teal, gadwall, common pochard)		Eurasia
H. lamellata (now *Staphylepis*)	Anseriformes: anatid (Radjah shelduck)		Australasia
H. lanceolata (now *Drepanidotaenia*)	Anseriformes: anatid (mallard, American black duck, greylag goose, brant, muscovy, whooper swan, red-crested pochard, common pochard, white-headed duck, black swan, African teal); Phoenicopteriformes: phoenicopterid (flamingo); Podicipediformes: podicipedid (grebe); Primates: hominid (human)	freshwater Copepoda: diaptomid (*Diaptomus sinosus*), cyclopid (*Cyclops*)	worldwide
H. lateralis (now *Laricanthus*)	Charadriiformes: larid (glaucous-winged gull)		North America
H. liguloides (now *Flamingolepis*)	Phoenicoptiformes: phoenicopterid (greater flamingo)		Africa
H. lintoni (now *Retinometra*)	Anseriformes: anatid (red-breasted merganser)		Holarctic
H. lobulata (now *Lobatolepis*)	Podicipediformes: podicipedid (pied-billed grebe)		Americas
H. longicirrosa (now *Cladogynia*)	Anseriformes: anatid (Eurasian teal, taiga bean goose, swan goose)		Eurasia
H. longistylosa	Anseriformes: anatid (taiga bean goose)		Eurasia

(now *Retinometra*)			
H. longivaginata (now *Hymenophenocanthus*)	Anseriformes: anatid (barnacle goose)		Holarctic
H. loossi (now *Staphylocystis*)	Eulipotyphla: soricid (musk shrew)		Africa
H. macracanthos (now *Retinometra*)	Anseriformes: anatid (common goldeneye, red-breasted merganser)		Holarctic
H. magniovata (now *Microsomacantha*)	Passeriformes: monarchid (Melanesian flycatcher)		Melanesia
H. magnisaccis (now *Nadejdolepis*)	Charadriiformes: scolopacid (little stint)		Eurasia
H. magniuncinata (now *Armadoskrjabinia*)	Pelecaniformes: pelecanid (great white pelican)		Eurasia
H. mayhewi (now *Microsomacantha*)	Anseriformes: anatid (common goldeneye)		Holarctic
H. medici (now *Echinorhynchotaenia*)	Pelecaniformes: pelecanid (great white pelican, pink-backed pelican)		Eurasia, Africa
H. megalorchis (now *Cladogynia*)	Phoenicoptiformes: phoenicopterid (greater flamingo)		Africa
H. meggitti (now *Retinometra*)	Anseriformes: anatid (goose)		Europe
H. microcirrosa (now *Dicranotaenia*)	Passeriformes: turdid (American robin)		North America
H. microps (now *Paradicranotaenia*)	Galliformes: phasianid (greater sage-grouse, red grouse, black grouse, western capercaillie)		North America, Eurasia
H. microscolecina (now *Variolepis*)	Passeriformes: cotingid (Guianan cock-of-the-rock)		South America
H. multiglandularis (now *Echinocotyle*)	Charadriiformes: larid (lesser black-backed gull)		Holarctic, Africa
H. multihamata (now *Skrjabinolepis*)	Accipitriformes: accipitrid (black kite)		Eurasia
H. muris-sylvatici (now *Staphylocystis*)	Rodentia: murid (wood mouse)		Europe
H. musculosa (now *Dicranotaenia*)	Galliformes: phasianid (turkey)		Europe
H. nagatyi (now *Hilmylepis*)	Eulipotyphla: soricid (musk shrew)		Eurasia
H. naja (now *Capiuterilepis*)	Passeriformes: certhiid (Eurasian treecreeper), sittid (Eurasian nuthatch)		Eurasia
H. neoarctica (now *Dicranotaenia*)	Charadriiformes: larid (European herring gull, great black-backed gull)		Holarctic
H. nishidai (now *Paramilinia*)	Chiroptera: rhinolophid (Japanese greater horseshoe bat)		Japan
H. nitidulans (now *Najedolepis*)	Charadriiformes: scolopacid (dunlin), charadriid (common ringed plover); Passeriformes: turdid (common blackbird); Anseriformes: anatid (greater scaup)		Holarctic
H. nyrocae (now *Drepanidotaenia*)	Anseriformes: anatid (mallard, greater scaup)		Eurasia
H. obvelata (now *Octacanthus*)	Pterocliformes: pteroclid (pin-tailed sandgrouse)		Eurasia
H. octacanthoides (now *Sobolevicanthus*)	Charadriiformes: larid (black-headed gull)		Holarctic
H. oena (now *Passerilepis*)	Columbiformes: columbid (Namaqua dove)		Africa
H. omissa (now *Coronacanthus*)	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
H. orientalis (now *Aploparaksis*)	Passeriformes: muscicapid (northern wheatear)		Europe
H. orthacantha	Anseriformes: anatid (Coscoroboa swan)		South America

(now *Variolepis*)			
H. oshimai (now *Retinometra*)	Anseriformes: anatid (mallard)		Asia
H. oweni (now *Echinocotyle*)	Charadriiformes: scolopacid (ruff)		Eurasia
H. pachycephala (now *Microsomacanthus*)	Anseriformes: anatid (harlequin duck)		North America
H. papillata (now *Sobolevicanthus*)	Anseriformes: anatid (muscovy)		North America
H. paramicrosoma (now *Microsomacanthus*)	Anseriformes: anatid (mallard, tufted duck)		Holarctic
H. parina (now *Passerilepis*)	Passeriformes: parid (great tit, coal tit)		Eurasia, Africa
H. parviceps (now *Dicranotaenia*)	Anseriformes: anatid (red-breasted merganser)		Holarctic
H. parviuncinata (possibly *Taenia*)	Pelecaniformes: pelecanid (great white pelican)		Eurasia
H. parvula (now *Microsomacanthus*)	Anseriformes: anatid (mallard)		Europe
H. passerina (now *Passerilepis*)	Passeriformes: turdid (thrush)		Europe
H. passeris (now *Passerilepis*)	Passeriformes: aegithalid (long-tailed tit), parid (Eurasian blue tit, European crested tit, great tit, coal tit, marsh tit), passerid (house sparrow, Eurasian tree sparrow), fringillid (common chaffinch, brambling, common linnet, Eurasian siskin), panurid (bearded reedling), sylviid (warbler); Accipitriformes: accipitrid (Eurasian sparrowhawk)		Eurasia, Africa
H. pauciannulata (now *Microsomacanthus*)	Anseriformes: anatid (northern shoveler)		Holarctic
H. pauciovata (now *Microsomacanthus*)	Tinamiformes: tinamid (red-legged tinamou)		South America
H. pellucida (now *Passerilepis*)	Passeriformes: icterid (oropendola, crested oropendola)		Central and South America
H. peramelidarum (syn. *Vampirolepis*) (now *Potorolepis*)	Peramelemorphia: peramelid (northern brown bandicoot, southern brown bandicoot, long-nosed bandicoot)		Australia
H. petteri (now *Lophurolepis*)	Rodentia: murid (rusty-bellied brush-furred rat)		Africa
H. phalacrocoracis (now *Woodlandia phalacrocorax*)	Suliformes: phalacrocoracid (great cormorant)		Eurasia, North America
H. phasianina (now *Mayhewia*)	Galliformes: phasianid (red-legged partridge, grey partridge, ring-necked pheasant)		Eurasia
H. pingi (now *Dicranotaenia*)	Anseriformes: anatid (taiga bean goose)		Eurasia
H. pistillum (now *Staphylocystis*)	Eulipotyphla: soricid (greater white-toothed shrew, common shrew, alpine shrew)		Europe, Africa
H. pittalugai (now *Retinometra*)	Anseriformes: anatid (common goldeneye)		North America
H. planestici (now *Variolepis*)	Passeriformes: sturnid (common myna, American robin)		Americas
H. podicipina (now *Variolepis*)	Podicipediformes: podicipedid (horned grebe, great crested grebe, black-necked grebe)		Arctic
H. polyacantha (now *Echinocotyle*)	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia
H. porale (now *Dicranotaenia*)	Charadriiformes: glareolid (collared pratincole)		Africa
H. porzana (now *Aploparaksis*)	Gruiformes: rallid (spotted crake)		Eurasia
H. przewalskii	Anseriformes: anatid (greylag goose)		Europe

(now *Drepanidotaenia*)			
H. pycnonoti (now *Variolepis*)	Passeriformes: pycnonotid (yellow-vented bulbul)		Indochina
H. querquedula (now *Dicranotaenia*)	Anseriformes: anatid (Eurasian teal)		Eurasia
H. raillieti (now *Hilmylepis*)	Eulipotyphla: soricid (greater white-toothed shrew)		Europe
H. rapida (now *Drepanidotaenia*)	Anseriformes: anatid (black swan)		Australia
H. rara (now *Microsomacanthus rarus*)	Anseriformes: anatid (red-crested pochard)		Eurasia
H. rectacantha (now *Microsomacanthus*)	Charadriiformes: charadriid (common ringed plover)		Eurasia
H. recurvirostrae (now *Wardium*)	Charadriiformes: recurvirostrid (black-winged stilt, pied avocet)		Eurasia, Africa
H. retracta (now *Wardium*)	Anseriformes: anatid (king eider)		Holarctic
H. rhodesiensis (now *Schmelzia*)	Piciformes: lybiid (black-collared barbet)		Africa
H. riggenbachi (now *Dicranotaenia*)	Anseriformes: anatid (red-crested pochard)		Eurasia
H. rosethali (now *Octacanthum*)	Pterocliformes: pteroclid (pin-tailed sandgrouse)		Eurasia
H. rostellata (now *Microsomacanthus*)	Gaviiformes: gaviid (black-throated loon, common loon, red-throated loon); Podicipediformes: podicipedid (red-necked grebe)		Arctic
H. sagitta (now *Drepanidotaenia*)	Anseriformes: anatid (mallard)		Europe
H. scalaris (now *Staphylocystis*)	Eulipotyphla: soricid (greater white-toothed shrew, common shrew)		Europe, Africa
H. schaldybini (now *Neoskrjabinolepis*)	Eulipotyphla: soricid (common shrew, Eurasian pygmy shrew)	Coleoptera: staphylinid (*Anthobium unicolor*)	Europe
H. scutigera (now *Monopylidium*)	Eulipotyphla: soricid (common shrew, Eurasian pygmy shrew)		Europe
H. sengeri (now *Lineolepis*)	Eulipotyphla: soricid (marsh shrew)		North America
H. serpentulus (now *Mayhewia*)	Passeriformes: sturnid (crested myna), motacillid (tree pipit), corvid (western jackdaw, common raven, hooded crow, carrion crow, collared crow, Eurasian jay, Eurasian magpie, spotted nutcracker, rook), icterid (Baltimore oriole), alaudid (crested lark), turdid (wood thrush, common thrush, black-throated thrush, American robin, fieldfare, ring ouzel, mistle thrush), laniid (woodchat shrike), muscicapid (spotted flycatcher), sturnid (common starling)		Eurasia, Africa, North America
H. serrata (now *Retinometra*)	Columbiformes: columbid (speckled pigeon, rock dove, European turtle dove, Oriental turtle dove, red turtle dove, laughing dove, spotted dove)		Eurasia, Africa
H. setigera (now *Vigissotaenia*)	Anseriformes: anatid (mallard, greater white-fronted goose, greylag goose, taiga bean goose, brant goose, barnacle goose, whooper swan, mute swan, pochard, tufted duck); Gruiformes: rallid (Eurasian coot)		Holarctic
H. sibirica (now *Staphylocystis*)	Anseriformes: anatid (king eider)		Holarctic
H. simplex (now *Dicranotaenia*)	Anseriformes: anatid (northern pintail, Eurasian teal, common shelduck)		Holarctic
H. singularis (now *Neoskrjabinolepis*)	Eulipotyphla: soricid (common shrew, Eurasian pygmy shrew)		Europe

H. solitaria (now *Pseudohymenolepis*)	Eulipotyphla: soricid (musk shrew)		Europe
H. soricis (now *Soricinia*)	Eulipotyphla: soricid (alpine shrew)		Europe
H. southwelli (now *Australiolepis*)	Anseriformes: anatid (black swan)		Australia
H. spinulosa (now *Vigisolepis*)	Eulipotyphla: soricid (common shrew, musk shrew)		Europe
H. streptopeliae (now *Passerilepis*)	Columbiformes: columbid (ring-necked dove, Oriental turtle dove)		Eurasia, Africa
H. styloides (now *Microsomacanthus*)	Charadriiformes: scolopacid (common snipe), pluvianid (Egyptian plover), rostratulid (greater painted-snipe)		Eurasia, Africa
H. taiwanensis (now *Passerilepis*)	Pelecaniformes: ardeid (purple heron)		Asia
H. tenerrima (now *Retinometra*)	Anseriformes: anatid (greater scaup)		Holarctic
H. tenuirostris (now *Anatinella*)	Anseriformes: anatid (mallard, greylag goose, velvet scoter, smew, common merganser, red-breasted merganser, tufted duck, greater scaup, common eider); Charadriiformes: larid (black-legged kittiwake)		Holarctic
H. teresoides (now *Hamatolepis*)	Anseriformes: anatid (gadwall)		Holarctic
H. terraereginae (now *Sobolevicanthus*)	Anseriformes: anatid (magpie goose)		Australia
H. tetracis (now *Hispaniolepis*)	Otidiformes: otidid (little bustard)		Eurasia
H. tiara (now *Staphylocystis*)	Eulipotyphla: soricid (greater white-toothed shrew, common shrew)		Europe, Africa
H. tonkinensis (now *Staphylepis*)	Cuculiformes: cuculid (square-tailed drongo-cuckoo)		Asia
H. trichorhyncha (now *Dicranotaenia*)	Anseriformes: anatid (Eurasian teal)		Eurasia
H. trifolium (now *Microsomacanthus*)	Anseriformes: anatid (mallard)		Europe
H. tubicirrosa (now *Armadoskrjabinia*)	Cariamiformes: cariamid (red-legged seriema)		South America
H. urceus (now *Paradilepis* (syn) *Meggittiella*))	Pelecaniformes: pelecanid (great white pelican), threskiornithid (glossy ibis, Eurasian spoonbill, plumbeous ibis)		Eurasia
H. vaginata (now *Avocetolepis*)	Charadriiformes: recurvirostrid (pied avocet)		Eurasia
H. vallei (now *Nadejdolepis*)	Charadriiformes: scolopacid (little stint, long-toed stint)		Holarctic
H. variabilis (now *Variolepis*)	Passeriformes: corvid (American crow)		Americas
H. varicanthos (now *Paradilepis*)	Pelecaniformes: threskiornithid (ibis)		Eurasia
H. varsoviensis (now *Dicranotaenia*)	Charadriiformes: scolopacid (dunlin)		Holarctic
H. venusta (now *Retinometra*)	Anseriformes: anatid (mallard)		Europe
H. villosa (now *Hispaniolepis*)	Galliformes: phasianid (chicken, black grouse, western capercaillie, Himalayan snowcock); Otidiformes: otidid (houbara bustard, great bustard, little bustard)		Eurasia, Africa
H. villosoides (now *Hispaniolepis*)	Anseriformes: anatid (tufted duck, greater scaup)		Eurasia
H. woodsholei (now *Variolepis*)	Podicipediformes: podicipedid (horned grebe, red-necked grebe)		Arctic
H. zosteropsis	Passeriformes: leiothrichid (white-throated		Asia

(now *Passerilepis*)	laughingthrush)		
R. gnoskei (now *Pararodentolepis*)	Eulipotyphla: soricid (lesser dwarf shrew)		Africa
V. heleni (now *Neomylepis*)	Eulipotyphla: soricid (Eurasian water shrew)		Eurasia

Parasite morphology: Hymenolepid tapeworms form 3 different sequential stages in their developmental cycles: eggs, larvae (cysticeroids) and adults. Eggs have a colourless to yellow transparent shell and are round to oval in shape and quite variable in size ranging from 30-90 µm in length (those of *H. nana* are smaller than *H. diminuta*, 30-50 cf. 60-90 µm). Each egg contains a non-ciliated hexacanth (6-hooked) oncosphere (embryo) enclosed in thin inner membrane and a thicker striated outer membrane. The embryophore of *H. nana* has 2 polar thickenings, each with 4-8 filaments extending into the space between membranes, while that of *H. diminuta* has neither polar thickenings nor filaments. The larval metacestode (cysticercoid) has an elongate lacunate body with a well-developed retracted scolex and a prominent broad spade-shaped tail (cercomer) containing longitudinal fibres without lateral outgrowths (modified cysticercoids with caudal appendages are also formed by some species and have been called cercocysts). Adult tapeworms are elongate with an anterior scolex, a short skinny neck and a posterior ribbon-like body (strobila) with numerous segments (proglottids). The dwarf tapeworm *H. nana* is small in size measuring 1.5-5.0 cm long and 1 mm wide even though up to 200 segments may be present, while the rat tapeworm *H. diminuta* is larger ranging from 20-60 cm long (some up to 90 cm) and containing up to 1,000 segments. Proglottids are much wider than they are long (up to 4 times wider). The scolex is globular (knob-like) and possesses 4 muscular suckers surmounted by a small retractable rostellum (which can be withdrawn into a rostellar sac). The rostellum of different *Hymenolepis* spp. varies in its armature, some species bearing 20-30 small thorn-like hooks (e.g. *H. nana*), while others are unarmed (e.g. *H. diminuta*). The rostella of *Vampirolepis* and *Rodentolepis* spp. are armed, the former with fraternoid-type hooks and the latter with cricetoid-type hooks. Adult tapeworms are hermaphroditic with each segment containing a single set of male and female reproductive organs. Mature proglottids have 3 clearly-defined testes (sometimes 1-4), large seminal vesicles, a single ovary, sacculate uterus and unilateral genital pores. Posterior proglottids become gravid (fill with up to 200 eggs) and then drop off the tapeworm body and break down in the digestive tract releasing the eggs to be passed in faeces.

Site of infection: Adult hymenolepid tapeworms infect the small intestines of their vertebrate definitive hosts, sometimes extending to the bile ducts and gall bladder. In humans, *H. nana* and *H. diminuta* preferentially infect the ileum. Larval metacestodes (cysticercoids) infect the body cavities of their invertebrate intermediate hosts, usually insects (beetles, flies, moths, fleas) although annelids (earthworms) and gastropods (snails) have occasionally been implicated in life-cycles. Most *Hymenolepis* spp. infect birds and small insectivorous mammals (rodents, shrews, primates), *Vampirolepis* spp. infect bats, and *Rodentolepis* spp. infect rodents.

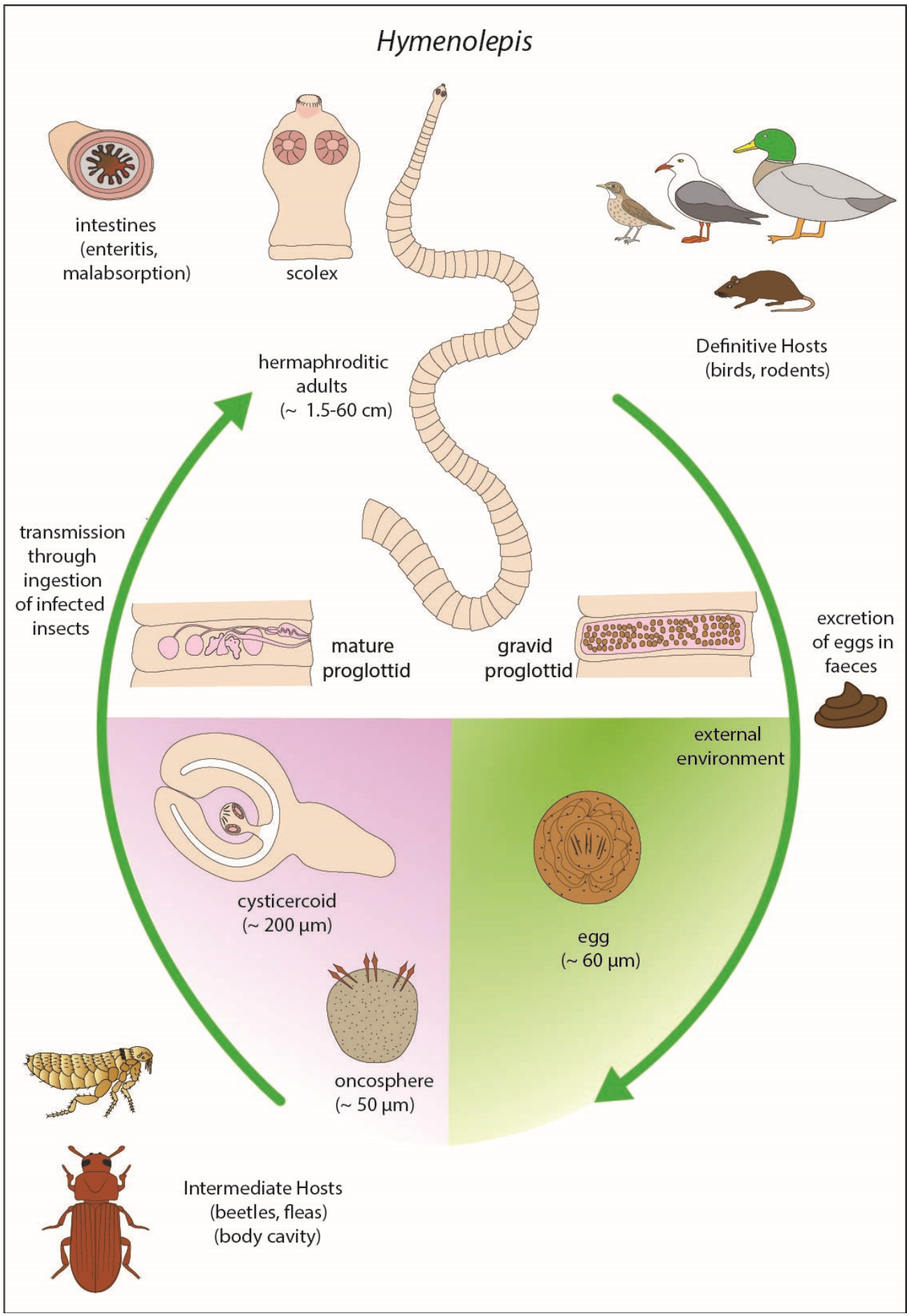
Pathogenesis: Infections are generally asymptomatic but prolonged infections or heavy infections may produce clinical signs consistent with catarrhal enteritis and malabsorption. Adult tapeworms do not feed on host tissues but absorb nutrients from the gut lumen. However, their sites of attachment may cause physical damage to the gut wall and compromise gut function. Several *Hymenolepis* spp. infecting domestic poultry may cause production losses in meat and egg production due to gut inflammation, reduced absorption, nutrient depletion and retarded growth. Infections are often moderate and not pathogenic, although heavier infections cause clinical signs including diarrhoea (sometimes haemorrhagic), weight loss, emaciation, intestinal obstruction, nodular growths, ruffled and dry plumage, and sometimes death. Heavy and chronic infections may also induce stress and predispose birds to other infectious diseases. Infections in humans are predominantly associated with the dwarf tapeworm *H. nana,* and to a lesser extent the rat tapeworm *H. diminuta,* particularly common in children in developing countries with warm-temperate climates. Chronic infections by *H. nana* in children have frequently been associated with crowded environments, unsanitary conditions, institutionalized settings, nutritional disorders and immunocompromising disorders. Light to mild infections are generally asymptomatic, but very heavy infections, particularly those developing due to direct infection or auto-infection, may cause severe clinical disease characterized by enteritis, diarrhoea (sometimes bloody), abdominal pain, anal pruritus, anorexia, restlessness, irritability, weakness, insomnia, headaches, dizziness, convulsions, epileptic seizures, and behavioural disturbances. Initial symptoms are thought to be exacerbated by allergenic responses caused by tapeworm metabolic (excretory and/or secretory) products resulting in toxaemia with localized and systemic eosinophilia. This can lead to an increase in the production of toxic oxygen radicals (superoxides, hydrogen peroxide, oxidant halide) which can cause degeneration of the intestinal mucosa, oedema and villous atrophy. Some species (including *H. nana*) may also cause physical damage to the gut wall when cysticercoid stages penetrate to the submucosa where they develop and when adult worms use their armed rostellum to attach to the mucosa. The resultant trauma and accompanying inflammation impairs intestinal absorption and increases protein loss.

Developmental cycle and mode of transmission: Most *Hymenolepis* spp. have indirect heteroxenous aquatic or terrestrial life-cycles that involve encysted cysticercoid larvae in invertebrate intermediate hosts being transmitted to vertebrate definitive hosts via predation. Hymenolepid tapeworms often exhibit rapid development and have short lifespans, thereby contributing to their wide distribution and abundance. Many genera and species have been reported in a wide range of definitive hosts (birds, mammals, reptiles and amphibians) and intermediate hosts (arthropods, annelids and molluscs). Gravid proglottids released from adult tapeworms may be passed in host faeces but they often disintegrate in the gut releasing eggs which are then passed in faeces. Eggs

are immediately infective but can survive in the external environment for several weeks. When eggs are ingested by an invertebrate intermediate host, they hatch releasing their oncospheres which penetrate the gut wall and form larval cysticercoids in the body cavity. If the infection occurs in the larval stage of the intermediate host (e.g. beetle larvae), the encysted larval cysticercoid persists through moulting and morphogenesis into the adult stage. When infected invertebrates are eaten by definitive hosts, the cysticercoids attach to the gut wall and develop into adult tapeworms. The prepatent period (time from infection to release of first eggs) is quire variable and may range from several weeks to months, and adult tapeworms tend to live only for several months. Infections in humans are usually acquired by the ingestion of foodstuffs (often precooked cereals) contaminated with infected insects (e.g. flour beetles) or by children ingesting invertebrates from the environment. An exceptional example of transmission adaptability is shown by the dwarf tapeworm *H. nana* which may also undergo direct transmission between definitive hosts (without using intermediate hosts) and even auto-infect the same definitive host. Direct transmission occurs when definitive hosts ingest eggs which hatch releasing their oncospheres which penetrate intestinal villi to the submucosa where they develop over several days into modified cysticercoid larvae (known as cercocysts). The cercocysts then rupture the villi to emerge to the lumen where they attach to the mucosa and develop into adult worms. Auto-infection occurs when eggs hatch internally without ever leaving the host. They complete their larval developmental in the submucosa and emerge to the gut lumen to form adults. Direct transmission and auto-infection cycles facilitate chronic infections and the development of large worm burdens with more severe pathological consequences.

Differential diagnosis: Infections are diagnosed by the microscopic detection of tapeworm eggs in faecal samples following formol-ether concentration or floatation in saturated salt solutions (high specific gravity). Egg production is often sporadic so repeated tests are recommended to improve diagnostic sensitivity. Infections can also be diagnosed at necropsy by dissecting the small intestine in warm water to detect adult tapeworms. Various immunoserological tests (immnodiffusion, complement fixation, fluorescence, haemagglutination and enzyme immunoassays) have also been developed to detect host antibodies against *H. nana*, but they generally had low sensitivity and specificity. More recently, molecular biological techniques have been used to characterize species by polymerase chain reaction (PCR) amplification of specific gene sequences (nuclear small subunit ribosomal DNA (18S) and internal transcribed spacer regions, and mitochondrial cytochrome c oxidase subunit 1).

Treatment and control: Clinical infections have been successfully treated with broad-spectrum anthelmintics, including isoquinolines (praziquantel), benzimidazole-methylcarbamates (albendazole, mebendazole), benzimidazole-thiazolyls (thiabendazole), salicylanilides (niclosamide), and also the aminoglycoside antibiotic (paromomycin). These drugs have been shown to be effective against adult tapeworms of many hymenolepid species, but they appeared to have limited efficacy against *H. nana* cysticercoid stages developing in submucosal sites so repeated doses may be required. It is also important to remember the potential for *H. nana* to undergo direct transmission so care should be taken when handling fomites, foodstuffs and even laboratory animals potentially contaminated by faeces containing tapeworm eggs. Various preventive strategies have been proposed to minimize the transmission of infections to the environment (waste disposal, effluent treatment, rodent control), reduce intermediate host populations (insect-proof food-stores using barriers or chemicals) and limit their uptake by definitive hosts (improve food and personal hygiene). Public health education campaigns have proven successful in raising awareness of infections.


Hymenolepis
intestines
(enteritis,
malabsorption)
scolex
hermaphroditic
adults
(~ 1.5-60 cm)
Definitive Hosts
(birds, rodents)
transmission
through
ingestion
of infected
insects
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
external
environment
cysticercoid
(~ 200 µm)
egg
(~ 60 µm)
oncosphere
(~ 50 µm)
Intermediate Hosts
(beetles, fleas)
(body cavity)



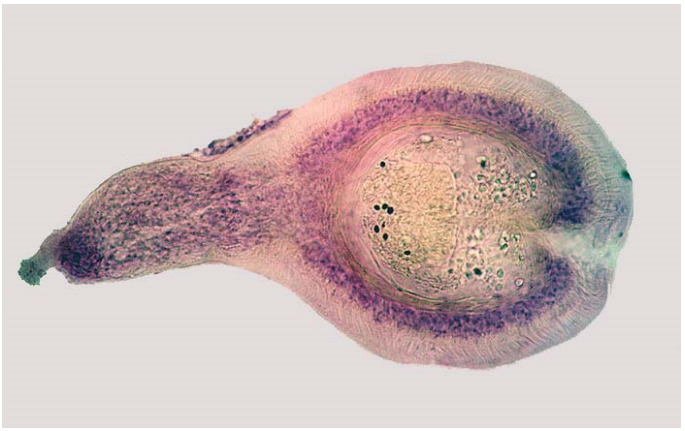
Hymenolepis scolex



Hymenolepis segments



Hymenolepis egg



Hymenolepis cysticercoid

Diphyllobothrium*, *Dibothriocephalus
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Diphyllobothriidean (formerly pseudophyllidean) tapeworms are intestinal parasites of fish-eating birds and mammals and have an anterior scolex (holdfast organ with two elongate grooved bothria) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). They have indirect life-cycles involving two intermediate hosts. Eggs shed into water release motile coracidia which are ingested by copepods and develop into first-stage larvae (procercoids). When ingested by fish, they form second-stage larvae (plerocercoids or spargana) in host tissues which are transmitted to final hosts by piscivory. Aquatic animals may also act as paratenic hosts for plerocercoids. Infections by *Dibothriocephalus latus* occur in humans and fish-eating mammals, sometimes causing enteric disorders.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Diphyllobothriidea (Pseudophyllidea) (aquatic hosts, scolex with bothria, central genital pores, two IH)
Family:	Diphyllobothriidae (coracidium, procercoid in copepods, pleroceroids in frogs, often PHs)
Genus:	*Diphyllobothrium, Dibothriocephalus* (parasitic in small intestines in piscivorous mammals)
Species:	various species cause enteritis in humans and carnivores

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce

eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Diphyllobothriidean (= Pseudophyllidean) cestodes are polyzoic with complete or incomplete segmentation. They possess an anterior scolex with 2 shallow grooves (bothria) which are unarmed and their genital organs and pores are centrally located on the ventral surface. Adult worms are found in vertebrate definitive hosts, usually aquatic mammals such as seals and cetaceans, but infections have also been recorded in piscivorous mammals and birds (canids, felids, rodents, occasionally humans) as well as in reptiles (pythons, varanids) and amphibians (African frogs). Larval stages (metacestodes) are usually formed in two intermediate hosts: cercoids (procercoid-type) forming in first intermediate hosts (copepods); then metacercoids (plerocercoid-type) developing in second intermediate hosts (fish, amphibians, reptiles, mammals, occasionally humans). Over 240 species have been described in 19 genera in 3 families: Cephalochlamydidae, Diphyllobothriidae, and Solenophoridae (earlier works also recognized another 3 families (Ligulidae, Schistocephalidae, and Scyphocephalidae) but they are no longer considered valid).

Members of the family Diphyllobothriidae are characterized by adult tapeworms possessing a spatulate scolex with 2 shallow elongated grooves (bothria) located dorsally and ventrally, craspedote proglottids with a small common genital atrium on the midventral surface and reproductive organs comprising a bilobed ovary, numerous testes and a cirrus sac, and eggs containing a coracidium (hexacanth embryo sheathed in a ciliated embryophore). Some 13 diphyllobothriid genera have been described: including *Adenocephalus*, *Baylisia*, *Baylisiella*, *Dibothriocephalus*, *Diphyllobothrium*, *Flexobothrium*, *Glandicephalus*, *Ligula*, *Plicobothrium*, *Pyramicocephalus*, *Schistocephalus*, *Spirometra* and *Tetragonoporus*. The genera *Diphyllobothrium* and *Dibothriocephalus* are characterized by adult worms having a rosette-shaped uterus (as opposed to a spiral-shaped uterus in *Spirometra*). *Diphyllobothrium* species are commonly known as fish or broad tapeworms and more than 50 species have been described in the intestines of piscivorous definitive hosts (predominantly mammals but also birds) with larval stages developing first as procercoids in copepodid intermediate hosts and then as plerocercoids in piscine intermediate hosts (freshwater, marine or anadromous host species). On the basis of recent molecular and biological data, several workers resurrected the genus *Dibothriocephalus* essentially for *Diphyllobothrium* spp. from terrestrial carnivores, while those species infecting cetaceans have been retained in the genus *Diphyllobothrium sensu stricto* ('in the strictest sense') and those infecting pinnipeds in the genus *Diphyllobothrium sensu lato* ('in the broadest sense'). Molecular studies also suggested that the genus *Diplogonoporus* should be considered a junior synonym of *Diphyllobothrium*. Infections have been found in various human populations, notably involving *Dib. latus* (= *Dip. latum*), *Dib. nihonkaiensis* (= *Dip. nihonkaiense*) and *Adenocephalus pacificus* (= *Dip. pacificum*) in fish-eating communities in Europe, Asia and North America. It is estimated that more than 20 million people harbour infections, with the incidence varying considerably spatially and temporally reflecting differences in sanitation, food hygiene, dietary and cultural practices and public health awareness.

Diphyllobothriid species	**Definitive host (DH) [adults in intestines]**	**First intermediate hosts [procercoids in tissues]**	**Second intermediate hosts [plerocercoids in tissues]**	**Distribution**
Dibothriocephalus (terrestrial carnivores as DH)				
Dib. alascensis (syn. *Dip. alascense, alaskensi*)	Carnivora: canid (dog), phocid (harbor seal); Primates: hominid (humans)		Gadiformes: lotid (burbot); Osmeriformes: osmerid (rainbow smelt)	North America
Dib. dalliae (syn. *Dip. dalliae*)	Carnivora: canid (dog, Arctic fox); Charadriiformes: larid (glaucous-winged gull); Primates: hominid (human)		Esociformes: esocid (Alaska blackfish); Salmoniformes: salmonid (dolly varden)	North America
Dib. dendriticus (syn. *Dib. sebago, Dip. dendriticum, fissiceps, cordiceps, exile, minor, canadense, strictus, obdoriense, nenzi, laruei, oblongatum, medium, minus, microcordiceps, norvegicum, sebago, Bothriocephalus cordiceps*)	Carnivora: canid (dog, red fox, American red fox, Arctic fox), ursid (grizzly bear, Kodiak bear, black bear), mustelid (Eurasian otter), felid (cat), phocid (ringed seal, Baikal seal); Rodentia: cricetid (golden hamster, golden mouse), murid (brown rat, rakali, Australian water rat); Primates: hominid (human); Passeriformes: corvid (common raven) Charadriiformes: larid (common gull, glaucous gull, European herring gull, great black-backed gull, Bonaparte's gull, ring-billed gull, California gull, kelp gull, black-headed gull, lesser black-headed gull, brown hooded gull, black-legged kittiwake, common tern), stercorarid (skua); Pelecaniformes: pelecanid	Copepoda: diaptomid (*Aglaodiaptomus* (*D.*) *leptopus*, *Arctodiaptomus acutilobatus, A. bacillifer, Diaptomus gracilis, D. graciloides, D. leptodus, Eudiaptomus gracilis, Leptodiaptomus* (*D.*) *minutus*), cyclopid (*Acanthocyclops* (*C.*) *vernalis, Cyclops abyssorum, C. kolensis, C. lacustris, C. scutifer, C. serrulatus, C. strenuus, Diacyclops* (*C.*) *bicuspidatus, Mesocyclops leuckarti*)	Salmoniformes: salmonid (Atlantic salmon, pink salmon, coho salmon, sockeye salmon, sharp-snouted lenok, Siberian taimen, kokanee, char, Arctic char, grayling, Arctic grayling, Mongolian grayling, white-spotted char, Arctic cisco, shortjaw cisco, blackfin cisco, chub, kiyi, lavaret, Dolly Varden trout, rainbow trout, brown trout, brook trout, cutthroat trout, lake trout, common whitefish, lake whitefish, northern whitefish, Valaan whitefish, mountain whitefish, vendace, peled, Baikal omul); Osmeriformes: osmerid (rainbow smelt); Gasterosteiformes: gasterosteid (threespine stickleback, fourspine	Holarctic, Australia

	(American white pelican); Gaviiformes: gaviid (black-throated loon, red-throated loon); Anseriformes: anatid (merganser, red-breasted merganser); Suliformes: phalacrocoracid (great cormorant); Podicipediformes: podicipedid (horned grebe, great crested grebe)		stickleback, ninespine stickleback); Scorpaeniformes: abyssocottid (deepwater sculpin, Vitim sculpin), comephorid (Baikal oilfish, little Baikal oilfish), cottid (fourhorn sculpin), cottocomephorid (yellowfin Baikal sculpin, longfin Baikal sculpin, Kessler's sculpin); Atheriniformes: atherinopsid (silverside, cauque); Galaxiiformes: galaxiid (common galaxias); Perciformes: percid (Eurasian ruffe, European perch), percichthyid (creole perch); Gadiformes: lotid (burbot); Cypriniformes: nemacheilid (stone loach); Osmeriformes: osmerid (European smelt, rainbow smelt, grayling, puye), Siluriformes: silurid (tollo)	
Dib. ditremus (syn. *Dip. ditremum, colymbi, vogeli, hottai, osmeri, Bothriocephalus ditremus, osmeri*)	Anseriformes: anatid birds (merganser, greater scaup); Gaviiformes: gaviid (common loon, yellow-billed loon, red-throated loon, black-throated loon); Charadriiformes: larid (European herring gull, ring-billed gull, common tern, black-legged kittiwake), alcid (red-throated guillemot); Pelecaniformes: ardeid (grey heron); Podicipediformes: podicipedid (red-necked grebe); Suliformes: phalacrocoracid (cormorant); Carnivora: phocid (Weddell seal, common seal, harbor seal, ringed seal, Saimaa ringed seal), canid (dog, wolf), felid (cat); Rodentia: cricetid (golden hamster), murid (rat)	Copepoda: cyclopid (*Cyclops strenuus*)	Salmoniformes: salmonid (brown trout, rainbow trout, cutthroat trout, lake trout, brook trout, Dolly Varden trout, grayling, Atlantic salmon, sockeye salmon, bloater, kokanee, chinook salmon, coho salmon, Arctic char, cisco, Arctic cisco, sardine cisco, tugun, vendace, lake whitefish, common whitefish, broad whitefish, northern whitefish); Osmeriformes: osmerid (Japanese surf smelt, olive rainbow smelt, pond smelt, European smelt); Gasterosteiformes: gasterosteid (threespine stickleback, fourspine stickleback, ninespine stickleback); Scorpaeniformes: cottid (Baikal oilfish), cottocomephorid (Baikal yellowfin, longfin Baikal sculpin), abyssocottid (vitim sculpin); Gadiformes: lotid (burbot); Cypriniformes: nemacheilid (stone loach)	Europe, Southern Ocean, Pacific Ocean
Dib. latus (broad tapeworm, broad fish tapeworm, pseudo-	Primates: hominid (human); Carnivora: canid (dog, red fox, Iberian fox,	Copepoda: cyclopid (*Cyclops insignis, C. lacustris, C.*	Perciformes: percid (European perch, yellow perch, pikeperch, creole	Eurasia, India, Americas

tapeworm) (syn. *Dip. latum, americanus, fuscus/fuscum, luxi, parvum, stictus, tungussicum, skrjabini, Taenia lata, vulgaris, membranacea, tenella, dentata, grisea, Bothriocephalus fuscus*, *latus, balticus, cristatus, reticulatus*, *taenioides, Dibothrium latum, serratum, Bothriocephalus cristatus, Dibothriocephalus cristatus, Diancyrobothrium taenioidoes*)	Arctic fox, crab-eating fox, coyote, wolf, golden jackal, raccoon dog), felid (cat, jungle cat, European wildcat, leopard, leopard cat, clouded leopard, jaguar, lynx, tiger, long-tailed tiger cat, ocelot), ursid (brown bear, American black bear, polar bear), procyonid (raccoon), mustelid (wolverine, Eurasian otter, European pine marten, sable, European badger, American mink), odobenid (Pacific walrus), phocid (ringed seal, bearded seal, hooded seal, leopard seal, Mediterranean monk seal, common seal, harbor seal); Artiodactyla: phocoenid (harbor porpoise), suid (pig); Rodentia: cricetid (golden hamster); Charadriiformes: larid (kelp gull, brown-headed gull)	*strenuus* (= *C. furcifer*), *C. vicinus, Ectocyclops phaleratus, Acanthocyclops viridis, Acanthocyclops vernalis, Eucyclops serrulatus, Microcyclops varicans, Mesocyclops leuckarti, M. araucanus, Thermocyclops* (*M.*) *oithonoides, Tropocyclops prasinus*), centropagid (*Gladioferens brevicornis, Boeckella gracilis, B. minuta*), diaptomid (*Acanthodiaptomus denticornis, Aglaodiaptomus leptopus* (= *D. piscinae*), *Arctodiaptomus ulomskyi, Diaptomus vulgaris, Eudiaptomus zachariasi, E. transylvanicus* (= *E. coeruleus*), *E.* (*D.*) *gracilis, E.* (*D.*) *graciloides, Hemidiaptomus ignatovi, Leptodiaptomus* (*D.*) *minutus L.* (*D.*) *siciloides, Mastigodiaptomus* (*D.*) *albuquerquensis, Onychodiaptomus* (*D.*) *sanguineus, Skistodiaptomus* (*D.*) *oregonensis*, *S.* (*D.*) *mississippiensis, Tumeodiaptomus diabolicus* (= *D. diabolicus*), calanoid (*Eurytemora affinis*); Diptera: muscid (*Musca domestica*)	perch, ruffe, Eurasian ruffe, zander, walleye, sauger), centropomid (common snook), zoarcid (viviparous eelpout); Esociformes: esocid (northern pike), Salmoniformes: salmonid (pink salmon, chum salmon, sockeye salmon, masu, char, Arctic char, white-spotted char, Atlantic salmon, rainbow trout, brown trout, brook trout, Biwa trout, common whitefish, grayling, vendace); Atheriniformes: atherinid (cauque, silverside); Gadiformes: lotid (burbot); Mugiliformes: mugilid (redlip mullet, so-iuy mullet); Osmeriformes: osmerid (puye, European smelt); Siluriformes: silurid (wels catfish), heteropneustid (Asian stinging catfish); Gasterosteiformes: gasterosteid (ninespine stickleback); Cypriniformes: cyprinid (long-spine bream, common bleak, common minnow, common roach), nemacheilid (stone loach); Anguilliformes: anguillid (European eel); Scorpaeniformes: cottid (European bullhead); Aulopiformes: synodontid (bummalo); Gobiiformes: gobiid (sand goby)	
Dib. nihonkaiensis (syn. *Dip. nihonkaiense, klebanovskii, giljacicum*)	Carnivora: ursid (brown bear, grizzly bear), American black bear, Asian black bear); canid		Salmoniformes: salmonid (cherry salmon, chum salmon, sockeye, pink salmon, Japanese huchen,	Asia, North Pacific

	(wolf, dog, fox), mustelid (American mink); Artiodactyla: suid (pig); Rodentia: cricetid (golden hamster); Primates: hominid (human)		whitespotted char, taimen); Mugiliformes: mugilid (so-iuy mullet)	
Dib. ursi (syn. *Diphyllobothrium*)	Carnivora: ursid (Kodiak bear, brown bear, American black bear); Primates: hominid (human); Charadriiformes: larid (glaucous-winged gull)		Salmoniformes: salmonid (sockeye salmon)	North America
Diphyllobothrium (comprising 2 groups, one with cetaceans as DH, one with pinnipeds as DH)				
Dip. archeri (syn. *Dibothriocephalus*)	Carnivora: phocid (Weddell seal)			Southern Ocean
Dip. balaenopterae (syn. *Dip. brauni, Krabbea grandis, Diplogonoporus balanopterae, fukuokaensis*)	Artiodactyla: balaenopterid (sei whale, common minke whale, blue whale, fin whale, humpback whale); Carnivora: canid (dog), felid (cat); Primates: hominid (human)		Clupeiformes: engraulid (Japanese anchovy), clupeid (Japanese pilchard); Scombriformes: scombrid (skipjack tuna)	circumpolar
Dip. cameroni	Carnivora: phocid (Hawaiian monk seal); Primates: hominid (human)			Pacific
Dip. cordatum (syn. *Dib. cordatus, Bothriocephalus, Dibothrium*)	Carnivora: phocid (bearded seal, harp seal, spotted seal, harbor seal, common seal, Greenland seal), otariid (Stellar sea lion), odobenid (walrus); canid (dog); Primates: hominid (human);			Holarctic
Dip. elegans (syn. *Dip. pterocephalum, Bothriocephalus, Dibothriocephalus*)	Carnivora: phocid (Mediterranean monk seal, harbour seal, hooded seal, common seal), otariid (Steller's sera lion)			Arctic Ocean
Dip. fasciatus (syn. *Bothriocephalus*)	Carnivora: phocid (ringed seal)			Greenland
Dip. fayi	Carnivora: odobenid (Pacific walrus)			Pacific
Dip. fuhrmanni	Artiodactyla: delphinid (Pacific white-sided dolphin, long-snouted dolphin, spotted dolphin), phocoenid (finless porpoise)			Asia
Dip. gondo (syn. *Dip. subtile*)	Artiodactyla: delphinid (short-finned pilot whale)			Atlantic
Dip. hians (syn. *Dib. hians, polycalceolus, variabile*)	Carnivora: phocid (Hawaiian monk seal, Mediterranean monk seal, harbour seal, bearded seal, ringed seal, hooded seal, common seal); Primates: hominid (human);			circumpolar
Dip. lanceolatum (syn. *Dibothriocephalus, Bothriocephalus,*	Carnivora: phocid (bearded seal, ringed seal, harp seal, common seal,		Salmoniformes: salmonid (sardine cisco)	circumpolar

Cordiocephalus)	ribbon seal, harbor seal, Mediterranean monk seal), otariid (Stellar sea lion); Artiodactyla: phocoenid (harbour porpoise), monodontid (beluga whale); Carnivora: canid (dog); Primates: hominid (human)			
Dip. lashleyi (syn. *Dibothriocephalus tectus*)	Carnivora: phocid (Weddell seal, Ross seal, leopard seal, southern elephant seal)			Southern Ocean
Dip. lobodoni	Carnivora: phocid (crabeater seal)			Southern Ocean
Dip. macroovatum	Artiodactyla: balaenopterid (minke whale), eschrichtiid (gray whale	Copepoda: acartiid (*Acartia clausi*), oithinid (*Oithina nana*), pontellid (*Labidocera japonica*)		Asia
Dip. minutus	Carnivora: phocid (Hawaiian monk seal)			Pacific Ocean
Dip. mobile (syn. *Dibothriocephalus*)	Carnivora: phocid (Ross seal, Weddell seal)			Southern Ocean
Dip. orcini	Artiodactyla: delphinid (killer whale); Primates: hominid (human)			Pacific
Dip. polyrugosum	Artiodactyla: delphinid (long-finned pilot whale)			Atlantic
Dip. pseudowilsoni	Carnivora: phocid (leopard seal)			Southern Ocean
Dip. quadratum (syn. *Dip. resimum, Dib. coatsi, Bothriocephalus*)	Carnivora: phocid (leopard seal, Weddell seal, crabeater seal)			Indian, Southern Oceans
Dip. rauschi	Carnivora: phocid (Hawaiian monk seal)			Pacific Ocean
Dip. roemeri (syn. *Dibothriocephalus*)	Carnivora: odobenid (walrus), phocid (bearded seal, harp seal)			Atlantic
Dip. schistochilos (syn. *Dib. schistochilus, coniceps, macrophallus p.p., Bothriocephalus coniceps*)	Carnivora: phocid (bearded seal, harbor seal, harp seal, common seal, Greenland seal, Mediterranean monk seal)			Arctic Ocean
Dip. scoticum (syn. *Dibothriocephalus scoticus*, *pygoscelis*)	Carnivora: phocid (leopard seal, Weddell seal, southern elephant seal), otariid (southern sea lion); Primates: hominid (human)			circumpolar
Dip. stemmacephalum (syn. *Dip. yonagoensis, ponticum*)	Artiodactyla: phocoenid (harbor porpoise), delphinid (common dolphin, bottle-nosed dolphin, spinner dolphin, Risso's dolphin, Pacific white-sided dolphin, long-finned pilot whale); Primates: hominid (human)			circumpolar
Dip. tetrapterum (syn. *Bothriocephalus*	Carnivora: phocid (common seal, harbor		Salmoniformes: salmonid (pink salmon)	Holarctic

tetrapterus, dubius, fasciatus, variabilis, Diplogonoporus, Dip. septrionalis, violettae, mutabilis, Dib. variabilis)	seal, bearded seal, hooded seal, ribbon seal, harp seal, spotted seal, ringed seal, monk seal), otariid (northern fur seal, Steller sea lion), mustelid (sea otter, American mink), canid (dog); Rodentia: murid (brown rat)			
Dip. ventropapillatum	Carnivora: phocid (leopard seal)			Russia (zoo)
Dip. wilsoni (syn. *Dip. scotti, Dib. mobilis, Dibothriocephalus*)	Carnivora: phocid (Ross seal, Weddell seal, crabeater seal, leopard seal)			Southern Ocean
Adenocephalus (pinnipeds and terrestrial carnivores as DH)				
A. pacificus (syn. *Dip. pacificum, glaciale, giljacicum, arctocephali, arctocephalinum, krotovi, atlanticum, A. septentrionalis Bothriocephalus macrophallus p.p.*) (Pacific broad tapeworm)	Carnivora: otariid (South American fur seal, Antarctic fur seal, Kurile fur seal, Alaskan fur seal, Juan Fernandez fur seal, brown fur seal, Subantarctic fur seal, northern fur seal, Steller sea lion, Afro-Australian fur seal, Australian sea lion, South American sea lion, California sea lion, Galapagos sea lion), canid (dog, black-backed jackal); Primates: hominid (human)		Perciformes: sciaenid (Lorna drum, Callao drum, Peruvian banded croaker, snakehead king croaker, Peruvian weakfish, kingfish), carangid (Paloma pompano, Chilean jack mackerel), haemulid (Peruvian grunt), coryphaenid (dolphinfish), serranid (Peruvian rock seabass); Scombriformes: centrolophid (palm ruff), scombrid (eastern Pacific bonito, chub mackerel, Atlantic Spanish mackerel); Siluriformes: ariid (Tete sea catfish, Peruvian sea catfish); Pleuronectiformes: paralichthyid (fine flounder); Gadiformes: merlucciid (Peruvian hake); Ophidiiformes: ophidiid (pink cusk-eel); Mugiliformes: mugilid (flathead grey mullet); Carcharhiniformes: triakid (sickle fin smooth-hound)	Pacific, Indian, Atlantic, Southern Oceans
Reassigned species				
Dip. antarcticus (syn. *Bothriocephalus, Dibothrium, Diplogonoporus, Dibothriocephalus*) (now *Glandicephalus*)	Carnivora: phocid (Ross seal)			Antarctic
Dip. perfoliatum (syn. *Dip. rufum, clavatum*) (now *Glandicephalus*)	Carnivora: phocid (Weddell seal)			Antarctic
Dip. phocarum (now *Pyramicocephalus*)	Carnivora: phocid (hooded seal, bearded seal, spotted seal, common seal, ringed seal, Caspian seal), otariid (Stellar sea lion, northern fur seal)			circumpolar, Caspian Sea
Dip. tectum	Carnivora: phocid			Southern Ocean

(now *Baylisiella*)	(southern elephant seal, Weddell seal, leopard seal)			

Parasite morphology: These aquatic tapeworms form 4 developmental stages: eggs, larval procercoids, larval plerocercoids and adults. The eggs are ovoid in shape and variable in size depending on species, ranging from 35-85 µm in length by 25-65 µm in width (those of *Dib. latus* range from 50-85 x 40-60 µm). They have smooth tanned eggshells which are yellow-brown and have an ellipsoidal operculum at one pole (some species also having a small knob at the opposite (abopercular) pole). The eggs are laid unembryonated and are polylecithal (containing a large amount of yolk). The eggs mature in the aquatic environment to contain a hexacanth (6-hooked) embryo (oncosphere) covered with a ciliated outer envelope (embryophore), this stage being called a coracidium. In intermediate hosts, the parasites form 2 sequential larval stages, first procercoids then plerocercoids, both being alacunate (without internal cavities). Procercoids are elongate and globular growing to 500 µm in length and they are essentially undifferentiated stages filled with parenchymal tissue. They lack an anterior scolex but have a posterior knob-like tail (cercomer) with 6 embryonic hooks. Plerocercoids (or spargana) are elongate and lanceolate measuring from several mm to several cm in length (e.g. < 5 cm for *Dib. latus*, but 10-20 cm for *Dip. dendtriticus*). They appear as white corrugated (pseudo-segmented) tubes with an anterior everted scolex with 2 shallow bothria and several internal cellular masses corresponding to developing organs. Adult tapeworms are large in size ranging from 3-15 m in length (some species reaching 25 m). They have a small spatulate unarmed scolex (2.5 mm long) with 2 shallow elongated (1-2 mm) sucker-like grooves (bothria) located dorsally and ventrally. The tapeworm body has a narrow proliferative zone (neck) giving rise to the elongate dorso-ventrally flattened strobila containing up to 4,000 craspedote proglottids that are wider (10-20 mm) than long (2-7 mm). Adults are hermaphroditic with each segment containing a single set of male and female reproductive organs. Mature segments have numerous ovoid testes connected to a common sperm duct which enlarges distally to form an external seminal vesicle that enters the cirrus sac containing the muscular cirrus (copulatory organ). Segments also contain numerous vitelline follicles, a bilobed ovary (germarium), a central rosette-shaped uterus (spiral uterus in the case of *Spirometra*) and a tubular vagina. The cirrus and vaginal pores are fused into a common genital atrium on the midventral surface (those of *Spirometra* spp. remain separated), yet separate from the uterine (birth) pore. Gravid proglottids release numerous dark operculate eggs but eventually become spent and degenerate (process of anapolysis).

Site of infection: Adult diphyllobothriid tapeworms infect the small intestines of their piscivorous definitive hosts: one *Diphyllobothrium* group infecting cetaceans; another group infecting pinnipeds; *Dibothriocephalus* infecting terrestrial carnivores; and the monospecific *Adenocephalus* infecting pinnipeds and terrestrial carnivores. Adult worms usually attach to the ileal or jejunal wall, and on rare occasion to the bile duct. Procercoid larvae develop in the haemocoel (body cavity) of copepods (first intermediate hosts) while plerocercoid larvae develop in the tissues and organs of many fish species, particularly salmonids (second intermediate hosts).

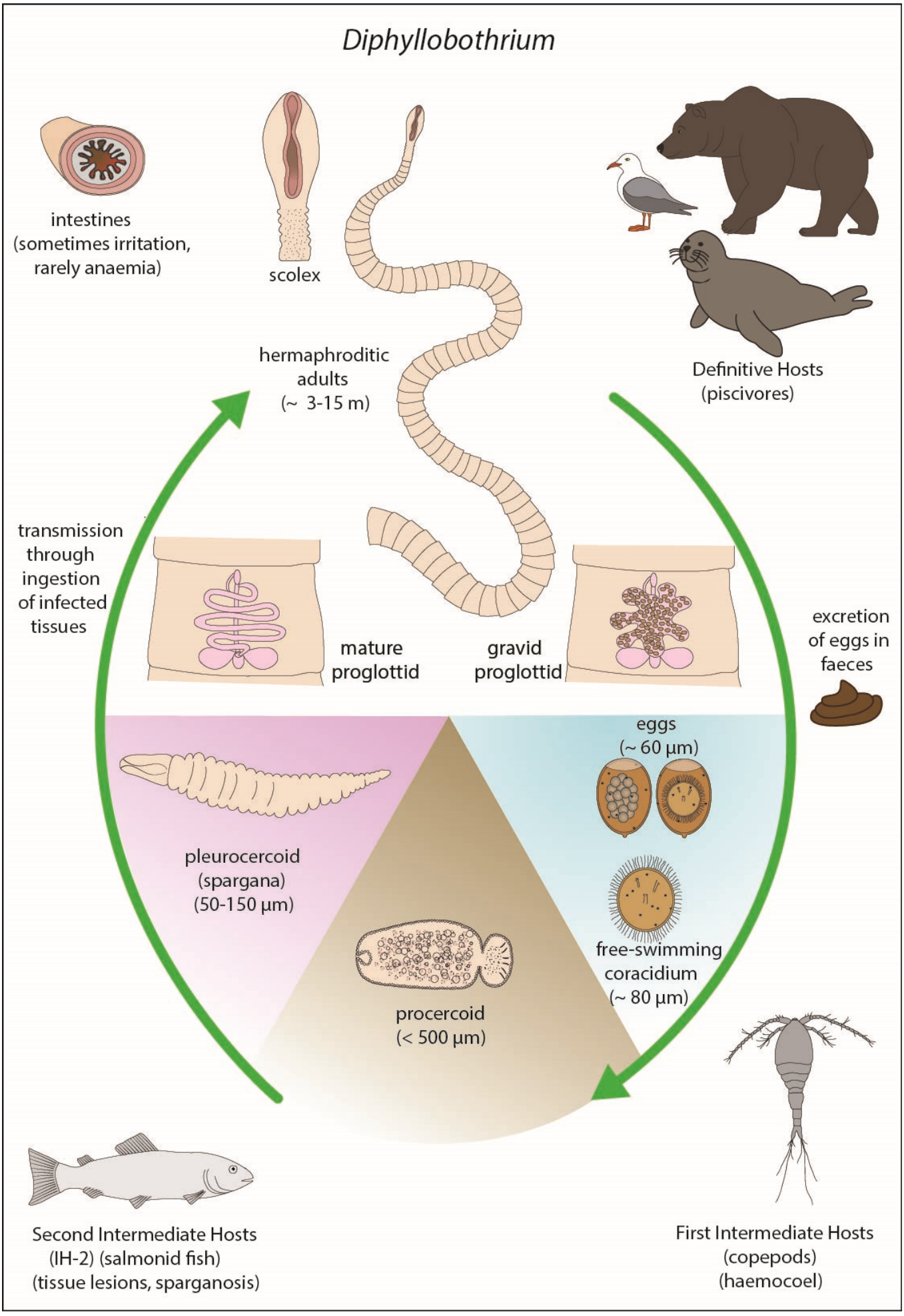
Pathogenesis: Despite the large size of adult tapeworms, most infections are asymptomatic as the worms lack digestive tracts and do not feed on host tissues but absorb nutrients from the gut lumen. Many infections in humans have also been found to consist of only one worm. Chronic and/or heavy infections may cause clinical manifestations attributable to host responses to parasite metabolic wastes, degenerating proglottids, mucosal irritation and inflammation, including constipation, diarrhoea, abdominal pain, nausea, vomiting, weight loss, anorexia, asthenia (physical weakness), vertigo (dizziness), numbness of extremities, sensation of hunger, craving for salt, sometimes headache, allergic reactions, eosinophilia, psychosomatic disorders (often when the patient learns of the presence of the worm) and less commonly, intestinal obstruction, cholecystitis or cholangitis (inflammation of the bile duct or gall bladder). Some patients with protracted infections may also develop megaloblastic pernicious anaemia (hyperchromic, macrocytic, low platelet counts, low leucocyte counts) due to the worms causing vitamin B_{12} deficiency through the dissociation of vitamin B_{12}-intrinsic factor complex. This manifestation is particularly common in Finland, where individuals have a genetic predisposition to pernicious anaemia. Anaemic patients develop pallor, breathlessness, weakness, numbness and disturbances in coordination due to degeneration of spinal and peripheral nerves. On occasion, humans may become infected with larval stages of the parasite and develop a condition known as sparganosis, which is caused by the encystment of plerocercoids in host tissues after they have ingested infected copepods. While the cysts are often benign, physical stress may impact on organ structure and/or function, with the most severe symptoms occurring when spargana infect the brain or eye.

Developmental cycle and mode of transmission: *Diphyllobothrium/Dibothriocephalus* tapeworms have indirect aquatic life-cycles involving 3 hosts with predator-prey transmission occurring between first and second intermediate hosts and definitive hosts. Adult tapeworms release numerous eggs from gravid segments until their uterine contents become exhausted. Terminal segments become senile and degenerate often detaching in chains of spent segments of variable length. Eggs passed in host faeces are unembryonated and require 1-3 weeks in water (depending on temperature) for embryonic development to be completed. The eggs then hatch releasing a ciliated coracidium which swims sporadically in the water column to attract the attention of zooplanktonic crustaceans (copepods) which act as first intermediate hosts. Coracidia will perish if not ingested by copepods within 24 hours of hatching. Once consumed, the coracidium sheds its ciliated embryophore and the hexacanth larva penetrates the gut wall and develops into a procercoid larva in the haemocoel within 14-18 days. Infections have been recorded in over 40 copepod species, mostly diaptomid,

cyclopoid, centropagid and temorid genera. Procercoids deplete host copepod nutrients and impair their mobility, thus increasing their chances of predation. Infected copepods are eaten by a variety of fish species which act as second intermediate hosts, particularly anadromous salmonids, freshwater predatory fish (pike, perch, burbot) and marine foraging fish (mullet, anchovy, sardines). Many infections have been reported in fish from cold waters in circumpolar regions, but an increasing number are being detected in subtropical and even tropical regions. Digestion of the infected copepods in the fish gut releases the procercoid larvae which burrow though gut wall and develop to infective plerocercoid larvae over 1-5 weeks. Plerocercoids (or spargana) occur free (unencapsulated) in most host tissues and organ (even the abdominal cavity) or encysted (encapsulated) within connective tissues in muscles, viscera, gut or gonads. Some plerocercoids have also been observed migrating from the viscera to the muscles after death of the host. Plerocercoids often ascend piscivorous food chains as they may re-establish in the tissues of larger predatory fish which have eaten smaller infected prey fish (the larger fish thus acting as a paratenic host). Plerocercoids may remain dormant (inactive) for several years, and they can re-establish several times in successive predatory fish. Plerocercoids are ultimately infective to piscivorous definitive hosts; both aquatic (cetaceans, pinnipeds) and terrestrial (carnivores, birds). When ingested, plerocercoids attach to the intestinal wall and develop rapidly into adult tapeworms (prepatent period of 2-6 weeks). Adult tapeworms grow sometimes at the rate of several cm per day, often reaching a length of several metres. Some species may live for up to 20 years and produce up to 1 million eggs per day. Sylvatic cycles may be maintained indefinitely in many countries between a wide range of wild animals, while domestic cycles in humans and companion animals may be regionally specific depending on cultural practices regarding the consumption of uncooked, partly-cooked or pickled fish. Human infections commonly occur in communities eating sashimi (raw sliced fish), sushi (rice balls with fish, egg, vegetables wrapped in seaweed), carpaccio (thin slices of raw fish), tartare maison (raw salmon), ceviche (raw fish pieces freshly marinated in lemon and salt), gefilte fish (balls of finely chopped fish mixed with crumbs, eggs and seasoning, cooked in broth), caviar (raw or partly cooked roe), or lightly cured fish (salted, smoked or marinated). The geographic distribution of infections has changed markedly over recent years with the globalization of trade (import/export of fish products) and growing cosmopolitanism (esp. shared dietary practices). Humans may also become infected with larval plerocercoids (spargana) after accidentally ingesting copepods (harbouring procercoids) in drinking water.

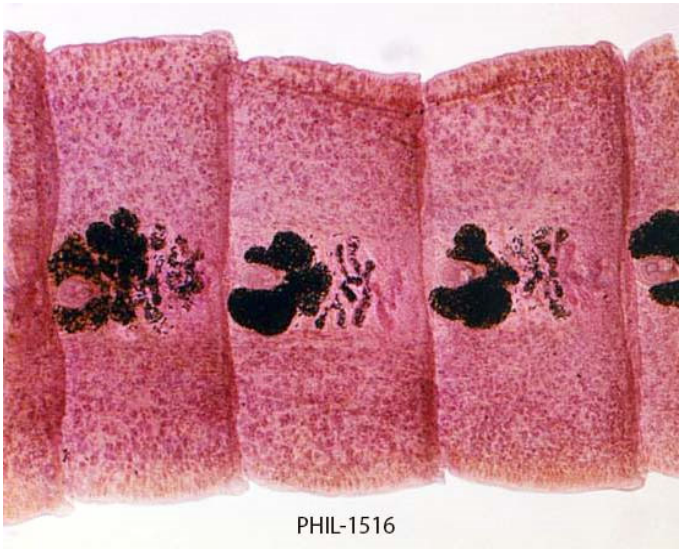
Differential diagnosis: Infections by adult tapeworms are readily diagnosed in definitive hosts by the microscopic detection of tapeworm eggs in faecal samples. Sometimes chains or strands of spent proglottids may be detected visually in samples, while a range of egg concentration and high contrast microscopic illumination methodologies have been used to improve diagnostic sensitivity, including sedimentation and/or floatation techniques. Infections by larval stages (procercoids in copepods and plerocercoids in fish) may be detected upon post-mortem dissection, but their specific identification is difficult due to their similar morphologies. Nonetheless, the plerocercoids of several species common in Holarctic fishes have been reliably differentiated on basis of several morphological characteristics (body surface wrinkled or smooth, length and density of microtriches, retraction of scolex, number of subtegumental longitudinal muscles). More recently, molecular characterization techniques have been applied to the differentiation of species and reconciling larval and adult stages. Isoenzyme and immuno-electrophoresis were used to characterize parasite proteins and antigens, restriction fragment length polymorphism (RFLP) analyses were used as species-specific markers, and polymerase chain reaction (PCR) amplification was used to sequence both nuclear DNA (18S ribosomal RNA (rRNA), internal transcribed spacers 1 and 2 (ITS1 and ITS2), elongation factor 1-alpha) and mitochondrial DNA (cytochrome c oxidase subunit 1 (cox1) and subunit 3 (cox3), cytochrome b (cob), tRNA pro, tRNA Ile, tRNA lys, NADH dehydrogenase subunits 1, 3 and 4 (nad1, nad3, nad4)) for diagnostic and phylogenetic purposes.

Treatment and control: Infections by adult tapeworms in humans and animals have been successfully treated with the anthelmintics praziquantel, niclosamide and albendazole. There may be some vague side-effects following praziquantel treatment, including abdominal discomfort with nausea, headache, dizziness, malaise/fatigue, fever, lower back pain and rarely urticaria. Niclosamide treatment has not been associated with many side-effects as it is not absorbed from the gastrointestinal tract. There is some evidence that the anti-ulcer agent gastropin and the contrast medium gastrografin may cause worms to detach and be excreted. In patients with pernicious anaemia, worms must be eliminated to allow the anaemia to resolve and vitamin B_{12} supplementation is recommended. Patients infected with spargana often go untreated as the larvae eventually die, but chemotherapy can be used should clinical problems arise or accessible cysts may be surgically removed (lumpectomy). Various prevention and control strategies have been proposed for domestic settings and aquaculture facilities to break the parasite life-cycle by stopping water contamination by faeces (better sanitation, sewage treatment), reducing copepod populations (water filtration/treatment), and minimizing transmission to fish-eating mammals (improving food hygiene, handling and cooking). Plerocercoids in fish products have been rendered nonviable by freezing (at least 24-48 hours at -10 to -35°C), desiccation (completely dried), brining (in 12% salt) or cooking (at 55°C for 5 minutes). Translocations (import/export) of partially processed fish products should be avoided, particularly from endemic regions.

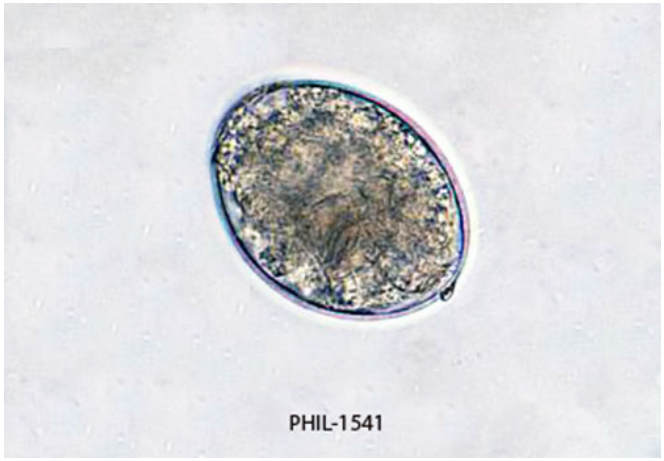

Diphyllobothrium
intestines
(sometimes irritation,
rarely anaemia)
scolex
hermaphroditic
adults
(~ 3-15 m)
Definitive Hosts
(piscivores)
transmission
through
ingestion
of infected
tissues
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
eggs
(~ 60 µm)
pleurocercoid
(spargana)
(50-150 µm)
free-swimming
coracidium
(~ 80 µm)
procercoid
(< 500 µm)
Second Intermediate Hosts
(IH-2) (salmonid fish)
(tissue lesions, sparganosis)
First Intermediate Hosts
(copepods)
(haemocoel)



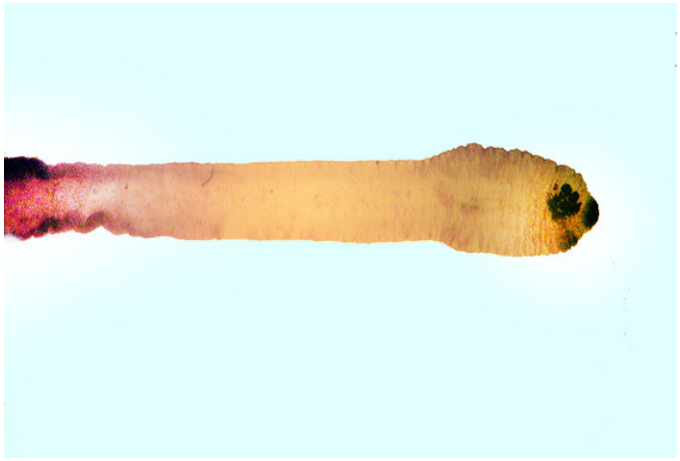
Diphyllobothrium scolex



Diphyllobothrium segments



Diphyllobothrium egg



Diphyllobothrium pleurocercoid

Spirometra
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Diphyllobothriidean (formerly pseudophyllidean) tapeworms are intestinal parasites of fish-eating birds and mammals and have an anterior scolex (holdfast organ with two elongate grooved bothria) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). They have indirect life-cycles involving two intermediate hosts. Eggs shed into water release motile coracidia which are ingested by copepods and develop into first-stage larvae (procercoids). When ingested by fish, they form second-stage larvae (plerocercoids or spargana) in host tissues which are transmitted to final hosts by piscivory. Aquatic animals may also act as paratenic hosts for plerocecoids. Infections by *Spirometra* spp. occur in humans and fish-eating mammals, sometimes causing enteric disorders.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Diphyllobothriidea (= Pseudophyllidea) (aquatic hosts, scolex with bothria, central genital pores, two IH)
Family:	Diphyllobothriidae (coracidium, procercoid in copepods, plerocercoids in frogs, often PHs)
Genus:	*Spirometra* (parasitic in small intestines of carnivores)
Species:	various species cause sparganosis in humans, dogs and cats

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce

eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10 hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Diphyllobothriidean (= Pseudophyllidean) cestodes are polyzoic with complete or incomplete segmentation. They possess an anterior scolex with 2 shallow grooves (bothria) which are unarmed and their genital organs and pores are centrally located on the ventral surface. Adult worms are found in vertebrate definitive hosts, usually aquatic mammals such as seals and cetaceans, but infections have also been recorded in piscivorous mammals and birds (canids, felids, rodents, occasionally humans) as well as in reptiles (pythons, varanids) and amphibians (African frogs). Larval stages (metacestodes) are usually formed in two intermediate hosts: cercoids (procercoid-type) forming in first intermediate hosts (copepods); then metacercoids (plerocercoid-type) developing in second intermediate hosts (fish, amphibians, reptiles, mammals, occasionally humans). Over 240 species have been described in 19 genera in 3 families: Cephalochlamydidae, Diphyllobothriidae, and Solenophoridae (earlier works also recognized another 3 families (Ligulidae, Schistocephalidae, and Scyphocephalidae) but they are no longer considered valid).

Members of the family Diphyllobothriidae are characterized by adult tapeworms possessing a spatulate scolex with 2 shallow elongated grooves (bothria) located dorsally and ventrally, craspedote proglottids with a small common genital atrium on the midventral surface and reproductive organs comprising a bilobed ovary, numerous testes and a cirrus sac, and eggs containing a coracidium (hexacanth embryo sheathed in a ciliated embryophore). Some 13 diphyllobothriid genera have been described: including *Adenocephalus*, *Baylisia*, *Baylisiella*, *Dibothriocephalus*, *Diphyllobothrium*, *Flexobothrium*, *Glandicephalus*, *Ligula*, *Plicobothrium*, *Pyramicocephalus*, *Schistocephalus*, *Spirometra* and *Tetragonoporus*. The genus *Spirometra* is characterized by diphyllobothrids with a spiral-shaped uterus (as opposed to the rosette-shaped uterus in *Diphyllobothrium*). Around 40 *Spirometra* species have been described as intestinal parasites of mammalian definitive hosts (wild and domestic carnivores) with larval stages developing as procercoids in first intermediate hosts (copepods, crustaceans) and then as plerocercoids (spargana) in a range of second intermediate hosts (frogs, reptiles, mammals, some birds, but not fish). Humans usually act as intermediate or paratenic hosts for tissue infections with spargana (becoming infected after drinking water contaminated with copepods, or applying animal flesh to open wounds as poultices), but occasionally humans may act as definitive hosts for intestinal infections with adult tapeworms (becoming infected after eating animal flesh containing pleroceroids). It is estimated that more than 20 million people harbour infections; most reported throughout Asia, with sporadic cases recorded in the Americas, Africa, Europe and Australia.

***Spirometra* species**	**Definitive host [adults in intestines]**	**First intermediate hosts [procercoids in tissues]**	**Second intermediate hosts, incl. paratenic hosts [plerocercoids in tissues]**	**Distribution**
Hosts for adult stages known				
S. bresslaui (syn. *Diphyllobothrium*)	Didelphimorphia: didelphid (common opossum)			South America
S. decipiens (syn. *S. longicolle, longicollis, Dibothrium, Diphyllobothrium, Dibothriocephalus*)	Carnivora: felid (jaguar, jaguarundi, cat, clouded leopard, kodkod, margay, cougar), canid (dog, crab-eating fox, South American gray fox), mephitid (Molina's hog-nosed skunk), mustelid (lesser grison, southern river otter); Didelphimorphia: didelphid (white-eared opossum, lutrine opossum); Rodentia: cricetid (olive grass mouse), murid (black rat, brown rat); Primates: hominid (human)		Anura: leptodactylid (butter frog), microhylid (painted chorus frog), ranid (dark-spotted frog)	India, China, South America
S. didelphidis (syn. *Bothriocephalus, Diphyllobothrium*)	Didelphimorphia: didelphid (big-eared opossum)			South America
S. erinaceieuropaei (syn. *Dubium, Diphyllobothrium, S. erinacei, felis, Bothriocephalus felis, maculatus, Dibothriocephalus felis, Sparganum lanceolatum, proliferum, Plerocercoides prolifer*) (zipper worm)	Carnivora: felid (cat, wildcat, leopard cat, jungle cat, leopard, clouded leopard, fishing cat, lion, tiger), canid (red fox, Japanese red fox, Pampas fox, dog, wolf, golden jackal, raccoon dog), mephitid (Molina's hog-nosed skunk); Primates: hominid (human)	Copepoda: cyclopid (*Mesocyclops leuckarti*, *Eucyclops serrulatus*)	Eulipotyphla: erinaceid (European hedgehog, Chinese hedgehog, southern white-breasted hedgehog, northern white-breasted hedgehog), soricid (Dsinezumi shrew, bicolored shrew, lesser white-toothed shrew, Mediterranean water shrew, common shrew), talpid (European mole, Japanese shrew mole); Peramelemorphia: peramelid (northern brown bandicoot, long-nosed bandicoot); Dasyuromorphia: dasyurid (fawn antechinus, brown antechinus, dusky antechinus, northern quoll, tiger quoll, eastern quoll, brush-tailed phascogale, common planigale, sandstone false	Eurasia, Americas, Australia

			antechinus, fat-tailed false antechinus, Tasmanian devil); Rodentia: murid (mouse, small Japanese field mouse, large Japanese field mouse, striped field mouse, yellow-necked mouse, rakali, brown rat), sciurid (red squirrel), cricetid (red-backed vole, golden hamster, Japanese grass vole); Carnivora: felid (cat), mustelid (Eurasian otter, beech marten, European pine marten, European badger, stoat, least weasel, ferret, American mink, Japanese marten, European polecat); Artiodactyla: suid (pig); Monotremata: ornithorhynchid (platypus), tachyglossid (short-beaked echidna); Primates: hominid (human), cercopithecid (vervet monkey, Sykes monkey, baboon); Anura: bufonid (cane toad, Argentine common toad), ranid (dark-spotted frog, poor frog, marsh frog, edible frog, rice field frog, Otton frog), hylid (desert tree frog); Serpentes: colubrid (Chinese ratsnake, Japanese striped snake, grass snake, dice snake, tiger keelback, large whip snake), pythonid (Asian rock python, Indian rock python), elapid (death adder), viperid (common European viper, painted carpet viper); Sauria: agamid (Okinawa tree lizard), anguid (European glass lizard)	
S. folium (syn. *Dibothrium*)	Carnivora: herpestid (white-tailed mongoose)			Africa
S. gracile (syn. *Diphyllobothrium*)	Carnivora: felid (long-tailed tiger cat, jaguarundi, Geoffroy's cat, margay)			South America
S. houghtoni (syn. *Diphyllobothrium*)	Carnivora: canid (golden jackal, dog), felid (cat); Primates: hominid (human)			Europe, Asia
S. janickii	Carnivora: felid (Eurasian lynx), canid (wolf)			Europe
S. mansoni (syn. *Sparganum mansoni, Bothriocephalus, Diphyllobothrium, Ligula*)	Carnivora: canid (golden jackal, dog), felid (cat, clouded leopard, lion, fishing cat), viverrid (masked palm civet); Artiodactyla: suid (pig); Primates: hominid (human)	Copepoda: cyclopid (*Cyclops*)	Anura: bufonid (cane toad), dicroglossid (Chinese edible frog, Asian grass frog), ranid (American bullfrog, darkspotted frog, common water frog); Serpentes: colubrid (Chinese garter snake, Amur rat snake, slender racer, Steppe ratsnake, tiger keelback, red-banded snake), viperid (Siberian pit viper), pythonid (Indian rock python); Artiodactyla: suid (pig);	Eurasia, South America, Australia

			Carnivora: mustelid (Siberian weasel, yellow-throated marten), canid (raccoon dog, red fox); Eulipotyphla: erinaceid (Amur hedgehog); Rodentia: murid (mouse); Primates: hominid (human); Galliformes: phasianid (chicken); Passeriformes: passerid (sparrow)	
S. mansonoides (syn. *Diphyllobothrium*)	Carnivora: felid (bobcat, cat, jungle cat, clouded leopard, fishing cat, Geoffroy's cat, ocelot, jaguar, jaguarundi, cougar, lion), canid (dog, crab-eating fox, Pampas fox), procyonid (raccoon); Didelphimorphia: didelphid (Virginia opossum); Artiodactyla: suid (pig); Primates: callitrichid (moustached tamarin), hominid (human); Pelecaniformes: pelecanid (American white pelican)	Copepoda: cyclopid (*Cyclops bicuspidatus, C. leuckarti, C. vernalis, C. viridis*)	Serpentes: colubrid (military ground snake, false coral snake, goldbauch-buntnatter), pythonid (Indian rock python); Anura: ranid (American bullfrog, leopard frog): Rodentia: murid (rats, field mouse, house mouse), cricetid (hamster, cotton mouse), caviid (guinea pig); Didelphimorphia: didelphid (opossum); Lagomorpha: leporid (cottontail rabbit); Carnivora: procyonid (raccoon), canid (grey fox), felid (cat), ursid (black bear); Primates: cercopithecid (rhesus macaque), cebid (ringtail monkey), hominid (human)	Americas
S. marginatus nom. nud. (syn. *Bothriocephalus*)	Diprotodontia: macropodid (pademelon)			Australia
S. okumurai (syn. *Diphyllobothrium*)	Carnivora: canid (dog), felid (lion)			Africa, China
S. pretoriensis (syn. *Lueheella, Diphyllobothrium*)	Carnivora: canid (bat-eared fox, African wild dig, hyena)			Africa
S. raillieti (syn. *Sparganum*)	Artiodactyla: suid (pig)			Europe
S. ranarum (syn. *Ligula*)	Carnivora: felid (cat, fishing cat, clouded leopard, lion), canid (dog, raccoon dog); Artiodactyla: suid (pig); Primates: hominid (human); Serpentes: pythonid (python)		Anura: ranid (edible frog), dicroglossid (Chinese edible frog, Indian bullfrog), leptodactylid (butter frog); Serpentes: colubrid (grass snake)	Eurasia
S. ratticola (syn. *Bothriocephalus*)	Rodentia: murid (black rat)			Asia
S. reptans (syn. *Ligula*)	Primates: cebid (common squirrel monkey), callitrichid (black-tailed marmoset); Chiroptera: noctilionid (greater bulldog bat); Carnivora: canid (dog, crab-eating fox), felid (ocelot, oncilla, leopard), mustelid (tayra, neotropical otter, giant otter, wolverine, marmoset), procyonid (South American coati, coatimundi); Rodentia: cricetid (Brazilian marsh rat); Didelphimorphia: didelphid (yellow-sided opossum, southeastern four-eyed opossum, northern red-		Anura: leptodactylid (butter frog); Sauria: amphisbaenid (red worm lizard); Serpentes: colubrid (two-headed sipo, mussurana, false coral snakes, parrot snake, Rio tropical racer, green snake, chicken snake, Wagler' snake), elapid (Caatinga coral snake), viperid (jacaraca, Neuweid's lancehead, yara, fer-de-lance); Carnivora: canid (dog); Didelphimorphia: didelphid (white-eared opossum, lutrine opossum)	South America

	sided opossum); Coraciiformes: alcedinid (green kingfisher, ringed kingfisher); Anseriformes: anatid (Brazilian merganser); Pelecaniformes: ardeid (cocoi heron, rufescent tiger heron, great white heron, wood stork), threskiornithid (white-necked ibis); Piciformes: bucconid (rusty-breasted nunlet), ramphastid (channel-billed toucan, toco toucan); Ciconiiformes: ciconiid (wood stork); Passeriformes: corvid (curl-crested jay, purplish jay, plush-crested jay), furnariid (anabates), icterid (brown-headed cowbird, crested oropendola), turdid (pale-breasted thrush, rufous-bellied thrush), tyrannid (strange-tailed tyrant); Accipitriformes: pandionid (osprey); Strigiformes: strigid (burrowing owl); Tinamiformes: tinamid (red-winged tinamou); Galliformes: cracid (nocturnal curassow)			
S. serpentis sp. inq. (syn. *Diphyllobothrium*)	Serpentes: elapid (Taiwan cobra)			Asia
S. serratum (syn. *Dibothrium*)	Carnivora: canid (crab-eating fox, dog)			South America
S. sulcatum (syn. *Dibothrium*)	Carnivora: felid (leopard)			Europe
S. tangalongi (syn. *Dibothrium*)	Carnivora: viverrid (Malayan civet)			Asia
S. theileri (syn. *Diphyllobothrium*)	Carnivora: felid (serval, southern African wildcat, lion), canid (dog); Primates: hominid (human)	Copepoda: cyclopid (*Cyclops*)	Rodentia: murid (mice, rats), cricetid (hamster); Artiodactyla: suid (warthog); Primates: cercopithecid (rhesus macaque)	Africa
S. trinitatis (syn. *Diphyllobothrium*)	Carnivora: procyonid (crab-eating raccoon, South American coati)			Americas
S. urichi (syn. *Diphyllobothrium*)	Carnivora: felid (ocelot)			Americas
Hosts for adult stages unknown				
S. affine (syn. *Sparganum*)			Urodela: salamandrid (newt)	Europe
S. ameiva (syn. *Sparganum*)			Sauria: teiid (South American ground lizard)	South America
S. ardeae (syn. *Sparganum*)			Pelecaniformes: ardeid (little blue heron)	South America
S. baxteri (syn. *Sparganum*)			Primates: hominid (human)	Africa
S. canis (syn. *Sparganum*)			Carnivora: canid (dog)	South America
S. cuniculi (syn. *Sparganum*)			Lagomorpha: leporid (European rabbit)	Europe
S. ellipticum (syn. *Sparganum*)			Carnivora: mustelid (beech marten)	Europe
S. falconis			Falconiformes: falconid	ns

(syn. *Sparganum*)			(unspecified falcon sp.)	
S. fausti (syn. *Diphyllobothrium*)			Eulipotyphla: erinaceid (Amur hedgehog)	Asia
S. fernandezi (syn. *Sparganum*)			Artiodactyla: bovid (goat)	South America
S. lanii (syn. *Sparganum*)			Passeriformes: vangid (rufous vanga)	Africa
S. leptodactyli (syn. *Sparganum*)			Anura: leptodactylid (butter frog)	South America
S. liguloides (syn. *Bothriocephalus*)			Primates: hominid (human)	Asia
S. mygales (syn. *Sparganum*)			Carnivora: mustelid (Chinese ferret-badger)	Asia
S. okapiae (syn. *Sparganum*)			Artiodactyla: giraffid (okapi)	Africa
S. pancerii (syn. *Ligula*)			Serpentes: colubrid (grass snake)	Europe
S. philippinensis (syn. *Sparganum*)			Carnivora: viverrid (Asian palm civet)	Asia
S. strigis (syn. *Sparganum*)			Strigiformes: strigid (short-eared owl)	ns

Parasite morphology: *Spirometra* spp. form 4 sequential stages in their developmental cycles: eggs, procercoid larvae, plerocercoid larvae and adult tapeworms. Eggs are ovoid-ellipsoid in shape measuring from 55-70 x 31-50 µm, but are slightly asymmetrical with uneven lateral curvature. They are surrounded by a smooth transparent yellow-brown eggshell with a conical operculum at one end and a thickening at the abopercular end. The eggs are unembryonated when passed in faeces but then form an ovoid coracidium comprising a hexacanth (6 hooked) embryo (oncosphere) surrounded by ciliated embryonic membrane (embryophore). Procercoid larvae are pyriform measuring 55-145 µm long by 20-75 µm wide, alacunate (without internal cavities) and display an anterior invagination with minute spines and a knob-like tail (cercomer) containing oncospheral hooks. Plerocercoid larvae (spargana) have white ribbon-like bodies measuring 2-115 mm long by 1-6 mm wide and are surrounded by a thick tegument. The body is alacunate (without an internal cavity or bladder) and unsegmented but has a wrinkled-corrugated appearance (pseudo-segmented). Most possess an everted protoscolex (developing scolex) with 2 developing bothria (sucker-like grooves), although it is absent or inconspicuous in some species. Adult tapeworms have long dorso-ventrally flattened bodies measuring from 60-110 cm in length by 0.5-1.0 cm in width, some attaining a length of 1.5 m. They have an anterior spoon-shaped scolex measuring 1.8-2.0 x 0.2-0.5 mm which possesses 2 long shallow muscular grooves (bothria) measuring ~ 1 mm in length. The scolex is mounted on a thin unsegmented neck region which gives rise to a long robust segmented strobila formed by up to 1,000 segments (proglottids) which are wider than long (6-10 mm wide by 1.0-2.5 mm long) and sometimes with serrate margins. Adult worms are hermaphroditic with each proglottid containing a single set of male and female reproductive organs, including numerous ovoid testes connected to a common sperm duct, the seminal vesicle and cirrus sac fused together and containing a muscular cirrus (male copulatory organ), numerous vitelline follicles, a bilobed ovary connected to a centrally-located spiral-shaped uterus with 3-5 closely compressed coils (rosette-shaped in *Diphyllobothrium*) and a tubular vagina. The cirrus and vaginal pores open separately on the ventral surface anterior to the uterine (birth) pore. The central location of these pores gives the appearance of a zipper down the middle of the worm (hence the common name of 'zipper worm'). Gravid proglottids contain many eggs which are released through uterine pore into gut lumen and passed unembryonated in faeces. Egg production eventually becomes exhausted and the spent proglottids disintegrate or are shed in faeces.

Site of infection: Adult *Spirometra* worms infect the small intestines of their definitive hosts, mostly carnivorous mammals but sometimes possibly involving rodents, primates, birds and reptiles. Procercoid larvae develop in the body cavities of zooplanktonic crustaceans (notably copepods which act as first intermediate hosts), while plerocercoid larvae (spargana) form in the tissues in a range of vertebrate hosts (including amphibia, reptiles, birds, mammals (carnivores, herbivores, rodents, primates) which act as second intermediate hosts or paratenic transport hosts). Spargana may occur in a variety of tissues and organs, notably subcutaneous tissues, visceral organs, the orbit of the eye, and rarely the brain.

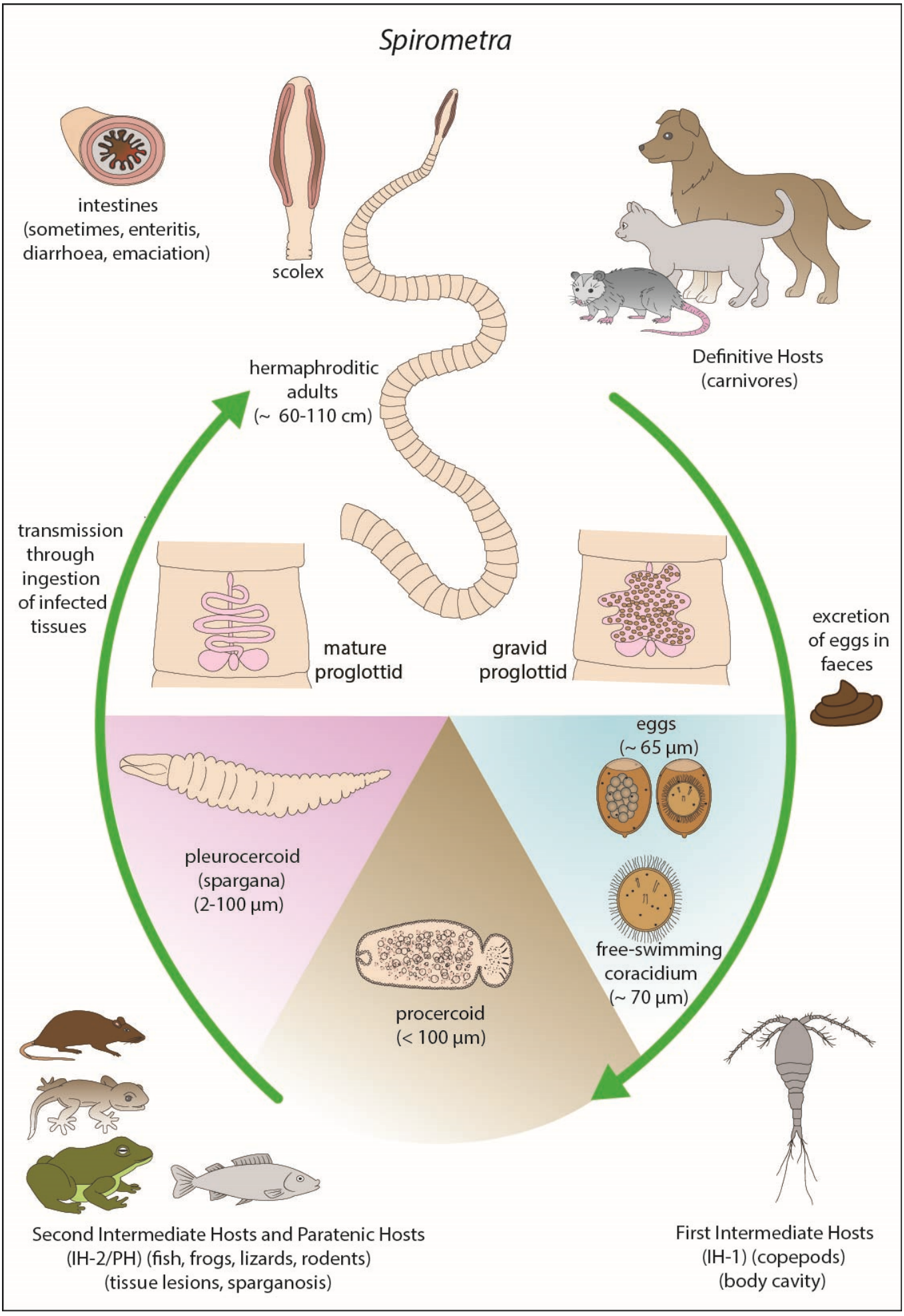
Pathogenesis: Infections by adult tapeworms rarely cause clinical signs in most definitive hosts, although heavy infections may cause enteritis in companion animals, resulting in diarrhoea, weight loss, emaciation, vomiting, irritability, abnormal or exaggerated appetite and occasionally stunted growth in nursing young. Adult worms and plerocercoid larvae have also been shown to deplete vitamin B_{12} from their hosts, possibly contributing to the development of anaemia (as occurs for some *Diphyllobothrium* infections). In contrast, infections by plerocercoid larvae (spargana) may cause a range of clinical conditions depending on which tissues have been infected. Infections have been recorded in a wide range of vertebrates acting as second intermediate and/or paratenic hosts, notably mammals (carnivores, herbivores, rodents and primates, including humans) but also in birds, reptiles and

amphibians. Once ingested, spargana migrate throughout the body but then settle and form nodules at various sites. The early migratory and developmental phases may be asymptomatic, but nodule formation and growth induces intense inflammatory reactions with erythema, oedema, heat, pain, pruritus, urticaria, leucocytosis, eosinophilia and fibrosis (although the larvae do not become encysted). Nodules often appear, disappear and migrate with time (the parasites apparently using a mimic of human growth factor to aid migration), persisting in the host for a long time (up to 20-30 years). The disease sparganosis may manifest in 5 different ways: subcutaneous, visceral, ocular, cerebral or proliferative. The most common form is subcutaneous sparganosis where irregular nodules (1-2 cm) develop in connective tissues in the abdomen, chest and scrotum, accompanied by inflammation, pruritus, urticaria and oedema (sometimes elephantitis). Visceral sparganosis occurs when nodules develop in the intestines, mesenteries, kidneys, pleural cavity, lungs, pericardium or heart resulting in organ malfunction, including gut obstruction or perforation leading to peritonitis or pericardial effusion. Infections in the inner ear have also been associated with vertigo or deafness. In Asia, the most common form is ocular sparganosis where larvae migrate to the conjunctiva and enter the orbit of the eye, producing intense pain, excessive watering, oedema, lacrimation, pruritus, exophthalmos (protrusion of eyeball), cellulitis, corneal ulceration and blindness. A rare form is cerebral sparganosis which occurs when nodules grow in the cerebrum or cerebellum leading to various neurological symptoms, including motor weakness, fatigue, headache, seizures, confusion, memory loss, paresthesias (tingling or numbing sensation of the skin), abscesses, paralysis and coma. A most severe form known as proliferative sparganosis occurs when larvae undergo massive asexual reproduction (by budding or branching) resulting in the spread of nodules often from subcutaneous sites to the muscles and internal organs. Such proliferation take place over years and can prove fatal. Most cases have been traced to infection by the pleomorphic species *S. proliferum* which forms irregular branches and proliferative buds, although several cases involving pleuritis and pneumothorax in dogs have characterized the species responsible as *S. erinacei.*

Developmental cycle and mode of transmission: *Spirometra* spp. have indirect life-cycles involving predator-prey transmission between at least 3 different hosts, with adult tapeworms infecting vertebrate definitive hosts, larval procercoids infecting invertebrate intermediate hosts, and larval plerocercoids developing in vertebrate intermediate and paratenic hosts. Unembryonated eggs released by adult tapeworms are passed in host faeces into the external environment. The eggs embryonate in water over several days depending on temperature (taking longer in cold water) and then hatch releasing a ciliated coracidium. The free-swimming coracidia are ingested by zooplanktonic crustaceans (invariably cyclopid copepods) which act as first intermediate hosts. After ingestion, the coracidia shed their cilia and the oncospheres penetrate the gut wall and form procercoid larvae in the body cavity over several weeks. Infected copepods are then consumed (often in contaminated drinking water) by a wide range of terrestrial and amphibious vertebrates (mammals, birds, reptiles, frogs), which act as second intermediate hosts. The larvae penetrate host tissues and develop over several weeks into worm-like plerocercoid larvae (also called spargana) which may persist for many years. Should animals infected with spargana be eaten by predators that are unsuitable as definitive hosts, the spargana may be transferred to their tissues, thus making them paratenic (transport) hosts. Spargana may ascend the food-chain by passing through several paratenic hosts before infection of the definitive host. Eventually, spargana are ingested by suitable definitive hosts, particularly hunters and scavengers preying on smaller rodents, reptiles and frogs (incl. tadpoles). The larval plerocercoids attach to the gut wall of the definitive host and develop into adult tapeworms. The prepatent period (time from infection to first egg release) ranges from 2-4 weeks and adult worms can live for 0.5-4.0 years. Humans can become infected with several *Spirometra* spp., usually by larval stages in the tissues and rarely by adult tapeworms in the gut. Infections are acquired by eating raw or poorly-cooked meat containing spargana (often from feral pigs, game animals, chickens, reptiles and frogs) resulting usually in the retention of larval spargana in the tissues (humans acting as paratenic hosts) and rarely the development of adult tapeworms in the gut (humans acting as definitive hosts). In Asia, sparagana have also developed in humans after the flesh of infected animals (usually frogs or snakes) has been applied to open wounds, ulcers or sore eyes as medicinal or ritualistic poultices (humans acting as paratenic hosts). Lastly, humans may develop spargana after drinking water containing copepods infected with procercoid larvae (humans acting as second intermediate hosts).

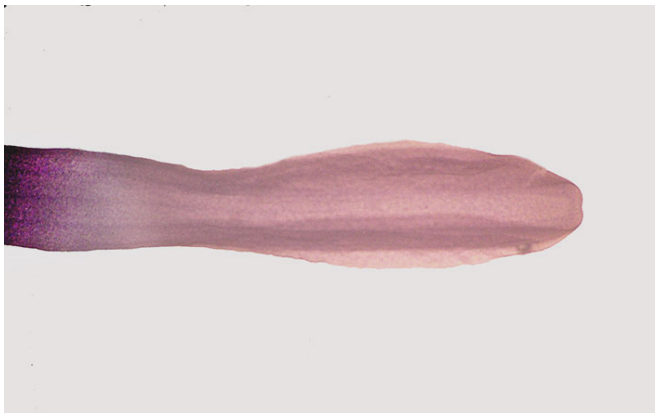
Differential diagnosis: Intestinal infections by adult tapeworms are usually diagnosed by the microscopic detection of eggs in faecal samples following concentration by sedimentation and/or floatation techniques. It is recommended that multiple consecutive samples be examined as egg excretion by worms may be cyclic. Occasionally, strands of spent proglottids may be detected in faecal or vomitus samples. Infections by larval spargana are more difficult to diagnose because pleurocercoids may be located in superficial tissues or deeper in vital organs, thus generating a broad spectrum of clinical symptoms/signs often associated with space-occupying nodules. Like many helminthiases, infections may be accompanied by a marked eosinophilia. Various medical imaging techniques have been applied to the diagnosis of sparganosis, including computed tomography (CT) and magnetic resonance imaging (MRI) scans which reveal migratory nodular lesions characterized by multifocal hypodense regions with irregular punctuate areas of calcification (referable to larval calcareous corpuscles). Differential diagnosis should also consider inflammatory granulomas, tuberculomas, benign and malignant tumours. Where possible, nodules may be surgically removed and the presence of plerocercoid larvae confirmed by microscopic examination. Enzyme immunoassays have been developed to detect host antibodies in serum or cerebrospinal fluid samples to spargana antigens, but some cross-reactivity was noted with other tapeworm genera. Molecular techniques have also been applied to the characterization of adult tapeworms and spargana by polymerase chain reaction (PCR) amplification and sequencing of nuclear (small (18S) and large (28S) subunit rRNA, internal transcribed spacers 1 and 2) and mitochondrial (cytochrome c oxidase subunits 1 and 3 (cox1, cox3), NADH dehydrogenase subunits 1, 3 and 4 (nad1, nad3, nad4) and succinate dehydrogenase subunit 3 (sdh3)) genes.

Treatment and control: Several anthelminthic drugs have been used to successfully treat *Spirometra* infections, both gut infections by adult worms and tissue infections by larval spargana. The isoquinoline, praziquantel, is effective against immature and mature worms and can be administered by many routes (oral, subcutaneous, transcutaneous, intramuscular), but higher and repeated doses may be required to avoid re-infection. The hexyloxynaphthamidine, bunamidine, has been used to treat companion animals but care should be taken to avoid unpleasant side-effects (diarrhoea, vomiting, ventricular fibrillation). The benzimidazole-methylcarbamates (albendazole, fenbendazole and mebendazole) and hydropyrazino-benzazepine (epsiprantel) have proven particularly effective in treating sparganosis, although dead and dying nodules of parasites may present significant challenges to the host. Alternatively, spargana may be surgically removed where feasible, usually by lumpectomy from subcutaneous sites. Various precautions may be taken to prevent infections in domestic and agricultural settings, while little can be done to limit sylvatic cycles in wildlife where many parasite species exhibit broad host specificities. Control strategies centre around minimizing faecal contamination of water (through proper waste/effluent disposal, sewage treatment), reducing transmission to and from copepods (by water treatment and/or filtration) and restricting transmission to vertebrates (by improved food hygiene, cooking meat, curbing hunting and scavenging behaviours, and prohibiting the use of raw meat poultices). Public health education campaigns are mandated as it is difficult to change the dietary habits and medicinal customs of human populations.


Spirometra
intestines
(sometimes, enteritis,
diarrhoea, emaciation)
scolex
hermaphroditic
adults
(~ 60-110 cm)
Definitive Hosts
(carnivores)
transmission
through
ingestion
of infected
tissues
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
eggs
(~ 65 µm)
pleurocercoid
(spargana)
(2-100 µm)
free-swimming
coracidium
(~ 70 µm)
procercoid
(< 100 µm)
Second Intermediate Hosts and Paratenic Hosts
(IH-2/PH) (fish, frogs, lizards, rodents)
(tissue lesions, sparganosis)
First Intermediate Hosts
(IH-1) (copepods)
(body cavity)



Spirometra adult worms



Spirometra scolex



Spirometra segments



Spirometra egg

***Bothriocephalus* (incl. *Schyzocotyle*)**
(platyhelminth: cestode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Cestodes (tapeworms) have elongate ribbon-like bodies ranging from a few millimetres to several metres in length. Diphyllobothriidean (formerly pseudophyllidean) tapeworms are intestinal parasites of fish-eating birds and mammals and have an anterior scolex (holdfast organ with two elongate grooved bothria) and a posterior tape (strobila) made up of segments (proglottids). Adult worms lack a gut (they absorb nutrients) and they are hermaphroditic (segments containing both male and female reproductive organs). They have indirect life-cycles involving larval development in invertebrate intermediate hosts. Eggs shed into water release motile coracidia that are ingested by copepods and develop into procercoids and/or plerocercoids which are transmitted to final hosts by piscivory. Infections by *Bothriocephalus* and *Schyzocotyle* spp. occur in freshwater fishes and transmission involves plerocercoid stages in copepods.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Cestoda (tapeworms, gut absent, anterior scolex, proglottid segments, heteroxenous, predator-prey cycles)
Subclass:	Eucestoda (larvae hexacanth (with six hooks))
Order:	Bothriocephalidea (aquatic hosts, scolex with 2 bothria)
Family:	Bothriocephalidae (hexacanth coracidia, procercoid larvae in copepods)
Genus:	*Bothriocephalus/Schyzocotyle* (parasitic in intestines of fish)
Species:	various species cause mortality or stunting in fish

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The cestodes (or tapeworms) lack digestive tracts and have elongate ribbon-like bodies (strobila); most being polyzoic (segmented) divided internally and/or externally into proglottids, although some are monozoic (unsegmented). Serial proglottids may be craspedote (overlapping) or acraspedote. Proglottids are generally hermaphroditic, possessing both male and female reproductive organs (those in which the male system matures first are protandrous, those in which the female system matures first are progynous). Terminal proglottids may detach from the strobila when they are immature (hyperapolytic), mature (euapolytic) or gravid (apolytic), or remain attached until they degenerate (anapolytic). Cestodes possess remarkable anterior attachment organs on the head (scolex): many divided into 4 membrane-bound muscular acetabula evident as suckers or bothridia (stalked, fused or bearing loculi); others bearing two weakly muscular bothria; some possessing a simple apical funnel (monobothriate); and some with a complex apical organ or rostellum that may be retractable, armed with hooks or bearing tentacles. Fertile tapeworms produce eggs in which larval stages develop as non-ciliated oncospheres or ciliated coracidia or lycophores. These stages possess 6 or 10

hooks which they use to invade the tissues of intermediate hosts where they form encysted metacestode stages: either alacunate forms (procercoid with tail-like cercomer, plerocercus with retracted scolex, plerocercoid with an everted scolex, or merocercoid with an invaginated scolex) or lacunate forms (cysticercoid with cercomer and a retracted scolex, or cysticercus with an invaginated scolex). Two main cestode subclasses are recognized: Cestodaria with decacanth larvae (with 10 hooks) and Eucestoda with hexacanth larvae (with 6 hooks). The Eucestoda are divided into 17 orders on the basis of many morphological and biological differences, many groups being well supported by contemporary molecular characterization studies. Acetabulate orders (with bothridia) include Lecanicephalidea, Tetraphyllidea, Proteocephalidea, Cyclophyllidea, Tetrabothriidea, Phyllobothriidea and Rhinebothriidea; those bearing bothria include Bothriocephalidea, Caryophyllidea, Diphyllidea, Diphyllobothriidea, Haplobothriidea, Spathebothridea and Trypanorhyncha; while others with apical pads/suckers include Cathetocephalidea, Litobothridea and Nippotaeniidea.

Order (+ no. families)	**No. spp.**	**DH[a]**	**Scolex**	**IH1[b]**	**Stage[d]**	**IH2[c]**	**Stage[d]**
Class: **Cestoda** (tapeworms, without gut, monoecious, endoparasites, heteroxenous, predator-prey cycles)							
monozoic (unsegmented)							
Subclass: Cestodaria (adult lacking scolex, larvae decacanth (with 10 hooks))							
Gyrocotylidea (1)	10	F,S,L	muscular sucker-like organ	-	-	-	-
Amphilinidea (1)	8	F,P	muscular proboscis, or absent	C	pro	-	-
Subclass: Eucestoda (‘true’ tapeworms, adult with variable scolex; larvae hexacanth (with six hooks))							
Caryophyllidea (4)	122	F	acetabula, loculi, bothria, apical disc or polymorphic	W	pro		
polyzoic (segmented)							
Cathetocephalidea (1)	6	S	apical pad, papillary band				
Diphyllidea (2)	59	S,R	2 bothria; armed rostellum	C,L	ple		
Trypanorhyncha (16)	315	S,R	2 or 4 bothria, 4 tentacles	C	pro	F,C,L	ple, plc
Litobothridea (1)	9	S	apical sucker, 3-5 segments				
Lecanicephalidea (3)	90	S,R	4 suckers or bothridia, and apical structure or tentacles	C,L,F	pro		
Rhinebothriidea (4)	136	R	4 stalked loculate bothridia	C	pro	F	ple
“Tetraphyllidea’ relics (6)	104	S,R,M	4 stalked bothridia	C	pro	F,L,C, M	ple, mer
Spathebothridea (4)	6	F	undifferentiated or 1-2 bothria	C	ple		
Haplobothriidea (1)	2	F	club-shaped, tentacles, bothria	C	pro	F	ple
Bothriocephalidea (7)	132	F,A	2 bothria	C	pro	F	ple
Nippotaeniidea (1)	6	F	single sucker	C			
Tetrabothriidea (1)	70	B,M	4 muscular bothridia	C,F			
Phyllobothriidea (1)	69	S,R	unarmed bothridia, apical suckers	C,F	ple		
Oncoproteocephalidea (2)	562	F,A,P,S,R	4 loculate bothridia,rostellum	C	pro	F	ple
Diphyllobothridea (6) (= Pseudophyllidea)	70	M,B,P,A	2 shallow bothria, unarmed	C	pro	F,A,P, M	ple
Cyclophyllidea (16) (incl. Mesocestoididae)	3,034	M,B,P	4 suckers, rostellum, often armed	M,A,B, L,T,I	ccc, ccs	-	-

LEGEND
[a] DH = definitive host; [b] IH1 = first intermediate host; [c] IH2 = second intermediate host;
[A = amphibian; B = bird; C = crustacean; F = teleost; I = insect; L = mollusc; M = mammal, P = reptile; R = ray; S = shark; T = acarine; W = annelid];
[d] Metacestode: pro = procercoid, plc = plerocercus; ple = plerocercoid, mer = merocercoid; ccc = cysticercoid; ccs = cysticercus, coenurus, strobilocercus or hydatid cyst

Molecular studies confirmed the order Pseudophyllidea to be paraphyletic so it was recently split into two monophyletic clades: Bothriocephalidea and Diphyllobothridea. Adult bothriocephalidean worms are polyzoic with proglottids wider than long surmounted on a distinctive heart-shaped scolex with 2 prominent bothria. They are endoparasitic in the intestines of vertebrate definitive hosts, usually aquatic animals (fish or amphibians). Over 130 species have been described in 48 genera in 7 families: Ancistrocephalidae, Amphicotylidae, Bothriocephalidae, Echinophallidae, Parabothriocephalidae, Ptychobothriidae and Triaenophoridae. Members of the family Bothriocephalidae are characterized by proglottids possessing a median genital pore, bilobed ovary, testes in 2 lateral fields and eggs containing a coracidium (hexacanth embryo sheathed in a ciliated embryophore). Some 17 genera bothriocephalid genera have been described: *Anantrum, Andycestus, Bothriocephalus, Clestobothrium, Ichthybothrium, Kirstenella, Oncodiscus, Penetrocephalus, Plicatobothrium, Plicocestus, Polyonchobothrium, Ptychobothrium, Regobothrium, Schyzocotyle, Senga, Taphrobothrium* and *Tetracampos*. Most genera are relatively uniform in strobilar morphology and they were often differentiated on the basis of minor differences in scolex morphology. Some of these parasites are also unusual in that their life-cycles involve one (not two) intermediate hosts. They use invertebrates (copepods) as the only intermediate hosts,

whereas diphyllobothridean species use invertebrates as first intermediate hosts and then small vertebrates as second intermediate hosts. This has led to some confusion concerning the terminology applicable to the larval stages, which are metacestode or cercoid stages now considered to be plerocercoids, but were formerly referred to as procercoids. Recent molecular studies have indicated that the family Bothriocephalidae is polyphyletic and in need of revision. Over 20 *Bothriocephalus* species have been described in 2 major clades: one infecting freshwater fish and the other marine fish. The Asian fish tapeworm *B. acheilognathi*, now widespread in ornamental and wild freshwater fish populations, has over 20 synonyms, and recent molecular characterization studies have led to its transfer to the resurrected genus *Schyzocotyle*.

Parasite species	**Definitive hosts [adults in intestines]**	**Intermediate hosts [plerocercoids in tissues]**	**Distribution**
Schyzocotyle (wide heart-shaped scolex, narrow deep bothria)			
S. acheilognathi (Asian fish tapeworm) (syn. *Bothriocephalus acheilognathi, aegypticus*, *barbus, barilii, chelai, clupeoidesii, discusae, elongata, fluviatilis*, *gambusiense, gowkongensis*, *khami, kivuensis*, *maesae, monodi, mystacoleucysi, oitense, opsariichthydis*, *phoxini, phuloi, rectangulum, rojanapaibuli, sinensis, spiraliceps, teleostei*)	Cypriniformes: cyprinid (Amur false gudgeon, bitterling, common bream, common carp, gila longfin dace, grass carp, silver carp, common bleak, Caucasian bleak, Danube bleak, Sellal bleak, Patzcuaro chub, mountain chub, spottail chub, Kura chub, Kura barbel, Balkan barbel, Hamilton's barila, white bream, Aztec chub, white-eye bream, kalabans, bangana, common barbel, Niger barb, Algerian barb, striped bystranka, shabout, pike asp, Mexican stone roller, sevan khramulya, Levantine scraper, longspine scraper, Tigris scraper, sharpray, Mesopotamian himri, goldfish, crucian carp, Prussian carp, dace, ornate shiner, largemouth bronze gudgeon, topmouth culter, blue sucker, gibbous shiner, red shiner, Proserpine shiner, spotfin shiner, blacktail shiner, Cuatro Cienegas shiner, kangal fish,, Amur carp, Manantial roundnose minnow, Devils River fish, roundnose minnow, kanyu, broadstriped barb, rosefin barb, hyphen barb, shortfin barb, papermouth, Neumayer's barb, straightfin barb, threespot barb, suckerhead, Jalisco chub, pale chub, Nazas chub, humpback chub, bonytail chub, headwater chub, arroyo chub, conchos chub, roundtail chub, field gudgeon, goby, gudgeon, naked osman, ussuri sharpbelly, sharpbelly, bighead carp, lake stargazer, predatory carp, common nase, Mesopotamian nase, rohu, smallmouth yellowfish, ripon barbel, Niger barb, largemouth yellowfish, largescale yellowfish, Ethiopian yellowfish, Virgin River spinedace, kissing loach, asp, ide, zeravshan dace, Tigris asp, Aral barbel, Bulatmai barbel, Ankara barbel, mangar, Maghreb barb, mursa, Rebot barbel, Rifian barbel, yellowfin barbel, Yahyaoui barbel, long spikyhead carp, Wuchang bream, black Amur bream, binni, spotted sucker, redmouth sucker, black carp, yellowtail barb, golden shiner, emerald shiner, Balsas shiner, Tamaulipas shiner, yellow shiner, spottail shiner, Chihuahua shiner, Papaloapan chub, Nazas shiner, sand shiner, Topeka shiner, pygmy shiner, mimic shiner, Chinese hooksnout carp, three-lips, white Amur bream, sabre carp, rosy barb, sonnenflek barb, common minnow, bluntnose minnow, fathead minnow, woundfin, fat spring minnow, stone moroko, Colorado pikeminnow, northern pikeminnow, spotted barb, speckled dace, European bitterling, white-finned gudgeon, kutum, common roach, Bloch razorbelly minnow, finescale razorbelly minnow, common rudd, creek chub, Alghad snowtrout, false osman, tui chub, barbel chub, chub, marmara chub, Aegean chub, Mesopotamian pike chub, Sakarya chub, Javean barb, olive barb, bicolor minnow, lantern minnow, tench, Javan mahseer, tor mahseer, bigscaled redfin, vimba, Yangtze gudgeon), cobitid (golden-spined loach), nemacheilid (mottled zipper loach, western crested loach, stone loach,	Copepoda: cyclopid (*Acanthocyclops robustus, A. americanus, Cyclops strenus, C. vicinus, Diacyclops thomasi, Eucyclops agilis, Mesocyclops edax, Paracyclops fimbriatus, Tropocyclops prasinus*)	worldwide

	Tibetan stone loach), catostomid (river carpsucker, white sucker, bluehead sucker, Modoc sucker, gray redhorse), gyrinocheilid (Siamese algae-eater), balitorid (Angoran loach); Cyprinodontiformes: cyprinodontid (Kizilirmak toothcarp, Mezquital pupfish, cachorrito del aquanaval), poeciliid (western mosquitofish, eastern mosquitofish, robust gambusia, blotched gambusia, Gulf gambusia, Yucatan gambusia, twospot livebearer, barred killifish, green swordtail, southern platyfish, highland swordtail, variable platyfish, Pacific molly, shortfin molly, common molly, guppy, golden livebearer, porthole livebearer, Lerma livebearer, Yaqui topminnow), fundulid (plains killifish), profundulid (headwater killifish, Guatemalan killifish, brown spotted killifish, Oaxaca killifish, portillo killifish), goodeid (bulldog goodeid, rainbow goodeid, Picotee goodeid, green goodea, dark-edged splitfin, freckled splitfin, Balsas splitfin, chapultepec splitfin, jeweled splitfin, La Luz splitfin, Patzcuaro allotoca, zacapu allotoca, White River springfish, bold characodon, twoline skiffia, olive skiffia, spotted skiffia); Perciformes: percid (European perch, zander, schraetzer), channid (northern snakehead), cichlid (convict cichlid, sieve cichlid, redside cichlid, threespot cichlid, Madagascar cichlid, Mayan cichlid, Sam Borstein's cichlid, Texas cichlid, curve-bar cichlid, blue tilapia, Mozambique tilapia, Nile tilapia, Bay snook, blue discus, red discus firemouth cichlid, Angosturan cichlid), gobiid (scribbled goby, black goby, monkey goby, round goby, tubenose goby), eleotrid (oopu, western carp gudgeon, flathead gudgeon), centrarchid (green sunfish, pumpkinseed, bluegill, largemouth bass), moronid (white bass), nanid (Gangetic leaffish); Atheriniformes: atherinid (bigscale sand-smelt), atherinopsid (Gulf silverside, Balsas silverside, blackfin silverside, largetooth silverside, slender silverside, pike silverside, bigeye silverside, shortfin silverside, mesa silverside, sharpnose silverside, longjaw silverside, Toluca silverside, Alchichica silverside, La Preciosa silverside, Quechulac silverside); Siluriformes: ictalurid (yellow bullhead, channel catfish), clariid (African sharptooth catfish), claroteid (whitehead catfish), bagrid (Tigris catfish, giant river catfish), silurid (wels catfish, Tigris catfish); Characiformes: characid (banded astyanax, Mexican tetra, cardinal tetra, neon tetra), bryconid (macabi tetra), alestid (African triggerfish); Esociformes: esocid (northern pike); Mugiliformes: mugilid (mullet); Synbrachiformes: synbranchid (Asian swamp eel); Acipenseriformes: acipenserid (Amu Darya sturgeon); Percopsiformes: percopsid (trout-perch); Salmoniformes: salmonid (rainbow trout); Beloniformes: adrianichthyid (Japanese rice fish), belonid (maya needlefish); Osmeriformes: retropinnid (Australian smelt); Urodela: ambystomatid (Patzcuaro salamander); Anura: bufonid (European green toad), hylid (European tree frog), ranid (bigfoot leopard frog, marsh frog, long-legged wood frog); Serpentes: colubrid (blackbelly garter snake); Anseriformes: anatid (mallard); Falconiformes: falconid (sooty falcon); Charadriiformes: sternid (black tern); Pelecaniformes: ardeid (little bittern); Primates: hominid (human)		
S. nayarensis (syn. *Ptychobothrium*)	Cypriniformes: cyprinid (trout barb, common snowtrout)		India
Bothriocephalus (fleshy arrowhead-shaped scolex, weakly-developed apical disc, elongate bothria)			
B. andesi	Pleuronectiformes: citharid (spotted flounder)		Atlantic

B. antarcticus	Perciformes: channichthyid (mackerel icefish)		Indian Ocean
B. apogonis	Kurtiformes: apogonid (cardinalfish)		Pacific
B. atherinae	Atheriniformes: atherinid (bigscale sand smelt)		Atlantic
B. auriculatus (syn. *Anthobothrium*)	Torpediniformes: torpedinid (marbled electric ray)		Atlantic
B. australis	Scorpaeniformes: platycephalid (southern sand flathead)		Australia
B. bengalensis	Perciformes: carangid (barcheek trevally)		Indian Ocean
B. branchiostegi	Perciformes: malacanthid (red tilefish)		Pacific
B. brotulae	Ophidiiformes: ophidiid (goatsbeard brotula)		Pacific
B. carangis	Perciformes: carangid (blue trevally)		Pacific
B. celineae	Perciformes: serranid (golden hind)		Pacific
B. cepolae	Perciformes: cepolid (red bandfish)		Atlantic
B. clavibothrium	Pleuronectiformes: bothid (Mediterranean scaldfish)		Atlantic
B. claviceps (syn. *B. anguillae, Taenia claviceps, T. anguilla*)	Anguilliformes: anguillid (European eel, American eel, sharp-nosed eel, giant mottled eel); Percopsiformes: percopsid (trout-perch); Gasterosteiformes: gasterosteid (threespine stickleback); Perciformes: centrarchid (rock bass, largemouth bass, smallmouth bass, warmouth, green sunfish, longear sunfish, pumpkinseed, bluegill), sciaenid (freshwater drum), percid (sauger)	Copepoda: cyclopid (*Macrocyclops albidus, M. fuscus, Megacyclops viridis, Cyclops strenuus, C. vicinus, Acanthocyclops vernalis*)	Holarctic
B. cuspidatus (syn. *B. musculosus, B. texomensis*)	Perciformes: percid (walleye, Johnny darter, sauger, Iowa darter, yellow perch, common logperch, channel darter), centrarchid (green sunfish, rock bass, pumpkinseed, bluegill, smallmouth bass, largemouth bass), moronid (white bass); Hiodontiformes: hiodontid (goldeye, mooneye); Cichliformes: cichlid (Jack Dempsey); Clupeiformes: clupeid (American gizzard shad); Salmoniformes: salmonid (whitefish, Dolly Varden trout, lake trout); Esociformes: esocid (northern pike, muskellunge); Cypriniformes: cyprinid (emerald shiner); Siluriformes: ictalurid (brown bullhead); Gadiformes: lotid (burbot)		North America
B. euryciensis	Urodela: plethodontid (long-tailed salamander)		North America
B. formosus	Percopsiformes: percopsid (trout-perch); Cypriniformes: cyprinid (creek chub); Perciformes: percid (Iowa darter, Johnny darter, common logperch)		North America
B. gadellus	Gadiformes: morid (beardless codling)		Atlantic
B. japonicus (syn. *B. brachysoma*)	Anguilliformes: anguillid (Japanese eel, giant mottled eel)		Japan
B. kerguelensis	Perciformes: nototheniid (blue rockcod)		Indian Ocean
B. lateolabracis	Perciformes: lateolabracid (Japanese seabass)		Pacific
B. manubriformis (syn. *B. histiophorus*, *B. laciniatus*)	Istiophoriformes: istiophorid (white marlin, Indo-Pacific sailfish); Elopiiformes: megalopid (Atlantic tarpon)		cosmopolitan
B. monticelli	Lampriformes: trachipterid (scalloped ribbonfish)		Atlantic
B. nigropunctatus	Scorpaeniformes: sebastid (rockfish)		Atlantic
B. occidentalis	Scorpaeniformes: sebastid (rockfish)		Atlantic
B. pearsei	Cichliformes: cichlid (Mayan cichlid)		North America
B. rarus	Urodela: salamandrid (eastern newt)		North America
B. sciaenae	Perciformes: sciaenid (white croaker)		Pacific
B. scorpii (syn. *B. bipunctatus, luehei, punctatus, rhombi*)	Scorpaeniformes: cottid (shorthorn sculpin, European bullhead); Pleuronectiformes: scophthalmid (brill)		cosmopolitan
B. suecicus	Salmoniformes: salmonid (Atlantic salmon)		Atlantic
B. tetragonus	Perciformes: anarhichadid (spotted wolffish)		Atlantic
B. timii	Perciformes: bovichtid (Channel bull blenny)		South America
B. travassosi	Anguilliformes: anguillid (giant mottled eel)		Pacific
B. typhlotritonis	Urodela: plethodontid (grotto salamander)		North America

Reassigned *Bothriocephalus* species	Definitive hosts [adults in intestines]	Intermediate hosts [plerocercoids in tissues]	Distribution
B. abyssmus (now *Andycestus*)	Perciformes: zoarcid (eelpout)		Atlantic
B. belones (syn. *B. restiformis*) (now *Ptychobothrium*)	Beloniformes: belonid (Atlantic needlefish)		Europe
B. bicolor (now *Tentacularia coryphaenae*)	Scombriformes: scombrid (skipjack tuna)		
B. cestus (syn. *Dibothrium*) (now *Eubothrium*)	Salmoniformes: salmonid (char)		North America
B. claviger (now *Hepatoxylon trichuri*)	Carangiformes: coryphaenid (mahi-mahi)		North America
B. coniceps (now *Diphyllobothrium schistochilus*)	Carnivora: phocid (bearded seal)		Arctic Ocean
B. cordatus (now *Diphyllobothrium*)	Carnivora: canid (dog)		Europe
B. cordiceps (now *Dibothriocephalus dendriticus*)	Salmoniformes: salmonid (brook trout)		North America
B. corollatus (now *Nybelinia lingualis*)	Rajiformes: rajid (common skate)		Atlantic
B. coronatus (now *Acanthobothrium*)	Torpediniformes: torpedinid (marbled electric ray)		Europe
B. crassiceps (now *Clestobothrium*)	Gadiformes: merlucciid (European hake)		Europe
B. cristatus (now *Dibothriocephalus latus*)	Primates: hominid (human)		
B. dalmatinus (now *Fistulicola plicata*)	Zeiformes: zeid (John Dory)		Europe
B. dendriticus (now *Dibothriocephalus*)	Charadriiformes: larid (black-legged kittiwake)		North America
B. didelphidis (syn. *Diphyllobothrium*) (now *Spirometra*)	Didelphimorphia: didelphid (big-eared opossum)		South America
B. ditremus (now *Dibothriocephalus*)	Gaviiformes: gaviid (common loon); Anseriformes: anatid (red-breasted merganser)		Europe
B. dubius (now *Diphyllobothrium tetrapterum*)	Carnivora: canid (dog)		Iceland
B. elegans (now *Diphyllobothrium*)	Carnivora: phocid (hooded seal)		Europe
B. ellipticus (now *Abothrium gadi*)	Gadiformes: gadid (Atlantic cod)		Atlantic
B. eriocis (now *Eubothrium crassum*)	Salmoniformes: salmonid (brown trout)		North America
B. fasciatus (now *Diphyllobothrium tetrapterum*)	Carnivora: phocid (ringed seal)		Europe
B. felis (now *Spirometra erinaceieuropaei*)	Carnivora: felid (cat)		Europe
B. fuscus (now *Dibothriocephalus latus*)	Carnivora: canid (dog)		Iceland
B. ganapatti (syn. *B. penetratus*) (now *Penetrocephalus*)	Aulopiformes: synodontid (greater lizardfish)		Indian Ocean
B. heteropleurus (now *Amphicotyle*)	Scombriformes: centrolophid (black ruff)		Pacific
B. indicus (now *Oncodiscus sauridae*)	Aulopiformes: synodontid (greater lizardfish)		Indian Ocean

B. janickii (now *Plicocestus*)	Perciformes: coryphaenid (dolphinfish)		Indian Ocean
B. lanceolatus (now *Diphyllobothrium lanceolatum*)	Carnivora: phocid (bearded seal)		Greenland
B. liguloides (now *Spirometra erinaceieuropaei*)	Primates: hominid (human)		Japan
B. lonchinobothrium (now *Echinophallus*)	Perciformes: coryphaenid (dolphinfish)		Indian Ocean
B. maculatus (now *Spirometra erinaceieuropaei*)	Carnivora: felid (leopard)		Africa
B. mansoni (now *Spirometra*)	Primates: hominid (human)		China
B. microcephalus (syn. *B. monorchis*) (now *Anchistocephalus*)	Tetraodontiformes: molid (ocean sunfish)		Europe
B. neglectus (now *Clestobothrium*)	Gadiformes: gadid (tadpole fish)		Atlantic
B. osmeri (now *Dibothriocephalus ditremus*)	Osmeriformes: osmerid (European smelt)		Europe
B. peltocephalus (now *Echinobothrium*)	Scombriformes: centrolophid (Imperial blackfish)		Atlantic
B. pilula (now *Clestobothrium crassiceps*)	Gadiformes: merlucciid (European hake)		Europe
B. platycephalus (now *Australicola*)	Beryciformes: berycid (alfansino)		Pacific
B. plicatus (now *Fistulicola*)	Istiophoriformes: xiphiid (swordfish)		Pacific
B. polycalceolus (now *Diphyllobothrium hians*)	Carnivora: phocid (harbour seal)		Atlantic
B. polypteri (now *Polyoncobothrium*)	Anabantiformes: channid (striped snakehead); Cypriniformes: cyprinid (rohu)		India
B. proboscideus (now *Eubothrium crassum*)	Salmoniformes: salmonid (Atlantic salmon)		Atlantic
B. prudhoei (now *Kirstenella gordoni*)	Siluriformes: clariid (mudfish)		Africa
B. pycnomerus (now *Senga*)	Anabantiformes: channid (bullseye snakehead)		India
B. quadratus (now *Diphyllobothrium quadratum*)	Carnivora: phocid (leopard seal)		Southern Ocean
B. ratticola (now *Spirometra*)	Rodentia: murid (black rat)		Asia
B. reticulatus (now *Dibothriocephalus latus*)	Carnivora: canid (dog)		Europe
B. sagittatus (now *Anchistrocephalus microcephalus*)	Tetraodontiformes: molid (ocean sunfish)		Europe
B. schistochilos (now *Diphyllobothrium*)	Carnivora: phocid (bearded seal)		Europe
B. solinosomum (syn. *B. centrolophipompilii*) (now *Bothriocotyle*)	Scombriformes: centrolophid (black ruff)		Pacific, Atlantic
B. taenioides (now *Dibothriocephalus latus*)	Primates: hominid (human)		Europe
B. tectus (syn. *Baylisiella tecta*) (now *Diphyllobothrium lashleyi*)	Carnivora: phocid (southern elephant seal)		Southern Ocean
B. tetrapterus (now *Diphyllobothrium tetrapterum*)	Carnivora: phocid (harbour seal)		Europe
B. variabilis (now *Diphyllobothrium tetrapterum*)	Carnivora: phocid (harp seal)		Europe
B. wagneri (now *Echinophallus*)	Scombriformes: centrolophid (black ruff)		Pacific
B. zschokkei (now *Schistocephalus pungitii*)	Gasterosteiformes: gasterosteid (ninespine stickleback)		Eurasia

A number of other species have been named but subsequent revisions have disputed their identity: either as *species inquirena* (species of doubtful identity requiring further investigation): *B. alessandrinii* (from river trout), *B. affinis* (from red scorpionfish), *B. angustatus* (from red scorpionfish), *B. angusticeps* (from rose fish), *B. bramae* (from Atlantic pomfret), *B. breviceps* (from cutthroat eel), *B. capillicollis* (from Ballan wrasse, ide), *B. columbae* (from pigeon), *B. granularis* (from carp), *B. hirondellei* (from sargassum pipefish), *B. labiatus* (from Atlantic pomfret), *B.labracis* (from European bass), *B. levinseni* (from lumpfish), *B. longispiculus* (from crake), *B. lophii* (from angler monkfish), *B. macrobothrium* (from scalloped ribbonfish), *B. marietani* (from water rail), *B. minutus* (from greater pipefish), *B. motellae* (from fourbeard rockling), *B. palumbi* (from piper gunard), *B. parvus* (from lesser sand eel), *B. pusillus* (from rock partridge), *B. salvelini* (from Arctic char), *B. sauridae* (from clouded lizardfish), *B. schilbeodis* (from easterm madtom), *B. sciuri* (from fox squirrel), *B. similis* (from arctic fox), *B. speciosus* (from tesellated darter), *B. spinachidae* (from sea stickleback), *B. squali* (from blue shark), *B. tintinnabulus* (from dragonet), *B. trachypteri* (incl. *B. trachypteri-iris*, *B. trachypteri-liopteri*) (from Mediterranean dealfish, ribbonfish) and *B. vallei* (from red mullet); or as *nomen dubium* (doubtful name): *B. barbatulae* (from stone loach), *B. barbatus* (from brill), *B. funiculus* (from fivebeard rockling); *B. gregarius* (from turbot), *B. sinensis* (from long spiky-head carp), and *B. ursi* (from brown bear).

Parasite morphology: Bothriocephalid parasites form 3 developmental stages: eggs, larvae (cercoids) and adult tapeworms. The eggs are ovoid in shape measuring from 32-63 µm in length by 21-41 µm in width. They are thick-walled with an operculum (10-11 µm wide) at the narrower pole and are unembryonated when laid. Embryonated eggs contain a coracidium consisting of a hexacanth (6-hooked) embryo (oncosphere) surrounded by a ciliated envelope (embryophore). Cercoid larvae are alacunate (without internal cavities) and vary considerably in size growing from small ovoid stages some 30 µm in diameter to larger elongate stages measuring up to 380 µm long by 140 µm wide. Early stages sometimes possessed knob-like tails (cercomers) containing remnants of embryonic hooks (thus resembling procercoids), but the cercomers were soon lost as the larvae matured and developed anterior indentations and an everted scolex (thus better conforming to descriptions of plerocercoids). Adult tapeworms have long ribbon-like bodies ranging in size depending not only on parasite species but also host species, host size, host age, intensity of infection and possibly prevailing ecological conditions. Most species grow to a length of 3.5-8.0 cm, but some species may reach 60-100 cm. They have an elongate anterior scolex (0.4-1.4 mm long) immediately giving rise to flattened segments (proglottids). The scolex has a distinctive arrowhead shape and is fleshy being wider than the first body segments. The scolex is unarmed but possesses a weakly-developed apical disc measuring 100-200 µm wide and 2 elongate anterolaterally-directed attachment grooves (bothria) with non-crenulate margins. The genus *Schyzocotyle* has been resurrected mostly on the basis of molecular evidence, although its 2 cognate species are considered to be morphologically characterised by the occurrence of a wide heart-shaped scolex with narrow deep bothria. The strobila of both genera is comprised firstly of immature segments (lacking fully developed genitalia) that are wider than long, then mature segments (with developed genitalia) and gravid segments (containing eggs) that are rectangular and longer than wide. Adult worms are hermaphroditic with proglottids containing one set of male and female reproductive organs. Proglottids contain numerous spherical testes in 2 lateral medullary fields, and a muscular cirrus sac that opens into a common genital atrium. They also contain numerous corticular vitelline follicles, a bilobed ovary, a short sinuous vagina that opens into the common genital atrium, and a saccular uterus that opens to a dorso-median uterine (birth) pore from which eggs are released.

Site of infection: Infections by adult tapeworms occur in the small intestines of their piscine definitive hosts, while procercoid larvae develop in the body cavities of their copepodid intermediate hosts.

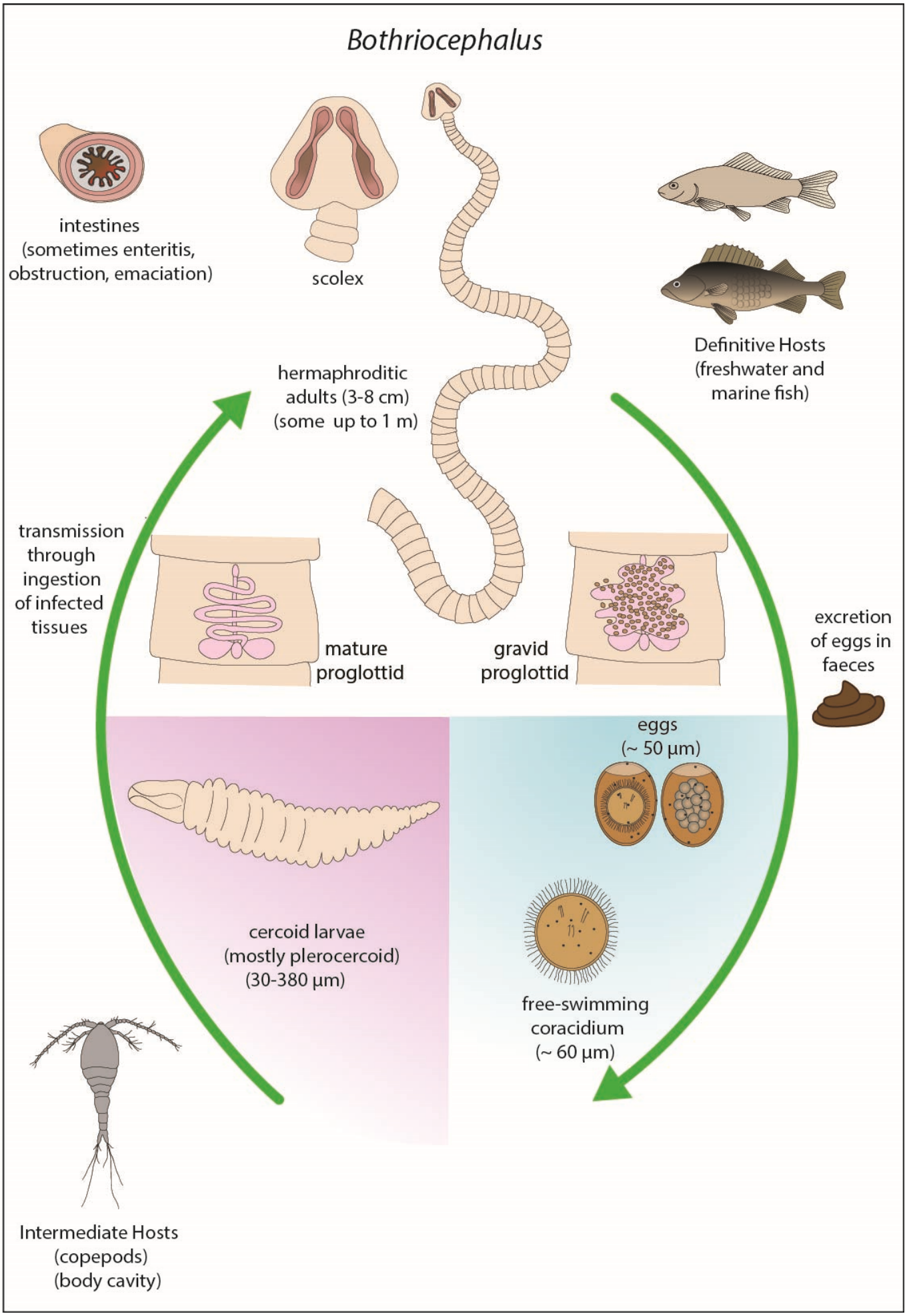
Pathogenesis: Tapeworms attach to the wall of the anterior small intestines, just posterior to the bile duct. Adult worms lack digestive tracts and do not feed on host tissues but absorb nutrients from the gut lumen. Nonetheless, infections can cause significant pathology, not only at their sites of attachment, but also posteriad where their presence may perturb gut function. Attachment of the worm produces an inflammatory response, leading to desquamative catarrhal enteritis, necrosis, haemorrhage, ulceration, fibrosis, increased mucus production, and degeneration of the intestinal wall with extensive destruction of villi. Heavy tapeworm burdens (or the presence of large tapeworms) may block the intestinal tract causing severe distention, congestion, compression, pressure necrosis, mucosal atrophy, perforation and death. Occluded organs often become grossly enlarged, very thin-walled and stretched to the point of transparency, revealing the presence of squirming white worms. Clinical signs in affected fish vary greatly depending on the site and extent of infection, most often including inappetence, weight loss, slow growth, loss of condition, emaciation, anaemia, and mortality (especially in juveniles). Other internal organs may also be affected, particularly the gall bladder becoming swollen and turgid, and the liver exhibiting signs of hepatocyte atrophy contributing to nutritional deficiencies, in some cases consistent with starvation. Infected fish may also become more susceptible to secondary bacterial infections. The Asian fish tapeworm (*S. acheilognathi*) presents significant problems to cyprinid aquaculture by causing severe damage to the intestinal tracts of young fish, physiological disturbances (protein depletion, altered digestive enzyme activity, elevated muscle fatigue), reduced growth, loss of condition and mortality (sometimes as high as 100% in hatchery ponds).

Developmental cycle and mode of transmission: Bothriocephalid tapeworms have indirect heteroxenous (2-host) life-cycles, alternating between adult stages in fish (definitive hosts) and larval stages in copepods (intermediate hosts). Unembryonated eggs

are passed in host faeces into water where they embryonate over several days (1-28 days depending on water temperature, longer in colder water). The eggs hatch releasing a ciliated coracidium which swims sporadically in the water attracting the attention of zooplanktonic crustaceans, in this case cyclopoid copepods. Coracidia eaten by copepods shed their ciliated embryophore and the oncosphere penetrates the gut and forms plerocercoid larval stages within the body cavity over 6-12 days. When infected copepods are eaten by fish definitive hosts, the plerocercoids attach to the gut wall and develop into adult tapeworms over 20–23 days. Gravid segments produce and shed eggs which are passed in host faeces. While fishes normally become infected by eating infected copepods, there is some evidence that adult worms may be transmitted directly to piscivorous fishes (a phenomenon known as postcyclic transmission). Several experiments have implicated aquatic birds in the spread of infections, although they may simply eat infected fish and spread worm eggs with their faeces. The Asian fish tapeworm (*S. acheilognathi*) has spread widely throughout the world from East Asia due to many translocations of fish for aquaculture, ornamental and bait fish supply, aquatic weed control, and even mosquito control. Many patterns of infection have been observed, particularly intermittent and seasonal patterns with peak incidence in summer.

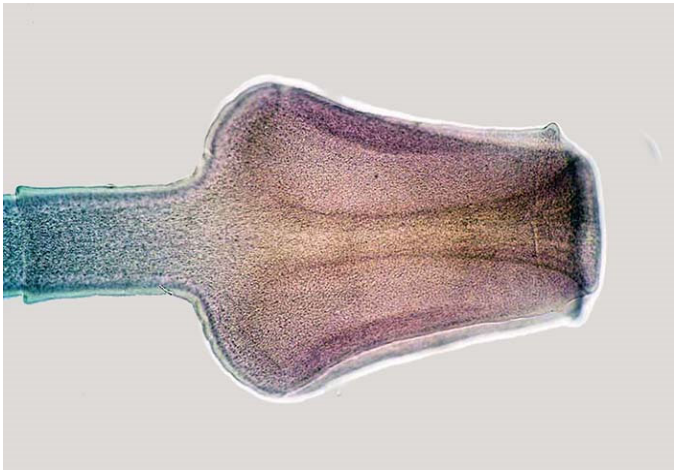
Differential diagnosis: Infections may be diagnosed ante-mortem by the microscopic detection of worm eggs in faecal samples, but are most often diagnosed post-mortem by the detection of adult worms in dissected gut samples. Mature worms are usually conspicuous within the intestines of infected fish, but the presence of plerocercoid larvae or juvenile immature worms is best facilitated by the microscopic examination of mucosal scrapings, washes or squash preparations. More recently, molecular techniques have been used to characterize species following polymerase chain reaction (PCR) amplification of nuclear (18S ribosomal RNA) and mitochondrial (cytochrome c oxidase subunit 1 (cox1), large subunit (16S) mitochondrial rRNA (rrnL)) genes.

Treatment and control: Infections in fish have been treated with various anthelmintic drugs exhibiting cestodicidal activity, notably the isoquinoline (praziquantel) applied as a bath or given orally (mixed in fish food with oil), but also including the inhibitory salicylanilide (niclosamide) and the purgative halogenated hydrocarbon (butynorate). Various natural products have also shown some limited efficacy; including infusions of lupin seeds, conifer needles, tobacco dust and horse radish leaves. A wide range of preventive measures have been developed in attempts to curb the worldwide spread of infections. Many governments have introduced legislation within the aquaculture and aquarium trades for the screening, impoundment, treatment and quarantine of live fish and broodstock. Various industry recommendations have also been made to modify management practices designed to reduce the likelihood of transmission of parasites to juvenile fish, particularly with respect to providing clean holding facilities, reducing overstocking stress, and reducing copepod intermediate host populations by water treatment (filtration, disinfection) or pond management (draining, drying, liming). Several experiments were also conducted using insecticides to reduce copepod populations, but their overt use should be curtailed due to environmental and health concerns.

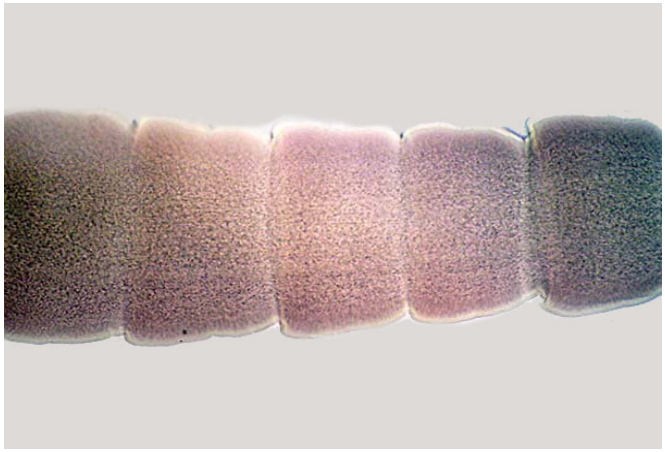

Bothriocephalus
intestines
(sometimes enteritis,
obstruction, emaciation)
scolex
Definitive Hosts
(freshwater and
marine fish)
hermaphroditic
adults (3-8 cm)
(some up to 1 m)
transmission
through
ingestion
of infected
tissues
mature
proglottid
gravid
proglottid
excretion
of eggs in
faeces
eggs
(~ 50 µm)
cercoid larvae
(mostly plerocercoid)
(30-380 µm)
free-swimming
coracidium
(~ 60 µm)
Intermediate Hosts
(copepods)
(body cavity)



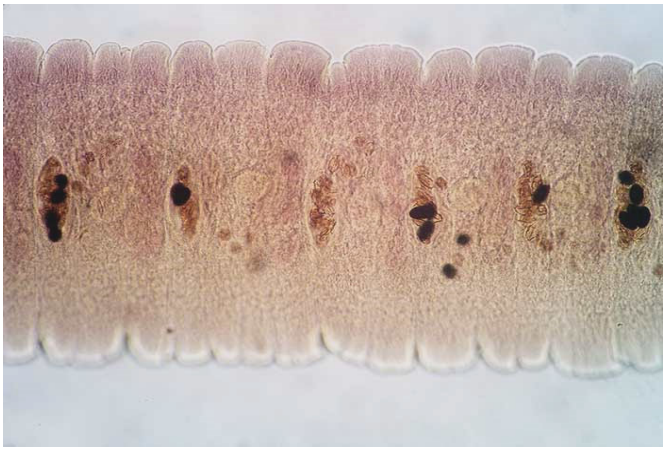
Bothriocephalus scolex



Bothriocephalus scolex



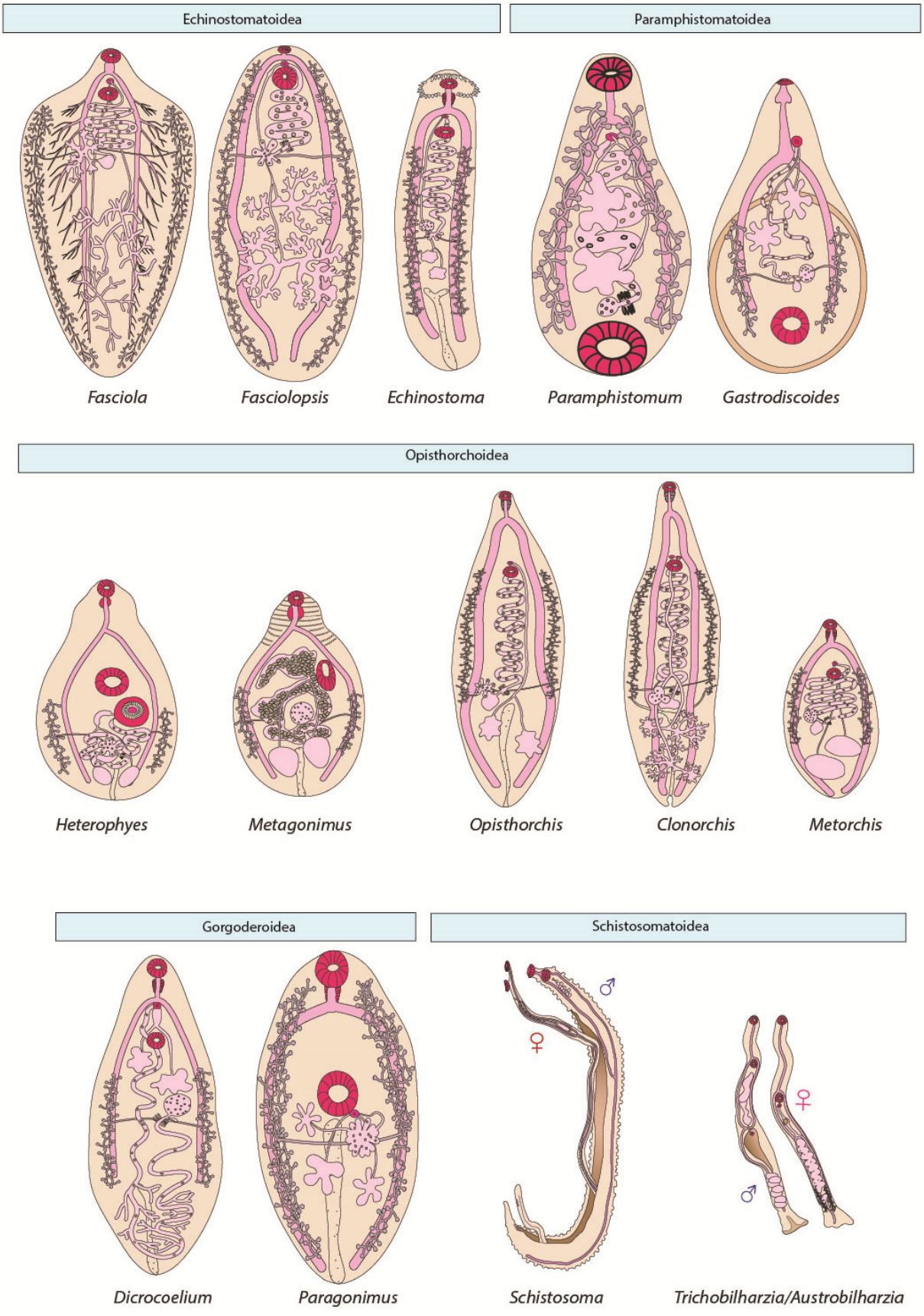
Bothriocephalus segments

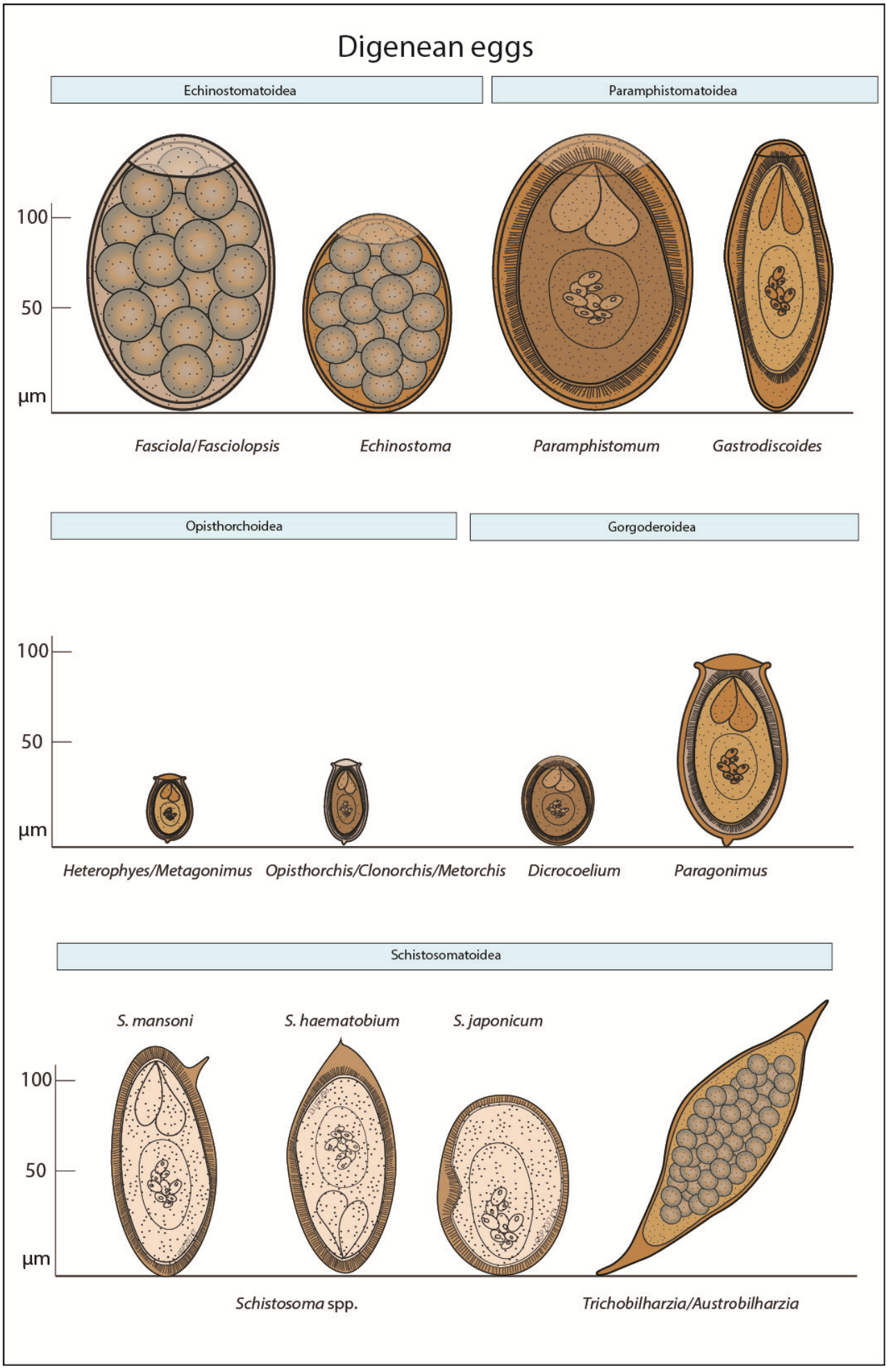


Bothriocephalus segments

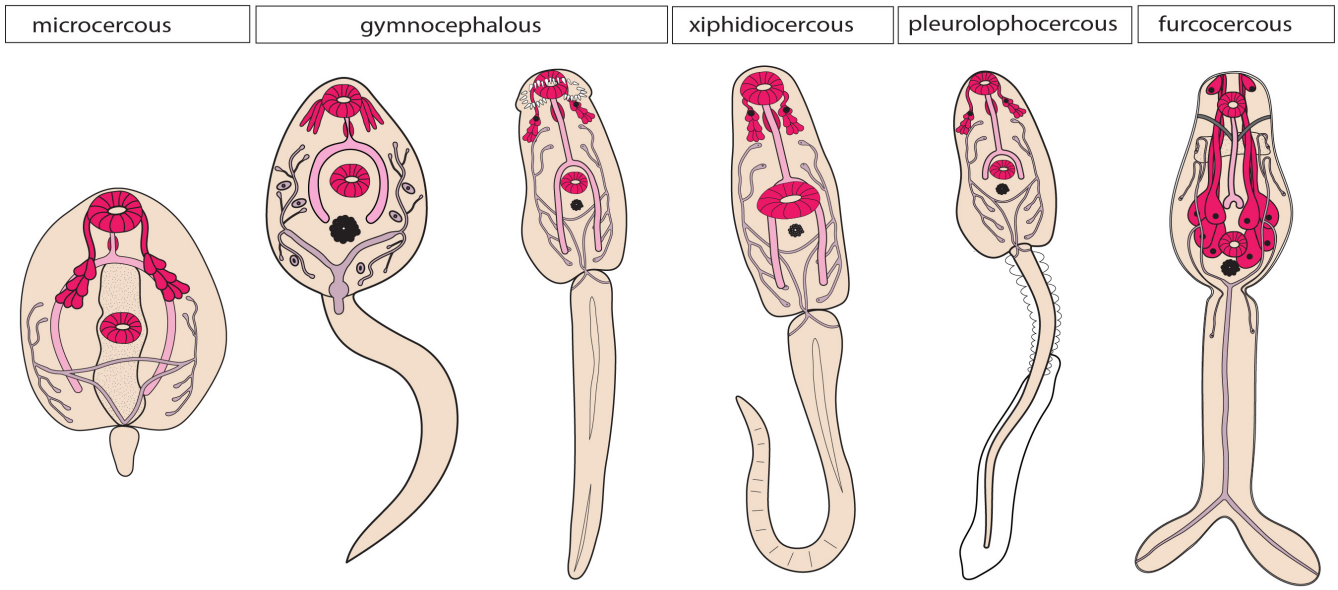
Trematoda
(digenetic flukes)

Digenean adult flukes




Digenean eggs
Echinostomatoidea
Paramphistomatoidea
100
50
µm
Fasciola/Fasciolopsis
Echinostoma
Paramphistomum
Gastrodiscoides
Opisthorchoidea
Gorgoderoidea
100
50
µm
Heterophyes/Metagonimus
Opisthorchis/Clonorchis/Metorchis
Dicrocoelium
Paragonimus
Schistosomatoidea
S. mansoni
S. haematobium
S. japonicum
100
50
µm
Schistosoma spp.
Trichobilharzia/Austrobilharzia

Cercariae of digenean trematodes



Paragonimus

Fasciola
Fasciolopsis
Paramphistomum
Gastrocoides

Echinostoma

Dicrocoelium

Opisthorchis
Clonorchis
Metorchis
Heterophyes
Metagonimus

Schistosoma
Trichobilharzia

Fasciola
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies, oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult echinostomatids often have well-developed scales or spines on the anterior tegument and the ventral sucker is near the oral sucker. Fasciolids occur as large flukes in the livers of herbivores and infections by *Fasciola* spp. cause chronic debilitating hepatic diseases in domestic ruminants, and sometimes humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Plagiorchiida (‘echinostomatids’, plagiorchiids’, mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder:	Echinostomata (miracidium penetrates gastropod IH, redia formed, simple-tailed cercariae, encysts in open or in second IH, metacercariae eaten by DH)
Superfamily:	Echinostomatoidea (slender worms, adult with scales or spines)
Family:	Fasciolidae (large leaf-shaped flukes, in herbivores, conical anterior end, ventral sucker at level of shoulders)
Genus:	*Fasciola* (parasitic in liver of mammals)
Species:	*F. hepatica* (causes hepatic fibrosis in ruminants and humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs, fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of

their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. The suborder Echinostomata contains one superfamily Echinostomatoidea whose members have simple-tailed cercariae that encyst in the open or in second intermediate hosts and the resultant metacercariae are eaten by definitive hosts. Ten families are recognized (Calycodidae, Cyclocoelidae, Echinostomatidae (including Echinochasmidae), Eucotylidae, Fasciolidae, Himasthlidae, Philophthalmidae, Psilostomidae, Rhytidodidae, and Typhlocoelidae). By far the most clinically important family is the Fasciolidae which contains 6 genera (*Fasciola, Fasciolopsis, Fascioloides, Parafasciolopsis, Protofasciola* and *Tenuifasciola*). These are large (sometimes up to several

cm long) leaf-shaped flukes that infect the liver, gall bladder and intestines of herbivores and undergo asexual development in freshwater snails from the superfamily Lymnaeoidea. Two main *Fasciola* spp. are widely distributed and abundant throughout many sheep and cattle producing areas around the world, particularly temperate regions with high rainfall or irrigated pastures where snail vectors are common. *F. hepatica* has been reported in sheep, cattle, goats, pigs, macropods, rats, rabbits and many other animals, including humans (mainly from western Europe, northern Africa and South America). More than 2 million people are thought to be infected from over 60 countries, and over 180 million people are considered to be at risk of infection. *F. gigantica* is found mostly in cattle and buffalo in tropical regions, including parts of Africa, India and South-East Asia. It has been estimated that some 250 million sheep and 350 million cattle are at risk of fascioliasis. Another species *F. jacksoni* has been described from the livers of elephants in India, Burma and Malaysia, but recent molecular studies have transferred the species to the genus *Fascioloides*. Likewise, many fasciolid infections in deer have now been attributed to the pathogenic species *Fascioloides magna* (giant liver fluke, deer fluke). Some workers have grouped the genera *Fasciola* and *Fascioloides* into the subfamily Fasciolinae on the basis of shared morphotypic characters (cephalic cone, branched intestinal caeca, dendritic testes and ovaries), tissue tropism (bile ducts or liver parenchyma of definitive hosts) and intermediate host specificity (lymnaeid snails).

Parasite species	Definitive hosts [adults in bile ducts of liver]	Intermediate hosts [sporocysts/rediae in tissues]	Infective stages	Distribution
Fasciola				
F. hepatica (syn. *Planaria latiuscula, Distoma hepaticum, F. humana, F. lanceolata*) (common liver fluke, sheep liver fluke)	Artiodactyla: bovid (sheep, goat, cattle, buffalo, bison), cervid (mule deer, black-tailed deer, white-tailed deer, sika deer, fallow deer, red deer, roe deer, moose), camelid (camel), suid (pig); Proboscidea: elephantid (elephant); Perissodactyla: equid (horse, donkey); Lagomorpha: leporid (rabbit, jackrabbit, cottontail, European hare, mountain hare, snowshoe hare); Rodentia: castorid (beaver), echimyid (coypu); occasionally Primates: hominid (human)	amphibious Gastropoda: lymnaeid (*Austropeplea* (*Lymnaea*) *tomentosa, A.* (*L.*) *viridis, A. ollula, Fossaria* (*L.*) *viatrix/viator, F.* (*L.*) *diaphana, F. cubensis, F. bulimoides, Galba* (*L.*) *truncatula, Lymnaea cousini, L. cubensis, L. diaphana, L. humilis, L. neotropica, L. occulta, L. palustris, L. stagnalis, Omphiscola glabra, Potamopygrus antipodarum, Pseudosuccinea* (*L.*) *columella, Radix auricularia, R. balthica, R. lagotis, R. natalensis, R. peregra, R. rubiginosa, Stagnicola caperata, S. fuscus, S. palustris, S. turricula, Succinea*)	metacercariae on herbage	worldwide
F. gigantica (syn. *Distomum giganteum, Fasciola gigantea*) (tropical large liver fluke)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, blue wildebeest, sassaby, waterbuck, kob, puku, hartebeest), cervid (deer), suid (pig), camelid (camel), giraffid (giraffe), hippopotamid (hippopotamus); Perissodactyla: equid (horse, donkey, mule); Lagomorpha: leporid (rabbit); occasionally Primates: hominid (human)	aquatic Gastropoda: lymnaeid (*Radix auricularia, R. luteola, R.* (*Lymnaea*) *natalensis, R. peregra, R. rubiginosa, R. gedrosiana, Austropeplea* (*L.*) *tomentosa, A. ollula, A. viridis, Galba* (*L.*) *truncatula, Lymnaea acuminata, L. cailliaudi, L. rufescens, Pseudosuccinea* (*L.*) *columella*)	metacercariae on herbage	Africa, Asia, Europe, North America
F. nyanzae	Artiodactyla: hippopotamid (hippopotamus)	unknown		Africa
Fascioloides				
Fa. magna (syn. *Distomum magnum, D. texanicum, Fasciola magna, Fasciola carnosa, Fasciola americana*) (giant liver fluke, large American liver fluke, deer fluke)	Artiodactyla: cervid (black-tailed deer, white-tailed deer, mule deer, wapiti, caribou, moose, fallow deer, red deer, roe deer, sika deer, sambar), bovid (cattle, yak, buffalo, bison, sheep, bighorn sheep, goat, chamois, nilgai), camelid (llama), suid (pig), tayassuid (collared peccary); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig)	aquatic Gastropoda: lymnaeid (*Lymnaea trunculata, L. palustris*)	metacercariae on herbage	North America. Europe
Fa. jacksoni	Proboscidea: elephantid (Asiatic elephant)	unknown		India, Pakistan, Burma, Malaysia

Protofasciola				
P. robusta	Proboscidea: elephantid (African elephant)	unknown		Africa
Tenuifasciola				
T. tragelaphi	Artiodactyla: bovid (sitatunga)	unknown		Africa

Many putative *Fasciola* species have also been recorded from fish: including *F. alosae*, *F. appendiculata* and *F. halecis* from herring; *F. polymorpha* from eels; *F. bramae* and *F. transversalis* from cyprinids; *F. bramae* and *F. gibbosa* from pike; *F. aeglefini* and *F. scabra* from gadids; *F. crenata* from sticklebacks; *F. bramae, F. coryphaenae*, *F. fusca*, *F. lagena*, *F. luciopercae, F. tereticollis* and *F. blennii* from perch, bream and dolphinfish; *F. atomon* and *F. platessae* from flounder and plaice; *F. eriocis, F. farionis*, *F. truttae*, *F. umblae* and *F. varica* from salmon, char and trout; and *F. clavata* and *F. scorpii* from bonito and sculpins (most piscine species subsequently assigned to other trematode genera, incl. *Allocreadium*, *Crepidostomum*, *Dendrocoelum*, *Distoma*, *Podocotyle* and *Spaherostoma*); several species have been reported from birds: including *F. anatis* from ducks, *F. ardeae* from heron, *F. bilis* from falcons, *F. buteonis* from buzzards, *F. denticulata* from terns, *F. elegans* from finches, *F. gruis* from cranes, and *F. milvi* from kites (all avian species assigned to the genus *Distoma*); and one species has even been recorded from reptiles (*F. colubri* from colubrid snakes).

Parasite morphology: These flatworms form 7 different developmental stages: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae, and adult flukes. The eggs are brown, ovoid and operculate (with a 'hatch' at one end). *F. hepatica* eggs are 130-150 µm in length by 63-90 µm in width, while those of *F. gigantica* are 156-197 µm long by 80-104 µm wide. Miracidia are pyriform motile larval stages (150-200 µm long) covered with cilia and they have apical papillae, glands and two pigmented eyespots. Sporocysts are pleomorphic sac-like bodies (0.3-1.5 mm in diameter) covered with a thin tegument and containing germinal cells which give rise to rediae (embryos). Rediae are elongate (1-2 mm long) with muscular collars and ventral processes (lappets or procruscula). Mature cercariae (~0.5 mm long) are free-swimming stages with simple elongate club-shaped tails. The body has rudimentary organs, including suckers (oral and ventral), a bifurcated digestive system, excretory bladder and genitalia (this cercarial form is known as 'gymnocephalous'). The cercariae swim to aquatic vegetation where they shed their tails and encyst to form membrane-bound metacercariae (~ 0.2 mm in diameter). Mature flukes are dorsoventrally flattened and leaf-shaped with a conical apex demarcated by wider 'shoulders'. *F. hepatica* adults are 2.0-3.5 cm long by 0.8-1.5 cm wide, while those of *F. gigantica* are 2.5-7.5 cm long by 0.5-1.2 cm wide. The tegument is covered with scaly spines, and they have two suckers (distome arrangement with the oral and ventral suckers close together). They have a bifurcate blind gut and each worm is hermaphroditic, possessing both male and female reproductive organs.

Site of infection: Immature flukes undergo transient migration through the liver parenchyma and then settle as mature flukes in the bile ducts of their mammalian definitive hosts. In some (uncommon) hosts, aberrant flukes may be found encapsulated in lungs, skin or other organs. In snail intermediate hosts, several asexual multiplicative stages are formed; sporocysts first developing in tissues near the site of penetration (foot, antenna, gill), rediae then migrating to glandular tissue (hepatopancreas and gonads) and culminating in the emergence of tailed cercariae.

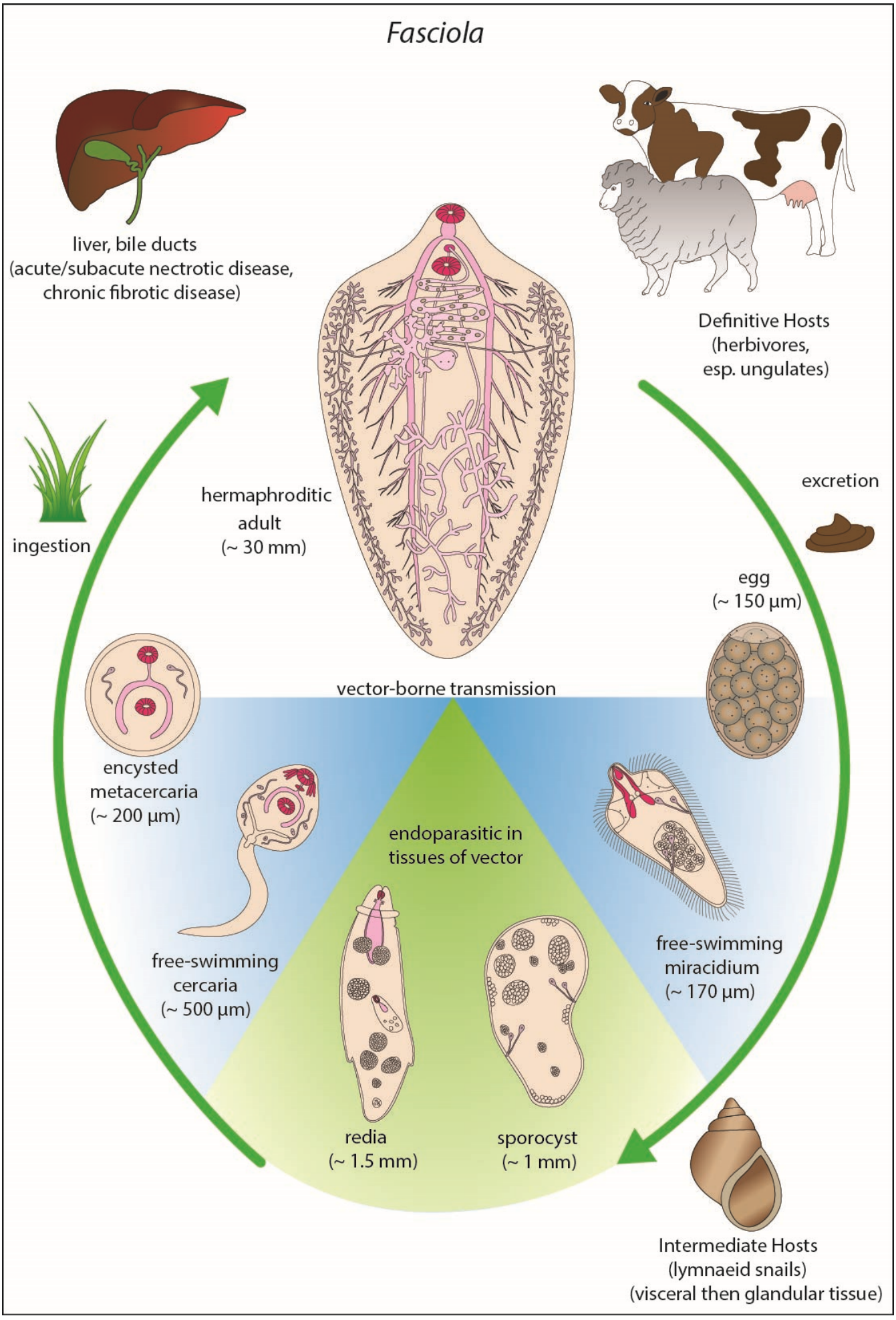
Pathogenesis: Infections are associated with 2 types of liver disease in domestic animals: acute or subacute necrotic disease due to juvenile flukes (parenchymal (migratory) phase of infection); and chronic fibrotic disease due to adult flukes (biliary phase of infection). Penetration of the liver capsule by immature flukes generally does not cause much damage, but their subsequent migration through the liver parenchyma may cause significant necrosis (liver rot), bile duct degeneration and acute verminous hepatitis. Mass migration of juveniles may produce extensive traumatic tissue damage, coagulative necrosis, haemorrhage, anaemia, hepatomegaly, urticaria, eosinophilia, leucocytosis, jaundice, pallor, ascites, fever, vomiting, diarrhoea, abdominal pain and can be fatal. Acute infections in sheep can also be complicated by secondary bacterial infection causing clostridial necrotic hepatitis ('black disease'). Chronic infections by the long-lived spiny adults living and feeding in the bile ducts may result in progressive loss of condition with biliary epithelial hyperplasia, biliary colic, cholecystitis, bile duct calcification, duct obstruction, cirrhosis, cholangitis, jaundice, anaemia, hepatomegaly and eventually a fibrotic hardened liver. Interference with protein metabolism and loss of protein from the ducts leads to hypoproteinaemia. Infections have also been associated with abdominal pain, nausea, pruritus, cardiac disorders, pancreatitis and fatty food intolerance. Occasionally, ectopic infections have been reported involving the peritoneal cavity, intestinal wall, lungs, lymph nodes, subcutaneous tissues and eyes. Sheep develop hypochromic macrocytic anaemia with eosinophilia and become emaciated developing submandibular oedema (bottle-jaw) and ascites. In cattle, the bile ducts become fibrotic and sometimes calcified producing a 'clay-pipe' or 'pipe-stem' liver. Chronic fascioliasis causes significant economic losses to many animal industries through mortality, general ill-thrift, debilitation, scouring, reduced meat, milk and fibre production, condemned livers, secondary infections and expensive treatments. Infected animals develop little in the way of protective immunity but continue to accumulate flukes as long as they graze infected pasture. However, some host species and breeds appear to be more resistant or resilient to infections than others; e.g. buffalo calves are more resistant to *F. gigantica* than *Bos indicus* breeds.

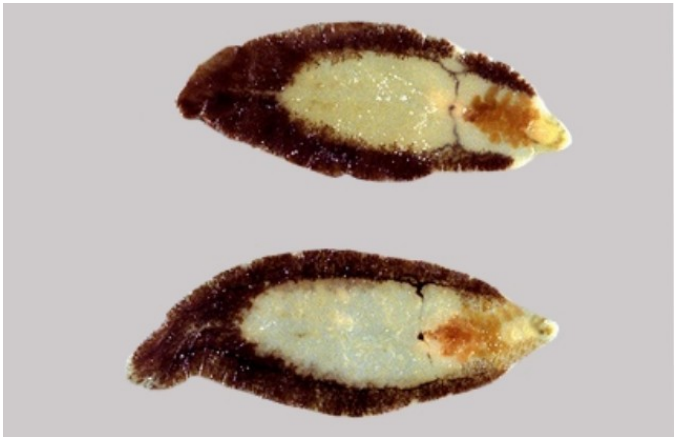
Developmental cycle and mode of transmission: Digenean trematodes have indirect life-cycles, involving mammalian definitive hosts and molluscan intermediate hosts. Transmission between the two hosts occurs within water, via the formation of motile and encysted larval stages. Adult flukes may live for several years in their hosts and they produce hundreds to thousands of eggs each day which pass out of the liver in bile and are shed in host faeces. The eggs embryonate in water in a few days to form miracidia which hatch out in 9-10 days in warm weather (longer when colder). Miracidia actively seek snail hosts by chemotaxis, and must penetrate snail tissues (usually through the foot) within a few hours or die after 24 hours. *F. hepatica* exhibits high intermediate host-specificity and will only develop in freshwater amphibious lymnaeid snails. These snails are pulmonate (with lungs), small (0.5-2.5 cm long) and delicate; their shells being thin, fragile, lacking an operculum and the apertures located on the right-hand side (dextral). They live in freshwater and/or wet soils and survive dry periods by burrowing and aestivating (parasites can survive for months in aestivating snails). Various lymnaeid genera and species (whose classification is undergoing considerable revision) are suitable intermediate hosts; the most common vectors for *F. hepatica* being *Galba* (*Lymnaea*) *truncatula* in most continents, *Austropeplea* (*L.*) *tomentosa* in Australia, *A.* (*L.*) *viridis* in China, *Pseudosuccinea* (*L.*) *columella* in the Americas, *Fossaria* (*L.*) *viator/viatrix* and *F.* (*L.*) *diaphana* in South America, and *F.* (*L.*) *bulimoides* in North America; and those for *F. gigantica* being *Radix auricularia* in many countries, *Radix natalensis* in Africa, *R. rubiginosa* in Malaysia, and *L. acuminata* and *L. rufescens* in India. These aquatic/amphibious snails vary in their habitat preferences, some preferring wet mud, others free water. They can readily colonize transient habitats, such as puddles in depressions, wheel ruts and hoof marks, especially after heavy rainfall, irrigation or flooding. These snails breed readily when mean daily ambient temperatures are above 10-15°C, a similar temperature threshold required for parasite development within the snails. Once miracidia penetrate the tissues of a snail, they transform into the 'larval' stages which undergo massive asexual multiplication (formerly and inappropriately called polyembryony). The miracidia lose their cilia, glands and eyespots and become simple sac-like sporocysts that lack digestive organs and feed by absorption. Germinal cells within the sporocyst develop into 5-8 small elongate rediae which emerge from the mother sporocyst. Rediae have mouths and guts and feed on snail tissues. Germinal cells within rediae develop into another generation of daughter rediae (usually during summer months). Those daughter rediae ultimately produce the motile single-tailed cercariae. Each redia produces 14-20 cercariae which emerge through the redial birth pore and then escape from the snail (usually by migrating through the digestive gland into the pulmonary sac where they pass out into water). Cercariae begin emerging 5-7 weeks after infection and several hundred (sometimes thousands) of cercariae may be produced. Within 2-3 days, emergent cercariae swim to suitable substrates (such as blades of grass) and form encysted metacercariae by shedding their tails and secreting thick cyst walls. Metacercariae are quiescent infective stages which can survive in water for several months or on sodden herbage for several weeks (they usually encyst within 10 cm of the waterline). Mammals become infected when they ingest metacercariae with food or water (many human infections have been linked to the consumption of watercress, water lettuce and alfalfa). Metacercariae excyst in the small intestines releasing juvenile worms which penetrate the gut wall and migrate around the body cavity for several days. They then move to the liver and burrow through the capsule into the parenchyma where they feed and grow for 5-8 weeks before entering the bile ducts where they feed on mucosa, blood and bile. Worms become sexually mature and begin producing eggs 6-14 weeks after infection. Even though each adult fluke is hermaphroditic, cross-fertilization is common with copulation occurring in the bile ducts. Adult flukes can live for many years in sheep but not in cattle, although infections in domestic animals exhibit marked seasonal variation. Acute disease is most common in sheep during summer-autumn while chronic disease is most common in cattle during autumn-spring.

Differential diagnosis: Fasciolosis may be suspected in domestic animals grazing in endemic regions on the basis of clinical signs and history (illthrift, anaemia, deaths). Infections are conventionally diagnosed by coprological examination for fluke eggs in faecal samples, usually following their concentration by sedimentation techniques (fluke eggs are 'heavy' and do not float well in many floatation media). Despite the fecundity of mature flukes, faecal egg counts may vary due to sporadic egg production/release and the intermittent flow of bile into the intestines. Serial samples should therefore be examined. Blood biochemical tests can also be used to show elevated plasma levels of hepatic enzymes, notably glutamate dehydrogenase (GLDH) during acute stages and gamma glutamyl transpeptidase (GGT) during chronic stages. Medical imaging techniques may be used to reveal worms in bile ducts and assess attendant pathology (burrow tracts, duct dilation), including radiology, ultrasound, computerized tomography (CT) and magnetic resonance imaging (MRI). Infections may be detected in carcases during meat inspection by observing characteristic fibrotic lesions in the liver and finding flukes in sectioned bile ducts. Immunological tests (enzyme immunoassays, Western blots) have been developed to detect host antibodies in serum samples (and even in bulk milk samples) or parasite antigens in faecal samples in attempts to facilitate early diagnosis. Molecular studies based on polymerase chain reaction (PCR) amplification of parasite gene sequences (ribosomal RNA, internal transcribed spacers, noncoding repetitive DNA fragments, mitochondrial cytochrome c oxidase subunit 1) are currently being used to examine parasite strain variation in definitive and intermediate hosts, identify putative virulence factors and screen for protective immunogens.

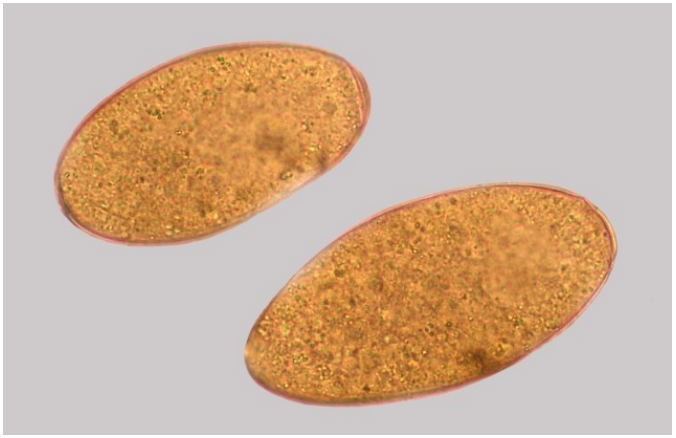
Treatment and control: Subacute and chronic infections may be treated with triclabendazole or bithionol, which show excellent trematocidal activity with few side-effects. A range of other anthelmintics show variable activity depending on the phase of infection, including other halogenated phenols (hexachlorophene, nitroxynil), other benzimidazoles (albendazole, mebendazole, luxabendazole, ricobendazole), probenzimidazoles (netobimin), salicylanilides (closantel, rafoxanide, niclofolan, oxyclozanide), sulfonamides (clorsulon), phenoxyalkanes (diamphenetide) and halogenated hydrocarbons (carbon tetrachloride, hexachlorethane), but their use may be confounded by issues with toxicity, residues and with-holding periods (esp. in lactating females). Strategic

longitudinal drenching programs should be instituted for livestock depending on local conditions, particularly over summer-autumn periods to control clinical disease and minimize pasture contamination. Several forecasting models have been developed based on meteorological data (ground surface wetness or rainy days) to predict the distribution, timing and intensity of infections in livestock thereby facilitating timely interventions. Preventive measures are based on breaking the cycle of transmission by reducing faecal contamination of water bodies, reducing snail populations using molluscicides (usually copper sulphate), pasture management by draining or fencing off riparian habitats (especially swampy fields), strategic grazing by rotating and treating stock, reticulating water supplies to troughs rather watering stock from dams or streams, restricting access of livestock to aquatic vegetation, and avoiding using watercress in salads or as garnish. Farmers harvesting grass for penned stock should avoid sodden grass or should only cut grass 15 cm above the waterline. Snail control is often difficult, particularly in high rainfall areas where even temporary pools may harbour large snail populations (they aestivate in the ground during dry conditions). Feral or wild animals (such as rabbits) may also act as reservoirs of infection for domestic livestock.


Fasciola
liver, bile ducts
(acute/subacute nectrotic disease,
chronic fibrotic disease)
Definitive Hosts
(herbivores,
esp. ungulates)
hermaphroditic
adult
(~ 30 mm)
ingestion
excretion
egg
(~ 150 µm)
vector-borne transmission
encysted
metacercaria
(~ 200 µm)
endoparasitic in
tissues of vector
free-swimming
cercaria
(~ 500 µm)
free-swimming
miracidium
(~ 170 µm)
redia
(~ 1.5 mm)
sporocyst
(~ 1 mm)
Intermediate Hosts
(lymnaeid snails)
(visceral then glandular tissue)



Fasciola adult worms



Fasciola eggs



Fasciola miracidia



Fasciola redia



Fasciola cercaria



Fasciola snail vectors

Fasciolopsis
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies, oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult echinostomatids often have well-developed scales or spines on the anterior tegument and the ventral sucker is near the oral sucker. Fasciolids occur as large flukes in the small intestines and infections by *Fasciolopsis buski* cause enteric diseases in dogs, pigs and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Plagiorchiida (‘echinostomatids’, plagiorchiids’, mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder:	Echinostomata (miracidium penetrates gastropod IH, redia formed, simple-tailed cercariae, encysts in open or in second IH, metacercariae eaten by DH)
Superfamily:	Echinostomatoidea (slender worms, adult with scales or spines)
Family:	Fasciolidae (large leaf-shaped flukes, in herbivores, conical anterior end, ventral sucker at level of shoulders)
Genus:	*Fasciolopsis* (parasitic in intestines of man/pigs)
Species:	*F. buski* causes enteritis in dogs, pigs and humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs, fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in

molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. The suborder Echinostomata contains one superfamily Echinostomatoidea whose members form simple-tailed cercariae that encyst in the open or in second intermediate hosts, and the resultant metacercariae are eaten by definitive hosts. Ten families are recognized (Calycodidae, Cyclocoelidae, Echinostomatidae (including Echinochasmidae), Eucotylidae, Fasciolidae, Himasthlidae, Philophthalmidae, Psilostomidae, Rhytidodidae, Typhlocoelidae). The family Fasciolidae contains 6 genera (*Fasciola, Fasciolopsis, Fascioloides, Parafasciolopsis,*

Protofasciola, Tenuifasciola) which form large leaf-shaped adult flukes in the liver, gall bladder and intestines of herbivorous mammals and undergo asexual development in freshwater snails from the superfamily Lymnaeoidea. The genus *Fasciolopsis* is monotypic with a single species (*F. buski*) described from pigs and humans, with proven zoonotic transmission. More than 10 million people are thought to be infected; mostly in the Indo-Asian subcontinent, particularly in communities consuming freshwater plants as part of their culinary traditions. Several other animal species (dogs, rabbits, rodents) may also act as reservoirs for infection.

***Fasciolopsis* species**	**Definitive hosts [adults in small intestines]**	**Intermediate hosts [sporocysts/rediae in tissues]**	**Infective stages**	**Distribution**
F. buski (giant intestinal fluke)	Artiodactyla: suid (pig); Primates: hominid (human), cebid (squirrel monkey), cercopithecid (rhesus macaque); Carnivora: canid (dog); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig)	freshwater Gastropoda: planorbid (*Segmentina* (*Trochorbis*) *hemisphaerula* (syn. *S. coenosus, S. nitidella, S. calathus, S. largeillierti*), *S. trochoideus, S. hemisphaerula, Hippeutis* (*Helicorbis*) *cantori* (syn. *Hi. smackeri*), *Hi. umbilicalis, He. coenosus, Gyraulus convexiusculus, G. chinensis, Indoplanorbis exustus*, *Polypylis, Planorbis*); and rarely (doubtfully) ampullariid (*Pila,*), lymnaeid (*Lymnaea*)	metacercariae on herbage	cosmopolitan (most prevalent in Asia)

Parasite morphology: *Fasciolopsis buski* forms 7 different stages in its developmental cycle: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae and adult flukes. Eggs are quinone-coloured (yellow-brown, bile-stained), ellipsoidal measuring 130-150 x 65-90 μm, thin-shelled, and have a small operculum at one end (hatching point). They are passed unembryonated and contain yolk cells with uniformly distributed lipid granules. As the eggs mature, they embryonate and eventually hatch releasing ovoid ciliated free-swimming miracidia about 150-200 μm long. The miracidia penetrate snails, lose their cilia and transform into elliptical sac-like mother sporocysts which lack a mouth and a gut. The sporocysts grow in size (ranging from 0.07-1.5 mm) and undergo asexual proliferation whereby germinal cells develop into a second generation (called rediae). In contrast to sporocysts, rediae possess a mouth, pharynx and saccular gut and actively ingest and digest food. Mature rediae are cylindrical in shape measuring 1-1.5 x 0.2-0.3 mm. Rediae escape from the mother sporocyst, invade neighbouring tissue and either produce cercariae or another generation of redia. Cercariae are elongate free-swimming stages with bodies measuring 0.21-0.23 x 0.12-0.15 mm and trailing a long simple club-shaped (leptocercous) tail (2-3 times body length). They possess a mouth, gut, oral sucker, ventral sucker (previously called acetabulum), excretory flame cells and numerous cystogenous glands which impart a dark colouration. Mature cercariae attach themselves to aquatic plants, drop their tails and encyst to become metacercariae. The cysts are ovoid, measure 0.13-0.2 mm in diameter and are surrounded by a conspicuous double-layered wall approximately 7 μm thick. Adult flukes have large dorsoventrally-flattened (0.5-3.5 mm thick) leaf-shaped pink-brown bodies and are distinguished from other fasciolids by their blunt anterior ends lacking cephalic cones and shoulders, possessing unbranched gut caeca and inhabiting the intestines rather than the liver of their definitive hosts. The tegument is covered with transverse rows of small spines facing backwards, occurring mostly around the muscular ventral sucker which is 3-4 times larger than the oral sucker. As worms mature, they grow from 1.0-1.6 x 0.5-0.6 mm to 17-75 x 8-20 mm while developing functional genitalia. Adults are hermaphroditic with two dendritic testes located one behind the other (tandem) in the posterior body, a highly branched ovary located in the midline, a short anterior uterus, and extensive vitellaria (vitelline follicles) located laterally.

Site of infection: Adult *Fasciolopsis* flukes attach to the intestinal mucosa of their vertebrate definitive hosts, unlike other fasciolids which infect the liver. In light infections, the parasites reside in the duodenum and the jejunum while in moderate to heavy infections the parasites inhabit most of the small intestines and can also be found in the stomach and sometimes the colon. Larval stages in snails vary in their location with most sporocysts forming near the site of miracidial penetration in the foot pad while rediae migrate towards glandular tissue (hepatopancreas and gonads) before finally releasing free-swimming cercariae.

Pathogenesis: The clinical consequences of infections by *Fasciolopsis buski* can be negligible, mild or severe, depending largely on the intensity of infection (number of worms per individual host). Most infections are clinically asymptomatic and significant worm burdens (in the order of hundreds) are usually required to cause clinical disease (called fasciolopsiasis). Worms feed actively on the intestinal mucosa, causing inflammation, ulceration and abscesses. Infections are typically over-dispersed in endemic regions, with many individuals having light infections (involving < 100 worms) that remain asymptomatic or produce mild nonspecific symptoms such as fever, headaches, dizziness, abdominal pain and discomfort, loose stools with alternating constipation, anaemia with eosinophilia, asthenia (weakness) and pallor. Clinical disease worsens in moderate to heavy infections (involving hundreds to thousands of worms), with most symptomatology attributed to traumatic, obstructive and/or toxic effects, often cumulatively. The

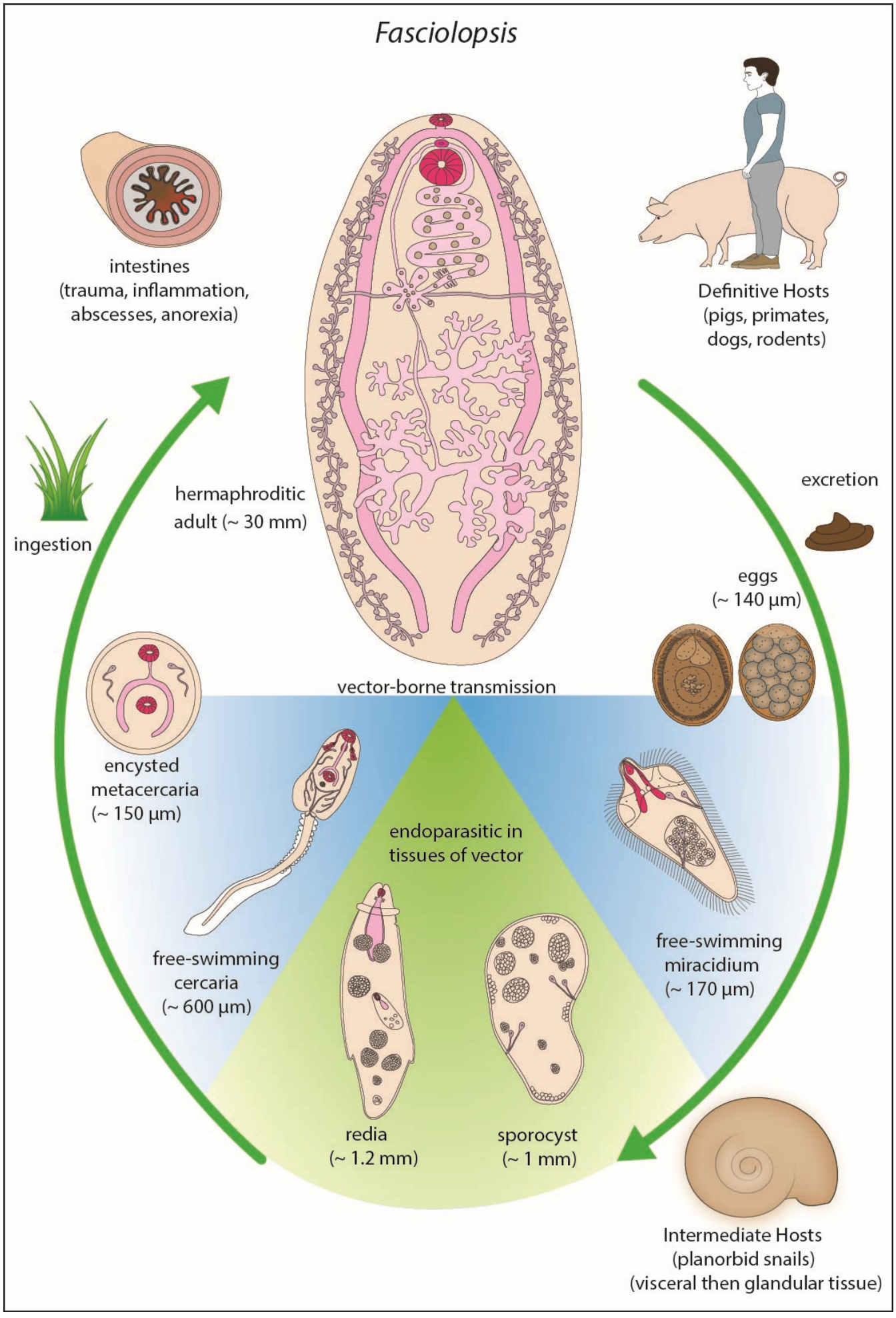
presence of > 400 worms may prove fatal in children. Adult worms attach to the intestines causing mechanical damage, irritation, erosion, ulceration, abscesses, sometimes perforation, haemorrhage, anaemia, catarrhal inflammation, excessive mucus production, hyperaemia, maldigestion, malnutrition, anorexia and weight loss. Heavy infections by these large worms may also cause partial or complete intestinal obstruction with abdominal colic, epigastric pain, fever, acute ileus and nausea. The absorption of worm metabolites may provoke allergic and toxigenic responses, involving the development of ascites (fluid accumulation in peritoneal cavity), facial or orbital edema, anasarca (generalized oedema) and toxaemia. Both mechanical and metabolite effects lead to inflammatory responses, often involving tissue invasion by leucocytes and eosinophils. Clinical disease may progress through 3 different stages: latency (often asymptomatic for months then developing mild anaemia); diarrhoeic (intestinal inflammation, erosion and ulceration with excessive mucus secretion producing epigastric pain, diarrhoea (yellowish stools without blood), nausea, vomiting and anorexia, sometimes accompanied by allergy and toxaemia); and oedematous (progressive anaemia with fluid accumulation in abdomen (ascites), then genitals, lower limbs, upper limbs, face and lungs culminating in dyspnoea, cardiac insufficiency, hypothermia, dry skin, weakness and possibly death from exhaustion). The intensity of infection and severity of disease is strongly linked to impoverished economic status, rural communities with limited health infrastructures, poor sanitation and unhygienic dietary practices. It is estimated that 10 million human *Fasciolopsis* infections occur annually, infections being more prevalent in children 2-10 years of age who become infected when playing in lakes and ponds.

Developmental cycle and mode of transmission: This trematode species has an indirect heteroxenous life-cycle involving sexual developmental stages (adults) in mammalian definitive hosts, free-swimming aquatic stages, asexual developmental stages (larvae) in molluscan intermediate hosts, free-swimming and then encysted stages on aquatic vegetation. Unembryonated eggs released by adult worms are shed in host faeces into the external environment. The eggs embryonate in water over 2-12 weeks depending on temperature (slower in cold water) and then hatch releasing their enclosed miracidia. These stages are ciliated and actively swim about using chemotactic cues to find aquatic pulmonate snails which they must invade within 6-52 hours or die. They can only undergo further development in specific snail species (planorbids) which act as intermediate hosts suitable for parasite asexual development. Miracidia invade the snails by penetrating through the head, foot, tentacles or mantle shedding their ciliated plates in the process. They develop into larger mother sporocysts within snail tissues (often in haemolymph sinuses) which undergo asexual reproduction producing and releasing first-generation rediae that penetrate the snail digestive gland and respiratory cavity where they settle and undergo further asexual reproduction to produce second-generation (daughter) rediae or cercariae. Sporocysts do not have digestive organs but absorb nutrients from their snail hosts, while rediae have mouths and guts to actively feed on snail tissues. Cercariae are transmissive stages which use their mouthparts and glandular secretions to penetrate host tissues and escape from snails into the surrounding environment. The time from infection of the snail to the first release of cercariae ranges from 4-7 weeks, but parasites can survive for months in aestivating snails which bury themselves in soil during dry periods. Cercariae often emerge from snails during the day, although some variation has been observed in their daily pattern. The cercariae are free-swimming stages and can survive in water for up to 64-72 days. Eventually, the cercariae drop their tails and form encysted metacercariae sometimes at the surface of the water but mostly on floating or submerged aquatic vegetation, including edible varieties of water chestnuts, water caltrop, watercress, water spinach, water lotus, water lily, water hyacinth, water bamboo, gankola or water morning glory. Definitive hosts become infected when they ingest raw aquatic plants or drink water containing metacercariae, although some infections may be contracted during food preparation when cooks peel pods or stalks using their teeth. Ingested metacercariae excyst in the gut releasing immature worms which attach and develop into adults over 1-3 months. Mature worms may produce up to 25,000 eggs daily and adults generally live for 6-12 months.

Differential diagnosis: Infections by adult *F. buski* are conventionally diagnosed by the microscopic detection of eggs in faecal preparations, including smears (e.g. Kato-Katz) and sediments (e.g. formalin-ethyl-acetate, merthiolate-iodine-formalin), but their specific identification is difficult due to the similar egg morphologies of many fasciolid species. Eggs, and sometimes adult worms, may also be recovered occasionally from other biological samples, such as vomitus, gastric washes and duodenal aspirates. The relatively large adult worms may also be detected *in situ* by gastrointestinal endoscopy. Infections are often associated with a systemic inflammatory eosinophilia and sometimes by a developing anaemia, as revealed by haematological assessments. Immunoserological tests (enzyme immunoassays) have been developed to detect host antibodies against parasite excretory/secretory antigens, but they have demonstrated problems with sensitivity and specificity. Molecular techniques have recently been applied to the characterization of fasciolid species and strain variations following the polymerase chain reaction (PCR) amplification of nuclear (18S and 28S ribosomal RNA, internal transcribed spacer regions 1 and 2 (ITS1, ITS2)) and mitochondrial (NADH dehydrogenase subunit 1 (Nad1), cytochrome c oxidase subunit 1 (cox1) gene sequences.

Treatment and control: Various anthelmintics have been used to treat fasciolopsiasis in humans and animals; including isoquinolines (praziquantel) interfering with parasite muscles, benzimidazoles (thiabendazole, mebendazole, triclabendazole) inhibiting microtubules, tetrahydropyrimidines (pyrantel) and imidazothiazole (levamisole (causing neurointerference, salicylanilides (niclosamide, oxyclozanide, rafoxanide), halogenated phenols (bithionol) and substituted dihydroxybenzene (hexylresorcinol) inhibiting energy provision, and even the halogenated hydrocarbon (tetrachloroethylene) acting as a purgative. These drugs exhibited variable efficacy and produced few side-effects, with praziquantel being very effective even in severe cases with mild transient side-effects, including dizziness, drowsiness and epigastric pain. Attention should be paid to contra-indications for agricultural use as many have mandatory meat with-holding periods after application to livestock. Various preventive strategies

have been developed to break the parasite life-cycle between snail vectors and definitive hosts. It must be remembered that digenean trematodes are unique in that they may undergo massive proliferation in both definitive and intermediate hosts (sexual in the former, asexual in the latter) leading potentially to widespread and heavy contamination of freshwater sources. Every effort should be made to eliminate faecal contamination of water by improving sanitation to limit promiscuous defaecation, introducing sewage and water treatment and prohibiting the use of human 'night soil' and pig excrement as fertilizers in agriculture. Reducing snail populations by the application of molluscicides may be feasible in some peri-domestic situations, but the potential always exists for considerable ecological harm (to crops, fish and the environment). Definitive hosts must avoid eating uncooked aquatic vegetation and cooks should not use their teeth to peel aquatic plants. Drying vegetables or steeping (immersing) them in boiling water for at least 30 seconds has been shown to be effective in killing attached metacercariae. Aquatic green fodder should not be used to feed pigs and farm animals should have access to clean treated water supplies. Regrettably, changes in dietary and agricultural practices are difficult to institute in many circumstances due to entrenched local customs, poverty, unhygienic conditions and the abundance of stagnant waters in wet tropical regions. Nonetheless, education programmes should target not only mothers within families (most often involved in food preparation) but also school children (before cultural norms develop).


Fasciolopsis
intestines
(trauma, inflammation,
abscesses, anorexia)
Definitive Hosts
(pigs, primates,
dogs, rodents)
ingestion
hermaphroditic
adult (~ 30 mm)
excretion
eggs
(~ 140 µm)
vector-borne transmission
encysted
metacercaria
(~ 150 µm)
endoparasitic in
tissues of vector
free-swimming
cercaria
(~ 600 µm)
free-swimming
miracidium
(~ 170 µm)
redia
(~ 1.2 mm)
sporocyst
(~ 1 mm)
Intermediate Hosts
(planorbid snails)
(visceral then glandular tissue)



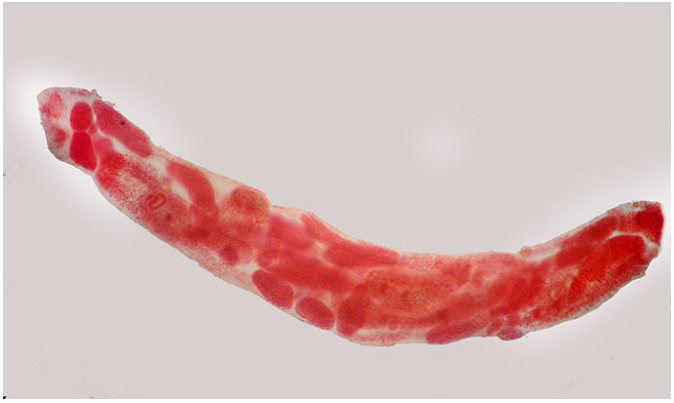
Fasciolopsis adult worm



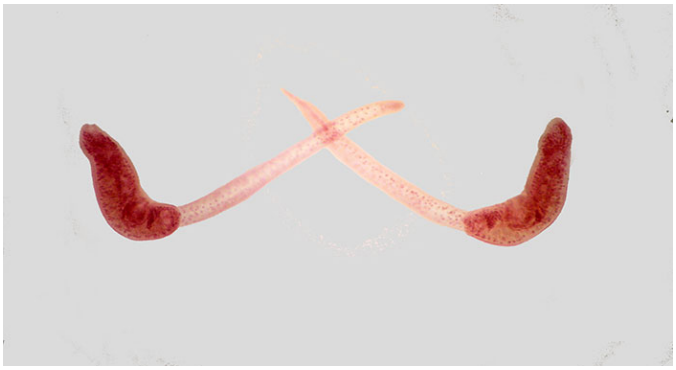
Fasciolopsis egg



Fasciolopsis miracidium



Fasciolopsis redia



Fasciolopsis cercariae

Echinostoma
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult echinostomatids often have well-developed scales or spines on the anterior tegument and the ventral sucker is near the oral sucker. Echinostomes ('spiny mouth') are slender worms with a circumoral collar of peg-like spines and they form metacercariae in second intermediate hosts (small aquatic invertebrates, amphibians and fish). Most species are parasites in the intestines of fish-eating birds and mammals, sometimes associated with enteric diseases in waterfowl, domestic carnivores and humans.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum: Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade: Neodermata (syncytial tegument = neodermis)
Class: Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass: Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order: Plagiorchiida ('echinostomatids', plagiorchiids', mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder: Echinostomata (miracidium penetrates gastropod IH, redia formed, simple-tailed cercariae, encysts in open or in second IH, metacercariae eaten by DH)
Superfamily: Echinostomatoidea (slender worms, adult with scales or spines)
Family: Echinostomidae (in piscivores, adult with collar of peg-like spines, ventral sucker near oral sucker, rediae with appendages, cercariae without eyespots and with simple tail, miracidia with one pair protonephridia)
Genus: *Echinostoma* (parasitic in gut of birds/mammals)
Species: various species cause enteritis in birds, carnivores and humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs,

fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

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[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

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[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. The suborder Echinostomata contains one superfamily Echinostomatoidea whose members form simple-tailed cercariae that encyst in the open or in second intermediate

hosts, and the resultant metacercariae are eaten by definitive hosts. Ten families are recognized (Calycodidae, Cyclocoelidae, Echinostomatidae, Eucotylidae, Fasciolidae, Himasthlidae, Philophthalmidae, Psilostomidae, Rhytidodidae and Typhlocoelidae). The family Echinostomatidae (syn. Cathaemasiidae, including Echinochasmidae) contains 40-50 genera of slender worms with a distinctive collar of peg-like spines. Adult flukes have been found in various organs in fish, reptiles, birds and mammals (including humans) while larval stages develop in freshwater and marine snails, mussels, insects, amphibians and reptiles. A variety of morphotypic and biologic characters have been used to recognize some 45 genera in 10-11 subfamilies, a recent review listing Echinostomatinae (*Bashkirovitrema, Drepanocephalus, Echinodollfusia, Echinoparyphium, Echinostoma* (syn. *Echinostomum*)*, Euparyphium, Hypoderaeum, Isthmiophora* (syn. *Echinocirrus*)*, Longicollia, Lyperorchis, Moliniella, Neoacanthoparyphium, Pameileenia, Parallelotestis, Petasiger* (syn. *Paryphostomum*)*, Prionosoma, Prionosomoides, Singhia*), Echinochasminae (*Dissurus, Echinochasmus, Episthmium, Mehratomum, Microparyphium, Pulchrosomoides, Saakotrema, Stephanoprora, Stephanoprora, Uroproctepisthmium*), Chaunocephalinae (*Chaunocephalus, Balfouria*), Himasthlinae (*Himasthla, Acanthoparyphium, Aporchis, Artyfechinostomum, Caballerotrema, Cloeophora, Curtuteria*), Ignaviinae (*Ignavia*), Nephrostominae (*Nephrostomum, Patagifer*), Pegosominae (*Pegosomum*), Pelmatostominae (*Pelmatostomum*), Singhiatreminae (*Singhiatrema*), Sodalinae (*Sodalis*) and one unplaced (*Ruffetrema*).

The genus *Echinostoma* is speciose with over 120 nominal species recorded worldwide from a wide range of birds, mammals, occasionally reptiles and fish as definitive hosts, freshwater snails as first intermediate hosts, and many aquatic animals (snails, clams, fish, amphibians, planaria and leeches) as second intermediate hosts. Several attempts have been made to revise the systematics of the heterogeneous echinostomes and many phenotypic characters (morphological and biological) have been used to differentiate taxa and identify major groups (possibly species-flocks); the most robust being the number of collar spines on adults and the divisions of paraoesophageal glands in cercariae. The genus *Echinostoma* has been characterized by most workers as comprising adult worms possessing a collar with 27-55 spines (lateral, dorsal and angle spines arranged in 1-2 rows). More recently, a comprehensive comparison of larval and adult stages revealed that the number of spines was consistent between different life-cycle stages and was always uneven (reports of worms with even numbers of spines were considered to represent specimens with spines lost, retracted or supernumerary). Preliminary molecular phylogenetic studies have identified several dominant clades, with strong support found for the 37-collar-spined '*E. revolutum'* group. Infections by *Echinostoma* spp. are prevalent in humans throughout Asia, and zoonotic infections have been recorded throughout Europe, Africa and the Americas. Most human infections occur in children and young women in poor rural areas with limited sanitation and healthcare and where dietary customs include the consumption of raw or insufficiently cooked foods derived from aquatic animals (molluscs, shellfish, amphibians, fish), important sources of supplemental protein in human nutrition. It has been estimated that 40-50 million people throughout the world are at risk of infection by echinostomes, with some 15% developing disease.

***Echinostoma* species**	**Definitive hosts [adults in intestines]**	**First intermediate hosts [sporocysts/rediae in tissues]**	**Second intermediate hosts [metacercariae in tissues]**	**Distribution**
27-collar-spined				
E. hortense (syn. *Isthmiophora*)	Carnivora: canid (dog), felid (cat), mustelid (Japanese weasel); Rodentia: murid (rats, mice, field mice), cricetid (reed vole); Primates: hominid (human); Suliformes: phalacrocoracid (cormorants); Anseriformes: anatid (duck, mallard, spot-billed duck)	freshwater Gastropoda: lymnaeid (*Lymnaea pervia*, *Radix auricularia*)	freshwater Cypriniformes: cobitid (pond loach, Chinese fine-scaled loach), cyprinid (Chinese minnow, gudgeon); Perciformes: percichthyid (redfin perch); Gobiiformes: odontobutid (dark sleeper), oxudercid (yellowfin goby); Anura: ranid (American bullfrog, tadpoles); Clitellata: hirudinid (leeches); Gastropoda: lymnaeid (snails)	Asia
E. melis (syn. *Isthmiophora, E. trigonocephalum, Euparyphium jassyenese, Eu. spiculator, Eu. suinum*)	Carnivora: mustelid (European badger, European polecat, American mink); Eulipotyphla: erinaceid (European hedgehog); Rodentia: murid (striped field mouse); Primates: hominid (human)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*)	freshwater Osteichthyes (fish); Anura: ranid (tadpoles)	Eurasia, North America

29-collar-spined				
E. ignavum	Charadriiformes: charadriid (Australian masked plover)			Australia
31-collar-spined				
E. anseris	Anseriformes: anatid (duck)			Asia, North America
E. donosoi		freshwater Gastropoda: ampullariid (*Marisa cornuarietis*)		South America
E. govindum	Charadriiformes: scolopacid (ruff)			India
E. parcespinosum	Gruiformes: rallid (spotted rail, plumbeous rail)			South America
E. sudanense	Pelecaniformes: ardeid (heron), Anseriformes: anatid (duck)			Africa, Europe, North America
33-collar-spined				
E. chasma	Anseriformes: anatid (garganey)			North America
E. operosum	Charadriiformes: scolopacid (common snipe); Suliformes: anhingid (Surinam darter)			Americas
E. stantschinskii	Charadriiformes: scolopacid (common sandpiper)			Japan
35-collar-spined				
E. amurzetica	Anseriformes: anatid (duck)			Asia, North America
E. bhattacharyai	Anseriformes: anatid (duck)			Asia, North America
E. crotophagae	Cuculiformes: cuculid (greater ani, guira cuckoo)			South America
E. distinctum	Passeriformes: icterid (solitary cacique)			South America
E. elongatum	Anseriformes: anatid (ducks); Caprimulgiformes: podargid (tawny frogmouth)			China, Australia
E. emollitum	Cuculiformes: cuculid (pheasant coucal)			Australia
E. grandis	Anseriformes: anatid (duck); Gruiformes: rallid (coot)			Eurasia, North America
E. guirae	Cuculiformes: cuculid (guira cuckoo)			South America
E. parvum	Columbiformes: columbid (rock dove)			South America
E. pekinensis	Anseriformes: anatid (duck)			China, North America
E. porteri	Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Rodentia: murid (rats)	freshwater Gastropoda: lymnaeid (*Lymnaea natalensis*)	freshwater Gastropoda: planorbid (*Bulinus* (*Physopsis*) *globosus*, *Bulinus* (*Bulinus*) *forskalii*), lymnaeid (*Lymnaea natalensis*)	Africa
E. uncatum	Cuculiformes: cuculid (greater ani, smooth-billed ani, squirrel cuckoo)			South America
E. uitalica	Galliformes: phasianid (common pheasant)			Russia
E. valentini	Suliformes: phalacrocoracid (Indian cormorant)			Pakistan

37-collar-spined (*Echinostoma* '*revolutum'* group)				
E. acuticauda	Pelecaniformes: threskiornithid (straw-necked ibis)			Australia
E. atrae	Gruiformes: rallid (black coot)			Pakistan
E. caproni (syn. *E. liei, E. togoensis, E. parasensei*)	Galliformes: phasianid (chicken); Anseriformes: anatid (duck); Columbiformes: columbid (pigeon); Passeriformes: fringillid (finch); Falconiformes: falconid (falcon); Rodentia: murid (mice, jirds, rats, roof rat), cricetid (golden hamster); Eulipotyphla: soricid (Egyptian giant shrew); Lagomorpha: leporid (rabbit)	freshwater Gastropoda: planorbid (*Biomphalaria glabrata, Bulinus*)	freshwater Gastropoda (snails), Bivalvia (clams), Anura (tadpoles)	Africa
E. chloephagae	Anseriformes: anatid (upland goose)			South America
E. cinetorchis	Carnivora: canid (dog); Primates: hominid (human); Rodentia: murid (rats, mice)	freshwater Gastropoda: viviparid (*Cipangopaludina chinensis*), lymnaeid (*Austropeplea ollula*), planorbid (*Hippeutis* (*Helicorbis*) *cantori*, *Segmentina hemispaerula, S. nitidella*, *Gyraulus convexiusculus*)	freshwater Gastropoda: planorbid (*Segmentina hemispaerula*, *S. nitidella, Gyraulus convexiusculus*, *Hippeutis* (*Helicorbis*) *cantori, H. cantori, Planorbis compressus*), lymnaeid (*Radix auricularia, Lymnaea japonica*), physid (*Physa* (*Physella*) *acuta*), viviparid (*Cipangopaludina chinensis*); Bivalvia: cyrenid (*Corbicula*, basket clams); Cypriniformes: cobitid (pond loach, muddy loach); Anura: ranid (dark-spotted frog, American bullfrog)	Asia
E. deserticum	Rodentia: murid (African grass rat)	freshwater Gastropoda: planorbid (*Bulinus trancatus, B. globosus*)	freshwater Gastropoda (snails)	Africa
E. echinatum (syn. *E. lindoense, E. barbosai, E. robustum*)	Rodentia: murid (rats, mice); Primates: hominid (human); Columbiformes: columbid (spotted dove); Anseriformes: anatid (duck, mallard, mottled duck, goldeneye, wigeon, muscovy, shelduck, ferruginous duck, gadwall, pochard, shoveler, whooper swan, mute swan, greylag goose); Podicipediformes: podicipedid (great crested grebe, little grebe); Suliformes: phalacrocoracid (red-legged cormorant, pygmy cormorant); Pelecaniformes: ardeid (black-crowned night heron, crowned heron, squacco heron); Gruiformes:	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*), planorbid (*Planorbarius*, *Planorbis corneas*, *Anisus*, *Gyraulus*, *Biomphalaria glabrata*), viviparid (*Viviparus* (*Paludina*) *vivipara*, *V. achatina*)	freshwater Gastropoda: viviparid (*Idiopoma javanica*); Bivalvia: cyrenid basket clams (*Corbicula lindoensis, C. sucplanta*), unspecified mussels	South America, Europe, Asia, Australia?

	gruid (common crane)			
E. erraticum	Columbiformes: columbid (pigeon, ground dove); Gruiformes: rallid (common gallinule, coot, russet-crowned crake); Pelecaniformes: ardeid (yellow-crowned night heron); Cuculiformes: cuculid (smooth-billed ani)	freshwater Gastropoda: planorbid (*Biomphalaria*, *Drepanotrema*)	freshwater Gastropoda: physid (*Physa rivalis*), planorbid (*Planorbis*)	Europe
E. friedi	Rodentia: murid (rats, mice), cricetid (hamster); Galliformes: phasianid (chicken)	freshwater Gastropoda: lymnaeid (*Lymnaea peregra*, *L. corvus*, *Radix*), planorbid (*Gyraulus chinensis*, *Biomphalaria*, *Bulinus*)	freshwater Gastropoda: lymnaeid (*Lymnaea*), planorbid (*Gyraulus*)	Europe
E. jurini (syn. *E. bolschewense, E. sisjakowi, E. orlovi*)	Rodentia: cricetid (golden hamster, muskrat), murid (rats, mice); Columbiformes: columbid (pigeon)	freshwater Gastropoda: viviparid (*Viviparus contectus, V. viviparus, V. acerosus*)	freshwater Gastropoda: physid (*Physa acuta, P. fontinalis*), viviparid (*Viviparus viviparus*, *V. contectus*), lymnaeid (*Lymnaea stagnalis, L. tomentosa, L. truncatula, L. palustris, L. peregra, L. auricularia*), planorbid (*Planorbarius corneus, Planorbis planorbis, Biomphalaria glabrata, B. alexandrina*), bithynid (*Bithynia tentaculata, B. leachi*); Bivalvia (thick-shelled river mussels, zebra mussels); Anura: ranid (European grass frog, marsh frog); Testudines: emydid (European pond turtle)	Eurasia
E. londonense	Columbiformes: columbid (pigeon)	freshwater Gastropoda: planorbid (*Planorbis corneus*)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*, *L. pereger*), planorbid (*Planorbis corneus*)	Europe
E. luisreyi	Rodentia: murid (mice), cricetid (hamster)	freshwater Gastropoda: physid (*Physa marmorata*)	freshwater Gastropoda: physid (*Physa*), planorbid (*Biomphalaria*)	Central/South America
E. mendax	Anseriformes: anatid (black-necked swan, white-faced whistling duck)			South America
E. miyagawai	Anseriformes: anatid (duck, tufted duck); Galliformes: phasianid (chicken)	freshwater Gastropoda: planorbid (*Planorbis planorbis*,	freshwater Gastropoda (snails)	Europe, Asia, Australia, New Zealand

		Planorbarius corneus, *Anisus vortex*), lymnaeid (*Lymnaea*)		
E. nasincovae	Rodentia: cricetid (golden hamster)	freshwater Gastropoda: planorbid (*Planorbarius corneus*)		Europe
E. novaezealandense	Anseriformes: anatid (Canada goose, duck, black swan)			New Zealand
E. nudicaudatum	Columbiformes: columbid (pigeon)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*)	Europe
E. paraensei	Rodentia: cricetid (hamster, scaly-footed water-rat), murid(mice, rats)	freshwater Gastropoda: planorbid (*Biomphalaria glabrata*), physid (*Physa rivalis, P. marmorata, P. gyrina, Glyptophysa*)	freshwater Gastropoda (snails)	Central and South America, Australia
E. parvocirrus	Anseriformes: anatid (muscovy duck); Passeriformes: fringillid (canary)	freshwater Gastropoda: planorbid (*Biomphalaria glabrata*)	freshwater Gastropoda: planorbid (*Biomphalaria glabrata*), physid (*Physa marmorata*); Anura: bufonid (cane toad, tadpoles)	Central and South America
E. revolutum (syn. *E. audyi, E. paraulum, E. ivaniosi, E. columbae, E. neglectum, E. nephrocystis, E. microrchis, E. echinocephalum?*)	Anseriformes: anatid (duck, black duck, tufted duck, mallard, spot-billed duck, greater scaup, goose, pied goose, white-fronted goose, Canada goose, black swan, green goose teal, falcated teal); Columbiformes: columbid (pigeon, little cuckoo dove); Podicipediformes: podicipedid (crested grebe); Galliformes: phasianid (chicken); Passeriformes: sturnid (starling), estrildid (Java sparrow, black-headed munia, spotted munia); turdid (thrush); Falconiformes: falconid (falcon, Eurasian hobby); Accipitriformes: accipitrid (northern goshawk, lesser spotted eagle, common buzzard, rough-legged buzzard, short-toed snake eagle, red kite); Strigiformes: strigid (little owl, tawny owl), tytonid (barn owl); Ciconiiformes: ciconiid (white stork); Gruiformes: rallid (common gallinule); Charadriiformes: larid (black-backed gull); Rodentia: cricetid (hamster), echimyid (coypu), murid (rat); Carnivora: felid (cat); Primates: hominid (human)	freshwater Gastropoda: lymnaeid (*Lymnaea elodes, perega, rubiginosa, stagnalis, Radix Auricularia, peregra, Stagnicola palustris*), viviparid (*Filopaludina*), physid (*Physa occidentalis*), planorbid (*Segmentina*)	freshwater Gastropoda (pulmonate and prosobranch snails) physid (*Physa occidentalis*), lymanaeid (*Lymnaea*); Bivalvia (mussels, basket clams) cyrenid (*Corbicula producta*); Anura: ranid (frogs, tadpoles); Testudines (turtles)	Eurasia, Americas, Africa, Australia
E. rodriguesi	Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Rodentia: cricetid (hamster), murid (mice)	freshwater Gastropoda: physid (*Physa rivalis*)	freshwater Gastropoda: physid (*Physa rivalis*), planorbid (*Biomphalaria*	Brazil

			glabrata)	
E. serratum (syn. *Echinoparyphium*)	Anseriformes: anatid (duck)	freshwater Gastropoda: planorbid (*Isidorella brazieri*)		Australia
E. trivolvis (syn. *E. rodriguesi, E. armigerum, E. coalitum, E. callawayensis, E. multispinosum, Echinoparyphium contiguum*)	Anseriformes: anatid (duck, mallard, pintail, wigeon, teals, mottled duck, shoveler duck, shelduck, goldeneye, black duck, tufted duck, goose, emden goose, greylag goose, magpie goose, bean goose, scaup, ring-necked duck, fulvous whistling duck, common scoter, muscovy, mute swan, whooper swan,); Galliformes: phasianid (chicken, partridge); Passeriformes: icterid (grackle), corvid (carrion crow, jackdaw); Charadriiformes: larid (black-headed gull); Phoenicopteriformes: phoenicopterid (flamingo); Podicipediformes: podicipedid (great crested grebe); Columbiformes: columbid (mourning dove, pigeon); Accipitriformes: accipitrid (rough-legged buzzard); Strigiformes: strigid (horned owl); Rodentia: caviid (guinea pig), cricetid (golden hamster, muskrat), murid (mice, rats); Didelphimorphia: didelphid (opossum); Lagomorpha: leporid (rabbit); Carnivora: canid (dog, red fox), felid (cat): Artiodactyla: suid (pig); Primates: hominid (human)	freshwater Gastropoda: planorbid (*Helisoma trivolvis, Biomphalaria*), lymnaeid (*Lymnaea*), physid (*Physa*), bithyniid (*Bithynia*)	freshwater Gastropoda (pulmonate and prosobranch snails); Bivalvia (mussels); Rhabditophora (planarians); Anura (bullfrogs, green frogs, leopard frogs, tadpoles); Testudines (turtles); Osteichthyes (fish)	Americas, Europe
39-collar-spined				
E. aphylactum	Gruiformes: rallid (purple gallinule); Primates: callitrichid (Geoffroy's tamarin)			South America
E. platensis	Rodentia: cricetid (Argentine swamp rat)			South America
E. rufinae	Anseriformes: anatid (red-crested pochard)			Eurasia, North America
E. uralensis	Charadriiformes: scolopacid (woody sandpiper, Eurasian curlew, little curlew)		freshwater Gastropoda: bithynid (*Bithynia tentaculata, B. trocheli*), lymnaeid (*Lymnaea stagnalis*)	Russia
41-collar-spined				
E. alepidotum	Gruiformes: rallid (azure gallinule)			Brazil
E. angustitestis	Carnivora: canid (dog); Primates: hominid (human)		freshwater fish	Asia
E. rafiae	Pelecaniformes: ardeid (little egret)			Pakistan
E. turkestanica	Anseriformes: anatid (duck)			Eurasia, North America
43-collar-spined				
E. academica	Charadriiformes: scolopacid (black-tailed godwit)			Europe
E. aegyptiacum	Rodentia: murid (albino rat)			Japan
E. azerbaidjanicum	Galliformes: phasianid (chicken)			India
E. coronale	Passeriformes: corvid (carrion crow)			Russia
E. dietzi	Anseriformes: anatid (duck)			Eurasia,

				North America
E. macrorchis	Rodentia: murid (field mice, rats), cricetid (field vole); Eulipotyphla: talpid (mole); Charadriiformes: scolopacid (common snipe); Primates: hominid (human)	freshwater Gastropoda: lymnaeid (*Lymnaea luteola*)	freshwater Gastropoda: viviparid (*Cipangopaludina chinensis, C. malleata, C. japonica*), planorbid (*Segmentina nitidella*; Anura: ranid (frog)	Asia
E. malayanum (syn. *Artyfechinostomum*)	Carnivora: canid (dog), Artiodactyla: suid (pig); Rodentia: murid (mice, rats), cricetid (hamsters); Primates: hominid (human)	freshwater Gastropoda: planorbid (*Indoplanorbis exustus, Gyraulus convexisuculus*)	freshwater Gastropoda: lymnaeid (*Radix, Bullastra* (*Lymnaea cumingiana*), ampullariid (*Pila scutata*), planorbid (*Indoplanorbis exustus, Gyraulus convexisuculus*), Anura: dicroglassid (skittering frog, tadpoles); Osteichthyes (fish)	Southeast Asia, India
45-collar-spined				
E. attenuatum	Gruiformes: rallid (king rail, mangrove rail)			North America
E. australasianum	Gruiformes: gruid (brolga)			Australia
E. coromandum	Pelecaniformes: ardeid (cattle egret)			Germany (ex: India)
E. exile	Columbiformes: columbid (rock dove); Gruiformes: rallid (American purple gallinule)			South America
E. gotoi	Anseriformes: anatid (mallard, spot-billed duck)			Asia
E. jacanae	Charadriiformes: jacanid (wattled jacana)			South America
E. lahorensis	Galliformes: phasianid (chicken)			Pakistan
E. pindchi (formerly *Euparyphium*)	Podicipediformes: podicipedid (little grebe)			India
E. siticulosum	Tinamiformes: tinamid (undulated tinamou, variegated tinamou, yellow-legged tinamou)			South America
47-collar-spined				
E. chloropodis	Gruiformes: rallid (coots, gallinules, common moorhen); Anseriformes: anatid (duck)			Eurasia, North America
E. corvi	Passeriformes: corvid (carrion crow)			Japan
E. garzetti	Pelecaniformes: ardeid (little egret)			Pakistan
E. hilliferum	Gruiformes: pallid (Australasian swamphen)			Australia
E. hystricosum	Passeriformes: estrildid (white-headed munia, spotted munia); Columbiformes: columbid (zebra dove)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*), planorbid (*Gyraulus convexisulcus, Indoplanorbis exustus*)	Malaya
E. militare	Charadriiformes: scolopacid (Eurasian	freshwater		Eurasia

	curlew, jack snipe); Gruiformes: rallid (spotted crake)	Gastropoda: lymnaeid (*Lymnaea stagnalis*), viviparid (*Viviparus* (*Paludina*) *vivipara*)		
E. necopinum	Pelecaniformes: threskiornithid (bald ibis)			Brazil
E. rousseloti	Gruiformes: rallid (Allen's gallinule)			Africa
E. sarcinum	Gruiformes: gruid (common carne); Anseriformes: anatid (duck)			Eurasia, Africa, North America
E. travassosi	Passeriformes: corvid (gray crow)			Russia
49-collar-spined				
E. coecale	Galliformes: phasianid (chicken)			India
E. condignum	Caprimulgiformes: caprimulgid (scissor-tailed nightjar)			Brazil
E. ilocanum (syn. *Euparyphium*)	Carnivora: felid (cat), canid (dog); Rodentia: murid (rats, rice field rat); Primates: cercopithecid (baboon), hominid (human)	freshwater Gastropoda: planorbid (*Gyraulus, Hippeutis*)	freshwater Gastropoda: ampullariid (*Pila conica*), viviparid (*Viviparus javanicus*), lymnaeid (*Lymnaea rubiginosa*)	Asia, Philippines
51-collar-spined				
E. sindhenses	Pelecaniformes: ardeid (western cattle egret)			Pakistan
E. transfretanum	Gruiformes: rallid (red-gartered coot)			Brazil
Reptile species				
E. jacaretinga	Crocodilia: alligatorid (caiman)			Brazil
E. ornatum (= *Stephanoprora ornata*)	Crocodilia: crocodylid (Nile crocodile)			Egypt
E. umbonatum (= *Allechinostomum crocodili*)	Crocodilia: crocodylid (Nile crocodile, Siamese crocodile)			Africa, Southeast Asia
Piscine species				
E. annulatum	Gymnotiformes: gymnotid (electric eel)			South America
E. cristatum	Scombriformes: stromateid (blue butterfish)			Mediterranean
E. dujardinii	Pleuronectiformes: pleuronectid (European plaice), scophthalmid (turbot)			Europe
E. fallax	Trachiniformes: uranoscopid (Atlantic stargazer)			Atlantic
E. hispidum	Acipenseriformes: acipenserid (European sea sturgeon, starry sturgeon, sterlet)			Eurasia
E. pristis	Gadiformes: gadid (blue whiting)			Atlantic
E. scabrum	Gadiformes: lotid (common ling), gadid (Atlantic cod)			Atlantic
As yet unplaced				
E. apiculatum	Strigiformes: strigid (brown owl, tawny owl, short-eared owl)			North America
E. asiatica	Anseriformes: anatid (duck)			North America
E. bancrofti	Gruiformes: rallid (Eurasian coot)			India
E. bilobum	Gruiformes: rallid (Eurasian coot), Pelecaniformes: threskiornithid (Eurasian spoonbill, white ibis)			Eurasia, Australia
E. chishtii	Accipitriformes: accipitrid (black kite)			India

E. cinctum	Charadriiformes: charadriid (lapwings)			Europe
E. crecci	Anseriformes: anatid (duck)			North America
E. danubiana	Gruiformes: rallid (Eurasian coot)			Europe
E. denticulatum	Charadriiformes: larid (common tern, black tern, sandwich tern)			Northern Hemisphere
E. dilatatum	Galliformes: phasianid (junglefowl)			Asia
E. echiniferum	Charadriiformes: scolopacid (ruff)			Europe
E. echymiperae	Peramelemorphia: peramelid (spiny bandicoot)			Papua New Guinea
E. egregium (syn. *Dietziella*)	Pelecaniformes: threskiornithid (bald ibis); Anseriformes: anatid (piken duck)			Brazil, Middle-East
E. ferox	Ciconiiformes: ciconiid (white stork, black stork);Pelecaniformes: ardeid (brown bittern)			Europe, Africa
E. fotedari	Passeriformes: acrocephalid (clamorous reed warbler)			India
E. fulicae	Anseriformes: anatid (duck)			North America
E. koisarensis	Anseriformes: anatid (duck)			North America
E. leptosomum	Charadriiformes: scolopacid (dunlin, sanderling)			Eurasia
E. minimus	Anseriformes: anatid (duck)			North America
E. nephrocephalum	Passeriformes: muscicapid (rock thrush)			
E. nordiana	Anseriformes: anatid (greater scaup)			Europe
E. novum	Anseriformes: anatid (duck)			North America
E. ralli	Gruiformes: rallid (water rail)			Japan
E. spinulosum	Podicipediformes: podicipedid (great crested grebe); Anseriformes: anatid (garganey); Charadriiformes: alcid (black guillemot), larid (herring gull, glaucous gull, black-headed gull), scolopacid (curlew); Suliformes: phalacrocoracid (spectacled cormorant); Anseriformes: anatid (goldeneye)			Northern Hemisphere
E. stromi	Anseriformes: anatid (duck)			North America
E. turdi	Passeriformes: turdid (Tickell's thrush)			India
E. uncinatum	Gruiformes: rallid (moorhen)			

Parasite morphology: *Echinostoma* spp. form 7 different developmental stages: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae and adults. Eggs are typically oval-elliptical in shape and variable in size depending on the species, ranging from 58-150 µm in length by 36-88 µm in width. They are surrounded by a thin refractory tanned eggshell (yellow-brown or silver-white in colour) with an operculum (often small and inconspicuous) at one end and a small abopercular wrinkle, knob or thickening at the other end. Unembryonated ectolecithal eggs are passed in faeces, but embryonate in water to contain miracidia which are released upon hatching. Free-swimming miracidia are elongate measuring 65-120 x 45-70 µm, broad anteriorly and tapering posteriorly. They possess ciliated epidermal plates, apical papilla, 2 eyespots, and a pair of protonephridia with 2 excretory ducts and pores. In snails, they transform to non-ciliated contractile pleomorphic sacs (sporocysts) initially measuring around 100 µm long but growing to 200-250 µm. Sporocysts do not have defined organs but contain germ balls which form larval embryos (rediae) by asexual reproduction. Rediae are motile colourless elongate larvae measuring 0.5–2.0 x 0.07–0.2 mm and they possess an anterior mouth, pharynx, saccular gut, an anterior collar-like tegumentary ring, and 2 posterior stumpy locomotor appendages (ambulatory buds). There are 2-3 rediae generations with small mother rediae producing slightly larger daughter rediae and some forming grand-daughter redia. Daughter and grand-daughter rediae ultimately produce cercariae. Larval cercariae measure 0.2–0.6 x 0.1–0.2 mm

and are gymnocephalous with elongate bodies and simple cylindrical tails with finger-like tips. They are active swimmers and have oral and ventral suckers, an oral collar of spines, anterior cystogenous penetration glands and several finfolds (dorsal, ventral and ventrolateral). Metacercariae are tail-less cercariae that have encysted becoming surrounded by several cyst wall layers (thick outer wall, thin inner opaque wall). The cysts are spherical measuring from 100-200 µ in diameter and contain stages similar to immature worms with collar spines, excretory granules and an oesophagus. Adult trematodes have elongate-oval ventrally-curved bodies ranging in size from 2.5-30 mm in length by 0.6–6.0 mm in width, depending on species. The tegument is spinose (covered with scale-like spines), the number and size of which is reduced in the posterior half of the body. *Echinostoma* adults are characterized by the possession of a prominent circumoral collar armed with 27-55 large spines (up to 110 µm long) arranged in 1-2 ventrally interrupted rows. The oral and ventral suckers are well developed and the gut comprises a mouth, prepharynx, pharynx, oesophagus, and 2 blind caeca. Adult worms are hermaphroditic, with smooth or lobate testes in tandem in the posterior half of the body, and spherical or ovoid ovaries in the anterior body. Other male organs comprise the vas efferentia, vas deferens, cirrus sac (with seminal vesicle, ejaculatory duct, cirrus and prostate gland) terminating in a median genital pore. Other female organs consist of an oviduct (with seminal receptacle), numerous vitelline follicles (with ducts), an ootype (oviduct enlargement) surrounded by glandular tissue (Mehlis' gland) and a uterus also terminating in the genital pore.

Site of infection: Adult echinostomes infect the small intestines of their definitive hosts, including domestic and wild mammals (carnivores, rodents, primates) and aquatic birds (many families). In heavy infections, adults can also be found in stomach, liver, gall-bladder and pancreas of their vertebrate hosts. Larval sporocysts and rediae infect the tissues and organs of their first intermediate hosts (aquatic snails). Sporocysts often form near the site of miracidial penetration (foot, head) but rediae move to the heart and then the digestive gland-gonad complex. Encysted metacercariae form in the tissues of their second intermediate hosts (molluscs, crustaceans, fish and amphibians), particularly in the kidney-pericardial region of molluscs, the gills and gonads in clams, the kidneys and cloaca of frogs, and the skin and muscles of fish.

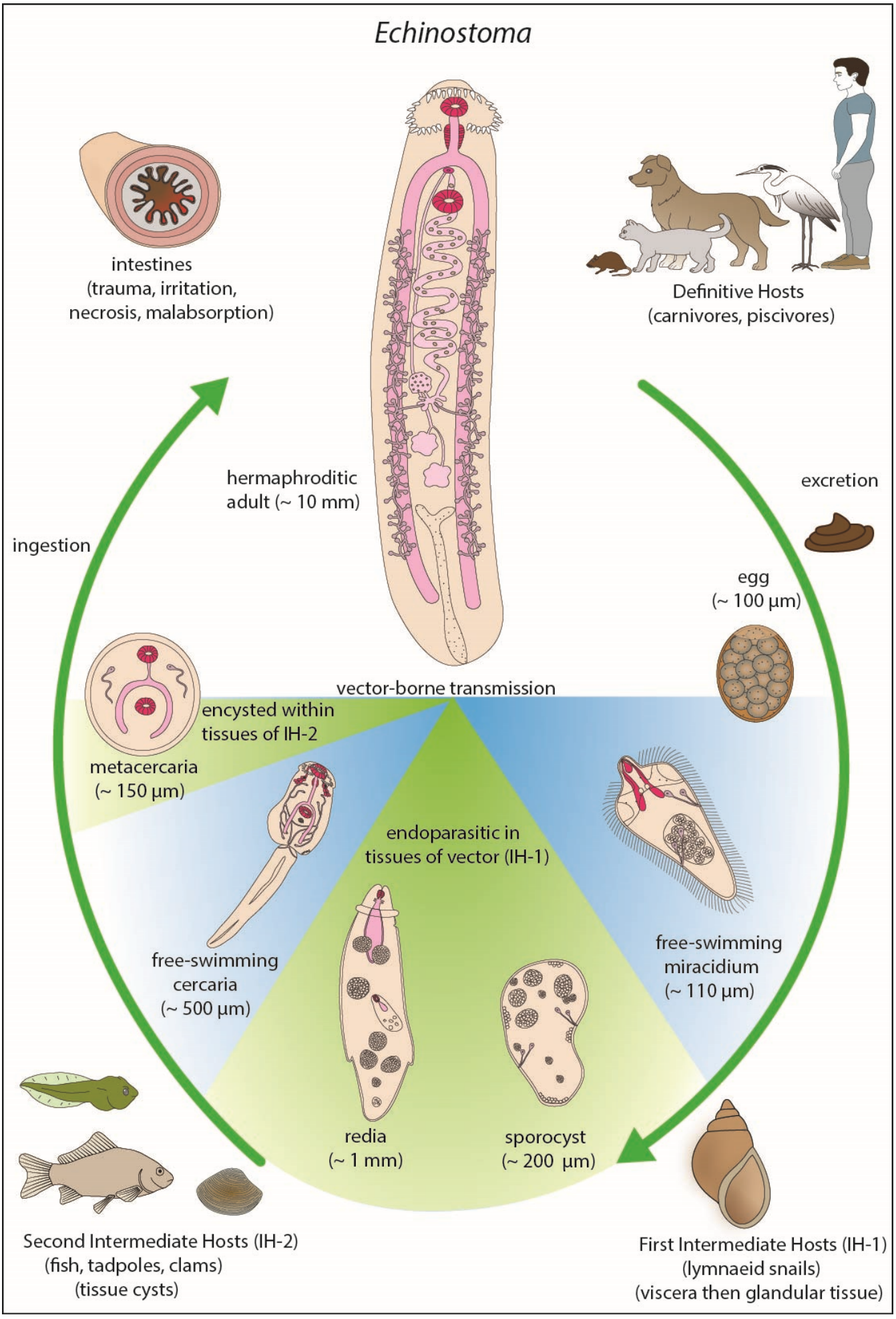
Pathogenesis: Trematodes have mouths (oral suckers) and saccular guts (blind caeca lacking an anus) which are used to feed on the intestinal mucosa of their vertebrate hosts. Light infections may be asymptomatic or subclinical, while heavier infections may cause clinical manifestations attributable to trauma/irritation at the site of attachment and to host immune/allergic responses to the flukes and their metabolites. Young and adult flukes attach to the mucosa using their oral and ventral suckers and collar spines to penetrate to subepithelial layers. They feed using their oral suckers to imbibe and pinch off tissue plugs which causes tissue damage, ulceration and inflammation. This may result in epithelial desquamation, villous blunting and atrophy, crypt hyperplasia, necrosis, enteritis, cellular infiltration, oedema, haemorrhages and vascular congestion. Adult flukes also secrete and excrete many metabolites (e.g. digestive enzymes, waste products) into the host gut which trigger physiological and immunological responses, including diarrhoea, anaemia and malabsorption with inflammatory, allergenic and hypersensitivity reactions. Light to moderate infections have been associated with intermittent diarrhoea, epigastric and abdominal pain, intestinal colic and flatulence, postprandial burning, headaches, dizziness, anorexia, weight loss, fatigue, mild anaemia and eosinophilia. Heavy infections may produce profuse watery diarrhoea, mucosal ulceration and haemorrhages, catarrhal enteritis, oedema, severe epigastric pain and abdominal discomfort, anorexia, malnutrition, weight loss, emaciation, weakness and a developing anaemia with elevated white blood cell counts, including eosinophilia. In heavy infections, adult worms may migrate up the common bile duct to the liver, gall-bladder and pancreas damaging tissues, causing haemorrhages and forming granulomas. While infections are unlikely to cause death in humans, they have severe consequences for patients in remote rural communities with limited healthcare by causing chronic diarrhoea with dehydration and malnutrition as well as predisposing them to other opportunistic infections, which collectively may prove fatal. In animals, heavy infections have been associated with severe disease and mortality, particularly in domestic fowl exhibiting haemorrhagic diarrhoea and emaciation.

Developmental cycle and mode of transmission: *Echinostoma* spp. have indirect life-cycles involving 3 different types of hosts: adult trematodes infecting definitive hosts (vertebrates), asexual stages multiplying within first intermediate hosts (molluscs), and metacercariae encysting within second intermediate hosts (vertebrates and invertebrates). Transmission from definitive to intermediate hosts involves free-swimming aquatic stages, while parasites move from second intermediate to definitive hosts by predator-prey transmission. Eggs produced by adult flukes are passed with host faeces to contaminate the external environment. Those deposited in water embryonate over 2-3 weeks depending on temperature (longer in colder water) and some have been observed to remain viable for up to 5 months. Most eggs hatch around 3 weeks releasing a non-feeding ciliated miracidium which swims around for 2-15 hours seeking a suitable aquatic snail host using positive phototaxis (swim to light), negative geotaxis (swim up) as well as chemotaxis (swim towards macromolecules secreted in snail mucus). *Echinostoma* spp. have been found within ampullariid, lymnaeid, physid, planorbid and viviparid snails, and their host specificity is generally confined to a few related snail species. The snails act as first intermediate hosts as the miracidia penetrate their tissues and undergo massive asexual multiplication forming several larval generations (a single sporocyst generation then 2 rediae generations). Sac-like sporocysts are formed within organs (usually the heart cavity) within 2 days and their germ balls produce first-generation (mother) rediae after 5 days. These rediae migrate to the gonads and/or digestive gland and produce second-generation (daughter) rediae which in turn produce numerous cercariae within 28-42 days of initial infection. Cercariae migrate to the mantle cavity and exit the host via the sinuses. They are free-swimming stages that periodically swim to the surface of the water and then sink to the bottom for up to 5 days. They may infect a wide range of second intermediate hosts, including the same or different snail species, bivalves (river mussels, basket

clams), amphibians (including tadpoles) or fish (particularly cyprinids). When cercariae penetrate host tissues, they shed their tails and encyst as metacercariae. Definitive hosts living in or near fresh-water or brackish-water habitats become infected when they eat infective metacercariae within the tissues of prey. Metacercariae excyst in the ileum releasing immature flukes which migrate to the lower small intestines where they attach to the gut wall and develop into adult flukes over 1-3 weeks. Mature flukes may produce from 300-2,000 eggs per day and they may live for several months. Human infections are most often associated with the consumption of raw or undercooked fish, clams or snails, particularly in specialized dishes in Asian cuisine: e.g. lab-pla or plasom (raw fish), kinilaw (raw fish or snails dipped in salt and vinegar), kukhol or kiambu-ay (raw fish in coconut milk), tinola (lightly boiled fish), gintaan (fish stewed in coconut milk), sinugba (charcoal-grilled fish), sashimi (raw sliced fish), and sushi (raw fish roll in rice).

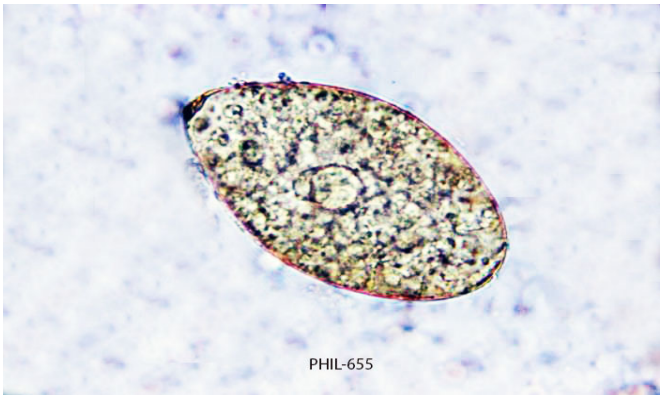
Differential diagnosis: Echinostome infections may be diagnosed by the detection of worm eggs in faecal samples, but the identification of particular species relies on the examination of whole adult worms recovered from hosts. Coprological tests may detect eggs in faecal smears (e.g. Kato-Katz thick smears, merthiolate-iodine-formalin fixation) or following their concentration by sedimentation (in water) and/or floatation (in saturated salt or sugar solutions). Adult flukes may be recovered from hosts ante-mortem following anthelmintic treatment or by endoscopic biopsy around the duodenal bulb, or post-mortem by dissection. *Echinostoma* spp. are differentiated mainly on the basis of the number and arrangement of the circumoral spines and the topography of the genital systems in adult flukes. Haematological and biochemical tests conducted on blood and urine samples have associated infections with reductions in erythrocyte parameters (anaemia), plasma choline, formate, acetate, lactate, urine creatine, increases in eosinophil counts, plasma glucose and distortions in neutral lipid and amino acid profiles, but such changes are mostly nonspecific and may be attributable to other causes. Enzyme immunoassays have been developed to detect class-specific host antibodies in serum samples (typified by early transient increases in IgM and secretory IgA, followed by more persistent IgG responses) as well as to detect parasite copro-antigens in faecal samples. These immunological tests were reported to vary considerably in their sensitivity and specificity, with cross-reactions found between various trematode species. Molecular biological techniques have recently been used to characterize DNA from adult flukes, metacercariae and eggs of various echinostome species (particularly those with 37 collar spines); mostly following polymerase chain reaction (PCR) amplification of restriction fragment length polymorphisms (RFLP), random amplified polymorphic DNA (RAPD) or particular gene sequences (nuclear DNA (small (18S) and large (28S) subunit ribosomal RNA and internal transcribed spacers 1 and 2) and mitochondrial DNA (nicotinamide adenine dinucleotide dehydrogenase subunit 1, and cytochrome c oxidase subunit 1).

Treatment and control: A range of anthelminthics have proven effective in treating echinostomiasis in humans, including the broad-spectrum benzimidazoles (albendazole, mebendazole), isoquinolines (praziquantel), halogenated phenols (bithionol), salicylanilides (nicolsamide, rafoxanide, oxyc1ozanide) and substituted dihydroxybenzene (hexylresorcinol). Most drugs had few side-effects, mostly nausea, abdominal pain, headaches and dizziness. Recent experiments have also reported some success *in vitro* using the trematodicide clorsulon, the anthelmintic tribendimidine and the antiprotozoal artemisinin (dihydroartemisinin). The halogenated hydrocarbons (tetrachloroethylene and carbon tetrachloride) have been used to treat infections in birds and some mammals, but their use in humans in contraindicated due to toxic or adverse interactions with dietary components. Despite regular treatment programmes in many endemic regions, re-infection was found to be common as the parasites may be maintained in sylvatic or peridomestic cycles involving aquatic birds and mammals. Preventive measures are based on breaking transmission cycles by reducing faecal contamination of water bodies (through proper effluent treatment and disposal), reducing intermediate host snail populations (using molluscicides or draining swampy fields), and avoiding the consumption of raw or improperly cooked foods (notably fish, clams, snails and frogs). Public health education campaigns may be used to inform at-risk groups although their impact may be eroded in endemic rural communities by poor living conditions, the lack of alternative food sources and entrenched dietary customs.

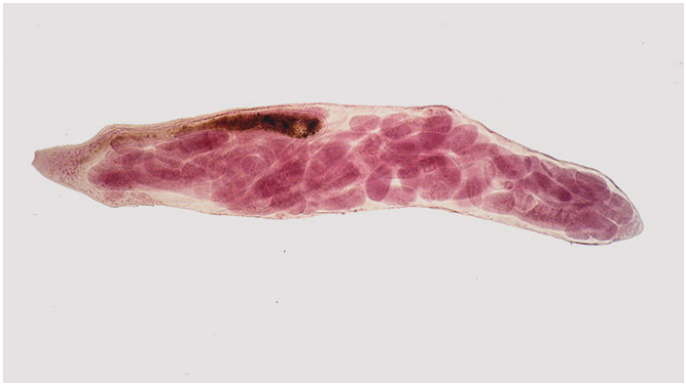

Echinostoma
intestines
(trauma, irritation,
necrosis, malabsorption)
Definitive Hosts
(carnivores, piscivores)
hermaphroditic
adult (~ 10 mm)
excretion
ingestion
egg
(~ 100 µm)
vector-borne transmission
encysted within
tissues of IH-2
metacercaria
(~ 150 µm)
endoparasitic in
tissues of vector (IH-1)
free-swimming
cercaria
(~ 500 µm)
free-swimming
miracidium
(~ 110 µm)
redia
(~ 1 mm)
sporocyst
(~ 200 µm)
Second Intermediate Hosts (IH-2)
(fish, tadpoles, clams)
(tissue cysts)
First Intermediate Hosts (IH-1)
(lymnaeid snails)
(viscera then glandular tissue)



Echinostoma adult worm



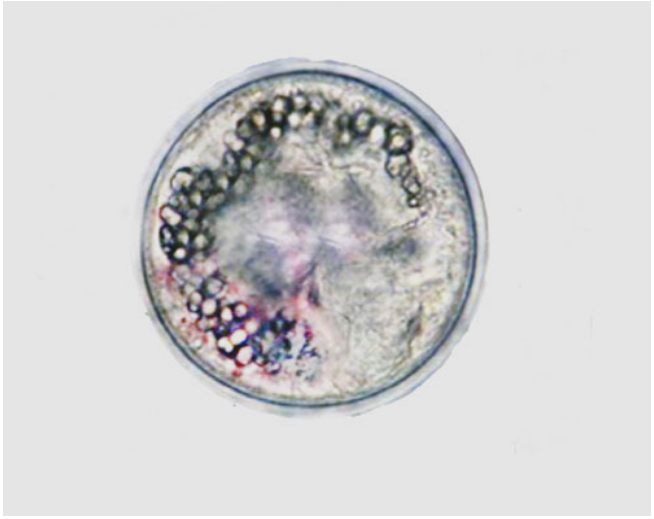
Echinostoma egg



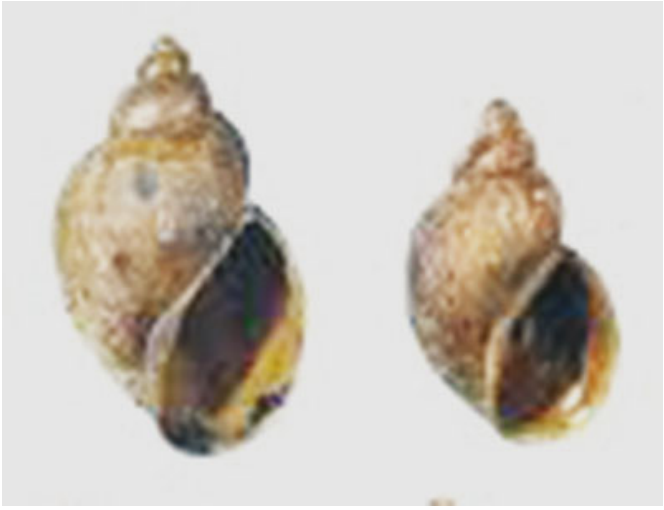
Echinostoma redia



Echinostoma cercaria



Echinostoma metacercaria



Echinostoma lymnaeid snail vectors

Sister genera to *Echinostoma*

Parasite species	Definitive hosts [adults in intestines]	First intermediate hosts [sporocysts/rediae in tissues]	Second intermediate hosts [metacercariae in tissues]	Distribution
Subfamily: Echinochasminae				
Echinochasmus				
E. accipeteri	Accipitriformes: accipitrid (shikra)			Pakistan
E. amphibolus (syn. *E. botauri*)	Pelecaniformes: ardeid (Eurasian bittern, black-crowned night heron); Suliformes: phalacrocoracid (great cormorant); Gruiformes: rallid (common moorhen)			Europe, Pakistan
E. antigonus	Gruiformes: gruid (sarus crane)			India
E. bagulai	Pelecaniformes: ardeid (Indian pond heron)	freshwater Gastropoda: thiarid (*Thiara tuberculata*)	freshwater Cyprinodontiformes: aplocheilid (blue panchax), poeciliid (western mosquitofish); Beloniformes: adrianichthyid (medaka); Anabantiformes: channid (spotted snakehead)	Asia, India
E. beleocephalus	Passeriformes: sittid (Eurasian nuthatch); Pelecaniformes: ardeid (black-crowned night heron, grey heron); Galliformes: phasianid (chicken)	freshwater Gastropoda: bithyniid (*Parafossarulus*)	freshwater Cypriniformes: cyprinid (goldfish); Anura: ranid (*Rana dubowskii* tadpoles); freshwater Gastropoda: bithyniid (*Parafossarulus*)	Europe
E. coaxatus (syn. *E. squamatus)*	Anseriformes: anatid (mallard); Podicipediformes: podicipedid (black-necked grebe, red-necked grebe, great crested grebe); Ciconiiformes: ciconiid (white stork); Columbiformes: columbid (pigeon)	freshwater Gastropoda: bithyniid (*Bithynia tentaculata*)	freshwater Cypriniformes: cyprinid (spined loach, Caspian roach, rudd, tench, bleak, silver bream); Perciformes: percid (European perch); Gasterosteiformes: gasterosteid (Ukrainian stickleback); Gobiformes: gobiid (bighead goby, round goby)	Eurasia, North America
E. cohensi	Charadriiformes: larid (European herring gull)			Europe
E. colymbi (= *E. schigini*) (= *Episthmium*?)	Podicipediformes: podicipedid (grebes)			Eurasia
E. dietzevi	Pelecaniformes: threskiornithid (roseate spoonbill); Anseriformes: anatid (teal); Podicipediformes: podicipedid (great crested grebe, black-necked grebe)			Europe, North America
E. donaldsoni	Pelecaniformes: pelecanid (brown pelican, American white pelican);	freshwater Gastropoda: amnicolid (*Amnicola limosa, A.*	freshwater fish	North America

	Columbiformes: columbid (pigeon); Podicipediformes: podicipedid (pied-billed grebe)	*lustrica*)		
E. euryporus	Accipitriformes: accipitrid (buzzard, western marsh harrier, pallid harrier, red kite, black kite); Pelecaniformes: ardeid (grey heron, great egret, little egret)			Eurasia, Africa
E. famelicus	Ciconiiformes: ciconiid (lesser adjutant)			Sri Lanka
E. fujianensis	Carnivora: canid (dog), felid (cat); Artiodactyla: suid (pig); Rodentia: murid (rats); Primates: hominid (human)	freshwater Gastropoda: viviparid (*Bellamya aeruginosa*)	freshwater Cypriniformes: cyprinid (stone moroko, common carp)	China
E. gorsakii	Pelecaniformes: ardeid (Japanese night heron)			Japan
E. japonicus	Galliformes: phasianid (chicken); Anseriformes: anatid (duck); Pelecaniformes: ardeid (egret); Carnivora: canid (dog), felid (cat); Rodentia: murid (rats, mice); Primates: hominid (human)	freshwater Gastropoda: bithyniid (*Parafossarulus striatulus, P. manchouricus, Boreoelona*)	freshwater Cypriniformes: cyprinid (stone moroko, Manchurian gudgeon); Osmeriformes: osmerid (pond smelt); Anura: ranid (Dybowski's frog, tadpoles)	Asia, Europe
E. jamshorensi	Pelecaniformes: ardeid (Indian pond heron)			Pakistan
E. jiufoensis	Primates: hominid (human)			China
E. liliputanus	Primates: hominid (human); Carnivora: canid (dog, fox), felid (cat), mustelid (badger), procyonid (raccoon), birds?	freshwater Gastropoda: viviparid (*Bellamya aeruginosa*), bithyniid (*Parafossarulus striatulus*)	freshwater Cypriniformes: cyprinid (stone moroko, goldfish) [plus drinking water containing cercariae]	Middle-East, China
E. leopoldinae	Galliformes: phasianid (chicken)	aquatic Gastropoda: hydrobiid (*Pyrgophorus coronatus*)	brackish water Cichliformes: cichlid (Mayan cichlid, firemouth cichlid, Nile tilapia)	Mexico
E. macrocaudatus	Galliformes: phasianid (chicken); Anseriformes: anatid (duck)	aquatic Gastropoda: hydrobiid (*Pyrgophorus coronatus*)	freshwater Characiformes: characid (Mexican tetra); Cyprinodontiformes: poeciliid (variegated platy, Yucatan molly)	Mexico
E. mathevossianae (syn. *Schiginella*)	Anseriformes: anatid (pochard, goldeneye)			Russia
E. mazharuddini	Passeriformes: sturnid (bank myna)			Pakistan
E. megavitellus	Pelecaniformes: ardeid (Indian pond heron)			India
E. mergi (syn. *Stephanoprora mergi*, *Mesorchis mergi*) (incl. subspp. *E. m. mergi, E. m. palaearcticus*)	Anseriformes: anatid (merganser)			Europe, North America
E. microacetabulum	Charadriiformes: larid (European herring gull)			Russia
E. militaris	Pelecaniformes: ardeid (grey heron)			Europe
E. milvi	Accipitriformes: accipitrid (black kite)			Japan

E. mirus	Anseriformes: anatid (common eider)			Europe
E. mohiuddini	Pelecaniformes: ardeid (Indian pond heron)			Pakistan
E. mordax	Podicipediformes: podicipedid (great crested grebe); Pelecaniformes: pelecanid (Dalmatian pelican)			Eurasia, Africa
E. muraschkinzevi	Pelecaniformes: pelecanid (Dalmatian pelican)			Russia
E. narayani	Accipitriformes: accipitrid (black kite)			India
E. passeri	Passeriformes: passerid (house sparrow)			Pakistan
E. perfoliatus	Carnivora: canid (dog, red fox), felid (cat); Artiodactyla: suid (pig); Rodentia: murid (rats); Primates: hominid (human); Galliformes: phasianid (chicken)	freshwater Gastropoda: bithyniid (*Parafossarulus manchouricus*, *Bithynia leachi*), lymnaeid (*Lymnaea stagnalis*)	freshwater Cypriniformes: cyprinid (goldfish, carp, pale chub, dark chub, stone moroko)	Asia, Europe
E. prakashi	Pelecaniformes: ardeid (black-crowned night heron)			Pakistan
E. reniovarus	Passeriformes: corvid (house crow)			India
E. ruficapensis	Pelecaniformes: ardeid (black-crowned night heron); Podicipediformes: podicipedid (little grebe)			Europe
E. schwartzi	Anseriformes: anatid (ducks); Rodentia: murid (mouse)		freshwater Cyprinodontiformes: fundulid (mummichog)	North America
E. skrjabini	Gaviiformes: gaviid (red-throated loon); Podicipediformes: podicipedid (great crested grebe)			Europe
E. spinulosus	Anseriformes: anatid (ducks)			Europe
E. swabiensis	Accipitriformes: accipitrid (black kite)			Pakistan
E. tobi	Accipitriformes: accipitrid (black kite)			Japan
E. vindhianae	Accipitriformes: accipitrid (Asian tawny eagle)			India
E. zubedakhaname	Passeriformes: tyrannid (pied water tyrant); Columbiformes: columbid (pigeon); Galliformes: phasianid (chicken)	freshwater Gastropoda: ampullariid (*Pomacea glauca*)	freshwater Cyprinodontiformes: poeciliid (rainbow fish)	Americas
Episthmium				
E. bilqeesae	Pelecaniformes: ardeid (little egret)			Pakistan
E. bursicola (syn. *Uroproctepisthmium*)	Pelecaniformes: ardeid (grey heron)			Europe
E. caninum	Carnivora: canid (dog), felid (cat); Primates: hominid (human)		freshwater fish	Asia
E. colymbi	Pelecaniformes: ardeid (little egret)			Pakistan
Subfamily: Echinostominae				

Euparyphium				
E. albuferensis	Rodentia: murid (rats, mice), cricetid (hamster)	freshwater Gastropoda: planorbid (*Gyraulus chinensis*)	freshwater Gastropoda: planorbid (*Gyraulus chinensis*), lymnaeid (*Lymnaea trunculata, L. peregra, L. palustris*), physid (*Physa acuta*)	Europe
E. beaveri (syn. *Isthmiophora*)	Carnivora: mustelid (mink, otter); Lagomorpha: leporid (snowshoe hare)	freshwater Gastropoda: lymnaeid (*Stagnicola* (*Lymnaea*) *angulata*)	freshwater Anura (tadpoles, frogs)	North America
E. capitaneum (syn. *E. anhingae*)	Suliformes: anhingid (darter)			North America
E. guerreroi	Rodentia: murid (brown rat)			
E. inermis (syn. *Isthmiophora*)	Carnivora: mustelid (North American river otter)			North America
E. lukjanovi (syn. *Isthmiophora*)	Artiodactyla: bovid (goitered gazelle)			Russia
E. melis (syn. *Isthmiophora*)	Carnivora: felid (cat), canid (fox), mustelid (European polecat, mink, badger, otter); Eulipotyphla: erinaceid (hedgehog); Rodentia: murid (rats)	freshwater Gastropoda: lymnaeid (*Lymnaea*)	freshwater Cypriniformes: cobitid (loach); Anura: ranid (tadpoles)	Europe
E. murinum	Rodentia: murid (rats); Anseriformes: anatid (ducks); Galliformes: phasianid (chicken)	freshwater Gastropoda: lymnaeid (*Lymnaea peregra*), planorbid (*Gyraulus chinensis*), lymnaeid (*Lymnaea ollula*	freshwater Gastropoda: lymnaeid (*Lymnaea peregra*), planorbid (*Gyraulus chinensis, Segmentina hemisphaerula, Hippeutis cantori*), lymnaeid (*Lymnaea ollula*), bithynid (*Parafossarulus striatulus*), viviparid (*Viviparus*); Anura: ranid (tadpoles)	Philippines, China
E. paramurinum	Rodentia: caviid (guinea pig)	freshwater Gastropoda: viviparid (*Vivipara angularis*)	freshwater Gastropoda: viviparid (*Vivipara angularis*)	Philippines
E. vietnamensis	Carnivora: mustelid (Eurasian otter)			Vietnam
Echinoparyphium				
E. aconiatum	Galliformes: phasianid (ruffed grouse); Charadriiformes: scolopacid (black-tailed godwit); Anseriformes: anatid (ducks)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis, L. corvus*)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis, L. corvus, Stagnicola turricula, Radix peregra, R. auricularia*), bithyniid (*Bithynia tentaculata, B. troscheli*), planorbid (*Planorbarius corneus, Planorbis planorbis*), physid (*Physella acuta*)	Eurasia, North America
E. agnatum	Anseriformes: anatid (mallard)			Europe
E. baculoides	Charadriiformes: larid (whiskered tern)			Eurasia
E. baculus	Anseriformes: anatid (smew, scaup, goldeneye, northern shoveler, velvet scoter); Gaviiformes: gaviid (black-throated loon)			Eurasia
E. bagulai	Anseriformes: anatid (Indian spot-billed duck)	freshwater Gastropoda: lymnaeid	freshwater Gastropoda: lymnaeid (*Lymnaea luteola*)	India

		(*Lymnaea luteola*)		
E. chinensis	Anseriformes: anatid (duck)			China
E. cinctum	Anseriformes: anatid (duck); Charadriiformes: scolopacid (black-tailed godwit)	freshwater Gastropoda: lymnaeid (*Lymnaea*)	freshwater Gastropoda: lymnaeid (*Lymnaea*); Anura: ranid (frogs); Testudines (turtles)	Europe
E. clerci (syn. *Echinostoma*?)	Anseriformes: anatid (domestic duck); Charadriiformes: scolopacid (black-tailed godwit)			India
E. combesi	Galliformes: phasianid (chicken); Rodentia: murid (mouse)	freshwater Gastropoda: planorbid (*Bulinus truncatus*), physid (*Physa acuta*)	freshwater Gastropoda: planorbid (*Bulinus truncatus, Planorbarius metidjensis*), physid (*Physa acuta*); Anura: ranid (marsh frog tadpoles)	Africa
E. contiguum	Rodentia: cricetid (muskrat)			North America
E. dollfusi (syn. *Paryphostomum*?)	Suliformes: anhingid (Indian darter)			India
E. dunni	Anseriformes: anatid (duck); Columbiformes: columbid (pigeon); Passeriformes: estrildid (white-capped munia, spotted munia, Java sparrow)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*), planorbid (*Gyraulus convexiusculus, Indoplanorbis exustus*), viviparid (*Bellamya ingallsiana*)	Malaysia
E. elegans	Anseriformes: anatid (ducks); Pelecaniformes: ardeid (western cattle egret); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Passeriformes: fringillid (canary); Rodentia: murid (rats); Carnivora: felid (cat)	freshwater Gastropoda: planorbid (*Bulinus truncatus, B. tropica*)	freshwater Gastropoda: planorbid (*Bulinus truncatus, B. globosus, B. tropica, Biomphalaria glabrata*), physid (*Physa acuta*)	Africa
E. ellisi	Anseriformes: anatid (duck, black swan)	freshwater Gastropoda: planorbid (*Glyptophysa*)		Australia, New Zealand
E. flexum	Anseriformes: anatid (blue-winged teal, black scoter), Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon)	freshwater Gastropoda: lymnaeid (*Lymnaea* (*Stagnicola*) *palustris*)	freshwater Gastropoda: lymnaeid (*Lymnaea* (*Stagnicola*) *palustris*), viviparid (*Viviparus bengalensis*), physid (Physa); Anura (ranid, hylid tadpoles)	North America
E. gallinarum	Galliformes: phasianid (chicken)			China
E. gizzardai	Anseriformes: anatid (black swan)			India
E. indicum	Accipitriformes: accipitrid (Egyptian vulture)			India
E. groenlandicum	Charadriiformes: scolopacid (purple sandpiper)			Greenland
E. hirundonis (syn. *Euparyphium*)	Passeriformes: hirundinid (red-rumped swallow)			Taiwan
E. hydromys	Rodentia: murid (Australian water rat, dusky rat)	freshwater Gastropoda: planorbid (*Plananisis* (*Gyraulus*) *isingi*)	Anura: ranid (tadpoles)	Australia
E. ichthyophilum	Pelecaniformes: ardeid (grey heron)			Eurasia
E. kashmirensis	Galliformes: phasianid			India

	(chicken)			
E. limosorum	Charadriiformes: scolopacid (black-tailed godwit)			Europe
E. longicirrus	Anseriformes: anatid (mute swan)			India
E. macrovitellatum	Suliformes: phalacrocoracid (great cormorant)			Russia
E. megacirrus	Galliformes: phasianid (chicken); Rodentia: murid (mouse)		freshwater Bivalvia: hyriid (*Diplodon chilensis*); and Platyhelminthes: temnocephalid (*Temnocephala chilensis*) ectosymbiotic on Decapoda: aeglid (Patagonian crab)	South America
E. mordvilkowi	Charadriiformes: charadriid (northern lapwing, plovers, killdeers), scolopacid (black-tailed godwit)	freshwater Gastropoda: valvatid (*Valvata piscinalis*)	freshwater Gastropoda: valvatid (*Valvata piscinalis*)	Eurasia
E. montgomeriana	Columbiformes: columbid (pigeon)	freshwater Gastropoda: planorbid (*Bulinus africanus*)		Africa
E. nordianum	Anseriformes: anatid (Eurasian wigeon)			Eurasia
E. oscitansi	Ciconiiformes: ciconiid (Asian openbill stork)			Asia
E. paracinctum	Charadriiformes: scolopacid (black-tailed godwit)			Europe
E. petrowi (syn. *Neoacanthoparyphium*?)	Anseriformes: anatid (duck, goose); Galliformes: phasianid (chicken)		freshwater Gastropoda: viviparid (*Viviparus viviparous*)	Russia
E. phasianinum	Galliformes: phasianid (pheasant)			Russia
E. politus (syn. *Echinostoma*?)	Charadriiformes: scolopacid (green sandpiper)			Europe
E. poulini	Anseriformes: anatid (black swan)			New Zealand
E. pseudorecurvatum	Anseriformes: anatid (duck); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon)	freshwater Gastropoda: planorbid (*Planorbis planorbis*)	freshwater Gastropoda: planorbid (*Planorbis planorbis*); Anura (frogs, tadpoles)	Europe
E. ralphaudyi	Anseriformes: anatid (duck); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Passeriformes: fringillid (finch); Rodentia: murid (mouse, rat), cricetid (hamster)	freshwater Gastropoda: planorbid (*Bulinus truncatus, B. forskalii, B. sericinus*)	freshwater Gastropoda: planorbid (*Bulinus truncatus, B. forskalii, B. sericinus*)	Africa
E. recurvatum (syn. *E. bioccalerouxi*)	Anseriformes: anatid (mallard, greater scaup, tufted duck, spot-billed duck, brahmany duck, graylag goose); Podicipediformes: podicipedid (greater crested grebe); Galliformes: phasianid (chicken, pheasant, ruffed grouse, turkey); Columbiformes: columbid (pigeon); Charadriiformes: larid (southern black-backed gull, red-billed gull), charadriid (common ringed plover), scolopacid (common	freshwater Gastropoda: lymnaeid (*Radix peregra, R. auricularia, Lymnaea peregra, L. stagnalis*), valvatid (*Valvata piscinalis*), physid (*Physa fontinalis)*, planorbid (*Planorbis carinatus, Planorbarius corneus, Bulinus truncatus*)	freshwater Gastropoda: lymnaeid (*Radix auricularia, Lymnaea peregra, L stagnalis*), physid (*Physa fontinalis*), planorbid (*Planorbis planorbis, Biomphalaria glabrata*); Bivalvia (clams, mussels); Anura: ranid (European grass frog, tadpoles); Cypriniformes: cobitid (loach)	worldwide

	snipe, black-tailed godwit); Accipitriformes: accipitrid (common buzzard); Rodentia: murid (rats): Carnivora: canid (dog); Primates: hominid (human)			
E. rubrum	Galliformes: phasianid (pheasant); Accipitriformes: accipitrid (red-tailed hawk); Rodentia: cricetid (golden hamster)	freshwater Gastropoda: physid (*Physa gyrina, P. occidentalis)*		North America
E. scapteromae	Rodentia: cricetid (Argentine swamp rat)			South America
E. schulzi	Columbiformes: columbid (pigeon)			Europe
E. serratum	Anseriformes: anatid (duck); Galliformes: phasianid (chicken)	freshwater Gastropoda: planorbid (*Isidorella brazieri*)	freshwater Gastropoda: planorbid (*Isidorella brazieri*)	Australia
E. sinorchis	Anseriformes: anatid (garganey), Passeriformes: corvid (azure-winged magpie)			Europe
E. speotyto	Strigiformes: strigid (burrowing owl)			North America
E. spiniferum	Anseriformes: anatid (Pekin duck)	freshwater Gastropoda: planorbid (*Planorbarius corneus*)		Asia
E. spinosus	Charadriiformes: charadriid (spur-winged plover)			India
E. syrdariense	Galliformes: phasianid (chicken)			Russia
E. westsibiricum	Galliformes: phasianid (chicken)			Russia
Hypoderaeum				
H. batanguensis	Gruiformes: rallid (moorhen)			Eurasia
H. conoideum	Anseriformes: anatid (duck, mallard, garganey, scaup, northern shoveler, merganser, swan, goose); Podicipediformes: podicipedid (grebes); Galliformes: phasianid (chicken, turkey); Columbiformes: columbid (pigeon); Primates: hominid (humans)	freshwater Gastropoda: planorbid (*Indoplanorbis exustus, Planorbis corneus*), lymnaeid (*Radix rubiginosa, Lymnaea peregra, L. auricularia, L. trunculata, L. stagnalis, L. ovata, L. limosa, L. tumida, L. corvus*)	freshwater Gastropoda: lymnaeid (*Lymnaea trunculata, L. stagnalis, L. limosa, L. tumida, L. ovata*), planorbid (*Planorbis planorbis, P. corneus*); Bivalvia (clams, mussels); Anura (frogs, tadpoles)	Eurasia
H. cubanicum	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (*Lymnaea tumida*)	freshwater Gastropoda: lymnaeid (*Lymnaea tumida*), planorbid (*Planorbis planorbis*)	Cuba
H. dingeri	Anseriformes: anatid (duck, goose)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*), lymnaeid (*Gastrothylax crumenifer*)		Thailand
H. essexensis	Anseriformes: anatid (duck)			England
H. gnedini	Anseriformes: anatid (red-necked duck, pouting duck, green-winged duck, mallard, spotted duck, white-browed			China, Russia

	duck, red-headed duck); Galliformes: phasianid (chicken)			
H. longitestis (syn. *Euparyphium, Vermatrema*)	Anseriformes: anatid (black swan)			India
H. magnocirrusa	Anseriformes: anatid (pintail)			India
H. mainpuria	Anseriformes: anatid (shoveler)			Europe
H. microspina	Anseriformes: anatid (pintail)			India
H. sinensis	Anseriformes: anatid (duck)			China
H. skrjabini	Anseriformes: anatid (duck)			Russia
H. vigi	Anseriformes: anatid (greater scaup); Charadriiformes: scolopacid (little stint, dunlin)			Eurasia

Paramphistomum
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult paramphistomids are thick fleshy worms and the ventral sucker is near the posterior end. Paramphistomes are conical (rather than flat) in shape and most occur as parasites in the forestomach of ruminants (rumen/stomach flukes), although some infect the intestines of pigs and horses. Infections by a range of species belonging to several genera have been associated with enteritis and diarrhoea in domestic animals.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum: Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade: Neodermata (syncytial tegument = neodermis)
Class: Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass: Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order: Plagiorchiida ('echinostomatids', plagiorchiids', mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder: Pronocephalata (gastropod IH, sporocyst and redia formed; simple-tailed cercariae, encysts in open, metacercariae eaten by DH)
Superfamily: Paramphistomoidea (rumen flukes, miracidium penetrates gastropod IH)
Family: Paramphistomidae (thick fleshy worms, conical shape, ventral sucker near posterior end, rediae with appendages, cercariae with two eyespots)
Genus: *Paramphistomum* (parasitic in rumen/reticulum of cattle/sheep)
Species: various species cause diarrhoea

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs, fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the

tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. The suborder Pronocephalata is characterized by species forming simple-tailed cercariae which encyst in the open and the resultant metacercariae are eaten by herbivorous/omnivorous definitive hosts. One important superfamily is the Paramphistomoidea which contains thick fleshy worms from the stomach and intestines of a wide range of omnivores and herbivores. Adult worms have a pharynx rather than an oral

sucker at the anterior end and a ventral sucker at the posterior end (amphistome arrangement, as distinct from monostome, holostome, distome, echinostome or schistosome). Hundreds of species have been described in over 140 genera in 10 families (Balanorchiidae, Brumptiidae, Cladorchiidae, Diplodiscidae, Gastrodiscidae, Gastrothylacidae, Mesometridae, Microscaphidiidae, Paramphistomidae and Zygocotylidae). Familial designations have been extensively reviewed on the basis of morphotypic and biotypic characters with significant reclassifications of individual genera and species. Hopefully, contemporary molecular characterization studies will help resolve their phylogenetic affinities. Amphistome stomach flukes have been detected in a broad range of definitive hosts encompassing all vertebrate classes (mammals, birds, reptiles, amphibians and fish) widely distributed throughout the world.

Paramphistome families and subfamilies	**Genera**	**Definitive Hosts**
Paramphistomidae		
Paramphistominae	*Calicophoron, Cotylophoron, Explanatum, Gigantocotyle, Paramphistomum* (syn. *Liorchis, Srivastavaia*), *Ugandocotyle*	artiodactyls
Orthocoeliinae	*Bilatorchis, Buxifrons, Gemellicotyle, Gigantoatrium, Glyptamphistoma, Leiperocotyle, Macropharynx, Nilocotyle, Orthocoelium* (syn. *Ceylonocotyle*), *Palamphistomum, Paramphistomoides, Platyamphistoma, Pseudoparamphistoma, Sellsitrema*	artiodactyls
Gastrothylacidae		
	Carmyerius, *Duttiella, Fischoederius*, *Gastrothylax, Velasquezotrema*	artiodactyls
Zygocotylidae		
Olveriinae	*Olveria, Sureshiella*	artiodactyls
Pseudodiscinae	*Macropotrema, Pseudodiscus*	perissodactyls, proboscids, macropodids
Stephanopharynginae	*Stephanopharynx*	artiodactyls
Watsoniinae	*Gastrodiscoides*, *Homalogaster*, *Skrjabinocladorchis, Watsonius*	primates, artiodactyls, rodents
Zygocotylinae	*Choerocotyloides, Wardius, Zygocotyle*	birds, artiodactyls, rodents
Gastrodiscidae		
	Gastrodiscus	proboscids, perissodactyls
Brumptiidae		
	Brumptia, Choerocotyle, Hawkesius	proboscids, rhinocerotids
Balanorchiidae		
	Balanorchis	artiodactyls
Cladorchiidae		
Caballerodiscinae	*Cabellerodiscus, Elseyatrema*	reptiles
Caballeroiinae	*Bancroftrema, Cabelleroia, Platycladorchis*	fish
Chiorchiinae	*Chiorchis, Chiostichorchis, Paraibatrema*	testudines, rodents, sirenia
Cladorchiinae	*Australodiscus, Catadiscus, Cladorchis, Dermatemytrema, Diplodiscus, Progonimodiscus, Pseudodiplodiscus, Taxorchis*	mainly amphibians
Dadaytrematinae	*Alphamphistoma, Anavilhanatrema, Annelamphistoma, Australotrema, Betamphistoma, Cleptodiscus, Dadayius, Dadaytrema, Dadaytremoides, Deltamphistoma, Gammamphistoma, Inpamphistoma, Macrorchitrema, Neocladorchis, Ophioxenus, Pacudistoma, Panamphistomum, Pronamphistoma*	fish, amphibians
Helostomatinae	*Amurotrema, Helostomatis, Protocladorchis*	fish
Megalodiscinae	*Megalodiscus, Opisthodiscus, Pseudopisthodiscus*	mainly amphibians
Microrchiinae	*Brevicaecum, Colocladorchis, Kalitrema, Micramphistoma, Microrchis, Nicollodiscus, Pseudocladorchis*	fish
Nemathophilinae	*Halltrema, Nematophila, Parachiorchis, Pseudoalassostoma*	reptiles
Orientodiscinae	*Australotrema, Basidiodiscus, Orientodiscus, Pretestis, Pseudoorientodiscus, Sandonia*	fish
Osteochilotrematinae	*Osteochilotrema*	fish
Pfenderiinae	*Pfenderius*	proboscids
Pisciamphistominae	*Pisciamphistomum*	fish
Schizamphistominae	*Alassostoma, Alassostomoides, Lobatodiscus, Pseudoalassostomoides, Pseudoceloiptodiscus, Quasichiorchis,*	mainly reptiles, amphibians

	Schizamphistomum, Schizamphistomoides, Stunkardia	
Solenorchiinae	*Solenorchis*	dugongs
Stichorchiinae	*Stichorchis*	rodents, artiodactyls
Transvassosiniinae	*Travassosinia, Zetamphistoma*	fish
Mesometridae		
	Centroderma, Elstia, Mesometra, Neowardula, Parawardula, Wardula	fish
Microscaphidiidae (syn. Angiodictyidae)		
	Angiodictyum, Curumai, Denticauda, Deuterobaris, Dictyangium, Doodytrema, Hexangitrema, Hexangium, Microscaphidium, Neoctangium, Neodeuterobaris, Neohexangitrema, Octangioides, Octangium, Paradeuterobaris, Podocnemitrema, Polyangium, Polygorgyra, Pseudohexangium, Pseudoparabaris	testudines

Most of the known paramphistomoids of ruminants (commonly known as paramphistomes) belong to 2 families Paramphistomidae and Gastrothylacidae. The family Paramphistomidae comprises the rumen flukes whose adults lack a ventral pouch, and some 20 genera have been classified in 2 major subfamilies: the Paramphistominae (Laurer's canal crosses excretory duct); and the Orthocoeliinae (Laurer's canal and excretory duct do not cross). Some classifications include other subfamilies within the Paramphistomidae but subsequent reviews have reassigned them elsewhere. Notably, the subfamily Pseudodiscinae was transferred to the family Zygocotylidae; the subfamily Cladorchiinae to the family Cladorchiidae (although the genus *Olveria* was established in a new subfamily Olveriinae in the family Zygocotylidae); and the subfamily Gastrodiscinae was split with the genus *Gastrodiscus* placed in the family Gastrodiscidae and the genera *Gastrodiscoides* and *Homalogaster* allocated to the subfamily Watsoniinae in the family Zygocotylidae. The family Gastrothylacidae contains rumen flukes whose adults possess a ventral pouch, and 4 genera are recognized. Various species of rumen flukes impact on domestic livestock industries by causing morbidity and production losses (rarely mortality).

Amphistome species	**Definitive hosts [location]**	**First intermediate hosts [sporocysts/rediae in tissues]**	**Infective stages**	**Distribution**
Family: Paramphistomidae				
Subfamily: Paramphistominae (Laurer's canal crosses excretory duct)				
Paramphistomum				
P. bothriophoron	Artiodactyla: bovid (zebu)			Africa
P. cephalophi	Artiodactyla: bovid (black-fronted duiker) [small intestines]			Africa
P. cervi (rumen fluke)	Artiodactyla: bovid (cattle, banteng, buffalo, bison, yak, sheep, argali, goat, ibex, roan antelope, hartebeest, waterbuck, kob, lechwe, gemsbok, oryx, reedbuck), cervid (moose, red deer, roe deer, fallow deer, reindeer, sika, sambar, chital, muntjac); Perissodactyla: equid (Przewalski's horse) [rumen, reticulum]	freshwater Gastropoda: planorbid (*Planorbis planorbis, P. carinatus, Anisus cornetus, A. leucostomus, A. septemgyratus, A. spirorbis, A. vortex, Armiger crista, Ar. inermis, Bathyomphalus contortus, Choanophalus anophalus, Gyraulus albus, G. ehrenbergi, G. gredleri, Hippeutis complanatus, Segmentina nitida, Indoplanorbis exustus, Helicorbis, Polypylis*)	metacercariae on herbage	Eurasia, Americas
P. clavula	Artiodactyla: bovid (zebu, buffalo)			Africa
P. epiclitum	Artiodactyla: bovid (cattle, zebu,	freshwater Gastropoda:	metacercariae on	India,

(syn. *P. indicum p.p., P. thapari, P. malayi, Cotylophoron madrasense, C. chauhani*)	buffalo, guar, sheep, goat, sable antelope), cervid (chital) [rumen]	planorbid (*Indoplanorbis exustus*)	herbage	Southeast Asia
P. gotoi	Artiodactyla: bovid (cattle, buffalo, blackbuck, sheep) [rumen]	freshwater Gastropoda: planorbid (*Segmentina nitidella, Gyraulus largielli*)		Southeast Asia, Egypt
P. gracile (syn. *P. indicum p.p., P. bombayiensis*)	Artiodactyla: bovid (cattle, zebu, nilgai, buffalo, sheep) [rumen]			Indochina
P. hiberniae	Artiodactyla: bovid (cattle, buffalo, argali), cervid (red deer) [rumen]	freshwater Gastropoda: planorbid (*Anisus leucostomus*)		United Kingdom
P. ichikawai (syn. *Cotylophoron vigisi*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat), cervid (roe deer, red deer, sika) [rumen]	freshwater Gastropoda: planorbid (*Helicorbis australiensis, H. suiffunensis, Anisus centrifugus, A. minusculus, A. spirorbis, A. subfilialis, Gyraulus corinna, G. filialis, Hippeutis complanatus, Planorbis carinatus, Segmentina nitida, S. semiglobosa, S. hemisphaerula*)	metacercariae on herbage	Eurasia, South America, Australia, New Zealand
P. leydeni (syn. *P. scotiae, P. julimarinorum, P. nicabrasilorum, P. procapri, Cotylophoron skrjabini p.p.*)	Artiodactyla: bovid (cattle, bison, buffalo, argali, goa), cervid (red deer, roe deer, red deer, reindeer, sika, moose) [rumen, reticulum]	freshwater Gastropoda: planorbid (*Anisus leucostoma, A. septemgyratus, A. spirorbis, A. vortex, Armiger crista, Bathyomphalus contortus, Gyraulus albus, G. gredleri, Hippeutis complanatus, Planorbis planorbis, Segmentina nitida*)		Europe, Asia, Americas
P. liorchis	Artiodactyla: cervid (red brocket, gray brocket, brown brocket, white-tailed deer, moose, marsh deer, sambar, pampas deer), bovid (cattle, buffalo, goat, argali) [rumen])	freshwater Gastropoda: planorbid (*Helisoma campanulata, H. trivolvis*)		Americas, Southeast Asia
P. phillerouxi	Artiodactyla: bovid (zebu, buffalo)			Africa
Explanatum				
E. anisocotyle (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, goat)			Indochina
E. bathycotyle (syn. *Paramphistomum*)	Artiodactyla: cervid (chital), bovid (cattle, buffalo, goat, argali)	freshwater Gastropoda: planorbid (*Gyraulus convexiusculus*)		Indochina
E. explanatum (syn. *Paramphistomum fraternum, P. siamense*)	Artiodactyla: bovid (cattle, banteng, bison, buffalo, yak, sheep, argali, goat, hartebeest, blackbuck, reedbuck, bontebok, roan antelope), cervid (sambar)	freshwater Gastropoda: planorbid (*Gyraulus convexiusculus*)	metacercariae on herbage	Asia, India, Middle-East, Africa
E. symmeri	Artiodactyla: bovid (buffalo)			Africa
Cotylophoron				

C. bareilliense (syn. *C. skrjabini*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat)			India, Philippines, South America
C. chauhani	Artiodactyla: bovid (sheep, goat)			India
C. cotylophorum (syn. *C. indicum, C. guongdongense, Paramphistomum cotylophorum*)	Artiodactyla: bovid (cattle, buffalo, yak, sheep, goat, impala, hartebeest, Harvey's duiker, tsessebe, Thomson's gazelle, roan antelope, royal antelope, sable antelope, klipspringer, waterbuck, bushbuck, marshbuck, kob, lechwe, puku, oribi, argali, steinbok, reedbuck, bohor reedbuck, duiker, eland, nyala, kudu), cervid (chital, gray brocket), hippopotamid (hippopotamus); Proboscidea: elephantid (African elephant); Perissodactyla: equid (zebra) [rumen, reticulum]	freshwater Gastropoda	metacercariae on herbage	Africa, Southeast Asia, India, Australia
C. dilipticus	Artiodactyla: bovid (cattle)			Africa
C. fulleborni (syn. *C. kwantungensis, C. noveboracensis, C. shangkiangensis, C. sinuointestinum*)	Artiodactyla: bovid (cattle, buffalo, impala, duiker, bongo)			Africa
C. jacksoni	Artiodactyla: bovid (cattle, hartebeest, sable antelope, waterbuck)			Africa
C. macrosphinctris	Artiodactyla: bovid (buffalo, hartebeest, oribi)			Africa
C. madrasensis	Artiodactyla: bovid (sheep)			India
C. panamense	Artiodactyla: bovid (cattle, sheep)			America
C. travassosi	Artiodactyla: bovid (cattle)			Brazil
C. xiangjiangense	Artiodactyla: bovid (buffalo)			China
Ugandocotyle				
U. pisum (syn. *Paramphistomum*)	Artiodactyla: hippopotamid (hippopotamus) [stomach, intestines]			Africa
Calicophoron				
C. bothriophoron (syn. *Amphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, waterbuck, reedbuck)			Africa, India
C. calicophorum (syn. *C. fusum, C. orientalis, C. ovillum, C. zhejiangense, Paramphistomum calicophorum, P. cauliorchis, P. crassum, P. erschovi, P. ijimai*)	Artiodactyla: bovid (cattle, buffalo, tamaraw, sheep, goat, impala, moose, hartebeest, wildebeest, roan antelope, sable antelope, waterbuck, lechwe, springbok, bontebok, eland, nyala, kudu), cervid (chital, sika, sambar, red deer, muntjac, fallow deer, reindeer) [rumen, reticulum]	freshwater Gastropoda: planorbid (*Gyraulus scottianus* (syn. *Pygmanisis pelorius*), *G. corinna, G. pulcher, Anisus spirorbis, Bulinus tropicus, Planorbis kahuika, P. planorbis, Helicorbis suiffunensis*)	metacercariae on herbage	Africa, Eurasia, India, Australia, New Zealand
C. clavula (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, goat, impala, hartebeest, waterbuck, reedbuck, kob, puku, oribi, roan antelope, sable antelope)	freshwater Gastropoda: planorbid (*Bulinus abyssinicus*)		Africa
C. daubneyi (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, gemsbok), cervid (roe deer, red deer) [rumen]	freshwater Gastropoda: lymnaeid (*Galba trunculata, Lymnaea peregra*)	metacercariae on herbage	Africa, Europe
C. microbothrioides (syn. *Paramphistomum microbothrium, Ceylonocotyle petrowi*)	Artiodactyla: bovid (cattle, bison, sheep), cervid (sika, sambar, muntjac)	freshwater Gastropoda: planorbid (*Anisus minusculus*), lymnaeid (*Galba trunculata, Lymnaea peregra, L. cubensis, L. humilis*)		Europe, Asia, North America

C. microbothrium (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, ibex, impala, hartebeest, bontebok, tsessebe, red-fronted gazelle, Thomson's gazelle, roan antelope, waterbuck, reedbuck, kob, lechwe, puku, serow, gemsbok, oribi, eland, nyala, kudu), camelid (camel), cervid (roe deer, red deer) [rumen]	freshwater Gastropoda: planorbid (*Bulinus tropicus, B. truncatus, B. liratus, B. mariei, B. forskalii, B. natalensis, B. octoploidus, Physopsis globosus, P. nasutus*)	metacercariae on herbage	Africa, Europe
C. papilligerum (syn. *Paramphistomum*)	Artiodactyla: cervid (Eld's deer)			Asia
C. papillosum (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep)			India, Asia
C. phillerouxi (syn. *Paramphistomum togolense, P. vangrenbergeri*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, impala, tsessebe, roan antelope, sable antelope, waterbuck, kob, puku, kudu, reedbuck)	freshwater Gastropoda: planorbid (*Bulinus cercinus, B. forskalii, B. senegalensis*)		Africa
C. raja	Artiodactyla: bovid (cattle, buffalo, sheep, goat, impala, hartebeest, wildebeest, tsessebe, Thomson's gazelle, roan antelope, sable antelope, waterbuck, reedbuck, lechwe, puku, gemsbok, eland, bushbuck, kudu)	freshwater Gastropoda: planorbid (*Physopsis globosus*)		Africa
C. shillongensis	Artiodactyla: bovid (sheep, goat)			India
C. sukari (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat)	freshwater Gastropoda: planorbid (*Biomphalaria pfeifferi*)		Africa
C. sukumum (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, wildebeest, tsessebe, roan antelope, waterbuck, reedbuck, lechwe, eland)			Africa
C. wuchengense	Artiodactyla: bovid (buffalo)			China
Subfamily: Orthocoeliinae (Laurer's canal and excretory duct do not cross)				
Orthocoelium				
O. arambuloi	Artiodactyla: bovid (cattle, buffalo)			Indonesia, Philippines
O. bovini (syn. *Ceylonocotyle*)	Artiodactyla: bovid (cattle)			India
O. brevicaeca (syn. *Ceylonocotyle*)	Artiodactyla: bovid (cattle, buffalo)			China
O. dawesi (syn. *Ceylonocotyle*)	Artiodactyla: bovid (cattle, sheep, goat)			India
O. dicranocoelium (syn. *Ceylonocotyle tamilensis, Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat) [rumen]	freshwater Gastropoda: bithyniid (*Digoniostoma pulchella*)	metacercariae on herbage	India, Southeast Asia
O. dinniki	Artiodactyla: bovid (cattle, buffalo, sheep, goat)			India, Asia
O. gigantopharynx (syn. *Ceylonocotyle hsui, C. chinensis*)	Artiodactyla: bovid (blackbuck, buffalo)			India, Southeast Asia
O. indonesiense	Artiodactyla: bovid (cattle, sheep)			Indonesia
O. narayanai (syn. *Ceylonocotyle*)	Artiodactyla: bovid (cattle, buffalo)			India
O. orthocoelium (syn. *O. saccocoelium, Paramphistomum chinensis, P. spinicephalus, Chenocoelium kiangsiensis*)	Artiodactyla: bovid (cattle, buffalo, goat, sheep)			India, Asia
O. parastreptocoelium	Artiodactyla: bovid (cattle, buffalo)			China

(syn. *Ceylonocotyle*)				
O. parvipapillatum (syn. *Paramphistomum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat)			India
O. scoliocoelium (syn. *Ceylonocotyle cheni, C. longicoelium, Cotylophoron ovatum, Paramphistomum, P. shipley*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat), cervid (chital, barasingha, muntjac, red deer) [rumen]	freshwater Gastropoda: bithyniid (*Bulimus* (*Bithynia*) *pulchella, Digoniostoma pulchella*), planorbid (*Anisus natalensis, Gyraulus convexiusculus, Indoplanorbis exustus*), lymnaeid (*Lymnaea luteola*)	metacercariae on herbage	Africa, India, Asia
O. serpenticaecum	Artiodactyla: bovid (swamp buffalo)			Philippines
O. sinuocoelium (syn. *Ceylonocotyle*)	Artiodactyla: bovid (cattle)			China
O. streptocoelium (syn. *Ceylonocotyle, Paramphistomum, P. malayi*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, Thomson's gazelle, waterbuck, bushbuck), cervid (barasingha, muntjac, sambar) [rumen]	freshwater Gastropoda: planorbid (*Gyraulus gilberti, G. isingi, G. waterhousei, G. chinensis*)	metacercariae on herbage	Australia, India, Asia
O. thapari	Artiodactyla: bovid (cattle, buffalo)			India
Family: Gastrothylacidae				
Gastrothylax				
G. caraphilensis	Artiodactyla: bovid (cattle)			Philippines
G. compressus (syn. *G. glandiformis, G. indicus*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat,), cervid (barasingha, sambar)			India, Asia
G. crumenifer (syn. *G. orientalis, G. chinensis, Paramphistomum magnum*)	Artiodactyla: bovid (cattle, buffalo, yak, banteng, bison, sheep, goat, blackbuck, nilgai, lechwe, sitatunga), cervid (chital, hog deer, barasingha, Philippine deer, sambar) [rumen]	freshwater Gastropoda: planorbid (*Gyraulus convexiusculus, G. albus, G. ehrenbergi, Armiger crista, Planorbis planorbis, P. sieversi*)	metacercariae on herbage	India, Asia, southern Africa
G. globoformis	Artiodactyla: bovid (buffalo)			China
G. magnadiscus	Artiodactyla: bovid (buffalo)			China
G. zhonghuaensis	Artiodactyla: bovid (cattle, buffalo)			China, Philippines
Carmyerius				
C. bubalis (syn. *C. gretillati, Gastrothylax*)	Artiodactyla: bovid (cattle, buffalo, hartebeest, bongo)			Africa, China
C. bulbosus	Artiodactyla: bovid (buffalo), cervid (sambar)			Asia
C. chabaudi	Artiodactyla: bovid (Thomson's gazelle)			Africa
C. cruciformis (syn. *Gastrothylax*)	Artiodactyla: hippopotamid (hippopotamus)			Africa
C. diplopharyngialis	Artiodactyla: bovid (?)			Africa
C. endopapillatus (syn. *C. papillatus*)	Artiodactyla: bovid (cattle, buffalo, Thomson's gazelle, roan antelope, waterbuck, kob, reedbuck), hippopotamid (hippopotamus)			Africa
C. exoporus	Artiodactyla: bovid (cattle, buffalo, sheep, tsessebe, sitatunga, roan antelope)	freshwater Gastropoda: planorbid (*Anisus natalensis*)		Africa
C. graberi	Artiodactyla: bovid (cattle, buffalo, sheep, red-fronted gazelle, Thomson's gazelle, hartebeest, waterbuck, bohor reedbuck, harnessed bushbuck)			Africa

C. gregarius (syn. *Gastrothylax*)	Artiodactyla: bovid (cattle, buffalo, sheep, blackbuck, bushbuck)	freshwater Gastropoda: planorbid (*Bulinus truncatus, B. forskalii*)		India, Asia, Africa
C. mancupatus (syn. *C. dollfusi, C. minutus, Wellmanius wellmani, Gastrothylax*)	Artiodactyla: bovid (cattle, buffalo, goat, waterbuck, roan antelope, eland, bushbuck)	freshwater Gastropoda: planorbid (*Bulinus liratus, B. mariei, Anisus natalensis*)		Africa
C. multivitellarius	Artiodactyla: bovid (Thomson's gazelle)			Africa
C. parvipapillatus (syn. *C. gregarius p.p.*)	Artiodactyla: bovid (cattle, sheep, goat, tsessebe, waterbuck, kob)	freshwater Gastropoda: planorbid (*Physopsis globosus*)		Africa
C. schoutedeni	Artiodactyla: bovid (buffalo, black-fronted duiker, waterbuck, kob, reedbuck, bongo), hippopotamid (hippopotamus)			Africa
C. spatiosus (syn. *Gastrothylax*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, reedbuck, waterbuck, kob,lechwe, puku, hartebeest, tsessebe, Thomson's gazelle, roan antelope, eland, bushbuck, sitatunga), cervid (muntjac) [rumen]		metacercariae on herbage	Africa, India, Southeast Asia
C. synethes (syn. *Gastrothylax*)	Artiodactyla: bovid (cattle, buffalo, goat), cervid (sambar)			Southeast Asia
C. wenyoni (syn. *Gastrothylax*)	Artiodactyla: bovid (Nile lechwe)			Africa
Fischoederius				
F. bubalis	Artiodactyla: bovid (buffalo)			China
F. cobboldi (syn. *F. poyangensis, Gastrothylax)*	Artiodactyla: bovid (cattle, buffalo, gayal, banteng, yak, nilgai, sheep, goat), cervid (sambar) [rumen]	freshwater Gastropoda	metacercariae on herbage	India, Asia
F. elongatus (syn. *F. ceylonensis, F. compressus, F. fischoederi, F. siamensis, Gastrothylax elongatus)*)	Artiodactyla: bovid (cattle, banteng, gayal, anoa, buffalo, sheep, goat), cervid (chital, Philippine deer, Javan rusa, sambar, muntjac, water deer, reindeer); rarely Primates: hominid (human)	freshwater Gastropoda: lymnaeid (*Radix luteola*, *Lymnaea luteola, L. acuminata*), planorbid (*Gyraulus euphraticus, G. pulcher*)	metacercariae on herbage	India, Asia
F. japonicus (syn. *Gastrothylax*)	Artiodactyla: bovid (cattle, buffalo), cervid (sambar, muntjac)			Asia
F. ovatus (syn. *F. ovis*)	Artiodactyla: bovid (cattle, buffalo, sheep)			China
F. philippinensis	Artiodactyla: bovid (cattle, buffalo, goat)			Philippines
F. skrjabini	Artiodactyla: bovid (cattle, buffalo), cervid (moose, roe deer, red deer)			Asia
Family: Gastrodiscidae				
Gastrodiscus				
G. aegyptiacus (syn. *Cotylogaster cochleariformis, Distoma, G. sonsini, G. minor, G. polymastos, G. equi*)	Artiodactyla: bovid (cattle), suid (pig, forest hog, desert warthog); Perissodactyla: rhinocerotid (white rhinoceros), equid (horse, donkey, mule, zebras, Przewalski's horse) [caecum, colon]	freshwater Gastropoda: planorbid (*Bulinus forskalii, B. senegalensis*)	metacercariae on herbage	Africa, India, Asia, Australia
G. secundus	Proboscidea: elephantid (Asian elephant); Perissodactyla: equid (donkey, Przewalski's horse) [caecum, colon]	freshwater Gastropoda: planorbid (*Indoplanorbis exustus*)	metacercariae on herbage	India, Asia, Egypt
Family: Zygocotylidae				

Subfamily: Pseudodiscinae				
Pseudodiscus				
P. collinsi (syn. *Amphistoma, P. stenleyi*)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse, mule, donkey, Przewalski's horse); Proboscidea: elephantid (Asian elephant) [caecum, colon]	freshwater Gastropoda: planorbid (*Indoplanorbis exustus*)	metacercariae on herbage	India
Macropotrema				
M. pertinax	Diprotodontia: macropodid (agile wallaby)			Australia
Subfamily: Olveriinae				
Olveria				
O. indica (syn. *O. thapari*)	Artiodactyla: bovid (cattle, buffalo, sheep) [rumen]	freshwater Gastropoda: planorbid (*Gyraulus convexiusculus*)	metacercariae on herbage	India
O. bosi	Artiodactyla: bovid (cattle, buffalo, sheep)		metacercariae on herbage	India
Subfamily: Watsoniinae				
Homalogaster				
H. paloniae (syn. *H. poirieri, H. philippiensis, H. taiwana*)	Artiodactyla: bovid (cattle, buffalo, gayal, banteng, sheep, goat, blackbuck, lechwe), cervid (Javan rusa, muntjac); Proboscidea: elephantid (Asian elephant) [large intestines]	freshwater Gastropoda: planorbid (*Indoplanorbis exustus, Polypylis* (*Segmentina*) *hemisphaerula*)	metacercariae on herbage	Asia, Australasia, Africa
Watsonius				
W. watsoni (syn. *Amphistoma, Cladorchis, Gastrodiscus, Paramphistomum, Pseudodiscus*)	Primates: cercopithecid (grivet, crab-eating macaque, mandrill), hominid (human)			Africa
W. noci (syn. *Chiorchis, Prochiorchis*)	Primates: cercopithecid (rhesus macaque)			Asia
W. macaci	Primates: cercopithecid (rhesus macaque)			Asia
W. deschiensi	Primates: cercopithecid (mandrill, hamadryas baboon)			Africa
W. capri	Artiodactyla: bovid (goat)			Pakistan
Gastrodiscoides (considered in detail separately in next section)				
G. hominis (syn. *Amphistoma, Gastrodiscus*) (colonic fluke)	Rodentia: cricetid (water vole, muskrat), murid (bandicoot rats, ricefield rat, brown rat, black rat), echimyid (coypu); Artiodactyla: suid (pig, bushpig, warthog), tragulid (mouse-deer); Primates: cercopithecid (crab-eating macaque, Philippine long-tailed macaque, rhesus macaque, Sumatran surili), hominid (orangutan, human)	freshwater Gastropoda: planorbid (*Helicorbis coenosus*, *Anisus acronicus*), lymnaeid (*Lymnaea stagnalis*)	on herbage (esp. water caltrop)	India, Asia, Russia, Africa

Parasite morphology: Paramphistomes form 7 different developmental stages in their life-cycles: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae and adults. Eggs are yellow-green to white, oval to spherical and vary considerably in size depending on the parasite species: most ranging from 100-170 µm in length by 60-100 µm in width (e.g. *Explanatum explanatum, Cotylophoron cotylophorum, Calicophoron calicophorum, Orthocoelium scoliocoelium, Pseudodiscus collinsi, Homalogaster paloniae, Gastrothylax crumenifer, Carmyerius spatiosus, Fischoederius cobboldi*); a few species produce larger eggs measuring 170-200 x 100-120 µm (e.g., *Gastrodiscus aegyptiacus*); and several species produce smaller eggs measuring 35-100 x 30-60 µm (e.g., *Paramphistomum cervi*). The eggs are enveloped within transparent eggshells which are thin in species developing in freshwater and thicker in species developing in marine/brackish-water. The eggs taper anteriorly to a small operculum and have a knob-like posterior polar thickening. They embryonate in the external environment forming miracidia which are released when the

eggs hatch. Miracidia have elongated streamlined bodies, measuring 110-200 µm long by 35-50 µm wide, and are covered with ciliated epidermal plates, often arranged anteriorly in staggered longitudinal rows. They have a prominent terminal papilla and a primitive gut with elongated cellular masses. Sporocysts appear as elongated sac-like structures up to 1.5 mm in length without internal organs but with germ balls undergoing asexual reproduction to form rediae. Two redial generations are formed, with mother rediae forming daughter rediae which then form cercariae. Each developing redia is sausage-shaped measuring from 140-750 µm long by 45-140 µm wide (daughters are larger) and they have a mouth, pharynx, saccular gut, and 3 pairs of flame cells. Cercariae have light brown ovoid bodies measuring from 200–900 µm in diameter with an elongate unforked tail measuring 450–900 µm in length and containing a conspicuous excretion tube. The amphistome cercariae have 2 eyespots, a pharynx with a pair of well-developed oral pouches, an oesophagus with a muscular bulb, 2 simple intestinal caeca, and a prominent posterior ventral sucker. Metacercariae consist of the cercarial body which has encysted after shedding its tail. They appear brown and are hemispherical measuring 200-300 µm in length. Adult paramphistomes have thick fleshy bodies that are mostly conical but somewhat flattened to form pyriform 'jelly-bean' shapes. They are often orange to pink-red and are variable in size depending on species; ranging from 3-20 mm in length by 1-8 mm in width. Many species are medium-sized measuring 6-14 x 2-5 mm (e.g. *Paramphistomum cervi, Explanatum explanatum Cotylophoron cotylophorum*), some are larger measuring 11-20 x 5-8 mm (e.g. *Gastrothylax crumenifer*), and some smaller measuring 2-5 x 1-2 mm (e.g. *Orthocoelium scoliocoelium*). Adult worms are covered with a smooth tegument (without spines) and they have a muscular apparatus (the pharynx) at the anterior oral opening, and a well-developed muscular ventral sucker located at the posterior end (amphistome arrangement). They contain internal organs constituting digestive, reproductive, excretory, lymphatic and nervous systems. The digestive system comprises 3 parts: the anterior pharynx (with primary pharyngeal sacs or pharyngeal bulb and secondary pharyngeal sacs); the middle oesophagus (with or without muscular thickening); and the posterior caeca (blind-ended bifurcated gut). The excretory system is stenosome in type, consisting of solenocytes, capillaries, 2 main canals, connecting vesicle, excretory bladder and excretory pore. Adult flukes are hermaphroditic, possessing both male and female reproductive organs, most lying between the intestinal caeca except the extensive vitelline follicles. Female organs comprise an oval-conical ovary, oviduct, Laurer's canal, vitellaria, Mehlis' gland, ootype, uterus with muscular distal end (metraterm) opening into a hermaphroditic sac, while male organs consist of 2 large lobulated testes, vasa efferentia, a vas deferens, an ejaculatory duct (some species in lower vertebrates also have a cirrus sac) with erectile genital papilla (instead of a cirrus). The genital papilla is surrounded by a depression known as the genital atrium with walls strengthened by muscular elements around the genital pore (terminal genitalium). Species belonging to the family Gastrothylacidae also have a blind ventral pouch associated with the atrium. Paramphistome genera are distinguished primarily on the basis of differences in the types of pharynx (5 main types with numerous subtypes), terminal genitalium (4 main types with numerous subtypes) and ventral sucker (3 main types with numerous subtypes). Adult amphistomes of most warm-blooded vertebrates are oviparous (produce eggs) whereas those of cold-blooded vertebrates may be ovoviviparous (eggs hatching internally) or viviparous (bearing live young).

Site of infection: Most paramphistomes occur as parasites in the gastrointestinal tracts of ruminants, with juvenile (sub-adult) stages in the small intestines and/or abomasum migrating to the rumen or reticulum to develop as adults (hence the common name of rumen or stomach flukes). Some species infect the small intestines of non-ruminants, such as pigs and horses. Asexual generations form in tissues of aquatic snails, mainly bithyniids, planorbids and lymnaeids. Miracidia and cercariae are free-swimming aquatic stages, while metacercariae encyst on herbage.

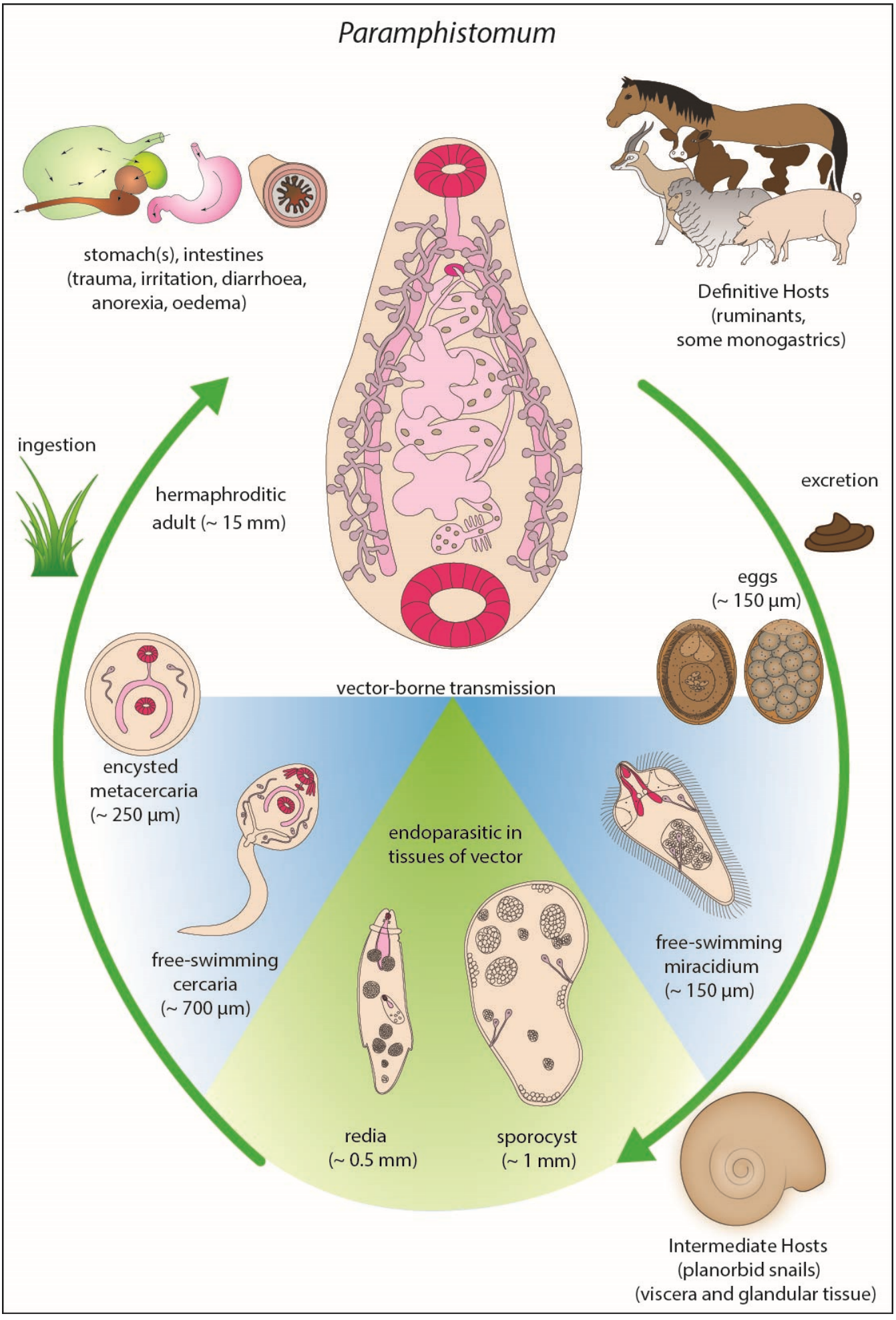
Pathogenesis: Infections by small numbers of paramphistome flukes rarely cause disease, but large numbers of immature flukes developing and migrating in the small intestinal mucosa may cause severe clinical disease, especially in young ruminants as adult animals develop immunity with repeated exposure. Juvenile worms cause traumatic damage to the mucosa by adhering using their posterior sucker. Continuous attachment and detachment during migration amplifies the damage and may result in mucosal irritation, enteritis, ulceration, haemorrhage, foetid diarrhoea (scours), dehydration, anorexia, rapid weight loss, loss of electrolytes and hypoproteinaemia (often with submandibular oedema and sometimes generalized oedema such as hydrothorax, hydropericardium, ascites, lung oedema), anaemia, lethargy, recumbency and death. In addition, the development of young flukes may be retarded in heavy infections so they remain in the small intestine for months causing severe disease through cumulative damage. The parasites are considered to be a leading cause of livestock morbidity in tropical and subtropical regions, with considerable production and economic losses. Moderate infections by immature flukes have also been associated with reduced weight gain, lower milk production and ill-thrift. Recent studies have indicated that infections by mature flukes in the stomach may also be responsible for production losses by causing atrophy and ulceration of ruminal papillae at attachment sites.

Developmental cycle and mode of transmission: Paramphistomes have indirect life-cycles involving transmission between vertebrate definitive hosts and molluscan intermediate hosts by aquatic developmental stages. Eggs passed with host faeces embryonate in water over several weeks and then hatch releasing their enclosed miracidia (hatching may be delayed in cold water). The miracidia are ciliated and swim about in water seeking molluscan hosts, apparently using chemotactic cues to home in on snail mucus and then penetrating soft tissues. Paramphistomes develop in aquatic snails (mostly planorbids, lymnaeids and bithyniids) which act as intermediate hosts for the massive asexual reproduction of larval cercariae. Parasite distribution is largely delimited by the distribution of suitable snail hosts, with higher incidence recorded in wet high rainfall and irrigation areas. Miracidia move to the heart, shed their ciliated plates and form sporocysts in surrounding mantle tissues. Sporocysts contain little other than balls of germinal cells which develop into rediae which are feeding stages with functional mouths and guts. Two generations of rediae are

formed, with mother rediae migrating to the digestive gland, gut, gonads or mantle tissue where their germ balls form daughter rediae which eventually release cercariae to complete their development in snail tissues over several days. The prepatent period in snails (time from infection to first release of cercariae) ranges from 35-65 days and infected snails can shed cercariae for over 1 year. Mature cercariae released from the snail pulmonary aperture swim about actively for several hours but then shed their tails and encyst as metacercariae on subaquatic vegetation. Metacercariae may remain viable for up to 6 months under favourable environmental conditions (wet humid). When ingested on herbage by grazing animals, the metacercariae excyst in the duodenum and the immature flukes attach to the small intestinal mucosa for 3-6 weeks before migrating to the stomach(s) where they develop into mature adults. The prepatent period in vertebrates (time from infection to first release of eggs) ranges from 55-75 days and adult flukes may live for up to 1 year. Animals are usually exposed to subclinical trickle infections (slow and continuous) under normal grazing conditions, but heavy infections and severe disease may ensue when numerous metacercariae are ingested over short periods from grazing wetlands, marshlands, flooded or irrigated pastures, saturated pastures or around lakes and rice paddies.

Differential diagnosis: Infections may be suspected on the basis of clinical symptomatology and history of exposure, i.e. when diarrhoea, illthrift and mortalities occur in livestock in endemic regions. Confirmation of diagnosis is afforded by the microscopic detection of fluke eggs in faecal samples, often following filtration (using sieves), sedimentation (in water) and contrast staining (with methylene blue or methyl green rather than iodine). However, clinical disease is often caused by immature stages migrating through the intestinal mucosa, which may occur before any adults have matured in the stomach and produced eggs. Infections may be diagnosed at post-mortem by the detection of immature stages from suspicious haemorrhagic lesions in the intestinal mucosa, or by the detection of adult worms in the stomach. Immunodiagnostic tests may become available in the future as research studies have developed enzyme immunoassays to detect host antibodies in serum, saliva and milk samples using protein extracts from whole worms. Molecular diagnostic techniques may also become more widely available, with the polymerase chain reaction (PCR) amplification of specific nuclear genes (ribosomal RNA and internal transcribed spacer region 2) and mitochondrial genes (cytochrome c oxidase subunit 1) already being used to examine phylogenetic and geographic variation between adults of a growing number of species.

Treatment and control: Clinical infections have been successfully treated using a range of anthelmintic drugs, including salicylanilides (oxyclozanide, niclosamide, resorantel), probenzimidazoles (febantel), benzimidazoles (albendazole), halogenated phenols (bithionol, hexachlorophene) and halogenated hydrocarbons (hexachloroethane, carbon tetrachloride). In particular, the salicylanilides proved to be most effective against both immature and mature worms when multiple doses were given several days apart. Regular drenching also provides prophylactic protection against infections, especially during periods when pastures are wet and snails vectors abound. Various control strategies have been used to reduce parasite transmission between hosts, particularly by avoiding faecal contamination of water sources (exclusion fences, waste management), reducing snail populations (drain affected areas, repair leaking dams and troughs, use molluscicides) and managing grazing livestock (barrier fences, herd/flock rotation, not grazing weaners with adults, and avoiding wet pastures prior to winter when they are more heavily contaminated). More recently, vaccination studies have demonstrated some promise in the control of infections as cattle, sheep and goats were found to develop some protective immunity against clinical challenge that persisted for at least a year.


Paramphistomum
stomach(s), intestines
(trauma, irritation, diarrhoea,
anorexia, oedema)
Definitive Hosts
(ruminants,
some monogastrics)
ingestion
hermaphroditic
adult (~ 15 mm)
excretion
eggs
(~ 150 µm)
vector-borne transmission
encysted
metacercaria
(~ 250 µm)
endoparasitic in
tissues of vector
free-swimming
cercaria
(~ 700 µm)
free-swimming
miracidium
(~ 150 µm)
redia
(~ 0.5 mm)
sporocyst
(~ 1 mm)
Intermediate Hosts
(planorbid snails)
(viscera and glandular tissue)



Paramphistomum adult worms



Paramphistomum adult worms



Paramphistomum adult worms



Paramphistomum cercaria

Gastrodiscoides
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult paramphistomids are thick fleshy worms and the ventral sucker is near the posterior end. Paramphistomes are conical (rather than flat) in shape and most occur as parasites in the forestomach of ruminants (rumen/stomach flukes), although some infect the intestines of pigs and horses. Infections by a range of species belonging to several genera have been associated with enteritis and diarrhoea in domestic animals.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Plagiorchiida (‘echinostomatids’, plagiorchiids’, mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder:	Pronocephalata (gastropod IH, sporocyst and redia formed; simple-tailed cercariae, encysts in open, metacercariae eaten by DH)
Superfamily:	Paramphistomoidea (rumen flukes, miracidium penetrates gastropod IH)
Family:	Paramphistomidae (thick fleshy worms, conical shape, ventral sucker near posterior end, rediae with appendages, cercariae with two eyespots)
Genus:	*Gastrodiscoides* (parasitic in intestines of pigs/humans)
Species:	various species cause diarrhoea

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs, fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the

tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. The suborder Pronocephalata is characterized by species forming simple-tailed cercariae which encyst in the open and the resultant metacercariae are eaten by herbivorous/omnivorous definitive hosts. One cognate superfamily is the Paramphistomoidea which contains thick fleshy worms from the stomach and intestines of ruminants and some omnivores. Adult worms possess a pharynx rather than an oral sucker at the

anterior end, and a ventral sucker at the posterior end (amphistome arrangement, as distinct from monostome, holostome, distome, echinostome or schistosome). Hundreds of species have been described in over 140 genera in 10 families (Balanorchiidae, Brumptiidae, Cladorchiidae, Diplodiscidae, Gastrodiscidae, Gastrothylacidae, Mesometridae, Microscaphidiidae, Paramphistomidae and Zygocotylidae). Familial designations have been extensively reviewed on the basis of morphotypic and biotypic characters with significant reclassifications of individual genera and species. Hopefully, contemporary molecular characterization studies will help resolve their phylogenetic affinities. Amphistome stomach flukes have been detected in a broad range of definitive hosts encompassing all vertebrate classes (mammals, birds, reptiles, amphibians and fish) widely distributed throughout the world.

Paramphistome families and subfamilies	**Genera**	**Definitive Hosts**
Paramphistomidae		
Paramphistominae	*Calicophoron, Cotylophoron, Explanatum, Gigantocotyle, Paramphistomum* (syn. *Liorchis, Srivastavaia*), *Ugandocotyle*	artiodactyls
Orthocoeliinae	*Bilatorchis, Buxifrons, Gemellicotyle, Gigantoatrium, Glyptamphistoma, Leiperocotyle, Macropharynx, Nilocotyle, Orthocoelium* (syn. *Ceylonocotyle*), *Palamphistomum, Paramphistomoides, Platyamphistoma, Pseudoparamphistoma, Sellsitrema*	artiodactyls
Gastrothylacidae		
	Carmyerius, *Duttiella, Fischoederius*, *Gastrothylax, Velasquezotrema*	artiodactyls
Zygocotylidae		
Olveriinae	*Olveria, Sureshiella*	artiodactyls
Pseudodiscinae	*Macropotrema, Pseudodiscus*	perissodactyls, proboscids, macropodids
Stephanopharynginae	*Stephanopharynx*	artiodactyls
Watsoniinae	*Gastrodiscoides*, *Homalogaster*, *Skrjabinocladorchis, Watsonius*	primates, artiodactyls, rodents
Zygocotylinae	*Choerocotyloides, Wardius, Zygocotyle*	birds, artiodactyls, rodents
Gastrodiscidae		
	Gastrodiscus	proboscids, perissodactyls
Brumptiidae		
	Brumptia, Choerocotyle, Hawkesius	proboscids, rhinocerotids
Balanorchiidae		
	Balanorchis	artiodactyls
Cladorchiidae		
Caballerodiscinae	*Cabellerodiscus, Elseyatrema*	reptiles
Caballeroiinae	*Bancroftrema, Cabelleroia, Platycladorchis*	fish
Chiorchiinae	*Chiorchis, Chiostichorchis, Paraibatrema*	testudines, rodents, sirenia
Cladorchiinae	*Australodiscus, Catadiscus, Cladorchis, Dermatemytrema, Diplodiscus, Progonimodiscus, Pseudodiplodiscus, Taxorchis*	mainly amphibians
Dadaytrematinae	*Alphamphistoma, Anavilhanatrema, Annelamphistoma, Australotrema, Betamphistoma, Cleptodiscus, Dadayius, Dadaytrema, Dadaytremoides, Deltamphistoma, Gammamphistoma, Inpamphistoma, Macrorchitrema, Neocladorchis, Ophioxenus, Pacudistoma, Panamphistomum, Pronamphistoma*	fish, amphibians
Helostomatinae	*Amurotrema, Helostomatis, Protocladorchis*	fish
Megalodiscinae	*Megalodiscus, Opisthodiscus, Pseudopisthodiscus*	mainly amphibians
Microrchiinae	*Brevicaecum, Colocladorchis, Kalitrema, Micramphistoma, Microrchis, Nicollodiscus, Pseudocladorchis*	fish
Nemathophilinae	*Halltrema, Nematophila, Parachiorchis, Pseudoalassostoma*	reptiles
Orientodiscinae	*Australotrema, Basidiodiscus, Orientodiscus, Pretestis, Pseudoorientodiscus, Sandonia*	fish
Osteochilotrematinae	*Osteochilotrema*	fish
Pfenderiinae	*Pfenderius*	proboscids
Pisciamphistominae	*Pisciamphistomum*	fish
Schizamphistominae	*Alassostoma, Alassostomoides, Lobatodiscus, Pseudoalassostomoides, Pseudoceloiptodiscus, Quasichiorchis,*	mainly reptiles, amphibians

	Schizamphistomum, Schizamphistomoides, Stunkardia	
Solenorchiinae	*Solenorchis*	dugongs
Stichorchiinae	*Stichorchis*	rodents, artiodactyls
Transvassosiniinae	*Travassosinia, Zetamphistoma*	fish
Mesometridae		
	Centroderma, Elstia, Mesometra, Neowardula, Parawardula, Wardula	fish
Microscaphidiidae (syn. Angiodictyidae)		
	Angiodictyum, Curumai, Denticauda, Deuterobaris, Dictyangium, Doodytrema, Hexangitrema, Hexangium, Microscaphidium, Neoctangium, Neodeuterobaris, Neohexangitrema, Octangioides, Octangium, Paradeuterobaris, Podocnemitrema, Polyangium, Polygorgyra, Pseudohexangium, Pseudoparabaris	testudines

Most of the known paramphistomes of ruminants belong to the families Paramphistomidae and Gastrothylacidae. The family Paramphistomidae comprises the rumen flukes whose adults lack a ventral pouch, and some 20 genera have been classified in 2 major subfamilies: the Paramphistominae (Laurer's canal crosses excretory duct); and the Orthocoeliinae (Laurer's canal and excretory duct do not cross). Some classifications include other subfamilies within the Paramphistomidae but subsequent reviews have reassigned them elsewhere. Notably, the subfamily Gastrodiscinae was split with the genus *Gastrodiscus* placed in the family Gastrodiscidae and the genera *Gastrodiscoides* and *Homalogaster* allocated to the subfamily Watsoniinae in the family Zygocotylidae. The genus *Gastrodiscoides* is monotypic and only contains one species *G. hominis* which infects the intestines mostly of pigs and humans throughout Asia.

***Gastrodiscoides* species**	**Definitive hosts [adults in intestines]**	**First intermediate hosts [sporocysts/rediae in tissues]**	**Infective stages [metacercariae]**	**Distribution**
G. hominis (syn. *Amphistoma, Gastrodiscus*) (colonic fluke)	Rodentia: cricetid (water vole, muskrat), murid (bandicoot rats, ricefield rat, brown rat, black rat), echimyid (coypu); Artiodactyla: suid (pig, bushpig, warthog), tragulid (napu mouse-deer); Primates: cercopithecid (crab-eating macaque, Philippine long-tailed macaque, rhesus macaque, Sumatran surili), hominid (orangutan, human)	freshwater Gastropoda: planorbid (*Helicorbis coenosus, Anisus acronicus*), lymnaeid (*Lymnaea stagnalis*)	on herbage (esp. water caltrop)	India, Asia, Russia, Africa

Parasite morphology: *Gastrodiscoides hominis* forms 7 different stages in its developmental cycle: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae and adult flukes. Unembryonated eggs are ovoid-rhomboidal measuring 120-165 x 60-75 µm and are surrounded by a transparent green-brown eggshell with a small polar operculum and an abopercular thickening (rarely with a spine-like projection). Eggs embryonate in water to form a miracidium which is released when eggs hatch. Free miracidia have elongated streamlined bodies measuring 115-140 x 35-50 µm with long cilia (arranged in staggered longitudinal rows anteriorly), prominent papilla, a primitive gut and cellular masses representing developing organs. Sporocysts have sac-like bodies measuring up to 1.5 mm in length and they do not contain any organs other than balls of germinal cells which develop into rediae. Two generations of rediae are formed, with first generation (mother) rediae forming second-generation (daughter) rediae. Rediae have sausage-shaped bodies that vary in size ranging from 150-750 x 45-150 µm (daughter rediae are larger). They are parasitic stages possessing a mouth, pharynx and saccular gut, but lacking locomotory organs. Cercariae have light brown ovoid bodies ranging in dimensions from 190-920 x 400–860 µm and have long unforked tails measuring 470-920 µm in length with central excretion tubes. They have 2 hemispherical eyespots, an oral region with 2 well-developed oral pouches, an oesophagus with a muscular bulb, 2 blind caeca, an excretory system (with a cross-connection between the 2 main trunks), developing reproductive organs and a ventral sucker. Metacercariae are brown and hemispherical ranging from 200–230 µm in diameter and they consist essentially of cercariae bodies that have shed their tails and become encapsulated within several cyst walls. Adult *G. hominis* have pyriform fleshy bodies measuring from 5-10 x 4-6 mm (generally smaller in pigs than humans) with distinctive anterior conical and posterior discoidal regions. They are covered by smooth (aspinose) tegument which is pink-red in colour. They have an anterior conical projection bearing the pharynx and a well-developed posterior concave ventral sucker separated from surrounding tissue by a deep narrow groove. Worms have a conspicuous alimentary tract comprising a pair of lateral pouches arising from the pharynx, a torturous pharyngeal tube and bifurcate caeca which are blind-ended. Adult worms are hermaphroditic and possess both male and female reproductive organs lying mostly between the caeca, except for the vitellaria. Worms have 2 large lobulated testes with vas

efferentia, a single ovoid ovary with oviduct, extensive vitelline glands, Laurer's canal, and a curved uterus terminating in a prominent genital cone. Fertile worms are oviparous and produce unembryonated eggs.

Site of infection: Infections by adult flukes occur in the large intestines (caecum and/or colon) of their definitive hosts (hence the common name of colonic fluke). However, juvenile worms first emerge from metacercariae in the small intestines (usually duodenum) from where they migrate posteriad to their final predilection sites to develop as adults. Larval stages (sporocysts and rediae) develop in various tissues of their snail intermediate hosts, particularly the digestive gland.

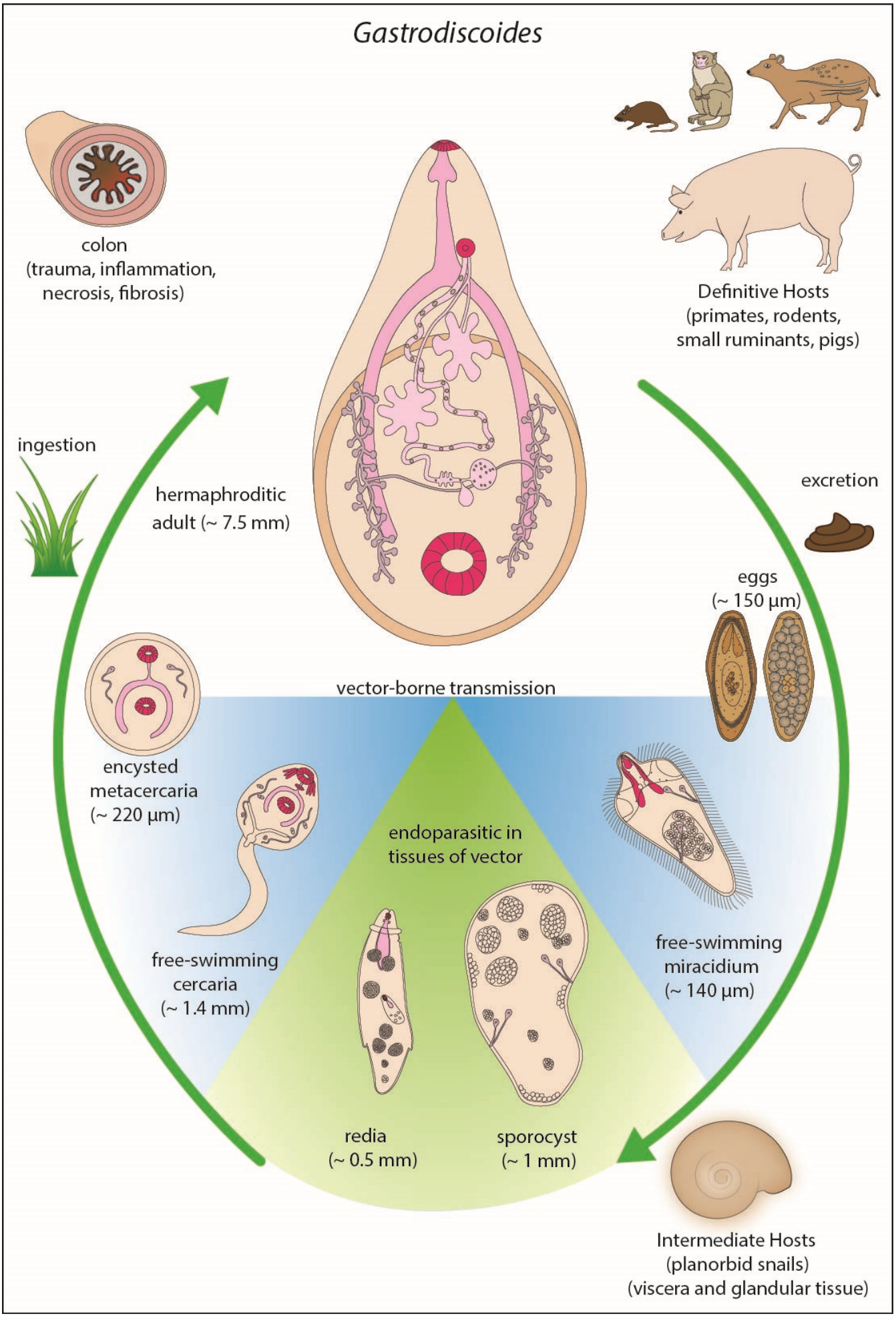
Pathogenesis: Adult flukes attach to the intestinal mucosa producing focal lesions characterized by hyperaemia, epithelial loss, necrosis, ulceration, neutrophilic infiltrates, and submucosal sclerosis due to connective tissue fibrosis and lymphoplasmacytic cellular infiltrates. Heavy infections in humans may cause oedematous catarrhal typhlitis (inflammation of the caecum) and/or chronic necrotizing typhlocolitis (inflammation of both the caecum and colon) with increased mucus production, mucoid diarrhoea, dehydration, abdominal pain, colic, fever and sometimes cachexia (weakness/wasting) and death. In severe cases, the presence of large number of eggs and worms may cause tissue reactions in the heart or mesenteric lymphatics, and untreated patients (esp. children) may die. On occasion, infections have been so extreme that the caecum and ascending colon are completely filled with parasites causing malabsorption, hypoalbuminaemia and intestinal obstruction. Infections in animals are less severe and generally involve chronic inflammation of the caecum and/or colon with mucosal desquamation, submucosal infiltrates and diarrhoea.

Developmental cycle and mode of transmission: *G. hominis* has an indirect digenetic (2-host) life-cycle with transmission occurring between vertebrates (definitive hosts) and molluscs (intermediate hosts) via free-swimming aquatic stages and encysted stages on vegetation. Unembryonated eggs are passed into the external environment with host faeces. They embryonate in water over 9-28 days depending on temperature (longer in cold water), forming a miracidium which hatches 1-5 days later. The free-swimming miracidia actively seek snail intermediate hosts using chemotactic cues to find snail mucus, but some may slowly settle on sediments until a snail host comes into contact. The miracidia penetrate snail tissues shedding their ciliated plates and forming sac-like sporocysts, usually in the snail digestive gland. Asexual development occurs primarily in the freshwater planorbid snail *Helicorbis coenosus,* although development has also been noted in another planorbid *Anisus acronicus* and the lymnaeid *Lymnaea stagnalis*. Sporocysts produce 2 generations of rediae: the first generation (mother) rediae being released from sporocysts into host tissues where they produce second generation (daughter) rediae. Cercariae are ultimately produced in daughter rediae and released into lymph spaces to complete their development before emerging from the snails. The prepatent period for infections in snails (time from infection to emergence of first cercariae) ranges from 28-152 days. Snails may shed from 7-238 cercariae and they usually emerge during morning hours. Cercariae swim about in water for up to 24 hours and then shed their tails and encyst as metacercariae on the external surfaces of aquatic plants (esp. water caltrop). A recent study detected metacercariae on market vegetables (cabbages), but how they became contaminated was not determined. It has also been suggested that metacercariae may form on other substrates such as the external surfaces of aquatic animals ["crustaceans (crayfish), squid, molluscs, or amphibians (frogs, tadpoles)"], or even in their tissues after they have consumed snails infected with cercariae. However, these suppositions are speculative and appear to be based on comparisons with other amphistomes (esp. *Gastrodiscus*) that have been perpetuated in textbooks and review papers without citing substantiating evidence (confirmatory primary scientific publications apparently lacking). Definitive hosts become infected by ingesting metacercariae on contaminated vegetation. The metacercaria excyst in the small intestines and the juvenile worms migrate posteriad to the caecum and/or ascending colon where they attach and mature to adults. Fertilized worms produce hundreds of eggs which are released and excreted with host faeces. The prepatent and patent periods in definitive hosts is unknown and it is unsure how long adult worms live.

Differential diagnosis: Infections are readily diagnosed by the microscopic detection of characteristic fluke eggs in faecal samples, usually following concentration by sedimentation. Adult worms may be collected ante-mortem following colonoscopic biopsy, soap-water enemas or anthelmintic treatment, or at post-mortem by gut dissection. Worms may be identified by their morphological characteristics with specific anatomical features (esp. with respect to genitalia) verified by microscopy. Haematological assessment often detects high levels of eosinophils in association with patent infections. Molecular characterization techniques have recently been used to confirm diagnoses and examine parasite strain variation by the polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (18S and 28S ribosomal RNA, internal transcribed spacer regions 1 and 2).

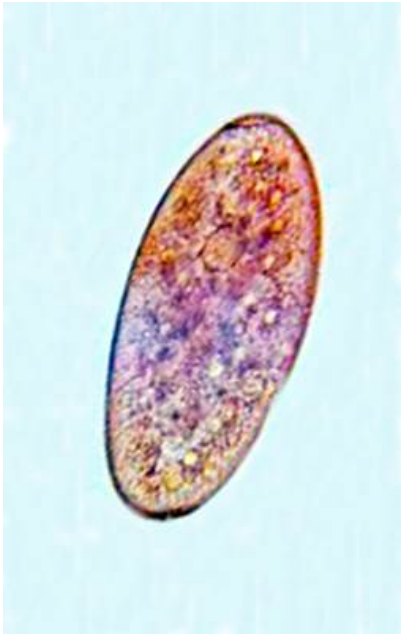
Treatment and control: Several anthelmintic drugs have been used to treat clinical infections in humans and pigs, including the isoquinoline (praziquantel), halogenated hydrocarbons (carbon tetrachloride, tetrachloroethylene) and benzimidazole (mebendazole). Soapy water enemas have also been used to cleanse the bowels of worms, presumably by their detergent and washing action detaching worms from the mucosa. The prevention of infections is based on interrupting parasite transmission between hosts; by reducing faecal contamination of the environment (through better sanitation, preventing promiscuous defaecation, not using 'night-soil' to fertilize crops, sewage collection and treatment, water treatment); reducing snail intermediate host populations (using physical barriers or chemical molluscicides); and preventing metacercarial uptake by vertebrates (cooking or blanching vegetation in boiling water, not using aquatic green fodder in piggeries, water treatment). Public health educational

campaigns should be used to alert communities to the dangers of infections, particularly in high-risk endemic regions, and suggest appropriate courses of preventive action.


Gastrodiscoides
colon
(trauma, inflammation,
necrosis, fibrosis)
Definitive Hosts
(primates, rodents,
small ruminants, pigs)
ingestion
hermaphroditic
adult (~ 7.5 mm)
excretion
eggs
(~ 150 µm)
vector-borne transmission
encysted
metacercaria
(~ 220 µm)
endoparasitic in
tissues of vector
free-swimming
cercaria
(~ 1.4 mm)
free-swimming
miracidium
(~ 140 µm)
redia
(~ 0.5 mm)
sporocyst
(~ 1 mm)
Intermediate Hosts
(planorbid snails)
(viscera and glandular tissue)



Gastrodiscoides adult worm



Gastrodiscoides egg

Opisthorchis
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult opisthorchiideans are small to medium flukes, often spinose, living in the alimentary tracts of mammals, birds, reptiles and fish. They produce embryonated eggs which only hatch after ingestion by snails (first intermediate hosts) and metacercariae develop in fish (second intermediate hosts). Opisthorchids are parasitic in the bile ducts of fish-eating mammals and infections by *Opisthorchis, Clonorchis* and *Metorchis* spp. have been associated with liver disorders in dogs, cats and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Plagiorchiida ('echinostomatids', plagiorchiids', mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder:	Opisthorchiata (egg eaten by gastropod IH, rediae formed, simple-tailed cercariae, encysts in second IH, metacercariae eaten by DH)
Superfamily:	Opisthorchioidea (small-medium flukes, often spinose, piscivorous DH)
Family:	Opisthorchiidae (medium leaf-shaped flukes, in bile ducts of mammals, rediae without appendages, cercariae with two eyespots, metacercariae in second IH)
Genus:	*Opisthorchis* (parasitic in liver of piscivorous mammals)
Species:	various species cause biliary obstruction, cholangitis and possibly cholangiocarcinoma in animals and humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs,

fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. The suborder Opisthorchiata contains one superfamily Opisthorchioidea comprising tiny to medium-sized flukes which form rediae without appendages, then simple-tailed cercariae that encyst in second intermediate hosts forming metacercariae. Over 400 species have been described in 90 genera

in 3 families (Opisthorchiidae, Cryptogonimidae, Heterophyidae). The family Opisthorchiidae is found primarily in the bile ducts of piscivorous mammals and some 30 genera have been recognized in 13 subfamilies: Allogomtiotrematinae (*Allogomtiotrema, Satyapalia*); Aphallinae syn. Witenbergiinae (*Witenbergia*); Delphinicolinae (*Delphinicola*); Diasiellinae (*Diasiella*); Metorchiinae (*Holometra, Metametorchis, Metorchis, Parametorchis*); Oesophagicolinae (*Oesophagicola*); Opisthorchiinae (*Agrawalotrema* (syn. *Thaparotrema*)*, Amphimerus, Cladocystis, Clonorchis, Cyclorchis, Evranorchis, Nigerina, Opisthorchis* (syn. *Hepatiarius*)*, Paropisthorchis, Pseudogomtiotrema* (syn. *Gomtia*)*, Trionychotrema*); Pachytrematinae (*Pachytrema*); Plotnikoviinae (*Plotnikovia*); Pseudamphimerinae (*Erschoviorchis, Euamphimerus, Pseudamphimerus*); Pseudamphistominae (*Microtrema, Pseudamphistomum*); Ratziinae (*Ratzia*); and Tubangorchiinae (*Tubangorchis*). The subfamily Opisthorchiinae is characterized by small-medium elongate flukes whose uterus and vitellaria do not extend anteriorly beyond the level of the ventral sucker. The genus *Opisthorchis* contains over 50 species which have been found in a wide range of fish-eating animals (9 species in mammals, 20 in birds, 17 in fish (most reassigned to genus *Agrawalotrema* (syn. *Thaparotrema*), 2 in turtles, 1 each in snakes and frogs), mostly in Indochina and eastern Europe. Several species infect humans and it is estimated that 17-30 million people are currently infected and that over 400 million are at risk of infection. Molecular and biological studies suggest that the species *Opisthorchis viverrini* may actually be a species complex predominantly infecting humans inhabiting different watersheds throughout Asia, while the species *Opisthorchis felineus* infects a broader range of carnivores and only occasionally causes disease in humans. Another Oriental liver fluke similar to *Opisthorchis felineus* and *Opisthorchis viverrini* in its biological characteristics is *Clonorchis sinensis* (considered separately in detail in next section). The genera *Opisthorchis* and *Clonorchis* are conventionally differentiated on the basis of adult worm morphology, particularly in the position and shape of testes and vitellaria (*Opisthorchis* spp. have lobular testes and vitelline glands arranged in clusters, while *C. sinensis* has highly-branched testes positioned tandemly and vitellaria distributed continuously along both lateral margins). Nonetheless, some workers consider the genera to be synonymous, and molecular studies have indeed shown them to be very closely-related (forming sister clades).

***Opisthorchis* species**	**Definitive hosts [adults in hepatic bile ducts]**	**First intermediate hosts [sporocysts/rediae in tissues]**	**Second intermediate hosts [metacercariae in tissues]**	**Distribution**
Mammalian definitive hosts				
O. chabaudi	Carnivora: felid (cat)	freshwater Gastropoda: bithyniid (*Gabbia neumanni*)	tadpoles of Anura: bufonid (African toad), ranid (white-lipped frog), conrauid (Togo slippery frog)	Europe
O. felineus (cat liver fluke)	Carnivora: felid (cat), canid (dog, red fox, silver fox, Arctic fox, corsac fox, wolf, raccoon dog), pinniped (Caspian seal, bearded seal, grey seal), mustelid (marten, wolverine, European polecat, Steppe polecat, American mink, European mink, ermine, weasel, Siberian weasel, sable, European badger, European otter), procyonid (raccoon); Artiodactyla: suid (pig), phocoenid (porpoise); Eulipotyphla: erinaceid (European hedgehog); Primates: hominid (human); Rodentia: murid (brown rat), cricetid (muskrat, European water vole, golden hamster, black-bellied hamster), castorid (beaver), sciurid (chipmunk), caviid (guinea pig); Lagomorpha: leporid (European rabbit)	freshwater Gastropoda: bithyniid (*Bithynia siamensis, B. inflata, B. leachi, B. troscheli, B. tentaculata*)	freshwater Cypriniformes: cyprinid (bream, ide, asp, Eurasian dace, common roach, tench, minnows)	Asia, Europe, Russia, Canada
O. noverca (syn *O. caninus*)	Carnivora: canid (dog); Artiodactyla: suid (pig); Primates: hominid (human)		Cypriniformes: cyprinid (carp)	India
O. pricei	Didelphimorphia: didelphid (woolly opossum)			South America
O. pseudofelineus	Carnivora: felid (cat), canid		Cypriniformes: catostomid	Americas

(syn. *O. guayaquilensis*, *Amphimerus*)	(coyote, dog); Didelphimorphia: didelphid (opossum); Primates: hominid (human)		(suckers)	
O. starkovi	Carnivora: felid (serval)			Africa
O. tonkae	Rodentia: cricetid (muskrat), caviid (guinea pig), murid (white rat); Carnivora: felid (cat), canid (dog)		Cypriniformes: cyprinid (minnow)	North America
O. viverrini (Southeast Asian liver fluke)	Carnivora: felid (cat, civet cat, Indian fishing cat, leopard cat), canid (dog); Artiodactyla: suid (pig); Rodentia: murid (rat); Primates: hominid (human)	freshwater Gastropoda: bithyniid (*Bithynia siamensis siamensis, B. siamensis goniompharus, B funiculata, Codiella* (*B.*) *inflata, C. troscheli, C. leachi*)	freshwater Cypriniformes: cyprinid (silver barb, Java barb, Javean barb, Smith's barb, beardless barb, swamp barb, Siamese mud carp, Hampala barb, spotted Hampala barb, sa, hard-lipped barb, thin-lipped barb, mrigal, saitan takhao, pa sou, soi pik daeng, dok niew, sicklefin barb, striped flying barb, blunt-snouted barb, shovel-jaw carp, common carp, grass carp, silver carp, topmouth gudgeon, Amur bream, goldfish)	South-East Asia
O. wardi	Carnivora: felid (cat)			Philippines
Avian definitive hosts				
O. ahingii	Suliformes: anhingid (Oriental darter)			India
O. allahabadii	Accipitriformes: accipitrid (red-headed vulture)			India
O. brahmini	Anseriformes: anatid (Brahminy duck)			India
O. choledochum	Anseriformes: anatid (duck)			Europe
O. dendriticus	Gruiformes: gruid (sarus crane)			India
O. entzi	Pelecaniformes: ardeid (purple heron)			
O. geminus (syn. *O. altaevi, O. allahabadii, O. tenuicollis, O. cheelia, O. milvusensis*)	Anseriformes: anatid (duck, white-faced whistling duck, spur-winged goose); Pelecaniformes: ardeid (grey heron, purple heron, squacco heron); Accipitriformes: accipitrid (greater spotted eagle, tawny eagle, western marsh harrier, eastern marsh harrier, hen harrier, pied harrier, black kite, yellow-billed kite, red-headed vulture); Gruiformes: rallid (Eurasian coot)			Europe, Asia, India, Africa
O. giddhis	Accipitriformes: accipitrid (red-headed vulture)			India
O. hardoiensis	Suliformes: phalacrocoracid (little cormorant)			India
O. interruptus	Coraciiformes: alcedinid (green kingfisher)			
O. jonesae	Accipitriformes: accipitrid (black kite)			Pakistan
O. kashmirensis	Anseriformes: anatid (duck)			India
O. longissimus (syn. *O.* (*Notaulua*) *asiaticus*)	Gruiformes: gruid (sarus crane); Anseriformes: anatid (duck, northern shoveler, Eurasian teal, ferruginous duck);			Europe, Asia, India, North America

	Pelecaniformes: ardeid (grey heron, purple heron, Chinese pond heron, Eurasian bittern, black-crowned night heron); Accipitriformes: accipitrid (eastern imperial eagle, western marsh harrier, cinereous harrier, black kite)			
O. obsequens (syn. *O. indicus*)	Accipitriformes: accipitrid (goshawk); Anseriformes: anatid (duck, red-crested pochard)			India, Asia, Australia
O. parageminus	Anseriformes: anatid (duck)			Vietnam
O. pelecani	Pelecaniformes: pelecanid (rosy pelican)			India
O. simulans (syn. *O. anatis*)	Anseriformes: anatid (greylag goose, greater white-fronted goose, duck, tufted duck, greater scaup, Eurasian wigeon); Pelecaniformes: ardeid (little egret); Accipitriformes: accipitrid (western marsh harrier, European honey buzzard); Gruiformes: rallid (Eurasian coot)			Europe, Asia, Africa
O. skrjabini	Anseriformes: anatid (duck)			Asia
O. tsingkiapuensis	Anseriformes: anatid (duck)			
O. vitellatus	Suliformes: phalacrocoracid (double-crested cormorant)			China
Piscine definitive hosts				
O. attui	Anabantiformes: channid (great snakehead) [intestines]			India
O. attuai	Siluriformes: silurid (wallago catfish)			India
O. bagarius	Siluriformes: sisorid (goonch)			India
O. caudalspinutum	Siluriformes: silurid (wallago catfish)			India
O. dayali	Siluriformes: bagrid (catfish)			India
O. elongatum	Siluriformes: sisorid (goonch) [intestines]			India
O. gomtii	Siluriformes: silurid (catfish) [intestines]			India
O. gorakhpurensis	Siluriformes: bagrid (striped dwarf catfish)			India
O. gurdaspurensis	Cypriniformes: cyprinid (rohu)			India
O. gwaliorensis	Siluriformes: sisorid (goonch)			India
O. parasiluri (syn. *Thaparotrema*)	Siluriformes: bagrid (yellowhead catfish)			China
O. pedicellata (syn. *Thaparotrema*, *O. mehrai, O. thaparae, O. thapari*)	Siluriformes: bagrid (rita catfish, tengan), sisorid (goonch), silurid (wallago catfish); Synbranchiformes: mastacembelid (tire track eel)			India
O. piscicola (syn. *Thaparotrema*)	Osteoglossiformes: gymnarchid (frankfish); Siluriformes: clariid (African sharptooth catfish)			Africa
O. raptii	Siluriformes: bagrid (catfish) [intestines]			India
O. ritai	Siluriformes: bagrid (rita catfish)			India
O. thapari (syn. *Thaparotrema*)	Siluriformes: bagrid (catfish), sisorid (goonch)			India

Other definitive hosts				
O. lomeensis	Anura: pyxicephalid (brown ball frog)			Africa
O. ophidiarum	Serpentes: elapid (spine-bellied sea snake)			Philippines
O. ovalis	Testudines: trionychid (smooth softshell turtle, spiny softshell turtle)			North America
O. wuhanensis	Testudines: trionychid (Chinese softshell turtle)			China

Parasite morphology: *Opisthorchis* spp. form 7 different stages in their developmental cycles: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae, and adult flukes. Eggs are small and oval, measuring 21-36 µm in length by 11-22 µm in width. They appear bile-stained (yellow-brown colour) and are surrounded by an eggshell with a roughened surface (musk-melon pattern). The eggs have an operculum with a distinct shoulder and some species also have a small knob-like abopercular appendage. Eggs voided by the host are embryonated and contain a ciliated miracidium with conspicuous germinal cells and flame cells. Sporocysts are elongated sac-like structures measuring up to 1.1 x 0.6 mm. They are thin-walled and contain little other than balls of germinal cells. Rediae are elongate stages measuring around 500 x 90 µm without lateral ambulatory appendages. They are surrounded by an aspinose tegument and possess a mouth, a thick-walled pharynx, a short saccular gut, ciliated flame cells and tubular cells (protonephridial system). Cercariae are pleurolophocercous with tubular shapes comprising elongate bodies (150 x 75 µm) surmounting long powerful tails (400 x 25 µm) with dorsal and ventral fins. Cercariae have spinose teguments with sensory hairs, rudimentary ventral suckers, without stylets but with 2-3 short transverse rows of oral spines, and developing organ systems. Metacercaria are tail-less cercarial bodies that have encysted and become surrounded by several cyst wall layers (derived from both parasite and host); their final morphology tends to be intermediate between that of the cercaria and the sexual adult. Adult flukes are lancet-shaped with dorsoventrally flattened bodies measuring from 7-12 mm long by 1-3 mm wide. They are covered with a translucent tegument and appear red-yellow in colour. They possess a subterminal oral sucker, pharynx, oesophagus, bifurcate caeca, mid-body ventral sucker and a tubular excretory bladder. Adult worms are hermaphroditic and possess both male and female reproductive organs. The generic name *Opith-orchis* actually means 'behind'-'testis', referring to the posterior location of the testes with respect to the ovary. Worms have 2 testes located in diagonal or tandem apposition and they may be lobular or branched (*O. viverrini* has deeply lobed testes cf. *O. felineus*). The testes are connected to a muscular seminal vesicle that ends in the ejaculatory duct (no cirrus sac) opening into the genital pore. Worms possess a single multilobed ovary connected to lateral vitelline follicles (both *O. viverrini* and *O. felineus* have vitelline clusters, but those of the latter species have transversely compressed patterns) and a coiled uterus opening into the genital pore. Internal fertilization occurs resulting in the production of numerous small and embryonated eggs.

Site of infection: Adult *Opisthorchis* worms infect the biliary tract of their vertebrate definitive hosts (mammals, birds, fish, reptiles), being found predominantly in intrahepatic bile ducts, sometimes in extrahepatic bile ducts, the gall bladder or pancreas, and a few species in fish even occur in the intestines. Asexual developmental stages (sporocysts, rediae) are found within various tissues of their first intermediate hosts (snails), while metacercariae develop in the muscles of their second intermediate hosts (fish).

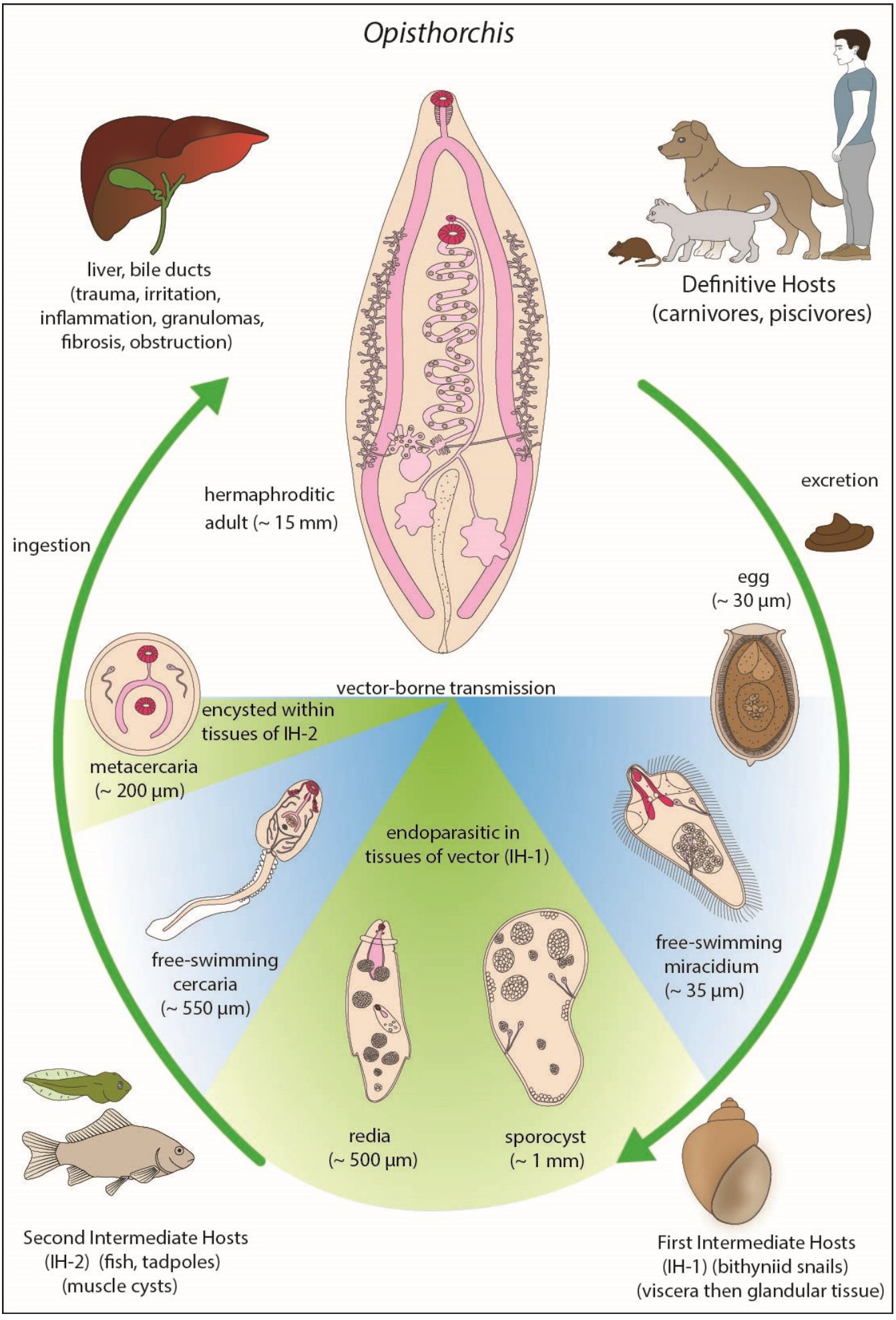
Pathogenesis: Adult liver flukes cause tissue damage by mechanical irritation (when attaching, feeding and moving), by chemical irritation (releasing parasite metabolic products that are toxigenic and/or antigenic) and by immune-mediated reactions (provoking chemical and cellular inflammatory responses that have cytotoxic, proliferative and mutagenic effects). The flukes live in the bile ducts and while light infections may be asymptomatic, heavier infections (> 100 worms) may cause mild, moderate or severe disease manifestations due to tissue trauma, persistent inflammation and obstruction. A range of acute and chronic clinical symptoms/signs have been reported, including diarrhoea, abdominal pain, flatulence, indigestion, anorexia, malaise, fatigue, fever, eosinophilia, tender hepatomegaly, cholangitis, cholecystitis and biliary obstruction with jaundice and mild scleral icterus. In acute infections caused by *O. felineus*, symptoms may also include urticaria, nausea, vomiting, arthralgia, sometimes lymphadenopathy and rarely an acute serum sickness-like presentation. Chronic infections cause cumulative damage to bile ducts as epithelial cells undergo adenomatous hyperplasia, goblet cell metaplasia increases mucus production and periductal areas become fibrotic and sclerotic (esp. left hepatic lobe). Persistent inflammation and granuloma formation may occur throughout tissues in association with adult flukes and eggs, but cholelithiasis is uncommon even though eggs and worm fragments may be found in gallstones. Obstructive jaundice, intrahepatic duct stones and recurrent suppurative cholangitis (occasionally with liver abscesses) are considered to be strongly indicative of opisthorchiasis. Both children and adults may be clinically affected, although symptomatic infection is more common in adults as worm burdens accumulate due to repeated infection and the lack of any acquired protective immunity (possibly due to immunosuppressive factors). Serious complications may also develop in adults with progressive hepatic cirrhosis, cholecystitis and pancreatitis. Heavy *O. viverrini* infections have also been implicated in the development of bile duct cancer, cholangiocarcinoma (CCA), due to the constant irritation, hypersecretion and extensive fibrosis making the biliary epithelium more susceptible to malignant transformation (chronic inflammation induces oxidative and nitrative stress with consequential DNA damage). *O. viverrini* is now classified as a class 1 carcinogen for CCA in humans (together with *Clonorchis*

sinensis) and risk factors include geographic location, high alcohol consumption, advancing age, male gender, a specific GST-M1 (glutathione S-transferase enzyme) genetic polymorphism, and exposure to nitrosamines in foods and betel nut tobacco.

Developmental cycle and mode of transmission: *Opisthorchis* spp. have indirect life cycles involving 3 hosts: definitive hosts (vertebrates) infected with adult flukes; first intermediate hosts (gastropods) in which asexual reproduction of larval stages occurs; and second intermediate hosts (fish) infected with encysted metacercariae. Transmission between hosts involves motile aquatic developmental stages that actively seek hosts. Embryonated eggs produced by fertile worms (up to 300 eggs per day) are passed in host faeces into the external environment. Those contaminating freshwater sources may be ingested by bithyniid snails which act as first intermediate hosts. The eggs hatch in the snail digestive tract releasing their enclosed miracidia which penetrate the gut wall and form sac-like sporocysts. Germ balls within the sporocysts form rediae which are released into adjacent tissues. Germ balls within the rediae then form cercariae which are released into lymph spaces to undergo maturation. Eventually, the cercariae emerge from the snails, typically with diurnal periodicity (peaking in early morning). Cercariae may emerge from snails for up to 2 months. They swim about in the water column, particularly in stagnant or slow-moving waters (including ponds, streams, rivers, swamps, rice fields), and penetrate the skin of freshwater fish, mostly cyprinids, which act as second intermediate hosts. In particular, infections have been associated with rural communities that have established rice paddies for agriculture and carp ponds for aquaculture, with the boundaries between these pursuits often becoming blurred. The cercariae penetrate the fish skin dropping their tails and encyst as metacercariae in the skin, fins and muscles within 3 weeks. Piscivorous hosts become infected by eating infective metacercariae in raw, undercooked, dried, smoked, salted or pickled fish. Freshwater fish dishes are very common in the cuisine of Laos and Thailand as koi-pla (raw fish), larb-pla (raw fish in spicy salad), pla-ra, pla-som and som-fak (salted semi-fermented fish). Infections may also be exported outside of endemic regions with frozen, dried and pickled fish. Following ingestion, metacercariae excyst in the small intestines releasing the juvenile worms which migrate through the common bile duct to reach the intrahepatic bile ducts where they mature into adult worms 3-4 weeks later. Gravid worms release embryonated eggs that are carried with bile into the gut to be passed with faeces. The prepatent period (time from infection to first egg release) ranges from 4-6 weeks in definitive hosts, and infections have been shown to persist for 10-30 years.

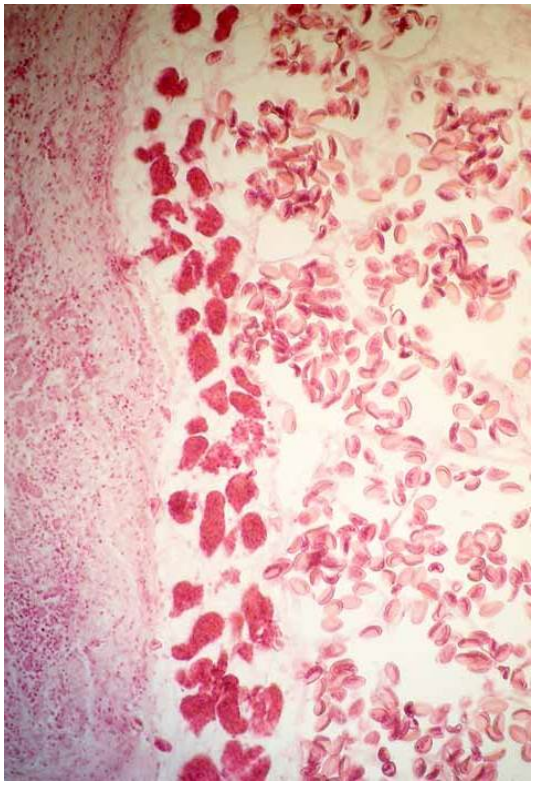
Differential diagnosis: Infections are routinely diagnosed by the microscopic detection of fluke eggs in faecal samples or in bile or duodenal fluid biopsy samples. Coprological examination may require multiple stool samples due to irregular egg excretion. While eggs may be detected in wet faecal preparations or faecal smears (Kato-Katz thick smears), they are better concentrated from stool samples by sedimentation (e.g. formalin-ethyl acetate technique) rather than floatation (eggs do not float readily in saturated salt or sugar solutions). Many fluke eggs resemble each other so specific diagnosis based on egg morphology alone is difficult. Adult flukes may be recovered from hosts ante-mortem by surgery, endoscopy (such as gastroscopy or endoscopic retrograde cholangiopancreatography (ERCP)) or following chemotherapy, or at post-mortem by dissection. Key anatomical features of adult worms may be examined by microscopy to facilitate differential diagnosis. Infections may also be revealed by modern medical imaging techniques, including ultrasonic or X-ray (cholecystocholangiography) examination, or computed tomography (CT) or magnetic resonance imaging (MRI) scans. The severity and extent of associated pathological changes (inflammation, fibrosis) may be indicated by enlargements, thickenings, dilations, strictures or filling defects. Infections by metacercariae in fish may be detected by microscopic examination of dissected muscles, usually in squash preparations or following pepsin-acid digestion. A range of immunodiagnostic tests (including immunoelectrophoresis, haemagglutination, fluorescent-antibody tests and enzyme immunoassays) have been developed to detect host antibodies in serum samples, but they are unable to differentiate between recent infections and prior exposure. An enzyme immunoassay has recently been developed to detect parasite copro-antigens in faecal samples, although some cross-reactivity problems were encountered. Research laboratories have recently used molecular techniques to detect and characterize DNA from adult worms and eggs in mammals and from metacercariae in fish, via DNA hybridization assays or by polymerase chain reaction (PCR) amplification of repetitive DNA elements or by random amplified polymorphic DNA (RAPD) analyses.

Treatment and control: Anthelmintics have been used for the chemotherapeutic treatment of individual patients as well as for the chemoprophylactic treatment of cohorts/communities most at-risk of infection. The isoquinoline (praziquantel) has proven most efficacious in eradicating adult worms, despite some minor side-effects such as headache, dizziness, insomnia, nausea and vomiting. Good results have also been obtained using the broad-spectrum benzimidazoles (mebendazole and albendazole) as well as the new diamidine derivative (tribendimidine). However, prognosis is poor once cholangiocarcinoma (CCA) develops. Surgical resection may be attempted in early cases of CCA, while bile drainage may be carried out as palliative treatment to relieve symptoms of obstructive jaundice in later cases. Regrettably, re-infection commonly occurs in endemic areas due to the high frequency of eating raw or improperly cooked fish in Asia. Preventive measures developed to break transmission patterns centre around 3 strategies: limiting faecal contamination of water (avoiding promiscuous defaecation and night-soil fertilizers, improving sanitation, sewage treatment, treating humans and companion animals (dogs and cats are important reservoirs of infection)); reducing snail intermediate host populations (using barriers or molluscicides); and killing metacercariae in fish products (cooking above 63°C, freezing at -20°C for > 7 days). Public health education campaigns are mandatory to raise awareness of the consequences of acute and chronic infections (particularly cancer development), to promote community treatment programs, to improve food and water hygiene, and to advocate for changes in culinary customs (cook fish).


Opisthorchis
liver, bile ducts
(trauma, irritation,
inflammation, granulomas,
fibrosis, obstruction)
Definitive Hosts
(carnivores, piscivores)
hermaphroditic
adult (~ 15 mm)
excretion
ingestion
egg
(~ 30 µm)
vector-borne transmission
encysted within
tissues of IH-2
metacercaria
(~ 200 µm)
endoparasitic in
tissues of vector (IH-1)
free-swimming
cercaria
(~ 550 µm)
free-swimming
miracidium
(~ 35 µm)
redia
(~ 500 µm)
sporocyst
(~ 1 mm)
Second Intermediate Hosts
(IH-2) (fish, tadpoles)
(muscle cysts)
First Intermediate Hosts
(IH-1) (bithyniid snails)
(viscera then glandular tissue)



Opisthorchis adult worm



Opisthorchis section through worm in liver



Opisthorchis egg

Clonorchis
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult opisthorchiideans are small to medium flukes, often spinose, living in the alimentary tracts of mammals, birds, reptiles and fish. They produce embryonated eggs which only hatch after ingestion by snails (first intermediate hosts) and metacercariae develop in fish (second intermediate hosts). Opisthorchids are parasitic in the bile ducts of fish-eating mammals and infections by *Opisthorchis, Clonorchis* and *Metorchis* spp. have been associated with liver disorders in dogs, cats and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Plagiorchiida ('echinostomatids', plagiorchiids', mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder:	Opisthorchiata (egg eaten by gastropod IH, rediae formed, simple-tailed cercariae, encysts in second IH, metacercariae eaten by DH)
Superfamily:	Opisthorchioidea (small-medium flukes, often spinose, piscivorous DH)
Family:	Opisthorchiidae (medium leaf-shaped flukes, in bile ducts of mammals, rediae without appendages, cercariae with two eyespots, metacercariae in second IH)
Genus:	*Clonorchis* (parasitic in liver of piscivorous mammals)
Species:	*C. sinensis* causes biliary obstruction, cholangitis and possibly cholangiocarcinoma in humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs,

fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. The suborder Opisthorchiata contains one superfamily Opisthorchioidea comprising tiny to medium-sized flukes which form rediae without appendages, then simple-tailed cercariae that encyst in second intermediate hosts forming metacercariae. Over 400 species have been described in 90 genera

in 3 families (Opisthorchiidae, Cryptogonimidae, Heterophyidae). The family Opisthorchiidae is found primarily in the bile ducts of piscivorous mammals and some 30 genera have been recognized in 13 subfamilies: Allogomtiotrematinae (*Allogomtiotrema, Satyapalia*); Aphallinae syn. Witenbergiinae (*Witenbergia*); Delphinicolinae (*Delphinicola*); Diasiellinae (*Diasiella*); Metorchiinae (*Holometra, Metametorchis, Metorchis, Parametorchis*); Oesophagicolinae (*Oesophagicola*); Opisthorchiinae (*Agrawalotrema* (syn. *Thaparotrema*)*, Amphimerus, Cladocystis, Clonorchis, Cyclorchis, Evranorchis, Nigerina, Opisthorchis* (syn. *Hepatiarius*)*, Paropisthorchis, Pseudogomtiotrema* (syn. *Gomtia*)*, Trionychotrema*); Pachytrematinae (*Pachytrema*); Plotnikoviinae (*Plotnikovia*); Pseudamphimerinae (*Erschoviorchis, Euamphimerus, Pseudamphimerus*); Pseudamphistominae (*Microtrema, Pseudamphistomum*); Ratziinae (*Ratzia*); and Tubangorchiinae (*Tubangorchis*). The subfamily Opisthorchiinae is characterized by small-medium elongate flukes whose uterus and vitellaria do not extend anteriorly beyond the level of the ventral sucker. The genus *Clonorchis* is monotypic and contains only one species (the Chinese liver fluke *C. sinensis*) found in fish-eating mammals throughout Asia (Far-East, South-East Asia, Japan, Siberia), mostly humans, pigs, dogs and cats. It is estimated that 20-30 million people are currently infected and that 600 million are at risk of infection. *C. sinensis* is very similar in its biological characteristics to other Oriental liver flukes commonly infecting humans in Asia; namely *Opisthorchis felineus* and *Opisthorchis viverrini*. The genera *Clonorchis* and *Opisthorchis* are conventionally differentiated on the basis of adult worm morphology, particularly in the position and shape of testes and vitellaria (*Clonorchis* having highly branched testes positioned tandemly and vitellaria distributed continuously along both lateral margins, while *Opisthorchis* spp. have lobular testes and vitelline glands arranged in clusters). Nonetheless, some workers consider the genera to be synonymous and have transferred the species *C. sinensis* to the genus *Opisthorchis*. Molecular studies have confirmed their close identity but most often depict them as closely-related sister clades.

***Clonorchis* species**	**Definitive hosts [adults in bile ducts]**	**First intermediate hosts [sporocysts/rediae in tissues]**	**Second intermediate hosts [metacercariae in tissues]**	**Distribution**
C. sinensis (syn. *C. endemicum, Opisthorchis sinensis*) (Chinese liver fluke, Oriental liver fluke)	Primates: hominid (human); Carnivora: canid (dog), felid (cat), mustelid (mink, badger); Artiodactyla: suid (pig), camelid (camel), bovid (cattle); Lagomorpha: leporid (rabbit); Rodentia: murid (rats, mice), caviid (guinea pig), cricetid (muskrat)	freshwater Gastropoda: bithyniid (*Parafossarulus anomalospiralis, manchouricus, sinensis, striatulus, Bithynia fuchsianus, longicornis, misella, robustus*); assimineid (*Assiminea lutea*), thiarid (*Melanoides tuberculata*), semisulcospirid (*Semisulcospira amurensis, cancellate, libertine, Koreoleptoxis amurensis*)	freshwater Cypriniformes: cyprinids (common carp, crucian carp, predatory carp, grass carp, black carp, silver carp, mud carp, bighead carp, goldfish, dark chub, pale chub, sharpbelly, stone moroko, Korai moroko, ito moroko, Amur false gudgeon, topmouth gudgeon, Korean southern gudgeon, Manchurian gudgeon, three-lips, pike gudgeon, mugitsuku, Chinese lake gudgeon, Chinese lizard gudgeon, rainbow gudgeon, variegated gudgeon, rosy bitterling, Khanka spiny bitterling, Amur bitterling, slender bitterling, Korean bitterling, kanehira, Yamatsuta paljasloug, Chinese bleak, Korean splendid dace, common sawbelly, spotted steed, barbel steed, barbel chub, zunaga-nigoi, Chinese minnow, big-scaled redfin, wataka, common dace, black Amur bream, white Amur bream, hiina laikviidikas, hiina morukas, bangana, kamatsuka, mugitsuku, lake minnow), cobitid (pond loach); Siluriformes: bagrid (Korean stumpy bullhead, yellowhead catfish, orca-whip, Brazhnikov's catfish), silurid (Amur catfish, Chinese large-mouth catfish); Gobiformes: oxudercid (pseudogoby), eleotrid (sleeper); Mugiliformes: mugilid (mullet); Perciformes: percichthyid (oriental perch, golden mandarin	Asia, India, Eastern Russia

			fish), ephippid (orbfish), odontobutid (Chinese sleeper); Clupeiformes: pristigasterid (slender shad); Anabantiformes: osphronemid (paradise fish, paradise gourami); Osmerifoirmes: osmerid (pond smelt); Cichliformes: cichlid (Mozambique tilapia); Beloniformes: adrianichthyid (Japanese rice fish)	

Parasite morphology: *Clonorchis sinensis* forms 7 different developmental stages: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae and adult flukes. Embryonated eggs passed in faeces are small and ovoid to flask-shaped, with dimensions ranging from 25-35 x 12-19 µm. They are surrounded by a thick tanned (yellow-brown) eggshell with a distinct operculum sporting prominent opercular shoulders at one end and a small knob-like protuberance at the other end. The eggs contain a fully-developed pyriform miracidium with 2 simple eyespots, a ciliated covering, lateral sensory papillae and 8-25 germinal cells. Sporocysts are elongate pleomorphic sacs measuring up to 0.5 mm long with thin walls containing balls of germinal cells that give rise to small rediae (embryos). Rediae grow into large elongate stages measuring over 1mm in length and possess a mouth, pharynx and simple digestive tract. They contain balls of germ cells which develop into more rediae or cercariae. Cercariae are long brown pleurolophocercous stages with elliptical bodies (around 200 µm long) and elongate unforked tails (up to 500 µm long) with long dorsal fins and shorter ventral fins. They have a pair of eyespots, well-developed anterior glands (penetration and cystogenous), a rudimentary ventral sucker, without stylets but with 2-3 short transverse rows of oral spines, and their cuticle is covered with delicate bristles and tiny spines. Metacercaria are essentially tail-less cercariae whose bodies have become folded and encapsulated in a thin cyst wall. Cysts are elliptical, ranging from 120-280 x 85-220 µm, and are usually white with brown pigment granules. Metacercariae have oral and ventral suckers (of approx. equal size) and a sac-like excretory bladder. Adult flukes have long flat narrow lanceolate bodies that are tapered anteriorly and rounded posteriorly. Their size ranges from 4-28 x 1-7 x 1 mm, but most are 8-15 x 1.5-4.0 x 1 mm. They are covered by a delicate translucent aspinose tegument and are whitish-brown. They have an anterior oral sucker and a ventral sucker located in the upper mid-body. The digestive tract comprises a mouth, pharynx, oesophagus and simple bifurcate caeca that are blind-ended (no anus). Mature adult flukes are hermaphroditic, each worm containing both male and female reproductive organs. The generic name *Clon-orchis* (meaning 'rear'-'testis') refers to 2 large branched testes located in tandem near the posterior end (*C. sinensis* has branched rather than lobed testes like *Opisthorchis*). The testes are connected to a large, serpentine seminal vesicle leading to the ejaculatory duct which opens into the genital pore (both cirrus and cirrus sac are absent). The single pretesticular ovary has several lobes and is connected to a broad looped uterus with numerous folds and numerous small dense vitelline follicles continuously distributed in both lateral fields (cf. *Opisthorchis* spp. have clustered vitelline glands). The uterus opens into the common genital duct and is normally filled with many small embryonated eggs.

Site of infection: Adult *C. sinensis* flukes usually infect the intrahepatic bile ducts in the livers of their definitive hosts (mammals), although in heavy infections flukes may also occur in extrahepatic bile ducts, the gall bladder and sometimes in pancreatic ducts. Asexual developmental stages (sporocysts and rediae) are found associated with the digestive tracts and haemolymph spaces in their first intermediate hosts (snails), while metacercariae encyst within the muscles and connective tissues of their second intermediate hosts (fish).

Pathogenesis: Adult liver flukes live in the bile ducts and feed on epithelia which may result in profound inflammatory responses due to mechanical irritation (worm attachment, feeding and movement) and chemical irritation (release of toxic and/or allergenic worm metabolites invoking molecular and cellular host immune responses with immunopathological consequences). Many infections are light and benign (involving < 100 worms), but the risk of symptomatic infection and complications increases with heavier and more persistent infections. Nevertheless, only around 10% of patients develop clinical disease, manifest usually by diarrhoea, obstructive jaundice, and even cancer formation. Infections do not lead to the acquisition of any solid protective immunity, so repeated infections in endemic areas result in increasing worm burdens with age. Symptomatic infections are more common in aging adults and disease onset may be delayed for years following primary infection. Three stages of disease progression have been observed for heavier infections. An acute phase occurs around 1 week after infection, with relatively nonspecific clinical signs including anorexia, weight loss, diarrhoea, flatulence, fever, rigors and chills, colic abdominal pain, indigestion, slight icterus, rash, liver enlargement, swollen abdomen, oedema, fatigue, leucocytosis and eosinophilia. A prolonged chronic phase then ensues, with progressive gall bladder enlargement, oedema, meteorism (intestinal gas accumulation), cachexia, recurrent pyogenic liver cholangitis, diarrhoea, hepatomegalia, growth retardation and neuropsychiatric symptoms. Various complications may then arise, ranging from obstructive jaundice, cholangitis, cholestasis, liver cirrhosis, hepatolithiasis, pancreatitis, ascites, portal hypertension, night blindness (lack of vitamin A) and hepatic tumours. Adult flukes cause erosion of the biliary epithelial lining, adenomatous epithelial hyperplasia, mucin-secreting metaplasia and sometimes the formation of crypts. Profuse leucocytic infiltrates (eosinophils and mononuclear cells) occur around ducts, with necrosis and atrophy of adjacent hepatocytes. The ducts become fibrotic, thickened

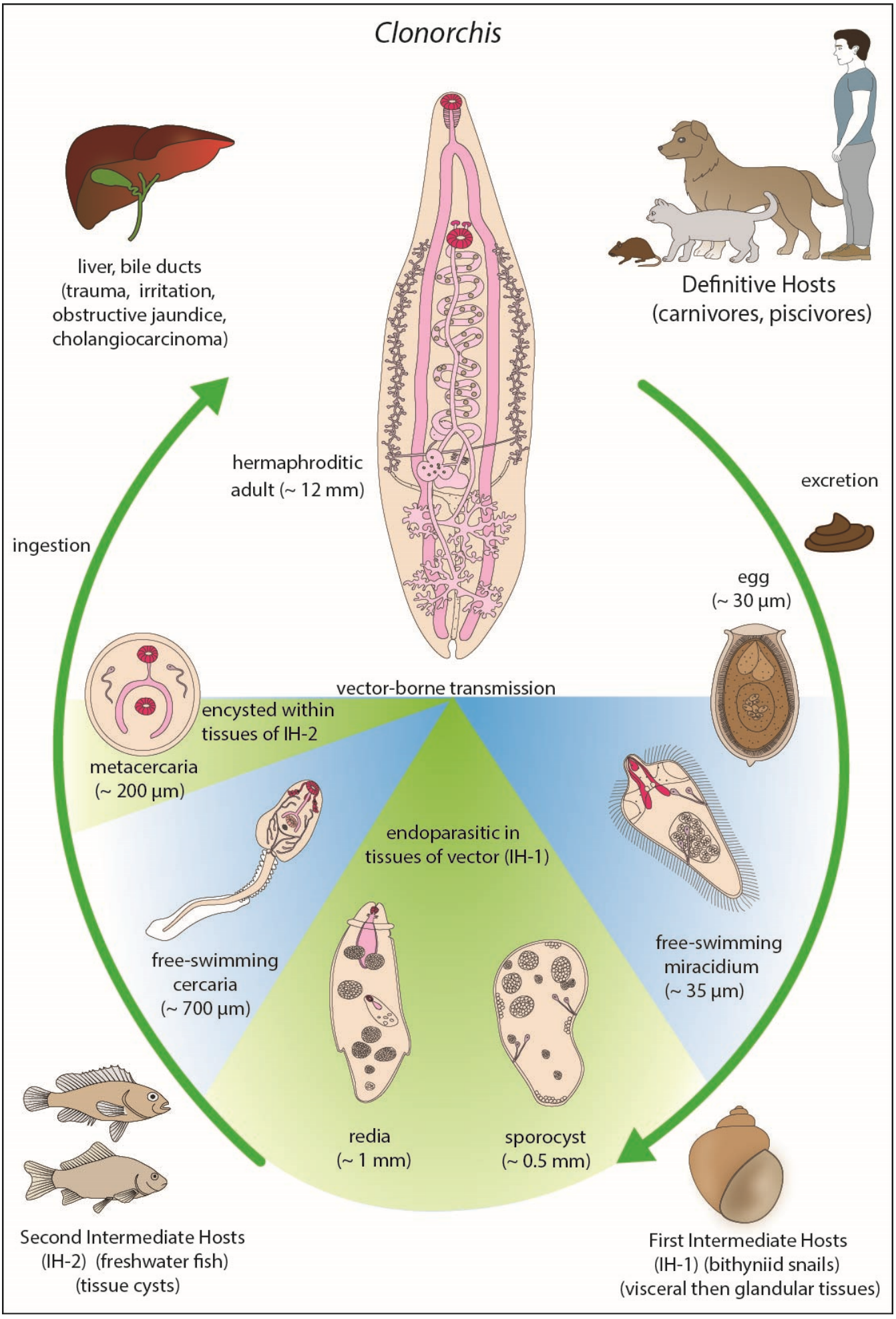
and obstructed, with cholangitis, stenosis and bile retention. The gall bladder often becomes enlarged and nonfunctional with worms causing cholecystitis, cholelithiasis (gallstones), intrahepatic pigment stones and pancreatitis. Infiltrating eggs may also result in granuloma formation further interfering with liver function. Recurrent infection and inflammation of the bile duct by C. *sinensis* can lead to dysplasia or neoplasia of biliary epithelial cells, particularly cholangiocarcinoma (CCA) which is malignant and invariably fatal unless a liver transplant is performed. *C. sinensis* has recently been classified as a group 1 biocarcinogen with causative mechanisms involving chronic irritation and inflammation, nitric oxide formation, protein dysregulation, and parasite excretory-secretory (ES) products.

Developmental cycle and mode of transmission: *Clonorchis* flukes have indirect life cycles involving 3 different types of hosts: asexual larval stages occurring in first intermediate hosts (snails), encysted infective stages in second intermediate hosts (fish), and adult worms in piscivorous definitive hosts (mammals). Transmission between the two intermediate hosts involves aquatic developmental stages, while final hosts become infected by predator-prey transmission when they consume infected fish. Embryonated eggs are excreted with definitive host faeces into the external environment, some ending up in water where they are ingested by freshwater snails (first intermediate hosts). The most suitable snails are bithyniid species living in slow-moving water bodies such as rice paddies, aquaculture ponds, and lakes used for commercial fishing. Reports in assimineid, thiarid and semisulcospirid snail species may represent mis-identifications and remain to be confirmed by molecular characterization studies. The eggs hatch in the snail digestive tract releasing their enclosed miracidia which penetrate the gut wall and develop into sporocysts in haemolymph spaces within 4 hours of infection. Sporocysts feed by absorption (lack mouths) and their germ balls undergo asexual reproduction forming 20-50 rediae over several weeks. Rediae have functional digestive tracts and they feed actively on snail tissues. At least 2 generations of rediae are produced; mother rediae forming daughter rediae which eventually produce up to 50 cercariae which emerge from the snail into water. The prepatent period in snails (time from infection to first release of cercariae) is around 95 days. Cercaria use their tails to swim around in water for 1-2 days actively seeking a suitable second intermediate host (freshwater fish, mainly cyprinids). Chinese publications have recorded over 130 fish species (and 4 shrimp species?) as second intermediate hosts for *C. sinensis.* When cercariae find a fish host, they invade the skin shedding their tails and then encyst as metacercariae in the muscles and subcutis where they may survive for up to 1 year. Young small fish are particularly susceptible to heavy infections due to their thinner skins and naive immune status. Infections are transmitted to piscivorous definitive hosts when they eat fish containing infective metacercariae. Humans become infected by eating raw, undercooked, salted, smoked or slightly pickled fish. Wine, vinegar, mustard, wasabi, and spices do not destroy encysted flukes. In Asia, many traditional dishes include raw freshwater fish (yu sang, sushi), lightly pickled fish (koi pla), fermented fish several days old (pla som), fermented and salted fish several weeks old (pla ra, jaewbhong), and lightly cooked fish (yusheng zhou, fish congee, hotpot, thick fillets). Ingested metacercariae excyst in the duodenum releasing immature flukes which quickly migrate to the bile ducts where they develop into adult flukes. The prepatent period in mammals (time from infection to first release of eggs) is around 4 weeks and adult worms may produce from 2,500-4,000 eggs per day for at least 6 months. Infections have been recorded to persist for decades and there is circumstantial evidence to suggest that adult worms may live for 25-30 year.

Differential diagnosis: The disease clonorchiasis manifests with relatively nonspecific biliary or hepatic signs, but should be suspected in symptomatic patients with a history of residence in, or travel to, endemic areas and a dietary intake of raw freshwater fish. Infections are usually diagnosed by the microscopic detection of fluke eggs in faecal samples, either in smears (Kato-Katz technique) or concentrates (formalin-ether technique), although their differentiation from other liver flukes (esp. *Opisthorchis*) is difficult due to their morphological similarity. Eggs may also be detected in duodenal aspirates or bile specimens collected when there is complete obstructive jaundice. Adult flukes may also be recovered from host faecal samples following anthelmintic therapy, or from fluids collected by endoscopy (esp. retrograde cholangiopancreatography). Modern imaging techniques have been used to gauge the extent and severity of infections by assessing tissue/organ changes, although it is difficult to distinguish between pathology caused by current infection or prior exposure. Ultrasonography, computed tomography (CT), magnetic resonance imaging (MRI) and cholangiography may reveal intrahepatic bile duct inflammation and periductal fibrosis with dilatation, stenosis or wall irregularities, gall bladder enlargement and filling defects. Infections by metacercariae in fish may be detected by microscopic examination of dissected muscles, usually in squash preparations or following pepsin-acid digestion. Various immunoserological tests have been developed to detect host antibodies against whole worm extracts, excretory-secretory (ES) products or recombinant antigens, including intradermal tests, complement fixation, haemagglutination, fluorescence antibody tests and enzyme immunoassays, but problems with specificity and cross-reactivity have been encountered. Molecular biological techniques have been developed to detect and characterize parasites in mammals, fish and snails, mostly by polymerase chain reaction (PCR, including realtime-PCR) or loop-mediated isothermal (LAMP) amplification of random amplified polymorphic DNA (RAPD), mobile genetic elements (MGE), nuclear DNA (internal transcribed spacer regions of ribosomal RNA) or mitochondrial DNA (cytochrome c oxidase subunits 1 and 2, nicotinamide adenine dinucleotide dehydrogenase subunits 1 and 2).

Treatment and control: The isoquinoline anthelmintic praziquantel is currently the drug of choice for the chemotherapeutic treatment of *C. sinensis* infections in clinical patients as well as for preventive chemoprophylaxis in high-risk communities. Cure rates up to 100% have been reported with minimal side-effects (headache, dizziness, insomnia, nausea and vomiting). Acute and chronic infections have also been treated successfully with the broad-spectrum benzimidazoles, albendazole and mebendazole. The concurrent administration of antibiotics is used to treat recurrent pyogenic cholangitis. Other interventions may also be required in

cases of obstructive jaundice, including biliary drainage and/or surgery. If cholangiocarcinoma (CCA) develops, however, a complete liver resection with clear margins gives the greatest chance for long-term survival because CCA responds poorly to chemotherapy. Many regions have implemented control programs based around mass population treatments with praziquantel, but re-infection is quite common in endemic areas. Other strategies have been integrated into preventive programs to reduce transmission cycles between piscivorous and aquatic hosts. Much can be done to prevent the faecal contamination of freshwater bodies, such as preventing promiscuous defaecation, installing sewers or septic tanks, treating sewage, fencing out feral and wild mammals which may be reservoir hosts, banning night-soil fertilizers, and especially by preventing the ingress of faeces into aquaculture ponds (some communities actually build toilets over carp ponds). Parasites infect and multiply in snail intermediate hosts but attempts to control their population numbers in domestic, peridomestic and wild situations have met with limited success. Various molluscicides have been used to kill snails but their indiscriminate use has been associated with serious environmental and public health problems because snails are integral to healthy aquatic ecosystems. Some aquaculture ventures regularly drain ponds to control aquatic biota, but this is difficult to do in regions with wet seasons involving monsoons and periodic flooding. The greatest impact for control in endemic regions has been to reduce transmission to humans by encouraging them not to eat raw freshwater fish. Cooking fish at temperatures above 63ºC, or freezing them at -20ºC for at least 7 days, has been shown to kill metacercariae. Proactive public health educational campaigns are required to get communities to change entrenched culinary practices perceived to be normal. Food hygiene regulations should also be upgraded to check the exportation of potentially contaminated fish products (frozen, dried, salted or pickled) from endemic areas. Lastly, some preliminary research on vaccine development has shown promising results, despite the apparent lack of acquired protective immunity in natural infections. Two DNA vaccines, one encoding a cysteine proteinase and another encoding a fatty-acid binding protein, and an oral vaccine, using tegumental protein fused with bacterial spore coat, have provided some protection (30-45%) in experimental animal models.

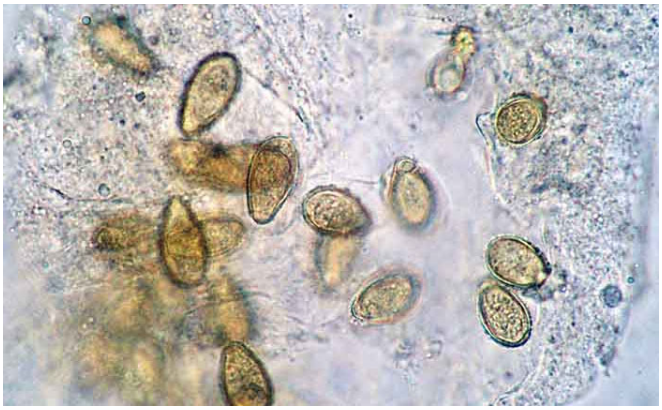

Clonorchis
liver, bile ducts
(trauma, irritation,
obstructive jaundice,
cholangiocarcinoma)
Definitive Hosts
(carnivores, piscivores)
hermaphroditic
adult (~ 12 mm)
excretion
ingestion
egg
(~ 30 µm)
vector-borne transmission
encysted within
tissues of IH-2
metacercaria
(~ 200 µm)
endoparasitic in
tissues of vector (IH-1)
free-swimming
cercaria
(~ 700 µm)
free-swimming
miracidium
(~ 35 µm)
redia
(~ 1 mm)
sporocyst
(~ 0.5 mm)
Second Intermediate Hosts
(IH-2) (freshwater fish)
(tissue cysts)
First Intermediate Hosts
(IH-1) (bithyniid snails)
(visceral then glandular tissues)



Clonorchis adult worm



Clonorchis section through worm in liver



Clonorchis eggs



Clonorchis cercaria

Metorchis
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult opisthorchiideans are small to medium flukes, often spinose, living in the alimentary tracts of mammals, birds, reptiles and fish. They produce embryonated eggs which only hatch after ingestion by snails (first intermediate hosts) and metacercariae develop in fish (second intermediate hosts). Opisthorchids are parasitic in the bile ducts of fish-eating mammals and infections by *Opisthorchis, Clonorchis* and *Metorchis* spp. have been associated with liver disorders in dogs, cats and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Plagiorchiida ('echinostomatids', plagiorchiids', mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder:	Opisthorchiata (egg eaten by gastropod IH, rediae formed, simple-tailed cercariae, encysts in second IH, metacercariae eaten by DH)
Superfamily:	Opisthorchioidea (small-medium flukes, often spinose, piscivorous DH)
Family:	Opisthorchiidae (medium leaf-shaped flukes, in bile ducts of mammals, rediae without appendages, cercariae with two eyespots, metacercariae in second IH)
Genus:	*Metorchis* (parasitic in bile ducts of piscivorous animals)
Species:	various species cause cholangiohepatitis in mammals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs,

fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. The suborder Opisthorchiata contains one superfamily Opisthorchioidea comprising tiny to medium-sized flukes which form rediae without appendages, then

simple-tailed cercariae that encyst in second intermediate hosts forming metacercariae. Over 400 species have been described in 90 genera in 3 families (Opisthorchiidae, Cryptogonimidae, Heterophyidae). The family Opisthorchiidae is found primarily in the bile ducts of piscivorous mammals and some 30 genera have been recognized in 13 subfamilies: Allogomtiotrematinae (*Allogomtiotrema, Satyapalia*); Aphallinae syn. Witenbergiinae (*Witenbergia*); Delphinicolinae (*Delphinicola*); Diasiellinae (*Diasiella*); Metorchiinae (*Holometra, Metametorchis, Metorchis, Parametorchis*); Oesophagicolinae (*Oesophagicola*); Opisthorchiinae (*Agrawalotrema* (syn. *Thaparotrema*)*, Amphimerus, Cladocystis, Clonorchis, Cyclorchis, Evranorchis, Nigerina, Opisthorchis* (syn. *Hepatiarius*)*, Paropisthorchis, Pseudogomtiotrema* (syn. *Gomtia*)*, Trionychotrema*); Pachytrematinae (*Pachytrema*); Plotnikoviinae (*Plotnikovia*); Pseudamphimerinae (*Erschoviorchis, Euamphimerus, Pseudamphimerus*); Pseudamphistominae (*Microtrema, Pseudamphistomum*); Ratziinae (*Ratzia*); and Tubangorchiinae (*Tubangorchis*). The subfamily Metorchiinae is characterized by small elongate flukes whose uterus and vitellaria extend anteriorly beyond the level of the ventral sucker. The genus *Metorchis* contains over 25 species which have been found in a wide range of fish-eating mammals (8 species) and birds (18 species), mostly from the Northern Hemisphere (Eurasia and North America). *Metorchis* infections in humans are uncommon apart from isolated outbreaks which are often traced to common infected food sources, especially raw sucker fish consumed by indigenous populations. *Metorchis* spp. differ from *Clonorchis* and *Opisthorchis* spp. in that the adult flukes are smaller (shorter and wider), the oesophagus is very short (almost absent), the caeca extend posteriorly to the end of the body, and the 2 testes are usually entire rather than lobed or branched.

***Metorchis* species**	**Definitive hosts [adults in bile ducts]**	**First intermediate hosts [sporocysts/rediae in tissues]**	**Second intermediate hosts [metacercariae in tissues]**	**Distribution**
M. bilis (syn. *M. albidus, M. crassiusculus*)	Carnivora: canid (dog, fox), felid (cat), mustelid (Eurasian otter, mink), ursid (bear); Rodentia: cricetid (hamster, muskrat); Pinnipedia: phocid (seal); Primates: hominid (human), Suliformes: phalacrocoracid (great cormorant); Accipitriformes: accipitrid (white-tailed sea-eagle, eastern imperial eagle, golden eagle, long-legged buzzard, rough-legged buzzard, marsh harrier); Anseriformes: anatid (red-breasted merganser, garganey, mallard, duck)	freshwater Gastropoda: bithyniid (*Bythinia tentaculata, B. inflata, B. troscheli*)	freshwater Cypriniformes: cyprinid (ide, roach, dace, tench, minnow, gudgeon, verkhovka, crucian carp, silver carp)	Eurasia, North America
M. butoridi	Pelecaniformes: ardeid (striated heron)			Russia
M. conjunctus (syn. *Distoma conjunctum*, *Parametorchis noveboracensis, P. canadensis, P. manitobensis*) (Canadian liver fluke)	Carnivora: canid (dog, red fox, gray fox, silver fox, red wolf, gray wolf, coyote), procyonid (raccoon), mustelid (American mink, fisher, ferret), ursid (bear), felid (cat); Rodentia: cricetid (muskrat, cotton rat); Primates: hominid (human)	freshwater Gastropoda: amnicolid (*Amnicola limosa*)	freshwater Cypriniformes: catostomid (white sucker, longnose sucker), cyprinid (creek chub, fallfish); Perciformes: percid (yellow perch); Salmoniformes: salmonid (brook trout, char); Esociformes: esocid (northern pike)	North America
M. hovorkai	Anseriformes: anatid (ferruginous duck)			Europe
M. kimbangensis	Siluriformes: silurid (Amur catfish)			Vietnam
M. orientalis (syn. *M. felis*)	Carnivora: canid (dog), felid (cat); Primates: hominid (human); Anseriformes: anatid (duck, goose); Galliformes: phasianid (chicken)	freshwater Gastropoda: bithyniid (*Parafossarulus striatulus*)	Cypriniformes: cyprinid (stone moroko, Chinese false gudgeon, pseudogoby)	Asia
M. taiwanensis	Anseriformes: anatid (duck)	freshwater Gastropoda: bithyniid (*Bythinia fuchsianus, Parafossarulus striatulus*)	Cypriniformes: cyprinid (stone moroko); Gobiiformes: odontobutid (sleeper)	Asia
M. tener	Anseriformes: anatid (common			Europe

	merganser)			
M. ussuriensis	Anseriformes: anatid (duck)	freshwater Gastropoda: bithyniid (*Parafossarulus spiridonovi, Boreoelona ussuriensis*)	freshwater fish: Gobiformes: odontobutid (Chinese sleeper); Cypriniformes: cyprinid (lake minnow); tadpoles: Anura: ranid (Dybowski's frog); snails: Gastropoda: bithyniid (*Parafossarulus spiridonovi, Boreoelona ussuriensis*)	Russia
M. xanthosomus (syn *M. coeruleus, M. intermedius, M. pinguinicola, M. nettioni*)	Anseriformes: anatid (duck, garganey, red-throated diver, common scoter, red-breasted merganser, teal); Gruiformes: rallid (coot, western swamphen); Podicipediformes: podicipedid (little grebe); Charadriiformes: alcid (razorbill), Accipitriformes: accipitrid (marsh harrier, long-legged buzzard); Passeriformes: corvid (carrion crow); Sphenisciformes: spheniscid (African penguin); Galliformes: phasianid (chicken)	freshwater Gastropoda: bithyniid (*Bythinia tentaculata*)		Europe, Africa, Indochina, Asia, South America
M. zacharovi	Anseriformes: anatid (duck)			Russia

Parasite morphology: *Metorchis* spp. form 7 different developmental stages: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae, and adult flukes. Eggs are ovoid in shape measuring from 22-32 µm in length by 11-20 µm in width. They are yellow-brown and slightly constricted anteriorly with a distinct subterminal operculum. The eggs are embryonated and contain a well-developed lanceolate miracidium with a covering of cilia, small primitive gut cells at the pointed anterior end and larger central granular cells. Sporocysts are pleomorphic sac-like structures with thin walls and no organs other than balls of germinal cells. Sporocysts undergo asexual reproduction producing rediae which then produce cercariae. Rediae are also sac-like structures, measuring 1.6-1.9 x 0.2-0.3 mm, but they have digestive tracts comprising a prominent oral sucker with a mouth, pharynx, oesophagus and bifurcate caecum. Cercariae are pleurolophocercous with oval-trapezoidal bodies (up to 0.3 mm long by 0.05-0.11 mm wide) and elongate tubular tails (up to 0.9 mm long) with dorsoventral fin folds. Their bodies are covered by spinose tegument and contain 2 eyespots, a sucker-like mouth and prominent anterior penetration glands. Metacercaria are essentially tail-less cercariae that have become encapsulated by a thin cyst wall (0.02-0.07 mm) forming transparent ovoid cysts (0.21-0.42 mm in diameter). Adult flukes are worms are distinctively pyriform, measuring from 1.8-6.8 mm long by 0.3-1.6 mm wide. They have a translucent spiny cuticle, 2 weakly developed suckers (oral and ventral) almost equal in size, an oval pharynx, short oesophagus (almost absent), and bifurcate intestinal caeca extending to the posterior end of the body but still blind-ended (no anus). Adult worms are hermaphroditic and possess both male and female reproductive organs. They have 2 spherical testes diagonally apposed to each other in the posterior body, the testes being entire (not branched or lobed). A single round ovary is located immediately anterior to the testes (pre-testicular) and is connected to a highly folded uterus opening into a genital pore located just in front of the ventral sucker. A large seminal receptacle is present near the ovary and numerous vitelline follicles are located in lateral fields extending anteriorly past the ventral sucker. The uterus in gravid worms is filled with numerous small embryonated eggs.

Site of infection: Adult *Metorchis* flukes infect bile ducts in the livers of their definitive hosts (piscivorous mammals), but in heavy infections they may also occur in extrahepatic ducts, the gall bladder and sometimes pancreatic ducts. Asexual developmental stages (sporocysts and rediae) form in the digestive glands and gonads of their first intermediate hosts (snails), while encysted metacercaria develop in the tissues of their second intermediate hosts (fish).

Pathogenesis: Light infections by *Metorchis* are often asymptomatic while heavier infections (> 200 worms) may cause clinical disease characterized by inflammation (cholangiohepatitis) and sometimes obstructive jaundice. Mature flukes cause mechanical and chemical irritation to the bile ducts by moving, attaching and feeding on epithelial tissues, releasing excretory-secretory (ES)

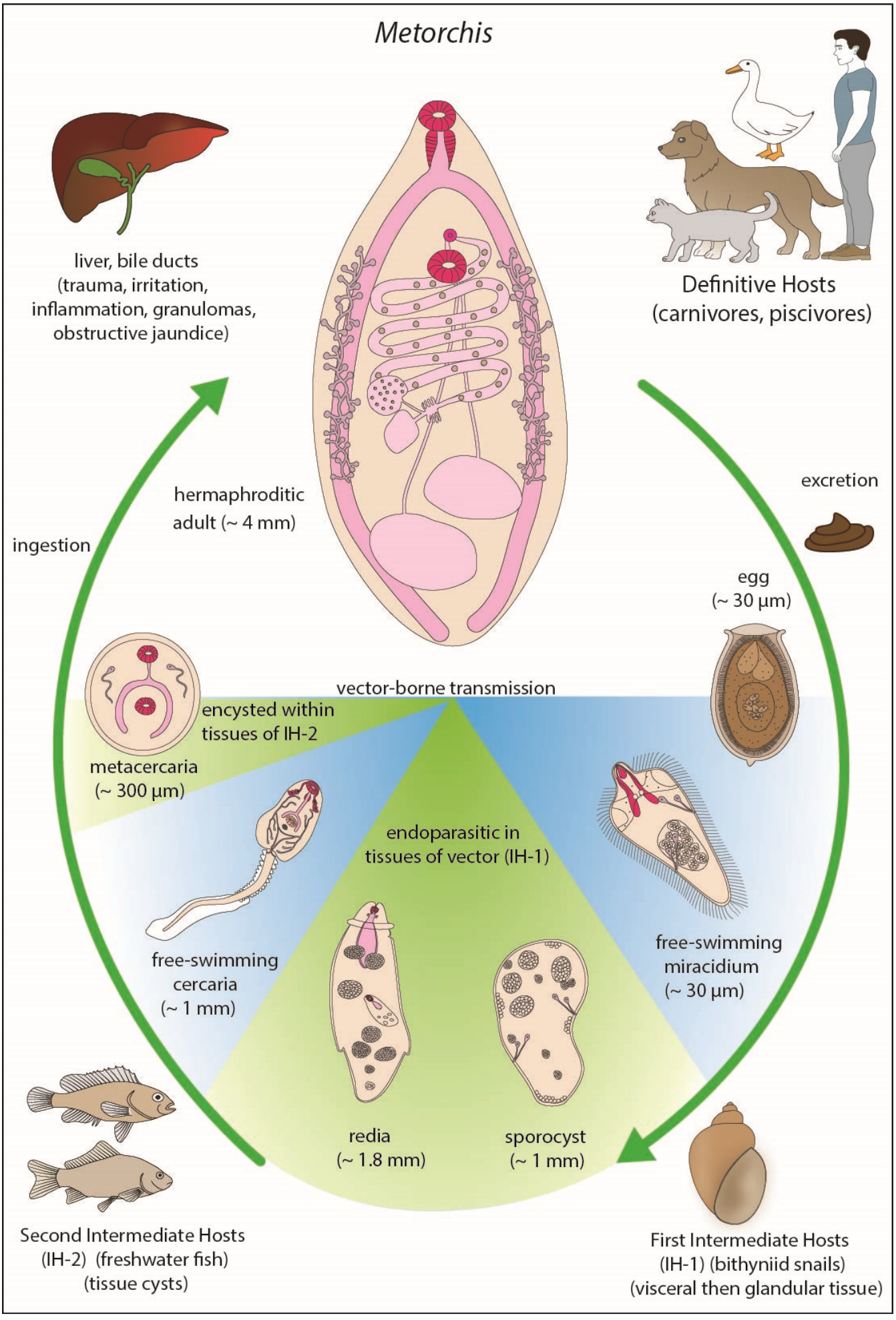
products with toxic/allergenic properties, and stimulating molecular and cellular host immune responses which may contribute to tissue damage. Infections have been associated with epithelial hyperplasia, inflammation, ductal thickenings, nodular or cord-like swellings in the hepatic parenchyma, the accumulation of viscid yellow-green fluid, and verminous granulomas. Common symptoms of acute infections include abdominal pain, urine discolouration, headache, fever, and eosinophilia. Heavy and/or chronic infections may cause cholangiohepatitis with periductular fibrosis, liver cirrhosis, hepatic and biliary lesions, ulceration and necrosis of hepatic and biliary tissue, haemorrhage, anaemia, jaundice, anorexia, emaciation, and rarely death. Chronic infections in pancreatic ducts may result in pancreatic inflammation and fibrosis leading to impairment of both endocrine and exocrine functions. While disease is rare in humans (mostly occurring in indigenous communities in North America), infections have been associated with emaciation and mortality in companion animals, esp. sled dogs and cats. Infected dogs experience severe weight loss with marked bile duct and periductal inflammation, cirrhosis and verminous granulomas. Chronic infections in cats caused biliary epithelial hyperplasia resulting in icterus, bloody urine, and severe intermittent diarrhoea that recurred over months.

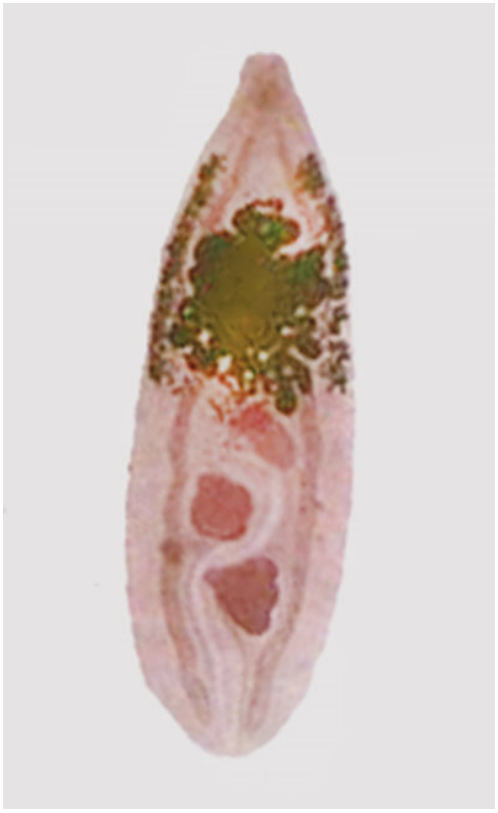
Developmental cycle and mode of transmission: These liver flukes have indirect 3-host life-cycles involving transmission between hermaphroditic adult parasites in fish-eating mammals, asexual multiplicative larval stages in freshwater snails, free-swimming aquatic stages and then encysted infective stages in freshwater fish. Adult liver flukes lay embryonated eggs which pass through the bile ducts to the intestines and are excreted with host faeces into the external environment. Eggs ending up in freshwater are ingested by aquatic snails, mostly bithyniid and amnicolid species, which act as first intermediate hosts. The eggs hatch in the snail intestines releasing the ciliated miracidia which penetrate through the gut wall into the hepatopancreas where they shed their cilia and form sac-like sporocysts. These stages undergo asexual reproduction forming rediae which escape and invade the digestive gland and gonads where they feed on snail tissues and produce more rediae or cercariae. Mature cercariae emerge from snails into the surrounding aquatic environment. They have powerful tails and actively swim about for up to 3 days exhibiting positive phototaxis (towards light), negative geotaxis (against gravity) and chemotaxis (swim towards chemicals released by fish). When they encounter freshwater fish, the cercariae penetrate the skin or gills shedding their tails and encysting as metacercariae in subcutaneous or muscular tissues. Various species of freshwater fish may act as second intermediate hosts, particularly catostomids and cyprinids, but also including some percids, salmonids and esocids. Metacercariae of several *Metorchis* spp. have also been found in tadpoles of several ranid frog species as well as some bithyniid snails infected by cercariae. Infections may accumulate over time in freshwater fish and the encysted metacercariae may survive in host tissues for over 1 year. Definitive hosts become infected when they consume raw or undercooked freshwater fish containing viable metacercariae which excyst in the intestines releasing juvenile stages that migrate through the common bile duct to the intrahepatic bile ducts. Here they attach, feed and develop into adults worms which cross-fertilize and produce embryonated eggs. Final hosts are generally piscivorous vertebrates, mostly wild carnivores or birds that live near water to hunt fish, but companion animals (esp. sled dogs) and humans may also be infected in domestic situations. The prepatent period (time from infection to first release of eggs) is around 1 month and it is thought the adult worms may live for up to 7 years.

Differential diagnosis: Patent infections are conventionally diagnosed by the microscopic detection of fluke eggs in faecal samples, either in smears or following concentration. However, the eggs of many liver fluke species (and genera) appear similar in morphology so differential diagnosis is difficult. Adult worms may be recovered from faecal samples following chemotherapy or from duodenal or bile samples obtained by endoscopy or exploratory surgery. Indeed, medical imaging techniques such as X-rays (cholecystyocholangiography), ultrasound, computed tomography (CT) and magnetic resonance imaging (MRI) may be used to aid diagnoses by demonstrating structural anomalies due to inflammation, fibrosis, blockage or filling defects. Infections by metacercariae in fish may be detected by microscopic examination of dissected muscles, usually in squash preparations or following pepsin-acid digestion. An enzyme immunoassay has been developed to detect specific antibodies in host serum samples against crude worm antigens, but varying levels of cross-reactivity were observed. Molecular characterization techniques have been used to explore parasite genetic variation by polymerase chain reaction (PCR, including realtime PCR) amplification of nuclear (18S ribosomal RNA, internal transcribed spacer regions 1 and 2) and mitochondrial (cytochrome c oxidase subunit 1, NADH dehydrogenase subunit 1) gene sequences.

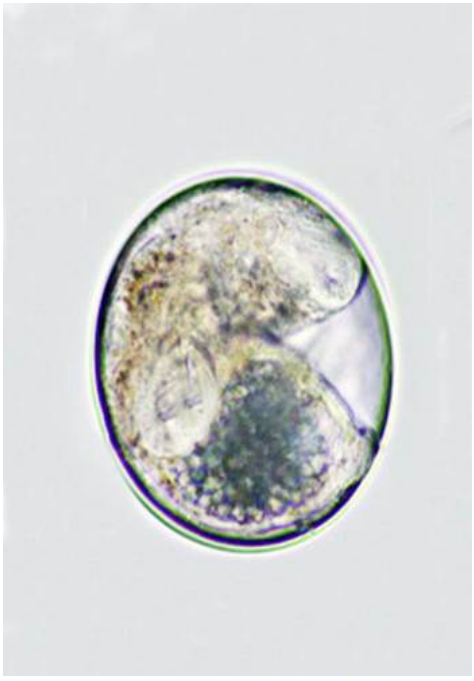
Treatment and control: Clinical *Metorchis* infections have been successfully treated with broad spectrum anthelmintics: notably the isoquinoline (praziquantel) and the benzimidazole (mebendazole), with low toxicity and minor side effects such as abdominal pain, nausea and diarrhoea. Various preventive strategies targeting transmission cycles have been implemented in endemic regions even though their effectiveness is often diminished due to the abundance of aquatic environments in Holarctic (Nearctic and Palaearctic) zoogeographic zones with suitable snail vectors, freshwater fish and wild animals supporting sylvatic cycles, and indigenous populations, companion animals, nomadic life-styles and dietary customs supporting peridomestic cycles and rapid re-infection. Where possible, every effort should be undertaken to prevent faecal contamination of water by providing facilities for better sanitation, including sewage and water treatment. While it may be desirable to reduce freshwater snail populations (first intermediate hosts) to minimize parasite asexual amplification, the indiscriminate use of toxic molluscicides in natural waterways is not advised due to unforeseen ecological consequences. Similarly, attempts to reduce freshwater fish populations (second intermediate hosts) in natural lakes, ponds and streams are at best impractical and at worst harmful to aquatic ecosystems and associated biota. The best way to reduce infections in humans and domestic animals has proven to be reducing or eliminating their consumption of raw, undercooked or lightly salted fish as part of their traditional dietary practices. Metacercariae are killed when

fish are cooked at temperatures above 63°C, or freezing them at -20°C for at least 7 days. Public health education campaigns have targeted indigenous communities in endemic regions to convince them to change their culinary customs and to stop feeding untreated trash fish to working dogs.


Metorchis
liver, bile ducts
(trauma, irritation,
inflammation, granulomas,
obstructive jaundice)
Definitive Hosts
(carnivores, piscivores)
hermaphroditic
adult (~ 4 mm)
excretion
ingestion
egg
(~ 30 µm)
vector-borne transmission
encysted within
tissues of IH-2
metacercaria
(~ 300 µm)
endoparasitic in
tissues of vector (IH-1)
free-swimming
cercaria
(~ 1 mm)
free-swimming
miracidium
(~ 30 µm)
redia
(~ 1.8 mm)
sporocyst
(~ 1 mm)
Second Intermediate Hosts
(IH-2) (freshwater fish)
(tissue cysts)
First Intermediate Hosts
(IH-1) (bithyniid snails)
(visceral then glandular tissue)



Metorchis adult worm



Metorchis metacercaria

Heterophyes
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult opisthorchiideans are small to medium spinose flukes living in the alimentary tracts of mammals, birds, reptiles and fish. They produce embryonated eggs which only hatch after ingestion by snails (first intermediate hosts) and metacercariae develop in fish (second intermediate hosts). Heterophyids are parasitic in the intestines of fish-eating birds and mammals and infections by *Heterophyes* and *Metagonimus* spp. have been associated with enteritis and diarrhoea in cats, dogs and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Plagiorchiida ('echinostomatids', plagiorchiids', mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder:	Opisthorchiata (egg eaten by gastropod IH, rediae formed, simple-tailed cercariae, encysts in second IH, metacercariae eaten by DH)
Superfamily:	Opisthorchioidea (small-medium flukes, often spinose, piscivorous DH)
Family:	Heterophyidae (tiny pyriform flukes, in intestines of mammals/birds, two IH (snails and fishes/frogs))
Genus:	*Heterophyes* (parasitic in intestines of carnivores)
Species:	various species cause diarrhoea in dogs, cats and humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs, fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the

tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND
[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc
[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1
[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod
[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst
[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet
[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore
[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. The suborder Opisthorchiata contains one superfamily Opisthorchioidea comprising tiny to medium-sized flukes which form rediae without appendages, then simple-tailed cercariae that encyst in second intermediate hosts forming metacercariae. Over 400 species have been described in 90 genera in 3 families (Opisthorchiidae, Cryptogonimidae, Heterophyidae). The family Heterophyidae are found as intestinal parasites in

mammals and birds with asexual developmental occurring in gastropods and metacercariae forming in fish and amphibians. The family is characterized by adults with small bodies where the ventral sucker (previously called acetabulum) is usually enclosed in a genital sinus containing a protuberance (gonotyl) and the male and female reproductive tracts fuse terminally to form a hermaphroditic duct. Some 40 heterophyid genera have been described in 8 subfamilies: Heterophyinae (no genital sinus, posterolateral gonotyl with chitinous rodlets, e.g. *Heterophyes, Heterophyopsis*); Metagoniminae (lateral ventral sucker in genital sinus, inconspicuous papilla-like gonotyl, e.g. *Metagonimus, Metagonimoides*); Cryptocotylinae (median ventral sucker in muscular genital sinus, papilla-like gonotyl, e.g. *Cryptocotyle, Seaphanocephalus*); Apophallinae (well-developed ventral sucker in non-muscular genital sinus, 1-2 papilla-like gonotyls, e.g. *Apophallus, Euryhelmis*); Galactosominae (ventral sucker reduced or absent, globular gonotyl usually with spines, e.g. *Galactosomum, Acanthotrema, Stictodora*); Centrocestinae (circumoral spines present, well-developed ventral sucker in genital sinus, 1-2 papilla-like gonotyls, e.g. *Centrocestus, Ascocotyle, Phagicola, Pygidiopsis, Pygidiopsoides*); Haplorchiinae (rudimentary ventral sucker, large gonotyl with chitinous rodlets superimposed on ventral sucker, single testis, e.g. *Haplorchis*); and Stellantchasminae (small lateral ventral sucker, large spiny gonotyl, distal seminal vesicle forms muscular expulsor, e.g. *Stellantchasmus, Procerovum*). The genus *Heterophyes* contains some 8 species of small distome flukes found in the intestines of piscivorous mammals which become infected by eating fish or amphibians containing encysted metacercariae. Heterophyiasis is endemic in human populations in Egypt, the Middle-East and East Asia, and an emerging problem in the Philippines. It is difficult to estimate the number of people suffering from heterophyiasis because symptoms are usually mild and similar to other common ailments. People most at risk are those residing next to freshwater sources, particularly where fish consumption is high and sanitation is poor.

***Heterophyes* species**	**Definitive hosts [adults in intestines]**	**First intermediate hosts [sporocysts/rediae in tissues]**	**Second intermediate hosts [metacercariae in tissues]**	**Distribution**
H. aequalis	Primates: hominid (human); Carnivora: canid (dog, red fox, golden jackal, Indian wolf), felid (cat, jungle cat); Rodentia: murid (rats); Artiodactyla: suid (pig); Pelecaniformes: pelecanid (white pelican), ardeid (reef heron); Accipitriformes: accipitrid (black kite)	brackish-water Gastropoda: potamidid (*Pirinella conica*)	freshwater/brackish-water Mugiliformes: mugilid (flathead grey mullet, thinlip mullet, golden grey mullet); Cypriniformes: cyprinid (himri); Cichliformes: cichlid (Nile tilapia, redbelly tilapia); Perciformes: serranid (white grouper), sciaenid (croaker), carangid (leerfish); Pleuronectiformes: soleid (common sole)	Asia Minor, Southern Europe
H. bucalis sp. inq.	Pelecaniformes: ardeid (night heron)			South America
H. dispar (syn. *H. limatus*)	Primates: hominid (human); Carnivora: canid (dog, golden jackal, red fox, Indian wolf), felid (cat, jungle cat); Lagomorpha: leporid (rabbit); Rodentia: murid (rats); Accipitriformes: accipitrid (black kite)	brackish-water Gastropoda: potamidid (*Pirinella conica*)	freshwater/brackish-water Mugiliformes: mugilid (flathead grey mullet, thinlip mullet, golden grey mullet); Cypriniformes: cyprinid (barbels, himri); Cichliformes: cichlid (Nile tilapia, redbelly tilapia); Perciformes: serranid (white grouper), sciaenid (croaker), carangid (leerfish); Pleuronectiformes: soleid (common sole)	North Africa, Middle-East, Korea, Thailand
H. heroni	Pelecaniformes: ardeid (cattle egret); Columbiformes: columbid (pigeon)		freshwater Cichliformes: cichlid (Nile tilapia)	Egypt
H. heterophyes (syn. *H. aegyptiaca, fraternus, persicus, inops, palidus*)	Primates: hominid (human), cercopithecid (macaque); Carnivora: canid (dog, red fox, polar fox, golden jackal, Indian wolf), felid (cat, jungle cat), mustelid (badger); Lagomorpha: leporid (rabbit); Rodentia: murid (rats); Chiroptera: rhinolophid (Geoffrey's horseshoe bat);	freshwater/brackish-water Gastropoda: potamidid (*Pirenella conica, Cerithidea cingulata* (syn. *Tympanotonus micropterus*), *Certhideopsilla conica*), thiarid (*Tarebia*)	brackish-water Mugiliformes: mugilid (flathead grey mullet, thinlip mullet, thicklip grey mullet, golden grey mullet, green mullet, so-iuy mullet, leaping mullet); Cyprinodontiformes: cyprinodontid (Mediterranean killifish), poeciliid (mosquitofish), fundulid	North Africa, Middle-East, southern Europe, India, Asia, Hawaii

	Artiodactyla: suid (pig); Accipitriformes: accipitrid (short-toed eagle, black kite); Pelecaniformes: pelecanid (white pelican); Charadriiformes: larid (gull)		(killifish); Gobiiformes: gobiid (tank goby), oxudercid (yellowfin goby, dusky tripletooth goby); Cichliformes: cichlid (Nile tilapia, redbelly tilapia, Mozambique tilapia); Pleuronectiformes: soleid (black sole); Perciformes: sciaenid (croaker), moronid (European bass, spotted seabass), sparid (seabream); and unspecified Decapoda (shrimp), Odonata (dragonfly naiads)	
H. indica	Carnivora: canid (dog)			India
H. nocens (syn. *H. katsuradai*)	Carnivora: canid (dog, fox), felid (cat); Rodentia: murid (rats, mice, rakali); Primates: hominid (human)	brackish-water Gastropoda: potamidid (*Cerithidea cingulata* (= *Tympanotomus microptera*), *C. fluviatilis*), pleurocerid (*Melania obliquegranosa*), thiarid (*Stenomelania juncea*, *Melanoides tuberculata*)	brackish-water Mugiliformes: mugilid (flathead grey mullet, so-iuy mullet); Gobiiformes: oxudercid (dusky tripletooth goby, yellowfin goby, mudskipper, bluespotted mudskipper), gobiid (goby, tank goby); Perciformes: terapontid (sharpbeak terapon)	Korea, Japan, China, Thailand, Australia
H. pleomorphis	Carnivora: canid (dog)			Africa

Other *Heterophyes* species described from mammals and birds have been assigned to several other heterophyid genera mainly on the basis of the morphological characteristics of adults and metacercariae: e.g. *H. bitorquatus, H. chini* and *H. superspinata* transferred to *Alloheterophyes*; *H. continua* to *Heterophyopsis*; *H. lari* returned to *Stictodora*; and *H. reticulatum* assigned variously to *Distomum*, *Mesogonimus* and *Climastomatopsis* before being synonymized with *Clinostomum dictyotum.*

Parasite morphology: *Heterophyes* spp. form 7 different stages in their developmental cycles: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae, and adult flukes. Embryonated eggs are small and ovoid, measuring 19-30 x 13-17 µm, yellow-brown and thick-shelled with an operculum set on thickened opercular shoulders. Eggs contain fully developed embryos in the form of pyriform ciliated miracidia. Sporocysts are pleomorphic non-ciliated sac-like bodies containing few internal elements other than balls of germinal cells. Rediae are elongate sac-like structures, measuring from 0.3-1.2 mm in length by 0.1-0.2 mm in width, and they possess an anterior mouth, tubular pharynx and short simple caecum. Cercariae are pleurolophocercous with ellipsoidal bodies (175-225 x 70-90 µm), eyespots and elongate finned tails (470-510 x 25-30 µm). They have oral and ventral suckers, mouths, guts, numerous glands and tegumental spines. Metacercariae are ovoid encysted stages (130-380 x 80-170 µm), opalescent with scattered brown pigment granules. They have a rounded oral sucker and a larger elliptical ventral sucker, a triangular excretory bladder filled with concretions, a digestive tract and developing genitalia. Adult flukes have small grey leaf-shaped bodies ranging from 0.3-3 mm in length by 0.3-0.9 mm in width. Their forebodies are flatter and narrower than their hindbodies with the junction often demarcated by shoulders. The tegument is covered with scale-like spines which are larger over the forebody and minute over the hindbody. The anteroventral oral sucker is small (around 90 µm in diameter) while the median-located ventral sucker is larger (up to 250 µm in diameter) and contains approximately 70 spines [cf. *Metagonimus* spp. have smaller submedian-located ventral suckers]. The digestive system consists of a mouth in the oral sucker, a short prepharynx, pharynx, long oesophagus, and 2 blind intestinal caeca (no anus). Worms have a conspicuous tubular excretory bladder terminating posteriorly. Adult *Heterophyes* worms are hermaphroditic and have both male and female reproductive organs. They possess 2 ovoid testes located posteriorly in tandem connected to a vas deferens that firstly expands to form a large seminal vesicle and then narrows to form an ejaculatory duct (no cirrus). A single ovoid ovary located mid-body is connected to numerous vitelline follicles. The ovary is also connected to a long tubular uterus which joins the ejaculatory duct leading to the genital pore from where eggs are released. The genital pore is surrounded by a prominent genital sucker (gonotyl) which measures ~150 µm in diameter and is armed with 14-90 toothed or digitate spines (chitinous rodlets) depending on species [cf. *Metagonimus* spp. lack genital suckers]. For example, the gonotyls of *H. heterophyes* have 70-85 chitinous rodlets, *H. nocens* have 50-62, *H. dispar* have 22-35 and *H. aequalis* have 14-25. Genera within the family Heterophyidae (and the 8 subfamilies) differ mostly in adult body morphology: particularly in the number of gonotyl spines; location of the genital pores; extensions of the uterus and vitellaria; structure of the testes; and length of the intestinal caeca.

Site of infection: Adult *Heterophyes* flukes infect the small intestines in their piscivorous definitive hosts, with many species exhibiting some tissue tropism independent of host species or size: e.g. *H. heterophyes* often infects the duodenum and jejunum; *H. dispar* the duodenum; and *H. aequalis* the posterior jejunum and ileum. Asexual developmental stages develop in the intestines and

tissues (esp. hepatopancreas) of their first intermediate hosts (freshwater snails), while metacercariae encyst in the muscles, fins or gills of their second intermediate hosts (fish).

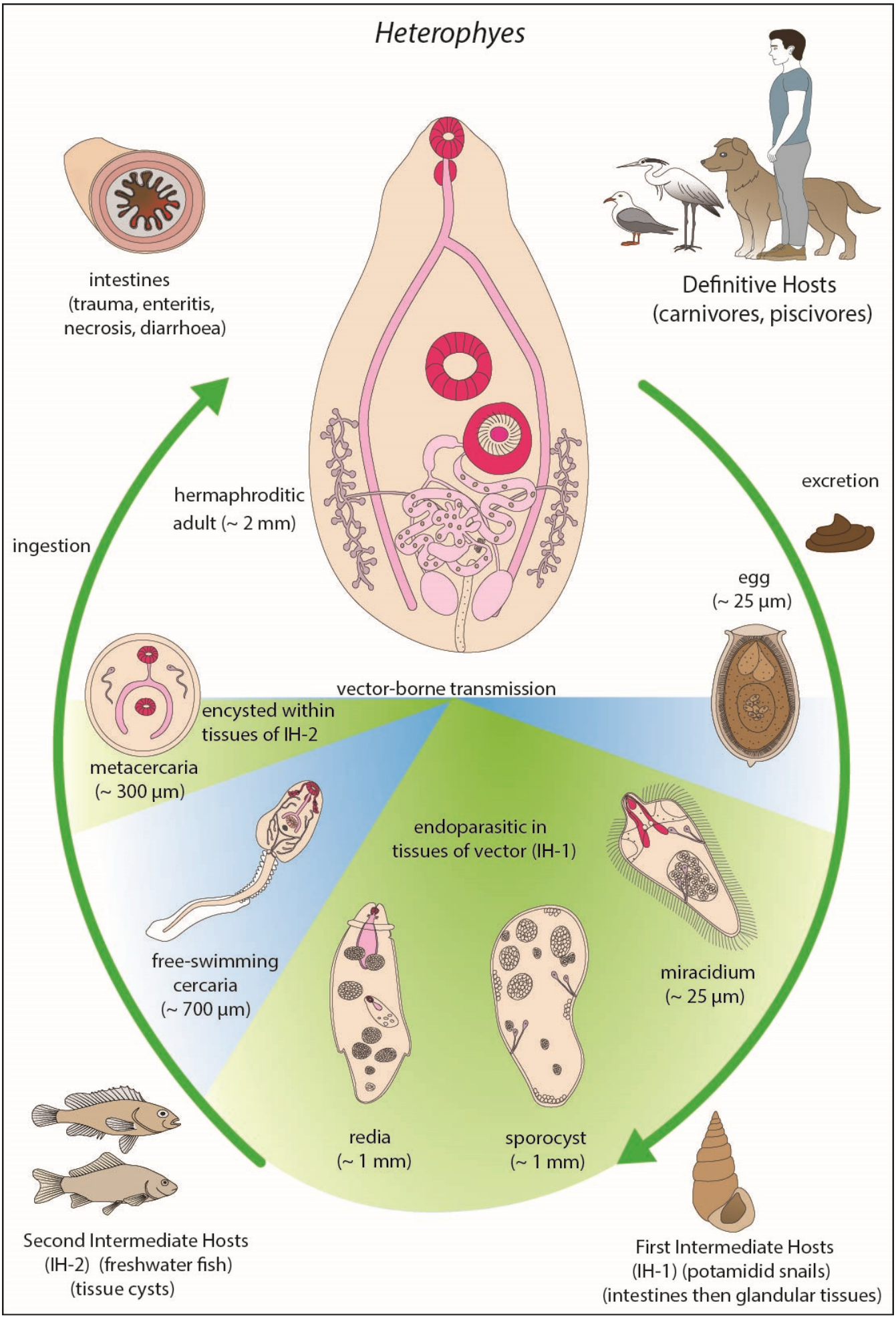
Pathogenesis: These intestinal flukes invade the intervillous spaces, often burrowing into the mucosal layer and crypts of Lieberkuhn and sometimes penetrating the intestinal wall. The resultant pathology arises from traumatic mucosal damage with hyperplasia, villous atrophy, hyperplasia, inflammation and sometimes ectopic granulomas. The severity of disease largely depends on the intensity of the infection but is also influenced by host susceptibility and the degree of acquired protective immunity. Light infections are often asymptomatic although some have been associated with mild enteritis, transient intestinal pain and intermittent diarrhoea. Moderate infections may cause more intense symptoms, such as abdominal tenderness and pain, vomiting and chronic (sometimes blood-tainted) diarrhoea, but these indications are also common in patients with peptic or duodenal ulcers. Heavy infections involving hundreds of worms may cause extensive mucosal necrosis producing severe symptoms including persistent abdominal pain, mucoid (often bloody) diarrhoea, haemorrhages, nausea, indigestion, dyspepsia, vomiting and anorexia. Adult worms and eggs embedded in the mucosa elicit significant inflammatory responses with cellular infiltrates of neutrophils and eosinophils. Complications may arise when eggs in eroded tissues are swept away by the circulatory and/or lymphatic systems and lodge in ectopic sites (such as the heart, lungs, brain and spinal cord) leading to fibrosis and granuloma formation. Lesions in the myocardium and mitral valve have been associated with heart failure, and those in the brain and spinal cord have apparently caused various neurological disorders, sometimes contributing to death. Complications due to disseminated infections appear to be more prevalent in patients with immuno-compromised status due to concomitant diseases, immunosuppression or malnutrition.

Developmental cycle and mode of transmission: *Heterophyes* spp. have indirect life-cycles involving transmission between 3 different types of hosts associated with aquatic environments: adults worms infecting fish-eating mammals and birds (definitive hosts); asexual stages multiplying within aquatic snails (first intermediate hosts); and metacercariae encysting within fish (second intermediate hosts). Gravid adult worms produce embryonated eggs which are excreted with host faeces. Eggs contaminating water sources are ingested by aquatic snails whereupon they hatch releasing the enclosed ciliated miracidium in the snail gut. The miracidium penetrates the gut wall shedding its cilia and developing into a sac-like sporocyst usually within the digestive gland. A small range of snails act as suitable first intermediate hosts for *Heterophyes* spp., notably several amphibious prosobranch (operculate) families, including potamidids (freshwater and brackish-water snails common on mud flats, mangroves, periphyton), thiarids, pleurocerids and semisulcospirids (freshwater snails). Sporocysts undergo asexual multiplication and produce 2 generations of rediae in the snail tissues over 3-5 months, although parasites can survive longer in aestivating snails. The rediae feed on snail tissues and ultimately produce numerous cercariae which emerge actively from the snail. Free cercariae swim up towards the water surface and then slowly descend through the water column. If they contact a fish, they actively penetrate the skin shedding their tails and encyst in the musculature as metacercariae. A range of freshwater and brackish-water fish act as suitable second intermediate hosts, including Mugiliformes (mugilid), Gobiiformes (oxudercid, gobiid), Perciformes (terapontid, sciaenid, moronid, sparid, serranid, carangid), Cypriniformes (cyprinid), Cyprinodontiformes (cyprinodontid, poeciliid, fundulid), Cichliformes (cichlid), and Pleuronectiformes (soleid). Food-borne transmission occurs to piscivorous definitive hosts (mammals and birds) when they consume infected fish. The metacercariae excyst in the intestines, attach to the gut wall and develop into adult worms over several weeks. Infections are transmitted to humans when they eat raw, undercooked or newly salted, pickled or smoked fish in which metacercariae may survive for several days. Adult flukes live for a few months to a year in the final host.

Differential diagnosis: While infections may be suspected on the basis of clinical presentation and history of exposure, the symptoms of heterophysiasis are often similar to those of other gut ailments, notably peptic ulcer disease. Infections by *Heterophyes* spp. are conventionally diagnosed by the microscopic detection of fluke eggs in faecal samples, either in direct smears (Kato-Katz technique) or following concentration (Lumbreras rapid sedimentation or ether-formalin concentration). It is suggested that at least 3 stool samples be examined due to intermittent egg excretion, and that samples be stained with potassium permanganate to accentuate structural features on eggs. Alternatively, adult flukes may be recovered for examination following anthelmintic treatment or by endoscopic biopsy. Infections in fish by metacercariae may be detected by microscopic examination of dissected muscles, usually in squash preparations or following pepsin-acid digestion. Several immunoserological tests have been developed to detect host antibodies in serum samples, including counter-current immunoelectrophoresis, intradermal tests, indirect fluorescent-antibody tests and enzyme immunoassays, but they often exhibited poor specificity presumably due to antigenic cross-reactivity. Molecular techniques have been applied to the characterization of parasite DNA extracted from adult flukes, eggs, sporocysts/rediae, and cercariae; by polymerase chain reaction (PCR) amplification of restriction fragment length polymorphisms (RFLP), random amplified polymorphic DNA (RAPD) and sequencing nuclear (18S, 5.8S and 28S ribosomal DNA, internal transcribed spacers regions 1 and 2) and mitochondrial genes (cytochrome c oxidase subunit 1).

Treatment and control: Clinical infections have been successfully treated with broad spectrum anthelmintics; notably the isoquinoline praziquantel, and the salicylanilide niclosamide. Repeated treatments and community treatments are recommended in endemic regions due to rapid re-infection rates. Patients with suspected ectopic infections should be carefully monitored post-treatment as dying worms and eggs may cause intense reactions. Preventive strategies are centred around breaking transmission cycles but most interventions are only suitable for domestic or peridomestic situations, rather than natural ecosystems. Every effort

should be made to reduce faecal contamination of water bodies, by improving sanitation, building latrines, proper waste disposal (human and animal), and treating sewage. While it is desirable to reduce snail populations in which parasites reproduce asexually, the indiscriminate use of molluscicides in aquatic environments may have unintended consequences due to the toxic nature of the chemicals and their effect on other biota. Indeed, snail control is often difficult as they aestivate in the ground during dry conditions and even temporary pools may harbour large snail populations, especially in high rainfall regions. In rural village settings and aquaculture ventures, various physical, chemical and biological control strategies have been integrated with pond management to reduce the suitability of the habitat for snails (e.g. periodic drainage, clearing periphyton, installing screens, small-scale use of molluscicides, introducing predatory crustaceans and/or fish). The most effective means of controlling infections, however, appears to be denying piscivores access to raw fish or improperly cooked fish products. Companion animals should not be fed raw trash fish, and humans should not consume raw or improperly-prepared fish. While metacercariae may survive for days in raw, lightly salted, lightly pickled or lightly smoked fish products, they are killed by cooking at temperatures above 63ºC, or by freezing at -20ºC for at least 7 days. Public education campaigns should be undertaken in regions where raw or undercooked fish are regarded as traditional cultural cuisine, particularly targeting people who prepare foods or schoolchildren who have not yet been ingrained with dietary customs.


Heterophyes
intestines
(trauma, enteritis,
necrosis, diarrhoea)
Definitive Hosts
(carnivores, piscivores)
hermaphroditic
adult (~ 2 mm)
ingestion
excretion
egg
(~ 25 µm)
vector-borne transmission
encysted within
tissues of IH-2
metacercaria
(~ 300 µm)
endoparasitic in
tissues of vector (IH-1)
free-swimming
cercaria
(~ 700 µm)
miracidium
(~ 25 µm)
redia
(~ 1 mm)
sporocyst
(~ 1 mm)
Second Intermediate Hosts
(IH-2) (freshwater fish)
(tissue cysts)
First Intermediate Hosts
(IH-1) (potamidid snails)
(intestines then glandular tissues)



Heterophyes adult worm



Heterophyes egg



Heterophyes adult worm

Metagonimus
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult opisthorchiideans are small to medium spinose flukes living in the alimentary tracts of mammals, birds, reptiles and fish. They produce embryonated eggs which only hatch after ingestion by snails (first intermediate hosts) and metacercariae develop in fish (second intermediate hosts). Heterophyids are parasitic in the intestines of fish-eating birds and mammals and infections by *Heterophyes* and *Metagonimus* spp. have been associated with enteritis and diarrhoea in cats, dogs and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Plagiorchiida ('echinostomatids', plagiorchiids', mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder:	Opisthorchiata (egg eaten by gastropod IH, rediae formed, simple-tailed cercariae, encysts in second IH, metacercariae eaten by DH)
Superfamily:	Opisthorchioidea (small-medium flukes, often spinose, piscivorous DH)
Family:	Heterophyidae (tiny pyriform flukes, in intestines of mammals/birds, two IH (snails and fishes/frogs))
Genus:	*Metagonimus* (parasitic in intestines of carnivores)
Species:	various species cause diarrhoea in dogs, cats and humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs, fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the

tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. The suborder Opisthorchiata contains one superfamily Opisthorchioidea comprising tiny to medium-sized flukes which form rediae without appendages, then simple-tailed cercariae that encyst in second intermediate hosts forming metacercariae. Over 400 species have been described in 90 genera in 3 families (Opisthorchiidae, Cryptogonimidae, Heterophyidae). The family Heterophyidae are found as intestinal parasites in

mammals and birds with asexual developmental occurring in molluscs (Prosobranchia) and encysted stages forming mostly in fish and amphibians. The family is characterized by adults with small bodies where the ventral sucker (previously called the acetabulum) is usually enclosed in a genital sinus containing a cirrus-like body (gonotyl) and the male and female reproductive tracts fuse terminally to form a hermaphroditic duct. Some 40 heterophyid genera have been described in 8 subfamilies: Heterophyinae (no genital sinus, posterolateral gonotyl with chitinous rodlets, e.g. *Heterophyes, Heterophyopsis*); Metagoniminae (lateral ventral sucker in genital sinus, inconspicuous papilla-like gonotyl, e.g. *Metagonimus, Metagonimoides*); Cryptocotylinae (median ventral sucker in muscular genital sinus, papilla-like gonotyl, e.g. *Cryptocotyle, Seaphanocephalus*); Apophallinae (well-developed ventral sucker in non-muscular genital sinus, 1-2 papilla-like gonotyls, e.g. *Apophallus, Euryhelmis*); Galactosominae (ventral sucker reduced or absent, globular gonotyl usually with spines, e.g. *Galactosomum, Acanthotrema, Stictodora*); Centrocestinae (circumoral spines present, well-developed ventral sucker in genital sinus, 1-2 papilla-like gonotyls, e.g. *Centrocestus, Ascocotyle, Phagicola, Pygidiopsis, Pygidiopsoides*); Haplorchiinae (rudimentary ventral sucker, large gonotyl with chitinous rodlets superimposed on ventral sucker, single testis, e.g. *Haplorchis*); and Stellantchasminae (small lateral ventral sucker, large spiny gonotyl, distal seminal vesicle forms muscular expulsor, e.g. *Stellantchasmus, Procerovum*). The genus *Metagonimus* contains around 9 species of small flukes found in the intestines of piscivorous mammals and birds which become infected by eating fish containing encysted metacercariae. Human infections are most prevalent in riverine and coastal fishing communities where raw fish are traditionally eaten, especially in Asia (Korea, China, Japan, eastern Russia) but also including Indonesia, the Middle-East (Israel and Balkan states) and Spain. The geographic distribution of infections is not confined to regions where snail intermediate hosts are found, as many fish hosts undergo extensive migration. Human infections outside endemic areas can also result from eating pickled fish or sushi imported from endemic areas.

***Metagonimus* species**	**Definitive hosts [adults in small intestines]**	**First intermediate hosts [sporocysts/rediae in tissues]**	**Second intermediate hosts [metacercariae in tissues]**	**Distribution**
M. hakubaensis	Carnivora: canid (dog), felid (cat), Rodentia: murid (mice, rats), cricetid (hamster); Eulipotyphla: soricid (Japanese water shrew); Galliformes: phasianid (chicken, quail)	freshwater Gastropoda: semisulcospirid (*Semisulcospira nakasekoae*)	freshwater Petromyzontiformes: petromyzontid (Far Eastern brook lamprey)	Japan
M. katsuradai	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Rodentia: murid (mice, rats), cricetid (golden hamster); Lagomorpha: leporid (rabbit); Anseriformes: anatid (duck)	freshwater Gastropoda: semisulcospirid (*Semisulcospira libertina, Juga tegulata* (= *Melania amurensis*))	freshwater Cypriniformes: cyprinid (stone moroko, pale chub, napjaru, oily bitterling, kanehira, tamoroko)	Japan, Russia
M. minutus	Primates: hominid (human); Carnivora: canid (dog, red fox), felid (cat); Rodentia: murid (mice); Accipitriformes: accipitrid (black kite)		freshwater Mugiliformes: mugilid (flathead grey mullet)	China, Taiwan
M. miyatai (syn. *M. yokogawai* Miyata type)	Primates: hominid (human); Carnivora: canid (dog, raccoon dog, red fox), procyonid (raccoon); Rodentia: murid (mice, rats), cricetid (golden hamster); Eulipotyphla: soricid (Japanese water shrew); Accipitriformes: accipitrid (black kite)	freshwater Gastropoda: semisulcospirid (*Semisulcospira globus*, *S. libertina*, *S. dolorosa, Koreanomelania nodifila*)	freshwater Osmeriformes: plecoglossid (sweetfish); Cypriniformes: cyprinid (big-scaled redfin, dace, Amur minnow, fat-minnow, pale chub, dark chub, hasu)	Japan, Korea
M. otsurui	Rodentia: cricetid (golden hamster); Eulipotyphla: soricid (Japanese water shrew)		freshwater Gobiiformes: oxudercid (dusky tripletooth goby, tripletooth goby, gobies)	Japan
M. pusillus	Rodentia: murid (brown rat); Anseriformes: anatid (duck)	freshwater Gastropoda: semisulcospirid (*Parajuga subtegulata, P. subextensa*)	freshwater Cypriniformes: cyprinid (Amur bitterling)	Russia
M. suifunensis	Rodentia: murid (brown rat)	freshwater Gastropoda:	freshwater Cypriniformes:	Russia

		semisulcospirid (*Parajuga subtegulata, P. subextensa, P. subcalculus, P. heukelomiana, P. nodosa, P. amurensis, P. buettneri*)	cyprinid (Amur bitterling, carp)	
M. takahashii (syn. *M. yokogawai* var. *takahashii,* or *M. y.* Koga type)	Primates: hominid (human); Carnivora: canid (dog, red fox, raccoon dog), felid (cat), procyonid (raccoon); Eulipotyphla: soricid (Japanese water shrew); Rodentia: murid (mice, rats), cricetid (hamster); Lagomorpha: leporid (rabbit); Accipitriformes: accipitrid (black kite); Pelecaniformes: pelecanid (pelican)	freshwater Gastropoda: semisulcospirid (*Semisulcospira coreana*, *S. libertina Koreanomelania nodifila*)	freshwater Mugiliformes: mugilid (flathead grey mullet); Cypriniformes: cyprinid (carp, crucian carp, goldfish, gudgeon, big-scaled redfin); Perciformes: lateolabracid (Japanese sea bass)	Japan, Korea
M. yokogawai (syn. *M. ovatus, M. romanicus, M. dobrogiensis*)	Primates: hominid (human); Carnivora: canid (dog, fox), felid (cat); Rodentia: murid (mice, rats, gerbil), cricetid (golden hamster); Lagomorpha: leporid (rabbit): Artiodactyla: suid (boar); Pelecaniformes: pelecanid (pelican); Accipitriformes: accipitrid (kite); Anseriformes: anatid (duck)	freshwater Gastropoda: semisulcospirid (*Semisulcospira libertina, S. coreana*, *S. cancellata, S. laevigata, Koreanomelania nodifila*)	freshwater Osmeriformes: plecoglossid (sweetfish), salangid (Japanese icefish), Cypriniformes: cyprinid (goldfish, common carp, chub, Amur fat-minnow, slender bitterling, stone moroko, big-scaled redfin, Pacific redfin); Mugiliformes: mugilid (flathead grey mullet); Gobiiformes: oxudercid (yellowfin goby), odontobutid (dark sleeper); Perciformes: lateolabracid (Japanese seabass); Salmoniformes: salmonid (Japanese huchen)	Asia, Middle-East, Balkans, Spain

Parasite morphology: *Metagonimus* spp. form 7 different developmental stages: eggs, miracidia, sporocysts, rediae, cercariae, metacercariae and adult flukes. Eggs are ovoid-ellipsoid and small, measuring from 26-36 µm in length by 14-23 µm in width. They are brown-yellow and surrounded by a thick eggshell with a distinct operculum set on thickened opercular shoulders. The eggs are embryonated and contain an ellipsoidal well-developed miracidium which is covered with cilia. Sporocysts have elongate pleomorphic sac-like bodies without organs but containing balls of germinal cells which give rise to rediae by asexual reproduction. Rediae have elongate bodies measuring 700-1050 x 95-150 µm and they possess an anterior mouth with sensory hairs, a spherical pharynx, a short saccular gut and their body cavity contains germinal balls which give rise to daughter rediae or cercariae. Free cercariae are pleurolophocercous with spinose bodies (180-230 x 55-75 µm) containing conspicuous eyespots and a long slender tail (340-400 x 10-14 µm) with lateral fluting (fins), They are brown and have sensory papillae (hairs) located along the lateral body margins. They possess 2 suckers, an anterior oval oral sucker and a larger midbody ventral sucker. Metacercariae are encysted cercariae that have shed their tails and developed thin cyst walls. The cysts are ovoid in shape, measuring 130-500 µm in diameter, and contain yellow-brown pigment granules. The enclosed larvae have spinose teguments and possess an anterior oral sucker with sensory papillae, a ventral sucker located to one side, a short prepharynx, an oval pharynx, a V-shaped excretory bladder and 2 developing testes. Mature flukes are dorsoventrally-flattened and pyriform in shape, small in size ranging 0.5-2.5 x 0.2-0.8 mm, and their tegument is covered with small spines. They possess a small subterminal oral sucker and a larger ventral sucker (not as large as *Heterophyes* spp.) that is unusual in being located submedian and dextral (to right of midline) within a genital sinus. Worms have a short prepharynx, a tubular pharynx opening into 2 saccular caeca that are blind-ended (no anus) and a Y-shaped excretory vesicle. Mature adults are hermaphroditic and possess both male and female reproductive organs. They have 2 globular testes located posteriorly and diagonally adjacent to each other, a large seminal vesicle and receptacle and a short ejaculatory duct opening into the genital pore (cirrus absent). The single globular ovary is connected to a short oviduct, numerous vitellaria located in posterior lateral fields, and a large tubular uterus that is often filled with eggs and opens into the genital pore. Unlike *Heterophyes* spp., *Metagonimus* worms lack a separate genital sucker but have a ventrogenital complex (combination of ventrogenital sac and ventral sucker) with an inconspicuous papilla-like gonotyl. Characters used to differentiate *Metagonimus* spp. include the locations of the oral and ventral suckers, uterine tubule patterns, vitelline follicle distribution, and morphometrics of the ovary, seminal vesicle and eggs.

Site of infection: Adult flukes infect the small intestines of their definitive hosts, beginning in the mucosa and progressing to the crypts and intervillous spaces. Asexual developmental stages (sporocysts and rediae) occur mostly in the digestive glands of their first intermediate hosts (snails), while metacercariae encyst within the muscles, subcutaneous tissues and sometimes the scales of their second intermediate hosts (fish).

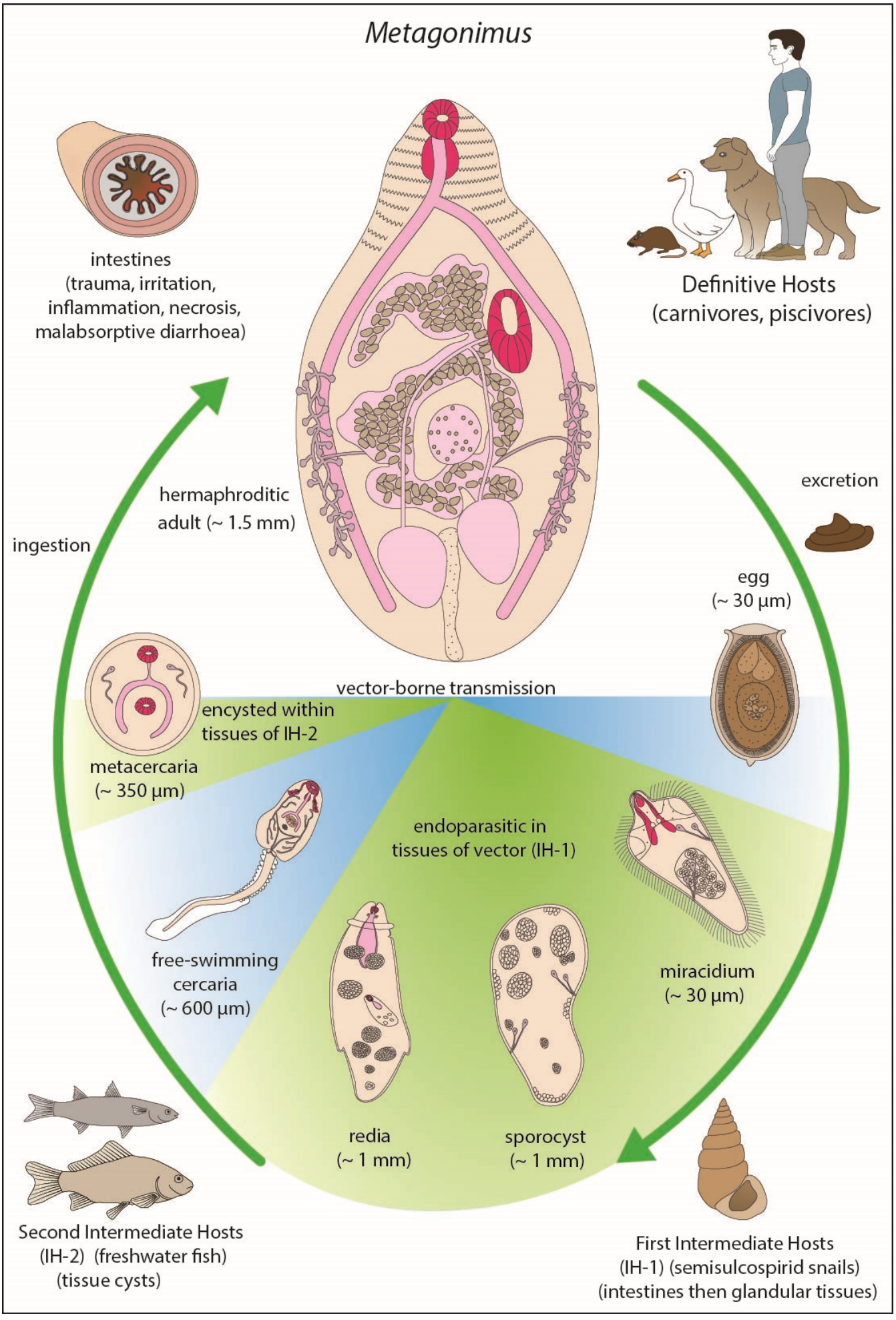
Pathogenesis: The severity of the disease metagonimiasis varies depending on the intensity and duration of infection, the immune status of the host and possibly the frequency of prior exposure leading to protective immune responses. While infections in endemic regions have been shown to accumulate in susceptible hosts over time, milder symptoms often occur in long-term residents than in newly infected patients with similar worm burdens (ranging from hundreds to thousands of worms). Adult flukes feed on to the intestinal mucosa causing irritation, tissue trauma, erosive lesions, necrosis, villous atrophy, crypt hyperplasia, and inflammation. Nevertheless, most light infections are asymptomatic and many moderate infections are subclinical or have only been associated with mild symptoms, such as fatigue, vague epigastric pain, intermittent diarrhoea, nausea, anorexia, and weight loss. Heavier infections cause more severe symptoms, particularly malabsorptive diarrhoea, abdominal pain, ulcers, nausea, vomiting, malaise, anorexia and weight loss. Flukes may penetrate deeply into the small intestinal mucosa, causing villous atrophy, oedema, lymphatic dilatation, crypt hyperplasia with excessive mucus production, and cellular inflammation (neutrophils and eosinophils). Severe infection may lead to mucosal ulceration and malabsorption with hypoalbuminemia, protein loss, impaired vitamin B_{12} absorption, anaemia, oedema, anasarca, malnutrition and sometimes obstruction. Complications may arise in immunocompromised hosts where worms invade submucosal tissues and deposit eggs which are carried by the circulation and/or lymphatics to internal organs where they may cause emboli, granulomas and/or fibrosis. Cases of myocardial sclerosis, heart valve calcification and cardiac failure attributable to ectopic infections have been reported in humans.

Developmental cycle and mode of transmission: *Metagonimus* spp. have indirect heteroxenous life-cycles involving cyclic transmission between 3 different types of hosts: adult worms in mammals and birds (definitive hosts); larval stages in snails (first intermediate hosts) and infective stages in fish (second intermediate hosts). Adult flukes lay embryonated eggs into the host gut lumen and they are voided with host faeces into the external environment. Eggs are ingested by freshwater snails feeding on aquatic plants in contaminated waters. Intermediate host specificity is high and only semisulcospirid snails (*Parajuga, Semisulcospira, Juga, Koreanomelania*) act as suitable first intermediate hosts. These gilled snails have robust high-spired or turreted shells with opercula and are found in many rivers, streams and lakes throughout Asia. The eggs hatch in the snail gut releasing the contained miracidium which penetrates the gut wall shedding its cilia and forming a sporocyst in the digestive gland. Mother sporocysts feed by absorption (they lack digestive organs) whilst their germ balls produce multiple rediae by asexual reproduction. Rediae are released into adjacent snail tissues where they feed (they possess mouths and guts) while their germ balls produce numerous cercariae. Mature cercariae are released from the rediae and exit the snail into the surrounding waters where they use their tails to swim about seeking fish hosts. Upon contact, the cercariae penetrate the skin of the fish shedding their tails and forming metacercarial cysts in fish tissues (scales, subcutis, muscles). Various species of freshwater (some brackish-water) fish act as suitable second intermediate hosts, including Osmeriformes (plecoglossids, salangids), Cypriniformes (cyprinids), Mugiliformes (mugilids), Gobiiformes (oxudercids, odontobutids), Perciformes (lateolabracids), Salmoniformes (salmonids) and Petromyzontiformes (petromyzontid lampreys). Infections are transmitted to piscivorous definitive hosts when they ingest fish tissues. Metacercariae are thought to remain viable in live fish for up to 2.5 years and they can survive in raw, undercooked, lightly preserved or pickled fish products for several days. Following ingestion, the metacercariae excyst in the host duodenum releasing the juvenile worms which attach to the mucosa and mature into adults around 1 week later. The prepatent period (time from infection to first release of eggs) ranges from 2-3 weeks and adult worms may produce from 14-280 eggs per day and live in vertebrate hosts for up to 18 months.

Differential diagnosis: Infections may be suggested on the basis of symptomatology and history of exposure (residence or travel in endemic regions, dietary intake of under-processed fish), but most clinical signs are nonspecific and other aetiological agents may be implicated. Coprological tests are usually conducted to confirm diagnoses by the microscopic detection of worm eggs in faecal samples, either in smears (direct smear, glycerin-jelly mounts, cellophane thick smears, Kato-Katz thick smears) or concentrates (formalin-ether sedimentation, some floatation techniques). Multiple samples from consecutive days should be examined due to intermittent or low egg excretion, although the differential diagnosis of fluke species (and genera) is difficult due to their similar appearance. Adult worms may be recovered for microscopic examination following anthelmintic treatment or by using purgatives or endoscopy. Infections by metacercariae in fish may be detected at necropsy by microscopic examination of dissected muscles, usually in squash preparations or following pepsin-acid digestion. Several immunoserological tests have been developed to detect host serum antibodies, including intradermal and indirect fluorescent-antibody tests and enzyme immunoassays, but they have often yielded poor specificity due to the use of crude worm antigens. Chromosome karyotyping techniques have been used in research settings to differentiate between several *Metagonimus* spp. (*M. miyatai, M. yokogawai, M. takahashii*) but they have not found widespread application. More recently, molecular biological techniques have been used to characterize various species by polymerase chain reaction (PCR) amplification of restriction fragment length polymorphisms (RFLP), simple sequence repeats PCR

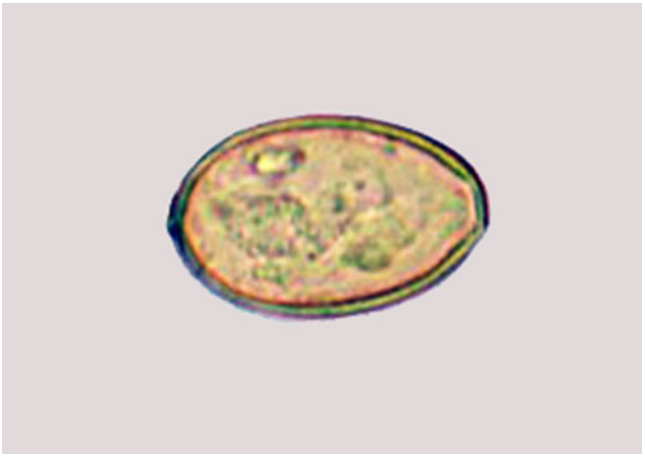
(SSR) or sequencing nuclear (28S ribosomal RNA, internal transcribed spacer region 1) or mitochondrial (cytochrome c oxidase subunit 1) genes.

Treatment and control: The drug of choice for treating *Metagonimus* infections is the isoquinoline anthelmintic praziquantel, despite some minor side-effects, such as nausea, vomiting, headaches, dizziness and insomnia. Alternative anthelmintics include the salicylanilides (niclofolan and niclosamide) and halogenated phenols (bithionol) but they were not as effective. The potential for re-infection following chemotherapy is high in endemic regions so various control strategies have been explored to break transmission cycles. The prevention of water contamination by faecal material is paramount in domestic and aquaculture settings and many attempts have been made to reduce snail populations in ponds used for fishing. However, the widespread use of toxic chemicals in aquatic ecosystems should not be considered due to environmental concerns. It is better to improve sanitary practices around water bodies and prevent definitive hosts from consuming unprocessed fish products. Public education campaigns should encourage people, especially in endemic areas, to fully cook fish and eliminate raw or undercooked fish meals from their dietary practices, despite some dishes being regarded as traditional delicacies. Many salting, smoking and pickling processes practiced in endemic communities do not effectively kill metacercariae, and freezing only renders them nonviable if fish products are deep-frozen (-20ºC for at least 7 days). Experimental studies have also shown that gamma-irradiation of fish at 200 Gy also destroys metacercariae.

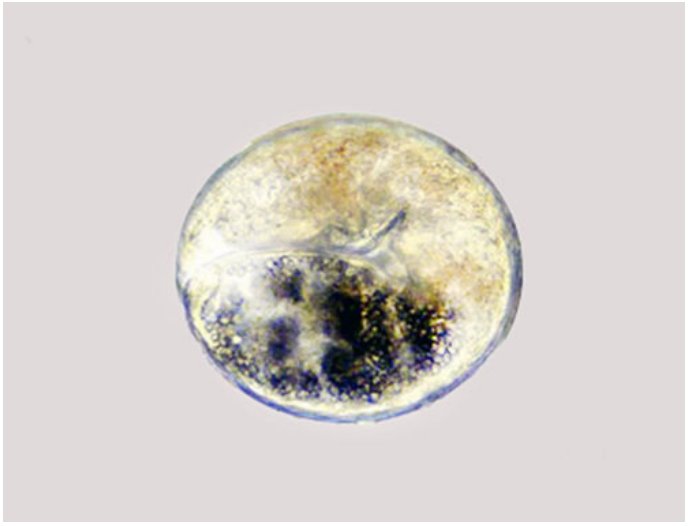

Metagonimus
intestines
(trauma, irritation,
inflammation, necrosis,
malabsorptive diarrhoea)
Definitive Hosts
(carnivores, piscivores)
hermaphroditic
adult (~ 1.5 mm)
ingestion
excretion
egg
(~ 30 µm)
vector-borne transmission
encysted within
tissues of IH-2
metacercaria
(~ 350 µm)
endoparasitic in
tissues of vector (IH-1)
free-swimming
cercaria
(~ 600 µm)
miracidium
(~ 30 µm)
redia
(~ 1 mm)
sporocyst
(~ 1 mm)
Second Intermediate Hosts
(IH-2) (freshwater fish)
(tissue cysts)
First Intermediate Hosts
(IH-1) (semisulcospirid snails)
(intestines then glandular tissues)



Metagonimus adult worm



Metagonimus egg



Metagonimus metacercaria

other taxa sister to *Heterophyes*/*Metagonimus*

Parasite species	Definitive hosts [adults in tissues]	First intermediate hosts [sporocysts/rediae in tissues]	Second intermediate hosts [metacercariae in tissues]	Distribution
Subfamily: Cryptocotylinae (median ventral sucker (acetabulum) in muscular genital sinus, papilla-like gonotyl)				
Cryptocotyle				
C. badamshini	Carnivora: phocid (Caspian seal)			Russia
C. concava (*concavum*)	Carnivora: felid (cat) mammals birds		brackish water Gobiiformes: gobiid (knot goby, round goby, monkey goby)	Korea, Russia
C. cryptocotyloides	Gaviiformes: gaviid (black-throated loon)			Russia
C. delamurei (syn. *Ciureana*)	Carnivora: otariid (northern fur seal)			Russia
C. jejuna	Carnivora: canid (dog); Charadriiformes: larid (gull)		brackish water Gobiiformes: gobiid (knot goby, round goby, monkey goby)	Russia
C. lata	Anseriformes: anatid (duck)	freshwater Gastropoda: bithyniid (*Boreoelona ussuriensis*)	freshwater Cypriniformes: cyprinid (swamp minnow); Anura: ranid (Dybowski's frog, tadpoles)	Russia
C. lingua (syn. *C. americana, C. macrorhinis*)	Primates: hominid (human); Carnivora: canid (dog, fox), felid (cat), procyonid (raccoon), phocid (harbor seal, northern elephant seal), otariid (California sea lion); Rodentia: murid (rat); Charadriiformes: larid (black-backed gull, European herring gull, tern); Pelecaniformes: ardeid (heron)	marine Gastropoda: littorinid (*Littorina littorea*)	marine Gobiiformes: gobiid (two-spotted goby); Perciformes: labrid (Ballan wrasse); Mugiliformes: mugilid (thicklip grey mullet)	Greenland, Eurasia, North America
C. quinqueangularis	Carnivora: felid (cat)			Russia
C. ransomi sp. inq.	Carnivora: canid (dog); Rodentia: murid (brown rat)			Russia
C. thapari	Carnivora: mustelid (giant otter, neotropical river otter)			South America
Subfamily: Centrocestinae (circumoral spines present, well-developed ventral sucker (acetabulum) in genital sinus, 1-2 papilla-like gonotyls)				
Centrocestus				
C. armatus	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Lagomorpha: leporid (rabbit): Rodentia: murid (rats, mice), cricetid (hamster); Pelecaniformes: ardeid (large egret, heron); Accipitriformes: accipitrid (kite)	freshwater Gastropoda: semisulcospirid (*Semisulcospira libertina*)	freshwater Cypriniformes: cyprinid (bitterling, rosy bitterling, stone moroko, pale chub, dark chub), cobitid (pond loach); Gobiformes: oxudercid (Amur goby); Siluriformes: bagrid (yellowhead catfish)	Russia, Korea, Japan
C. caninus (syn. *C. longus, C. yokogawai, C. asadai*)	Carnivora: canid (dog), felid (cat); Rodentia: murid (mouse); Primates: hominid (human); Pelecaniformes: ardeid (egret, heron)	freshwater Gastropoda: semisulcospirid (*Semisulcospira*)	brackish water Mugiliformes: mugilid (flathead grey mullet); Cypriniformes: cyprinid (European carp, goldfish, Chinese barb, dace), cobitid (pond loach); Gobiiformes: oxudercid (yellowfin goby); Abantiformes: channid (small snakehead), osphronemid	Asia

			(paradise fish); Perciformes: leiognathid (ponyfish); Beloniformes: hemiramphid (halfbeak); Anura: dicroglossid (rice field frog), bufonid (Asian toad)	
C. cuspidatus	Primates: hominid (human); Carnivora: canid (dog, fox), felid (cat); Rodentia: murid (rats); Galliformes: phasianid (chicken); Accipitriformes: accipitrid (yellow-billed kite)		freshwater Cyprinodontiformes: poeciliid (mosquitofish); Cichliformes: cichlid (eastern happy)	Middle East, Asia
C. formosanus	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Rodentia: murid (mice, rats); Lagomorpha: leporid (rabbit); Anseriformes: anatid (duck); Galliformes: phasianid (chicken); Pelecaniformes: ardeid (night heron, green heron, heron, pond heron, great egret)	freshwater Gastropoda: semisulcospirid (*Semisulcospira libertina*), thiarid (*Stenomelania newcombi, Melanoides tuberculata*)	freshwater Anabantiformes: anabantid (climbing perch), channid (striped snakehead); Characiformes: characid (blind cave fish); Cypriniformes: cyprinid (goldfish, mudcarp, barb, hardlip barb, repasson, hampala, common carp, forktail blenny, minnow, pla-kamung, swamp barb, Java barb, pale chub), nemacheilid (stone loach), cobitid (pond loach); Perciformes: percid (fountain darter); Cyprinodontiformes: poeciliid (mosquitofish); Cichliformes: cichlid (blue tilapia, Nile tilapia, redbelly tilapia); Anura: ranid (Asian grass frog), bufonid (Asian toad)	Asia, Philippines, North America, Hawaii
C. kurokawai	Primates: hominid (human)		freshwater fish?	Japan
C. nycticoracis	Pelecaniformes: ardeid (black-crowned night heron, grey heron); Suliformes: phalacrocoracid (great cormorant); Accipitriformes: accipitrid (black kite); Carnivora: felid (cat)			Japan
C. polyspinosus	Carnivora: canid (dog)		brackish water Anabantiformes: channid (blotched snakehead), anabantid (climbing perch); Siluriformes: clariid (catfish); Cypriniformes: cobitid (weather loach)	Japan
Pygidiopsis				
P. ardeae	Pelecaniformes: ardeid (grey heron); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Carnivora: canid (dog)		marine Pleuronectiformes: pleuronectid (plaice, flounder)	Europe
P. australis	Galliformes: phasianid (chicken); Rodentia: murid (mouse)			South America
P. anterouteria (syn. *Caiguira*)	Charadriiformes: recurvirostrid (black-winged stilt); Carnivora: felid (cat)			South America
P. cambodiensis	Rodentia: cricetid (golden hamster)		marine Mugiliformes: mugilid (largescale mullet)	Asia
P. crassus	Galliformes: phasianid (chicken); Rodentia: murid (mouse)			South America
P. genata	Primates: hominid (human); Carnivora: felid (cat), canid (wolf, dog, fox): Eulipotyphla: soricid (shrew); Rodentia: murid (rats,	freshwater Gastropoda: thiarid (*Melanoides tuberculata*),	brackish-water Cypriniformes: cyprinid (Jordan himri); Cyprinodontiformes: poeciliid (western mosquitofish);	Middle East, Eurasia

	mice), cricetid (hamster); Pelecaniformes: pelecanid (pelican); Accipitriformes: accipitrid (kite); Anseriformes: anatid (duck); Suliformes: phalacrocoracid (cormorant)	melanopsid (*Melanopsis costata*)	Mugiliformes: mugilid (thinlip mullet); Cichliformes: cichlid (Nile tilapia)	
P. himantopae (syn. *Caiguira*)	Charadriiformes: recurvirostrid (black-necked stilt)			North America
P. macrostomum	Rodentia: cricetid (hamster), murid (rat)	brackish water Gastropoda: cochliopid (*Heleobia australis*)	freshwater Cyprinodontiformes: poeciliid (January carpling, molly), anablepid (Rio de la Plata onesided livebearer)	South America
P. marivillai	Accipitriformes: accipitrid (sea eagle)			Philippines
P. pelecani	Pelecaniformes: pelecanid (pelican)			China
P. phalacrocoracis	Suliformes: phalacrocoracid (common cormorant)			Japan
P. piclaumoreli	Charadriiformes: larid (common tern)			Africa
P. plana	Pelecaniformes: ardeid (green heron)			North America
P. summa	Primates: hominid (human); Carnivora: canid (dog), felid (cat), procyonid (raccoon); Rodentia: murid (rats, mice)	brackish-water Gastropoda: potamidid (*Tympanotonus microptera* (= *Cerithidea fluvialitis*), *Cerithidea cingulata*)	brackish-water Mugiliformes: mugilid (flathead gray mullet, so-iuy mullet); Gobiiformes: oxudercid (yellowfin goby, mudskipper, walking goby); Perciformes: lateolabracid (Japanese seabass); Clupeiformes: clupeid (dotted gizzard shad)	Asia
Ascocotyle				
A. (*Phagicola*) *angeloi*	Pelecaniformes: ardeid (least bittern); Galliformes: phasianid (chicken); Rodentia: murid (mouse)	freshwater Gastropoda: cochliopid (*Littoridina* (*Heleobia*) *castellanosae*)	freshwater Cyprinodontiformes: anablepid (onesided livebearer)	South America
A. (*Phagicola*) *ampullacea*	Carnivora: procyonid (raccoon)		freshwater Cyprinodontiformes: poeciliid (western mosquitofish)	North America
A. angrense	Pelecaniformes: ardeid (striated heron, green heron, tricolored heron, yellow-crowned night heron, black-crowned night heron, great egret, snowy egret); Anseriformes: anatid (wood duck); Galliformes: phasianid (chicken); Suliformes: sulid (northern gannet); Charadriiformes: larid (herring gull); Carnivora: canid (dog, Alaskan fox), felid (cat), procyonid (raccoon); Rodentia: cricetid (muskrat, hamster), murid (mouse, rat)		freshwater Cyprinodontiformes: poeciliid (top minnow, sailfin molly, black molly), cyprinodontid (sheepshead pupfish), fundulid (longnose killifish, Gulf killifish, golden topminnow, mummichog, saltmarsh topminnow, striped killifish, rainwater killifish)	Americas
A. arnoldoi	Rodentia: murid (mouse); Carnivora: canid (dog), felid (cat); Procellariiformes: diomedeid (albatross)			South America
A. (*Phagicola*) *ascolonga*	Carnivora: canid (dog), felid (cat)		brackish water Cichliformes: cichlid (tilapia, Galilean comb)	Middle East
A. (*A.*) *branchialis*			Anura: ranid (edible frog,	Europe

			tadpoles)	
A. byrdi	Accipitriformes: cathartid (turkey vulture)			North America
A. (*Phagicola*) *cameliae*	Sphenisciformes: spheniscid (Magellanic penguin)			South America
A. (*A.*) *chandleri*			brackish water Cyprinodontiformes: cyprinodontid (sheepshead pupfish), fundulid (longnose killifish), poeciliid (sailfin molly)	North America
A. (*A.*) *coleostoma*	Pelecaniformes: pelecanid (pelican); Primates: hominid (human)			Middle East
A. (*Phagicola*) *diminuta*	Galliformes: phasianid (chicken); Anseriformes: anatid (duck); Pelecaniformes: ardeid (great egret, snowy egret); Carnivora: procyonid (raccoon); Rodentia: murid (mouse, rat), cricetid (hamster)	brackish water Gastropoda: hydrobiid (*Pyrgophorus coronatus, Littoridina castellanosae, L. parchappei*)	brackish water Cyprinodontiformes: poeciliid (Yucatan molly, Peten molly, top minnow, variatus platy), fundulid (longnose killifish, Gulf killifish), cyprinodontid (goldspotted killifish)	Americas
A. (*A.*) *felippei* (syn. *A. puertoricensis*)	Pelecaniformes: ardeid (least bittern)		freshwater Cyprinodontiformes: poeciliid (guppy)	Americas
A. (*A.*) *gemina*	Gruiformes: rallid (mangrove rail); Galliformes: phasianid (chicken); Anseriformes: anatid (duck)	freshwater Gastropoda: hydrobiid (*Litterodinops monroensis*)	brackish water Cyprinodontiformes: cyprinodontid (sheepshead pupfish),	North America
A. (*Leighia*) *hadra*	Galliformes: phasianid (chicken); Rodentia: murid (mouse)	freshwater Gastropoda: hydrobiid (*Littoridina parchappei*)	freshwater Cyprinodontiformes: poeciliid (ten-spotted livebearer), anablepid (onesided livebearer)	South America
A. intermedius	Accipitriformes: accipitrid (Indian fishing eagle)			India
A. langeniformis	Rodentia: cricetid (muskrat)			North America
A. (*A.*) *leighi*	Carnivora: procyonid (raccoon); Galliformes: phasianid (chicken); Pelecaniformes: arceid (tricolored heron, great egret)		brackish water Cyprinodontiformes: cyprinodontid (sheepshead pupfish), poeciliid (sailfin molly); Cichliformes: cichlid (Bay snook)	Americas
A. (*Phagicola*) *longa*	Carnivora: canid (dog, Alaskan fox); Rodentia: cricteid (hamster); Primates: hominid (human); Pelecaniformes: pelecanid (pelican); Accipitriformes: accipitrid (eagle); Sphenisciformes: spheniscid (Magellanic penguin)	brackish water Gastropoda: cochliopid (*Heleobia australis*)	brackish water Mugiliformes: mugilid (liza)	Americas, Africa, Europe, Middle-East
A. (*Phagicola*) *longicollis*	Carnivora: canid (dog), felid (cat)		brackish water Mugiliformes: mugilid (mullet); Cichliformes: cichlid (tilapia)	Middle East
A. (*Phagicola*) *macrostomus*	Galliformes: phasianid (chicken); Accipitriformes: cathartid (turkey vulture)		brackish water Cyprinodontiformes: poeciliid (Yucatan molly)	North America
A. mcintoshi	Pelecaniformes: threskiornithid (American white ibis); Galliformes: phasianid (chicken)	brackish water Gastropoda: hydrobiid (*Littoridinops*	brackish water Cyprinodontiformes: poeciliid (sailfin molly, western mosquitofish)	North America

		monroensis)		
A. (*Leighia*) *megalocephala*	Pelecaniformes: ardeid (great egret)		brackish water Cyprinodontiformes: poeciliid (Yucatan molly)	North America
A. (*Phagicola*) *minuta*	Carnivora: canid (dog), felid (cat); Pelecaniformes: ardeid (grey heron)			Middle East
A. (*Phagicola*) *nana*	Pelecaniformes: pelecanid (American white pelican), ardeid (great egret, great blue heron, least bittern); Galliformes: phasianid (chicken); Accipitriformes: accipitrid (black hawk); Suliformes: sulid (northern gannet); Carnivora: canid (Alaskan fox), procyonid (raccoon); Didelphimorphia: didelphid (Virginia opossum); Rodentia: murid (mouse), cricteid (muskrat, Syrian hamster)		freshwater Cichliformes: cichlid (Mayan cichlid, Jack Dempsey, firemouth cichlid, golden cichlid); Characiformes: characid (banded astyanax); Cyprinodontiformes: poeciliid (Yucatan molly)	Americas
A. (*A.*) *nunezae*	Pelecaniformes: ardeid (great egret); Galliformes: phasianid (chicken)		freshwater Cichliformes: cichlid (firemouth cichlid, Jack Dempsey)	America
A. (*A.*) *pachycystis*	Carnivora: procyonid (raccoon), felid (cat)	brackish water Gastropoda: hydrobiid (*Littoridinops tenuipes*)	brackish water Cyprinodontiformes: cyprinodontid (sheepshead pupfish)	North America
A. (*A.*) *patagoniensis*	Carnivora: otariid (South American sea lion); Sphenisciformes: spheniscid (Magellanic penguin)		marine Atheriniformes: atherinopsid (silversides)	South America
A. (*Phagicola*) *pindoramensis*	Pelecaniformes: ardeid (least bittern, stripe-backed bittern, great blue heron, striated heron, yellow-crowned night heron, black-crowned night heron), threskiornithid (roseate spoonbill); Suliformes: phalacrocoracid (Neotropic cormorant); Accipitriformes: pandionid (osprey); Anseriformes: anatid (duck); Galliformes: phasianid (chicken); Rodentia: cricetid (marsh rice rat, golden hamster), murid (mouse); Carnivora: canid (dog)		brackish water Cyprinodontiformes: poeciliid (January carp, Catemaco molly, shortfin molly, guppy, swordtail); Cichliformes: cichlid (tilapia)	Americas
A. pithecophagicola	Accipitriformes: accipitrid (monkey-eating eagle)			Philippines
A. (*A.*) *secunda*	Galliformes: phasianid (chicken)	freshwater Gastropoda: hydrobiid (*Heleobia castellanosae, H. parchappei*)	freshwater Cyprinodontiformes: poeciliid (tenspotted livebearer, western mosquitofish), anablepid (onesided livebearer)	South America
A. (*A.*) *sexidigita*	Galliformes: phasianid (chicken)		marine Cyprinodontiformes: fundulid (California killifish)	North America
A. (*A.*) *tenuicollis*	Pelecaniformes: ardeid (great egret, American bittern, little blue heron, tricolored heron); Accipitriformes: accipitrid (black hawk); Galliformes: phasianid (chicken)	brackish water Gastropoda: hydrobiid (*Pyrgophorus coronatus*)	brackish water Cyprinodontiformes: fundulid (mummichog), poeciliid (southern platyfish, Peten molly, Yucatan molly, broadspotted molly, western mosquitofish,	Americas, Middle East

			speckled mosquitofish, sailfin molly, ten-spotted livebearer); Characiformes: characid (Mexican tetra); Perciformes: centrarchid (warmouth); Cichliformes: cichlid (Jack Dempsey, yellowjacket cichlid, sepelkirjoahven, Pantani cichlid, redhead cichlid)	
A. (*A.*) *tertia*	Galliformes: phasianid (chicken)	freshwater Gastropoda: hydrobiid (*Heleobia castellanosae, H. parchappei*)	freshwater Cyprinodontiformes: poeciliid (tenspotted livebearer, western mosquitofish), anablepid (onesided livebearer)	South America
Subfamily: Galactosominae (ventral sucker (acetabulum) reduced or absent, globular gonotyl usually with spines)				
Stictodora				
S. (*S.*) *adulecentia*	Charadriiformes: larid (gull)			Japan
S. allicoli	Charadriiformes: larid (Indian skimmer)			India
S. (*S.*) *caballeroi*	Charadriiformes: larid (ring-billed gull)			North America
S. cablei	Charadriiformes: larid (royal tern)			North America
S. (*S.*) *diplacantha*	Suliformes: phalacrocoracid (pied cormorant)			Australia
S. (*S.*) *fuscata*	Carnivora: felid (cat), canid (dog); Primates: hominid (human)		brackish-water Mugiliformes: mugilid (flathead grey mullet, largescale mullet, so-iuy mullet); Gobiiformes: oxudercid (yellowfin goby)	Japan, Korea
S. (*S.*) *guerreroi*	Charadriiformes: larid (black-headed gull)			Philippines
S. (*S.*) *hainanensis*	Carnivora: canid (dog)			China
S. (*S.*) *japonica*	Anseriformes: anatid (red-breasted merganser)			Japan
S. (*Galactosomoides*) *johnsoni*	Suliformes: sulid (brown booby); Charadriiformes: larid (royal tern)			Central America
S. (*S.*) *lari*	Charadriiformes: larid (black-tailed gull); Carnivora: felid (cat), canid (dog); Primates: hominid (human)	brackish-water Gastropoda: batillariid (*Velacumantus australis*)	estuarine Perciformes: gobiid (southern longfin goby, pale mangrove goby); Atheriniformes: atherinid (smallmouth hardyhead); Syngnathiformes: syngnathid (hairy pipefish); Cyprinodontiformes: poeciliid (western mosquitofish)	Japan, Korea, Russia, Vietnam, Australia
S. (*S.*) *lariformicola*	Charadriiformes: larid (herring gull, laughing gull, ring-billed gull, royal tern)			North America
S. (*S.*) *macrotestis*	Charadriiformes: scolopacid (wandering tattler)			Russia
S. (*S.*) *manilensis*	Carnivora: felid (cat), canid (dog); Rodentia: murid (mouse, rat)			Philippines
S. (*S.*) *mergi*	Anseriformes: anatid (red-breasted merganser)			Japan
S. (*S.*) *morosovi*	Charadriiformes: larid (Mediterranean gull)			Russia
S. (*S.*) *palmifera*			marine Perciformes: sillaginid (trumpeter whiting)	Philippines

S. (*S.*) *perpendiculum*	Charadriiformes: larid (gull); Carnivora: canid (dog), felid (cat)			Japan
S. (*S.*) *petrowi*	Charadriiformes: larid (gull)			Russia
S. (*S.*) *pusilla*	Charadriiformes: larid (gull)			Japan
S. (*S.*) *sawakinensis*	Charadriiformes: larid (gull); Procellariiformes: procellariid (Cory's shearwater)			Middle-East, Russia, Philippines
S. (*S.*) *sclerogonocotyla*	Pelecaniformes: ardeid (purple heron)			Middle-East
S. (*S.*) *thaparai*	Carnivora: felid (cat)			Middle East
S. ubelakeri	Carnivora: otariid (California sea lion)			North America
Acanthotrema				
A. acanthotrema (syn. *Stictodora*)	Charadriiformes: larid (royal tern)			Central America
A. armata	Charadriiformes: larid (Audouin's gull)			Europe
A. cursitans (syn. *Stictodora*)	Rodentia: cricteid (marsh rice rat); Carnivora: procyonid (raccoon); Didelphimorphia: didelphid (opossum)	brackish water Gastropoda: potamidid (*Cerithidea scalariformis*)	Cyprinodontiformes: fundulid (killifish)	North America
A. felis	Carnivora: felid (cat); Primates: hominid (human)		brackish water Gobiiformes: oxudercid (yellowfin goby)	Korea
A. hancocki	Galliformes: phasianid (chicken)			North America
A. martini	Charadriiformes: larid (black skimmer)			North America
A. tanayensis (syn. *Stictodora*)	Carnivora: felid (cat)			Philippines
A. tridactyla (syn. *Stictodora*)	Galliformes: phasianid (chicken); Carnivora: felid (cat)			Middle-East
Subfamily: Heterophyinae (no genital sinus, posterolateral gonotyl with chitinous rodlets)				
Heterophyopsis				
H. continua (syn. *Heterophyes expentans*)	Primates: hominid (human); Carnivora: felid (cat), canid (dog); Anseriformes: anatid (duck); Galliformes: phasianid (chicken); Charadriiformes: larid (seagull); Gaviiformes: gaviid (black-throated loon)		fresh and brackish water Cypriniformes: cyprinid (common carp); Mugiliformes: mugilid (flathead gray mullet); Clupeiformes: clupeid (shad, spotted sardine); Gobiiformes: oxudercid (yellowfin goby, mudskipper, walking goby); Osmeriformes: plecoglossid (sweetfish); Perciformes: serranid (dusky-tail grouper, orange-spotted grouper), lateolabracid (Asian seabass); Anguilliformes: congrid (white-spotted conger)	Asia
Subfamily: Stellantchasminae (small lateral ventral sucker (acetabulum), large spiny gonotyl, distal seminal vesicle forms muscular expulsor)				
Procerovum				
P. calderoni	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Galliformes: phasianid (chicken)	brackish water Gastropoda: thiarid (*Thiara riquetti*)	marine and freshwater Gobiiformes: gobiid (tank goby, robust mangrove goby); Anabantiformes: channid (striped snakehead), anabantid (climbing perch); Perciformes: gerreid (whipfin silver-biddy), eleotrid (olive flathead gudgeon), ambassid (Buru glass perchlet), terapontid (trumpeter	Asia, Egypt

			perch), siganid (streaked spinefoot), polynemid (fourfinger threadfin); Mugiliformes: mugilid (gray mullet); Gonorynchiformes: chanid (milkfish); Cyprinodontiformes: poeciliid (sailfin molly); Scorpaeniformes: platycephalid (bartail flathead); Beloniformes: hemiramphid (halfbeak)	
P. cheni	Anseriformes: anatid (duck); Galliformes: phasianid (chicken)	freshwater Gastropoda: thiarid (*Melanoides tuberculata*)	freshwater Anabantiformes: osphronemid (paradisefish)	China
P. varium	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Rodentia: murid (water rat, mouse); Pelecaniformes: pelecanid (Australian pelican), ardeid (great egret, yellow-billed egret, white-faced heron, nankeen night heron); Accipitriformes: accipitrid (whistling kite); Anseriformes: anatid (duck); Galliformes: phasianid (chicken)	brackish water Gastropoda: thiarid (*Melanoides (Thiara) tuberculata*)	brackish water Mugiliformes: mugilid (flathead grey mullet, eastern keelback mullet); Scorpaeniformes: platycephalid (bartail flathead); Cyprinodontiformes: poeciliid (sailfin molly); Perciformes: scatophagid (spotted scat); Gonorynchiformes: chanid (milkfish); Gobiiformes: oxudercid (maned goby); Beloniformes: hemiramphid (halfbeak); Anabantiformes: anabantid (climbing perch)	Asia, India, Australia
Stellantchasmus				
S. aspinosus	Rodentia: murid (Australian water rat, rat); Carnivora: felid (cat); Suliformes: phalacrocoracid (little pied cormorant); Galliformes: phasianid (chicken)			Australia
S. batillans	Rodentia: murid (Australian water rat); Anseriformes: anatid (duck)			Australia
S. falcatus	Carnivora: canid (dog), felid (cat); Primates: hominid (human); Artiodactyla: suid (pig); Rodentia: murid (rat, mouse); Galliformes: phasianid (chicken); Pelecaniformes: ardeid (nankeen night heron); Accipitriformes: accipitrid (whistling kite)	brackish-water Gastropoda: thiarid (*Stenomelania newcombi, Melanoides tuberculata, Thiara granifera*)	brackish and freshwater Mugiliformes: mugilid (thinlip mullet, flathead grey mullet, so-iuy mullet); Gobiiformes: oxudercid (yellowfin goby); Anabantiformes: anabantid (climbing perch); Beloniformes: zenarchopterid (wrestling halfbeak)	Asia, Oceania
S. gallinae	Galliformes: phasianid (chicken)			Vietnam
Subfamily: Haplorchiinae (rudimentary ventral sucker (acetabulum), large gonotyl with chitinous rodlets superimposed on ventral sucker, single testis)				
Haplorchis				
H. butei (*nom. nud.?*)	Accipitriformes: accipitrid (long-legged buzzard)			India
H. gyanpuri	Accipitriformes: accipitrid (black kite)			India
H. parapumilio	Suliformes: phalacrocoracid (pygmy cormorant)			Indonesia
H. parataichui	Carnivora: felid (cat)		freshwater Atheriniformes: melanotaeniid (Pacific blue-eye)	Australia
H. paravanissimus	Pelecaniformes: ardeid (rufous night heron), pelecanid (Australian pelican), Accipitriformes: accipitrid (whistling kite); Suliformes:			Australia

	phalacrocoracid (little black cormorant)			
H. pearsoni (*sp. inq.*)	Strigiformes: strigid (brown fish owl)			Sri Lanka
H. popelkae	Testudines: chelid (northern snapping turtle, red-faced turtle)			Australia
H. pumilio (syn. *H. taihokui*, *H. milvi, H. pleurolophocerca, Monorchotrema taihokui*)	Primates: hominid (human), cercopithecid (crab-eating macaque (= cynomolgus monkey)); Carnivora: canid (dog, fox), felid (cat); Eulipotyphla: soricid (African giant shrew); Rodentia: murid (mice, rat, water rat), cricetid (hamster), caviid (guinea pig); Lagomorpha: leporid (rabbit); Pelecaniformes: ardeid (night heron, yellow-billed egret), pelecanid (great white pelican, grey pelican), threskiornithid (red-naped ibis); Suliformes: phalacrocoracid (little pied cormorant); Accipitriformes: accipitrid (black kite); Charadriiformes: larid (gull), scolopacid (whimbrel); Columbiformes: columbid (pigeon); Anseriformes: anatid (duck)	freshwater Gastropoda: potamidid (*Pirenella conica*), thiarid (*Thiara granifera* (= *Melania reiniana, M. obliquegranosa*), *Melanoides tuberculata, Me. chinensis*), semisulcospirid (*Semisulcospira libertina*)	fresh and brackish water Cypriniformes: cyprinid (hampala barb, spotted barb, Mekong flying barb, barb, grass carp); Cyprinodontiformes: poeciliid (mosquitofish); Mugiliformes: mugilid (mullet, thinlip mullet); Anabantiformes: channid (striped snakehead), anabantid (climbing perch), osphronemid (paradisefish); Gobiiformes: oxudercid (goby), gobiid (tank goby); Centrarchiformes: terapontid (silver perch); Perciformes: siganid (spinefoot), anabantid (climbing gourami), gerreid (whipfin silver-biddy); Cichliformes: cichlid (tilapia, happy); Percomorpha: ambassid (Buru glass perchlet)	Middle-East, Asia, Australia
H. solus	Serpentes: colubrid (green tree snake)			India
H. sprenti	Carnivora: felid (cat); Rodentia: murid (water rat, rat); Suliformes: phalacrocoracid (little black cormorant, little pied cormorant, pied cormorant); Pelecaniformes: pelecanid (Australian pelican), ardeid (great egret, plumed egret, white-faced heron); Galliformes: phasianid (chicken)			Australia
H. tagoreai (*nom. nud.?*)	Carnivora: canid (dog)			India
H. taichui (syn. *H. microrchis*)	Carnivora: canid (dog), felid (cat); Rodentia: murid (mice, rats), caviid (guinea pig), cricetid (hamster); Lagomorpha: leporid (rabbit); Artiodactyla: bovid (cattle); Primates: hominid (human); Pelecaniformes: ardeid (night heron, egret), pelecanid (spot-billed pelican), threskiornid (red-naped ibis); Accipitriformes: accipitrid (black kite, brahminy kite)	freshwater Gastropoda: thiarid (*Thiara granifera* (= *Melania reiniana, M. obliquegranosa*), *M. juncea, Melanoides tuberculata, Tarebia granifera*), semisulcospirid (*Semisulcospira libertina*)	freshwater Mugiliformes: mugilid (keelback mullet); Cypriniformes: cyprinid (dace, goldfish, common carp, grass carp, repasson, hampala, thinlip barb, spotted barb, swamp barb, Java barb, marginated barb, srang, stone moroko, rosy bitterling, pale chub, Burmese trout, Siamese mud carp); Cyprinodontiformes: poeciliid (mosquitofish); Cichliformes: cichlid (tilapia)	Asia, India, Middle-East
H. vanissimus	Primates: hominid (human); Carnivora: canid (dog); Suliformes: phalacrocoracid (little black cormorant): Accipitriformes: accipitrid (whistling kite); Pelecaniformes: ardeid (Nankeen night heron)		freshwater fish?	Philippines, Australia
H. wellsi	Coraciiformes: alcedinid (ruddy kingfisher)			Taiwan

H. yokogawai (syn. *H. vagabundi, Monorchotrema*)	Primates: hominid (human), cercopithecid (crab-eating macaque (= cynomolgus monkey)); Carnivora: canid (dog), felid (cat); Artiodactyla: bovid (cattle); Rodentia: murid (mouse, water rat); Accipitriformes: accipitrid (whistling kite, black kite); Pelecaniformes: ardeid (night heron, cattle egret), pelecanid (spot-billed pelican), threskiornithid (red-naped ibis); Passeriformes: corvid (rufous treepie)	freshwater Gastropoda: thiarid (*Stenomelania newcombi, Melanoides* (*Thiara*) *tuberculata*)	brackish water Mugiliformes: mugilid (flathead grey mullet, eastern keelback mullet); Perciformes: siganid (streaked spinefoot), ambassid (Buru glass perchlet), gerreid (silver biddy), mullid (red mullet); Anabantiformes: anabantid (climbing perch), channid (snakehead); Cypriniformes: cyprinid (goldfish, mud carp, beardless barb, spotted hampala barb, serrated anal-spine carp), cobitid (weather loach); Cyprinodontiformes: poeciliid (western mosquitofish); Suliformes: clariid (Hong Kong catfish), ariid (Manila sea catfish); Beloniformes: hemiramphid (long-billed halfbeak); Cichliformes: cichlid (Nile tilapia); Decapoda: penaeid (shrimp)	Asia, India, Australia, Mediterranean
Subfamily: Apophallinae (well-developed ventral sucker (acetabulum) in non-muscular genital sinus, 1-2 papilla-like gonotyls)				
Apophallus				
A. bacalloti	Anseriformes: anatid (duck); Passeriformes: fringillid (canary)		freshwater Gasterosteiformes: gasterosteid (three-spined stickleback); Cyprinodontiformes: poeciliid (western mosquitofish)	Europe
A. brevis	Charadriiformes: larid (ring-billed gull, herring gull); Gaviiformes: gaviid (common loon); Carnivora: felid (cat); Rodentia: murid (rat)	freshwater Gastropoda: amnicolid (*Amnicola limosa*)	freshwater Perciformes: percid (yellow perch); Salmoniformes: salmonid (trout)	North America
A. crami	Charadriiformes: larid (California gull)			North America
A. donicus	Carnivora: canid (dog, fox), felid (cat); Rodentia: murid (white rat, gerbil), cricetid (golden hamster); Lagomorpha: leporid (rabbit); Primates: hominid (human); Galliformes: phasianid (chicken); Charadriiformes: larid (black-headed gull, sandwich tern); Accipitriformes: accipitrid (common buzzard); Anseriformes: anatid (merganser); Pelecaniformes: ardeid (black-crowned night heron); Ciconiiformes: ciconiid (white stork); Strigiformes: strigid (owl); Columbiformes: columbid (wood dove, pigeon); Siluriformes: ictalurid (channel catfish)	freshwater Gastropoda: lithoglyphid (*Fluminicola virens*)	freshwater Cypriniformes: cyprinid (bleak, roach, blackside dace, speckled dace, redside shiner, squawfish, white bream, common bream, rudd, gudgeon, northern pikeminnow), catostomid (largescale sucker); Salmoniformes: salmonid (coho salmon, rainbow trout); Perciformes: percid (European perch, zander, ruffe, striped ruffe, zingel)	Europe, North America
A. eccentricus	Carnivora: canid (dog)			Philippines
A. imperator	Pelecaniformes: ardeid (great blue heron); Anseriformes: anatid (common merganser, hooded merganser)	freshwater Gastropoda: amnicolid (*Amnicola limosa*), planorbid (*Helisoma*)	freshwater Salmoniformes: salmonid (brook char, brown trout); Perciformes: percid (perch); Cypriniformes: catostomid (sucker)	North America
A. itascensis			freshwater Perciformes: percid (yellow perch); Cypriniformes:	North America

			cyprinid (eastern shiner)	
A. lerouxi	Charadriiformes: scolopacid (red shank)			Europe
A. microsoma	Galliformes: phasianid (chicken)		Salmoniformes: salmonid (coho salmon)	North America
A. microtestis	Pelecaniformes: ardeid (black-crowned night heron)			Europe
A. muhlingi (syn. *A. major*)	Charadriiformes: larid (black-headed gull, lesser black-headed gull), recurvirostrid (stilt); Pelecaniformes: pelecanid (pelican), ardeid (heron); Suliformes: phalacrocoracid (cormorant); Gaviiformes: gaviid (loon); Carnivora: canid (dog), felid (cat)	freshwater Gastropoda: lithoglyphid (*Lithoglyphus naticoides*)	brackish water Cypriniformes: cyprinid (crucian carp, common bream, silver bream, dace, bitterling, rudd); Perciformes: percid (perch)	Europe
A. similis	Carnivora: phocid (harbour seal)			North America
A. venustus	Carnivora: canid (dog, Arctic fox), felid (cat), procyonid (raccoon); Pelecaniformes: ardeid (blue heron); Charadriiformes: larid (gulls)	terrestrial Gastropoda: endodontid (*Goniobasis livescens*)	freshwater Lepisosteiformes: lepisosteid (garpike); Cypriniformes: cyprinid (carp), catostomid (sucker); Siluriformes: bagrid (catfish); Perciformes: centrarchid (smallmouth bass)	North America
A. zalophi (syn. *Pricetrema*)	Carnivora: otariid (sea lion)			North America

Dicrocoelium
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult plagiorchidans are varied in appearance, most bearing spines and a median ventral sucker and many producing small eggs which hatch after ingestion by snails (first intermediate hosts). Dicrocoeliids multiply in land (not aquatic) snails through multiple sporocyst generations (no redia) and they then form metacercariae in ants (second intermediate hosts). *Dicrocoelium* spp. are small lance-like liver flukes responsible for hepatic cirrhosis and production losses in domestic animals.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum: Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade: Neodermata (syncytial tegument = neodermis)
Class: Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass: Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order: Plagiorchiida ('echinostomatids', plagiorchiids', mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder: Xiphidiata (xiphidiocercariae with penetrating stylet in anterior margin of oral sucker)
Superfamily: Gorgoderoidea (miracidia penetrate gastropod, bivalve IH, sporocysts and rediae formed, simple-tailed cercariae with stylet, encysts in open or in second IH, metacercariae eaten by DH)
Family: Dicrocoeliidae (small lancet-like flukes, eggs ingested by snails, no redial stage, two-three IH)
Genus: *Dicrocoelium* (parasitic in liver of ruminants)
Species: various species cause cirrhosis of the liver in domestic animals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs, fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the

tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. Members of the suborder Xiphidiata are characterized by forming xiphidio-cercariae with a penetrating stylet in the anterior margin of the oral sucker which is used to penetrate second intermediate hosts where metacercariae are formed. Over 1,680 species have been described in 44 families in 4

superfamilies: Allocreadioidea (1,118 spp. in 6 families), Gorgoderoidea (106 spp. in 10 families), Microphalloidea (414 spp. in 12 families) and Plagiorchioidea (47 spp. in 16 families). The superfamily Gorgoderoidea parasitizes fish and tetrapods and the 10 cognate families comprise Atractotrematidae, Cadenatellinae, Haploporidae, Callodistomidae, Dicrocoeliidae, Gorgoderidae, Encyclometridae, Orchipedidae, Paragonimidae, and Troglotrematidae. The family Dicrocoeliidae contains more than 400 species in over 30 genera: including *Allocorrigia, Anchitrema, Athesmia, Brachydistomum, Brachylecithum, Brodenia, Caballerolecythus, Canaania, Concinnum, Conspicuum, Controrchis, Corrigia, Dicrocoelium, Dictyonograptus, Euparadistomum, Eurytrema, Leipertrema, Leptophallus, Lubens, Lutztrema, Lyperosomum, Metadelphis, Paradistomum, Platynosomum, Prosolecithus, Pseudathesmia, Pseudoparadistomum, Robertdigenea, Skrjabinus, Stromitrema, Unilaterilecithum, Yungasicola* and *Zonorchis*. They are small lanceolate flukes infecting the liver, bile ducts, gall bladder, pancreas or intestines of herbivores (ruminants, marsupials, reptiles, amphibians, birds) with indirect life-cycles involving 2 intermediate hosts (firstly molluscs, then insects). The genus *Dicrocoelium* contains some 15 species of liver flukes of domestic and wild herbivores that become infected during grazing when they ingest ants containing metacercariae. Infections have been reported in Europe, Russia, Africa, Asia, North America and South America.

***Dicrocoelium* species**	**Definitive hosts [adults in liver, bile ducts]**	**First intermediate hosts [sporocysts in tissues]**	**Second intermediate hosts [metacercariae in tissues]**	**Distribution**
D. albicolle (syn. *Distoma*)	Accipitriformes: accipitrid (booted eagle)			Europe
D. antechini	Dasyuromorphia: dasyurid (dusky antechinus, brown antechinus)			Australia
D. chinensis (syn. *D. suppereri, D. orientale*)	Artiodactyla: cervid (sika deer, roe deer), bovid (mouflon)	Stylommatophora (terrestrial snails): bradybaenid (*Bradybaena*), helicid (*Xeropicta*), pleurodontid (*Ganesella*)	Hymenoptera (ants): formicid (*Formica*, *Camponotus*)	China, Japan, Europe
D. colobusicola	Primates: cercopithecid (red colobus, eastern black-and-white colobus)			Africa
D. dendriticum (syn. *D. lanceatum, D. lanceolatum, D. macaci, D. vitrinus*) (little liver fluke, lanceolate fluke, lancet fluke)	Artiodactyla: bovid (sheep, mouflon, goat, chamois, serow, cattle, buffalo, yak), cervid (red deer, fallow deer, roe deer, sika deer, white-tailed deer, mule deer, wapiti, moose, elk), camelid (camel, lama, alpaca), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit, jackrabbit, hare, mountain hare), ochotonid (pika); Rodentia: murid (mice, rats), sciurid (woodchuck, marmot); Carnivora: canid (North American red fox), mustelid (mink); Primates: hominid (humans)	Stylommatophora (terrestrial snails): enid (*Zebrina* (*Napaeopsis*) *hohenackeri, Z. detrita*), hygromiid (*Helicella corderoi, H. jamuzensis, H. obvia, H. itala, H. candicans, H. madritensis, H. ordenensis, Helicopsis* (*Xeropicta*) *derbentina H.* (*X.*) *krynickii,*), cochliocopid (*Cionella* (*Cochlicopa*) *lubrica*), geomitrid (*Cernuella* (*Cernuella*) *virgata, C.* (*Xeromagna*) *cespitum, C.* (*Microxeromagna*) *vestita, Cochlicella acuta, C. barbara* (= *C. ventricosa*)), bradybaenid (*Bradybaena alma-atini, B. lantzi, B. plectotropis, B. rubens, B. semenovi, Eulota* (*B.*) *maacki*), helicid (*Helicella itala, H. obvia, Helix* (*Monacha*) *carthusiana, Cepaea nemoralis, C. vindobonensis*), clausiliid (*Clausilia bidentata*, *Laciniaria varnensis*), buliminid (*Chondrula microtraga, C.* (*Jaminia*)	Hymenoptera (ants): formicid (*Formica fusca, F. pratensis, F. rufibarbis, F. cinerea, F. mesasiatica, F. gagates, F. sanguinea, F. lugubris, F. cunicularia* (= *F. glebaria*), *F. polyctena, F. nigricans, F. picea, F. subpilosa, Proformica nasuta, Cataglyphus bicolor, Cataglyphis aenescens*)	worldwide, except South Africa and Australia

		tridens, J. potaniniana), zonitid (*Aegopis acies*)		
D. eurynorhynchi (syn. *D. kronschnepi*)	Charadriiformes: scolopacid (spoon-billed sandpiper)			Russia
D. hospes	Artiodactyla: bovid (cattle, buffalo, sheep, goat); Lagomorpha: leporid (rabbit); Sauria: varanid (savannah monitor); occasionally Primates: hominid (human)	Stylommatophora (terrestrial snails): achatinid (*Limicolaria flammea, L. felina*)	Hymenoptera (ants): formicid (*Camponotus, Crematogaster, Dorylus* spp.)	Africa
D. infidum (syn. *Eurytrema*)	Serpentes: boid (green anaconda, Brazilian smooth snake)			South America
D. ivoriense	Rodentia: murid (Tullberg's soft-furred mouse)			Africa
D. lasiuri	Chiroptera: vespertilionid (eastern red bat)			Central America
D. lobatum (syn. *Brachylecithum*)	Accipitriformes: accipitrid (Eurasian sparrowhawk)			Europe
D. macaci	Primates: cercopithecid (Japanese macaque)			Japan
D. macrostomum	Galliformes: numidid (helmeted guineafowl)			Africa
D. moschiferi	Artiodactyla: moschid (musk deer)			Asia
D. panduriforme (syn. *Lyperosomum*)	Passeriformes: corvid (Eurasian magpie)			Europe
D. petrowi	Galliformes: phasianid (chukar partridge)			Russia
D. proxillicens (syn. *Platynosomum*)	Psittaciformes: cacatuid (sulphur-crested cockatoo)			North America
D. rileyi	Chiroptera: vespertilionid (big brown bat)			North America
D. sciuri	Rodentia: sciurid (squirrel)			Russia
D. soricis	Eulipotyphla: soricid (common shrew)			Europe

Parasite morphology: *Dicrocoelium* spp. form 6 different developmental stages: eggs, miracidia, sporocysts, cercariae, metacercariae and adults. The eggs are relatively small (35-45 x 22-30 µm), asymmetrically oval (slightly flattened on one side), surrounded by a thick dark brown shell with a large indistinct operculum and are embryonated when laid. They contain a pyriform miracidium (25 x 20 µm) which is covered with flattened ciliated epidermal plates with ridged cytoplasmic junctions, an apical papilla with stylet, sensory organs and secretory glands and well-developed circular and longitudinal muscles. Sporocysts have pleomorphic saccular non-ciliated bodies (140-420 µm) with syncytial tegument (derived from the miracidial cytoplasmic ridges) and a thin parenchymal lining forming a brood chamber containing balls of germinal cells. The germ balls in mother sporocysts undergo asexual multiplication to form daughter sporocysts which are released into surrounding tissues. Germ balls within daughter sporocysts multiply asexually producing cercariae directly (rediae stages are not produced). Cercariae are known as xiphidiocercariae as they possess an anterior oral perforator stylet on their elongate ellipsoidal bodies (360-760 x 50-165 µm) and have long simple tails (200-1,000 µm) with a dorsal finfold. They possess an oral sucker, mouth, foregut, bifurcate caeca and numerous glands (notably mucoid glands). Cercariae released from daughter sporocysts come together in groups of 100-600 forming spherules, which then join together to form slimeballs up to 1cm in diameter containing up to 8,000 cercariae. Metacercariae are ellipsoidal encysted stages (480-600 x 260-320 µm) surrounded by cyst walls varying in thickness from 5-96 µm. They contain juvenile flukes that have tissues and organs similar to adults except for primordial developing genitalia. Adult flukes are thin and translucent with dorsoventrally flattened lanceolate bodies (5-15 x 0.9-3.0 mm) strongly tapered at each end. They are covered by an aspinose tegument and have 2 suckers located close to each other - the oral sucker being subterminal and slightly larger than the ventral sucker. They possess a mouth, small pharynx, long oesophagus, 2 blind-ended caeca that do not reach the posterior end (no anus) and an I- or Y-shaped posterior excretory vesicle. Mature adult worms are hermaphroditic and possess both female and male reproductive organs. They contain 2 lobed testes located diagonally next to each other in the anterior third of the body, an elongate cirrus sac and median genital pore. The single globular ovary is located post-testicular and connected to an extensive uterus filling the posterior body and numerous white vitellaria located in 2 lateral midbody bands. *Dicrocoelium* spp. are commonly differentiated on the basis of differences in testes morphology, uterus orientation and adult fluke size.

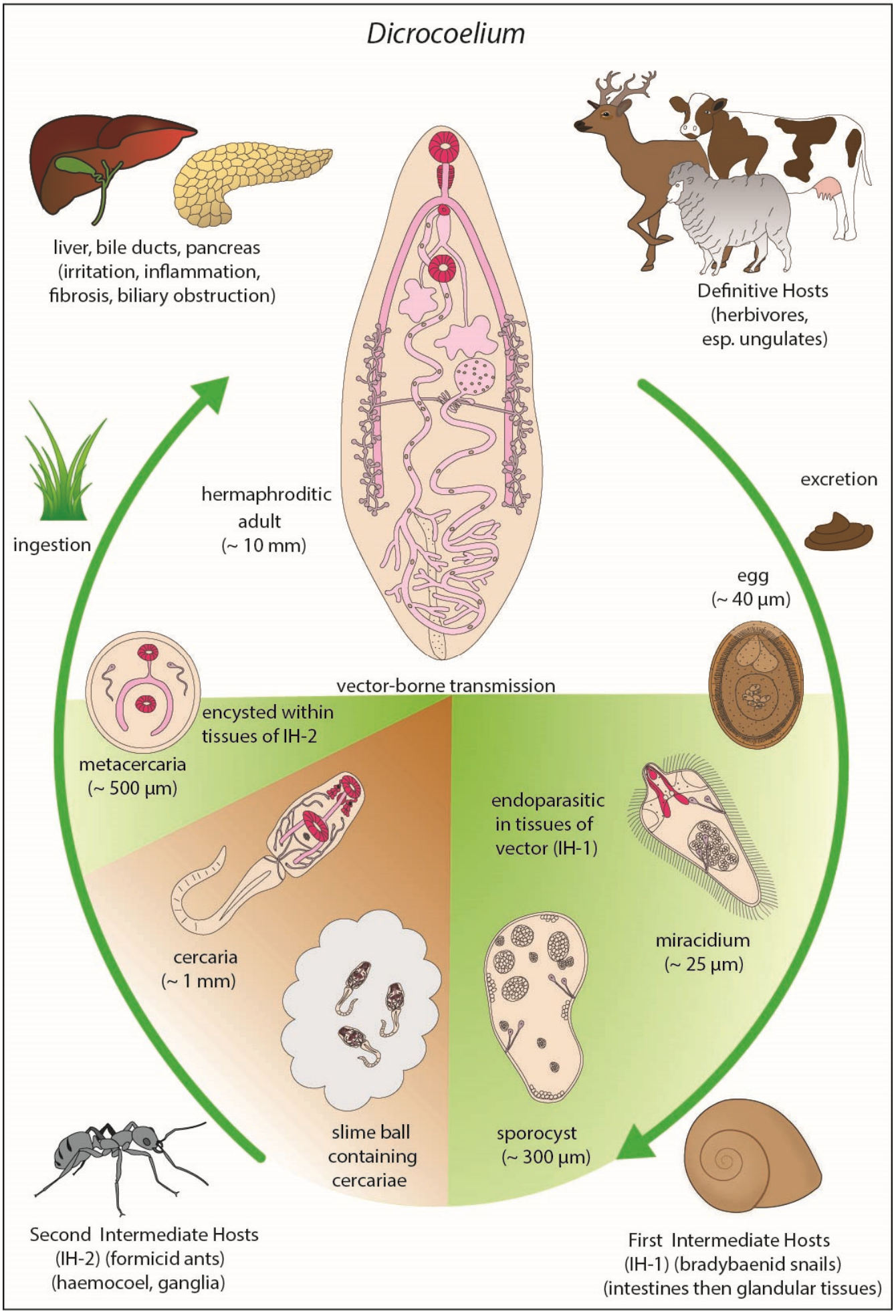
Site of infection: Adult flukes infect the bile ducts of their definitive hosts (mammals, birds), sometimes being found in the gall bladder and pancreas in heavy infections. Asexual stages are found predominantly in the digestive glands of their first intermediate hosts (terrestrial snails), while metacercariae are found encysted in the haemocoel, and some in the suboesophageal ganglia, of their second intermediate hosts (ants).

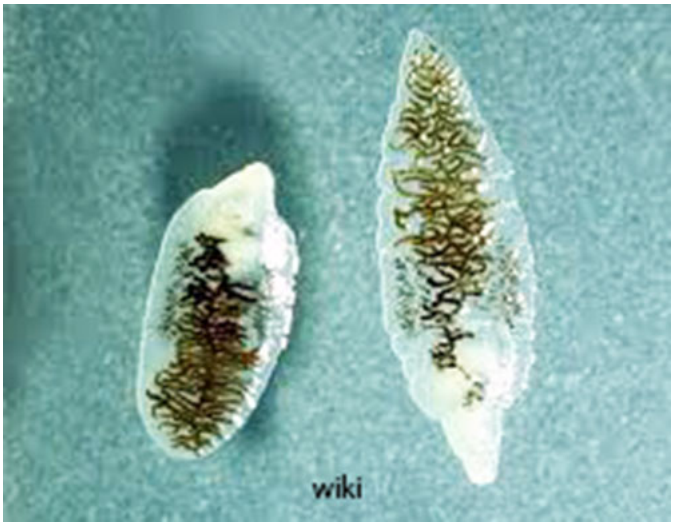
Pathogenesis: Immature flukes migrate up hepatic bile ducts but do not penetrate host tissues. Mature flukes have buccal stylets which irritate the bile duct walls inducing epithelial proliferation and periductal fibrosis resulting in firm, thickened and distended bile ducts (cholangiectasia) with biliary obstruction and dysfunction. The severity of disease depends largely on the intensity of infection, with most light infections being asymptomatic but heavier infections being associated with acute and chronic signs. Most clinical infections in ruminants are chronic in presentation with progressive fibrosis (cirrhosis) initially at hepatic portal triads and then along connecting bile ducts with the accumulation of bright viscid exudates. Symptoms/signs include anaemia, jaundice, eosinophilia, oedema, loss of condition, weight loss, emaciation and reduced meat, milk and/or wool production, while changes in clinical parameters included elevated levels of albumin, total bilirubin, bile acids and others consistent with oxidative liver damage such as increased aspartate aminotransferase (AST), alanine aminotransferase (ALT), glutamate dehydrogenase (GDH) and sometimes gamma-glutamyl transpeptidase (GGT). Acute and severe infections may prove fatal in domestic ruminants and protracted infections have been associated with significant inflammation of the liver (cholangiohepatitis), and sometimes the gall bladder (cholecystitis). Up to 50,000 flukes have been detected in ruminants with severe clinical disease. Several cases of verminous hepatitis have been reported in humans infected with lancet flukes, with abdominal pain, weight loss, recurrent watery diarrhoea, constipation, eosinophilia and anaemia.

Developmental cycle and mode of transmission: *Dicrocoelium* spp. have indirect heteroxenous life-cycles involving 3 different types of hosts: adult flukes undergo sexual reproduction in mammals and birds (definitive hosts); asexual stages reproduce in land snails (first intermediate hosts); and metacercariae form in ants (second intermediate hosts). Gravid flukes produce embryonated eggs which are released into the gut lumen and excreted with host faeces onto pastures where they remain viable for extended periods. The eggs are ingested by snails, but in this case by terrestrial snails rather than aquatic snails like most other Digenea. A wide range of pulmonate land snails (Stylommatophora) may act as first intermediate hosts in which parasites reproduce asexually; with reports including members of the superfamilies Helicoidea (bradybaenids, geomitrids, helicids, hygromiids, pleurodontids), Cochliocopoidea (cochliocopids), Zonitoidea (zonitids), Enoidea (enids (buliminids)), Clausilioidea (clausiliids), and Achatinoidea (achatinids). Ingested eggs hatch releasing their enclosed ciliated miracidia in the snail gut which then penetrate the gut wall shedding their cilia and forming sporocysts in snail tissues, predominantly the digestive gland (hepatopancreas). Two generations of sporocysts are formed over a period of 3-5 months, with germ balls in mother sporocysts giving rise daughter sporocysts whose germ balls then produce cercariae (redial stages are not formed). Cercariae migrate to the pulmonary chamber of the snail where they secrete a thin cyst wall and become coated with snail mucus forming small spherules that join together to make up slime balls. These mucilaginous balls are coughed up and expelled through the respiratory orifice (pneumostome) onto plants or other substrates when snails move. The slime balls are then eaten by field ants which act as second intermediate hosts. In the ant, the cercariae penetrate the gut, shedding their tails, and form encysted metacercariae in the body cavity (haemocoel) over 1-2 months. Within each ant, 1-2 cercariae also migrate to the suboesophageal ganglia where they encyst becoming 'brain-worms' which alter the ant's behaviour and cause tetany. When the environmental temperature drops each evening (< 15-20°C), infected ants move up vegetation and clamp onto grass tips when their mandibles undergo tetanic seizures (muscle spasms or cramps). The torpid ants are more susceptible to ingestion by grazing animals during peak foraging times at dusk and dawn (as temperatures warm again in the morning, the ants return to normal). When infected ants are ingested by suitable definitive hosts, the metacercariae excyst in the duodenum releasing juvenile worms which migrate up into the bile ducts within hours of infection and then mature to adult flukes over several weeks. The prepatent period (time from infection to first egg release) ranges from 48-96 days and the whole parasite life-cycle may be completed within 6 months. Transient infections may occur in humans following the accidental ingestion of infected ants on fruit, vegetables, salads, herbs or in drinking water.

Differential diagnosis: Infections in animals are conventionally diagnosed by the microscopic detection of characteristic fluke eggs in faecal samples, usually following concentration by sedimentation and/or floatation. Alternatively, infections may be diagnosed at necropsy by the detection of adult flukes in dissected bile ducts. Coprological examination may be used to diagnose infections in humans, but care should be taken to rule out pseudo-parasitism in people who have eaten uncooked infected liver (they do not become infected but simply pass intact eggs in their faeces). Blood biochemical profiles may reveal increased levels of albumin, total bilirubin, bile acids, alkaline phosphate, aspartate aminotransferase (AST), alanine aminotransferase (ALT), glutamate dehydrogenase (GDH), sometimes gamma-glutamyl transpeptidae (GGT) and immunoglobulin E, although such changes are relatively nonspecific. Immunoserological tests (complement fixation, haemagglutination, immunofluorescence, enzyme immunoassays) have been used to detect host antibodies against somatic and excretory-secretory antigens, but they have demonstrated poor specificity. Molecular characterization techniques have revealed genetic variation between a limited range of species from humans and domestic animals following polymerase chain reaction (PCR) amplification of nuclear genes (18S, 5.8S and 28S ribosomal RNA, internal transcribed spacer region 2).

Treatment and control: Infections by adult flukes have been successfully treated with several anthelmintic drugs, notably praziquantel (isoquinoline), triclabendozole (halogenated benzimidazole-thiol) and mirazid (oleoresin extract of myrrh), but they were less effective against juvenile or immature stages. Other broad-spectrum anthelmintic drugs, including benzimidazole-methylcarbamates (albendazole, fenbendazole, luxabendazole, mebendazole), benzimidazole-thiazolyls (cambendazole, thiabendazole) and probenzimidazole (thiophanate), have been used to treat infections, but at higher doses than recommended for other helminth infections. Treatment with the deacetylated (amine) metabolite of diamphenethide also appeared effective, but high doses were found to have serious side-effects. It is also recommended that repeat treatments be used to prevent re-infection as ants hibernate and may carry infections over seasons. The prevention of infections in free-range and natural ecosystems is particularly difficult due to the faecal contamination of pastures by livestock and the wide distribution and abundance of both land snails and formicid ants. Management of intermediate host populations using molluscicides and insecticides is contraindicated in most ecosystems due to concerns over toxicity and unintended ecological consequences. Several attempts have been made to reduce intermediate host populations in domestic and peridomestic situations by introducing poultry to eat snails and ants. Other farm management practices have included rotating livestock between pastures, restricting their grazing in evenings and mornings using barriers, and optimizing regular anthelmintic drenching regimes (for therapy and prophylaxis).

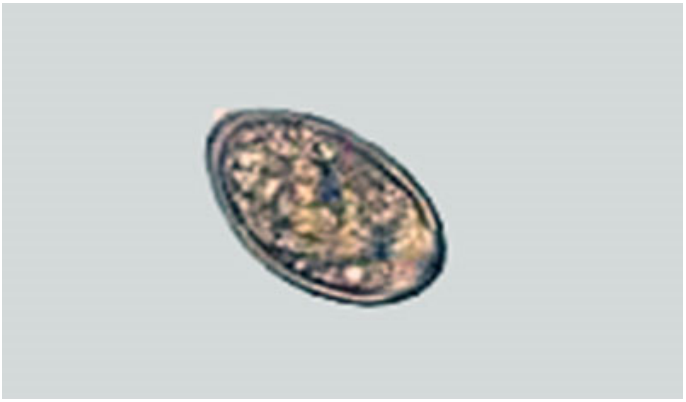

Dicrocoelium
liver, bile ducts, pancreas
(irritation, inflammation,
fibrosis, biliary obstruction)
Definitive Hosts
(herbivores,
esp. ungulates)
ingestion
hermaphroditic
adult
(~ 10 mm)
excretion
egg
(~ 40 µm)
vector-borne transmission
encysted within
tissues of IH-2
metacercaria
(~ 500 µm)
endoparasitic
in tissues of
vector (IH-1)
cercaria
(~ 1 mm)
miracidium
(~ 25 µm)
slime ball
containing
cercariae
sporocyst
(~ 300 µm)
Second Intermediate Hosts
(IH-2) (formicid ants)
(haemocoel, ganglia)
First Intermediate Hosts
(IH-1) (bradybaenid snails)
(intestines then glandular tissues)



Dicrocoelium adult worms



Dicrocoelium adult worm



Dicrocoelium egg



Dicrocoelium cercaria

Other pancreatic flukes

***Eurytrema* species**	**Definitive hosts [adults in pancreatic ducts, sometimes bile ducts]**	**First intermediate hosts [sporocysts in tissues]**	**Second intermediate hosts [metacercariae in tissues]**	**Distribution**
E. brumpti	Primates: hominid (chimpanzee, gorilla)			Africa
E. cladorchis	Artiodactyla: cervid (deer), bovid (cattle, goat)			China, India
E. coelomaticum	Artiodactyla: bovid (sheep, cattle, goat, buffalo), camelid (camel); Lagomorpha: leporid (hare)	terrestrial Gastropoda: bradybaenid (*Bradybaena similaris*)	Orthoptera: tettogoniid (*Conocephalus maculatus*)	Brazil, Asia
E. escuderoi	Artiodactyla: bovid (cattle, carabao)			Philippines
E. fukienensis	Artiodactyla			Asia
E. hydropotes	Artiodactyla: cervid (water deer)			Asia
E. pancreaticum (syn. *E. media, E. dajii, E. ovis, E. parvum*)	Artiodactyla: bovid (cattle, water buffalo, sheep, goat), camelid (camel), cervid (deer), suid (pig); Lagomorpha: leporid (hare); Primates: tarsiid (Philippine tarsier), hominid (human)	terrestrial Gastropoda: bradybaenid (*Bradybaena similaris, B.* (*Cathaica*) *ravida*), eulotid (*Eulota lantzi*)	Orthoptera: tettogoniid (*Conocephalus maculatus*), gryllid (*Oecanthus*)	Southeast Asia, India, South America
E. procyonis	Carnivora: procyonid (raccoon), felid (cat), canid (fox)	terrestrial Gastropoda: polygyrid (*Mesodon thyroidus*)	arthropod?	North America
E. satoi	Primates: cercopithecid (macaques), hominid (gorilla)			Africa
E. sphaeriorchis	Artiodactyla			Asia
E. tonkinense	Artiodactyla: bovid (cattle)			Vietnam

Paragonimus
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult plagiorchidans are varied in appearance, most bearing spines and a median ventral sucker and many producing small eggs which hatch after ingestion by snails (first intermediate hosts). Paragonimids are atypical for the group as their eggs release miracidia to find snails, they form metacercariae in freshwater crustaceans and insects (second intermediate hosts), and crustacean-eating animals may act as paratenic (transport) hosts for metacercariae. *Paragonimus* spp. (lung flukes) are thick oval spiny flukes in the respiratory systems of birds and mammals, and infections have been associated with respiratory and neurological diseases in cats, dogs and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Plagiorchiida ('echinostomatids', plagiorchiids', mainly fish hosts, some tetrapods, infection by ingestion of cercariae or metacercariae)
Suborder:	Xiphidiata (xiphidiocercariae with penetrating stylet in anterior margin of oral sucker)
Superfamily:	Gorgoderoidea (miracidia penetrate gastropod, bivalve IH, sporocysts and rediae formed, simple-tailed cercariae with stylet, encysts in open or in second IH, metacercariae eaten by DH)
Family:	Paragonimidae (thick oval flukes, scale-like spines, miracidia, snail IH-1, crustacean/insect IH-2)
Genus:	*Paragonimus* (parasitic in lungs of carnivores)
Species:	various species cause respiratory and neurological signs in carnivores

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs,

fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

Thirteen plagiorchidan suborders have been recognized containing 19 superfamilies. Members of the suborder Xiphidiata are characterized by forming xiphidio-cercariae with a penetrating stylet in the anterior margin of the oral sucker which is used to penetrate second intermediate hosts where metacercariae are formed. Over 1,680 species have been described in 44 families in 4

superfamilies: Allocreadioidea (1,118 spp. in 6 families), Gorgoderoidea (106 spp. in 10 families), Microphalloidea (414 spp. in 12 families) and Plagiorchioidea (47 spp. in 16 families). The superfamily Gorgoderoidea parasitizes fish and tetrapods and the 10 cognate families comprise Atractotrematidae, Cadenatellinae, Haploporidae, Callodistomidae, Dicrocoeliidae, Gorgoderidae, Encyclometridae, Orchipedidae, Paragonimidae and Troglotrematidae. The family Paragonimidae contains 3 genera (*Paragonimus, Euparagonimus, Pagumogonimus*) of thick oval flukes that infect the lungs of carnivores that feed on crustaceans infected with metacercariae. The genus *Paragonimus* contains around 20 species that infect mammals mostly in Asia but also in Africa and the Americas. In particular, *P. westermani* is most prevalent in humans in South-East Asia (including China), *P. kellicotti* in North America, and *P. africanus* in West Africa. Contemporary molecular phylogenetic studies have helped resolve many species-synonymies and have identified major clades comprising species-complexes (species-groups) represented by *P. westermani, P. skrjabini, P. bangkokensis, P. heterotremus, P. mexicanus* and *P. ohirai*. Infection rates in Asia are higher than elsewhere due to the higher consumption of raw shellfish. Several species are considered zoonotic, as many other mammalian species may support completion of the parasite life-cycle through freshwater snails and crustaceans as first and second intermediate hosts. Infections are common in riverine areas with slow-flowing or still waters throughout tropical, subtropical and temperate regions. It is currently estimated that there are some 20 million *Paragonimus* infections per year worldwide and that over 300 million people are at risk of infection.

***Paragonimus* species**	**Definitive hosts (adults in lungs)**	**First intermediate hosts (sporocyst/rediae in tissues)**	**Second intermediate hosts (metacercariae in tissues)**	**Distribution**
***P. westermani* complex**				
P. westermani (syn. *P. edwardsi, P. ringeri, P. philippinensis,* and triploid type, *P. pulmonalis*) (Asian or Oriental lung fluke)	Primates: hominid (human), cercopithecid (crab-eating macaque); Carnivora: canid (dog, fox, wolf, raccoon-dog), felid (cat, leopard, panther, tiger), viverrid (civet cat, palm civet), herpestid (mongoose); Artiodactyla: suid (pig), bovid (cattle); Rodentia: murid (rats)	amphibious and freshwater Gastropoda: pachychilid (*Brotia asperata, Sulcospira quangtriensis*), semisulcospirid (*Semisulcospira libertina, S. bensoni, S. japonica, S. amurensis*), thiarid (*Thiara toucheana, T. granifera*)	freshwater Decapoda: potamid (*Sinopotamon, Potamiscus manipurensis, Geothelphusa, Potamon* (*Ranguna*), *Alcomon superciliosum*), gecarcinucid (*Parathelphusa, Sundathelphusa*), varunid (*Eriocheir japonicus, E. sinensis*), cambarid (*Cambaroides similis*), plus crustacean-eating paratenic hosts (rodents)	Eurasia, India, Pacific Islands
P. siamensis	Carnivora: felid (cat); Rodentia: murid (rats, bandicoot rats)		freshwater Decapoda: gecarcinucid crabs (*Parathelphusa germaini*)	Thailand
***P. skrjabini* complex**				
P. skrjabini (incl. subspecies: *P. s. skrjabini, P. s. miyazakii*) (syn. *P. miyazakii, P. szechuanesis, P. hueitungensis, P. veocularis, P. macrorchis, P. proliferus* (*P. hokuoensis*), *P. heterorchis, P. fukienensis*)	Primates: hominid (human); Carnivora: felid (cat), viverrid (palm civet), canid (dog, raccoon-dog), mustelid (marten, weasel, badger); Rodentia: murid (rats, bandicoot rat); Artiodactyla: suid (boar)	freshwater Gastropoda: pomatiopsid (*Neotricula* (*Tricula*) *cristella*), amnicolid (*Akiyoshia chinensis, Erhaia*, *Bythinella nipponica*), pachychilid (*Sulcospira quangtriensis*)	freshwater Decapoda: potamid (*Potamiscus manipurensis*, *P. mieni*, *Sinopotamon, Geothelphusa*); Anura: ranid (frogs)	China, Japan, Southeast Asia, India
***P. ohirai* complex**				
P. ohirai (syn. *P. sadoensis, P. iloktsuenensis*)	Primates: hominid (human); Carnivora: felid (cat), canid (dog, raccoon-dog); Rodentia: murid (rats); Artiodactyla: suid (pig)	aquatic Gastropoda: assimineid (*Angustassiminea lutea, A. parasitologica*), pomatiopsid (*Oncomelania nosophora, O. hupensis, Tricula minima, T. chiui*)	estuarine Decapoda: sesarmid (*Sesarma* (*Holometopus*) *dehaani*)	South-East Asia
P. bangkokensis (syn. *P. paishuihoensis, P. menglaensis, P.*	Carnivora: canid (dog), felid (cat), mustelid (ferret), herpestid (Indian mongoose, Javan	freshwater Gastropoda: pomatiopsid (*Tricula gregoriana*?)	freshwater Decapoda: potamid (*Potamon smithianus, P. lipkei, Potamiscus mieni, Po.*	Asia

xiangshanensis)	mongoose); Rodentia: murid (rats, bandicoot rat)		*tannanti, Larnaudia beusekomae, Apotamonautes hainanensis, Ranguna smalleyi*)	
P. harinasutai (syn. *P. microrchis*)	Carnivora: felid (cat), canid (dog)		freshwater Decapoda: potamid (*Potamon smithianus, P. lipkei, Larnaudia beusekomae, L. larnaudii, Sinopotamon chekiangenes, Indochinamon ou*), gecarcinucid (*Siamthelphusa paviei, Chulathelphusa brandti*)	Asia
***P. heterotremus* complex**				
P. heterotremus (syn. *P. tuanshanensis*)	Primates: hominid (human); Carnivora: felid (cat, leopard), canid (dog); Rodentia: murid (rats, bandicoot rat)	freshwater Gastropoda: pomatiopsid (*Tricula gregoriana*), assimineid (*Assiminea*)	freshwater Decapoda: potamid (*Sinopotamon*, *Ranguna, Potamiscus manipurensis*, *P. mieni*, *Potamon lipkei*, *Po. smithianus*), gecarcinucid (*Barythelphusa* (*Maydelliathelphusa*) *lugubris, Alcomon superciliosum*), pachychilid (*Sulcospira quangtriensis*)	China, South-East Asia, India
P. pseudoheterotremus	Carnivora: felid (cat)		freshwater Decapoda: potamid (*Larnaudia larnaudii*)	Asia
Unplaced species				
P. africanus	Primates: hominid (human), cercopithecid (drill), lorisid (potto); Carnivora: viverrid (civet cat), canid (dog), herpestid (mongoose)	freshwater Gastropoda: pachychilid (*Potadoma freethii*)	freshwater Decapoda: potamonautid (*Sudanonautes*)	West Africa
P. amazonicus	Didelphimorphia: didelphid (four-eyed opossum, water opossum); Carnivora: felid (margay?)		Decapoda: pseudothelphusid (*Pseudothelphusa chilensis*?)	South America
P. caliensis	Didelphimorphia: didelphid (common opossum, gray four-eyed opossum)		Decapoda: pseudothelphusid (*Strengeria*)	South America
P. compactus	Carnivora: herpestid (Indian mongoose)			India
P. kellicotti (lung fluke) (syn. *P. rudis*)	Carnivora: canid (dog, red fox, coyote), felid (cat, bobcat), procyonid (raccoon), mephitid (skunk, hooded skunk), mustelid (giant otter, mink); Rodentia: cricetid (muskrat); Didelphimorphia: didelphid (North American opossum); Artiodactyla: bovid (goat), suid (pig); Primates: hominid (human)	amphibious Gastropoda: pomatiopsid (*Pomatiopsis lapidaria, P. cincinnatiensis*, *Oncomelania hupensis*)	freshwater Decapoda: cambarid (*Orconectes*, *Cambarus*), plus crayfish-eating paratenic hosts (rodents)	Americas, South Africa
P. mexicanus (syn. *P. peruvianus, P.*	Primates: hominid (human); Carnivora:	brackish-water Gastropoda: hydrobiid	freshwater Decapoda: pseudothelphusid	Central and South

inca, P. ecuadoriensis)	canid (dog, fox), felid (cat, jaguar, ocelot), procyonid (raccoon, coati); Artiodactyla: tayassuid (peccary); Didelphimorphia: didelphid (opossum)	(*Aroapyrgus costaricensis, A. alleei, A. colombiensis*)	(*Pseudothelphusa, Ptychophallus, Potamocarcinus, Strengeria, Hypolobocera guayaquilensis, H. aequatorialis, H. chilensis*), trichodactylid (*Zilchiopsis, Trichodactylus faxoni, Moreirocarcinus emarginatus*)	America
P. tuanshenensis	Carnivora: canid (dog), felid (cat, leopard); Primates: hominid (human)	freshwater Gastropoda: pomatiopsid (*Tricula gregoriana*)	freshwater Decapoda: potamid (*Potamon*)	China
P. uterobilateralis	Primates: hominid (human); Carnivora: canid (dog), felid (civet cat), herpestid (mongoose); Eulipotyphla: soricid (shrew); Rodentia: murid (rats)	terrestrial and freshwater Gastropoda: achatinid (*Homorus* (*Striosubulina*) *striatella*), ampullariid (*Afropomus balanoides*), pachychilid (*Potadoma sanctipauli*)	freshwater Decapoda: potamonautid (*Liberonautes*, *Sudanonautes*)	West Africa
P. vietnamensis	Carnivora: canid (dog), felid (cat)		freshwater Decapoda: potamid (*Potamiscus tannanti, P. mieni*)	Vietnam
P. yunnanensis	Carnivora: canid (dog)			China

Parasite morphology: *Paragonimus* spp. form 7 different developmental stages in their life-cycles: namely, eggs, miracidia, sporocysts, rediae, cercariae, metacercariae and adults. Eggs are unembryonated, ovoid (70-125 x 40-80 µm), yellowish brown, thick-shelled and operculate with a raised shoulder surrounding the operculum. Miracidia are ovoid (approximately 80 x 30 µm), covered with cilia, and have apical papillae with ducts to penetration glands. Sporocysts are pleomorphic sacs (300-500 µm long) without organs but containing germinal cells which give rise to small rediae. Mature rediae have yellow elliptical bodies (460–850 x 170–360 µm) with a mouth, well-developed pharynx and saccular gut. Cercariae are chaetomicrocercous in type with an ovoid body (160-250 x 65-100 µm) and a very small knob-like tail. The body is covered with tegumental spines and possesses an anterior mouth, a muscular oral sucker, ventral sucker and penetration glands. Metacercariae are white-pink, round-oval (ranging from 200-900 µm in diameter), surrounded by a bilayered cyst wall and contain oral and ventral suckers, saccular intestines and prominent granules. Metacercariae of most *Paragonimus* spp. can be allocated to 3 size groups: < 300 µm in diameter (e.g. *P. heterotremus*); 300-500 µm (e.g. *P. westermani, P. skrjabini*); and > 700 µm (e.g. *P. harinasutai, P. vietnamensis*), and it has been suggested that different species can be differentiated by their internal morphological features, e.g. *P. westermani* with colourless intestines and red dorsal granules, *P. mexicanus* with yellow intestines and red ventral granules. Adult lung flukes are usually found paired in capsules up to 2 cm in diameter in the lungs. Individual worms are thick-bodied, reddish-brown (but often grayish-white in ectopic sites) and are roughly the size of coffee beans (4-16 x 2-8 x 3-6 mm). They are elliptical to concave ovoid in shape and their tegument is covered with tiny thorn-like cuticular spines scattered around the body. The spines may be split distally or develop longitudinal grooves; those on the anterior dorsal surface sometimes forming comb-like groups. The body possesses an oral and a ventral sucker (usually similar in size), a truncated pharynx and oesophagus that bifurcates early into paired caeca, and a posterior excretory bladder. Adult worms are hermaphroditic, possessing both male and female reproductive organs. They contain 2 testes situated side-by-side (the name *Para-gonimus* literally translates to 'side-by-side gonads'). The testes are located posteriorly, irregularly lobed (4-5 lobes) and connected to seminal receptacles (no cirrus pouch). The ovary and uterus are located midbody either side of the midline and the vitelline follicles are located in 2 extensive lateral fields. The single ovary is typically six-lobed and the uterus is tightly coiled into a rosette shape and connects to a genital atrium which opens into a genital pore located posterior to the ventral sucker. The uterus is often dark coloured when packed with heavily tanned unembryonated eggs.

Site of infection: Juvenile worms released in the intestines of their definitive hosts penetrate the gut wall and peritoneum and migrate through the diaphragm and pleura to reach bronchioles in the lungs where they mature as paired adults in capsules. Some flukes may migrate to ectopic sites, including subcutaneous, nervous, muscular, glandular, hepatic, mesenteric and reproductive tissues and organs. Asexual developmental stages (sporocysts and redia) usually form within the digestive gland of their first intermediate hosts (snails), and metacercaria encyst within the viscera and muscles of their second intermediate hosts (crustaceans).

Pathogenesis: Infection by *Paragonimus* spp. may cause a zoonotic disease known as paragonimiasis (sometimes called pulmonary distomatosis or benign endemic haemoptysis) which usually manifests as a subacute to chronic inflammatory granulomatous lung

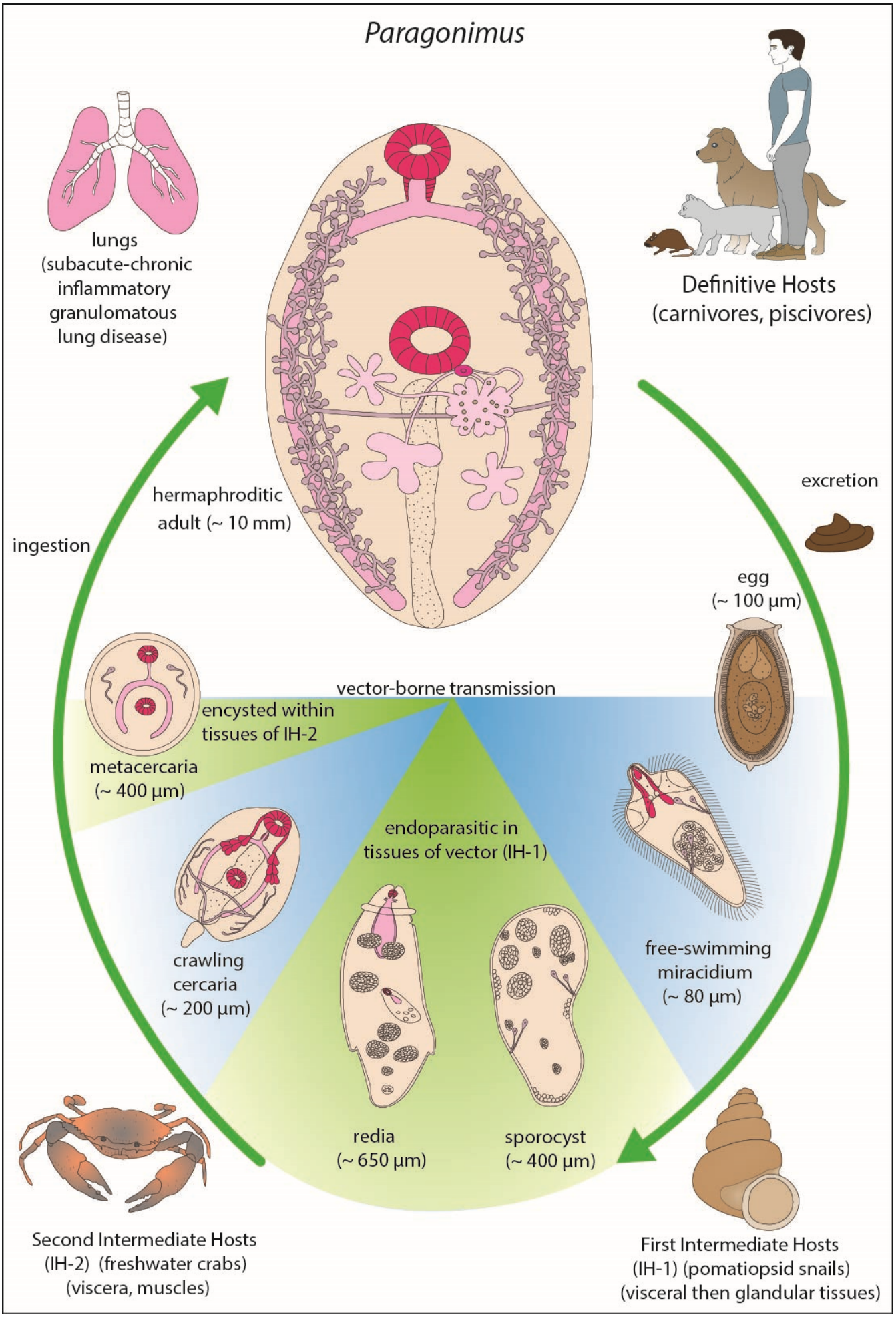
disease. Infections become established when flukes migrate from the gut through tissues to internal organs (typically the lungs) where they mature and produce eggs. Adult flukes feed on host tissues and proteins causing traumatic damage and eliciting host inflammatory, fibrotic and immune responses. Pathological changes vary in severity and type depending on the parasite species/strain, the intensity of infection, the susceptibility of the mammalian host, the route of migration and the site of infection, adult maturation and egg production. Many infections remain asymptomatic or subclinical, while others may produce mild to moderate symptoms for years before medical attention is sought. Clinical infections have been associated with three disease phases: acute (manifestations soon after infection), chronic (pleuropulmonary manifestations) and ectopic (manifestations arising from infections elsewhere than the lungs). The acute phase occurs 2-15 days after infection in response to immature worms migrating through tissues in the abdominal and thoracic cavities to invade the lungs. The mechanical damage and host inflammatory responses result in abdominal pain, diarrhoea, hepatosplenomegaly, fever, leucocytic infiltration, coughing, eosinophilia and urticaria, particularly in patients with heavy worm burdens. Worm migration in the lungs may cause transient haemorrhage, pleuritic chest pain, pleural effusions, bronchiectasis, interstitial pneumonitis and bronchopneumonia. The chronic phase occurs weeks after infection when worms arrive in the lungs, pair up, form capsules and produce eggs. Infections may cause parenchyma-based disease, pleura-based disease, or more usually both (pleuro-pulmonary disease). Capsules usually form in the lung parenchyma near airspaces so eggs may escape in respiratory secretions, but capsules (and eggs) in the pleura lead to pronounced inflammation with cellular infiltrates (neutrophils and eosinophils). Pulmonary manifestations include chronic cough, hoarseness, the expulsion of viscoid bloody or rusty sputum (containing eggs and Charcot-Leyden crystals), haemoptysis, mild anaemia, chronic bronchitis, crepitation/wheezing, pleurisy with dyspnoea, breathlessness, fever, fatigue, anorexia and headache. Immunopathological responses result in pleural thickening, interlobar pleuritis, pleural effusion, and sometimes pneumothorax or haemothorax. Symptoms and chest radiographic abnormalities are similar to those associated with pneumonia and tuberculosis. Inflammatory reactions work to encapsulate worms and eggs producing granulomas which sometimes ulcerate and heal slowly, giving the lungs a peppered appearance. Occasionally complications occur in the form of gross haemorrhages or bacterial superinfections, leading to pneumonia or pulmonary abscesses. Ectopic infections develop when worms migrate not into the lungs but into other tissues and internal organs, such as subcutis, heart, skeletal muscles, liver, brain, spinal cord, mesenteries, adrenal glands, ovary and epididymis. The worms, and sometimes their eggs, provoke serious inflammatory and immunopathological responses with cellular infiltrates, fibrosis, granuloma formation and calcifications. Migrating worms in the brain may cause meningitis or meningoencephalitis, while encapsulated and calcifying worms may cause expansive space-occupying lesions. Symptoms include fever, headache, seizures, convulsions, nausea, vomiting, visual disturbances, motor weakness, decline in cognitive function, personality changes, localized or generalized paralysis, coma and occasionally death. Cerebral paragonimiasis may be confused with other central nervous system diseases such as epilepsy, brain tumours, cysticercosis or echinococcosis. Cutaneous paragonimiasis may present with slow-moving lesions under the skin (especially on the abdomen or chest) but other parasites may cause similar signs (e.g. *Gnathostoma*). Infections have been detected in children and adults, males and females, and immunocompetent and immunocompromised individuals.

Developmental cycle and mode of transmission: *Paragonimus* spp. have indirect heteroxenous life-cycles involving cyclic transmission between definitive hosts (mammals infected with adult flukes), first intermediate hosts (snails infected with asexual stages) and second intermediate hosts (crustaceans infected with metacercariae). Adult flukes release unembryonated eggs into respiratory airspaces from where they are expectorated with sputum or swallowed and excreted with host faeces. Eggs reaching freshwater embryonate over at least 2 weeks and then hatch releasing ciliated miracidia which swim about actively seeking snail hosts by chemotaxis. Free-swimming miracidia do not live long and must find a snail host within 24 hours or die. A range of aquatic, terrestrial and amphibious snails act as suitable first intermediate hosts, including members of the superfamilies Cerithioidea (pachychilids, semisulcospirids, thiarids), Truncatelloidea (pomatiopsids, amnicolids, assimineids, hydrobiids), Ampullarioidea (ampullariids), and Achatinoidea (achatinids) which inhabit habitats as diverse as fast-flowing streams and still ponds. The miracidia penetrate the soft tissues of the snail shedding their cilia and develop into saccular sporocysts in the body cavity where they undergo 2 generations of asexual reproduction. Mother sporocysts give rise to first generation rediae which produce second generation rediae that produce and release cercariae. The prepatent period in snails (time from infection to first release of cercariae) is around 11 weeks. The knob-like tails of the cercariae are ineffective for swimming, so the cercariae crawl over substrates until they encounter crustaceans which they infect by penetrating the exoskeleton using their sharp cuticular stylets. It is thought that some crustaceans may also become infected when they eat infected snails. Once inside, the cercariae encyst in various tissues (muscles, gills, heart, liver and other viscera) forming metacercariae which mature to contain elongate (extended) juvenile worms (rather than ventrally folded juveniles like other flukes). A range of freshwater and estuarine decapod crustaceans act as suitable second intermediate hosts; including members of the crab superfamilies Potamoidea (potamids, potamonautids), Gecarcinucoidea (gecarcinucids), Grapsoidea (varunids, sesarmids), Pseudothelphusoidea (pseudothelphusids), Trichodactyloidea (trichodactylids), and the crayfish superfamily Astacoidea (cambarids). Metacercariae of some *Paragonimus* spp. have also been found in tadpoles of ranid frogs, and a few species apparently utilize paratenic (transport) hosts, such as crustacean-eating rodents and wild boar. Definitive hosts (carnivores, rodents, primates, pigs) become infected by eating raw, undercooked or inadequately cured, dried, salted or pickled freshwater crabs and crayfish containing infective metacercariae. Many countries have local culinary customs supporting the consumption of improperly prepared crustaceans; such as Chinese/Korean kejeng (live crustaceans with soybean sauce), Japanese oboro-kiro (crab juice added to miso (bean paste) soup), Mexican cerviche (uncooked crustaceans), Philippine kilano (raw crab in citrus juice, coconut milk and alcohol), and Asian drunken crab (uncooked crabs pickled in rice wine). On occasion, food handlers have been infected with metacercariae contaminating cooking utensils after being dislodged from crustacean tissues. There are also recorded instances of humans becoming infected as part of traditional folk medicine practices,

such as drinking juices from crushed crabs to treat measles in Korea, or eating raw crab to increase fertility in women in Africa. Following ingestion, metacercariae excyst in the small intestines and juvenile worms penetrate the gut wall into the body cavity and begin their migration through abdominal and thoracic tissues to the lungs (or other ectopic sites). Once in host tissues, worms mature, pair, mate and become encapsulated by host connective tissue over 8-12 weeks. If a migrating juvenile worm cannot find a mate, it may continue searching for several weeks, or it may form a single worm cyst. Despite adult worms being hermaphroditic, cross-fertilization between pairs of worms is generally required to produce fertile eggs (although some self-fertilization may occur). Unembryonated eggs released into airspaces are either expectorated in sputum or swallowed and then excreted with host faces. The prepatent period in mammalian definitive hosts (time from infection to first egg release) ranges from 65-90 days and it is thought that worms may live for up to 20 years.

Differential diagnosis: Clinical infections may be suspected on the basis of symptomatology and/or radiographic features, but such indications are not unique or pathognomic for paragonimiasis. Provisional diagnoses must be confirmed by the direct detection of fluke eggs in sputum or faecal samples, usually following their concentration by filtration, sedimentation and floatation techniques. Eosinophils and Charcot-Leyden crystals are commonly found in respiratory secretions and stools, and haematological investigations may reveal eosinophilia, elevated erythrocyte sedimentation rates (ESR) and sometimes leucocytosis. Modern medical imaging techniques, such as X-rays, computed tomography (CT) and magnetic resonance imaging (MRI) scans, often yield nonspecific results possibly attributable to other diseases (e.g. tuberculosis), including calcified spots, nodular shadows, patchy infiltrates, linear streaks (worm tracts), and cystic lesions in the lungs, pleural thickenings, interlobar pleuritis and pleural effusions in the thorax, and various types of calcifications in the brain (punctate, nodular, congregated or 'bubble-like'). More invasive diagnostic procedures may be used to detect parasites in surgical or needle biopsy samples (e.g. decortications and aspirates). Infections by metacercariae in crustaceans may be detected by microscopic examination of dissected tissues, usually in squash preparations or following pepsin-acid digestion. Several immunological tests have been developed to detect host antibodies or parasites antigens in serum or faecal samples, including immunodiffusion, immunoelectrophoresis, immunoblot, intradermal, complement fixation and haemagglutination tests and enzyme immunoassays (polyclonal and monoclonal-antibody based). Several tests were useful for detecting early and ectopic infections, but they do not differentiate between current, recent or past infection. Molecular biological techniques have been used to characterize different developmental stages (adults, eggs, cercariae, metacercariae) of several parasite species by polymerase chain reaction (PCR) amplification of restriction fragment length polymorphisms (RFLP), random amplified polymorphic DNA (RAPD), highly repetitive DNA fragments, and sequencing specific gene fragments (nuclear ribosomal RNA and internal transcribed spacer region 2, and mitochondrial cytochrome c oxidase subunit 1).

Treatment and control: Pulmonary and extrapulmonary infections by *Paragonimus* spp. have been successfully treated using the isoquinoline anthelmintic praziquantel, which was well tolerated, low in toxicity and only produced mild transient side-effects (headaches, dizziness, gastrointestinal upset, blurred vision). The halogenated benzimidazole triclabendazole has also proven to be highly effective, as has the salicylanilide niclofolan despite problems with neurotoxicity and hepatotoxicity. In the past, the halogenated bisphenol bithionol was used but often required extended treatment and side-effects were common (urticaria, rash, abdominal pain, nausea, vomiting, diarrhoea, dizziness). Treatment of individual cases with heavy and/or ectopic infections may involve surgical removal of parasites and infected tissues. Efforts to prevent infections centre around minimizing faecal contamination of water, reducing intermediate host populations (both snails and crustaceans), and rendering crustaceans safe for human and animal consumption. These strategies are difficult, if not impossible, to implement in natural ecosystems where parasites are transmitted between wildlife by free-living aquatic stages or by predator-prey relationships. The chemical control of snail and crustacean intermediate hosts is also impractical and inadvisable due to concerns about toxic residues and untoward ecological consequences. The prevention of infections in humans and domestic animals has been more successful through public health education campaigns designed to raise awareness, improve sanitation, promote safe food preparation and cooking practices, and provide contemporary alternatives to folk medicine treatments. Thorough cooking kills metacercariae in crustacean flesh and consumers should be encouraged to avoid raw or improperly prepared culinary dishes in endemic regions despite local customs. Globally, there has been a reduction in the incidence of paragonimiasis in humans which has been attributed to improved socioeconomic conditions, higher education standards, better sanitation, improved food hygiene, rural industrialization, and restricted intermediate host distribution due to habitat loss through deforestation and environmental pollution.

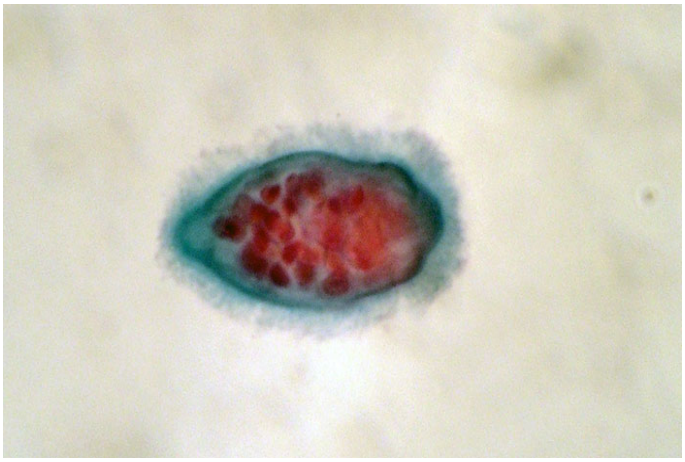

Paragonimus
lungs
(subacute-chronic
inflammatory
granulomatous
lung disease)
Definitive Hosts
(carnivores, piscivores)
hermaphroditic
adult (~ 10 mm)
excretion
ingestion
egg
(~ 100 µm)
vector-borne transmission
encysted within
tissues of IH-2
metacercaria
(~ 400 µm)
endoparasitic in
tissues of vector (IH-1)
crawling
cercaria
(~ 200 µm)
free-swimming
miracidium
(~ 80 µm)
redia
(~ 650 µm)
sporocyst
(~ 400 µm)
Second Intermediate Hosts
(IH-2) (freshwater crabs)
(viscera, muscles)
First Intermediate Hosts
(IH-1) (pomatiopsid snails)
(visceral then glandular tissues)



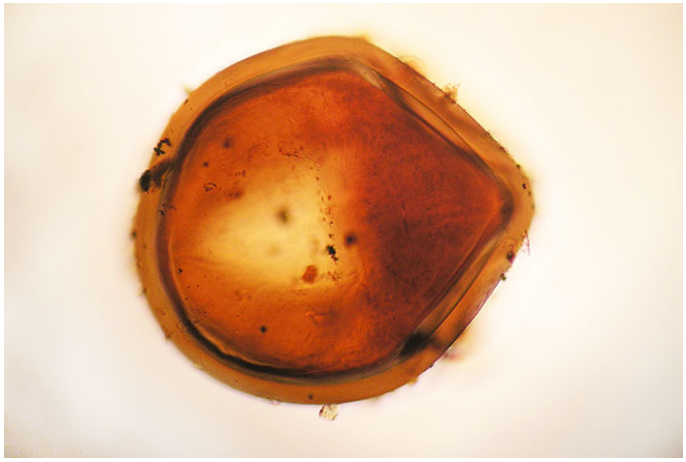
Paragonimus adult worm



Paragonimus egg



Paragonimus miracidium



Paragonimus metacercaria

Schistosoma
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult diplostomatids are diverse in morphology and biology, some having bizarre divided bodies, some appearing tubular, and one extraordinary group (the schistosomes) being dioecious, forming separate sexes. Male schistosomes have a unique gynaecophoral canal along the length of the body (schisto-soma = split body), in which a female worm resides. The copulatory partners live together inside visceral blood vessels and are commonly known as blood flukes. Eggs are deposited in the circulation and must penetrate the gut or bladder to be excreted with faeces or urine, or become trapped in host tissues causing severe granulomatous reactions. Schistosomes form multiple sporocyst (no redia) stages in snails which produce fork-tailed cercariae that emerge and actively seek hosts (metacercariae are not formed). Infections by *Schistosoma* spp. cause chronic debilitating diseases (schistosomiasis/bilharzia) in humans and some domestic ruminants.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Diplostomatida (‘strigeids’, blood and intestinal flukes mainly of tetrapods, some fish, infection usually by cercarial penetration)
Suborder:	Diplostomata (furcocercous (fork-tailed) cercariae)
Superfamily:	Schistosomatoidea (miracidium penetrates gastropod, bivalve, annelid IH, sporocysts formed, fork-tailed cercariae, penetrates DH)
Family:	Schistosomatidae (blood flukes, cylindrical bodies, in blood vessels of alimentary/urinary tract, separate sexes, male with gynaecophoric canal to hold female)
Genus:	*Schistosoma* (parasitic in blood vessels of mammals/birds)
Species:	various species cause schistosomiasis/bilharzia in humans and ruminants

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs, fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

One diplostomatid suborder has been recognized containing 3 superfamilies. The suborder Diplostomata is characterized by species forming furcocercous (fork-tailed) cercariae which either penetrate invertebrate intermediate hosts (forming metacercariae) or directly penetrate vertebrate definitive hosts (forming adults). Members of the superfamily Schistosomoidea do not form metacercariae in second intermediate hosts and their cercariae have been found to develop not only in gastropods but sometimes in bivalves or annelids. Some 430 species have been described in 5 families (Clinostomatidae, Aporocotylidae, Sanguicolidae, Spirorchiidae, Schistosomatidae), the latter 4 families comprising the blood flukes. The family Schistosomatidae contains the blood flukes living in venous blood vessels of tetrapods, the only trematodes that live in the bloodstream of warm-blooded hosts (rich in glucose and amino acids). Schistosomatids are also unique in that the adults are not hermaphroditic but form separate sexes (males resemble rolled leaves with ventral gynaecophoric canals in which the long slender females reside). At present, 15 genera have been classified into 4 subfamilies distinguished by differences in adult morphology and host specificity: Bilharziellinae (short gynaecophoric canal, female genital pore posterior to ventral sucker; *Bilharziella, Trichobilharzia*); Dendritobilharziinae (short canal, anterior pore, dendritic caeca; *Dendritobilharzia*); Gigantobilharziinae (short canal, anterior pore, no ventral sucker; *Gigantobilharzia*); and Schistosomatinae (well-developed canal; *Austrobilharzia* (incl. *Microbilharzia*)*, Ornithobilharzia, Macrobilharzia, Jilinobilharzia, Allobilharzia, Anserobilharzia, Bivitellobilharzia, Heterobilharzia, Schistomatium, Schistosoma* (incl. *Orientobilharzia*) and *Griphobilharzia*). The first 10 genera infect birds, the next 4 genera infect mammals and the last genus infects reptiles.

Parasite genus	Definitive hosts	Location	Intermediate hosts (gastropod family)	Distribution
Bilharziella	Anseriformes, Gruiformes, Ciconiformes, Podicipediformes	visceral	freshwater Planorbidae	Europe
Trichobilharzia	Anseriformes (Anatidae)	visceral, nasal	freshwater Lymnaeidae, Physidae	Global
Dendritobilharzia	Anseriformes, Gruiformes, Pelicaniformes, Gaviiformes	visceral	freshwater Planorbidae	Global
Gigantobilharzia	Passeriformes	visceral	freshwater Physidae	North America
Austrobilharzia (incl. *Microbilharzia*)	Charadriiformes	visceral	marine Nassariidae, Batillaridae, Littoriniidae, Potamididae	Global
Ornithobilharzia	Charadriiformes	visceral	marine Batillaridae	Global
Macrobilharzia	Suliformes	visceral	unknown	North America, Africa
Jilinobilharzia	Anseriformes (Anatidae)	visceral	unknown	China
Allobilharzia	Anseriformes (swans)	visceral	unknown	Northern Hemisphere
Anserobilharzia	Anseriformes (geese)	visceral	freshwater Planorbidae	Northern Hemisphere
Bivitellobilharzia	Elephantidae, Rhinocerotidae	visceral	unknown	Africa, Asia
Heterobilharzia	Carnivora, Artiodactyla, Rodentia	visceral	freshwater Lymnaeidae	North America
Schistosomatium	Rodentia	visceral	freshwater Lymnaeidae	North America
Schistosoma (including *Orientobilharzia*)	Primates, Artiodactyla, Rodentia	visceral, nasal	freshwater Planorbidae, Lymnaeidae, Pomatiopsidae	Eurasia, Africa, South America, China
Griphobilharzia	Crocodilia	visceral	unknown	Australia

Schistosoma spp. are important human and animal parasites throughout Africa, Asia and South America, predominantly in rural areas supporting agriculture and inland fisheries. Parasite distribution is linked to that of their snail intermediate hosts, which differ in their habitat preferences for slow-flowing or still waters. Many human activities also influence parasite distribution, especially the construction of irrigation channels and dams, and flood irrigation of crops. It has been estimated that over 200 million people may be infected worldwide. Infections have been recorded throughout human history, first being mentioned in ancient Egyptian papyri dated from 2000-1000 BC. Haematuria (bloody urine) became the scourge of Napoleon's army in northern Africa at the turn of the 18th century, and the disease later became known as bilharzia in honour of the discoverer of the causative agent. *Schistosoma* spp. vary in their specificity for intermediate hosts, some only developing in humans (and possibly primates) while others may infect domestic and wild animals, acting as reservoirs for human infection. Over twenty species have been described, including four recently transferred from the genus *Orientobilharzia.* Four main groups are recognized on the basis of multiple biological and molecular characteristics: namely, the *japonicum*, *haematobium, mansoni* and *indicum* groups. The epidemiology and host preferences of schistosomes in Africa is complicated by the occurrence of hybrid forms.

Schistosoma	**Egg size**	**Definitive hosts**	**Intermediate hosts**	**Distribution**

species		[location] {clinical disease}	[sporocysts in tissues]	
S. haematobium group (African distribution)(terminal-spined eggs) (Pulmonata snails)				
S. haematobium (bladder fluke)	112-170 x 40-70 µm	Primates: hominid (human), cercopithecid (mangabey), plus experimental infections in Primates: cercopithecid (green monkey, baboon, rhesus monkey, macaques); Eulipotyphla: erinaceid (hedgehog); Rodentia: murid (mouse, rat, gerbil), cricetid (hamster); rarely Artiodactyla: bovid (goat) [bladder and mesenteric veins] {haematuria, granulomas}	aquatic Gastropoda: planorbid (*Bulinus africanus* (syn. *Physopsis africana*), *Bu. globosus* (syn. *Ph. globosa*), *Bu. nasutus, Bu. abyssinicus, Bu. umbilicatus, Bu. truncatus, Bu. rohlfsi, Bu. forskalii, Bu. senegalensis, Bu. cernicus, Bu. reticulatus, Bu. ugandae, Bu. beccarii, Bu. nyassanus, Bu. jousseaumei, Bu. guernei, Bu. obtusispira, Bu. wrighti, Ferrissia tenuis*)	Africa, India, Southwest Asia
S. intercalatum	140-240 x 50-85 µm	Primates: hominid (human); Artiodactyla: bovid (cattle, sheep, goat); Rodentia: murid (mice, rats) [mesenteric veins] {diarrhoea}	aquatic Gastropoda: planorbid (*Bulinus forskalii, Bu. africanus* (syn. *Physopsis africana*))	Africa
S. bovis (blood fluke)	182-248 x 45-80 µm	Artiodactyla: bovid (cattle, sheep, goat), suid (pig), camelid (camel); Perissodactyla: equid (horse); Rodentia: murid (mice, rats) [portal, mesenteric & urogenital veins] {diarrhoea, haematuria}	aquatic Gastropoda: planorbid (*Bulinus contortus, Bu. truncatus, Bu. africanus* (syn. *Physopsis africana*), *Bu.* (*Ph.*) *nasutus, Bu. guernei, Bu. forskalii, Bu. abyssinicus, Bu. senegalensis, Bu. globosus, Bu. umbilicatus, Planorbarius metidjensis*)	Africa, Middle East, Southern Europe
S. mattheei	145-250 x 40-70 µm	Artiodactyla: bovid (cattle, sheep, goat, wild ruminants), camelid (camel); Rodentia: murid (mice, rats); Primates: hominid (human) [portal, mesenteric & bladder veins] {diarrhoea, haematuria}	aquatic Gastropoda: planorbid (*Bulinus africanus* (*Physopsis africana*), *Bu. globosus*)	Africa, Middle East
S. curassoni	146 x 63 µm	Artiodactyla: bovid (sheep, goat, cattle) [mesenteric, rectal & bladder veins] {liver, bowel lesions}	aquatic Gastropoda: planorbid (*Bulinus umbilicatus*)	West Africa
S. guineensis	151-189 x 57-64 µm	Primates: hominid (human); Rodentia: murid (mice, rats) [rectal veins]	aquatic Gastropoda: planorbid (*Bulinus forskalii*)	West Africa
S. kisumuensis	123-143 x 49-58 µm	Rodentia: murid (mice, rats) [vascular system]	unknown	Central Africa
S. leiperi	210-305 x 38-65 µm	Artiodactyla: bovid (cattle, antelope, wild ruminants); Rodentia: murid (mice, rats) [mesenteric & portal veins]	aquatic Gastropoda: planorbid (*Bulinus africanus* (syn. *Physopsis africana*))	Africa
S. margrebowiei	70-97 x 50-68 µm	Artiodactyla: bovid (antelope, wild ruminants, cattle, sheep, goat); Primates: hominid (human) [mesenteric & portal veins]	aquatic Gastropoda: planorbid (*Bulinus forskalii, Bu. scalaris, Bu. tropicus, Bu. Bu. natalensis, Bu. bavayi, Bu. beccarii*)	Africa
S. mansoni group (African distribution)(lateral-spined eggs) (Pulmonata snails)				
S. mansoni (Manson's blood fluke)	110-175 x 40-70 µm	Primates: hominid (human), cercopithecid (green monkey, macaque, baboon, rhesus monkey), cebid (capuchin); Eulipotyphla: soricid (shrew), erinaceid (hedgehog); Rodentia: murid (rats, mice, gerbil), cricetid (hamster), caviid (guinea pig); Didelphimorphia: didelphid (opossum); Lagomorpha: leporid	aquatic Gastropoda: planorbid (*Biomphalaria pfeifferi, Bi. alexandrina, Bi. glabrata* (*Australorbis glabratus*), *Bi. sudanica, Bi. camerunensis, Bi. angulosa, Bi. tenagophila, Bi. straminea, Bi. amazonica, Bi. arabica, Bi. peregrina, Bi. choanomphala, Bi. stanleyi, Bi. smithi, Au. olivaceus, Tropicorbis centimetralis*); terrestrial Gastropoda: achatinid (*Achatina fulica*)	Africa, Southwest Asia, Caribbean, South America

		(rabbit); Cingulata: chlamyphorid (armadillo); Artiodactyla: suid (pig), bovid (goat); Carnivora: felid (cat), canid (dog) [portal and mesenteric veins] {dermatitis, swamp fever, granulomas, ascites}		
S. rodhaini	120-170 x 48-70 µm	Rodentia: murid (rats, mice); Carnivora: canid (dog), felid (serval cat) [mesenteric & portal veins] {diarrhoea}	aquatic Gastropoda: planorbid (*Biomphalaria pfeifferi, Bi. sudanica*)	Africa
S. edwardiense	47-62 x 28-53 µm	Artiodactyla: hippopotamid (hippopotamus) [mesenteric veins]	aquatic Gastropoda: planorbid (*Biomphalaria sudanica,*)	Central Africa
S. hippopotami	93 x 40 µm	Artiodactyla: hippopotamid (hippopotamus) [hepatic veins, pulmonary circulation]	aquatic Gastropoda: planorbid (*Bulinus truncatus*)	Central Africa
S. japonicum group (Asian distribution)(minutely-spined or spineless eggs) (Prosobranchia snails)				
S. japonicum (blood fluke)	70-100 x 50-70 µm	Primates: hominid (human), cercopithecid (macaque); Artiodactyla: bovid (cattle, buffalo, sheep, goat), suid (pig), cervid (water deer, muntjac, sambar); Perissodactyla: equid (horse, donkey); Carnivora: canid (dog, raccoon dog, fox), felid (cat, leopard cat, leopard), mustelid (weasel, ferret-badger, badger), herpestid (mongoose), viverrid (civet); Lagomorpha: leporid (rabbit, hare); Rodentia: murid (mice, rats), cricetid (vole), sciurid (squirrel), hystricid (porcupine); Eulipotyphla: soricid (shrew), erinaceid (hedgehog) [portal & mesenteric veins] {dermatitis, abscesses, anaemia, diarrhoea, granulomas, ascites}	amphibious Gastropoda: pomatiopsid (*Oncomelania hupensis, O. nosophora, O. quadrasi, O. formosana, O. lindoensis, O. chiui, Robertsiella kaporensis, Pomatiopsis lapidaria, Tricula aperta*)	South-East Asia, Philippines, Indonesia
S. mekongi	50-65 x 30-55 µm	Primates: hominid (human); Carnivora: canid (dog), felid (cat) [mesenteric veins] {diarrhoea}	amphibious Gastropoda: pomatiopsid (*Neotricula* (*Tricula*) *aperta, T. bollingi*)	South-East Asia
S. malayensis	50 x 28 µm	Rodentia: murid (rats); rarely Primates: hominid (human) [portal veins]	amphibious Gastropoda: pomatiopsid (*Robertsiella gismanni, R. kaporensis, R. silvicola*)	South-East Asia
sister to *japonicum* clade				
S. sinensium	95-115 x 40-50 µm	Rodentia: murid (rats) [mesenteric veins]	amphibious Gastropoda: pomatiopsid (*Neotricula* (*Tricula*) *aperta, T. bollingi*)	China
S. ovuncatum	65-80 x 40-45 µm	Rodentia: murid (rats, mice) [mesenteric veins]	amphibious Gastropoda: pomatiopsid (*Tricula bollingi*)	Thailand
S. indicum group (Asian distribution)(polymorphic eggs)(Pulmonata snails)				
S. indicum	100-150 x 48-68 µm	Artiodactyla: bovid (cattle, buffalo, sheep, goat), camelid (camel); Perissodactyla: equid (horse, donkey) [portal, mesenteric, pancreatic, hepatic & pulmonary veins] {diarrhoea}	aquatic Gastropoda: planorbid (*Indoplanorbis exustus*)	India, Thailand
S. spindale	284-400 x 80-90 µm	Artiodactyla: bovid (cattle, buffalo, sheep, goat), suid (pig); Perissodactyla: equid (horse,	aquatic Gastropoda: planorbid (*Indoplanorbis exustus*)	India, South-East Asia

		donkey); Carnivora: canid (dog); Rodentia: murid (rats) [portal & mesenteric veins] {diarrhoea, plus cercarial dermatitis}		
S. nasalis (*nasale*)	316-508 x 40-75 µm	Artiodactyla: bovid (cattle, buffalo, sheep, goat); Perissodactyla: equid (horse) [nasal mucosa veins] {coryza, sneezing, dyspnoea, snoring disease}	aquatic Gastropoda: planorbid (*Indoplanorbis exustus*), lymnaeid (*Lymnaea luteola, L. acuminata*)	India, South-East Asia
S. incognitum (syn. *S. suis*)	90-148 x 41-81 µm	Artiodactyla: suid (pig), bovid (cattle); Carnivora: canid (dog); Rodentia: murid (rats) [mesenteric & portal veins] {diarrhoea}	aquatic Gastropoda: lymnaeid (*Radix luteola, R. rubiginosa*)	India, South-East Asia
formerly *Orientobilharzia* (differ from *Schistosoma s.s*. only in number of testes)				
S. turkestanicum	108-135 x 42-48 µm	Artiodactyla: bovid (cattle, buffalo, sheep, goat), camelid (camel); Perissodactyla: equid (horse, donkey); Carnivora: felid (cat) [mesenteric/portal veins] {cirrhosis}	aquatic Gastropoda: lymnaeid (*Radix gedrosiana, R. auricularia, Lymnaea tenera*)	Eurasia
S. harinasutai	111-127 x 27-52 µm	Artiodactyla: bovid (buffalo) [portal & mesenteric veins]	aquatic Gastropoda: lymnaeid (*Radix rubiginosa*)	Thailand
S. bomfordi	125-136 x 53-60 µm	Artiodactyla: bovid (cattle) [mesenteric veins]	aquatic Gastropoda: lymnaeid (*Radix luteola*)	India
S. dattai	120-170 x 43-60 µm	Artiodactyla: bovid (cattle, buffalo, sheep, goat) [portal veins]	aquatic Gastropoda: lymnaeid (*Radix luteola*)	India
Schistosomatium (rodent blood flukes established as laboratory models)				
Schistosomatium douthitti	150 x 60 µm	Rodentia: murid (muskrat, meadow mouse, redback mouse, deer mouse, field mouse, white mouse, rat), echimyid (nutria), cricetid (hamster), caviid (guinea pig); Lagomorpha: leporid (rabbit); Carnivora: canid (dog), felid (cat); Primates: cercopithecid (rhesus monkey), hominid (human) [mesenteric and intra-hepatic veins]	aquatic Gastropoda: lymnaeid (*Stagnicola* spp., *Lymnaea palustris, L. stagnalis, L. emarginata*, *L. natalensis, Pseudosuccinea columella*), planorbid (*Bulinus tropicus, Physa* spp.)	North America, Africa?
Schistosomatium pathlocopticum (possibly syn. of *Sc. douthitti*)	80-126 x 58-87 µm	Rodentia: murid (mice, rats) [mesenteric veins]	aquatic Gastropoda: lymnaeid (*Stagnicola (Lymnaea) palustris*)	North America

Parasite morphology: Blood flukes form five different developmental stages: eggs, miracidia, sporocysts, cercariae and adult worms. Eggs are round to oval in shape, light yellow-brown in colour, most lacking a distinct operculum, but all containing a developing embryonic larva (miracidium). Differences in egg morphology can be used to distinguish between *Schistosoma* species: *S. mansoni* producing oval eggs (114-175 x 45-68 µm) with a sharp lateral spine, *S. japonicum* forming oval eggs (70-100 x 50-70 µm) with a rudimentary lateral spine; and *S. haematobium* producing oval eggs (112-170 x 40-70 µm) with a sharp terminal spine. Miracidia are elliptical free-swimming larval stages (~200 µm long) covered with cilia. Sporocysts appear as pleomorphic sac-like bodies which contain another generation of sporocysts or cercariae. Mature cercariae are elongate free-swimming larval stages (400-600 µm long) consisting of a tapering head (with prominent escape and penetration glands) and a forked tail (furcocercous). Adult flukes are elongate tubular worms (9-28 mm long by 1-2 mm wide), with rudimentary oral and ventral suckers close together near the anterior end. The digestive system comprises the mouth (surrounded by the oral sucker), oesophagus (no pharynx), oesophageal glands and paired caeca which reunite posteriorly forming a single caecum extending the remaining length of the body. Unlike most trematodes, adult schistosomes are not hermaphroditic but are sexually dimorphic. Males are shorter and stouter than females (9-22 mm cf. 12-28 mm long), and they have a longitudinal ventral groove (gynaecophoral canal or schist) in which the longer slender

female lies. The suckers on the males are spiny and most of their bodies are finely tuberculated. Males possess 5-9 testes and have a ventral genital pore opening immediately posterior to the ventral sucker. Females possess a single ovary connected to the ventral genital pore by an elongate uterus.

Site of infection: Paired adult worms live inside venous blood vessels in specific sites within the bodies of their mammalian definitive hosts. In humans, *S. mansoni* lives principally in the portal veins draining the large intestine, *S. japonicum* in the mesenteric veins of the small intestines, and *S. haematobium* infects veins of the urinary bladder plexus. Fluke eggs penetrate into the lumen of the intestines or bladder to be voided with host faeces or urine. Many eggs, however, may be swept away in the host circulation and become trapped in various host tissues and organs. Asexual developmental stages (sporocysts) develop throughout the tissues and organs of freshwater snail intermediate hosts.

Pathogenesis: Schistosomiasis (or bilharziasis) is unusual amongst helminth diseases for two reasons: much of the pathogenesis is due to the eggs (rather than larvae or adults); and most of the pathology is caused by host immune responses (delayed-type hypersensitivity and granulomatous reactions). However, the severity of disease is dependent not only on the strength of the inflammatory and immune responses but also on the intensity of infection, previous exposure, extent of hepatic fibrosis, age, nutritional status and genetic background affecting host susceptibility/resistance. The course of infection is often divided into three phases: migratory, acute and chronic. The migratory phase begins when cercariae penetrate and migrate through the skin. This is often asymptomatic, but in sensitized patients, it may cause transient hypersensitivity, pruritus and dermatitis ('swimmers' itch') within the first few days after infection. Cercarial excretory/secretory (ES) products have been shown to induce oedema and neutrophil infiltration in the skin. Schistosomula then migrate from the lungs to the liver over several weeks, occasionally causing pulmonary lesions, congestion, pneumonitis and toxic reactions. The acute phase (sometimes called Katayama fever) occurs 2-8 weeks after infection and is coincident with schistosomula migration and the onset of egg laying by adult worms. It is characterized by allergic responses (serum sickness due to overwhelming immune complex formation), pyrexia, rash, urticaria, fatigue, aches, cough, dyspnoea, lymphadenopathy, gastrointestinal discomfort and eosinophilia. Hosts exhibit strong proinflammatory cell-mediated immune responses during the acute phase, where non-egg antigens (cercariae, schistosomula, schistosomes) elicit type 1 $CD4^+$ helper T-lymphocyte (T_h1) responses via effector cytokines (interleukin-1 (IL-1), IL-6 and tumour necrosis factor-alpha (TNF-α). The chronic phase occurs months to years after infection in response to the cumulative deposition of fluke eggs in tissues and the host reactions that develop against them. In order to complete the life-cycle, eggs deposited in small venules must exit the host by traversing vascular endothelia, interstitial tissues and mucosal linings to reach the lumen of the bladder or gut. Miracidia developing within the eggs secrete hydrolytic enzymes among other molecules, which are released through the porous eggshell. In addition to their lytic activity, these secretions elicit granulomatous responses involving motile immune cells (macrophages, neutrophils, eosinophils) which assist in the movement of the granuloma through the tissues. Not all the eggs laid by female worms successfully penetrate the gut or bladder walls, however, and many are swept away in the circulation and become trapped in various organs. The strong granulomatous responses result in extensive fibrosis with the deposition of collagen leading to fibro-obstructive disease. Eggs surrounded by inflammatory cells form characteristic pseudotubercles (abscesses), sometimes coalescing to form larger granulomatous reactions (polyps), which become encapsulated and eventually calcified. The resultant effects on host tissues are manifold and clinical symptoms vary depending on organ involvement, the most frequent being urinary, intestinal and hepatosplenic symptoms. Urinary infections by *S. haematobium* may cause irritative micturition syndrome with dysuria, proteinuria and haematuria (blood in urine), progressing to thickening of the bladder wall, chronic cystitis, polyps, vesical masses, fibrosis and calcification resulting in hydroureter and hydronephrosis. Constant disruption of the bladder wall may also be precancerous leading to bladder carcinoma (other *Schistosoma* spp. have not been associated with colon or liver cancer). Infections in the gut may cause intestinal hyperplasia, micro-abscesses, polyposis, ulceration, abdominal pain, diarrhoea and sometimes complicated enteropathies (erosive lesions, occlusions, prolapses, fistulas). Hepatosplenic symptoms arise from egg congestion of the portal venous circulation with occlusion of intrahepatic veins and periportal (Symmer's clay pipe-stem) fibrosis. The resultant portal hypertension often leads to hepatomegaly, splenomegaly, ascites, and sometimes gross enlargement of oesophageal and gastric veins (varices) which may burst. Other organ systems may be impacted, with cardiopulmonary, renal, genital and neurological symptoms arising infrequently (loosely designated as ectopic). Eggs may reach the lungs from vesical veins or through the porto-cava shunt leading to pulmonary fibrosis and arteritis, with the resultant pulmonary hypertension contributing to right cardiac insufficiency. Lesions may develop in the kidney parenchyma causing glumerulonephritis leading to renal failure. Genital lesions may be inflammatory, hypertrophic or fibrotic: involving the prostate and seminal vesicles in men and the vulva, vagina and uterus in women. Neurological symptoms include cerebral and medullar syndromes, cerebral granulomas being associated with focal encephalitis and epileptic convulsions, and medullar lesions causing transverse, ischaemic or vascular myelitis or myeloradiculitis. Host cell-mediated immune responses during the chronic phase switch to prohumoral and delayed-type hypersensitivity responses, where egg-antigens elicit T_h2 cellular responses via effector cytokines (particularly IL-10); such responses being more conducive to fibrogenesis and healing (also possibly providing protection against severe disease). Schistosomiasis in domestic animals is more severe in small rather than large ruminants: sheep often developing anaemia and hypoalbuminaemia due to mucosal haemorrhages and dyshaemopoesis, while cattle only occasionally display haematuria due to bladder damage. At necropsy, haemorrhagic lesions may be present in the intestinal mucosa during the acute phase of infection, but as disease progresses there may be marked thickening, oedema, fibrosis, and organ enlargement due to egg granulomata and associated inflammation. An unusual species (*S. nasalis*) found in the nasal mucosa mainly of cattle has been associated with copious mucopurulent discharge, snoring, dyspnoea, abscess formation and occlusion of nasal

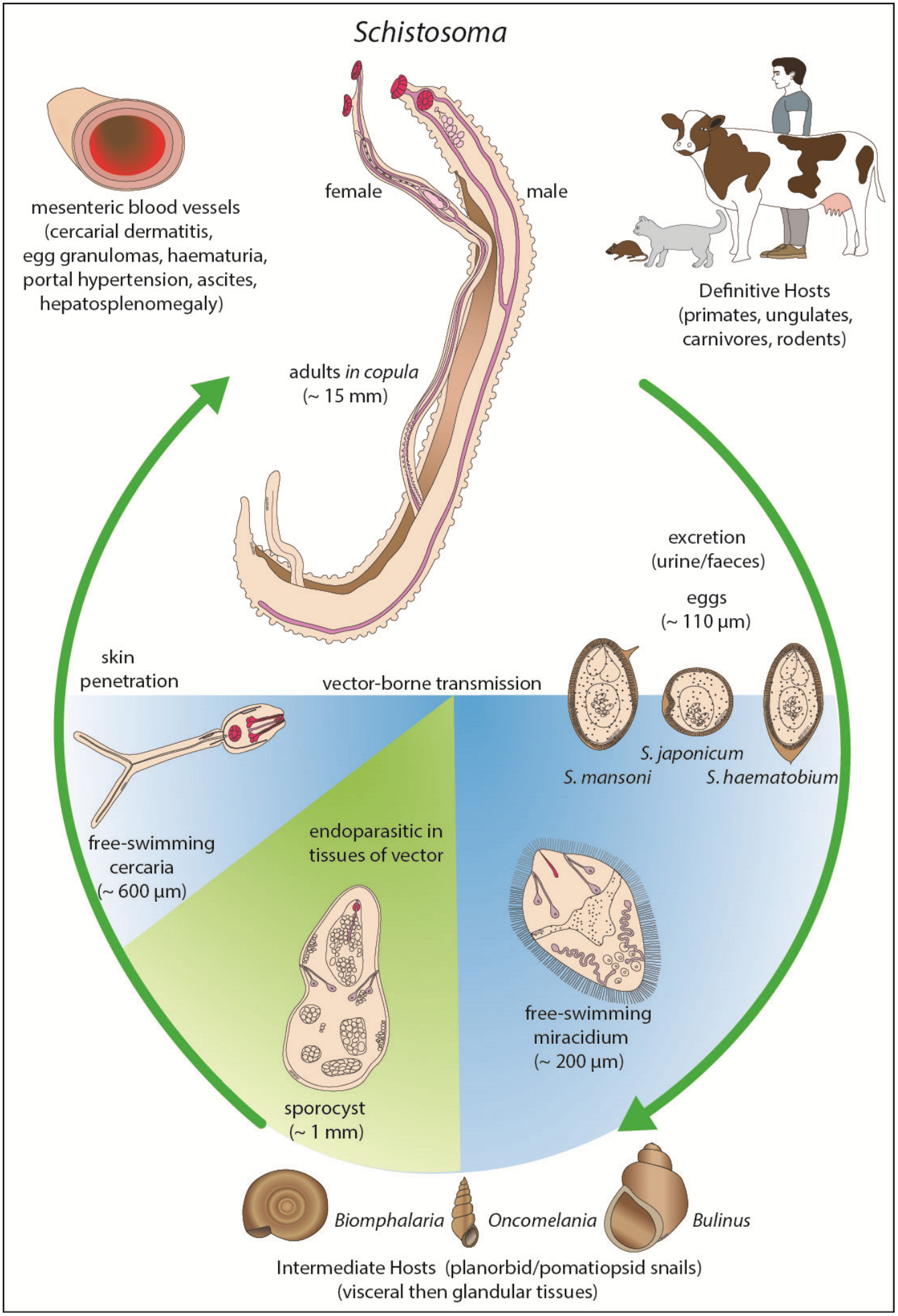
passages. Other schistosomes, such as those that normally infect birds (e.g. *Trichobilharzia* and *Austrobilharzia*) may also cause 'swimmers' itch' in humans when the cercariae penetrate the skin but are unable to complete their development.

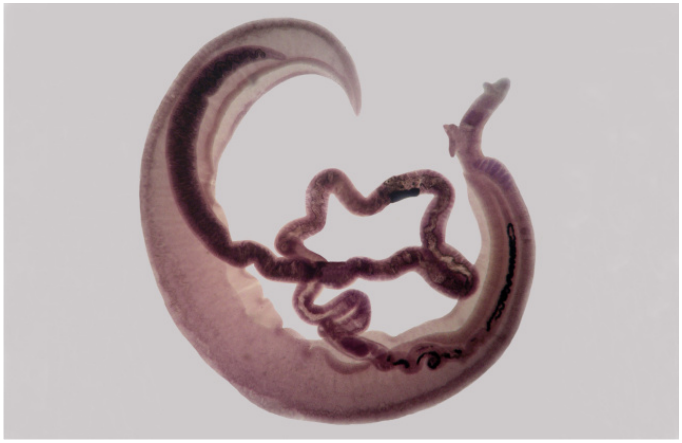
Developmental cycle and mode of transmission: Schistosomes have indirect digenetic life-cycles, involving sexual reproduction in vertebrate definitive hosts and asexual reproduction in snail intermediate hosts. The transmission and epidemiology of infections is dependent on water as a medium for motile parasite stages to actively seek hosts (miracidia seeking snails and cercariae seeking vertebrates). Infections are more prevalent in children who are in contact with infected water and in adults labouring in or near water (washing clothes and utensils, farmers, fishermen). Female worms in host veins produce numerous eggs (200-3,000 per day) which use proteolytic enzymes (and sometimes spines) to penetrate the gut or bladder wall and exit the host in faeces or urine. When deposited in water, the embryonated eggs hatch releasing free-swimming miracidia which only live for several hours. In that time, they actively seek suitable intermediate hosts (aquatic or amphibious snails) using chemotaxis and phototaxis (despite absence of eyespots). All *Schistosoma* spp. demonstrate quite narrow host specificity for particular snails: *S. mansoni* infects aquatic *Biomphalaria* spp. (large flat spiral snails ~14 mm in diameter with ~3 whorls and apical aperture), *S. japonicum* infects amphibious *Oncomelania* spp. (small elongate snails ~8 mm long with 4-5 whorls and dextral (right-sided) aperture), and *S. haematobium* infects aquatic *Bulinus* spp. (medium ovoid snails ~12 mm long with 2-3 whorls and sinistral (left-sided) aperture). The snails live in aquatic habitats, including standing waters, flowing streams, irrigated areas, marshy grounds and wet savannah, and they are quite resistant to drought, climate change and pollution. The miracidia invade the soft tissues of the snail and form a mother sporocyst near the site of penetration. Daughter sporocysts are produced 2-6 weeks after infection and they migrate to other organs in the snail (especially the digestive gland or gonads). Schistosomes do not produce redia stages; instead the daughter sporocysts produce cercariae which emerge into the water in their thousands beginning 4 weeks after infection. The fork-tailed cercariae are rapid swimmers and they periodically swim to the surface of the water and then sink in the water column, repeating this fixed behaviour for up to 2-3 days. Hosts entering water bodies in close proximity induce changes in this cyclic swimming behaviour, with cercariae swimming laterally beneath the water surface. The cercariae are attracted to skin secretions and when they come into contact with a prospective definitive host, they attach and actively penetrate the skin within minutes, losing their tails in the process. After 2-3 days, the schistosomula ('little schistosomes') enter the blood and/or lymphatic system and are carried to the right side of the heart and then the pulmonary circulation where they undergo rapid growth for 7-10 days. Schistosomules then move through the left side of the heart and are carried via the systemic circulation to hepatic portal veins where they develop for 3 weeks. Young adult worms then pair, mate and migrate to their predilection sites in the veins of the gut or bladder. Egg production begins from 4-8 weeks after infection, and adult worms normally live for 2-5 years, although some may survive much longer.

Differential diagnosis: Infections are conventionally diagnosed by the microscopic detection of fluke eggs in faecal or urine samples, often after concentration by sedimentation/floatation or filtration techniques. The eggs are sufficiently characteristic to facilitate specific diagnosis. The eggshell is acid-fast when stained with modified Ziehl-Neelsen stains. Various refinements of coprological tests have been developed to improve sensitivity, including incubating faeces to hatch miracidia which migrate towards a light source. On occasion, microscopy of rectal biopsies (snips) has been used to diagnose *S. haematobium* infections. Various medical imaging techniques may be used to locate worms *in situ*, including radiology, ultrasonography, computerized tomography (CT) and magnetic resonance imaging (MRI). Many immunoserological tests (agglutination, fluorescence, enzyme immunoassays) have been developed to detect host antibodies against infection, but most have experienced cross-reactivity problems and cannot discriminate between active and previous infections. Several techniques (electrophoresis, immunoblotting, chromatography) have also been developed to detect parasite antigens in blood, urine and even milk samples, but most are not species-specific. More recently, molecular techniques have been used to detect, quantify and characterize parasite DNA in host samples by polymerase chain reaction (PCR) amplification of specific gene sequences (nuclear 18S and 28S ribosomal DNA, repetitive sequences, mitochondrial DNA). Excellent results have been obtained in species discrimination, molecular epidemiology and quantifying parasite burdens, but most assays are not yet available outside of specialist laboratories.

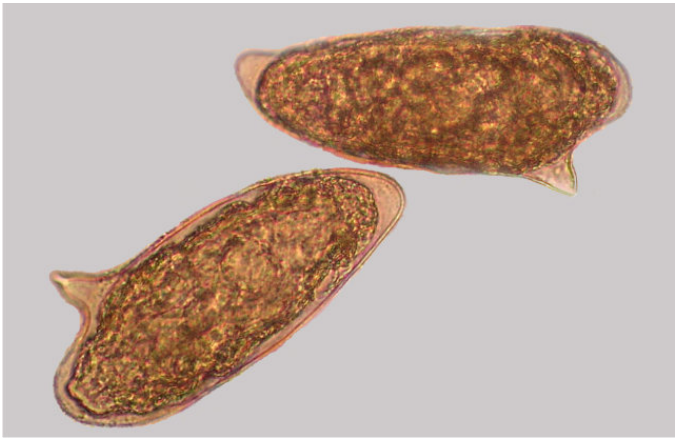
Treatment and control: The drug of choice for the treatment of *Schistosoma* infections is praziquantel, a single oral dose being very effective, with low toxicity and good tolerance, even in severe clinical cases. Nitridazole and metrifonate are effective against *S. haematobium*, and oxamniquine against *S. mansoni*, but they have mild side-effects. In some areas, domestic livestock are still treated with older drugs such as antimonial, stibophen, niridazole and trichlorphon, although dosages are protracted. Caution is advised in treating clinical cases as the dislodgement of damaged flukes may result in emboli and occlusion of major veins. While timely treatment is effective, cured individuals rapidly become re-infected in endemic areas. Various control programmes have therefore been developed based on mass chemotherapy in conjunction with preventive measures, including improved sanitation, snail vector control, modifying habitats and farming practices, and public education campaigns. Water contamination can be reduced by preventing the ingress of parasite eggs as well as curtailing the asexual amplification cycle in snail hosts. The provision and use of latrines contains sources of infection, and modern biocomposting toilets appear to be effective in killing parasite eggs when used properly. Snail populations may be reduced by the strategic use of molluscicides (niclosamide or copper sulphate), draining marshes and swamps, and clearing channels of vegetation. Irrigation practices can be modified to avoid long-standing still waters, and different or improved crops can be used which are less dependent on lengthy immersion in water. In endemic areas, farmers (and visitors) need to be aware of the dangers of immersion in potentially contaminated waters. Considerable resources have

been devoted to the development of cellular, subcellular and recombinant vaccines, and promising results have been obtained with parasite membrane proteins in animal models of disease.


Schistosoma
mesenteric blood vessels
(cercarial dermatitis,
egg granulomas, haematuria,
portal hypertension, ascites,
hepatosplenomegaly)
female
male
adults in copula
(~ 15 mm)
Definitive Hosts
(primates, ungulates,
carnivores, rodents)
excretion
(urine/faeces)
eggs
(~ 110 µm)
skin
penetration
vector-borne transmission
S. mansoni
S. japonicum
S. haematobium
free-swimming
cercaria
(~ 600 µm)
endoparasitic in
tissues of vector
free-swimming
miracidium
(~ 200 µm)
sporocyst
(~ 1 mm)
Biomphalaria
Oncomelania
Bulinus
Intermediate Hosts (planorbid/pomatiopsid snails)
(visceral then glandular tissues)



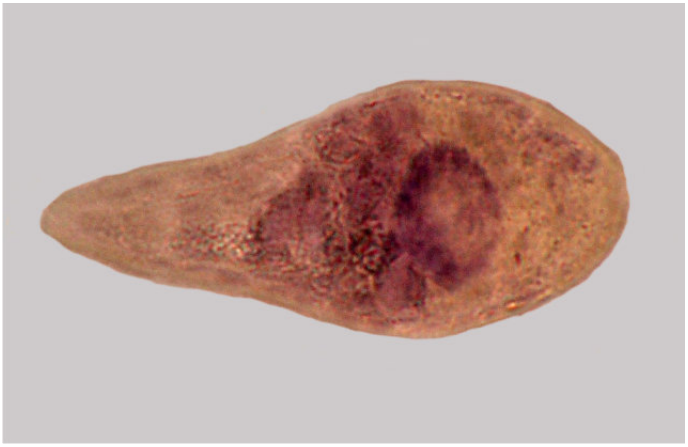
Schistosoma adult worms *in copula*



Schistosoma mansoni eggs



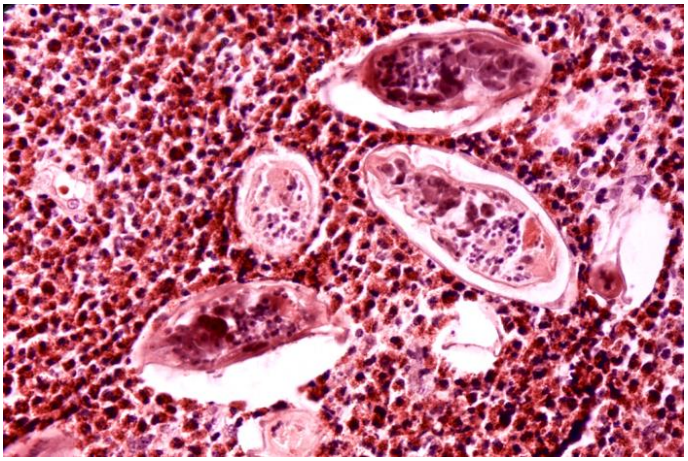
Schistosoma japonicum egg



Schistosoma miracidium



Schistosoma cercaria



Schistosoma haematobium egg granulomas

Trichobilharzia, Austrobilharzia
(platyhelminth: trematode)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Trematodes (flukes) have soft leaf-like bodies with oral and ventral suckers, a blind gut (mouth but no anus) and both male and female reproductive organs (hermaphroditic). Digeneans have indirect life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs. Miracidia released from eggs infect snails (obligate intermediate hosts) where they undergo massive asexual proliferation through sac-like sporocyst and redia stages eventually releasing larval cercariae into the water. Vertebrate (definitive) hosts become infected by penetration of the skin by cercariae or by eating encysted stages (metacercariae) on herbage or in second intermediate hosts. Adult diplostomatids are diverse in morphology and biology, some having bizarre divided bodies, some appearing tubular, and one extraordinary group (the schistosomes) being dioecious, forming separate sexes. Male schistosomes have a unique gynaecophoral canal along the length of the body (schisto-soma = split body), in which a female worm resides. The copulatory partners live together inside visceral blood vessels and are commonly known as blood flukes. Eggs are deposited in the circulation and must penetrate the gut or bladder to be excreted with faeces or urine, or become trapped in host tissues causing severe granulomatous reactions. Schistosomes form multiple sporocyst (no redia) stages in snails which produce fork-tailed cercariae that emerge and actively seek hosts (metacercariae are not formed). Many genera and species have been recorded in birds, but not in association with disease. However, the cercariae can penetrate and migrate in the skin of humans bathing in natural freshwater bodies causing transient dermatitis (swimmer's itch).

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Trematoda (flukes, most with dorsoventrally-flattened bodies, sac-like gut)
Subclass:	Digenea (heteroxenous, larval miracidium, sac-like sporocyst/redia stages in mollusc, cercariae/metacercariae)
Order:	Diplostomatida ('strigeids', blood and intestinal flukes mainly of tetrapods, some fish, infection usually by cercarial penetration)
Suborder:	Diplostomata (furcocercous (fork-tailed) cercariae)
Superfamily:	Schistosomatoidea (miracidium penetrates gastropod, bivalve, annelid IH, sporocysts formed, fork-tailed cercariae, penetrates DH)
Family:	Schistosomatidae (blood flukes, cylindrical bodies, in blood vessels of alimentary/urinary tract, separate sexes, male with gynaecophoric canal to hold female)
Genus:	*Trichobilharzia* (parasitic in blood vessels of birds)
Genus:	*Austrobilharzia* (parasitic in blood vessels of birds)
Species:	various species cause dermatitis (swimmer's itch) in humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

The trematodes (flukes) and monogeneans have blind sac-like guts (lacking an anus) while the cestodes (tapeworms) lack digestive tracts. Trematodes have leaf-like bodies well adapted to living in confined spaces in tubular organs of vertebrate hosts. Two trematode subclasses are recognized: the Aspidogastrea with relatively few species (obligate external parasites of molluscs, fish and turtles, adults possessing a large ventral disc divided with numerous alveoli (suckerlets) or rows of suckers and the tegument having short protrusions (microtubercles)); and the speciose Digenea (obligate endoparasites of vertebrates, adults bearing undivided ventral suckers (when present) and life-cycles involving alternation of sexual stages in vertebrates and asexual stages in molluscs). The success of digeneans as widespread parasites has been attributed to their ability to proliferate at 2 separate parts of their life-cycles. Adults worms in vertebrate definitive hosts produce numerous eggs which are excreted and release free-swimming miracidia which seek molluscan intermediate hosts. Massive asexual proliferation occurs in molluscs involving unique sporocysts and rediae. Both stages are sac-like structures with almost no anatomical features (no suckers, no reproductive organs). The difference is that sporocysts lack a gut (they absorb their food), whereas rediae have a mouth, a muscular pharynx and a sac-like gut (they browse on molluscan tissues). Sequential development of these stages varies considerably, with mother sporocysts producing daughter sporocysts or rediae over multiple generations, culminating in the production of cercariae. The infected molluscs are typically rendered sterile ('castrated') with parasites replacing their gonads and producing dozens to thousands of infective cercariae every day. The cercariae are larval forms, almost always with tails, and they actively emerge from molluscs and swim around in water. There is enormous variation in cercarial behaviour, but the 3 most important routes of infection for definitive hosts are by penetration of the skin by cercariae (e.g. blood flukes), by ingestion of encysted stages (metacercariae) on vegetation (e.g. sheep liver flukes), or ingestion of encysted metacercariae in the tissues of a second intermediate host (e.g. human liver flukes). Some 6,700 digenean species belonging to 22 superfamilies have been described in fish and tetrapods. The subclass Digenea is divided into 2 orders: Diplostomida characterized by furcocercous cercariae that penetrate definitive hosts; and Plagiorchiida with variable life-cycles but often involving cercariae being ingested by definitive hosts.

Superfamily (+ no. families)	**No. spp.**	**DH[a]**	**Egg[b]**	**IH1[c]**	**Asexual[d]**	**Cercaria[e]**	**IH2[f]**	**Mode[g]**
Subclass: Aspidogastrea (large ventral disc with numerous alveoli (suckerlets) or rows of suckers, tegument with short protrusions (microtubercles), obligate ectoparasites on molluscs, turtles, fish)								
Aspidogastroidea (4)	65	M,F,C,T	A	G,B	-	-	-	8
Subclass: Digenea (oral and ventral sucker; syncytial tegument; obligate endoparasites of vertebrates)								
Order: Diplostomida (blood flukes, 'strigeids') ~1,480 species								
Brachylaimoidea (2)	250	T	E	G	S	S,F	M	6,7
Diplostomoidea (5)	800	T	P	G	S	F	C,M,A	6
Schistosomatoidea (5)	430	F,C,T	P	G,B,A	R,S	F	-	1,6
Order: Plagiorchiida ('echinostomatids', 'plagiorchiids') ~5,200 species								
Allocreadioidea (6)	1,118	F,T	P	G,B	R,S	S,Y	C,M,R,A	6
Apocreadioidea (1)	94	F	P	G	R	S	M,A	6
Azygioidea (1)	43	F,C	E	G	R	F	C	3,4
Bivesiculoidea (1)	28	F	P	G	R	F	C	3,4
Bucephaloidea (2)	410	F	P	B	S	F	C	4
Echinostomatoidea (10)	112	F,T	P	G	R	S	C,M,R	5,6,7
Gorgoderoidea (10)	106	F,C,T	P	G,B	R,S	S,Y	C,M,R	5,6,7
Gymnophalloidea (4)	200	F,T	P	B	S	F	C,M,R,A,E,N	3,4,6
Haplosplanchnoidea (1)	51	F	P	G	S	S	-	5
Hemiuroidea (15)	1,160	F,C,T	E	G,B,S	R,S	F	C,M,R,N	4
Heronimoidea (1)	1	T	P	G	S	S	-	7
Lepocreadioidea (8)	473	F	P	G	R	S	C,M,R,A,E,N	6
Microphalloidea (12)	414	F,T	P	G,B	S	S,Y	C,M,R,A,E	6.7
Monorchioidea (3)	270	F	E	G,B	R,S	S	C,R,A,E	6
Opisthorchioidea (3)	436	F,T	E	G	R	S	C	6
Paramphistomoidea (5)	74	F,T	P	G	R	S	-	5
Plagiorchioidea (16)	47	F,T	P	G	R,S	S,Y	C,M,R,A	6
Pronocephaloidea (6)	131	F,T	E	G	R	S	-	5
Transversotrematoidea (1)	27	F	P	G	R	F	-	2

LEGEND

[a] DH = definitive host: F = teleost fish; C = chondrichthyan fish; T = tetrapod; M = mollusc

[b] Fate of egg: A = larva hatches and attaches to IH1, E = eaten by IH1, P = hatches releasing miracidium which penetrates IH1

[c] IH1 = first intermediate host: G = gastropod, B = bivalve, A = annelid, S = scaphopod

[d] Asexual reproduction involves formation of secondary: R = redia, S = sporocyst

[e] F = fork-tailed cercaria, S = simple tailed cercaria, Y = cercaria with stylet

[f] IH2 = second intermediate host: C = chordate, M = mollusc, R = arthropod, A = annelid, E = echinoderm, N = cnidaria, ctenophore

[g] Mode of infection for DH: 1 = cercaria penetrates DH; 2 = cercaria attaches to DH; 3 = cercaria eaten by DH; 4 = cercaria eaten by IH2; 5 = cercaria emerges, encysts in open and eaten by DH; 6 = cercaria emerges, penetrates IH2, encysts and eaten by DH; 7 = cercaria remains in IH1, encysts and eaten by DH; 8 = no cercarial stage, infected IH1 eaten by DH.

One diplostomatid suborder has been recognized containing 3 superfamilies. The suborder Diplostomata is characterized by species forming furcocercous (fork-tailed) cercariae which either penetrate invertebrate intermediate hosts (forming metacercariae) or directly penetrate vertebrate definitive hosts (forming adults). Members of the superfamily Schistosomoidea do not form metacercariae in second intermediate hosts and their cercariae have been found to develop not only in gastropods but sometimes in bivalves or annelids. Some 430 species have been described in 5 families (Clinostomatidae, Aporocotylidae, Sanguicolidae, Spirorchiidae, Schistosomatidae), the latter 4 families comprising the blood flukes. The family Schistosomatidae contains the blood flukes living in venous blood vessels of tetrapods, the only trematodes that live in the bloodstream of warm-blooded hosts (rich in glucose and amino acids). Schistosomatids are also unique in that the adults are not hermaphroditic but form separate sexes (males resemble rolled leaves with ventral gynaecophoric canals in which the long slender females reside). At present, 15 genera have been classified into 4 subfamilies distinguished by differences in adult morphology and host specificity: Bilharziellinae (short gynaecophoric canal or absent, female genital pore posterior to ventral sucker; *Bilharziella, Trichobilharzia*); Dendritobilharziinae (short canal, anterior pore, dendritic caeca; *Dendritobilharzia*); Gigantobilharziinae (short canal, anterior pore, no ventral sucker; *Gigantobilharzia*); and Schistosomatinae (well-developed canal; *Austrobilharzia* (incl. *Microbilharzia*)*, Ornithobilharzia, Macrobilharzia, Jilinobilharzia, Allobilharzia, Anserobilharzia, Bivitellobilharzia, Heterobilharzia, Schistomatium, Schistosoma* (incl. *Orientobilharzia*) and *Griphobilharzia*). The first 10 genera infect birds, the next 4 genera infect mammals and the last genus infects reptiles.

Parasite genus	Definitive hosts	Location	Intermediate hosts (gastropod family)	Distribution
Bilharziella	Anseriformes, Gruiformes, Ciconiformes, Podicipediformes	visceral	freshwater Planorbidae	Europe
Trichobilharzia	Anseriformes (Anatidae)	visceral, nasal	freshwater Lymnaeidae, Physidae	Global
Dendritobilharzia	Anseriformes, Gruiformes, Pelicaniformes, Gaviiformes	visceral	freshwater Planorbidae	Global
Gigantobilharzia	Passeriformes	visceral	freshwater Physidae	North America
Austrobilharzia (incl. *Microbilharzia*)	Charadriiformes	visceral	marine Nassariidae, Batillaridae, Littoriniidae, Potamididae	Global
Ornithobilharzia	Charadriiformes	visceral	marine Batillaridae	Global
Macrobilharzia	Suliformes	visceral	unknown	North America, Africa
Jilinobilharzia	Anseriformes (Anatidae)	visceral	unknown	China
Allobilharzia	Anseriformes (swans)	visceral	unknown	Northern Hemisphere
Anserobilharzia	Anseriformes (geese)	visceral	freshwater Planorbidae	Northern Hemisphere
Bivitellobilharzia	Elephantidae, Rhinocerotidae	visceral	unknown	Africa, Asia
Heterobilharzia	Carnivora, Artiodactyla, Rodentia	visceral	freshwater Lymnaeidae	North America
Schistosomatium	Rodentia	visceral	freshwater Lymnaeidae	North America
Schistosoma (including *Orientobilharzia*)	Primates, Artiodactyla, Rodentia	visceral, nasal	freshwater Planorbidae, Lymnaeidae, Pomatiopsidae	Eurasia, Africa, South America, China
Griphobilharzia	Crocodilia	visceral	unknown	Australia

Many avian schistosome species infect the blood vessels in the viscera or nasal mucosa of waterfowl and shorebirds that have become infected by penetration of cercariae released from aquatic snails. Cercariae from many of these species may also penetrate the skin of humans coming into contact with contaminated water. The parasites do not complete their development in these aberrant hosts but their migration can produce a painful transient creeping dermatitis (colloquially known as swimmer's itch, clam-digger's itch or duck itch), negatively impacting on recreational water use and tourism.

Parasite species	Definitive hosts [adults in blood vessels]	Intermediate hosts [sporocysts in tissues]	Distribution
Bilharziella			
B. littlebi (syn. *Trichobilharzia*)	Passeriformes: parulid (chestnut-sided warbler)		North America
B. polonica	Anseriformes: anatid (duck, mallard, teal, mute	freshwater Gastropoda:	Europe,

(syn. *B. indica, Ornithobilharzia*)	swan, goose); Gruiformes: rallid (crested coot); Podicipediformes: podicipedid (great crested grebe)	planorbid (*Planorbis corneus, Planorbarius corneus, Bulinus africanus*)	Africa, Asia, North America
Trichobilharzia			
adults in nasal veins			
T. arcuata	Anseriformes: anatid (wandering whistling duck, muscovy); Columbiformes: columbid (pigeons)	freshwater Gastropoda: lymnaeid (*Lymnaea lessoni*)	Australia
T. aureliani	Podicipediformes: podicipedid (crested grebe, dabchick)		Africa
T. australis	Anseriformes: anatid (Pacific black duck)	freshwater Gastropoda: lymnaeid (*Radix* spp.)	Australia
T. duboisi	Anseriformes: anatid (African pygmy goose)		Africa
T. nasicola	Anseriformes: anatid (yellow-billed duck)		Africa
T. regenti	Anseriformes: anatid (mallard, muscovy); Galliformes: phasianid (chicken)	freshwater Gastropoda: lymnaeid (*Radix lagotis, R. labiata, R. peregra, R. ovata, R. auricularia*)	Europe, Middle-East
T. rodhaini	Pelecaniformes: threskiornithid (Hadada ibis)		Africa
T. spinulata	Anseriformes: anatid (Egyptian goose, spur-winged goose)		Africa
adults in viscera			
T. adamsi	Anseriformes: anatid (Pekin duck)	freshwater Gastropoda: physid (*Physa coniformis, P. gyrina*)	North America
T. alaskensis	Anseriformes: anatid (Pekin duck)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*)	North America
T. anatina (syn. *T. berghei*)	Anseriformes: anatid (yellow-billed duck)		Africa
T. brevis	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*)	Malaysia
T. brantae	Anseriformes: anatid (Canada goose)		North America
T. burnetti	Anseriformes: anatid (ring-necked duck)		North America
T. cameroni	Anseriformes: anatid (duck); Passeriformes: fringillid (canary); Columbiformes: columbid (pigeon)	freshwater Gastropoda: physid (*Physa gyrina*)	North America
T. cerylei	Coraciiformes: alcedinid (pied kingfisher)		Africa
T. corvi	Passeriformes: corvid (carrion crow, Australian raven); emberizid (yellow bunting); Galliformes: phasianid (chicken)	freshwater Gastropoda: pleurocerid (?)	Asia, Australia
T. elvae	Anseriformes: anatid (black duck, Pekin duck), Passeriformes: fringillid (canary)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis*)	North America
T. filiformis	Anseriformes: anatid (mute swan)		Europe
T. franki	Anseriformes: anatid (mallard)	freshwater Gastropoda: lymnaeid (*Radix auricularia, R. ovata*)	Europe
T. guandongensis	?		Asia
T. horiconensis	Anseriformes: anatid (American wigeon)		North America
T. indica	Anseriformes: anatid (common teal)		India
T. jequitibaensis	Anseriformes: anatid (muscovy)	freshwater Gastropoda: lymnaeid (?), physid (?)	South America
T. jianensis	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (?)	Asia
T. kegonsensis	Anseriformes: anatid (canvasback)		North America
T. kowalewski	Anseriformes: anatid (common teal)		Eurasia
T. limnaeae	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (?)	Asia
T. lonchurae (*Pseudobilharziella*)	Passeriformes: estrildid (mannikin)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*)	Malaysia
T. maegraithi	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (*Lymnaea rubiginosa*)	Asia
T. mergi	Anseriformes: anatid (red-breasted merganser)	freshwater Gastropoda: lymnaeid (*Radix balthica* (= *R. peregra*, = *R. ovata*))	Iceland

T. ocellata (syn. *T. kossarewi*)	Anseriformes: anatid (duck, teal)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis, Stagnicola palustris*), planorbid (*Planorbarius corneus, Planorbis rotundatus*)	Eurasia, North America
T. oregonensis	Anseriformes: anatid (Pekin duck)	freshwater Gastropoda: physid (*Physa ampullacea, P. gyrina*)	North America
T. paoi	Anseriformes: anatid (mallard)	freshwater Gastropoda: lymnaeid (*Radix swinhoei, Galba pervia*)	Asia
T. parocellata	Anseriformes: anatid (muscovy duck, Sunda teal, Pacific black duck)	freshwater Gastropoda: lymnaeid (*Lymnaea ovata, L. stagnalis, L. lessoni*)	Europe, Australia
T. physellae	Anseriformes: anatid (mallard); Columbiformes: columbid (pigeon); Passeriformes: fringillid (canary)	freshwater Gastropoda: physid (*Physa parkeri, P. magnalacustris*)	North America
T. querquedulae	Anseriformes: anatid (blue-winged teal, northern shoveler)	freshwater Gastropoda: physid (*Physa gyrina*)	North America
T. salmanticensis	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (*Radix ovata*)	Europe
T. schoutedeni	Anseriformes: anatid (white-backed duck)		Africa
T. stagnicolae	Passeriformes: fringillid (canary); Anseriformes: anatid (duck); Charadriiformes: larid (gull)	freshwater Gastropoda: lymnaeid (*Lymnaea emarginata*)	North America
T. szidati	Anseriformes: anatid (duck)	freshwater Gastropoda: lymnaeid (*Lymnaea stagnalis, L. ovata*)	Europe
T. waubesensis	Anseriformes: anatid (American wigeon, ring-necked duck)		North America
T. zongshani	Anseriformes: anatid (duck)		Asia
Austrobilharzia (incl. *Microbilharzia*)			
A. penneri	Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Psittaciformes: psittacid (parakeet)	marine Gastropoda: potamidid (*Cerithidea scalariformis*)	North America
A. terrigalensis (syn. *A. variglandis, Microbilharzia*)	Pelecaniformes: ardeid (Pacific reef heron); Charadriiformes: larid (silver gull, brown noddy, sooty tern), scolopacid (ruddy turnstone); Galliformes: phasianid (chicken); Anseriformes: anatid (duck, canvasback, red-breasted merganser, lesser scaup)	marine Gastropoda: littorinid (*Littorina pintado*), planaxid (*Planaxis sulcatus*), batillariid (*Velacumantus australis, Pyrazus (Batillaria) australis*), nassarid (*Ilyanassa* (*Nassa*) *obsoleta*)	Australia, North America
A. odhneri (syn. *Ornithobilharzia, Sinobilharzia*)	Charadriiformes: scolopacid (Eurasian curlew)		China
A. pricei (syn. Ornithobilharzia)	Anseriformes: anatid (Canada goose)		North America
A. hoepplii (syn. *Ornithobilharzia, Microbilharzia*)	Charadriiformes: scolopacid (Swinhoe's snipe)		China
A. lari (syn. *Ornithobilharzia, Microbilharzia*)	Charadriiformes: larid (European herring gull, ring-billed gull, Bonaparte's gull)		Canada
A. bayensis	Charadriiformes: scolopacid (common snipe)		Philippines
Heterobilharzia			
H. americana	Carnivora: canid (dog, coyote), felid (bobcat, mountain lion), procyonid (raccoon), mustelid (mink); Rodentia: castorid (beaver), echimyid (coypu); Lagomorpha: leporid (swamp rabbit); Didelphimorphia: didelphid (opossum); Artiodactyla: cervid (white-tailed deer)	freshwater Gastropoda: lymnaeid (*Lymnaea cubensis*, *Pseudosuccinea columella*)	North America
Gigantobilharzia			
G. acotylea	Charadriiformes: larid (common gull, lesser black-backed gull, little gull, black-headed gull,	aquatic Gastropoda: physid (*Physa fontinalis*), planorbid	Europe

	common tern, white-winged tern); Passeriformes: hirundinid (sand martin); Podicipediformes: podicipedid (great crested grebe); Anseriformes: anatid (duck)	(*Anisus spirorbis*)	
G. adami	Anseriformes: anatid (African pygmy goose)		Africa
G. ardeola	Pelecaniformes: ardeid (Malagasy pond heron)		Madagascar
G. elongata	Podicipediformes: podicipedid (pied-billed grebe)	freshwater Gastropoda: planorbid (*Gyraulus parvus*)	North America
G. gyrauli	Passeriformes: icterid (red-winged blackbird, yellow-headed blackbird, brown-headed cowbird, common grackle)	freshwater Gastropoda: planorbid (*Gyraulus parvus*), physid (*Physa* sp.)	North America
G. huronensis	Passeriformes: fringillid (American goldfinch), cardinalid (northern cardinal)	freshwater Gastropoda: physid (*Physa gyrina)*	North America
G. huttoni	Psittaciformes: psittacid (parakeets)	marine Gastropoda: bullid (*Haminoea antillarum*)	North America
G. lawayi	Charadriiformes: larid (European herring gull, ring-billed gull, Bonaparte's gull)		North America
G. nettapi	Anseriformes: anatid (African pygmy goose)		Africa
G. plectropteri	Anseriformes: anatid (spur-winged goose)		Africa
G. sturniae	Passeriformes: corvid (carrion crow), sturnid (chestnut-cheeked starling)	freshwater Gastropoda: planorbid (*Segmentina nitidella, Polypylis hemisphaerula*)	Japan
G. tantali	Ciconiiformes: ciconiid (yellow-billed stork)		Africa
G. vittensis	Charadriiformes: larid (common gull)	freshwater Gastropoda: planorbid (*Anisus leucostomus*)	Europe
Ornithobilharzia			
O. canaliculata (syn. *O. intermedia, O. kowalewskii*)	Charadriiformes: larid (gulls, terns); Procellariiformes: procellariid (puffin); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon)	marine Gastropoda: batillariid (*Batillaria minima*)	Eurasia, Americas

Parasite morphology: These avian schistosomes form 5 different stages in their developmental cycles: eggs, miracidia, sporocysts, cercariae and adults. Eggs may be spindle-shaped, cresentic or ellipsoidal, measuring around 180 µm in length (depending on species), often with a small projection or hook at one end. As they mature, they embryonate to contain a well-developed miracidium. Hatched miracidia are pyriform in shape, measure ~110 µm in length, and are covered by a mosaic of ciliated plates often arranged in 4 tiers and separated by ridges, some with lateral horns. They contain prominent apical and lateral glands and the posterior body is filled with clusters of germinal cells. Sporocysts are pleomorphic sac-like structures without any conspicuous organ systems other than balls of germinal cells that undergo asexual reproduction to produce another generation of sporocysts. Daughter sporocysts produce cercariae measuring up to 1mm in length which have elongate tubular bodies (~300 µm long) with distinctive furcocercous (forked) tails (stem 250-500 µm long, 2 prongs each 150-250 µm long). The cercarial body has an anterior head organ, prominent penetration glands located around the ventral sucker (previously called the acetabulum), 1-2 pigmented eyespots (ocellate), a spiny tegument but is apharyngate. Adult flukes have long, slender filiform bodies, measuring from 3-10 mm in length and 20-100 µm in diameter, and the posterior end is spatulate. The tegument is often covered by tubercles or spines and they possess oral and ventral suckers. The digestive tract lacks a pharynx, but has a long oesophagus which bifurcates into 2 caeca with then recombine posteriorly. Schistosomes are not hermaphroditic but dioecious forming separate males and females. Adult worms are invariably found in male-female pairs, with male worms possessing short gynaecophoric canals that partly contain female worms. Males have numerous posterior testes, an elongate seminal vesicle between the ventral sucker and gynaecophoric canal, a small cirrus and a genital pore located at the anterior end of the canal. Females have a single elongate coiled ovary located anteriorly and connected to a well-developed posterior seminal receptacle and numerous vitellaria, an anterior ootype and an elongate uterus that opens immediately posterior to the ventral sucker. Fertilized female worms generally only contain a single egg in the uterus.

Site of infection: Adult schistosomes live in blood vessels in visceral organs or the nasal mucosa of their definitive hosts (birds). Asexual developmental stages (sporocysts) develop in the tissues, predominantly the hepatopancreas, of their intermediate hosts (aquatic snails).

Pathogenesis: Most avian schistosomes are not pathogenic in their definitive hosts, but some species have been associated with significant tissue injuries in birds, caused by migration of cercariae, schistosomula, adult flukes, eggs or miracidia. Migrating stages cause tracking trauma, focal lesions, petechial haemorrhages, inflammation, cellular infiltration and other host immune responses. Parasites may become trapped in host tissues where they provoke fibrosis and granuloma formation. Most fluke species migrate through the viscera of their hosts, but those species with a predilection for nasal mucosa migrate through nervous tissue (esp. white

matter) and may cause neuromotor disorders. Outbreaks of trichobilharziasis have been recorded in ducks and geese with significant morbidity (esp. leg paralysis and balance disorders) and low mortality. The impact of infections on wild bird species is not known although miscellaneous case reports have been published. Avian schistosomes have also been associated with clinical disease in humans and other mammals, when cercariae penetrate the skin causing painful transient creeping dermatitis (colloquially known as swimmer's itch, clam-digger's itch or duck itch), more intense in sensitized hosts. Symptoms include erythema, oedema, thickening and itching of immersed skin, followed by the development of pruritic hyperaemic papules which may become vesicular. Scratching the affected areas may result in secondary bacterial infections. In repeated infections, cellular infiltration (neutrophils, eosinophils, macrophages, lymphocytes, mast cells) is more severe and may lead to the formation of large abscesses, epidermal and/or dermal necrosis. Cases of cercarial dermatitis can occur in both fresh and brackish water environments. Several parasite species seem to be responsible for the majority of dermatitis outbreaks in humans, particularly *Trichobilharzia franki*, *T. physellae*, *T. querquedulae* and *Austrobilharzia variglandis* associated with aquatic environments used for tourism and recreational purposes. Interestingly, while experimental studies have shown that avian schistosomes do not mature in nonpermissive (incompatible) mammalian hosts, they have also recently shown that not all parasites are trapped and eliminated in the skin, but may wander for extended periods through nervous tissues and viscera, possibly contributing to more complications than previously thought.

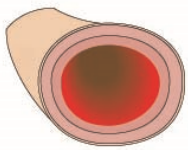
Developmental cycle and mode of transmission: Like other digenetic trematodes, avian schistosomes have indirect heteroxenous life-cycles involving transmission between definitive (bird) and intermediate (snail) hosts with free-swimming aquatic larval stages. Adult flukes living in blood vessels of birds deposit eggs into the circulation where they release proteolytic enzymes to pass through different tissue layers to reach the gut or nasal mucosa. Eggs of visceral species reach the gut lumen and are excreted with host faeces where they hatch releasing their enclosed miracidia. Eggs of nasal species reach the nasal cavity and hatch when they come into contact with water when the host feeds/drinks (an exception is the species *T. regenti* whose eggs hatch directly in the mucosa and the freed miracidia await contact with water). Once in water, the ciliated miracidia swim for up to 24 hours actively seeking snail hosts using chemotactic cues. A small range of aquatic snails act as suitable intermediate hosts; including freshwater lymnaeids, physids, planorbids (rarely pleurocerids) and marine potamidids, littorinids, planaxids, batillariids, nassarids and bullids. The miracidia penetrate snail tissues in the head-foot region shedding their cilia and developing into sac-like sporocysts. The parasites undergo 2 generations of asexual reproduction whereby mother sporocysts produce daughter sporocysts which migrate to the hepatopancreas before producing cercariae. The prepatent period in snails (time from infection to first release of cercariae) ranges from 3-10 weeks. Cercariae emerge from snails into water and use their forked tails to swim about seeking vertebrate hosts. A range of migratory and territorial bird species act as suitable definitive hosts, notably those associated with aquatic ecosystems such as waterfowl and shorebirds. Cercariae penetrate the skin shedding their tails and transforming into schistosomula which migrate via the circulation, lymphatics or peripheral nerves to their final predilection sites (blood vessels in the viscera or nasal mucosa). Cercariae may also cause transient infections in non-permissive vertebrate hosts, mostly mammals swimming or bathing in contaminated waters.

Differential diagnosis: Infections in avifauna are usually diagnosed at post-mortem by the detection of adult flukes in tissues from dead birds, often incidentally as the worms are located in cryptic sites. The detection of eggs in faecal samples, nasal swabs, aspirates or exudates is often difficult due to their low numbers, sporadic excretion and short longevity (eggs may hatch internally or upon contact with water). Furcocercariae may also be recovered from snail hosts following their dissection or after their emergence in wet cultures. Clinical infections in aberrant hosts (mammals) present with cercarial dermatitis, usually manifest by characteristic allergenic reactions (creeping eruptions). Blood tests often reveal a concurrent systemic eosinophilia and elevated IgE levels. A small number of serological tests have been developed to detect specific host antibodies to cercarial antigens, including complement fixation, immunofluorescence and enzyme immunoassays, but they often yield low sensitivity and specificity. Researchers have detected differences between several common types of cercariae by karyotypic studies, while molecular characterization techniques have discriminated between adult and larval stages of several *Trichobilharzia* spp. by polymerase chain reaction (PCR) amplification of nuclear genes (5.8S and 28S ribosomal RNA, internal transcribed spacer regions 1 and 2) and mitochondrial genes (cytochrome c oxidase subunit 1, NADH dehydrogenase subunits 2, 4 and 6).

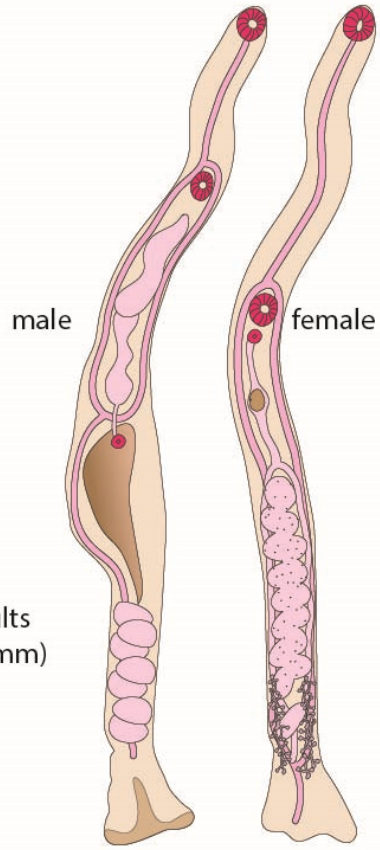
Treatment and control: Clinical infections in birds have responded well to treatment with the broad-spectrum anthelmintic praziquantel, although advanced cases (particularly those involving neurological signs) did not fully resolve. Nonetheless, drug treatment significantly reduced egg production and excretion in individuals not cured. The prevention of infections is based around breaking the transmission cycle between snails and birds, thus reducing the numbers of infective cercariae present in water. Various attempts have been made to reduce the contamination of water bodies by parasite eggs and miracidia, either by treating birds or relocating them. While some success has been reported in small scale peridomestic situations, efforts to control wild bird populations are untenable. Greater success has been achieved in reducing snail populations by chemical, mechanical and biological control, but the widespread application of molluscicides may have untoward toxicological and environmental consequences. Disturbing snail habitats in shallow ponds and lakes by mechanized tilling or raking has proven effective in reducing snail numbers, particularly when carried out during their breeding seasons. Removing aquatic vegetation, introducing natural predators (e.g. fish) and temporarily draining small ponds have also been successful in reducing snail numbers. Considerable effort has been made in several endemic areas (especially those frequented by tourists) to prevent cercariae from infecting humans. Advisory notices, and even legal regulations, have attempted to prohibit or restrict human access to contaminated waters, but they are often ignored by

swimmers and bathers. Most cases of cercarial dermatitis involve skin openly exposed to water, prompting studies that have shown some protection may be afforded by protective clothing, thoroughly drying the skin immediately after water contact, and coating the skin with vaseline or recently-developed chemical repellents.

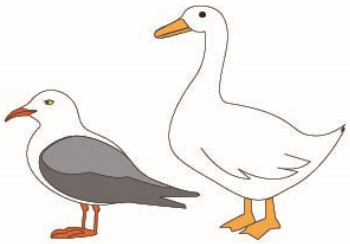
Trichobilharzia, Austrobilharzia



blood vessels
(viscera, nasal mucosa)
(cercarial dermatitis,
egg granulomas,
fibro-obstructive disorders)



adults
(~ 7 mm)



Definitive Hosts
(freshwater waterfowl,
marine shore birds)

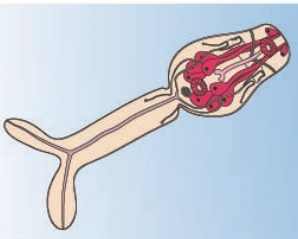
excretion
(faeces,
nasal mucus)

eggs
(~ 180 µm)



skin
penetration

vector-borne transmission





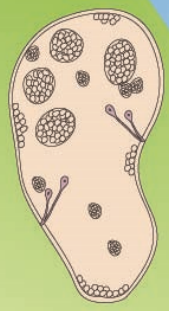
endoparasitic in
tissues of vector

free-swimming
cercaria
(~ 1 mm)

free-swimming
miracidium
(~ 110 µm)



redia
(~ 1 mm)



sporocyst
(~ 1 mm)



Intermediate Hosts (freshwater lymnaeid snails, marine potamidid snails)
(visceral then glandular tissues)



Trichobilharzia eggs



Trichobilharzia cercaria

2020

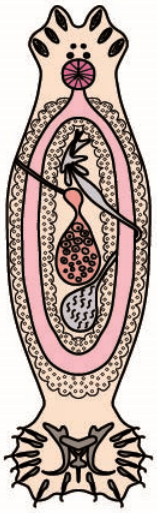
Monogenea
(monogenetic flukes)

Monogenea

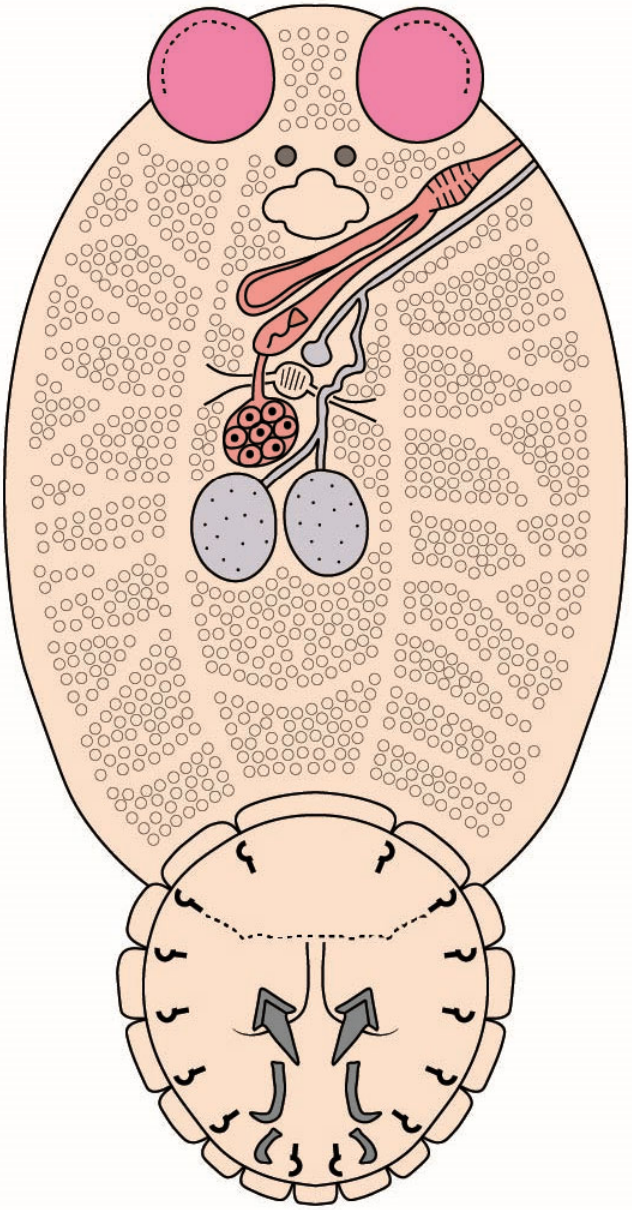
Gyrodactylus
adult (ventral)
(~ 1 mm)



Dactylogyrus
adult (ventral)
(~ 1.5 mm)



Benedenia
adult (ventral)
(~ 9 mm)



Gyrodactylus
(platyhelminth: monogenean)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Monogeneans are elongate to oval flatworms that are ectoparasitic on the skin and gills of fish, although a few are found in the urinary tracts of turtles, frogs, fishes and the eye of the hippopotamus. They have an anterior adhesive organ (prohaptor) and a conspicuous posterior adhesive organ (opisthaptor) armed with hooks or spines, often highly modified for attachment to specific sites. They are hermaphroditic and have direct life-cycles mostly where eggs hatch releasing a free-swimming larva (oncomiracidium) which actively seeks a new host. Monopisthocotyleans have an opisthaptor that forms a single symmetrical attachment unit lacking haptoral clamps. Gyrodactylids are unusual in that they are viviparous (produce live young); some even exhibiting hyperviviparity where subadults retained in the uterus develop their own young (cf. Russian nested dolls). Gyrodactylids are small long worms with an opisthaptor possessing a pair of large central hooks and 16 small marginal hooks. Various *Gyrodactylus* spp. are significant pests in fish ponds and heavy infestations of the gills may cause mortalities through blood loss and mucoid congestion.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Monogenea (monoxenous ectoparasites, sac-like gut, direct cycles, oncomiracidium with 3 ciliary bands)
Order:	Monopisthocotylea (posterior haptor comprising a single symmetrical attachment unit, no haptoral clamps)
Family:	Gyrodactylidae (posterior haptor, armed with hooks; viviparous, sometimes hyperviviparity)
Genus:	*Gyrodactylus* (parasitic in skin/fins/gills of fish)
Species:	various species cause respiratory signs in fish

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

Monogeneans and trematodes (flukes) have blind sac-like guts (lacking an anus) while cestodes (tapeworms) lack digestive tracts. Some 3,500 monogenean species have been described: most being ectoparasitic on the skin and gills of fish, although a few are found in the urinary tracts of turtles, frogs, fish and the eye of the hippopotamus. They have an anterior adhesive organ (prohaptor) and a conspicuous posterior adhesive organ (opisthaptor) armed with hooks, hooklets, hamuli (anchors) or clamps, often highly modified for attachment to specific sites. They are monoecious (hermaphroditic) and have direct monoxenous life-cycles mostly where eggs release free-swimming larvae (oncomiracidia with 3 ciliary bands) that actively seek new hosts (gyrodactylids are the exception as they are viviparous and produce live young). While the higher taxonomy of the Monogenea is often disputed with respect to rank, some 67 families have been resolved on the basis of morphological, biological and molecular studies. Three main groups are recognized: 28 families of Monopisthocotylea (opisthaptor with hooks, ectoparasitic on fish skin and gills, feed on

epithelia); 37 families of Polyopisthocotylea (opisthaptor with clamps, ectoparasitic on fish gills, feed on blood); and 2 families of Polystomatoinea (opisthaptor with suckers, endoparasitic in tetrapods).

Order	No. families	No. spp.	DH	Characters
Class: Monogenea (= Monogenoidea) (monogenetic life-cycles, ectoparasitic mainly on fish) ~ 3,500 spp.				
Subclass: Monopisthocotylea (= Polyonchoinea) (opisthaptor with hooks, feed on fish epithelia) ~2,500 spp.				
Capsalidea	2	200	mostly marine teleosts, some elasmobranchs	2 anterior suckers, 2 pairs anchors, 14 marginal haptoral hooks, some loculi
Dactylogyridea (= Monoaxonematidea)	17	1,000	freshwater and marine teleosts, coelacanths, squalea	sperm with single axoneme, 12-14 haptoral hooks, 2 pairs anchors, 1 transverse bar
Gyrodactylidea	5	1,500	freshwater and marine teleosts, squid, copepods	16 marginal 'hinged' haptoral hooks,1 pair anchors, dorsal and ventral bars, most viviparous (some nested polyembryony)
Monocotylidea	3	90	marine elasmobranchs	14 marginal haptoral hooks, some loculi
Montchadskyellidea	1	10	marine teleosts	14 marginal haptoral hooks, gut diverticulate, some endoparasitic in gut
Subclass: Polyopisthocotylea (= Heteronchoinea) (opisthaptor with clamps, most feed on blood of fish) ~1,000 spp.				
Chimaericolidea	1	5	marine holocephalans (chimaeras)	clamps, 1 pair anchors, haptor with 14 marginal hooks (each with domus)
Diclybothriidea	2	70	marine elasmobranchs, holocephalans, freshwater acipenseriform teleosts	clamps open and act as suckers, lateral sclerites absent
Mazocraeidea	34	920	numerous freshwater and marine teleost families	clamps with various structures incl. additional sclerites, hooks, spines; oral sucker a buccal organ, eggs with 2 polar filaments
Subclass: Polystomatoinea (parasitize aquatic tetrapods and lungfish)				
Polystomatidea	2	100	tetrapods (turtles, amphibians, hippopotamus), lungfish	haptor with 3 pairs suckers, egg filaments absent, some endoparasitic in tubular organs

Monopisthocotyleans have an opisthaptor that forms a single symmetrical attachment unit lacking haptoral clamps. Five orders are recognized on the basis of differences in parasite morphology, development and host occurrence; including the order Gyrodactylidea characterized by worms having a posterior haptor with 16 marginal articulated ('hinged') hooks and a single pair of hamuli (anchors) with a connective dorsal bar. A total of 1,500 species belonging to 5 families (Acanthocotylidae, Anoplodiscidae, Bothitrematidae, Gyrodactylidae, Tetraonchoididae and Udonellidae) have been described from marine and freshwater bony (teleost) fishes with occasional reports on crustaceans (copepods), cephalopods (squid) and amphibians (frogs). Gyrodactylids are characterized by the possession of multiciliate 'spike' sensilla (one on each cephalic lobe), all stages lacking pigmented eyespots, and the adult male and female reproductive systems having separate openings (intromittent organ tubular and reinforced with rings, accessory sclerites or spines). Most members of the family Gyrodactylidae are not oviparous (do not lay eggs or produce oncomiracidia) but are viviparous (produce live unciliated crawling juveniles); many even exhibiting hyperviviparity (polyembryony) where subadults retained in the uterus develop their own young (cf. Russian nested dolls).

The family Gyrodactylidae was erected to accommodate only the viviparous genus *Gyrodactylus*. Subsequently, a series of subfamilies were proposed to include other genera primarily on the basis of differences in haptor morphology (e.g. Isancistrinae lacking bars and hamuli, Polyclithrinae with numerous supporting bars, and the remainder placed in the catch-all Gyrodactylinae), but these subfamilies have received little support in molecular phylogenies. Most authors continue to recognise a major division between viviparous and oviparous forms as they are profoundly different biologically. The oviparous genera are protandrous hermaphrodites that lay eggs with a sticky droplet. The eggs hatch to release unciliated crawling larvae with prominent spike sensillae. Seven genera have been described from South American catfish primarily on the basis of differences in the structure of the male reproductive system and the vitelline system; namely, *Aglaiogyrodactylus, Hyperopletes, Nothogyrodactylus, Ooegyrodactylus, Onychogyrodactylus, Phanerothecium* and *Phanerothecioides.* The viviparous genera exhibit little variation in internal anatomy. While some morphological differences have been observed in penis structure, the occurrence of hamuli and bars, and the presence of accessory sclerites on the haptor, molecular studies indicate that considerable variation, not reflected in morphology, occurs between and within genera. Six *Gyrodactylus* subgenera (*Gyrodactylus, Mesonephrotus, Paranephrotus, Metanephrotus, Neonephrotus, Limnonephrotus*) have been differentiated on the basis of type of excretory system and host occurrence, but these groupings have not been supported by molecular studies. Several genera have recently been synonymized with *Gyrodactylus* on the basis of morphological and/or molecular studies, including *Afrogyrodactylus, Paragyrodactylus, Paragyrodactyloides*, *Fundulotrema* and *Metagyrodactylus*. Other gyrodactylid genera described include *Accessorius, Macrogyrodactylus* (syn. *Neogyrodactylus*), *Mormyrogyrodactylus, Gyrocerviceanseris*, *Scleroductus, Swingleus* and *Ieredactylus*

from freshwater fishes, *Acanthoplacatus, Archigyrodactylus, Gyrodactyloides, Polyclithrum* (syn. *Micropolyclithrum*), *Citharodactylus* and *Laminiscus* (syn. *Archigyrodactylus*) from marine fishes, *Isancistrum* from cephalopods (squid) and *Gyrdicotylus* from amphibians (toads).

Some 400 *Gyrodactylus* spp. have been described from wild, captive and cultured freshwater and marine bony fish belonging to 19 different orders; namely, Anguilliformes (4 *Gyrodactylus* spp.), Clupeiformes (3), Cypriniformes (191), Characiformes (6), Siluriformes (14), Esociformes (6), Osmeriformes (2), Salmoniformes (19), Percopsiformes (2), Gadiformes (17), Mugiliformes (4), Atheriniformes (1), Beloniformes (1), Cyprinodontiformes (22), Gasterosteiformes (14), Scorpaeniformes (20), Perciformes (59), Pleuronectiformes (10) and Tetraodontiformes (3). They are absent or occur infrequently on primitive fishes (agnathans, chondrichthyans, acipenserids, sarcopterygians, neopterygians, osteoglossids), but mostly infect more recently divergent teleost fishes. Despite the broad host range for the genus, most species infect only a narrow range of hosts; many being stenoxenous (specialists) and some being euryxenous or oioxenous (generalists). Species on salmonids tend to infest more hosts than those on cyprinids, and Eurasian fish families host more species than American fish families. Heavy infestations have been found on ornamental fish in aquaria and on fish reared in aquaculture facilities.

***Gyrodactylus* species**	**Habitat**	**Hosts**	**Distribution**
G. acanthorhodei	freshwater	Cypriniformes: cyprinid (Russian bitterling)	Asia
G. ackerti	marine	Pleuronectiformes: pleuronectid (starry flounder)	Northern Pacific
G. actzu	freshwater	Cyprinodontiformes: poeciliid (shortfin molly)	Mexico
G. adspersi	marine	Labriformes: labrid (cunner)	West Atlantic
G. aeglefini	marine	Gadiformes: gadid (haddock)	Nort Atlantic
G. afghanensis	freshwater	Cypriniformes: nemacheilid (stone loach)	China
G. aggregatus	marine	Perciformes: embiotocid (shiner perch)	Northeast Pacific
G. aideni	marine	Pleuronectiformes: pleuronectid (winter flounder)	North America
G. aksuensis	freshwater	Cypriniformes: cyprinid (naked osman)	Asia
G. alabamensis	freshwater	Cypriniformes: cyprinid (bluehead chub)	North America
G. albeoli	freshwater	Cypriniformes: cyprinid (river shiner)	North America
G. alberti	freshwater	Siluriformes: clariid (North African catfish)	Africa
G. albolacustris	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Russia
G. alburnoidesi	freshwater	Cypriniformes: cyprinid (bleak)	Europe
G. aldrichi	freshwater	Cypriniformes: cyprinid (lake chub)	North America
G. alekosi	freshwater	Siluriformes: clariid (North African catfish)	Africa
G. alexanderi	freshwater	Gasterosteiformes: gasterosteid (three-spined stickleback)	Eurasia, North America
G. alexgusevi	freshwater	Gadiformes: lotid (burbot)	Eurasia, North America
G. alviga	marine	Pleuronectiformes: scophthalmid (turbot), pleuronectid (European flounder); Clupeiformes: engraulid (anchovy), clupeid (pontic shad); Perciformes: sparid (annular seabream, salema), mullid (red mullet), pomatomid (bluefish); Atheriniformes: atherinid (bigscale sand smelt), Gadiformes: gadid (whiting); Gobiiformes: gobiid (round goby); Ophidiiformes: ophidiid (cusk-eel); Trachiniformes: uranoscopid (stargazer); Salmoniformes: salmonid (Black Sea salmon); Rajiformes: rajid (thornback skate)	Europe
G. ambystomae	freshwater	Urodela: ambyostomatid (long-toed salamander)	North America
G. ammodyti	marine	Trachiniformes: ammodytid (Pacific sand lance)	North Pacific
G. amphiliusi	freshwater	Siluriformes: amphiliid (loach catfish)	Africa
G. anabantii	freshwater	Anabantiformes: anabantid (ocellated labyrinth fish)	Africa
G. anarhichatis	marine	Perciformes: anarhichadid (Atlantic wolffish, spotted wolffish)	North Atlantic
G. angorae	freshwater	Cypriniformes: nemacheilid (Angora loach)	Middle-East
G. anguillae	marine, freshwater	Anguilliformes: anguillid (American eel, speckled longfin eel, Japanese eel, short-finned eel, European eel)	Atlantic, Pacific
G. anisopharynx	freshwater	Siluriformes: callichthyid (peppered corydoras)	South America
G. antarcticus	marine	Perciformes: nototheniid (dusky rockcod)	Southern Ocean
G. anudarinae	freshwater	Cypriniformes: cobitid (spine loach)	China
G. apazapanensis	freshwater	Cyprinodontiformes: poeciliid (shortfin molly, green	Mexico

		swordtail)	
G. aphredoderi	freshwater	Percopsiformes: aphredoderid (pirate perch)	North America
G. aphyae	freshwater, marine	Salmoniformes: salmonid (Atlantic salmon), Cypriniformes: cyprinid (Eurasian minnow)	North Atlantic
G. aquilinus	freshwater	Cypriniformes: catostomid (longnose sucker)	North America
G. arcuatoides	marine	Gobiiformes: gobiid (sand goby)	Europe
G. arcuatus	marine, freshwater	Perciformes: zoarcid (eelpout); Salmoniformes: salmonid (Atlantic salmon); Trachiniformes: ammodytid (small sandeel); Pleuronectiformes: pleuronectid (European flounder, European plaice); Cypriniformes: cyprinid (white bream); Esociformes: esocid (northern pike); Gasterosteiformes: gasterosteid (ninespine stickleback); Gobiiformes: gobiid (two-spotted goby, tubenose goby)	Europe, North America
G. armatus	marine	Scorpaeniformes: cottid (Pacific staghorn sculpin)	Northeast Pacific
G. asiaticus	freshwater	Salmoniformes: salmonid (lenok)	Asia
G. asperus	freshwater	Cypriniformes: cyprinid (rough shiner)	North America
G. atherinae	marine, freshwater	Atheriniformes: atherinid (bigscale sand smelt)	Europe
G. atratuli	freshwater	Cypriniformes: cyprinid (blacknose dace, longnose dace, Allegheny pearl dace), catostomid (longnose sucker)	North America
G. aurorae	freshwater	Anura: ranid (northern red-legged frog, tadpoles)	North America
G. australis	marine	Perciformes: nototheniid (crowned rockcod)	Southern Ocean
G. avaloniae	freshwater	Perciformes: centrarchid (pumpkinseed); Gasterosteiformes: gasterosteid (ninespine stickleback, fourspine stickleback, three-spined stickleback, blackspotted stickleback); Cyprinodontiformes: fundulid (banded killifish); Salmoniformes: salmonid (rainbow trout, brook trout); Cypriniformes: cyprinid (blacknose dace)	North America, Eurasia
G. baeacanthus	freshwater	Cypriniformes: cyprinid (comely shiner)	North America
G. baicalensis	freshwater	Scorpaeniformes: cottocomephorid (bighead sculpin)	Asia
G. bairdi	freshwater	Scorpaeniformes: cottid (mottled sculpin, slimy sculpin)	North America
G. barbatuli	freshwater	Cypriniformes: nemacheilid (stone loach)	Eurasia
G. barbi	freshwater	Cypriniformes: cyprinid (barbel, Mediterranean barbel, Kura barbel)	Europe, Middle-East
G. benedeni	freshwater	Gobiiformes: gobiid (western Greece goby)	Europe
G. bimaculatus	freshwater	Characiformes: lebiasinid (twospot lebiasina)	South America
G. bimicroforatus	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
G. bios	freshwater	Gobiiformes: gobiid (Thessaly goby)	Europe
G. birmani	marine, freshwater	Salmoniformes: salmonid (Arctic char)	Eurasia, North America
G. bliccensis	freshwater	Cypriniformes: cyprinid (bleak, white bream)	Europe
G. bodegiensis	marine, freshwater	Scorpaeniformes: cottid (sharpnose sculpin)	East Pacific
G. bohemicus	freshwater	Salmoniformes: salmonid (rainbow trout, brook trout)	North Pacific
G. bolonensis	freshwater, marine	Osmeriformes: osmerid (pond smelt)	Arctic
G. botnicus	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Russia
G. brachymystacis	freshwater	Salmoniformes: salmonid (lenok)	Asia
G. branchialis	freshwater	Gobiiformes: gobiid (common goby)	Europe, Africa
G. branchicus	freshwater	Gasterosteiformes: gasterosteid (three-spined stickleback)	Eurasia
G. branchius	marine	Pleuronectiformes: pleuronectid (starry flounder)	North America
G. bretinae	freshwater	Perciformes: percid (speckled darter)	North America
G. brevis	freshwater	Salmoniformes: salmonid (rainbow trout), Cypriniformes: cyprinid (California roach)	North America, Asia
G. bubyri	marine	Gobiiformes: gobiid (Caucasian dwarf goby)	Europe
G. bueni	freshwater	Siluriformes: callichthyid (banded corydoras, bigfin corydoras)	South America
G. bulbacanthus	freshwater	Cyprinodontiformes: fundulid (Plains killifish)	North America

G. bullatarudis	freshwater	Cyprinodontiformes: poeciliid (molly, green swordtail, guppy, eastern mosquitofish, two-spot livebearer)	Americas, Australia
G. bychowskianus	freshwater	Scorpaeniformes: cottocomephorid (yellowfin Baikal sculpin)	Russia
G. byrdi	marine	Perciformes: nototheniid (dusky rockcod)	Southern Ocean
G. caledoniensis	marine	Salmoniformes: salmonid (sea trout, Atlantic salmon)	North Pacific
G. californiensis	marine	Gadiformes: gadid (Pacific tomcod)	Northeast Pacific
G. callariatis	marine	Gadiformes: gadid (Atlantic cod)	North Atlantic
G. callawayensis	freshwater	Cypriniformes: cyprinid (red shiner)	North America
G. cameroni	marine, freshwater	Gasterosteiformes: gasterosteid (fourspine stickleback)	North America
G. camerunensis	freshwater	Siluriformes: clariid (walking catfishes)	Africa
G. campostomae	freshwater	Cypriniformes: cyprinid (central stoneroller)	North America
G. canadensis	freshwater	Gasterosteiformes: gasterosteid (fourspine stickleback, three-spined stickleback, ninespine stickleback)	North America, Eurasia
G. capoetai	freshwater	Cypriniformes: cyprinid (seven khramulya)	Asia
G. carassii	freshwater	Cypriniformes: cyprinid (roach, rudd, gudgeon, common dace, Eurasian minnow, bleak, white bream, Crucian carp, belica, chub)	Europe
G. carolinae	freshwater	Characiformes: crenuchid (South American darter)	South America
G. carpio	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
G. catesbeianae	freshwater	Anura: ranid (American bullfrog, tadpoles)	North America
G. centronoti	marine	Perciformes: nototheniid (sharp-spined notothenia)	Southern Ocean
G. cernuae	freshwater	Perciformes: percid (ruffe, European perch, pike-perch)	Europe, Asia
G. charon	freshwater	Gobiiformes: gobiid (Acheron spiny goby)	Europe
G. chileani	marine	Blenniformes: tripterygiid (triplefin blenny)	South America
G. chitandiri	freshwater	Cichliformes: cichlid (redbreast tilapia, southern mouthbrooder)	Africa
G. chologastris	freshwater	Percopsiformes: amblyopsid (spring cavefish)	North America
G. chondrostomi	freshwater	Cypriniformes: cyprinid (common nase)	Europe
G. cichlidarum	freshwater	Cichliformes: cichlid (blackchin tilapia, mango tilapia, blue tilapia, Guinean tilapia, redbelly tilapia, banded jewelfish, jewelfish)	Eurasia, Africa
G. clarii	freshwater	Siluriformes: clariid (North African catfish)	Africa
G. cobitis	freshwater	Cypriniformes: cobitid (spined loach)	Eurasia
G. colemanensis	marine, freshwater	Salmoniformes: salmonid (sea trout, rainbow trout, lake trout)	Eurasia, North America
G. comephori	freshwater	Scorpaeniformes: comephorid (Baikal oilfish)	Russia
G. commersoni	marine	Scombriformes: scombrid (narrow-barred Spanish mackerel)	South-East Asia
G. coriicepsi	marine	Perciformes: nototheniid (black rockcod)	Southern Ocean
G. corleonis	marine	Syngnathiformes: syngnathid (broad-nosed pipefish)	Europe
G. corti	marine	Perciformes: anarhichadid (wolf-eel)	North Pacific
G. corydori	freshwater	Siluriformes: callichthyid (peppered corydoras)	South America
G. costaricensis	freshwater	Cyprinodontiformes: poeciliid (molly)	Americas
G. costatae	freshwater	Cypriniformes: nemacheilid (eightbarbel loach)	Asia
G. cotti	freshwater	Scorpaeniformes: cottid (bullhead, alpine bullhead, slimy sculpin)	Eurasia, North America
G. cottinus	marine	Scorpaeniformes: cottid (Arctic sculpin)	North Atlantic, North Pacific
G. couesius	freshwater	Cypriniformes: cyprinid (lake chub)	North America
G. cranei	marine	Gadiformes: gadid (Pacific tomcod)	Northeast Pacific
G. crenilabri	marine	Labriformes: labrid (five-spotted wrasse, East Atlantic peacock wrasse, ocellated wrasse, grey wrasse)	Mediterranean
G. cryptarum	marine	Gadiformes: gadid (Atlantic cod)	North Atlantic
G. crysoleucas	freshwater	Cypriniformes: cyprinid (golden shiner)	North America
G. ctenopharyngodontis	freshwater	Cypriniformes: cyprinid (grass carp)	China

G. ctenopomi	freshwater	Anabantiformes: anabantid (ocellated labyrinth fish)	Africa
G. curemae	marine	Mugiliformes: mugilid (white mullet)	West Atlantic
G. curiosus	freshwater	Cypriniformes: nemacheilid (eightbarbel loach)	Asia
G. cyclopteri	marine	Scorpaeniformes: cyclopterid (lumpfish)	North Atlantic
G. cylindriformis	freshwater	Esocifoimes: umbrid (central mudminnow)	North America
G. cyprini	freshwater	Cypriniformes: cyprinid (freshwater bream, common carp, rudd)	Europe
G. cyprinodontis	freshwater	Cyprinodontiformes: cyprinodontid (Amargosa pupfish)	North America
G. cytophagus	freshwater	Cyprinodontiformes: poeciliid (Tanganyika lampeye, Norman's lampeye, Bitschumbi lampeye)	Africa
G. dakotensis	freshwater	Cypriniformes: catostomid (bigmouth buffalo, river carpsucker)	North America
G. danastriae	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Russia
G. dechtiari	freshwater	Cypriniformes: cyprinid (longnose dace, blacknose dace)	North America
G. decorus	freshwater	Cypriniformes: cyprinid (common roach, sunbleak)	Europe
G. derjavini	marine, freshwater	Salmoniformes: salmonid (Arctic char, brook trout, sea trout, rainbow trout, Atlantic salmon), Cypriniformes: cyprinid (common carp, Kura nase)	Eurasia, North America
G. derjavinoides	marine	Salmoniformes: salmonid (sea trout)	Europe
G. dogieli	marine	Pleuronectiformes: pleuronectid (common dab)	Europe
G. donghuensis	freshwater	Cypriniformes: cyprinid (bitterling)	China
G. dorlodoti	freshwater	Gobiiformes: gobiid (western Greece goby)	Europe
G. dorosomae	marine	Clupeiformes: clupeid (American gizzard shad, threadfin shad)	Northwest Atlantic
G. douglasadamsi	freshwater	Gobiiformes: gobiid (Neretva dwarf goby)	Europe
G. dubius	freshwater	Cypriniformes: nemacheilid (stone loach)	Europe
G. dulmaae	freshwater	Cypriniformes: nemacheilid (stone loach)	Europe
G. dykovae	freshwater	Cypriniformes: cyprinid (gudgeon)	Europe
G. dzhalilovi	freshwater	Cypriniformes: cyprinid (false osman)	Asia
G. editus	freshwater	Cypriniformes: cyprinid (false osman)	Asia
G. egregius	freshwater	Cypriniformes: cyprinid (Lahontan redside)	North America
G. egusae	freshwater	Anguilliformes: anguillid (Japanese eel)	Asia
G. elegans	freshwater	Cypriniformes: cyprinid (white-eye bream, freshwater bream)	Eurasia
G. elegini	marine	Gadiformes: gadid (Navaga)	Arctic
G. elongatus	marine	Gadiformes: gadid (Pacific tomcod)	Northeast Pacific
G. emembranatus	marine	Gadiformes: gadid (Atlantic cod)	North Atlantic
G. ensatus	freshwater	Urodela: cryptobranchid (California giant salamander, larvae)	North America
G. eos	freshwater	Cypriniformes: cyprinid (northern redbelly dace)	North America
G. ergensi	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
G. errabundus	marine	Labriformes: labrid (Ballan wrasse); Perciformes: zoarcid (eelpout), anarhichadid (Atlantic wolffish); Pleuronectiformes: pleuronectid (European plaice); Gadiformes: gadid (poor cod); Scorpaeniformes: cottid (longspined bullhead); Squaliformes: squalid (picked dogfish)	cosmopolitan
G. esomi	freshwater	Cypriniformes: cyprinid (Mekong flying barb)	Asia
G. etheostomae	freshwater	Perciformes: percid (mud darter, speckled darter, rainbow darter, orangethroat darter, splendid darter, Iowa darter, orangebelly darter, Johnny darter)	North America
G. eucaliae	freshwater	Gasterosteiformes: gasterosteid (brook stickleback)	North America
G. eutheraponensis	marine	Perciformes: terapontid (largescaled terapon)	Southeast Asia
G. euzeti	freshwater	Cypriniformes: cyprinid (spirlin)	Eurasia
G. exocoeti	marine	Beloniformes: exocoetid (barbel flyingfish, tropical two-wing flyingfish)	tropics
G. eyipayipi	marine	Syngnathiformes: syngnathid (greater pipefish)	Europe
G. fairporti	freshwater	Cypriniformes: cyprinid (common carp); Siluriformes: ictalurid (black bullhead)	Eurasia, North America
G. fernandoi	freshwater	Siluriformes: clariid (Philippine catfish)	Southeast Asia

G. flavescensis	marine	Gobiiformes: gobiid (two-spotted goby)	Europe
G. flesi	marine	Perciformes: pomatomid (bluefish), carangid (Mediterranean horse mackerel), sparid (blotched picarel); Pleuronectiformes: pleuronectid (European flounder, European plaice); Gobiiformes: gobiid (black goby, round goby); Trachiniformes: uranoscopid (stargazer); Rajiformes: rajid (thornback ray)	cosmopolitan
G. flexibiliradix	marine	Pleuronectiformes: pleuronectid (European flounder)	Europe
G. fossilis	freshwater	Cypriniformes: cobitid (weatherfish), nemacheilid (Angora loach)	Europe, Middle-East
G. foxi	marine	Mugiliformes: mugilid (flathead grey mullet)	cosmopolitan
G. freemani	freshwater	Perciformes: percid (American yellow perch)	North America
G. fryi	freshwater	Esociformes: esocid (muskellunge)	North America
G. funduli	marine	Cyprinodontiformes: fundulid (longnose killifish)	West Atlantic
G. fuscus	freshwater	Siluriformes: clariid (Hong Kong catfish)	Asia
G. gambusiae	freshwater	Cyprinodontiformes: poeciliid (mosquitofish)	North America
G. gasterostei	freshwater	Cypriniformes: cyprinid (roach, white bream, tench, chub); Perciformes: percid (European perch); Gasterosteiformes: gasterosteid (three-spined stickleback)	Eurasia, North America
G. gelnari	freshwater	Siluriformes: clariid (mudfish)	Africa
G. gemini	freshwater	Characiformes: prochilodontid (silver prochilodus)	South America
G. geophagensis	freshwater	Cichliformes: cichlid (pearl cichlid)	South America
G. gerdi	marine	Clupeiformes: clupeid (Pacific herring); Gadiformes: gadid (navaga, saffron cod)	Arctic
G. glaseri	freshwater	Cypriniformes: cyprinid (bleak)	Europe
G. glehnii	freshwater	Gobiiformes: odontobutid (Chinese sleeper)	Asia
G. gloriosi	freshwater	Perciformes: centrarchid (bluespotted sunfish)	North America
G. gnathopogonis	freshwater	Cypriniformes: cyprinid (Khanka gudgeon)	Asia
G. gobiensis	freshwater	Cypriniformes: cyprinid (gudgeon, Kessler's gudgeon)	Europe
G. gobii	freshwater	Cypriniformes: cyprinid (gudgeon, white-finned gudgeon, Siberian gudgeon, spotted steed); Salmoniformes: salmonid (rainbow trout)	Eurasia
G. gobioninum	freshwater	Cypriniformes: cyprinid (gudgeon, Cherskii's thicklip gudgeon, Amur whitefin gudgeon, Amur longnose gudgeon, Chinese lake gudgeon, Kessler's gudgeon, stone moroko, spotted steed)	Asia
G. goerani	freshwater	Perciformes: centrarchid (bluegill, rock bass, pumpkinseed)	North America
G. gondae	marine	Gobiiformes: gobiid (sand goby, Lozano's goby)	Europe
G. gracilihamatus	freshwater	Cypriniformes: cyprinid (spirlin, white bream, chub, roach, bleak)	Eurasia
G. granoei	freshwater	Cypriniformes: cobitid (spine loach)	China
G. groenlandicus	marine	Scorpaeniformes: cottid (warty sculpin, shorthorn sculpin, antlered sculpin, belligerent sculpin, Arctic sculpin); Clupeiformes: clupeid (Pacific herring); Perciformes: stichaeid (prickleback)	North Pacific, North Atlantic, Arctic
G. groschafti	freshwater	Siluriformes: clariid (North African catfish)	Africa
G. gurleyi	freshwater	Cypriniformes: cyprinid (common carp, goldfish)	Eurasia
G. gussevi	freshwater	Siluriformes: silurid (Soldatov's catfish, Amur catfish)	Asia
G. gvosdevi	freshwater	Cypriniformes: nemacheilid (gray loach)	Russia
G. gymneli	marine	Perciformes: zoarcid (fish doctor)	Arctic
G. haiteji	freshwater	Scorpaeniformes: cottid (Amur sculpin)	Asia
G. haplochromi	freshwater	Cichliformes: cichlid (cichlids)	Africa
G. harengi	marine	Clupeiformes: clupeid (Atlantic herring, Pacific herring, European sprat)	Arctic, Europe
G. hargisi	marine	Cyprinodontiformes: cyprinodontid (sheepshead minnow)	Americas
G. hellemansi	freshwater	Gobiiformes: gobiid (Neretva dwarf goby)	Europe

G. hemibarbi	freshwater	Cypriniformes: cyprinid (barbel, Kura barbel, chub)	Europe
G. hemiculteris	freshwater	Cypriniformes: cyprinid (Ussuri sharpbelly)	Asia
G. hemivicinus	freshwater	Cypriniformes: cyprinid (common marinka)	Asia
G. heterodactylus	freshwater	Perciformes: elassomatid (banded pygmy sunfish)	North America
G. hildae	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
G. hoffmani	freshwater	Cypriniformes: cyprinid (fathead minnow)	Americas
G. honghuensis	freshwater	Cypriniformes: cyprinid (humpback)	Asia
G. hrabei	freshwater	Scorpaeniformes: cottid (bullhead, Alpine bullhead)	Eurasia
G. hronosus	freshwater	Cypriniformes: cyprinid (spirlin, bleak)	Eurasia
G. hunanensis	freshwater	Cypriniformes: cyprinid (predatory carp)	Asia
G. hyderabadensis	freshwater	Anabantiformes: channid (snakehead)	India
G. hypophthalmichthydis	freshwater	Cypriniformes: cyprinid (silver carp)	Asia
G. ibragimovi	freshwater	Cypriniformes: cyprinid (seven khramulya)	Asia
G. ictaluri	freshwater	Siluriformes: ictalurid (Channel catfish)	North America
G. ihkahuili	freshwater	Cyprinodontiformes: poeciliid (shortfin molly)	Mexico
G. illigatus	freshwater	Cypriniformes: cyprinid (silverband shiner)	North America
G. imperialis	marine	Gobiiformes: gobiid (longjaw mudsucker)	North America
G. incognitus	freshwater	Cypriniformes: nemacheilid (spotted thicklip loach)	Russia
G. inesperatus	freshwater	Characiformes: crenuchid (South American darter)	South America
G. iunuri	freshwater	Cyprinodontiformes: goodeid (blackfin goodea)	Mexico
G. ivindoensis	freshwater	Cypriniformes: cyprinid (barbel)	Europe
G. jalalii	freshwater	Cichliformes: cichlid (Iranian mouthbrooder)	Middle-East
G. japonicus	marine	Osmeriformes: plecoglossid (Ayu sweetfish)	Northwest Pacific
G. jarocho	freshwater	Cyprinodontiformes: poeciliid (green swordtail)	Mexico
G. jennyae	freshwater	Anura: ranid (American bullfrog, tadpoles)	North America
G. jiroveci (syn. *papernai*)	freshwater	Cypriniformes: cyprinid (gudgeon), nemacheilid (stone loach)	Eurasia
G. joi	marine	Anguilliformes: anguillid (Japanese eel)	Asia
G. jussii	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Eurasia
G. kafirniganensis	freshwater	Cypriniformes: cyprinid (common marinka)	Asia
G. karabekovi	freshwater	Cypriniformes: cyprinid (naked osman)	Asia
G. karatagensis	freshwater	Cypriniformes: nemacheilid (Tibetan stone loach)	Asia
G. katamba	freshwater	Cyprinodontiformes: goodeid (blackfin goodea)	Mexico
G. katharineri	freshwater	Cypriniformes: cyprinid (common carp, Crucian carp, bighead carp, silver carp, goldfish, barbel, Mediterranean barbel, Balkan barbel, seven khramulya, gudgeon, bleak)	Eurasia
G. kearni	freshwater	Cypriniformes: cyprinid (chub)	Eurasia
G. kessleri	freshwater	Cypriniformes: nemacheilid (spotted thicklip loach)	Russia
G. kherulensis	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
G. kobayashii	freshwater	Cypriniformes: cyprinid (goldfish)	Asia
G. konovalovi	freshwater	Cypriniformes: cyprinid (Amur minnow)	Asia
G. kottelati	freshwater	Cypriniformes: cyprinid (Mekong flying barb)	Asia
G. kutikovana	marine	Gadiformes: gadid (Polar cod)	Arctic
G. kyogae	freshwater	Cypriniformes: cyprinid (Neumayer's barb, threespot barb)	Africa
G. lacusgrandis	freshwater	Scorpaeniformes: cottid (mottled sculpin)	North America
G. lacustricolae	freshwater	Cypriniformes: catostomid (Lake chubsucker)	North America
G. lacustris	freshwater	Cypriniformes: cyprinid (fathead minnow)	Americas
G. laevis	freshwater	Cypriniformes: cyprinid (belica, chub, bleak, Eurasian minnow, roach, bitterling, freshwater bream, white bream, zope, rudd, Dalmatian nase)	Eurasia
G. laevisoides	freshwater	Cypriniformes: cyprinid (redbelly dace)	North America
G. lagowskii	freshwater	Cypriniformes: cyprinid (Amur minnow)	Asia
G. lambanus	freshwater	Cypriniformes: cyprinid (longnose shiner)	North America
G. lamberti	freshwater	Cypriniformes: cyprinid (chub)	Eurasia
G. lamothei	freshwater	Cyprinodontiformes: goodeid (blackfin goodea, dark-edged splitfin)	Mexico
G. laruei	freshwater	Cypriniformes: cyprinid (central stoneroller)	North America
G. lateolabrax	marine	Perciformes: lateolabracid (Japanese seabass)	West Pacific
G. latus	freshwater	Cypriniformes: nemacheilid (eightbarbel loach),	Eurasia

		cobitid (spined loach)	
G. lavareti	freshwater	Salmoniformes: salmonid (rainbow trout, European whitefish, broad whitefish)	Eurasia, North America
G. lebiasinus	freshwater	Characiformes: lebiasinid (twospot lebiasina)	South America
G. lefua	freshwater	Cypriniformes: nemacheilid (eightbarbel loach)	Asia
G. lenoki	marine, freshwater	Salmoniformes: salmonid (Atlantic salmon, lenok)	North Atlantic, Asia
G. leopardinus	marine	Gobiiformes: gobiid (marbled goby)	Mediterranean
G. leptorhynchi	freshwater	Syngnathiformes: syngnathid (Bay pipefish)	North America
G. leucisci	freshwater	Cypriniformes: cyprinid (chub, common dace, roach)	Eurasia
G. lhkahuili	freshwater	Cyprinodontiformes: poeciliid (shortfin molly)	Mexico
G. lichuanensis	freshwater	Cypriniformes: cyprinid (Amur minnow)	Asia
G. limi	freshwater	Esociformes: umbrid (central mudminnow)	North America
G. limneus	freshwater	Cypriniformes: cyprinid (Eurasia minnow)	Eurasia
G. lineadactylus	freshwater	Perciformes: centrarchid (black crappie)	North America
G. lingulatus	freshwater	Cypriniformes: catostomid (Alabama hog sucker)	North America
G. llewellyni	freshwater	Cypriniformes: cyprinid (Eurasian minnow, Czekanowski's minnow, Altai osman)	Eurasia
G. lomi	freshwater	Cypriniformes: cyprinid (chub)	Eurasia
G. longidactylus	marine	Gobiiformes: gobiid (Lozano's goby)	Northeast Atlantic
G. longihamus	freshwater	Cypriniformes: cyprinid (naked osman)	Asia
G. longipes	marine	Perciformes: sparid (gilthead seabream)	Mediterranean
G. longiradix	freshwater	Perciformes: percid (ruffe, European perch, pike-perch)	Eurasia
G. longoacuminatus	freshwater	Cypriniformes: cyprinid (common carp, Crucian carp, Prussian carp)	Eurasia
G. lotae	freshwater	Gadiformes: lotid (burbot)	Eurasia, North America
G. lucii	freshwater	Esociformes: esocid (northern pike); Perciformes: percid (European perch, pike-perch); Anguilliformes: anguillid (European eel)	North America, Eurasia
G. luciopercae	freshwater	Perciformes: percid (European perch, ruffe, Volga pike-perch, Danube streber)	Eurasia
G. luckyi	freshwater	Cypriniformes: nemacheilid (spotted thicklip loach)	Russia
G. lythruri	freshwater	Cypriniformes: cyprinid (blacktip shiner)	North America
G. macracanthus	freshwater	Cypriniformes: cobitid (pond loach)	Asia
G. macrochiri	freshwater	Perciformes: centrarchid (green sunfish, spotted sunfish, orangespotted sunfish, bluegill, largemouth black bass, warmouth, pumpkinseed); Scorpaeniformes: cottid (mottled sculpin)	North America
G. macrocornis	freshwater	Cypriniformes: cyprinid (common nase)	Europe
G. macronychus	marine, freshwater	Salmoniformes: salmonid (sea trout); Cypriniformes: cyprinid (Eurasian minnow)	Europe
G. maculatus	freshwater	Anabantiformes: channid (blotched snakehead)	Asia
G. maculosi	marine	Scorpaeniformes: cottid (tidepool sculpin)	North Pacific
G. magniclypeus	freshwater	Cypriniformes: catostomid (blacktip jumprock)	North America
G. magnificus	freshwater	Cypriniformes: cyprinid (roach, Eurasian minnow); Salmoniformes: salmonid (European whitefish)	Eurasia
G. magnus	freshwater	Salmoniformes: salmonid (Arctic grayling)	North America
G. major	freshwater	Siluriformes: callichthyid (banded corydoras, bigfin corydoras)	South America
G. malalai	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
G. malmbergensis	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Eurasia
G. malmbergi	freshwater	Cypriniformes: cyprinid (barbel, Mediterranean barbel)	Europe
G. mantschuricus	freshwater	Cypriniformes: cyprinid (lake minnow)	Eurasia
G. margaritae	freshwater	Cypriniformes: cyprinid (Allegheny pearl dace)	North America
G. mariannae	freshwater	Scorpaeniformes: cottid (Alpine bullhead)	Eurasia
G. marinus	marine	Gadiformes: gadid (Alaska pollock, Atlantic cod)	North Pacific
G. marjami	freshwater	Cypriniformes: cyprinid (common marinka)	Asia
G. markakulensis	freshwater	Cypriniformes: cyprinid (gudgeon, Danubian	Eurasia

		longbarbel gudgeon, white-finned gudgeon, Amur whitefin gudgeon)	
G. markevitschi	freshwater	Cypriniformes: cyprinid (barbel, Mediterranean barbel); Perciformes: percid (ruffe)	Europe
G. masu	marine, freshwater	Salmoniformes: salmonid (masu salmon, sockeye salmon, rainbow trout, Japanese amago)	Northwest Pacific, North America, Asia
G. matovi	freshwater	Cypriniformes: cobitid (spined loach)	Eurasia
G. medaka	freshwater	Beloniformes: adrianichthyid (medaka)	Japan
G. mediotorus	freshwater	Cypriniformes: cyprinid (spottail shiner)	North America
G. medius	freshwater	Cypriniformes: cyprinid (roho labeo, common carp, Crucian carp, freshwater bream, goldfish), cobitid (weatherfish)	Eurasia, Indo-China
G. meelkopae	freshwater	Gobiiformes: gobiid (Trichonis dwarf goby)	Europe
G. megacanthus	freshwater	Cyprinodontiformes: fundulid (Bayou topminnow, blackspotted topminnow)	North America
G. menschikowi	freshwater	Cypriniformes: nemacheilid (stone loach)	Eurasia
G. mexicanus	freshwater	Cyprinodontiformes: goodeid (blackfin goodea, olive skiffia)	Mexico
G. micracanthus	freshwater	Cypriniformes: cobitid (pond loach)	Asia
G. microalestis	freshwater	Characiformes: alestid (sharptooth tetra)	Africa
G. microanchoratus	marine	Perciformes: anarhichadid (Atlantic wolffish)	Northeast Atlantic
G. microdactylus	freshwater	Cyprinodontiformes: poeciliid (shortfin molly)	Mexico
G. micropogonus	marine	Perciformes: sciaenid (Atlantic croaker)	West Atlantic
G. micropsi	marine	Gobiiformes: gobiid (common goby, Lozano's goby, sand goby)	East Atlantic
G. micropteri	freshwater	Perciformes: centrarchid (smallmouth bass)	North America
G. mikailovi	freshwater	Cypriniformes: cyprinid (seven khramulya)	Asia
G. milleri	freshwater	Cyprinodontiformes: poeciliid (cauca molly)	South America
G. minimus	freshwater	Cypriniformes: cyprinid (Eurasian minnow)	Eurasia
G. minytremae	freshwater	Cypriniformes: catostomid (spotted sucker)	North America
G. mirabilis	marine, freshwater	Scorpaeniformes: cottid (prickly sculpin)	North America
G. misgurni	freshwater	Cypriniformes: cobitid (weatherfish, pond loach)	Eurasia
G. mizellei	freshwater	Siluriformes: bagrid (striped dwarf catfish); Perciformes: percid (sauger, walleye)	Indo-China, North America
G. mobilensis	marine, freshwater	Cyprinodontiformes: cyprinodontid (sheepshead minnow)	Americas
G. molnari	freshwater	Cypriniformes: cobitid (spined loach)	Eurasia
G. mongolicus	freshwater	Cypriniformes: cyprinid (Altai osman, dwarf Altai osman)	Asia
G. monstruosus	freshwater	Cypriniformes: cobitid (spined loach, pond loach), nemacheilid (eightbarbel loach)	Eurasia
G. montanus	freshwater	Cypriniformes: cyprinid (Eurasian minnow, common marinka)	Eurasia
G. montealbani	freshwater	Cyprinodontiformes: profundulid (killifish)	Mexico
G. moraveci	freshwater	Cypriniformes: nemacheilid (Sistan loach)	Asia
G. mugelus	marine, freshwater	Mugiliformes: mugilid (flathead grey mullet)	cosmopolitan
G. mugili	marine	Mugiliformes: mugilid (so-iuy mullet)	Asia
G. mutabilitas	freshwater	Cypriniformes: cyprinid (seven khramulya)	Asia
G. nagibinae	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
G. nainum	marine	Scorpaeniformes: cottid (fourhorn sculpin)	Arctic
G. nannus	freshwater	Atheriniformes: atherinopsid (inland silverside)	North America
G. narzikulovi	freshwater	Cypriniformes: cyprinid (false osman, marinka)	Asia
G. nataliae	freshwater	Cypriniformes: cyprinid (bigeye chub)	North America
G. navarroensis	freshwater	Cypriniformes: cyprinid (California roach)	North America
G. nebraskensis	freshwater	Cypriniformes: cyprinid (northern redbelly dace)	North America
G. nebulosus	freshwater	Siluriformes: ictalurid (brown bullhead, Channel catfish)	North America
G. neili	freshwater	Esociformes: esocid (chain pickerel)	North America
G. nemacheili	freshwater	Cypriniformes: nemacheilid (stone loach, gray loach, Tibetan stone loach, spotted thicklip loach)	Eurasia
G. neonephrotus	freshwater	Siluriformes: heteropneustid (stinging catfish)	Asia

G. neotropicalis	freshwater	Characiformes: characid (banded astyanax)	Americas
G. neretum	marine	Syngnathiformes: syngnathid (Gulf pipefish)	West Atlantic
G. nerkae	marine, freshwater	Salmoniformes: salmonid (sockeye salmon, brook trout)	North Pacific
G. nevadensis	freshwater	Cyprinodontiformes: cyprinodontid (Amargosa pupfish)	North America
G. nigritae	freshwater	Siluriformes: mochokid (false upsidedown catfish)	Africa
G. nigrum	freshwater	Perciformes: percid (Johnny darter)	North America
G. niloticus	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
G. nipponensis	freshwater	Anguilliformes: anguillid (Japanese eel)	Asia
G. nordmanni	freshwater	Cypriniformes: cyprinid (Altai osman)	Asia
G. notatae	marine	Atheriniiformes: atheriniid (Atlantic silverside)	Atlantic
G. nudifronsi	marine	Perciformes: nototheniid (gaudy notothen)	Southern Ocean
G. nyanzae	freshwater	Cichliformes: cichlid (Victoria tilapia)	Africa
G. nyongensis	freshwater	Siluriformes: clariid (catfishes)	Africa
G. occupatus	freshwater	Cichliformes: cichlid (southern mouthbrooder, Nile tilapia, dwarf bream)	Africa
G. olsoni	marine	Gobiiformes: gobiid (longjaw mudsucker)	East Pacific
G. onegensis	freshwater	Scorpaeniformes: cottid (bullhead)	Europe
G. ophiocephali	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
G. orecchiae	marine	Perciformes: sparid (gilthead seabream)	Europe
G. oreoleucisci	freshwater	Cypriniformes: cyprinid (Altai osman, dwarf Altai osman)	Asia
G. osmeri	marine	Osmeriformes: osmerid (European smelt)	North Atlantic
G. osoblahensis	freshwater	Cypriniformes: cyprinid (common carp, common dace, chub)	Eurasia
G. ostendicus	freshwater	Gobiiformes: gobiid (common goby)	Europe
G. ouluensis	freshwater	Cypriniformes: cyprinid (roach)	Europe
G. oxycephali	freshwater	Cypriniformes: cyprinid (Chinese minnow)	Asia
G. pacificus	marine	Gadiformes: gadid (Pacific tomcod)	East Pacific
G. pakan	freshwater	Characiformes: characid (banded tetra)	Mexico
G. pannonicus	freshwater	Cypriniformes: cyprinid (barbel, Eurasian minnow)	Europe
G. parabotia	freshwater	Cypriniformes: cobitid (loach)	Asia
G. paraminimus	freshwater	Cypriniformes: cyprinid (common nase)	Europe
G. paranemacheili	freshwater	Cypriniformes: nemacheilid (spotted thicklip loach, gray loach)	Asia
G. parasiluri	freshwater	Siluriformes: silurid (Amur catfish)	Asia
G. pardalidis	marine, freshwater	Tetraodontiformes: tetraodontid (finepatterned puffer)	Northwest Pacific
G. parisellei	freshwater	Cichliformes: cichlid (Nile tilapia, southern mouthbrooder)	Africa
G. parvae	freshwater	Cypriniformes: cyprinid (stone moroko)	Asia
G. parvicirrus	freshwater	Cypriniformes: cyprinid (emerald shiner)	North America
G. parvus	freshwater	Cypriniformes: nemacheilid (gray loach, Tibetan stone loach, plain thicklip loach, spotted thicklip loach), cyprinid (Seven River's minnow)	Asia
G. patersoni	marine	Atheriniformes: atherinid (Atlantic silverside)	Atlantic
G. pavlovskyi	freshwater	Cypriniformes: nemacheilid (stone loach)	Eurasia
G. perccotti	freshwater	Gobiiformes: odontobutid (Amur sleeper)	Asia
G. percinae	freshwater	Perciformes: percid (blackbanded darter)	North America
G. percnuri	freshwater	Cypriniformes: cyprinid (lake minnow)	Eurasia
G. perforatus	marine	Gobiiformes: gobiid (arrow goby)	East Pacific
G. perlucidus	marine	Perciformes: zoarcid (eelpout)	Northeast Atlantic
G. pewzowi	freshwater	Cypriniformes: cyprinid (Altai osman, dwarf Altai osman)	Asia
G. pharyngicus	marine	Gadiformes: gadid (haddock, Atlantic cod)	Northeast Atlantic, Artic
G. phoxini	freshwater, marine	Cypriniformes: cyprinid (Eurasian minnow, lake minnow); Salmoniformes: salmonid (Atlantic salmon)	Eurasia, North Atlantic
G. pictae	freshwater	Cyprinodontiformes: poeciliid (scarlet livebearer)	Central America

G. pimelodellus	freshwater	Siluriformes: heptapterid (three-barbeled catfish)	South America
G. pisculentus	marine	Syngnathiformes: syngnathid (northern pipefish)	Europe
G. planensis	freshwater	Cypriniformes: cyprinid (bigmouth shiner)	North America
G. plecoglossi	marine	Osmeriformes: plecoglossid (Ayu sweetfish)	Northwest Pacific
G. pleuronecti	marine	Pleuronectiformes: pleuronectid (winter flounder)	West Atlantic
G. plotosi	marine	Siluriformes: plotosid (striped eel catfish)	Indo-Pacific
G. plumbeae	freshwater	Cypriniformes: cyprinid (lake chub)	North America
G. poeciliae	freshwater	Cyprinodontiformes: poeciliid (cauca molly, guppy)	South America, Central America
G. pomeraniae	freshwater	Cypriniformes: cyprinid (roach)	Europe
G. presidencyus	freshwater	Anabantiformes: channid (snakehead)	India
G. procerus	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
G. prolongis	marine, freshwater	Cyprinodontiformes: fundulid (mummichog, banded killifish, Gulf killifish); Cyprinodontiformes: cyprinodontid (sheepshead minnow)	West Atlantic, Americas
G. prostae	freshwater	Cypriniformes: cyprinid (roach, ide, chub, belica, freshwater bream, white bream, vimba bream, zope, common dace, Eurasian minnow)	Eurasia
G. proterorhini	marine	Gobiiformes: gobiid (giant goby, round goby, black goby, tubenose goby)	Europe, Mediterranean
G. protruberus	freshwater	Cypriniformes: cyprinid (skygazer shiner)	North America
G. proximus	marine	Scorpaeniformes: agonid (tubenose poacher)	North Pacific
G. pseudobullatarudis	freshwater	Cyprinodontiformes: poeciliid (green swordtail, porthole livebearer, shortfin molly)	Mexico
G. pseudonemacheili	freshwater	Cypriniformes: nemacheilid (gray loach, spotted thicklip loach)	Russia
G. pterygialis	marine	Gadiformes: gadid (saithe, Atlantic cod); Clupeiformes: clupeid (Pacific herring)	East Atlantic, Arctic
G. pungitii	marine, freshwater	Gasterosteiformes: gasterosteid (ninespine stickleback)	Eurasia, North America
G. quadratidigitus	marine	Gobiiformes: gobiid (leopard-spotted goby)	East Atlantic
G. rachelae	freshwater	Cypriniformes: cyprinid (shiner)	North America
G. rafinesqueii	freshwater	Perciformes: percid (Kentucky darter)	North America
G. raipurensis	freshwater	Abantiformes: channid (snakehead, spotted snakehead)	Asia
G. rarus	marine, freshwater	Gasterosteiformes: gasterosteid (ninespine stickleback)	Eurasia, North America
G. rasini	freshwater	Cyprinodontiformes: poeciliid (green swordtail)	Europe
G. recurvensis	freshwater	Cyprinodontiformes: aplocheilid (green panchax, blue panchax)	Asia, India
G. rhigophilae	marine	Perciformes: zoarcid (eelpout)	Southern Ocean
G. rhinichthius	freshwater	Cypriniformes: cyprinid (speckled dace)	North America
G. rhinogobius	freshwater	Gobiiformes: gobiid (goby)	Asia
G. rhodei	freshwater	Cypriniformes: cyprinid (bitterling, Russian bitterling, European bitterling, Chinese bitterling, giant Chinese bitterling)	Eurasia
G. richardsonius	freshwater	Cypriniformes: cyprinid (Lahontan redside)	North America
G. rivularae	freshwater	Cypriniformes: cyprinid (Chinese false gudgeon)	Asia
G. robustus	marine, freshwater	Clupeiformes: clupeid (Pacific herring); Pleuronectiformes: pleuronectid (European flounder, starry flounder)	Palearctic
G. rogatensis	freshwater	Scorpaeniformes: cottid (bullhead)	Europe
G. rogersi	marine	Gadiformes: gadid (Pacific tomcod)	East Pacific
G. rubripedis	marine	Tetraodontiformes: tetraodontid (Japanese pufferfish)	Asia
G. rugiensis	marine, freshwater	Gobiiformes: gobiid (common goby, sand goby)	East Atlantic
G. rugiensoides	marine	Gobiiformes: gobiid (Lozano's goby, sand goby, painted goby)	Northeast Atlantic
G. rutilensis	freshwater	Cypriniformes: cyprinid (roach)	Europe
G. rysavyi	freshwater	Siluriformes: clariid (North African catfish)	Africa
G. salaris	freshwater, marine	Salmoniformes: salmonid (Atlantic salmon, sea trout, Arctic char, grayling, European whitefish,	Eurasia, North America

		Adriatic trout, lake trout, brook trout, rainbow trout); Gasterosteiformes: gasterosteid (three-spined stickleback, ninespine stickleback); Cypriniformes: cyprinid (Eurasian minnow)	
G. salinae	freshwater	Cyprinodontiformes: cyprinodontid (European toothcarp)	Europe
G. salmonis	marine, freshwater	Salmoniformes: salmonid (cutthroat trout, sea trout, golden trout, rainbow trout, brook trout, Atlantic salmon, coho salmon)	Pacific, Atlantic, North America
G. salvelini	marine, freshwater	Salmoniformes: salmonid (Arctic char)	Arctic
G. samirae	freshwater	Siluriformes: callichthyid (peppered corydoras)	South America
G. saratogensis	freshwater	Cyprinodontiformes: cyprinodontid (Amargosa pupfish)	North America
G. scardiniensis	freshwater	Cypriniformes: cyprinid (rudd, chub)	Eurasia
G. schmidti	freshwater	Perciformes: percid (walleye)	North America
G. scleromystaci	freshwater	Siluriformes: callichthyid (banded corydoras, bigfin corydoras)	South America
G. sculpinus	marine	Scorpaeniformes: cottid (Pacific staghorn sculpin)	East Pacific
G. sedelnikowi	freshwater	Cypriniformes: nemacheilid (stone loach)	Eurasia
G. seravschani	freshwater	Cypriniformes: cyprinid (common marinka)	Asia
G. sergeji	freshwater	Cypriniformes: cyprinid (Amur ide)	Asia
G. shariffi	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
G. shorti	marine, freshwater	Syngnathiformes: syngnathid (Gulf pipefish)	West Atlantic
G. shulmani	freshwater	Cypriniformes: cyprinid (common carp, Prussian carp, silver carp, crucian carp)	Eurasia
G. sibiricus	freshwater	Cypriniformes: cobitid (spine loach)	Asia
G. slendrus	freshwater	Characiformes: lebiasinid (twospot lebiasina)	South America
G. slovacicus	freshwater	Esociformes: umbrid (mudminnow)	Europe
G. sommervillae	freshwater	Cypriniformes: cyprinid (freshwater bream)	Eurasia
G. somnaensis	freshwater, marine	Cypriniformes: cyprinid (Eurasian minnow); Salmoniformes: salmonid (chum salmon)	Eurasia
G. spathulatus	freshwater	Cypriniformes: catostomid (longnose sucker)	North America
G. sphinx	marine	Blenniformes: blenniid (sphinx blenny)	East Atlantic
G. sprostonae	freshwater	Cypriniformes: cyprinid (common carp, Prussian carp, redfin)	Eurasia
G. squaliobarbi	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
G. stableri	freshwater	Cyprinodontiformes: fundulid (Plains killifish)	North America
G. stankowici	freshwater	Cypriniformes: cyprinid (common carp)	Eurasia
G. stegurus	freshwater	Cyprinodontiformes: fundulid (banded killifish)	North America
G. stellatus	marine	Pleuronectiformes: pleuronectid (English sole, starry flounder), paralichthyid (speckled sanddab)	Pacific
G. stephanus	freshwater, marine	Cyprinodontiformes: fundulid (Gulf killifish, mummichog); Gasterosteiformes: gasterosteid (ninespine stickleback)	Palearctic
G. strelkovi	freshwater	Cypriniformes: cobitid (weatherfish, pond loach)	Eurasia
G. stunkardi	freshwater	Cypriniformes: cyprinid (blacknose dace, longnose dace), catostomid (Sacremento sucker); Perciformes: percid (Johnny darter); Anura: ranid (American bullfrog, tadpoles)	North America
G. sturmbaueri	freshwater	Cichliformes: cichlid (southern mouthbrooder)	Africa
G. superbus	freshwater	Siluriformes: callichthyid (peppered corydoras)	South America
G. syngnathi	marine	Syngnathiformes: syngnathid (Nilsson's pipefish)	Northeast Atlantic
G. synodonti	freshwater	Siluriformes: mochokid (false upsidedown catfish)	Africa
G. szanagai	freshwater	Scorpaeniformes: cottid (alpine bullhead)	Eurasia
G. taimeni	freshwater	Salmoniformes: salmonid (taimen)	Eurasia
G. takoke	freshwater	Cyprinodontiformes: poeciliid (two-spot livebearer, porthole livebearer)	Mexico
G. teken	freshwater	Characiformes: characid (banded tetra)	Mexico
G. tenesseensis	freshwater	Cypriniformes: cyprinid (southern redbelly dace)	North America
G. tepari	freshwater	Cyprinodontiformes: goodeid (blackfin goodea)	Mexico
G. teuchis	marine, freshwater	Salmoniformes: salmonid (rainbow trout, Atlantic salmon, sea trout)	North America, Europe

G. thlapi	freshwater	Cichliformes: cichlid (southern mouthbrooder)	Africa
G. thymalli	freshwater	Salmoniformes: salmonid (grayling, Arctic grayling)	Europe, North America
G. thysi	freshwater	Cichliformes: cichlid (southern mouthbrooder)	Africa
G. tibetanus	freshwater	Cypriniformes: nemacheilid (Tibetan stone loach)	Asia
G. tincae	freshwater	Cypriniformes: cyprinid (tench)	Eurasia
G. tokobaevi	freshwater	Cypriniformes: cyprinid (naked osman)	Asia
G. tomahuac	freshwater	Cyprinodontiformes: goodeid (blackfin goodea)	Central America
G. tominagai	marine, freshwater	Osmeriformes: plecoglossid (Ayu sweetfish)	Northwest Pacific
G. tonii	freshwater	Cypriniformes: nemacheilid (stone loach)	Eurasia
G. trairae	freshwater	Characiformes: erythrinid (wolf fish)	South America
G. transvaalensis	freshwater	Siluriformes: clariid (North African catfish)	Africa
G. trematoclithrus	freshwater	Cyprinodontiformes: fundulid (bluefin killifish)	North America
G. trematomi	marine	Perciformes: nototheniid (dusky rockcod)	Southern Ocean
G. truttae	freshwater, marine	Salmoniformes: salmonid (sea trout, rainbow trout, brook trout, grayling, Atlantic salmon)	North America, Europe
G. tularosae	freshwater	Cyprinodontiformes: cyprinodontid (White Sands pupfish)	North America
G. tulensis	freshwater	Cypriniformes: cyprinid (ide, Siberian dace)	Eurasia
G. turkanaensis	freshwater	Siluriformes: clariid (African sharptooth catfish)	Africa
G. turnbulli	freshwater	Cyprinodontiformes: poeciliid (guppy, livebearer)	Europe, South America
G. ulinganisus	freshwater	Cichliformes: cichlid (Mozambique tilapia)	Africa
G. umbrae	freshwater	Esociformes: umbrid (mudminnow)	Europe
G. unami	freshwater	Cyprinodontiformes: poeciliid (porthole livebearer)	Mexico
G. unicopula	marine	Pleuronectiformes: pleuronectid (Arctic flounder, starry flounder, European plaice)	Arctic
G. unipons	marine	Pleuronectiformes: pleuronectid (European plaice)	Europe
G. vancleavei	marine	Scorpaeniformes: hexagrammid (rock greenling)	East Pacific
G. variabilis	freshwater	Cypriniformes: cyprinid (golden shiner)	North America
G. varicorhini	freshwater	Cypriniformes: cyprinid (seven khramulya)	Asia
G. vicinoides	freshwater	Cypriniformes: cyprinid (common marinka)	Asia
G. vicinus	freshwater	Cypriniformes: cyprinid (Eurasian minnow, common marinka)	Eurasia
G. vimbi	freshwater	Cypriniformes: cyprinid (gudgeon, rudd, Tiber rudd, roach, chub, freshwater bream, vimba bream, white bream, white-eye bream, common carp, crucian carp, Mediterranean barbel, pigo, common dace, bleak)	Eurasia
G. viriosus	freshwater	Cypriniformes: catostomid (northern hog sucker, Alabama hog sucker)	North America
G. wardi	freshwater	Cypriniformes: catostomid (longnose sucker, Sacramento sucker)	North America
G. wellborni	freshwater	Cypriniformes: cyprinid (golden shiner)	North America
G. wilkesi	marine	Perciformes: nototheniid (striped rockcod, emerald rockcod)	Southern Ocean
G. wuchangensis	freshwater	Cypriniformes: cyprinid (Chinese bitterling)	China
G. xalapensis	freshwater	Cyprinodontiformes: poeciliid (two-spot livebearer)	Mexico
G. xiamenensis	marine	Mugiliformes: mugilid (largescale mullet)	Indian Ocean, Pacific
G. xtachuna	freshwater	Cyprinodontiformes: poeciliid (porthole livebearer, two-spot livebearer, shortfin molly)	Mexico
G. xynus	marine	Gerreiformes: gerreid (common silverbelly)	Australia
G. yacatli	freshwater	Cichliformes: cichlid (Nile tilapia)	Africa
G. yukhimenkoi	freshwater	Cypriniformes: cobitid (spine loach)	China
G. zapoteco	freshwater	Cyprinodontiformes: profundulid (killifish)	Mexico
G. zhukovi	marine	Mugiliformes: mugilid (so-iuy mullet)	Asia
G. zimbae	freshwater	Cichliformes: cichlid (southern mouthbrooder)	Africa

Parasite morphology: *Gyrodactylus* spp. are unique parasites because they effectively have only adult stages in their developmental cycles. The worms are viviparous and produce live unciliated young whereas all other monogeneans are oviparous and produce eggs containing ciliated oncomiracidia. In addition, many *Gyrodactylus* spp. exhibit hyperviviparity (polyembryony)

where unborn individuals (subadults retained in the uterus) develop their own young (cf. Russian nested dolls). The adults are hermaphroditic and contain an ovovitellarium which is a fused mass of ova and vitelline cells (vitellaria are not distinct). In gravid worms, body organs are usually compressed by the extensive volume of developing embryos curled within the uterus. Indeed, the internal anatomy of viviparous gyrodactylids has often been misinterpreted because they lack many structures present in oviparous monogeneans. Most gyrodactylid species do not possess a vagina but have a birth pore. Adults have small fusiform bodies < 1 mm in length often curved with the dorsal surface convex. They have a syncytial tegument characteristic of monogeneans and there are three body regions: cephalic (anterior to pharynx), trunk (body) and penduncle (tapered end of body). Although usually transparent and colourless, worms may vary in colour (grey, yellow, brown, black, pink, red) depending on ingested food. All worms possess a prominent posterior attachment organ (opisthaptor) apparent as a circular-semicircular disc bearing 16 small marginal hooks (often appearing as radial pins) and a central pair of large ventrally-orientated hamuli (appearing as fish-hooks) linked by separate dorsal and ventral bars. Adults also have two conspicuous anterior cephalic processes (bilobed head) bearing adhesive glands and spike sensilla involved in attachment and sensation.

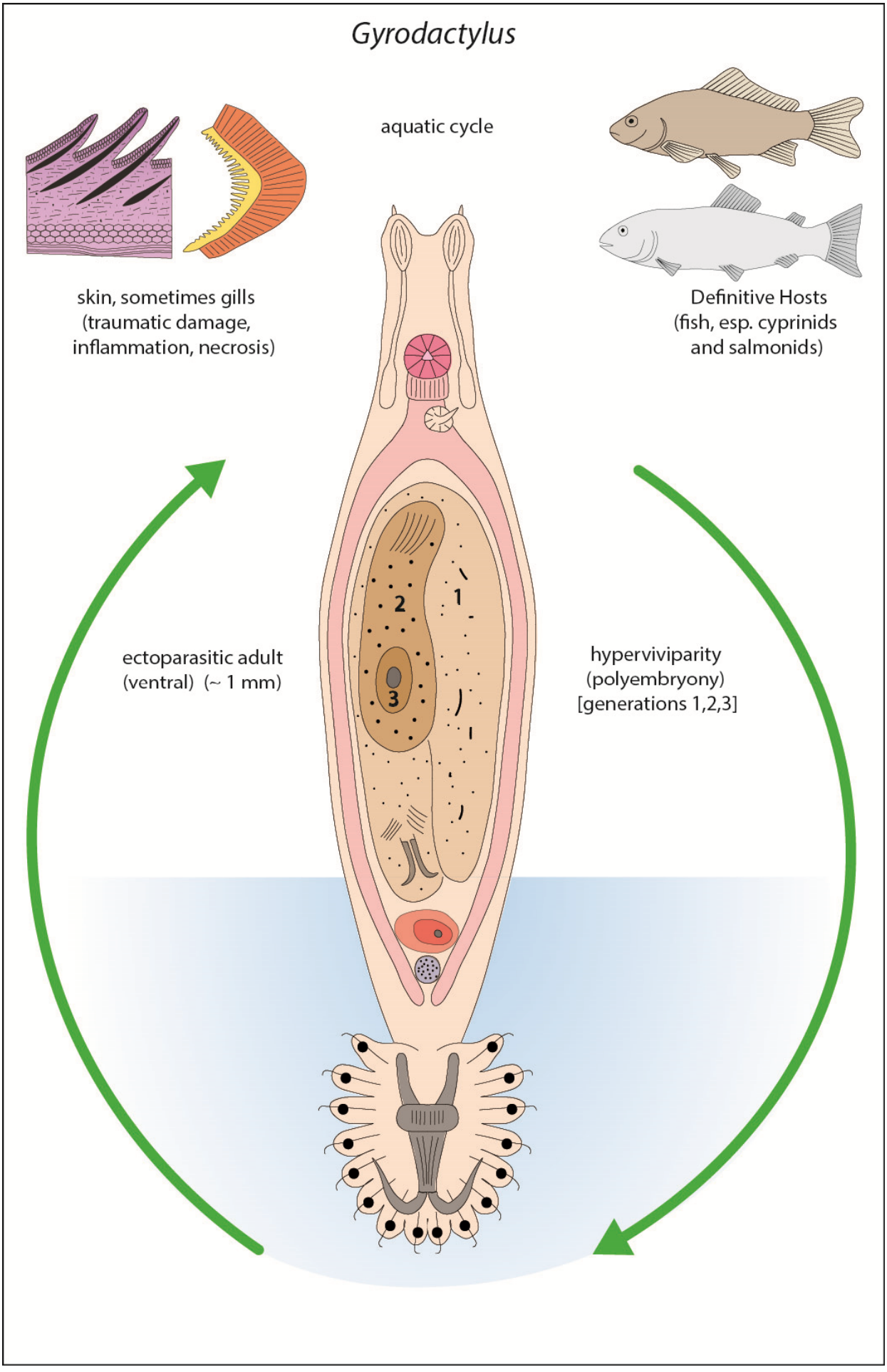
Site of infection: Gyrodactylids are commonly known as skin flukes as they usually infect the skin and fins of their fish hosts, but some species may also infect the gills. Several studies have shown many species to exhibit pronounced tissue tropism (site specificity), but it appears to be highly variable depending on environmental conditions, host age and condition, and stage of parasite development. Many gyrodactylid species apparently undergo characteristic migrations between sites as they mature e.g. juvenile *G. salaris* attach preferentially to the dorsal fin but migrate to the pectoral and anal fins as they mature. However, worms are less selective when infection densities are high and they may attach to any area of open skin. Other species have been shown to develop in infection foci ('hot-spots') when newborn worms attach alongside their mothers using their posterior attachment organ (opisthaptor). Worms have also been observed moving freely over their hosts in an 'inch-worm' or 'caterpillar'-like fashion involving alternate attachment of their posterior and anterior attachment organs.

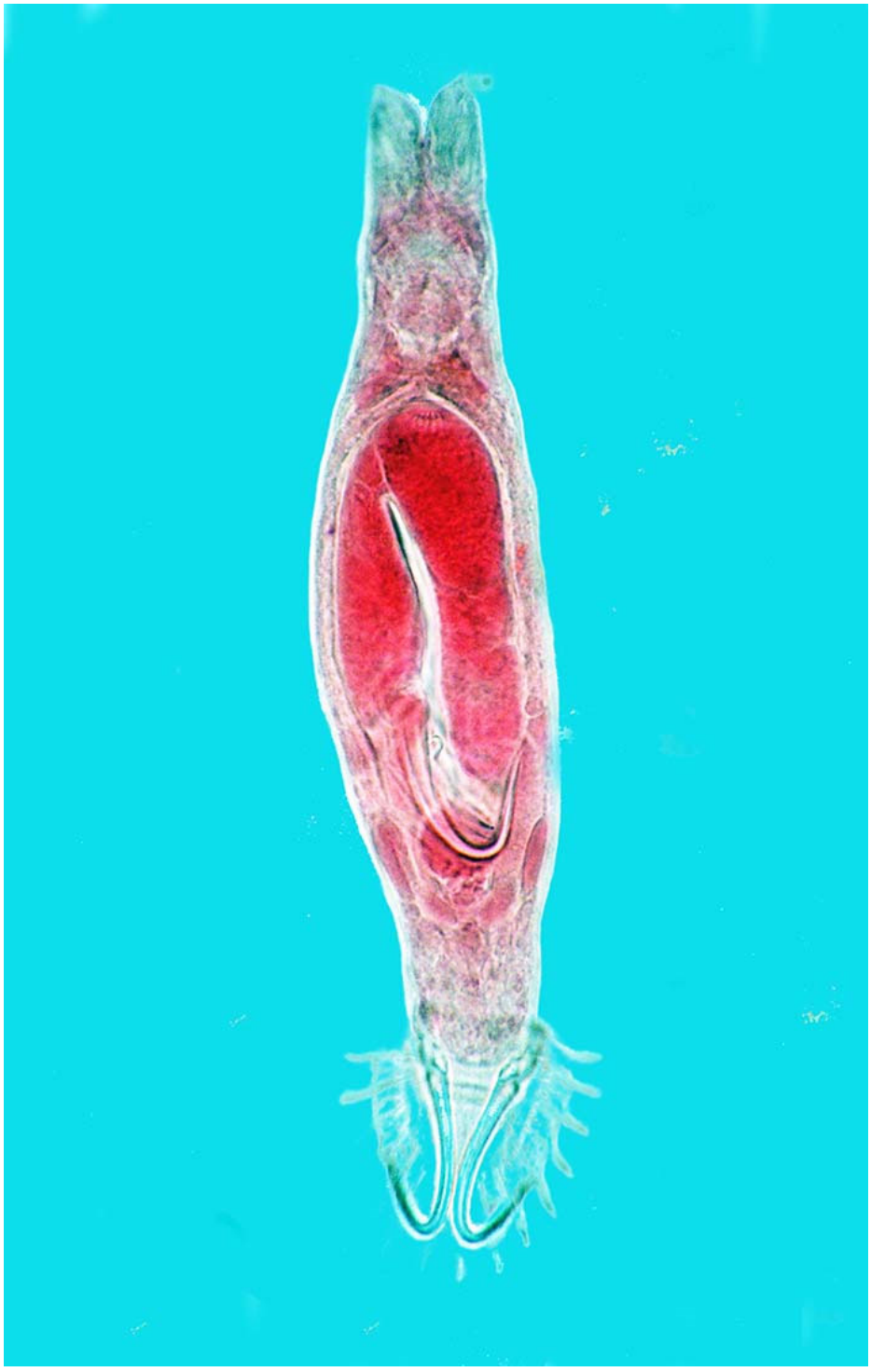
Pathogenesis: Following attachment to the external surfaces of fish, gyrodactylid worms feed on host epithelial cells and mucus and may cause significant damage to the skin, fins and even gills of the host. Even low levels of infections may cause disease (known as gyrodactylosis) which has been associated with morbidity and mortality in wide variety of fish species. Clinical signs include skin pallor (due to excessive mucus production and epithelial hyperplasia), mottling, necrosis, ulceration, focal haemorrhagic lesions, erosion, desquamation, loss of scales, fin erosion, fin clamping, restlessness, lethargy, anorexia, flashing behaviours and secondary bacterial and fungal infections are common. Infection of the gills may result in lamellar hyperplasia, excessive mucus production, rapid respiratory movements and severe distress. Mortalities are often attributed to a combination of problems associated with secondary infections and osmotic problems due to puncture wounds. Some infections have been observed to decline spontaneously over time, this being attributed to the development of host protective immune responses, but considerable heterogeneity was found within and between host populations. Gyrodactylid infections do present significant problems to the aquarium trade and they have caused significant economic losses in aquaculture (esp. salmonids, cod, flatfish, wolf fish, eels and cyprinids), with increasing drug resistance reported in farmed fish.

Developmental cycle and mode of transmission: Gyrodactylids are transmitted horizontally and directly between hosts when worms move from fish-to-fish by direct physical contact, or by being dislodged and then contaminating the immediate aquatic environment. Infections are, therefore, more easily transmitted between gregarious hosts or those kept in crowded or confined conditions. This direct mode of transmission is rare in that no specific transmissive stage is involved as the parasites reproduce *in situ* on their hosts. They also exhibit accelerated reproductive development (progenesis) and bear live young (viviparity). Gyrodactylids give birth to fully grown young which already contain second-generation (F1) embryos which in turn develop third-generation (F2) embryos. This 'Russian nested doll' succession of embryos occurs through a process of polyembryology. Viviparous gyrodactylids are protogynous hermaphrodites, in that the female system matures first although it remains structurally simple characterised by syncytial structures. Worms do not develop extensive internal organ systems but retain extensive syncytial layers in which metabolic functions take place. Newborn worms give birth at least twice before the male reproductive system develops and insemination occurs. Daughters are usually created asexually from a ball of germ cells, while subsequent daughters develop from eggs released from an oocyte before self-fertilization. Unlike other helminths, the eggs do not have eggshells normally created by vitelline cells. Cross-fertilization has been observed for some species when one individual pierces the body of another and injects sperm to fertilize developing embryos thus creating genetically different offspring. In addition to asexual and sexual development, some species have recently been reported to undergo parthenogenesis. Irrespective, all newborn worms immediately function as adults, attach and begin feeding on mucus and epithelial cells. Generation times are typically quite short (1-5 days), as are the lifespans of adults (6-15 days). Various patterns of infection have been reported: some being seasonal and apparently associated with decreased host activity in winter; others with host migrations and increased activity around breeding; and several being sporadic and seemingly influenced by parasite population density (asexual reproduction when population density is low and sexual reproduction when population density is high). The processes of progenesis, polyembryology and hyperviviparity, combined with rapid generation times, means parasite populations can potentially grow exponentially on hosts leading to outbreaks, particularly in aquaria or intensive culture.

Differential diagnosis: Whole parasites can be detected microscopically in wet mounts made from skin scrapings or gill snips. The genus *Dactylogyrus* can be differentiated by the characteristic arrangement of hooks on the haptor and the presence of developing embryos within the body, but their specific identification is difficult as the worms have simple anatomical features. Many species have been identified simply on the basis of host occurrence.

Treatment and control: Early diagnosis and treatment is essential because parasite numbers may increase exponentially over a short period (often days). Standard treatments involve bathing freshwater fish in saltwater, bathing marine fish in freshwater, or bathing either in dilute formalin or potassium permanganate solutions. Some success has been reported treating ornamental fish with trichlorfon or praziquantel. Control in the aquarium trade is best facilitated by screening exports and imports and using quarantine procedures to minimize parasite translocations. The species *G. salaris* has wrought havoc in Europe by causing epidemics in salmon aquaculture as well as endangering wild salmon stocks in rivers. Rotenone poisoning of entire river systems was used for many years, largely unsuccessfully, and recent efforts involving heavy metal (aluminium) dosing are similarly unequivocal.


Gyrodactylus
aquatic cycle
skin, sometimes gills
(traumatic damage,
inflammation, necrosis)
Definitive Hosts
(fish, esp. cyprinids
and salmonids)
ectoparasitic adult
(ventral) (~ 1 mm)
hyperviviparity
(polyembryony)
[generations 1,2,3]
1
2
3



Gyrodactylus adult worm

Dactylogyrus
(platyhelminth: monogenea)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Monogeneans are elongate to oval flatworms that are ectoparasitic on the skin and gills of fish, although a few are found in the urinary tracts of turtles, frogs and fishes. They have an anterior adhesive organ (prohaptor) and a conspicuous posterior adhesive organ (opisthaptor) armed with hooks or spines, often highly modified for attachment to specific sites. They are hermaphroditic and have direct life-cycles mostly where eggs hatch releasing a free-swimming larva (oncomiracidium) which actively seeks a new host. Monopisthocotyleans have an opisthaptor that forms a single symmetrical attachment unit lacking haptoral clamps. Dactylogyrids are small short worms and the opisthaptor has two pairs of large ventral anchors and 14 small marginal hooks. Several *Dactylogyrus* spp. are serious pathogens of hatchery fish and heavy infestations of the gills may cause mortalities through blood loss and mucoid congestion.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Monogenea (monoxenous ectoparasites, sac-like gut, direct cycles, oncomiracidium with 3 ciliary bands)
Subclass:	Monopisthocotylea (posterior haptor comprising a single symmetrical attachment unit, no haptoral clamps)
Order:	Dactylogyridea (sperm with single axoneme, 12-14 haptoral hooks, 2 pairs anchors, 1 transverse bar)
Family:	Dactylogyridae (posterior haptor, armed with hooks, oviparous)
Genus:	*Dactylogyrus* (parasitic in gills of fish)
Species:	various species cause respiratory signs in fish

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

Monogeneans and trematodes (flukes) have blind sac-like guts (lacking an anus) while cestodes (tapeworms) lack digestive tracts. Some 3,500 monogenean species have been described: most being ectoparasitic on the skin and gills of fish, although a few are found in the urinary tracts of turtles, frogs, fish and the eye of the hippopotamus. They have an anterior adhesive organ (prohaptor) and a conspicuous posterior adhesive organ (opisthaptor) armed with hooks, hooklets, hamuli (anchors) or clamps, often highly modified for attachment to specific sites. They are monoecious (hermaphroditic) and have direct monoxenous life-cycles mostly where eggs release free-swimming larvae (oncomiracidia with 3 ciliary bands) that actively seek new hosts (gyrodactylids are the exception as they are viviparous and produce live young). While the higher taxonomy of the Monogenea is often disputed with respect to rank, some 67 families have been resolved on the basis of morphological, biological and molecular studies. Three main groups are recognized: 28 families of Monopisthocotylea (opisthaptor with hooks, ectoparasitic on fish skin and gills, feed on

epithelia); 37 families of Polyopisthocotylea (opisthaptor with clamps, ectoparasitic on fish gills, feed on blood); and 2 families of Polystomatoinea (opisthaptor with suckers, endoparasitic in tetrapods).

Order	No. families	No. spp.	DH	Characters
Class: Monogenea (= Monogenoidea) (monogenetic life-cycles, ectoparasitic mainly on fish) ~ 3,500 spp.				
Subclass: Monopisthocotylea (= Polyonchoinea) (opisthaptor with hooks, feed on fish epithelia) ~2,500 spp.				
Capsalidea	2	200	mostly marine teleosts, some elasmobranchs	2 anterior suckers, 2 pairs anchors, 14 marginal haptoral hooks, some loculi
Dactylogyridea (= Monoaxonematidea)	17	1,000	freshwater and marine teleosts, coelacanths, squalea	sperm with single axoneme, 12-14 haptoral hooks, 2 pairs anchors, 1 transverse bar
Gyrodactylidea	5	1,500	freshwater and marine teleosts, squid, copepods	16 marginal 'hinged' haptoral hooks,1 pair anchors, dorsal and ventral bars, most viviparous (some nested polyembryony)
Monocotylidea	3	90	marine elasmobranchs	14 marginal haptoral hooks, some loculi
Montchadskyellidea	1	10	marine teleosts	14 marginal haptoral hooks, gut diverticulate, some endoparasitic in gut
Subclass: Polyopisthocotylea (= Heteronchoinea) (opisthaptor with clamps, most feed on blood of fish) ~1,000 spp.				
Chimaericolidea	1	5	marine holocephalans (chimaeras)	clamps, 1 pair anchors, haptor with 14 marginal hooks (each with domus)
Diclybothriidea	2	70	marine elasmobranchs, holocephalans, freshwater acipenseriform teleosts	clamps open and act as suckers, lateral sclerites absent
Mazocraeidea	34	920	numerous freshwater and marine teleost families	clamps with various structures incl. additional sclerites, hooks, spines; oral sucker a buccal organ, eggs with 2 polar filaments
Subclass: Polystomatoinea (parasitize aquatic tetrapods and lungfish)				
Polystomatidea	2	100	tetrapods (turtles, amphibians, hippopotamus), lungfish	haptor with 3 pairs suckers, egg filaments absent, some endoparasitic in tubular organs

Monopisthocotyleans have an opisthaptor that forms a single symmetrical attachment unit lacking haptoral clamps. Five orders are recognized on the basis of differences in parasite morphology, development and host occurrence; including the order Dactylogyridea (= Monoaxonematidea) characterized mainly by worms producing sperm with a single axoneme. Over 1,000 species belonging to 17 dactylogyridean families (Amphibdellatidae, Ancylodiscoididae, Ancyrocephalidae (syn. Engraulitrematidae), Calceostomatidae, Dactylogyridae, Diplectanidae, Fridericianellidae, Iagotrematidae, Neocalceostomatidae, Neodactylodiscidae, Neotetraonchidae, Protogyrodactylidae, Pseudodactylogyridae, Pseudomurraytrematidae, Sundanonchidae, Tetraonchidae and Urogyridae) have been described from freshwater and marine teleosts (esp. cyprinids), coelacanths and some cartilaginous squalean sharks.

Members of the family Dactylogyridae are represented by small worms with a posterior haptor containing 2 pairs large ventral anchors and 14 small marginal hooks. They are oviparous and produce eggs which hatch to release a free-swimming ciliated larva (oncomiracidium) that actively seeks hosts. Almost 170 dactylogyrid genera have been described but there is little consensus as to collective groupings into subfamilies. Some studies recognized up to 10 dactylogyrid subfamilies on the basis of morphological, biological and preliminary single-locus molecular analyses, but subsequent multi-locus molecular studies found considerable variation between genera suggesting their para- or poly-phyletic origins. Recent parsimony analyses using multiple characters have identified 2 macroclades, one tentatively represented by the subfamily Dactylogyrinae (including the genus *Dactylogyrus* (syn. *Aplodiscus, Falciunguis, Gussevianus, Microncotrema, Microncotrematoides, Neodactylogyrus, Paradactylogyrus, Skrjabinonchus*)) but also containing another 20 genera previously assigned to other subfamilies. Clearly, further studies are required to determine phylogenetic relationships between members of this diverse family. The genus *Dactylogyrus* is speciose with over 900 species recorded mostly from the gills of freshwater fishes, particularly cyprinids.

Dactylogyrus species	**Habitat**	**Hosts**	**Distribution**
D. absidatus	freshwater	Cypriniformes: cyprinid (chub, bigeye chub)	North America
D. acanthobramae	freshwater	Cypriniformes: cyprinid (bleak)	Middle-East
D. acanthobramis	freshwater	Cypriniformes: cyprinid (bleak)	Middle-East
D. acanthorhodei	freshwater	Cypriniformes: cyprinid (bitterling)	Europe
D. achmerowi	freshwater	Cypriniformes: cyprinid (carp)	Eurasia

D. achmerowianus	freshwater	Cypriniformes: cyprinid (yellowcheek)	Asia
D. acicularis	freshwater	Cypriniformes: catostomid (redhorse)	North America
D. aciculus	freshwater	Cypriniformes: cyprinid (barbel)	Asia
D. acinacus	freshwater	Cypriniformes: cyprinid (red garra)	Asia
D. acrossocheili	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. acus	freshwater	Cypriniformes: cyprinid (stoneroller, eastern shiner)	North America
D. acutanchoratus	freshwater	Cypriniformes: cyprinid (?)	China
D. aegyptiacus	marine	Atheriniformes: atherinid (silverside)	Africa
D. aequipinnati	freshwater	Cypriniformes: cyprinid (danio)	Asia
D. afer	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. aferoides	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. affinis	freshwater	Cypriniformes: cyprinid (barbel, bleak, white bream)	Eurasia, Africa
D. afrobarbae	freshwater	Cypriniformes: cyprinid (barbel), centropomid (perch)	Africa
D. afrochelatus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. afrofluviatilis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. afrolongicornis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. afropsilovaginus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. afroruahae	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. afrosclerovaginus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. afrotoxopous	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. agolumaccessorius	freshwater	Cypriniformes: cyprinid (bigmouth shiner)	North America
D. agopovae	freshwater	Cypriniformes: cyprinid (riffle minnows)	Asia
D. akaraicus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. alabamensis	freshwater	Cypriniformes: cyprinid (bigeye chub)	North America
D. alaeonchus	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. alatocirrus	freshwater	Cypriniformes: cyprinid (redknife)	China
D. alatoideus	freshwater	Cypriniformes: cyprinid (yellowfin, sharpbelly)	Eurasia
D. alatus	freshwater	Cypriniformes: cyprinid (riffle minnows, bleak, sun bleak, asp, white bream, ide, chub, roach)	Eurasia
D. albanicus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. albertensis	freshwater	Cypriniformes: cyprinid (bigeye chub, flathead chub)	North America
D. albori	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. allolongionchus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. amblops	freshwater	Cypriniformes: cyprinid (bigeye chub)	North America
D. amelliformis	freshwater	Cypriniformes: cyprinid (bitterling)	China
D. amieti	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. amphibothrium	freshwater	Cypriniformes: cyprinid (tench, ide, chub); Perciformes: percid (ruffe)	Eurasia
D. amplexicirrus	freshwater	Cypriniformes: cyprinid (blackfish)	Asia
D. amurensis	freshwater	Cypriniformes: cyprinid (minnow)	Europe
D. ancherythroculteri	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. anchoracanthus	freshwater	Cypriniformes: cyprinid (chela, carp)	Indo-China
D. anchoratus	freshwater, marine	Cypriniformes: cyprinid (bream, minnow, riffle minnow, tench, scraper, barbel, carp, grass carp, Crucian carp, silver carp, gudgeon, sharpbelly, sun bleak, ide, chub, roach); Salmoniformes: salmonid (whitefish); Esociformes: esocid (pike); Gasterosteiformes: gasterosteid (sticklebacks)	Eurasia, North America
D. anchoricirrus	freshwater	Cypriniformes: cyprinid (?)	China
D. ancistroides	freshwater	Cypriniformes: cyprinid (smallscale yellowfin)	Asia
D. ancyleus	freshwater	Cypriniformes: cyprinid (lizard gudgeon)	Asia
D. ancylostylus	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. andalousiensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. angularis	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. annelus	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. anylocirrus	freshwater	Cypriniformes: cyprinid (Guichenot gidgeon)	Asia
D. apogonis	marine	Kurtiformes: apogonid (cardinalfish)	Japan

D. apos	freshwater	Cypriniformes: catostomid (hogsucker)	North America
D. araxicus	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. archaeopenis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. arciformis	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. arcuatus	freshwater	Cypriniformes: cyprinid (carp, crucian carp)	Eurasia
D. arcus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. argenteus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. aristichthys	freshwater	Cypriniformes: cyprinid (bighead carp, silver carp)	Asia
D. asper	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. aspili	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. assimovi	freshwater	Cypriniformes: cobitid (stone loach)	Asia
D. atlasensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. atratuli	freshwater	Cypriniformes: cyprinid (riffle dace)	North America
D. atripinnei	freshwater	Cypriniformes: catostomid (redhorse)	North America
D. atromaculatus	freshwater	Cypriniformes: cyprinid (creek chub)	North America
D. attenuatus	freshwater	Cypriniformes: cyprinid (creek chub)	North America
D. aureus	freshwater	Cypriniformes: cyprinid (golden shiner); Percopsiformes: aphredoderid (pirate perch); Perciformes: centrarchid (warmouth bass)	North America
D. auriculatus	freshwater	Cypriniformes: cyprinid (carp, bream, white bream, tench, minnow, roach); Perciformes: percid (perch)	Eurasia, North America
D. auriformis	freshwater	Cypriniformes: cyprinid (smallscale yellowfin)	Asia
D. austrosinensis	freshwater	Cypriniformes: cyprinid (mahseer)	Asia
D. aviformis	freshwater	Cypriniformes: cyprinid (grey mullet)	Asia
D. aviunguis	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. babensis	freshwater	Cypriniformes: cyprinid (carp, silver carp)	Asia
D. bacailai	freshwater	Cypriniformes: cyprinid (oxygaster)	Indo-China
D. bakanensis	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. balistae	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. balkanicus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. banghami	freshwater	Cypriniformes: cyprinid (lake chub, creek chub, silvery minnow, highscale shiner, redside shiner, eastern shiner, riffle dace)	North America
D. barbatuli	freshwater	Cypriniformes: cobitid (stone loach)	Asia
D. barbi	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. barbioides	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. barbuli	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. barbus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. barbusi	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. barisicirrus	freshwater	Cypriniformes: cyprinid (minnow)	China
D. barnae	freshwater	Cypriniformes: cyprinid (barna baril)	India
D. batae	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. batesii	freshwater	Cyprinodontiformes: cyprinodontid (rivulines)	Africa
D. bati	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. baueri	freshwater	Cypriniformes: cyprinid (Crucian carp)	Europe
D. beckeri	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. bellicae	freshwater	Cypriniformes: cyprinid (bigeye chub, river chub)	North America
D. belligobio	freshwater	Cypriniformes: cyprinid (gudgeon)	China
D. benhoussai	freshwater	Cypriniformes: cyprinid (Algerian barbel)	Africa
D. bialatus	freshwater	Gobiiformes: gobiid (goby)	Asia
D. bicornis	freshwater	Cypriniformes: cyprinid (bitterling)	Eurasia
D. bicurvitubus	freshwater	Cypriniformes: cyprinid (labeo)	China
D. bifidus	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. bifurcatus	freshwater	Cypriniformes: cyprinid (bluntnose minnow)	North America
D. binotati	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. biporosus	freshwater	Cypriniformes: cyprinid (Amur bream)	Asia
D. birgii	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. bispiralis	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. biwaensis	freshwater	Cypriniformes: cyprinid (carp)	Eurasia
D. boaiensis	freshwater	Cypriniformes: cyprinid (ink carp)	China
D. bocageii	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa

D. boli	freshwater	Cypriniformes: cyprinid (trout barb)	Africa, Asia
D. boopsi	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. bopeleti	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. borealis	freshwater	Cypriniformes: cyprinid (minnow)	Europe
D. borjensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. bovicornutus	freshwater	Cypriniformes: cyprinid (redwing fish)	Asia
D. brachius	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. brachydiscus	freshwater	Cypriniformes: cyprinid (black 'shark')	Eurasia
D. branchialis	freshwater	Cypriniformes: cyprinid (redknife)	China
D. brevicardus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. brevicirrus	freshwater	Cypriniformes: cyprinid (barbel, minnow, black 'shark')	Eurasia, Africa
D. brevicornis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. brevifurcatus	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. brevitignus	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. brevitubus	freshwater	Cypriniformes: cyprinid (black 'shark')	Eurasia
D. bucephalophoroides	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. bucinus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. buddi	freshwater	Scorpaeniformes: cottid (sculpin)	North America
D. bulbus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. bullosus	freshwater	Cypriniformes: cyprinid (highscale shiner, eastern shiner)	North America
D. bului	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. bychowskyii	freshwater	Cypriniformes: cyprinid (riffle minnows, bluntnose minnow)	North America, Asia
D. caballeroi	freshwater	Cypriniformes: cyprinid (roach)	Eurasia
D. caecus	freshwater	Cypriniformes: cyprinid (ide, chub)	Eurasia
D. calbasi	freshwater	Cypriniformes: cyprinid (black 'shark')	Eurasia
D. californiensis	freshwater	Cypriniformes: cyprinid (pikeminnow)	North America
D. calyciformis	freshwater	Cypriniformes: cyprinid (thicklip gudgeon)	Asia
D. capoetae	freshwater	Cypriniformes: cyprinid (scraper)	Asia
D. capoetobramae	freshwater	Cypriniformes: cyprinid (sharpray)	Asia
D. carassioides	freshwater	Cypriniformes: cyprinid (blackfish)	Asia
D. carassobarbi	freshwater	Cypriniformes: cyprinid (himris)	Asia
D. carmeli	freshwater	Cypriniformes: cyprinid (bleak)	Middle-East
D. carolinensis	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. carpathicus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. catlaius	freshwater	Cypriniformes: cyprinid (Indian carp, black 'shark')	Asia
D. caucasicus	freshwater	Cypriniformes: cyprinid (riffle minnows)	Asia
D. caudoluminis	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. cauveryi	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. centrarchidi	freshwater	Perciformes: centrarchid (warmouth bass)	North America
D. ceratoides	freshwater	Cypriniformes: cyprinid (barbel)	Asia
D. cernyi	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. chagunionis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. chalcalburni	freshwater	Cypriniformes: cyprinid (riffle minnows, bleak, barbel chub, mullet)	Asia
D. changjiangensis	freshwater	Cypriniformes: cyprinid (danio)	China
D. charbinensis	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. chauhani	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. chelicirrus	freshwater	Cypriniformes: cyprinid (grey mullet)	Asia
D. cheligenitalis	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. cheloideus	freshwater	Cypriniformes: cyprinid (riffle dace)	North America
D. chenchihleui	freshwater	Cypriniformes: cyprinid (barbel chub, redknife)	Asia
D. cheni	freshwater, marine	Gobiiformes: gobiid (goby)	Asia
D. chenjiagengi	freshwater	Cypriniformes: cyprinid (jaw beard)	China
D. chenminjungae	freshwater	Cypriniformes: cyprinid (topmouth culter, redknife, sharpbelly)	Asia
D. chenshuchenae	freshwater	Cypriniformes: cyprinid (silver carp)	Asia
D. chenyenhsinae	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. chernyshevae	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia

D. chinensis	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. chini	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. chinyejiangensis	freshwater	Cypriniformes: cyprinid (barb)	China
D. chishuiensis	freshwater	Cypriniformes: cyprinid (?)	China
D. chitravanshii	freshwater	Cypriniformes: cyprinid (black 'shark')	Eurasia
D. chondrostomi	freshwater	Cypriniformes: cyprinid (white bream, nase)	cosmopolitan
D. chongqingensis	freshwater	Cypriniformes: cyprinid (rosy bitterling)	Japan
D. chramulii	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. chranilowi	freshwater	Cypriniformes: cyprinid (bream, white bream, bleak, crucian carp)	cosmopolitan
D. chrosomi	freshwater	Cypriniformes: cyprinid (minnow)	Europe
D. ciliensis	freshwater	Cypriniformes: cyprinid (cultrine)	Asia
D. cincinnatus	freshwater	Cypriniformes: cyprinid (scraper)	Asia
D. circumflexus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. circumphallus	freshwater	Cypriniformes: cyprinid (chela)	India
D. cirrhini	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. clani	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. clasterocirrus	freshwater	Cypriniformes: cyprinid (ink carp)	China
D. clavaeformis	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. clavatovaginus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. claviformis	freshwater	Cypriniformes: cyprinid (creek chub)	North America
D. clypeatus	freshwater	Cypriniformes: cyprinid (jaw beard)	China
D. coartatus	freshwater	Cypriniformes: cyprinid (tricolor sharkminnow)	Asia
D. colonus	freshwater	Scorpaeniformes: cottocomephorid (deepwater sculpins)	Europe
D. colpodes	freshwater	Cypriniformes: cyprinid (jaw beard)	China
D. columbiensis	freshwater	Cypriniformes: cyprinid (pikeminnow)	North America
D. comizae	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. concavusiformis	freshwater	Cypriniformes: cyprinid (mahseer)	Asia
D. condylus	freshwater	Cypriniformes: cyprinid (percocypris carp)	Asia
D. confusus	freshwater	Cypriniformes: cyprinid (dace, eastern shiner)	North America
D. contortus	freshwater	Cypriniformes: cyprinid (redknife)	China
D. contrarmatus	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. convolvugenitalis	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. cordus	freshwater	Cypriniformes: cyprinid (bleak, ide, chub)	Eurasia, North America
D. coreiusi	freshwater	Cypriniformes: cyprinid (gudgeon)	China
D. cornoides	freshwater	Cypriniformes: cyprinid (vimba bream, white bream)	Europe
D. cornu	freshwater, marine	Cypriniformes: cyprinid (bream, white bream, bleak, mahseer, vimba bream, barbel, nase, kingfish, ide, chub, roach, rudd), silurid (catfish), mugilid (mullet)	Eurasia, Middle-East
D. cornucirrus	freshwater	Cypriniformes: cyprinid (carp)	Eurasia
D. cornutus	freshwater	Cypriniformes: cyprinid (silverjaw minnow, eastern shiner)	North America
D. corporalis	freshwater	Cypriniformes: cyprinid (creek chub)	North America
D. cotius	freshwater	Cypriniformes: cyprinid (rohtee)	India
D. cranoglanis	freshwater	Siluriformes: bagrid (armorhead catfish)	China
D. crassus	freshwater	Cypriniformes: cyprinid (carp, crucian carp)	Eurasia
D. crescenticleithrium	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. cristatocleithrium	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. cristatus	freshwater	Cypriniformes: cyprinid (gudgeon)	Europe
D. crivellius	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. crossocheili	freshwater	Cypriniformes: cyprinid (mudcarp)	Asia
D. crucifer	freshwater	Cypriniformes: cyprinid (carp, bream, white bream, bleak, vimba bream, ide, chub, roach, rudd), esocid (pike)	Eurasia
D. crucis	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. crucitrabus	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. cryptomeres	freshwater	Cypriniformes: cyprinid (barbel, gudgeon)	Eurasia, Africa

D. ctenopharyngodonis	freshwater	Cypriniformes: cyprinid (grass carp)	Eurasia, North America
D. curiosus	freshwater	Cypriniformes: cyprinid (rasbora)	Asia
D. curriculi	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. cursitans	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. curvicirrus	freshwater	Cypriniformes: cyprinid (topmouth culter, redknife)	Asia
D. cyathus	freshwater	Cypriniformes: cyprinid (rectoris)	Asia
D. cyclocirrus	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. cymbidioides	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. cymtiformis	freshwater	Cypriniformes: cyprinid (redwing fish)	China
D. cyprini	freshwater	Cypriniformes: cyprinid (carp, koi carp)	Eurasia
D. cyprinioni	freshwater	Cypriniformes: cyprinid (kingfish)	Asia
D. cystovagina	freshwater	Cypriniformes: cyprinid (ink carp)	China
D. czerskii	freshwater	Cypriniformes: cyprinid (minnow)	Europe
D. dachuanensis	freshwater	Cypriniformes: cyprinid (tchangi)	China
D. daliensis	freshwater	Cypriniformes: cyprinid (snowtrout)	China
D. daniconii	freshwater	Cypriniformes: cyprinid (rasbora)	Asia
D. daojiensis	freshwater	Cypriniformes: cyprinid (flying fox)	Asia
D. decaspirus	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. delicatus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. dembae	freshwater	Cypriniformes: cyprinid (African carp)	Africa
D. denticulati	freshwater	Cypriniformes: cyprinid (barbel, spiny barbel)	Asia
D. deziensioides	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. deziensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. difformis	freshwater	Cypriniformes: cyprinid (carp, bream, white bream, ide, chub, roach, rudd)	Eurasia
D. difformoides	freshwater	Cypriniformes: cyprinid (rudd)	Eurasia
D. digitalis	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. digitformis	freshwater	Cypriniformes: cyprinid (Chinese lizard gudgeon)	Asia
D. dimitrovae	freshwater	Cypriniformes: cyprinid (riffle minnows, bleak)	Asia
D. dirigerus	freshwater	Cypriniformes: cyprinid (nase)	Europe
D. dissimili	freshwater	Cypriniformes: cyprinid (bigeye chub)	North America
D. distinctus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. distinguendus	freshwater	Cypriniformes: cyprinid (bream, vimba bream, white bream, ide, chub, rudd)	Eurasia
D. distoechodoni	freshwater	Cypriniformes: cyprinid (redwing fish)	Asia
D. doadrioi	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. dogieli	freshwater	Cypriniformes: cyprinid (Crucian carp)	Europe
D. dolus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. dominici	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. dorsalis	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. draaensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. drjagini	freshwater	Cypriniformes: cyprinid (osman, snowtrout)	Asia
D. dubii	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. dubius	freshwater	Cypriniformes: cyprinid (eastern shiner, creek chub)	North America
D. dujardinianus	freshwater	Cypriniformes: cyprinid (bream, bleak, carp, crucian carp, ide, chub, roach)	Eurasia
D. dulkeiti	freshwater	Cypriniformes: cyprinid (Crucian carp)	Europe
D. duplus	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. duquesni	freshwater	Cypriniformes: catostomid (redhorse)	North America
D. dyki	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. editus	freshwater	Cypriniformes: cyprinid (false osman)	China
D. effusus	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. egregius	freshwater	Cypriniformes: cyprinid (redside shiner)	North America
D. ehrenbergii	freshwater	Cypriniformes: cyprinid (?)	China
D. eigenmanni	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. elegantis	freshwater	Cypriniformes: cyprinid (nase)	Europe
D. elongatus	freshwater	Cypriniformes: cyprinid (carp, ide, chub)	Eurasia
D. emeiheensis	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. enidae	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa

D. eos	freshwater	Cypriniformes: cyprinid (dace, minnow)	North America, Europe
D. epalzeorhynchus	freshwater	Cypriniformes: cyprinid (flying fox)	Asia
D. ergensi	freshwater	Cypriniformes: cyprinid (nase)	Europe
D. erhaiensis	freshwater	Cypriniformes: cyprinid (barbel)	Asia
D. erhardovae	freshwater	Cypriniformes: cyprinid (roach)	Eurasia
D. ericymbae	freshwater	Cypriniformes: cyprinid (silverjaw minnow)	North America
D. ersinensis	freshwater	Cypriniformes: cyprinid (osman, minnow)	Eurasia
D. erythroculteris	freshwater	Cypriniformes: cyprinid (redknife)	China
D. erythropteris	freshwater	Cypriniformes: cyprinid (topmouth culter, redknife)	Asia
D. erythropteroides	freshwater	Cypriniformes: cyprinid (kanglang)	China
D. eslamii	freshwater	Cypriniformes: cyprinid (Gangetic latia)	India
D. eucalius	freshwater	Gasterosteiformes: gasterosteid (sticklebacks)	North America
D. euryanceps	freshwater	Cypriniformes: cyprinid (scaly fish)	China
D. exiguus	freshwater	Cypriniformes: cyprinid (barbel)	Asia
D. extensus	freshwater	Cypriniformes: cyprinid (carp, bighead carp, crucian carp, koi carp, barbel, ide, chub), cobitid (weather loach); Perciformes: centrarchid (black bass)	North America, Asia
D. facetus	freshwater	Cypriniformes: cyprinid (pseudogoby, lizard gudgeon)	Asia
D. falcatus	freshwater	Cypriniformes: cyprinid (carp, bream, white bream, sharpray, roach, lizard gudgeon)	Eurasia
D. falciformis	freshwater	Cypriniformes: cyprinid (carp)	Eurasia
D. falcilocus	freshwater	Cypriniformes: cyprinid (scraper, barbel, black 'shark')	Eurasia
D. falciunguis	freshwater	Cypriniformes: cyprinid (white bream)	Asia
D. fallax	freshwater	Cypriniformes: cyprinid (carp, sabre carp, bream, white bream, bleak, tench, ide, chub, roach, rudd); Gobiiformes: gobiid (tubenose goby)	Eurasia
D. falsiphallus	freshwater	Cypriniformes: cyprinid (Maghreb barbel)	Africa
D. faridpaki	freshwater	Cypriniformes: cyprinid (Gangetic latia)	India
D. fasciati	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. fasciculi	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. fasciola	freshwater	Cypriniformes: cyprinid (Lagowski's minnow)	Asia
D. fenghuaensis	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. fernandoi	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. fileicirrus	freshwater	Cypriniformes: cyprinid (ink carp)	China
D. fimbriphallus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. finitimus	freshwater	Cypriniformes: cyprinid (bleak, gudgeon)	Palearctic
D. fistuliformis	freshwater	Cypriniformes: cyprinid (lizard gudgeon)	Asia
D. flagellatus	freshwater	Cypriniformes: cyprinid (redknife, sharpbelly, bonelip)	Asia
D. flagellicirrus	freshwater	Cypriniformes: cyprinid (minnow, topmouth culter, redknife, sharpbelly)	Asia
D. flagristylus	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. flammulatus	freshwater	Cypriniformes: cyprinid (silverfish)	Asia
D. flexianchoratus	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. flexibilis	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. flexiformis	freshwater	Cypriniformes: cyprinid (striped minnow)	Asia
D. floricirrus	freshwater	Cypriniformes: cyprinid (redknife)	China
D. fluvialis	freshwater	Cypriniformes: cyprinid (pseudogoby)	Asia
D. foliicirrus	freshwater	Cypriniformes: cyprinid (redknife, sharpbelly)	Asia
D. folkmanovae	freshwater	Cypriniformes: cyprinid (ide, chub, roach)	Eurasia
D. forcipatus	freshwater	Cypriniformes: cyprinid (bitterling)	Europe
D. formosus	freshwater	Cypriniformes: cyprinid (crucian carp, carp)	Eurasia
D. fotedari	freshwater	Cypriniformes: cyprinid (black 'shark')	Eurasia
D. fragilis	freshwater	Cypriniformes: cyprinid (redknife)	China
D. fraternus	freshwater	Cypriniformes: cyprinid (bleak, sun bleak, ide, chub, roach, rudd)	Eurasia, North America
D. frisii	freshwater	Cypriniformes: cyprinid (ide, chub, roach)	Eurasia

D. fulcrum	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. fungulus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. furcatus	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. furcellatus	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. fustis	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. gabonensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. galilensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. garrae	freshwater	Cypriniformes: cyprinid (mudcarp, red garra)	Asia
D. geei	freshwater	Cypriniformes: cyprinid (Crucian carp)	Europe
D. gemellus	freshwater	Cypriniformes: cyprinid (bream, ide, chub, roach)	Eurasia
D. gemmicirrus	freshwater	Cypriniformes: cyprinid (?)	China
D. georgiensis	freshwater	Cypriniformes: cyprinid (stoneroller)	North America
D. gigihamatus	freshwater	Cypriniformes: cyprinid (percocypris carp)	Asia
D. glossogobii	freshwater, marine	Gobiiformes: gobiid (goby)	Africa, Australia
D. gnathopogonis	freshwater	Cypriniformes: cyprinid (jaw beard, longnose gudgeon)	China
D. gobii	freshwater	Cypriniformes: cyprinid (gudgeon)	Europe
D. gobiocypris	freshwater	Cypriniformes: cyprinid (rare minnow)	China
D. gobioninum	freshwater	Cypriniformes: cyprinid (gudgeon, pseudogoby, lizard gudgeon), alestid (tigerfish)	Africa, Asia
D. goktschaicus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. gotoi	marine	Perciformes: percichthyid (seabass)	Asia
D. gracilis	freshwater	Characiformes: alestid (tigerfish)	Africa
D. graciliuncinatus	freshwater	Cypriniformes: cyprinid (bream)	Eurasia
D. grandicirrus	freshwater	Cypriniformes: cyprinid (doty barbel)	Korea
D. greenei	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. grislaginis	freshwater	Cypriniformes: cyprinid (ide, chub)	Eurasia
D. guadianensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. guangxiensis	freshwater	Cypriniformes: cyprinid (lizard gudgeon)	Asia
D. gudaoensis	freshwater, marine	Gobiiformes: gobiid (goby)	Asia
D. guirensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. guizhouensis	freshwater	Cypriniformes: cyprinid (blackfish, lizard gudgeon)	Asia
D. gussevi	freshwater	Cypriniformes: cyprinid (yellowcheek, redknife)	Asia
D. gvosdevi	freshwater	Cypriniformes: cyprinid (minnow)	Europe
D. gyrocirrus	freshwater	Cypriniformes: cyprinid (ink carp)	China
D. hainanensis	freshwater	Cypriniformes: cyprinid (false halfknife)	Asia
D. hamatus	freshwater	Cypriniformes: catostomid (hogsucker, redhorse)	North America
D. hankinsoni	freshwater	Cypriniformes: cyprinid (silvery minnow)	North America
D. haplogonoides	freshwater	Cypriniformes: cyprinid (vimba bream, ide, chub)	Eurasia
D. haplogonus	freshwater	Cypriniformes: cyprinid (vimba bream, mullet, ide, chub, roach)	Eurasia
D. harmandi	freshwater	Cypriniformes: cyprinid (silver carp)	Asia
D. hauyingensis	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. hejiangensis	freshwater	Cypriniformes: cyprinid (?)	China
D. helicoides	freshwater	Cypriniformes: cyprinid (pseudogyrinocheilid)	China
D. helicoidus	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. helicophallus	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. helictocirrus	freshwater	Cypriniformes: cyprinid (topmouth culter)	Asia
D. hemiamphibothrium	freshwater	Perciformes: percid (ruffe, perch)	Eurasia
D. hemibarbi	freshwater	Cypriniformes: cyprinid (doty barbel)	Korea
D. hemiculteris	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. hemipetaloideus	freshwater	Cypriniformes: cyprinid (false halfknife)	Asia
D. hemiphysodes	freshwater	Cypriniformes: cyprinid (thornside)	China
D. hemitermedioides	freshwater	Cypriniformes: cyprinid (blackfish)	Asia
D. hemitremiae	freshwater	Cypriniformes: cyprinid (chub)	North America
D. hemivolutus	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. heterolepis	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. heteromorphus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. hirundinis	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. hirundinoides	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. holciki	freshwater	Cypriniformes: cyprinid (mullet)	Asia

D. hovorkai	freshwater	Cypriniformes: cyprinid (carp)	Eurasia
D. huhangensis	freshwater	Cypriniformes: cyprinid (thicklip gudgeon)	Asia
D. hui	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. hybognathus	freshwater	Cypriniformes: cyprinid (silvery minnow)	North America
D. hyderabadensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. hydrophloxi	freshwater	Cypriniformes: cyprinid (rough shiner)	North America
D. hypophthalmichthys	freshwater	Cypriniformes: cyprinid (bighead carp, silver carp)	Asia
D. idus	freshwater	Cypriniformes: cyprinid (ide)	Europe
D. imberbis	freshwater	Cypriniformes: cyprinid (jaw beard)	China
D. indicus	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. inexpectatus	freshwater	Cypriniformes: cyprinid (Crucian carp, grass carp)	Europe
D. insolitus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. intermedioides	freshwater	Cypriniformes: cyprinid (Crucian carp)	Europe
D. intermedius	freshwater	Cypriniformes: cyprinid (carp, crucian carp); Esociformes: esocid (pike)	Eurasia
D. intestinalis	freshwater	Cypriniformes: cyprinid (sharpray)	Asia
D. inutilis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. inversus	marine	Scombriformes: scombrid (mackerel); Perciformes: percichthyid (seabass)	Eurasia
D. iridescens	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. irinae	freshwater	Cypriniformes: cyprinid (false osman)	China
D. iskanderensis	freshwater	Cypriniformes: cyprinid (barbel, roach, cherry barb)	Eurasia, Africa
D. ivanovici	freshwater	Cypriniformes: cyprinid (Albanian roach)	Europe
D. iwani	freshwater	Cypriniformes: cyprinid (moggel, Orange River mudfish)	Africa
D. izjumovae	freshwater	Cypriniformes: cyprinid (ide, chub, rudd)	Eurasia
D. jaculus	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. jaei	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. jaini	freshwater	Cypriniformes: cyprinid (silverjaw minnow)	North America
D. jainisachali	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. jamansajensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. jiangjingensis	freshwater	Cypriniformes: cyprinid (Guichenot’s gudgeon)	China
D. jiayuensis	freshwater	Cypriniformes: cyprinid (bleak, yellowfin)	Middle-East, Eurasia
D. jubbstrema	freshwater, marine	Gobiiformes: gobiid (goby)	Africa, Australia
D. joriensis	freshwater	Cypriniformes: cyprinid (riffle minnows)	Asia
D. jucundus	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. jukhimenkoi	freshwater	Cypriniformes: cyprinid (white bream)	Asia
D. julieae	freshwater	Cypriniformes: cyprinid (silverjaw minnow)	North America
D. jullieni	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. junchisi	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. juveniformis	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. kalyanensis	freshwater	Cypriniformes: cyprinid (Indian carp)	Asia
D. kamang	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. kanchanaburiensis	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. katherineae	freshwater	Cypriniformes: cyprinid (stoneroller)	North America
D. kendalanicus	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. kersini	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. kii	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. kikuchii	marine	Perciformes: percichthyid (seabass)	Asia
D. knobihamatus	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. kontii	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. kritskyi	freshwater	Cypriniformes: cyprinid (hitch)	North America
D. ksibii	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. ksibioides	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. kulindrii	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. kulwieci	freshwater	Cypriniformes: cyprinid (barbel, ide, chub)	Eurasia, Africa
D. kunminensis	freshwater	Cypriniformes: cyprinid (kanglang)	China
D. kurematsui	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. kurenkowi	freshwater	Cypriniformes: cyprinid (minnow, three-lips)	Asia

D. kwainensis	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. labei	freshwater	Cypriniformes: cyprinid (black 'shark')	Eurasia
D. labeous	freshwater	Cypriniformes: cyprinid (black 'shark')	Eurasia
D. labiatus	freshwater	Siluriformes: bagrid (armorhead catfish)	China
D. lachneri	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. lali	freshwater, marine	Gobiiformes: gobiid (goby)	Africa, Australia
D. lamellatus	freshwater	Cypriniformes: cyprinid (mahseer, barbel, carp, grass carp, black carp)	Asia
D. lampam	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. lanka	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. laokajensis	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. larindae	freshwater	Cypriniformes: cyprinid (moggel, Orange River mudfish)	Africa
D. larrymilleri	freshwater	Cypriniformes: cyprinid (greenhead shiner, yellowfin shiner)	North America
D. lateolabracis	marine	Perciformes: percichthyid (seabass)	Asia
D. latihamatus	freshwater	Cypriniformes: cyprinid (Guichenot's gudgeon)	China
D. latirictus	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. latituba	freshwater	Cypriniformes: cyprinid (kingfish, sharpbelly)	Asia
D. laymani	freshwater	Cypriniformes: cyprinid (Crucian carp)	Europe
D. laymanianus	freshwater	Cypriniformes: cyprinid (thicklip gudgeon)	Asia
D. lebedevi	freshwater	Cypriniformes: cyprinid (lizard gudgeon)	Asia
D. leewanweii	freshwater	Cypriniformes: cyprinid (three-lips)	China
D. legionensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. lenkorani	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. lenkoranoides	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. leonis	freshwater	Cypriniformes: cyprinid (African carp)	Africa
D. lepidus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. leptobarbus	freshwater	Cypriniformes: cyprinid (mad barb)	Asia
D. leptosiphonius	freshwater	Cypriniformes: cyprinid (redwing fish)	Asia
D. leptostylus	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. leshanensis	freshwater	Cypriniformes: cyprinid (pseudogyronicheilid)	China
D. leucisci	freshwater	Cypriniformes: cyprinid (ide, chub)	Eurasia
D. leucisculus	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. liangshiyani	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. lianshanensis	freshwater	Cypriniformes: cyprinid (garra)	Asia
D. liaohoensis	freshwater	Cypriniformes: cyprinid (bitterling)	Europe
D. limaciformis	freshwater	Cypriniformes: cyprinid (rectoris)	Asia
D. limae	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. limleehongae	freshwater	Cypriniformes: cyprinid (yellowfin, nase)	Eurasia
D. limulus	freshwater	Cypriniformes: cyprinid (bigeye chub, river chub)	North America
D. lindbergi	freshwater	Cypriniformes: gyrinocheilid (sucking loach)	Asia
D. lineatus	freshwater	Cypriniformes: cyprinid (creek chub)	North America
D. lingualis	freshwater	Cypriniformes: cyprinid (red garra)	Asia
D. linstowi	freshwater	Cypriniformes: cyprinid (barbel, snowtrout)	Eurasia, Africa
D. linstowoides	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. lishuiensis	freshwater	Cypriniformes: cyprinid (redwing fish)	Asia
D. lohanii	freshwater	Cypriniformes: cyprinid (black 'shark')	Eurasia
D. longiacus	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. longicirrus	freshwater	Cypriniformes: cyprinid (mahseer, barbel, cherry barb, topmouth culter, carp, snowtrout)	Asia
D. longicopula	freshwater	Cypriniformes: cyprinid (barbel, snowtrout)	Eurasia, Africa
D. longilamenatus	freshwater	Cypriniformes: cyprinid (spikyhead carp)	Asia
D. longionchus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. longiphalloides	freshwater	Cypriniformes: cyprinid (black 'shark')	Eurasia
D. longiphallus	freshwater	Cypriniformes: cyprinid (barbel, black 'shark')	Eurasia, Africa
D. longissimus	freshwater	Cypriniformes: cyprinid (redknife)	China
D. longituba	freshwater	Cypriniformes: cyprinid (barb)	Asia
D. longivagina	freshwater	Cypriniformes: cyprinid (topmouth culter)	Asia
D. longquanensis	freshwater	Cypriniformes: cyprinid (barbel)	Asia
D. longsoi	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia

D. lophogonus	freshwater	Cypriniformes: cyprinid (bitterling)	Eurasia
D. lopuchinae	freshwater	Cypriniformes: cyprinid (carp)	Eurasia
D. loricirrus	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. luciosomis	freshwater	Cypriniformes: cyprinid (shark minnow)	Asia
D. lumpycirrus	freshwater	Cypriniformes: cyprinid (Tarim schizothoracin)	China
D. luxili	freshwater	Cypriniformes: cyprinid (golden shiner, eastern shiner)	North America
D. mabianensis	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. macracanthus	freshwater	Cypriniformes: cyprinid (tench); Perciformes: percid (ruffe)	Eurasia
D. macrocleithrum	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. macrocolpius	freshwater	Cypriniformes: cyprinid (tricolor sharkminnow)	Asia
D. macroformis	freshwater	Cypriniformes: cyprinid (barb)	China
D. macrogaster	freshwater	Siluriformes: clariid (catfish)	India
D. macrostomi	freshwater	Cypriniformes: cyprinid (kingfish)	Asia
D. maculatus	freshwater	Cypriniformes: cyprinid (riffle dace)	North America
D. magnibulbus	freshwater	Cypriniformes: cyprinid (longnose shiner, orangefin shiner)	North America
D. magnicirrus	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. magnicordus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. magnicystocirrus	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. magnihamatus	freshwater	Cypriniformes: cyprinid (bighead carp, crucian carp, grass carp, silver carp, black carp, topmouth culter, redknife, sharpbelly, Amur bream, white bream, danio, three-lips)	Asia
D. magnolium	freshwater	Cypriniformes: cyprinid (grey mullet)	Asia
D. magnus	freshwater	Cypriniformes: cyprinid (bigeye chub)	North America
D. maillardi	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. malayanus	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. malewitzkajae	freshwater	Cypriniformes: cyprinid (minnow)	Europe
D. malleolus	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. malleus	freshwater	Cypriniformes: cyprinid (asp, barbel, ide, chub)	Eurasia
D. manairensis	freshwater	Synbranchiformes: mastacembelid (spiny eel)	Asia
D. manicatus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. mantschuricus	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. markewitschi	freshwater	Cypriniformes: cyprinid (gudgeon, lizard gudgeon, pseudogoby)	Asia
D. marocanus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. martinovici	freshwater	Cypriniformes: cyprinid (roach)	Europe
D. mascomai	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. mawli	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. maximus	freshwater	Cypriniformes: cyprinid (thicklip gudgeon)	Asia
D. megastoma	freshwater	Cypriniformes: cyprinid (carp, white bream, bitterling)	Eurasia, Americas
D. megastylus	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. megatuba	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. melanopteri	freshwater	Cypriniformes: cyprinid (tricolour sharkminnow)	Asia
D. mendehei	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. meridionalis	freshwater	Cypriniformes: cyprinid (bleak, roach), cobitid (stone loach)	Asia
D. merus	freshwater	Cypriniformes: cyprinid (minnow)	Europe
D. micracanthus	freshwater	Cypriniformes: cyprinid (bleak, ide, chub, roach, rudd)	Eurasia, North America
D. microcirrus	freshwater	Cypriniformes: cyprinid (scraper)	Asia
D. microdontoides	freshwater	Cypriniformes: cyprinid (lizard gudgeon)	Asia
D. microlepidotus	freshwater	Cypriniformes: cyprinid (hitch, blackfish)	North America
D. microphallus	freshwater	Cypriniformes: cyprinid (creek chub)	North America
D. micropogoni	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. microtheloides	freshwater	Cypriniformes: cyprinid (doty barbel)	Korea
D. mikailovi	freshwater	Cypriniformes: cyprinid (scraper, barbel, ide, chub)	Eurasia
D. millieae	freshwater	Cypriniformes: cyprinid (river chub)	North America

D. minjiangensis	freshwater	Cypriniformes: cyprinid (pseudogyrinocheilid)	China
D. minor	freshwater	Cypriniformes: cyprinid (bleak, sun bleak, white bream, mullet, carp)	Eurasia, North America
D. minutus	freshwater	Cypriniformes: cyprinid (bream, white bream, bleak, asp, carp, koi carp)	Eurasia
D. mississippiensis	freshwater	Cypriniformes: cyprinid (river chub)	North America
D. mizellei	freshwater	Cyprinodontiformes: poeciliid (swordtail)	North America
D. mobedii	freshwater	Cypriniformes: cyprinid (morari)	Middle-East
D. modestus	freshwater	Cypriniformes: cyprinid (bleak, tench, carp, snowtrout)	Eurasia, North America
D. molitorelli	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. mollis	freshwater	Cypriniformes: cyprinid (bleak, tench, carp)	Eurasia, North America
D. molnari	freshwater	Cypriniformes: cyprinid (carp)	Eurasia
D. mongolicus	freshwater	Cypriniformes: cyprinid (redknife)	China
D. monocornis	freshwater	Cypriniformes: cyprinid (tench)	Eurasia
D. montschadskyi	freshwater	Cypriniformes: cyprinid (topmouth culter, redknife, sharpbelly)	Asia
D. moorei	freshwater	Cypriniformes: cyprinid (bigeye chub, eastern shiner)	North America
D. moorthyi	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. moximui	freshwater	Cypriniformes: cyprinid (dusky barbel)	China
D. mrazeki	freshwater	Cypriniformes: cyprinid (carp)	Eurasia
D. mrigali	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. mursae	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. muscariformis	freshwater	Cypriniformes: cyprinid (biglip gudgeon)	China
D. myersi	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. mylocheilus	freshwater	Cypriniformes: cyprinid (lake chub, peamouth chub)	North America
D. nanocirrus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. nanoides	freshwater	Cypriniformes: cyprinid (ide, chub)	Eurasia
D. nanus	freshwater	Cypriniformes: cyprinid (bream, white bream, bleak, scraper, ide, chub, roach, thicklip gudgeon)	Eurasia
D. nasalis	freshwater	Cypriniformes: cyprinid (white bream, roach, rudd)	Eurasia
D. narimani	freshwater	Cypriniformes: cyprinid (riffle minnows)	Asia
D. narzikulovi	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. nasali	freshwater	Cypriniformes: cyprinid (black carp)	Asia
D. nathaliae	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. navarroensis	freshwater	Cypriniformes: cyprinid (roach)	North America
D. navicularis	freshwater	Cypriniformes: cyprinid (thicklip gudgeon)	Asia
D. naviculoides	freshwater	Cypriniformes: cyprinid (ide, chub)	Eurasia
D. neoparvus	freshwater	Cypriniformes: cyprinid (riffle minnows)	Asia
D. newensis	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. nicolettae	freshwater	Cypriniformes: cyprinid (moggel, Orange River mudfish)	Africa
D. niedashui	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. niger	freshwater	Cypriniformes: catostomid (redhorse)	North America
D. nikolskyi	freshwater	Cypriniformes: cyprinid (minnow, sharpbelly)	Asia
D. nobilis	freshwater	Cypriniformes: cyprinid (bighead carp, grass carp, silver carp)	Asia
D. nuchalis	freshwater	Cypriniformes: cyprinid (silvery minnow)	North America
D. nuntuis	freshwater	Cypriniformes: cyprinid (bigeye chub, eastern shiner)	North America
D. nybelini	freshwater	Cypriniformes: cyprinid (nase, roach)	Europe
D. nyongensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. oblongus	freshwater	Cypriniformes: cyprinid (bitterling)	Eurasia
D. obscurus	freshwater	Cypriniformes: cyprinid (topmouth gudgeon)	Asia
D. occidentalis	freshwater	Cypriniformes: cyprinid (roach)	North America
D. olfactorius	freshwater	Cypriniformes: cyprinid (fathead minnow)	North America
D. oligospirophallus	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. omega	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia

D. omeiensis	freshwater	Cypriniformes: cyprinid (bitterling)	China
D. omenti	freshwater	Cypriniformes: cyprinid (Balkan barbelgudgeon)	Europe
D. onychoaccessorius	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. onychocirrus	freshwater	Cypriniformes: cyprinid (red garra)	Asia
D. onychorhini	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. oodeus	freshwater	Cypriniformes: cyprinid (doty barbel)	Korea
D. opsopoeodi	freshwater	Cypriniformes: cyprinid (pugnose minnow)	North America
D. orbus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. orchis	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. oreoleucisci	freshwater	Cypriniformes: cyprinid (osman)	Asia
D. orientalis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. ornatus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. ornithopodus	freshwater	Cypriniformes: cyprinid (yellowfin, smallscale yellowfin, sharpbelly)	Eurasia
D. ornithorrhynchus	freshwater	Cypriniformes: cyprinid (yellowfin, smallscale yellowfin, topmouth culter, redknife)	Eurasia
D. orphoidi	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. orthodon	freshwater	Cypriniformes: cyprinid (blackfish)	North America
D. oryziasi	freshwater	Beloniformes: adrianichthyid (medaka)	Asia
D. osculus	freshwater	Cypriniformes: cyprinid (riffle dace)	North America
D. osmanovi	freshwater	Cypriniformes: cyprinid (bream, carp, grass carp, ide, chub)	Eurasia
D. osteochili	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. ostraviensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. oumiensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. pahangensis	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. pakistanensis	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. pallens	freshwater	Cypriniformes: cyprinid (snowtrout)	China
D. palliatus	freshwater	Cypriniformes: cyprinid (Amur bream, white bream)	Asia
D. pallicirrus	freshwater	Cypriniformes: cyprinid (kingfish)	Asia
D. pamirensis	freshwater	Cypriniformes: cyprinid (false osman)	China
D. panchinpeii	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. pandus	freshwater	Cypriniformes: cyprinid (jaw beard)	China
D. pani	freshwater	Cypriniformes: cyprinid (kanglang)	China
D. pannosus	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. papernai	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. papillus	freshwater	Cypriniformes: cyprinid (bitterling)	Eurasia
D. parabramis	freshwater	Cypriniformes: cyprinid (Amur bream, white bream)	Asia
D. paracanthrobrama	freshwater	Cypriniformes: cyprinid (thornside)	China
D. paracurvituboides	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. paracymbidioides	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. paradinosaurinus	freshwater	Cypriniformes: cyprinid (barbel)	Asia
D. paradoxus	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. parahastatus	freshwater	Cypriniformes: cyprinid (redknife)	China
D. parahirundinus	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. parapeleci	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. parapterocleidus	freshwater	Cypriniformes: cyprinid (topmouth culter)	Asia
D. parawaldronii	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. partipentazonae	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. parvaccessorius	freshwater	Cypriniformes: cyprinid (bigeye chub)	North America
D. parvianchoris	freshwater	Cypriniformes: cyprinid (chela)	India
D. parvibulbus	freshwater	Cypriniformes: cyprinid (highscale shiner, weed shiner)	North America
D. parvicirrus	freshwater	Cypriniformes: cyprinid (golden shiner, roach)	North America, Eurasia
D. parviphallus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. parvisarcocheilichthysi	freshwater	Cypriniformes: cyprinid (thicklip gudgeon)	Asia
D. parvus	freshwater	Cypriniformes: cyprinid (riffle minnow, bleak, ide,	Eurasia

		chub)	
D. pavlovskyi	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. pectenatus	freshwater	Cypriniformes: cyprinid (bluntnose minnow)	North America
D. pectinate	freshwater	Cypriniformes: cyprinid (mahseer)	Asia
D. peculiaris	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. pekinensis	freshwater	Cypriniformes: cyprinid (Amur bream, white bream)	Asia
D. pedunculatus	freshwater	Cypriniformes: cyprinid (rasbora)	Asia
D. pellucidus	freshwater	Cypriniformes: cyprinid (redknife)	China
D. peltatus	freshwater	Cypriniformes: cyprinid (topmouth culter, redknife)	Asia
D. pentabrachiatus	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. pentabrachicleithrium	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. perakensis	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. percobromus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. percocypris	freshwater	Cypriniformes: cyprinid (percocypris carp)	Asia
D. perlus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. persis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. petaloideus	freshwater	Cypriniformes: cyprinid (smallscale yellowfin)	Asia
D. petenyi	freshwater	Cypriniformes: cyprinid (Danubian barbel, Romanian barbel)	Europe
D. petitjeanii	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. petkovici	freshwater	Cypriniformes: cyprinid (barbel, roach)	Eurasia, Africa
D. petruschewskyi	freshwater	Cypriniformes: cyprinid (Amur bream, white bream, silverfish)	Asia
D. petticoatus	freshwater	Cypriniformes: cyprinid (bitterling)	Europe
D. pharyngocephalus	freshwater, marine	Gobiiformes: gobiid (goby)	Africa, Australia
D. photogenis	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. phoxini	freshwater	Cypriniformes: cyprinid (carp, osman, minnow)	Eurasia
D. phymatachilus	freshwater	Cypriniformes: cyprinid (danio)	China
D. pienaari	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. pinleensis	freshwater	Cypriniformes: cyprinid (discogoby)	Asia
D. placentiformis	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. plegadus	freshwater	Cypriniformes: cyprinid (bigeye chub)	North America
D. pleioschizopetalus	freshwater	Cypriniformes: cyprinid (redknife)	China
D. plumbeus	freshwater	Cypriniformes: catostomid (redhorse)	North America
D. pokoase	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. pollens	freshwater	Cypriniformes: cyprinid (snowtrout)	China
D. pollex	freshwater	Cypriniformes: cyprinid (highscale shiner, eastern shiner)	North America
D. polycheirodactylus	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. polylepidis	freshwater	Cypriniformes: cyprinid (nase, ide, chub)	Eurasia
D. prespensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. primarius	freshwater	Cypriniformes: cyprinid (minnow, three-lips)	Asia
D. procypri	freshwater	Cypriniformes: cyprinid (ink carp)	China
D. pronatus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. propinquus	freshwater	Cypriniformes: cyprinid (bream, vimba bream)	Eurasia
D. proprius	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. prostae	freshwater	Cypriniformes: cyprinid (ide, chub)	Eurasia
D. protozysron	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. pseudanchoratus	freshwater	Cypriniformes: cyprinid (scraper, barbel, black ‘shark’)	Eurasia
D. pseudaspii	freshwater	Cypriniformes: cyprinid (ide, chub, redfin)	Eurasia
D. pseudoflagillicirrus	freshwater	Cypriniformes: cyprinid (topmouth culter, redknife)	Asia
D. pseudogobii	freshwater	Cypriniformes: cyprinid (gudgeon, lizard gudgeon, pseudogoby)	Asia
D. pseudohemiculteri	freshwater	Cypriniformes: cyprinid (minnow)	China
D. pseudominor	freshwater	Cypriniformes: cyprinid (riffle minnows)	Asia
D. pseudosphyrna	freshwater	Cypriniformes: cyprinid (beardless barb, cherry barb)	Asia
D. pterocleidus	freshwater	Cypriniformes: cyprinid (redknife)	China
D. pterygialis	freshwater	Cypriniformes: cyprinid (topmouth culter, redknife)	Asia

D. ptychidionis	freshwater	Cypriniformes: cyprinid (ratmouth barbel)	China
D. ptychocheilus	freshwater	Cypriniformes: cyprinid (pikeminnow)	North America
D. pulcher	freshwater	Cypriniformes: cyprinid (asp, scraper, barbel)	Eurasia
D. puntii	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. puntioplites	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. pusillus	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. pyriformis	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. qingshuihaiensis	freshwater	Cypriniformes: cyprinid (kanglang)	China
D. quadricurvitubus	freshwater	Cypriniformes: cyprinid (dusky barbel)	China
D. quangfami	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. qujiangensis	freshwater	Cypriniformes: cyprinid (ink carp)	China
D. quxianensis	freshwater	Cypriniformes: cyprinid (?)	China
D. ramosus	freshwater	Cypriniformes: cyprinid (scraper)	Asia
D. ramulosus	freshwater	Cypriniformes: cyprinid (ide, chub, roach)	Eurasia
D. rarissimus	freshwater	Cypriniformes: cyprinid (roach)	Eurasia
D. rarus	freshwater	Cypriniformes: cyprinid (doty barbel)	Korea
D. rastellus	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. reciprocus	freshwater	Cypriniformes: cyprinid (bigeye chub, river chub)	North America
D. rectotrabus	freshwater	Cypriniformes: cyprinid (red garra)	Asia
D. reinii	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. remicirrus	freshwater	Cypriniformes: cyprinid (barbel)	Asia
D. retiformis	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. retroversus	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. rhadicirrus	freshwater	Cypriniformes: cyprinid (minnow)	China
D. rhinichthius	freshwater	Cypriniformes: cyprinid (riffle dace)	North America
D. rhinogobii	freshwater	Gobiiformes: gobiid (goby)	Asia
D. rhodeusi	freshwater	Cypriniformes: cyprinid (bitterling)	Eurasia
D. rhombocarpus	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. rhynchoideus	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. richardsonius	freshwater	Cypriniformes: cyprinid (redside shiner)	North America
D. rimskykorsakowi	freshwater	Cypriniformes: cyprinid (bleak, yellowfin, smallscale yellowfin)	Middle-East, Eurasia
D. ritius	freshwater	Siluriformes: bagrid (catfish)	Asia
D. rizvii	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. robisoni	freshwater	Cypriniformes: cyprinid (bluehead shiner)	North America
D. robustus	freshwater	Esociformes: esocid (pike, asp, ide, chub)	Eurasia
D. rohdeianus	freshwater	Cypriniformes: cyprinid (scraper)	Asia
D. rongjianensis	freshwater	Cypriniformes: cyprinid (barb)	China
D. rosickyi	freshwater	Cypriniformes: cyprinid (roach)	Europe
D. rostellum	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. rostricirrus	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. rostrum	freshwater	Cypriniformes: cyprinid (doty barbel)	Korea
D. ruahae	freshwater	Cypriniformes: cyprinid (scraper, barbel)	Eurasia
D. rubellus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. rufijii	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. rutilus (*rutili*)	freshwater	Cypriniformes: cyprinid (roach)	Eurasia
D. rysavyi	freshwater	Cypriniformes: cyprinid (riffle minnow, asp)	Asia
D. sacrati	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. sagittavaginalis	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. sagmaformis	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. sahelensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. sahuensis	freshwater	Cypriniformes: cyprinid (carp)	Eurasia
D. salutaris	freshwater	Cypriniformes: cyprinid (jaw beard)	China
D. sanhuiensis	freshwater	Cypriniformes: cyprinid (ink carp)	China
D. sanjiangensis	freshwater	Cypriniformes: cyprinid (biglip gudgeon)	China
D. sarani	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. sarcocheilichthydis	freshwater	Cypriniformes: cyprinid (thicklip gudgeon)	Asia
D. saurogobii	freshwater	Cypriniformes: cyprinid (lizard gudgeon)	Asia
D. scalpelliformis	freshwater	Cypriniformes: cyprinid (redknife)	China
D. sceptici	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. schizocypris	freshwater	Cypriniformes: cyprinid (snow trout)	Asia

D. schizopygopsis	freshwater	Cypriniformes: cyprinid (false osman)	China
D. sclerovaginalis	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. scorpius	freshwater	Cypriniformes: cyprinid (Rifian barbel)	Africa
D. scroticirrus	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. scutatus	freshwater	Cypriniformes: cyprinid (cutlip minnow)	North America
D. seamsteri	freshwater	Cypriniformes: cyprinid (suckermouth minnow)	North America
D. securiformis	freshwater	Cypriniformes: cyprinid (doty barbel)	Korea
D. seenghali	freshwater	Siluriformes: bagrid (catfish)	Asia
D. sekerai	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. sekulovici	freshwater	Cypriniformes: cyprinid (roach)	Europe
D. selliformis	freshwater	Cypriniformes: cyprinid (?)	China
D. sematus	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. semifasciolatae	freshwater	Cypriniformes: cyprinid (scraper)	Asia
D. semilabeo	freshwater	Cypriniformes: cyprinid (pseudogyrinocheilid)	China
D. semotilus	freshwater	Cypriniformes: cyprinid (stoneroller, bluntnose minnow, creek chub)	North America
D. senegalensis	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. shantungensis	freshwater	Cypriniformes: cyprinid (yellowcheek)	Asia
D. shengxianensis	freshwater	Cypriniformes: cyprinid (silverfish)	Asia
D. siamensis	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. sichuansis	freshwater	Cypriniformes: cyprinid (ya-fish)	China
D. simiae	freshwater	Cypriniformes: cyprinid (barb)	Europe
D. similis	freshwater	Cypriniformes: cyprinid (bream, vimba bream, white bream, bleak, asp, tench, nase, osman, bluntnose minnow, ide, chub, sabre carp, roach, rudd)	Eurasia
D. simplex	freshwater	Cypriniformes: cyprinid (osman)	Asia
D. simplexus	freshwater	Cypriniformes: cyprinid (bluntnose minnow)	North America
D. simplicimalleata	freshwater	Cypriniformes: cyprinid (bream, white bream, sabre carp, roach)	Eurasia
D. singularis	freshwater	Cypriniformes: cyprinid (thicklip gudgeon)	Asia
D. sinibramis	freshwater	Cypriniformes: cyprinid (silverfish)	Asia
D. sinilabe	freshwater	Cypriniformes: cyprinid (biglip gudgeon)	China
D. sinogastromyzoni	freshwater	Cypriniformes: homalopterid (loach)	Eurasia
D. skrjabinensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. skrjabini	freshwater	Cypriniformes: cyprinid (silver carp)	Asia
D. slastnikowi	freshwater	Cypriniformes: cyprinid (smallscale yellowfin)	Asia
D. soikhaonensis	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. solidus	freshwater	Cypriniformes: cyprinid (carp)	Eurasia
D. soni	freshwater, marine	Gobiiformes: gobiid (goby)	Africa, Australia
D. soufii	freshwater	Cypriniformes: cyprinid (ide, chub)	Eurasia
D. sparsus	freshwater	Cypriniformes: cyprinid (gudgeon)	China
D. spatulus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. speciosus	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. sphyrna	freshwater	Cypriniformes: cyprinid (bream, vimba bream, white bream, bleak, mullet, gudgeon, ide, chub, sabre carp, bitterling, roach, rudd)	Eurasia, Middle-East
D. sphyrnoides	freshwater	Cypriniformes: cyprinid (barbel, tor barb)	Eurasia, Africa
D. spinibarbichthi	freshwater	Cypriniformes: cyprinid (barbel, spiny barbel)	Asia
D. spinicirrus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. spinitubus	freshwater	Cypriniformes: cyprinid (Indian carp)	Asia
D. spiralis	freshwater	Cypriniformes: cyprinid (Crucian carp)	Europe
D. spirocirrus	freshwater	Cypriniformes: cyprinid (doty barbel)	Korea
D. spirotubivagina	freshwater	Cypriniformes: cyprinid (red garra)	Asia
D. spirovagina	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. spiruli	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. sprostonae	freshwater	Cypriniformes: cyprinid (barbel chub, ide, chub)	Eurasia
D. squaliobarbi	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. squameus	freshwater	Cypriniformes: cyprinid (gudgeon, topmouth gudgeon)	Asia
D. stankovici	freshwater	Cypriniformes: cobitid (stone loach)	Asia

D. strelkowi	freshwater	Cypriniformes: cyprinid (Amur bream, white bream)	Asia
D. strombus	freshwater	Cypriniformes: cyprinid (rectoris)	Asia
D. subtilis	freshwater	Cypriniformes: cyprinid (barbel, cherry barb)	Eurasia, Africa
D. suchengtaii	freshwater	Cypriniformes: cyprinid (bighead carp, silver carp)	Asia
D. suecicus	freshwater	Cypriniformes: cyprinid (roach)	Eurasia
D. sukkurensis	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. sungariensis	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. symavesi	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. tabellaeformis	freshwater	Cypriniformes: cyprinid (rock carp)	China
D. taihuensis	freshwater	Cypriniformes: cyprinid (bighead carp)	Asia
D. takahashii	freshwater	Cypriniformes: cyprinid (carp)	Eurasia
D. talimuensis	freshwater	Cypriniformes: cyprinid (Tarim schizothoracin)	China
D. tapienensis	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. tauricus	freshwater	Cypriniformes: cyprinid (riffle minnows)	Asia
D. tchangi	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. tenax	freshwater	Cypriniformes: cyprinid (creek chub)	North America
D. tendiculus	freshwater	Cypriniformes: cyprinid (bleak, yellowfin, smallscale yellowfin)	Middle-East, Eurasia
D. tenuis	freshwater	Perciformes: percid (perch)	cosmopolitan
D. teresae	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. tetraradiatus	marine	Clupeiformes: clupeid (herring)	India
D. texomensis	freshwater	Cypriniformes: cyprinid (bigeye chub)	North America
D. thailandensis	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. thapari	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. tihsiukangi	freshwater	Cypriniformes: cyprinid (bleak, yellowfin, smallscale yellowfin)	Middle-East, Eurasia
D. tincae	freshwater	Cypriniformes: cyprinid (tench)	Eurasia
D. tissensis	freshwater	Cypriniformes: cyprinid (riffle minnow, bleak)	Asia
D. titus	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. tongrenensis	freshwater	Cypriniformes: cyprinid ()	
D. tongtinensis	freshwater	Cypriniformes: cyprinid (redknife)	China
D. tonguthaii	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. tonii	freshwater	Cypriniformes: cobitid (stone loach)	Asia
D. tonkinensis	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. tori	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. torquegenitalis	freshwater	Cypriniformes: cyprinid (bonelip)	Indo-China
D. toxostomi	freshwater	Cypriniformes: cyprinid (nase)	Europe
D. triappendixis	freshwater	Cypriniformes: cyprinid (?)	?
D. tridactylus	freshwater	Cypriniformes: cyprinid (pikeminnow)	North America
D. tridens	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia
D. tridigitatus	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. trifucellatoides	freshwater	Cypriniformes: cyprinid (blackfish)	Asia
D. trioxonis	freshwater	Cypriniformes: cyprinid (bitterling)	Europe
D. tripathii	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. trulIaeformis	freshwater	Cypriniformes: cyprinid (jaw beard)	China
D. tuba	freshwater	Cypriniformes: cyprinid (riffle minnow, asp, pike asp, tench, vimba bream, barbel, crucian carp, ide, chub, roach, rudd); Perciformes: percid (perch); Esociformes: esocid (pike),	Eurasia, North America
D. tubarius	freshwater	Cypriniformes: cyprinid (black ‘shark’)	Eurasia
D. tubatus	freshwater	Cypriniformes: cyprinid (barbel chub)	Asia
D. tubulus	freshwater	Cypriniformes: cyprinid (false halfknife)	Asia
D. tunisiensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. turaliensis	freshwater	Cypriniformes: cyprinid (roach)	Eurasia
D. turkestanikus	freshwater	Cypriniformes: cyprinid (sharpray)	Asia
D. tylognathi	freshwater	Cypriniformes: cyprinid (mudcarp, red garra)	Asia
D. umbelliformis	freshwater	Cypriniformes: cyprinid (mahseer)	Asia
D. unguiformis	freshwater, marine	Salmoniformes: salmonid (whitefish); Scorpaeniformes: cottid (sculpin)	cosmopolitan
D. ungulatus	freshwater	Cypriniformes: cyprinid (yellowfin)	Eurasia

D. urus	freshwater	Cypriniformes: catostomid (redhorse)	North America
D. uyeni	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. vaginulatus	freshwater	Cypriniformes: cyprinid (bighead carp, grass carp, silver carp)	Asia
D. valeti	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. validus	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. vancleavei	freshwater	Cypriniformes: cyprinid (chiselmouth, pikeminnow)	North America
D. vannus	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. varicorhini	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. varicorhinoides	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. varius	freshwater	Cypriniformes: cyprinid (Maghreb barbel)	Africa
D. vastator	freshwater	Cypriniformes: cyprinid (scraper, vimba bream, barbel, carp, crucian carp, grass carp), cobitid (weather loach), Esociformes: esocid (pike)	Eurasia
D. venusti	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. vicinus	freshwater	Cypriniformes: cyprinid (black 'shark')	Eurasia
D. vistulae	freshwater	Cypriniformes: cyprinid (nase, ide, chub, roach)	Eurasia
D. viticulus	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. volfi	freshwater	Cypriniformes: cyprinid (cherry barb)	Asia
D. volgensis	freshwater	Cypriniformes: cyprinid (white bream)	cosmopolitan
D. volutus	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. vranoviensis	freshwater	Cypriniformes: cyprinid (ide, chub)	Eurasia
D. wegeneri	freshwater	Cypriniformes: cyprinid (carp, crucian carp)	Eurasia
D. weishanensis	freshwater	Cypriniformes: cyprinid (bitterling)	Europe
D. welakae	freshwater	Cypriniformes: cyprinid (eastern shiner)	North America
D. wuae	freshwater	Cypriniformes: cyprinid (topmouth culter)	Asia
D. wuhanensis	freshwater	Cypriniformes: cyprinid (smallscale yellowfin)	Asia
D. wuhuensis	freshwater	Cypriniformes: cyprinid (silver carp)	Asia
D. wunderi	freshwater	Cypriniformes: cyprinid (bream, white bream, sharpray, mullet, roach)	Eurasia
D. wurtzii	freshwater	Cypriniformes: cyprinid (scraper)	Eurasia
D. xenocypris	freshwater	Cypriniformes: cyprinid (yellowfin, smallscale yellowfin)	Eurasia
D. xichangensis	freshwater	Cypriniformes: cyprinid (minnow)	China
D. xihuensis	freshwater	Cypriniformes: cyprinid (sharpbelly)	Asia
D. xinjiangensis	freshwater	Cypriniformes: cyprinid (ide)	Asia
D. xiondareni	freshwater	Cypriniformes: cyprinid (?)	China
D. xiyangjiangensis	freshwater	Cypriniformes: cyprinid (false halfknife)	Asia
D. yassensis	freshwater	Cypriniformes: cyprinid (African carp)	Africa
D. yinjiangensis	freshwater	Cypriniformes: cyprinid (pseudogyrinocheilid)	China
D. yinwenyingae	freshwater	Cypriniformes: cyprinid (bream, white bream, asp, nase, carp, grass carp, silver carp, ide, chub, minnow, roach, rudd, biglip gudgeon)	Eurasia
D. yogendrai	freshwater	Cypriniformes: cyprinid (carp, black 'shark')	Asia
D. youjiangensis	freshwater	Cypriniformes: cyprinid (false halfknife)	Asia
D. yousefpouri	freshwater	Cypriniformes: cyprinid (morari)	Middle-East
D. yuyaoensis	freshwater	Cypriniformes: cyprinid (redwing fish)	Asia
D. zaccoi	freshwater	Cypriniformes: cyprinid (minnow)	Asia
D. zachvatkini	freshwater	Cypriniformes: cyprinid (jaw beard)	China
D. zalesskyi	freshwater	Cypriniformes: cyprinid (bream, white bream, yellowfin, smallscale yellowfin)	Eurasia
D. zandti	freshwater	Cypriniformes: cyprinid (bream, white bream)	Eurasia
D. zatensis	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa
D. zoanyngi	freshwater	Cypriniformes: cyprinid (carp)	Asia
D. zulfikari	freshwater	Cypriniformes: cyprinid (barbel)	Eurasia, Africa

Parasite morphology: Dactylogyrid monogenean parasites have 3 distinct developmental stages: eggs, larvae (oncomiracidia) and adults. The eggs are oval in shape and quite variable in size depending on the species: dimensions ranging from 32-120 µm in length by 28-60 µm in width. The eggs have large tanned egg capsules, sometimes with a short polar filament at the posterior end. Eggs

hatch to release a free-swimming ciliated larva (called an oncomiracidium) which is elongate measuring 95-130 x 35-50 µm. The larvae are covered with tufts of ciliated locomotory cells, usually have 2 pairs of large pigmented eye and already have a distinct posterior haptor (opisthaptor) with developed marginal hooks and primordial anchors. The worms progress through immature juvenile stages (sometimes called post-oncomiracidia) to form hermaphroditic adults which are protandrous (male reproductive organs develops before female organs, so immature stages often possess no or little pigmented vitellaria). Adult worms are small measuring 0.3-2.0 mm in length by 0.15-0.30 mm in width and have shed their oncomiracidial ciliated cells. Members of the genus *Dactylogyrus* are readily recognized by the possession of a 4-lobed head usually with 2 pairs of pigmented eyes (some species with only 1 pair) and a posterior haptor (opisthaptor) with 1 conspicuous pair of large ventral anchors (sometimes called hooks), 1-2 connective dorsal bars and up to 14 small marginal hooks (sometimes called hooklets). Adults have a sclerotized copulatory apparatus composed of a copulatory tube and an accessory piece, and the internal female reproductive organs comprise a germarium (producing oocytes) and extensive pigmented vitellaria (vitelline cells provide nourishment for developing embryo and contribute to eggshell formation). Adult worms are oviparous (egg-laying) and extrude mature eggs.

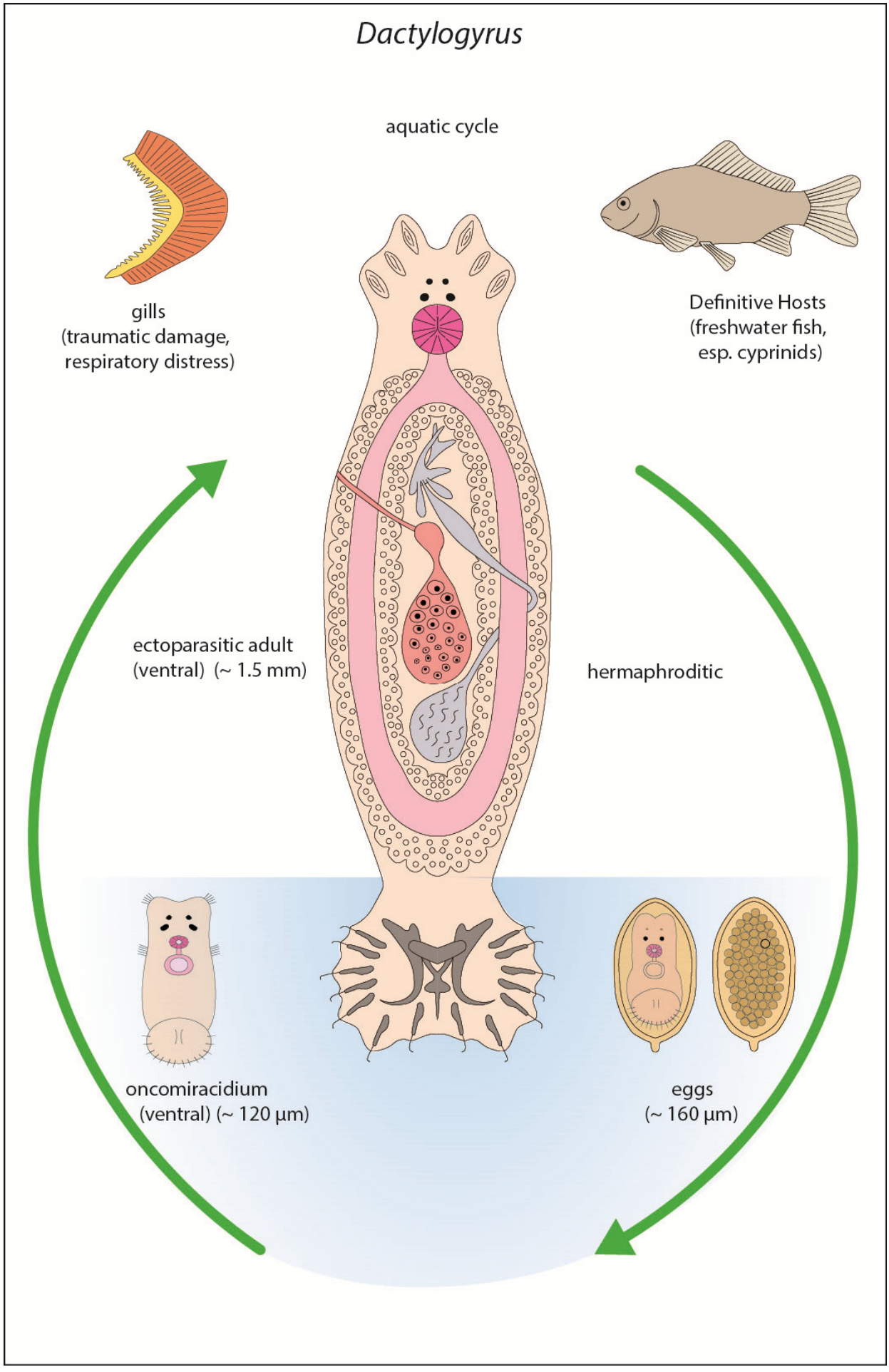
Site of infection: Dactylogyrids are commonly known as gill flukes and are found predominantly on the gills of their fish hosts (mainly cyprinids), although in heavy infections, worms may be found attached to the skin, fins and inside the buccal cavity. Oncomiracidia are free-swimming within their aquatic environments.

Pathogenesis: Adult worms attach to gill tissues and feed on epithelial cells and mucus, thus causing traumatic damage which becomes the focal point for haemorrhage, inflammation, necrosis, gill metaplasia and/or hyperplasia, excessive mucus production and often secondary bacterial and fungal infections. Infected fish may exhibit significant morbidity and mortality, with clinical signs including anorexia, lethargy and respiratory distress with aberrant behaviours (elevated respiration, opercular flapping or flaring, swimming near the surface, gasping, scratching gills on rocks, and leaping out of water). The severity of disease is often dependent on the intensity of infection, with many worms causing more severe signs, although some fish species appear to be more resistant to clinical infections and can tolerate larger worm populations with less ill effect. Some hosts have also demonstrated spontaneous declines in infection rates, apparently associated either with the development of protective immune responses or the rate of gill growth and repair (faster in fingerling stages).

Developmental cycle and mode of transmission: *Dactylogyrus* spp. undergo direct transmission between fish hosts involving free-swimming larval stages (oncomiracidia) which seek new hosts. Mature worms lay from 4-60 (usually 4-10) eggs per day which are released into the aquatic environment and sediment to the benthos (although some species produce eggs with short polar filaments which aid in their suspension or entanglement with substrates). Depending on temperature, the eggs hatch within several days to release ciliated oncomiracidium which actively swim about seeking new hosts. Although the larvae may live for 1-2 days, they apparently lose their infectivity after 4-8 hours. Larvae infect new hosts either by attaching directly to the gills when washed through with inhaled water, or by attaching to the skin and then migrating to the gills. Once the oncomiracidia attach, they shed their ciliated cells and develop into hermaphroditic adults over 4-5 days. Adult worms usually live for 5-40 days and spend their entire lives on the same host. While the whole life-cycle may be completed in several days in water temperatures around 20ºC, it may take substantially longer (weeks to months) when water temperatures are lower. A few species have exhibited prolonged lifespans (over a year) with reproduction limited to warmer seasons and peak infections occurring in late autumn or early winter. Heavier infections have also been detected in fish during their spawning seasons.

Differential diagnosis: Infections are best diagnosed by the direct microscopic detection of parasites in wet mounts of fresh gill biopsies (smears, scrapes or snips). Specimens should be recovered without excessive blood or mucus and then fixed in 1-2% formalin. Sclerotized organs are best viewed in samples embedded under pressure in glycerin mounts. Members of the genus *Dactylogyrus* can be readily identified by their characteristic morphological features (notably their 4-lobed heads, 4 eyespots, and opisthaptor with anchors and hooks), although it can be difficult to resolve individual species due to their morphotypic heterogeneity.

Treatment and control: Prompt diagnosis and treatment is paramount for controlling gyrodactylid outbreaks as their short generation times can lead to rapid increases in parasite populations in susceptible fish. Infections can spread rapidly through aquaria and culture systems, especially where stocking densities are high. Effective methods for controlling infections involve bathing fish in various chemical solutions, including anthelmintics (praziquantel, levamisole, fenbendazole, albendazole), organophosphates (metrifonate, dichlorvos, trichlorfon, bromex), salts (sodium chloride, copper sulphate), oxidising agents (hydrogen peroxide, peracetic acid, sodium percarbonate, potassium permanganate) and reducing agents (formaldehyde, formalin). However, gyrodactylid eggs are very resistant to chemical treatment so multiple treatments are required to control infections. Consideration should be given to ambient environmental conditions (water quality, temperature, salinity, organic content) as well as drug retention times and with-holding periods.


Dactylogyrus
aquatic cycle
gills
(traumatic damage,
respiratory distress)
Definitive Hosts
(freshwater fish,
esp. cyprinids)
ectoparasitic adult
(ventral) (~ 1.5 mm)
hermaphroditic
oncomiracidium
(ventral) (~ 120 µm)
eggs
(~ 160 µm)



Dactylogyrus adult worm



Dactylogyrus adult worm

Benedenia
(platyhelminth: monogenea)

Overview

Platyhelminths have triploblastic acoelomate soft bodies which are markedly flattened in profile (hence their common name as flatworms). They undergo protostomial embryonic development but do not moult during growth. On the basis of molecular evidence, they are classified within the Lophotrochozoa despite the absence of lophophore mouthparts and trochophore larvae. Three classes are composed entirely of parasitic flatworms (Cestoda, Trematoda and Monogenea), which have prominent attachment organs (suckers or bothria), syncytial teguments, shell glands and vitellaria involved in ectolecithal egg development, and life-cycles involving a variety of larval stages. Monogeneans are elongate to oval flatworms that are ectoparasitic on the skin and gills of fish, although a few are found in the urinary tracts of turtles, frogs and fishes. They have an anterior adhesive organ (prohaptor) and a conspicuous posterior adhesive organ (opisthaptor) armed with hooks or spines, often highly modified for attachment to specific sites. They are hermaphroditic and have direct life-cycles, mostly where eggs hatch releasing a free-swimming larva (oncomiracidium) which actively seeks a new host. Monopisthocotyleans have an opisthaptor that forms a single symmetrical attachment unit lacking haptoral clamps. Capsalids are large oval worms and the opisthaptor has a pair of anterior suckers and two pairs of posterior hooks. Infestations by *Benedenia* spp. have been associated with skin lesions, mortality and reduced productivity in cultured fish populations.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Lophotrochozoa (lophophore feeding structure or trochophore larva or neither)
Phylum:	Platyhelminthes (flatworms, acoelomate, most hermaphroditic, prominent attachment organs)
Clade:	Neodermata (syncytial tegument = neodermis)
Class:	Monogenea (monoxenous ectoparasites, sac-like gut, direct cycles, oncomiracidium with 3 ciliary bands)
Order:	Monopisthocotylea (posterior haptor comprising a single symmetrical attachment unit, no haptoral clamps)
Family:	Capsalidae (large worms, haptor with pair anterior suckers and two pairs of posterior hooks)
Genus:	*Benedenia* (parasitic in skin/gills of fish)
Species:	various species cause skin lesions in fish

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that do not moult during their life-cycles are grouped together in the enigmatic clade Lophotrochozoa, including the platyhelminths, rotifers, lophophorates, annelids and molluscs. Platyhelminths (flatworms) have soft acoelomate flat bodies with three-dimensional arrays of muscles that generate a typical writhing motion (cf. longitudinal muscles in nematodes producing a thrashing motion). Flatworms do not have a single unifying characteristic (synapomorphy) but comprise diverse free-living (most Turbellaria) and parasitic (Neodermata) assemblages. Neodermata have non-ciliated syncytial (multinucleate) teguments and 3 classes are recognized, all with prominent attachment organs, namely, Cestoda with anterior bothridia/bothria (true/false suckers), Trematoda with oral and ventral suckers (previously called acetabula), and Monogenea with posterior haptors (opisthaptors). All have shell glands surrounding the ootype, and most exhibit ectolecithal egg development (yolk not present in egg but secreted by accessory glands called vitellaria or yolk glands). Most have indirect life-cycles involving the development of adult worms in vertebrates and larval stages in intermediate hosts (usually invertebrates).

Monogeneans and trematodes (flukes) have blind sac-like guts (lacking an anus) while cestodes (tapeworms) lack digestive tracts. Some 3,500 monogenean species have been described: most being ectoparasitic on the skin and gills of fish, although a few are found in the urinary tracts of turtles, frogs, fish and the eye of the hippopotamus. They have an anterior adhesive organ (prohaptor) and a conspicuous posterior adhesive organ (opisthaptor) armed with hooks, hooklets, hamuli (anchors) or clamps, often highly modified for attachment to specific sites. They are monoecious (hermaphroditic) and have direct monoxenous life-cycles mostly where eggs release free-swimming larvae (oncomiracidia with 3 ciliary bands) that actively seek new hosts (gyrodactylids are the exception as they are viviparous and produce live young). While the higher taxonomy of the Monogenea is often disputed with respect to rank, some 67 families have been resolved on the basis of morphological, biological and molecular studies. Three main groups are recognized: 28 families of Monopisthocotylea (opisthaptor with hooks, ectoparasitic on fish skin and gills, feed on epithelia); 37 families of Polyopisthocotylea (opisthaptor with clamps, ectoparasitic on fish gills, feed on blood); and 2 families of Polystomatoinea (opisthaptor with suckers, endoparasitic in tetrapods).

Order	No. families	No. spp.	DH	Characters
Class: Monogenea (= Monogenoidea) (monogenetic life-cycles, ectoparasitic mainly on fish) ~ 3,500 spp.				
Subclass: Monopisthocotylea (= Polyonchoinea) (opisthaptor with hooks, feed on fish epithelia) ~2,500 spp.				
Capsalidea	2	200	mostly marine teleosts, some elasmobranchs	2 anterior suckers, 2 pairs anchors, 14 marginal haptoral hooks, some loculi
Dactylogyridea (= Monoaxonematidea)	17	1,000	freshwater and marine teleosts, coelacanths, squalea	sperm with single axoneme, 12-14 haptoral hooks, 2 pairs anchors, 1 transverse bar
Gyrodactylidea	5	1,500	freshwater and marine teleosts, squid, copepods	16 marginal 'hinged' haptoral hooks,1 pair anchors, dorsal and ventral bars, most viviparous (some nested polyembryony)
Monocotylidea	3	90	marine elasmobranchs	14 marginal haptoral hooks, some loculi
Montchadskyellidea	1	10	marine teleosts	14 marginal haptoral hooks, gut diverticulate, some endoparasitic in gut
Subclass: Polyopisthocotylea (= Heteronchoinea) (opisthaptor with clamps, most feed on blood of fish) ~1,000 spp.				
Chimaericolidea	1	5	marine holocephalans (chimaeras)	clamps, 1 pair anchors, haptor with 14 marginal hooks (each with domus)
Diclybothriidea	2	70	marine elasmobranchs, holocephalans, freshwater acipenseriform teleosts	clamps open and act as suckers, lateral sclerites absent
Mazocraeidea	34	920	numerous freshwater and marine teleost families	clamps with various structures incl. additional sclerites, hooks, spines; oral sucker a buccal organ, eggs with 2 polar filaments
Subclass: Polystomatoinea (parasitize aquatic tetrapods and lungfish)				
Polystomatidea	2	100	tetrapods (turtles, amphibians, hippopotamus), lungfish	haptor with 3 pairs suckers, egg filaments absent, some endoparasitic in tubular organs

Monopisthocotyleans have an opisthaptor that forms a single symmetrical attachment unit lacking haptoral clamps. Five orders are recognized on the basis of differences in parasite morphology, development and host occurrence; including the order Capsalidea characterized by worms possessing 2 anterior suckers, 2 pairs of anchors and a posterior haptor with 14 marginal hooks and accessory sclerites. A total of 250 species belonging to 2 families (Capsalidae and Enoplocotylidae) have been described mostly from marine bony (teleost) and some cartilaginous (chondrichthyan) fishes. Nine capsalid subfamilies have been erected containing 49 genera and over 220 species; most parasitizing teleost fishes although 2 species are found on sturgeons and 15 species on elasmobranchs. The combination of ancient (shark, ray, sturgeon) and modern (teleost) fish lineages as hosts suggests that capsalid evolution is likely a blend of host-parasite co-evolution and host-switching.

Capsalidae subfamilies	Haptor morphology	Number of testes	Hosts	Genera (number of species)
Benedeniinae	aseptate	2	mostly teleosts, some elasmobranchs	*Allobenedenia* (2), *Allometabenedeniella* (1), *Ancyrocotyle* (2), *Benedenia* (syn. *Tareenia*) (30), *Benedeniella* (2), *Calicobenedenia* (1), *Dioncopseudobenedenia* (1), *Lagenivaginopseudobenedenia* (2), *Menziesia* (5), *Metabenedeniella* (2), *Neobenedenia* (6), *Oligoncobenedenia* (1), *Pseudallobenedenia* (2), *Trimusculotrema* (4)
Capsalinae	septate	multiple	teleosts	*Caballerocotyla* (24), *Capsala* (14) , *Capsaloides* (10), *Nasicola* (2), *Tricotyla* (3), *Tristoma* (8), *Tristomella* (8)
Dioncinae	septate	2	teleosts, elasmobranchs	*Dioncus* (11)
Encotyllabinae	septate	2	teleosts	*Alloencotyllabe* (1), *Encotyllabe* (17)
Entobdellinae	aseptate	2	elasmobranchs (esp batoids), some teleosts (esp. flatfish)	*Branchobdella* (1), *Entobdella* (9), *Listrocephalos* (2), *Neoentobdella* (6), *Pseudoentobdella* (1)

Interniloculinae	septate	4	teleosts	*Interniloculus* (2)
Nitzschiinae	aseptate	multiple	acipenserids (sturgeons)	*Nitzschia* (2)
Pseudonitzschiinae	aseptate	multiple	teleosts	*Pseudonitzschia* (1)
Trochopodinae	septate	most 2, some 4 or multiple	mostly teleosts, some elasmobranchs	*Allomegalocotyla* (2), *Macrophyllida* (1), *Mediavagina* (2), *Megalobenedenia* (2), *Megalocotyle* (6), *Megalocotyloides* (6), *Pseudobenedenia* (3), *Pseudobenedeniella* (1), *Pseudobenedenoides* (2), *Pseudomegalocotyla* (1), *Sessilorbis* (1), *Sprostonia* (2), *Sprostoniella* (3), *Tetrasepta* (1), *Trilobiodiscus* (1), *Trochopella* (1), *Trochopus* (15)

Over 30 *Benedenia* spp. have been described as ectoparasites on the skin and fins, and sometimes gills, of marine teleost fishes around the world, mainly in tropical and subtropical regions near coral reefs. Several species have been associated with significant production problems mainly in sea cage aquaculture of marine finfish.

***Benedenia* species**	**Habitat**	**Hosts**	**Distribution**
B. acanthopagri	marine	Perciformes: sparid (sea bream, twobar sea bream, Sobaity sea bream)	Middle-East
B. anticavaginata	marine	Perciformes: sparid (yellowfin bream, goldsilk sea bream)	Australia
B. beverleyburtonae	marine	Perciformes: haemulid (slate sweetlip)	Australia
B. bodiani	marine	Labriformes: labrid (saddleback pigfish)	Australia
B. disciliata	marine	Perciformes: haemulid (slate sweetlip)	Australia
B. elongata (syn. *kintoki*)	marine	Perciformes: lutjanid (lavender jobfish, ruby snapper, flame snapper, bulleye)	West Pacific
B. epinepheli	marine	Perciformes: serranid (redspotted grouper, kelp grouper, convict grouper, Hong Kong grouper, orange-spotted rockcod), cheilodactylid (spottedtail morwong), echeneidid (slender sharksucker), pomacanthid (threadfin butterflyfish); Pleuronectiformes: pleuronectid (Japanese flounder); Anguilliformes: anguillid (whitespotted conger); Tetraodontiformes: monacanthid (unicorn filefish), balistid (clown triggerfish), diodontid (longspined porcupine fish), ostraciid (yellow boxfish, blue-spotted boxfish), tetraodontid (panther puffer, purple puffer, fine-patterned puffer, grass puffer, pear puffer, nashifugu); Labriformes: labrid (Asian sheepshead wrasse); Centrarchiformes: oplegnathid (spotted knifejaw), latrid (spotted-tail morwong); Scorpaeniformes: scorpaenid (Korean rockfish, false kelpfish, red lionfish)	Pacific
B. ernsti	marine	Perciformes: lutjanid (Chinamanfish, emperor red snapper)	Pacific
B. fieldsi	marine	Perciformes: serranid (blue-lined coralcod, blue-spotted rockcod, purple rockcod, blacktip rockcod, specklefin grouper, camouflage grouper, longfin grouper, saddle grouper, greasy rockcod, coral trout, yellowedge coronation trout, red-cheeked fairy basslet)	Pacific
B. hawaiiensis (syn. *sargocentron*)	marine	Perciformes: priacanthid (glasseye), mullid (yellowstripe goatfish, banded goatfish, doublebar goatfish, sidespot goatfish, whitesaddle goatfish, goldsaddle goatfish), pomacentrid (Hawaiian domino, green damselfish, oval chromis), acanthurid (brown tang, pencil surgeonfish, sleek unicornfish), chaetodontid (millet butterflyfish); Tetraodontiformes: monacanthid (honeycomb filefish, Indo-Pacific dumerili, scribbled leatherjacket filefish, fantail filefish), balistid (Sargassum triggerfish); Aulopiformes: synodontid (banded lizardfish); Beryciformes: holocentrid (yellow-striped squirrelfish, sabre squirrelfish); Labriformes: scarid (bullethead parrotfish)	Pacific, Atlantic
B. haywardi	marine	Perciformes: lutjanid (Chinamanfish)	Pacific
B. hendorffii	marine	Perciformes: coryphaenid (dolphinfish, pompani dolphinfish)	tropics
B. hoshinai	marine	Centrarchiformes: oplegnathid (striped beakfish)	Pacific
B. innobilitata	marine	Perciformes: serranid (comber)	Mediterranean
B. ishikawae	marine	Perciformes: lethrinid (Chinese emperor)	Pacific

B. jaliscana	marine	Perciformes: serranid (starry grouper, spotted grouper)	Pacific
B. lolo	marine	Labriformes: labrid (yellowtail coris wrasse, yellowstripe coris, blackeye thicklip wrasse)	Pacific
B. lutjani	marine	Perciformes: lutjanid (Spanish flag snapper)	Australia
B. madai (*sp. inquir.)*	marine	Perciformes: sparid (red seabream)	Pacific
B. malaboni	marine	Perciformes: serranid (humphead wrasse)	Pacific
B. merinthe	marine	Scorpaeniformes: scorpaenid (ulukau)	Pacific
B. monticellii	marine	Mugiliformes: mugilid (grey mullet, golden grey mullet, thinlip mullet, flathead grey mullet, greenback mullet, keeled mullet, bluespot mullet); Gobiiformes: gobiid (rock goby)	Red Sea, Pacific
B. noblei	marine	Scorpaeniformes: scorpaenid (Bocaccio rockfish)	North America
B. ovalis	marine	Perciformes: lutjanid (deepwater red snapper), priacanthid (bigeye)	Pacific
B. ovata (syn. *akaisaki*)	marine	Perciformes: serranid (sunrise perch)	Pacific
B. pagrosomi (*sp. inquir.)*	marine	Perciformes: sparid (red seabream)	Asia
B. pompatica	marine	Perciformes: sciaenid (meagre), carangid (amberjack)	East Atlantic
B. rohdei	marine	Perciformes: lutjanid (Spanish flag snapper)	Australia
B. scari	marine	Labriformes: scarid (bullethead parrotfish)	Indo-Pacific
B. sciaenae (syn. *elegans*)	marine	Perciformes: sciaenid (meagre, corb, shi drum), serranid (brown spotted grouper)	Europe, Pacific
B. sebastodis	marine	Scorpaeniformes: scorpaenid (Japanese stingfish)	Pacific
B. sekii	marine	Perciformes: sparid (red seabream)	Pacific
B. seriolae	marine	Perciformes: carangid (yellowtail amberjack, Japanese amberjack, yellowtail kingfish)	Indo-Pacific
B. synagris	marine	Tetraodontiformes: tetraodontid (scribbled toadfish)	IndoPacific

Parasite morphology: Capsalid monogeneans have 3 distinct developmental stages: eggs, larvae (oncomiracidia) and monoecious (hermaphroditic) adults. The eggs are tetrahedral, usually 100-200 μm along their long axes and each possesses a pronounced filamentous appendage measuring 0.9-2.3 mm long. The oncomiracidia are elongate measuring 170-400 μm in length and those of most species have patches or zones of epidermal cells bearing locomotory cilia. These larval stages have prominent anterior glandular elements (combinations of lateral and median head glands), pigmented eyes, flame bulbs, and a disc-like posterior haptor with hamuli (sometimes called anchors or hooks), accessory sclerites and marginal hooklets (sometimes called hooks). Adult worms have flattened leaf-like bodies up to 3-12 mm in length with 2 anterior disc-like attachment organs (often hooded or bipartite) and a well-developed posterior saucer-shaped opisthaptor armed with 2 pairs of ventrally directed hamuli, 1 pair of median accessory sclerites, 14 small marginal hooklets and a thin membranous marginal valve which is often scalloped. Some species possess pigmented bodies (black, brown, red, blue, green) producing an overall colouration or fragmented mottled appearance. Mature worms are hermaphroditic, possessing male (2 testes, accessory glands, vas deferens, penis enclosed in muscular sac) and female reproductive organs (germarium with internal chamber, extensive vitellaria, vitelline reservoir, ootype, uterus, vagina) with the male and female genital apertures usually common (sometimes separate). Capsalids are oviparous and usually produce and lay eggs one at a time although some species have been observed with up to 6 developing eggs in or near an expanded uterus.

Site of infection: Adult worms infect the external surfaces of their fish hosts, being found on the skin, fins, buccal cavities (lip folds, tooth pads), branchial chamber and gills (lamellae, arches, rakers) of euryhaline and marine teleosts and elasmobranchs. Oncomiracidia are free-swimming within their aquatic environments before attaching to hosts.

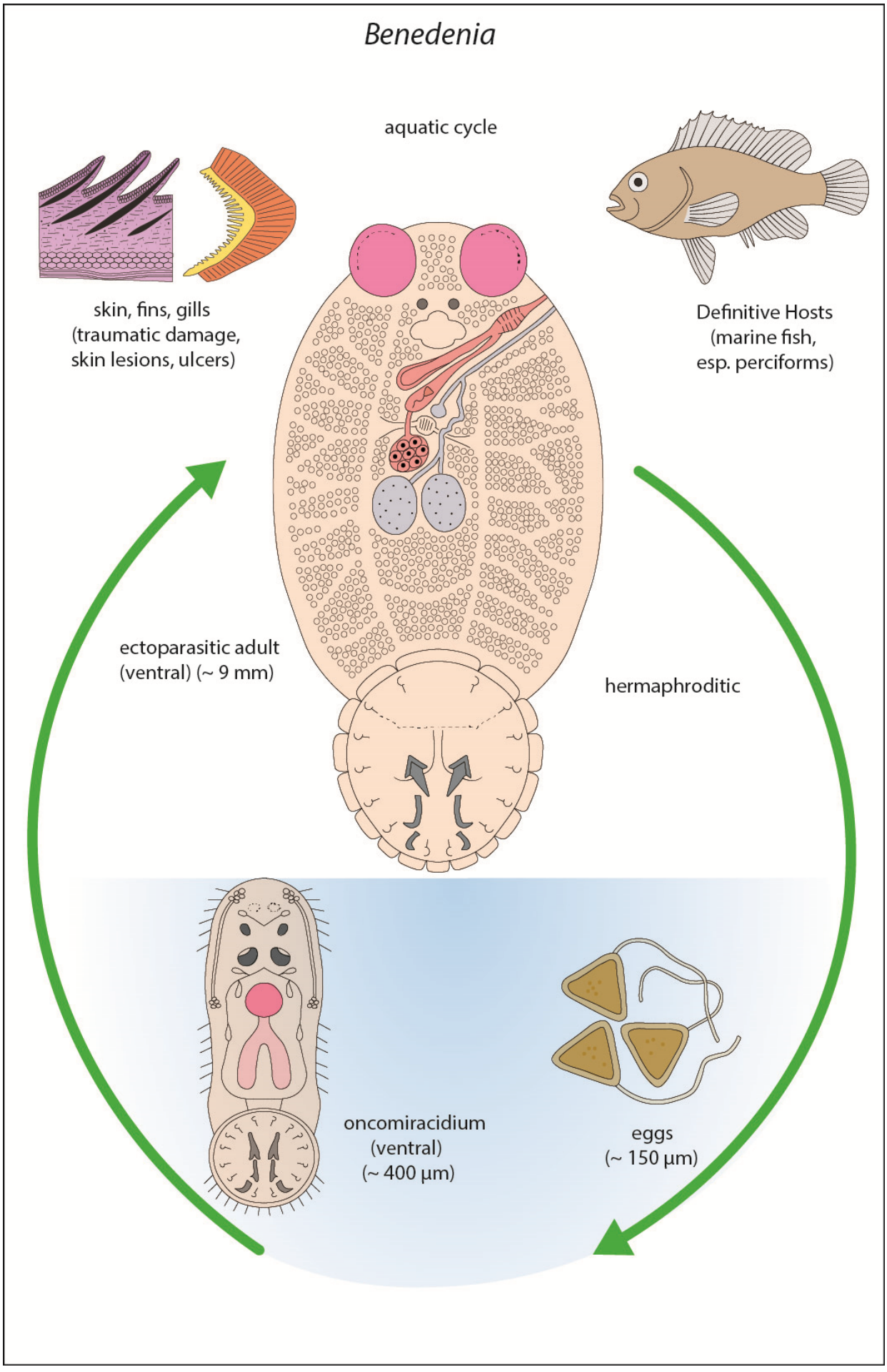
Pathogenesis: Capsalid monogeneans attach to the body surface and feed on epithelial cells and mucus, sometimes causing haemorrhages, ulcers, partial fin loss, decreased growth rate and mortality. Skin lesions are erosive and lead to excessive mucus production and wound sites are prone to secondary bacterial infection. Skin damage may be exacerbated by fish scratching on substrates (incl. nets) to alleviate skin irritation. Infections may cause serious economic losses in mariculture (esp. marine finfish in semi-open systems) with production losses (due to death and disease), reduced market value (remaining product with unsightly lesions) and increased production costs (for labour and treatment).

Developmental cycle and mode of transmission: Like most monogeneans, most capsalids have direct life-cycles with transmission occurring between fish hosts by free-swimming larvae. Mature hermaphroditic adults lay eggs with long sticky filamentous threads which become entangled on substrates and in organic material (including mucus). The eggs hatch after several days at water temperatures around 20ºC, but hatching may be delayed for several months at lower water temperatures. Hatching also depends on photoperiod duration and intensity, with hatching rates being greater during the day and under intense light. The eggs release larvae (oncomiracidia) which are ciliated and swim about seeking new hosts. Larvae attach to the external surfaces of susceptible fish using their haptors and hooks, shed their cilia and begin to feed and mature to adult worms. Depending on the ambient water

temperature, the whole life-cycle may be completed in days to months. The combination of direct transmission, short generation times, and moderate fecundity can facilitate rapid increases in parasite population densities in susceptible host populations, especially those kept in crowded culture conditions.

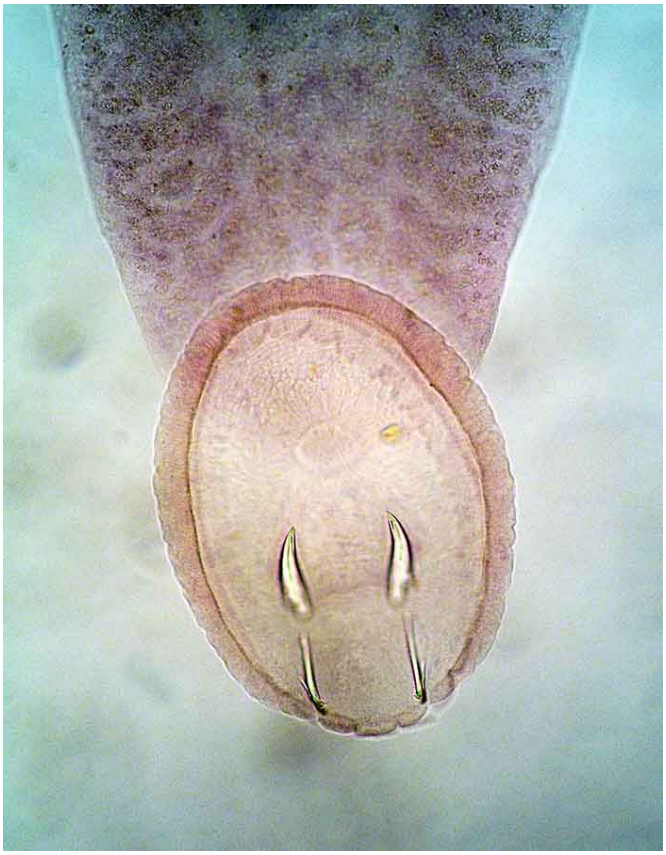
Differential diagnosis: Infections are diagnosed by the direct demonstration of parasites on fish in biopsy or necropsy tissue samples. Worms are best fixed and mounted as flattened preparations to better observe anatomical features. In some species, however, internal morphology can be obscured by extensive pigmentation and/or vitellaria. Generic identification is made on the basis of morphotypic features, especially the configuration of the opisthaptor and its hooks, the male genitalia and the anterior attachment organs.

Treatment and control: In mariculture, infected fish are conventionally treated by immersion in freshwater baths or dilute hydrogen peroxide. The anthelmintic praziquantel is also effective as a bath or orally via medicated feed (although it reduces feed palatability). The eggs are resistant to these treatments so repeated treatments are required for parasite control. Environmental management is difficult because the eggs entangle on equipment and local substrates. Reducing stocking densities in net pens has met with limited success as the eggs still hatch releasing free-swimming larvae that actively seek whatever hosts are available.


Benedenia
aquatic cycle
skin, fins, gills
(traumatic damage,
skin lesions, ulcers)
Definitive Hosts
(marine fish,
esp. perciforms)
ectoparasitic adult
(ventral) (~ 9 mm)
hermaphroditic
oncomiracidium
(ventral)
(~ 400 µm)
eggs
(~ 150 µm)



Benedenia adult worm



Benedenia opisthaptor



Benedenia oncomiracidia

ARTHROPODS

ARTHROPOD PARASITES

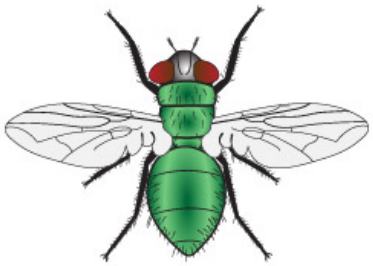
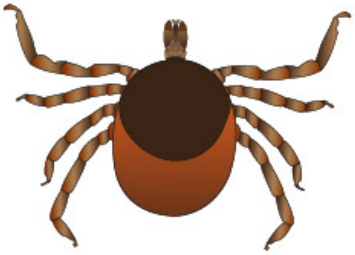
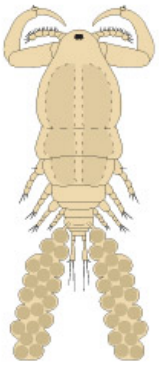
Arthropods form a huge assemblage of small coelomate animals with "jointed limbs" (hence the name arthro-pods). They exhibit segmentation of their bodies (metamerism) which is often masked in adults because their 10-25 body segments are combined into 2-3 functional groups (called tagmata). They exhibit varying degrees of cephalization whereby neural elements, sensory receptors and feeding structures are concentrated in the head region. Arthropods possess a rigid cuticular exoskeleton consisting mainly of tanned proteins and chitin. The exoskeleton is usually hard, insoluble, virtually indigestible and impregnated with calcium salts or covered with wax. The exoskeleton provides physical and physiological protection and serves as a place for muscle attachment. Skeletal plates are joined by flexible articular membranes and the joints are hinges or pivots made from chondyles and sockets.

The main arthropod assemblages include crustaceans (crabs, lobsters, crayfish, shrimp), arachnids (spiders, scorpions, ticks, mites) and insects (beetles, bugs, earwigs, ants, bees, termites, butterflies, moths, crickets, roaches, fleas, flies, mosquitoes, lice). Most parasitic arthropods belong to 2 main groups: the 6-legged insects; the 8-legged arachnids; and the multi-legged crustaceans.

- Insects have 3 distinct body parts, commonly called the head, thorax and abdomen. The head has 2 antennae and the thorax has 6 legs arranged in 3 bilateral pairs. Many insect species also have 2 pairs of wings attached to the thorax. Parasitic insect species include fleas, flies and lice which actively feed on host tissues and fluids at some stage in their life-cycles.

- Arachnids have 2 body parts known as the prosoma (or cephalothorax) and opisthosoma (or abdomen). The cephalothorax has 8 legs arranged in 4 bilateral pairs and arachnids do not have wings or antennae. Important parasitic assemblages include the ticks and mites which bite into tissues and feed off host fluids.

- Crustaceans have 16-20 segments (sometimes more) with one or more thoracic segments fused with the head to form a cephalothorax. They have 2 pairs of antennae, 2 pairs of maxillae and a pair of mandibles on the head, followed by a pair of biramous appendages on most body segments. Several assemblages contain parasitic groups; notably copepods and branchiurans on fish and pentastomes in reptiles and mammals.

insects	arachnids	crustaceans
		

Taxonomic classification

Traditionally, arthropod assemblages were classified together on the basis of their shared morphological characteristics; notably the possession of hardened exoskeletons and articulated joints. Various groups were recognized apparently representing variations on these unifying themes. However, phylogenetic studies conducted using extended character sets, particularly developmental biology and molecular gene sequences, revealed many new clades not previously recognized using traditional characters. While the integrity (monophyly) of many lower taxa (families and genera) were frequently validated, alternative hypotheses regarding their kinship (higher taxonomic relationships) were warranted.

Metazoa are multicellular eukaryotes with differentiated tissues that form a major division in the animal kingdom, exclusive of the sponges. They are triploblastic (with three body germ layers), most have a coelom (body cavity) and they exhibit bilateral symmetry (except the cnidaria (jellyfish) which exhibit radial symmetry). Their embryonic development includes a blastula stage, and two major lineages are recognized depending on the type of cleavage at the 8-cell embryonic stage and the fate of the blastopore: the protostomes (exhibiting determinate cleavage, mostly spiral, the blastopore becoming the mouth) and the deuterostomes (indeterminate radial cleavage, the blastopore becoming the anus). The deuterostomes comprise the echinoderms (starfish) and the chordates (including all vertebrates) while the protostomes contain most of the invertebrate animals. Molecular studies found that two major protostome lineages were well supported: the enigmatic Lophotrochozoa containing the platyhelminth parasites and the unique Ecdysozoa containing the nematode and arthropod parasites.

The Ecdysozoa are typified by organisms which have hard cuticles and can only grow by periodic moulting (ecdysis). They comprise the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (with jointed limbs). The latter three groups were grouped together in the Panarthropoda as they possessed coelomate bodies (in contrast to the pseudocoelomate nematodes), but their coelomic compartments were reduced to open circulatory systems (haemocoels). The arthropods are considered to have undergone ‘arthropodization’ by having hardened cuticles, segmented bodies with flexible jointed appendages and moulting cycles controlled by hormones. The development of hard exoskeletons that provide protection (against predators and desiccation) and facilitate movement (anchoring muscles and appendages) are considered to have allowed aquatic arthropods to have colonized terrestrial environments and even facilitated flight. Arthropods are both numerous and speciose, with representatives inhabiting all available habitats on Earth, both free-living (aquatic and terrestrial) and symbiotic (commensals, mutualists, parasites).

Morphotypic studies had previously identified two types of arthropods: those with uniramous appendages (single branches) and those with biramous appendages (two branches). The centipedes, millipedes, pauropods, symphylans and insects were classified together in the group Uniramia, but subsequent molecular phylogenetic studies did not support this classification. More recently, the myriapods, hexapods and crustaceans were classified in the group Mandibulata, based on their possession of mouthparts comprising mandibles rather than chelicerae. However, the mandibles of the cognate assemblages are quite different and do not appear to have evolved from a common ancestor. Those of crustaceans are multi-jointed and gnathobasic (biting/chewing surfaces on mandible bases) while those of myriapods and hexapods are single-jointed and ‘entire-limb’ (biting surface on distal edge). On the basis of all available evidence, five arthropod subphyla are currently recognized: Trilobita (‘three-lobed’ trilobites, extinct), Myriapoda (‘many-footed’ centipedes, millipedes, pauropods, symphylans), Chelicerata (‘claw-horned’ spiders, horseshoe crabs, ticks, mites), Crustacea (‘shelled’ crabs, lobsters, barnacles, tongue worms) and Hexapoda (‘six-footed’ insects). The latter two subphyla (Crustacea and Hexapoda) are regarded to be sister assemblages and have been placed in the clade Pancrustacea on the basis of shared gene sequences, tripartite brains, appendages of the third post-acronal segment forming the mandibles, and all head appendages (except the first antennae) being used for feeding sometime in their life-cycles.

Chelicerates have two tagmata (cephalothorax (prosoma) and abdomen (opisthosoma)) and six pairs of cephalo-thoracic appendages that include a pair of chelicerae (mouthparts), a pair of pedipalps (but no antennae) and four pairs of legs. Three classes are recognized: Pycnogonida (‘compact-kneed’ sea spiders), Merostomata (‘thigh-mouthed’ horseshoe crabs and extinct eurypterids) and Arachnida (‘spiders’ and allies). The cephalothorax of arachnids forms a carapace-like shield, their abdominal appendages are reduced, lost or modified, and the first or second abdominal somite is modified as a genital somite. Four arachnid groups are recognized: Araneae (spiders), Scorpiones (scorpions), Opiliones (harvestmen = daddy longlegs) and Acari (ticks and mites). The cephalothorax and abdomen of acarines is completely fused and their mouthparts (comprising central chelicerae with lateral pedipalps fusing ventrally to form a hypostome) are carried on a small anterior projection (capitulum) often covered by a dorsal rostrum or tectum. Ticks are macroscopic haematophagous ectoparasites with respiratory spiracles (stigmata) posterior to their legs (order Metastigmata). Mites are microscopic acarines that may be free-living, particularly in leaf litter, or parasitic in the epidermal tissues of vertebrate hosts. Gamesid mites have spiracles between the second and fourth pair of legs (order Mesostigmata), trombidiform mites have spiracles on the capitulum (order Trombidiformes, suborder Prostigmata), while sarcoptiform mites do not have spiracles but respire through the body surface (order Sarcoptiformes, suborder Astigmata).

Crustaceans are shelled arthropods with gnathobasic mandibles, biramous appendages, second antennae, unique nauplius larvae and most have stalked compound eyes. Six classes are recognized: including the rare Remipedia (‘oar-footed’ remipeds in caves) and Cephalocarida (‘shrimp-headed’ cephalocarids in marine sediments); the prevalent Brachiopoda (‘gill-footed’ fairy-, brine-, tadpole-, clam-shrimp and water fleas in aquatic environments) and Ostracoda (‘shelled’ mussel- and seed-shrimp in aquatic environments); and the highly speciose Maxillopoda (‘jawbone-footed’ shrimp, barnacles, copepods, brachiurans, pentastomes) and Malacostraca (‘soft-shelled’ crabs, lobsters, shrimp, isopods, amphipods and allies). Maxillopod subclasses include Mystacocarida (‘moustache-shrimp’ on beaches), Tantulocarida (‘tiny shrimp’ in marine benthos), Cirripedia (‘curly hair-footed’ free-living or parasitic barnacles), Copepoda (‘oar-footed’ copepods free-living in aquatic environments or parasitic on aquatic hosts), Brachiura (‘gill-tailed’ parasitic fish lice), and Pentastomida (‘five-mouthed’ tongue worms parasitic in lungs of reptiles). Of the 14 malacostracan orders, four prevalent groups include the Isopoda (‘equal-footed’ isopods in terrestrial and aquatic environments and some ectoparasites of fish and other crustaceans), Amphipoda (‘both-sided’ amphipods in aquatic environments, some being parasitic on aquatic hosts), Euphausiacea (‘shining-bright’ planktonic krill) and the speciose Decapoda (‘ten-footed’ crabs, shrimps, lobsters).

Hexapods are better known as insects. They have three tagmata (head, thorax and abdomen), an exoskeleton composed of plates (sclerites), whole-limb mandibles, one pair of antennae, six uniramous legs, Malpighian tubules and usually two pairs of wings. Two classes are recognized: the Entognatha whose mouthparts have their bases within the head capsule and mandibles with one articulation; and the speciose Insecta with ectognathous mouthparts (bases lie outside the head capsule) and mandibles usually with two regions of articulation. The entognathan orders Protura (‘first-tailed’ proturans), Diplura (‘double-tailed’ japygids and campodeids) and Collembola (‘glue-wedged’ springtails, jumping bristletails and snow fleas) are represented by small insects living mostly in soil or humus. The ectognathus insects are divided into two subclasses: the Apterygota without wings and the Pterygota with wings (usually two pairs, sometimes reduced to one pair or none). The wingless apterygotes are represented by the order Thysanura (‘tassel-tailed’ silverfish and bristletails). The winged pterygotes have been classified into two infraclasses: Paleoptera with outspread wings and Neoptera with wings that fold back over the body. The paleopterans are divided into two orders which undergo hemimetabolous (incomplete) development: Odonta (‘toothed’ dragonflies and damselflies) and Ephemeroptera (‘day-winged’ mayflies) with massive or vestigial mouthparts respectively. The neopterans are divided into 3 superorders; Orthopterodea with straight wings and biting/chewing mouthparts, Hemipterodea (Exopterygota) with piercing/sucking mouthparts and hemimetabolous (incomplete) development where the young resemble adults but have externally developing wings, and Holometabola (Endopterygota) with holometabolous (complete) development) where the young do not resemble adults and develop wings inside the body.

Orthopterodeans comprise nine orders: Orthoptera (‘straight-winged’ grasshoppers, locusts, crickets, katydids); Blattodea (‘roach-formed’ cockroaches); Phasmatodea (‘apparition-formed’ stick and leaf insects); Mantodea (‘soothsayer-formed’ mantids); Mantophasmatodea (‘soothsayer-apparition-formed’ gladiators); Isoptera (‘equal-winged’ termites); Plecoptera (‘twisted-winged’ stoneflies); Embiidina (‘lively-formed’ webspinners); and Dermaptera (‘skin-winged’ earwigs). Hemipterodeans are divided into 15 orders, including the Zoraptera (‘pure-wingless’ zorapterans); Psocoptera (‘rub-away-winged’ psocids, book lice, bark lice); Hemiptera (‘half-winged’ true bugs, hoppers, cicadas, whiteflies, aphids, scale insects); Thysanoptera (‘tassel-winged’ thrips); and Phthiraptera (‘wingless lice’). Holometabolans are classified into several broad groups: neuropteroids containing the orders Neuroptera (‘net-veined’ dobsonflies, ant lions, lacewings), Megaloptera (alderflies) and Raphidioptera (snakeflies); coleopteroids containing the orders Coleoptera (sheath-winged’ beetles, fireflies, weevils) and Strepsiptera (‘twisted-winged’ stylops, twisted wing parasites); hymenopteroids comprising the Hymenoptera (‘membrane-winged’ ants, bees, wasps) with highly developed social systems; and the panorpoid complex of orders Mecoptera (‘long-winged’ scorpion-flies), Trichoptera (‘hair-winged’ caddisflies), Lepidoptera (‘scale-winged’ butterflies, moths), Siphonaptera (‘siphon-bearing wingless’ fleas) and Diptera (‘two-winged’ true flies, midges and mosquitoes).

Supergroup: Amorphea (unikonts, with single flagellum, or nonflagellated amoebae)
Opisthokonta (stages with single posterior flagellum)
Holozoa (metazoans, filasterans, ichthyosporeans, choanomonads)
Metazoa (multicellular eukaryotes)
Protostomia (triploblastic, spiral cleavage)

▪ Group: Ecdysozoa (cuticle moulted = ecdysis)

Nematoidea (collagenous cuticle without microvilli)
Phylum: Nematoda (= Nemata) (pseudocoelomate roundworms, tubular digestive tract, dioecious)
Phylum: Nematomorpha (horsehair worms, aquatic)

Phylum: Kinorhyncha (spine-necked worms, marine sediments)
Phylum: Priapulida (priapulids, marine sediments)
Phylum: Loricifera (loriciferans, marine sediments)

Panarthropoda (haemocoel, ventrolateral appendages)
Phylum: Onychophora (velvet worms, litter)
Phylum: Tardigrada (water bears, mosses, lichen, moist soil)
Phylum: Arthropoda (calcification of chitinous cuticle, jointed limbs, segmental sclerites, cephalic ecdysial glands, setae, lateral compound eyes)

♦ Subphylum: Chelicerata (2 tagmata (cephalothorax + abdomen), chelicera, no antennae)
• Class: Pycnogonida (sea spiders)
• Class: Merostomata (horseshoe crabs)
• Class: Arachnida (spiders and allies, 4 pairs legs, carapace, slit sensilla)
•• Order: Araneae (spiders)
•• Order: Scorpiones (scorpions)
•• Order: Opiliones (harvestmen = daddy longlegs)
• Subclass: Acari (ticks and mites, segmentation inconspicuous, with capitulum)
•• Superorder: Parasitiformes (ticks and some mites)
••• Order: Metastigmata (Ixodida) (ticks, macroscopic, spiracles/stigmata posterior to legs)
••• Order: Mesostigmata (gamesid mites, spiracles/stigmata between second and fourth legs)
•• Superorder: Acariformes (diverse mites)
••• Order: Trombidiformes (trombidiform mites)
••• Suborder: Prostigmata (spiracles/stigmata on capitulum)
••• Order: Sarcoptiformes (sarcoptiform mites mites)
••• Suborder: Astigmata (without spiracles, respire through body surface)

♦ Subphylum: Crustacea (shells, biramous, 2 pairs antennae, 2 pairs maxillae, nauplius larva)
• Class: Remipedia (remipeds)
• Class: Cephalocarida (cephalocarids)
• Class: Brachiopoda (fairy-, brine-, tadpole, clam-shrimp, water fleas)
• Class: Ostracoda (mussel- and seed-shrimp, some fish parasites)
• Class: Malacostraca (crabs, lobsters, shrimp)
•• Order: Euphausiacea (krill)
•• Order: Isopoda (dorsoventrally flattened, lack carapace, some fish parasites)
•• Order: Amphipoda (laterally compressed, thoracic gills, mostly free-living)
•• Order: Decapoda (crabs, crayfish, lobster, shrimp, 5 pairs walking legs)
• Class: Maxillipoda (nauplius with maxillipodan eye, 5 cephalic, 6 thoracic and usually 4 abdominal segments plus telson)
• Subclass: Mystacocarida (marine beaches)
• Subclass: Tantulocarida (parasitic on deep-sea crustaceans)
• Subclass: Cirripedia (barnacles, some crustacean parasites)
• Subclass: Copepoda (elongate body, naupliar then copepodid instars, some fish parasites)
• Subclass: Branchiura (fish lice, flattened bilobed head, carapace expands laterally)
• Subclass: Pentastomatida (tongue worms, anterior end with mouth and two pairs tiny claws)
•• Order: Cephalobaenida (obliquely-paired hooks, medial genital opening, single oviduct)
•• Order: Porocephalida (horizontally-aligned hooks, posterior genital opening, two oviducts)

- Subphylum: Hexapoda (3 tagmata (head+thorax+abdomen), 3 pairs uniramous legs, whole-limb mandibles, Malpighian tubules)

  - Class: Entognatha (entognathous mouthparts (bases inside head capsule))
    - Order: Protura (proturans)
    - Order: Diplura (diplurans)
    - Order: Collembola (springtails)

  - Class: Insecta (ectognathous mouthparts (bases lie outside head capsule))

    - Subclass: Apterygota (wingless)
      - Order: Thysanura (silverfish, bristletails)
    - Subclass: Pterygota (winged)
      - Infraclass: Paleoptera (outspread wings)
        - Order: Odonta (dragonflies, damselflies)
        - Order: Ephemeroptera (mayflies)
      - Infraclass: Neoptera (wings fold back over body)
        - Superorder: Orthopterodea (biting/chewing mouthparts)
        - Order: Orthoptera (grasshoppers, locusts, crickets, katydids)
        - Order: Blattodea (cockroaches)
        - Order: Phasmatodea (walking-sticks, leaf insects)
        - Order: Mantodea (mantids)
        - Order: Mantophasmatodea (gladiators)
        - Order: Isoptera (termites)
        - Order: Ptecoptera (stoneflies)
        - Order: Embiidina (webspinners)
        - Order: Dermaptera (earwigs)
        - Superorder: Hemipterodea (= Exopterygota) (young resemble adults, have externally developing wings, piercing/sucking mouthparts)
        - Order: Zoraptera (zorapterans)
        - Order: Psocoptera (psocids, book lice, bark lice)
        - Order: Hemiptera (true bugs, hoppers, cicadas, whiteflies, aphids, scale insects)
        - Order: Thysanoptera (thrips)
        - Order: Phthiraptera (lice, wingless, sucking (anoplura), chewing (mallophaga))
        - Superorder: Holometabola (= Endopterygota) (young do not resemble adults, holometabolous (complete) development, with internally developing wings)

          Neuropteroid groups (net-veined flies)
        - Order: Neuroptera (dobsonflies, ant lions, lacewings)
        - Order: Megaloptera (alderflies)
        - Order: Raphidioptera (snakeflies)

          Coleopteroid groups (beetle-shaped)
        - Order: Coleoptera (beetles, fireflies, weevils)
        - Order: Strepsiptera (stylops, twisted wing parasites)

          Hymenopteroid group (highly developed social systems)
        - Order: Hymenoptera (ants, bees, wasps)

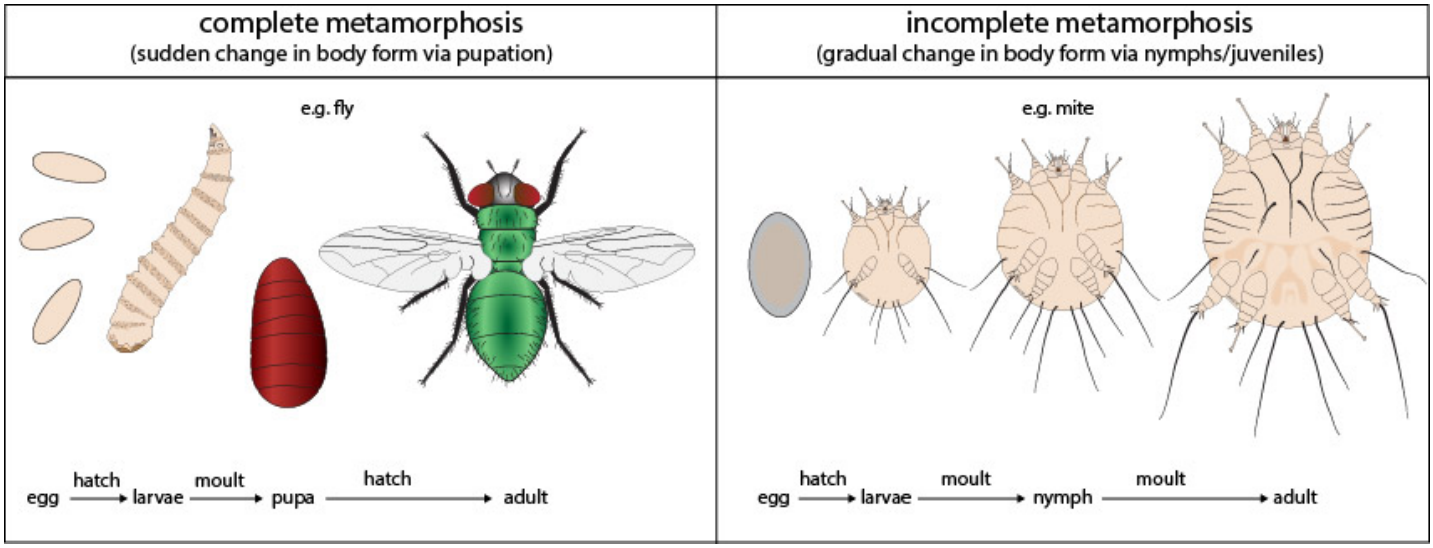
          Panorpoid groups (complex of orders)
        - Order: Mecoptera (scorpionflies)
        - Order: Lepidoptera (butterflies, moths)
        - Order: Trichoptera (caddisflies)
        - Order: Siphonaptera (fleas, laterally compressed, pupation)
        - Order: Diptera (true flies, nematocera with long filamentous antennae (midges, mosquitoes), brachycera with short stout antennae (flies))

Biodiversity

Collectively, arthropods account for a substantial share of global biodiversity, both in terms of species richness and relative abundance. There are over 1,000,000 species of insects, 50,000 species of arachnids and 67,000 species of crustaceans. They are very successful and adaptable organisms and are capable of forming large populations due to their rapid and fertile reproduction rates. Many species are also able to withstand adverse environmental conditions by undergoing periods of developmental arrest (diapause). The protection afforded by their exoskeletons allows them to colonize many habitats and they overcome the problem of growing larger in a non-expandable exoskeleton by undergoing periodic moulting (or ecdysis) which is mediated by hormones. Developmental stages between moults are referred to as instars. Moulting is a complex process and its timing is mediated by many environmental and physiological cues. It involves detachment of the hypodermis from the procuticle, partial resorption of the old cuticle, production of a new epicuticle, dehiscence (splitting) of the old cuticle, emergence of the animal, stretching and expansion of the new cuticle by air and/or water intake, and then sclerotization of the new cuticle.

Life-cycles

Adult arthropods are generally small in size, most are visible but some remain microscopic. Arthropod sexes are separate and fertilization is internal. A wide range of mating behaviours, insemination and egg production strategies are involved. In most species, the egg develops into a larva: i.e. a life-cycle stage that is structurally distinct from the adult and must undergo metamorphosis (structural reorganization) before becoming an adult. This metamorphosis may be complete (involving major changes during a pupation stage) or incomplete (involving gradual changes in nymph stages). For example, the grub-like larval stages of flies and fleas form cocoon-like pupae where they undergo complete metamorphosis and emerge as radically different adult insects. In contrast, the larval instars (or nymphs) of lice, ticks and mites undergo incomplete metamorphosis through a series of moults gradually becoming more adult-like in appearance, as do the nauplii, copepodid and juvenile stages of crustaceans.

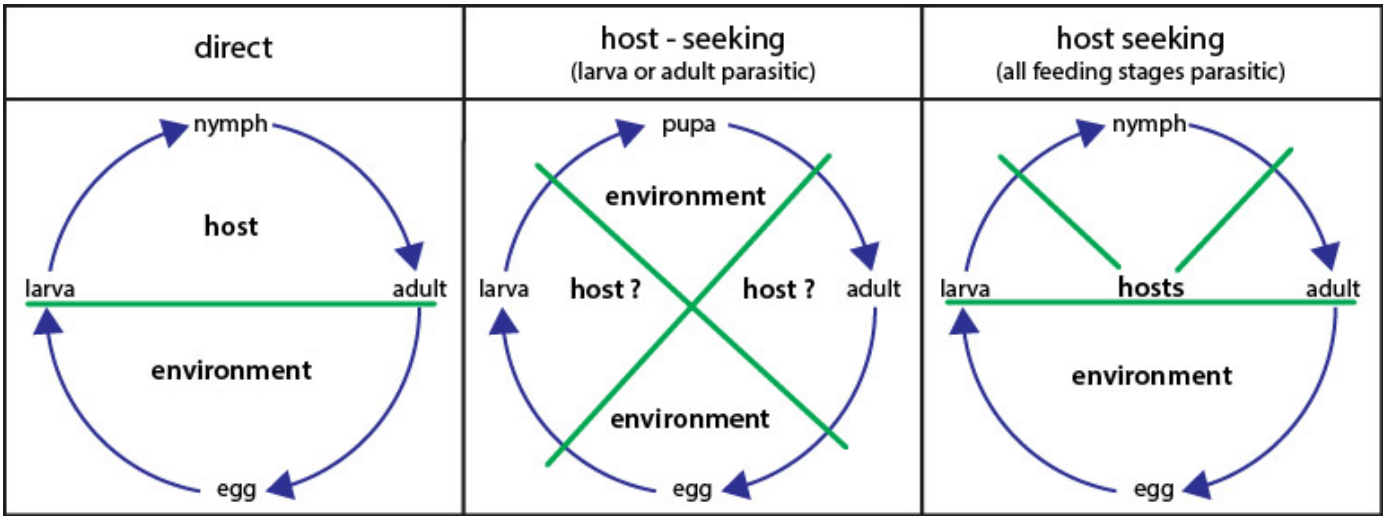


Arthropods are involved in nearly every kind of parasitic relationship, either as parasites themselves or as hosts/vectors for other micro-organisms (including viruses, bacteria, protozoa and helminths). They are generally ectoparasitic on, or in, the skin of vertebrate hosts. Many species are haematophagous (suck blood) while others are histophagous (tissue-feeders) and bite or burrow in dermal tissues causing trauma, inflammation and hypersensitivity reactions. Infestations are transmitted from host-to-host either by direct contact or by free-living larvae or adults actively seeking hosts.

- Direct transmission of infective stages occurs when hosts come into close contact with each other in terrestrial or aquatic environments. Larvae, nymphs or adults may cross from one host to another, while eggs may contaminate shared holding facilities, bedding, clothing or equipment. Insects (fleas and lice) and arachnids (mites) rely on close contact between hosts..

- Many adult insects actively seek hosts in order to feed or lay eggs. Winged insects (mosquitoes, flies) fly to new hosts to feed while fleas jump onto passing hosts. Some adult flies (bot flies) do not feed on their hosts but deposit eggs from which larvae emerge and feed on host tissues and exudates. When replete, larvae leave their hosts to pupate in the external environment.

- Tick larvae actively seek hosts by climbing vegetation and questing for passing hosts. Some species complete their life-cycle on the same host (one-host ticks) while others detach after feeding and drop to the ground to moult before seeking new hosts as nymphs or adults (two-host or three-host ticks). Larval and juvenile stages of crustaceans actively swim about in aquatic environments actively seeking hosts.



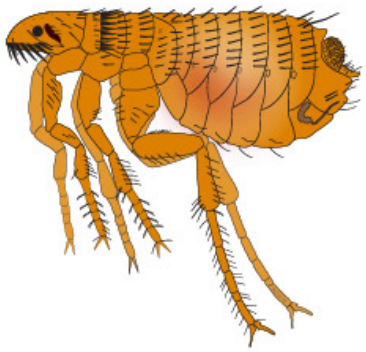
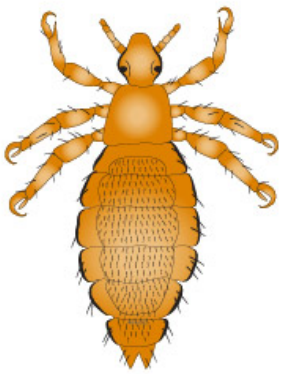
Overview of major arthropod groups parasitizing animals

Insects are incredibly biodiversity forming numerous species and large populations in aquatic and terrestrial habitats as well as in association with other organisms acting as hosts. Most parasitic insect species belong to three main groups: the jumping fleas (Siphonaptera); the winged flies (Diptera); and the wingless lice (Phthiraptera).

- Fleas are bilaterally-flattened wingless insects with enlarged hindlimbs specially adapted for jumping (up to 100 times their body length). Jumping feats are accomplished using elastic resilin pads which expand explosively when uncocked from the compressed state. Fleas undergo complete metamorphosis whereby grub-like larvae form pupae from which adult fleas emerge. The larvae are not parasitic but feed on debris associated mainly with bedding, den or nest material, whereas the adult stages are parasitic and feed on host blood. There are some 2,500 flea species, most parasitic on mammals (especially rodents) and some on birds. They vary in the time spent on their hosts ranging from transient feeders (rodent fleas) to permanent attachment (sticktight fleas and burrowing chigoes).

- Flies and mosquitoes are winged insects with two pairs of wings attached to the thorax and a well-developed head with sensory and feeding organs. They undergo complete metamorphosis involving a pupation stage. Different species vary in their feeding habits, both as adults (parasitic or free-living) and larvae (parasitic or free-living). There are over 120,000 species belonging to 140 families. Two main suborders are recognized on the basis of structural differences, Nematocera (adult stages parasitic, larval stages often free-swimming) and Brachycera (adult stages parasitic or free-living, larvae stages often predaceous).

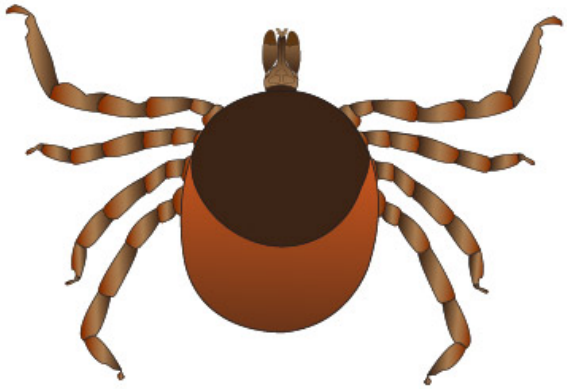
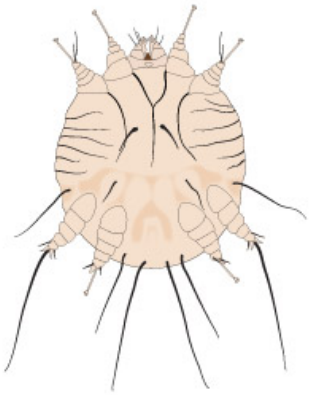
- Lice are small wingless insects, dorsoventrally flattened, with reduced or no eyes and enlarged tarsal claws for clinging. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to hair/feathers whereas nymphs and adults cling to hair/feathers. Two orders of lice are recognized on the basis of their mouthparts: the Mallophaga (chewing/biting lice) with some 3,000 species infesting birds and mammals; and the Anoplura (sucking lice) with 500 species found on mammals

fleas	flies	lice
		

Many non-spider arachnids (subclass Acari) are found as parasites on animal or plant hosts. They belong to two main groups: the macroscopic ticks and the microscopic mites. Many species are important in human and animal medicine as causes of disease or as transmission vectors for other pathogens.

- Ticks are epidermal parasites of terrestrial vertebrates that may cause anaemia, dermatosis, paralysis, otoacariasis and other infections (transmit viral, bacterial, rickettsial, spirochaete, protozoal and helminth pathogens). They feed mainly on blood and their mouthparts are armed with small backward-facing teeth to aid in attachment. All ticks undergo gradual/incomplete metamorphosis whereby larval and nymphal instars resemble adults. The integument is relatively thick and respiration occurs via spiracles (usually only one pair) and trachea. Two major families of ticks are recognized on the basis of many morphological features: the Ixodidae (hard ticks with a tough cuticle and a large anterodorsal scutum) with some 650 species that infest mammals, birds and reptiles; and the Argasidae (soft ticks with a leathery integument and no scutum) with 160 species that infest mainly birds and some mammals.

- Mites are microscopic arachnids which undergo gradual or incomplete metamorphosis. Adults and nymphs have 4 pairs of legs whereas larvae have 3 pairs. Over 30,000 species of mites have been described, many are free-living species, some are plant parasites while others are parasitic on terrestrial and aquatic hosts. Most parasitic species feed on skin debris or suck lymph, some burrow into the skin, some live in hair follicles, and some in the ear canals. Their mouthparts are variable in form but the hypostome is never armed with teeth. The integument is usually thin and three orders are recognized on the basis of their respiratory systems: the Mesostigmata with respiratory spiracles (stigmata) near the third coxae; the Prostigmata (Trombidiformes) with spiracles between the chelicerae or on the dorsal hysterosoma; and the Astigmata (Sarcoptiformes) without tracheal systems as they respire through the tegument.

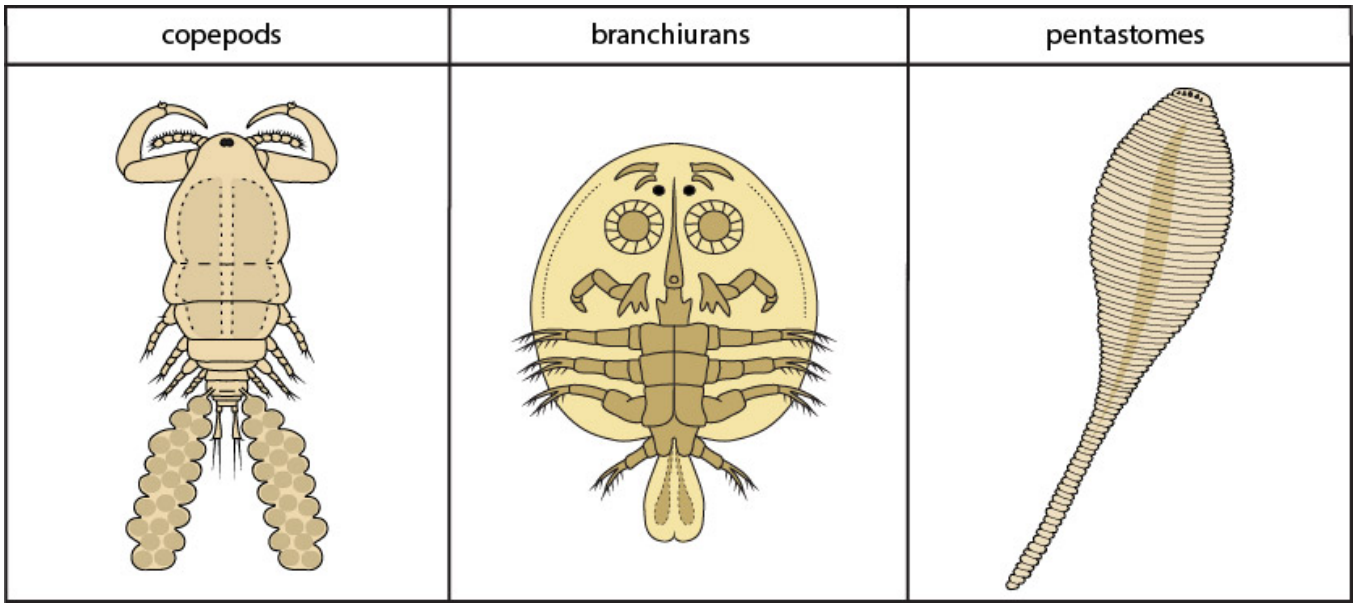
ticks	mites
	

Most crustaceans are free-living in aquatic or terrestrial environments, but some have become parasitic on or in other animals residing in the same habitats. Parasitic representatives belong to 3 main maxillipodan assemblages: Copepoda and Branchiura which are ectoparasitic on fish, and Pentastomida which are endoparasitic in reptiles and mammals.

- Copepods have elongate segmented bodies and they undergo gradual metamorphosis involving nauplii and copepodid developmental stages prior to adult formation. Some species are ectoparasitic on the skin and gills of freshwater fish and have been associated with lesions, respiratory difficulties and mortalities, with *Lernaea* and *Ergasilus* spp. causing problems in aquaculture facilities.

- Branchiurans (commonly known as fish lice) have round flat bodies with mouthparts modified for sucking blood from fish hosts. They have direct cycles with eggs releasing larvae (metanauplii) that gradually develop to juveniles then adults. Many *Argulus* spp. have been reported as ectoparasites on the skin and gills of marine and freshwater fish causing painful bites and haemorrhagic lesions.

- Pentastomes have elongate worm-like bodies with few appendages, apart from 2 pairs of tiny claws near the mouth contributing to their 'penta-stome' appearance. They are alternatively known as tongue worms as the adults are parasitic in the respiratory passages of snakes or carnivorous mammals, with heteroxenous life-cycles involving larval and nymphal stages in rodent intermediate hosts.

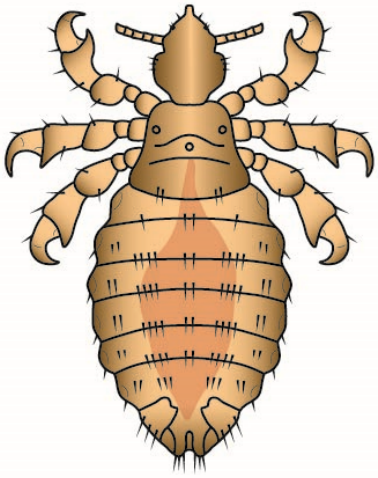


Phthiraptera
(lice)

Phthiraptera: Anoplura

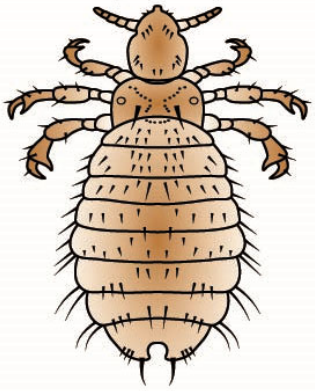
Haematopinus

adult (dorsal)
(~ 5 mm)



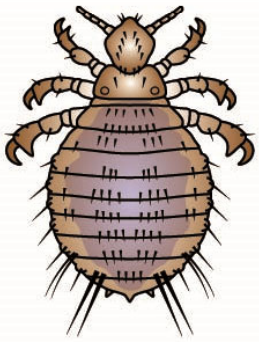
Linognathus

adult (dorsal)
(~ 3 mm)



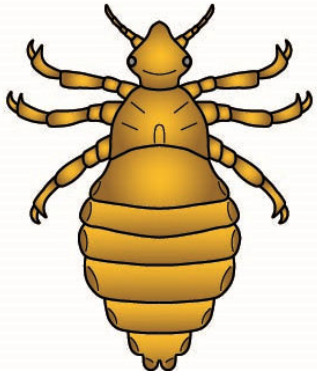
Solenopotes

adult (dorsal)
(~ 1.8 mm)



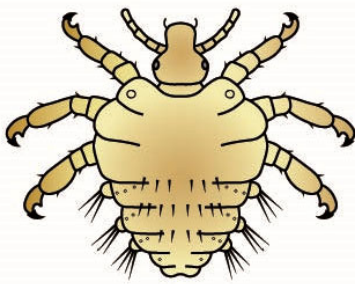
Pediculus

adult (dorsal)
(~ 3 mm)



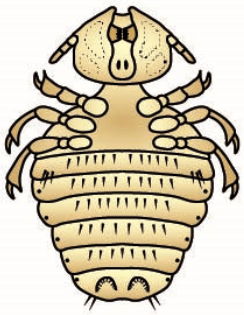
Pthirus

adult (dorsal)
(~ 2 mm)

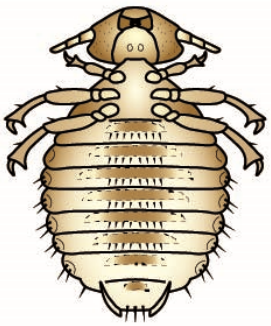


Phthiraptera: Ischnocera (chewing lice)

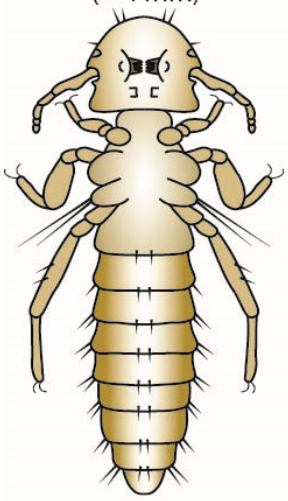
Trichodectes
adult (ventral)
(~ 2 mm)



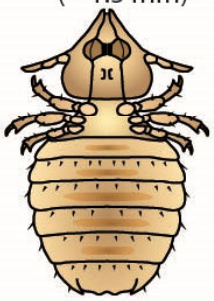
Bovicola
adult (ventral)
(~ 2 mm)



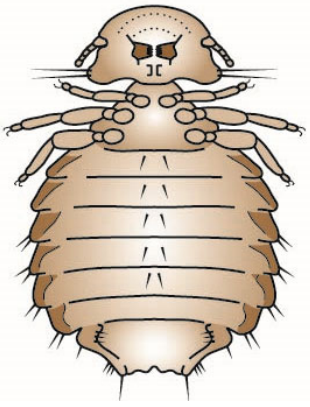
Lipeurus
adult (ventral)
(~ 4 mm)



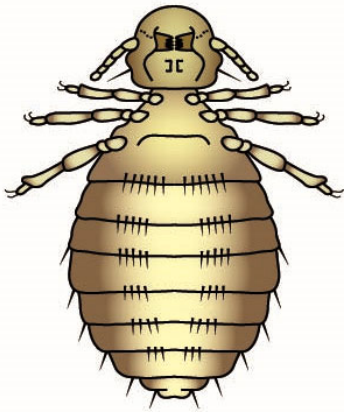
Felicola
adult (ventral)
(~ 1.5 mm)



Goniodes
adult (ventral)
(~ 3 mm)

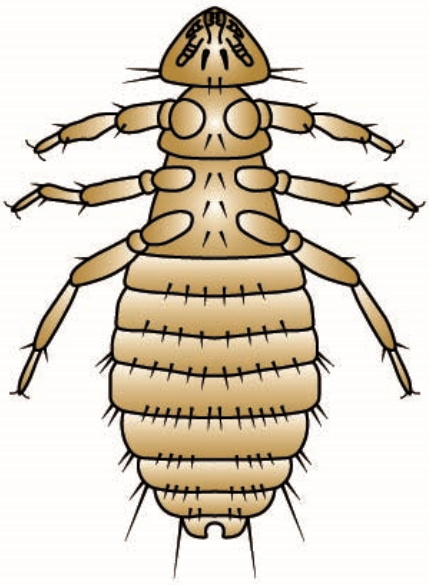


Cuclotogaster
adult (ventral)
(~ 3 mm)

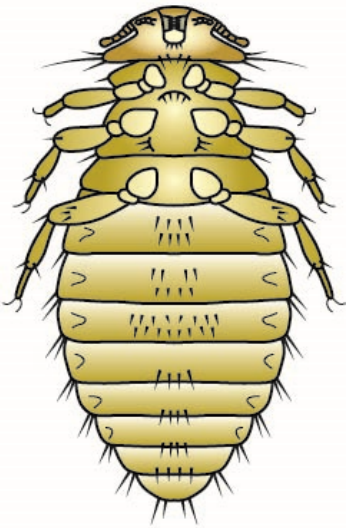


Phthiraptera: Amblycera (chewing lice)

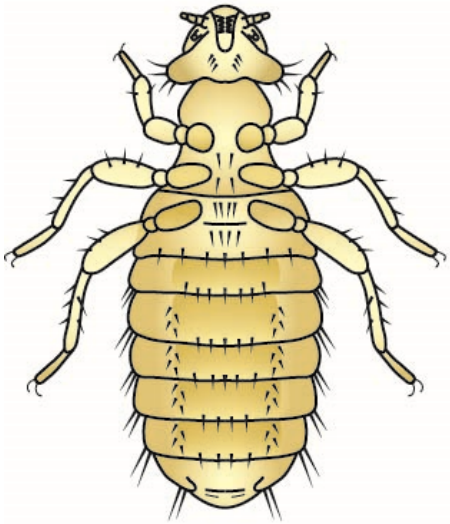
Heterodoxus
adult (ventral)
(~ 2.5 mm)



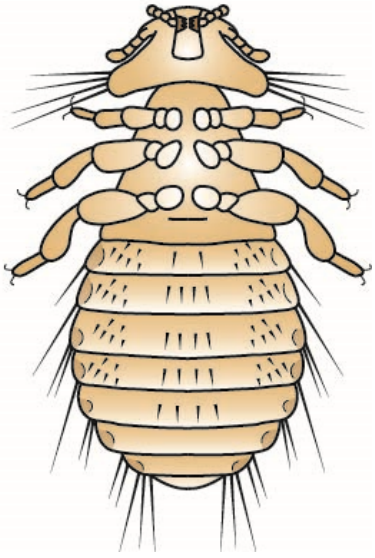
Menopon
adult (ventral)
(~ 2 mm)



Menacanthus
adult (ventral)
(~ 2 mm)



Holomenopon
adult (ventral)
(~ 2 mm)



Haematopinus
(insect: louse)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Anopluran (sucking) lice have narrow pointed heads adapted to piercing the skin and feeding on tissue fluids (solenophage mode of feeding). Sucking lice are ectoparasitic on mammals and most species are highly host specific and even site-specific, being found predominantly in areas with coarse hairs. Haematopinids are short-nosed lice whose tarsal claws are equal in size. *Haematopinus* spp. are commonly found on the skin/hair of domestic animals and infestations have been associated with dermatitis, anaemia, pruritus, alopecia, excoriation and self-wounding, especially in cattle.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order: Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder: Anoplura (sucking lice, narrow pointed head, pierce skin and feed on fluids (solenophagy))
Family: Haematopinidae (short-nosed lice, ectoparasites of domestic animals, claws on ends of legs of similar size)
Genus: *Haematopinus* (parasitic on skin/hair of horses/cattle/pigs)
Species: various species cause skin lesions/anaemia in domestic livestock

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Lice are small wingless hemipterodeans that undergo gradual (hemimetabolous) metamorphosis and are permanent obligate ectoparasites on other animals. Four suborders are recognized: the Anoplura containing the haematophagous sucking lice of placental mammals; the Ischnocera and Amblycera (previously classified together as Mallophaga) comprising the chewing or biting lice of birds, marsupials and placental mammals; and the Rhynchophthirina confined to elephants and warthogs in Africa.

Major parasitic phthirapteran families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Suborder: Anoplura (sucking lice of placental mammals) (narrow pointed head, pierce skin and feed on fluids (solenophagy)) [16 families, 51 genera, 694 species]					
Haematopinidae (ungulate lice, short-nosed lice)	1 genus, 21 spp.	mammals (equids, bovids, suids)	nymphs, adults	blood-sucking	viral, bacterial

Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-
Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial
Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-
Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
Suborder: Ischnocera [Mallophaga p.p.] (chewing lice of mammals and birds, broad rounded head, without maxillary palps, prominent filiform antennae, keratin feeders) [2 families, 158 genera, 3,371 species]					
Trichodectidae (fur lice)	20 genera, 413 spp.	mammals (bovids, equids, carnivores)	nymphs, adults	biting	helminth
Philopteridae (bird lice)	138 genera, 2,958 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					
Menoponidae (bird lice)	68 genera, 1,150 spp.	birds	nymphs, adults	biting, chewing	-
Boopiidae (marsupial chewing lice)	8 genera, 57 spp.	mammals (incl. marsupials)	nymphs, adults	biting	helminth

Some 700 species of anopluran sucking lice have been described in 51 genera in 16 families, namely: Echinophthiriidae (*Antarctophthirus*, *Echinophthirius*, *Latagophthirus*, *Lepidophthirus*, *Proechinophthirus*); Enderleinellidae (*Atopophthirus*, *Enderleinellus*, *Microphthirus*, *Phthirunculus*, *Werneckia*); Haematopinidae (*Haematopinus*); Hamophthiriidae (*Hamophthirius*); Hoplopleuridae (*Ancistroplax*, *Ferrisella*, *Haematopinoides*, *Hoplopleura*, *Paradoxophthirus*, *Pterophthirus*, *Schizophthirus*, *Typhlomyophthirus*); Hybophthiridae (*Hybophthirus*); Linognathidae (*Linognathus*, *Prolinognathus*, *Solenopotes*); Microthoraciidae (*Microthoracius*); Mirophthiridae (*Mirophthirus*); Neolinognathidae (*Neolinognathus*); Pecaroecidae (*Pecaroecus*); Pedicinidae (*Pedicinus*); Pediculidae (*Pediculus*); Polyplacidae (*Abrocomaphthirus*, *Ctenophthirus*, *Cuyana*, *Docophthirus*, *Eulinognathus*, *Fahrenholzia*, *Galeophthirus*, *Haemodipsus*, *Johnsonpthirus*, *Lagidiophthirus*, *Lemurpediculus*, *Lemurphthirus*, *Linognathoides*, *Neohaematopinus*, *Phthirpediculus*, *Polyplax*, *Proenderleinellus*, *Sathrax*, *Scipio*); Pthiridae (*Pthirus*); and Ratemiidae (*Ratemia*). Those of medical significance are found in the families Pediculidae (hominids, New World primates) and Pthiridae (hominids), while those of particular veterinary significance occur in the families Haematopinidae (equids, bovids, suids), Linognathidae (bovids, canids), Hoplopleuridae (rodents), Pedicinidae (Old World primates) and Polyplacidae (rabbits, rodents). Haematopinids are commonly known as ungulate lice or short-nosed lice. The tarsal claws at the ends of their legs are similar in size and used to grip host hairs. Over 20 *Haematopinus* spp. have been described from ungulates, both domestic and sylvatic. These species are mostly host-specific and their geographic distribution generally mirrors that of their hosts, with lice of domestic livestock being cosmopolitan due to frequent translocations, while those of wild animals are more restricted to their native host ranges (e.g. African antelope, zebra, etc.).

***Haematopinus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
H. acuticeps	Perissodactyla: equid (plains zebra)	skin		Africa
H. apri (syn. *H. aperis, urius p.p.*)	Artiodactyla: suid (pig)	skin		Eurasia
H. asini (syn. *H. elegans, equi, macrocephalus, minor*) (horse sucking louse)	Perissodactyla: equid (horses, donkeys)	skin (head, neck, back, brisket, upper legs, belly)	dermatitis, irritation, excoriation, alopecia, anaemia	worldwide
H. breviculus	Artiodactyla: bovid (eland)	skin		Africa
H. bufali (syn. *H. neumanni, papillosus, phthiropsis*)	Artiodactyla: bovid (buffalo)	skin		Africa
H. channabasavannai	Artiodactyla: bovid (cattle)	skin		India
H. eurysternus (syn. *H. brevipes, palpebrae*) (short-nosed cattle louse)	Artiodactyla: bovid (cattle)	skin (around poll, horns, ears, eyes, nostrils, tail switch)	dermatitis, pruritus, rubbing, licking	worldwide
H. gorgonis	Artiodactyla: bovid (wildebeest)	skin		Africa
H. jeannereti	Artiodactyla: bovid (giant eland)	skin		Africa

H. latus (syn. *H. incisus, peristictus p.p.*)	Artiodactyla: suid (river hog, bushpig)	skin		Africa
H. longus	Artiodactyla: cervid (sambar)	skin		Indo-China
H. ludwigi	Artiodactyla: suid (Philippine pig, bearded pig)	skin		South-East Asia
H. meinertzhageni	Artiodactyla: suid (giant forest hog)	skin		Africa
H. nigricantis	Artiodactyla: cervid (Philippine brown deer)	skin		South-East Asia
H. oliveri	Artiodactyla: suid (pygmy hog)	skin		India
H. oryx	Artiodactyla: bovid (gemsbok)	skin		Africa
H. phacochoeri (syn. *H. peristictus p.p.*)	Artiodactyla: suid (warthog)	skin		Africa
H. quadripertusus (syn. *H. parviprocursus*) (cattle tail louse)	Artiodactyla: bovid (cattle)	skin (tail, perineum)	dermatitis, pruritus	worldwide
H. suis (syn. *H. adventicus, chinensis, irritans*) (swine/hog louse)	Artiodactyla: suid (pig)	skin (neck, jowls, flanks, legs)	irritation, scratching, weight loss [plus vector for swine pox virus]	worldwide
H. taurotragi	Artiodactyla: bovid (kudu, eland)	skin		Africa
H. tuberculatus (syn. *H. punctatus*) (buffalo louse)	Artiodactyla: bovid (buffalo, cattle)	skin (tail, dorsal mid-line)	dermatitis	worldwide

Parasite morphology: Lice form three different types of developmental stages: eggs; nymphs (3 instars); and adults. Eggs are ovoid-ellipsoidal stages (0.9-1.1 x 0.4-0.5 mm) that are glued onto host hairs by their bases, sometimes on a short peduncle or stalk, and generally lay almost parallel to the hair. The eggs are translucent and white-beige in colour, the surface covering is pitted with numerous aeropyle pores, the apical end is bluntly rounded and contains an opercular lid, and they contain developing embryos. The eggs, and the empty eggshells, are commonly called nits. Newly-hatched nymphs moult through another two nymphal stages (instars) before developing into adult lice (imagoes). Developing stages undergo gradual (incomplete) metamorphosis (hemimetabolous) whereby the nymphs appear morphologically similar to adults but are smaller, less sclerotized, have fewer body setae, and lack genitalia. Haematopinids are the largest lice found on domestic animals, with adults ranging in length from 2-8 mm depending on species. They are usually grey to brown in colour and are dorso-ventrally flattened (dorsal tergum, ventral sternum) with three distinct body parts (head, thorax, abdomen). The head is long and narrow (longer than wide, narrower than thorax) with an anterior point containing the mouthparts, two antennae extending laterally (each comprised of five segments) and two lateral ocular points (eyeless projections) behind the antennae. The long thin mouthparts are modified for piercing and sucking and are located in a snout-like proboscis (labrum) containing a tubular haustellum which is eversible, armed with prostomal teeth (for attachment) and supports four retractable stylets (two supported by maxillae to form a food channel, one derived from the hypophyarnx and connected to the salivary gland, and one derived from the labium which is flattened with a serrated tip and guides the other stylets). The mouthparts are retracted into a pocket in the head when not used for feeding. Sucking lice lack maxillary palps (present in amblyceran chewing lice), and they lack mandibles and pulvinus pads (present in other chewing/biting lice). Although some early texts suggested that *Haematopinus* lice retained rudimentary mandibles, subsequent embryological studies revealed them only in developing eggs and they never became sclerotized and had disappeared before adults were formed. The alimentary tract consists of a foregut (with buccal funnel, cibarial pump, pharynx and oesophagus), a large midgut (with ventriculus, anterior caeca and round mycetome (special organ, sometimes called bacteriome or stomach disc, harbouring bacterial/fungal symbionts)), and a hindgut (with pylorus, papillae and rectum). The thorax is relatively small and consists of 3 fused segments without obvious divisions although a notal pit is present in the tergum and the sternal plate is large and dark. The thorax contains three pairs of legs, all similar in size. Each leg contains five sections (proximal coxa, trochanter, femur, tibia and distal tarsus), the latter bearing a large specialized claw that closes onto a thumb-like tibial spur next to a tibial pad. These modified tibiotarsal claws are similar in size and well adapted for grasping host hairs (the claw diameter closely corresponds to the diameter of host hairs). The elongate elliptoid abdomen consists of nine segments with well-sclerotized dorsal tergal plates, ventral sternal plates and paratergal plates bulging laterally and associated with respiratory spiracles (openings in the body wall connected to the tracheal system). Mature female lice are slightly larger than males (2-6 cf. 2-4 mm long). The female reproductive tract lacks a spermatheca but has ovaries with polytrophic ovarioles, tubular oviducts, and a globular uterus with accessory glands (produce eggshells and glue). The posterior abdominal segment is distinctly bifurcated (with apical lobes) and the genital opening (vagina) is supported by a sclerotized genital plate and well-developed gonopods armed with setae. Males have a more rounded abdomen containing compact bilobed testes, tubular vas deferens which coalesce to form the seminal vesicle, and then a prominent posterior genital sac containing a well-sclerotized asymmetrical aedeagus (copulatory intromittent organ comprising a penis-like tube with dorsal gonopore and terminal V-shaped pseudopenis) supported by a thick basal apodeme (plate-like sclerite) and small lateral parameres

(rod-like sclerites). [Note that some texts refer to the whole aedeagus as the pseudo-penis, while others reserve the latter term for the terminal portion of the aedeagus]. *Haematopinus* spp. are differentiated by variations in their morphological characteristics, particularly their heads, ocular points, thoracic sternites, sternal pits and genital plates.

Site of infection: Haematopinid lice are obligate ectoparasites of ungulates, parasitizing even-toed artiodactyls (pigs, cattle, buffalo, antelopes, deer) and odd-toed perissodactyls (horses, donkeys, zebras). Nymphal stages and adult lice are found crawling around on the skin and hair of their hosts. Most species are remarkably host specific and are found on individual host species, occasionally on several closely-related hosts. Many species exhibit some site specificity and are found preferentially on particular body parts, although they may be more widespread in heavy infestations. *H. eurysternus* (short-nosed cattle louse) is commonly found on the neck, dewlap and brisket, sometimes around the eyes, horns, tail and withers. During the summer, lice have been observed to shelter around the ears, horns and under the tail. *H. quadripertusus* (cattle tail louse) normally infests the tail, although nymphs may also be found on the perineum and vulva. *H. asini* (horse sucking louse) is found on the coarse hairs of the mane, forelock, brisket, back, tail and on the legs above the hooves. *H. suis* (hog louse) is found under scurf of the skin usually in protected areas such as neck folds, jowls, around the ears and eyes, the inner flanks and between the legs.

Pathogenesis: These sucking lice are haematophagous and all nymph and adult stages feed by piercing the skin with their slender mouthparts, injecting saliva and sucking blood. Light infestations are often well tolerated by their hosts and may go unnoticed, but heavier infestations may cause mild to severe disease characterized by dermatitis, anaemia, allergic reactions and reduced productivity. Bite sites may become irritated and inflamed due to physical trauma and local reactions to louse antigens/allergens (in saliva and/or faeces). Skin lesions may be conspicuous as red pruritic spots with inflammatory cellular infiltrates (polymorphonuclear leucocytes and eosinophils) sometimes progressing to dermal granulomas due to hypersensitivity responses. Infested animals become restless and endeavour to relieve the itching by grooming (licking, biting, scratching or rubbing) afflicted body parts which can become unsightly and unthrifty in appearance. Animals may develop rough coats (matted, dry, broken fibres, pulled appearance) and alopecia (loss of hair) with thickened areas of skin, superficial flecks, cracks, scales or crusts, and local scarification due to self-trauma. They may exhibit impaired thermoregulation and damaged hides are prone to secondary infections by bacteria or fly larvae. Over time, heavily or chronically infested animals lose body condition due to inappetence or anorexia, with production losses due to suboptimal meat, milk or fibre production. Heavy infestations by sucking lice may also cause significant blood loss with anaemia and compromised nutrition contributing to further weight loss, deteriorating health and sometimes reproductive losses (through abortion), shortened life-spans and death (particularly in pigs). Young, old, sick or stressed animals are more susceptible to severe infestations due to their compromised immunological and/or physiological states, with heavy infestations often developing in association with some underlying condition such as malnutrition or concurrent infection. Animals in good body condition with good nutrition generally keep louse populations in check by regular self-grooming. Studies have shown that individuals unable to groom themselves develop heavier and more persistent infestations, shed their winter coats later and may act as chronic carriers between seasons, locations and herds.

Some haematopinid species have been shown to act as vectors for several infectious microbial diseases of livestock: notably *H. suis* transmitting the virus causing swine pox and the bacterium *Eperythrozoon suis* causing eperythrozoonosis in pigs. Recent molecular screening studies have used polymerase chain reaction (PCR) techniques to detect DNA sequences from a range of potential microbial pathogens in lice; including the bacteria *Anaplasma marginale* in *H. tuberculatus* from cattle and in *H. suis* from pigs, *Mycoplasma* sp. in *H. tuberculatus* from buffalo, *Bartonella* spp. in *H. quadripertusus* and *H. tuberculatus* from cattle, *Rickettsia africae* in *H. quadripertusus* from cattle, *Rickettsia* sp. in *H. eurysternus* from cattle, and the haemoprotozoans *Trypanosoma evansi* in *H. tuberculatus* from cattle, and *Theileria orientalis* in *H. eurysternus* from cattle; but their roles in disease transmission are uncertain. Both sucking and chewing lice of cattle have also been shown to act as mechanical vectors for the skin fungus *Trichophyton verrucosum* which causes dermatomycosis (ringworm).

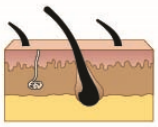
Developmental cycle and mode of transmission: Sucking lice are permanent obligate ectoparasites whose entire life-cycle occurs on the host with transmission between hosts occurring by direct contact or via fomites. Mature female lice attach their eggs (nits) to hairs close to the skin surface. The eggs hatch in 11-14 days releasing first-stage nymphs (N1) which crawl over the skin and begin to suck blood within hours. The nymphs resemble adult lice and undergo simple (incomplete) metamorphosis, moulting through another two nymphal stages (N2 and N3) before moulting to adults after 9-22 days. After feeding and mating, female lice lay 1-5 eggs each day for 2-4 weeks and may live for up to 8 weeks. The whole life cycle may be completed in 3-5 weeks, particularly in cool moist conditions. Transmission to other animals occurs by direct contact when lice (nymphs or adults) crawl from one host to another, although it may also occur by contamination of the immediate environment, notably when lice infest fomites, such as shared bedding, grooming equipment, harnesses, saddles, blankets or rugs. Lice do not survive for long off the host (maximum of 3-4 days), so infestations are generally transmitted during periods of high contact between hosts, such as mothers suckling young, commercial milking times, or crowding in feed-lots, yards, barns, stalls or pens. Occasional examples of phoresis or phoretic transfer have been reported whereby lice have become temporarily attached to insects (muscids) which act as paratenic (transport) hosts; e.g. *H. eurysternus* nymphs from cattle attached to horn flies (*Haematobia irritans*). Many infestations exhibit seasonal patterns, being most prevalent during cooler winter months when lower temperatures, rain and less daylight favour louse development, and hosts generally have poorer nutrition, longer hair, and crowd together for warmth. Infestations decline prevalence

and intensity approaching summer with warmer drier conditions, loss of winter coats, better nutrition and less crowding or gregarious behaviour. The exception is the cattle tail louse *H. quadripertusus* which is most abundant during summer months due to delayed hatching of their eggs.

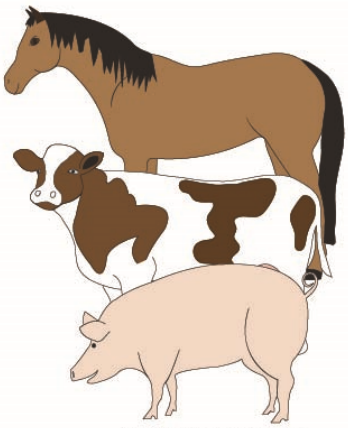
Differential diagnosis: Most infestations are diagnosed by direct detection of lice (nymphs and adults) on the skin of their hosts. Sucking lice move slowly and are often found with their mouthparts embedded in the skin. Occasionally, their eggs or egg cases (nits) may be observed attached to hairs near the skin surface. Macroscopic inspections of livestock are best conducted by parting the coat (if necessary, breaking apart matted hairs) particularly on the face, neck, back, legs, scrotum and tail. Lice may be collected and examined microscopically for positive identification. Recent studies have used molecular biological techniques to characterize several species following the polymerase chain reaction (PCR) amplification of nuclear DNA (ribosomal RNA gene) and mitochondrial DNA (revealing fragmented mitochondrial genomes with 37 genes arranged on 9 minichromosomes).

Treatment and control: Clinical infestations may be effectively controlled by combining chemotherapy with preventive management strategies. A range of insecticides have demonstrated good activity against haematopinid lice on domestic livestock and performance animals: including organochlorides (dichloro-diphenyl-trichloroethane (DDT), lindane, methoxychlor); organophosphates (tetrachlorvinphos, chlorpyrifos, diazinon, famphur, fenthion, malathion); carbamates (carbaryl, propoxur); synthetic pyrethroids (permethrin, fenvalerate, deltamethrin, flumethrin, cypermethrin); macrocyclic lactones (abamectin, doramectin, eprinomectin, ivermectin, moxidectin); amidines (amitraz); spinosyns (spinosad); and several insect growth regulators such as benzoylphenylureas (diflubenzuron). Most chemicals were not very effective against egg stages so treatments needed to be repeated, although some formulations had residual activity long enough to act against newly-emergent nymphs. Domestic animals may be treated using topical formulations (showers/baths/dips, shampoos/rinses, sprays/aerosols, powders/dusts, neck collars, ear/tail tags) or systemic chemicals (oral, spot-ons, injectable, gut boluses), while wild or feral animals may be treated using self-application devices (back rubbers, oilers, dust bags). Careful attention should be paid to regulations governing chemical usage (including with-holding periods, residues, contra-indications, environmental toxicity). It is also important to differentiate between infestations by sucking and chewing lice as not all chemicals are effective against both types of lice. Generally, injectable macrocyclic lactones are less efficient against chewing lice while pour-on formulations are active against both. Matted coats may need clipping prior to treatment, and a range of grooming devices (brushes and combs) may assist in easing tangles and exposing lice. Preventive measures revolve around minimizing contact between susceptible and infested individuals (through isolation, quarantine, treating new livestock) or decontaminating shared facilities and equipment (by cleaning, washing or chemical treatment). Insecticides may be used on absorbent materials (saddlery, harnesses, rugs, bedding, clothing, grooming equipment) while impervious materials (brushes, combs, stalls/pens) may be subject to heat sterilization (steam-cleaning). Animals should be kept well-nourished and healthy, as infestations are worse in sick or stressed hosts. Husbandry practices should avoid over-crowded unsanitary conditions and animals should be pre-emptively treated in autumn to prevent louse populations from escalating during the colder months, particularly in animals housed indoors.

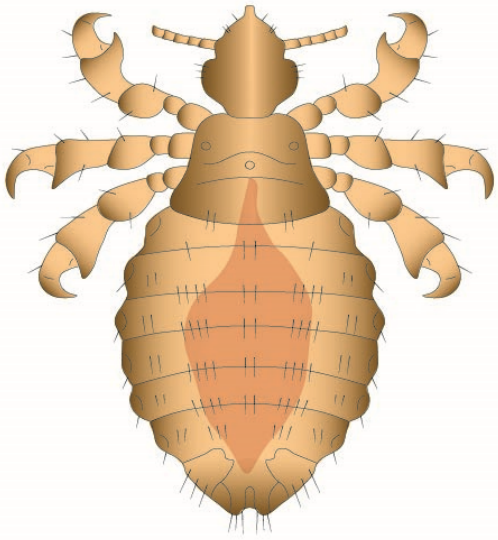
Haematopinus



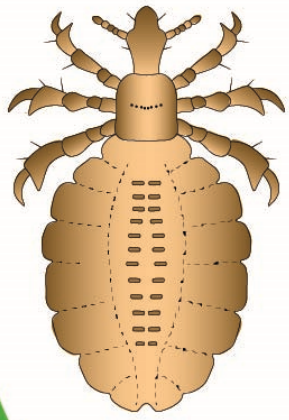
skin/pelage
(dermatitis,
anaemia,
allergy,
reduced
productivity)



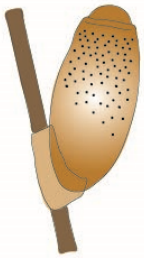
Definitive Hosts
(ungulates)



adult (dorsal)
(~ 5 mm)



nymph (dorsal)
(~ 3 mm)



egg
(~ 1 mm)

all stages ectozoic on host
(motile stages feed on blood)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites



Haematopinus adult on pig skin



Haematopinus adult



Haematopinus egg



Haematopinus nymph

Linognathus
(insect: louse)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Anopluran (sucking) lice have narrow pointed heads adapted to piercing the skin and feeding on tissue fluids (solenophage mode of feeding). Sucking lice are ectoparasitic on mammals and most species are highly host specific and even site-specific, being found predominantly in areas with coarse hairs. Linognathids are long-nosed lice whose tarsal claws are smaller on the first legs than on other legs. *Linognathus* spp. are commonly found on the skin/hair of ruminants and carnivores and infestations have been associated with dermatitis, anaemia, pruritus, alopecia, excoriation and self-wounding. Some species may transmit other infectious micro-organisms, including bovine anaplasmosis, theileriosis, dermatomycosis (ringworm) and ovine eperythrozoonosis.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order: Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder: Anoplura (sucking lice, narrow pointed head, pierce skin and feed on fluids (solenophagy))
Family: Linognathidae (long-nosed lice, claws on first leg smaller than those on other legs)
Genus: *Linognathus* (parasitic on skin/hair of ruminants/dogs/foxes)
Species: various species cause skin lesions in domestic animals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Lice are small wingless hemipterodeans that undergo gradual (hemimetabolous) metamorphosis and are permanent obligate ectoparasites on other animals. Four suborders are recognized: the Anoplura containing the haematophagous sucking lice of placental mammals; the Ischnocera and Amblycera (previously classified together as Mallophaga) comprising the chewing or biting lice of birds, marsupials and placental mammals; and the Rhynchophthirina confined to elephants and warthogs in Africa.

Major parasitic phthirapteran families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Suborder: Anoplura (sucking lice of placental mammals) (narrow pointed head, pierce skin and feed on fluids (solenophagy)) [16 families, 51 genera, 694 species]					
Haematopinidae (ungulate lice,	1 genus, 21 spp.	mammals (equids,	nymphs,	blood-	viral, bacterial

short-nosed lice)		bovids, suids)	adults	sucking	
Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-
Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial
Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-
Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
Suborder: Ischnocera [Mallophaga p.p.] (chewing lice of mammals and birds, broad rounded head, without maxillary palps, prominent filiform antennae, keratin feeders) [2 families, 158 genera, 3,371 species]					
Trichodectidae (fur lice)	20 genera, 413 spp.	mammals (bovids, equids, carnivores)	nymphs, adults	biting	helminth
Philopteridae(bird lice)	138 genera, 2,958 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					
Menoponidae (bird lice)	68 genera, 1,150 spp.	birds	nymphs, adults	biting, chewing	-
Boopiidae (marsupial chewing lice)	8 genera, 57 spp.	mammals (incl. marsupials)	nymphs, adults	biting	helminth

Some 700 species of anopluran sucking lice have been described in 51 genera in 16 families, namely: Echinophthiriidae (*Antarctophthirus*, *Echinophthirius*, *Latagophthirus*, *Lepidophthirus*, *Proechinophthirus*); Enderleinellidae (*Atopophthirus*, *Enderleinellus*, *Microphthirus*, *Phthirunculus*, *Werneckia*); Haematopinidae (*Haematopinus*); Hamophthiriidae (*Hamophthirius*); Hoplopleuridae (*Ancistroplax*, *Ferrisella*, *Haematopinoides*, *Hoplopleura*, *Paradoxophthirus*, *Pterophthirus*, *Schizophthirus*, *Typhlomyophthirus*); Hybophthiridae (*Hybophthirus*); Linognathidae (*Linognathus*, *Prolinognathus*, *Solenopotes*); Microthoraciidae (*Microthoracius*); Mirophthiridae (*Mirophthirus*); Neolinognathidae (*Neolinognathus*); Pecaroecidae (*Pecaroecus*); Pedicinidae (*Pedicinus*); Pediculidae (*Pediculus*); Polyplacidae (*Abrocomaphthirus*, *Ctenophthirus*, *Cuyana*, *Docophthirus*, *Eulinognathus*, *Fahrenholzia*, *Galeophthirus*, *Haemodipsus*, *Johnsonpthirus*, *Lagidiophthirus*, *Lemurpediculus*, *Lemurphthirus*, *Linognathoides*, *Neohaematopinus*, *Phthirpediculus*, *Polyplax*, *Proenderleinellus*, *Sathrax*, *Scipio*); Pthiridae (*Pthirus*); and Ratemiidae (*Ratemia*). Those of medical significance are found in the families Pediculidae (hominids, New World primates) and Pthiridae (hominids), while those of particular veterinary significance occur in the families Haematopinidae (equids, bovids, suids), Linognathidae (bovids, canids), Hoplopleuridae (rodents), Pedicinidae (Old World primates) and Polyplacidae (rabbits, rodents). Linognathids are commonly known as pale lice or long-nosed lice. The tarsal claws on the first pair of legs are smaller than those on the second and third pairs of legs. Two genera are of particular veterinary importance: several *Linognathus* spp. cause disease in domestic ruminants and companion animals; and several *Solenopotes* spp. cause disease in cattle and deer. Over 50 *Linognathus* species have been described, most associated with ungulates (especially African artiodactyls) and six species with carnivores (canids). They are highly host-specific and are found wherever their hosts occur, those of domestic livestock being cosmopolitan in distribution.

***Linognathus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
L. aepycerus	Artiodactyla: bovid (impala)	skin		Africa
L. africanus (African blue louse)	Artiodactyla: bovid (goats, sheep, gazelle); cervid (deer)	skin	irritation, dermatitis, anaemia	worldwide
L. angasi	Artiodactyla: bovid (nyala)	skin		Africa
L. angulatus (syn. *L. ungulatus*)	Artiodactyla: bovid (duiker)	skin		Africa
L. antennatus	Artiodactyla: bovid (hartebeest)	skin		Africa
L. antidorcitis	Artiodactyla: bovid (springbok)	skin		Africa
L. armatus	Artiodactyla: bovid (springbok)	skin		Africa
L. bedfordi	Artiodactyla: bovid (springbok)	skin		Africa
L. bhatii	Carnivora: canid (Bengal fox)	skin		India
L. breviceps (syn. *L. gazella, gilvus*)	Artiodactyla: bovid (Maxwell's duiker, blue duiker, red forest duiker, common duiker)	skin		Africa
L. brevicornis	Artiodactyla: giraffid (giraffe)	skin		Africa
L. cervicaprae	Artiodactyla: bovid (blackbuck)	skin		Africa
L. contractus	Artiodactyla: bovid (oribi)	skin		Africa
L. damaliscus	Artiodactyla: bovid (bontebok)	skin		Africa

(syn. *L. albifrontis*)				
L. damarensis	Artiodactyla: bovid (dikdik)	skin		Africa
L. digitalis	Artiodactyla: bovid (springbok)	skin		Africa
L. elblae	Artiodactyla: bovid (duiker)	skin		Africa
L. euchore	Artiodactyla: bovid (springbok)	skin		Africa
L. fahrenholzi (syn. *L. forficula*)	Artiodactyla: bovid (southern reedbuck, mountain reedbuck, Bohor reedbuck)	skin		Africa
L. fenneci	Carnivora: canid (fennec)	skin		North Africa, Middle-East
L. fractus	Artiodactyla: bovid (bushbuck)	skin		Africa
L. geigyi	Artiodactyla: bovid (Salt's dik-dik, Kirk's dikdik)	skin		Africa
L. gnu (syn. *L. ferrisi*)	Artiodactyla: bovid (wildebeest)	skin		Africa
L. gonolobatus	Artiodactyla: bovid (roan antelope)	skin		Africa
L. gorgonus	Artiodactyla: bovid (wildebeest)	skin		Africa
L. hippotragi	Artiodactyla: bovid (sable antelope)	skin		Africa
L. kimi	Artiodactyla: bovid (Sharpe's grysbok, Cape grysbok)	skin		Africa
L. lewisi	Artiodactyla: bovid (Thomson's gazelle, dorcas gazelle)	skin		Africa
L. limnotragi	Artiodactyla: bovid (sitatunga, bushbuck)	skin		Africa
L. nesotragi	Artiodactyla: bovid (suni)	skin		Africa
L. nevilli	Artiodactyla: bovid (impala)	skin		Africa
L. oryx	Artiodactyla: bovid (gemsbok)	skin		Africa
L. ourebiae	Artiodactyla: bovid (oribi)	skin		Africa
L. ovillus (sheep face louse)	Artiodactyla: bovid (sheep)	skin (face)	irritation, dermatitis, anaemia	worldwide
L. panamensis (syn. *L. tragelaphi*)	Artiodactyla: bovid (kudu, bushbuck); cervid (white-tailed deer)	skin		Africa, North America
L. pedalis (syn. *L. micerocephalus*) (sheep foot louse)	Artiodactyla: bovid (sheep, mountain goat)	skin (feet, legs, belly)	irritation, dermatitis, anaemia	worldwide
L. peleus	Artiodactyla: bovid (rhebok)	skin		Africa
L. petasmatus	Artiodactyla: bovid (oryx, addax)	skin		Africa
L. pithodes	Artiodactyla: bovid (blackbuck)	skin		Africa
L. raphiceri	Artiodactyla: bovid (steenbok, impala)	skin		Africa
L. reduncae	Artiodactyla: bovid (mountain reedbuck, southern reedbuck)	skin		Africa
L. samburi	Artiodactyla: bovid (Gunther's dik-dik)	skin		Africa
L. setosus (syn. *L. bicolor, flavidus, isopus, piliferus*) (dog sucking louse)	Carnivora: canid (dog, gray wolf, red fox, Ruppell's fox, jackal, coyote, Arctic fox); otariid (sea lion)	skin (head, neck)	irritation, anaemia	worldwide
L. sosninae	Carnivora: canid (red fox)	skin		Europe
L. spicatus	Artiodactyla: bovid (wildebeest)	skin		Africa
L. stenopsis (syn. *L. hirci, schistopyga, rupicaprae*) (goat sucking louse)	Artiodactyla: bovid (goat, ibex, chamois)	skin	irritation, dermatitis, anaemia	worldwide
L. taeniotrichus	Carnivora: canid (maned wolf, crab-eating fox)	skin		South America
L. taurotragus	Artiodactyla: bovid (kudu, eland)	skin		Africa
L. tibialis	Artiodactyla: bovid (dama gazelle, mountain gazelle, red-fronted gazelle, goitered gazelle)	skin		Africa
L. vituli (syn. *L. oxyrrhynchus, tenuirostris*) (long-nosed cattle louse)	Artiodactyla: bovid (cattle)	skin (head, neck, dewlap)	irritation, dermatitis, pruritus	worldwide
L. vulpis	Carnivora: canid (red fox, Bengal fox)	skin		Europe, India
L. weissei	Artiodactyla: bovid (impala)	skin		Africa

L. zumpti	Artiodactyla: bovid (common duiker, steenbok)	skin		Africa

Parasite morphology: *Linognathus* spp. form three different types of developmental stages: eggs; nymphs (3 instars); and adults. The eggs are ellipsoidal measuring around 500 μm in length and are attached by their bases to host hairs but lay longitudinally with their straight side along the hair. They are dark brown-blue in colour and are operculate with a distinct anterior cap (operculum) with a ridged lip. The eggs contain a developing embryo which hatches as a first-stage nymph (sometimes designated N1) measuring 1-2 mm in length. Nymphs resemble adult lice but are smaller, less sclerotized, have fewer body setae, and lack genitalia. They undergo incomplete (gradual) metamorphosis and moult through another two instars (N2, N3) before moulting to adults which measure up to 2.5 mm long. Adult lice are dorsoventrally flattened (dorsal tergum, ventral sternum), tan-coloured with dark blue-black markings, and have three prominent body parts (head, thorax, abdomen). *Linognathus* spp. have narrow elongate heads, twice as long as broad (in contrast to short blunt heads in members of the sister genus *Solenopotes*). Their heads lack eyes and ocular points, but have two short stout lateral antennae, each consisting of 5 segments. The head is pointed anteriorly and has long thin mouthparts modified for piercing and sucking. The mouthparts are located in a snout-like proboscis (labrum) comprising an eversible tubular haustellum armed with teeth and 4 retractable stylets (2 supported by maxillae to form a food channel, one derived from the hypophyarnx and connected to the salivary gland, and one derived from the labium which is flattened with a serrated tip and guides the other stylets). When not in use, the mouthparts are retracted into a pocket in the head. Sucking lice lack maxillary palps (present in amblyceran chewing lice), and mandibles and pulvinus pads (present in other chewing/biting lice). Adults have an elaborate alimentary tract comprising a foregut (with buccal funnel, cibarial pump, pharynx and oesophagus), a large midgut (with ventriculus, caeca and special mycetome (stomach disc containing endosymbiotic bacteria and/or fungi)), and a short hindgut (with pylorus, papillae and rectum). The thorax has three segments fused together without obvious divisions, and has a distinct dorsal notal pit but lacks a ventral sternal plate (present in *Solenopotes* spp.). The ventral thorax gives rise to three pairs of legs, each consisting of five segments (coxa, trochanter, femur, tibia, tarsus). The legs have highly specialized pincer-like tibiotarsal claws closing on tibial spurs, and the fore-legs and claws are smaller than mid- and hind-legs and claws (the diameter enclosed by the latter typically conforms to the hair diameter of the host). The abdomen is elongate and consists of 9 membranous segments without sclerotized plates except for those associated with genital or terminal segments. Each segment has two rows of ventral setae and the lateral spiracles (openings to the respiratory (tracheal) system) are not located on raised tubercles (present in *Solenopotes*). Female lice are slightly larger than males (average of 2.4 cf. 1.8 mm) and they are readily identified by the appearance of their posterior abdominal segments (bifurcated in females and rounded in males). Mature males have compact bilobed testes, tubular vas deferens which coalesce to form the seminal vesicle, and a genital sac with a conspicuous copulatory (intromittent) organ called the aedeagus (penis-like tube with dorsal gonopore and terminal pseudopenis) supported by a slender basal plate-like sclerite (apodeme) and well-developed lateral rod-like sclerites (parameres). Mature females have paired ovaries with polytrophic ovarioles, tubular oviducts and glue-producing accessory glands connected to a globular uterus, a weakly sclerotized spermatheca (sperm storage organ), and a genital opening (vagina) supported by a genital plate, valvula, and well-developed gonopods with terminal horns and/or long pointed genital setae. Gravid females often contain 1-2 large eggs developing in the uterus.

Site of infection: *Linognathus* spp. are blood-sucking ectoparasites on the skin of artiodactyls (mostly bovids) and carnivores (mostly canids). They are highly host specific (oioxenous) although a few may be found on closely-related host species (stenoxenous). Most species also exhibit some tissue tropism (site specificity) with lice being found preferentially on particular parts of the body, although they may be more widespread over the body in heavy infestations. For example, the long-nosed cattle louse (*L. vituli*) is commonly found on cattle occur in distinct clusters, mainly on the head, face, neck (esp. dewlap) and sometimes the shoulders, back, rump, udder and perineum. The sheep face louse (*L. ovillus*) and the sheep foot louse (*L. pedalis*) are found on sheep on the hairy (non-woolled) areas of the face and foot, respectively. The dog sucking louse (*L. setosus*) is found mainly on dogs (esp. long-haired breeds) on the neck and shoulders.

Pathogenesis: While sucking lice are not considered to be highly pathogenic, infestations may cause clinical disease depending on the numbers present and the general health of the hosts (infestations more severe in individuals with compromised physiological and/or immunological status). Nymphs and adult lice feed by piercing the skin, injecting saliva with anticoagulant properties and then sucking host blood. Clinical signs are usually limited to superficial dermatitis and secondary self-trauma, although blood loss in heavy infestations may result in mild anaemia. Lice moving and feeding on their hosts irritate the skin causing inflammation (dermatitis) with pruritus (itching), and then induration (fibrosis) and granuloma formation. These responses appear to be exacerbated by host allergic responses to louse antigens (saliva and/or faeces), but they do not progress to disruption and scabbing of the skin surface that is commonly associated with psoroptic scab mites. Infested animals endeavour to relieve the irritation by intense grooming (biting, licking, scratching, rubbing) which may lead to self-trauma with skin lesions (scaling and crust formation), alopecia (loss of hair, fur, fibre), unsightly appearance (matted dull coats, wool breaks in sheep) and sometimes hide damage (superficial spots or flecks). Female lice may also pull several hairs together and attach their eggs, accentuating matting particularly in sheep and goats. Chronically infested areas develop thick tender skin which may crack in severe cases resulting in further hide damage evident at slaughter. Infested animals become restless and unthrifty and may exhibit impaired thermoregulation, poor feed conversion efficiency and reduced productivity (suboptimal meat, milk, fibre production). Clinical manifestations are

worse in young, old, malnourished or stressed individuals, as well as those sick with other disease conditions. Animals that are well nourished, healthy and able to groom can usually keep louse burdens low and minimize or avoid clinical disease.

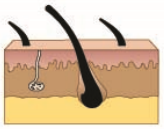
The species *L. setosus* from dogs has also been shown to act as a transmission vector for the nematode *Dipetalonema reconditum.* Recent molecular biological studies using polymerase chain reaction (PCR) amplification techniques have detected DNA from a range of bacteria in sucking lice; including *Acinetobacter soli, Anaplasma marginale, Anaplasma ovis, Rickettsia helvetica* and *Rickettsia africae* in *L. vituli* from cattle, *Anaplasma marginale* and *Rickettsia helvetica* in *L. stenopsis* from goats, *Rickettsia africae* in *L. africanus* from goats, and *Rickettsia felis* in *L. setosus* from dogs; but their role in disease transmission remains to be determined. Similar molecular studies have detected DNA from the haemoprotozoan *Theileria orientalis* in *L. vituli* from cattle, supporting previous work implicating sucking lice in the mechanical transmission of this piroplasm (via regurgitation, rather than cyclic transmission via saliva as occurs in ticks).

Developmental cycle and mode of transmission: These lice complete their whole life-cycles in the pelage (fur, hair, wool) of their hosts, with each mobile stage requiring a bloodmeal to develop further. Gravid female lice glue their eggs to host hairs/fibres using an adhesive cement. The eggs hatch in 1-2 weeks and release first-stage nymphs (N1) which feed and undergo hemimetabolous (incomplete) metamorphosis moulting through another two nymphal stages (N2, N3) before forming adult lice. After feeding and mating, female lice lay on average one egg per day for several weeks. Adults live for 6-10 weeks but the entire life-cycle may be completed within 3-4 weeks. Lice do not survive longed periods off hosts and die within 3-5 days if dislodged (the exception being the sheep foot louse *L. pedalis* which can survive in pastures for up to 18 days). Transmission occurs when lice (adults and sometimes nymphs) crawl from one host to another or temporarily contaminate fomites (especially shared bedding and grooming equipment). The highest transmission rates occur when hosts come into close contact, such as when herded, yarded, stabled or kennelled. Populations of lice increase during cooler months when lower temperatures, rainfall, reduced daylight, crowding and poor nutrition favour the breeding and spread of lice. Conversely, populations decrease during warmer months when drier conditions, loss of winter coats, better nutrition and less gregarious behaviours are detrimental to louse development. Nevertheless, lice persist over the summer months on a small number of highly susceptible animals.

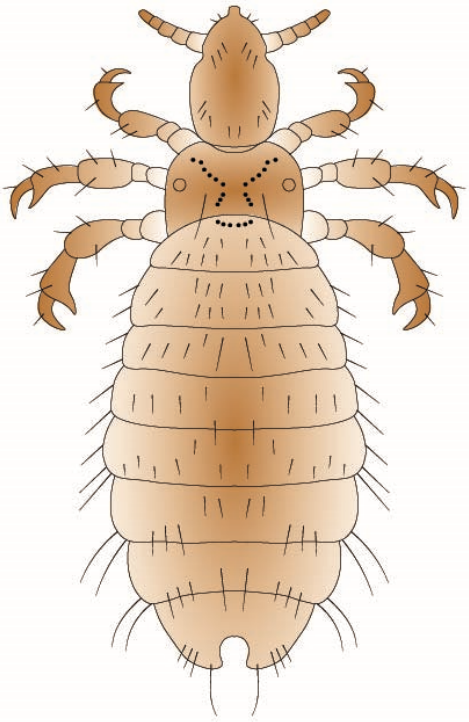
Differential diagnosis: Infestations may be suspected on the basis of clinical symptomatology involving manic self-grooming leading to traumatic lesions and alopecia, especially in cooler months over winter. Definitive diagnosis relies on the direct detection of lice (nymphs and adults) and/or their eggs (nits) in the host pelage. The parasites are large enough to be visible when parting the coat and they are slow moving and generally do not move to avoid light (while biting/chewing lice move readily to avoid light). Lice may be collected using tweezers (or sticky-tape impression smears) for microscopic examination to confirm identity. Modern molecular biological techniques have been used to infer phylogenetic relationships between various species following the PCR amplification of nuclear genes (18S ribosomal RNA).

Treatment and control: A range of insecticidal chemicals have shown good efficacy in the treatment of louse infestations: including organochlorides (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (chlorpyrifos, diazinon, malathion), synthetic pyrethroids (permethrin, deltamethrin, flumethrin, cypermethrin), macrocyclic lactones (milbemycin, selamectin, moxidectin, ivermectin, abamectin, eprinomectin, doramectin), formamidine (amitraz), chloronicotinyl (imidacloprid), arylpyrazole (fipronil), spinosyns (spinosad), and insect growth regulators (diflubenzuron). Most insecticides are not very effective against eggs, so treatments are usually repeated after several weeks to kill newly-emergent stages, although some formulations with good residual activity only require single applications. It is advisable to treat all animals at risk, particularly new animals before they are released into the general population. Treatment is best conducted in autumn to counter louse populations increases during the cold months over winter. Chemical usage should conform to government regulations regarding residues, with-holding periods and environmental toxicity. Insecticides may be applied to animals as topical (powders/fogs, aerosols/sprays, shampoos/rinses) or systemic preparations (oral, injectable, pour-ons, impregnated tags), and some are suitable for use in self-treatment devices (dust bags, back rubbers, oilers). A variety of grooming devices (brushes, combs) and lotions (essentially conditioners) may be used to help remove lice, although they are unsuited for use on long, curly or woolly coats. Matted coats on heavily infested animals should also be trimmed or clipped before treatment. Animals kept healthy and well-nourished are often able to control louse populations if they are able to self-groom, so husbandry practices should avoid over-crowded unsanitary conditions. Other preventive control measures involve decontaminating facilities and equipment (by washing, chemical or heat treatments) and restricting contact between individuals (isolate infested individuals, quarantine new livestock).

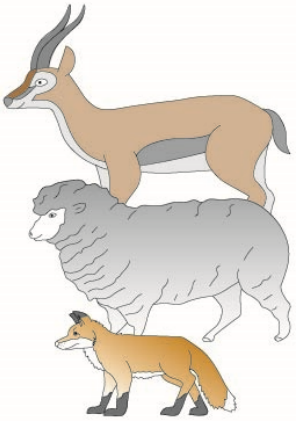
Linognathus



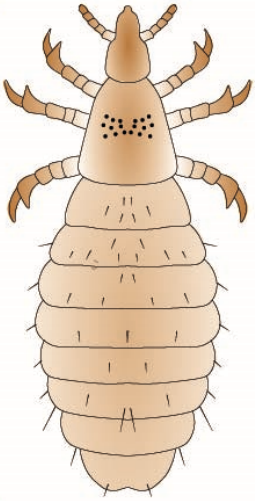
skin/pelage
(dermatitis, anaemia,
alopecia, excoriation)
(vectors for infectious
microbial diseases)



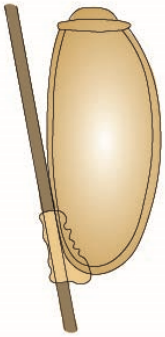
adult (dorsal)
(~ 3 mm)



Definitive Hosts
(ruminants, carnivores)



nymph (dorsal)
(~ 2 mm)



egg
(~ 0.5 mm)

all stages ectozoic on host
(motile stages feed on blood)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites



Linognathus adult



Linognathus adult



Linognathus egg

Linognathus adult

Solenopotes
(insect: louse)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Anopluran (sucking) lice have narrow pointed heads adapted to piercing the skin and feeding on tissue fluids (solenophage mode of feeding). Sucking lice are ectoparasitic on mammals and most species are highly host specific and even site-specific, being found predominantly in areas with coarse hairs. Linognathids are long-nosed lice whose tarsal claws are smaller on the first legs than on other legs. *Solenopotes* spp. are commonly found on the skin/hair of cattle/deer and infestations have been associated with irritation, dermatitis, pruritus, alopecia, excoriation and self-wounding.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order: Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder: Anoplura (sucking lice, narrow pointed head, pierce skin and feed on fluids (solenophagy))
Family: Linognathidae (long-nosed lice, claws on first leg smaller than those on other legs)
Genus: *Solenopotes* (parasitic on skin/hair of cattle)
Species: various species cause skin lesions on cattle

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Lice are small wingless hemipterodeans that undergo gradual (hemimetabolous) metamorphosis and are permanent obligate ectoparasites on other animals. Four suborders are recognized: the Anoplura containing the haematophagous sucking lice of placental mammals; the Ischnocera and Amblycera (previously classified together as Mallophaga) comprising the chewing or biting lice of birds, marsupials and placental mammals; and the Rhynchophthirina confined to elephants and warthogs in Africa.

Major parasitic phthirapteran families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Suborder: Anoplura (sucking lice of placental mammals) (narrow pointed head, pierce skin and feed on fluids (solenophagy)) [16 families, 51 genera, 694 species]					
Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-

Haematopinidae (ungulate lice, short-nosed lice)	1 genus, 21 spp.	mammals (equids, bovids, suids)	nymphs, adults	blood-sucking	viral, bacterial
Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial
Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-
Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
Suborder: Ischnocera [Mallophaga p.p.] (chewing lice of mammals and birds, broad rounded head, without maxillary palps, prominent filiform antennae, keratin feeders) [2 families, 158 genera, 3,371 species]					
Trichodectidae (fur lice)	20 genera, 413 spp.	mammals (bovids, equids, carnivores)	nymphs, adults	biting	helminth
Philopteridae(bird lice)	138 genera, 2,958 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					
Menoponidae (bird lice)	68 genera, 1,150 spp.	birds	nymphs, adults	biting, chewing	-
Boopiidae (marsupial chewing lice)	8 genera, 57 spp.	mammals (incl. marsupials)	nymphs, adults	biting	helminth

Some 700 species of anopluran sucking lice have been described in 51 genera in 16 families, namely: Echinophthiriidae (*Antarctophthirus*, *Echinophthirius*, *Latagophthirus*, *Lepidophthirus*, *Proechinophthirus*); Enderleinellidae (*Atopophthirus*, *Enderleinellus*, *Microphthirus*, *Phthirunculus*, *Werneckia*); Haematopinidae (*Haematopinus*); Hamophthiriidae (*Hamophthirius*); Hoplopleuridae (*Ancistroplax*, *Ferrisella*, *Haematopinoides*, *Hoplopleura*, *Paradoxophthirus*, *Pterophthirus*, *Schizophthirus*, *Typhlomyophthirus*); Hybophthiridae (*Hybophthirus*); Linognathidae (*Linognathus*, *Prolinognathus*, *Solenopotes*); Microthoraciidae (*Microthoracius*); Mirophthiridae (*Mirophthirus*); Neolinognathidae (*Neolinognathus*); Pecaroecidae (*Pecaroecus*); Pedicinidae (*Pedicinus*); Pediculidae (*Pediculus*); Polyplacidae (*Abrocomaphthirus*, *Ctenophthirus*, *Cuyana*, *Docophthirus*, *Eulinognathus*, *Fahrenholzia*, *Galeophthirus*, *Haemodipsus*, *Johnsonpthirus*, *Lagidiophthirus*, *Lemurpediculus*, *Lemurphthirus*, *Linognathoides*, *Neohaematopinus*, *Phthirpediculus*, *Polyplax*, *Proenderleinellus*, *Sathrax*, *Scipio*); Pthiridae (*Pthirus*); and Ratemiidae (*Ratemia*). Those of medical significance are found in the families Pediculidae (hominids, New World primates) and Pthiridae (hominids), while those of particular veterinary significance occur in the families Haematopinidae (equids, bovids, suids), Linognathidae (bovids, canids), Hoplopleuridae (rodents), Pedicinidae (Old World primates) and Polyplacidae (rabbits, rodents). Linognathids are commonly known as pale lice or long-nosed lice. The tarsal claws on the first pair of legs are smaller than those on the second and third pairs of legs. Two genera are of particular veterinary importance: several *Linognathus* spp. cause disease in domestic ruminants and companion animals; and several *Solenopotes* spp. cause disease in cattle and deer. Nine *Solenopotes* spp. have been described from artiodactyls, including domesticated and wild animals. Most species are host-specific and occur only within the geographic ranges of their hosts, although species on domestic livestock may be found worldwide due to large scale translocations.

***Solenopotes* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
S. binipilosus (syn. *S. coassus*)	Artiodactyla: cervid (white-tailed deer, brown brocket)	skin	irritation, dermatitis, pruritus	Americas
S. burmeisteri (syn. *S. crassicornis*)	Artiodactyla: cervid (red deer, sika deer)	skin	irritation, dermatitis, pruritus	Eurasia
S. capillatus (little blue cattle louse, tubercle-bearing louse)	Artiodactyla: bovid (cattle)	skin (head, neck, shoulders, back, tail)	irritation, dermatitis, pruritus	worldwide
S. capreoli	Artiodactyla: cervid (roe deer)	skin	irritation, dermatitis, pruritus	Eurasia
S. ferrisi	Artiodactyla: cervid (red deer, white-tailed deer, mule deer)	skin	irritation, dermatitis, pruritus	North America
S. hologastrus	Artiodactyla: bovid (wildebeest); Rodentia: sciurid (red-legged sun squirrel)	skin		Africa
S. muntiacus (syn. *S. sinensis*)	Artiodactyla: cervid (Indian muntjac, Reeve's muntjac)	skin	irritation, dermatitis, pruritus	Southern Asia
S. natalensis	Artiodactyla: bovid (steenbok, Cape grysbok, Sharpe's grysbok)	skin		Africa
S. tarandi	Artiodactyla: cervid (reindeer,	skin	irritation, dermatitis,	Eurasia, North

	caribou)		pruritus	America

Parasite morphology: *Solenopotes* spp. form three different types of morphological stages during their developmental cycles: eggs (nits); nymphs (three instars); and adult lice (male and female). The eggs of these sucking lice are small measuring around 0.7 mm in length, elongate and asymmetrical in shape and dark brown-blue in colour. They are glued by their bases to hair shafts and often lay along the hair which is sometime bent at the point of attachment. Eggs contain a developing embryo with darkened internal elements. They hatch to release first-stage nymphs (N1) which moult by gradual (incomplete) metamorphosis through another two nymphal stages (N2, N3) before forming adults. All nymphs are similar in appearance to adult lice but are less sclerotized, lack genitalia, have fewer setae, and are smaller in size (N1 measure on average 0.7 mm in length, N2 0.8 mm, N3 1.0 mm, and adults range from 1.0-1.8 mm). Adult lice are dorso-ventrally flattened (dorsal tergum, ventral sternum) and have three distinct body parts (head, thorax, abdomen) which range from brown to blue/gray in colour (abdomen darkest). The head is short, blunt and rhomboidal in shape (compared to long thin heads in the sister genus *Linognathus*), lacks eyes and ocular points, but has two lateral antennae, each composed of 5 segments with terminal sensoria. The piercing/sucking mouthparts are located in an anterior snout-like proboscis (labrum) and are retracted into a pocket in the head when not used for feeding. The mouthparts comprise an eversible tubular haustellum armed with teeth and 4 retractable stylets (2 flanked by maxillae to form a food channel, one arising from the hypophyarnx and forming a salivary channel, and one originating from the flattened labium to guide the other stylets). *Solenopotes* lack maxillary palps (present in amblyceran lice), and they lack mandibles and pulvinus pads (present in chewing/biting lice). Lice have an elongate alimentary tract divided into 3 sections: a tubular foregut (with cibarial pump, pharynx and oesophagus), an expansive midgut (with anterior caeca, ventriculus and globular mycetome (special organ, sometimes called bacteriome or stomach disc, harbouring bacterial/fungal symbionts)), and a short hindgut (with pylorus, papillae and rectum). The thorax consists of three segments fused together without obvious divisions, but contains a distinctive dark hexagonal sternal plate (absent in *Linognathus* spp.). The ventral thorax gives rise to 3 pairs of stout legs which are dissimilar in that the fore-legs are shorter and thinner than the mid- and hind-legs. Each leg consists of 5 segments (coxa, trochanter, femur, tibia, tarsus) terminating in specialized tarsal claws closing on tibial spurs (spurs absent on fore-legs). The abdomen is large, dark, elliptical, and consists of 9 membranous segments without paratergal plates but with rows of ventral setae and spiracles (respiratory pores) located on conspicuous protruding lateral tubercles (absent in *Linognathus* spp.). Female lice are slightly larger than males (average 1.5 cf. 1.1 mm in length) and their posterior abdominal segments have two distinctive pointed lobes (called gonopods or gonapophyses) which aid in oviposition. Mature females have globular ovaries with polytrophic ovarioles, tubular oviducts leading to the uterus together with accessory glands (produce glue), saccular spermatheca (store sperm after mating) and a rounded vagina with a sclerotized genital plate, valvula and genital setae. Males have compact bilobed testes, tubular vas deferens which join to form the seminal vesicle, and a distinct genital sac containing the copulatory aedeagus (penis-like tube with dorsal gonopore and terminal pseudopenis) supported by a basal plate-like sclerite (apodeme) and lateral rod-like sclerites (parameres).

Site of infection: These sucking lice are ectoparasitic on artiodactyls (bovids and cervids), moving amongst the hair and feeding on blood through the skin. Most louse species are host specific and are found only on one or a few closely-related host species. They are also highly site specific and prefer particular body parts of their hosts, although they may move to surrounding areas in heavy infestations. For example, the little blue cattle louse *S. capillatus* is usually found clustered on the face of cattle (on the cheeks, ears and around the muzzle and eyes), sometimes extending to the neck and dewlap, but they may invade the shoulders, back and tail in heavier infestations developing over winter.

Pathogenesis: Most infestations are light and often remain asymptomatic going unnoticed by their hosts. Heavier louse burdens are not highly pathogenic, although they may occasionally cause mild disease involving dermatitis and secondary self-trauma. Adults and nymphs feed on host blood but rarely do infestations cause anaemia although persistent blood loss must contribute to deteriorating health. More often, sucking lice cause discomfort and annoyance when feeding by piercing the skin, injecting saliva and sucking blood. Bites sites may become inflamed (local dermatitis) and pruritic (itchy), responses which appear to be exacerbated by hypersensitivity responses to allergens in louse saliva or faeces. Infested animals become restless and try to relieve the irritation by grooming (biting, licking, scratching or rubbing) afflicted body parts which may appear as dark blue patches due to aggregations of lice. Manic grooming can result in self- trauma with skin lesions, excoriations, scales, crusts, alopecia and secondary infections. Infested animals may be distracted and eat less exhibiting reduced productivity (poor growth and development) and their hides may be damaged by superficial erosive spots at slaughter. Heavier infestations develop on young, old, sick or stressed animals due to their compromised physiological and immunological states. Indeed, secondary increases in louse burdens often occur on animals with concomitant diseases as well as on individuals unable to groom effectively. Well-nourished animals in good health are generally able to tolerate infestations and keep louse populations low.

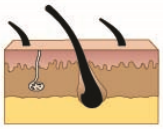
Developmental cycle and mode of transmission: The entire life-cycle of *Solenopotes* spp. may be completed in the pelage of individual hosts, and transmission between hosts occurs by close contact. Adult female lice glue their eggs to hair shafts close to the skin where they hatch in around 12 days to release first-stage nymphs which commence to feed. They undergo gradual (incomplete) metamorphosis (hemimetabolous) and moult through another two nymphal stages before moulting to adults. After mating, female lice lay 1-2 eggs per day during the first half of their 6-10 week lifespans. The whole life-cycle may be completed in as little as 4

weeks. Transmission occurs when motile stages (nymphs, adults) crawl onto new hosts in close contact or via contaminated fomites (bedding, equipment). Lice only survive off hosts for a short period (3-4 days) so most transmission occurs when animals are crowded in confined surroundings for protracted periods, either naturally (during mating, nursing, feeding or sheltering in herds) or artificially (when brought into yards, pens, barns or feedlots). Most clinical infestations occur over winter when environmental conditions favour louse development (cooler temperatures, available moisture, short daylight) and hosts become more susceptible (poorer nutrition, greater thermoregulatory stress, increased gregarious behaviours).

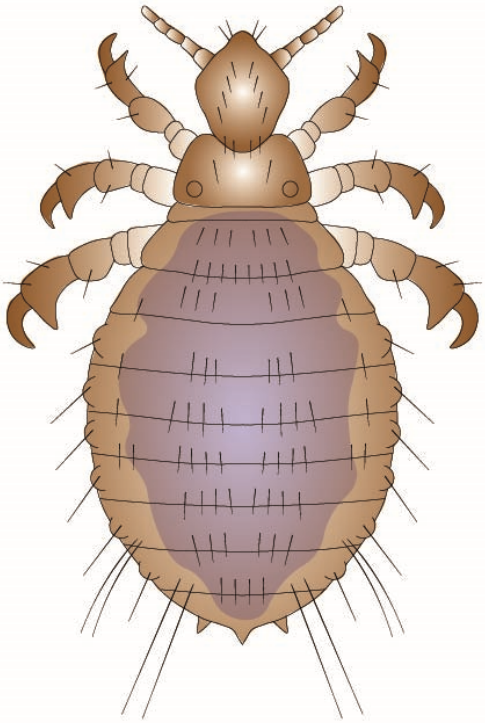
Differential diagnosis: Infestations may be suspected on the basis of clinical symptomatology (focal dermatitis, pruritus and increased grooming/rubbing in cooler months). Aggregations of the little blue cattle louse *S. capillatus* may even appear as dark blue patches on the faces of infested cattle. Definitive diagnosis is made by the direct detection of lice and sometimes their eggs in the host coat. The lice move slowly and tend not to avoid light when the coat is parted (unlike the rapid motility and photo-avoidance behaviours of chewing/biting lice). Lice may be readily collected and identified by microscopic examination of their unique morphological features. Modern molecular biological techniques have been used to examine phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear genes sequences (18S ribosomal RNA).

Treatment and control: A range of insecticidal chemicals have proven effective against immature and mature lice: including organochlorines (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (chlorpyrifos, diazinon, malathion), pyrethroids (permethrin, deltamethrin, flumethrin, cypermethrin), macrocyclic lactones (ivermectin, eprinomectin, moxidectin, abamectin, doramectin, milbemycin), formamidine (amitraz), chloronicotinyl (imidacloprid), spinosyns (spinosad), and insect growth regulators (diflubenzuron). Chemicals are available as topical applications (shampoos/rinses, sprays/aerosols, powders/fogs) or as systemic formulations (oral, injectable, spot-on, impregnated tags), and some may also be used in self-treatment devices (dust bags, back rubbers/oilers). Most chemicals are not very effective against louse eggs (nits) so treatment may need to be repeated after 1-2 weeks to kill newly-emergent nymphs, although products with long residual activity may only require a single application. It is advisable to treat all animals in the cohort at the same time, and treatment is best conducted in autumn to prevent louse populations from escalating over winter. Treatments should also comply with government regulations concerning contra-indications, with-holding periods, residues and environmental toxicity. Various grooming devices (brushes, combs) may be used to assist in louse removal and matted coats may need to be trimmed/clipped beforehand. Preventive control strategies should be implemented to decontaminate shared equipment and facilities (through heat or chemical treatment) and to reduce contact with infested animals (through isolation or quarantine). Livestock management should avoid over-crowded unsanitary conditions and hosts should be kept healthy, well-nourished and well-groomed.

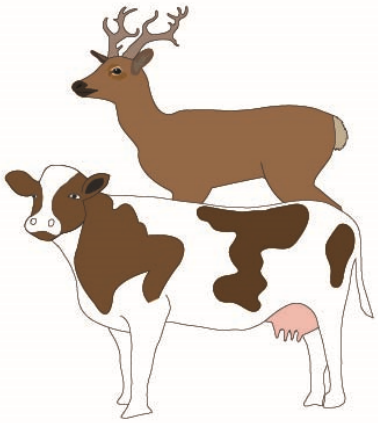
Solenopotes



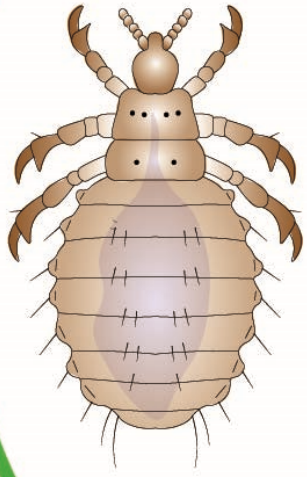
skin/pelage
(dermatitis, anaemia,
alopecia, excoriation)



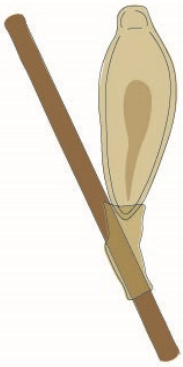
adult (dorsal)
(~ 1.8 mm)



Definitive Hosts
(ruminants)



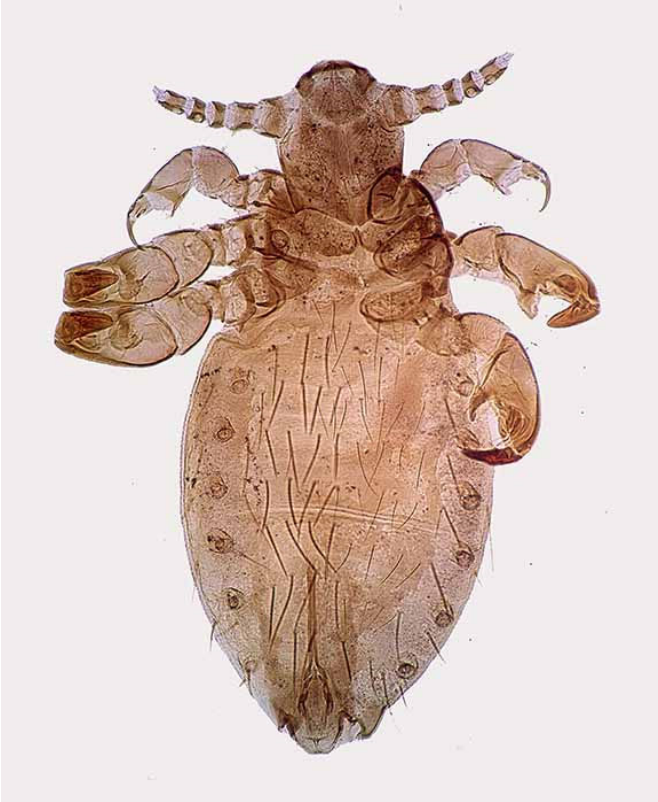
nymph (dorsal)
(~ 1 mm)



egg
(~ 0.7 mm)

all stages ectozoic on host
(motile stages feed on blood)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites



Solenopotes adult



Solenopotes egg

Pediculus
(insect: louse)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Anopluran (sucking) lice have narrow pointed heads adapted to piercing the skin and feeding on tissue fluids (solenophage mode of feeding). Sucking lice are ectoparasitic on mammals and most species are highly host specific and even site-specific, being found predominantly in areas with coarse hairs. Pediculids occur on primates, with different *Pediculus* spp. or subspecies infesting the head and body of humans causing irritation, dermatitis, pruritus and excoriation. Human body lice may also transmit bacterial pathogens, including rickettsias (causing epidemic or louse-borne typhus, and trench fever) and spirochaetes (causing relapsing or recurrent fever).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order: Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder: Anoplura (sucking lice, narrow pointed head, pierce skin and feed on fluids (solenophagy))
Family: Pediculidae (head/body lice of primates)
Genus: *Pediculus* (parasitic on skin/hair of primates)
Species: two species cause pruritus in humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Lice are small wingless hemipterodeans that undergo gradual (hemimetabolous) metamorphosis and are permanent obligate ectoparasites on other animals. Four suborders are recognized: the Anoplura containing the haematophagous sucking lice of placental mammals; the Ischnocera and Amblycera (previously classified together as Mallophaga) comprising the chewing or biting lice of birds, marsupials and placental mammals; and the Rhynchophthirina confined to elephants and warthogs in Africa.

Major parasitic phthirapteran families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Suborder: Anoplura (sucking lice of placental mammals) (narrow pointed head, pierce skin and feed on fluids (solenophagy)) [16 families, 51 genera, 694 species]					
Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial

Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-
Haematopinidae (ungulate lice, short-nosed lice)	1 genus, 21 spp.	mammals (equids, bovids, suids)	nymphs, adults	blood-sucking	viral, bacterial
Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-
Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
Suborder: Ischnocera [Mallophaga p.p.] (chewing lice of mammals and birds, broad rounded head, without maxillary palps, prominent filiform antennae, keratin feeders) [2 families, 158 genera, 3,371 species]					
Trichodectidae (fur lice)	20 genera, 413 spp.	mammals (bovids, equids, carnivores)	nymphs, adults	biting	helminth
Philopteridae(bird lice)	138 genera, 2,958 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					
Menoponidae (bird lice)	68 genera, 1,150 spp.	birds	nymphs, adults	biting, chewing	-
Boopiidae (marsupial chewing lice)	8 genera, 57 spp.	mammals (incl. marsupials)	nymphs, adults	biting	helminth

Some 700 species of anopluran sucking lice have been described in 51 genera in 16 families, namely: Echinophthiriidae (*Antarctophthirus*, *Echinophthirius*, *Latagophthirus*, *Lepidophthirus*, *Proechinophthirus*); Enderleinellidae (*Atopophthirus*, *Enderleinellus*, *Microphthirus*, *Phthirunculus*, *Werneckia*); Haematopinidae (*Haematopinus*); Hamophthiriidae (*Hamophthirius*); Hoplopleuridae (*Ancistroplax*, *Ferrisella*, *Haematopinoides*, *Hoplopleura*, *Paradoxophthirus*, *Pterophthirus*, *Schizophthirus*, *Typhlomyophthirus*); Hybophthiridae (*Hybophthirus*); Linognathidae (*Linognathus*, *Prolinognathus*, *Solenopotes*); Microthoraciidae (*Microthoracius*); Mirophthiridae (*Mirophthirus*); Neolinognathidae (*Neolinognathus*); Pecaroecidae (*Pecaroecus*); Pedicinidae (*Pedicinus*); Pediculidae (*Pediculus*); Polyplacidae (*Abrocomaphthirus*, *Ctenophthirus*, *Cuyana*, *Docophthirus*, *Eulinognathus*, *Fahrenholzia*, *Galeophthirus*, *Haemodipsus*, *Johnsonpthirus*, *Lagidiophthirus*, *Lemurpediculus*, *Lemurphthirus*, *Linognathoides*, *Neohaematopinus*, *Phthirpediculus*, *Polyplax*, *Proenderleinellus*, *Sathrax*, *Scipio*); Pthiridae (*Pthirus*); and Ratemiidae (*Ratemia*). Those of medical significance are found in the families Pediculidae (hominids, New World primates) and Pthiridae (hominids), while those of particular veterinary significance occur in the families Haematopinidae (equids, bovids, suids), Linognathidae (bovids, canids), Hoplopleuridae (rodents), Pedicinidae (Old World primates) and Polyplacidae (rabbits, rodents). Pediculids have pointed heads with eyes, elongate bodies, 6 similar legs, and conspicuous abdominal paratergites. The family comprises a single genus, *Pediculus*, containing four recognized species, although over 40 names had been proposed for different isolates but are now considered to be junior synonyms or invalid. Humans are infested by head and body lice which are highly host-specific and will not infest other animals, although body lice colonies can be bred in the laboratory after their adaptation to feeding on rabbits. Head and body lice are remarkably similar morphologically and genetically but they normally do not interbreed, although they have been shown to so with partial success under experimental conditions. Some authors regard them to be separate species (*P. capitis* and *P. humanus*), while others consider them to be subspecies or ecotypes of *P. humanus*. There is no doubt that they exhibit significant differences in biology; particularly in tropism, development, ecology, pathogenicity and vectorial capacity. Two additional species have also been recorded from non-human primates; *P. schaeffi* from chimpanzees and bonobos and *P. mjobergi* (or *P. humanus mjobergi*) from South American monkeys.

Pediculus species	Hosts	Location	Clinical signs	Distribution
P. humanus (syn. *P. h. humanus, P. h. corporis, P. corporis, P. vestimenti*) (human body louse, clothing louse)	Primates: hominid (human)	skin (body), clothing	irritation, dermatitis, pruritus [plus vector for bacterial pathogens causing epidemic (louse-borne) typhus, trench fever, relapsing (recurrent) fever]	Africa, Asia, Americas
P. capitis (syn. *P. h. capitis*) (human head louse)	Primates: hominid (human)	skin (head)	irritation, dermatitis, pruritus	worldwide
P. mjobergi (syn. *P. h. mjobergi, atelophilus, chapini, lobatus*)	Primates: cebid (Columbian white-faced capuchin, tufted capuchin), atelid (black-headed	skin (head, body)	irritation, dermatitis, pruritus	zoos, South America

	spider monkey, black-handed spider monkey, red-faced spider monkey, white-bellied spider monkey, red-handed howler, black howler, mantled howler, Guatemalan howler)			
P. schaeffi	Primates: hominid (chimpanzee, bonobo)	skin (head, body)	irritation, dermatitis, pruritus	zoos, Africa

Parasite morphology: Lice form three developmental stages: eggs, nymphs (3 instars) and adults. Eggs appear as white-tan ellipsoidal operculate bodies (0.8 x 0.3 mm) glued along half of one side to hair shafts (head lice) or clothing fibres (body lice). Eggs are colloquially called nits by some authorities, whereas others reserve the term for empty eggshells. There are three nymphal instars which are similar in appearance to adults (or imagoes). All have three body parts (head, thorax and abdomen), but the nymphs are smaller measuring 1.0-2.5 mm in length, are less sclerotized, possess fewer body setae, and lack genitalia. Adult lice have elongated dorsoventrally flattened bodies (1.0-4.5 mm long) which appear opaque although darker internal organs can be seen mainly in the abdomen. Head lice are slightly smaller than body lice, with females being 1.8-3.3 mm and males 1.0-2.6 mm long, compared to 2.0-4.5 mm and 2.0-3.0 mm respectively. They are sucking lice and have small pointed rhomboidal heads (as wide as long) with long thin terminal mouthparts modified for piercing and sucking. The mouthparts are located in a snout-like proboscis (labrum) containing an eversible tubular haustellum armed with teeth and supporting four retractable stylets (two supported by maxillae to form a food channel, one derived from the hypophyarnx and connected to the salivary gland, and one derived from the flattened labium and serving to guide the other stylets). The mouthparts are retracted into a pocket in the head when not used for feeding. The mouthparts lack sensory maxillary palps (present in amblyceran chewing lice), and they lack mandibles and pulvinus pads (present in other chewing/biting lice). The head has two prominent noncompound eyes (lateral ocelli) and a pair of short antennae (each with 5 segments). The alimentary tract consists of a foregut (with buccal funnel, cibarial pump, pharynx and oesophagus), a large midgut (with ventriculus, anterior caeca and round mycetome (special organ, sometimes called bacteriome or stomach disc, harbouring bacterial/fungal symbionts)), and a hindgut (with pylorus, papillae and rectum). The thorax appears as a truncated cone possessing a reduced tergum with a small notal pit, and three pairs of stout jointed legs of similar size, each with five sections (coxa, trochanter, femur, tibia, and tarsus). The legs terminate in large tarsal claw closing onto a small tibial spur (thumb) with small bristles. The diameter enclosed by the modified tibiotarsal claws conforms to the diameter of the host hair shafts at the predilection sites of infection. The elongate abdomen is membranous with seven segments having prominent sclerotized paratergal plates (the first six segments each have a pair of spiracles for breathing and the last segment contains the genitalia and anus). The terminal abdominal segment in males is pointed and contains a well-developed genital apparatus visible through the cuticle. Male genitalia comprise compact lobular testes, tubular vas deferens, saccular seminal vesicle, and an elaborate genital sac with an aedeagus (penis-like tube with dorsal gonopore and terminal V-shaped pseudopenis) supported by large basal apodeme (plate-like sclerite) and short lateral parameres (rod-like sclerites). The terminal abdominal segment in females is W-shaped with two well-developed gonopods used to assist oviposition. Female genitalia comprise ovaries with polytrophic ovarioles, tubular oviducts, an ovoid uterus with accessory glands (for eggshell and cement/glue production), and a vagina supported by a large transverse genital plate, valvula and setae (spermatheca indistinct or absent).

Site of infection: Head lice are known colloquially as cooties, greybacks, or mechanized dandruff. All developmental stages are found attached to, or grasping, hairs on the head, especially at the back of the neck and behind the ears. They are highly site-specific and head lice transplanted to other body regions attempt to migrate back to the head. Body lice spend most of their time in host clothing, especially around the waist and beneath armpits. Nymphs and adults visit the host skin to feed and then return to clothing where mature female lay eggs (hence their colloquial name of seam squirrels in some countries).

Pathogenesis: Louse infestation causes a condition known as pediculosis. In humans, the variant pediculosis capitis is caused by head lice and that of pediculosis corporis (also known as pediculosis vestimenti, vagabond's or hobo's disease) is caused by body lice. Nymphs and adults of both species feed by piercing the skin with their elongate mouthparts and sucking blood (solenophage mode of feeding) about every 2-3 hours. Light infestations by head lice may only cause moderate itching of the scalp exacerbated by sensitization to louse saliva. Heavy infestations, however, may cause considerable discomfort as the bites produce red papules and intense pruritus (itching) which induces scratching leading to dermatitis and secondary infections with impetigo and pyoderma and occasional swelling of local lymph nodes and fever. Head lice infestations are endemic worldwide, with children aged from 3-13 years being frequently infested (particularly girls with long hair), and outbreaks occurring during winter months (possibly due to host crowding). Persistent head lice infestations may cause matting of the hair with concomitant fungal growth contributing to a fetid odour (condition known as plica polonica). Body lice also cause considerable discomfort and skin irritation due to their feeding activities, resulting in intense pruritus, red papules, aches and fever. Infestations persisting over years may cause thickened darkened skin (vagabond's disease). While significant outbreaks have been described in many countries throughout human history, notably in times of great deprivation and war (esp. World War I), the current geographic distribution of body lice is restricted to temperate regions and high elevations of Africa, Asia and the Americas. Heavy infestations have often been associated with crowded and unsanitary conditions, often occurring after population displacements (translocations) associated with civil unrest, war, famine or

natural disasters. Infestations of monkeys by other *Pediculus* spp. have been associated with irritation, papulocrustous dermatitis, self-excoriation, alopecia, anaemia, illthrift and poor weight gain.

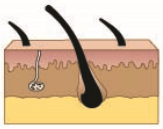
Body lice have been shown to act as vectors for the transmission of several bacterial pathogens to humans, including *Rickettsia prowazekii* causing epidemic or louse-borne typhus, *Bartonella* (formerly *Rochalimaea*) *quintana* causing trench fever, bacillary angiomatosis bacteraemia, endocarditis and chronic lymphadenopathy, and the spirochaete *Borrelia recurrentis* causing relapsing or recurrent fever. Microbial transmission usually occurs when lice or their wastes are crushed or smeared into feeding sites or contaminate wounds. Experimental studies have implicated body lice as potential vectors for other bacteria (*Acinetobacter baumannii, A. lwoffii, Rickettsia akari, R. conorii, R. rickettsia, R. typhi* and *Yersinia pestis*), and recent molecular biological studies have detected bacterial DNA from *Anaplasma phagocytophilum* and *Coxiella burnetii* in body lice and from *Acinetobacter* spp., *Anaplasma* sp., *Borrelia theileri*, *Coxiella burnetii*, *Ehrlichia* spp., *Rickettsia aeschlimannii*, *Yersinia pestis* and Moraxellaceae in head lice, but their significance in disease transmission is unknown.

Developmental cycle and mode of transmission: Once hatched, lice undergo gradual metamorphosis whereby nymphs moult several times before forming adults. Eggs hatch within seven days and there are three nymphal moults taking 8-9 days. Adult lice then mate and fertilized female lice begin laying eggs shortly thereafter (laying from 50-150 eggs at a rate of around 10 per day). The whole life-cycle may be completed in 2-3 weeks. Head lice attach to hairs and do not survive long off their hosts. Infestations are therefore transmitted between hosts by direct physical contact when nymphs or adults crawl from one host to another, however, some transmission may occur via contaminated fomites (headwear, clothing or bedding). Head louse populations often exhibit pronounced seasonal fluctuations, apparently linked to crowding during winter housing, particularly in temperate regions. Body lice spend most of the time in host clothing and their eggs are attached to fibres in clothes, usually along seams. The whole life-cycle of body lice can take longer at lower temperatures (2-4 weeks), such as when clothing is removed at night or worn intermittently, but the lice will die if clothing is not worn for several days. Infestations can be transmitted by physical contact with infested people or with articles (clothing, bedding and towels) shared with infested persons. Transmission is highest between people living in impoverished conditions in institutions (orphanages, psychiatric hospitals), prisons (penal, political), camps (concentration, refugee, disaster-relief) and shelters (transients, homeless), particularly where clothing cannot be laundered and/or changed frequently. Body lice were more common in cooler parts of the world; in tropical areas people who wear less clothing usually have only head lice.

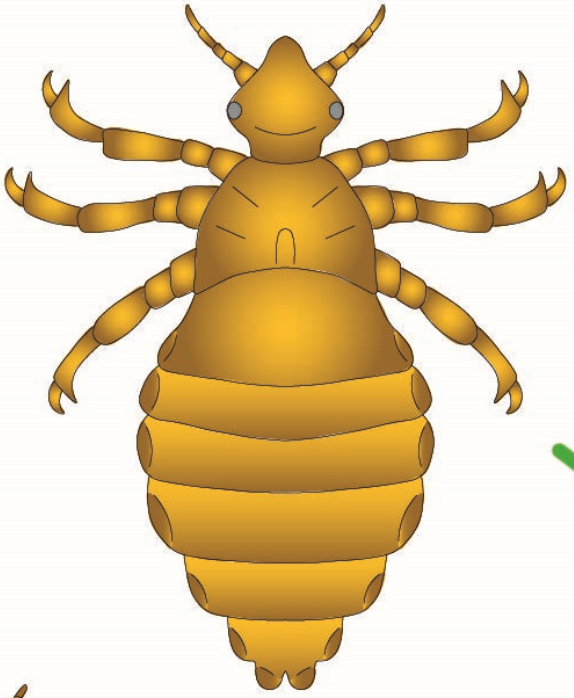
Differential diagnosis: Infestations are diagnosed by the direct detection of live lice in hair or clothing or their egg cases (nits) attached to hairs or clothing fibres. Fine-toothed combs have been used for millennia to remove head lice and nits, often in conjunction with hair conditioner to untangle hairs and trap lice. Close visual inspection of clothing along the seams may reveal body lice and nits, which can subsequently be removed (nit-picking). Molecular characterization techniques have been used to examine the phylogenetic relationships between various *Pediculus* species and isolates using polymerase chain reaction (PCR) amplification of nuclear (18S ribosomal RNA, elongation factor 1-apha, RNA polymerase II) and mitochondrial (cytochrome b, cytochrome c oxidase subunit I, and NADH-ubiquinone oxidoreductase chain 4) gene sequences.

Treatment and control: Various insecticides have been used to control louse infestations on humans and other primates. Most conventional insecticides are available as topical formulations (medicated shampoos, lotions or creams) but some newer drugs are systemic (pour-on, oral or injectable formulations). Conventional organophosphates (malathion, chlorpyriphos, diazinon), organochlorides (dichloro-diphenyl trichloroethane (DDT), lindane), pyrethrins, synthetic pyrethroids (permethrin), carbamates (carbamyl, carbaryl), formamidine (amitraz), chloronicotinyl (imidacloprid), spinosyns (spinosad), arylpyrazole (fipronil), and macrocyclic lactones (ivermectin, selamectin) have shown good efficacy, particularly against nymphs and adult lice. Repeat treatments are required within 10 days as most insecticides have limited activity against eggs. Careful attention should also be paid to drug contra-indications as some formulations exhibit toxicity or produce adverse side-effects. Unfortunately, varying degrees of resistance have been detected in louse populations to most insecticides (except spinosad), so researchers have begun to explore a range of alternative or herbal remedies. Other chemicals have also been used to occlude respiratory function or disrupt the structural integrity of lice, including synthetic silicone oils (dimeticone), esters (isopropyl myristate), detergents (octanediol) and aromatic alcohols (benzyl alcohol). During infestations, daily grooming with nit combs is recommended to remove head lice and their eggs, usually using conditioners or lubricants to ease tangles and help dislodge nits. A medieval remedy of last resort is to shave the hair from the head and impose strict hygiene. Some countries still enforce home quarantine of infested school-children to curtail outbreaks. Mass treatments for body lice infestations have involved blowing talcum powder mixed with permethrin, lindane or even DDT between the body and underclothes, regularly changing clothes, washing soiled clothing and bedding in warm water (heated to at least 60°C) with soap containing DDT, and ironing clothes, particularly over seams. Inter-personnel hygiene must be improved and shared clothing, bedding and grooming implements (brushes, combs) should be avoided. Continuous surveillance programs should be maintained because the potential exists for the wider dissemination of lice in our modern world of international travel, refugee translocations and globalization.

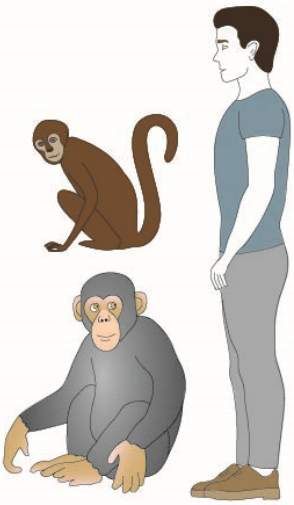
Pediculus



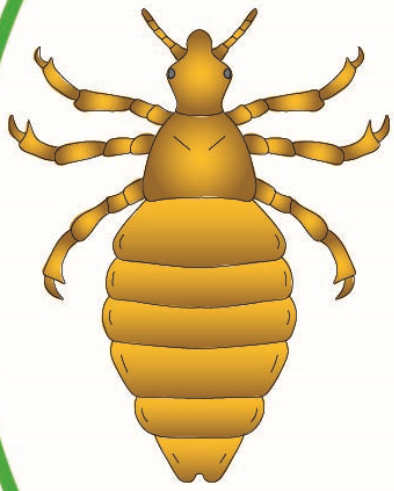
skin/pelage
(irritation, pruritus,
dermatitis, excoriation)
(some vector infectious
microbial diseases)



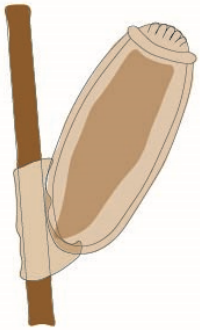
adult (dorsal)
(~ 3 mm)



Definitive Hosts
(primates)



nymph (dorsal)
(~ 2 mm)



egg
(~ 0.8 mm)

all stages ectozoic on host
(motile stages feed on blood)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites



Pediculus adult female



Pediculus adult male



Pediculus adult



Pediculus nymph

Pthirus
(insect: louse)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Anopluran (sucking) lice have narrow pointed heads adapted to piercing the skin and feeding on tissue fluids (solenophage mode of feeding). Sucking lice are ectoparasitic on mammals and most species are highly host specific and even site-specific, being found predominantly in areas with coarse hairs. Pthirids occur on primates, with different species found on humans and gorillas. Infestations by human pubic lice (*Pthirus pubis*) are transmitted mainly by sexual contact and may cause irritation, dermatitis and intense pruritus.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order: Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder: Anoplura (sucking lice, narrow pointed head, pierce skin and feed on fluids (solenophagy))
Family: Pthiridae (pubic lice of primates)
Genus: *Pthirus* (parasitic on skin/hair of humans)
Species: *P. pubis* causes irritation/dermatitis in humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Lice are small wingless hemipterodeans that undergo gradual (hemimetabolous) metamorphosis and are permanent obligate ectoparasites on other animals. Four suborders are recognized: the Anoplura containing the haematophagous sucking lice of placental mammals; the Ischnocera and Amblycera (previously classified together as Mallophaga) comprising the chewing or biting lice of birds, marsupials and placental mammals; and the Rhynchophthirina confined to elephants and warthogs in Africa.

Major parasitic phthirapteran families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Suborder: Anoplura (sucking lice of placental mammals) (narrow pointed head, pierce skin and feed on fluids (solenophagy)) [16 families, 51 genera, 694 species]					
Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-

Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial
Haematopinidae (ungulate lice, short-nosed lice)	1 genus, 21 spp.	mammals (equids, bovids, suids)	nymphs, adults	blood-sucking	viral, bacterial
Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-
Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
Suborder: Ischnocera [Mallophaga p.p.] (chewing lice of mammals and birds, broad rounded head, without maxillary palps, prominent filiform antennae, keratin feeders) [2 families, 158 genera, 3,371 species]					
Trichodectidae (fur lice)	20 genera, 413 spp.	mammals (bovids, equids, carnivores)	nymphs, adults	biting	helminth
Philopteridae(bird lice)	138 genera, 2,958 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					
Menoponidae (bird lice)	68 genera, 1,150 spp.	birds	nymphs, adults	biting, chewing	-
Boopiidae (marsupial chewing lice)	8 genera, 57 spp.	mammals (incl. marsupials)	nymphs, adults	biting	helminth

Some 700 species of anopluran sucking lice have been described in 51 genera in 16 families, namely: Echinophthiriidae (*Antarctophthirus*, *Echinophthirius*, *Latagophthirus*, *Lepidophthirus*, *Proechinophthirus*); Enderleinellidae (*Atopophthirus*, *Enderleinellus*, *Microphthirus*, *Phthirunculus*, *Werneckia*); Haematopinidae (*Haematopinus*); Hamophthiriidae (*Hamophthirius*); Hoplopleuridae (*Ancistroplax*, *Ferrisella*, *Haematopinoides*, *Hoplopleura*, *Paradoxophthirus*, *Pterophthirus*, *Schizophthirus*, *Typhlomyophthirus*); Hybophthiridae (*Hybophthirus*); Linognathidae (*Linognathus*, *Prolinognathus*, *Solenopotes*); Microthoraciidae (*Microthoracius*); Mirophthiridae (*Mirophthirus*); Neolinognathidae (*Neolinognathus*); Pecaroecidae (*Pecaroecus*); Pedicinidae (*Pedicinus*); Pediculidae (*Pediculus*); Polyplacidae (*Abrocomaphthirus*, *Ctenophthirus*, *Cuyana*, *Docophthirus*, *Eulinognathus*, *Fahrenholzia*, *Galeophthirus*, *Haemodipsus*, *Johnsonpthirus*, *Lagidiophthirus*, *Lemurpediculus*, *Lemurphthirus*, *Linognathoides*, *Neohaematopinus*, *Phthirpediculus*, *Polyplax*, *Proenderleinellus*, *Sathrax*, *Scipio*); Pthiridae (*Pthirus*); and Ratemiidae (*Ratemia*). Those of medical significance are found in the families Pediculidae (hominids, New World primates) and Pthiridae (hominids), while those of particular veterinary significance occur in the families Haematopinidae (equids, bovids, suids), Linognathidae (bovids, canids), Hoplopleuridae (rodents), Pedicinidae (Old World primates) and Polyplacidae (rabbits, rodents). Pthirids have short heads with eyes, compact ovoid bodies, mid- and hind-legs and claws stouter than the fore-legs, and 4 pairs of lateral abdominal tubercles. The family contains a single genus, *Pthirus*, with two species: human pubic lice *P. pubis* (commonly called 'crabs' because they have grasping tarsi reminiscent of crab pincers); and gorilla lice *P. gorillae*. [Note that the correct spelling for the genus is *Pthirus* according to the International Code of Zoological Nomenclature (ICZN), with the names *Phthirus* and *Phthirius* designated as invalid emendations of the original.] *P. pubis* is host-specific for humans and infestations have been found worldwide in all races and ethnic groups.

***Pthirus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
P. pubis (syn. *P. inguinalis, chavesi, Pediculus ferus, pubis*) (human pubic louse, crab louse)	Primates: hominid (humans)	skin (pubis, occasionally eyebrows, eyelashes, beard, moustache)	irritation, dermatitis, pruritus	worldwide
P. gorillae (gorilla louse)	Primates: hominid (gorillas)	skin (groin, armpits, legs, arms)	irritation, pruritus	Rwanda, DR Congo

Parasite morphology: *Pthirus* spp. form three different types of morphological stages during their life-cycles: eggs (nits); nymphs (3 instars); and adult lice. The eggs are oval shaped (0.5-1.0 x 0.3 mm), brown to opalescent white in colour, operculate (with convex caps perforated by air holes), and glued by their bases (rather than their sides) to hair shafts. Nymphs are similar in morphology to adult lice but are smaller (measuring 1.1-1.3 mm long), less sclerotized (slightly transparent and whitish-grey in colour), have fewer body setae, and lack genitalia. Adult lice are yellow-green in colour but turn red-brown after blood meals. They have small oval dorso-ventrally flattened bodies (dorsal tergum, ventral sternum) measuring 1.1-2.2 mm in length (smaller than head and body lice). They superficially resemble crabs (hence their common name of crab lice) and have three body segments comprising a short blunt head, broad rectangular thorax and short conical abdomen. The head has a pair of short five-segmented antennae in front of a pair of simple noncompound eyes (ocelli) laterally positioned (on protuberances in gorilla lice). The ventral mouthparts

are long and thin and modified for piercing and sucking. They are located in a snout-like proboscis (labrum) containing an eversible tubular haustellum armed with teeth and supporting 4 retractable stylets (2 stylets supported by lateral maxillae to form a food channel, one derived from the hypophyarnx and connected to the salivary gland, and one derived from a flattened labium with a serrated tip). When not used for feeding, the mouthparts are retracted into a pocket in the head. Pthirid lice lack maxillary palps (present in amblyceran lice) and do not have mandibles or pulvinus pads (present in most chewing/biting lice). Internally, the alimentary tract consists of a foregut (with buccal funnel, cibarial pump, pharynx and oesophagus), a large midgut (with ventriculus, anterior caeca and round mycetome (special organ, sometimes called bacteriome or stomach disc, harbouring bacterial/fungal symbionts)), and a hindgut (with pylorus, papillae and rectum). The small head fits into an anterior notch in the wide thorax which lacks a sternal plate and notal pit. The thorax gives rise to three pairs of legs, each with 5 segments (coxa, trochanter, femur, tibia, tarsus). The fore-legs are slim and adapted for holding onto the skin during feeding, while the mid- and hind-legs are stouter and terminate in robust tarsal claws that close onto tibial spurs (thumbs) to grasp the coarse hairs of the pubis (and sometimes those of the armpits, eyebrows or eyelashes). The abdomen is unique for the genus *Pthirus* in that the first 5 segments are combined while the posterior 4 segments are membranous and bear dorsal spiracles located on conspicuous lateral hump-shaped tubercles (body wall protrusions) with conspicuous setae. Male lice are slightly smaller than female lice and have rounded posterior ends while those of females appear bifurcated with 2 small lateral gonopods (lobes that assist in oviposition). The male reproductive system consists of compact bilobed testes connected to tubular vas deferens which coalesce to form a seminal vesicle opening into the genital sac equipped with an aedeagus (copulatory or intromittent organ with dorsal gonopore and terminal pseudopenis) supported by a large basal plate (apodeme) and flanked by thick lateral plates (parameres). The female reproductive system comprises elongate ovaries with polytrophic ovarioles connected to tubular oviducts joined to a globular uterus with accessory glands (secrete glue/cement), a large spermatheca (for sperm storage after mating), and a genital opening (vagina) with a broad genital plate, valvula and lateral gonopods with setae.

Site of infection: The enlarged tarsi of pubic lice are adapted to gripping coarse hairs and most infestations are confined to the pubic region, but can involve the peri-anal region, upper thighs, genitals and lower abdomen. Occasionally, pubic lice may be found in other coarse-hair locations, including the armpits, beard, moustache, eyebrows and eyelashes.

Pathogenesis: Infestations by pubic (crab) lice generally cause discomfort and local inflammation, with symptoms becoming more severe in heavier infestations. The disease is known as pthiriasis pubis (earlier called pediculosis pubis or pediculosis inguinalis). Nymphs and adult lice feed by piercing the skin with their mouthparts, injecting saliva containing anticoagulants and sucking blood. They may remain attached for hours or even days feeding intermittently (4-5 times daily). Bite sites appear as small red papules or light-blue macules (maculae caerulae) blue-grey in colour due to haemosiderin deposits, especially in chronic infestations. Inflammatory responses (erythema, dermatitis) often cause irritation with intense pruritus in infested areas, particularly the groin but sometimes the armpits, eyebrows or eyelashes. Some individuals may exhibit allergic (hypersensitive) reactions to bites with pruritus intensifying nocturnally. Hosts attempt to relieve the itching by scratching, often causing minor lesions (abrasions/ulcerations with crusting) which are susceptible to secondary bacterial or fungal infections leading to pus formation, lymphadenopathy and sometimes fever. Infestation of the eyelashes may cause inflammation of the eyelids (condition known as pthiriasis palpebrarum) which may be seborrheic or eczematous, with bilateral ocular itching, irritation, erythematous lesions, secondary blepharitis, marginal keratitis and follicular conjunctivitis. Unlike body lice, pubic lice do act as a mechanical or biological vectors for other infectious microbial diseases.

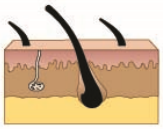
Developmental cycle and mode of transmission: Pubic lice are obligatory ectoparasites with all developmental stages occurring on hosts. Direct transmission occurs when nymphs/adults crawl from one host to another during periods of intimate contact (sexual contact or close body contact) or via recently-contaminated fomites (bedding, towels, clothing). Mature female lice lay eggs which are glued to host hairs and hatch after a 7-8 day incubation period releasing first stage nymphs (N1). The nymphs grasp hairs near their bases and feed on blood by piercing the skin with their sucking mouthparts. Unfed nymphs die within a day, and all subsequent stages require bloodmeals for further development, feeding regularly but intermittently. They undergo gradual (incomplete) metamorphosis (hemimetabolous development) moulting through another 2 nymphal stages before moulting to immature adults after 13-17 days. Pubic lice are not highly mobile and they do not move far (several millimetres-centimetres per day). Male lice are more active than females and seek mates. Female lice have a spermatheca (sperm storage organ) and only need to be fertilized once to become fertile. Gravid females begin laying eggs 1-2 days after mating and lay on average a total of 30 eggs (up to 3 eggs daily for up to 15-17 days). The entire life-cycle may be completed on a single host in 20-25 days. Transmission between hosts occurs when lice (nymphs or adults) are dislodged and crawl to infest new hosts (transmission may involve a single fertilized female). Dislodged stages cannot live long without feeding and will die within 20-24 hours if they do not find a host. Most transmission occurs directly between humans during interludes of close physical contact (predominantly sexual intercourse but also foreplay and other intimate activities). Lice may be transferred from genital areas to facial hairs (eyelashes, eyebrows, beard, moustache) by hand or oral sexual contact. Pubic lice are most prevalent in patients that are sexually active aged between 15 and 40 years (more common in females aged 15-19 and males aged 20 years and older). Infestations are rare in countries or communities where genital hair is removed for social or cosmetic reasons. Transmission may occasionally occur via the contamination of shared items (such as clothing, bedding, towels and sometimes upholstered seating). There have been well-documented instances of infestations in young children sharing beds with parents, amongst soldiers sharing barrack facilities, and sometimes between patrons of cinemas with

recurring sessions. Epidemiological studies have shown pubic lice infestations to be generally associated with poor hygiene, overcrowding, slum dwellings and rural-to-urban translocations. Infestations by gorilla lice are transmitted between animals during close contact (including rest, play, fighting, embracing as well as coitus) and lice populations are usually well regulated by communal grooming (especially mothers grooming infants).

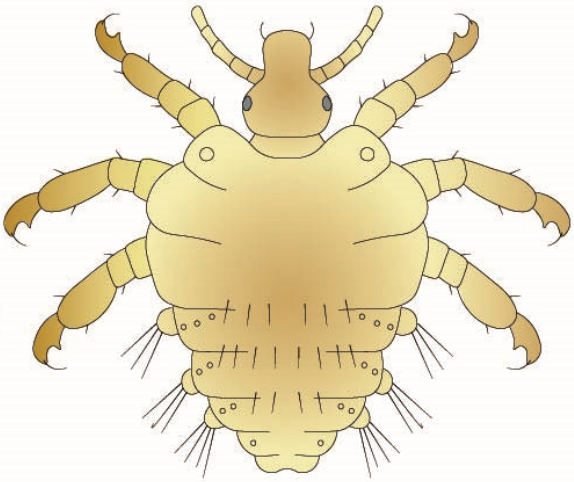
Differential diagnosis: Infestations may be suspected by developing pruritus in the groin region and discovering small spot-stains on underwear (due to blood, crusts or flecks of louse faeces). Confirmation is then made by direct detection of lice (nymphs, adults) and/or eggs (nits) by close visual inspection of infested areas, often assisted by using magnification devices (hand lenses or dermoscopic micro-cameras) and incident illumination sources (torches, lanterns or slit lamps). Nits glued to hair shafts and lice grasping hairs may be collected using forceps, fine-toothed combs, adhesive (sticky) tape or cutting infested hairs with scissors. Samples may be examined microscopically for characteristic morphological features. Molecular characterization techniques have been used to examine the phylogenetic relationships between various *Pthirus* isolates following polymerase chain reaction (PCR) amplification of nuclear (18S ribosomal RNA) and mitochondrial (cytochrome b, cytochrome c oxidase subunit I) gene sequences.

Treatment and control: A range of insecticidal chemicals available as topical creams, lotions or shampoos have been used to treat infestations by pubic lice: including pyrethrins and pyrethroids (permethrin, phenothrin, some with synergists such as piperonyl butoxide); organochlorides (lindane); organophosphates (malathion); carbamates (carbamyl); RID (containing insecticides DEET (N,N-diethyl-m-toluamide) and di-n-propyl isocinchomeronate, with synergist N-octyl bicycloheptene dicarboximide and antimicrobial agent triclosan) and in some countries, macrocyclic lactones (ivermectin) for stubborn or severe cases. Most treatments were effective against nymphal and adult stages but less so against eggs, so repeat treatments after 10 days may be required. Most treatments are considered safe over-the-counter formulations (prescriptions not required), but careful attention should be paid to contra-indications as some drugs may exhibit toxicity or cause adverse side-effects such as allergic responses (e.g. lindane). Louse populations have also demonstrated some drug resistance to certain formulations, notably pyrethroids. Treatment is assisted by the mechanical removal of lice from infested areas using grooming devices (tweezers, fine-toothed combs, even fingernails) and solvents (to facilitate nit removal). When such methods prove ineffective (due to drug resistance or heavy infestations), recourse may be made to partial or complete hair removal from affected areas (by trimming, clipping or shaving). Infestations of eyelashes have been successfully treated by coating with petroleum jelly or permethrin lotion, washing with pilocarpine or povidone iodine solutions, applying sulphur or yellow mercuric oxide ointments, using fluorescein or physostigmine eyedrops, cryotherapy, argon laser photocoagulation, or even giving oral ivermectin. Preventive measures are based on breaking transmission cycles by educating patients to increase personal hygiene and restrict social contacts while infested and undertaking environmental decontamination. Education campaigns should enable sensible behavioural modifications to be implemented minimizing social stigmas and taboos so patients undertake voluntary abstinence, permit contact tracing of sexual partners and avoid sharing clothing, bedding or towels. In some countries, pubic lice infestations are considered to be sexually-transmitted diseases and government intervention is mandated. It should be noted, however, that safe-sex via condom use is ineffective in preventing infestations. Surfaces in contaminated areas should be cleaned with chemicals (bleach) or heat (steam) and floor coverings should be similarly cleaned or vacuumed. Clothing, bedding and towelling should be washed in hot water (> 55°C) for at least 20 minutes and then thoroughly dried. Items that cannot be washed or dry-cleaned may be sealed in plastic bags for 2 weeks so any lice present will starve and die.

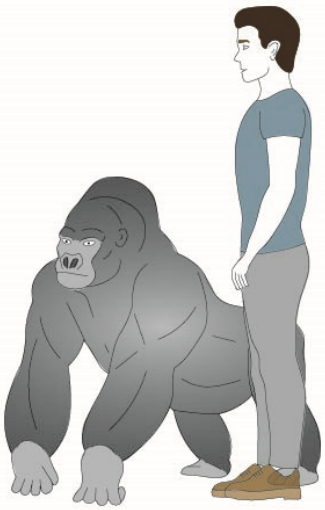
Pthirus



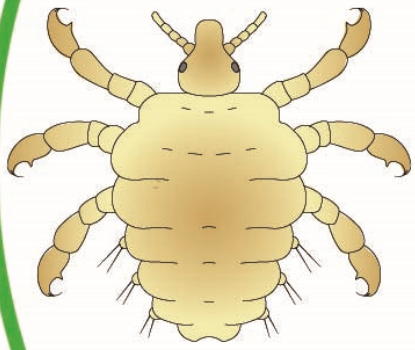
skin/pelage
(irritation, pruritus,
erythema, dermatitis)



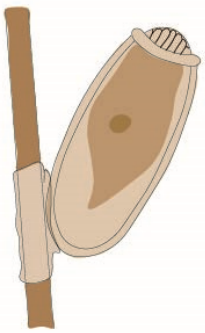
adult (dorsal)
(~ 2 mm)



Definitive Hosts
(primates)



nymph (dorsal)
(~ 1.2 mm)



egg
(~ 1 mm)

all stages ectozoic on host
(motile stages feed on blood)

transmission between hosts
through transfer of motile stages
by direct contact (often sexual)
or via freshly-contaminated fomites



Pthirus adult



Pthirus adult

Trichodectes
(insect: louse)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Mallophagan (chewing) lice have blunt rounded heads with mouthparts adapted for feeding on keratin in superficial skin layers. Chewing lice are ectoparasitic on mammals and birds, most species being highly host specific and even site-specific. Ischnoceran lice have prominent filiform antennae but lack maxillary palps. Trichodectids have three antennal segments, single tarsal claws and are found on mammals. Infestations by *Trichodectes canis* in dogs have been associated with irritation, inflammation, pruritus, alopecia and excoriation.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order: Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder: Mallophaga (= wool-eating) (chewing lice, broad rounded head, feed on keratin, host/site specific)
Superfamily: Ischnocera (without maxillary palps, prominent filiform antennae, keratin feeders (hairs/feathers))
Family: Trichodectidae (parasitize mammals, 3-segmented antennae, single claw on tarsi)
Genus: *Trichodectes* (parasitic on skin/hair of dogs)
Species: *T. canis* (causes pruritus and dermatitis in dogs)

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		equids, carnivores)	adults		
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Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					
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Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
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Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-
Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial
Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-

Over 4,900 species of biting/chewing lice have been described in 253 genera in 8 families, around 4,400 species associated with birds and 500 species with mammals. Members of the suborder Ischnocera have broad rounded heads with conspicuous filiform antennae but lacking maxillary palps, while members of the suborder Amblycera have large rounded heads with maxillary palps and inconspicuous antennae hidden in grooves. Some 158 ischnoceran genera have been assigned to 2 families (Trichodectidae and Philopteridae), while 96 amblyceran genera have been classified in 6 families (Boopiidae; Gyropidae, Laemobothriidae, Menoponidae, Ricinidae, Trimenoponidae). Species of veterinary importance include members of the ischnoceran families Trichodectidae (bovids, canids, equids) and Philopteridae (poultry), and the amblyceran families Menoponidae (poultry) and Boopiidae (carnivores). Most ischnoceran lice are parasitic on birds but the trichodectids are found on mammals and are commonly known as fur lice. Members of the family Trichodectidae possess antennae with 3 segments and their legs terminate in tarsi with single claws (in contrast to members of the family Philopteridae which have 5-segmented antennae and paired tarsal claws). Over 400 trichodectid species have been described from 20 genera, namely *Bisonicola*, *Bovicola*, *Cebidicola*, *Damalinia*, *Dasyonyx*, *Eurytrichodectes*, *Eutrichophilus*, *Felicola*, *Geomydoecus*, *Lorisicola*, *Lutridia*, *Neotrichodectes*, *Procavicola*, *Procaviphilus*, *Protelicola*, *Thomomydoecus*, *Tragulicola*, *Trichodectes*, *Werneckiella* and *Werneckodectes*. The subfamily Trichodectinae (subgenital lobes present on females, often with serrate margin, six or fewer abdominal spiracles, carnivora/primate hosts) contains the genus *Trichodectes* (at least one pair of abdominal spiracles present, small abdominal tergal and sternal setae), and 3 subgenera are recognized: *T.* (*Trichodectes*) (other than 5 pairs of abdominal spiracles, subgenital lobe bifurcate, mesomeres unfused, parameres fused), *T.* (*Paratrichodectes*) (5 pairs of abdominal spiracles, subgenital lobe not bifurcate, parameres not fused, mesomeres absent, abdominal terga with median setal groups comprising at least 3 setae) and *T.* (*Stachiella*) (other than 5 pairs of abdominal spiracles, subgenital lobe often with basal lateral processes, parameres fused, abdominal terga with median setal group reduced to one seta). Over 20 *Trichodectes* spp. have been described from carnivores, particularly canids and mustelids, and some viverrids, procyonids and ursids.

***Trichodectes* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
Subgenus *T.* (*Trichodectes*) [other than 5 pairs of abdominal spiracles, subgenital lobe bifurcate, mesomeres unfused, parameres fused]				
T. canis (syn. *T. floridanus, latifrons, latus, octopunctatus, riveti*) (dog biting louse)	Carnivora: canid (dog, raccoon dog, wolf, jackal, coyote, Andean fox, crab-eating fox, Bengal fox, Darwin's fox); viverrid (African civet)	skin (head, neck, tail)	irritation, pruritus, matted coat, inflammation, excoriation, alopecia [plus vector for double-pored tapeworm (*Dipylidium caninum*)]	worldwide
T. emersoni	Carnivora: mustelid (ferret-badger)	skin		Malaysia
T. euarctidos	Carnivora: ursid (black bear)	skin		North America
T. galictidis (syn. *T. paranensis*)	Carnivora: mustelid (wolverine)	skin		South America

T. kuntzi	Carnivora: mustelid (ferret-badger)	skin		South-East Asia
T. melis (syn. *T. crassus*)	Carnivora: mustelid (European badger)	skin		Europe
T. pinguis	Carnivora: ursid (brown bear)	skin		North America, Scandinavia
T. vosseleri	Carnivora: mustelid (honey badger)	skin		Africa
Subgenus *T.* (*Paratrichodectes*) [5 pairs of abdominal spiracles, subgenital lobe does not bifurcate, parameres not fused, mesomeres absent, abdominal terga with median setal groups comprising at least 3 setae]				
T. ovalis	Carnivora: mustelid (striped polecat, African striped weasel)	skin		Africa
T. ugandensis	Carnivora: mustelid (African striped weasel)	skin		Africa
T. zorillae	Carnivora: mustelid (Sahara striped polecat)	skin		Africa
Subgenus *T.* (*Stachiella*) [other than 5 pairs of abdominal spiracles, subgenital lobe often with basal lateral processes, parameres fused, abdominal terga with median setal group reduced to one seta]				
T. divaricatus	Carnivora: mustelid (lesser grison)	skin		South America
T. emeryi	Carnivora: mustelid (yellow-throated marten)			Asia
T. ermineae	Carnivora: mustelid (stoat)	skin		North America, Europe, New Zealand
T. fallax	Carnivora: procyonid (crab-eating raccoon)	skin		Americas
T. jacobi	Carnivora: mustelid (European polecat)	skin		Eurasia, Africa
T. kingi	Carnivora: mustelid (least weasel)	skin		Eurasia, North America
T. larseni	Carnivora: mustelid (American mink)			North America, Eurasia
T. martis	Carnivora: mustelid (American marten)	skin		North America
T. mustelae (syn. *S. dubia, pusilla*)	Carnivora: mustelid (Siberian weasel, least weasel)	skin		Eurasia
T. octomaculatus (syn. *S. procyonis*)	Carnivora: mustelid (common raccoon)	skin		North America
T. potus	Carnivora: procyonid (kinkajou)	skin		Americas
T. retusa	Carnivora: mustelid (beech marten, weasel)	skin		Eurasia
T. salfii	Carnivora: mustelid (European pine marten)	skin		Europe

Parasite morphology: Like all lice, *Trichodectes* spp. form three different types of developmental stages: eggs (nits); nymphs (3 instars); and adults. The eggs are subcylindrical around 1 mm long and have rounded ends with the posterior ends glued to host hairs and the anterior ends having a convex operculum (cap) with aeropyles (breathing holes). The eggs are embryonated and hatch to release first-stage nymphs (N1). These stages undergo gradual (incomplete) metamorphosis and moult through another two nymphal stages before forming adults. All nymphs are similar in morphology to adult lice but are smaller, less sclerotized, have fewer body setae (hairs) and lack genitalia. Adult lice are small (1.6-2.0 mm long), pale yellow, dorsoventrally flattened (dorsal tergum, ventral sternum) and have three distinct body parts (broad blunt head, small triangular thorax, and large ovoid abdomen). The head is wider than the thorax and is rounded anteriorly with a groove in the ventral surface which accommodates hair shafts of their hosts. They have a pair of short filiform antennae situated laterally and often projecting posteriorly. The antennae are clearly visible and not hidden in grooves (like amblyceran lice) and they have three segments (rather than 5 segments like those of bird lice in the family Philopteridae). Trichodectid lice are chewing lice and do not have long piercing/sucking mouthparts but feed by the biting or scraping action of large ventral dentate mandibles with food particles pushed into the preoral cavity by the posterior plate-like labrum, often with an anterior hyaline pad-like protrusion (pulvinus), lateral maxillae and an anterior labium (salivary secretions added through a central hypopharynx). In ischnoceran lice, the sclerotized ridged mandibles are inserted at right angles to the head (such that the condyles are posterior and the ginglymus is anterior), the maxillae and labium are reduced in size with single-lobed maxillae attached to the tripartite labium, and they lack maxillary palps (present in amblyceran lice). The mouth opens to the foregut

(with pharynx, oesophagus and tubular crop) connected to the large midgut (with ventriculus and anterior caeca) and hindgut (with pylorus, papillae and rectum). In ischnoceran chewing lice, the midgut also contains a rounded mycetome (special organ, sometimes called bacteriome or stomach disc) harbouring bacterial/fungal symbionts (mycetome more developed in anopluran sucking lice, but absent in amblyceran chewing lice). The thoracic segments are fused together with indistinct boundaries and the ventral surface gives rise to three pairs of legs which are similar in size. The legs consist of 5 segments (coxa, trochanter, femur, tibia, tarsus) and terminate in single tarsal claws (in contrast to the double claws found on members of the family Philopteridae on birds) but the claws do not close on tibial spurs (i.e. they are not specialized tibiotarsal claws like those found on anopluran lice). The large rounded abdomen has nine distinct segments each bearing a transverse row of long dense setae both dorsally and ventrally. The abdomen also possesses six pairs of respiratory spiracles located along the dorsal edges of segments 4 to 9. Adult lice are sexually dimorphic with males being smaller than females (1.6-1.7 mm cf. 1.7-2.0 mm long) and males having a larger first antennal segment. Male genitalia are large and conspicuous comprising 2 pairs of compact testes (3 pairs in amblyceran lice) connected to tubular vas deferens which join to form a seminal vesicle basal to the genital sac containing a spiny aedeagus (tube-like copulatory or intromittent organ with dorsal gonopore and terminal endophallus) supported by a basal plate-like sclerite (apodeme) and lateral rod-like sclerites (parameres). Female genitalia consist of ovaries with polytrophic ovarioles connected to tubular oviducts joined to a globular uterus with accessory glands (produce glue) and spermatheca (store sperm) opening into a vagina with genital plate, valvula, setae and two posterior finger-like gonopods (lobes on posterior segment to aid in oviposition).

Site of infection: Trichodectids are commonly known as fur lice as they are ectoparasitic in the fur on the external surfaces of their carnivorous hosts. Many species are considered to be host specific and most show some site specificity as ischnoceran chewing lice are more sedentary and specialized than the more mobile unspecialized amblyceran chewing lice. For example, the dog biting louse *T. canis* is commonly found on the head, neck and tail of canids and tends to aggregate around body openings and wounds.

Pathogenesis: Infestations by a few lice may remain asymptomatic and go unnoticed by their hosts but heavier burdens may cause mild-severe disease with inflammation, pruritus and unkempt coats. Lice may cause irritation and annoyance when moving and feeding on their hosts. Nymphs and adults feed on flakes of skin and host fluids using their mandibular mouthparts to scrape epidermal tissues, often congregating around body openings or wounds seeking moisture. Their feeding behaviour may cause inflammation (dermatitis) which is often exacerbated by host allergic responses to louse antigens in saliva and/or faeces. Heavy infestations may result in intense pruritus with restlessness, sleeplessness, nervousness, and biting-stress with animals attempting to relieve the itching by self-grooming (biting, licking, scratching or rubbing afflicted body parts) which may cause unsightly matted dull coats with alopecia (hair loss) and excoriations (lesions) prone to crusting and secondary bacterial infections. Louse populations are usually readily controlled on well-nourished, healthy, well-groomed pets but louse numbers and clinical manifestations may be worse on very young, old, sick or stressed animals because of their compromised immunological and/or physiological conditions.

The species *T. canis* has also been shown to act as an intermediate host for *Dipylidium caninum* (the double-pore or cucumber tapeworm). Lice which ingest tapeworm eggs from dog faeces harbour cysticercoid stages which remain quiescent until ingested by dogs during grooming, or accidentally by humans (usually children playing with pets). Enigmatically, recent molecular studies have detected DNA from spirochaete bacteria *Borrelia* spp. in *Trichodectes melis* lice recovered from badgers but without detecting bacterial infections in those badgers. Further studies are required to determine whether chewing lice may be involved as mechanical or biological vectors in the transmission of borreliosis (including Lyme disease and relapsing fevers).

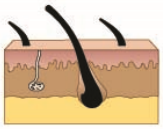
Developmental cycle and mode of transmission: Fur lice are obligate ectoparasites that live permanently in the host pelage, with transmission occurring when nymphs and/or adult lice are dislodged and crawl onto new hosts in close proximity. Gravid female lice glue their eggs to hair shafts where they develop and hatch after 5-14 days releasing first-stages nymphs. The emergent undergo hemimetabolous development with simple (incomplete) metamorphosis involving moults through another two nymphal stages before forming adult lice after 2 weeks. Each stage must feed in order to undergo further development. Adult lice mate and fertilized females begin laying eggs at the rate of several eggs per day for up to 30 days. The entire life-cycle may be completed on the same host in 3-6 weeks. Lice do not survive for long off the host and usually die within a week, although *T. canis* has been shown to withstand a range of environmental conditions but not for protracted periods. Infestations are transmitted between hosts when lice move from one to another either by direct contact or via contaminated bedding or grooming equipment (shared brushes and combs). Louse populations generally increase during cooler months of the year, with peak infestations typically occurring in late autumn or winter. Some lice (mostly ischnoceran chewing lice) have also been observed to be transmitted by phoresy when they use their mandibles to become temporarily attached to other larger insects that move between hosts. Stages of several *Trichodectes* spp. have been found attached to hippoboscid louse-flies and several times to adult fleas collected from wild animals, notably badgers.

Differential diagnosis: Infestations are usually detected by the direct demonstration of parasites on hosts, either eggs or empty egg cases (nits) attached to the bases of hair shafts, or motile stages (nymphs, adults) clinging to hairs or feeding on skin. Parasites may be visible to the naked eye when parting the coat, but the use of strong lights and magnifying lenses greatly aids their detection. Parasites may also be collected using tweezers, sticky tape impression smears or brisk coat brushings for subsequent light microscopic examination and identification. Potassium hydroxide digestion techniques have also been used to recover lice from

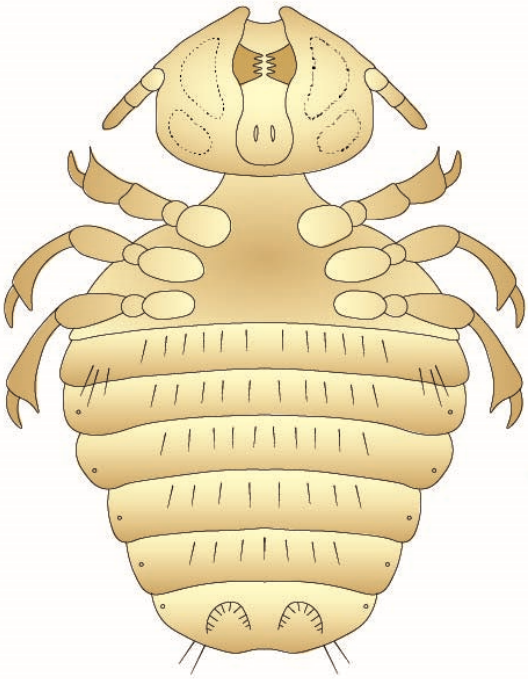
fresh wolf hides. Molecular studies have recently shown that the mitochondrial genome of trichodectid lice from mammals is fragmented into many mini-chromosomes like that of anopluran and rhynchophthirinid lice, while that of philopterid lice from birds is retained in a single chromosome. The shared derived feature of mitochondrial genome fragmentation has prompted the erection of a novel clade (Mitodivisia) which has been tentatively supported by phylogenetic studies on mitochondrial genes (cytochrome c oxidase subunit I).

Treatment and control: Infestations may be treated effectively using insecticidal chemicals applied at least twice at an interval of 7-14 days to ensure that any nymphs hatching from resistant eggs are killed. Insecticides exhibiting good activity have included chloronicotinyl (imidacloprid), pyrethroids (permethrin), carbamates (carbaryl), organochlorides (lindane, dichloro-diphenyl-trichloroethane (DDT)), organophosphates (malathion, chlorpyrifos, diazinon), arylpyrazole (fipronil) and macrocyclic lactones (selamectin, ivermectin). Most chemicals are available as topical applications (shampoos/rinses, sprays/aerosols, powders/fogs) although some are available as systemic formulations (injectable, oral or spot-on). Careful attention should be paid to regulations governing chemical usage (especially contra-indications, residues and environmental toxicity). Various grooming devices (brushes and fine-toothed combs) may be used to assist in the removal of lice, although adherent nits can be difficult to dislodge without using conditioners to lubricate coats and ease tangles. It is advisable to treat all animals in contact if possible, and to ensure they are kept healthy, well-nourished and well-groomed. Control through preventive management practices are based around minimizing contact with infested individuals (through quarantine, isolation or exclusion) and decontaminating shared facilities (through cleaning, washing or chemical treatment of pens, cages, bedding and grooming equipment).

Trichodectes



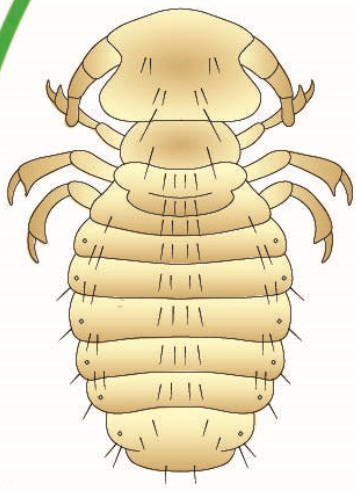
skin/pelage
(dermatitis, pruritus,
alopecia, excoriation)
(some vector infectious
microbial diseases)



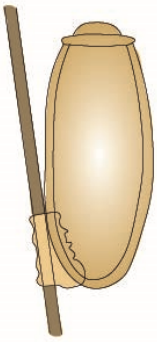
adult (ventral)
(~ 2 mm)



Definitive Hosts
(carnivores)



nymph (dorsal)
(~ 1.5 mm)



egg
(~ 1 mm)

all stages ectozoic on host
(motile stages feed on skin/scurf)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites



Trichodectes adult

Bovicola, Damalinia
(insect: louse)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Mallophagan (chewing) lice have blunt rounded heads with mouthparts adapted for feeding on keratin in superficial skin layers. Chewing lice are ectoparasitic on mammals and birds, most species being highly host specific and even site-specific. Ischnoceran lice have prominent filiform antennae but lack maxillary palps. Trichodectids have three antennal segments, single tarsal claws and are found on mammals. Many species were originally described in the genera *Damalinia* and *Werneckiella* but have subsequently been transferred to the genus *Bovicola* on the basis of molecular phylogenetic studies. Infestations by *Bovicola* spp. have been associated with dermatitis, pruritus, alopecia and excoriation in ruminants and horses.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order:	Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder:	Mallophaga (= wool-eating) (chewing lice, broad rounded head, feed on keratin, host/site specific)
Superfamily:	Ischnocera (without maxillary palps, prominent filiform antennae, keratin feeders (hairs/feathers))
Family:	Trichodectidae (parasitize mammals, 3-segmented antennae, single claw on tarsi)
Genus:	*Bovicola, Damalinia* (parasitic on skin/fleece/hair of sheep/cattle/horses)
Species:	various species cause pruritus and dermatitis in livestock

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Lice are small wingless hemipterodeans that undergo gradual (hemimetabolous) metamorphosis and are permanent obligate ectoparasites on other animals. Four suborders are recognized: the Anoplura containing the haematophagous sucking lice of placental mammals; the Ischnocera and Amblycera (previously classified together as Mallophaga) comprising the chewing or biting lice of birds, marsupials and placental mammals; and the Rhynchophthirina confined to elephants and warthogs in Africa.

Major parasitic phthirapteran families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Suborder: Ischnocera [Mallophaga p.p.] (chewing lice of mammals and birds, broad rounded head, without maxillary palps, prominent filiform antennae, keratin feeders) [2 families, 158 genera, 3,371 species]					

Trichodectidae (fur lice)	20 genera, 413 spp.	mammals (bovids, equids, carnivores)	nymphs, adults	biting	helminth
Philopteridae(bird lice)	138 genera, 2,958 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					
Menoponidae (bird lice)	68 genera, 1,150 spp.	birds	nymphs, adults	biting, chewing	-
Boopiidae (marsupial chewing lice)	8 genera, 57 spp.	mammals (incl. marsupials)	nymphs, adults	biting	helminth
Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
Suborder: Anoplura (sucking lice of placental mammals) (narrow pointed head, pierce skin and feed on fluids (solenophagy)) [16 families, 51 genera, 694 species]					
Haematopinidae (ungulate lice, short-nosed lice)	1 genus, 21 spp.	mammals (equids, bovids, suids)	nymphs, adults	blood-sucking	viral, bacterial
Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-
Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial
Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-

Over 4,900 species of biting/chewing lice have been described in 253 genera in 8 families, around 4,400 species associated with birds and 500 species with mammals. Members of the suborder Ischnocera have broad rounded heads with conspicuous filiform antennae but lacking maxillary palps, while members of the suborder Amblycera have large rounded heads with maxillary palps and inconspicuous antennae hidden in grooves. Some 158 ischnoceran genera have been assigned to 2 families (Trichodectidae and Philopteridae), while 96 amblyceran genera have been classified in 6 families (Boopiidae; Gyropidae, Laemobothriidae, Menoponidae, Ricinidae, Trimenoponidae). Species of veterinary importance include members of the ischnoceran families Trichodectidae (bovids, canids, equids) and Philopteridae (poultry), and the amblyceran families Menoponidae (poultry) and Boopiidae (carnivores). Most ischnoceran lice are parasitic on birds but the trichodectids are found on mammals and are commonly known as fur lice. Members of the family Trichodectidae possess antennae with 3 segments and their legs terminate in tarsi with single claws (in contrast to members of the family Philopteridae which have 5-segmented antennae and paired tarsal claws). Over 400 trichodectid species have been described from 20 genera, namely *Bisonicola*, *Bovicola*, *Cebidicola*, *Damalinia*, *Dasyonyx*, *Eurytrichodectes*, *Eutrichophilus*, *Felicola*, *Geomydoecus*, *Lorisicola*, *Lutridia*, *Neotrichodectes*, *Procavicola*, *Procaviphilus*, *Protelicola*, *Thomomydoecus*, *Tragulicola*, *Trichodectes*, *Werneckiella* and *Werneckodectes*. The subfamily Bovicolinae contains the genera *Bovicola* (subgenera *Bovicola*, *Holakartikos*, *Lepikentron*, *Spinibovicola*), *Bisonicola*, *Damalinia* (subgenera *Damalinia*, *Cervicola*, *Tricholipeurus*), *Tragulicola*, and *Werneckiella.* Taxonomic ranks differ in various classification schemes as many early descriptions were inconsistent and species were assigned to pleomorphic genera, sometimes to the point that texts used the names *Bovicola* and *Damalinia* almost interchangeably. A comprehensive cladistic analysis provided some structure to taxonomic classifications, although the author conceded that most genera/subgenera be considered *sedis mutabilis* ("of uncertain relationship") pending detailed molecular phylogenetic analyses. Currently, some 15 *Bovicola* spp., 51 *Damalinia* spp., 7 *Werneckiella* spp., 1 *Bisonicola* sp. and 1 *Tragulicola* sp. are considered valid from artiodactyls (bovids, cervids, camelids, tragulids) and perissodactyls (equids) around the world. Most species are highly host specific and their distributions mirror those of their hosts, with many species infesting domestic animals being cosmopolitan. These lice have interesting sex lives and many species are regarded to be parthenogenetic as male lice are rare or absent.

Bovicolinid species	Hosts	Location	Clinical signs	Distribution
***Bovicola* (subgenus *Bovicola*)** [body and head with short setae, gonopods conspicuous but not distinctly lobular, mesomeres not pentagonal, never bipartite, bovid/cervid hosts]				
B. alpinus (syn. *B. rupicaprae*)	Artiodactyla: bovid (chamois)			Europe
B. bovis (syn. *B. scalaris, tauri*) (cattle chewing louse, cattle biting louse, red louse)	Artiodactyla: bovid (cattle)	skin (head, neck, shoulders, back, rump, tail switch)	irritation, pruritus, inflammation, excoriation, alopecia, anorexia	worldwide
B. caprae	Artiodactyla: bovid (goats)	skin	irritation,	worldwide

(syn. *B. climacius, climax, mambricus, peregrinus, solidus*) (goat biting louse, red louse)		(shoulders, back, rump)	pruritus, inflammation, excoriation, alopecia	
B. concavifrons	Artiodactyla: cervid (red deer)			cosmopolitan
B. jellisoni	Artiodactyla: bovid (Dall sheep, bighorn sheep)			North America
B. limbatus (syn. *B. madagascarensis, painei, sachtlebeni, wernecki*) (red louse)	Artiodactyla: bovid (Angora goat)	skin (shoulders, back, rump)	irritation, pruritus, inflammation, excoriation, alopecia	worldwide
B. longicornis (syn. *B. americanus, similis*)	Artiodactyla: cervid (red deer)	skin	irritation, pruritus, inflammation	Europe
B. oreamnidis	Artiodactyla: bovid (mountain goat)			North America
B. ovis (syn. *B. ovisarietis, sphaerocephalus*) (sheep biting louse)	Artiodactyla: bovid (sheep)	skin (shoulders, back, rump)	irritation, pruritus, inflammation, wool matting, excoriation, alopecia	worldwide
B. tarandi	Artiodactyla: cervid (reindeer)			Europe
B. tibialis (syn. *B. punctus*)	Artiodactyla: cervid (fallow deer, chital, black-tailed deer, Rocky Mountain mule deer)	skin	irritation, pruritus, inflammation, hair loss syndrome	Europe, North America
***Bovicola* (subgenus *Holakartikos*)** [body and head with long dense setae, gonopods small and lobose, mesomeres not pentagonal and fused apically, caprine hosts]				
B. crassipes (syn. *B. hermsi, ibicis, penicillatus*) (Angora goat biting louse)	Artiodactyla: bovid (goat, ibex)			Europe
***Bovicola* (subgenus *Lepikentron*)** [body with short setae, head with long fine setae, gonopods conspicuous and distinctly lobular, mesomeres not pentagonal and bipartite, camelid hosts]				
B. breviceps (syn. *B. aucheniaelamae, inaequalemaculatus*)	Artiodactyla: camelid (llama, guanaco, alpaca)			South America
***Bovicola* (subgenus *Spinibovicola*)** [body and head with medium setae, gonopods rounded, parameres fused, mesomeres absent, ovine hosts]				
B. hemitragi	Artiodactyla: bovid (Himalayan tahr)			Himalayas
B. multispinosus	Artiodactyla: bovid (blue sheep)			Himalayas
Bisonicola [body and head with short setae, gonopods wide and truncate, parameres separate and attached to mesomeral arch, bison hosts]				
B. sedecimdecembrii	Artiodactyla: bovid (American bison, European bison)			North America
Werneckiella [gonopods broad and truncate, mesomeres pentagonal, equid/bovid hosts]				
W. aspilopygus	Perissodactyla: equid (plains zebra)			Africa
W. equi (syn. *W. hemioni, B. parumpilosus, pilosus, pubescens, trampel, vestitus*) (horse biting louse)	Perissodactyla: equid (horse, onager); Artiodactyla: camelid (Bactrian camel?)	skin (neck, mane, flanks, tail base)	irritation, pruritus, inflammation, hair matting, excoriation, alopecia	worldwide
W. fulva	Artiodactyla: bovid (Barbary sheep)			North Africa
W. neglecta	Artiodactyla: bovid (Barbary sheep)			North Africa
W. ocellata	Perissodactyla: equid (horse, donkey, plains zebra)			Africa

W. zebrae	Perissodactyla: equid (mountain zebra)			Africa
W. zuluensis	Perissodactyla: equid (plains zebra)			Africa
Tragulicola [gonopods broad and tapering, mesomeres fused apically, tragulid (mouse-deer) hosts]				
T. balabacensis	Artiodactyla: cervid (Philippine mouse-deer)	skin		Philippines
T. traguli	Artiodactyla: cervid (Java mouse-deer, greater mouse-deer)	skin		South-East Asia
***Damalinia* (subgenus *Damalinia*)** [broad lice, subgenital lobe absent or reduced to flap, gonopods not hook-shaped, mesomeres fused to parameres, bovid hosts]				
D. adenota	Artiodactyla: bovid (kob, puku)	skin		Africa
D. appendiculata	Artiodactyla: bovid (goitered gazelle)	skin		Indo-Asia
D. baxi	Artiodactyla: bovid (sassabies)	skin		Africa
D. chorleyi	Artiodactyla: bovid (hartebeest)	skin		Africa
D. crenelata	Artiodactyla: bovid (sassabies)	skin		Africa
D. dimorpha	Artiodactyla: bovid (goral)	skin		Himalayas
D. fahrenholzi	Artiodactyla: bovid (Arabian gazelle)	skin		Arabian Peninsula
D. harrisoni	Artiodactyla: bovid (gnu)	skin		Africa
D. hilli	Artiodactyla: bovid (waterbuck)	skin		Africa
D. neotheileri	Artiodactyla: bovid (wildebeest)	skin		Africa
D. orientalis	Artiodactyla: bovid (serow)	skin		Japan, Taiwan
D. ornata	Artiodactyla: bovid (hartebeest)	skin		Africa
D. pelea	Artiodactyla: bovid (rhebok)	skin		Africa
D. semitheileri	Artiodactyla: bovid (wildebeest)	skin		Africa
D. theileri	Artiodactyla: bovid (wildebeest)	skin		Africa
D. thompsoni	Artiodactyla: bovid (serow)	skin		China
***Damalinia* (subgenus *Cervicola*)** [broad lice, subgenital lobe absent or reduced to flap, gonopods hook-shaped, endopallus lacking spicular patch, mesomeres unfused, bovid/cervid hosts]				
D. annectens	Artiodactyla: bovid (sitatunga, kewel)	skin		Africa
D. cordillerai	Artiodactyla: cervid (samba deer)	skin		Indo-Asia
D. forficula	Artiodactyla: cervid (chital, Indian hog deer, muntjac)	skin	irritation, pruritus, inflammation	Asia
D. hendrickxi	Artiodactyla: bovid (duiker)	skin		Africa
D. hopkinsi	Artiodactyla: bovid (eland)	skin		Africa
D. hydropotis	Artiodactyla: cervid (water deer)	skin		China
D. lerouxi	Artiodactyla: bovid (bush duiker)	skin		Africa
D. maai	Artiodactyla: cervid (sika deer)	skin	irritation, pruritus, inflammation	Eurasia
D. martinaglia	Artiodactyla: bovid (lechwe)	skin		South Africa
D. meyeri (syn. *D. tibialis*)	Artiodactyla: cervid (roe deer)	skin	irritation, pruritus, inflammation	Eurasia
D. muntiaca	Artiodactyla: cervid (muntjac)	skin		Indo-Asia
D. natalensis	Artiodactyla: bovid (kewel)	skin		Africa
D. reduncae	Artiodactyla: bovid (reedbuck)	skin		southern Africa
D. siamensis	Artiodactyla: cervid (muntjac)	skin		Indo-Asia
D. trabeculae	Artiodactyla: bovid (reedbuck)	skin		Africa
D. ugandae	Artiodactyla: bovid (reedbuck)	skin		Africa
***Damalinia* (subgenus *Tricholipeurus*)** [long slender lice, subgenital lobe present, endophallus with dense patch of spicules, mesomeres unfused, bovid/cervid hosts]				
D. aepycerus	Artiodactyla: bovid (impala)	skin		Africa
D. albimarginata	Artiodactyla: cervid (gray brocket, red brocket)	skin		South America
D. antidorcus	Artiodactyla: bovid (springbok)	skin		Africa
D. balanicus	Artiodactyla: bovid (blackbuck)	skin		Africa
D. bedfordi	Artiodactyla: bovid (blue duiker)	skin		Africa

D. clayi	Artiodactyla: bovid (royal antelope)	skin		Africa
D. conectens	Artiodactyla: bovid (klipspringer)	skin		Africa
D. cornuta	Artiodactyla: bovid (blackbuck, dorcas gazelle)	skin		Africa
D. dorcephali	Artiodactyla: cervid (Pampas deer)	skin		South America
D. elongata	Artiodactyla: bovid (impala)	skin		Africa
D. indica	Artiodactyla: cervid (Reeve's muntjac, Indian muntjac)	skin		Indo-China
D. lineata	Artiodactyla: bovid (steenbok, Cape grysbok, Sharpe's grysbok)	skin		Africa
D. lipeuroides (syn. *D. mazama*, *mexicanus, virginianus*)	Artiodactyla: cervid (white-tailed deer, mule deer, sambar deer)	skin		North America
D. longiceps	Artiodactyla: bovid (Arabian gazelle)	skin		Middle-East
D. moschatus	Artiodactyla: bovid (suni)	skin		Africa
D. ourebiae	Artiodactyla: bovid (oribi)	skin		Africa
D. pakenhami	Artiodactyla: bovid (Ader's duiker, common duiker)	skin		Africa
D. parallela (syn. *D. odocoilei*)	Artiodactyla: cervid (white-tailed deer, mule deer, sambar deer)	skin		North America
D. parkeri	Artiodactyla: bovid (Thomson's gazelle)	skin		Africa
D. spinifer	Artiodactyla: bovid (Grant's gazelle)	skin		Africa
D. victoriae	Artiodactyla: bovid (Kirk's dik-dik, Gunther's dik-dik)	skin		Africa
D. zaganseeri	Artiodactyla: bovid (Mongolian gazelle)	skin		Eurasia

Parasite morphology: Chewing lice belonging to the subfamily Bovicolinae form three different types of morphological stages during their development: namely, eggs (nits); nymphs (3 instars); and adults. Eggs are small beige barrel-shaped stages ranging in length from 0.5-1.0 mm depending on species. They are attached to hair shafts at their posterior ends and their anterior ends have a convex operculum (cap) with a small rim. Mature eggs are embryonated and they release first-stage nymphs (N1) when they hatch. These lice undergo gradual (incomplete) metamorphosis and moult through another two nymphal stages before moulting to adults. All nymphal stages resemble adult lice but are smaller, less sclerotized, have fewer body setae (hairs) and lack abdominal bands and genitalia. Adult lice have pale red-brown dorsoventrally-flattened bodies ranging from 1.0-2.5 mm in length with three distinct body parts (comprising a broad blunt head, cylindrical thorax and ellipsoidal abdomen). The head is short, broader than long and rounded anteriorly with a longitudinal groove in the ventral surface that accommodates host hairs. The head possesses a pair of prominent filiform antennae projecting laterally and not confined to antennal grooves. The antennae of trichodectid lice are composed of three segments (while those of philopterid lice from birds are composed of five segments). These ischnoceran chewing/biting lice do not have long piercing mouthparts like anopluran sucking lice, but feed by the biting/scraping action of large ventral dentate mandibles inserted at right angles to the head (such that the condyles are posterior and the ginglymus is anterior). Food particles are delivered to the preoral cavity by a posterior plate-like labrum (often with an anterior hyaline pad-like protrusion (pulvinus)), 2 lateral maxillae and an anterior labium (salivary secretions added through a central hypopharynx). In ischnoceran chewing lice, the maxillae and labium are reduced in size (compared to anopluran sucking lice), the maxillae are single lobed and attached to the lateral margins of the tripartite labium, and maxillary palps are absent (present in amblyceran lice). The mouth opens into the foregut (with pharynx, oesophagus and fusiform crop), a large midgut (with ventriculus and anterior caeca) and a hindgut (with pylorus, papillae and rectum). The midgut also contains a special organ known as a mycetome (or bacteriome or stomach disc) harbouring bacterial/fungal symbionts (but the mycetome is less developed than in anopluran sucking lice and is absent in amblyceran chewing lice). The segments of the thorax are fused with indistinct boundaries and the ventral surface gives rise to three pairs of legs, each composed of five segments (coxa, trochanter, femur, tibia, tarsus) and terminating in a single tarsal claw (in contrast to double claws on philopterid lice from birds, and specialized tibio-tarsal claws on anopluran lice). The fore-legs on the prothorax are slightly smaller than the mid- or hind-legs and are used to grasp host hairs together with the mandibles in the ventral groove. The abdomen is ellipsoidal in shape and appears yellow-white in colour with distinct brown transverse bands on most segments. Each segment bears at least one row of short to medium setae and respiratory spiracles are located dorsolaterally on segments 2 to 7. Adult lice are sexually dimorphic with male lice slightly smaller than females, but sex ratios are highly female biased (males unknown, particularly in cervid species, or few in number (<5% in bovid species or <1% in equid species) and parthenogenesis appears to a common phenomenon in many species. Females have polytrophic ovarioles connected by tubular oviducts to a globular uterus with accessory glands (that produce the cement used to glue eggs) and a saccular spermatheca (used to store sperm after mating). The uterus opens into the vagina which has a genital plate with valvula, and the gonopore is located between two lateral terminal gonopods or gonapophyses (protuberances of the terminal abdominal segment that aid oviposition)

often bearing long setae. When present, males have 2 pairs of compact testes (3 pairs in amblyceran lice) with tubular vas deferens joining to form a seminal vesicle which is connected to the genital sac containing a tubular copulatory aedeagus (intromittent organ with dorsal gonopore and endophallus) supported by sclerotized elements (basal apodemal plate, lateral paramere rods and dorsal arched mesomeres). Different bovicolinid genera and subgenera are recognized primarily by differences in their setate ornamentation, genital structures and host ranges. Members of the subgenus *B.* (*Bovicola*) have short setae, conspicuous non-lobular gonopods, rod-like non-bipartite mesomeres and bovid/cervid hosts, those of *B.* (*Spinibovicola*) have medium setae, rounded gonopods, fused parameres but not mesomeres and ovine hosts, those of *B*. (*Holakartikos*) have long dense setae, small lobose gonopods, fused rod-like mesomeres and caprine hosts, and those of *B.* (*Lepikentron*) have long head setae but short body setae, conspicuous lobular gonopods, rod-like bipartite mesomeres and camelid hosts. Members of the subgenus *D.* (*Damalinia*) are broad lice with subgenital lobes reduced to flaps, tapering gonopods and fused mesomeres, those of *D.* (*Cervicola*) are similar but have hook-shaped gonopods and unfused mesomeres, while those of *D.* (*Tricholipeurus*) are long slender lice with rounded subgenital lobes, unfused mesomeres, and the endophallus bears a dense patch of spicules. The genus *Bisonicola* comprises species with short setae, wide truncate gonopods, separate parameres fused to the mesomeral arch, and bison hosts, *Werneckiella* contains species with broad truncate gonopods, pentagonal mesomeres, and equid/bovid hosts, while *Tragulicola* has species with broad tapering gonopods, fused mesomeres and tragulid (mouse-deer) hosts.

Site of infection: These chewing lice are ectoparasitic on the skin of their ungulate hosts and crawl amongst hairs/fibres close to the skin surface. Most louse species are highly host-specific and have a clumped or aggregated distribution as they have preferred sites of infestation, especially along the top line of the back, particularly the shoulders and withers from where they may spread to the neck, head, rump and poll. These lice avoid light and are usually found in regions with long hair or wool, but they avoid areas with coarse hairs such as the ears, mane, tail and lower legs. In heavy infestations, they may be found underneath heavily encrusted scurf.

Pathogenesis: Light infestations involving a few lice often remain asymptomatic and are unnoticed by their hosts, but heavier infestations by feeding nymphs and adults may cause clinical signs predominantly involving skin irritation, inflammation and sometimes lesions. Feeding stages abrade the skin using their chewing mouthparts and eat scurf (dead skin cells), skin secretions (oils/lipids from sebaceous and sweat glands, including wool grease) and skin bacteria. The surface of the skin usually remains intact although there may be some abrasion of the upper superficial layers (moist scabs do not form as occurs in infestations by psoroptic mange mites). The lice may cause skin irritation, discomfort, hyperkeratosis, inflammation (dermatitis) and intense itching (pruritus), which may be exacerbated by allergic responses to louse antigens (some animals have been shown to develop antibodies to louse salivary secretions). Infested animals attempt to relieve the annoyance by vigorous self-grooming (by biting, licking, scratching or rubbing afflicted body parts) which may result in unsightly coats/fleeces (matting, discolouration), loss of hair/wool (alopecia), skin damage (scaling, crusts) and self-trauma (sores, wounds) which are susceptible to secondary microbial infections. Infested animals may exhibit distress, impaired thermoregulation, poor feed conversion efficiency, suboptimal meat/milk/fibre production, and even hide damage (thickened discoloured patches or nodules known as ‘spot and fleck’ in cattle hides and ‘scatter cockle’ in sheep skins).Healthy animals able to groom effectively often do not develop severe infestations, and there is growing evidence that animals develop resistance after protracted exposure. Infestations are generally worse on young, old, sick or stressed (undernourished, overcrowded) animals due to their compromised physiological and/or immunological states. Lice are more prevalent during winter when animals have long coats and environmental conditions are more conducive to louse multiplication and survival.

Ischnoceran chewing lice (*Werneckiella equi*) have also been implicated in the mechanical transmission of equine infectious anaemia, a blood-borne disease caused by a horse specific lentivirus normally transmitted by dipteran insects (horseflies, deer flies and stable flies). Both sucking and chewing lice of cattle have also been shown to act as mechanical vectors for the skin fungus *Trichophyton verrucosum* which causes dermatomycosis (ringworm).

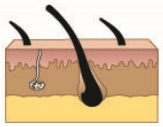
Developmental cycle and mode of transmission: Chewing lice are obligate ectoparasites that live permanently in the host pelage and are able to complete their entire life-cycles on individual hosts. Transmission between hosts occurs by direct intimate contact when dislodged lice crawl onto new hosts or are transferred on contaminated equipment. Mature female lice lay eggs attaching them to hair shafts close to the skin, where they hatch after 5-14 days depending on temperature and humidity (favouring warm humid conditions). Emergent nymphs feed on the host and undergo gradual (hemimetabolous) metamorphosis moulting through another 2 nymphal stages over the next 14-21 days and then moulting to adults 3-4 days later. Most adult lice are female (comprising 95-99% of the population) and males are only occasionally seen. Many species are parthenogenetic and females can reproduce without mating. Female lice lay 1-2 eggs each day for 6-10 weeks. The whole life-cycle may be completed in 25-42 days but may be extended in warmer conditions (higher temperatures inhibit egg laying and survival of lice). None of the developmental stages are free-living and nymphs and adult lice can only survive for short periods (3-4 days) if dislodged from hosts. Direct transmission therefore occurs when lice move from host to host through close contact or via infested equipment. Transmission often occurs when animals are in close contact during feeding (including suckling) or when crowded into yards, stalls, barns or feedlots. Infestations may also be transmitted between hosts by contaminated bedding, rugs, harnesses or shared grooming equipment (combs, brushes). Some lice (mostly ischnoceran chewing lice) have occasionally been observed to be transmitted between hosts by phoresy, that is, when lice become temporarily attached to the external surfaces of larger winged insects (particularly hippoboscid and muscid flies)

which move between hosts. Infestations are common in domestic ungulates in most grazing areas around the world, except those with very hot or very wet climates. Most infestations exhibit marked seasonal changes in prevalence and abundance, increasing during the cooler months of winter and spring when animals have longer coats, crowd together for warmth, have poorer nutrition and reduced vigour (all of which favour the breeding and spread of lice).

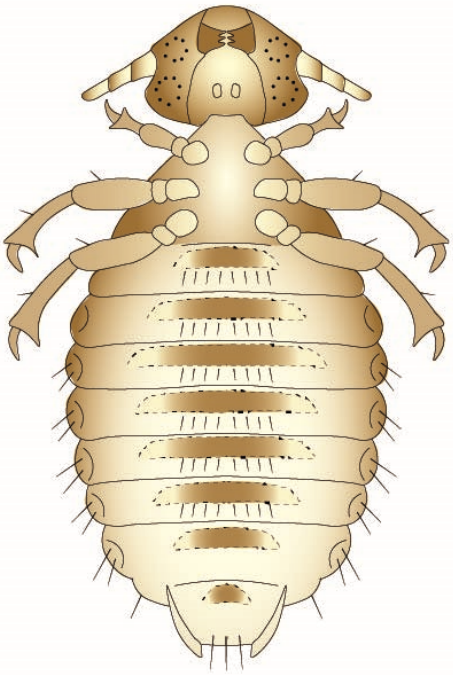
Differential diagnosis: Infestations may be suspected when animals show signs of irritation with rubbing resulting in unkempt coats (hair loss/matting) and skin lesions (due to self-trauma) in cooler months (late autumn, winter, early spring). Infested animals may also exhibit reduced feed intake and even weight loss. Visual examination of affected body regions by several partings of the coat may reveal the presence of lice (whitish nits or red-brown nymphs/adults). Most species are colonial and their motile stages are photophobic moving quickly away from light. Searches may be assisted by using magnifying glasses or fine-toothed combs, although light infestations may be overlooked. Any lice detected may be collected for microscopic examination and identification. Molecular techniques have recently been used to characterize louse species following polymerase chain reaction (PCR) amplification and sequencing of nuclear genes (18S ribosomal RNA).

Treatment and control: Clinical infestations may be treated with a range of insecticidal compounds, including synthetic pyrethroids (permethrin, cypermethrin, alphamethrin, deltamethrin, flumethrin, zetacypermethrin, cyfluthrin, cyhalothrin), synergized pyrethrins, organophosphates (diazinon, tetrachlorvinphos, coumaphos, chlorfenvinphos, chlorpyrifos, crotoxyphos, trichlorfon, phosmet, propetamphos, famphur), organochlorides (dieldrin, aldrin), macrocyclic lactones (ivermectin, eprinomectin, abamectin, moxidectin, doramectin), insect growth regulators (diflubenzuron), spinosyns (spinosad) and formamidines (amitraz), although the latter 2 have been discontinued in many countries as have some organochlorines and organophosphates. Animals may be treated by external topical applications (baths/dips, showers/sprays) or systemic treatments (oral, injectable, pour-on or impregnated ear tags), but careful attention should be given to drug guidelines and regulations concerning contra-indications, side-effects and toxic residues, particularly since some animal breeds have drug hypersensitivities (e.g. certain Brahman-cross cattle and some dairy cattle react adversely to organophosphates) and some drugs differ in their efficacy depending on their route of administration (e.g. injectable macrocyclic lactones are generally less effective against chewing lice). In most cases, treatment should be repeated after 1-2 weeks, because the chemicals are not effective against egg stages and most have little residual activity. Some louse species have also developed resistance to various insecticides, including cypermethrin, deltamethrin, cyhalothrin, diazinon, aldrin and dieldrin, and it is recommended that periodic treatments rotate between different chemical classes to reduce the risk of selection for further resistance. Animals are generally treated in autumn to prevent the escalation of louse populations during cooler months and all animals on the property should be treated. Good control through preventive management practices are based around maintaining healthy animals (well-nourished groomed individuals are less susceptible), minimizing contact between animals (avoiding overcrowding, quarantining new livestock or infested individuals) and decontaminating shared facilities and equipment (through cleaning, washing or chemical treatment of pens, stalls, rugs, harnesses, saddlery and grooming devices). Fibre-producing animals should be shorn before or during summer to reduce louse burdens (exposure to solar radiation and dehydration markedly reduce louse reproduction and survival).

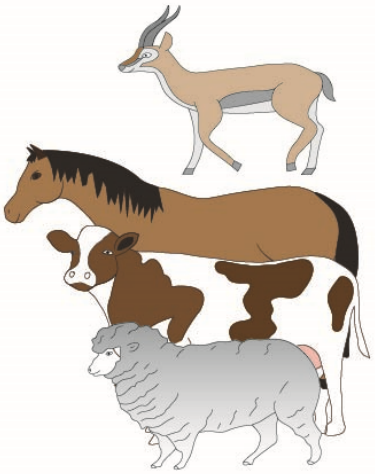
Bovicola, Damalinia



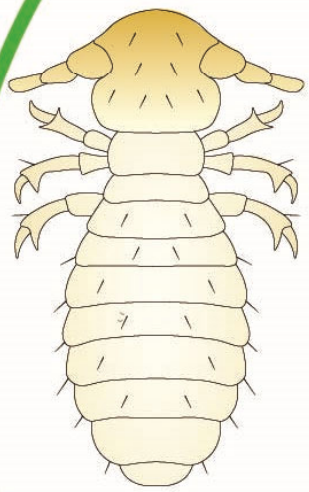
skin/pelage
(dermatitis, pruritus,
alopecia, excoriation)
(some vector infectious
microbial diseases)



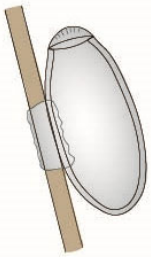
adult (ventral)
(~ 2 mm)



Definitive Hosts
(ungulates)



nymph (dorsal)
(~ 1.5 mm)



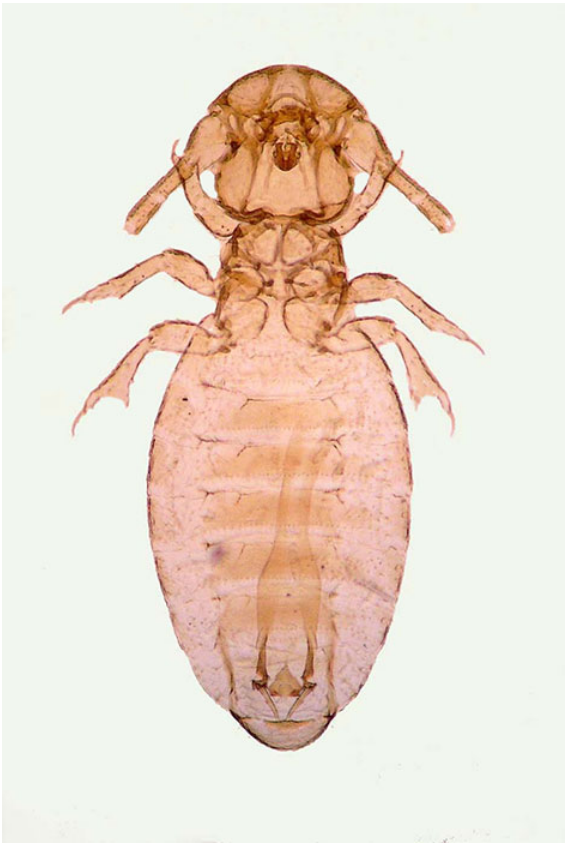
egg
(~ 1 mm)

all stages ectozoic on host
(motile stages feed on skin/scurf)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites



Bovicola adult female



Bovicola adult male

Felicola
(insect: louse)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Mallophagan (chewing) lice have blunt rounded heads with mouthparts adapted for feeding on keratin in superficial skin layers. Chewing lice are ectoparasitic on mammals and birds, most species being highly host specific and even site-specific. Ischnoceran lice have prominent filiform antennae but lack maxillary palps. Trichodectids have three antennal segments, single tarsal claws and are found on mammals. Infestations by *Felicola subrostrata* have been associated with dermatitis in cats.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order: Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder: Mallophaga (= wool-eating) (chewing lice, broad rounded head, feed on keratin, host/site specific)
Superfamily: Ischnocera (without maxillary palps, prominent filiform antennae, keratin feeders (hairs/feathers))
Family: Trichodectidae (parasitize mammals, 3-segmented antennae, single claw on tarsi)
Genus: *Felicola* (parasitic on skin/hair of cats)
Species: *Felicola subrostrata* (causes dermatitis in cats)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Lice are small wingless hemipterodeans that undergo gradual (hemimetabolous) metamorphosis and are permanent obligate ectoparasites on other animals. Four suborders are recognized: the Anoplura containing the haematophagous sucking lice of placental mammals; the Ischnocera and Amblycera (previously classified together as Mallophaga) comprising the chewing or biting lice of birds, marsupials and placental mammals; and the Rhynchophthirina confined to elephants and warthogs in Africa.

Major parasitic phthirapteran families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Suborder: Ischnocera [Mallophaga p.p.] (chewing lice of mammals and birds, broad rounded head, without maxillary palps, prominent filiform antennae, keratin feeders) [2 families, 158 genera, 3,371 species]					
Trichodectidae (fur lice)	20 genera, 413 spp.	mammals (bovids, equids, carnivores)	nymphs, adults	biting	helminth

Philopteridae(bird lice)	138 genera, 2,958 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					
Menoponidae (bird lice)	68 genera, 1,150 spp.	birds	nymphs, adults	biting, chewing	-
Boopiidae (marsupial chewing lice)	8 genera, 57 spp.	mammals (incl. marsupials)	nymphs, adults	biting	helminth
Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
Suborder: Anoplura (sucking lice of placental mammals) (narrow pointed head, pierce skin and feed on fluids (solenophagy)) [16 families, 51 genera, 694 species]					
Haematopinidae (ungulate lice, short-nosed lice)	1 genus, 21 spp.	mammals (equids, bovids, suids)	nymphs, adults	blood-sucking	viral, bacterial
Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-
Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial
Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-

Over 4,900 species of biting/chewing lice have been described in 253 genera in 8 families, around 4,400 species associated with birds and 500 species with mammals. Members of the suborder Ischnocera have broad rounded heads with conspicuous filiform antennae but lacking maxillary palps, while members of the suborder Amblycera have large rounded heads with maxillary palps and inconspicuous antennae hidden in grooves. Some 158 ischnoceran genera have been assigned to 2 families (Trichodectidae and Philopteridae), while 96 amblyceran genera have been classified in 6 families (Boopiidae; Gyropidae, Laemobothriidae, Menoponidae, Ricinidae, Trimenoponidae). Species of veterinary importance include members of the ischnoceran families Trichodectidae (bovids, canids, equids) and Philopteridae (poultry), and the amblyceran families Menoponidae (poultry) and Boopiidae (carnivores). Most ischnoceran lice are parasitic on birds but the trichodectids are found on mammals and are commonly known as fur lice. Members of the family Trichodectidae possess antennae with 3 segments and their legs terminate in tarsi with single claws (in contrast to members of the family Philopteridae which have 5-segmented antennae and paired tarsal claws). Over 400 trichodectid species have been described from 20 genera, namely *Bisonicola*, *Bovicola*, *Cebidicola*, *Damalinia*, *Dasyonyx*, *Eurytrichodectes*, *Eutrichophilus*, *Felicola*, *Geomydoecus*, *Lorisicola*, *Lutridia*, *Neotrichodectes*, *Procavicola*, *Procaviphilus*, *Protelicola*, *Thomomydoecus*, *Tragulicola*, *Trichodectes*, *Werneckiella* and *Werneckodectes*. The subfamily Trichodectinae (subgenital lobes present on females, often with serrate margins, six or fewer abdominal spiracles, carnivora/primate hosts) contains the genus *Felicola* (head triangular or broadly rounded, variable number of abdominal spiracles, setae sparse, subgenital lobe without scales or spines, parameres narrow and rod-like) and 2 subgenera are recognized: *F.* (*Felicola*) (gonopod with rounded lobe, terminal endophallus thinly sclerotized) and *F.* (*Suricatoecus*) (gonopod with rectangular-round lobe and spur, terminal endophallus not sclerotized). All *Felicola* spp. have been reported from carnivores, mostly felids (cats and allies), herpestids (mongooses) and viverrids (civets and genets), although a small number have been found on canids (foxes). Most species are considered to be host-specific and their distribution mirrors that of their hosts.

***Felicola* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
Subgenus *F.* (*Felicola*) [gonopod with rounded lobe, terminal endophallus thinly sclerotized]				
F. calogaleus	Carnivora: herpestid (slender mongoose, Cape gray mongoose)	skin		South Africa
F. congoensis	Carnivora: herpestid (kusimanse)	skin		West Africa
F. cynictis	Carnivora: herpestid (yellow mongoose)	skin		South Africa
F. genettae	Carnivora: viverrid (genet)	skin		Africa
F. helogale	Carnivora: herpestid (dwarf mongoose)	skin		Africa
F. helogaloidis	Carnivora: herpestid (dwarf mongoose)	skin		Africa
F. hopkinsi	Carnivora: nandiniid (palm civet)	skin		Africa
F. inaequalis (syn. *F. rammei*)	Carnivora: herpestid (Egyptian mongoose)	skin		North Africa
F. liberiae	Carnivora: herpestid (Liberian mongoose)	skin		Liberia
F. minimus	Carnivora: herpestid (marsh mongoose)	skin		Africa
F. occidentalis	Carnivora: herpestid (long-nosed kusimanse)	skin		Africa

F. rahmi	Carnivora: herpestid (water mongoose)	skin		Africa
F. robertsi	Carnivora: herpestid (Meller's mongoose)	skin		Africa
F. rohani	Carnivora: herpestid (crab-eating mongoose)	skin		Indo-Asia
F. setosus	Carnivora: herpestid (Selous's mongoose)	skin		South Africa
F. subrostratus (syn. *F. rostratus, Trichodectes, Felicina, Bedfordia helogale*) (cat biting louse)	Carnivora: felid (cat, civet, bobcat), herpestid (brown-tailed mongoose)	skin (face, pinnae, back)	dull ruffled coat, scaling, crusts, alopecia	worldwide
F. viverriculae	Carnivora: viverrid (small Indian civet)	skin		India
F. zeylonicus	Carnivora: herpestid (stripe-necked mongoose)	skin		Africa
Subgenus *F.* (*Suricatoecus*) [gonopod with rectangular-round lobe and spur, terminal endophallus not sclerotized, herpestid/canid hosts]				
F. acutirostris	Carnivora: herpestid (marsh mongoose)	skin		Africa
F. bedfordi	Carnivora: herpestid (Jackson's mongoose, bushy-tailed mongoose, black-footed mongoose)	skin		Africa
F. cooleyi	Carnivora: herpestid (meerkat)	skin		Africa
F. decipiens	Carnivora: herpestid (banded mongoose)	skin		Africa
F. fahrenholzi	Carnivora: canid (crab-eating fox, Patagonian fox)	skin		South America
F. fennecus	Carnivora: canid (fennec fox)	skin		Egypt
F. guinlei	Carnivora: canid (bat-eared fox)	skin		Africa
F. macrurus	Carnivora: herpestid (water mongoose)	skin		Africa
F. pygidialis	Carnivora: herpestid (water mongoose)	skin		Africa
F. quadraticeps	Carnivora: canid (gray fox, swift fox)	skin		North and Central America
F. vulpis (syn. *F. abnormis, micropus*)	Carnivora: canid (red fox), Primates: cheirogaleid (brown mouse lemur?)	skin		Africa

A range of species formerly recognized as *Felicola* spp. have now been reclassified into the sister genus *Lorisicola* (gonopore with spicular patch, gonopod lobes comprising two fused tubercles, subgenital lobe with scales or spines, parameres broad) with two subgenera: *L.* (*Lorisicola*) (male antennal flagellum with teeth on projection) and *L.* (*Paradoxuroecus*) (male antennal flagellum with teeth not on projection).

Lorisicola species	**Hosts**	**Location**	**Clinical signs**	**Distribution**
Subgenus *L.* (*Lorisicola*) [male antennal flagellum with teeth on projection]				
L. americanus	Carnivora: felid (bobcat)	skin		North America
L. braziliensis	Carnivora: felid (pampas cat)	skin		South America
L. caffra	Carnivora: felid (cat)	skin		Africa
L. felis	Carnivora: felid (ocelot, pampas cat, puma)	skin		Americas
L. hercynianus	Carnivora: felid (cat)	skin		Europe
L. isidoroi	Carnivora: felid (Spanish lynx)	skin		Europe
L. malaysianus	Carnivora: felid (otter civet)	skin		South-East Asia
L. mjoebergi (syn. *F. brachycephalus*)	Primates: lorisid (slow loris)	skin		South-East Asia
L. neofelis	Carnivora: felid (Geoffrey's cat)	skin		South America
L. oncae	Carnivora: felid (jaguar)	skin		Americas
L. siamensis	Carnivora: felid (leopard cat)	skin		Asia
L. similis	Carnivora: felid (jaguarundi)	skin		Americas
L. spenceri	Carnivora: felid (Eurasian lynx, Canadian lynx)	skin		Eurasia, North America
L. sudamericanus	Carnivora: felid (tigrillo)	skin		Central

				America
Subgenus *L.* (*Paradoxuroecus*) [male antennal flagellum with teeth not on projection]				
L. acuticeps (syn. *F. genetta*)	Carnivora: viverrid (large-spotted genet, Abyssinian genet)	skin		Africa
L. africanus	Carnivora: viverrid (small-spotted genet)	skin		Africa
L. aspidorhynchus	Carnivora: prionodontid (banded linsag)	skin		South-East Asia
L. bengalensis	Carnivora: viverrid (Asian palm civet)	skin		South-East Asia
L. juccii	Carnivora: viverrid (masked palm civet)	skin		Indo-Asia
L. laticeps	Carnivora: herpestid (marsh mongoose)	skin		Africa
L. lenicornis	Carnivora: viverrid (giant genet, large-spotted genet)	skin		Africa
L. mungos	Carnivora: herpestid (slender mongoose)	skin		Africa
L. neoafricanus	Carnivora: viverrid (large-spotted genet)	skin		Africa
L. paralaticeps	Carnivora: herpestid (water mongoose)	skin		Africa
L. philippinensis	Carnivora: viverrid (Asian palm civet)	skin		Philippines
L. sumatrensis	Carnivora: prionodontid (banded linsag)	skin		South-East Asia
L. wernecki	Carnivora: viverrid (Haussa genet, large-spotted genet)	skin		Africa

Parasite morphology: *Felicola* spp. form 3 different types of stages during their development: eggs (sometimes called nits); nymphs (3 consecutive instars); and adult lice (male and female). The eggs are white-cream in colouration and elongate-oval in shape measuring 0.8-1.0 x 0.2-0.4 mm. They have an anterior operculum (lid) and are attached (glued) to host hairs by their bases sometimes on a short stalk. They contain a developing embryo which hatches as a first-stage nymph (N1) and then moults through another 2 nymphal stages (N2, N3) before moulting to adult lice. All nymphs are similar in morphology to adults but are smaller, less sclerotized, contain fewer body setae, and lack genitalia. Adult lice are elongate measuring 1.0-1.5 mm in length, dorso-ventrally flattened, pale in colour (often pale yellow sometimes with tan bands) and they have 3 body parts (broad head, small thorax, and oval abdomen). Members of the genus *Felicola* are characterized by a large triangular head notched at the apex rather than having broad rounded heads like other members of family Trichodectidae. The notch is continuous with a median longitudinal groove in the ventral surface of the head which fits a host hair shaft. The biting/chewing mouthparts comprise large ventral opposing sclerotized mandibles used to sever small pieces of food which are guided to the preoral cavity by a posterior plate-like labrum (often with an anterior hyaline pad-like protrusion (pulvinus)), 2 lateral maxillae and an anterior labium with salivary secretions provided through a central hypopharynx. In ischnoceran lice, the mandibles are inserted at right angles to the head (such that the condyles are posterior and the ginglymus is anterior), the maxillae and labium are reduced in size (compared to anopluran lice) with single-lobed maxillae attached to the sides of the tripartite labium. The mandibles and pulvinus assist in anchoring the louse to the host. The head lacks maxillary palps (present in amblyceran lice) but possesses stout filiform antennae that extend laterally (not in grooves) and consist of three short segments (rather than 5 segments as occurs in the family Philopteridae in birds). The alimentary tract comprises a foregut (pharynx, oesophagus, crop), midgut (ventriculus, caeca, mycetome (sometimes called bacteriome or stomach disc, harbouring bacterial/fungal symbionts)), and hindgut (pylorus, papillae, rectum). The thorax is small and trapezoidal and composed of segments fused together with indistinct boundaries. The ventral surface gives rise to 3 pairs of legs, each composed of 5 segments (coxa, trochanter, femur, tibia, tarsus). The hind-legs are slightly smaller than the fore- and mid-legs, and all legs terminate in a single tarsal claw (whereas those of philopterid lice from birds terminate in pairs of claws). The abdomen is oval-shaped and smooth in appearance with a few short setae and a variable number of dorsal spiracles (openings to tracheal (breathing) system) but numbering 6 or fewer in the subfamily Trichodectinae. Adult lice possess conspicuous genitalia, and male lice are slightly smaller than female lice. Males have 2 pairs of compact testes (3 pairs in amblyceran lice) connected to tubular vas deferens which coalesce to form a seminal vesicle opening into a large spinous genital sac equipped with a tubular intromittent organ (aedeagus with terminal endophallus and dorsal gonopore surrounded by a spicular patch) supported by basal plate-like apodeme and narrow rod-like lateral parameres. In males belonging to the subgenus *F.* (*Felicola*), the endophallus is thinly sclerotized whereas that in males of the subgenus *F.* (*Suricatoecus*) is not sclerotized. Females possess ovaries with polytrophic ovarioles, tubular oviducts, a globular uterus with accessory glands (produce glue) and a spermatheca (sperm storage vesicle), a genital opening (vagina) with a lobular genital plate and the posterior segment is bifurcated forming lateral gonopods with subgenital lobes (often with serrate margins, but without scales or spines). In females belonging to the subgenus *F.* (*Felicola*), the gonopods have rounded lobes while those in females of the subgenus *F.* (*Suricatoecus*) are rectangular and bear lateral spurs.

Site of infection: These chewing lice (also known as fur lice) are ectoparasitic on the skin and hair of carnivorous hosts, especially felids but also including some herpestids, viverrids and a few canids. Most species are relatively sedentary and tend to congregate in their predilection sites, particularly on the face, pinnae, along the back and tail, and in areas of higher moisture (near body openings or skin abrasions).

Pathogenesis: Light infestations may be asymptomatic and go unnoticed by their hosts, but heavier infestations may cause mild-severe disease characterized by intense skin irritation, hyperkeratosis and inflammation (dermatitis), often exacerbated by allergic responses to louse antigens. Lice feed using their mandibles to bite or scrape hairs and epidermal debris, and probably opportunistically on body fluids and blood from scabs and lesions. Their feeding behaviour results in skin inflammation with pruritus (itching), alopecia (hair loss) and epidermal sloughing (dandruff). Infested animals endeavour to relieve the pruritus by repetitive grooming (licking, scratching, rubbing) of afflicted body parts, which can lead to lesions due to self-excoriation, seborrhoea, unsightly coat, impaired thermoregulation, and secondary infections. Animals that are able to groom themselves properly appear to be able to control the clinical consequences of infestations, but old, poorly-nourished, sick, neglected or stray felids, especially long-haired breeds, may develop severe disease.

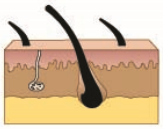
Several trichodectid species, possibly including *Felicola subrostratus,* have been implicated in the transmission of the double-pored tapeworm *Dipylidium caninum* by acting as an intermediate host for cysticercoid stages that may infect humans or dogs and cats when they ingest infected lice.

Developmental cycle and mode of transmission: All stages occur as ectoparasites in the fur of individual hosts: eggs being attached to hair shafts, and motile nymphs and adults using their claws and mouthparts to hold onto hairs. Transmission between hosts occurs when motile stages become dislodged from one host and crawl onto new hosts in direct/close contact or are transferred via contaminated grooming equipment or bedding. Gravid female lice glue their eggs onto hairs using an adhesive cement-like substance. The eggs hatch 10-12 days later releasing first-stage nymphs (N1) which commence feeding and undergo simple/incomplete (hemimetabolous) metamorphosis moulting through another 2 nymphal stages before forming adult lice in 2-3 weeks. After mating, female lice begin laying eggs several days later. Any developmental stages dislodged from hosts do not survive long in the external environment, dying within hours in warm dry conditions, but also within days in cool moist conditions. Transmission relies on close contact between hosts, as occurs during breeding, nursing, nesting or gregarious hosts. Some lice (mostly ischnoceran chewing lice) have also been observed to be transmitted between hosts by phoresy: i.e. temporary attachment to the external surfaces of larger insects that move between hosts (usually hippoboscid or muscid flies). Louse populations tend to increase in the cooler months of the year, when conditions are more favourable for louse development and survival and when hosts congregate for breeding or shared thermoregulation.

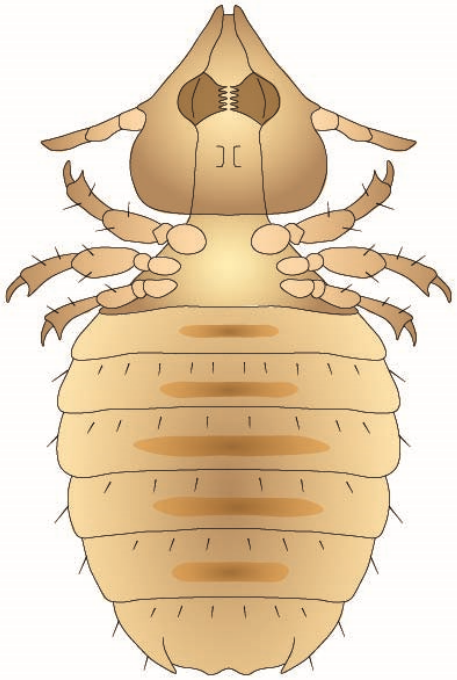
Differential diagnosis: While infestations may be suspected on clinical grounds (dermatitis and pruritus), diagnosis is made by direct demonstration of lice and/or their eggs upon clinical examination (visual examination of parted fur, sometimes aided by using magnifying glasses or grooming equipment). Sticky-tape impression smears may assist in the collection of eggs or lice for microscopic examination. Alternatively, infestations may sometimes be detected fortuitously when the undigested cuticular remains of lice are found upon routine coprological examination of host faecal samples (smears, sediments or floats). Molecular biological techniques have been used to characterize species and examine phylogenetic relationships between lice following polymerase chain reaction (PCR) amplification of nuclear (18S ribosomal RNA, elongation factor-1α) and mitochondrial (16S rRNA, cytochrome oxidase 1) gene sequences.

Treatment and control: A range of insecticidal chemicals have been used to treat clinical infestations, including organophosphates (dichlorvos, fenitrothion, fenthion), pyrethrins, pyrethroids (permethrin), macrocyclic lactones (ivermectin, selamectin), arylpyrazoles (fipronil), and chloronicotinyls (imidacloprid). Most chemicals are applied topically as shampoos/foams, rinses/sprays, aerosols or powders, although some recent formulations are given systemically as injectables, orals or spot-ons. Careful attention should be paid to product information regarding usage (side-effects, contra-indications) as well as to government regulation (concerning with-holding periods, environmental toxicity). Most chemicals have little residual activity and do not work effectively against egg stages, so treatments are best repeated 7-14 days later to kill any emergent nymphs before they mature to adults. A variety of fine-toothed combs have been designed to assist grooming in the removal of lice, but adherent nits (eggs and egg cases) are difficult to dislodge without using lubricants (conditioners) to ease tangles. Heavy infestations in long-haired animals may sometimes result in matted coats which are best clipped prior to treatment. Preventive control measures are based around minimizing contact with infested individuals (through quarantine, isolation or exclusion), decontaminating shared facilities and items (clothing, bedding, cages, pens and grooming equipment by washing with insecticidal chemicals), avoiding over-crowded unsanitary conditions, and maintaining healthy, well-nourished and well-groomed hosts (as they are better able to resist clinical infestations).

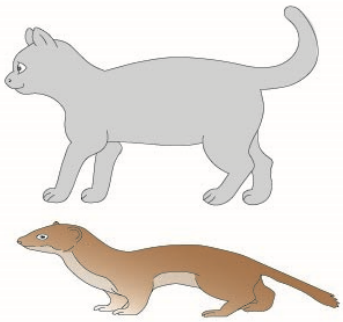
Felicola



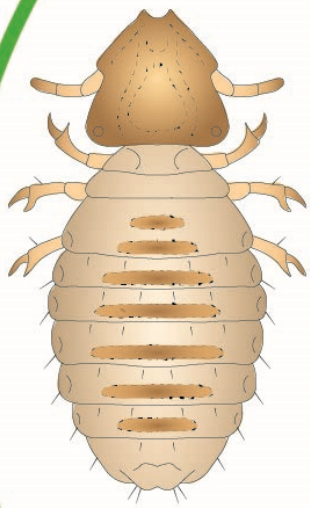
skin/pelage
(dermatitis, pruritus,
alopecia, dandruff)
(some vector infectious
microbial diseases)



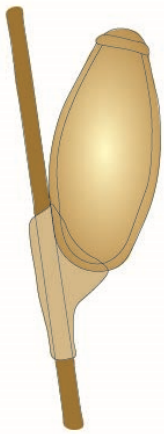
adult (ventral)
(~ 1.5 mm)



Definitive Hosts
(carnivores)



nymph (dorsal)
(~ 1.2 mm)



egg
(~ 1 mm)

all stages ectozoic on host
(motile stages feed on skin/scurf/hairs)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites



Felicola adult



Felicola egg

Lipeurus, Goniocotes, Goniodes, Cuclotogaster, Chelopistes
(insect: louse)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Mallophagan (chewing) lice have blunt rounded heads with mouthparts adapted for feeding on keratin in superficial skin layers. Chewing lice are ectoparasitic on mammals and birds, most species being highly host specific and even site-specific. Ischnoceran lice have prominent filiform antennae but lack maxillary palps. Philopterids have five antennal segments, paired tarsal claws and are found on birds. Infestations by *Lipeurus, Goniodes, Goniocotes, Cuclotogaster* and *Chelopistes* spp. have been associated with restlessness and reduced productivity in poultry and gamebirds.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order:	Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder:	Mallophaga (= wool-eating) (chewing lice, broad rounded head, feed on keratin, host/site specific)
Superfamily:	Ischnocera (without maxillary palps, prominent filiform antennae, keratin feeders (hairs/feathers))
Family:	Philopteridae (parasitize birds, five-segmented antennae, paired claws on tarsi)
Genus:	*Lipeurus* (parasitic on skin/feathers of birds)
Genus:	*Goniocotes* (parasitic on skin/feathers of birds)
Genus:	*Goniodes* (parasitic on skin/feathers of birds)
Genus:	*Cuclotogaster* (parasitic on skin/feathers of birds)
Genus:	*Chelopistes* (parasitic on skin/feathers of birds)
Species:	various species cause restlessness and reduced productivity in poultry and gamebirds

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Lice are small wingless hemipterodeans that undergo gradual (hemimetabolous) metamorphosis and are permanent obligate ectoparasites on other animals. Four suborders are recognized: the Anoplura containing the haematophagous sucking lice of placental mammals; the Ischnocera and Amblycera (previously classified together as Mallophaga) comprising the chewing or biting lice of birds, marsupials and placental mammals; and the Rhynchophthirina confined to elephants and warthogs in Africa.

Major parasitic phthirapteran families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Suborder: Ischnocera [Mallophaga p.p.] (chewing lice of mammals and birds, broad rounded head, without maxillary palps, prominent filiform antennae, keratin feeders) [2 families, 158 genera, 3,371 species]					
Philopteridae(bird lice)	138 genera, 2,958 spp.	birds	nymphs, adults	biting, chewing	-
Trichodectidae (fur lice)	20 genera, 413 spp.	mammals (bovids, equids, carnivores)	nymphs, adults	biting	helminth
Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					
Menoponidae (bird lice)	68 genera, 1,150 spp.	birds	nymphs, adults	biting, chewing	-
Boopiidae (marsupial chewing lice)	8 genera, 57 spp.	mammals (incl. marsupials)	nymphs, adults	biting	helminth
Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
Suborder: Anoplura (sucking lice of placental mammals) (narrow pointed head, pierce skin and feed on fluids (solenophagy)) [16 families, 51 genera, 694 species]					
Haematopinidae (ungulate lice, short-nosed lice)	1 genus, 21 spp.	mammals (equids, bovids, suids)	nymphs, adults	blood-sucking	viral, bacterial
Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-
Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial
Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-

Over 4,900 species of biting/chewing lice have been described in 253 genera in 8 families, around 4,400 species associated with birds and 500 species with mammals. Members of the suborder Ischnocera have broad rounded heads with conspicuous filiform antennae but lacking maxillary palps, while members of the suborder Amblycera have large rounded heads with maxillary palps and inconspicuous antennae hidden in grooves. Some 158 ischnoceran genera have been assigned to 2 families (Trichodectidae and Philopteridae), while 96 amblyceran genera have been classified in 6 families (Boopiidae; Gyropidae, Laemobothriidae, Menoponidae, Ricinidae, Trimenoponidae). Species of veterinary importance include members of the ischnoceran families Trichodectidae (bovids, canids, equids) and Philopteridae (poultry), and the amblyceran families Menoponidae (poultry) and Boopiidae (carnivores). Most ischnoceran lice are parasitic on birds, including the philopterids which are found mainly on galliform birds. Members of the family Philopteridae possess antennae with 5 segments and their legs terminate in tarsi with paired claws (in contrast to members of the family Trichodectidae which have 3-segmented antennae and single tarsal claws). Almost 3,000 philopterid species have been described from 138 genera: namely *Acidoproctus*, *Acutifrons*, *Aegypoecus*, *Alcedoecus*, *Alcedoffula*, *Anaticola*, *Anatoecus*, *Aquanirmus*, *Ardeicola*, *Ardeiphagus*, *Auricotes*, *Austrogoniodes*, *Austrophilopterus*, *Bedfordiella*, *Bizarrifrons*, *Bothriometopus*, *Brueelia*, *Bucerocophorus*, *Buceroemersonia*, *Buceronirmus*, *Bucorvellus*, *Buerelius*, *Campanulotes*, *Capraiella*, *Caracaricola*, *Carduiceps*, *Centropodiella*, *Chelopistes*, *Cirrophthirius*, *Colilipeurus*, *Colinicola*, *Coloceras*, *Columbicola*, *Cotingacola*, *Craspedonirmus*, *Craspedorrhynchus*, *Cuclotocephalus*, *Cuclotogaster*, *Cuculicola*, *Cuculoecus*, *Cummingsiella*, *Dahlemhornia*, *Degeeriella*, *Discocorpus*, *Docophoroides*, *Echinophilopterus*, *Emersoniella*, *Episbates*, *Esthiopterum*, *Falcolipeurus*, *Falcolius*, *Forficuloecus*, *Formicaphagus*, *Formicaricola*, *Fulicoffula*, *Furnariphilus*, *Galliphilopterus*, *Goniocotes*, *Goniodes*, *Haffneria*, *Halipeurus*, *Harrisoniella*, *Heptapsogaster*, *Hopkinsiella*, *Ibidoecus*, *Incidifrons*, *Kelloggia*, *Kodocephalon*, *Labicotes*, *Lagopoecus*, *Lamprocorpus*, *Lipeurus*, *Lunaceps*, *Megaginus*, *Megapeostus*, *Megapodiella*, *Meinertzhageniella*, *Meropoecus*, *Mulcticola*, *Nakicola*, *Naubates*, *Neophilopterus*, *Neopsittaconirmus*, *Nesiotinus*, *Nothocotus*, *Nyctibicola*, *Ornicholax*, *Ornithobius*, *Osculotes*, *Otidoecus*, *Oxylipeurus*, *Pachyskelotes*, *Paraclisis*, *Paragoniocotes*, *Paroncophorus*, *Passonomedea*, *Pectenosoma*, *Pectinopygus*, *Pelmatocerandra*, *Penenirmus*, *Perineus*, *Philoceanus*, *Philopterus*, *Physconella*, *Physconelloides*, *Picicola*, *Podargoecus*, *Pseudocophorus*, *Pseudolipeurus*, *Pseudonirmus*, *Pseudophilopterus*, *Psittaconirmus*, *Psittoecus*, *Pterocotes*, *Quadraceps*, *Rallicola*, *Rhopaloceras*, *Rhynonirmus*, *Rotundiceps*, *Saemundssonia*, *Splendoroffula*, *Strigiphilus*, *Strongylocotes*, *Struthiolipeurus*, *Sturnidoecus*, *Syrrhaptoecus*, *Theresiella*, *Tinamotaecola*, *Trabeculus*, *Trichodopeostus*, *Trichophilopterus*, *Trogoniella*, *Trogoninirmus*, *Turnicola*, *Turturicola*, *Upupicola*, *Vernoniella*, and *Wilsoniella*. Several species infest domestic poultry sometimes in association with disease, but most have been described from wild, game or aviary galliform birds. Nearly all species are considered to be host-specific, only a few occurring on closely-related hosts, and many are also thought to site-specific being restricted to specific parts of the body where particular feathers occur. The chewing lice *Lipeurus* (43 species) are frequently found on the skin and feathers of galliform birds, including domestic poultry. *Chelopistes* (34 species) are usually found in quill bases of phasianids in Palearctic and Oriental zoogeographic subregions and cracids in the Neotropical subregion, while *Cuclotogaster* (39 species), *Goniocotes* (46 species) and *Goniodes* (103 species) parasitize the skin and feathers of domestic and wild fowl from most continents.

***Lipeurus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
L. alexandermuelleri	Galliformes: megapodid (scrub fowl)	skin, feathers		Polynesia
L. boonsongi	Galliformes: phasianid (partridge)	skin, feathers		Thailand
L. brunneipictus (syn. *L. intermedius*)	Galliformes: phasianid (crested fireback)	skin, feathers		Asia
L. caponis (syn. *L. antennatus, bakeri, dovei, tesselatus, variabilis*) (wing louse)	Galliformes: phasianid (chicken, quail, jungle-fowl, pheasant, turkey, guineafowl), Pelecaniformes: ardeid (bittern)	skin, feathers (wing, tail)	restlessness, irritation	worldwide
L. charltonii	Galliformes: phasianid (hill partridge, tree partridge)	skin, feathers		Indochina
L. crassus	Galliformes: megapodid (brush turkey)	skin, feathers		Australia
L. crinitus	Galliformes (golden pheasant, Amherst's pheasant)	skin, feathers		Northern Hemisphere
L. deignani	Galliformes: phasianid (fireback pheasant)	skin, feathers		Thailand
L. dekkeri	Galliformes: megapodid (Micronesian scrubfowl)	skin, feathers		Micronesia
L. delta	Galliformes: phasianid (Reeve's pheasant)	skin, feathers		China
L. differens	Galliformes: phasianid (white-breasted guineafowl)	skin, feathers		West Africa
L. epsilon	Galliformes: phasianid (Cape francolin)	skin, feathers		South Africa
L. eurycnemis	Galliformes: phasianid (monal pheasant)	skin, feathers		Himalayas
L. fimbriatus	Galliformes (black partridge)	skin, feathers		South-East Asia
L. fradei	Accipitriformes: accipitrid (long-crested eagle)	skin, feathers		Africa
L. hamatus	Galliformes: phasianid (bobwhite quail)	skin, feathers		Americas
L. introductus (syn. *L. sellatus, subsellatus*)	Galliformes: phasianid (silver pheasant, Kalij pheasant)	skin, feathers		Indochina
L. jonesi	Galliformes: megapodid (brush turkey)	skin, feathers		New Guinea
L. keleri	Galliformes: phasianid (brown-eared pheasant, white-eared pheasant)	skin, feathers		China
L. latifasciatus	Galliformes: megapodid (dusky scrubfowl, Bismarck scrubfowl)	skin, feathers		Indonesia, New Guinea
L. lawrensis	Galliformes: phasianid (helmeted guineafowl)	skin, feathers		South Africa
L. lewisi	Galliformes: phasianid (ferruginous partridge)	skin, feathers		South-East Asia
L. maculosus	Galliformes: phasianid (grey partridge, common pheasant)	skin, feathers		Eurasia
L. meyeri	Galliformes: megapodid (brush turkey)	skin, feathers		New Guinea
L. moluccensis	Galliformes: megapodid (Wallace's scrubfowl)	skin, feathers		Indonesia, New Guinea
L. namalaius	Galliformes: megapodid (Banks Island scrubfowl)	skin, feathers		Vanuatu
L. nodosus	Galliformes: megapodid (collared brush turkey)	skin, feathers		New Guinea
L. numidae (syn. *L. numidianus*)	Galliformes: phasianid (helmeted guineafowl)	skin, feathers		South Africa
L. palauensis	Galliformes: megapodid (Micronesian scrubfowl)	skin, feathers		Micronesia
L. parkeri (syn. *L. sejugatus*)	Galliformes: megapodid (mallee fowl)	skin, feathers		Australia
L. parumsetosus (syn. *L. uncinatus*)	Galliformes: phasianid (crested wood partridge)	skin, feathers		South-East Asia
L. pavo	Galliformes: phasianid (common peafowl, green peafowl)	skin, feathers		South-East Asia
L. phasidus	Galliformes: phasianid (black guineafowl)	skin, feathers		Africa
L. polyplectron	Galliformes: phasianid (Malay peacock-pheasant, grey peacock-pheasant)	skin, feathers		South-East Asia
L. raymondi	Galliformes: phasianid (vulturine guineafowl)	skin, feathers		Africa
L. rheinardia	Galliformes: phasianid (crested argus)	skin, feathers		South-East Asia
L. sarissa	Galliformes: phasianid (long-billed partridge)	skin, feathers		South-East Asia

L. schoutedeni	Galliformes: phasianid (Congo peafowl)	skin, feathers		Africa
L. silvai	Galliformes: phasianid (crested guineafowl)	skin, feathers		South Africa
L. sinuatus	Galliformes: megapodid (dusky scrubfowl, Philippine scrubfowl, orange-footed scrubfowl)	skin, feathers		South-East Asia
L. talautensis	Galliformes: megapodid (Philippine scrubfowl)	skin, feathers		South-East Asia
L. tropicalis	Galliformes: phasianid (chicken)	skin, feathers		?
L. tsade	Galliformes: megapodid (wattled brush turkey, maleo)	skin, feathers		Africa, Indonesia

***Goniocotes* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
G. afer	Galliformes: phasianid (red-necked francolin)	feathers		Africa
G. afropavo	Galliformes: phasianid (Congo peafowl)	feathers		Africa
G. albidus (syn. *G. homocerus, phasiani*)	Galliformes: phasianid (silver pheasant)	feathers		South-East Asia
G. castaneicollis	Galliformes: phasianid (chestnut-naped francolin)	feathers		Africa
G. chapini	Galliformes: phasianid (Congo peafowl)	feathers		Africa
G. chrysocephalus	Galliformes: phasianid (ruffed grouse, common pheasant)	feathers		North America
G. clayae	Galliformes: phasianid (double-spurred francolin)	feathers		Africa
G. congolensis	Galliformes: phasianid (helmeted guineafowl)	feathers		Africa
G. coxatus	Tinamiformes: tinamid (solitary tinamou)	feathers		South America
G. crassicauda	Galliformes: phasianid (vulturine guineafowl)	feathers		Africa
G. creber	Galliformes: phasianid (silver pheasant)	feathers		South-East Asia
G. crossoptiloni	Galliformes: phasianid (white-eared pheasant)	feathers		Himalayas
G. diasi	Galliformes: phasianid (crested guineafowl)	feathers		Africa
G. diplogonus	Galliformes: phasianid (satyr tragopan)	feathers		Himalayas
G. eurygaster	Galliformes: phasianid (white-throated hill partridge)	feathers		Taiwan
G. gallinae (syn. *G. hologaster*) (fluff louse)	Galliformes: phasianid (chicken, turkey, ferruginous wood partridge)	feathers (back, rump)	restlessness, damaged plumage, anaemia	worldwide
G. gregarius	Galliformes: phasianid (grey-winged francolin)	feathers		South Africa
G. haplogonus	Galliformes: phasianid (monal pheasant)	feathers		Himalayas
G. ictiorhynchi	Galliformes: phasianid (yellow-billed francolin)	feathers		Africa
G. ignitus	Galliformes: phasianid (crested-fireback pheasant)	feathers		Indonesia
G. jirufti	Galliformes: phasianid (black francolin)	feathers		India
G. keleri	Galliformes: phasianid (red-necked francolin)	feathers		Africa
G. keniensis	Galliformes: phasianid (grey-winged francolin)	feathers		Africa
G. kivuensis	Galliformes: phasianid (handsome francolin)	feathers		Africa
G. maculatus (syn. *G. meleagris, nigromaculatus, numidae, valdezi*)	Galliformes: phasianid (chicken, helmeted guineafowl)	feathers		Africa
G. mayuri	Galliformes: phasianid (common peafowl)	feathers		South Asia
G. megalocephalus (syn. *G. macrocephalus*)	Galliformes: phasianid (hazel grouse)	feathers		Japan
G. microcephalus	Galliformes: phasianid (white-throated hill partridge)	feathers		Taiwan
G. microthorax (syn. *G. alatus, simillimus*)	Galliformes: phasianid (chukar partridge, grey partridge)	feathers		Europe
G. nahanii	Galliformes: phasianid (forest partridge)	feathers		Africa
G. obscurus	Galliformes: phasianid (red-legged partridge)	feathers		Europe
G. pallidiflavus	Galliformes: megapodid (mallee fowl)	feathers		Indonesia

G. pallidomaculatus	Galliformes: phasianid (bar-backed partridge, chestnut-headed partridge, chestnut-bellied partridge, grey-breasted partridge, rufous-throated partridge)	feathers		Indonesia
G. parviceps (syn. *G. yngarejsuf*)	Galliformes: phasianid (common peafowl, green peafowl)	feathers		South Asia
G. plumiferae	Galliformes: phasianid (plumed guineafowl)	feathers		Africa
G. pternistis	Galliformes: phasianid (yellow-necked francolin)	feathers		Africa
G. pucherani	Galliformes: phasianid (crested guineafowl)	feathers		Africa
G. punctatus	Apodiformes: trochilid (green-throated carib)	feathers		Central America
G. pusillus	Galliformes: phasianid (chukar partridge, Barbary partridge)	feathers		North Africa
G. rectangulatus (syn. *G. rectangulus*)	Galliformes: phasianid (common peafowl)	feathers		South Asia
G. reticulatus	Galliformes: phasianid (Kalij pheasant, green pheasant)	feathers		Indochina
G. rotundiceps	Galliformes: phasianid (Reeve's pheasant)	feathers		China
G. schraderi	Galliformes: phasianid (Erckel's francolin)	feathers		Africa
G. shelleyii	Galliformes: phasianid (Shelley's francolin)	feathers		Africa
G. tetraophasis	Galliformes: phasianid (monal partridge)	feathers		China
G. vulturini	Galliformes: phasianid (vulturine guineafowl)	feathers		Africa

***Goniodes* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
G. aepypodius	Galliformes: megapodid (Bruijn's brush turkey)			Indonesia
G. agelastes (syn. *G. latifasciatus*)	Galliformes: phasianid (white-breasted guineafowl, crested fireback pheasant)			Africa, South-East Asia
G. ammoperdix	Galliformes: phasianid (sand partridge, see see partridge)			Arabia
G. antennatus	Galliformes: phasianid (yellow-necked spurfowl)			Africa
G. arfakianus	Galliformes: megapodid (wattled brush turkey)			Indonesia
G. argus	Galliformes: phasianid (great argus pheasant)			Southeast Asia
G. assimilis (syn. *G. pternistis*)	Galliformes: phasianid (red-necked francolin, Ahanta spurfowl, double-spurred spurfowl, Cape spurfowl, chestnut-naped spurfowl, Clapperton's spurfowl, Coqui francolin, Erckel's spurfowl, Hildebrandt's spurfowl, yellow-necked spurfowl, red-winged francolin, Orange River francolin, Natal spurfowl, crested francolin, scaly spurfowl, Swainson's spurfowl, stone partridge)			Africa
G. astrocephalus (syn. *G. gracilis*)	Galliformes: phasianid (common quail, harlequin quail, rain quail)			Europe, Africa, Indochina
G. australis (syn. *G. maorianus*)	Galliformes: megapodid (mallee fowl)			Australia
G. bambusicolus	Galliformes: phasianid (mountain bamboo partridge)			Indo-Asia
G. bifurcus	Galliformes: phasianid (crested guineafowl)			Africa
G. biordinatus	Galliformes: megapodid (scrub fowl)			New Guinea, Micronesia
G. bituberculatus	Galliformes: phasianid (western capercaillie)			Europe, Russia
G. bonasus	Galliformes: phasianid (ruffed grouse)			North America
G. capitatus	Galliformes: phasianid (common pheasant)			Asia
G. centrocerci	Galliformes: phasianid (sage grouse)			North America
G. cervinicornis	Galliformes: phasianid (silver pheasant, Kalij pheasant)			Indo-Asia
G. chloropus	Galliformes: phasianid (green-legged hill partridge)			Thailand
G. chrysolophi	Galliformes: phasianid (golden pheasant, Lady			Eurasia, Americas

	Amherst's pheasant)			
G. colchici	Galliformes: phasianid (common pheasant)			Asia
G. columbianus (syn. *G. latiorfasciatus*)	Galliformes: phasianid (crested bobwhite)			South America
G. confusio	Galliformes: megapodid (Nicobar scrub fowl)			India
G. coronatus (syn. *G. laevis, obscrurus*)	Galliformes: phasianid (crested wood partridge)			Southeast Asia
G. corpulentus	Galliformes: phasianid (spruce grouse)			North America
G. costatus (syn. *G. tetraogallae*)	Galliformes: phasianid (Tibetan snowcock, Himalayan snowcock, Altai snowcock)			Himalayas
G. crassipes	Galliformes: megapodid (red-billed brush turkey)			Indonesia
G. crossoptilon	Galliformes: phasianid (blue-eared pheasant, black-billed brush turkey)			Asia, New Guinea
G. cupido	Galliformes: phasianid (prairie chickens)			North America
G. curtiprothorax	Galliformes: megapodid (collared brush turkey)			New Guinea
G. curvicornis	Galliformes: phasianid (great argus pheasant)			Southeast Asia
G. diardi	Galliformes: phasianid (Siamese fireback pheasant)			Asia
G. discogaster	Galliformes: megapodid (dusky scrub fowl)			Indonesia
G. dispar (syn. *G. breviantennatus, cypricus, flaviceps, truncatus*)	Galliformes: phasianid (chukar partridge, rock partridge, red-legged partridge, grey partridge)			Europe
G. dissimilis (brown chicken louse)	Galliformes: phasianid (chicken, grey junglefowl, Sri Lankan jungle-fowl)	feathers (body)	restlessness, damaged plumage, reduced productivity	worldwide
G. dolani	Galliformes: phasianid (white-eared pheasant)			Indo-China
G. emersoni	Galliformes: phasianid (montane francolin)			Africa
G. eurygaster	Galliformes: phasianid (monal pheasant)			Himalayas
G. fissus	Galliformes: megapodid (wattled brush turkey, Waigeo brush turkey, Australian brush turkey)			Indonesia, New Guinea
G. gigas (syn. *G. abdominalis, hologaster*) (large chicken louse)	Galliformes: phasianid (chicken, plumed guineafowl, crested guineafowl, helmeted guineafowl)	skin, feathers (body)	restlessness, damaged plumage, reduced productivity	worldwide, esp. tropics
G. graecus	Galliformes: phasianid (rock partridge)			Europe
G. gutterae	Galliformes: phasianid (plumed guineafowl)			Africa
G. hopkinsi	Galliformes: phasianid (crested guineafowl)			Africa
G. humiae	Galliformes: phasianid (Hume's pheasant, Elliot's pheasant)			Indochina
G. inaequalis	Galliformes: phasianid (crested guineafowl)			Africa
G. indicus	Galliformes: phasianid (rufous-throated partridge, hill partridge)			Indo-Asia
G. intermedius	Galliformes: phasianid (koklass)			Indochina
G. isogenos	Galliformes: phasianid (greyling francolin)			Africa
G. ithaginis	Galliformes: phasianid (blood pheasant)			Indochina
G. keleri	Galliformes: phasianid (brush turkey, Madagascar partridge)			Australia
G. klockenhoffi	Galliformes: phasianid (helmeted guineafowl)			Africa
G. lagopi (syn. *G. chelicornis, lagopodis*)	Galliformes: phasianid (rock ptarmigan, red grouse, western capercaillie)			Eurasia, North America
G. leipoae	Galliformes: megapodid (Mallee fowl)			Australia
G. leucurus	Galliformes: phasianid (snow quail)			North America
G. longus	Galliformes: phasianid (king quail, crested			Asia

(syn. *G. pallidus*)	fireback pheasant, crestless fireback pheasant)			
G. lootensi	Galliformes: phasianid (king quail)			Asia
G. lophurus	Galliformes: phasianid (Kalij pheasant)			Himalayas
G. macrocephalus	Galliformes: megapodid (brush turkey)			Australia
G. major (syn. *G. meyeri*)	Galliformes: megapodid (blue-eared pheasant, New Guinea scrubfowl, dusky megapode, Philippine megapode, Melanesian megapode, Micronesian megapode, Nicobar megapode, black-billed brush turkey)			Asia
G. megaceros	Galliformes: phasianid (Himalayan monal, Slater's monal)			India
G. meinertzhageni	Galliformes: phasianid (common peafowl)			South Asia
G. merriamanus (syn. *G. simoni*)	Galliformes: phasianid (dusky grouse)			North America
G. meyi	Galliformes: phasianid (helmeted guineafowl)			Africa
G. minimus	Galliformes: megapodid (orange-footed scrubfowl)			New Guinea
G. minor	Galliformes: megapodid (Philippine scrubfowl, Sula scrubfowl, orange-footed scrubfowl)			Philippines, Indonesia, Australasia
G. montschadskyi	Galliformes: phasianid (black-billed capercaillie)			Russia, China
G. moucheti	Galliformes: phasianid (handsome francolin)			Africa
G. nebraskensis	Galliformes: phasianid (sharp-tailed grouse)			North America
G. neokeleri	Galliformes: megapodid (brush turkey)			Australia
G. numidae (syn. *G. fimbriatus, perlatus*) (guinea feather louse)	Galliformes: phasianid (helmeted guineafowl)			Africa
G. ocellatus (syn. *G. dentatus*)	Galliformes: phasianid (Kalij pheasant, koklass)			Himalayas
G. ocrea	Galliformes: megapodid (Moluccas scrub fowl)			Indonesia
G. oreophilus	Galliformes: phasianid (Jackson' spurfowl, Shelley's francolin)			Africa
G. ortygis	Galliformes: phasianid (bobwhite)			North America
G. ovoidalis	Galliformes: phasianid (California quail)			North America
G. pavonis (syn. *G. falcicornis, tetragonocephalus*)	Galliformes: phasianid (green peafowl, common peafowl)			South Asia
G. phasidus	Galliformes: phasianid (black guineafowl)			Africa
G. pictus	Galliformes: phasianid (mountain quail)			North America
G. plumiferae	Galliformes: phasianid (plumed guineafowl)			Africa
G. processus	Galliformes: phasianid (bar-backed partridge, white-cheeked partridge, white-necklaced partridge, rufous-throated partridge, hill partridge)			Indo-Asia
G. reichenowii	Galliformes: phasianid (helmeted guineafowl)			Africa
G. retractus	Galliformes: phasianid (brown quail)			Australia
G. rhynchortyx	Galliformes: phasianid (tawny-faced quail)			Central and South America
G. schoutedenii	Galliformes: phasianid (crested guineafowl)			Africa
G. scleroptilus	Galliformes: phasianid (Orange River francolin)			Africa
G. sectus	Galliformes: phasianid (cheer pheasant)			India
G. securiger	Galliformes: phasianid (Barbary partridge)			North Africa
G. sinensis	Galliformes: phasianid (Mikado pheasant)			Taiwan
G. soueefi (syn. *G. elongatus*)	Galliformes: phasianid (quail, fireback pheasant)			Eurasia
G. spinicornis (syn. *G. bicuspidatus*)	Galliformes: phasianid (Blyth's tragopan, Temminck's tragopan, satyr tragopan)			Indochina
G. squamatus	Galliformes: phasianid (scaled quail)			North America
G. stefani	Galliformes: phasianid (California quail)			North America

(syn. *G. mamillatus*)				
G. submamillatus	Galliformes: phasianid (Gambel's quail)			North America
G. talegallae	Galliformes: megapodid (black-billed brush turkey)			New Guinea
G. temporalis (syn. *G. extraneus*)	Galliformes: phasianid (swamp partridge)			India
G. tetraonis (syn. *G. heterocerus*)	Galliformes: phasianid (black grouse)			Eurasia
G. tetraophasis	Galliformes: phasianid (monal partridge)			China
G. tibetanus	Galliformes: phasianid (Tibetan snowcock)			Himalayas
G. tragopan	Galliformes: phasianid (western tragopan)			Himalayas
G. wilsoni	Galliformes: phasianid (Congo peafowl)			Africa
G. zairensis	Galliformes: phasianid (plumed guineafowl)			Africa

***Chelopistes* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
C. bicolor	Galliformes: cracid (Marail guan)	feathers		South America
C. calvus	Galliformes: phasianid (marbled wood quail)	feathers		South America
C.chamaepetes	Galliformes: cracid (sickle-winged guan)	feathers		South America
C.costaricensis	Galliformes: cracid (black guan)	feathers		Central America
C. craxae	Galliformes: cracid (blue-billed curassow)	feathers		South America
C.dendrortyx	Galliformes: phasianid (singing quail, buffy-crowned wood partridge, long-tailed wood partridge)	feathers		South America
C. elongatus	Galliformes: phasianid (rufous-fronted wood quail)	feathers		South America
C. erythrops	Galliformes: phasianid (rufous-fronted wood quail)	feathers		South America
C. eximius	Galliformes: cracid (horned guan)	feathers		Central America
C. guttatus	Galliformes: phasianid (spot-winged wood quail)	feathers		South America
C. heterurus	Galliformes: phasianid (rufous-fronted wood quail)	feathers		South America
C.hyperythra	Galliformes: phasianid (chestnut wood quail)	feathers		South America
C. jacquacu	Galliformes: cracid (Spix's guan)	feathers		South America
C. karachiensis	Galliformes: phasianid (turkey)	feathers		India
C. latafrons	Galliformes: cracid (grey-headed chachalaca, chestnut-winged chachalaca, little chachalaca, West Mexican chachalaca, rufous-vented chachalaca)	feathers		Americas
C. lervicola	Galliformes: phasianid (snow partridge)	feathers		Indochina
C. leucolaema	Galliformes: phasianid (white-throated wood quail)	feathers		South America
C. longicephalus	Galliformes: phasianid (marbled wood quail)	feathers		South America
C. longipes	Galliformes: cracid (helmeted curassow)	feathers		South America
C. longisetosus	Galliformes: phasianid (wood quail)	feathers		South America
C. macropoda	Galliformes: phasianid (marbled wood quail)	feathers		South America
C. melanonotus	Galliformes: phasianid (black-backed wood quail)	feathers		South America
C. meleagridis (syn. *C. stylifer*) (large turkey louse)	Galliformes: phasianid (turkey, ocellated turkey)	skin, feathers (body)	restlessness, damaged plumage, reduced productivity	worldwide, esp. tropics
C. mexicanus	Galliformes: phasianid (spotted wood quail)	feathers		North America
C. minutus	Galliformes: phasianid (black-fronted wood quail)	feathers		South America
C. oculari	Galliformes: cracid (crested guan, dusky-legged guan, Andean guan)	feathers		Central and South America
C. peruviana	Galliformes: phasianid (rufous-breasted wood quail)	feathers		South America
C. phasiani	Galliformes: cracid (little chachalaca)	feathers		South America

C. pilosus	Galliformes: cracid (Andean guan)	feathers		South America
C. quadratus	Galliformes: phasianid (stripe-faced wood quail)	feathers		South America
C. rotundus (syn. *C. diversus*)	Galliformes: cracid (highland guan)	feathers		Central America
C. setosus	Galliformes: phasianid (marbled wood quail, rufous-fronted wood quail)	feathers		South America
C. stigmatus	Galliformes: cracid (band-tailed guan)	feathers		South America
C. subquadratus	Galliformes: cracid (sickle-winged guan)	feathers		South America
C. texanus	Galliformes: cracid (plain chachalaca)	feathers		North America

***Cuclotogaster* species (syn. *Cuclutogaster*)**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
C. acuminatus	Galliformes: phasianid (king quail)	skin, feathers		South-East Asia
C. aethiopicus	Galliformes: phasianid (chestnut-naped francolin)	skin, feathers		North Africa
C. arabicus	Galliformes: phasianid (Arabian chukar)	skin, feathers		Arabia
C. barbara	Galliformes: phasianid (Barbary partridge)	skin, feathers		North Africa
C. bicalcaratus	Galliformes: phasianid (double-spurred francolin)	skin, feathers		Africa
C. cameratus	Galliformes: phasianid (black grouse)	skin, feathers		Eurasia
C. cinereus	Galliformes: phasianid (common quail, Japanese quail)	skin, feathers		Europe, North Africa, Asia
C. erckelii	Galliformes: phasianid (Erckel's francolin)	skin, feathers		Africa
C. gedgii	Galliformes: phasianid (Clapperton's francolin)	skin, feathers		Africa
C. haydocki	Galliformes: phasianid (coqui francolin)	skin, feathers		Africa
C. heterogrammicus	Galliformes: phasianid (grey partridge)	skin, feathers		Eurasia
C. heterographus (syn. *C. burnetti, eynsfordii, laticorpus, pallidus*) (chicken head louse)	Galliformes: phasianid (chicken, Chukar partridge, green peafowl, pheasant), Tinamiformes (tinamou)	skin, feathers (head, neck)	scales, scabs, feather loss, weakness	worldwide
C. heyi	Galliformes: phasianid (sand partridge)	skin, feathers		Arabia
C. hopkinsi	Galliformes: phasianid (greyling francolin)	skin, feathers		Africa
C. hungerfordi	Galliformes: phasianid (Jackson's francolin)	skin, feathers		Africa
C. insolitus	Galliformes: phasianid (rufous-throated partridge)	skin, feathers		Indochina
C. maculipes	Galliformes: phasianid (bobwhite quail)	skin, feathers		North America
C. madagascariensis	Galliformes: phasianid (Madagascar partridge)	skin, feathers		Madagascar
C. maranensis	Galliformes: phasianid (scaly francolin)	skin, feathers		Africa
C. meinertzhageni	Galliformes: phasianid (yellow-necked francolin)	skin, feathers		Africa
C. moucheti	Galliformes: phasianid (Clapperton's francolin)	skin, feathers		Africa
C. nigromarginatus	Galliformes: phasianid (Kalij pheasant)	skin, feathers		Indo-Asia
C. notatus	Galliformes: phasianid (stone partridge)	skin, feathers		Africa
C. obscurior (syn. *C. obscurus*)	Galliformes: phasianid (red-legged partridge, rock partridge)	skin, feathers		Europe
C. occidentalis	Falconiformes: phasianid (palm-nut vulture)	skin, feathers		Africa
C. phayrei	Galliformes: phasianid (Chinese francolin)	skin, feathers		Asia
C. placentella	Galliformes: phasianid (grey-striped francolin)	skin, feathers		Africa
C. pternistis	Galliformes: phasianid (red-necked spurfowl, Swainson's francolin)	skin, feathers		Africa
C. rosalindae	Galliformes: phasianid (Shelley's francolin)	skin, feathers		Africa
C. sephaenae	Galliformes: phasianid (crested francolin)	skin, feathers		Africa
C. spinicaudatus	Galliformes: phasianid (jungle bush quail)	skin, feathers		Asia
C. subinsolitus	Galliformes: phasianid (bar-backed partridge)	skin, feathers		Thailand
C. synoicus	Galliformes: phasianid (brown quail)	skin, feathers		Australasia

C. tetraogallus	Galliformes: phasianid (Tibetan snowcock, Caucasian snowcock, Altai snowcock)	skin, feathers		Indochina
C. theresae	Galliformes: phasianid (black francolin)	skin, feathers		India
C. ugandanus	Galliformes: phasianid (Clapperton's francolin)	skin, feathers		Africa
C. zumpti	Galliformes: phasianid (coqui francolin)	skin, feathers		Africa

Parasite morphology: Philopterid chewing lice form 3 different types of developmental stages: eggs (often called nits, although some restrict this term to empty egg-cases); nymphs (3 consecutive instars); and adult lice (males and females). The eggs are pale-coloured (tan to grey) and elongate oval-ellipsoidal in shape measuring around 0.7-1.0 mm in length. They are attached by their bases to feathers but appear to lay longitudinally along quills. The eggs are embryonated and eventually hatch to release first-stage nymphs which moult twice before forming adult lice. All 3 nymphal instars are similar in morphology to adults, but are smaller, less sclerotized, possess fewer body setae, and lack genitalia. Adult lice are generally small in size (1-5 mm long), range from pale-tan to grey to reddish-brown in colour, and have dorso- ventrally flattened bodies comprising 3 distinct parts (head, thorax and abdomen). The family Philopteridae is extremely biodiverse and contains almost 140 genera which are unified by several defining characteristics (notably the presence of 5-segmented antennae and paired tarsal claws) but otherwise display considerable pleomorphic variation. Adult lice belonging to the genera *Goniocotes, Goniodes* and *Chelopistes* have stout squat bodies, those of the genus *Cuclotogaster* have barrel-shaped bodies, and those of the genus *Lipeurus* have distinctive narrow elongate bodies. They all have prominent heads, rounded anteriorly (often described as circum-fasciate (rounded in an unbroken arc)), nearly as wide as the abdomen, and sometime helmet-like in appearance. Most heads bear setae, either several short anterior hairs (*Lipeurus*), both anterior and posterior hairs (*Cuclotogaster*), or 2-3 long posterolateral bristles (*Goniocotes, Goniodes, Chelopistes*). Philopterid lice lack maxillary palps (present in amblyceran lice) and all species have 2 lateral filiform antennae which are conspicuous (not confined to antennal grooves like amblyceran lice), each antenna composed of 5 segments (not 3 like trichodectid lice). The first antennal segment on male *Lipeurus, Chelopistes, Cuclotogaster* and *Goniodes* is enlarged, those of male *Goniodes* bears thumb-like prongs (absent on male *Gonicotes*) and the third antennal segment of male *Cuclotogaster* has spur-like extensions. These chewing lice have small ventral mouthparts with 2 opposing sclerotized mandibles closing over a posterior plate-like labrum (often with an anterior hyaline pad-like pulvinus), 2 lateral maxillae and an anterior labium. Food particles are maneuvered into the preoral cavity and salivary secretions are added through a central hypopharynx. The mandibles of ischnoceran lice are inserted at right angles to the head (so the condyles are posterior and the ginglymus is anterior), the maxillae are reduced to single lobes, and the labium is small and tripartite. The mouth opens to the alimentary tract which comprises a foregut (with hypopharynx, salivary glands, oesophagus and fusiform crop), a large midgut (with ventriculus and anterior caeca) and a hindgut (with pylorus, papillae and rectum). The midgut contains a rudimentary organ known as the mycetome (or bacteriome or stomach disc) harbouring bacterial/fungal symbionts (mycetome more developed in anopluran sucking lice, but absent in amblyceran lice). The thorax is small and narrow and composed of fused segments with indistinct boundaries, often with dorsal sternal plates bearing long lateral or posteriorly directed bristles. The ventral thorax gives rise to 3 pairs of legs, each composed of 5 segments (coxa, trochanter, femur, tibia, tarsus) and all bearing paired tarsal claws (in contrast to the single tarsal claws found on trichodectid lice). The legs are generally similar in size, although those of some genera differ in length (the hind-legs of *Lipeurus* are longer than the mid- and fore-legs, while the fore-legs of *Cuclotogaster* are shorter than the mid- and hind-legs). The abdomen is oval to elliptical in shape and has 8 conspicuous segments with well-developed sclerotized paratergal plates (except *Lipeurus*) with lateral spiracles (openings to the tracheal (breathing) system). The abdominal segments of the different genera differ in their chaetotaxy (arrangement of setae), ranging from sparse numbers (*Lipeurus*) to several rows of short dorsal and ventral setae (*Cuclotogaster*) or more frequently rows of short dorsal setae and tufts of long ventrolateral bristles (*Goniocotes, Goniodes, Chelopistes*). Adult lice exhibit sexual size dimorphism, with female lice being larger than males. The size differences between sexes of different philopterid species has been shown to generally conform to Rensch's rule (allometric increase in male body size relative to female size, i.e. larger lice produce proportionately larger males although they remain smaller than females). Male lice have 2 pairs of lobular testes (3 pairs in amblyceran lice) joined to tubular vas deferens which coalesce into a seminal vesicle connected to the genital sac equipped with a tubular copulatory/intromittent organ (aedeagus with dorsal gonopore and terminal endophallus (pseudopenis)) supported by a basal apodeme (plate-like sclerite) and 2 lateral parameres (rod-like sclerites). Female lice have saccular ovaries with polytrophic ovarioles and tubular oviducts connected to a globular uterus with spermatheca (sperm storage vesicle) and accessory glands (produce adhesive glue/cement used in oviposition). The uterus opens into a vaginal receptacle with a genital plate that is located between well-developed bifurcated gonopods often with elongate terminal setae.

Site of infection: Philopterid lice are ectoparasitic on the skin and/or feathers of their avian hosts. Eggs are attached to barbs near the bases of feather quills, while nymph and adult stages are mostly found amongst fluff and down at the bases of feathers. Most species are oioxenous (specific for individual host species) or stenoxenous (specific for a small number of closely-related host species). These ischnoceran chewing lice are relatively more sedentary than amblyceran chewing lice, and exhibit greater site specificity (tissue tropism) for particular regions of the head, neck, back, belly, wings, tail and vent (although they may be more widespread in heavy infestations). *Cuclotogaster* spp. seem to prefer the skin and feathers of the head (many known as head lice), *Lipeurus* spp. are usually found on the undersides of the wings and tail (many known as wing lice), *Chelopistes* spp. inhabit the bases of quills on the back, belly and wings, *Goniocotes* spp. mainly infest the back and vent (many known as fluff lice), and *Goniodes* spp. are more widespread over the body.

Pathogenesis: Light infestations by these bird lice are often asymptomatic and remain subclinical, but heavy infestations may cause mild-severe disease characterized by irritation, inflammation, self-trauma, damaged plumage and weight loss. These ischnoceran chewing lice feed on skin and/or feathers using a biting or scraping action of their mandibles. Some species have occasionally been observed to feed on blood either by scraping the integument until it bleeds or by chewing on blood clots associated with skin lesions. Lice foraging and feeding on skin and feathers can be extremely irritating to birds and may cause damage to underlying tissues, with local inflammation, pruritus and hyperkeratosis (possibly exacerbated by allergic responses to louse antigens). Birds become restless and endeavor to relieve the annoyance by repetitive grooming (scratching the skin, preening and pulling feathers) which may result in self-trauma with skin lesions (scabs, scales, crusts) and unsightly appearance due to damaged plumage (broken rough feathers losing colour, dirty feathers near the vent) and depluming (feather loss, bald spots). This may result in impaired thermoregulation (birds unable to keep warm), poor health (weakness, debility, inappetence, pallor, sometimes anaemia, predisposition to secondary infections) and reduced productivity (reduced growth, poor weight gain or weight loss, decreased egg production, and occasionally death). Birds can often control philopterid louse populations through preening as these lice are relatively sedentary and hide in the plumage (they are less agile than amblyceran lice and therefore less able to escape preening). Lice numbers increase on birds unable to groom effectively, and debeaked birds become more heavily infested. Clinical infestations are more prevalent in colder weather, particularly on younger birds, presumably due to their immunological immaturity, gregarious behaviour and limited grooming skills.

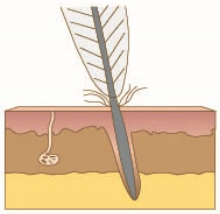
Developmental cycle and mode of transmission: Bird lice are intimate ectoparasites that live permanently in the plumage of their avian hosts. Gravid female lice attach eggs to feathers singly or in clusters where they develop and hatch after 4-7 days releasing first-stage nymphs. These stages feed and undergo hemimetabolous development with gradual (incomplete) metamorphosis through another 2 nymphal stages before moulting to adults. All motile stages (nymphs and adults) cling to feathers and feed on keratinized elements (feathers and/or skin). Each nymphal stage lasts for 5-15 days depending on prevailing environmental conditions (shorter duration in mild moist conditions) and adult lice may live for up to 36 days. After mating, female lice begin laying around 2 eggs per day for up to 30 days. The entire life-cycle may be completed in 18-35 days. There are no free-living stages and any lice dislodged from hosts do not survive long (hours to days depending on climatic conditions). Transmission between hosts is therefore direct and only occurs when lice move from one host to another when in prolonged close or direct contact. Lice are more active and abundant in autumn and winter when temperature and moisture conditions favour louse development and survival and hosts may exhibit more gregarious behaviours associated with shared thermoregulation (flocking) and reproduction (mating and nesting). While ischnoceran philopterid lice are well adapted to move about feathers and hide in plumage, they are more sedentary and not as agile as amblyceran menoponid lice and are therefore more susceptible to predation by host preening. Healthy fully-fledged birds are often able to control louse populations by grooming, including preening, sunning and dust-bathing, especially over summer months. Some lice (mostly ischnoceran chewing lice) have also been observed to be transmitted between hosts by phoresy, that is, by temporary attachment to external surfaces of larger arthropods that move between hosts (particularly hippoboscid or muscid flies).

Differential diagnosis: Infestations may be suspected on the grounds of symptomatology when birds become restless and relentlessly scratch and peck themselves. Definitive diagnosis is achieved by the direct detection of louse developmental stages (eggs, nymphs, adults) by visual examination of bird feathers and skin, performed by parting feathers in suspect areas (especially the vent if dirty) looking for attached eggs and lice moving away from light. Physical examination may be aided by using magnifying glasses and blunt instruments to probe feathers and fluffy down. Lice may be collected for microscopic examination and identification. Modern molecular biological techniques have been used to characterize various philopterid species and examine their phylogenetic relationships following polymerase chain reaction (PCR) amplification of nuclear (elongation factor 1-alpha) and mitochondrial (cytochrome oxidase 1) genes.

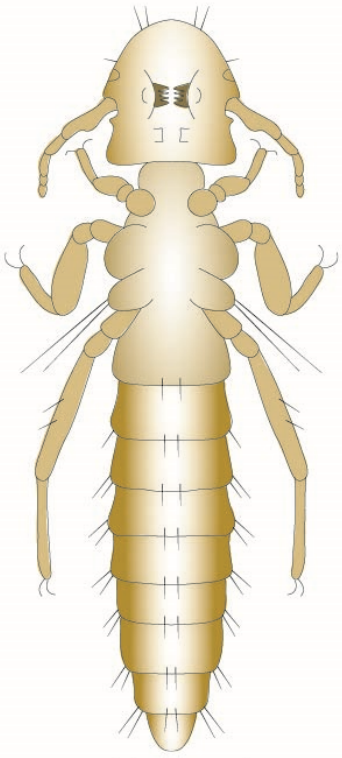
Treatment and control: A range of insecticides have been used to treat clinical infestations, including organophosphates (malathion, tetrachlorvinphos), pyrethroids (permethrin), spinosyns (spinosad), macrocyclic lactones (ivermectin, moxidectin) and some natural products (such as rotenone (recently banned in several countries). Careful attention should be given to recommendations and regulations governing chemical usage (including with-holding periods, residues, contra-indications, environmental toxicity). It is advisable to treat the entire flock simultaneously, and to repeat treatments 1-2 weeks later as the eggs are often resistant and may hatch to reinfest the flock. Chemicals are available as topical applications (powders, sprays, baths) or as systemic formulations (injectable, oral or spot-on). Small numbers of birds are often treated using insecticidal powders or spray solutions ensuring thorough coverage by manually ruffling the plumage. Head lice have also been treated by mixing powders with petroleum jelly or vaseline and rubbing the mixture onto affected areas. Powders may also be mixed with diatomaceous earth, sulphur dust, sand or wood ash and made available for self-administration in dust boxes in open aviaries, but not all bird species avail themselves of dust baths, nor do all individuals of compliant species. Liquid sprays, washes and baths have exhibited variable efficacy as feathers often provide waterproof barriers, and wet chilled birds may develop respiratory conditions. More recently, a range of liquids containing essential oil extracts were reported to have some efficacy, but some caused skin, eye or respiratory irritation, and many apparently acted only as repellents and birds quickly became re-infested. Several macrocyclic lactones have

been used for the systemic treatment of infestations, with better residual activity providing longer term protection, but they are not registered for use in poultry destined for human consumption (including both meat and egg production). Preventive control is based around disease detection (routine monitoring), minimizing contact with infested individuals (quarantine/isolation of infested birds, exclusion of wild birds), maintaining hygienic conditions (avoid crowded conditions, regular cleaning and decontamination of shared facilities and equipment) and maintaining healthy well-nourished birds (more resistant to infestations) which are able to self-groom (de-beaked birds are unable to preen effectively).

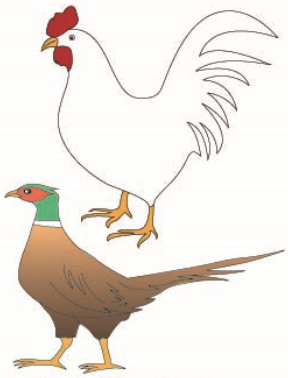
Lipeurus



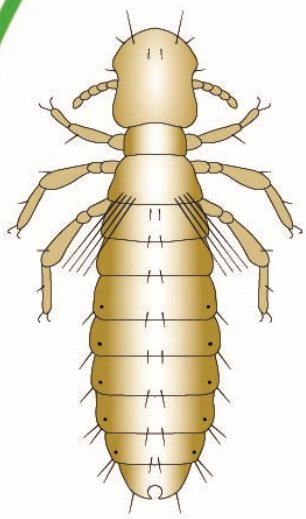
skin/plumage
(irritation, inflammation,
damaged feathers,
reduced productivity)



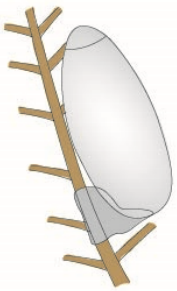
adult (ventral)
(~ 4 mm)



Definitive Hosts
(birds)



nymph (dorsal)
(~ 2 mm)

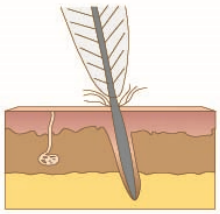


egg
(~ 1 mm)

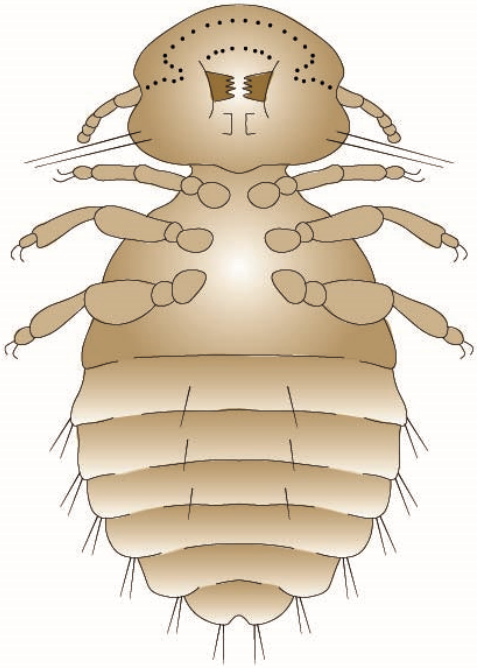
all stages ectozoic on host
(motile stages feed on skin/feathers)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites

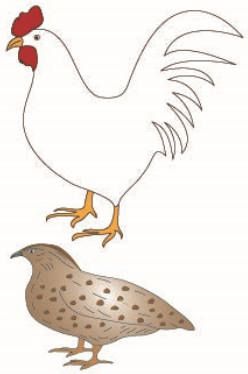
Goniocotes



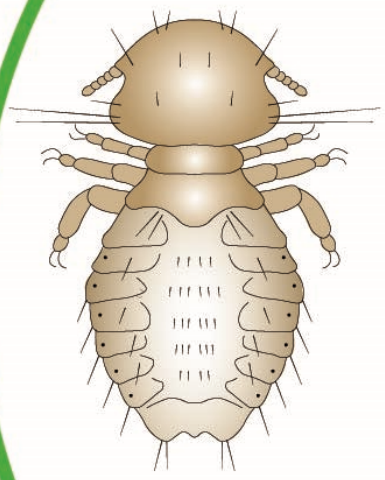
skin/plumage
(irritation, inflammation,
damaged feathers,
reduced productivity)



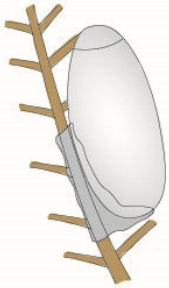
adult (ventral)
(~ 3 mm)



Definitive Hosts
(birds)



nymph (dorsal)
(~ 2 mm)

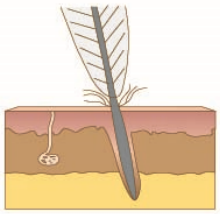


egg
(~ 1 mm)

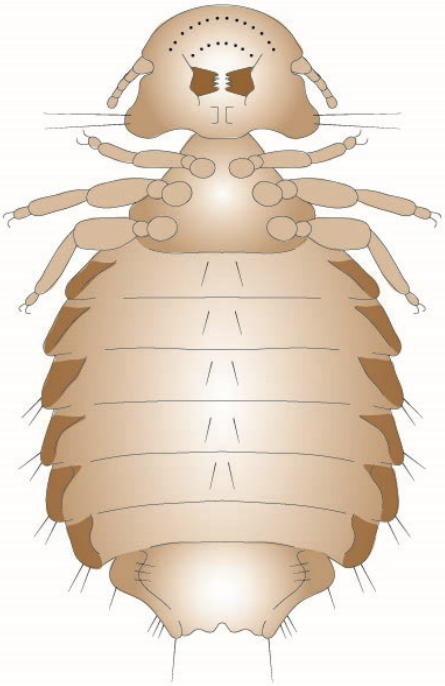
all stages ectozoic on host
(motile stages feed on skin/feathers)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites

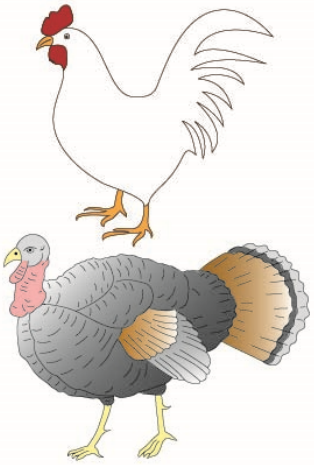
Goniodes



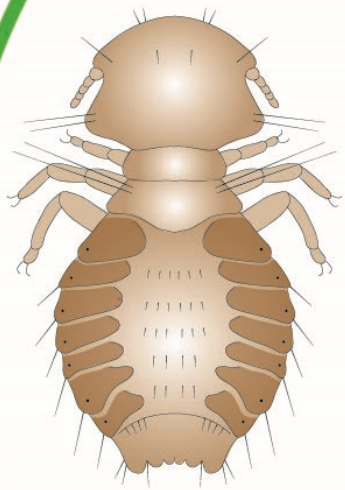
skin/plumage
(irritation, inflammation,
damaged feathers,
reduced productivity)



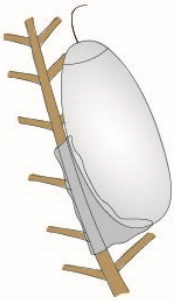
adult (ventral)
(~ 3 mm)



Definitive Hosts
(birds)



nymph (dorsal)
(~ 2 mm)

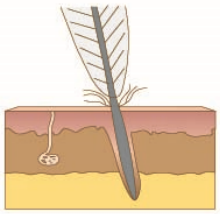


egg
(~ 1 mm)

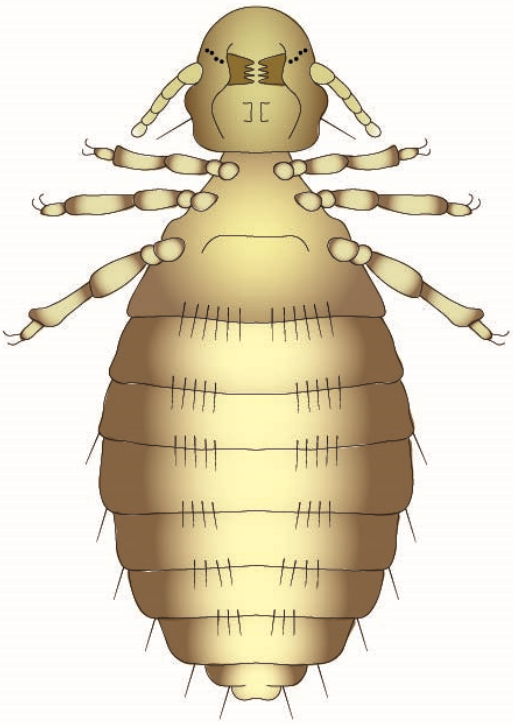
all stages ectozoic on host
(motile stages feed on skin/feathers)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites

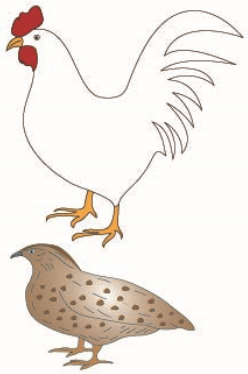
Cuclotogaster



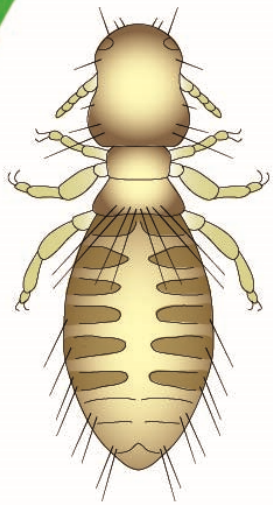
skin/plumage
(irritation, inflammation,
damaged feathers,
reduced productivity)



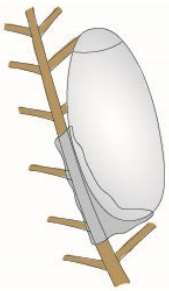
adult (ventral)
(~ 3 mm)



Definitive Hosts
(birds)



nymph (dorsal)
(~ 2 mm)

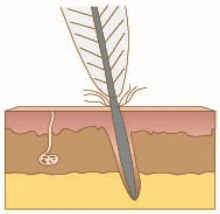


egg
(~ 1 mm)

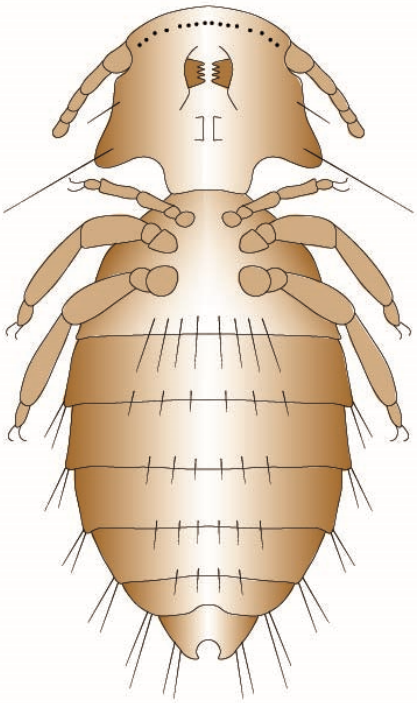
all stages ectozoic on host
(motile stages feed on skin/feathers)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites

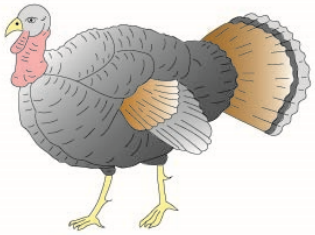
Chelopistes



skin/plumage
(irritation, inflammation,
damaged feathers,
reduced productivity)

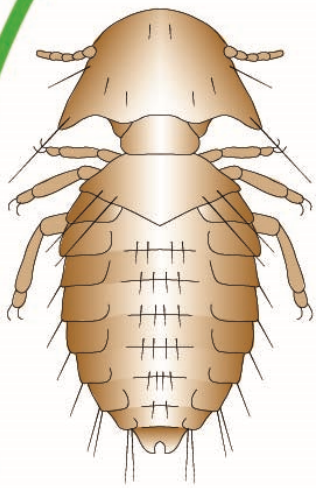


adult (ventral)
(~ 3 mm)

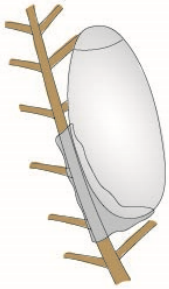




Definitive Hosts
(birds)



nymph (dorsal)
(~ 2 mm)



egg
(~ 1 mm)

all stages ectozoic on host
(motile stages feed on skin/feathers)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites



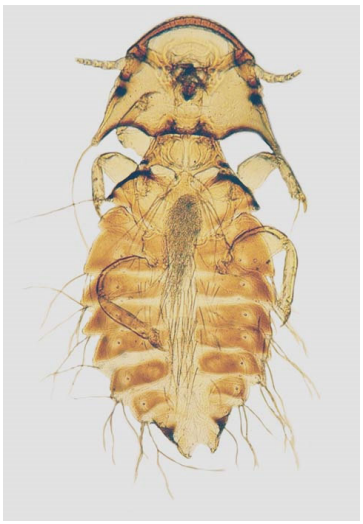
Lipeurus adult



Goniodes adult



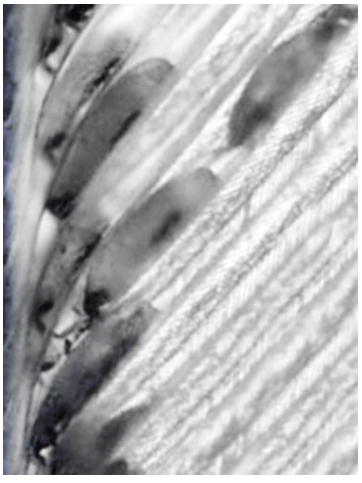
Gonicotes adult



Chelopistes adult



Cuclotogaster adult



Goniodes eggs

Menopon, Menacanthus, Holomenopon
(insect: louse)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Mallophagan (chewing) lice have blunt rounded heads with mouthparts adapted for feeding on keratin in superficial skin layers. Chewing lice are ectoparasitic on mammals and birds, most species being highly host specific and even site-specific. Amblyceran lice have maxillary palps and four-segmented antennae located in grooves. Menoponids occur on birds and infestations by *Menopon, Holomenopon* and *Menacanthus* spp. have been associated with restlessness, damaged plumage and reduced productivity in poultry and gamebirds.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order:	Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder:	Mallophaga (= wool-eating) (chewing lice, broad rounded head, feed on keratin, host/site specific)
Superfamily:	Amblycera (with maxillary palps, large rounded heads, 4-segmented antennae in antennal grooves)
Family:	Menoponidae (parasitize birds)
Genus:	*Menopon* (parasitic on skin/feathers of birds)
Genus:	*Holomenopon* (parasitic on skin/feathers of birds)
Genus:	*Menacanthus* (parasitic on skin/feathers of birds)
Species:	various species cause restlessness and reduced productivity in poultry and gamebirds

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Lice are small wingless hemipterodeans that undergo gradual (hemimetabolous) metamorphosis and are permanent obligate ectoparasites on other animals. Four suborders are recognized: the Anoplura containing the haematophagous sucking lice of placental mammals; the Ischnocera and Amblycera (previously classified together as Mallophaga) comprising the chewing or biting lice of birds, marsupials and placental mammals; and the Rhynchophthirina confined to elephants and warthogs in Africa.

Major parasitic phthirapteran families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					

Menoponidae (bird lice)	68 genera, 1,150 spp.	birds	nymphs, adults	biting, chewing	-
Boopiidae (marsupial chewing lice)	8 genera, 57 spp.	mammals (incl. marsupials)	nymphs, adults	biting	helminth
Suborder: Ischnocera [Mallophaga p.p.] (chewing lice of mammals and birds, broad rounded head, without maxillary palps, prominent filiform antennae, keratin feeders) [2 families, 158 genera, 3,371 species]					
Trichodectidae (fur lice)	20 genera, 413 spp.	mammals (bovids, equids, carnivores)	nymphs, adults	biting	helminth
Philopteridae(bird lice)	138 genera, 2,958 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
Suborder: Anoplura (sucking lice of placental mammals) (narrow pointed head, pierce skin and feed on fluids (solenophagy)) [16 families, 51 genera, 694 species]					
Haematopinidae (ungulate lice, short-nosed lice)	1 genus, 21 spp.	mammals (equids, bovids, suids)	nymphs, adults	blood-sucking	viral, bacterial
Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-
Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial
Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-

Over 4,900 species of biting/chewing lice have been described in 253 genera in 8 families, around 4,400 species associated with birds and 500 species with mammals. Members of the suborder Ischnocera have broad rounded heads with conspicuous filiform antennae but lacking maxillary palps, while members of the suborder Amblycera have large rounded heads with maxillary palps and inconspicuous antennae hidden in grooves. Some 158 ischnoceran genera have been assigned to 2 families (Trichodectidae and Philopteridae), while 96 amblyceran genera have been classified in 6 families (Boopiidae; Gyropidae, Laemobothriidae, Menoponidae, Ricinidae, Trimenoponidae). Species of veterinary importance include members of the ischnoceran families Trichodectidae (bovids, canids, equids) and Philopteridae (poultry), and the amblyceran families Menoponidae (poultry) and Boopiidae (carnivores). Members of the family Menoponidae are parasitic on birds and have 6 pairs of abdominal spiracles with 2 segments between the thorax and first abdominal segment bearing spiracles (whereas members of the family Boopiidae are parasitic on mammals and also have 6 pairs of abdominal spiracles but only one segment between the thorax and the first abdominal segment bearing spiracles). Some 1,150 menoponid species have been described from 68 genera, namely *Actornithophilus*, *Afrimenopon*, *Amyrsidea*, *Ancistrona*, *Apterygon*, *Ardeiphilus*, *Austromenopon*, *Bonomiella*, *Bucerocolpocephalum*, *Bucerophagus*, *Cavifera*, *Chapinia*, *Ciconiphilus*, *Clayia*, *Colimenopon*, *Colpocephalum*, *Comatomenopon*, *Coramenopon*, *Ctenigogus*, *Cuculimenopon*, *Cuculiphilus*, *Dennyus*, *Dicteisia*, *Eidmanniella*, *Elbelia*, *Eomenopon*, *Epiara*, *Eucolpocephalum*, *Eureum*, *Falcomenopon*, *Franciscoloa*, *Fregatiella*, *Gruimenopon*, *Heleonomus*, *Heterokodeia*, *Heteromenopon*, *Hoazineus*, *Hohorstiella*, *Holomenopon*, *Kaysius*, *Kelerimenopon*, *Kurodaia*, *Longimenopon*, *Machaerilaemus*, *Menacanthus*, *Menopon*, *Meromenopon*, *Microctenia*, *Mimemamenopon*, *Myrsidea*, *Neomenopon*, *Nosopon*, *Numidicola*, *Odoriphila*, *Osborniella*, *Pacifimenopon*, *Piagetiella*, *Plegadiphilus*, *Podargiphilus*, *Pseudomenopon*, *Psittacobrosus*, *Psittacomenopon*, *Pterophilus*, *Quateia*, *Rediella*, *Somaphantus*, *Trinoton*, and *Turacoeca*. Many species have been recorded from domestic birds (especially galliform and anseriform birds), while other species have been found on wild, game and aviary birds. Most species are thought to be host-specific, or to occur on closely-related hosts. Many species have also been found to be site-specific and only occur on particular body parts in association with particular feathers. In particular, some 13 *Menopon* spp. have been found on the feathers of domestic fowl, 16 *Holomenopon* spp. on the skin and feathers of waterfowl, and 96 *Menacanthus* spp. on the skin of domestic and game birds as well as numerous aviary perching birds. Infestations have been recorded around the world in most zoogeographic regions.

***Menopon* species**	**Hosts**	**Location**	**Distribution**
M. carrikeri	Galliformes: phasianid (Sumatran peacock-pheasant)	feathers	Indonesia
M. clayae	Galliformes: phasianid (Palawan peacock-pheasant)	feathers	Philippines
M. deryloi	Galliformes: phasianid (black grouse)	feathers	Europe
M. ferrisi	Galliformes: phasianid (mountain peacock-pheasant)	feathers	Malaysia
M. gallinae (syn. *M. brevipes, longicephalum, lunanale, pallidum, productum, trigonocephalum*) (shaft louse)	Galliformes: phasianid (chicken, turkey, ferruginous partridge, silver pheasant, brown-eared pheasant, Mikado pheasant, Bulwer's pheasant, Swinhoe's pheasant, Kalij pheasant, Siamese fireback, crested fireback, crestless fireback, grey junglefowl, Sri Lankan jungle-fowl, helmeted guineafowl, Satyr tragopan), Columbiformes: columbid (pigeon)	feathers (thigh, breast)	worldwide

M. hopkinsi	Galliformes: phasianid (Malay peacock-pheasant)	feathers	Malaysia
M. interpositum	Galliformes: phasianid (grey francolin)	feathers	South Asia
M. jellisoni	Galliformes: phasianid (Ceylon spurfowl)	feathers	Sri Lanka
M. kuntzi	Galliformes: phasianid (bamboo partridge)	feathers	Asia
M. pallens (syn. *M. pallascens*)	Galliformes: phasianid (Barbary partridge, rock partridge, red-legged partridge, grey partridge)	feathers	Europe, Africa
M. spinulosum	Galliformes: phasianid (Burmese peacock-pheasant)	feathers	Asia
M. subgallinae	Galliformes: phasianid (green jungle-fowl)	feathers	Indonesia

***Menacanthus* species**	**Hosts**	**Location**	**Distribution**
M. abdominalis	Galliformes: phasianid (common quail)	skin	Europe
M. aburris	Galliformes: cracid (wattled guan)	skin	South America
M. aeedonis	Passeriformes: troglodytid (Bewick's wren, house wren)	skin	Americas
M. affinis	Passeriformes: turdid (northern wheatear)	skin	Eurasia, North America
M. agilis (syn. *M. phylloscopi*)	Passeriformes: muscicapid (spotted flycatcher), sylviid (Tickell's leaf warbler, common chiff-chaff, willow warbler), turdid (common redstart, black redstart)	skin	Eurasia, Africa
M. alaudae (syn. *M. alaskensis, cannabinae, carduelis, citrinellae, mongolicus, parviceps, perforatus, stiefeli*)	Passeriformes: cinclid (American dipper), fringillid (pine grosbeak, common linnet, common redpoll, twite, European goldfinch, American goldfinch, pine siskin, common rosefinch, housefinch, Pallas's rosefinch, Asian rosy finch, pine grosbeak), alaudid (Eurasian skylark, horned lark, crested lark), emberizid (black-throated sparrow, yellowhammer, chestnut-eared bunting, snow bunting), icterid (eastern meadowlark, western meadowlark), ploceid (white-browed sparrow-weaver)	skin	Eurasia, Africa, Americas
M. albicans	Galliformes: phasianid (kalij pheasant)	skin	Himalayas
M. albicaudus	Galliformes: cracid (band-tailed guan)	skin	South America
M. annuliventer	Galliformes: cracid (blue-billed curassow)	skin	South America
M. arctifasciatus	Tinamiformes: tinamid (spotted nothura, red-winged tinamou)	skin	South America
M. aurocapillus	Passeriformes: parulid (black-and-white warbler, orange-crowned warbler, Colima warbler, ovenbird, northern waterthrush, Louisiana waterthrush)	skin	Americas
M. balfouri	Piciformes: ramphastid (yellow-throated toucan, white-throated toucan, Choco toucan, green-billed toucan, keel-billed toucan, channel-billed toucan, chestnut-mandibled toucan)	skin	South America
M. boliviensis	Galliformes: phasianid (marbled wood quail)	skin	South America
M. brachygaster	Tinamiformes: tinamid (grey tinamou)	skin	South America
M. brevispinus	Galliformes: phasianid (stripe-faced wood quail)	skin	South America
M. camelinus (syn. *M. aequalis, brevidentatus, dudiyalatora, guldum, inequalis, setosus*)	Passeriformes: laniid (great grey shrike, lesser grey shrike, red-backed shrike, brown shrike, loggerhead shrike, masked shrike, long-tailed shrike, woodchat shrike, bay-backed shrike, Chinese grey shrike, Burmese shrike)	skin	Eurasia, Africa
M. campephili	Piciformes: picid (Magellanic woodpecker)	skin	South America
M. caudatus	Piciformes: galbulid (rufous-tailed jacamar)	skin	Central and South America
M. chaparensis	Galliformes: cracid (Spix's guan)	skin	South America
M. chrysophaeus (syn. *M. spodocephalae*)	Passeriformes: emberizid (black-faced bunting, swamp sparrow, song sparrow, savannah sparrow, fox sparrow, American tree sparrow, field sparrow)	skin	Eurasia, North America
M. cincinnatus	Galliformes: cracid (sickle-winged guan)	skin	South America
M. colinus	Galliformes: phasianid (crested bobwhite)	skin	South America
M. coniceps	Tinamiformes: tinamid (little tinamou)	skin	South America
M. cornuceps	Galliformes: cracid (sickle-winged guan, band-tailed guan, crested guan, black curassow)	skin	Central and South America
M. cornutus	Galliformes: phasianid (chicken)	skin	Asia
M. crateropus	Passeriformes: leiothrichid (southern pied babbler, arrow-marked babbler)	skin	Africa
M. curuccae	Passeriformes: sylviid (thick-billed warbler, great reed	skin	Eurasia, Africa,

(syn. *M. mauersbergi, verecundus, vistulanus, wegelini*)	warbler, aquatic warbler, sedge warbler, willow warbler, garden warbler, barred warbler, common whitethroat, lesser whitethroat, Eurasian blackcap), vireonid (yellow-throated vireo, white-eyed vireo, red-eyed vireo, blue-headed vireo)		Americas
M. daubentoni	Galliformes: cracid (yellow-knobbed curassow)	skin	South America
M. dendroicae	Passeriformes: parulid (prairie warbler, yellow-rumped warbler)	skin	North America
M. dennisi	Passeriformes: cracticid (grey currawong)	skin	Australia
M. distinctus	Passeriformes: tyrannid (Euler's flycatcher, ash-throated flycatcher, dusky-capped flycatcher, brown-crested flycatcher, greyish mourner)	skin	Americas
M. eichleri	Galliformes: phasianid (rock partridge)	skin	Europe
M. eisenachensis	Passeriformes: sylviid (reed warbler)	skin	Eurasia, Africa
M. elbeli	Passeriformes: artamid (ashy wood swallow, great wood swallow)	skin	India, Asia
M. eurysternus (syn. *M. annulatus, biaculeatus, brelihi, chabaroviensis, cornicis, dicruri, difficilis, dubius, festivus, flavus, fuscocinctus, germanus, gracilis, grandis, gulabimaina, himalayicus, inscitus, kevei, meniscus, microsceli, minisculus, monochromateus, mutabilis, parvulus, persignatus, pflegeri, picae, pius, polonicus, pyrrhulae, remizae, safedgal, schildmacheri, sittae, spiniferus, spinosus, subspinosus, tibialis, tichodrome, translucidus, tristisi, turkmeniscus, volkovi, wipszyckii*)	Passeriformes: bombycillid (northern phainopepla), cardinalid (rose-breasted grosbeak, vermilion cardinal), chloropseid (golden-fronted leafbird, blue-winged leafbird, yellow-throated leafbird, greater green leafbird), cisticolid (rufous-tailed tailorbird), corvid (carrion crow, western jackdaw, Eurasian jay, Florida scrub jay, blue jay, Steller's jay, black-headed jay, plush-crested jay, green jay, white-collared jay, Eurasian magpie, azure-winged magpie, yellow-billed magpie, Clark's nutcracker, piapiac, alpine chough), dicrurid (ashy drongo, black drongo, white-bellied drongo, hair-crested drongo, greater racket-tailed drongo, lesser racket-tailed drongo), emberizid (chestnut-capped brushfinch, rufous-winged sparrow, fox sparrow, Lapland longspur, northern cardinal, black-faced bunting, cinnamon-breasted bunting), estrildid (African silverbill, Indian silverbill, scaly-breasted munia, green-winged pytilia), fringillid (common redpoll, European greenfinch, red siskin, common chaffinch, Eurasian bullfinch, canary, streaky seedeater), grallariid (tawny antpitta, chestnut-crowned antpitta), icterid (red-winged blackbird, scarlet-headed blackbird, Baltimore oriole, bronzed cowbird, brown-headed cowbird, common grackle), irenid (Asian fairy-bluebird), laniid (red-backed shrike, brown shrike, long-tailed shrike), leiothrichid (Taiwan barwing, Nilgiri laughingthrush, chestnut-crowned laughingthrush), meliphagid (red wattlebird, New Zealand bellbird, New Holland honeyeater, tawny-breasted honeyeater, tui), mimid (tropical mockingbird, northern mockingbird, Bendire's thrasher, California thrasher, brown thrasher), motacillid (Australasian pipit, forest wagtail), muscicapid (Narcissus flycatcher, large niltava, Nilgiri blue robin), nectariniid (black-throated sunbird, copper-throated sunbird, southern double-collared sunbird, Mrs Gould's sunbird, little spiderhunter, streaked spiderhunter, long-billed spiderhunter), oriolid (black-naped oriole, black-hooded oriole), pachycephalid (grey shrikethrush, olive whistler), panurid (bearded reedling, bearded reedling), paramythiid (tit berrypecker, eastern crested berrypicker), parulid (ovenbird, American redstart), passerid (house sparrow, russet sparrow, yellow-throated sparrow), passerellid (green-tailed towhee, dark-eyed junco, white-crowned sparrow, Harris's sparrow), pellorneid (Abbott's babbler), petroicid (South Island robin, dusky robin), ploceid (Baya weaver), piprid (lance-tailed manakin), prunellid (dunnock), pycnonotid (brown-eared bulbul, sooty-headed bulbul, common bulbul, Ayeyarwady bulbul, red-vented bulbul, stripe-throated bulbul, yellow-vented bulbul, Himalayan bulbul, light-vented bulbul, Styan's bulbul, white-spectacled bulbul, crested finchbill), remizid (Eurasian penduline tit), rhinocryptid (unicolored tapaculo), sittid (Eurasian nuthatch), sturnid (common myna, bank myna,	skin	Eurasia, Australasia, Africa, Americas

	common hill myna, Indian pied myna, common starling, black-collared starling, Brahminy starling, rosy starling, Daurian starling, metallic starling, Micronesian starling, Asian glossy starling, long-tailed glossy starling, Pohnpei starling, wattled starling, greater blue-eared starling, Cape starling, Madagascar starling, slender-billed starling, grosbeak starling, coleto), sylviid (tawny-flanked prinia), thraupid (blue-and-yellow tanager), tichodromid (wallcreeper), timaliid (chestnut-capped babbler), turdid (black-breasted thrush, wood thrush, western bluebird, white-necked thrush, creamy-bellied thrush, Japanese thrush, brown-headed thrush, black-breasted thrush, Austral thrush, clay-coloured thrush, common blackbird, American robin, eyebrowed thrush, song thrush, fieldfare, mountain thrush, red-throated thrush, mistle thrush, scaly thrush, Siberian thrush), zosteropid (warbling white-eye, silvereye); Piciformes: capitonid (lemon-throated barbet), lybiid (white-headed barbet, black-breasted barbet, black-collared barbet), picid (common flameback, downy woodpecker, white-wedged piculet, arrowhead piculet)		
M. exilis	Passeriformes: turdid (wheatear)	skin	Eurasia
M. exsanguis	Piciformes: picid (cream-backed woodpecker, crimson-crested woodpecker)	skin	South America
M. extraneus	Piciformes: picid (red-necked woodpecker)	skin	South America
M. falcatus	Galliformes: phasianid (marbled wood quail)	skin	South America
M. fasciatus	Galliformes: cracid (red-faced guan)	skin	South America
M. fertilis (syn. *M. upupae*)	Coraciiformes: upupid (hoopoe)	skin	Eurasia, Africa
M. genitalis	Galliformes: cracid (crested guan)	skin	Americas
M. geothlypis	Passeriformes: parulid (common yellowthroat, Connecticut warbler, MacGillivray's warbler)	skin	North America
M. gonophaeus (syn. *M. corvus, laticeps, masudi, ovatus*)	Passeriformes: corvid (house crow, pied crow, little crow, large-billed crow, Cape crow, common raven, little raven, forest raven, Australian raven, Chihuahuan raven, rook, western jackdaw, red-billed chough)	skin	Africa, Eurasia, North America
M. hilensis	Passeriformes: drepanidid ('i'iwi)	skin	Hawaii
M. infumatus	Coraciiformes: alcedinid (kookaburra)	skin	Australia
M. kaddoui	Galliformes: phasianid (peafowl)	skin	South Asia
M. kalatitar	Galliformes: phasianid (black francolin)	skin	India
M. laticephalus	Tinamiformes: tinamid (great tinamou)	skin	Central and South America
M. latus	Galliformes: cracid (black guan)	skin	Central America
M. leistidis	Passeriformes: icterid (white-browed meadowlark)	skin	South America
M. longipalpis	Galliformes: phasianid (kalij pheasant)	skin	Himalayas
M. longispinus	Galliformes: phasianid (spot-winged wood quail)	skin	South America
M. lyali	Galliformes: phasianid (red-legged partridge)	skin	Europe
M. machadoi	Cuculiformes: musophagid (blue turaco)	skin	Africa
M. mamola	Passeriformes: turdid (spotted forktail)	skin	Indochina
M. menura	Passeriformes: menurid (superb lyrebird)	skin	Australia
M. meridionalis	Galliformes: phasianid (spot-winged wood quail, marbled wood quail, black-breasted wood quail)	skin	Central and South America
M. merisuoi	Passeriformes: corvid (house crow, grey treepie, spotted nutcracker, yellow-billed blue magpie)	skin	Eurasia
M. mikadokiji	Galliformes: phasianid (Mikado pheasant)	skin	Taiwan
M. mituensis	Galliformes: cracid (razor-billed curassow)	skin	Brazil
M. montagnii	Galliformes: cracid (Andean guan)	skin	South America
M. nelsoni	Passeriformes: artamid (dusky wood swallow)	skin	Australia
M. nogoma (syn. *M. orientalis*)	Passeriformes: motacillid (white wagtail), muscicapid (white-tailed robin, Siberian rubythroat, collared bush robin, golden bush robin, red-flanked bluetail)	skin	Indochina, Eurasia
M. nothoproctae	Tinamiformes: tinamid (brushland tinamou, curve-billed tinamou, Andean tinamou, Chilean tinamou)	skin	South America
M. numidae	Galliformes: phasianid (helmeted guineafowl)	skin	Africa

M. obsoleti	Passeriformes: troglodytid (rock wren)	skin	Americas
M. orioli	Passeriformes: malaconotid (black-backed puffback), oriolid (black-naped oriole, Eurasian golden oriole), pycnonotid (brown-cheeked bulbul, ochraceous bulbul, puff-throated bulbul, yellow-bellied bulbul, Asian red-eyed bulbul, stripe-throated bulbul, yellow-vented bulbul, black-capped bulbul)	skin	Asia, Africa
M. ortalidis	Galliformes: cracid (chestnut-winged chachalaca)	skin	Central America
M. pallidulus	Galliformes: phasianid (bamboo partridge, grey junglefowl, red junglefowl)	skin	Indochina
M. pallipes	Galliformes: phasianid (king quail)	skin	Asia, Oceania
M. pauxensis	Galliformes: cracid (helmeted curassow)	skin	South America
M. perijanus	Galliformes: phasianid (black-fronted wood quail)	skin	South America
M. phasiani	Galliformes: phasianid (common pheasant)	skin	Europe
M. pici (syn. *M. benii, bruneri, caquetae, ceophloeus, colaptis, dryobates, hoffmanni, koreae, picorum, pitius, praecursor, punensis*)	Piciformes: megalaimid (black-browed barbet, great barbet, brown-headed barbet), picid (northern flicker, Campo flicker, Chilean flicker, Andean flicker, green-barred woodpecker, lineated woodpecker, pileated woodpecker, golden-fronted woodpecker, red-bellied woodpecker, yellow-tufted woodpecker, red-headed woodpecker, acorn woodpecker, Hoffmann's woodpecker, grey-breasted woodpecker, Lewis's woodpecker, gila woodpecker, white-headed woodpecker, great spotted woodpecker, downy woodpecker, hairy woodpecker, grey-headed woodpecker, greater yellownape, European green woodpecker, yellow-bellied sapsucker)	skin	Americas, Europe, Indo-Asia
M. picicola	Piciformes: picid (black-backed woodpecker, Eurasian three-toed woodpecker)	skin	North America
M. pipilensis	Galliformes: cracid (piping guan)	skin	South America
M. pricei	Galliformes: phasianid (northern bobwhite)	skin	North America
M. pusillus (syn. *M. andalus, campestris, hispanicus, montanus, trivialis*)	Passeriformes: motacillid (tawny pipit, olive-backed pipit, Australasian pipit, meadow pipit, water pipit, tree pipit, African pied wagtail, white wagtail, western yellow wagtail)	skin	Eurasia, Africa, Australasia
M. quiscali	Passeriformes: icterid (rusty blackbird, brown-headed cowbird, boat-tailed grackle, great-tailed grackle, common grackle)	skin	North America
M. ralli	Gruiformes: rallid (water rail)	skin	Eurasia, Africa
M. robustus	Passeriformes: aegithalid (bushtit)	skin	North America
M. samaipatae	Galliformes: cracid (Spix's guan)	skin	South America
M. setifer	Galliformes: cracid (wattled guan)	skin	South America
M. sinuatus (syn. *M. bussei, minutus, subhorridus, subsimilis*)	Passeriformes: parid (coal tit, great tit, marsh tit, Eurasian blue tit, black-capped chickadee, mountain chickadee, chestnut-backed chickadee, tufted titmouse, whitethroat)	skin	North America, Eurasia
M. stramineus (syn. *M. biseriatus, meleagridis*) (yellow body louse, chicken body louse)	Galliformes: phasianid (chicken, kalij pheasant, ring-necked pheasant, turkey, helmeted guineafowl, Indian peafowl, satyr tragopan); Passeriformes: sturnid (common myna)	skin	worldwide
M. stubbei	Passeriformes: prunellid (brown accentor)	skin	Indochina
M. sturnellae	Passeriformes: bombycillid (cedar waxwing), sturnid (long-tailed meadowlark, eastern meadowlark, western meadowlark)	skin	Americas
M. takayamai (syn. *M. cettiae, obrteli*)	Passeriformes: cettid (Cetti's warbler, Japanese bush warbler), locustellid (Gray's grasshopper warbler, Middendorf's grasshopper warbler, lanceolated warbler, Savi's warbler), phylloscopid (Tickell's leaf warbler, dusky warbler)	skin	Japan
M. tarsatus (syn. *M. okadai*)	Galliformes: phasianid (crested partridge, crested wood partridge)	skin	Southeast Asia
M. tenuifrons	Passeriformes: troglodytid (marsh wren, sedge wren, Eurasian wren)	skin	Americas, Eurasia, Africa
M. tyranni	Passeriformes: tyrannid (grey kingbird, tropical kingbird, eastern kingbird, western kingbird, great kiskadee)	skin	Americas
M. unicolor	Galliformes: phasianid (black-backed partridge, chestnut-	skin	Southeast Asia

	bellied partridge)		
M. valenciae	Galliformes: phasianid (Venezuelan wood quail)	skin	South America
M. werneri	Galliformes: phasianid (peacock-pheasant)	skin	Taiwan

***Holomenopon* species**	**Hosts**	**Location**	**Distribution**
H. acutae	Anseriformes: anatid (northern pintail, Cape teal)		Eurasia, North America
H. boehmi	Anseriformes: anatid (coscoroba swan)		South America
H. brevithoracicum	Anseriformes: anatid (kelp goose, upland goose, ruddy-headed goose, black-necked swan)		South America
H. bucephalae	Anseriformes: anatid (common goldeneye, bufflehead)		North America
H. cairinae	Anseriformes: anatid (Muscovy duck)		Americas
H. clauseni	Anseriformes: anatid (wood duck, blue-winged teal, bufflehead)		North America
H. clypeilargum	Anseriformes: anatid (northern pintail, American wigeon, Eurasian wigeon, northern shoveler, Eurasian teal, cinnamon teal, blue-winged teal, yellow-billed teal, garganey, American black duck, yellow-billed duck, ring-necked duck, greater scaup, New Zealand scaup, canvasback, gadwall, hooded merganser, common merganser)		cosmopolitan
H. goliath	Anseriformes: anatid (magpie goose)		Australasia
H. leucoxanthum (syn. *H. albofasciatum, concii, dendrocygni, hansloehrli, lunarium, nyrocae*) (shaft louse)	Anseriformes: anatid (mallard, Muscovy duck, long-tailed duck, common shelduck, Radjah shelduck, knob-billed duck, Pacific black duck, Indian spot-billed duck, ring-necked duck, ruddy duck, white-faced whistling duck, wandering whistling duck, fulvous whistling duck, plumed whistling duck, lesser whistling duck, tufted duck, gadwall, common pochard, southern pochard, red-crested pochard, common scoter, northern pintail, Eurasian wigeon, American wigeon, cinnamon teal, Sunda teal, Eurasian teal, Auckland teal, northern shoveler, greater scaup, lesser scaup, canvasback, redhead, hardhead, bufflehead, greylag goose, common pygmy goose, Canada goose, black swan): Suliformes: phalacrocoracid (cormorant)	skin, feathers	worldwide
H. loomisii	Anseriformes: anatid (velvet scoter, red-breasted merganser, common eider, king eider)		Eurasia, North America
H. maxbeieri	Anseriformes: anatid (mallard, black duck)		cosmopolitan
H. obscurum	Anseriformes: anatid (Radjah shelduck)		Australasia
H. setigerum	Anseriformes: anatid (northern pintail, northern shoveler, Cape shoveler, Eurasian teal, cinnamon teal, blue-winged teal, garganey, gadwall, white-winged duck, Australian wood duck, maned goose)		Americas, Eurasia, Australasia
H. tadornae (syn. *H. boetticheri, eulasium, museigottingense*)	Anseriformes: anatid (Egyptian goose, Andean goose, brant, ruddy shelduck, common shelduck, Australian shelduck, paradise shelduck); Suliformes: phalacrocoracid (reed cormorant)		Africa, Americas, Australasia, Indochina
H. transvaalense	Anseriformes: anatid (mallard)		South Africa
H. tumidum (syn. *H. africanum*)	Anseriformes: anatid (spur-winged goose)		Africa

Parasite morphology: Menoponid lice form 3 different type of morphological stages during their development: eggs (nits); nymphs (3 instars); and adults. Eggs are oval-elliptical in shape measuring from 0.8-0.9 x 0.4-0.5 mm and attached to feathers or other eggs by several rows of anterior attachment structures with hooked processes (soft and pliable when freshly laid but then drying and hardening thus separating adjacent eggs and keeping their anterior ends free of obstructions). The eggs are operculate and have an anterior dome-shaped cap formed by 8-10 structures fused together. The posterior (anopercular) end of the egg bears an egg-stigma (group of canals which partly or completely traverse the chorion) which assist in egg attachment. The eggs are embryonated and hatch to release first-stage nymphs (N1) which feed and moult through another 2 nymphal stages (N2, N3) before forming adults. All nymphs are similar in structure to adults, but are smaller (ranging from 1.2-1.8 mm in length), less sclerotized, have fewer body setae and lack genitalia. Adult lice are elongate and dorso-ventrally flattened measuring from 1.4-4.0 mm in length (*Holomenopon* 1.4-2.0 mm, *Menopon* 1.6-2.5 mm, *Menacanthus* 1.9-4.0 mm). Adults are often pale yellow in colour and have 3 distinct body parts (short broad head, small oval thorax, and elongate elliptical abdomen). The head is broadly triangular (almost as wide as body) with

a prominent parabolic-rounded anterior margin and posterolateral bulges often bearing pairs of backwards directed spines. The head also bears a pair of compound eyes behind which are clavate (club-shaped) antennae (each composed of 4 segments) concealed in deep fossae (grooves). The ventral mouthparts consist of large opposing sclerotized mandibles used to shear or scrape host materials delivering food particles to the preoral cavity via a posterior plate-like labrum (often with an anterior hyaline pad-like protrusion (pulvinus)), lateral maxillae and an anterior labium with salivary secretions added through a central hypopharynx. In amblyceran lice, the mandibles lie parallel to the ventral surface of the head (such that the condyles are ventral and the ginglymus is dorsal), the maxillae and labium are reduced in size (compared to sucking lice) with single-lobed maxillae attached to the sides of the tripartite labium. Amblyceran lice also possess maxillary palps, each composed of 4 segments (palps absent in ischnoceran lice). The alimentary tract consists of a foregut (with pharynx, oesophagus and crop (expansion of oesophagus)), a large midgut (with ventriculus and anterior caeca) and a hindgut (with pylorus, papillae and rectum). Amblyceran chewing lice appear to lack a midgut mycetome (bacteriome or stomach disc) harbouring endosymbiotic microbes, although proteobacteria occur in the gut (mycetome well developed in anopluran sucking lice and less developed in ischnoceran chewing lice). The thorax is bipartite with a large anterior prothorax (oval in *Menacanthus*, semicircular in *Menopon* and *Holomenopon*) and a narrow mesothorax completely fused with the metathorax. The ventral thorax bears 3 pairs of legs, each comprising 5 segments (coxa, trochanter, femur, tibia, tarsus) and all ending in paired claws. The fore-legs are usually smaller than the mid- and hind-legs, and all legs usually have small groups of fine hairs. The abdomen is elongate, oval-elliptical in shape and often appears to have transverse bands or lateral patches of pigmented material. The abdomen is composed of 10 segments which are densely setate, with transverse rows of short-medium hairs and several long lateral bristles. Spiracles (openings to the tracheal (breathing) system) are visible at the dorsal edges of the abdominal segments. Adult lice exhibit sexual size dimorphism, with female lice being larger than males. The size differences between sexes of different menoponid species has been shown to generally conform to Rensch's rule (allometric increase in male body size relative to female size, i.e. larger lice produce bigger males although they remain smaller than females). Adult male lice have 3 pairs of testes (cf. 2 pairs in ischnoceran lice) with tubular vas deferens joining to form a seminal vesicle connected to the genital sac which is equipped with a tubular intromittent organ (aedeagus with dorsal gonopore and terminal endophallus) supported by a basal plate-like apodeme and 2 lateral rod-like parameres. Adult female lice have ovaries with polytrophic ovarioles connected via oviducts to a globular uterus with accessory glands (glue production), spermatheca (sperm storage) and a vaginal opening with a genital plate and valvula. Female lice do not have ovipositors but the terminal abdominal segment often has bifurcated apical lobes (gonopods) often bearing setae that aid in egg deposition.

Site of infection: These chewing lice are ectoparasitic on the feathers and skin of avian hosts, most parasite species being stenoxenous, that is, specific for closely-related host species (such as galliforms, anseriforms, passeriforms). Nymphs and adult lice usually live on the skin in the fluffy underlayer of the plumage and female lice attach their eggs around the bases of feathers. Menoponid amblyceran lice are less specialized than philopterid ischnoceran lice and may be found widely distributed over the body, although feeding and oviposition may be restricted to certain areas. *Menacanthus* spp. are found on the skin mostly in sparsely-feathered areas such as the vent, breast or thigh, but they may be more widespread in heavy infestations. *Menopon* spp. are most often seen resting in single files along shafts of breast and thigh feathers, but will disperse to the skin when disturbed. *Holomenopon* spp. are found on the skin and feathers of their anseriform hosts.

Pathogenesis: Light-mild infestations may be asymptomatic or remain subclinical, but heavier infestations may produce clinical disease, with morbidity (skin inflammation, irritation, hyperkeratosis, pruritus, plumage damage, scabs, anaemia, poor growth) and mortalities. Nymphs and adult lice use their modified mandibles to scrape and gnaw at the epidermis and bases of feathers, often penetrating to blood vessels to feed on blood. Infested birds may develop patches of skin with sloughing epithelial cells, small blood clots, oozing tissue exudates and scabs. Several *Menacanthus* spp. are particularly pathogenic in domestic poultry and some aviary birds (especially canaries), while many *Menopon* and *Holomenopon* spp. may cause plumage damage in fledged birds. Infested animals become restless and endeavour to relieve the pruritus by grooming (preening, scratching, rubbing) resulting in wet damaged plumage, unsightly appearance, feather loss (esp. *Menacanthus*), impaired thermoregulation, self-trauma, scabs (esp. *Menopon*), sometimes lameness and secondary infections, and reduced productivity (poor growth, weight loss, reduced egg production). Infestations are often worse on young birds, presumably due to their immature immune systems, poor grooming skills and gregarious behaviours, although most *Menopon* spp. do not bother chicks until they are fully feathered, and menoponid lice are quite agile (compared to philopterid lice) and are better able to escape preening.

Several reports have implicated other amblyceran chewing lice (notably *Trinoton*) as potential vectors for filarial nematodes (*Sarconema*) of wild waterfowl (swans and geese). There have also been a few suggestions that *Menopon gallinae* may act as a reservoir, and possible vector, for fowl cholera, typhoid and toxoplasmosis, and recent molecular studies have detected *Toxoplasma* DNA in *Menacanthus stramineus* from chickens.

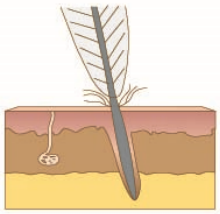
Developmental cycle and mode of transmission: The entire life-cycle of these chewing lice may occur on the skin and plumage of individual birds, with a generation time of 13-14 days. Transmission between hosts occurs when motile stages (nymphs, adults) are dislodged and move to new birds in direct or close contact. Female lice lay 1-4 eggs each day gluing them in clusters around the bases of feathers. The eggs hatch after 4–5 days releasing first-stage nymphs which begin feeding. The lice undergo hemimetabolous development with gradual (incomplete) metamorphosis through another 2 nymphal instars lasting around 3 days

each before moulting to adults. After feeding and mating, female lice produce eggs for up to 12 days with peak egg production occurring after 5-6 days. None of the developmental stages are free-living and do not survive for long when dislodged from the host, usually dying within hours (sometimes days). Direct transmission takes place when lice crawl onto new hosts in close proximity, often when birds are crowded together (particularly when breeding, nesting, or huddling for warmth). Amblyceran menoponid lice are more active and agile than ischnoceran philopterid lice and infestations may spread rapidly through a flock. Infestations often exhibit seasonal variation, with lice being more prevalent and abundant in autumn and winter. Some studies have reported an apparent synchronization between host and louse reproduction, with louse numbers escalating when host breed, thus allowing parasites to disperse from one generation to the next.

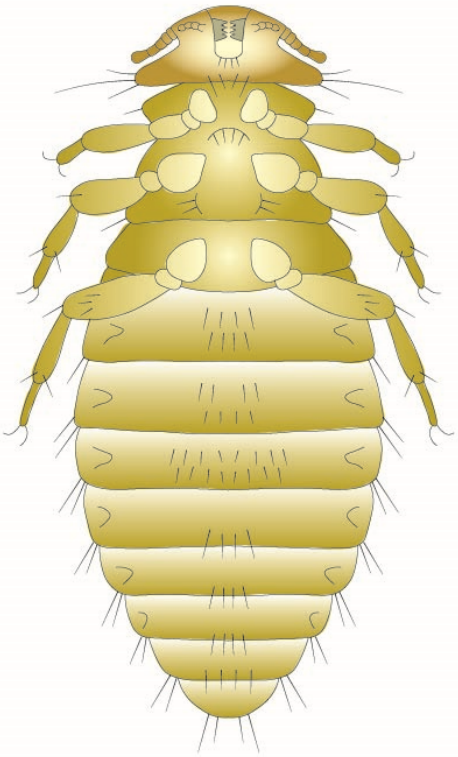
Differential diagnosis: Clinical infestations may be indicated by symptomatology, when birds exhibit restlessness, inflammation, irritation, pruritus, constant self-grooming and skin lesions with numerous small scabs and oozing exudates. Motile stages (nymphs, adults) may be detected moving around the skin and under plumage, although they rapidly scurry away from light when the feathers are parted. Louse eggs may be evident as pearl-coloured fans or masses at the bases of feathers. Louse developmental stages may be captured by hand or using forceps for subsequent microscopic examination and identification. Modern molecular biological techniques have been used to characterize some species and infer phylogenetic relationships following the polymerase chain reaction (PCR) amplification of parasite gene sequences, notably mitochondrial cytochrome oxidase I.

Treatment and control: Birds infested with chewing lice may be treated effectively using a range of insecticides, including organophosphates (malathion, tetrachlorvinphos), pyrethroids (permethrin), spinosyns (spinosad), macrocyclic lactones (ivermectin, moxidectin) and some natural products (such as rotenone (recently banned in several countries). However, louse eggs are often impervious to these chemicals so treatment needs to be repeated after 1-2 weeks to kill any emergent nymphs before they mature to adults and lay eggs. The whole flock should be treated at once and careful attention should be paid to regulations governing chemical usage in production animals (including with-holding periods, residues, contra-indications, environmental toxicity). Chemicals are available as topical applications (powders, sprays, baths) or as systemic formulations (injectable, oral or spot-on). Small numbers of birds are often treated using insecticidal powders or spray solutions ensuring thorough coverage by manually ruffling the plumage, rubbing the powder into the skin or mixing it with vaseline and applying to affected areas. Powders may also be scattered on litter or mixed with diatomaceous earth, sulphur dust, sand or wood ash and made available for self-administration in dust boxes in open aviaries, but not all bird species avail themselves of dust baths, nor do all individuals of compliant species. Liquid sprays, washes and baths have exhibited variable efficacy as feathers often provide waterproof barriers, and wet chilled birds may develop respiratory conditions. More recently, a range of liquids containing essential oil extracts were reported to have some efficacy, but some caused skin, eye or respiratory irritation, and many apparently acted only as repellents and birds quickly became re-infested. Several macrocyclic lactones have been used for the systemic treatment of infestations, with better residual activity providing longer term protection, but they are not registered for use in poultry destined for human consumption (including both meat and egg production). The prevention of infestations in farmed or aviary birds is based around providing clean facilities (washing or chemically treating cages, feeding and watering equipment), minimizing contact with infested individuals (through the isolation of infested individuals, the quarantine of new livestock, the exclusion of wild birds, avoiding over-crowding), maintaining healthy well-nourished birds (better able to resist clinical infestations) and ensuring they can preen (infestations worse in de-beaked birds).

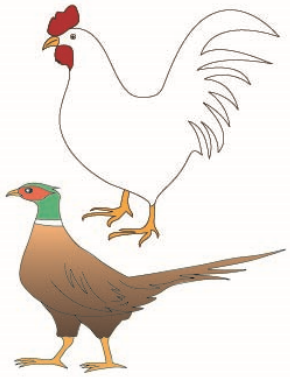
Menopon



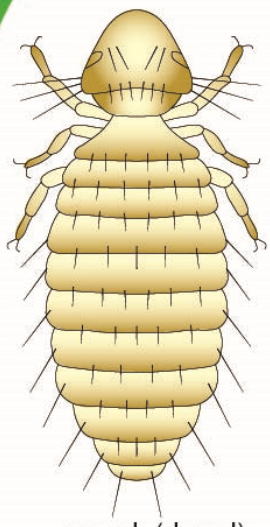
skin/plumage
(irritation, inflammation,
damaged feathers,
reduced productivity)



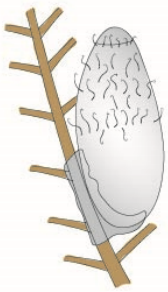
adult (ventral)
(~ 2 mm)



Definitive Hosts
(birds)



nymph (dorsal)
(~ 1.5 mm)

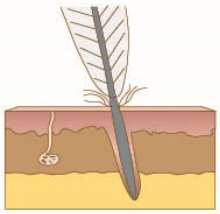


egg
(~ 0.9 mm)

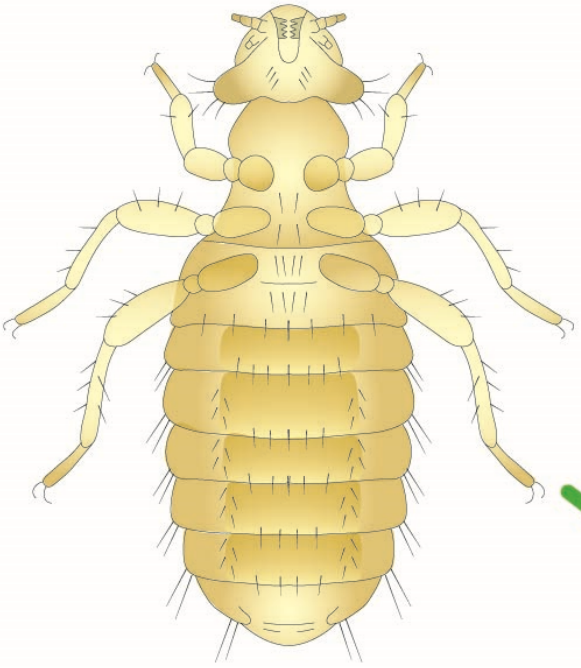
all stages ectozoic on host
(motile stages feed on skin/feathers)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites

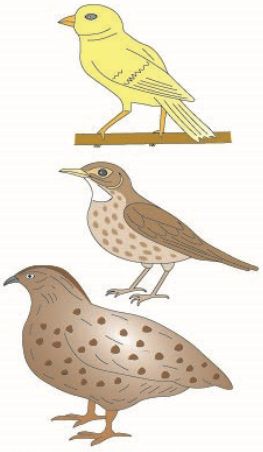
Menacanthus



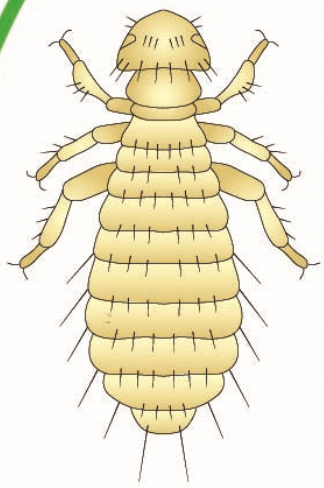
skin/plumage
(irritation, inflammation,
damaged feathers,
reduced productivity)



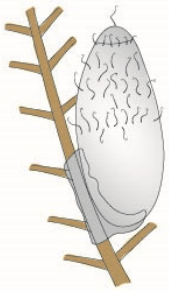
adult (ventral)
(~ 2 mm)



Definitive Hosts
(birds)



nymph (dorsal)
(~ 1.5 mm)

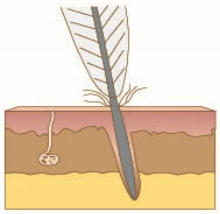


egg
(~ 0.9 mm)

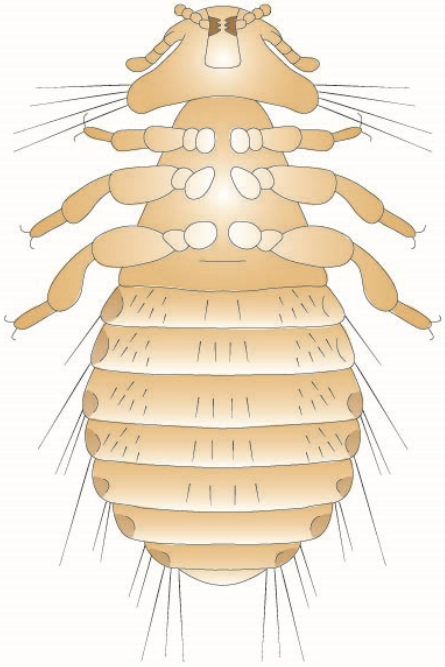
all stages ectozoic on host
(motile stages feed on skin/feathers)

transmission between hosts
through transfer of motile stages
by direct contact or via fomites

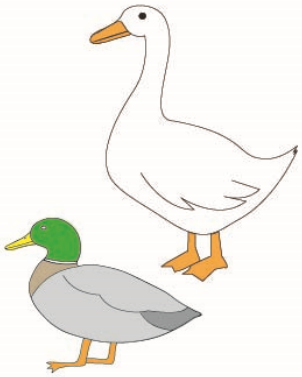
Holomenopon



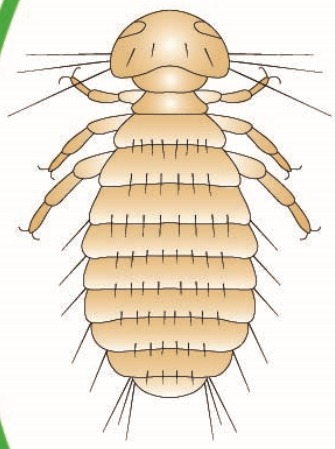
skin/plumage
(irritation, inflammation,
damaged feathers,
reduced productivity)



adult (ventral)
(~ 2 mm)



Definitive Hosts
(birds)



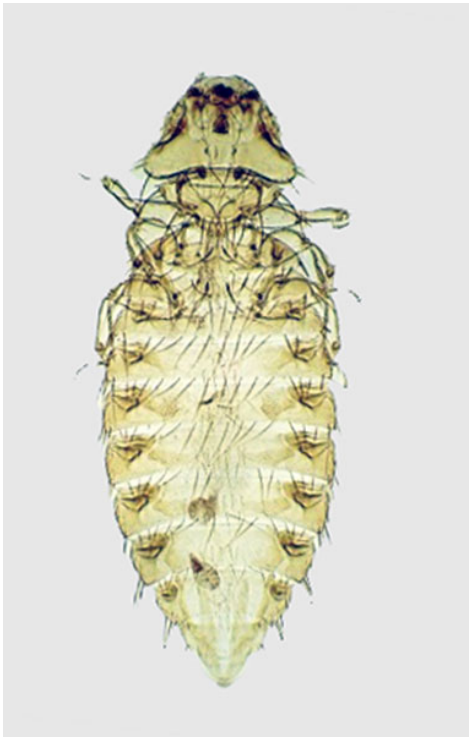
nymph (dorsal)
(~ 1.5 mm)



egg
(~ 0.9 mm)

all stages ectozoic on host
(motile stages feed on skin/feathers)

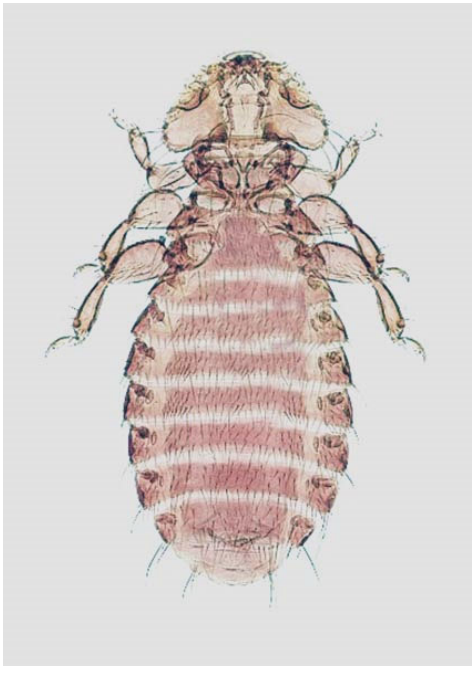
transmission between hosts
through transfer of motile stages
by direct contact or via fomites



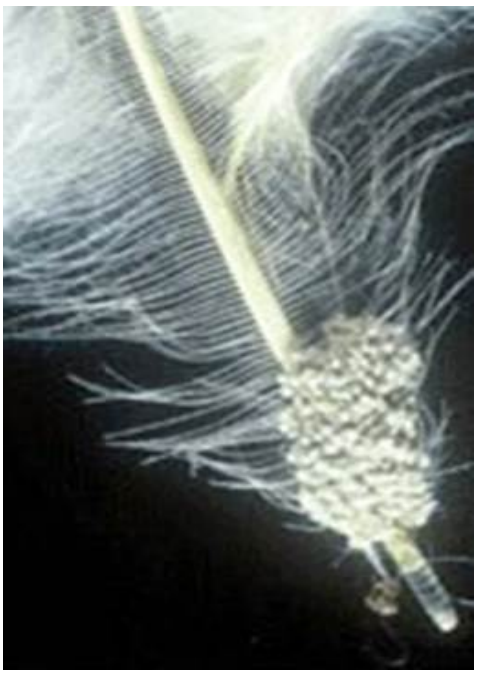
Menopon adult



Menacanthus adult



Holomenopon adult



Menopon eggs

Heterodoxus
(insect: louse)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Lice (Phthiraptera) are small wingless dorsoventrally-flattened hemipterodeans which are permanent obligate ectoparasites on other animals. All lice undergo gradual metamorphosis and there are no free-living stages. Eggs are cemented to host hairs whereas nymphs and adults cling to hairs using enlarged tarsal claws. Lice do not survive long off their hosts so transmission is usually by direct contact. Mallophagan (chewing) lice have blunt rounded heads with mouthparts adapted for feeding on keratin in superficial skin layers. Chewing lice are ectoparasitic on mammals and birds, most species being highly host specific and even site-specific. Amblycera lice have maxillary palps and four-segmented antennae located in grooves. Boopiids occur on mammals and marsupials, and infestations by *Heterodoxus* spp. have been associated with pruritus and dermatitis in dogs and macropods.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order: Phthiraptera (lice, wingless, ectoparasites, dorsoventrally flattened, stout legs, claws, eggs, nymphs, adults)
Suborder: Mallophaga (= wool-eating) (chewing lice, broad rounded head, feed on keratin, host/site specific)
Superfamily: Amblycera (with maxillary palps, large rounded heads, 4-segmented antennae in antennal grooves)
Family: Boopiidae (parasitize mammals/marsupials)
Genus: *Heterodoxus* (parasitic on skin/hair of dogs/macropods)
Species: *H. spiniger* (causes pruritus in dogs)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Lice are small wingless hemipterodeans that undergo gradual (hemimetabolous) metamorphosis and are permanent obligate ectoparasites on other animals. Four suborders are recognized: the Anoplura containing the haematophagous sucking lice of placental mammals; the Ischnocera and Amblycera (previously classified together as Mallophaga) comprising the chewing or biting lice of birds, marsupials and placental mammals; and the Rhynchophthirina confined to elephants and warthogs in Africa.

Major parasitic phthirapteran families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Suborder: Amblycera [Mallophaga p.p.] (chewing lice of mammals and birds, large rounded head, with maxillary palps, 4-segmented antennae in antennal grooves, keratin feeders) [6 families, 96 genera, 1,550 species]					
Boopiidae (marsupial chewing lice)	8 genera, 57 spp.	mammals (incl. marsupials)	nymphs, adults	biting	helminth

Menoponidae (bird lice)	68 genera, 1,150 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Ischnocera [Mallophaga p.p.] (chewing lice of mammals and birds, broad rounded head, without maxillary palps, prominent filiform antennae, keratin feeders) [2 families, 158 genera, 3,371 species]					
Trichodectidae (fur lice)	20 genera, 413 spp.	mammals (bovids, equids, carnivores)	nymphs, adults	biting	helminth
Philopteridae(bird lice)	138 genera, 2,958 spp.	birds	nymphs, adults	biting, chewing	-
Suborder: Rhynchophthirina (sucking lice of African wildlife) [1 family, 1 genus, 4 species]					
Haematomyzidae (elephant & warthog lice)	1 genus, 4 spp.	mammals (elephants, warthogs)	nymphs, adults	blood-sucking	-
Suborder: Anoplura (sucking lice of placental mammals) (narrow pointed head, pierce skin and feed on fluids (solenophagy)) [16 families, 51 genera, 694 species]					
Haematopinidae (ungulate lice, short-nosed lice)	1 genus, 21 spp.	mammals (equids, bovids, suids)	nymphs, adults	blood-sucking	viral, bacterial
Linognathidae (pale lice, long-nosed lice)	3 genera, 73 spp.	mammals (bovids, canids)	nymphs, adults	blood-sucking	-
Pediculidae (head & body lice)	1 genus, 4 spp.	mammals (hominids, New World primates)	nymphs, adults	blood-sucking	bacterial
Pthiridae (pubic lice)	1 genus, 2 spp.	mammals (hominids)	nymphs, adults	blood-sucking	-

Over 4,900 species of biting/chewing lice have been described in 253 genera in 8 families, around 4,400 species associated with birds and 500 species with mammals. Members of the suborder Ischnocera have broad rounded heads with conspicuous filiform antennae but lacking maxillary palps, while members of the suborder Amblycera have large rounded heads with maxillary palps and inconspicuous antennae hidden in grooves. Some 158 ischnoceran genera have been assigned to 2 families (Trichodectidae and Philopteridae), while 96 amblyceran genera have been classified in 6 families (Boopiidae; Gyropidae, Laemobothriidae, Menoponidae, Ricinidae, Trimenoponidae). Species of veterinary importance include members of the ischnoceran families Trichodectidae (bovids, canids, equids) and Philopteridae (poultry), and the amblyceran families Menoponidae (poultry) and Boopiidae (carnivores). Members of the family Boopiidae are parasitic on mammals and have 6 pairs of abdominal spiracles but only one segment between the thorax and the first abdominal segment bearing spiracles (whereas members of the family Menoponidae are parasitic on birds and also have 6 pairs of abdominal spiracles but have 2 segments between the thorax and first abdominal segment bearing spiracles). Some 57 boopiid species have been described from 8 genera (*Boopia*, *Heterodoxus*, *Latumcephalum*, *Macropophila*, *Paraboopia*, *Paraheterodoxus*, *Phacogalia*, *Therodoxus*). The genus *Heterodoxus* contains 24 species, one of which (*H. spiniger*) occurs on various canid and viverrid carnivores around the world, while the remaining 23 species are only found on particular macropodid marsupials in Australasia.

***Heterodoxus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
H. alatus	Diprotodontia: macropodid (pademelon)	skin		Australia
H. ampullatus	Diprotodontia: macropodid (brush-tailed rock wallaby)	skin		Australia
H. ancoratus	Diprotodontia: macropodid (whiptail wallaby)	skin		Australia
H. briscoei	Diprotodontia: macropodid (brush-tailed rock wallaby)	skin		Australia
H. calabyi	Diprotodontia: macropodid (tammar wallaby, black-striped wallaby)	skin		Australia
H. closei	Diprotodontia: macropodid (allied rock wallaby)	skin		Australia
H. harrisoni	Diprotodontia: macropodid (allied rock wallaby)	skin		Australia
H. hughendensis	Diprotodontia: macropodid (allied rock wallaby)	skin		Australia
H. insularis	Diprotodontia: macropodid (allied rock wallaby, unadorned rock wallaby)	skin		Australia
H. insulatus	Diprotodontia: macropodid (allied rock wallaby, unadorned rock wallaby)	skin		Australia
H. keleri	Diprotodontia: macropodid (brown dorcopsis)	skin		New Guinea
H. lesoueefi	Diprotodontia: macropodid (allied rock wallaby)	skin		Australia
H. longitarsus	Diprotodontia: macropodid (red-necked	skin		Australia

	wallaby)			
H. maai	Diprotodontia: macropodid (brown dorcopsis)	skin		New Guinea
H. macropus	Diprotodontia: macropodid (agile wallaby)	skin		Australia
H. maynesi	Diprotodontia: macropodid (brush-tailed rock wallaby, unadorned rock wallaby)	skin		Australia
H. mitratus	Diprotodontia: macropodid (lesser forest wallaby)	skin		New Guinea
H. murrayi	Diprotodontia: macropodid (Godman's rock wallaby)	skin		Australia
H. octoseriatus	Diprotodontia: macropodid (brush-tailed rock wallaby, unadorned rock wallaby)	skin		Australia
H. orarius	Diprotodontia: macropodid (Godman's rock wallaby)	skin		Australia
H. pygidialis	Diprotodontia: macropodid (Lumholtz's tree kangaroo)	skin		Australia
H. quadriseriatus	Diprotodontia: macropodid (quokka)	skin		Australia
H. spiniger (syn. *H. armiferus*)	Carnivora: canid (dog, red wolf, gray wolf, coyote, side-striped jackal, golden jackal, gray fox), viverrid (African civet, giant forest genet), rarely felid (cat); Diprotodontia: macropodid (agile wallaby)	skin (head, dorsum)	unkempt coat, pruritus	cosmopolitan in tropical and subtropical zones (except Europe)
H. ualabati	Diprotodontia: macropodid (swamp wallaby)	skin		Australia

Parasite morphology: Boopiid chewing lice form 3 different types of morphological stages: eggs (nits); nymphs (3 instars); and adult lice. The eggs are oval-elliptical measuring 0.8-0.9 mm in length and are often white-yellow in colour. They are glued (cemented) to host hairs along one side and surface of the eggs bears numerous small scales (pentagonal-rectangular scutes) arranged obliquely. The eggs are operculate and have an anterior disc-like ridged lid with a short central polar rod. Mature eggs hatch to release first-stage nymphs which moult through another 2 nymphal stages before forming adults. The nymphs are similar in morphology to adults but are smaller, less sclerotized, have fewer body setae, and lack genitalia. Adult lice are pale-tan to dark-brown in colour and have elongate dorsoventrally-flattened bodies measuring up to 2.5 mm in length. They have 3 distinct body parts (head, thorax, abdomen) usually covered in short setae. Their heads are broad (almost as wide as the body), hemispherical (with a smooth rounded anterior section) and sparsely setate (but with conspicuous posteriorly-directed lateral spines). They have small vestigial eyes positioned laterally in front of short clavate antennae (each composed of 4 segments) which are not conspicuous as they are concealed in deep grooves or fossae (like all other amblyceran lice, but grooves absent in ischnoceran lice). The biting/chewing mouthparts are ventrally located and consist of large opposing mandibles (lying parallel to the ventral surface such that the condyles are ventral and the ginglymus is dorsal), a posterior plate-like labrum (often with an anterior hyaline pad (pulvinus)), lateral maxillae, and an anterior labium. In chewing lice, the maxillae and labium are reduced in size (compared to sucking lice) and the maxillae are single lobed and attached to the lateral margins of the tripartite labium. Amblyceran chewing lice also have a pair of small maxillary palps, each composed of 4 segments (palps absent in ischnoceran lice). The oral cavity opens to the foregut (with pharynx, oesophagus and small crop (merely an enlargement of the oesophagus in amblyceran lice), a large midgut (with ventriculus and anterior caeca), and a hindgut (with pylorus, papillae and rectum). Amblyceran lice apparently lack a mycetome (bacteriome or stomach disc) harbouring bacterial/fungal endosymbionts, although proteobacteria are often present in the gut (in contrast, anopluran sucking lice have a well-developed mycetome and ischnoceran chewing lice have a weakly developed mycetome). The thorax is small, oval and bipartite with an anterior prothorax while the central and posterior segments are fused together. The ventral surface gives rise to 3 pairs of legs, each composed of 5 segments (coxa, trochanter, femur, tibia, tarsus) and terminating in paired tarsal claws. The abdomen in elliptical and composed of 8 segments, each with transverse rows of dense setae, lateral spines and spiracles (openings to the tracheal (breathing) system). Adult lice exhibit moderate sexual dimorphism, with male lice being slightly smaller than female lice. Mature males have 3 pairs of testes (cf. 2 pairs in ischnoceran lice), tubular vas deferens coalescing into a seminal vesicle opening into the genital sac equipped with a sclerotized aedeagus (tubular copulatory or intromittent organ with dorsal gonopore and terminal endophallus (pseudopenis)) supported by a basal apodeme (plate-like sclerite) and lateral parameres (rod-like sclerites). Mature females have ovaries with polytrophic ovarioles connected via tubular oviducts to a globular uterus fitted with accessory glands (for glue production) and spermatheca (for sperm storage after mating) opening into the vagina equipped with a genital plate and valvula. Females do not possess ovipositors but their terminal abdominal segment is bifurcated with apical sickle-shaped lobes (gonopods) with bluntly or sharply pointed appendages and setae to aid in egg deposition.

Site of infection: These chewing lice are obligate ectoparasites on the skin of their mammalian hosts, motile stages (nymphs, adults) living amongst the hair/fur close to the skin, and eggs (nits) attached to hair shafts. Most species are oioxenous (specific for individual host species) although *Heterodoxus spiniger* exhibits broader host specificity (described from a macropodid marsupial but more commonly found on canids and viverrids (rarely felids)). These ambylceran lice are less specialized and more mobile than ischnoceran lice and are often found widespread over their hosts, particularly over dorsal surfaces.

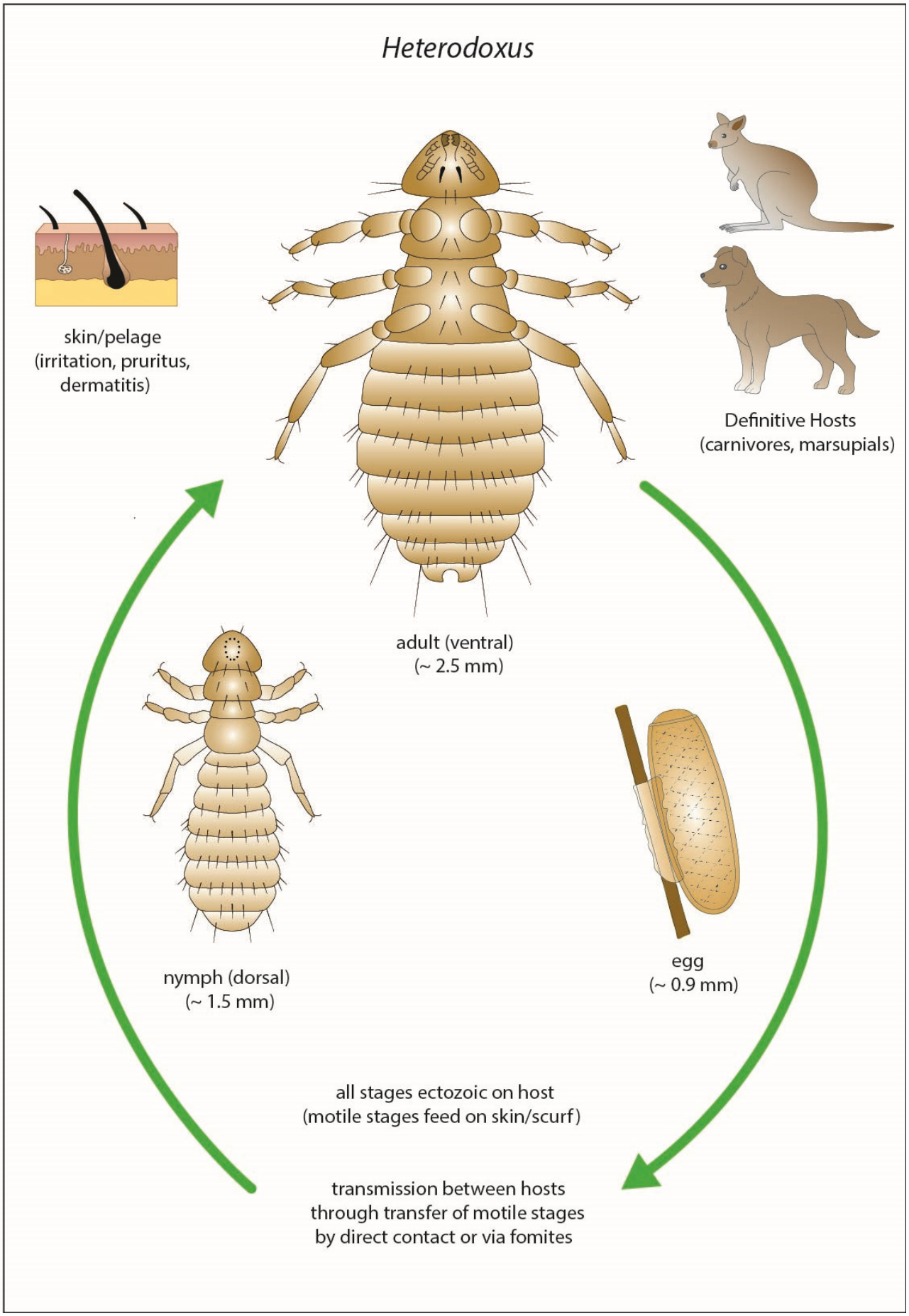
Pathogenesis: Many infestations are light and remain asymptomatic or subclinical, but heavier infestations may cause mild-severe clinical disease, characterized by inflammation, pruritus and unkempt coats. *H. spiniger* has been associated with clinical disease on canines on all continents except Antarctica and Europe. Nymphs and adult lice use their mandibles to chew or scrape host epidermal tissues feeding on sloughed skin and blood seeping from epidermal wounds. Feeding lice cause skin inflammation (dermatitis) with hyperkeratosis and variable levels of pruritus. Infested animals become restless, distressed and attempt to relieve the itching by frantic grooming (licking, biting, scratching and rubbing afflicted body parts) resulting in unsightly unkempt coats, alopecia (hair loss), skin lesions due to self-trauma and secondary infections, impaired thermoregulation, poor growth and even weight loss. Infestations are generally worse on young, old, sick or stressed animals due to their compromised physiological and/or immunological states.

Heterodoxus spiniger has been shown to act as an intermediate host for the double-pored tapeworm *Dipylidium caninum* of dogs whereby the cysticercoid stage develops in the louse and may be ingested during grooming. *H. spiniger* has also been found to harbour larval stages of the filarial nematode *Dipetalonema reconditum* which infects dogs. Recent molecular screening studies have also detected bacterial gene sequences (β subunit of RNA polymerase) from *Acinetobacter* spp. in *Heterodoxus spiniger* from dogs.

Developmental cycle and mode of transmission: Boopiid lice may complete their entire life-cycles in the pelage of individual hosts within 3-4 weeks, and there are no free-living transmissive stages. Female lice attach eggs to host hairs where they develop and hatch releasing first-stage nymphs. These stages undergo hemimetabolous development with gradual (incomplete) metamorphosis occurring through another 2 nymphal stages before moulting to adult lice. Nymphs and adult lice that become dislodged from hosts cannot survive for long periods off the host, usually dying within hours or a few days in the external environment. Transmission between hosts therefore occurs when dislodged lice crawl onto new hosts in direct or close contact or via infested bedding or grooming equipment. The transmission of infestations is greatest when hosts have prolonged contact as occurs in over-crowded groups, nursing groups, shared dens and resting places, and during cooler months of the year (autumn and winter) when animals may congregate for shared thermoregulation.

Differential diagnosis: Infestations may be suspected on clinical grounds when hosts exhibit restlessness, pruritus, repetitive grooming, skin lesions, and alopecia. Definitive diagnosis is made by the direct detection of lice and/or their eggs by visual examination when parting the coat. Detection may be assisted by using magnifying glasses and sticky tape impressions to retrieve eggs or lice for microscopic examination and identification (*Heterodoxus spiniger* should be distinguished from *Trichodectes canis* in regions where both species occur). Lice may also be collected from the skins of deceased hosts by combing or brushing the hair, scrubbing in detergent washes, performing alkaline skin digests, or by placing hides in plastic bags as lice rapidly abandon dead hosts (post-mortem examinations conducted after 24 hours are often negative for lice). Molecular biological techniques have been used to characterize species and examine phylogenetic relationships by polymerase chain reaction (PCR) amplification of nuclear gene sequences (18S ribosomal RNA).

Treatment and control: A wide range of insecticides have been used to effectively treat louse infestations, including organophosphates (diazinon), carbamates (propoxur, carbaryl), pyrethrin, pyrethroids (phenothrin, cyphenothrin, etofenprox, permethrin, cypermethrin, deltamethrin), formamidines (amitraz), macrocyclic lactones (ivermectin, moxidectin, selamectin), phenylpyrazole (fipronil), chloronicotinyl (imidacloprid), and several insect development inhibitors (methoprene or pyriproxifen but in combination with other insecticides). Most chemicals were not effective against eggs so repeat treatments were required 7-14 days later to avoid re-infestation. Care should also be given to guidelines and regulations governing chemical usage as some chemicals are quite toxic or may elicit adverse side-effects. Chemicals are available as topical applications (shampoos, sprays, powders/dusts, neck collars) or as systemic formulations (injectable, oral, spot-ons). Treatment may be aided by clipping matted fur and by using grooming devices (brushes and fine-toothed combs) to help remove lice, although adherent nits are difficult to dislodge without using conditioners to lubricate coats and ease tangles. It is advised to treat all animals in contact or confinement, and symptomatic relief may be provided using topical anti-inflammatory creams and antibiotics for damaged skin and secondary infections. Common-sense management practices may also be used for preventive control by minimizing contact with infested individuals (through quarantine, isolation or exclusion), maintaining clean housing and bedding (through washing or chemical treatment), decontaminating equipment (regular cleaning of food and water bowls, and grooming equipment), avoiding over-crowded unsanitary conditions, and keeping hosts healthy, well-nourished and well-groomed.


Heterodoxus
skin/pelage
(irritation, pruritus,
dermatitis)
adult (ventral)
(~ 2.5 mm)
Definitive Hosts
(carnivores, marsupials)
nymph (dorsal)
(~ 1.5 mm)
egg
(~ 0.9 mm)
all stages ectozoic on host
(motile stages feed on skin/scurf)
transmission between hosts
through transfer of motile stages
by direct contact or via fomites



Heterodoxus adult female



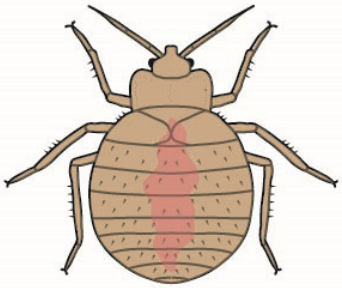
Heterodoxus adult male

Hemiptera
(bugs)

Bugs (Hemiptera)

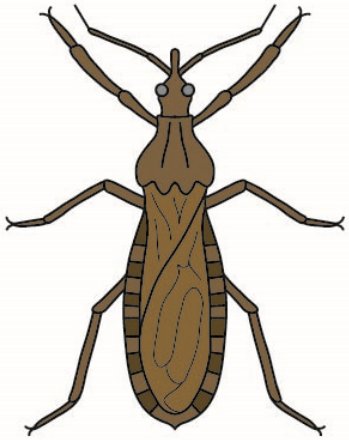
Cimex

adult (dorsal)
(~ 6 mm)



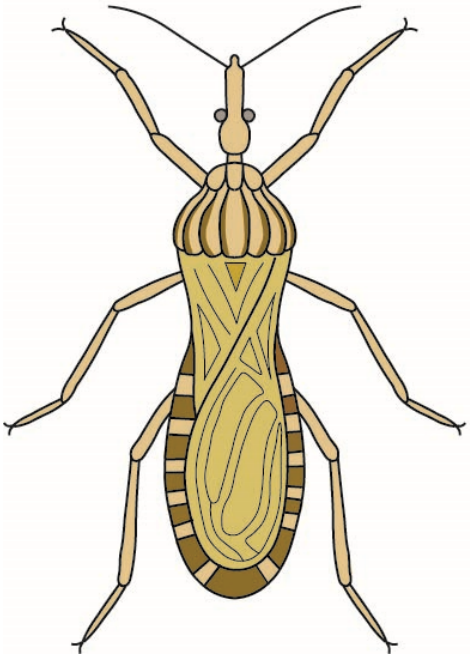
Panstrongylus

adult (dorsal)
(~ 25 mm)



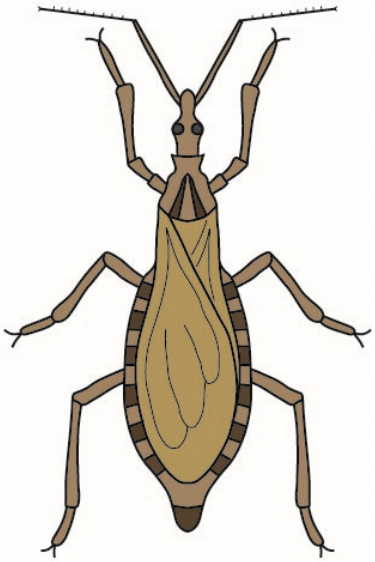
Rhodnius

adult (dorsal)
(~ 25 mm)



Triatoma

adult (dorsal)
(~ 25 mm)



Cimex
(insect: bug)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Bugs (Hemiptera) are hemipterodeans that undergo gradual metamorphosis where nymphal stages gradually become more like the adults with each moult. All bugs have sucking mouthparts for feeding on the juices mainly of plants, but sometimes on other arthropods or blood from vertebrate hosts. Cimicids are small wingless bugs that feed on warm-blooded animals, primarily birds and bats, but including bed-bugs which feed on humans. Infestations by several *Cimex* spp. have been associated with irritation, inflammation and skin lesions in birds and mammals, including humans.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order: Hemiptera (true bugs, mouthparts with stylet-like mandibles/maxillae, gradual metamorphosis)
Suborder: Heteroptera (some plant-feeders, some predatory on other arthropods, some blood-feeders on vertebrates)
Family: Cimicidae (small wingless bugs, incl. bed-bugs, blood feeders on animals)
Genus: *Cimex* (parasitic on skin of mammals/birds)
Species: various species cause skin lesions on humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Various arthropods occur as ectoparasites on other animals, mostly feeding on the blood or skin of vertebrates. Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Bugs are small winged hemipterodeans that undergo gradual (hemimetabolous) metamorphosis. They have stylet-like mouthparts and some prey on other arthropods while others feed on plants or blood from vertebrates.

Major parasitic hemipteran families	No. taxa	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Family: Cimicidae (bed bugs, bat bugs, swallow bugs)	6 subfamilies, 24 genera, 110 species	birds, mammals (bats, humans)	adults	biting, blood-feeding	-
Family: Reduviidae (assassin bugs, conenose bugs)	23 subfamilies				
Subfamily: Triatominae (kissing bugs)	5-6 tribes, 16-19 genera, 132-149 species		adults	blood-feeding	protozoa (trypanosomes)

The family Cimicidae contains 24 genera in 6 subfamilies: namely; Cimicinae (*Cimex, Bertilia, Oeciacus, Paracimex, Propicimex*); Afrocimicinae (*Afrocimex*); Latrocimicinae (*Latrocimex*); Primicimicinae (*Bucimex*, *Primicimex*); Cacodminae (*Aphrania, Cacodmus, Crassicimex, Leptocimex, Loxaspis, Passicimex, Rusingeria, Stricticimex*); and Haematosiphonae (*Caminicimex, Cimexopsis, Haematosiphon, Hesperocimex, Ornithocoris, Psitticimex, Synxenoderus*). These bugs are temporary haematophagous ectoparasites as they only come into physical contact with warm-blooded hosts in order to suck blood. They spend most of their time free-living in the external environment hiding in refuges. Most species are nidicolous and remain close to enclosed spaces in which gregarious hosts rest and sleep (such as nests, roosts, caves, and buildings). The genus *Cimex* contains 23 species which traditionally may be allocated to three groups based on biological and geographical differences, including their apparent host preferences for humans, bats or birds. While two species (*C. lectularius* and *C. hemipterus*) feed primarily on humans, another six species usually feeding on birds or bats may also occasionally feed on humans (*C. columbarius, C. limai, C. pipistrelli, C. pilosellus, C. adjunctus* and *C. dissimilis*). More recent molecular characterization studies recognize four species groups: *C. lectularius* group (but including *C. columbarius* of birds and *C. emarginatus* of bats); *C. hemipterus* group (but including *C. insuetus* of bats); *C. pilosellus* group (Nearctic bat bugs); and *C. pipistrelli* group (Palaearctic bat bugs). Archaeological records show that bed bugs have been living with humans for thousands of years, both in tropical and temperate regions, and they have been given a variety of common names (including buk, chinche, ekukulan, fusfus, heavy dragoon, klop, kunguni, lude, nachtkrabbler, nankinmusi, perceveja, piq-seq, pishpesh, plostice, punaise, red coat, rep, tapetenflunder, tokozirami, uddamsa, vaeggelus, wagglus, and wandlaus). Infestations were generally associated with rural populations living in rudimentary buildings, but increasing travel and urbanization saw infestations spread to towns and cities, with outbreaks associated with unsanitary living conditions (slums and cheap hotels). Control programmes using residual insecticides have previously worked well, but the emergence of insecticidal resistance has seen a global resurgence of infestations. Bed bugs have not been implicated in the transmission of any infectious diseases to humans, but several species of bat bugs have been found to act as vectors for the transmission of some protozoal and viral infections in bats.

***Cimex* species**	**Hosts**	**Clinical signs**	**Distribution**
C. adjunctus (Eastern bat bug)	Chiroptera: vespertilionid (big brown bat, little brown bat, silver haired bat, California bat, Indiana bat, northern long-eared bat, evening bat, Rafinesque's big-eared bat); Galliformes: phasianid (chicken); occasionally Primates: hominid (humans)		North America
C. antennatus	Chiroptera: vespertilionid (pallid bat, little brown bat), molossid (Mexican free-tailed bat)		North America
C. brevis	Chiroptera: vespertilionid (little brown bat)	experimental vector for *Trypanosoma hedricki* of bats	North America
C. burmanus	Chiroptera: vespertilionid (pipistrelle)		Asia
C. cavernicola	Chiroptera: rhinolophid (horseshoe bat), miniopterid (bent-winged bat), vespertilionid (mouse-eared bat)		Russia
C. columbarius	Columbiformes: columbid (pigeon); Passeriformes: muscicapid (pied flycatcher); Lagomorpha: leporid (rabbit); occasionally Primates: hominid (humans)		Europe
C. dissimilis	Chiroptera: vespertilionid (greater mouse-eared bat, common noctule); occasionally Primates: hominid (humans)		Eurasia
C. emarginatus	Chiroptera: vespertilionid (Geoffroy's bat)		Eurasia
C. flavifuscus	Chiroptera: vespertilionid (yellow bats); Rodentia: cricetid (Chinese striped hamster)	natural vector for *Trypanosoma scotophili* of bats	China
C. hemipterus (syn. *C. rotundatus*) (tropical bedbug)	Primates: hominid (humans); Chiroptera: vespertilionid (greater Asiatic yellow bat, lesser Asiatic yellow bat, Temminck's bat); Lagomorpha: leporid (rabbit); Rodentia: murid (rats); Galliformes (chickens); Apodiformes: apodid (common swift)	sleeplessness, sores, iron & haemoglobin deficiencies	Southeast Asia, Africa, Europe, South America
C. himalayanus	Chiroptera: vespertilionid (Himalayan whickered bat)		India
C. incrassatus	Chiroptera: vespertilionid (pallid bat, big brown bat, fringed myotis, cave myotis, Yuma myotis, canyon bat, Rafinesque's big-eared bat), molossid (Mexican free-tailed bat)		North America
C. insuetus	Chiroptera: molossid (wrinkle-lipped free-tailed bat)	vector for Kaeng Khoi virus of bats	Indochina
C. japonicus	Chiroptera: vespertilionid (greater noctule bat)		Asia
C. latipennis	Chiroptera: vespertilionid (fringed myotis)		North America

C. lectularius (common bedbug)	Primates: hominid (humans); Rodentia: murid (rats, mice); Chiroptera: vespertilionid (eastern red bat, greater mouse-eared bat, lesser mouse-eared bat, whiskered bat), rhinolophid (Mediterranean horseshoe bat); Lagomorpha: leporid (rabbit); Rodentia: murid (mouse); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon)	sleeplessness, sores, iron & haemoglobin deficiencies	Americas, Eurasia, Africa, Australasia
C. limai (syn. *Propicimex*)	Chiroptera: molossid (velvety free-tailed bat); occasionally Primates: hominid (humans)		Brazil
C. pilosellus (bat bug, Western bat bug)	Chiroptera: vespertilionid (big brown bat, silver haired bat, California myotis, long-legged myotis, Yuma myotis, pallid bat, canyon bat); Galliformes (chickens); occasionally Primates: hominid (humans)	experimentally supports *Trypanosoma cruzi*	North America
C. pipistrelli	Chiroptera: vespertilionid (common noctule, lesser noctule, common pipistrelle); occasionally Primates: hominid (humans)	natural vector for *Trypanosoma incertum* of bats	Eurasia
C. pulveratus	Chiroptera: vespertilionid (Chinese pipistrelle)		Vietnam
C. singeri	Chiroptera: vespertilionid (greater mouse-eared bat), rhinolophid (greater horseshoe bat)		Eurasia
C. stadleri	Chiroptera: rhinolophid (greater horseshoe bat), vespertilionid (greater mouse-eared bat, Geoffroy's bat)		Europe
C. usingeri	Chiroptera: rhinolophid (rufous horseshoe bat)		India

Parasite morphology: Cimicid bugs form three different types of developmental stages: eggs; nymphs (5 stages (instars) often designated N1-N5); and adults. The eggs are oval-elliptical in shape but slightly asymmetrical (bowed longitudinally). They are elongate and measure 0.9-1.1 x 0.3-0.4 mm and have a prominent operculum (anterior cap) that is bent obliquely. They are coated with a thin layer of transparent cement and appear milky-pearly white in colour. Eggs hatch to release first stage nymphs (N1) which undergo gradual (incomplete) metamorphosis whereby nymphs resembling adults moult after bloodmeals to form another four nymphal stages (N2-N5) and then adults. Successive stages gradually increase in size (from 1.5 mm long as N1 to 4.5 mm as N5 and 5-7 mm as adults) and their cuticle gradually darkens in colour (from pale yellow as N1 to dark brown as N5 and adults). All feeding stages are roughly oval and conspicuously dorsoventrally flattened. After a bloodmeal, they become swollen, and the gut turns reddish black (most obvious in the abdomen). The alimentary tract consists of a foregut (stomatodeum) with a buccal capsule, cybarium and oesophagus connected to salivary glands, a midgut (mesenteron) with a globular stomach and tubular ventricles connected to excretory Malpighian tubules and a mycetome (harbouring symbionts), and a hindgut (proctodeum) with a vesicular colon and short rectum terminating in a posterior anus. Nymphs and adults have three conspicuous body parts: a short stout head; a shield-like thorax; and an oval abdomen. The integument is densely covered with fine hairs (setae) which are most evident on adults, particularly on the margins of abdominal segments and on the legs. The head often appears triangular with a blunt tip, a pair of long slender antennae (each composed of four segments, with the distal three segments long and slender) and a pair of widely-separated lateral compound eyes. The mouthparts are located on a long slender ventral proboscis which is folded under the head when not in use for feeding. The mouthparts are of the piercing and sucking type with a basal labrum, a long slender labium forming a three-segmented rostellum (rostrum), and lateral maxillary and mandibular stylets that form two canals used for feeding and salivation. The thorax has a pronounced canoe-shaped pronotum (dorsal plate-like structure) with an anterior concavity where the head is joined). On adults, the pronotum contains numerous bristles that project outwards laterally along the margins. The thorax does not possess wings, but the forewings have been reduced to oval hemelytral pads that cover the dorsolateral mesonotum (pads absent on nymphs). The thorax possesses three bilateral pairs of slender well-developed legs inserted ventrally, and each ending in small paired claws. Bugs also possess an odorific apparatus comprising a pair of stink-glands which are located on the ventral thorax of adults but on the dorsal abdomen of later-stage nymphs. The abdomen has eleven segments that expand during feeding, exposing intersegmental membranes, and there are seven pairs of respiratory spiracles located laterally. Male bugs are slightly smaller than females, and their abdomen is narrower and the posterior tip is curved and more pointed than in females. The male reproductive system comprises globular testes, tubular vas deferens, a saccular seminal vesicle with accessory glands and a mesadenial reservoir, and then an elongate copulatory organ (aedeagus with basal paramere and terminal ejaculator bulb). The female reproductive system comprises ovoid ovaries, lateral tubular oviducts converging to a common duct and genital chamber (vagina). Females also possess a paragenital system comprising globose spermalege for sperm storage (alternatively known as the Ribaga or Berlese organ) near a narrow cleft or fissure (also known as the paragenital sinus) on the posterior margin of the fifth abdominal sternite. This system is involved in a unique form of copulation practiced by these bugs (called extra-genital, traumatic or integumentary insemination) whereby males use their lance-shaped external genitalia to pierce the female abdomen near the cleft to inject spermatozoa directly into her spermalege. A range of morphological features have been used to differentiate species, notably pronotal structure and paragenital sinus armature. For example, *C. lectularius* has broad lateral pronotal lobes while those of *C. hemipterus* are narrow. Both have a narrowly-clefted and bristled paragenital sinus (apparently an Old World feature). The bird bug *C. columbarius* is similar to *C. lectularius* but smaller, while bat bugs of the *C. pilosellus* and *C. pipistrelli* groups have narrow lateral pronotal lobes and a rounded paragenital sinus (with bristles in the *C. pilosellus* group, but naked in the *C. pipistrelli* group).

Site of infection: All cimicid bugs are obligate haematophagous ectoparasites, with nymphs required bloodmeals to moult and adults requiring blood to mature and reproduce. However, the bugs are temporary parasites as they only come into physical contact with their hosts when feeding. Several species feed on humans, biting exposed skin (face, neck, shoulders, back, limbs) often with three bites in a row (sometimes nicknamed as 'breakfast, lunch and dinner'). Bat bugs bite their hosts mostly on body surfaces with sparse hairs (particularly the wings and ears) while bird bugs often feed around sites with small downy feathers (face and vent). Most hosts are bitten at night whilst in small enclosed spaces routinely used for resting or sleeping, such as beds, buildings, caves or nests.

Pathogenesis: Bed bug infestations have been associated with a wide variety of dermatological manifestations in humans, ranging from erythematous macules or papules to bullous (blister) eruptions, and occasionally systemic and psychological disorders. Infestations of domestic poultry can be debilitating, causing significant irritability and sometimes anaemia, especially in young birds. Nymphs and adults (both sexes) feed on host blood, using their mouthparts to pierce the skin, inject saliva containing a variety of glyco- and lipo-proteins (many with anticoagulant and vasodilatory activity), and then sucking up blood. They do not remain on the host after feeding and the bites are generally painless and initially go unnoticed. However, host immunological reactions to the injected substances subsequently cause the feeding sites to become inflamed, thickened and painful. The most common local reaction is the development of pruritic (itchy) erythematous (red) maculopapular lesions (2-5 mm flat or raised bumps or wheals), which can take up to 9 days to appear but resolve within a week (often with temporary residual hyperpigmentation). The lesions may coalesce to form rashes when bites are clustered due to repeated probing by bugs to find capillary beds upon which to feed. In some cases, bullous lesions (blisters) may occur days after being bitten, and scratching may result in pruritic papules, wheals or nodules which can last for weeks. Individuals vary considerably in their immune reactions to bites, with previous exposure sometimes leading to desensitization but more frequently resulting in hypersensitivity with quicker onset and more severe lesions. On occasion, repeated infestations may lead to severe systemic allergic reactions including asthma, generalized urticaria and anaphylaxis. In heavy or protracted infestations, patients may also demonstrate varying degrees of pallor, anaemia, iron deficiency, diarrhoea, malnourishment, lethargy, malaise, sleeplessness, nervousness, irritability, anxiety, emotional and psychological distress (sometimes misdiagnosed as neurosis). Patients are also predisposed to secondary bacterial infections causing folliculitis, cellulitis and eczematoid dermatitis, with bruising and scar formation due to scratching. Infested people and premises may also develop a distinctive pungent sweet odour due to chemicals (pheromones) secreted from stink-glands in nymphal and adult bugs. Despite their reputation as one of the most common and annoying pests in human history, bed bugs have not been found to act as vectors for any infectious diseases, even though there are anecdotal reports they may harbour a range of bacteria and viruses but are unable to transmit them. Experimental studies have shown that *C. pilosellus* may support the limited development of *Trypanosoma cruzi* but there is no evidence that they are involved in the transmission of Chagas' disease. In contrast, studies involving bats have shown that *C. pipistrelli, C. flavifuscus, C. brevis* and *C. lectularius* may act as a vector for *Trypanosoma incertum, T. scotophili, T. hedricki* and *T. myoti* of bats, respectively, and that *C. insuetus* may act as a vector for Kaeng Khoi virus of bats.

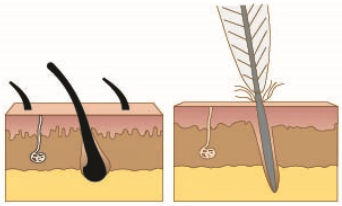
Developmental cycle and mode of transmission: The entire life-cycle of cimicid bugs is completed in the external environment, but each developmental instar requires at least one blood meal from a warm-blooded host in order to develop and moult, and adult females require larger blood meals for egg production. The bugs are therefore regarded as transient or temporary ectoparasites only coming into contact with hosts in order to feed. Indeed, the bugs lack appendages to enable them to cling to hair, fur or feathers. They are not transmitted between hosts via physical contact but spend most of their time hiding and resting within refuges. Bugs are generally nocturnal parasites and tend to feed in darkness when hosts are resting or sleeping. Nymphs and adults seek hosts within 24 hours of hatching or moulting and they are attracted by carbon dioxide, warmth, and possibly other chemicals. Having found a host, they probe exposed skin for suitable capillary beds and feed on host blood for several (3-15) minutes before leaving and seeking refuge. When prevailing temperatures exceed 10°C, they may feed several (1-3) times a week (less frequently in cooler conditions). Most cimicids are nidicolous, and well adapted to living in resting or sleeping areas of their hosts (beds, hides, nests, caves). Several species have become accustomed to invading, or even colonizing, man-made structures (buildings, pens, coops), particularly those made of poor quality materials (rough dry substrates) with numerous cracks or crevices in which to hide away from light. In refuges, mature females lay several eggs per day for 5-7 weeks, attaching the eggs to substrates in clusters using a secreted adhesive cement (sites sometimes called brood centres). The eggs hatch within 4-12 days depending on ambient temperature (longer in cooler conditions). Cimicids develop by gradual (incomplete) metamorphosis (hemimetabolous) whereby nymphs resembling adults undertake five successive moults to reach adulthood, each instar requiring a bloodmeal to develop further. Each instar develops over 2.5-10 days and adults may be formed within 6-8 weeks. Bug development, life-cycle duration and fecundity depends primarily on temperature and humidity (all being reduced in colder conditions). With regular blood meals, *C. lectularius* may complete its life-cycle in as little as 24 days at 30°C and as long as 128 days at 18°C, while *C. hemipterus* may take 25 days at 30°C and 265 days at 18°C. Without blood, adults may survive for one year in warm conditions, and even up to two years in cooler environments (bugs have been found to assimilate moisture from water vapor in the surrounding air). Different bug species vary in their climatic and geographic distributions as well as in their preferences for particular hosts. Nonetheless, they are widespread in tropical and temperate regions where human dwellings, bat caves and bird nests provide suitable habitats offering sheltered refuges, warmth and regular access to resident hosts. In human habitations, they prefer dark dry places in beds, bed frames,

mattresses (seams and stuffing), cracks/crevices in the walls and floors, behind wallpaper and wood panelling, under rugs and carpets, in furniture (particularly upholstered items), and amongst stacks or accumulations of papers and books. In severe infestations, bed bugs can be carried in the clothing and may be carried to public facilities such as theatres, office waiting rooms and upholstered seats on buses. Bed bugs may also be transported over large distances by vehicles (cars, planes, trains and ships) concealed in infested bedding, luggage, furniture and packing materials. Indeed, international travellers have been linked to the spread of infestations principally in lodging establishments around the world.

Differential diagnosis: Bed bug infestations are generally suspected following the detection of linear arrays of bites on the skin, bite sites later becoming inflamed and itchy. Visual examination of sheets and mattresses may reveal reddish-brown bloodstains as well as speckles of bug excrement. Careful examination of the immediate surroundings, particularly dark crevices which serve as hiding places, may reveal egg cases, shed skins and excrement around points of entry and exit. Infested areas may also acquire an unpleasant sickly-sweet or raspberry-like odour due to secretions from bug stink-glands. Despite such indications, infestations are best definitively confirmed by the capture and identification of bugs during or after feeding (nymphs and adults range from pale yellow to reddish-brown depending on stage and gut content). Molecular characterization studies have recently been used to examine cimicid phylogeny following the polymerase chain reaction (PCR) amplification of nuclear (ribosomal RNA) or mitochondrial (cytochrome oxidase) genes.

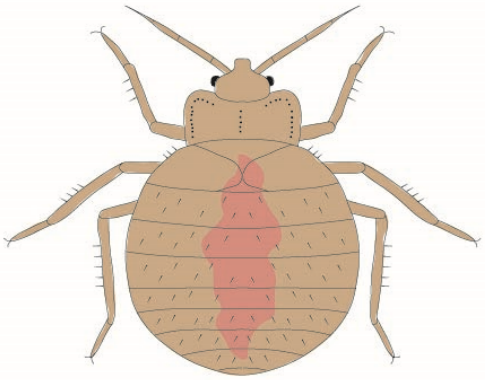
Treatment and control: Most bed bug bites resolve spontaneously in 3-10 days without treatment, but heavy or recurrent infestations may lead to persistent lesions, and even hypersensitivity. Inflammation and pruritus at the bite site may be temporarily relieved by the application of heat or ice, topical anti-pruritic agents, and topical or systemic corticosteroids or antihistamines, but they generally do not improve the appearance or duration of any dermatitis. Topical or systemic antibiotics may also be used to treat secondary bacterial infections, particularly those involving bullous lesions. In rare cases of hypersensitivity involving anaphylaxis, emergency intervention may be required with intramuscular adrenaline, antihistamines and corticosteroids. Infestations are generally controlled at source by improved hygiene and environmental disinfection using a range of chemical and non-chemical methods, which can be costly and prolonged as bugs are hardy and may survive for months. Every effort should be made to improve hygienic practices, especially with respect to sleeping quarters. Sheets and clothes should be laundered by washing in hot water with detergent or steam cleaning, and then thoroughly dried either in a hot clothes dryer for at least 20 minutes or by air-drying exposed to the sun. Bedding materials (mattresses, pillows, bedframes) should be regularly aired in the sun or cleansed by steam cleaning. Some agencies have used plastic zippered mattress covers with some success as bugs become trapped inside and die. Furniture, walls and floors should be cleaned thoroughly with commercial products, and hard-to-reach places may be dowsed with rubbing alcohol (although heavily infested upholstered furniture may have to be discarded and burned). Rugs and carpets should be regularly vacuumed and collections of papers, books or wood should be removed. Anecdotal reports suggest that sleeping under mosquito nets and keeping the lights on at night tend to reduce the frequency of being bitten. The most effective control programmes, however, also employ insecticidal chemicals to disinfect the surroundings and restrict bug populations. A range of insecticides with good residual activity are sprayed onto substrates around sites of infestations: including organochlorines (dichlorodiphenyltrichloroethane (DDT), dichlorovos, lindane, dieldrin, aldrin); organophosphates (malathion, diazinon, phosalon (on chicken farms)); pyrethrin and synthetic pyrethroids (permethrin, cypermethrin), diethyltoluamide (DEET) and some insect growth regulators (benzoylphenylureas). It may be difficult to treat all bug refuges in a single application, so a second treatment is often used 10 days later to kill any newly-emergent bugs. Given toxicity concerns associated with many of these insecticides, it is often best to employ professional pest exterminators. It is also advisable to treat luggage before and after travel to prevent the inadvertent translocation of bugs. Many successes have been recorded in controlling infestations around the world, but the emergence of insecticidal resistance and increasing globalization has seen a recent resurgence of infestations in many countries.

Cimex

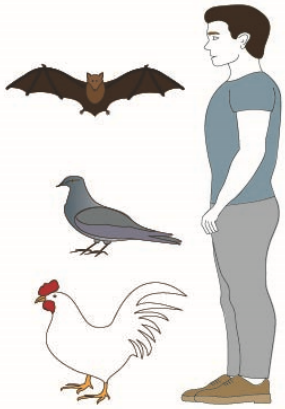


skin, pelage/plumage
(irritation,
inflammation,
skin lesions)

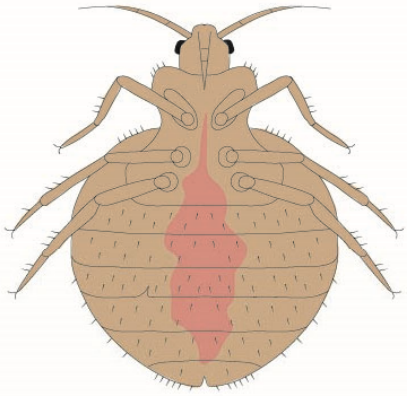
adults (~ 6 mm)



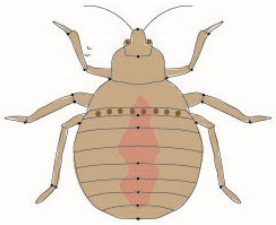
dorsal



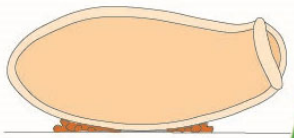
Definitive Hosts
(mammals, birds)



ventral



nymph (dorsal)
(~ 2.5 mm)



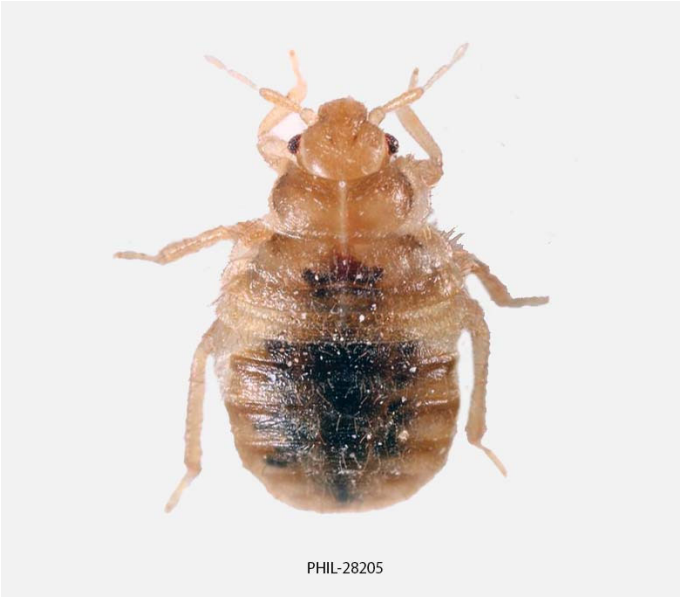
egg
(~ 1 mm)

all stages occur in external environment
(but motile stages are temporary
ectoparasites that feed on blood)

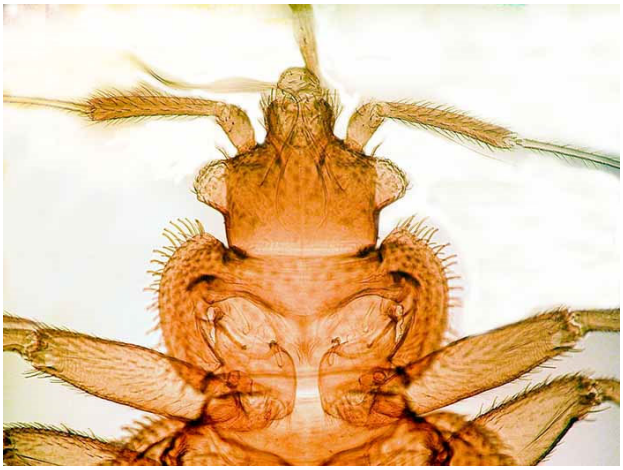
motile stages are nidiculous and
emerge nocturnally to feed on resting hosts



Cimex adult



Cimex adult



Cimex adult head



Cimex egg

Triatoma, Panstrongylus, Rhodnius
(insect: bug)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Bugs (Hemiptera) are hemipterodeans that undergo gradual metamorphosis where nymphal stages gradually become more like the adults with each moult. All bugs have sucking mouthparts for feeding on the juices mainly of plants, but sometimes on other arthropods or blood from vertebrate hosts. Reduviids are large elongate bugs, usually with wings folded in a concavity on the dorsal abdomen. Most reduviids are known as 'assassin bugs' because they prey on other insects and have a painful bite. However, the subfamily Triatominae feed on animal blood and have relatively painless bites; they are called 'kissing bugs' because they often bite the lips of sleeping persons. Various *Triatoma, Rhodnius* and *Panstrongylus* spp. feeding on humans in South and Central America may transmit Chagas' disease (caused by the kinetoplastid flagellate *Trypanosoma cruzi*).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Hemipterodea (Exopterygota) (young resemble adults, externally developing wings)
Order: Hemiptera (true bugs, mouthparts with stylet-like mandibles/maxillae)
Suborder: Heteroptera (some plant-feeders, some predatory on other arthropods, some blood-feeders on vertebrates)
Family: Reduviidae (large winged cone-nose/kissing/assassin bugs, incl. triatome bugs, blood feeders on animals)
Genus: *Triatoma* (parasitic on skin of mammals)
Species: various species feed on humans and transmit Chagas' disease

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Various arthropods occur as ectoparasites on other animals, mostly feeding on the blood or skin of vertebrates. Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Bugs are small winged hemipterodeans that undergo gradual (hemimetabolous) metamorphosis. They have stylet-like mouthparts and some prey on other arthropods while others feed on plants or blood from vertebrates.

Major parasitic hemipteran families	No. taxa	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Family: Reduviidae (large winged conenose bugs)	23 subfamilies				
Subfamily: Triatominae (kissing/assassin bugs)	5-6 tribes, 16-19 genera, 132-149 species	mammals, birds	adults	blood-feeding	protozoa (trypanosomes)
Family: Cimicidae (bed bugs, bat bugs, swallow bugs)	6 subfamilies, 24 genera,	birds, mammals (bats, humans)	nymphs, adults	biting, blood-	-

	110 species			feeding	

Members of the family Reduviidae have conical heads and are commonly known as cone-nosed bugs. Most are predatory and feed on other insects (hence being named assassin bugs or ambush bugs), but those of the single subfamily Triatominae are haematophagous and feed on vertebrate blood (known variously as kissing bugs, vampire bugs or barber bugs, as well as barbeiro, benchuca, bicudo, bush chinch, chinchorro, chipo, chirimacha, chupao, iquipito, pito or vinchuca in Latin America). The monophyletic nature of the blood-sucking Triatominae is strongly supported by molecular studies, but subsequent ranks within the subfamily vary with different tribes (and genera) proposed: namely, Alberprosseniini (*Alberprosenia*), Bolboderini (*Belminus, Bolbodera, Microtriatoma, Parabelminus*), Cavernicolini (*Cavernicola*), Linshcosteusini? (*Linshcosteus*), Rhodniini (*Psammolestes, Rhodnius*), and Triatomini (*Dipetalogaster, Eratyrus, Hermanlentia, Mepraia*?, *Meccus*?, *Nesotriatoma*?, *Paratriatoma, Panstrongylus, Triatoma* and the fossil genus *Paleotriatoma*). Most triatomine species occur in tropical and sub-tropical regions of the Americas but some occur in Southeast Asia and Africa. Morphotypic and genotypic studies on triatomines reveal a complex array of characteristics, with many discrepancies. Triatomines display a high degree of morphological plasticity (sometimes referred to as phenetic drift) with considerable pleomorphy within and between groups (particularly in size and color). Experimental studies have also revealed a large degree of inter-specific genetic variation, with evidence of inter-fertility, hybrid formation and chromosomal variation. Karyotyping studies on select American taxa have suggested two clades may exist: a northern clade comprising triatomines of North, Central and northern South America with multiple X chromosomes, and a southern clade comprising triatomines of western and southern South America with single X chromosomes, but more extensive studies are required. It has also become apparent that scientists need to agree on what constitutes a species, as different concepts yield confounding results (discrepancies between morphologic, biogeographic, reproductive and phylogenetic approaches due to pleomorphy, sympatry, inter-fertility, and gene plasticity).

Triatomine bugs spend most of their time free-living in the external environment in vegetation (esp. palm trees), animal nests and human habitations, and only come into temporary contact with vertebrate hosts in order to feed on blood. While bugs may feed on a range of available hosts, most species appear to have preferences for particular hosts (as determined by direct observations, proximity to host habitats (mostly human buildings and chicken coops), experimental feeding studies, and more recently by molecular analyses of ingested bloodmeals). Hosts include mammals (primates, carnivores, rodents, ruminants, insectivores, marsupials), birds (particularly galliforms), reptiles (lizards), and some amphibians. In particular, members of three genera are important with respect to human health, with various *Triatoma*, *Rhodnius* and *Panstrongylus* spp. acting as vectors for the transmission of Chagas' disease (New World or American trypanosomiasis) caused by the protozoan parasite *Trypanosoma cruzi* (stercorarian or contaminative transmission via bug faeces, rather than salivarian or inoculative transmission). While all triatomine species may potentially act as vectors, most transmission is limited to a few species (e.g. *T. infestans, T. brasiliensis, T. dimidiata, R. prolixus, P. megistus*) that have become well adapted to living with humans, particularly in rural areas within rudimentary buildings.

Triatomine species	Hosts	Clinical signs	Distribution
Genus *Triatoma*			
T. amicitiae			Sri Lanka
T. arthurneivai	Rodentia: caviid (Brazilian guinea pig, rock cavy); Sauria: tropidurid (Amazon lava lizard)		Brazil
T. baratai			Brazil
T. barberi	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Rodentia: murid (rats); Artiodactyla: bovid (goat); Galliformes: phasianid (chicken, turkey)	natural vector for *Trypanosoma cruzi*	Mexico
T. bolivari			Mexico
T. boliviana	Insecta: blattid (cockroach)		South America
T. bouvieri			Philippines, Vietnam
T. brailovskyi			Mexico
T. brasiliensis [incl. *T. b. brasiliensis, T. b. macromelasoma, T. b. melanica*] ['brasiliensis' complex]	Primates: hominid (human); Carnivora: canid (dog), felid (cat), mephitid (skunk); Rodentia: caviid (Spix's yellow-toothed cavy, rock cavy, Brazilian guinea pig), murid (rats); Cingulata: dasypodid (armadillo); Artiodactyla: bovid (goat); Galliformes: phasianid (chicken); birds (?); Sauria: tropidurid (calango), teiid (Argentine black and white tegu); Insecta: blaberid (cockroach)	natural vector for *Trypanosoma cruzi*	Brazil
T. breyeri	Rodentia: caviid (?), cricetid (?)		Argentina
T. carcavalloi	Primates: hominid (human)	natural vector for	Brazil

		Trypanosoma cruzi	
T. carrioni	Primates: hominid (human); Perissodactyla: equid (horse); wild animals	natural vector for *Trypanosoma cruzi*	South America
T. cavernicola	Primates: hominid (human)		Malaysia
T. circummaculata	Primates: hominid (human)	natural vector for *Trypanosoma cruzi*	Brazil, Argentina?
T. costalimai	Rodentia: caviid (rock cavy)		Brazil
T. deanei (syn. *T. deaneorum*)	Primates: hominid (human)		Brazil
T. delpontei [‘infestans’ subcomplex]	Psittaciformes: psittacid (monk parakeet); Passeriformes: furnariid (thorn bird); Rodentia: murid (rats); Didelphimorphia: didelphid (opossum)	natural vector for *Trypanosoma cruzi*	Argentina, Paraguay, Uruguay
T. dimidiata [incl. *T. d. dimidiata, T. d. capitata, T. d. maculipennis*]	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Chiroptera: phyllostomid (bat); Cingulata: dasypodid (armadillo); Artiodactyla: bovid (cattle, sheep/goat), suid (pig); Rodentia: murid (rat, mouse); Didelphimorphia: didelphid (opossum); Anseriformes: anatid (duck); Galliformes: phasianid (chicken)	natural vector for *Trypanosoma cruzi*	Central America, Mexico, Venezuela, Peru
T. dispar	Pilosa: choloepodid (Hoffmann’s two-toed sloth); Primates: hominid (human)		Central America, Ecuador
T. dominicana [fossil species]	from amber		South America
T. eratyrusiformis (syn. *T. ninoi*)	Primates: hominid (human); Perissodactyla: equid (horse); Rodentia: murid (rat), caviid (southern mountain cavy); Galliformes: phasianid (chicken)	natural vector for *Trypanosoma cruzi*	Argentina
T. flavida	Primates: hominid (human); Rodentia: capromyid (Desmarest’s hutia)		Cuba
T. gerstaeckeri	Primates: hominid (human); Rodentia: cricetid (southern plains woodrat); Didelphimorphia: didelphid (common opossum); Artiodactyla: suid (pig), bovid (cattle); Perissodactyla: equid (horse); Passeriformes: corvid (crow); Galliformes: phasianid (chicken); Serpentes: colubrid (indigo snake)	natural vector for *Trypanosoma cruzi*	Mexico, United States
T. gomeznunezi			Mexico
T. guasayana	Primates: hominid (human); Artiodactyla: bovid (goat); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Anura: bufonid (toad)	natural vector for *Trypanosoma cruzi*	Argentina, Bolivia, Paraguay
T. guazu			Paraguay
T. hegneri		natural vector for *Trypanosoma cruzi*	Mexico
T. huehuetenanguensis [*T*. sp. aff *dimidiata* (group 3)]	Primates: hominid (human)	natural vector for *Trypanosoma cruzi*	South America
T. incrassata			Mexico, United States
T. indictiva	Rodentia: cricetid (woodrat)		Mexico, United States
T. infestans (syn. *T. mazzae T. melanosome, T. oswaldoi, T. sordelli*) [‘infestans’ subcomplex] (winchuka, vinchuca, barbeiro, chipo, kissing bug, barber bug)	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Artiodactyla: suid (pig), bovid (goat, sheep); Perissodactyla: equid (donkey); Rodentia: cricetid (pale leaf-eared mouse, yellow-rumped leaf-eared mouse, Wolffsohn’s leaf-eared mouse, South American grass mouse), murid (rat), caviid (guinea pig, common yellow-toothed cavy, southern mountain cavy), chinchillid (southern viscacha), octodontid (mountain degu); Lagomorpha: leporid (rabbit);	natural vector for *Trypanosoma cruzi*	South America

	Didelphimorphia: didelphid (opossum); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Strigiformes: strigid (owl); Passeriformes: tyrranid (southern scrub flycatcher); Sauria: phyllodactylid (naked-toed gecko), tropidurid (neotropical ground lizard)		
T. jatai			Brazil
T. juazeirensis ['brasiliensis' complex]	Primates: hominid (human)	natural vector for *Trypanosoma cruzi*	Brazil
T. jurbergi			Brazil
T. klugi	Rodentia: murid (mouse); Galliformes: phasianid (chicken)	experimental vector for *Trypanosoma cruzi*	Brazil
T. lecticularia (syn. *T. heidemanni, T. occulta*)	Primates: hominid (human); Rodentia: cricetid (southern plains woodrat), sciurid (rock squirrel)	natural vector for *Trypanosoma cruzi*	Mexico, United States
T. lenti (syn. *T. bahiensis, T. pessoai*)	Primates: hominid (human); Artiodactyla: bovid (goat)		Brazil
T. leopoldi (syn. *T. novaeguineae*)			Indonesia, Australia
T. limai	Rodentia: murid (rats)		Argentina
T. longipennis ['phyllosoma' complex]	Didelphimorphia: didelphid (opossum); Artiodactyla: (suid (pig); Rodentia: murid (rat); Galliformes: phasianid (chicken)	natural vector for *Trypanosoma cruzi*	Mexico
T. maculata	Primates: hominid (human), cebid (white-fronted capuchin); Pilosa: choloepodid (Linnaeus's two-toed sloth); Carnivora: canid (dog), felid (cat), procyonid (kinkajou, raccoon); Artiodactyla: bovid (buffalo, cattle, zebu), suid (pig); Perissodactyla: equid (ass), tapirid (South American tapir); Chiroptera: phyllostomid (tailed tailless bat, Seba's short-tailed bat, spectral bat, Tilda's yellow-shouldered bat); Cingulata: chlamyphorid (six-banded armadillo), dasypodid (greater long-nosed armadillo, nine-banded armadillo); Didelphimorphia: didelphid (brown four-eyed opossum, common opossum); Rodentia: erethizontid (black-tailed hairy dwarf porcupine), murid (black rat, brown rat, mouse), sciurid (Brazilian squirrel, North American red squirrel, red-tailed squirrel); Anseriformes: anatid (muscovy duck); Cathartiformes: cathartid (Andean condor); Columbiformes: columbid (rock dove); Galliformes: phasianid (chicken, rufous-throated wood quail, spot-winged woodquail); Passeriformes: furnariid (rufous-throated thornbird); Piciformes: picid (golden-green woodpecker); Psittaciformes: psittaculid (budgerigar); Rheiformes: rheid (Darwin's rhea, greater rhea); Suliformes: fregatid (magnificent frigate bird), phalacrocoracid (neotropic cormorant), sulid (blue-footed booby); Tinamiformes: tinamid (ornate tinamou)	natural vector for *Trypanosoma cruzi*	Brazil, Colombia, Guyana, Surinam, Venezuela
T. matogrossensis			Brazil
T. mazzotti ['phyllosoma' complex]	Primates: hominid (human); Rodentia: cricetid (woodrat); Cingulata: dasypodid (armadillo)	natural vector for *Trypanosoma cruzi*	Mexico
T. melanocephala	Primates: hominid (human); Artiodactyla: bovid (goat)		Brazil
T. mexicana ['phyllosoma' complex]			Mexico

T. migrans (syn. *T. pallidula*)			India, South-East Asia
T. mopan [*T.* sp. aff *dimidiata* cave (group 4)]	Primates: hominid (human)	natural vector for *Trypanosoma cruzi*	Central America
T. neotomae	Rodentia: cricetid (southern plains woodrat, white-throated woodrat)	natural vector for *Trypanosoma cruzi*	United States
T. nigromaculata	Primates: hominid (human); Galliformes: phasianid (chicken)	natural vector for *Trypanosoma cruzi*	Venezuela
T. nitida		natural vector for *Trypanosoma cruzi*	Central America
T. obscura	Primates: hominid (human)		Jamaica
T. oliveirai	Rodentia: caviid (Brazilian guinea pig)		Brazil
T. pallidipennis (syn. *T. phyllosoma usingeri*) [‘phyllosoma’ complex]	Cingulata: dasypodid (nine-banded armadillo); Rodentia: cricetid (Allen’s woodrat)		Mexico
T. patagonica	Primates: hominid (human); Lagomorpha: leporid (rabbit); Rodentia: caviid (southern mountain cavy), cricetid (leaf-eared mouse); Galliformes: phasianid (chicken)	natural vector for *Trypanosoma cruzi*	Argentina
T. peninsularis	Rodentia: cricetid (desert woodrat)	natural vector for *Trypanosoma cruzi*	North America
T. petrochiae	Carnivora: canid (dog); Rodentia: caviid (rock cavy), murid (rats); Cingulata: dasypodid (armadillos); birds (?)		Brazil
T. phyllosoma [‘phyllosoma’ complex]	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Artiodactyla: bovid (sheep), suid (pig); Rodentia: murid (rat); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon)	natural vector for *Trypanosoma cruzi*	Mexico
T. picturata [‘phyllosoma’ complex]		natural vector for *Trypanosoma cruzi*	Mexico
T. pintodiasi			Brazil
T. platensis (syn. *T. rosenbuschi*) [‘infestans’ subcomplex]	Passeriformes: furnariid (firewood gatherer, lark-like brushrunner, brown cacholote); Psittaciformes: psittacid (monk parakeet); Galliformes: phasianid (chicken); Didelphimorphia: didelphid (latrine opossum); Rodentia: cricetid (leaf-eared mouse); Artiodactyla: bovid (goat)	natural vector for *Trypanosoma cruzi*	Argentina, Bolivia, Paraguay
T. protracta (western conenose)	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Artiodactyla: suid (pig); Didelphimorphia: didelphid (opossum); Rodentia: cricetid (white-throated woodrat, dusky-footed woodrat, desert woodrat, southern plains woodrat)	natural vector for *Trypanosoma cruzi*	Mexico, United States
T. pseudomaculata	Primates: hominid (human); Carnivora: canid (dog), mephitid (skunk); Rodentia: murid (rats); Artiodactyla: bovid (goat); birds (?); Insecta: blaberid (cockroach)	natural vector for *Trypanosoma cruzi*	Brazil
T. pugasi			Java
T. recurva (syn. *T. longipes*)	Primates: hominid (human); Didelphimorphia: didelphid (opossum); Rodentia: sciurid (rock squirrel); Carnivora: canid (dog, coyote); Sauria (lizards); Serpentes (snakes); Insecta: blattid (cockroach)	natural vector for *Trypanosoma cruzi*	Mexico, United States
T. rubida (syn. *T. ocellata, T. sonoriana, T. uhleri*)	Primates: hominid (human); Chiroptera: vespertilionid (fish-eating bat); Carnivora: canid (dog, wolf, coyote); Artiodactyla: bovid (sheep, bighorn sheep, goat), suid (pig); Rodentia: murid (rats, mice), cricetid (white-throated woodrat, desert woodrat)	natural vector for *Trypanosoma cruzi*	Mexico, United States, South-East Asia
T. rubrofasciata	Primates: hominid (human); Rodentia: murid	vector for	Indochina,

	(rats, mice); Carnivora: mephitid (skunk); Columbiformes: columbid (pigeon)	*Trypanosoma cruzi*, *conorhini* and *lewisi*	Americas, Africa
T. rubrovaria (syn. *T. bruchi, T. gomesi*)	Primates: hominid (human); Cingulata: dasypodid (armadillo); Sauria (lizards); experimentally Arachnida: mygalomorphid (tarantula); Lepidoptera: bombycid (silkworm)	natural vector for *Trypanosoma cruzi*	Argentina, Brazil, Uruguay, Java?
T. ryckmani			Central America
T. sanguisuga (syn. *T. ambigua, T. pintoi*) (eastern conenose)	Primates: hominid (human); Carnivora: canid (dog), procyonid (raccoon); Perissodactyla: equid (horse); Didelphimorphia: didelphid (opossum); Rodentia: cricetid (eastern woodrat, southern plains woodrat, hispid cotton rat); Galliformes: phasianid (chicken); Anura: hylid (frog)	natural vector for *Trypanosoma cruzi,* and possibly equine encephalitis virus	United States, India
T. sinaloensis	Rodentia: cricetid (sonoran woodrat, white-throated woodrat)	natural vector for *Trypanosoma cruzi*	Mexico
T. sinica			China
T. sordida (syn. *T. garciabesi*)	Primates: hominid (human); Carnivora: canid (dog), felid (cat); Didelphimorphia: didelphid (opossum); Lagomorpha: leporid (rabbit); Rodentia: murid (rats), caviid (guinea pig); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Passeriformes: passerid (sparrow), furnariid (rufous-throated thornbird, firewood gatherer, brown cacholote), troglodytid (thrush-like wren); Psittaciformes: psittacid (monk parakeet)	natural vector for *Trypanosoma cruzi*	South America
T. spinolai (syn. *T. chilena*)	Primates: hominid (human); Carnivora: canid (wolf); Lagomorpha: leporid (rabbit, hare); Rodentia: chinchillid (viscacha), murid (rats); Didelphimorphia: didelphid (mouse opossum); Columbiformes: columbid (pigeon), (guano shorebirds)	natural vector for *Trypanosoma cruzi*	Chile
T. tibiamaculata	Didelphimorphia: didelphid (opossum, mouse opossum); Rodentia: cricetid (marsh rice rat), echimyid (spiny rat)	natural vector for *Trypanosoma cruzi*	Brazil
T. vandae			Brazil
T. venosa	Primates: hominid (human), cebid (white-fronted capuchin); Carnivora: canid (dog), felid (cat); Artiodactyla: bovid (cattle, buffalo), suid (pig); Perissodactyla: equid (ass); Chiroptera: phyllostomid (spectral bat, Tilda's yellow-shouldered bat); Cingulata: chlamyphorid (six-banded armadillo); Pilosa: myrmecophagid (giant anteater, southern tamandua); Didelphimorphia: didelphid (brown four-eyed opossum, common opossum, northern red-sided opossum); Lagomorpha: leporid (rabbit); Rodentia: murid (brown rat, mouse), sciurid (Brazilian squirrel, North American red squirrel, red-tailed squirrel); Anseriformes: anatid (muscovy duck); Columbiformes: columbid (rock dove); Galliformes: phasianid (chicken, common quail, rufous-throated woodquail, spot-winged woodquail, turkey); Piciformes: picid (golden-green woodpecker); Suliformes: fregatid (magnificent frigate bird), phalacrocoracid (neotropic cormorant), sulid (blue-footed booby); Tinamiformes: tinamid (ornate tinamou)	natural vector for *Trypanosoma cruzi*	Central and South America
T. vitticeps (syn. *T. chagasi, T. holmbergi*)	Primates: hominid (human); Didelphimorphia: didelphid (opossum); Rodentia: caviid (rock cavy)	natural vector for *Trypanosoma cruzi*	Brazil

T. williami	Primates: hominid (human)	natural vector for *Trypanosoma cruzi*	Brazil
T. wygodzinskyi			Brazil
Genus *Panstrongylus*			
P. chinai (syn. *P. turpiali*)	Primates: hominid (human); Rodentia: murid (rats); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon)	natural vector for *Trypanosoma cruzi*	Ecuador, Peru
P. diasi	Primates: hominid (human)		Brazil, Bolivia
P. geniculatus (syn. *P. parageniculatus, Triatoma fluminensis, tenuis*)	Primates: hominid (human), cebid (white-fronted capuchin); Pilosa: choloepodid (Linnaeus's two-toed sloth), cyclopodid (silky anteater), myrmecophagid (southern tamandua); Carnivora: canid (dog), felid (cat), procyonid (kinkajou, raccoon); Artiodactyla: bovid (zebu, cattle, buffalo), suid (pig); Perissodactyla: equid (ass), tapirid (South American tapir); Chiroptera: phyllostomid (tailed tailless bat, common vampire bat, dwarf little fruit bat, Tilda's yellow-shouldered bat, stripe-headed round-eared bat, spectral bat); Didelphimorphia: didelphid (common opossum, brown four-eyed opossum); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig), murid (mouse, brown rat, black rat), octodontid (common degu), sciurid (Brazilian squirrel, red-tailed squirrel, North American red squirrel); Cingulata: chlamyphorid (southern rocket-tailed armadillo, six-banded armadillo), dasypodid (greater long-nosed armadillo, nine-banded armadillo); Galliformes: phasianid (chicken, turkey, spot-winged woodquail); Anseriformes: anatid (muscovy duck); Cathartiformes: cathartid (Andean condor); Columbiformes: columbid (rock dove); Piciformes: picid (golden-green woodpecker); Psittaciformes: psittaculid (budgerigar); Suliformes: phalacrocoracid (neotropic cormorant), fregatid (magnificent frigate bird), sulid (blue-footed booby); Tinamiformes: tinamid (ornate tinamou)	natural vector for *Trypanosoma cruzi*	South America
P. guentheri (syn. *P. larroussei, seai*)	Primates: hominid (human); Rodentia: murid (rats); Didelphimorphia: didelphid (opossums); birds (?)	natural vector for *Trypanosoma cruzi*	Argentina, Bolivia, Paraguay
P. hispaniolae (fossil species)	from amber		Central America
P. howardi (syn. *Triatoma*)	Primates: hominid (human); Rodentia: murid (rats)	natural vector for *Trypanosoma cruzi*	Ecuador
P. humeralis	Primates: hominid (human)	natural vector for *Trypanosoma cruzi*	Central America
P. lenti	Primates: hominid (human)		Brazil
P. lignarius (syn *P. herreri*)	Primates: hominid (human); Chiroptera: phyllostomid (bats); Didelphimorphia: didelphid (opossums); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig), echimyid (spiny rats), erethizontid (porcupine); Pilosa: cyclopedid (anteater); Galliformes: phasianid (chicken); Columbiformes: columbid (pigeon); Piciformes: ramphastid (toucan)	natural vector for *Trypanosoma cruzi*	Brazil, Guyana, Surinam, Venezuela, Peru
P. lutzi (syn. *P. sherlocki*)	Primates: hominid (human); Carnivora: canid (dog), felid (cat), mephitid (skunk); Artiodactyla: bovid (goat, cattle); Perissodactyla: equid (horse); Rodentia: murid (rats); Cingulata: dasypodid (armadillo); Insecta: blaberid (cockroach); birds (?)	natural vector for *Trypanosoma cruzi*	Brazil

P. martinezorum			Venezuela
P. megistus (syn. *Triatoma africana, wernickei*)	Primates: hominid (human); Chiroptera: phyllostomid (bats); Carnivora: canid (dog), felid (cat), mephitid (skunk); Artiodactyla: bovid (cattle, goat), suid (pig); Didelphimorphia: didelphid (opossums); Rodentia: murid (rats); Galliformes: phasianid (chicken); Insecta: blaberid (cockroach)	natural vector for *Trypanosoma cruzi*	South and Central America
P. mitarakaensis			French Guiana
P. rufotuberculatus	Primates: hominid (human); Chiroptera: phyllostomid (vampire bat); Carnivora: procyonid (kinkajou); Didelphimorphia: didelphis (opossum)	natural vector for *Trypanosoma cruzi*	South and Central America
P. tupynambai	Primates: hominid (human); Carnivora: canid (dog); Rodentia: cricetid (rats), murid (rats); Didelphimorphia: didelphid (opossums); birds (?); Sauria (lizards)	natural vector for *Trypanosoma cruzi*	Brazil
Genus *Rhodnius*			
R. arthuri			South America
R. barretti [‘prolixus-robustus’ group]			South America
R. brethesi [‘pictipes’ group]	Primates: hominid (human)	natural vector for *Trypanosoma cruzi*	Brazil, Venezuela
R. colombiensis [‘pictipes’ group]			South America
R. coreodes			South America
R. dalessandroi [‘prolixus-robustus’ group]			South America
R. domesticus [‘prolixus-robustus’ group]	Primates: hominid (human); Rodentia: murid (rats, mice), echimyid (golden Atlantic tree-rat, drab Atlantic tree-rat); Didelphimorphia: didelphid (opossum, mouse opossum)	natural vector for *Trypanosoma cruzi*	Brazil
R. ecuadoriensis [‘pictipes’ group]	Primates: hominid (human); Rodentia: caviid (guinea pig), murid (rats), sciurid (squirrels); birds (?)	natural vector for *Trypanosoma cruzi, rangeli*	Ecuador, Peru
R. marabaensis (syn. *R. jacundaensis*)			Brazil
R. micki			Bolivia
R. milesi [‘prolixus-robustus’ group]			Brazil
R. montenegrensis [‘prolixus-robustus’ group]			Brazil
R. nasutus (syn. *R. brumpti*) [‘prolixus-robustus’ group]	Primates: hominid (human); Artiodactyla: bovid (goat, sheep); Didelphimorphia: didelphid (opossums); Columbiformes: columbid (pigeon); Galliformes: phasianid (chicken)	natural vector for *Trypanosoma cruzi*	Brazil
R. neglectus [‘prolixus-robustus’ group]	Primates: hominid (human); Passeriformes: furnariid (firewood-gatherer); Columbiformes: columbid (pigeon); Galliformes: phasianid (chicken)	natural vector for *Trypanosoma cruzi*	Brazil
R. neivai [‘prolixus-robustus’ group]	Primates: hominid (human)		Colombia, Venezuela
R. pallescens (syn. *R. dunni*) [‘pictipes’ group]	Primates: hominid (human), cebid (white-fronted capuchin); Pilosa: choloepodid (Linnaeus’s two-toed sloth); cyclopodid (silky anteater), myrmecophagid (giant anteater, southern tamandua); Carnivora: canid (dog), felid (cat), procyonid (kinkajou, raccoon); Chiroptera: phyllostomid (Seba’s short-tailed bat, tailed tailless bat, common vampire bat, dwarf little fruit bat, spectral bat, stripe-headed round-eared bat, Tilda’s yellow-shouldered bat);	natural vector for *Trypanosoma cruzi*	Belize, Colombia, Panama

	Artiodactyla: bovid (buffalo, cattle, zebu), suid (pig); Perissodactyla: equid (ass), tapirid (South American tapir); Cingulata: chlamyphorid (southern rocket-tailed armadillo, six-banded armadillo), dasypodid (greater long-nosed armadillo, nine-banded armadillo); Didelphimorphia: didelphid (brown four-eyed opossum, common opossum, grey four-eyed opossum, white-eared opossum); Rodentia: caviid (guinea pig), erethizontid (black-tailed hairy dwarf porcupine), murid (black rat, brown rat, mouse), octodontid (common degu), sciurid (Brazilian squirrel, North American red squirrel, red-tailed squirrel); Lagomorpha: leporid (rabbit); Anseriformes: anatid (muscovy duck); Cathartiformes: cathartid (Andean condor); Columbiformes: columbid (rock dove); Galliformes: phasianid (chicken, common quail, rufous-throated woodquail, spot-winged woodquail); Pelecaniformes: pelecanid (brown pelican); Piciformes: picid (golden-green woodpecker); Psittaciformes: psittaculid (budgerigar); Rheiformes: rheid (Darwin's rhea, greater rhea); Suliformes: fregatid (magnificent frigate bird), phalacrocoracid (neotropic cormorant), sulid (blue-footed booby); Tinamiformes: tinamid (ornate tinamou); Anura: telmatobiid (Andean frog)		
R. paraensis ['pictipes' group]	Primates: hominid (human); Rodentia: echimyid (white-faced spiny tree-rat); Didelphimorphia: didelphid (opossum)	natural vector for *Trypanosoma cruzi*	Brazil
R. pictipes (syn. *R. amazonicus*) ['pictipes' group]	Primates: hominid (human), Columbiformes: columbid (pigeon)	natural vector for *Trypanosoma cruzi*	Central and South America
R. prolixus ['prolixus-robustus' group]	Primates: hominid (human), cebid (white-fronted capuchin); Pilosa: choloepodid (Linnaeus's two-toed sloth), myrmecophagid (giant anteater, southern tamandua); Carnivora: canid (dog), felid (cat), procyonid (kinkajou, raccoon), ursid (spectacled bear); Artiodactyla: bovid (zebu, cattle, buffalo), suid (pig); Perissodactyla: equid (ass), tapirid (South American tapir); Chiroptera: phyllostomid (tailed tailless bat, common vampire bat, dwarf little fruit bat, Seba's short-tailed bat, spectral bat, stripe-headed round-eared bat, Tilda's yellow-shouldered bat); Cingulata: chlamyphorid (six-banded armadillo, southern rocket-tailed armadillo), dasypodid (greater long-nosed armadillo, nine-banded armadillo); Didelphimorphia: didelphid (brown four-eyed opossum, common opossum, northern red-sided opossum, water opossum); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig), cuniculid (lowland paca), erethizontid (black-tailed hairy dwarf porcupine), murid (black rat, brown rat, mouse), octodontid (common degu), sciurid (Brazilian squirrel, fiery squirrel, North American red squirrel, red-tailed squirrel); Anseriformes: anatid (muscovy duck); Cathartiformes: cathartid (Andean condor); Ciconiiformes: ciconiid (jabiru, wood stork); Columbiformes: columbid (rock dove);	natural vector for *Trypanosoma cruzi*	South and Central America

	Cuculiformes: cuculid (yellow-billed cuckoo); Galliformes: phasianid (chicken, common quail, marbled woodquail, rufous-throated woodquail, spot-winged woodquail, turkey); Pelecaniformes: pelecanid (brown pelican); Piciformes: picid (golden-green woodpecker); Psittaciformes: psittaculid (budgerigar); Rheiformes: rheid (Darwin's rhea, greater rhea); Suliformes: fregatid (magnificent frigate bird), phalacrocoracid (neotropic cormorant), sulid (blue-footed booby); Tinamiformes: tinamid (ornate tinamou)		
R. robustus ['prolixus-robustus' group]	Primates: hominid (human)	natural vector for *Trypanosoma cruzi, rangeli*	Brazil, Bolivia, Colombia, Ecuador, Peru, Venezuela
R. stali ['pictipes' group]	Primates: hominid (human)	natural vector for *Trypanosoma cruzi*	Brazil
R. taquarussuensis			Brazil
R. zeledoni ['prolixus-robustus' group]			Brazil

Parasite morphology: Triatomine bugs form three different types of morphological stages during their development: eggs; nymphs; and adults. The eggs are oval-elliptical and slightly asymmetrical in shape, often developing a lateral flattening on one side (deemed dorsal) after several days (presumably due to drying). They range in size from 1.9-2.5 x 1.0-1.4 mm and have a convex operculum (smooth or ornamented) at one end (mounted on a short neck in the tribe Rhodniini). The eggs are pearly white (sometimes grey) when laid, but they often become brown-pink near hatching. The eggs contain a developing embryo (protonymph) whose eyespots become visible near the operculum in eggs that are > 14 days old. Newly emergent nymphs (first instar) are often pink and may be as small as 2 mm in length. Like all hemipteran bugs, triatomines undergo gradual (incomplete) metamorphosis (hemimetabolous) moulting between 5 nymphal instars (often termed N1-N5) before moulting to adults. All nymphal stages resemble adult bugs but are smaller in size, have smaller eyes, lack ocelli and mature genitalia, and are wingless but have thoracic lobes where the wings will develop. Adult bugs vary in size from 5-45 mm in length depending on species, but the majority range from 20-30 mm in length. They have elongated flattened bodies with three parts (head, thorax, abdomen) and are typically brown-black, but can have bright colouration with contrasting patterns of yellow, brown, orange, or red around the lateral edges of the abdomen. The head is elongate and cone-shaped, but small compared to the rest of the body. It has a conspicuous pair of dark hemispherical compound eyes (with multiple sensory units) at the base just in front of a pair of small ocelli (with single sensory units) located on small elevations. The head is constricted behind the eyes forming a neck without a transverse sulcus. A pair of long filiform antennae, each consisting of four segments, is mounted anterior to the eyes. The length of the anterior portion of the head and the insertion point for the antennae varies between different triatomine genera. *Rhodnius* spp. have long slender heads with the antennae inserted near the apex, *Triatoma* spp. have medium-sized heads with the antennae inserted between the eyes and the anterior apex, and *Panstrongylus* spp. have short heads with the antennae inserted close to eyes. *Panstrongylus* spp. also have large eyes relative to head size, with more and/or larger ommatidia (well adapted to dim illumination). All genera have a long three-segmented proboscis (sometimes called a beak or rostrum) which is folded beneath the head when not in use for feeding. The tip extends to a thoracic groove (the prosternal stridulatory sulcus) in all genera except *Cavernicola* and *Linshcosteus*. In blood-sucking triatomines, the proboscis is slender, straight and has a membranous connection between the second and third rostral segments, while that of predatory reduviids is thick, curved and heavily chitinized. The proboscis contains piercing/sucking mouthparts comprising a basal labrum and an elongate labium which encloses mandibular and maxillary stylets that form feeding and salivary channels. The alimentary tract consists of three sections: the foregut (stomodaeum) including the buccal cavity, pharynx (cibarial pump), oesophagus and saccular crop (stomach); the midgut (mesenteron) with ventriculus (small intestines) connected to excretory Malpighian tubules; and the hindgut (proctodeum) comprising the colon, rectum and anus. Cells in the midgut called mycetomes harbour endosymbiotic (yeast-like) micro-organisms that are involved in the digestion of bloodmeals and the production of essential vitamins. The thorax is usually dark brown and has a rough texture with large tubercles. The dorsal surface has a collar (neck), a triangular pronotum, an elongate scutellum turned down at the posterior margin but lacking lateral prongs, and two pairs of wings. The fore-wings (hemelytra) have a thickened basal section (corium and base of clavus) and an apical membranous section (apical clavus and membrane) which is often dusky, spotted or darkened along the wing veins, while the hindwings are completely membranous. When at rest, the forewings are folded over the hind wings over the dorsal abdomen. The ventral surface of the thorax has a prosternum with the stridulatory groove and gives rise to six long slender legs with simple paired terminal claws (some species also have spongy fossulae with adhesive setae at the apex of tibia on several legs). The abdomen is oval and consists of 11 segments with exposed lateral margins with distinct rims often with varied patterns of brown on a yellow or orange or red background. The abdomen is flat in unfed bugs, but becomes globose in fed bugs as it dilates considerably stretching the intersegmental and connexival membranes. Males are slightly smaller than females and their posterior abdomen is smoothly rounded rather than pointed, lobed or truncate as in females. Both sexes sclerotized external genitalia involved in reproduction. Females have two

ovaries (composed of ovarioles) connected to lateral oviducts that join into a common oviduct together with two lateral spermathecae (blind tubes for sperm storage) and accessory glands (produce proteinaceous cement). The common oviduct opens into the saccular vagina that is supported and framed by external sclerites (gonocoxites, gonapophyses and styloids). Males have two testes connected to a globular ejaculatory bulb by tubular vas deferens, as well as accessory glands connected to the bulb by seminal vesicle ducts. The ejaculatory bulb is connected to the copulatory organ (aedeagus) with a sclerotized articulatory apparatus supporting the intromittent phallus (sac-like phallosome containing an eversible endosome). These organs are contained within a genital capsule (pygophore) with sclerotized external club-shaped appendages (parameres) that hold the female during copulation. Males deposit spermatophores into the female vagina where they burst releasing spermatozoa which migrate to spermathecae.

Site of infection: Triatomine bugs are temporary ectoparasites of vertebrates, with nymphs and adults biting exposed skin and sucking blood before seeking refuge in the immediate vicinity. Various species feed on the face of resting or sleeping humans, especially around the lips (hence the common name of kissing bugs) or around the eyes, and less often on the hands, arms, feet and trunk (they are unable to feed through clothing or bedding). Many species have eclectic feeding habits and are able to feed on locally available mammals, birds, some reptiles and amphibians, although they often demonstrate strong host preferences. Host specificity is difficult to determine as bugs are rarely found on hosts and many host associations have been inferred from epidemiological records of proximity to hosts or host habitats. More recently, molecular sequencing of bloodmeals from bugs has revealed wide variations in sources suggesting broad host ranges. For example, several *Triatoma* spp. showing feeding preferences for primates, bats, rodents and birds, some *Rhodnius* spp. preferred artiodactyls and non-human primates, while some Panstrongylus spp. favoured canids and rodents.

Pathogenesis: All nymph and adult stages are obligate blood feeders and require bloodmeals for growth and development. They use their elongate mouthparts to pierce the skin, inject saliva and suck blood over periods ranging from 3-30 minutes. Despite the size of the bugs, their bites are frequently painless as their saliva contains chemicals with anaesthetic and analgesic properties as well as anticoagulant and vasodilatory activity. However, hosts may then develop immediate and delayed skin reactions to bites, the severity of which depends on the degree of allergic sensitivity. Reactions may range from wheals, papules or nodules around puncture sites to bullous (blister-like) lesions with pruritus (itching), oedema (swelling), and erythema (redness). Wheals may persist for weeks and the pruritus may be intense resulting in secondary traumatic lesions due to scratching. In rare cases, hosts may develop giant urticarial lesions or display systemic hypersensitivity responses such as anaphylaxis. Blood loss from the host may be significant as nymphs may imbibe 6-12 times their body weight and adults 2-3 times their weight in blood every 4-9 days. Heavy infestations in poultry houses may cause chronic blood loss with anaemia, morbidity and even mortality in young birds.

A range of triatomine species have gained notoriety as transmission vectors for the kinetoplastid flagellate *Trypanosoma cruzi*, the causative agent of Chagas' disease in humans in over 20 countries throughout South and Central America. Bugs ingest flagellates with bloodmeals and infective stages develop in the hindgut of the bugs. Subsequent transmission is contaminative (stercorarian) via bug faeces deposited near bite sites and then rubbed into wounds the puncture wounds when the host scratches themselves. Most bugs defaecate shortly after feeding and the interval between feeding and defaecation is one of the critical features determining the effectiveness of that species in disease transmission. Those species that cause pruritic lesions are also good vectors because they cause greater host scratching. The main vectors for Chagas' disease are those 'domestic' species (notably *T. infestans, T. brasiliensis, T. dimidiata, R. prolixus, P. megistus*) that live in close association with humans having invaded and colonized human and domestic animal habitations. However, an increasing number of sylvatic and peri-domestic species have also been shown to be natural and/or experimental vectors for *Trypanosoma cruzi*, and some consider that all triatomine species may be potential vectors. Studies have also shown that *Rhodnius robustus* and *R. ecuadorensis* may act as vectors for the less pathogenic *Trypanosoma rangeli* of mammals, and *T. rubrofasciata* may act as a vector for *Trypanosoma conorhini* and *Trypanosoma lewisi* of rodents. It has also been shown that triatomine bugs can be transiently infected with a range of viruses (including those causing hepatitis and acquired immunodeficiency syndrome in humans, and equine encephalitis), but there is no evidence to suggest that they are involved in disease transmission.

Developmental cycle and mode of transmission: All triatomine species exhibit gradual (incomplete) metamorphosis whereby eggs hatch to release nymphs which moult between five nymphal stages before forming adults. Nymphs and adults are haematophagous and must feed on blood from vertebrate hosts to develop further. They are not transmitted directly or indirectly between hosts, but only make physical contact with a host when feeding. They are nocturnal and feed at night every 2-9 days, although some have occasionally been observed feed during the day under adverse conditions. Rarely, some species have been found to be kleptohaematophagous (sucking blood already ingested by another triatomine), haemolymphagous (sucking haemolymph from other insects, notably cockroaches) or even coprophagous (ingest faeces). When not feeding, they live free in the surrounding environment taking shelter in small enclosed spaces. Many species are nidicolous and aggregate in natural or artificial constructs frequented by hosts, including nests, burrows, caves, animal houses and human habitations. Fertilised females lay 1-2 eggs per day for several weeks, each female producing around 200 eggs in total, although this may range from 50-1,000 eggs depending on species, lifespan, environment and food supply. Most eggs are oviposited singly or in small clusters free in the environment, although some species secrete an adhesive cement to stick eggs to substrates (sometimes including the feathers of nesting birds). Depending on environmental conditions (temperature and humidity), eggs hatch within 10-37 days releasing small wingless nymphs

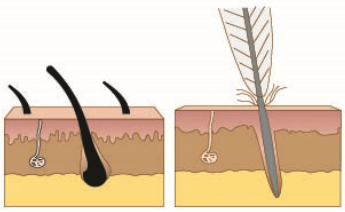
which begin feeding 2-3 days later. All subsequent nymphal and adult stages must engorge fully to develop, often requiring more than a single bloodmeal (N4 and N5 feed the most). The final moult produces winged adults (males and females) which mature rapidly and mate. Females start laying eggs 10-30 days after mating. The entire life cycle may be completed in 2-3 months, but more usually takes 1-2 years. Development occurs faster at higher ambient temperatures and at low relative humidity, suggesting that incipient global warming may accelerate life-cycles. Many species survive long periods of fasting (months) making them well adapted to nest habitats where hosts may be present intermittently. Adult bugs are good fliers but tend not to fly far from refuges (usually < 200 m although some have been recorded flying up to 1 km). During the night, the adults of several species have been found to be attracted to house lights. Behavioural studies have observed a circadian rhythm with two peak periods of spontaneous locomotory activity: one period around dusk when bugs begin seeking food; and one near dawn when they seek shelter. Host-seeking appears to involve thermoreceptors on antennae to detect heat sources as well as chemoreceptors to detect volatile host odours (carbon dioxide emanating from breath, ammonia, short chain amines and carboxylic acids from skin, hair and exocrine glands). The large compound eyes work well in conditions of dim illumination and vision serves for orientation. Studies have also shown that volatile chemical substances released in bug faeces may act as signals for refuges resulting in gregarious behaviour and aggregated distributions. The majority of triatomines are found in the New World (Americas) between latitudes 42°N and 46°S, although a few species have been found in East Asia and coastal Australia. Three major species groups are recognized on the basis of their habitats: comprising sylvatic species (inhabiting natural settings); peri-domestic species (occurring around shelters for domestic animals and humans); and domestic species (living within human habitations). Most sylvatic species are associated with wild nesting vertebrates in a variety of terrestrial or arboreal habitats, ranging from deserts, savannahs, steppe or thorny brushwood regions to dry, wet, moist and rain forests. Terrestrial habitats include subterranean ground burrows, tree root cavities, fallen logs, rock piles, caves and ruins, often inhabited by rodents (murids and porcupines) and armadillos, while arboreal habitats include hollow trees, tree holes, under tree bark, bird nests, palm-trees crowns and fronds, cactus mandacaru, bromeliads and other epiphytes, occupied by amphibians, lizards, opossums, sloths, bats and birds. *Triatoma* spp. are widespread in most sylvatic habitats while *Rhodnius* spp. primarily inhabit arboreal habitats and *Panstrongylus* spp. prefer terrestrial habitats. Numerous sylvatic species appear to be in the process of domiciliation due to changes in land use (deforestation, agricultural development, and urbanization), with some transiently invading man-made ecotopes and a few colonizing human habitations. Peri-domestic species utilize domestic animals as hosts and live near settlements usually in animal shelters, including chicken coops, aviaries, pens, hutches, sties and stables. A few species (e.g. *T. infestans*) have become truly domestic (domiciliary) and live in cracks and crevices in human dwellings where they depend on humans (and pets) for blood. They are well adapted to living in dilapidated or poorly constructed huts or shacks, especially older dwellings with mud and/or wooden walls, thatched or shingled roofs, earthen or timber floors, crude furniture, elementary furnishings (wall hangings and curtains), woodpiles and stacks of paper, clothing, and other materials. They prefer shaded refuges that provide extensive body contact with rough dry surfaces.

Differential diagnosis: Bugs are rarely captured or even observed feeding on hosts as they are nocturnal, stealthy and have painless bites. Persistent or recurrent feeding, however, may cause skin lesions, especially in allergic individuals, but the lesions are not pathognomic. Infestations in households may generally be indicated by the detection of bug faeces on floors or walls (both whitish streaks/strikes due to excreted uric acid and dark streaks containing heme), exuviae (moulted exoskeletons) or eggs (white-pink intact or empty casings) in nooks and crannies, and occasionally by the presence of nymphs or adults (lethargic after feeding). When disturbed, adults may also produce a pungent odour (secreting isobutyric acid) and they may also ‘chirp’ using their stridulatory apparatus. Various traps may be used to collect wild triatomines, but light traps only attract adults and live-baited traps only collect starved bugs, so trapping may seriously under-represent bug populations in remote areas with abundant food sources. A variety of genetic techniques have been used to characterize species and infer phylogenetic relationships, ranging from karyotyping (especially X chromosomes) to DNA sequencing (following polymerase chain reaction (PCR) amplification of nuclear (ribosomal RNA) or mitochondrial (cytochrome) genes).

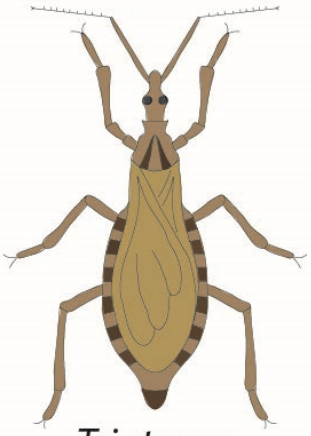
Treatment and control: Given the potential for triatomines to transmit Chagas’ disease via their faeces, it is important that bite sites are not rubbed or scratched but washed thoroughly with soap and water. Individuals developing pruritic lesions may seek relief using palliatives or antihistamines while those experiencing acute systemic reactions (anaphylaxis) may require epinephrine and other supportive measures. Several studies have reported some success with immunotherapeutic interventions where multiple measured injections of bug salivary gland extracts have been used to desensitize some individuals. Infestations in domestic animals may be treated or prevented using pour-on formulations of insecticides (notably synthetic pyrethroids) to repel or kill bugs. Effective control programs have been instituted in many countries by reducing bug populations through environmental decontamination and improving living conditions using chemical insecticides and better building methods. Various insecticidal formulations with good residual activity, notably the synthetic pyrethroids (deltamethrin, cyfluthrin, lambdacyhalothron, cypermethrin), may be used to spray inside and outside residences and outbuildings ensuring good coverage of walls, roofs and furniture. Although these chemicals may not be very effective against eggs wedged in cracks and crevices, their residual activity may be enough to kill newly emergent nymphs over longer periods. Alternatively, spray applications may be repeated at regular intervals, or wettable powders, concentrated suspensions or insecticidal paints may be used. Surface treatments are more effective on non-porous materials, such as hardwood sealed timber, fired bricks, ceramic tiles and plastered walls, than on porous surfaces such as mud adobe and rough dried timber. Homes and shelters constructed with smooth walls and ceilings, tiled or tin roofs, and concrete floors provide fewer refuges for bugs. It is also important that households be kept clear of accumulations of materials (clothing, papers, firewood, vegetation or debris), that furniture and furnishings be solidly constructed, and that domestic animals be

kept in separate quarters. Premises should undergo regular or continual surveillance for infestations, sometimes as simple as mounting paper swatches on walls to detect bug faeces. With increasing urbanization and globalization, it is important that luggage, furniture and household goods from endemic areas be treated before translocation. There have been several reports of insecticide resistance emerging in domestic bug species in several South American countries, but it does not appear to be widespread at present (possibly due to the long life-cycles of bugs and their allopatric distributions). Intensive public education programs using print and electronic media (radio, television, internet) have been used to alert communities to the risks associated with bugs and the transmission of Chagas' disease, particularly in schools and health-care facilities.

Reduviid bugs



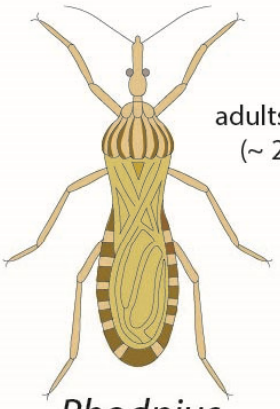
skin, pelage/plumage
(irritation, inflammation,
lesions, allergic reactions,
vector for infectious diseases
[trypanosomiases])



Triatoma

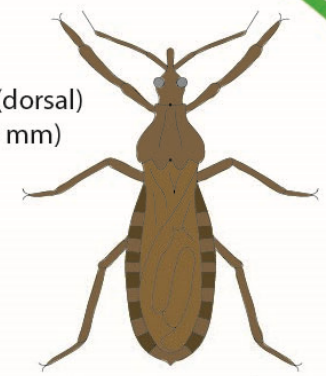


Definitive Hosts
(mammals, birds,
reptiles))

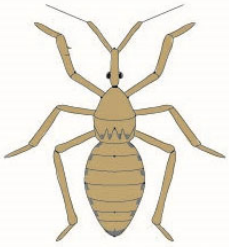


Rhodnius

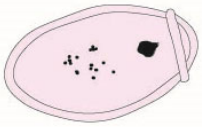
adults (dorsal)
(~ 25 mm)



Panstrongylus



nymph (dorsal)
(~ 10 mm)



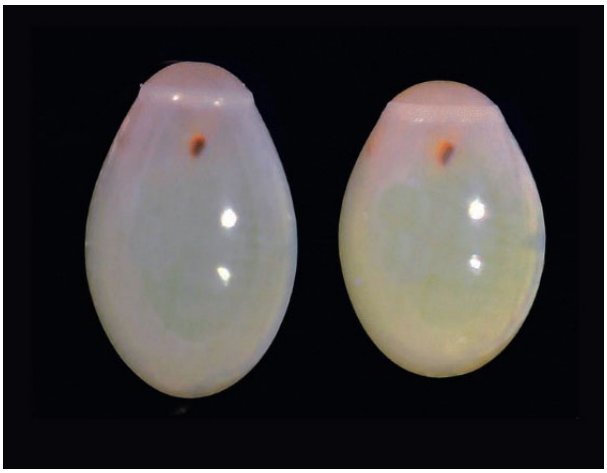
egg
(~ 2 mm)

all stages occur in external environment
(but motile stages are temporary
ectoparasites that feed on blood)

motile stages are nidiculous and
emerge nocturnally to feed on resting hosts



Triatoma adult

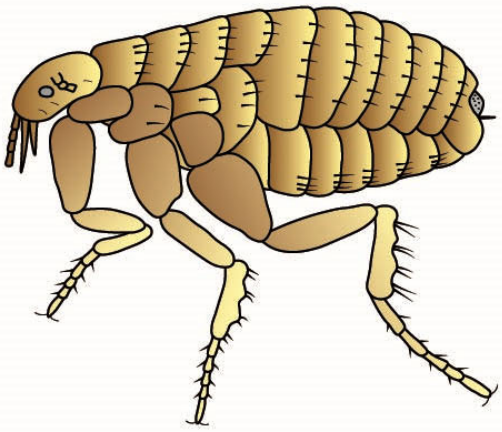


Triatoma eggs

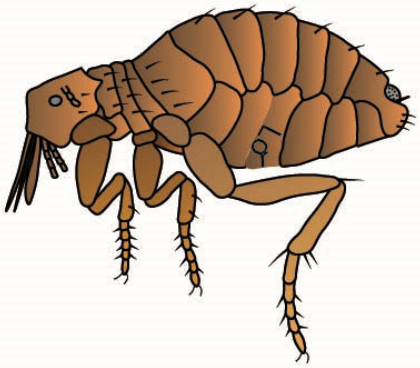
Siphonaptera
(fleas)

Siphonaptera: Pulicidae

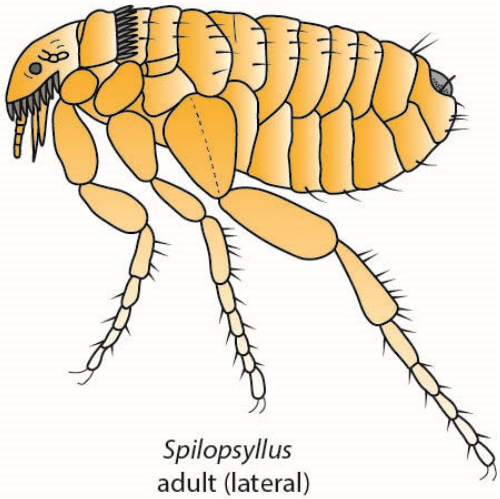
Pulex
adult (lateral)
(~ 3 mm)



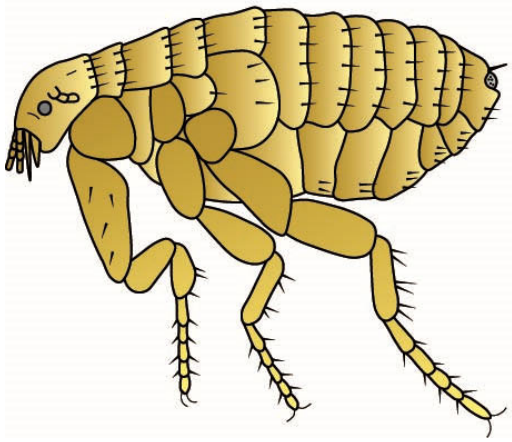
Echidnophaga
adult (lateral)
(~ 2 mm)



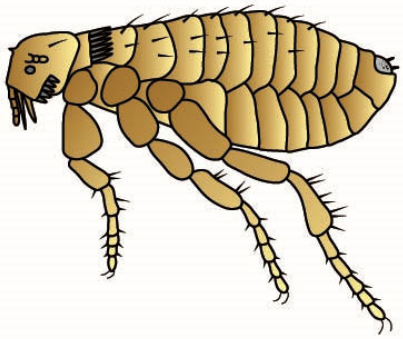
Ctenocephalides
adult (lateral)
(~ 3.5 mm)



Xenopsylla
adult (lateral)
(~ 3.5 mm)

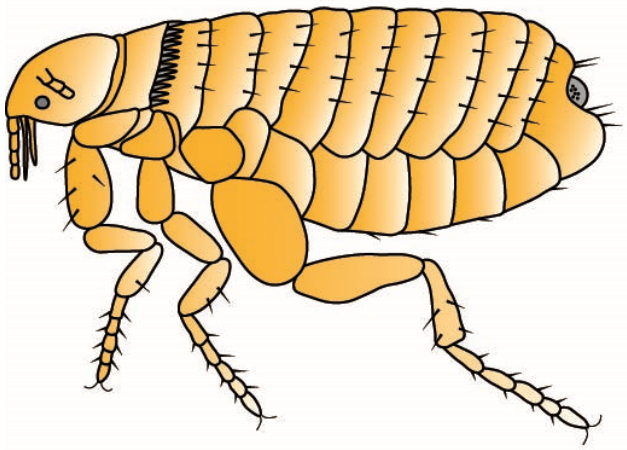


Spilopsyllus
adult (lateral)
(~ 2 mm)

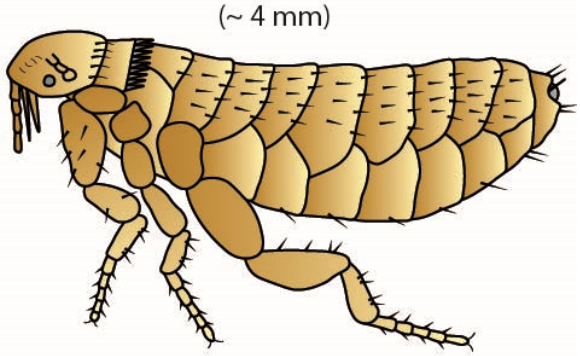


Siphonaptera: Ceratophyllidae

Ceratophyllus
adult (lateral)
(~ 4 mm)



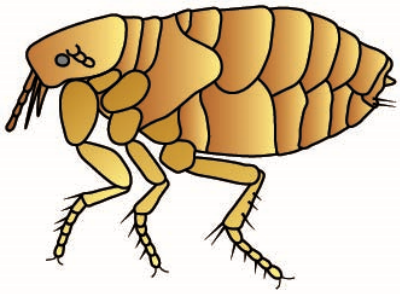
Nosophyllus
adult (lateral)
(~ 4 mm)



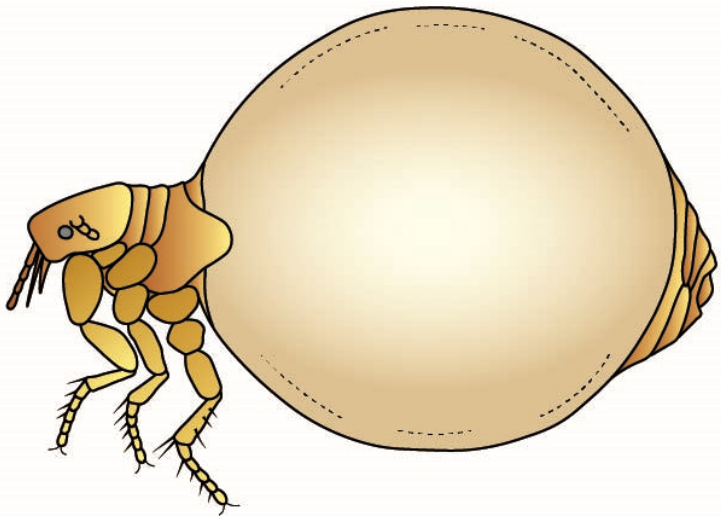
Siphonaptera: Tungidae

Tunga

adult female (lateral)
(~ 1 mm)



engorged female (lateral)
(~ 5 mm))



Pulex
(insect: flea)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Siphonaptera (fleas) are bilaterally-flattened wingless insects whose hindlimbs are enlarged and specially adapted for jumping (using elastic resilin pads rather than muscles). Fleas are holometabolans and undergo complete metamorphosis whereby grub-like larvae form pupae from which adult fleas emerge. The larvae are not parasitic but feed on debris associated mainly with bedding, den or nest material, whereas the adult stages are parasitic and feed on host blood. Pulicid fleas occur as ectoparasites on mammals, including humans, domestic and companion animals and wildlife, especially rodents. Adult *Pulex* spp. lack genal (oral) and pronotal (thoracic) combs and infestations have been associated with skin lesions and dermal hypersensitivity in humans, pigs, dogs and cats.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order: Siphonaptera (fleas, wingless, laterally compressed, third pair of legs adapted for jumping)
Family: Pulicidae (parasites of mammals)
Genus: *Pulex* (parasitic on skin of humans/dogs/cats)
Species: various species cause pruritus and allergic dermatitis in humans and companion animals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Fleas are small wingless insects that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. The adults are ectoparasitic and use siphon-like mouthparts to feed on blood from warm-blooded vertebrates [the name 'Siphon-aptera' literally translates as 'siphon' and 'wingless']. All adult fleas are further characterized by having laterally compressed bodies (allowing movement through hair/feathers), backward-pointing hairs and bristles (resisting grooming by host), strong tarsal claws (for grasping), and enlarged hindlegs (adapted for jumping). Around 2,200 flea species have been described in 250 genera on the basis of morphological and biological differences, and recent molecular phylogenetic studies have indicated some 18 families may occur in 4 infra-orders.

Siphonapteran families	Biodiversity	Hosts	Characters	Biogeographical distribution
Infraorder: Pulicomorpha (compact body, small thorax, pronotum with entire undivided ventral margin)				
Pulicidae (common fleas)	22 genera 207 species	carnivores, lagomorphs, rodents, artiodactyls, birds	sensilium with at most 14 pits, coxa with spiniform setae	pan-Tropical, cosmopolitan
Tungidae (sand fleas)	5 genera 23 species	rodents, insectivores, bats, suids, humans, birds	compression of 3 thoracic segments, neosomy	Neotropical, Holarctic

Vermipsyllidae	3 genera 39 species	carnivores, pikas, ungulates	frontal tubercle, large spiracles, reduced tergites	Holarctic
Ancistropsyllidae	1 genus 3 species	artiodactyls	metanotum and abdominal tergites with spinelets	Oriental
Coptopsyllidae	1 genus 19 species	rodents	combless, 2 spermathecae, tergal spinelets absent	Southern Palaearctic
Malacopsyllidae	2 genera 2 species	armadillos	high mesonotum, metanotum without spinelets	Patagonian
Rhopalopsyllidae	14 genera 126 species	rodents, insectivores, birds	metanotum and abdominal tergites with spinelets	Neotropical, Australasian
Infraorder: Ceratophyllomorpha (elongate body, long thorax, head without intergenal process, interantennal dimorphism)				
Ceratophyllidae	47 genera 540 species	birds, rodents, pikas, carnivores, insectivores	genal combs absent, males with interantennal suture	Cosmopolitan
Ischnopsyllidae (bat fleas)	20 genera 125 species	bats	genal comb with 2-4 flattened spines, interantennal furrow	Cosmopolitan
Leptopsyllidae	29 genera 260 species	insectivores, lagomorphs, rodents, carnivores, birds	head with tentorial arch, males with interantennal suture	Holarctic, Australasia
Xiphlopsyllidae	1 genus 8 species	rodents, shrews	squamulum absent, simple interantennal wall	Eastern African
Infraorder: Hystrichopsyllomorpha (elongate body, long thorax, head with intergenal process, clasper without process)				
Chimaeropsyllidae	8 genera 26 species	elephant shrews	sensilium with 14 pits, hind coxa with spiniform setae	African
Hystrichopsyllidae (nest fleas)	46 genera 582 species	rodents, insectivores, pikas, marsupials	highly variable structures, 2 spermathecae	Cosmopolitan
Macropsyllidae	2 genera 2 species	rodents	single head comb, 4 abdominal combs, 2 spermathecae	Australian
Stephanocircidae (helmet fleas)	9 genera 51 species	rodents, marsupials, birds	helmet (frons) with 2 separate combs, single spermatheca	Neotropical, Australian
Infraorder: Pygiopsyllomorpha (elongate body, long thorax, head with intergenal process, metanotum without spinelets)				
Pygiopsyllidae	10 genera 48 species	rodents, marsupials, birds	unique articulation between digitoid and main part of clasper	Australasian, Neotropical
Lycopsyllidae	4 genera 8 species	marsupials	genal lobe, simple interantennal wall, single mesopleural rod	Australian
Stivaliidae	23 genera 110 species	rodents, marsupials	strongly developed basal arm of Y-sclerite	Palaearctic, Australasia

Fleas from several families are found as ectoparasites on domestic and companion animals around the world: particularly those belonging to the families Pulicidae and Tungidae on mammals, and the family Ceratophyllidae on birds. Members of the family Pulicidae (syn. Archaeopsyllidae, Xenopsyllidae, Sarcopsyllidae p.p.) are characterized by compact bodies, small rounded heads and reduced chaetotaxy (small numbers of setae, spines and/or bristles). Over 20 genera have been recognized in 5 subfamilies: namely, Archaeopsyllinae (*Aphropsylla*, *Archaeopsylla*, *Centetipsylla*, *Ctenocephalides*, *Nesolagobius*), Moeopsyllinae (*Moeopsylla*), Pulicinae (*Delopsylla*, *Echidnophaga*, *Pulex*), Spilopsyllinae (*Actenopsylla*, *Cediopsylla*, *Euchoplopsyllus*, *Hoplopsyllus*, *Ornithopsylla*, *Spilopsyllus*), and Xenopsyllinae (*Parapulex*, *Pariodontis*, *Procaviopsylla*, *Pulicella*, *Synopsyllus*, *Synosternus*, *Xenopsylla*). Various pulicid species and genera are considered to be important parasites of medical and veterinary significance either as parasites in their own right (blood-sucking behaviour causing anaemia, dermatitis and hypersensitivity reactions) or as vectors for other infectious micro-organisms (including bacteria and helminths). Pulicid genera are differentiated mainly on the basis of whether the thoracic segments are very short (*Echidnophaga*), whether both genal (head) and pronotal (thorax) ctenidia (combs) are present (*Ctenocephalides, Spilopsyllus*) or absent (*Pulex, Echidnophaga, Xenopsylla*), and whether the axis of the genal comb is horizontal (*Ctenocephalides*) or vertical (*Spilopsyllus*).

Genera	**No. spp.**	**Hosts**	**Ctenidia (combs)**		**Disease**	**Vector**
			Genal (head)	**Pronotal (thorax)**		
Pulicidae						
Pulex	12	humans, carnivores, marsupials, rodents, birds	absent	absent	irritation, dermatitis, anaemia	plague, typhus, spotted fevers, tapeworms
Echidnophaga	23	birds, rodents, carnivores, marsupials	absent	absent	inflammation, ulceration	rickettsioses, plague, myxomatosis

Xenopsylla	76	rodents, carnivores, marsupials, birds	absent	absent	irritation	plague, typhus, rat tapeworms
Ctenocephalides	12	carnivores, rodents, rabbits, insectivores, ungulates, birds	horizontal	present	pruritus, anaemia, hypersensitivity (flea-bite allergy)	bartonelloses, typhus, plague, dog tapeworm, filarial nematode
Spilopsyllus	1	rabbits, rodents, carnivores, birds	vertical	present	irritation	myxomatosis, tularemia
Tungidae						
Tunga	13	humans, insectivores, rodents, carnivores	absent	absent	inflammation, ulceration	*Staphylococcus, Wolbachia*, tetanus
Ceratophyllidae						
Ceratophyllus	64	birds, rodents, carnivores, ungulates	absent	present	irritation, reduced productivity	
Nosopsyllus	52	rodents, carnivores, some birds	absent	present	irritation	plague, erysipeloid, rat tapeworm

Pulex spp. are characterized primarily by morphological features of adult flea stages, notably their small smooth rounded heads and setate bodies lacking genal and pronotal ctenidia (combs). Some 12 species have been described from mammals (mainly rodents, insectivores, marsupials, carnivores, sometimes humans) and some birds; many species being found on a range of hosts, often not closely-related but sharing similar habitats. Some authorities recognize 2 subgenera: *P.* (*Pulex*) comprising those species with shorter heads, medium mouthparts, large eyes, and a single bristle in place of the genal comb; and *P.* (*Juxtapulex*) comprising those species with longer heads, longer mouthparts, smaller eyes, and 2 short angulate spines in place of the genal comb. The human flea, *P. irritans*, once prevalent and widespread in human communities, is now found mainly on pigs and poultry in rural areas in developing countries. Health authorities continue to monitor distribution patterns, as the flea has previously been shown to act as a vector for the transmission of various bacterial diseases (notoriously including bubonic plague) as well as dog tapeworms.

***Pulex* species**	**Hosts**	**Clinical signs**	**Distribution**
P. (*Juxtapulex*) *alvarezi*	Perissodactyla: tapirid (Baird's tapir); Didelphimorphia: didelphid (common opossum)		Central America
P. arizonensis	Rodentia: murid (silvery mouse)		North America
P. brunneri	Rodentia: sciurid (Columbian ground squirrel)		South America
P. (*Juxtapulex*) *echidnophagoides*	Cingulata: dasypodid (nine-banded armadillo); Didelphimorphia: didelphid (gray four-eyed opossum); Carnivora: felid (cougar)		Americas
P. gillettei	Strigiformes: strigid (eastern screech owl)		North America
P. howardi	Rodentia: sciurid (woodchuck, flying squirrel), murid (silvery mouse)		Americas
P. (*Pulex*) *irritans* (syn. *P. conepati, orientalis, vulgaris*) (human flea)	Primates: hominid (human); Chiroptera: molossid (broad-eared bat), phyllostomid (big-eared woolly bat); Carnivora: canid (dog, culpeo, red fox), felid (cat), ailurid (red panda), mustelid (Eurasian otter, European badger); Artiodactyla: suid (pig); Perissodactyla: equid (horse); Eulipotyphla: erinaceid (European hedgehog); Rodentia: cricetid (short-tailed field vole), heteromyid (Gaumer's spiny pocket mouse), murid (brown rat, bush rat, house mouse, wood mouse); Dasyuromorphia: dasyurid (western quoll); Diprotodontia: phalangerid (common brushtail possum), pseudocheirid (western ringtail possum); Monotremata: tachyglossid (short-beaked echidna); Didelphimorphia: didelphid (Virginia opossum); Anseriformes: anatid (mallard); Charadriiformes: scolopacid (Eurasian woodcock); Galliformes: phasianid (chicken); Passeriformes: hirundinid (welcome swallow)	dermatitis (+ vector for bubonic plague, murine typhus, trench fever, spotted fevers, dog tapeworm, mouse tapeworm)	worldwide
P. (*Pulex*) *larimerius*	[fossil in amber]		Dominican Republic
P. multispinosus	Lagomorpha: leporid (cottontail rabbit)		Americas
P. (*Juxtapulex*) *porcinus*	Artiodactyla: tayassuid (peccary); Carnivora: felid (cougar, jaguar); Didelphimorphia: didelphid (common opossum); Cingulata: dasypodid (nine-banded armadillo)		Americas
P. (*Pulex*) *simulans* (syn. *P. dugesii*)	Primates: hominid (human); Artiodactyla: suid (pig), cervid (mule deer); Carnivora: canid (wolf, gray fox, savannah fox), mephitid (striped skunk); Rodentia: sciurid (ground squirrel, prairie dog); Didelphimorphia: didelphid (common opossum); Pilosa:	dermatitis	Americas

	myrmecophagid (collared anteater)		
P. (*Pulex*) *sinoculus*	Rodentia: geomyid (giant pocket gopher), sciurid (squirrel)		Central America

A number of other flea species were originally described as belonging to the genus *Pulex* but were subsequently transferred to other genera: including *P. coloradensis* to *Tarsopsylla, P. divisus* to *Typhlopsylla, P. grossiventris* to *Malacopsylla, P. hirsutus* to *Opisocrostis, P. ignotus* to *Foxella, P. keeni* to *Opisodasys, P. lutzii* to *Rhopalopsyllus, P. montanus* to *Oropsylla (Diamanus), P. penetrans* (syn. *P. penetrates*) to *Tunga, P. penicilliger* to *Trichopsylla, P. sciurorum* to *Monopsyllus,* and *P. segnis* to *Leptopsylla,* as well as two species names (*P. pungens* and *P. vespertilionis*) declared invalid.

Parasite morphology: Pulicid fleas form 4 different types of morphological stages during their development: eggs; larvae; pupae; and adults. The eggs are ovoid measuring around 0.5 mm long and appear pearly white in colour. Larvae emerge as elongate vermiform (worm-like) stages that become progressively larger as they moult through 3 instars growing from 1.5 to 4-6 mm in length by 0.5 mm in width. They are eruciform having soft cylindrical bodies (yellow-white in colour) with darker sclerotized heads with powerful mandibles and mandibular teeth well-adapted for biting and chewing. Larvae have 13 segments (3 thoracic, 10 abdominal) with bristles on each segment and the posterior segment having 2 small brown hooks. They lack eyes and legs but are active stages, the final instar folding back on itself prior to pupation. They become enclosed within loosely-woven silken cocoons which are initially white to yellow in colour but become brown as they are sticky and collect adherent debris. The cocoons range in size from 2-5 x 1-3 mm and contain pupae undergoing profound changes. The larval head and last 3 segments are lost during pupation and the body becomes compressed (shorter and wider). They are exarate pupae and their legs appear free from the body wall (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). Pupae come to resemble adult fleas without wings but with elongated mouthparts, short antennae, inconspicuous eyes, and developing setae and bristles. Adult fleas emerge as characteristically laterally-compressed stages that are heavily chitinized with hard plates (called sclerites) which make them very resistant to being squashed. Adults of different species range in size from 1.5-4.0 mm in length and are often shiny dark brown in colour, sometimes tan-red particularly after feeding. The sclerites have distinctive patterns (chaetotaxy) of setae, spines and/or bristles, usually facing backwards so as to not impede forward movement through pelage or plumage, but catching on hairs or feathers when dragged backwards by host grooming. Other flea genera possess comb-like rows of spines either on the head (genal ctenidia), on the thorax (pronotal ctenidia) or on both sites, but they are absent on *Pulex* spp. All adults have 3 separate body parts, with a small anterior head, a short thorax and an elongate abdomen (the latter 2 being almost continuous). The head is small and shield-like with a smoothly rounded frons (forehead), no frontal tubercle (brow), and gena (cheeks) with broad ventral lobes. They possess a pair of simple noncompound eyes (clusters of ocelli), a pair of short club-like antennae (3-segmented) held in protective grooves (fossae), and 3 strong bristle-like setae on each side; one on the genal margin, one behind the antennae, and one below the eye (in contrast to *Xenopsylla* spp. which have an ocular bristle in front of the eye). Early workers recognized 2 subgenera on the basis of morphometric differences: *P.* (*Pulex*) with shorter heads, medium mouthparts, large eyes, and a single genal bristle, and *P.* (*Juxtapulex*) with longer heads, longer mouthparts, smaller eyes, and 2 short angulate genal spines. All adults have conspicuous ventral piercing-sucking mouthparts (lacking mandibles and teeth) located between sensory palps used to probe the host skin for suitable feeding sites. The palps consist of a pair of long 4-segmented maxillary palps arising from the top of short blade-like maxillary lobes (stipes) as well as long 5-segmented labial palps arising from a short basal labium. The actual mouthparts (fascicle) consist of 3 long slender stylets: the 2 outer stylets (maxillary laciniae) being blade-like and serrated (sometimes with coarse teeth) and used to puncture the skin; and the third central stylet (labrum-epipharynx) being an outgrowth of the body wall (unique to fleas) and used to enter a capillary. All 3 stylets join to form a tube-like canal to inject saliva (via salivary pumps) and suck blood (via cibarial and pharyngeal pumps). The laciniae in *Pulex* spp. are elongate and extend halfway down the forecoxae in *P. irritans* and three-quarters the length of forecoxae in *P. simulans*. The alimentary tract comprises a tubular foregut (with anterior pharynx, salivary glands inserted apically, elongate oesophagus, and small globular proventriculus armed with spines to prevent regurgitation), a large expandable midgut (a simple undivided organ (without diverticula or caeca) for the storage, digestion and absorption of bloodmeals, unlike the more elaborate divided midguts of most other haematophagous arthropods), and a tubular hindgut (with excretory Malpighian tubules, and rectum). The thorax possesses 3 dorsal sclerites (pronotum, mesonotum, and metanotum) but does not have a meral rod (vertical thickening). Ventrally, the thorax is the point of attachment for 3 pairs of strong legs; each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) and ending in 2 claws. The hind-coxae bears a patch of small spines (8-12 spines in females, 7-10 in males). The third pair of legs are much longer and well-adapted for jumping using unique elastic resilin pads to store energy under compression (rather than muscular contraction). The oval abdomen contains 10 segments, most with lateral respiratory spiracles and a single row of setae, but the last 3 segments highly modified by genital structures. Both males and females have a flat dorsal plate-like organ (sensilium or pygidium) with a number of pitted and setate dome-like structures (sensory organs detecting air movement, vibrations and temperature gradients). A pair of anal stylets bearing apical setae and short bristles is also located behind the sensilium. Males are generally smaller than females (1.5-2.5 v. 2.5-4.0 mm long) and they have highly elaborate genitalia (arguably the most complex in the animal kingdom). Males have modified abdominal segments forming an exterior protective shield and movable claspers (each with a large central process covering 2 smaller processes). They have 2 testes connected by tubules to a seminal vesicle and ejaculatory duct leading to the genital apparatus consisting of an aedeagal apodeme (penis plate) with extendable penis rods coiled and retracted within an endophallic sac. The penis is thin and wispy and cannot enter the female without the support of the rods and claspers. Females have 2 ovaries with tubular oviducts connected to a globular uterus and vagina with a bursa copulatrix (depression to receive male organ)

and subglobular spermatheca (for sperm storage after mating). During mating, the male aedeagus dorsal lobe extends to the vagina, the thicker penis rod penetrates deep into the bursa copulatrix and the thinner penis rod penetrates deeper into the spermathecal duct. The thinner penis rod also has a cobra-shaped head thought to convey sperm as well as scoop out rival sperm.

Site of infection: Only the adult stages of *Pulex* spp. are obligate ectoparasites on warm-blooded vertebrates, while the eggs, larvae and pupae are free-living in the external environment (often associated with host resting places such as dens, beds and nests). Adult fleas require bloodmeals to become sexually mature and complete their development. Adults are very agile and may move rapidly though host pelage or plumage, feeding on blood through the skin at multiple sites. Nonetheless, they are transient ectoparasites feeding on hosts for 5-10 minutes and then often leaving the host to rest in the surrounding environment. Most species are stenoxenous or euryxenous feeding on the blood of a small range of mammals and birds, particularly rodents, insectivores, small carnivores, humans and non-passerine birds.

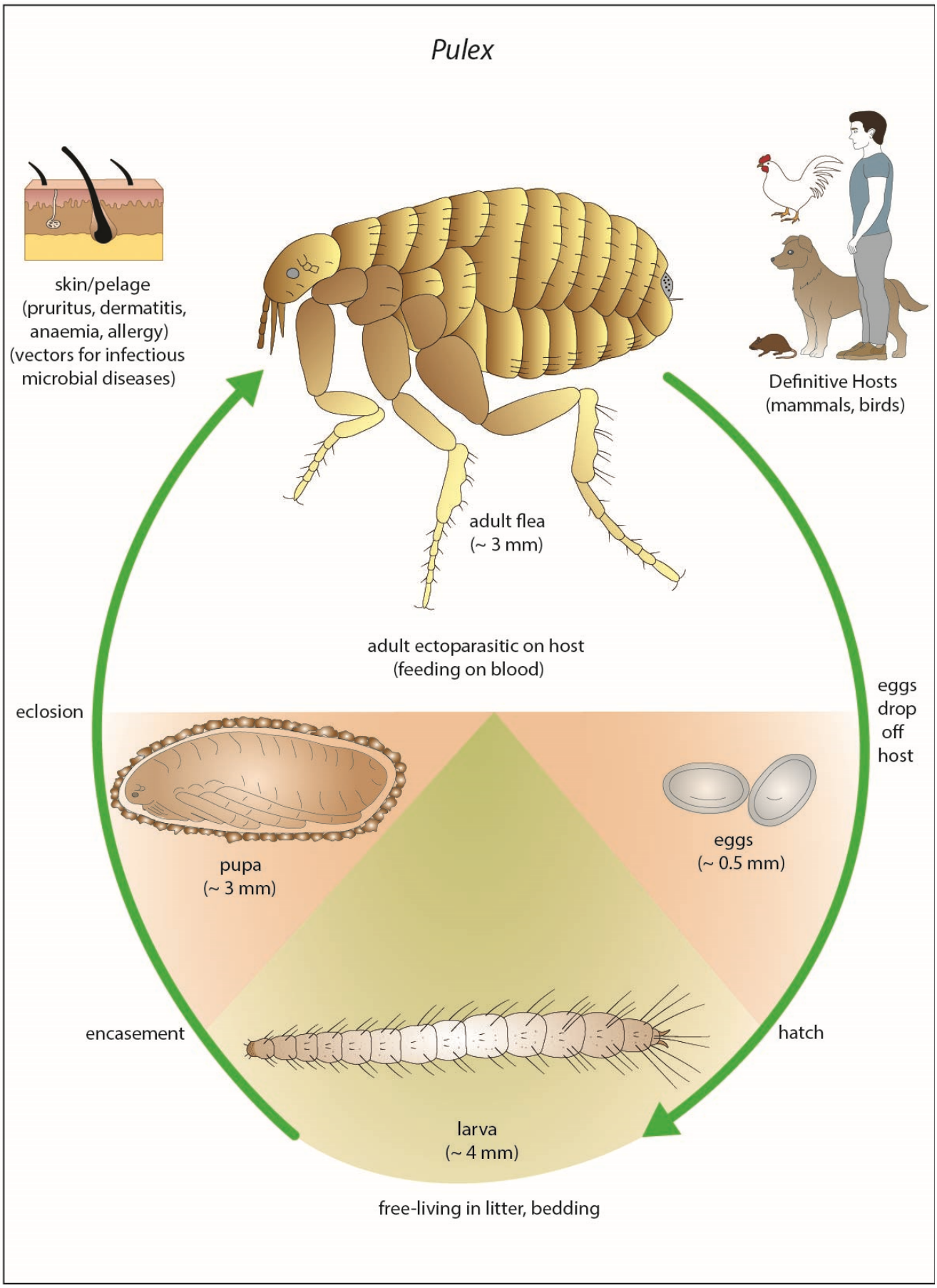
Pathogenesis: Adult fleas are haematophagous and use their mouthparts to pierce the skin and suck blood from their hosts, often taking more blood than they can digest. During feeding, they inject saliva containing vaso-active compounds, including anticoagulant, vasodilatory and anti-inflammatory substances. Bites often appear in clusters or small rows as the fleas feed at frequent intervals, causing traumatic skin damage at the puncture point (tiny purplish spot known as purpura pulicosa) surrounded by focal inflammation (known as roseola pulicosa). The lesions are often intensely pruritic (itchy) and may persist as urticarial and vesicular papules causing discomfort for several weeks. Individual hosts may also develop hypersensitivity responses to bites resulting in eczematous skin disease known as flea allergy dermatitis. Obviously, flea bites represent a considerable nuisance to their hosts with persistent irritation and annoyance, often leading to biting stress. Hosts attempt to relieve the irritation by aggressive self-grooming (biting, pecking, scratching, rubbing), sometimes causing self-trauma and hair/feather loss, making them more susceptible to secondary bacterial infections. Heavy infestations may also cause a slow but progressive anaemia due to sustained blood loss. In addition to being parasites in their own right, *Pulex* spp. have become notorious for the transmission of many infectious microbial diseases, including bacterial bubonic plague, rickettsial murine typhus, feline spotted fever, Rocky Mountain spotted fever and Mediterranean spotted fever, trench fever, cat scratch fever, tularemia (rabbit fever), and erysipeloid skin infection. The fleas have also been shown to act as intermediate hosts for larval stages of the dog tapeworm *Dipylidium caninum* and the mouse tapeworm *Vampirolepis nana*.

Developmental cycle and mode of transmission: *Pulex* spp. have holometabolous life-cycles where grub-like larvae undergo complete metamorphosis in pupae to become adults. The adults feed on host blood and void faeces containing partially-digested blood (called flea dirt) which usually fall off the host. Gravid female fleas lay non-sticky eggs in small batches (2-8) which also usually fall off the host, contaminating the immediate environment (often host resting places, burrows, or nests). Provided adequate moisture is present (humidity usually >70%), the eggs hatch in 3–6 days (up to 14 days in colder conditions) releasing larvae. The maggot-like larvae avoid sunlight and keep to dark humid places (sand, loose soil, cracks, crevices, carpets, bedding, etc.) feeding on organic debris (vegetable material, dead insects, faeces, especially flea dirt). The larvae develop through 3 instars over 4-18 days under ideal conditions, but the duration depends on prevailing temperatures and humidity, and may be delayed for several months (in some cases up to 200 days) in cooler drier conditions. Mature larvae then curve back on themselves forming a U-shape and weave silken cocoons (pupae) which become covered by debris from the environment (sand, pebbles, etc.). Within the pupae, the fleas undergo complete transformation into adult stages, with pupation occurring in as little as 4-10 days, but often taking longer in more adverse conditions (several weeks in colder conditions). The pre-emergent adults wait within their pupae for suitable occasions to emerge and engage hosts, sometimes waiting for several months for the right combination of stimuli. They have numerous sensory organs and are triggered to eclose (emerge) by the close proximity of hosts as detected by changes in carbon dioxide concentrations, certain odours, heat, vibrations, air currents, and light patterns. Indeed, the passing of a warm-blooded animal may trigger the mass emergence of adults from pupae. Once emerged, adult fleas must find a host and feed within several days (although there a few reports of unfed fleas surviving up to 100 days in cool humid conditions). Adults are anautogenous and require a bloodmeal to become sexually mature, as the meal stimulates dissolution of a testicular plug in males and maturation of the ovaries in females. Unfed fleas cannot mate and virgin females may lay nonviable eggs. Fed adults may mate several times and it is thought that males may use their long thinner penis rods to scoop out sperm left in the female spermatheca by rivals. Fertilized females lay eggs in small batches (2-8) after each bloodmeal. They usually live for 2-3 months and may produce over 400 eggs, but they do not have to reside on hosts and actually spend much of their time off hosts between feeds. It has been estimated that only 5% of the adult flea population occurs on a host at any given time. If a continuous food supply is available and females feed regularly, some have been found to live up to a year under ideal conditions of temperature and humidity.

Differential diagnosis: Infestations may be suspected on clinical grounds by the detection of pruritic papular bites on hosts exhibiting biting stress. Careful visual examination usually reveals the presence of adult fleas in the pelage or plumage, particularly when fine combs are used to part hairs or feathers. The fleas are very agile and hard to catch for macroscopic or microscopic examination, but they are very hardy and can withstand considerable pinch pressure. Different taxa are readily identified by their morphological characteristics, particularly with respect to the presence of absence of genal and/or ctenidial combs. Molecular biological techniques have been used for generic and species differentiation and phylogeny following polymerase chain reaction

(PCR) amplification of nuclear (18S and 28S ribosomal DNA, internal transcribed spacer regions 1 and 2, elongation factor 1-alpha) and mitochondrial (cytochrome c oxidase subunit I, cytochrome b, 16S ribosomal DNA) gene sequences.

Treatment and control: Clinical infestations may be treated by removing or killing fleas on hosts using various grooming strategies and the application of insecticidal chemicals, but long-term management depends on preventing rapid re-infestations by free-living stages. Washing hosts in immersion baths may remove and drown fleas. Flea soaps can also be used as they contain fatty acids acting as detergents to remove the waxy coats of fleas making them susceptible to subsequent desiccation. Many different types of flea combs have been developed and hair conditioners may be used to help untangle matted coats, although recourse if often taken to clipping or shaving severely affected regions. A wide range of insecticides have been used to treat flea infestations, many as topical preparations (sprays, shampoos, washes, powders, mousses, dips, dusts) or as systemic products (oral, spot-on, impregnated collars). Good results have been obtained using organochlorines (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (coumaphos, chlorfenvinphos, diazinon, dioxathion, fenchlorvos, malathion, phosmet, stirofos, trichlorfon), carbamates (carbaryl), neonicotinoids (dinotefuran), chloronicotinyles (nitenpyram, imidacloprid), spinosyns (spinosad), pyrethrin and synthetic pyrethroids (permethrin, cyfluthrin, cypermethrin, etofenprox), macrocyclic lactones (selamectin, ivermectin), semicarbazones (metaflumizone), phenylpyrazoles (fipronil), benzoylphenylureas (lufenurin) and some insect growth regulators (methoprene, pyriproxyfen), although some resistance have been reported against many conventional formulations (some organochlorines, organophosphates and pyrethroids). The use of products with long residual activities has done much to simplify treatment protocols, as they only need to be treated once and do not become rapidly re-infested when returned to contaminated environments. However, it is important to regularly re-treat hosts with formulations with short residual activities. All in-contact hosts should be treated at the same time, and any hosts with severe lesions should be given supportive therapies in the form of anti-pruritics, anti-inflammatories (anti-histamines or glucocorticoids) and possibly antibiotics in the event of secondary bacterial infections. Human patients may seek relief from flea bites by using various cooling preparations, such as menthol, camphor, calamine, propylene glycol, vaseline or even ice. Some personal protection can be afforded to individuals by the application of insect repellents (such as diethylmethylbenzamide (DEET), ethyl butylacetylaminopropionate (EBAAP, or IR3535), and permethrin) to skin or clothing. The prevention of flea infestations relies on decontamination of the environment by removing or killing flea eggs, larvae, pupae and adults by physical and/or chemical cleaning processes. Flooring, especially carpets, should be regularly cleaned and vacuumed (which also stimulates adults to eclose from pupae), bedding and clothing should be thoroughly washed or replaced, and inanimate objects (including grooming equipment) can be sterilized by steam-cleaning or using stringent disinfectants. Various insecticidal chemicals with good residual activity can be used indoors (and sometimes outdoors) as sprays (organophosphates, pyrethroids, and insect growth regulators methoprene or pyriproxyfen with permethrin and pyrethrin synergists) and powders (pyriproxyfen, linalool and pyrethrin synergists), although many commercial flea bombs and foggers (methoprene or pyriproxyfen with permethrin, pyrethrins or esfenvalerate synergists) have proven to be not as effective against pulicid fleas. Other methods of reducing flea populations have involved the use of various traps (intermittent light traps, sticky traps, and pan traps), spreading desiccants in animal bedding or rest areas (diatomaceous earth, sodium polyborate), restricting animal movements (quarantine, preventing pets from roaming) and implementing rodent control (with many attendant public health benefits).

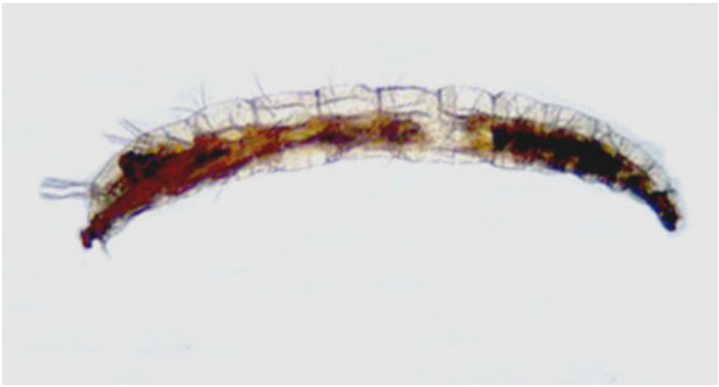

Pulex
skin/pelage
(pruritus, dermatitis,
anaemia, allergy)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, birds)
adult flea
(~ 3 mm)
adult ectoparasitic on host
(feeding on blood)
eclosion
eggs
drop
off
host
pupa
(~ 3 mm)
eggs
(~ 0.5 mm)
encasement
hatch
larva
(~ 4 mm)
free-living in litter, bedding



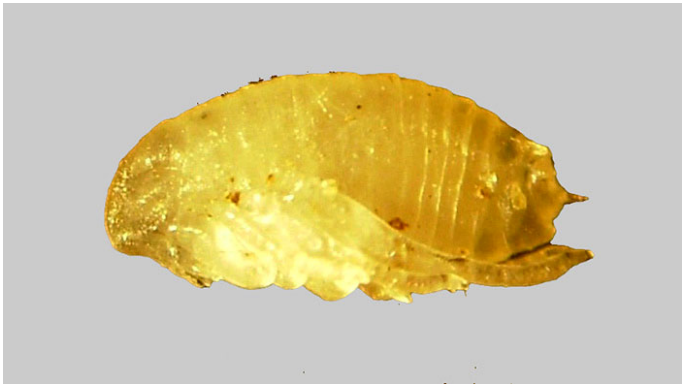
Pulex adult



Pulex eggs



Pulex larva



Pulex pupa

Echidnophaga
(insect: flea)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Siphonaptera (fleas) are bilaterally-flattened wingless insects whose hindlimbs are enlarged and specially adapted for jumping (using elastic resilin pads rather than muscles). Fleas are holometabolans and undergo complete metamorphosis whereby grub-like larvae form pupae from which adult fleas emerge. The larvae are not parasitic but feed on debris associated mainly with bedding, den or nest material, whereas the adult stages are parasitic and feed on host blood. Pulicid fleas occur as ectoparasites on mammals, including humans, domestic and companion animals and wildlife, especially rodents. Adult *Echidnophaga* spp. have short thoracic segments and infestations by these stick-tight (stick-fast) fleas have been associated with irritation and dermatitis in domestic and companion animals.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order: Siphonaptera (fleas, wingless, laterally compressed, third pair of legs adapted for jumping)
Family: Pulicidae (parasites of mammals)
Genus: *Echidnophaga* (parasitic on skin of mammals/birds, sticktight/stickfast fleas)
Species: various species cause dermal lesions on wild and some domestic animals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Fleas are small wingless insects that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. The adults are ectoparasitic and use siphon-like mouthparts to feed on blood from warm-blooded vertebrates [the name 'Siphon-aptera' literally translates as 'siphon' and 'wingless']. All adult fleas are further characterized by having laterally compressed bodies (allowing movement through hair/feathers), backward-pointing hairs and bristles (resisting grooming by host), strong tarsal claws (for grasping), and enlarged hindlegs (adapted for jumping). Around 2,200 flea species have been described in 250 genera on the basis of morphological and biological differences, and recent molecular phylogenetic studies have indicated some 18 families may occur in 4 infra-orders.

Siphonapteran families	Biodiversity	Hosts	Characters	Biogeographical distribution
Infraorder: Pulicomorpha (compact body, small thorax, pronotum with entire undivided ventral margin)				
Pulicidae (common fleas)	22 genera 207 species	carnivores, lagomorphs, rodents, artiodactyls, birds	sensilium with at most 14 pits, coxa with spiniform setae	pan-Tropical, cosmopolitan
Tungidae (sand fleas)	5 genera 23 species	rodents, insectivores, bats, suids, humans, birds	compression of 3 thoracic segments, neosomy	Neotropical, Holarctic

Vermipsyllidae	3 genera 39 species	carnivores, pikas, ungulates	frontal tubercle, large spiracles, reduced tergites	Holarctic
Ancistropsyllidae	1 genus 3 species	artiodactyls	metanotum and abdominal tergites with spinelets	Oriental
Coptopsyllidae	1 genus 19 species	rodents	combless, 2 spermathecae, tergal spinelets absent	Southern Palaearctic
Malacopsyllidae	2 genera 2 species	insectivores	high mesonotum, metanotum without spinelets	Patagonian
Rhopalopsyllidae	14 genera 126 species	rodents, insectivores, birds	metanotum and abdominal tergites with spinelets	Neotropical, Australasian
Infraorder: Ceratophyllomorpha (elongate body, long thorax, head without intergenal process, interantennal dimorphism)				
Ceratophyllidae	47 genera 540 species	rodents, pikas, carnivores, insectivores, birds	genal combs absent, males with interantennal suture	cosmopolitan
Ischnopsyllidae (bat fleas)	20 genera 125 species	bats	genal comb with 2-4 flattened spines, interantennal furrow	cosmopolitan
Leptopsyllidae	29 genera 260 species	insectivores, lagomorphs, rodents, carnivores, birds	head with tentorial arch, males with interantennal suture	Holarctic, Australasia
Xiphlopsyllidae	1 genus 8 species	rodents, shrews	squamulum absent, simple interantennal wall	Eastern African
Infraorder: Hystrichopsyllomorpha (elongate body, long thorax, head with intergenal process, clasper without process)				
Chimaeropsyllidae	8 genera 26 species	rodents, shrews	sensilium with 14 pits, hind coxa with spiniform setae	African
Hystrichopsyllidae (nest fleas)	46 genera 582 species	rodents, insectivores, pikas, marsupials	highly variable structures, 2 spermathecae	cosmopolitan
Macropsyllidae	2 genera 2 species	rodents	single head comb, 4 abdominal combs, 2 spermathecae	Australian
Stephanocircidae (helmet fleas)	9 genera 51 species	rodents, marsupials, birds	helmet (frons) with 2 separate combs, single spermatheca	Neotropical, Australian
Infraorder: Pygiopsyllomorpha (elongate body, long thorax, head with intergenal process, metanotum without spinelets)				
Pygiopsyllidae	10 genera 48 species	rodents, marsupials, birds	unique articulation between digitoid and main part of clasper	Australasian, Neotropical
Lycopsyllidae	4 genera 8 species	marsupials	genal lobe, simple interantennal wall, single mesopleural rod	Australian
Stivaliidae	23 genera 110 species	rodents, marsupials	strongly developed basal arm of Y-sclerite	Palaearctic, Australasia

Fleas from several families are found as ectoparasites on domestic and companion animals around the world: particularly those belonging to the families Pulicidae and Tungidae on mammals, and the family Ceratophyllidae on birds. Members of the family Pulicidae (syn. Archaeopsyllidae, Xenopsyllidae, Sarcopsyllidae p.p.) are characterized by compact bodies, small rounded heads and reduced chaetotaxy (small numbers of setae, spines and/or bristles). Over 20 genera have been recognized in 5 subfamilies: namely, Archaeopsyllinae (*Aphropsylla*, *Archaeopsylla*, *Centetipsylla*, *Ctenocephalides*, *Nesolagobius*), Moeopsyllinae (*Moeopsylla*), Pulicinae (*Delopsylla*, *Echidnophaga*, *Pulex*), Spilopsyllinae (*Actenopsylla*, *Cediopsylla*, *Euchoplopsyllus*, *Hoplopsyllus*, *Ornithopsylla*, *Spilopsyllus*), and Xenopsyllinae (*Parapulex*, *Pariodontis*, *Procaviopsylla*, *Pulicella*, *Synopsyllus*, *Synosternus*, *Xenopsylla*). Various pulicid species and genera are considered to be important parasites of medical and veterinary significance either as parasites in their own right (blood-sucking behaviour causing anaemia, dermatitis and hypersensitivity reactions) or as vectors for other infectious micro-organisms (including bacteria and helminths). Pulicid genera are differentiated mainly on the basis of whether the thoracic segments are very short (*Echidnophaga*), whether both genal (head) and pronotal (thorax) ctenidia (combs) are present (*Ctenocephalides, Spilopsyllus*) or absent (*Pulex, Echidnophaga, Xenopsylla*), and whether the axis of the genal comb is horizontal (*Ctenocephalides*) or vertical (*Spilopsyllus*).

Genera	**No. spp.**	**Hosts**	**Ctenidia (combs)**		**Disease**	**Vector**
			Genal (head)	**Pronotal (thorax)**		
Pulicidae						
Pulex	12	humans, carnivores, marsupials, rodents, birds	absent	absent	irritation, dermatitis, anaemia	plague, typhus, spotted fevers, tapeworms
Echidnophaga	23	birds, rodents, carnivores, marsupials	absent	absent	inflammation, ulceration	rickettsioses, plague, myxomatosis

Xenopsylla	76	rodents, carnivores, marsupials, birds	absent	absent	irritation	plague, typhus, rat tapeworms
Ctenocephalides	12	carnivores, rodents, rabbits, insectivores, ungulates, birds	horizontal	present	pruritus, anaemia, hypersensitivity (flea-bite allergy)	bartonelloses, typhus, plague, dog tapeworm, filarial nematode
Spilopsyllus	1	rabbits, rodents, carnivores, birds	vertical	present	irritation	myxomatosis, tularemia
Tungidae						
Tunga	13	humans, insectivores, rodents, carnivores	absent	absent	inflammation, ulceration	*Staphylococcus, Wolbachia*, tetanus
Ceratophyllidae						
Ceratophyllus	64	birds, rodents, carnivores, ungulates	absent	present	irritation, reduced productivity	
Nosopsyllus	52	rodents, carnivores, some birds	absent	present	irritation	plague, erysipeloid, rat tapeworm

Echidnophaga spp. are characterized by the presence of angular pentagonal heads (rather than smooth rounded heads like other pulicids) and the absence of genal and pronotal ctenidia (combs). Females of most flea genera detach from their hosts after feeding, but those of *Echidnophaga* spp. undergo partial neosomy (abdominal development) and remain attached to the skin for most of their lives (hence their common name as stick-fast or stick-tight fleas). [Note that tungid fleas undergo complete neosomy whereby adult females burrow into the skin and undergo accelerated development (tachygenesis) with marked abdominal distention and encystment.] Some 23 *Echidnophaga* spp. have been described from a range of avian and mammalian hosts, most species having a broad host specificity and occurring on sympatric hosts. These fleas are widespread throughout the world, particularly in tropical and subtropical regions where warm moist environmental conditions are more conducive to flea development. The are often prevalent in areas where domestic poultry are kept, and some species are responsible for significant economical losses on commercial chicken farms. Some species have also been implicated in the transmission of bacterial and viral diseases, including bubonic plague, rickettsial fevers, and myxomatosis.

***Echidnophaga* species**	**Hosts**	**Clinical signs**	**Distribution**
E. aethiops	Chiroptera: nycterid (Egyptian slit-faced bat, large slit-faced bat), rhinolophid (Darling's horseshoe bat, bushveld horseshoe bat), megadermatid (yellow-winged bat)		Africa
E. ambulans	Monotremata: tachyglossid (short-beaked echidna); Lagomorpha: leporid (rabbit)		Australia
E. aranka	Diprotodontia: potoroid (boodie)		Australia
E. bradyta	Carnivora: herpestid (meerkat, yellow mongoose, common slender mongoose); Rodentia: murid (bushveld gerbil), mustelid (striped polecat), petedid (South Africa springhare), sciurid (Cape ground squirrel)		Africa
E. calabyi	Diprotodontia: vombatid (common wombat, hairy nosed wombat)		Australia
E. cornuta	Diprotodontia: vombatid (common wombat, southern hairy nosed wombat)		Australia
E. eyrei	Diprotodontia: vombatid (wombat); Rodentia: murid (roof rat)		Australia
E. gallinacea (sticktight flea)	Galliformes: phasianid (chicken, red-winged francolin, turkey), numidid (guineafowl); Accipitriformes: accipitrid (black sparrowhawk); Anseriformes: anatid (duck); Columbiformes: columbid (crested pigeon, rock dove, Namaqua dove); Passeriformes: corvid (Australian magpie), estrilidid (quailfinch), fringillid (yellow canary), hirundinid (white-backed swallow, brown-throated martin), malaconotid (southern boubou), meliphagid (noisy miner), meropid (little bee-eater, white-fronted bee-eater), motacillid (Cape wagtail, African pied wagtail, long-legged pipit), muscicapid (Arnot's chat), ploceid (red-billed quelea); Strigiformes: strigid (marsh owl); Suliformes: phalacrocoracid (reed cormorant), sulid (Cape gannet); Carnivora: canid (dog, golden jackal, black-backed jackal, Cape fox, kit fox), felid (cat, African wildcat, black-footed cat, caracal, serval), herpestid (meerkat, yellow mongoose, common slender mongoose, marsh mongoose, Cape gray mongoose, white-tailed mongoose, Selous's mongoose, banded mongoose), hyaenid (aardwolf, striped	irritation, ulceration, pruritus, allergic dermatitis	worldwide

	hyena, brown hyena), mustelid (striped polecat), viverrid (common genet, rusty-spotted genet, African civet, small Indian civet); Lagomorpha: leporid (European rabbit, black-tailed jackrabbit, scrub hare, Jameson's red rock hare); Dasyuromorphia: dasyurid (brush-tailed phascogale), myrmecobiid (numbat); Diprotodontia: potoroid (boodie), phalangerid (common brushtail possum); Peramelemorphia: thylacomyid (greater bilby); Monotremata: tachyglossid (short-beaked echidna); Rodentia: hystricid (Cape porcupine), murid (brown rat, black rat, red rock rat, Namaqua rock rat, African grass rat, South African vlei rat, bush vlei rat, Brandt's whistling rat, creek groove-toothed swamp rat, greater sticknest rat, acacia rat, multimammate mouse, Griselda's striped grass mouse, four-striped grass mouse, Cape gerbil, Cape short-eared gerbil, hairy-footed gerbil, highveld gerbil), nesomyid (South African pouched mouse), pedetid (South African springhare), petromurid (dassie rat), sciurid (Cape ground squirrel); Macroscelidea: macroscelidid (rufous elephant shrew, western rock elephant shrew, round-eared elephant shrew, four-toed elephant shrew); Eulipotyphla: erinaceid (four-toed hedgehog, South African hedgehog), soricid (musk shrew); Artiodactyla: bovid (goat, cattle); Perissodactyla: equid (horse); Primates: cercopithecid (grivet, king colobus, Chacma baboon), hominid (humans)		
E. iberica	Lagomorpha: leporid (rabbit)		Europe
E. inexpectata	Artiodactyla: suid (desert warthog)		Africa
E. larina	Artiodactyla: suid (pig, desert warthog, red river hog), bovid (cattle, common duiker, red-flanked duiker harnessed bushbuck); Carnivora: canid (dog, African wild dog, black-backed jackal, Cape fox), felid (cat, black-footed cat, African wildcat, lion, leopard, serval), herpestid (meerkat, white-tailed mongoose), hyaenid (aardwolf, spotted hyena, striped hyena, brown hyena), viverrid (common genet); Lagomorpha: leporid (rabbit); Perissodactyla: equid (horse); Tubulidentata: orycteropodid (aardvark); Rodentia: hystricid (crested porcupine, Cape porcupine), murid (red rock rat); Anseriformes: anatid (white-faced whistling duck); Coliformes: coliid (red-faced mousebird)		Eurasia, Africa
E. liopus	Monotremata: tachyglossid (short-beaked echidna); Rodentia: murid (rat)		Australia, India
E. macronychia	Diprotodontia: potoroid (boodie)		Australia
E. murina	Rodentia: murid (Sundevall's jird, black rat), dipodid (greater Egyptian jerboa)		Middle-East
E. myrmecobii	Diprotodontia: macropodid (eastern grey kangaroo), phalangerid (common brushtail possum), potoroid (boodie), pseudocheirid (common ringtail possum), vombatid (common wombat); Peramelemorphia: thylacomyid (bilby); Dasyuromorphia: dasyurid (tiger quoll, eastern quoll, red-tailed phascogale, fat-tailed dunnart, kultarr), myrmecobiid (numbat); Rodentia: murid (long-haired rat, black rat, brown rat, greater sticknest rat, rakali, house mouse, Mitchell's hopping mouse); Lagomorpha: leporid (European rabbit); Carnivora: felid (cat), Canid (dog, red fox); Primates: hominid (human); Serpentes: elapid (eastern brown snake)		Australia
E. ochotona	Lagomorpha: ochotonid (pika)		China
E. octotricha	Diprotodontia: vombatid (hairy-nosed wombat)		Australia
E. oschanini	Rodentia: murid (great gerbil); Passeriformes: muscicapid (isabelline wheatear)		Asia
E. perilis	Diprotodontia: potoroid (boodie), vombatid (hairy-nosed wombat); Peramelemorphia: thylacomyid (bilby); Dasyuromorphia: myrmecobiid (numbat); Rodentia: murid (black rat); Lagomorpha: leporid (European rabbit); Carnivora: felid (cat), Canid (dog, red fox); Primates: hominid (human); Monotremata: tachyglossid (short-beaked echidna)		Australia
E. popovi	Carnivora: mustelid (European badger)		Europe
E. suricatta	Carnivora: herpestid (meerkat)		Africa
E. tarda	Carnivora: felid (African wildcat), hyaenid (striped hyaena)		Africa
E. tenerifensis	Rodentia: murid (rat)		Canary Islands
E. tiscadaea	Rodentia: dipodid (Gobi jerboa)		Mongolia

Parasite morphology: *Echidnophaga* spp. form 4 different types of morphological stages during their development: namely, eggs; larvae (3 instars); pupae; and adults. The eggs are shiny white ovoid stages approximately 0.5 mm long. They hatch to release elongate vermiform (worm-like) larvae which moult twice growing up to 6 mm long. The larvae have soft white-yellow segmented bodies (3 thoracic and 10 abdominal segments) with numerous stout bristles protruding from each segment. They have darker sclerotized heads possessing powerful dentate mandibles well adapted for biting and chewing. Mature third-stage larvae produce silk from mandibular glands and create loosely-woven pupal cocoons which are sticky and become covered with debris from the surrounding environment. Pupae are roughly ovoid measuring around 4 mm long and they are initially white-yellow in colour but become brown with adherent debris. The larval head and last 3 segments are lost during pupation and the pupal body becomes compressed (shorter and wider). They are exarate pupae with legs free from the body wall (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). The pupae have begun to develop elongated mouthparts, short antennae, inconspicuous eyes, and setae and bristles. Adult fleas are wingless dark brown insects, with laterally compressed bodies ranging from 1.0-2.5 mm long. They are covered by a heavily chitinized exoskeleton with hard plates (sclerites) but with reduced chaetotaxy; i.e. their covering of bristles and spines is sparse and limited to a few rows on thoracic and abdominal segments and legs. Unlike many other flea genera, *Echidnophaga* spp. do not have comb-like rows (ctenidia) of bristles on their cheeks (genal) or thorax (pronotal). Adult fleas have 3 conspicuous body parts: an angular head; small thorax; and ovoid abdomen. The head is highly distinctive and has a sharply angular dorsal profile forming a squarish-pentagonal shape. The frons (forehead) is heavily sclerotized and integricipit (without an interantennal suture). The antennae are composed of 3 short club-like segments held in protective grooves (fossae) with 2 setae posteriorly. The head bears 2 well-developed simple (non-compound) eyes (clusters of ocelli) located laterally, and has large mouthparts projecting conspicuously from the antero-ventral surface. The piercing-sucking mouthparts are located between sensory palps consisting of a pair of long 4-segmented maxillary palps as well as a pair of long unsegmented labial palps. The actual mouthparts (fascicle) consist of 3 long slender stylets: the 2 outer stylets (maxillary laciniae) being broad with serrated edges used to puncture skin; and the third central stylet (labrum-epipharynx) being an outgrowth of the body wall (unique to fleas) and used to enter a capillary. All 3 stylets join to form a tube-like canal to inject saliva (via salivary pumps) and suck blood (via cibarial and pharyngeal pumps). The alimentary tract consists of an anterior pharynx (with salivary glands inserted apically), elongate oesophagus, small globular proventriculus (armed with spines to prevent regurgitation), large expandable midgut (simple undivided organ lacking diverticula and caeca, unlike the more elaborate divided midguts of most other haematophagous arthropods), tubular hindgut (with excretory Malpighian tubules) and rectum. The thorax is short and narrowed dorsally, with 3 small segments (pronotum, mesonotum, and metanotum) lacking a meral rod (vertical thickening). The ventral thorax gives rise to 3 pairs of long muscular legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) with the hind-coxae having an inner patch of spiniform setae, and all legs terminating in 2 claws. The hindmost pair of legs are much larger than the others, and are well adapted for jumping (using unique elastic resilin pads to store energy under compression, rather than muscular contraction). The abdomen is ovate and has 10 segments, but the last 3 segments are highly modified by genital and sensory structures. Both sexes have a flat dorsal plate-like organ (sensilium or pygidium) with several (8-14) dome-like structures with central bristles. Males are smaller than females (1.0-2.0 v. 2.0-2.5 mm long) and have highly elaborate genitals (possibly the most complex in the animal kingdom). Males have 2 testes connected by vas deferens to a seminal vesicle and ejaculatory ducts leading to an aedeagal apodeme (penis plate) and extendable penis rods coiled and retracted within an endophallic sac. The penis is thin and pliable and cannot enter the female without the support of the rods and posterior claspers. Females have 2 ovaries connected by oviducts to the uterus leading to the vagina. The uterus has an associated bursa copulatrix (depression to receive male organ) and a subglobular spermatheca (for sperm storage) connected to the bursa by a sclerotized tube.

Site of infection: Adult fleas are obligate ectoparasites that live on the skin and feed on blood from warm-blooded vertebrate hosts. The fleas exhibit variable host specificity and usually infest small numbers of mammalian hosts (particularly rodents, carnivores, marsupials and ungulates) as well as some avian hosts (including passerines, fowl, and water birds). The fleas are photophobic and preferentially attach to dermal surfaces shielded from sunlight, and they also attach for long periods of time to bare skin or skin sparsely covered with hair/fur or feathers (hence their common names of sticktight or stickfast fleas). Adults usually attach to the ventral abdomen, ear canals, pinnae, periorbital skin, scrotum and interdigital webs of mammals, while they preferentially attach to the head, wattle, comb and anus of birds. Eggs, larvae and pupae are free-living stages in the environment and are strongly associated with animal resting sites (such as burrows, dens, hides and nests).

Pathogenesis: Infestations by adult fleas vary considerably in their pathogenic impacts on their hosts, ranging from transient irritating pests to persistent aetiological agents of mild-severe clinical disease (skin lesions, anaemia) contributing to poor health and production losses (reduced meat and egg production) with occasional mortalities. The severity of infestation depends on both host and parasite variables, including parasite virulence, site of infestation, host susceptibility (age and nutritional status) and host resistance (immunological status). Light infestations are generally subclinical, mild infestations may cause intermittent dermatitis and production losses, while heavy infestations may cause severe disease characterized by ulcerative lesions. Adult fleas feed on host blood using their mouthparts to pierce the skin and suck blood. Their mouthparts also have barbed edges that allow the fleas to attach and hold fast to their hosts. During feeding, the fleas inject saliva containing vaso-active compounds (anticoagulants, vasodilators and anti-inflammatories) to assist blood flow. Heavy infestations have been associated with blood loss severe enough to manifest as iron-deficiency anaemia. Female fleas also tend to burrow into the skin and remain attached using their mouthparts even

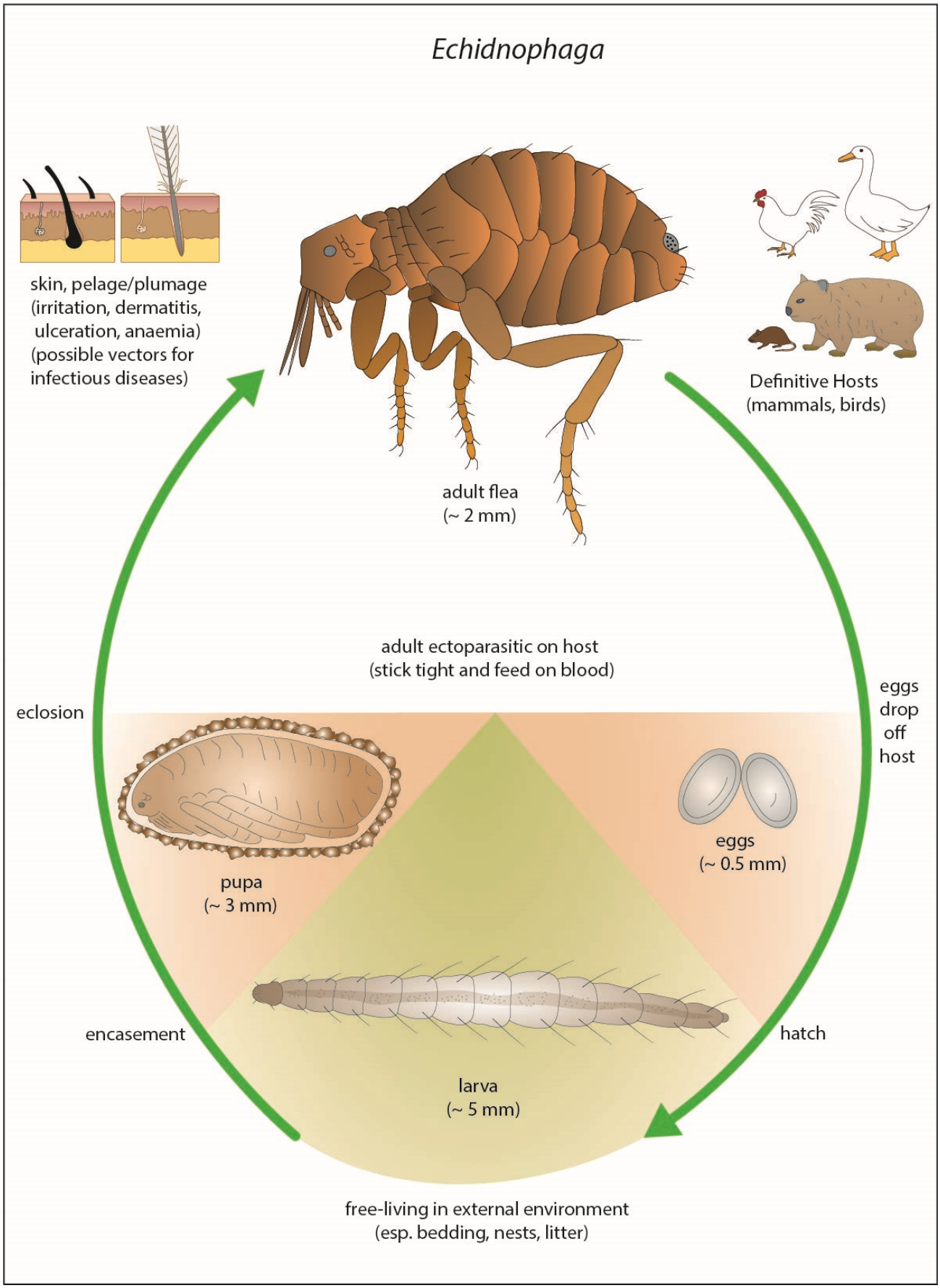
when not feeding. Flea bites cause tissue trauma with localized dermatitis, oedema and pruritus. Animals become restless and seek relief by vigorous grooming (biting/pecking, scratching, rubbing), often resulting in further trauma and opening wounds to secondary bacterial infections. Birds often show feather loss due to excessive preening. Attachment and bite sites may become ulcerated with serous discharges and small haemorrhages. Gravid female fleas may lay eggs in ulcerative subcutaneous wounds, which is thought to contribute to further inflammation due to the presence of foreign material. Infestations around the eyes and ears can lead to swelling and lesions which compromise sight and hearing in smaller animals, sometimes progressing to blindness and deafness. Infested animals have a reduced ability to forage or hunt and their general health declines with subsequent wasting due to starvation, and sometimes death. There are miscellaneous reports of these fleas harbouring potentially pathogenic microbes but their role in disease transmission is unclear due to the characteristic stick-tight behaviour of adult fleas on individual hosts. Molecular screening studies have detected various *Rickettsia* spp. (potentially involved in rickettsioses) and even *Yersinia pestis* (aetiological agent of bubonic plague). One species (*E. myrmecobii*) has been shown to transmit myxoma virus (causing myxomatosis) to rabbits, with virus particles residing in flea gut and mouthparts for several weeks.

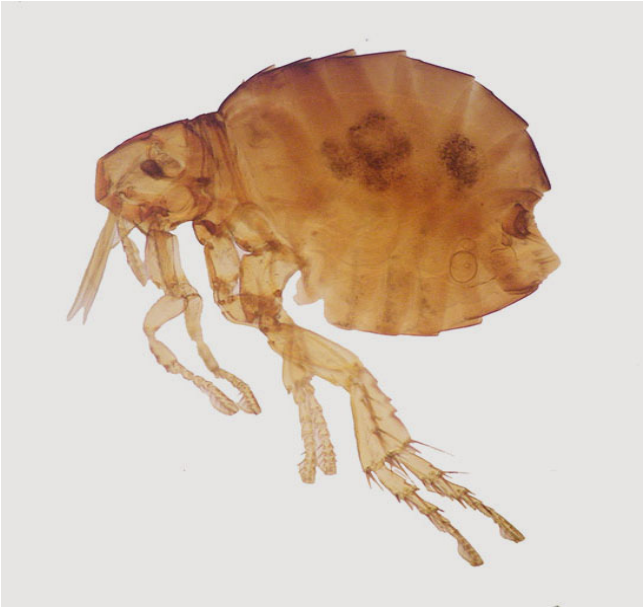
Developmental cycle and mode of transmission: Like all fleas, *Echidnophaga* spp. exhibit holometabolous development whereby vermiform larval stages undergo complete metamorphosis in pupae to form adult stages. Gravid female fleas lay 1-4 eggs each day on their hosts, even in ulcerations. The eggs usually drop from the hosts into the external environment, often being found in bedding or nesting materials. They hatch in 4-16 days depending on prevailing environmental conditions, taking longer in colder conditions. Vermiform (worm- or maggot-like) larval stages emerge and feed on organic debris using their biting/chewing mandibles. Food sources include manure, eggshells, flea dirt (adult flea faeces consisting of pellets of dried blood that have dropped from the host into the environment), and even other larvae. They are negatively phototactic (move away from light) and positively geotactic (move towards the earth) and are able to burrow into soil, leaf litter, nests and even carpets. There are 3 larval instars with 2 moults occurring over several weeks. Mature larvae burrow deeper into the soil and form cocoons in which they pupate to adult stages over 9-31 days, although they may remain as pupae for several months in harsh dry or cold environmental conditions. Adult fleas eclose (emerge) from pupae when environmental conditions (particularly temperature) are favourable, when disturbed by vibrations or mechanical pressure, and when stimulated by the presence of host body heat and increased carbon dioxide concentrations. They search for suitable hosts and are able to jump to heights of 20-40 cm. They need to find a host within 5-8 days as both male and female fleas are obligate haematophagous ectoparasites and require bloodmeals to survive and mature sexually. After mating, female fleas remain attached to their hosts for 2-6 weeks. Some authorities consider that stick-tight fleas exhibit partial neosomy (enlargement or formation of new external structures by secretion of new cuticle) during their attachment phase. Sticktight behaviour and prolonged feeding causes the formation of ulcers, in which the female lays her eggs. Most eggs drop out of wounds onto the ground, but some may remain caught up in secretions until they hatch whereupon the larvae drop out to the ground. The whole life-cycle may be completed in 30-60 days, but may take longer when environmental conditions fluctuate. Transmission between hosts generally occurs when newly emergent adult fleas quest for hosts, although adults (particularly males) may also move between hosts in close contact or proximity. Because *Echinophaga* spp. require organic material for their developmental cycles, infestations are most common in rural areas where domestic animals are free-ranging and may intermingle with other reservoir hosts. Infestations have been reported to spread into wildlife in adjacent areas such as woodlands, marshlands and nature reserves.

Differential diagnosis: Infestations can be suspected on clinical grounds (flea bites, ulcerated lesions) and the detection of flea dirt (faeces) in the pelage or plumage (which turns red when moistened). Provisional diagnoses are confirmed by the direct detection of adult fleas, usually clustered together in lesions particularly in areas of bare skin and around the head. However, fleas can sometimes be difficult to detect because of their small size and their habit of partially burrowing into the skin (stick-tight attachments). Because they are similar in size, shape and coloration to other ectoparasites (other fleas and ticks), specimens should be collected for microscopic examination. Most other fleas are readily detached or quickly move away from light, whereas stick-tight fleas are difficult to pull off and often tear. *Echidnophaga* spp. are easily identified under magnification due to the angular shape of the head, the sparse covering of setae and bristles and the absence of genal and pronotal combs. Molecular biological techniques have been applied to the characterization of species following the amplification of nuclear (ribosomal RNA) gene sequences by polymerase chain reaction (PCR).

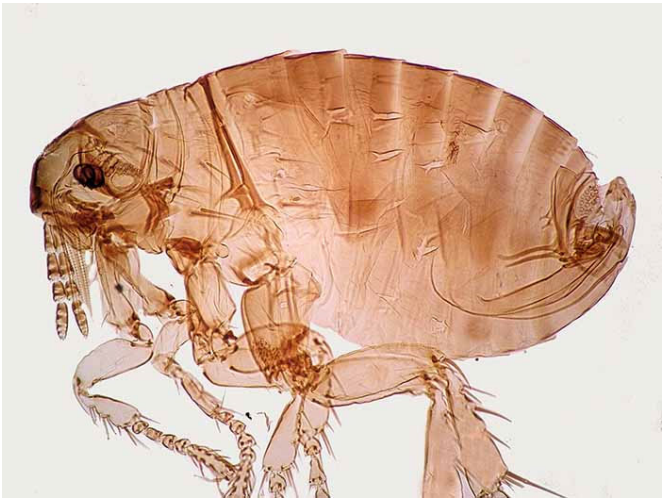
Treatment and control: Clinical infestations are usually treated with chemical insecticides, as the physical removal of fleas using tweezers or forceps is laborious and very difficult as the adult stick-tight fleas are firmly embedded in host skin. A range of commercial insecticides are available as topical preparations (sprays, shampoos, washes, pastes, mousse, powders) or as systemic preparations (oral, injectable, or spot-ons). Effective control has been reported following treatment with organophosphates (coumaphos, chlorfenvinphos, diazinon, dioxathion, fenchlorvos, malathion, phosmet, stirofos, trichlorfon), pyrethrin and synthetic pyrethroids (permethrin, cyfluthrin, cypermethrin), carbamates (carbaryl), arylpyrazoles (fipronil), natural products (rotenone) and some insect growth regulators (IGRs, such as lufenuron). It is recommended that animals with ulcerated lesions also be treated with antibiotics to prevent secondary bacterial infection. Single treatments with insecticides that have long-lasting residual activity may be sufficient to prevent reinfestation, while multiple treatments several weeks apart are required for products that have poor residual activity. It is further recommended that the immediate environment (particularly bedding, nests, burrows and hides) be treated with environmental insecticides (such as flea bombs and sprays containing organophosphates or pyrethroids) or desiccants (such as sodium polyborate). Various preventive strategies may be adopted to disrupt transmission cycles, particularly those involving

improved sanitation (regular removal of manure/litter, frequent changing of bedding/nesting materials), good hygiene (grooming, water/dust baths), isolating livestock (vermin-proof enclosures, pasture/pen rotation, quarantine), and regular health surveillance (screening and treatment).


Echidnophaga
skin, pelage/plumage
(irritation, dermatitis,
ulceration, anaemia)
(possible vectors for
infectious diseases)
adult flea
(~ 2 mm)
Definitive Hosts
(mammals, birds)
adult ectoparasitic on host
(stick tight and feed on blood)
eggs
drop
off
host
eclosion
pupa
(~ 3 mm)
eggs
(~ 0.5 mm)
encasement
hatch
larva
(~ 5 mm)
free-living in external environment
(esp. bedding, nests, litter)



Echidnophaga adult female



Echidnophaga adult male



Echidnophaga eggs



Echidnophaga larva

Ctenocephalides
(insect: flea)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Siphonaptera (fleas) are bilaterally-flattened wingless insects whose hindlimbs are enlarged and specially adapted for jumping (using elastic resilin pads rather than muscles). Fleas are holometabolans and undergo complete metamorphosis whereby grub-like larvae form pupae from which adult fleas emerge. The larvae are not parasitic but feed on debris associated mainly with bedding, den or nest material, whereas the adult stages are parasitic and feed on host blood. Pulicid fleas occur as ectoparasites on mammals, including humans, domestic and companion animals and wildlife, especially rodents. Adult *Ctenocephalides* spp. have genal (oral) and horizontal pronotal (thoracic) combs and infestations have been associated with skin lesions, pruritus and flea-allergy dermatitis (hypersensitivity) in dogs, cats and humans.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order: Siphonaptera (fleas, wingless, laterally compressed, third pair of legs adapted for jumping)
Family: Pulicidae (parasites of mammals)
Genus: *Ctenocephalides* (parasitic on skin of dogs/cats/humans)
Species: various species cause dermatoses in companion animals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Fleas are small wingless insects that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. The adults are ectoparasitic and use siphon-like mouthparts to feed on blood from warm-blooded vertebrates [the name 'Siphon-aptera' literally translates as 'siphon' and 'wingless']. All adult fleas are further characterized by having laterally compressed bodies (allowing movement through hair/feathers), backward-pointing hairs and bristles (resisting grooming by host), strong tarsal claws (for grasping), and enlarged hindlegs (adapted for jumping). Around 2,200 flea species have been described in 250 genera on the basis of morphological and biological differences, and recent molecular phylogenetic studies have indicated some 18 families may occur in 4 infra-orders.

Siphonapteran families	Biodiversity	Hosts	Characters	Biogeographical distribution
Infraorder: Pulicomorpha (compact body, small thorax, pronotum with entire undivided ventral margin)				
Pulicidae (common fleas)	22 genera 207 species	carnivores, lagomorphs, rodents, artiodactyls, birds	sensilium with at most 14 pits, coxa with spiniform setae	pan-Tropical, cosmopolitan
Tungidae	5 genera	rodents, insectivores, bats,	compression of 3 thoracic	Neotropical,

(sand fleas)	23 species	suids, humans, birds	segments, neosomy	Holarctic
Vermipsyllidae	3 genera 39 species	carnivores, pikas, ungulates	frontal tubercle, large spiracles, reduced tergites	Holarctic
Ancistropsyllidae	1 genus 3 species	artiodactyls	metanotum and abdominal tergites with spinelets	Oriental
Coptopsyllidae	1 genus 19 species	rodents	combless, 2 spermathecae, tergal spinelets absent	Southern Palaearctic
Malacopsyllidae	2 genera 2 species	insectivores	high mesonotum, metanotum without spinelets	Patagonian
Rhopalopsyllidae	14 genera 126 species	rodents, insectivores, birds	metanotum and abdominal tergites with spinelets	Neotropical, Australasian
Infraorder: Ceratophyllomorpha (elongate body, long thorax, head without intergenal process, interantennal dimorphism)				
Ceratophyllidae	47 genera 540 species	rodents, pikas, carnivores, insectivores, birds	genal combs absent, males with interantennal suture	cosmopolitan
Ischnopsyllidae (bat fleas)	20 genera 125 species	bats	genal comb with 2-4 flattened spines, interantennal furrow	cosmopolitan
Leptopsyllidae	29 genera 260 species	insectivores, lagomorphs, rodents, carnivores, birds	head with tentorial arch, males with interantennal suture	Holarctic, Australasia
Xiphlopsyllidae	1 genus 8 species	rodents, shrews	squamulum absent, simple interantennal wall	Eastern African
Infraorder: Hystrichopsyllomorpha (elongate body, long thorax, head with intergenal process, clasper without process)				
Chimaeropsyllidae	8 genera 26 species	rodents, shrews	sensilium with 14 pits, hind coxa with spiniform setae	African
Hystrichopsyllidae (nest fleas)	46 genera 582 species	rodents, insectivores, pikas, marsupials	highly variable structures, 2 spermathecae	cosmopolitan
Macropsyllidae	2 genera 2 species	rodents	single head comb, 4 abdominal combs, 2 spermathecae	Australian
Stephanocircidae (helmet fleas)	9 genera 51 species	rodents, marsupials, birds	helmet (frons) with 2 separate combs, single spermatheca	Neotropical, Australian
Infraorder: Pygiopsyllomorpha (elongate body, long thorax, head with intergenal process, metanotum without spinelets)				
Pygiopsyllidae	10 genera 48 species	rodents, marsupials, birds	unique articulation between digitoid and main part of clasper	Australasian, Neotropical
Lycopsyllidae	4 genera 8 species	marsupials	genal lobe, simple interantennal wall, single mesopleural rod	Australian
Stivaliidae	23 genera 110 species	rodents, marsupials	strongly developed basal arm of Y-sclerite	Palaearctic, Australasia

Fleas from several families are found as ectoparasites on domestic and companion animals around the world: particularly those belonging to the families Pulicidae and Tungidae on mammals, and the family Ceratophyllidae on birds. Members of the family Pulicidae (syn. Archaeopsyllidae, Xenopsyllidae, Sarcopsyllidae p.p.) are characterized by compact bodies, small rounded heads and reduced chaetotaxy (small numbers of setae, spines and/or bristles). Over 20 genera have been recognized in 5 subfamilies: namely, Archaeopsyllinae (*Aphropsylla*, *Archaeopsylla*, *Centetipsylla*, *Ctenocephalides*, *Nesolagobius*), Moeopsyllinae (*Moeopsylla*), Pulicinae (*Delopsylla*, *Echidnophaga*, *Pulex*), Spilopsyllinae (*Actenopsylla*, *Cediopsylla*, *Euchoplopsyllus*, *Hoplopsyllus*, *Ornithopsylla*, *Spilopsyllus*), and Xenopsyllinae (*Parapulex*, *Pariodontis*, *Procaviopsylla*, *Pulicella*, *Synopsyllus*, *Synosternus*, *Xenopsylla*). Various pulicid species and genera are considered to be important parasites of medical and veterinary significance either as parasites in their own right (blood-sucking behaviour causing anaemia, dermatitis and hypersensitivity reactions) or as vectors for other infectious micro-organisms (including bacteria and helminths). Pulicid genera are differentiated mainly on the basis of whether the thoracic segments are very short (*Echidnophaga*), whether both genal (head) and pronotal (thorax) ctenidia (combs) are present (*Ctenocephalides, Spilopsyllus*) or absent (*Pulex, Echidnophaga, Xenopsylla*), and whether the axis of the genal comb is horizontal (*Ctenocephalides*) or vertical (*Spilopsyllus*).

Genera	**No. spp.**	**Hosts**	**Ctenidia (combs)**		**Disease**	**Vector**
			Genal (head)	**Pronotal (thorax)**		
Pulicidae						
Pulex	12	humans, carnivores, marsupials, rodents, birds	absent	absent	irritation, dermatitis, anaemia	plague, typhus, spotted fevers, tapeworms
Echidnophaga	23	birds, rodents, carnivores,	absent	absent	inflammation, ulceration	rickettsioses, plague, myxomatosis

		marsupials				
Xenopsylla	76	rodents, carnivores, marsupials, birds	absent	absent	irritation	plague, typhus, rat tapeworms
Ctenocephalides	12	carnivores, rodents, rabbits, insectivores, ungulates, birds	horizontal	present	pruritus, anaemia, hypersensitivity (flea-bite allergy)	bartonelloses, typhus, plague, dog tapeworm, filarial nematode
Spilopsyllus	1	rabbits, rodents, carnivores, birds	vertical	present	irritation	myxomatosis, tularemia
Tungidae						
Tunga	13	humans, insectivores, rodents, carnivores	absent	absent	inflammation, ulceration	*Staphylococcus, Wolbachia*, tetanus
Ceratophyllidae						
Ceratophyllus	64	birds, rodents, carnivores, ungulates	absent	present	irritation, reduced productivity	
Nosopsyllus	52	rodents, carnivores, some birds	absent	present	irritation	plague, erysipeloid, rat tapeworm

The genus *Ctenocephalides* is classified within the Pulicidae together with other fleas of mammalian hosts, including humans. Adult fleas attach primarily to carnivores (especially canids and felids), but may also infest a range of other mammals (rodents, ungulates, lagomorphs, insectivores, primates, including humans) and occasionally some birds. Most flea species are considered to be host-preferential rather than host-specific – they have promiscuous feeding habits and will try to feed on any available host. The most common flea on cats and dogs is *C. felis*, but it will feed on many other mammals, including humans. In subtropical and temperate regions, infestations peak in prevalence and intensity in late summer and autumn, although fleas may often be found all year round.

***Ctenocephalides* species**	**Hosts**	**Clinical signs**	**Distribution**
C. arabicus	Hyracoidea: procaviid (rock hyrax)		Middle-East
C. brygooi	Carnivora: viverrid (civet)		Madagascar
C. canis (dog flea)	Carnivora: canid (dog, dingo, coyote, golden jackal, red fox, grey fox, crab-eating fox, South American grey fox), felid (cat, Iberian lynx, leopard), herpestid (meerkat, white-tailed mongoose), mephitid (eastern spotted skunk), otariid (brown fur seal), viverrid (common genet); Lagomorpha: leporid (European rabbit, European hare, scrub hare); Rodentia: cricetid (European water vole, common vole), hystricid (Cape porcupine), murid (black rat, brown rat, striped field mouse, wood mouse, house mouse); Eulipotyphla: erinaceid (European hedgehog, North African hedgehog, northern white-breasted hedgehog); Artiodactyla: bovid (goat, Asiatic mouflon), suid (pig); Peramelemorphia: peramelid (long-nosed bandicoot); Hyracoidea; procaviid (rock hyrax); Primates: cercopithecid (yellow baboon), hominid (human); Galliformes: phasianid (chicken)	wheal, pruritus, anaemia, flea-allergy dermatitis (+ vector for dog tapeworm, mouse tapeworm)	worldwide
C. chabaudi	Artiodactyla: bovid (duiker)		Africa
C. connatus	Carnivora: viverrid (meerkat, yellow mongoose); Rodentia: sciurid (African ground squirrel); Lagomorpha: leporid (hare); Eulipotyphla: erinaceid (hedgehog)		South Africa
C. crataepus	Rodentia: sciurid (African ground squirrel); Eulipotyphla: erinaceid (hedgehog)		Africa
C. craterus	Hyracoidea: procaviid (southern tree hyrax)		Africa
C. felis [incl. subspecies *felis, strongylus, damarensi, orientalis*] (cat flea)	Carnivora: felid (cat, wildcat, bobcat, Asian golden cat, lion, jaguar, jaguarundi, cougar, leopard, caracal, ocelot, oncilla, serval, cheetah), canid (dog, dingo, maned wolf, black-backed jackal, side-striped jackal, red fox, gray fox, hoary fox, crab-eating fox, Ruppell's fox), hyaenid (spotted hyaena), herpestid (meerkat, marsh mongoose, yellow mongoose, Egyptian mongoose, small Asian mongoose, common dwarf mongoose, crab-eating mongoose, white-tailed mongoose, banded mongoose, Selous's mongoose), mustelid (striped polecat, tayra, beech marten, honey badger, Burmese ferret-badger, least weasel, African striped weasel, European polecat, American mink), mephitid (striped skunk, eastern spotted skunk), procyonid	wheal, pruritus, anaemia, flea-allergy dermatitis (hypersensitivity) (+ vector for several bacterial infections, dog tapeworm, mouse tapeworm)	worldwide

	(South American coati, raccoon, crab-eating raccoon), ursid (brown bear), viverrid (common genet, Cape genet, civet cat, African civet); Rodentia: murid (black rat, brown rat, rakali, Tinfield's rock rat, house mouse, wood mouse, Kemp's spiny mouse, typical striped grass mouse, Misonne's soft-furred mouse, fringe-tailed gerbil, Shaw's jird), caviid (guinea pig, capybara, Spix's yellow-toothed cavy), cricetid (hispid cotton rat, cotton mouse, Yucatan deer mouse, terraced rice rat, Serra do Mar grass mouse, Atlantic forest climbing mouse, hairy-tailed bolo mouse, delta pygmy rice rat, black-footed pygmy rice rat, marsh rice rat, Robert's hocicudo, angular hocicudo), echimyid (common punare, Fischer's guara, white-spined Atlantic spiny rat), hystricid (Cape porcupine, crested porcupine), nesomyid (Mearn's pouched mouse), pedetid (South African springhare), sciurid (Brazilian squirrel, fox squirrel, striped ground squirrel, Cape ground squirrel), thryonomid (greater cane rat); Lagomorpha: leporid (European rabbit, European hare, Cape hare, scrub hare, Natal red rock hare, Jameson's red rock hare, common tapeti, eastern cottontail); Artiodactyla: bovid (goat, sheep, Asiatic mouflon, cattle, gaur, common duiker, red forest duiker, mountain gazelle, Rhim gazelle, hartebeest, klipspringer, Cape grysbok, harnessed bushbuck), cervid (mule deer, marsh deer), suid (desert warthog); Perissodactyla: equid (horse); Eulipotyphla: erinaceid (North African hedgehog, South African hedgehog, European hedgehog), soricid (lesser red musk shrew); Hyracoidea: procaviid (southern tree hyrax, rock hyrax); Cingulata: dasypodid (nine-banded armadillo); Pilosa: myrmecophagid (southern tamandua); Macroscelidea: macroscelid (rufous elephant shrew, western rock elephant shrew, four-toed elephant shrew); Didelphimorphia: didelphid (white-eared opossum, big-eared opossum, common opossum, Virginia opossum, big lutrine opossum, gray short-tailed opossum); Dasyuromorphia: dasyurid (eastern quoll); Diprotodontia: macropodid (eastern grey kangaroo, red-legged pademelon), phalangerid (common brushtail possum), potoroid (rufous rat-kangaroo); Peramelemorphia: peramelid (southern brown bandicoot, long-nosed bandicoot); Chiroptera: vespertilionid (southeastern myotis); Primates: atelid (Columbian red howler), cercopithecid (Guinea baboon, Chacma baboon), hominid (human); Galliformes: phasianid (chicken, red junglefowl), numidid (helmeted guineafowl); Strigiformes: strigid (lesser horned owl)		
C. grenieri	Hyracoidea: procaviid (rock hyrax)		Africa
C. orientis (Oriental cat flea)	Carnivora: felid (cat), canid (dog); Artiodactyla: bovid (sheep, goat)		India, Australia
C. paradoxuri	Carnivora: viverrid (palm civet)		Sri Lanka
C. rosmarus	Hyracoidea: procaviid (rock hyrax)		Ethiopia

Parasite morphology: Fleas form four different types of developmental stages: eggs; larvae; pupae and adults. The eggs are pearly-white ovoid bodies measuring 0.25-0.5 mm in length. Larvae are eruciform with slender cylindrical white-brown bodies 1-5 mm long. They have darker sclerotized heads with powerful mandibles and mandibular teeth well-adapted for biting and chewing. Their bodies are segmented (3 thoracic and 10 abdominal segments), each bearing a ring of bristles, and the caudal segment bearing 2 hooked processes (anal struts) used for gripping in locomotion. Pupae are opaque ellipsoidal stages around 0.5 mm long surrounded by thin silk cocoons, often with detritus adherent to the external surface. The larval head and last 3 segments are lost during pupation and the body becomes compressed (shorter and wider). They are exarate pupae with appendages free of the body wall (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). Pupae have begun to develop elongated mouthparts, short antennae, inconspicuous eyes, and numerous body setae and bristles. Adult fleas are wingless insects with heavily chitinized laterally-compressed bodies ranging in size from 2-3.5 mm long. Their shiny brown bodies are highly setate, with many spines and bristles usually facing backwards so as to not impede forward movement of the flea through pelage or plumage, but catching on hairs or feathers when dragged backwards by host grooming. Their chaetotaxy includes prominent comb-like rows of spines on the cheeks of the head (genal ctenidia) and on the thorax (pronotal ctenidia), the spacing of the spines generally correlated to the hair diameter of their hosts. The genal ctenidia are horizontal and have 5-9 vertical spines on each side, those of *C. felis* being similar in length, but the first spine of *C. canis* being shorter than the rest. The pronotal ctenidia are located along the posterior of the first thoracic segment and are vertical with 8-9 horizontal spines on each side. Adult fleas have 3 distinct body parts; a small flat head, a short thorax; and a globular abdomen. The dorsal profile of the head is smoothly rounded, being strongly convex in C. canis, and less convex and more elongate in C. felis (especially females). The frons (forehead) lacks a frontal

brow but has a conspicuous club-shaped internal incrassation. The head also possesses a pair of simple noncompound eyes (clusters of ocelli), a pair of short club-like antennae (3-segmented) held in protective grooves (fossae), and genal (cheek) processes with small sharp spines. All adults have conspicuous ventral piercing-sucking mouthparts (lacking mandibles and teeth) located between sensory palps used to probe the host skin for suitable feeding sites. The palps consist of a pair of long 4-segmented maxillary palps arising from the top of short blade-like maxillary lobes (stipes) as well as long 5-segmented labial palps arising from a short basal labium. The actual mouthparts (fascicle) consist of 3 long slender stylets: the 2 outer stylets (maxillary laciniae) being blade-like and serrated (sometimes with coarse teeth) and used to puncture the skin; and the third central stylet (labrum-epipharynx) being an outgrowth of the body wall (unique to fleas) and used to enter a capillary. All 3 stylets join to form a tube-like canal to inject saliva (via salivary pumps) and suck blood (via cibarial and pharyngeal pumps). The alimentary tract consists of an elaborate foregut (anterior pharynx, salivary glands inserted apically, elongate oesophagus, small globular proventriculus armed with spines to prevent regurgitation), a large expandable midgut (simple undivided organ (without diverticula or caeca) for the storage, digestion and absorption of bloodmeals, unlike the more elaborate divided midguts of most other haematophagous arthropods), and a tubular hindgut (with excretory Malpighian tubules, and rectum). The thorax contains 3 distinct dorsal sclerites (pronotum, mesonotum, metanotum) and there is a vertical thickening of the exoskeleton (meral rod) on the mid-thoracic segment. The ventral thorax gives rise to 3 pairs of strong legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) and all terminating in paired claws. There are 6 notches bearing setae along the dorsal border of the hind (metathoracic) tibia in *C. felis*, but 8 seta-bearing notches in *C. canis*. In all species, the hindmost pair of legs are greatly enlarged for jumping, using unique elastic resilin pads to store energy under compression (rather than muscular contraction) allowing fleas to jump some 50-200 times their own body length. The abdomen is ovate with 10 segments, some with lateral respiratory spiracles, and the numbers of spines reducing posteriad. Both sexes have a flat dorsal plate-like organ (sensilium or pygidium) with a number of dome-like structures from which bristles project. Fleas exhibit considerable sexual dimorphism, with males being smaller than females and having conspicuous posterior abdominal segments bearing copulatory structures. Indeed, male genital structures are highly elaborate and perhaps the most complex in the animal kingdom. Males have 2 testes connected by vas deferens to a seminal vesicle and ejaculatory ducts. They then have an aedeagal apodeme (penis plate) with extendable penis rods which are coiled and retracted within an endophallic sac. The penis is thin and wispy and cannot enter the female without the support of the rods and posterior claspers. Females have 2 ovaries with tubular oviducts connecting them to a globular uterus with a bursa copulatrix (depression to receive the male organ) and saccular spermatheca (for sperm storage after mating) located behind the vagina and vulva.

Site of infection: Adult fleas are obligate haematophagous ectoparasites living amongst the hair/fur on the skin of their hosts. They can also live off their hosts for extended periods in suitable micro-habitats (bedding, carpets, etc.) awaiting the arrival of new hosts on which to jump. Most species have preferred hosts but they do exhibit broad host specificity and may feed on a wide range of hosts as available (mainly mammals but including some birds). Adult fleas are agile and highly mobile and may infest many different regions of the body. Flea eggs, larvae and pupa are found in the external environment usually in the immediate vicinity of infested hosts, notably in their resting places.

Pathogenesis: Infestations by *Ctenocephalides* spp. are a major cause of skin disease in their natural hosts (dogs and cats), and they may also cause significant irritation when feeding or attempting to feed on other host species (even though they may not be able to complete their life-cycles feeding solely on aberrant hosts). Adult fleas are blood suckers that cause traumatic damage at the bite site. They have piercing mouthparts composed of cutting laciniae (back-and-forth action) and a stabbing epipharynx which enters small blood vessels. Saliva is ejected into the general area and bite sites develop erythematous (reddened) papules or wheals surrounding the central puncture site. Wounds may persist for days to several weeks and develop a crust of dried exudate. Host responses range from mild irritation to intense pruritus (itching) with restlessness, irritability, anaemia and weight loss. However, flea bites are often associated with severe allergic reactions; especially in inbred strains of dogs and cats and in young children. Flea-allergy dermatitis (FAD) is the result of hypersensitivity (immediate (type I), basophil, but mostly delayed (type IV)) reactions to flea salivary chemicals (enzymes, histamines, polypeptides and amino acids) injected into the skin. Reactions in sensitized individuals include intense pruritus, urticarial papules, excoriations, dermal infiltrates and rash. The skin may react to persistent inflammation by hardening and crusting with lichenification (thickening) and hyperpigmentation. Animals aggravate these conditions by inflicting self-trauma through over-grooming, barbering, licking, biting, chewing and scratching (itchy-scratchy syndrome) leading to significant hair loss (alopecia) and moist dermatitis (wet eczema). Secondary bacterial infections may lead to focal ‘hot-spots’ with or without pyoderma. Clinical signs are more common in mature dogs and cats and lesions are distributed more on the caudal half of the body. *Ctenocephalides* spp. tend to bite humans predominantly on the lower legs and ankles, often with several bites in a row. Adult fleas are voracious feeders and may ingest up to 15 µl blood per day, so persistent heavy infestations in companion animals may cause iron-deficiency anaemia, especially in small young animals. The intensity of infestation may vary considerably, with most infested hosts having few fleas (often < 20, rarely > 100). The severity of disease does not correlate well with the intensity of infestation, for it only takes one or several flea bites to cause serious allergic/hypersensitivity reactions in sensitized individuals. Two distinct clinical manifestations have been associated with flea allergy in cats: miliary dermatitis (crusted papules with variable hair loss, especially across the dorsum and trunk) and feline symmetrical alopecia (skin appear normal but distal hair tips become fractured by excessive grooming).

In addition to directly causing disease, *Ctenocephalides* fleas have also been shown to act as vectors for a range of bacterial diseases: including several bartonelloses (*Bartonella henselae, B. clarridgeiae, B. quintana, B. koehlerae*), haemobartonellosis

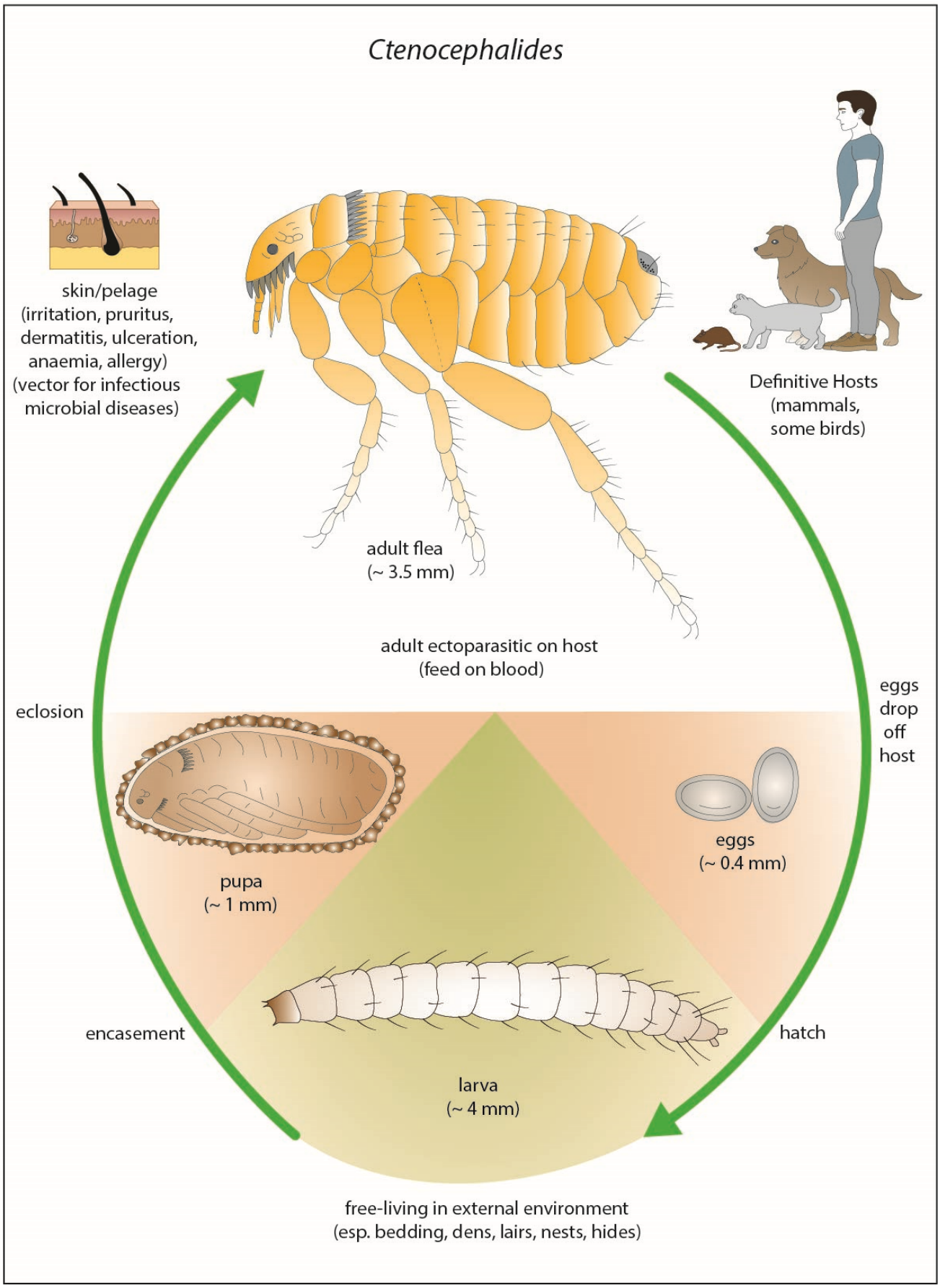
(*Mycoplasma haemofelis*), murine typhus (*Rickettsia typhi, R. felis*), Lyme disease (*Borrelia burgdorferi*) and possibly even bubonic plague (*Yersinia pestis*) that are transmitted variously to dogs, cats and humans. Fleas also serve as intermediate hosts for several helminth parasites, harbouring larval cysticerci of the dog tapeworm (*Dipylidium caninum*), the mouse tapeworm (*Vampirolepis nana*) and infective larvae of the filarial nematode (*Dipetalonema reconditum*), that are ingested during flea-grooming by dogs and cats, or accidentally by humans.

Developmental cycle and mode of transmission: Fleas have a holometabolous life cycle and undergo complete metamorphosis (egg-larva-pupa-adult). Only the adult fleas are ectoparasitic as all other life cycle stages occur in the environment. After feeding and mating, female fleas begin laying the first of hundreds of eggs in small groups of 4-8 eggs usually directly on the host. Egg production occurs at the rate of 20-50 eggs per day for several weeks, although it has sometimes been found to last up to 50-100 days. The eggs are not sticky and therefore drop off the host, usually in rest or sleeping areas frequented by hosts (bedding in dens, lairs, nests or hides). The eggs hatch within 2-21 days depending on prevailing environmental conditions (faster in warm moist conditions but unable to survive dry conditions). Hatched eggs release vermiform larvae which are legless and eyeless. The larvae avoid light by moving down into their surrounding substrata. They cannot close their spiracles and are therefore sensitive to low humidity and desiccation. They feed on dead skin and other debris within bedding materials, notably on flea dirt (excreta from adult fleas containing partially digested blood). The larvae moult through three larval instars over 8-150 days before forming pupae in silky cocoons which become covered in dust and debris. The pupa completes development to an adult over several days to weeks, although low temperatures and high humidity can extend larval and pupal stages for several months. Adults may remain in the cocoon for some time (usually 3-4 weeks but ranging from 14-170 days) until a passing host triggers their emergence via physical and chemical stimuli (vibration, heat, carbon dioxide). The hind-limbs of adult fleas are greatly enlarged and specially adapted for jumping, they possess elastic resilin pads which can be compressed and cocked, to be released with explosive force enabling them to make prodigious leaps (up to 100 times their own length). Newly emergent adults may jump onto a host immediately and begin feeding, or wait for a passing host after climbing on top of their surrounding substrata (vegetation, carpet pile, etc.) but they can only survive for several days without a blood meal. When feeding, adult fleas may consume up to 15 times their body weight in blood per day, but it transits the digestive tract very rapidly resulting in partially digested blood being excreted as reddish-black faecal pellets. This flea dirt falls off the host and acts as a food source for larval stages in host bedding. The whole life cycle may be completed under optimal conditions in as little as three weeks but it can be extended in suboptimal conditions for as long as 3-6 months. Adult fleas rarely leave their hosts so transmission is more reliant on hosts sharing contaminated environments than by direct host-host contact. The intensity of infestation can increase significantly over time but is restricted by the low survival of larval stages contaminating the environment, unless bedding or nesting behaviours and frequency provide suitable conditions for their persistence, thus leading to an aggregated distribution and focal points for transmission.

Differential diagnosis: Animals attempt to groom infested areas, and an 'itchy-scratchy' syndrome may develop, sometimes associated with intense inflammation or allergic reactions. Adult fleas and flea dirt can often be found in infested areas by visual examination (manually parting hairs or using a fine-toothed comb), although flea numbers on animals with FAD may be low or remain undetected. Flea dirt contains partially digested blood so when placed on moist filter paper it will often stain the surrounding area red. Using low power magnification, the species *C. felis* and *C. canis* may be differentiated on the basis of the length of the first two genal ctenidia (equal for *C. felis*, unequal for *C. canis*) and the number of seta-bearing notches on the dorsal margin of the hind limb tibia (six for *C. felis*, eight for *C. canis*). Several immunological tests have been developed to assist in the diagnosis of flea-allergy dermatitis (FAD) in pets, including intra-dermal skin tests with a panel of antigens to differentiate from atopic dermatitis (AD), and serological tests for specific immunoglobulins (IgE) against flea antigens. Molecular biological tests have been used to characterize flea isolates using polymerase chain reaction (PCR) amplification of specific gene sequences (nuclear 18S and 28S ribosomal RNA, internal transcribed spacer regions 1 and 2, elongation factor 1-alpha, mitochondrial cytochrome oxidase II, mitochondrial 16S ribosomal RNA).

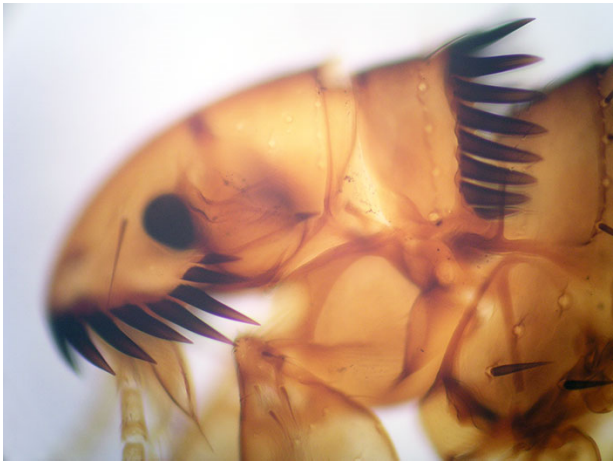
Treatment and control: Many chemicals have been developed to kill fleas, most acting on neurotransmitters, some on insect cuticle and several insect growth regulators (IGR). These insecticides may be used variously as tablets, in-feed medications, powders, washes, shampoos, sprays, pour-ons or impregnated into collars. Most conventional treatments consist of topical organophosphates (coumaphos, chlorfenvinphos, diazinon, dioxathion, fenchlorvos, crotoxyphos, malathion, phosmet, stirofos, trichlorfon), carbamates (carbaryl), and pyrethrum and its pyrethroid derivatives (permethrin, cypermethrin, cyfluthrin). Several new generation ectoparasiticides have also been developed as topical spray or spot-on formulations, including arylpyrazoles (fipronil), chloronicotinyles (imidacloprid), macrocyclic lactones (selamectin), neonicotinoid (dinotefuran), oxadiazine (indoxacarb), semicarbazone (metaflumizone) and juvenile hormone mimetics (methoprene, pyriproxyfen). Oral formulations include chloronicotinyles (nitenpyram), spinosyns (spinosad), isoxazoline-substituted benzamide derivatives (fluralaner) (dogs only), isoxazoline (afoxolaner) (dogs only) and benzoylphenylureas (lufenuron), the latter also available as an injectable for use in cats only. Most drugs act on adult fleas (adulticides), although many of the newer preparations also act against eggs (ovicides). Ideally, topical or systemic insecticides with good residual activity should be used to kill existing infestations (curative treatment) as well as to reduce environmental contamination and prevent re-infestation (prophylaxis). However, treatments should be repeated regularly (7-14 days) to avoid re-infestation from larval and pupal stages already present in the environment. Drug efficacy should also be monitored as there are growing reports of insecticide resistance developing in flea populations. Human patients may seek relief from

bite site reactions by using various cooling preparations, such as menthol, camphor, calamine, propylene glycol, vaseline or even ice. Corticosteroids (glucocorticoids, prednisone) are often used topically or systemically for palliative treatment of flea-bite allergy. Antibiotics may also be required to manage secondary bacterial infections and pyoderma. Experimental vaccination studies have shown some success in limiting infestations on dogs, cats and rabbits injected with midgut antigens of cat fleas. Control measures should include environmental management such as the provision of clean bedding, vacuuming carpets (which also stimulates adults to emerge from cocoons), rodent control and restricting pet roaming. Several methods of environmental decontamination have been developed including the use of intermittent light traps, insecticidal room foggers or flea bombs for confined indoor areas (flubenzuron, pyriproxyfen, methoprene), insecticidal sprays for small outdoor (organophosphates, pyrethroids, imidacloprid, cyfluthrin, fenvalerate) and even spreading desiccants (diatomaceous earth, sodium polyborate) in areas where animals rest.


Ctenocephalides
skin/pelage
(irritation, pruritus,
dermatitis, ulceration,
anaemia, allergy)
(vector for infectious
microbial diseases)
Definitive Hosts
(mammals,
some birds)
adult flea
(~ 3.5 mm)
adult ectoparasitic on host
(feed on blood)
eclosion
eggs
drop
off
host
pupa
(~ 1 mm)
eggs
(~ 0.4 mm)
encasement
hatch
larva
(~ 4 mm)
free-living in external environment
(esp. bedding, dens, lairs, nests, hides)



Ctenocephalides adult



Ctenocephalides adult head



Ctenocephalides larva



Ctenocephalides pupa



Ctenocephalides egg

Xenopsylla
(insect: flea)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Siphonaptera (fleas) are bilaterally-flattened wingless insects whose hindlimbs are enlarged and specially adapted for jumping (using elastic resilin pads rather than muscles). Fleas are holometabolans and undergo complete metamorphosis whereby grub-like larvae form pupae from which adult fleas emerge. The larvae are not parasitic but feed on debris associated mainly with bedding, den or nest material, whereas the adult stages are parasitic and feed on host blood. Pulicid fleas occur as ectoparasites on mammals, including humans, domestic and companion animals and wildlife, especially rodents. Adult *Xenopsylla cheopis* lack genal (oral) and pronotal (thoracic) combs and infestations have been associated with dermal irritation in humans and rats. The fleas may also transmit serious pathogens; including bubonic plague, murine typhus and tapeworms.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order: Siphonaptera (fleas, wingless, laterally compressed, third pair of legs adapted for jumping)
Family: Pulicidae (parasites of mammals)
Genus: *Xenopsylla* (parasitic on skin of rats/dogs/cats/humans)
Species: various species cause pruritus in humans and rats

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Fleas are small wingless insects that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. The adults are ectoparasitic and use siphon-like mouthparts to feed on blood from warm-blooded vertebrates [the name 'Siphon-aptera' literally translates as 'siphon' and 'wingless']. All adult fleas are further characterized by having laterally compressed bodies (allowing movement through hair/feathers), backward-pointing hairs and bristles (resisting grooming by host), strong tarsal claws (for grasping), and enlarged hindlegs (adapted for jumping). Around 2,200 flea species have been described in 250 genera on the basis of morphological and biological differences, and recent molecular phylogenetic studies have indicated some 18 families may occur in 4 infra-orders.

Siphonapteran families	Biodiversity	Hosts	Characters	Biogeographical distribution
Infraorder: Pulicomorpha (compact body, small thorax, pronotum with entire undivided ventral margin)				
Pulicidae (common fleas)	22 genera 207 species	carnivores, lagomorphs, rodents, artiodactyls, birds	sensilium with at most 14 pits, coxa with spiniform setae	pan-Tropical, cosmopolitan
Tungidae	5 genera	rodents, insectivores, bats,	compression of 3 thoracic	Neotropical,

(sand fleas)	23 species	suids, humans, birds	segments, neosomy	Holarctic
Vermipsyllidae	3 genera 39 species	carnivores, pikas, ungulates	frontal tubercle, large spiracles, reduced tergites	Holarctic
Ancistropsyllidae	1 genus 3 species	artiodactyls	metanotum and abdominal tergites with spinelets	Oriental
Coptopsyllidae	1 genus 19 species	rodents	combless, 2 spermathecae, tergal spinelets absent	Southern Palaearctic
Malacopsyllidae	2 genera 2 species	insectivores	high mesonotum, metanotum without spinelets	Patagonian
Rhopalopsyllidae	14 genera 126 species	rodents, insectivores, birds	metanotum and abdominal tergites with spinelets	Neotropical, Australasian
Infraorder: Ceratophyllomorpha (elongate body, long thorax, head without intergenal process, interantennal dimorphism)				
Ceratophyllidae	47 genera 540 species	rodents, pikas, carnivores, insectivores, birds	genal combs absent, males with interantennal suture	cosmopolitan
Ischnopsyllidae (bat fleas)	20 genera 125 species	bats	genal comb with 2-4 flattened spines, interantennal furrow	cosmopolitan
Leptopsyllidae	29 genera 260 species	insectivores, lagomorphs, rodents, carnivores, birds	head with tentorial arch, males with interantennal suture	Holarctic, Australasia
Xiphlopsyllidae	1 genus 8 species	rodents, shrews	squamulum absent, simple interantennal wall	Eastern African
Infraorder: Hystrichopsyllomorpha (elongate body, long thorax, head with intergenal process, clasper without process)				
Chimaeropsyllidae	8 genera 26 species	rodents, shrews	sensilium with 14 pits, hind coxa with spiniform setae	African
Hystrichopsyllidae (nest fleas)	46 genera 582 species	rodents, insectivores, pikas, marsupials	highly variable structures, 2 spermathecae	cosmopolitan
Macropsyllidae	2 genera 2 species	rodents	single head comb, 4 abdominal combs, 2 spermathecae	Australian
Stephanocircidae (helmet fleas)	9 genera 51 species	rodents, marsupials, birds	helmet (frons) with 2 separate combs, single spermatheca	Neotropical, Australian
Infraorder: Pygiopsyllomorpha (elongate body, long thorax, head with intergenal process, metanotum without spinelets)				
Pygiopsyllidae	10 genera 48 species	rodents, marsupials, birds	unique articulation between digitoid and main part of clasper	Australasian, Neotropical
Lycopsyllidae	4 genera 8 species	marsupials	genal lobe, simple interantennal wall, single mesopleural rod	Australian
Stivaliidae	23 genera 110 species	rodents, marsupials	strongly developed basal arm of Y-sclerite	Palaearctic, Australasia

Fleas from several families are found as ectoparasites on domestic and companion animals around the world: particularly those belonging to the families Pulicidae and Tungidae on mammals, and the family Ceratophyllidae on birds. Members of the family Pulicidae (syn. Archaeopsyllidae, Xenopsyllidae, Sarcopsyllidae p.p.) are characterized by compact bodies, small rounded heads and reduced chaetotaxy (small numbers of setae, spines and/or bristles). Over 20 genera have been recognized in 5 subfamilies: namely, Archaeopsyllinae (*Aphropsylla*, *Archaeopsylla*, *Centetipsylla*, *Ctenocephalides*, *Nesolagobius*), Moeopsyllinae (*Moeopsylla*), Pulicinae (*Delopsylla*, *Echidnophaga*, *Pulex*), Spilopsyllinae (*Actenopsylla*, *Cediopsylla*, *Euchoplopsyllus*, *Hoplopsyllus*, *Ornithopsylla*, *Spilopsyllus*), and Xenopsyllinae (*Parapulex*, *Pariodontis*, *Procaviopsylla*, *Pulicella*, *Synopsyllus*, *Synosternus*, *Xenopsylla*). Various pulicid species and genera are considered to be important parasites of medical and veterinary significance either as parasites in their own right (blood-sucking behaviour causing anaemia, dermatitis and hypersensitivity reactions) or as vectors for other infectious micro-organisms (including bacteria and helminths). Pulicid genera are differentiated mainly on the basis of whether the thoracic segments are very short (*Echidnophaga*), whether both genal (head) and pronotal (thorax) ctenidia (combs) are present (*Ctenocephalides, Spilopsyllus*) or absent (*Pulex, Echidnophaga, Xenopsylla*), and whether the axis of the genal comb is horizontal (*Ctenocephalides*) or vertical (*Spilopsyllus*).

Genera	**No. spp.**	**Hosts**	**Ctenidia (combs)**		**Disease**	**Vector**
			Genal (head)	**Pronotal (thorax)**		
Pulicidae						
Pulex	12	humans, carnivores, marsupials, rodents, birds	absent	absent	irritation, dermatitis, anaemia	plague, typhus, spotted fevers, tapeworms
Echidnophaga	23	birds, rodents, carnivores,	absent	absent	inflammation, ulceration	rickettsioses, plague, myxomatosis

		marsupials				
Xenopsylla	76	rodents, carnivores, marsupials, birds	absent	absent	irritation	plague, typhus, rat tapeworms
Ctenocephalides	12	carnivores, rodents, rabbits, insectivores, ungulates, birds	horizontal	present	pruritus, anaemia, hypersensitivity (flea-bite allergy)	bartonelloses, typhus, plague, dog tapeworm, filarial nematode
Spilopsyllus	1	rabbits, rodents, carnivores, birds	vertical	present	irritation	myxomatosis, tularemia
Tungidae						
Tunga	13	humans, insectivores, rodents, carnivores	absent	absent	inflammation, ulceration	*Staphylococcus, Wolbachia*, tetanus
Ceratophyllidae						
Ceratophyllus	64	birds, rodents, carnivores, ungulates	absent	present	irritation, reduced productivity	
Nosopsyllus	52	rodents, carnivores, some birds	absent	present	irritation	plague, erysipeloid, rat tapeworm

Xenopsylla spp. are primarily rat fleas, but they will readily feed opportunistically on other mammalian hosts, including humans. They are distributed throughout tropical, subtropical and temperate regions, rarely being found in cold regions as such conditions are not conducive to pupation. Studies on flea morphology and biology resulted in the differentiation of 8 species groups; *cheopis, trispinis, nilotica, eridos, brasiliensis, hirsuta, conformis* and *erilli* groups. Several flea species (particularly *X. cheopis*) are regarded to be primary vectors for the transmission of bacterial pathogens, including *Yersinia pestis* causing bubonic plague. Once the source of infection was discovered, flea and rodent control became prime concerns throughout human history in attempts to curb plague epidemics.

***Xenopsylla* species**	**Hosts**	**Clinical signs**	**Distribution**
'*cheopis'* group			
X. acomydis	Rodentia: murid (spiny mouse, Cyprus spiny mouse)		Cyprus
X. aequisetosa	Rodentia: nesomyid (Gambian pouched rat)		Africa
X. astia	Rodentia: murid (black rat, lesser bandicoot rat, greater bandicoot rat, flat-haired mouse, Indian gerbil); Strigiformes: strigid (spotted owlet)		Asia, Africa
X. australiaca	Rodentia: murid (black rat, brown rat, house mouse, spinifex hopping mouse, Mitchell's hopping mouse, ash-grey mouse)		Australia
X. bantorum	Rodentia: murid (field rats)		Africa
X. cheopis (syn. *Alaopsylla murinus, pachyruomyidids, philippinensis, tripolitanus, Pulex, cheopis, murinus*) (Oriental rat flea, tropical rat flea, black rat flea, plague flea)	Rodentia: murid (black rat, brown rat, grey spiny mouse, African grass rat, grassland melomys), sciurid (squirrel, chipmunk); Lagomorpha: leporid (European rabbit); Didelphimorphia: didelphid (Virginia opossum); Diprotodontia: macropodid (black wallaroo); Peramelemorphia: peramelid (northern brown bandicoot); Carnivora: canid (dog, fox), felid (cat), procyonid (raccoon), viverrid (common genet); Primates: hominid (human); Galliformes: phasianid (chicken)	irritation, pruritus (+ vector for plague, murine typhus, rat tapeworm, mouse tapeworm)	worldwide
X. dipodilli	Rodentia: murid (Wagner's gerbil)		Middle-East
X. guancha	Rodentia: murid (black rat, house mouse); Eulipotyphla: soricid (Canarian shrew)		Canary Islands
X. hussaini	Rodentia: murid (Indian gerbil)		India
X. nesiotes	Rodentia: murid (rat, mouse)		Christmas Island
X. nesokiae	Rodentia: murid (short-tailed bandicoot rat), cricteid (mole vole)		Central Asia
X. nubica	Rodentia: dipodid (jerboa, lesser Egyptian jerboa)		Middle-East
X. papuensis	Rodentia: murid (rat, mouse)		New Guinea
X. pestanai	Rodentia: murid (rock rat, striped grass mouse)		Africa
X. versuta	Rodentia: sciurid (African bush squirrel, African striped squirrel), glirid (African dormouse), murid (soft-furred mouse, African four-striped mouse, rock rat, vlei rat)		Africa
X. vexabilis	Rodentia: murid (greater sticknest rat, pale field rat, bush rat,		Australia,

	plains rat, common rock rat, dusky rat, dusky field rat, long-haired rat, Cape York rat, brush-tailed rabbit rat, fawn hopping mouse); Dasyuromorphia: dasyurid (northern quoll, antechinus, kowari, crest-tailed mulgara, fat-tailed dunnart); Peramelemorphia: peramelid (northern brown bandicoot)		Hawaii
'*trispinis'* group			
X. moucheti	Passeriformes: picarthartid (grey-necked rockfowl)		Africa
X. trispinis	Passeriformes: hirundinid (South African cliff swallow)		South Africa
'*nilotica'* group			
X. coppensi	Rodentia: murid (black-tailed gerbil)		Ethiopia
X. debilis	Rodentia: murid (gerbils)		Africa
X. difficilis	Rodentia: murid (gerbils)		Africa
X. humilis	Rodentia: murid (gerbils)		Africa
X. jorgei	Rodentia: murid (four-striped mouse, gerbil)		Africa
X. mulleri	Rodentia: murid (highveld gerbil)		Africa
X. nilotica	Rodentia: murid (gerbils)		Africa
X. orientalis	Rodentia: murid (bushveld gerbil)		Africa
X. raybouldi	Rodentia: murid (gerbils)		Africa
X. silvai	Rodentia: murid (gerbils)		Africa
X. tanganyikensis	Rodentia: murid (gerbils)		Africa
X. trifaria	Rodentia: murid (hairy-footed gerbil, Cape short-eared gerbil)		Africa
'*eridos'* group			
X. eridos	Rodentia: murid (whistling rat, vlei rat, gerbil)		South Africa
X. frayi	Rodentia: murid (bushveld gerbil)		Africa
X. geldenhuysi	Rodentia: murid (highveld gerbil)		Africa
X. hipponax	Rodentia: murid (rock rat, gerbil, soft-furred mouse)		Africa
X. occidentalis	Rodentia: murid (Littledale's whistling rat)		Africa
X. philoxera	Rodentia: murid (gerbils)		South Africa
X. phyllomae	Rodentia: murid (gerbils)		Africa
X. piriei	Rodentia: murid (gerbil, hairy-footed gerbil)		South Africa
'*brasiliensis'* group			
X. angolensis	Rodentia: nesomyid (pouched mouse)		Africa
X. bechuanae	Rodentia: nesomyid (South African pouched mouse)		Africa
X. brasiliensis	Rodentia: murid (black rat, brown rat)		cosmopolitan
X. cornigera	Rodentia: murid (savanna gerbil), glirid (woodland dormouse)		Africa
X. crinita	Rodentia: nesomyid (Gambian pouched rat)		Africa
X. cuisancei	Rodentia: murid (red rock rat, savanna gerbil)		Africa
X. georychi	Rodentia: bathyergid (common mole-rat)		Africa
X. graingeri	Rodentia: murid (acacia rat)		Africa
X. hamula	Rodentia: glirid (woodland dormouse), murid (woodland thicket rat)		Africa
X. morgandaviesi	Rodentia: murid (soft-furred mouse, striped grass mouse, spiny mouse); Eulipotyphla: soricid (musk shrew)		Africa
X. sarodes	Rodentia: nesomyid (South African pouched mouse)		Africa
X. scopulifer	Rodentia: nesomyid (South African pouched mouse)		Africa
X. syngenis	Rodentia: murid (soft-furred mouse, rock rat, gerbils), nesomyid (pouched mouse)		Africa
X. robertsi	Rodentia: murid (black rat, acacia rat, typical striped grass mouse)		Africa
X. torta	Rodentia: nesomyid (Gambian pouched rat)		Africa
X. zumpti	Rodentia: murid (acacia rat, thicket rat, rock rat); sciurid (African bush squirrel)		Africa
'*hirsuta'* group			
X. demeilloni	Rodentia: murid (hairy-footed gerbil, pygmy gerbil)		Africa
X. davisi	Rodentia: murid (hairy-footed gerbil, Cape gerbil)		Africa
X. hirsuta	Rodentia: murid (striped mouse, vlei rat, gerbils)		South Africa
X. lobengulai	Rodentia: murid (Cape gerbil)		South Africa
X. petteri	Rodentia: nesomyid (Malagasy giant rat)		Madagascar
X. sulcata	Rodentia: murid (Cape gerbil)		Africa
'*conformis'* group			
X. blanci	Rodentia: murid (house mouse)		North Africa

X. buxtoni	Rodentia: murid (gerbils)		Iran
X. conformis	Rodentia: murid (gerbil), dipodid (jerboa)		North Africa
X. cunicularis	Lagomorpha: leporid (European rabbit)		North Africa
X. gerbilli	Rodentia: murid (jird, great gerbil)		Central Asia
X. gratiosa	Procellariiformes: procellariid (streaked shearwater)		Atlantic
X. hirtipes	Rodentia: murid (great gerbil, jird)		Central Asia
X. magdalinae	Rodentia: murid (bandicoot rat), cricetid (mole vole)		Central Asia
X. minax [former subsp. of *X. gerbilli*]	Rodentia: murid (great gerbil, jird)		Central Asia
X. nuttalli	Rodentia: murid (gerbils), dipodid (jerboa)		Central Asia
X. persica	Rodentia: murid (Persian jird)		Central Asia
X. ramesis	Rodentia: murid (great gerbil, jird)		
X. skrjabini	Rodentia: murid (great gerbil, jird)		Central Asia
X. regis	Rodentia: murid (great gerbil, king jird)		Middle-East
X. taractes	Rodentia: murid (great gerbil, jird)		North Africa
X. tarimensis	Rodentia: dipodid (northern three-toed jerboa)		China
'*erilli'* group			
X. cryptonella	Rodentia: sciurid (Cape ground squirrel)		Africa
X. erilli	Rodentia: sciurid (Cape ground squirrel)		Africa

Parasite morphology: *Xenopsylla* spp. form 4 different types of developmental stages in their life-cycles; eggs; larvae (3 instars); pupae (cocoons); and adults (males and females). The eggs are white, ovoid (0.4-0.5 x 0.3-0.35 mm) and have small cephalic and caudal pores (aeropyles and micropyles, respectively). The larvae have elongated cylindrical vermiform (worm-like) bodies that are white-cream coloured with darker sclerotized heads possessing powerful mandibles and mandibular teeth well-adapted for biting and chewing. There are 3 larval instars growing in length from 0.5-4.5 mm and each possessing 14 bristly segments. Mature larvae form silken cocoons 2-4 mm long which become adorned with debris (small sand grains and dirt) from the surrounding environment. The enclosed stages transform into pupae by losing the larval head and last 3 segments while the rest of the body becomes compressed (shorter and wider). They are exarate pupae with free appendages (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). The emergent adult fleas are laterally compressed, measure from 1.5-4.0 mm in length and have shiny light-dark brown bodies with sclerotized plates (sclerites). They are moderately setate with strong setae, spines and/or bristles, usually facing backwards so as to not impede forward movement through pelage, but catching on hairs when dragged backwards by host grooming. However, *Xenopsylla* spp. do not possess genal (cheek) or pronotal (thoracic) ctenidia (combs of bristles). Adult fleas have small rounded heads, small compact thoracic segments and broad ovoid abdominal segments. The head is helmet-like, smoothly rounded and lacking a frontal tubercle (brow). The frons (forehead) is not heavily sclerotized and integricipit (without an interantennal suture). The head has a pair of small simple noncompound eyes (clusters of ocelli) located laterally with a stout ocular bristle present just in front but below each eye (whereas the ocular bristle in *Pulex* spp. is located beneath each eye). A pair of short compact club-like antennae (each comprising 3 segments) are held flat against the head behind the eyes. There are 6-8 large setae located on each side of the head behind the antennae, many conspicuous in a row along the posterior margin. All adults have conspicuous ventral piercing-sucking mouthparts (lacking mandibles and teeth) located between sensory palps consisting of a pair of long 4-segmented maxillary palps mounted on short blade-like maxillary lobes (stipes) as well as a pair of long 5-segmented labial palps arising from a short basal labium. The actual mouthparts (fascicle) consist of 3 long slender stylets: the 2 outer stylets (maxillary laciniae) being blade-like and serrated; and the third central stylet (labrum-epipharynx) being an outgrowth of the body wall (unique to fleas). All 3 stylets join to form a tube-like canal to inject saliva (via salivary pumps) and ingest blood (via cibarial and pharyngeal pumps). The alimentary tract consists of a tubular foregut (anterior pharynx with salivary glands inserted apically, elongate oesophagus, and small globular proventriculus), a large expandable digestive midgut (simple undivided organ lacking diverticula and caeca, unlike the elaborate divided midguts of other haematophagous arthropods), a tubular hindgut (with excretory Malpighian tubules) and rectum. The thorax has 3 conspicuous segments with a vertical thickening (meral rod) in the ventral mesopleuron. The ventral thorax gives rise to 3 pairs of strong legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) and all terminating in a pair of tarsal claws. The hindmost pair of legs are larger and well-adapted for jumping (using unique elastic resilin pads to store energy under compression, rather than muscular contraction). The legs are setate with prominent posterior tibial bristles and smaller tarsal bristles. The ovate abdomen has 8 visible segments consisting of dorsal tergites and ventral sternites with lateral respiratory spiracles. Most tergites have a single row of setae and the last segment bears a flat dorsal plate-like sensory organ (pygidium or sensilium). Male fleas are smaller than females and have highly elaborate genitals consisting of an aedeagal apodeme (penis plate) with long extendable penis rods held coiled and retracted within an endophallic sac. Female fleas are often recognizable by the presence of dark saccular spermatheca (sperm storage organs) located ventro-posteriorly. Females have 2 ovaries with tubular oviducts connected to the uterus and bursa copulatrix (depression to receive male organ).

Site of infection: Adult fleas are obligate ectoparasites of vertebrates, predominantly mammals (especially rodents but also some small marsupials, carnivores, lagomorphs and occasionally humans) as well as a few birds. Adults move through the pelage/plumage

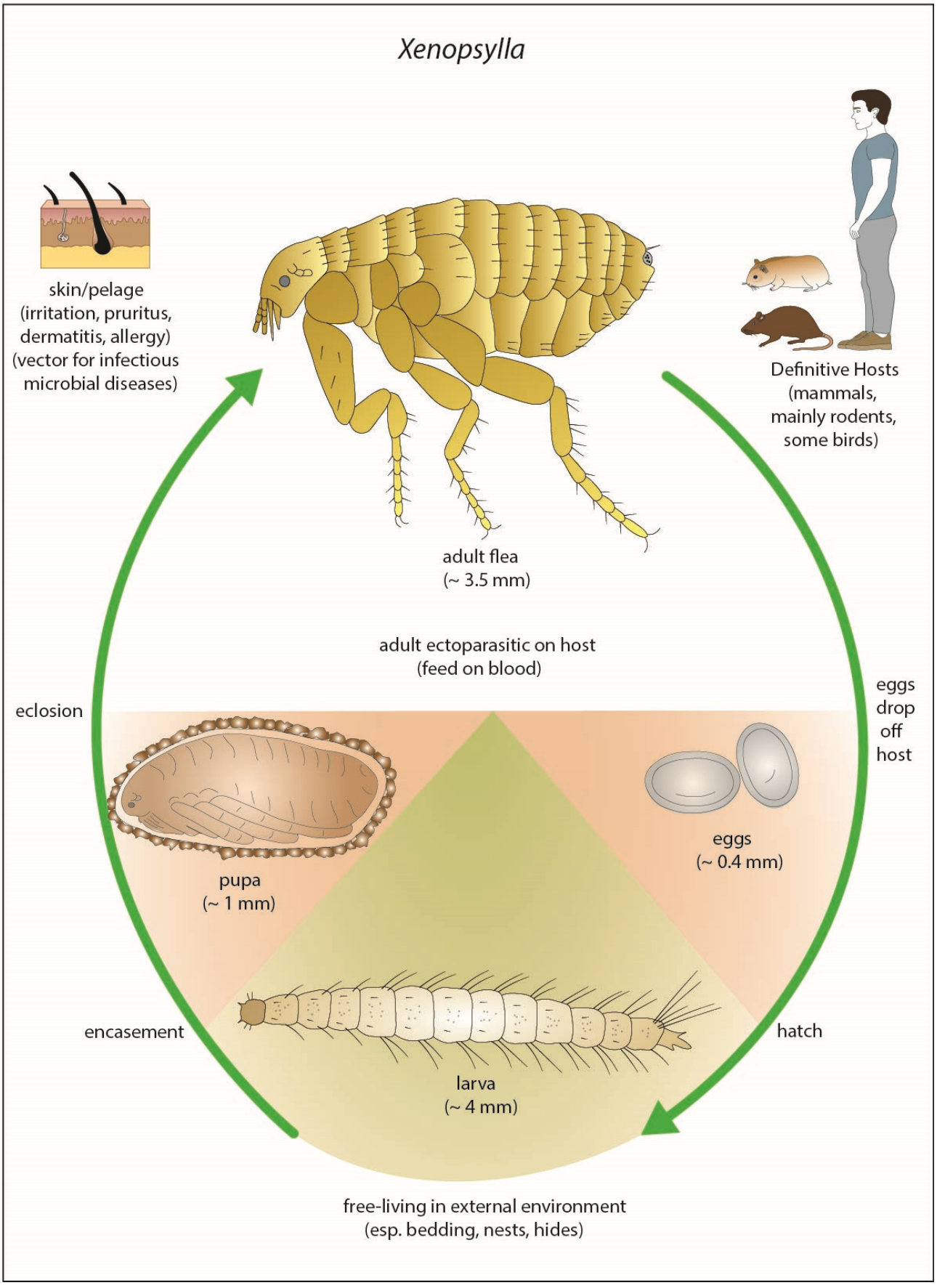
next to the skin and stop intermittently to feed on host blood. Between meals, adult fleas may remain on hosts or may drop off into burrows and nests (they are thought to dislike constant exposure to mammalian body temperatures). All other life stages (eggs, larvae and pupae) occur in the external environment, most being nidicolous and associated with host nests.

Pathogenesis: *Xenopsylla* spp. use their mouthparts to pierce the skin and then ingest blood by sucking from pools forming in the dermis (process known as telmophagy, as opposed to solenophagy where blood is sucked directly from blood vessels). Adults of both sexes feed on blood and some species are able to ingest up to 0.5 ml blood per meal. During feeding, they inject saliva containing numerous chemicals with anticoagulant, vasodilatory and anti-inflammatory properties. Nonetheless, bite sites often become irritated, inflamed and itchy, provoking hosts to scratch with the propensity to exacerbate wounds through self-trauma. Some individual hosts may also exhibit allergic and hypersensitivity responses to persistent infestations. In addition to being annoying pests causing transient skin lesions and anaemia, these rat fleas have gained notoriety as efficient vectors for the transmission of infectious diseases. In particular, the Oriental rat flea (*X. cheopis*) has been shown to transmit *Yersinia pestis* causing bubonic plague (lymph nodes), pneumonic plague (lungs) and septicaemia plague (skin, viscera) in humans. The bacteria multiply rapidly in the guts of the fleas often blocking the proventriculus and causing the hungry fleas to search for new hosts which become infected by regurgitative feeding. Adult fleas have also been shown to transmit other bacterial infections to humans, including *Rickettsia typhi* (the causative agent of murine or endemic typhus) and several *Bartonella* spp. (causing bartonellosis characterized by prolonged intraerythrocytic bacteraemia). Several flea species have also been found to act as vectors for the transmission of the nonpathogenic trypanosome (*T. lewisi*) in rats, and as intermediate hosts for *Hymenolepis diminuta* (rat tapeworm) and *H. nana* (mouse tapeworm).

Developmental cycle and mode of transmission: These rat fleas, like all fleas, exhibit holometabolous development where vermiform larvae undergo complete metamorphosis in pupal cocoons to form adult fleas. Gravid female fleas residing on hosts lay 15-20 eggs each day (sometimes up to 50 eggs per day). The eggs are not sticky and invariably drop off the host into the surrounding environment, particularly into dirt and crevices in nesting materials. Depending on prevailing environmental conditions, the eggs hatch in 2-12 days (or longer in colder conditions). The emergent larvae use their biting/chewing mandibles to feed on organic material in the environment (including plant detritus, cereal grains, and other micro-organisms), but rarely on 'flea dirt' (pellets of dried blood excreted by adults into the environment) like many other flea taxa. The larvae moult twice over 9-15 days, although it may take up to 200 days in unfavourable cold conditions. Mature third-stage larvae then weave silken cocoons around themselves and pupate into adult fleas over 5-14 days. The adult fleas usually remain in their pupal cases until they sense the presence of a nearby host by a combination of mechanical, chemical and thermal receptors (detecting vibration, pressure, noise, heat and increased carbon dioxide concentrations). Emergent fleas seek hosts and are able to jump up to 30-50 cm to engage hosts. Unfed fleas have been shown to survive for 6-10 weeks without feeding, but both sexes require bloodmeals to mature sexually. Fertilized females lay eggs regularly and may produce up to 600 eggs in their life-times. Adults have relatively long life-spans, and may survive for up to one year with regular access to bloodmeals. They are distributed throughout tropical, subtropical and temperate regions, and epidemiological and experimental studies have shown they flourish best when able to pupate in warm climatic conditions (temperatures of 20-25°C).

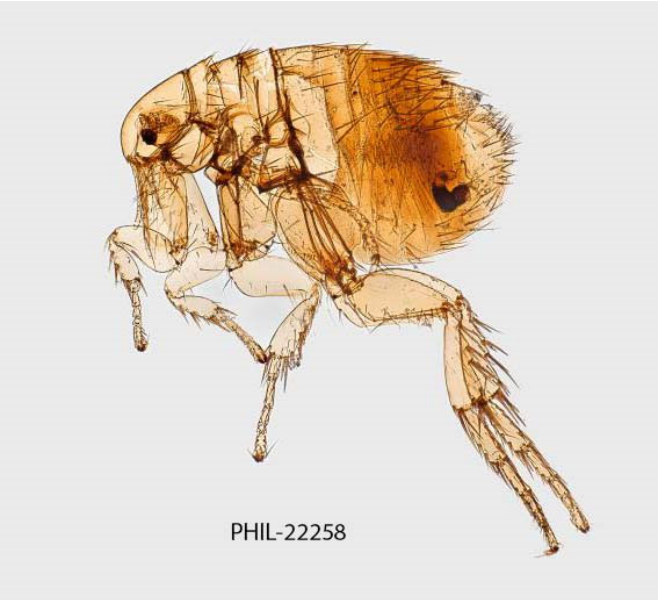
Differential diagnosis: Infestations are usually diagnosed by the direct detection of adult fleas on hosts, although they can be difficult to catch for microscopic examination. Fleas can be recovered from dead animals by roughly swabbing them with alcohol in plastic bags and then examining the washings. Adults can be identified by their morphological characteristics, particularly their rounded heads, setate bodies and the absence of genal and pronotal combs. Molecular biological techniques have been used to characterize species by polymerase chain reaction (PCR) amplification of nuclear (ribosomal RNA and internal transcribed spacer regions) and mitochondrial (16S ribosomal RNA) gene sequences.

Treatment and control: Many studies have been conducted on flea and vermin control in peri-urban environments due to the potential for rat fleas to transmit deadly infectious diseases to humans (such as plague). Considerable efforts have been made to eradicate rodents from communities by trapping, baiting or poisoning them. However, some initial caution is advised as starving fleas may seek alternative hosts on which to feed, including humans. Flea bites are generally treated with anti-inflammatory agents such as topical steroids (glucocorticoids, prednisolone), cooling preparations (propylene glycol, menthol, camphor, pramoxine, calamine, and ice compresses) together with antibiotics for secondary pyoderma. Animals may be treated with insecticidal chemicals, including organophosphates (coumaphos, chlorfenvinphos, diazinon, malathion, trichlorfon), pyrethroids (permethrin, cypermethrin), chloronictinyles (imidacloprid, nitenpyram), carbamates (carbaryl), arylpyrazoles (fipronil), macrocyclic lactones (selamectin) and some insect growth regulators (lufenuron, pyriproxyfen). Attempts should be made to decontaminate the surrounding environment (bedding, nests, burrows) with environmental insecticides (such as flea bombs and sprays containing organophosphates or pyrethroids) or desiccants (diatomaceous earth, sodium polyborate). Infested houses should be thoroughly cleaned by washing hard substrates and crevices with disinfectants, shampooing and vacuuming carpets, and fogging or spraying rooms with residual pyrethroid insecticides (cyfluthrin, fenvalerate).


Xenopsylla
skin/pelage
(irritation, pruritus,
dermatitis, allergy)
(vector for infectious
microbial diseases)
Definitive Hosts
(mammals,
mainly rodents,
some birds)
adult flea
(~ 3.5 mm)
adult ectoparasitic on host
(feed on blood)
eggs
drop
off
host
eclosion
pupa
(~ 1 mm)
eggs
(~ 0.4 mm)
encasement
hatch
larva
(~ 4 mm)
free-living in external environment
(esp. bedding, nests, hides)



Xenopsylla adult male



Xenopsylla adult female



Xenopsylla larva

Spilopsyllus
(insect: flea)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Siphonaptera (fleas) are bilaterally-flattened wingless insects whose hindlimbs are enlarged and specially adapted for jumping (using elastic resilin pads rather than muscles). Fleas are holometabolans and undergo complete metamorphosis whereby grub-like larvae form pupae from which adult fleas emerge. The larvae are not parasitic but feed on debris associated mainly with bedding, den or nest material, whereas the adult stages are parasitic and feed on host blood. Pulicid fleas occur as ectoparasites on mammals, including humans, domestic and companion animals and wildlife, especially rodents. Adult *Spilopsyllus* spp. have genal (oral) and vertical pronotal (thoracic) combs and infestations have been associated with irritation and tissue damage in rabbits. The fleas also act as vectors for the transmission of myxomatosis.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order: Siphonaptera (fleas, wingless, laterally compressed, third pair of legs adapted for jumping)
Family: Pulicidae (parasites of mammals)
Genus: *Spilopsyllus* (parasitic on skin of rabbits)
Species: various species cause irritation, skin lesions

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Fleas are small wingless insects that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. The adults are ectoparasitic and use siphon-like mouthparts to feed on blood from warm-blooded vertebrates [the name 'Siphon-aptera' literally translates as 'siphon' and 'wingless']. All adult fleas are further characterized by having laterally compressed bodies (allowing movement through hair/feathers), backward-pointing hairs and bristles (resisting grooming by host), strong tarsal claws (for grasping), and enlarged hindlegs (adapted for jumping). Around 2,200 flea species have been described in 250 genera on the basis of morphological and biological differences, and recent molecular phylogenetic studies have indicated some 18 families may occur in 4 infra-orders.

Siphonapteran families	Biodiversity	Hosts	Characters	Biogeographical distribution
Infraorder: Pulicomorpha (compact body, small thorax, pronotum with entire undivided ventral margin)				
Pulicidae (common fleas)	22 genera 207 species	carnivores, lagomorphs, rodents, artiodactyls, birds	sensilium with at most 14 pits, coxa with spiniform setae	pan-Tropical, cosmopolitan
Tungidae	5 genera	rodents, insectivores, bats,	compression of 3 thoracic	Neotropical,

(sand fleas)	23 species	suids, humans, birds	segments, neosomy	Holarctic
Vermipsyllidae	3 genera 39 species	carnivores, pikas, ungulates	frontal tubercle, large spiracles, reduced tergites	Holarctic
Ancistropsyllidae	1 genus 3 species	artiodactyls	metanotum and abdominal tergites with spinelets	Oriental
Coptopsyllidae	1 genus 19 species	rodents	combless, 2 spermathecae, tergal spinelets absent	Southern Palaearctic
Malacopsyllidae	2 genera 2 species	insectivores	high mesonotum, metanotum without spinelets	Patagonian
Rhopalopsyllidae	14 genera 126 species	rodents, insectivores, birds	metanotum and abdominal tergites with spinelets	Neotropical, Australasian
Infraorder: Ceratophyllomorpha (elongate body, long thorax, head without intergenal process, interantennal dimorphism)				
Ceratophyllidae	47 genera 540 species	rodents, pikas, carnivores, insectivores, birds	genal combs absent, males with interantennal suture	cosmopolitan
Ischnopsyllidae (bat fleas)	20 genera 125 species	bats	genal comb with 2-4 flattened spines, interantennal furrow	cosmopolitan
Leptopsyllidae	29 genera 260 species	insectivores, lagomorphs, rodents, carnivores, birds	head with tentorial arch, males with interantennal suture	Holarctic, Australasia
Xiphlopsyllidae	1 genus 8 species	rodents, shrews	squamulum absent, simple interantennal wall	Eastern African
Infraorder: Hystrichopsyllomorpha (elongate body, long thorax, head with intergenal process, clasper without process)				
Chimaeropsyllidae	8 genera 26 species	rodents, shrews	sensilium with 14 pits, hind coxa with spiniform setae	African
Hystrichopsyllidae (nest fleas)	46 genera 582 species	rodents, insectivores, pikas, marsupials	highly variable structures, 2 spermathecae	cosmopolitan
Macropsyllidae	2 genera 2 species	rodents	single head comb, 4 abdominal combs, 2 spermathecae	Australian
Stephanocircidae (helmet fleas)	9 genera 51 species	rodents, marsupials, birds	helmet (frons) with 2 separate combs, single spermatheca	Neotropical, Australian
Infraorder: Pygiopsyllomorpha (elongate body, long thorax, head with intergenal process, metanotum without spinelets)				
Pygiopsyllidae	10 genera 48 species	rodents, marsupials, birds	unique articulation between digitoid and main part of clasper	Australasian, Neotropical
Lycopsyllidae	4 genera 8 species	marsupials	genal lobe, simple interantennal wall, single mesopleural rod	Australian
Stivaliidae	23 genera 110 species	rodents, marsupials	strongly developed basal arm of Y-sclerite	Palaearctic, Australasia

Fleas from several families are found as ectoparasites on domestic and companion animals around the world: particularly those belonging to the families Pulicidae and Tungidae on mammals, and the family Ceratophyllidae on birds. Members of the family Pulicidae (syn. Archaeopsyllidae, Xenopsyllidae, Sarcopsyllidae p.p.) are characterized by compact bodies, small rounded heads and reduced chaetotaxy (small numbers of setae, spines and/or bristles). Over 20 genera have been recognized in 5 subfamilies: namely, Archaeopsyllinae (*Aphropsylla*, *Archaeopsylla*, *Centetipsylla*, *Ctenocephalides*, *Nesolagobius*), Moeopsyllinae (*Moeopsylla*), Pulicinae (*Delopsylla*, *Echidnophaga*, *Pulex*), Spilopsyllinae (*Actenopsylla*, *Cediopsylla*, *Euchoplopsyllus*, *Hoplopsyllus*, *Ornithopsylla*, *Spilopsyllus*), and Xenopsyllinae (*Parapulex*, *Pariodontis*, *Procaviopsylla*, *Pulicella*, *Synopsyllus*, *Synosternus*, *Xenopsylla*). Various pulicid species and genera are considered to be important parasites of medical and veterinary significance either as parasites in their own right (blood-sucking behaviour causing anaemia, dermatitis and hypersensitivity reactions) or as vectors for other infectious micro-organisms (including bacteria and helminths). Pulicid genera are differentiated mainly on the basis of whether the thoracic segments are very short (*Echidnophaga*), whether both genal (head) and pronotal (thorax) ctenidia (combs) are present (*Ctenocephalides, Spilopsyllus*) or absent (*Pulex, Echidnophaga, Xenopsylla*), and whether the axis of the genal comb is horizontal (*Ctenocephalides*) or vertical (*Spilopsyllus*).

Genera	**No. spp.**	**Hosts**	**Ctenidia (combs)**		**Disease**	**Vector**
			Genal (head)	**Pronotal (thorax)**		
Pulicidae						
Pulex	12	humans, carnivores, marsupials, rodents, birds	absent	absent	irritation, dermatitis, anaemia	plague, typhus, spotted fevers, tapeworms
Echidnophaga	23	birds, rodents, carnivores,	absent	absent	inflammation, ulceration	rickettsioses, plague, myxomatosis

		marsupials				
Xenopsylla	76	rodents, carnivores, marsupials, birds	absent	absent	irritation	plague, typhus, rat tapeworms
Ctenocephalides	12	carnivores, rodents, rabbits, insectivores, ungulates, birds	horizontal	present	pruritus, anaemia, hypersensitivity (flea-bite allergy)	bartonelloses, typhus, plague, dog tapeworm, filarial nematode
Spilopsyllus	1	rabbits, rodents, carnivores, birds	vertical	present	irritation	myxomatosis, tularemia
Tungidae						
Tunga	13	humans, insectivores, rodents, carnivores	absent	absent	inflammation, ulceration	*Staphylococcus, Wolbachia*, tetanus
Ceratophyllidae						
Ceratophyllus	64	birds, rodents, carnivores, ungulates	absent	present	irritation, reduced productivity	
Nosopsyllus	52	rodents, carnivores, some birds	absent	present	irritation	plague, erysipeloid, rat tapeworm

Spilopsyllus is a monotypic genus with a single species (*S. cuniculi*) originally described from rabbits in Europe but now distributed throughout the world due to the numerous translocations of hosts during colonization and more recently attempts using fleas as vectors for the spread of viral myxomatosis for the biological control of rabbits. Infestations may also be found on small mammals and some birds living in sympatry with rabbit populations, including companion animals.

***Spilopsyllus* species**	**Hosts**	**Clinical signs**	**Distribution**
S. cuniculi (rabbit flea)	Lagomorpha: leporid (European rabbit, European hare, mountain hare); Carnivora: felid (cat, wildcat), canid (dog, red fox), mustelid (Eurasian otter, stoat, least weasel, European polecat); Rodentia: cricetid (bank vole), sciurid (eastern gray squirrel); Eulipotyphla: soricid (common shrew); Artiodactyla: cervid (European fallow deer); Anseriformes: anatid (mallard); Charadriiformes: alcid (Atlantic puffin); Galliformes: phasianid (grey partridge); Passeriformes: parid (Eurasian blue tit); Procellariiformes: procellariid (Manx shearwater); Strigiformes: strigid (little owl); Suliformes: phalacrocoracid (great cormorant)	irritation, tissue damage (+ vector for myxoma virus causing myxomatosis; *Francisella tularensis* causing tularemia, nonpathogenic *Trypanosoma nabiasi*)	worldwide

Parasite morphology: Like all fleas, the rabbit flea *Spilopsyllus cuniculi* forms 4 different types of morphological stages during its development: namely, eggs; larvae; pupae; and adults. The eggs are pearly white and ovoid measuring around 0.5 mm in length. They hatch to release elongate vermiform (worm-like) larvae which develop through 3 instars growing in length from 1-5 mm. The larvae are eruciform having cylindrical segmented bristly bodies with darker sclerotized heads possessing powerful mandibles and mandibular teeth. Mature third-stage larvae form silken ellipsoidal cocoons around 2 mm long and transform through pupae into adults. The larval head and some abdominal segments are lost and the body becomes compressed (shorter and wider) during pupation. Pupae are exarate with free appendages (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). Following pupation, adult fleas eclose (emerge) from their pupal cocoons. Adults range from 1-2 mm in length and have laterally-compressed dark-brown bodies which are heavily chitinized with hard plates (called sclerites). They exhibit unique chaetotaxy (patterns of setation) with most spines, setae and bristles facing backwards so they do not impede forward movement of the flea through the pelage or plumage, but resist host grooming by catching on hairs or feathers when dragged backwards. In particular, *Spilopsyllus* has a unique combination of spines in comb-like rows (ctenidia) on the cheeks (genal) and thorax (pronotal). The pronotal ctenidia have a horizontal axis and contain 6-7 blunt spines on each side, while the genal ctenidia are oblique (almost vertical, and not horizontal like *Ctenocephalides* spp.) with 4-6 straight blunt spines on each side. The body has 3 conspicuous tagma: an angular head; a compact thorax; and a bulbous abdomen. The head has a rounded frons (forehead) with small frontal tubercle (brow) and the genal process (cheek) lacks a spine. There are 2 lateral simple noncompound eyes (clusters of ocelli) located high on the head, followed by a pair of short compact club-like antennae (3-segmented) held in protective grooves (fossae) and then 2 stout spines located behind them. Adult fleas have conspicuous ventral piercing-sucking mouthparts (lacking mandibles and teeth) located between 2 pairs of sensory palps: one pair consisting of long 4-segmented maxillary palps arising from short maxillary lobes (stipes); and the other pair consisting of long 5-segmented labial palps arising from a short basal labium. The mouthparts (fascicle) consist of 3 long slender stylets: the 2 outer stylets (maxillary laciniae) being blade-like and serrated; and the third central stylet (labrum-epipharynx) being an outgrowth of the body wall (unique to fleas). All 3 stylets join to form a tube-like canal to inject saliva (via salivary pumps) and suck blood (via cibarial and pharyngeal pumps). The alimentary canal consists of a tubular foregut (anterior pharynx, salivary glands inserted apically, elongate oesophagus, small globular proventriculus), a large

expandable digestive midgut (simple undivided gut, unlike the more elaborate divided midguts (with diverticula and caeca) in most other haematophagous arthropods), and a tubular hindgut (with excretory Malpighian tubules) and rectum. The thorax has 3 distinct segments (pronotum, mesonotum and metanotum), the former being more than half as long as the pronotal ctenidial spines. The ventral thorax gives rise to 3 pairs of strong legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) and all terminating in a pair of curved claws. The hindmost pair of legs are much longer and well-adapted for jumping (using unique elastic resilin pads to store energy under compression, rather than muscular contraction). The ovate abdomen has 10 segments but the last 3 are highly modified by sensory and genital structures. The dorsal sclerotized plates (tergites) of segments 2-7 have a single row of setae and respiratory spiracles are located laterally. Both male and female fleas have a flat dorsal plate-like organ (sensilium or pygidium) with several dome-like structures with small bristles. Male fleas are smaller than females, and have highly elaborate genitals (arguably the most complex in the animal kingdom) consisting of an aedeagal apodeme (penis plate) with extendable penis rods which are coiled and retracted within an endophallic sac. The penis is thin and delicate and cannot enter the female without the support of the rods and posterior claspers. Males have 2 testes connected by tubular vas deferens to a seminal vesicle opening into the ejaculatory duct. Female fleas have 2 ovaries joined by tubular oviducts to the globular uterus opening to the vagina with a bursa copulatrix (depression to receive male organ) and associated saccular spermatheca (for sperm storage).

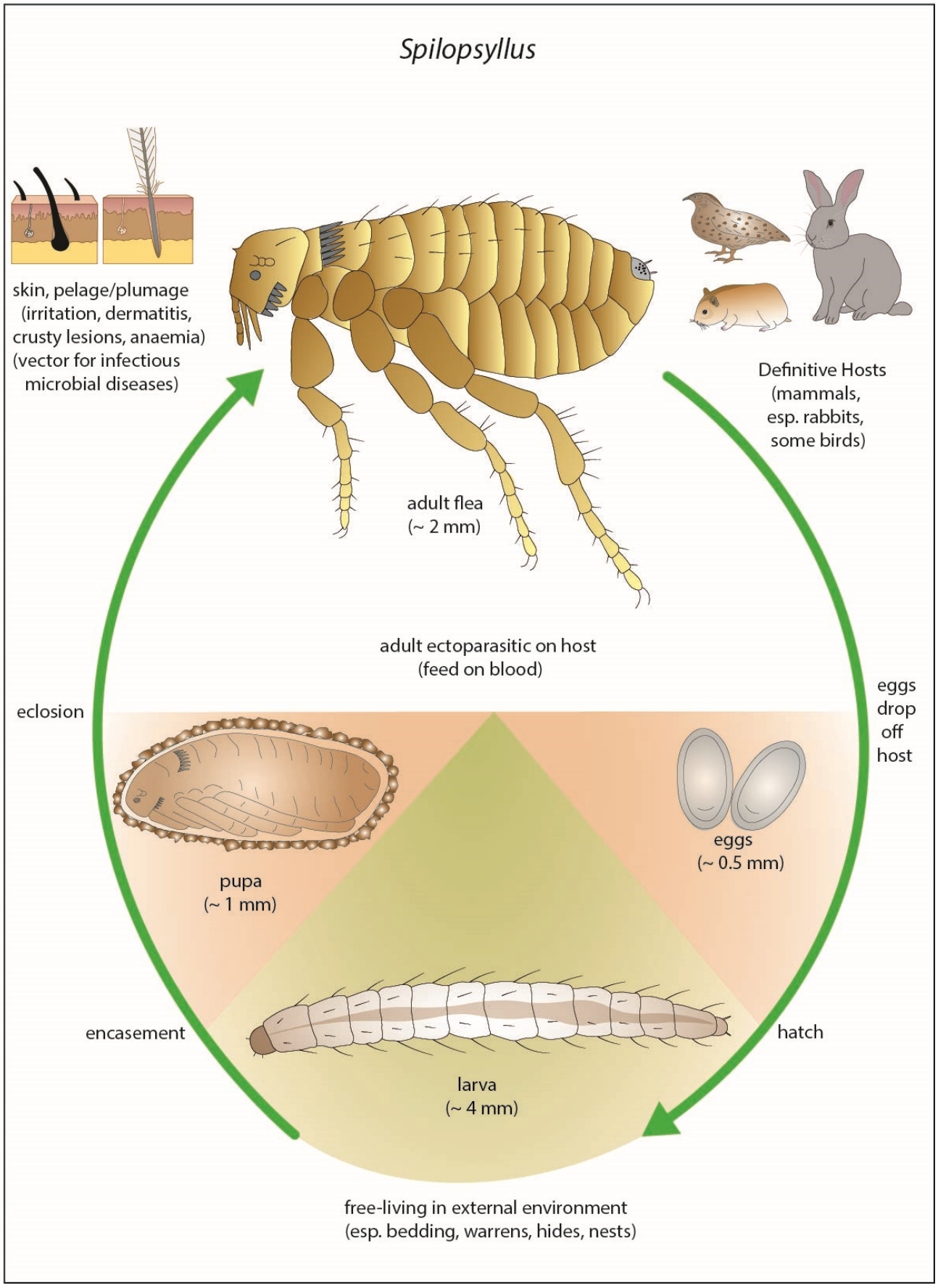
Site of infection: The adult stages of *S. cuniculi* are obligate ectoparasites of terrestrial mammals (mostly lagomorphs and a few small carnivores, rodents and shrews). On occasion, infestations have also been detected on several ground and water birds, often those close to or associated with burrows. Adults are often found clustered around the bases of the ears, along the ear margins, and sometimes the nose and eyelids of mammals, and around the neck and heads of birds. All other stages (eggs, larvae and pupae) occur in the external environment, particularly in burrows.

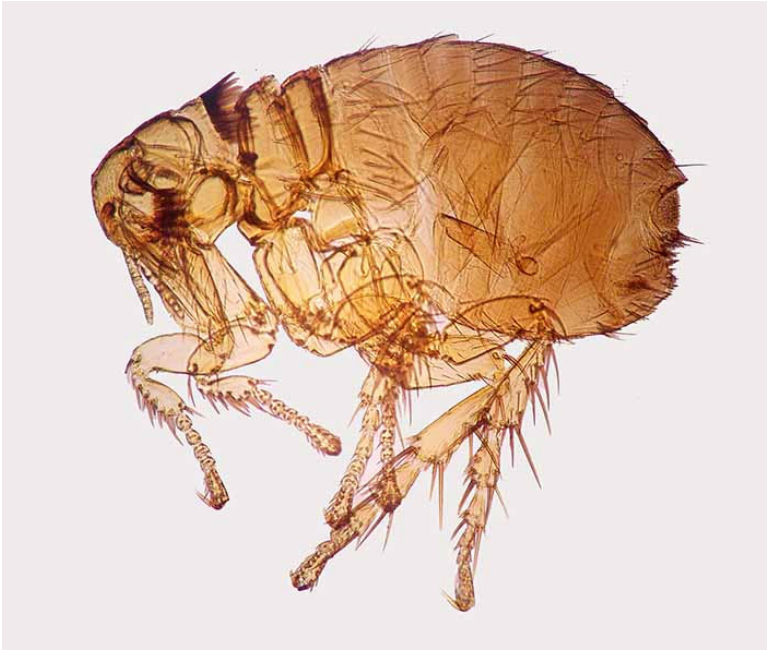
Pathogenesis: Adult rabbit fleas are relatively sedentary and remain attached to their hosts for long periods with their piercing-sucking mouthparts embedded in the skin while they periodically feed on host blood. Flea attachment and feeding causes traumatic structural damage to the skin with irritation, inflammation and pruritus. Light infestations often remain subclinical, but fleas tend to congregate on the ears of rabbits and their presence in large numbers may cause crusty lesions. Animals may attempt to groom infested regions by scratching or biting which may lead to self-trauma and wound exacerbation. Heavy infestations may cause blood loss sufficient enough to manifest as anaemia. When feeding, adult fleas inject saliva containing vaso-active compounds (anticoagulant, vasodilatory and anti-inflammatory chemicals) and some individual hosts exhibit allergic/hypersensitive reactions with expansive lesions but rarely with systemic effects. Lesions on other animals appear to be more subdued as fewer fleas appear to be involved in infestations (presumably due to the unique reproductive life cycle of the flea coinciding with that of the host (outlined below). Adult fleas have also been shown to act as vectors for infectious micro-organisms, including the bacterium *Francisella tularensis* causing tularemia (rabbit fever), the nonpathogenic protozoan parasite *Trypanosoma nabiasi,* and the myxoma virus causing myxomatosis. Indeed, rabbit fleas have been deliberately introduced into certain rabbit-infested regions to spread myxomatosis in attempts at biological control of pest populations (with good success due to the narrow host specificity of the fleas, their nidicolous burrow-inhabiting behaviour, their 'vertical' transmission between rabbit generations, and their ability to maintain viraemia for prolonged periods). Molecular screening studies have also detected the bacterium *Bartonella alsatica* in wild rabbits, but their involvement in the transmission of disease to humans (endocarditis and lymphadenitis) remains speculative.

Developmental cycle and mode of transmission: Rabbit fleas exhibit holometabolous development where grub-like larvae undergo complete metamorphosis in pupae to become adult fleas. Their life-cycle is quite unique, however, as flea reproduction is coincident and contingent on host reproduction. While fleas may parasitize rabbits of any age and gender, they only complete reproduction when in contact with female rabbits (does) in late pregnancy or with newborn rabbits (kits). Female fleas only mature and complete egg development when they feed on blood from pregnant does containing high levels of oestrogens and corticosteroids (the presence of progesterones in non-pregnant rabbits inhibits or delays flea maturation). The presence of the pregnancy-related hormones also enhances flea defaecation rates (up to 5-fold) thus facilitating greater contamination of the burrow with flea dirt (flea faeces containing partially digested blood). When young rabbits are born, fleas move onto them within hours to feed and lay eggs, as well as to mate. Newborn rabbits (1-10 days old) emit airborne and urinary kairomones (pheromone-like chemicals that only benefit the receiver rather than the emitter) which attract fleas and stimulates copulation. Gravid female fleas lay non-sticky eggs which drop off hosts into the surrounding environment, particularly in burrows where humidity levels are high enough (>50%) for their development. The eggs hatch after several days releasing larvae which feed on organic debris and detritus, especially flea dirt. The larvae develop through 3 instars over 15-45 days depending on environmental conditions (longer in colder conditions). Mature third-stage larvae form pupal cases (cocoons) in which they transform into adult fleas over 8-10 days. Adult fleas then emerge from cocoons, notably in response to vibrations caused by nearby hosts. They locate and feed on hosts within several days, but may survive without further feeding for several weeks (with some reporting periods up to 9 months in cold conditions). Sexual maturation of both male and female fleas occurs when they feed on pregnant does, and gravid females may lay up to 50 eggs per day for a few weeks around newborn kits. The whole life-cycle may be completed in as little as 14-21 days under ideal (warm humid) conditions, but may take as long as 6 months in adverse (dry cold) conditions. In many temperate and subtropical regions, infestations in wild lagomorphs appear to be seasonal, with peaks observed over summer.

Differential diagnosis: Infestations are generally detected by finding fleas, flea dirt or eggs when parting the pelage or using a fine-toothed flea comb, particularly near crusted lesions along the ear margins. Adult fleas are best recovered and examined microscopically for their distinctive morphological features (esp. rounded head with small tubercle, oblique genal comb, and horizontal pronotal comb). Molecular biological techniques have been used to examine flea phylogenetic relationships by polymerase chain reaction (PCR) amplification of several gene sequences (18S ribosomal DNA, 28S ribosomal DNA, elongation factor 1-alpha, and cytochrome oxidase II).

Treatment and control: Laboratory animals and pets may be treated with various conventional and modern insecticides, including organophosphates (chlorfenvinphos, diazinon, malathion, trichlorfon), pyrethroids (permethrin, cypermethrin), chloronictinyles (imidacloprid), carbamates (carbaryl), arylpyrazoles (fipronil), macrocyclic lactones (selamectin) and some insect growth regulators (lufenuron). Treatments are available as sprays/mousses, shampoos/washes, powders or spot-ons, but attention should be paid to any contra-indications as several products may have toxic side-effects on rabbits (e.g. impregnated anti-flea collars should never be used on rabbits as they cause severe irritation and burning of the skin). Symptomatic relief may be sought using glucocorticoids to alleviate dermatitis and pruritus, and systemic antibiotics may be required to combat any secondary bacterial infections associated with flea bites and skin lesions. It is advised that any animals being translocated be quarantined and screened for infestations and that all in-contact animals be treated at the same time. Animal holding facilities should also be decontaminated using environmental insecticides with good residual activity against free-living stages (eggs, larvae and/or pupae); such as organophosphates and pyrethroids in flea bombs or sprays. Facilities should be kept clean, with regular disinfection (washing, shampooing, vacuuming, or steam-cleaning but ensuring substrates dry thoroughly) and frequent changes of bedding materials (particularly during rabbit breeding seasons).


Spilopsyllus
skin, pelage/plumage
(irritation, dermatitis,
crusty lesions, anaemia)
(vector for infectious
microbial diseases)
adult flea
(~ 2 mm)
Definitive Hosts
(mammals,
esp. rabbits,
some birds)
adult ectoparasitic on host
(feed on blood)
eggs
drop
off
host
eclosion
pupa
(~ 1 mm)
eggs
(~ 0.5 mm)
encasement
hatch
larva
(~ 4 mm)
free-living in external environment
(esp. bedding, warrens, hides, nests)



Spilopsyllus adult



Spilopsyllus larva

Tunga
(insect: flea)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Siphonaptera (fleas) are bilaterally-flattened wingless insects whose hindlimbs are enlarged and specially adapted for jumping (using elastic resilin pads rather than muscles). Fleas are holometabolans and undergo complete metamorphosis whereby grub-like larvae form pupae from which adult fleas emerge. The larvae are not parasitic but feed on debris associated mainly with bedding, den or nest material, whereas the adult stages are parasitic and feed on host blood. Tungids (sand fleas, chiggers) are unusual in that female fleas are permanently attached to their mammalian hosts, residing in excavated sinuses in the skin and releasing eggs from their protruding abdominal segments. Infestations by *Tunga penetrans* have been associated with nodular and ulcerated skin lesions in humans and pigs.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order: Siphonaptera (fleas, wingless, laterally compressed, third pair of legs adapted for jumping)
Family: Tungidae (chigoes/jiggers/chiggers/chique/sand fleas, females burrow under skin, enclosed in sinus)
Genus: *Tunga* (parasitic on skin of mammals)
Species: *T. penetrans* (causes nodular/ulcerated lesions in humans and pigs)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Fleas are small wingless insects that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. The adults are ectoparasitic and use siphon-like mouthparts to feed on blood from warm-blooded vertebrates [the name 'Siphon-aptera' literally translates as 'siphon' and 'wingless']. All adult fleas are further characterized by having laterally compressed bodies (allowing movement through hair/feathers), backward-pointing hairs and bristles (resisting grooming by host), strong tarsal claws (for grasping), and enlarged hindlegs (adapted for jumping). Around 2,200 flea species have been described in 250 genera on the basis of morphological and biological differences, and recent molecular phylogenetic studies have indicated some 18 families may occur in 4 infra-orders.

Siphonapteran families	Biodiversity	Hosts	Characters	Biogeographical distribution
Infraorder: Pulicomorpha (compact body, small thorax, pronotum with entire undivided ventral margin)				
Pulicidae (common fleas)	22 genera 207 species	carnivores, lagomorphs, rodents, artiodactyls, birds	sensilium with at most 14 pits, coxa with spiniform setae	pan-Tropical, cosmopolitan
Tungidae (sand fleas)	5 genera 23 species	rodents, insectivores, bats, suids, humans, birds	compression of 3 thoracic segments, neosomy	Neotropical, Holarctic

Vermipsyllidae	3 genera 39 species	carnivores, pikas, ungulates	frontal tubercle, large spiracles, reduced tergites	Holarctic
Ancistropsyllidae	1 genus 3 species	artiodactyls	metanotum and abdominal tergites with spinelets	Oriental
Coptopsyllidae	1 genus 19 species	rodents	combless, 2 spermathecae, tergal spinelets absent	Southern Palaearctic
Malacopsyllidae	2 genera 2 species	insectivores	high mesonotum, metanotum without spinelets	Patagonian
Rhopalopsyllidae	14 genera 126 species	rodents, insectivores, birds	metanotum and abdominal tergites with spinelets	Neotropical, Australasian
Infraorder: Ceratophyllomorpha (elongate body, long thorax, head without intergenal process, interantennal dimorphism)				
Ceratophyllidae	47 genera 540 species	rodents, pikas, carnivores, insectivores, birds	genal combs absent, males with interantennal suture	cosmopolitan
Ischnopsyllidae (bat fleas)	20 genera 125 species	bats	genal comb with 2-4 flattened spines, interantennal furrow	cosmopolitan
Leptopsyllidae	29 genera 260 species	insectivores, lagomorphs, rodents, carnivores, birds	head with tentorial arch, males with interantennal suture	Holarctic, Australasia
Xiphlopsyllidae	1 genus 8 species	rodents, shrews	squamulum absent, simple interantennal wall	Eastern African
Infraorder: Hystrichopsyllomorpha (elongate body, long thorax, head with intergenal process, clasper without process)				
Chimaeropsyllidae	8 genera 26 species	rodents, shrews	sensilium with 14 pits, hind coxa with spiniform setae	African
Hystrichopsyllidae (nest fleas)	46 genera 582 species	rodents, insectivores, pikas, marsupials	highly variable structures, 2 spermathecae	cosmopolitan
Macropsyllidae	2 genera 2 species	rodents	single head comb, 4 abdominal combs, 2 spermathecae	Australian
Stephanocircidae (helmet fleas)	9 genera 51 species	rodents, marsupials, birds	helmet (frons) with 2 separate combs, single spermatheca	Neotropical, Australian
Infraorder: Pygiopsyllomorpha (elongate body, long thorax, head with intergenal process, metanotum without spinelets)				
Pygiopsyllidae	10 genera 48 species	rodents, marsupials, birds	unique articulation between digitoid and main part of clasper	Australasian, Neotropical
Lycopsyllidae	4 genera 8 species	marsupials	genal lobe, simple interantennal wall, single mesopleural rod	Australian
Stivaliidae	23 genera 110 species	rodents, marsupials	strongly developed basal arm of Y-sclerite	Palaearctic, Australasia

Fleas from several families are found as ectoparasites on domestic and companion animals around the world: particularly those belonging to the families Pulicidae and Tungidae on mammals, and the family Ceratophyllidae on birds. Although thought to be closely related to the Pulicidae, recent molecular studies have placed the Tungidae at the base of flea phylogeny in association with basal mammalian hosts. Members of the family Tungidae (= Dermatophilidae, Hectopsyllidae, Rhynchoprionidae, Echidnophagidae p.p., Sarcopsyllidae p.p.) are characterized by small simple bodies (small triangular heads and compressed thoracic segments) and reduced chaetotaxy (including the absence of both genal and pronotal ctenidial combs). Four tungid genera are recognized from a range of warm-blooded hosts: namely, *Hectopsylla* from nonvolant mammals, bats and birds, *Rhynchopsyllus* from bats, *Neotunga* from pangolins, and *Tunga* from small mammals. The latter two genera also exhibit a unique process known as neosomy whereby female fleas burrow into the host skin and undergo accelerated development (tachygenesis) with abdominal hypertrophy and encystment. In contrast, females of most other flea genera detach from their hosts after feeding, although pulicid stick-fast fleas, *Echidnophaga,* do undergo partial neosomy and remain attached. Neosomy (previously called teleomorphosis) has been defined as the pronounced interstadial growth of unsclerotized parts of the abdomen without moulting. It allows females to take maximum advantage of food resources and greatly increases their reproductive potential (readily producing over 1,000 eggs each).

Genera	**No. spp.**	**Hosts**	**Ctenidia (combs)**		**Disease**	**Vector**
			Genal (head)	**Pronotal (thorax)**		
Tungidae						
Tunga	13	humans, insectivores, rodents, carnivores	absent	absent	inflammation, ulceration	*Staphylococcus, Wolbachia*, tetanus
Pulicidae						
Pulex	12	humans, carnivores, marsupials, rodents,	absent	absent	irritation, dermatitis, anaemia	plague, typhus, spotted fevers, tapeworms

		birds				
Echidnophaga	23	birds, rodents, carnivores, marsupials	absent	absent	inflammation, ulceration	rickettsioses, plague, myxomatosis
Xenopsylla	76	rodents, carnivores, marsupials, birds	absent	absent	irritation	plague, typhus, rat tapeworms
Ctenocephalides	12	carnivores, rodents, rabbits, insectivores, ungulates, birds	horizontal	present	pruritus, anaemia, hypersensitivity (flea-bite allergy)	bartonelloses, typhus, plague, dog tapeworm, filarial nematode
Spilopsyllus	1	rabbits, rodents, carnivores, birds	vertical	present	irritation	myxomatosis, tularemia
Ceratophyllidae						
Ceratophyllus	64	birds, rodents, carnivores, ungulates	absent	present	irritation, reduced productivity	
Nosopsyllus	52	rodents, carnivores, some birds	absent	present	irritation	plague, erysipeloid, rat tapeworm

A total of 13 *Tunga* spp. have been described from wild and domestic mammals in tropical and subtropical regions, notably South and Central America, sub-Saharan Africa and parts of Indo-China. These species have been divided into two groups: the '*penetrans'* group (referable to the subgenus *T.* (*Tunga*)) containing 6 species (fusion of pronotum and mesonotum dorsally complete, spiracles of terga II-IV absent), and the '*caecata'* group (referable to the subgenus *T.* (*Brevidigitata*)) containing 7 species (fusion incomplete, spiracles present). Most *Tunga* spp. show little host specificity and infest multiple host species living in sympatry, particularly in areas with sandy soils in which immature fleas lay in wait of passing/resting hosts. Two species (*T. penetrans* and *T. trimamillata*) may infest humans causing ulcerative dermal lesions (tungiasis) mainly on the feet (around margins, toes and toenails), particularly in people who go barefoot. The lesions may become ulcerative and are highly prone to secondary bacterial infections, including tetanus which may prove fatal.

***Tunga* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
penetrans group (rodents, armadillos, anteaters, ungulates, carnivores and primates)				
T. bondari	Pilosa: myrmecophagid (southern tamandua); Cariamiformes: cariamid (red-legged seriema)	abdomen, legs	cysts	Brazil
T. hexalobulata	Artiodactyla: bovid (zebu)	foot	cysts	Brazil
T. penetrans (syn. *Pulex, Acarus, Rhynchoprion, Dermatophilus, Sarcopsylla*) (sand fleas, chiggers, jiggers, chigoes)	Primates: hominid (human, gorilla), atelid (southern brown howler monkey), cercopithecid (baboon, guenon); Artiodactyla: bovid (cattle, sheep, goat), camelid (llama, vicuna), suid (pig, bushpig), tayassuid (collared peccary); Perissodactyla: equid (horse, donkey, mule), tapirid (South American tapir); Proboscidea: elephantid (African bush elephant); Carnivora: canid (dog), felid (cat, jaguar); Rodentia: caviid (guinea pig, Brazilian guinea pig), cuniculid (lowland paca), dasyproctid (Central American agouti, red acouchi), hystricid (porcupine), murid (black rat, brown rat, house mouse); Cingulata: chlamydophorid (big hairy armadillo, six-banded armadillo), dasypodid (nine-banded armadillo, southern long-nosed armadillo); Pilosa: myrmecophagid (collared anteater, giant anteater)	feet, toes, scrotum, muzzle	cysts, pruritus, pain, ulceration	Latin America, Africa, Asia
T. terasma	Cingulata: chlamyphorid (giant armadillo, six-banded armadillo, southern naked-tail armadillo), dasypodid (nine-banded armadillo)	abdomen, toes	cysts	Brazil
T. travassosi	Cingulata: dasypodid (nine-banded armadillo)	abdomen	cysts	Brazil
T. trimamillata	Primates: hominid (human); Artiodactyla: suid (pig), bovid (cattle, sheep, goat); Rodentia: caviid (capybara)	feet, perianal	cysts	Ecuador, Peru
caecata group (primarily rodent hosts)				
T. bonneti	Rodentia: cricetid (yellow-rumped leaf-eared mouse, Darwin's leaf-eared mouse)	tail	cysts	Chile
T. bossi	Rodentia: cricetid (striped Atlantic forest rat)	tail	cysts	Brazil
T. caecata	Rodentia: murid (black rat, brown rat, house mouse), cricetid (Cursor grass mouse, bolo mouse, Atlantic	ears	cysts	Brazil

	forest climbing mouse, scaly-footed water rat, black-footed pygmy rice rat, hocicudo)			
T. caecigena	Rodentia: murid (black rat, brown rat, house mouse, southwestern Asian house mouse); Eulipotyphla: soricid (Asian house shrew)	ears	cysts	China, Japan
T. callida	Rodentia: murid (black rat, brown rat, southwestern Asian house mouse, Chevrier's field mouse), cricetid (southwest China vole)	perianal	cysts	China
T. libis	Rodentia: cricetid (soft grass mouse, Andean leaf-eared mouse, Darwin's leaf-eared mouse)	ears	cysts	Ecuador, Chile
T. monositus	Rodentia: cricetid (pack rat, desert wood rat, deer mouse, cactus mouse, canyon mouse)	ears	cysts	North America

Parasite morphology: *Tunga* spp. form 4 different and unique types of morphological stages during their developmental cycles: namely, eggs; larvae (2-3 instars); pupae (in cocoons); and adults (small laterally-flattened fleas but gravid females become large and swollen). The eggs are shiny white-yellow ovoid stages measuring approximately 0.6 x 0.3 mm. The larvae are yellow-brown vermiform (worm-like) stages with segmented bodies. Each of the 13 segments has an uneven circle of backwards-facing bristles and the last segment bears 2 lobes carrying an anal brace. The larvae have darker sclerotized heads with strong mandibles and mandibular teeth well-adapted for biting and chewing, and rudimentary maxillary palps and a labrum can be observed. The heads do not have eyes but have a pair of bar-like antennae that extend forwards. The larvae moult through several instars (2 for *T. penetrans*, 3 for other *Tunga* spp.) growing from 1-3 mm in length. Mature larvae void their guts of food and bend in a U-shape shortly before forming pupal cocoons. The cocoons are sticky and become covered with adherent sand grains and detritus. The enclosed pupae are exarate with free appendages (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). Adult fleas are reddish brown in colour with bilaterally symmetrical but laterally compressed bodies measuring 0.5-1.5 mm long (except for gravid females which become swollen and globular measuring up to 4-10 mm in diameter. Adults have hard chitinized plates (sclerites) and are sparsely setate (with few setae and entirely lacking genal and pronotal combs). They have 3 conspicuous body parts: a large angular double-curved head; a short narrow thorax; and an expandable abdomen. The head is flattened and angular, forming a triangular shape with a well pronounced frontal tubercle. Some species have a more rounded head while others have a slight depression on the top. The cheeks (gena) in *T. penetrans* have deep grooves which are absent in *T. trimamillata.* All species have a pair of short compact club-like antennae (3-segmented) flattened against the head and not within antennal grooves (fossae). They vary in their possession of eyes which, when present, may be small or large noncompound eyes (clusters of ocelli), sometimes pigmented. Adults have long ventral piercing-sucking mouthparts (lacking mandibles and teeth) that project conspicuously from the head. The mouthparts are located between 2 pairs of sensory palps: a pair of long 4-segmented maxillary palps (first segment longer in *T. trimamillata,* second segment longer for *T. penetrans*) arising from short lobes (stipes), and a pair of long 5-segmented labial palps arising from a short basal labium. The feeding mouthparts consist of 3 long slender stylets: the 2 outer stylets (maxillary laciniae) being blade-like and serrated, and the third central stylet (labrum-epipharynx) being an outgrowth of the body wall (unique to fleas). *Tunga* adults differ from other fleas in that they have well-developed laciniae and an epipharynx which facilitate burrowing. All 3 stylets join to form a tube-like canal to inject saliva (via salivary pumps) and suck blood (via cibarial and pharyngeal pumps). The alimentary tract consists of a tubular foregut (anterior pharynx, elongate oesophagus, globular proventriculus armed with spines), a large expandable midgut (simple undivided digestive organ, unlike the more elaborate divided midguts (with diverticula and caeca) of most other haematophagous arthropods), a tubular hindgut (with excretory Malpighian tubules) and rectum. The thorax has 3 distinct dorsal sclerites (pronotum, mesonotum, metanotum) that are surrounded by 3 humps in female *T. trimamillata* but absent in *T. penetrans.* The fusion of the pronotum and mesonotum is complete in the *T. penetrans* group, but incomplete in the *T. caecata* group. The ventral thorax is the point of attachment for 3 pairs of legs: each with 5 segments (coxa, trochanter, femur, tibia, and tarsus) and all ending in 2 claws. The legs are setate, with more spines on the first tarsal segment and hindleg tibia of *T. trimamillata* than *T. penetrans.* The hindlegs are enlarged which enables them to jump, but they are poor jumpers as the legs are very slender. Like all fleas, they jump using unique elastic resilin pads to store energy under compression, rather than muscular contraction. The expandable abdomen is segmented, with rows of hair-like structures on each segment. The *T. caecata* group has small lateral spiracles located laterally on dorsal abdominal sclerites (tergites II-IV) which are absent in the *T. penetrans* group. In non-gravid females, the last abdominal tergite in *T. trimamillata* protrudes outwards forming a small tail, but not in *T. penetrans.* The size and shape of the abdomen can be readily used to distinguish sexes, as marked sexual dimorphism occurs after maturation with females exhibiting considerable hypertrophic growth (up to 80-100 times) between abdominal segments II and III. This unique process is known as neosomy (previously called teleomorphosis) and has been defined as the pronounced interstadial growth of unsclerotized parts of the abdomen without moulting. This results in gravid females having dramatic size increase (up to 10 mm in diameter) accompanied by extensive morphological degeneration, major integumental chitin synthesis, and protracted and extensive egg development (200-1,000 eggs). Female fleas expose their posterior respiratory spiracles as well as their anal and vaginal apertures at the surface of the host skin, all contained within a caudal disc (varying in shape from flattened, conical to cylindrical, and in size from as wide as long, longer than wide, or wider than long). Different *Tunga* spp. can be distinguished by their hypertrophic forms, ranging from globular without lobes (*T. penetrans, caecata, travassoi, libis, bossii, bonneti*) or with 3 lobes (*T. trimamillata*), 4 lobes (*T. callida, terasmam, caecigena*), 6 lobes (*T. hexalobulata*), 8 lobes (*T. monositus*) or mushroom-shaped (*T. bondari*). Mature females have 2 ovaries with oviducts leading to the uterus which is connected to the vagina located in a bursa copulatrix (grooved depression to receive male organ) with an associated

spermatheca (sperm storage organ with a globular-elongate body (bulga) and a short-long thin-thick tail (hilla)). Male fleas remain small and do not undergo neosomy. However, they have distinctive and highly elaborate genitals (probably the most complex in the animal kingdom). They have 2 testes with tubular vas deferens leading to a seminal vesicle with an ejaculatory duct connected to a long thin delicate intromittent organ (penis). The penis is attached to an aedeagal apodeme (penis plate) and has extendable penis rods coiled and retracted within an endophallic sac. The phallosome has proximal and distal arms articulated in the middle just before the ejaculatory duct and almost as long as the penis plate. Copulation is aided by posterior claspers which have immovable processes (basimeres) and movable processes (telomeres) connected to a manubrium.

Site of infection: Adult *Tunga* fleas are obligate haematophagous ectoparasites of terrestrial vertebrates, whereas pre-adult stages (eggs, larvae and pupae) are free-living stages, usually in sandy soil. *Tunga* spp. exhibit variable host specificity, but most infest only a few host species living in sympatry. Collectively, members of the *T. penetrans* group have been found in 20 mammalian families (comprising rodents, armadillos, anteaters, ungulates, carnivores, and primates) and one avian family (a predatory terrestrial bird), while members of the *T. caecata* group are confined to 3 mammalian families (cricetid and murid rodents and Asian shrews). Only 3 species have been found on domestic animals (*T. penetrans, trimamillata,* and *hexalobulata*), the former 2 also being found on humans. While most other fleas leave their hosts after feeding, female *Tunga* fleas penetrate the epidermis forming furuncular nodules as they continue feeding and become grossly hypertrophied and filled with eggs. In humans, lesions are usually found in regions of body that regularly contact soil, notably periungual and subungual regions (around or under nails), the soles of the feet, and interdigital spaces, but other sites may also be involved, including the neck, upper limbs, buttocks and genital regions. In animals, female fleas usually burrow into the skin of the feet and legs but they can also invade ventral body surfaces and sometimes the neck and face.

Pathogenesis: Both male and female fleas feed on blood from vertebrate hosts, but males are transient feeders detaching after meals, whereas females burrow head-first into the skin and stay attached to feed, expand and produce eggs. Adults have well-developed mouthparts with cutting laciniae used to penetrate skin and a stabbing epipharynx used to suck blood from dermal blood vessels. Bite sites are evident as erythematous (reddened) papules surrounded by inflamed tissues, with inflammation heightened by allergic/hypersensitivity reactions to flea saliva. Inflammation may last for several days to weeks, and become encrusted with dried exudates. Female fleas burrow deeply into the skin causing lesions that appear as blisters or furuncular nodules. They undergo massive abdominal hypertrophy in a process known as neosomy (intrastadial development with new cuticle formation) and produce large numbers of eggs (200-1,000) as they stay *in situ* until death. The lesions appear as black-brown dots at the centre of swollen red tissues surrounded by white halos of thin skin. The central dots are where the female flea extends her spiracles, anus and vagina to breathe, defaecate and release eggs. The expanding lesions exert pressure on local tissues (including nerves and blood vessels) resulting in sensations ranging from mild irritation with pruritus to serious discomfort with great pain (sometimes crippling the host). Researchers have recognized 5 different stages in the development of lesions (Fortaleza classification). Stage 1 involves penetration of the female flea into the epidermis over 3-7 hours causing a focal red spot (~1 mm in diameter). This stage is initially asymptomatic but may produce some irritation, inflammation, erythema and pruritus. Stage 2 involves growth of the flea as it feeds over several days resulting in dark spots surrounded by erythema (~5 mm in diameter). The lesions are pruritic and host scratching may facilitate secondary bacterial infections, sometimes resulting in with nail deformation or loss. Stage 3 involves hypertrophy of the flea as it encysts over 1-2 weeks into a spherical nodule 7-10 mm in diameter which is evident as a white-gray-yellow papule with a brown-black center and surrounded by a halo of pale thin stretched hyperkeratotic skin. As the fleas engorge and lay eggs, hosts often experience pulsating pain that may limit their mobility and feeding efficiency. The lesions become covered by black scabs after the fleas expel their eggs. Stage 4 involves involution of the lesion after the majority of eggs are expelled and the hypertrophic zone crumples. Host reactions over several weeks cause the lesions to shrink and the surrounding skin becomes wrinkled and crusted. Stage 5 is the final repair period which lasts for several weeks as the host expels the flea carcass and repairs the skin, leaving a characteristic circular indurated scar. Two species (*T. trimamillata* and *T. penetrans*) cause tungiasis in humans (most commonly in children 5-9 years old and in males), with infestations by the former species being the most painful as the fleas are larger. In animals, infestations of the feet/hooves may compromise motility leading to feeding difficulties with reduced weight gain or weight loss, and decreased milk production. Infestations of the teats may lead to mastitis, agalactia and neonatal mortalities (young unable to suckle). Multiple lesions have been associated with the formation of pustules and suppuration, with lymphadenopathy and lymphoedema. Open or ulcerated lesions are highly susceptible to secondary bacterial infections, mostly by *Staphylococcus aureus* and Gram-negative bacteria, but also including Enterobacteriaceae, *Enterococcus faecalis*, *Streptococcus pyogenes*, *Bacillus* spp., *Pseudomonas* spp. and other anaerobic bacteria. Infected lesions become further enlarged leading to the formation of abscesses, cellulitis, phagedenic ulcers, hyperkeratosis, fissures, phlegmons, septicaemia, thrombophlebitis, lymphangitis, osteomyelitis, onycholysis (loss of nails), and gangrene with spontaneous amputation of toes. Lesions may also act as portals of entry for *Clostridium tetani* causing tetanus, which may be fatal. Molecular screening studies on sand fleas have also isolated *Yersinia pestis* (the cause of plague) as well as enigmatic *Wolbachia* spp. (Gram-negative bacteria that have been found as intracellular symbiotes (mutualists or parasites) in a range of insects and nematodes).

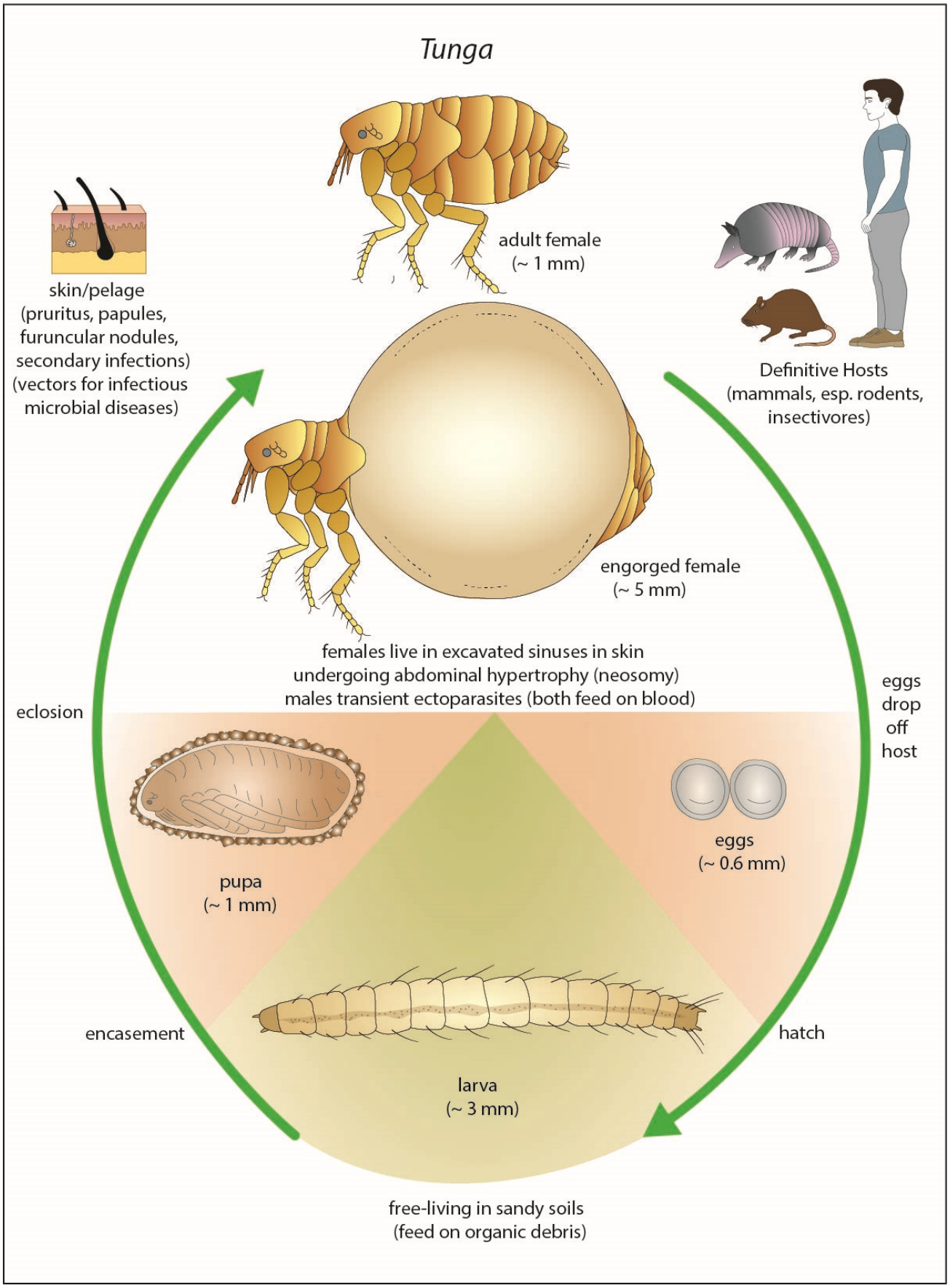
Developmental cycle and mode of transmission: Like other fleas, *Tunga* spp. exhibit holometabolous development where vermiform larvae undergo complete metamorphosis in pupae to form adult fleas. Unlike other fleas, however, the female fleas attach permanently to their hosts, even burrowing into the skin and undergoing massive hypertrophy of their abdomens as they produce

numerous eggs. Females lay eggs through their posterior genital aperture which protrude from the centre of the skin lesions. The eggs may become entangled in exudative material but most drop off the hosts into the surrounding environment. Hosts scratching at lesions also assist the release of eggs from lesions. Eggs landing in suitable substrates (fine-grained sandy soils that are warm and dry) hatch after 1-6 days releasing vermiform larvae. Larvae are usually found at depths of 2–5 cm as surface layers are too hot and deeper layers are too poor in oxygen for survival and growth. The larvae feed on organic debris in the environment and develop through 2 or 3 instars over 6-18 days. Mature larvae form thin-walled cocoons that become covered in particulate material. The enclosed stages undergo pupation to form adult fleas which emerge from the puparia after 5-15 days. Adult fleas may reside in the soil for several weeks to months while waiting for hosts. When they sense the presence of hosts (by vibration and odours), adults jump onto the skin to feed, sometimes making prodigious leaps of up to 35 cm. Both sexes require bloodmeals to become sexually mature (unfed free-living stages do not mate). Mature males search for receptive females feeding on hosts and mate before dropping off and dying. Unfertilized females also drop off hosts and die, whereas fertilized females burrow into the skin and continue feeding as they undergo considerable hypertrophy (by the process of neosomy) and produce eggs. Females may increase in size up to 80-100 times over 4-6 weeks and they may produce over 200-1,000 eggs when patent for the last 2-3 weeks before they die. Most *Tunga* spp. are univoltine and only breed once each year, with fleas being most abundant during the dry season (high soil humidity associated with rainy seasons impairs larval development and adult flea survival). Hosts that are most susceptible to infection are those that utilize habitual resting/sleeping places under trees, poor people that reside in huts/buildings with sandy earthen floors, and people who go barefoot or wear open sandals.

Differential diagnosis: Infestations are strongly indicated by the detection of characteristic skin lesions, even though they vary in appearance over time (initially small red spots but progressing to large pale papules with dark centres surrounded by halos of thin skin and then crusted nodules). Careful attention should be paid to patient history, symptoms and signs, as a range of other conditions may cause similar enigmatic lesions, including other arthropods (ticks, myiases, mange mites, fire ant bites), bacteria (abscesses, pustular dermatitis, acute paronychia, interdigital and pododermatitis, foot rot, mastitis), viruses (warts, vesicular diseases in swine and ruminants), fungi (mycotic granulomas), inflammatory conditions (foreign body granulomas, vasculitis), neoplasms (tumours, early melanoma) and developmental abnormalities (ingrown toenails, subungueal exostosis). Patent infestations are often diagnosed by the macroscopic or microscopic detection of shiny white flea eggs on or near skin lesions, sometimes associated with crusted blood and flea excreta (the spiracles, anus and vagina of resident fleas protrude from the central punctum). Careful examination may even reveal periodic pulsation of the central dark spot as the flea defaecates or lays eggs. The identification of *Tunga* spp. often relies on the examination of non-neosomic stages, as intact specimens of neosomic females are difficult to obtain (their hypertrophic status also obscures many morphological features). When hypertrophic forms are available, different species clusters may be recognized on the basis of their overall globular (e.g. *T. penetrans*) or multilobular structure (e.g. *T. trimamillata* with 3 lobes, *T. callida* with 4 lobes, *T. hexalobulata* with 6 lobes, and *T. monositus* with 8 lobes). Molecular biological techniques have been applied to the characterization of species and phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear (internal transcribed spacer regions I and II of ribosomal RNA) and mitochondrial (cytochrome oxidase II, large subunit (16S) ribosomal RNA) gene sequences.

Treatment and control: Most infestations are self-limiting and may resolve without treatment after 5 or more weeks. However, various treatment options may be sought depending on the number, size, location, age and severity of lesions. Various poultices have been used to some effect, most providing symptomatic relief, including mercury ointment, rocou tincture, turpentine, castor oil, palm oils, cassava and tobacco infusions. In the case of swollen painful lesions, recourse is usually made to the surgical removal of fleas. Folklore remedies practiced for centuries have involved flea extraction using heat-treated sharpened thorns or clean needles (auguring), but surrogate efforts using unsterilized safety pins, scissors, knives or wood splinters may aid the transmission of blood-borne infections (e.g. hepatitis, human papilloma virus, human immunodeficiency virus) as fleas cannot be removed without causing bleeding. Modern techniques involve local excision or sterile curettage by enlarging the wound around the posterior end of the flea and removing it using sterile tweezers, forceps or needles. It is important that fleas be removed in their entirety as any residual fragments may provoke inflammatory and hyperkeratotic reactions. Alternative but uncommon treatment options have included local cryotherapy and electro-desiccation of nodules. Every effort should be made to clean wounds to prevent secondary bacterial infections, using sterile saline or disinfectant washes, sterile dressings, anti-pruritic and anti-inflammatory ointments and topical or systemic antibiotics (notably to prevent pyoderma and tetanus). Attempts to suffocate fleas by occlusive coverings of oily compounds such as vaseline or petroleum jelly (as used against fly larvae causing myiases) are not recommended because they do not remove the flea or its remnants from the skin and do not give quick relief from painful lesions. There are no completely effective drug treatments for flea lesions, although several topical and a few systemic preparations do kill fleas, but their carcases remain within the lesions which complicates healing processes. Variable results have been reported in the treatment of infestations in humans and animals (particularly pigs and dogs) using volatile fixatives (formaldehyde, chloroform), some natural oils (coco oil, jojoba oil, *Aloe vera* extracts) and insecticidal chemicals, including organochlorides (lindane, dichloro-diphenyl-trichloroethane (DDT)), organophosphates (metrifonate, coumaphos, chlorfenvinphos, diazinon, dioxathion, fenchlorvos, malathion, phosmet, stirofos, trichlorfon), pyrethroids (permethrin, cyfluthrin, cypermethrin), arylpyrazoles (fipronil), macrocyclic lactones (ivermectin) and even some anthelmintics, including benzimidazoles (thiabendazole) and nitrothiazoles (niridazole). Many of the insecticidal chemicals had greater effect when used therapeutically to treat early infestations (before neosomic lesions were present) or when used prophylactically to prevent infections. It is advised that domestic animals (including pets) be regularly treated with anti-flea compounds, such as pyrethrin sprays or malathion powder. Flea control programmes must also include attempts to prevent

infestations or re-infestations by new fleas arising from free-living stages, as flea eggs, larvae and pupae can persist in sandy soils for extended periods. Some success has been reported when treating the immediate environment (especially soil in houses and animal pens) with insecticides that have long residual activities, including organophosphates (malathion), pyrethrum and synthetic pyrethroids (cypermethrin, deltamethrin), polycyclic aromatic hydrocarbon (naphthalene) and juvenile hormone mimetics (methoprene). The floors of animal pens and houses should be kept clean by regular sweeping or watering earthen floors, or by paving or cementing them. Domestic animals and humans should be housed separately, and domiciles should undertake vermin control using barriers, traps or baits. Humans living in endemic regions should adopt personal protection measures such as regularly washing hands and feet, wearing gloves when handling soil, wearing closed shoes and using insect repellent lotions, such as diethyltoluamide (DEET). Communities should also be made aware of tungiasis through public health education campaigns.


Tunga
adult female
(~ 1 mm)
skin/pelage
(pruritus, papules,
furuncular nodules,
secondary infections)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, esp. rodents,
insectivores)
engorged female
(~ 5 mm)
females live in excavated sinuses in skin
undergoing abdominal hypertrophy (neosomy)
males transient ectoparasites (both feed on blood)
eclosion
eggs
drop
off
host
pupa
(~ 1 mm)
eggs
(~ 0.6 mm)
encasement
hatch
larva
(~ 3 mm)
free-living in sandy soils
(feed on organic debris)



Tunga adult



Tunga eggs



Tunga lesions

Ceratophyllus
(insect: flea)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Siphonaptera (fleas) are bilaterally-flattened wingless insects whose hindlimbs are enlarged and specially adapted for jumping (using elastic resilin pads rather than muscles). Fleas are holometabolans and undergo complete metamorphosis whereby grub-like larvae form pupae from which adult fleas emerge. The larvae are not parasitic but feed on debris associated mainly with bedding, den or nest material, whereas the adult stages are parasitic and feed on host blood. Ceratophyllid fleas occur as ectoparasites on small rodents and birds, many being associated with nest habitats so adult fleas are transient parasites. Infestations by *Ceratophyllus* spp. have been associated with irritation, pruritus and allergic dermatitis in domestic birds and animals, including humans.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order: Siphonaptera (fleas, wingless, laterally compressed, third pair of legs adapted for jumping)
Family: Ceratophyllidae (parasites of small rodents and birds)
Genus: *Ceratophyllus* (parasitic on skin of rodents and birds)
Species: various species cause dermatitis

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Fleas are small wingless insects that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. The adults are ectoparasitic and use siphon-like mouthparts to feed on blood from warm-blooded vertebrates [the name 'Siphon-aptera' literally translates as 'siphon' and 'wingless']. All adult fleas are further characterized by having laterally compressed bodies (allowing movement through hair/feathers), backward-pointing hairs and bristles (resisting grooming by host), strong tarsal claws (for grasping), and enlarged hindlegs (adapted for jumping). Around 2,200 flea species have been described in 250 genera on the basis of morphological and biological differences, and recent molecular phylogenetic studies have indicated some 18 families may occur in 4 infra-orders.

Siphonapteran families	Biodiversity	Hosts	Characters	Biogeographical distribution
Infraorder: Pulicomorpha (compact body, small thorax, pronotum with entire undivided ventral margin)				
Pulicidae (common fleas)	22 genera 207 species	carnivores, lagomorphs, rodents, artiodactyls, birds	sensilium with at most 14 pits, coxa with spiniform setae	pan-Tropical, cosmopolitan
Tungidae (sand fleas)	5 genera 23 species	rodents, insectivores, bats, suids, humans, birds	compression of 3 thoracic segments, neosomy	Neotropical, Holarctic

Vermipsyllidae	3 genera 39 species	carnivores, pikas, ungulates	frontal tubercle, large spiracles, reduced tergites	Holarctic
Ancistropsyllidae	1 genus 3 species	artiodactyls	metanotum and abdominal tergites with spinelets	Oriental
Coptopsyllidae	1 genus 19 species	rodents	combless, 2 spermathecae, tergal spinelets absent	Southern Palaearctic
Malacopsyllidae	2 genera 2 species	insectivores	high mesonotum, metanotum without spinelets	Patagonian
Rhopalopsyllidae	14 genera 126 species	rodents, insectivores, birds	metanotum and abdominal tergites with spinelets	Neotropical, Australasian
Infraorder: Ceratophyllomorpha (elongate body, long thorax, head without intergenal process, interantennal dimorphism)				
Ceratophyllidae	47 genera 540 species	rodents, pikas, carnivores, insectivores, birds	genal combs absent, males with interantennal suture	cosmopolitan
Ischnopsyllidae (bat fleas)	20 genera 125 species	bats	genal comb with 2-4 flattened spines, interantennal furrow	cosmopolitan
Leptopsyllidae	29 genera 260 species	insectivores, lagomorphs, rodents, carnivores, birds	head with tentorial arch, males with interantennal suture	Holarctic, Australasia
Xiphlopsyllidae	1 genus 8 species	rodents, shrews	squamulum absent, simple interantennal wall	Eastern African
Infraorder: Hystrichopsyllomorpha (elongate body, long thorax, head with intergenal process, clasper without process)				
Chimaeropsyllidae	8 genera 26 species	rodents, shrews	sensilium with 14 pits, hind coxa with spiniform setae	African
Hystrichopsyllidae (nest fleas)	46 genera 582 species	rodents, insectivores, pikas, marsupials	highly variable structures, 2 spermathecae	cosmopolitan
Macropsyllidae	2 genera 2 species	rodents	single head comb, 4 abdominal combs, 2 spermathecae	Australian
Stephanocircidae (helmet fleas)	9 genera 51 species	rodents, marsupials, birds	helmet (frons) with 2 separate combs, single spermatheca	Neotropical, Australian
Infraorder: Pygiopsyllomorpha (elongate body, long thorax, head with intergenal process, metanotum without spinelets)				
Pygiopsyllidae	10 genera 48 species	rodents, marsupials, birds	unique articulation between digitoid and main part of clasper	Australasian, Neotropical
Lycopsyllidae	4 genera 8 species	marsupials	genal lobe, simple interantennal wall, single mesopleural rod	Australian
Stivaliidae	23 genera 110 species	rodents, marsupials	strongly developed basal arm of Y-sclerite	Palaearctic, Australasia

Fleas from several families are found as ectoparasites on domestic and companion animals around the world: particularly those belonging to the families Pulicidae and Tungidae on mammals, and the family Ceratophyllidae on birds. Ceratophyllid fleas are characterized by their elongate laterally-compressed bodies, the absence of genal combs but the presence of pronotal combs. Some 45 genera have been identified in 2 subfamilies: Ceratophyllinae (*Aenigmopsylla, Aetheca, Amalaraeus, Amaradix, Amphalius, Baculomeris, Brevictenidia, Callopsylla, Ceratophyllus, Citellophilus, Dasypsyllus, Eumolpianus, Glaciopsyllus, Hollandipsylla, Igioffius, Jellisonia, Kohlsia, Libyastus, Macrostylophora, Malaraeus, Margopsylla, Megabothris, Megathoracipsylla, Mioctenopsylla, Myoxopsylla, Nosopsyllus, Opisodasys, Orchopeas, Oropsylla, Paraceras, Paramonopsyllus, Pleochaetis, Plusaetis, Rostropsylla, Rowleyella, Smitipsylla, Spuropsylla, Syngenopsyllus, Tarsopsylla, Thrassis, Traubella, Psittopsylla*) and Dactylopsyllinae (*Dactylopsylla, Foxella, Spicata*). Species from several genera are considered to be serious pests of domestic poultry and companion animals, while the remainder infest a wide range of wild animals.

Genera	**No. spp.**	**Hosts**	**Ctenidia (combs)**		**Disease**	**Vector**
			Genal (head)	**Pronotal (thorax)**		
Ceratophyllidae						
Ceratophyllus	64	birds, rodents, carnivores, ungulates	absent	present	irritation, reduced productivity	
Nosopsyllus	52	rodents, carnivores, some birds	absent	present	irritation	plague, erysipeloid, rat tapeworm
Pulicidae						
Pulex	12	humans, carnivores, marsupials, rodents, birds	absent	absent	irritation, dermatitis, anaemia	plague, typhus, spotted fevers, tapeworms
Echidnophaga	23	birds, rodents,	absent	absent	inflammation,	rickettsioses, plague,

		carnivores, marsupials			ulceration	myxomatosis
Xenopsylla	76	rodents, carnivores, marsupials, birds	absent	absent	irritation	plague, typhus, rat tapeworms
Ctenocephalides	12	carnivores, rodents, rabbits, insectivores, ungulates, birds	horizontal	present	pruritus, anaemia, hypersensitivity (flea-bite allergy)	bartonelloses, typhus, plague, dog tapeworm, filarial nematode
Spilopsyllus	1	rabbits, rodents, carnivores, birds	vertical	present	irritation	myxomatosis, tularemia
Tungidae						
Tunga	13	humans, insectivores, rodents, carnivores	absent	absent	inflammation, ulceration	*Staphylococcus, Wolbachia*, tetanus

The genus *Ceratophyllus* contains some 64 species allocated to 6 subgenera: namely, *C.* (*Ceratophyllus*) with 37 spp., *C.* (*Celeophilus*) with 2 spp., *C.* (*Emmareus*) with 11 spp., *C.* (*Amonopsyllus*) with one sp., *C.* (*Monopsyllus*) with 10 spp., and *C.* (*Rosickyiana*) with a single species. The former 3 subgenera are found mainly on birds, and the latter 3 subgenera mainly on squirrels. The fleas are found mostly in temperate Holarctic regions, with some 38 spp. confined to the Palaearctic (Eurasia), 14 spp. to the Nearctic (North America), 4 spp. to the Neotropics (Central and South America), and the remainder occurring several other subregions. The species *C. gallinae* (hen flea or European chicken flea) is regarded to be a pest species in domestic poultry but is not considered to be an important vector of disease. Adult fleas, however, are highly agile and exhibit broad host specificity being able to infest a wide range of birds (particularly nesting birds) and some small mammals.

***Ceratophyllus* species**	**Hosts**	**Clinical signs**	**Distribution**
C. adustus	Charadriiformes: larid (herring gull); Passeriformes: artamid (white-browed wood swallow); Piciformes: picid (woodpecker); Rodentia: erethizontid (North American porcupine)		North America
C. affinis	Passeriformes: hirundinid (barn swallow)		Holarctic
C. altus	Falconiformes: falconid (American kestrel); Strigiformes: strigid (Andean pygmy owl)		Americas
C. (*M.*) *anisus*	Rodentia: murid (black rat, brown rat)		Eurasia
C. arcuegens	Passeriformes: hirundinid (cliff swallow)		North America
C. avicitelli	Passeriformes: muscicapid (isabelline wheatear, stonechat)		Eurasia
C. balati	Passeriformes: motacillid (rock pipit)		Europe
C. (*E.*) *borealis* (cliff/rock birds-nest flea)	Charadriiformes: alcid (Atlantic puffin), larid (European herring gull, Arctic tern); Passeriformes: alaudid (Eurasian skylark), cinclid (white-throated dipper), corvid (red-billed chough), motacillid (European rock pipit, grey wagtail, white-browed wagtail), muscicapid (northern wheatear, common redstart, African stonechat), passerid (snowfinch), prunellid (dunnock), sylviid (common whitethroat), troglodytid (Eurasian wren), turdid (thrush); Suliformes: sulid (northern gannet)		Holarctic
C. breviprojectus	Passeriformes: hirundinid (red-rumped swallow)		Tibet
C. calderwoodi	Charadriiformes: larid (herring gull); Passeriformes: artamid (white-browed wood swallow); Piciformes: picid (woodpecker)		Eurasia, Australia
C. caliotes	Passeriformes: hirundinid (common house martin, sand martin, cave swallow)		Holarctic
C. celsus	Passeriformes: hirundinid (sand martin, cliff swallow)		North and Central America
C. (*E.*) *chasteli*	Suliformes: phalacrocoracid (European shag)		Europe
C. chutsaensis	Passeriformes: muscicapid (isabelline wheatear); Lagomorpha: ochotonid (pika)		Asia
C. ciliatus	Rodentia: sciurid (chipmunk)		North America
C. coahuilensis	Passeriformes: hirundinid (cave swallow)		North America
C. (*E.*) *columbae* (pigeon flea, pigeon	Columbiformes: columbid (rock dove, blue rock pigeon, common wood pigeon); Carnivora: felid (cat); Primates: hominid (human)	irritation, anaemia,	Holarctic

nest flea)		allergic dermatitis	
C. delichoni	Passeriformes: hirundinid (common house martin)		Europe
C. diffinis	Podicipediformes: podicipedid (red-necked grebe)		North America
C. enefdeae	Passeriformes: tyrannid (Say's phoebe), muscicapid (wheatear), corvid (Eurasian magpie)		Holarctic
C. (*C.*) *farreni*	Columbiformes: columbid (common wood pigeon); Passeriformes: hirundinid (common house martin, barn swallow), passerid (house sparrow); Carnivora: felid (cat)		Palearctic, Asia
C. (E.) fionnus	Procellariiformes: procellariid (Manx shearwater)		Europe
C. frigoris	Passeriformes: motacillid (gray wagtail)		Russia
C. (*C.*) *fringillae* (house sparrow/starling flea)	Passeriformes: alaudid (Eurasian skylark), corvid (carrion crow), fringillid (common chaffinch), hirundinid (common house martin, sand martin, barn swallow), motacillid (European rock pipit, white-browed wagtail), muscicapid (spotted flycatcher), parid (Eurasian blue tit, great tit), passerid (house sparrow), prunellid (dunnock), sturnid (common starling), sylviid (common whitethroat); Strigiformes: strigid (tawny owl); Apodiformes: apodid (common swift); Carnivora: felid (cat); Primates: hominid (human)		Eurasia
C. (*C.*) *gallinae* (hen flea, European chicken flea)	Galliformes: phasianid (chicken, grey partridge, ring-necked pheasant, willow ptarmigan); Accipitriformes: accipitrid (Eurasian sparrowhawk, red kite); Anseriformes: anatid (kelp goose); Charadriiformes: larid (black-legged kittiwake), stercorariid (parasitic jaeger); Falconiformes: falconid (merlin); Gruiformes: rallid (corn crake, common moorhen); Passeriformes: acrocephalid (sedge warbler), aegothelid (long-tailed tit), alaudid (Eurasian skylark), apodid (common swift), calcariid (snow bunting), certhiid (Eurasian treecreeper), cinclid (white-throated dipper), corvid (common raven, carrion crow, rook, western jackdaw, Eurasian jay, red-billed chough), emberizid (yellowhammer, common reed bunting), fringillid (common linnet, European goldfinch, European greenfinch, common chaffinch, twite, Eurasian siskin, red crossbill), hirundinid (common house martin, sand martin, barn swallow), motacillid (European rock pipit, meadow pipit, tree pipit, white wagtail, grey wagtail, white-browed wagtail), muscicapid (European robin, common nightingale, northern wheatear, bluethroat, pied flycatcher, spotted flycatcher, black redstart, common redstart, African stonechat), parid (coal tit, Eurasian blue tit, great tit, marsh tit), passerid (house sparrow, Eurasian tree sparrow), phylloscopid (wood warbler, willow warbler), prunellid (dunnock), regulid (goldcrest), sittid (Eurasian nuthatch), sturnid (common starling), sylviid (Eurasian blackcap, garden warbler, common whitethroat, lesser whitethroat, barred warbler), troglodytid (Eurasian wren), turdid (redwing, common blackbird, song thrush, mistle thrush); Columbiformes: columbid (rock dove, stock dove, Eurasian collared dove, common wood pigeon); Piciformes: picid (great spotted woodpecker, Eurasian wryneck); Procellariiformes: procellariid (northern fulmar); Strigiformes: strigid (little owl, tawny owl); Suliformes: phalacrocoracid (European shag); Rodentia: cricetid (common vole, short-tailed field vole), echimyid (coypu), murid (brown rat, wood mouse), sciurid (eastern grey squirrel); Lagomorpha: leporid (European rabbit); Artiodactyla: bovid (cattle), cervid (Indian muntjac); Carnivora: canid (dog, red fox), felid (cat), mustelid (European pine marten, stoat, ferret, least weasel); Chiroptera: vespertilionid (common noctule); Primates: hominid (human)		Eurasia
C. (*E.*) *garei* (ground-nesting bird flea)	Anseriformes: anatid (northern shoveler, Eurasian teal, mallard, tufted duck, northern pintail, common scoter, common eider, red-breasted merganser); Charadriiformes: alcid (Atlantic puffin), charadriid (common ringed plover, northern lapwing), larid (European herring gull, common gull, lesser black-backed gull, great black-backed gull, black-headed gull, Arctic tern), scolopacid		Holarctic

	(dunlin, common snipe, Eurasian woodcock, common redshank); Columbiformes: columbid (rock dove); Galliformes: phasianid (red-legged partridge, willow ptarmigan, grey partridge, ring-necked pheasant); Gruiformes: rallid (common moorhen); Passeriformes: corvid (Eurasian skylark, hooded crow, carrion crow, western jackdaw, red-billed chough), emberizid (yellowhammer, common reed bunting, corn bunting), fringillid (common linnet, European greenfinch, common chaffinch), hirundinid (barn swallow), motacillid (European rock pipit, meadow pipit, white wagtail, grey wagtail, white-browed wagtail), muscicapid (European robin, northern wheatear, whinchat, African stonechat), panicrid (bearded reedling), passerid (house sparrow), prunellid (dunnock), regulid (goldcrest), sturnid (common starling), troglodytid (Eurasian wren), turdid (common blackbird, ring ouzel); Piciformes: picid (Eurasian wryneck, green woodpecker); Strigiformes: strigid (long-eared owl); Suliformes: phalacrocoracid (European shag); Rodentia: cricetid (bank vole), murid (wood mouse, Eurasian harvest mouse); Lagomorpha: leporid (European rabbit, European hare); Carnivora: mustelid (stoat)		
C. gilvus	Passeriformes: hirundinid (cliff swallow)		North America
C. glaphyrus	Passeriformes: parid (coal tit)		
C. hagoromo	Procellariiformes: procellariid (streaked shearwater); Charadriiformes: alcid (tufted puffin)		Japan
C. (*C.*) *hirundinis* (house martin flea	Passeriformes: hirundinid (common house martin, sand martin, barn swallow); Columbiformes: columbid (rock dove); Galliformes: phasianid (chicken)		Europe
C. idius	Passeriformes: hirundinid (barn swallow, tree swallow, purple martin)		North America
C. igii	Anseriformes: anatid (shelduck)		Russia
C. lari	Charadriiformes: larid (herring gull); Passeriformes: artamid (white-browed woodswallow); Piciformes: picid (woodpecker)		North America
C. (*Rosickyiana*) *lunatus*	Carnivora: mustelid (ermine, marten)		Holarctic
C. maculatus	Passeriformes: hirundinid (common house martin)		Russia
C. nanshanensis	Passeriformes: hirundinid (red-rumped swallow, Eurasian crag martin)		China
C. niger (western chicken flea, black hen flea)	Galliformes: phasianid (chicken); Strigiformes: strigid (northern saw-whet owl, long-eared owl); Piciformes: picid (green woodpecker, wryneck)		North America
C. olsufjevi	Passeriformes: hirundinid (common house martin)		Russia
C. orites	Passeriformes: hirundinid (common house martin); Rodentia: murid (Mongolian gerbil)		Asia
C. pelecani	Charadriiformes: larid (western gull); Pelecaniformes: pelecanid (pelican)		North America
C. petrochelidoni	Charadriiformes: larid (herring gull); Passeriformes: artamid (white-browed woodswallow), hirundinid (American cliff swallow); Piciformes: picid (woodpecker)		North America
C. phrillinae	Rodentia: murid (Himalayan field mouse)		Nepal
C. pullatus	Passeriformes: passerid (house sparrow, tree sparrow)		Europe
C. qinghaiensis	birds nest		China
C. rauschi	Charadriiformes: larid (herring gull); Passeriformes: artamid (white-browed woodswallow); Piciformes: picid (woodpecker, northern flicker)		North America
C. (C.) rossittensis	Passeriformes: corvid (carrion crow); Strigiformes: strigid (owl)		Holarctic
C. (*C.*) *rusticus* (house martin flea)	Passeriformes: hirundinid (common house martin, barn swallow); Columbiformes: columbid (common wood pigeon)		Europe
C. (*M.*) *sciurorum*	Rodentia: sciurid (eastern grey squirrel), cricetid (European water vole, bank vole), glirid (hazel dormouse, European edible dormouse), murid (wood mouse); Lagomorpha: leporid (European rabbit); Eulipotyphla: soricid (common shrew); Carnivora: canid (red fox), mustelid (pine marten, stoat, least weasel); Primates: hominid		Eurasia

	(human); Columbiformes: columbid (stock dove, common wood pigeon); Passeriformes: corvid (western jackdaw, Eurasian magpie), motacillid (white-browed wagtail), turdid (mistle thrush); Strigiformes: strigid (tawny owl)		
C. sclerapicalis	Passeriformes: hirundinid (common house martin, red-rumped swallow)		China
C. scopulorum	Passeriformes: hirundinid (cliff swallow)		North America
C. sinicus	Lagomorpha: ochotonid (pika)		China
C. spinosus	Falconiformes: falconid (lesser kestrel)		Eurasia
C. sternacuminatus	Passeriformes: hirundinid (tree swallow)		North America
C. (*C.*) *styx* (sand martin flea)	Passeriformes: hirundinid (sand martin, common house martin), cinchlid (white-breasted dipper), corvid (western jackdaw), parid (Eurasian blue tit), sturnid (common starling); Rodentia: cricetid (bank vole)		Holarctic
C. titicacensis	Suliformes: phalacrocoracid (Neotropic cormorant)		South America
C. tribulis (syn. *C. passerinus*)	Passeriformes: passerid (Eurasian tree sparrow)		Russia
C. (*C.*) *vagabundus* (corvid/heron nest flea)	Passeriformes: corvid (common raven, carrion crow, western jackdaw, Eurasian magpie, red-billed chough), motacillid (Eurasian rock pipit), muscicapid (spotted flycatcher, northern wheatear); Charadriiformes: alcid (Atlantic puffin, crested auklet, parakeet auklet), larid (European herring gull, black-legged kittiwake), scolopacid (ruddy turnstone); Columbiformes: columbid (rock dove); Falconiformes: falconid (peregrine falcon); Accipitriformes: accipitrid (European honey buzzard); Galliformes: phasianid (chicken); Pelecaniformes: ardeid (grey heron); Procellariiformes: procellariid (northern fulmar, manx shearwater); Strigiformes: strigid (tawny owl); Suliformes: phalacrocoracid (European shag, great cormorant, neotropical cormorant)		Holarctic
C. vison	Rodentia: sciurid (red squirrel)		Eurasia
C. wui	Apodiformes: apodid (Himalayan swiftlet)		Asia
C. yamane	Rodentia: glirid (Japanese dormouse)		Japan
C. zhovtyi	Strigiformes: strigid (Eurasian pygmy owl)		Russia

Parasite morphology: *Ceratophyllus* spp. form 4 different morphological types of developmental stages: eggs; larvae (3 instars); pupae (in cocoons); and adults (male and female fleas). The eggs are pearly white ovoid stages measuring 0.5-0.6 mm in length. Larvae are elongate grey-white vermiform (worm-like) stages with segmented bodies (13 segments) and brown sclerotized heads with powerful mandibles and mandibular teeth adapted for biting and chewing. The larvae are essentially cylindrical although the middle segments are somewhat flattened dorsoventrally and the caudal segment bears a pair of anal struts. Each segment is adorned with small backward-facing bristles that increase in length posteriad. Larvae develop though 3 instars growing in length from 1.6-4.0 mm. Mature larvae form silken cocoons that are roughly ovoid measuring 2-3 mm. The cocoons are sticky and become covered with small particulate matter from the environment. The enclosed pupae are considered to be exarate as their appendages appear free from the body wall (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). Adult fleas have shiny brown laterally-flatted bodies 2 to 4 mm in length that are covered with hard chitinized plates (sclerites). They have unique patterns of setation (chaetotaxy) with most setae, spines and bristles facing backwards so they do not hinder forward movement through the plumage or pelage, but will catch on feathers or hairs if dragged backwards by host grooming. In particular, *Ceratophyllus* spp. have a distinctive comb-like row of 12-14 horizontal spines on each side of the first thoracic segment (known as the pronotal comb or ctenidium). They lack genal (cheek) ctenidia like some other fleas (e.g. *Ctenocephalides* and *Spilopsyllus*). Adults have 3 conspicuous body parts (tagma): a small anterior head, a short thorax, and an elongate abdomen. The head is integricipit (without an interantennal suture) and has a smoothly-rounded frons (forehead) with a small downward-facing frontal tubercle. There are a pair of compact club-like lateral antennae (3-segmented) held flattened against the head but not within grooves (no antennal fossae). Large noncompound eyes (clusters of ocelli) are located below the antennae, and there are 3 strong setae located below each eye. Adult fleas have conspicuous ventral piercing-sucking mouthparts (lacking mandibles and teeth) located between 2 sets of sensory palps (a pair of 4-segmented palps arising from short maxillary lobes, and a pair of 5-segmented palps arising from a short basal labium). The functional mouthparts (fascicle) consist of 3 long slender stylets: the 2 outer stylets (maxillary laciniae) being blade-like and serrated; and the third central stylet (labrum-epipharynx) being an outgrowth of the body wall (unique to fleas). These 3 stylets join to form a tube-like canal to inject saliva (via salivary pumps) and suck blood (via cibarial and pharyngeal pumps). The alimentary tract consists of a tubular foregut (anterior pharynx, elongate oesophagus, small globular proventriculus armed with spines), a large expandable midgut (simple undivided digestive organ, unlike the more elaborate divided

midguts (with diverticula and caeca) of most other haematophagous arthropods), a tubular hindgut (with excretory Malpighian tubules) and rectum. The thorax has 3 distinct rectangular dorsal sclerites: an anterior pronotum (with pronotal comb), a middle mesonotum, and a posterior metanotum (with marginal spinelets). The thoracic mesopleuron (ventral sclerite) has a vertical thickening of the wall (known as a pleural ridge or meral rod). The ventral thorax gives rise to 3 pairs of strong legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) and all ending in a pair of strong claws. The legs are setate and characteristically have 4-6 bristles on inner surface of the hind-femur bit no spines on basal sections. The hindmost legs are considerably enlarged and well-adapted for jumping (using unique elastic resilin pads to store energy under compression, rather than muscular contraction). The abdomen is elongated and consists of 10 segments, although the last 3 segments are highly modified by sensory and genital structures. The dorsal sclerites (tergites) have more than one row of setae as well as lateral respiratory spiracles. Both males and females have a flat dorsal plate-like organ (sensilium or pygidium) with antesensillial setae. Male fleas are smaller than females, and have highly elaborate genitals (possibly the most complex in the animal kingdom). Males have 2 testes joined by tubular vas deferens to a seminal vesicle and an ejaculatory duct connected to an aedeagal apodeme (penis plate) with extendable penis rods held coiled and retracted within an endophallic sac. The penis is thin and delicate and must be supported during copulation by the penis rods and posterior claspers. Female fleas have 2 ovaries connected by tubular oviducts to a globular uterus opening to the vagina located within a bursa copulatrix (depression to receive male organ) with associated subglobular spermatheca (organ for sperm storage after mating).

Site of infection: Adult fleas are obligate blood-sucking ectoparasites of vertebrate hosts, while all pre-adult developmental stages are free-living in the external environment. *Ceratophyllus* spp. exhibit variable host specificity, with around half infesting mammals (belonging to 16 mammalian families, including carnivores, bats, shrews, rabbits, rodents, and humans), and half infesting birds (belonging to 25 passerine and 20 non-passerine families, including poultry, waterfowl, seabirds, shorebirds, several forest-dwellers and a few birds of prey). Only 9 species are found on both mammals and birds, particularly those infesting poultry and aviary birds that opportunistically feed on pets and humans in the immediate vicinity. Adult fleas often feed on hosts in sites that are difficult to groom: such as the head, neck, back and limbs of mammals; and the head (including the comb and wattles when present), breast, belly and around the vent of birds.

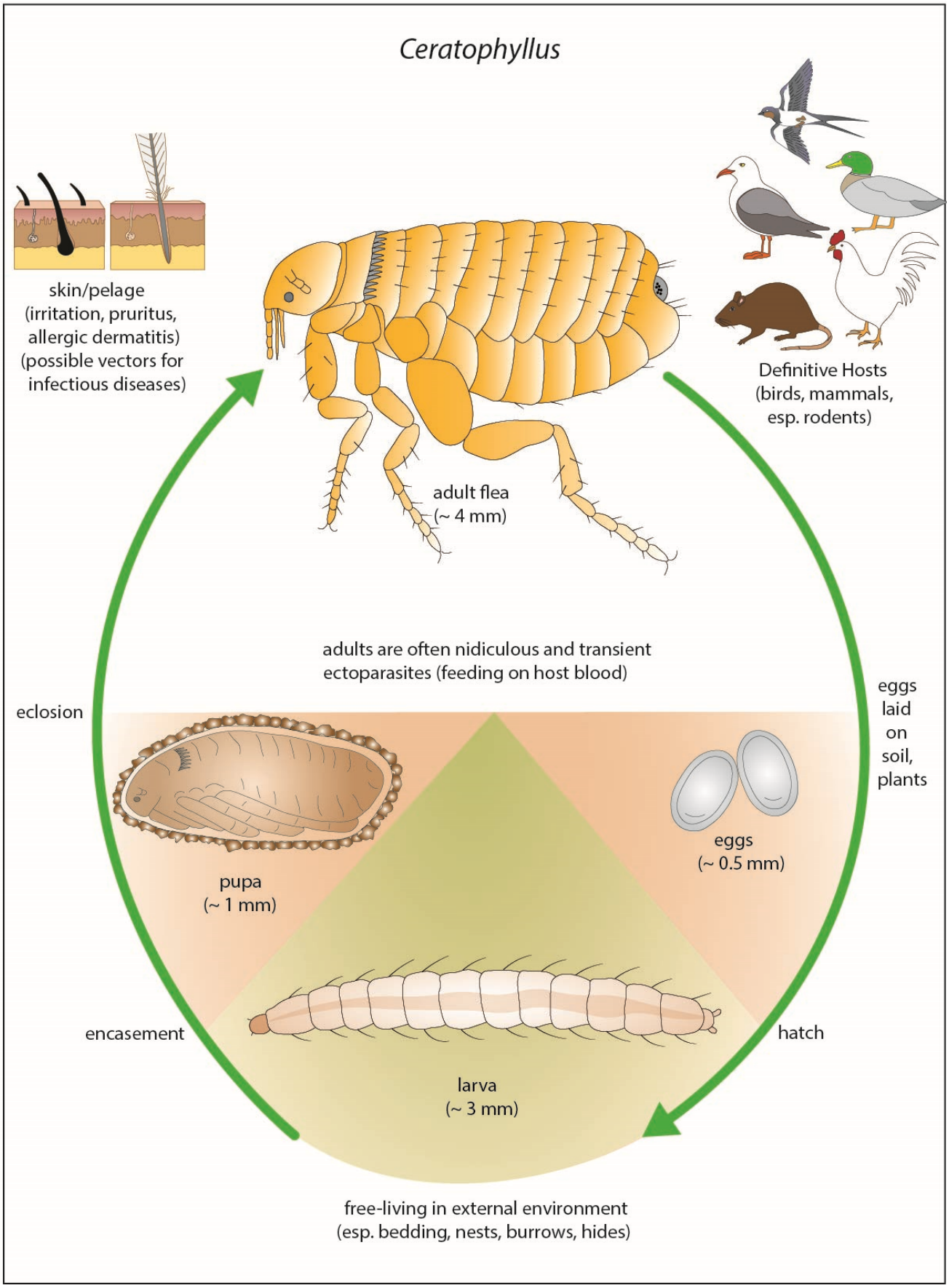
Pathogenesis: Adult fleas jump onto hosts to feed on blood by inserting their mouthparts into the skin and sucking blood from the dermal vasculature. The fleas are highly mobile on hosts and feed repeatedly until replete before dropping off to rest in the environment. Flea bites cause traumatic skin damage with variable inflammation depending on the sensitivity of the host animal (some animals become hypersensitive to flea saliva). Bite sites are often visible as small lesions on the skin surrounded by red inflamed tissues that are pruritic. Hosts often peck/bite, scratch or rub affected areas exacerbating wounds sometimes resulting in crusted papules with alopecia or feather damage. Animals may become agitated or restless and appear dishevelled. Open wounds are also prone to secondary bacterial infections. Sensitized animals may develop allergic dermatitis with severe itching and rashes. Humans that have been subjected to repeated attacks sometimes develop allergic urticarial reactions. While the volume of blood ingested by individual fleas may be small, repetitive feeding and heavy infestations may lead to anaemia with consequential iron deficiency, sometimes proving fatal especially in young fowl. Chronic infestations in domestic animals have been associated with production losses, manifest as decreased egg production, reduced weight gains (sometimes weight loss) and poor growth contributing to host emaciation and weakness. Experimental studies on nestling birds have shown infestations reduce host fitness as evidenced by reduced body mass and poorer bone development. The impact of the fleas on the growth performance of host nestlings was more noticeable in years with lower temperatures and higher precipitation. *Ceratophyllus* spp. are not considered to be important vectors for the transmission of infectious diseases, although recent molecular screening studies have shown they may carry various bacterial pathogens, including the Mountain Altai strain of plague, *Rickettsia africae* and several *Bartonella* spp.

Developmental cycle and mode of transmission: *Ceratophyllus* spp. exhibit holometabolous development in that grub-like larvae undergo complete metamorphosis in pupae to form adult fleas which are ectoparasitic on vertebrate hosts. Adult fleas of most species do not attach permanently to hosts but detach after feeding and rest in the environment to digest their bloodmeals (although a few species apparently reside longer on hosts). The adults and larvae of several species may be found in bird droppings, but most species are nidicolous and strongly associated with nests, dens or other resting sites; ranging from cavity nests in bushes and trees (passerines), nest holes and cliff crevices (seabirds), wet ground nests (water birds), and subterranean burrows (rodents). Fleas are known to infest other animals that come into contact with, or take over, nests and burrows, particularly pet animals. Humans may become infested when handling poultry or injured birds, and fleas may also invade houses from nests under the eaves. Gravid female fleas lay eggs singly or in small batches on firm substrates in the environment, particularly woody or leafy vegetation forming nests or particulate material forming burrows. The eggs hatch in 6-10 days releasing first-stage larvae which use their cutting/chewing mandibles to feed on organic debris, particularly flea dirt (pellets of dried blood excreted by adult fleas). The larvae develop through 3 instars over several weeks (15-37 days). Mature larvae form sticky cocoons which become covered in detritus from the environment. The encased larvae transform into pupae and then adult fleas over 10-23 days, but the adults generally do not eclose (emerge) until conditions are favourable. Fleas often overwinter in their cocoons and only emerge when temperatures rise is spring and when they sense that hosts may be present (combination of tactile stimuli such as vibration, body heat, and increased carbon dioxide concentrations). Emergent fleas are negatively geotactic and disperse upwards in vegetation taking up ready-postures oriented towards light. They jump onto hosts when triggered by reductions in light intensity (e.g. caused by shadows of passing

hosts). Adults are transient blood-feeders and attach to hosts only for short periods to feed while spending most of their time in nests or burrows. They may fast for long periods of time (months) and resume feeding when nests are re-occupied. They apparently do not require bloodmeals in order to copulate, but females only produce eggs after feeding. In wild bird populations in temperate regions, flea reproduction is often synchronized with the breeding season of the host. In warmer regions, some flea species may complete 2-3 generations each year, while infestations in domestic birds may occur year-round.

Differential diagnosis: Light infestations may remain asymptomatic or subclinical, while heavier infestations may be suspected on clinical grounds (irritated hosts with focal lesions, dermatitis and anaemia). Diagnosis is usually afforded by the direct detection of fleas on hosts upon macroscopic examination, even though their presence may be irregular and transient. Specimens are best collected for microscopic examination and identification by their unique morphological characteristics (particularly head shape, presence of pronotal comb and absence of genal comb, and chaetotaxy (patterns of setation)). Various molecular biological techniques have recently been used to characterize species and infer phylogenetic relationships, including polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA and internal transcribed spacer regions) and mitochondrial (cytochrome oxidase) gene sequences, analyses of nucleotide microsatellite loci, and determining the complete mitochondrial genome.

Treatment and control: It is important to isolate infested animals both to facilitate treatment and also prevent the spread of infestations. Individual fleas can be carefully removed from host pelage or plumage using fine-toothed combs, tweezers or forceps, but most fleas quickly detach and even leave their hosts when disturbed. A range of cleaning products have been used to moderate infestations and alleviate clinical signs in individual birds or mammals, including shampoos, sprays, balms and ointments with either flea repellent activity or soothing anti-inflammatory and anti-pruritic activity. Topical antibiotics may be applied to bite lesions to minimize the risk of secondary bacterial infections. Heavy or widespread infestations in domestic animals are usually treated with insecticidal chemicals, including boric acid powder, organophosphates (coumaphos, diazinon, malathion), pyrethroids (permethrin, cypermethrin), carbamates (carbaryl), chloronictinyles (imidacloprid), arylpyrazoles (fipronil), macrocyclic lactones (selamectin) and some natural products (rotenone, and even apple cider vinegar). However, careful attention should be paid to any contra-indications, as some flea products for pets may be highly toxic to birds (such permethrin, carbaryl or boric acid powder). Most of these flea species are nidicolous so every effort should be made to decontaminate the immediate environment to prevent rapid re-infestation. This can be done by improved sanitation (removing manure/litter), increased hygiene (regular change of nesting/bedding materials), applying environmental insecticides with long-lasting residual activity (sprays or powders with sulphur, carbaryl, coumaphos, malathion, permethrin, spinosad or insect growth regulators such as methoprene), or providing flea desiccants (such as diatomaceous earth which act to dehydrate fleas). Domestic animals may also be protected by regular health inspections, preventing roaming behaviours, excluding wild animals from holding facilities (improving barriers, and vermin control) and using quarantine procedures (for new or translocated animals).


Ceratophyllus
skin/pelage
(irritation, pruritus,
allergic dermatitis)
(possible vectors for
infectious diseases)
Definitive Hosts
(birds, mammals,
esp. rodents)
adult flea
(~ 4 mm)
adults are often nidiculous and transient
ectoparasites (feeding on host blood)
eclosion
eggs
laid
on
soil,
plants
pupa
(~ 1 mm)
eggs
(~ 0.5 mm)
encasement
hatch
larva
(~ 3 mm)
free-living in external environment
(esp. bedding, nests, burrows, hides)



Ceratophyllus adult

Nosopsyllus
(insect: flea)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Siphonaptera (fleas) are bilaterally-flattened wingless insects whose hindlimbs are enlarged and specially adapted for jumping (using elastic resilin pads rather than muscles). Fleas are holometabolans and undergo complete metamorphosis whereby grub-like larvae form pupae from which adult fleas emerge. The larvae are not parasitic but feed on debris associated mainly with bedding, den or nest material, whereas the adult stages are parasitic and feed on host blood. Ceratophyllid fleas occur as ectoparasites on small rodents and birds, many being associated with nest habitats so adult fleas are transient parasites. Infestations by *Nosopsyllus* spp. have been associated with irritation, pruritus and allergic dermatitis in small mammals (esp. rodents) and birds.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order: Siphonaptera (fleas, wingless, laterally compressed, third pair of legs adapted for jumping)
Family: Ceratophyllidae (parasites of small rodents and birds)
Genus: *Nosopsyllus* (parasitic on skin of rats)
Species: various species cause allergic dermatitis

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Fleas are small wingless insects that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. The adults are ectoparasitic and use siphon-like mouthparts to feed on blood from warm-blooded vertebrates [the name 'Siphon-aptera' literally translates as 'siphon' and 'wingless']. All adult fleas are further characterized by having laterally compressed bodies (allowing movement through hair/feathers), backward-pointing hairs and bristles (resisting grooming by host), strong tarsal claws (for grasping), and enlarged hindlegs (adapted for jumping). Around 2,200 flea species have been described in 250 genera on the basis of morphological and biological differences, and recent molecular phylogenetic studies have indicated some 18 families may occur in 4 infra-orders.

Siphonapteran families	Biodiversity	Hosts	Characters	Biogeographical distribution
Infraorder: Pulicomorpha (compact body, small thorax, pronotum with entire undivided ventral margin)				
Pulicidae (common fleas)	22 genera 207 species	carnivores, lagomorphs, rodents, artiodactyls, birds	sensilium with at most 14 pits, coxa with spiniform setae	pan-Tropical, cosmopolitan
Tungidae (sand fleas)	5 genera 23 species	rodents, insectivores, bats, suids, humans, birds	compression of 3 thoracic segments, neosomy	Neotropical, Holarctic

Vermipsyllidae	3 genera 39 species	carnivores, pikas, ungulates	frontal tubercle, large spiracles, reduced tergites	Holarctic
Ancistropsyllidae	1 genus 3 species	artiodactyls	metanotum and abdominal tergites with spinelets	Oriental
Coptopsyllidae	1 genus 19 species	rodents	combless, 2 spermathecae, tergal spinelets absent	Southern Palaearctic
Malacopsyllidae	2 genera 2 species	insectivores	high mesonotum, metanotum without spinelets	Patagonian
Rhopalopsyllidae	14 genera 126 species	rodents, insectivores, birds	metanotum and abdominal tergites with spinelets	Neotropical, Australasian
Infraorder: Ceratophyllomorpha (elongate body, long thorax, head without intergenal process, interantennal dimorphism)				
Ceratophyllidae	47 genera 540 species	rodents, pikas, carnivores, insectivores, birds	genal combs absent, males with interantennal suture	cosmopolitan
Ischnopsyllidae (bat fleas)	20 genera 125 species	bats	genal comb with 2-4 flattened spines, interantennal furrow	cosmopolitan
Leptopsyllidae	29 genera 260 species	insectivores, lagomorphs, rodents, carnivores, birds	head with tentorial arch, males with interantennal suture	Holarctic, Australasia
Xiphlopsyllidae	1 genus 8 species	rodents, shrews	squamulum absent, simple interantennal wall	Eastern African
Infraorder: Hystrichopsyllomorpha (elongate body, long thorax, head with intergenal process, clasper without process)				
Chimaeropsyllidae	8 genera 26 species	rodents, shrews	sensilium with 14 pits, hind coxa with spiniform setae	African
Hystrichopsyllidae (nest fleas)	46 genera 582 species	rodents, insectivores, pikas, marsupials	highly variable structures, 2 spermathecae	cosmopolitan
Macropsyllidae	2 genera 2 species	rodents	single head comb, 4 abdominal combs, 2 spermathecae	Australian
Stephanocircidae (helmet fleas)	9 genera 51 species	rodents, marsupials, birds	helmet (frons) with 2 separate combs, single spermatheca	Neotropical, Australian
Infraorder: Pygiopsyllomorpha (elongate body, long thorax, head with intergenal process, metanotum without spinelets)				
Pygiopsyllidae	10 genera 48 species	rodents, marsupials, birds	unique articulation between digitoid and main part of clasper	Australasian, Neotropical
Lycopsyllidae	4 genera 8 species	marsupials	genal lobe, simple interantennal wall, single mesopleural rod	Australian
Stivaliidae	23 genera 110 species	rodents, marsupials	strongly developed basal arm of Y-sclerite	Palaearctic, Australasia

Fleas from several families are found as ectoparasites on domestic and companion animals around the world: particularly those belonging to the families Pulicidae and Tungidae on mammals, and the family Ceratophyllidae on birds. Ceratophyllid fleas are characterized by their elongate laterally-compressed bodies, the absence of genal combs but the presence of pronotal combs. Some 45 genera have been identified in 2 subfamilies: Ceratophyllinae (*Aenigmopsylla, Aetheca, Amalaraeus, Amaradix, Amphalius, Baculomeris, Brevictenidia, Callopsylla, Ceratophyllus, Citellophilus, Dasypsyllus, Eumolpianus, Glaciopsyllus, Hollandipsylla, Igioffius, Jellisonia, Kohlsia, Libyastus, Macrostylophora, Malaraeus, Margopsylla, Megabothris, Megathoracipsylla, Mioctenopsylla, Myoxopsylla, Nosopsyllus, Opisodasys, Orchopeas, Oropsylla, Paraceras, Paramonopsyllus, Pleochaetis, Plusaetis, Rostropsylla, Rowleyella, Smitipsylla, Spuropsylla, Syngenopsyllus, Tarsopsylla, Thrassis, Traubella, Psittopsylla*) and Dactylopsyllinae (*Dactylopsylla, Foxella, Spicata*). Species from several genera are considered to be serious pests of domestic poultry and companion animals, while the remainder infest a wide range of wild animals.

Genera	**No. spp.**	**Hosts**	**Ctenidia (combs)**		**Disease**	**Vector**
			Genal (head)	**Pronotal (thorax)**		
Ceratophyllidae						
Nosopsyllus	52	rodents, carnivores, some birds	absent	present	irritation	plague, erysipeloid, rat tapeworm
Ceratophyllus	64	birds, rodents, carnivores, ungulates	absent	present	irritation, reduced productivity	
Pulicidae						
Pulex	12	humans, carnivores, marsupials, rodents, birds	absent	absent	irritation, dermatitis, anaemia	plague, typhus, spotted fevers, tapeworms
Echidnophaga	23	birds, rodents,	absent	absent	inflammation,	rickettsioses, plague,

		carnivores, marsupials			ulceration	myxomatosis
Xenopsylla	76	rodents, carnivores, marsupials, birds	absent	absent	irritation	plague, typhus, rat tapeworms
Ctenocephalides	12	carnivores, rodents, rabbits, insectivores, ungulates, birds	horizontal	present	pruritus, anaemia, hypersensitivity (flea-bite allergy)	bartonelloses, typhus, plague, dog tapeworm, filarial nematode
Spilopsyllus	1	rabbits, rodents, carnivores, birds	vertical	present	irritation	myxomatosis, tularemia
Tungidae						
Tunga	13	humans, insectivores, rodents, carnivores	absent	absent	inflammation, ulceration	*Staphylococcus, Wolbachia*, tetanus

The genus *Nosopsyllus* contains some 54 species allocated to 4 subgenera: namely, *N.* (*Nosophyllus*) with 32 spp., *N.* (*Gerbillophilus*) with 17 spp., *N.* (*Nosinius*) with one sp., and *N.* (*Penicus*) with one sp. (the remaining species are unplaced). These fleas were described from a range of rodents, mostly small terrestrial murine or cricetine species distributed throughout Palaearctic and Oriental regions, occasionally Africa. Several species are now cosmopolitan in their distribution due to their transport on synanthropic rodents and their dispersal through human activities. In particular, the northern rat flea, *N. fasciatus,* is found on domestic rats and house mice throughout North America and Europe, but has now become common in most temperate regions where it may infest wild rodents, and sometimes feed on humans.

***Nosopsyllus* species**	**Hosts**	**Clinical signs**	**Distribution**
N. (*G.*) *abramovi*	Rodentia: murid (Tamarisk jird, Libyan jird, gerbil)		Central Asia
N. aegaeus	Rodentia: murid (black rat, eastern broad-toothed field mouse)		Europe
N. afghanus	Rodentia: murid (midday jird, Libyan jird)		Asia
N. (*N.*) *alladinis*	Rodentia: sciurid (Indian palm squirrel)		India
N. (N.) antakyaicus	Rodentia: cricetid (Gunther's vole, Turkish hamster)		Asia
N. apicoprominus	Rodentia: murid (midday jird)		China
N. (*G.*) *aralis*	Rodentia: murid (Tamarisk jird, midday jird)		Russia
N. (*N.*) *arcotus*	Rodentia: sciurid (Indian palm squirrel)		India
N. (*N.*) *argutus*	Rodentia: murid (house mouse), sciurid (Indian palm squirrel)		India
N. (*N.*) *atlantis*	Rodentia: sciurid (Barbary ground squirrel)		North Africa
N. (*G.*) *baltazardi*	Rodentia: murid (great gerbil, Libyan jird)		Middle-East
N. (*N.*) *barbarus*	Rodentia: murid (house mouse, black rat, Barbary striped grass mouse); Eulipotyphla: soricid (Osorian shrew)		North Africa
N. (*G.*) *bunni*	Rodentia: murid (Sundevall's jird), dipodid (lesser Egyptian jerboa)		Middle-East
N. (*N.*) *ceylonensis*	Rodentia: sciurid (Indian palm squirrel)		India
N. chayuensis	host unknown		China
N. (*N.*) *consimilis*	Rodentia: cricetid (social vole, European water vole), murid (wood mouse)		Russia
N. (*N.*) *durii*	Rodentia: cricetid (social vole, Gunther's vole, Persian vole)		Middle-East
N. (*N.*) *elongatus*	Rodentia: murid (black rat)		China
N. (*G.*) *eremicus*	Rodentia: murid (Sundevall's jird)		Afghanistan
N. (*N.*) *farahae*	Rodentia: cricetid (social vole)		Middle-East
N. (*N.*) *fasciatus* (syn. *Ceratophyllus fasciatus*) (northen rat flea)	Rodentia: murid (black rat, brown rat, bush rat, Australian swamp rat, rakali, house mouse, yellow-necked mouse, wood mouse, Eurasian harvest mouse), cricetid (bank vole, short-tailed field vole, common vole, Cabrera's vole, golden hamster), sciurid (eastern grey squirrel, red-bellied tree squirrel); Eulipotyphla: erinaceid (European hedgehog), soricid (common shrew, lesser white-toothed shrew), talpid (European mole); Dasyuromorphia: dasyurid (eastern quoll); Lagomorpha: leporid (European rabbit, European hare); Artiodactyla: bovid (sheep); Carnivora: felid (cat), canid (dog, red fox), mustelid (stoat, ferret, least weasel, European polecat, American mink); Primates: hominid (human); Columbiformes: columbid (stock dove); Passeriformes: fringillid (common chaffinch), motacillid (meadow pipit), passerid (house sparrow), troglodytid (Eurasian wren)	pruritus, allergic dermatitis (+ vector for rat tapeworm, rat trypanosome)	worldwide in temperate zones
N. (*N.*) *fidus*	Rodentia: murid (house mouse, rat)		Central Asia
N. (*Penicus*) *geneatus*	Rodentia: murid (spiny mouse, golden spiny mouse)		Middle-East
N. (*G.*) *henleyi*	Rodentia: murid (Libyan jird, Tristram's jird, North African gerbil)		Middle-East

N. (*N.*) *incisus*	Rodentia: murid (common rufous-nosed rat, thicket rat, vlei rat, brush-furred mouse)		Africa
N. (*G.*) *iranus*	Rodentia: murid (Libyan jird, Tristram's jird, Vinogradov's jird, Sundevall's jird, Wagner's gerbil)		Middle-East
N. (*G.*) *laeviceps*	Rodentia: murid (Libyan jird, great gerbil), cricetid (northern mole-vole, Brandt's vole)		Asia
N. (*N.*) *londiniensis*	Rodentia: murid (black rat, brown rat, African grass rat, house mouse, wood mouse, silky mouse, New Holland mouse); Dasyuromorphia: dasyurid (fat-tailed dunnart); Diprotodontia: petauroid (honey possum); Carnivora: felid (cat), canid (dog)		Eurasia, Middle-East, Australia
N. (*G.*) *maurus*	Rodentia: murid (jird)		North Africa
N. (*N.*) *medus*	Rodentia: murid (black rat, brown rat, house mouse)		Middle-East
N. (*N.*) *mikulini*	Rodentia: murid (Libyan jird, Persian jird), cricetid (grey dwarf hamster)		Central Asia
N. (*N.*) *mokrzeckyi*	Rodentia: murid (house mouse, black rat), cricetid (grey dwarf hamster)		Russia
N. (*G.*) *monstrosus*	Rodentia: murid (jird, great gerbil)		Central Asia
N. (*N.*) *nicanus*	Rodentia: murid (black rat, brown rat, striped field mouse)		Asia
N. (*N.*) *nilgiriensis*	Rodentia: murid (black rat)		India
N. (*G.*) *oranus*	Rodentia: murid (Shaw's jird, gerbil)		North Africa
N. (*N.*) *philippovi*	Rodentia: cricetid (grey dwarf hamster, common vole); Lagomorpha: ochotonid (Afghan pika)		Central Asia
N. (*G.*) *pringlei*	Rodentia: murid (Wagner's gerbil, Sundevall's jird)		Middle-East
N. (*G.*) *pumilionis*	Rodentia: murid (Balochistan gerbil, Wagner's gerbil, Tristram's jird)		Middle-East
N. (*N.*) *punensis*	Rodentia: sciurid (Indian palm squirrel)		India
N. (*N.*) *punjabensis*	Rodentia: murid (house mouse, Turkestan rat, short-tailed bandicoot rat, Indian gerbil)		Palearctic
N. (*N.*) *sarinus*	Rodentia: murid (house mouse, Tristram's jird), cricetid (Gunther's vole, grey dwarf hamster)		Middle-East
N. (*N.*) *simla*	Rodentia: murid (house mouse, field mouse, Turkestan rat); Eulipotyphla: soricid (Asian house shrew)		Palearctic
N. (*Nosinius*) *sinaiensis*	Rodentia: murid (lesser Egyptian gerbil)		Egypt
N. (*N.*) *sincerus*	Rodentia: cricetid (Gunther's vole), spalacid (Middle-East blind mole-rat)		Middle-East
N. (*N.*) *tamilanus*	Rodentia: murid (black rat)		Sri Lanka
N. (*G.*) *tersus*	Rodentia: murid (great gerbil)		Russia
N. (*G.*) *turkmenicus*	Rodentia: murid (Persian jird, Libyan jird, midday jird, great gerbil)		Central Asia
N. (*N.*) *vauceli*	Rodentia: murid (soft-furred rat)		India
N. (*G.*) *vlasovi*	Rodentia: murid (jird, great gerbil)		Central Asia
N. (*N.*) *wualis*	Rodentia: murid (roof rat)		China
N. (*G.*) *ziarus*	Rodentia: murid (Persian jird, great gerbil)		Middle-East

Parasite morphology: These rodent fleas form 4 different types of stages during their developmental cycles; namely, eggs, larvae, pupae and adults. Eggs are ovoid stages measuring up to 0.5-0.6 mm long and have a white translucent appearance. Larvae are elongate vermiform (worm-like) stages which develop through 3 instars growing from 0.5-3.0 mm long. They are eruciform with cylindrical bodies with darker sclerotized heads containing powerful mandibles and mandibular teeth adapted for biting and chewing. They have 13 segments, each with prominent bristles projecting posteriorly. Mature larvae form silken ellipsoidal cocoons around 2 mm long which are sticky and become covered with particulate matter from the surrounding environment. The enclosed stages have lost the larval head and last 3 segments and the body has become compressed (shorter and wider). Although covered by debris, the pupae are exarate as their appendages are free from the body wall (in contrast to many other insects which form obtect pupae whose appendages are fused to the body wall). The emergent adults have elongated laterally-flattened bodies measuring 3-4 mm in length, although the females of a few species may grow up to 9 mm long. Adults fleas are usually shiny brown in appearance and have heavily chitinized plates (sclerites) adorned with numerous strong setae, spines and bristles facing backwards so they do not hinder forward movement of the flea through the pelage. In particular, *Nosopsyllus* spp. have distinctive horizontal pronotal ctenidia, i.e. comb-like rows of 9-10 spines on each side of the first thoracic segment (they lack genal ctenidia which are present on *Ctenocephalides* and *Spilopsyllus* spp.). The head has a rounded forehead (frons) with a small frontal tubercle conspicuous on both sexes. The frons is integricipit (without an interantennal suture) and contains a pair of short 3-segmented club-like antennae located in protective grooves (fossae). A pair of small simple noncompound eyes (clusters of ocelli) are located below the antennae but above rows of 3 stout setae. Adults have ventral piercing-sucking mouthparts (lacking mandibles and teeth) located between 2 pairs

of sensory palps (4-segmented maxillary palps and 5-segmented labial palps). The mouthparts (fascicle) consist of 3 long slender stylets: the 2 outer stylets (maxillary laciniae) appearing as serrated blades and the third central stylet (labrum-epipharynx) being an outgrowth of the body wall (unique to fleas). All 3 stylets join to form a tube-like canal to inject saliva (via salivary pumps) and suck blood (via cibarial and pharyngeal pumps). The alimentary tract consists of a tubular foregut (anterior pharynx, salivary glands inserted apically, elongate oesophagus, proventriculus armed with sclerotized teeth), a large expandable midgut (simple undivided digestive organ, unlike the more elaborate divided midguts (with diverticula and caeca) of most other haematophagous arthropods), a tubular hindgut (with excretory Malpighian tubules) and rectum. The thorax has 3 dorsal sclerites: a rectangular pronotum bearing the pronotal ctenidia, a short middle mesonotum, and a rectangular metanotum bearing marginal spinelets. The middle ventral thoracic sclerite has a vertical thickening known as a meral rod (also present in *Xenopsylla*, *Leptopsylla*, *Ceratophyllus* and *Ctenocephalides* spp.). The ventral thorax is the point of attachment for 3 pairs of strong legs, each consisting of 5 segments (coxa, trochanter, femur, tibia, and tarsus), the hind femur bearing 3-4 bristles on the inner surface and all tarsi terminating in a pair of claws. The hindlegs are enlarged and well-adapted for jumping (using unique elastic resilin pads to store energy under compression, rather than muscular contraction). The abdomen is elongate and has 8 visible segments (each with more than one row of dorsal setae and lateral respiratory spiracles) plus another 3 posterior segments modified by sensory and genital structures. Both sexes have a flat dorsal plate-like organ (sensilium or pygidium) from which antesensillial setae project. Males are generally smaller than females and are usually readily distinguished by the presence of long penis rods coiled within the abdomen. Male flea genitalia are highly elaborate (probably the most complex in the animal kingdom) and consist of an aedeagal apodeme (penis plate) with extendable penis rods coiled and retracted within an endophallic sac. The flea penis is thin and delicate and cannot enter the female without the support of the rods and posterior claspers. Males have 2 testes joined by tubular vas deferens to a seminal vesicle with an ejaculatory duct leading to the penis. Female fleas are often readily identified by the presence of a dark reniform spermatheca (for sperm storage after mating) located within the posterior abdomen. Females have 2 ovaries with tubular oviducts leading to a globular uterus opening to the vagina located in a bursa copulatrix (depression to receive male organ) with associated spermatheca.

Site of infection: Flea eggs, larvae and pupae are non-parasitic stages that live free in the environment, particularly nests, burrows and hides used by rodents. Adult fleas are external parasites on mammalian hosts, although they can spend much time off their hosts resting between bloodmeals. All *Nosopsyllus* spp. are parasitic on small terrestrial rodents (particularly murids, cricetids and sciurids) with records for several species also extending to eulipotyphlans (shrews, hedgehogs and moles), lagomorphs, several marsupials and some small carnivores (felids, canids and mustelids). The species *N. fasciatus* has also occasionally been detected on sheep, humans and several birds (mainly ground-foraging species). These rodent fleas are particularly numerous throughout Palearctic and Oriental regions and occasionally Africa, but several species have become common in most temperate regions due to numerous translocations. Fleas prefer to feed on the sacral and pelvic regions of rats and rarely move anteriad.

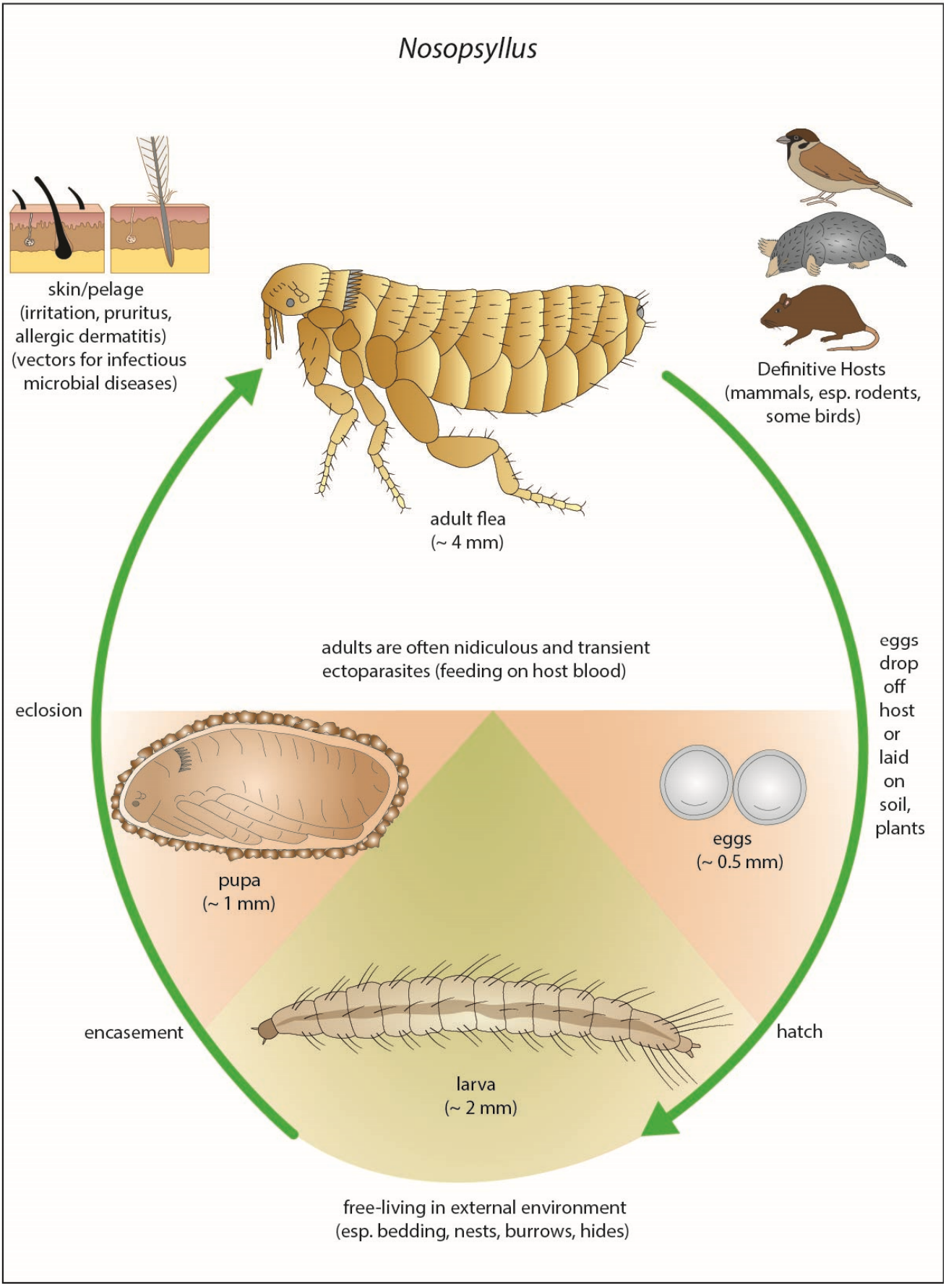
Pathogenesis: Adult fleas are haematophagous ectoparasites that use their mouthparts to pierce the skin and suck blood from small blood vessels (solenophagy). They jump onto hosts and feed for 2-3 hours even though they are able to take a full bloodmeal in as little as 10 minutes (they are often disturbed by host activity and must repeatedly find suitable blood vessels). Females take larger bloodmeals than males (up to 9-fold more). Flea bites cause significant irritation to their hosts with traumatic skin lesions, inflammation, pruritus, restlessness and even anaemia in heavy infestations. When feeding, fleas inject saliva containing vaso-active compounds and some hosts exhibit hypersensitivity reactions to the saliva with the development of allergic dermatitis. Laboratory studies on gerbils and voles have shown that *Nosopsyllus* infestations reduce host fitness as evidenced by reductions in body mass, impaired immune defences and the induction of iron deficiency. Epidemiological and experimental studies have also shown that several *Nosopsyllus* spp. may act as vectors for a variety of infectious micro-organisms: including those causing yersiniosis (plague), rickettsioses, bartonelloses, salmonellosis, and erysipeloid (Rosenbach's disease) in humans; tularemia, Q fever and myxomatosis in lagomorphs; and a nonpathogenic rat trypanosome (*T. lewisi*). Rat fleas have also been shown to act as intermediate hosts for the rat tapeworm *Hymenolepis diminuta* and the dwarf tapeworm *Hymenolepis nana*.

Developmental cycle and mode of transmission: Rat fleas exhibit holometabolous development whereby grub-like larvae undergo complete metamorphosis in pupae to for adult fleas. The fleas show strong nidicolous behaviour as they are usually intimately associated with the nests, burrows or dens of their hosts. Gravid female fleas may lay eggs on or off their hosts but they are not very sticky and generally drop off into the nest. The eggs are able to tolerate wide temperature variations (from 5-29°C) and hatch within 7 days. The emergent larvae feed on organic debris, particularly on flea dirt (faecal pellets of dried blood excreted by adults which also drop into the nest). They grow through 3 larval instars over 60 days and survive best in dark cool humid spaces filled with detritus containing numerous hiding places. Workers have also noticed a unique feeding behaviour where larvae solicit faecal bloodmeals from adult fleas by grasping their posterior regions with their mandibles which stimulates the adults to excrete semi-liquid stored blood which is ingested by the larvae. Mature larvae then form silken cocoons in which they undergo pupation for around 2 weeks. Adult fleas may remain in their pupal cases for many months and will not emerge at low temperatures. When they do emerge, they seek hosts on which to feed. Adult fleas have been observed to mate year round with copulation usually occurring off the host. Some researchers think fleas need to feed first in order to mate (requiring blood, warmth or both), but others have reported that unfed fleas kept under warm conditions were able to successfully mate. Gravid female fleas lay 2-8 eggs after each bloodmeal and they may live for 4-17 months depending on ready access to food and cryptic resting sites with moderate temperatures and high humidity. The whole life-cycle may be completed in 80 days, but it often takes longer in less favourable

conditions. Infestations are generally more prevalent during the summer months due primarily to the greater abundance and increased activities of suitable mammalian hosts.

Differential diagnosis: Many infestations remain asymptomatic or subclinical and are often overlooked. Clinical infestations may be suspected when hosts exhibit furtive grooming behaviours and skin lesions become apparent. Diagnoses are made by the direct demonstration of fleas in the pelage and confirmed by microscopic examination of specimens dislodged from hosts. Molecular biological techniques have been used to characterize flea species and infer phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear (18S ribosomal DNA and internal transcribed spacer regions 1 and 2) and mitochondrial (cytochrome c oxidase 1 and cytochrome b) gene sequences.

Treatment and control: Infestations in urban and peri-urban areas that may represent public health threats to human populations are generally controlled by vermin eradication (through trapping and/or baiting). Humans experiencing flea bites may be treated symptomatically with anti-inflammatory agents (glucocorticoids), cooling preparations (menthol, camphor, calamine, ice compresses) together with antibiotics for secondary bacterial infections. Infestations in laboratory animals and pets may be treated with insecticidal chemicals, including organophosphates (coumaphos, diazinon, malathion), pyrethroids (permethrin, cypermethrin), chloronictinyles (imidacloprid), arylpyrazoles (fipronil), and macrocyclic lactones (selamectin). Because rat fleas are nidicolous and usually develop in rodent nests, attempts should be made to decontaminate the immediate environment using residual insecticides. Some success has been reported spraying substrates with organophosphates, pyrethroids or insect growth regulators (methoprene, pyriproxyfen), but aerosol preparations (like foggers and flea bombs) have limited efficacy as they do not penetrate well into cryptic resting sites. Infested houses should be thoroughly cleaned by washing hard substrates with disinfectants and by vacuuming and steam-cleaning carpets. Animal holding facilities should also be cleaned regularly, nesting and bedding materials should be changed frequently, and wild animals should be excluded using suitable barriers and traps. Appropriate screening and quarantine procedures should also be used to avoid outbreaks in laboratory animal colonies.


Nosopsyllus
skin/pelage
(irritation, pruritus,
allergic dermatitis)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, esp. rodents,
some birds)
adult flea
(~ 4 mm)
adults are often nidiculous and transient
ectoparasites (feeding on host blood)
eggs
drop
off
host
or
laid
on
soil,
plants
eclosion
pupa
(~ 1 mm)
eggs
(~ 0.5 mm)
encasement
hatch
larva
(~ 2 mm)
free-living in external environment
(esp. bedding, nests, burrows, hides)

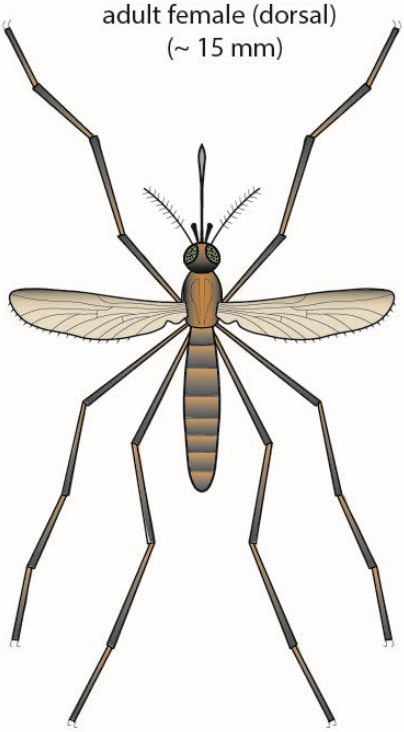


Nosopsyllus adult

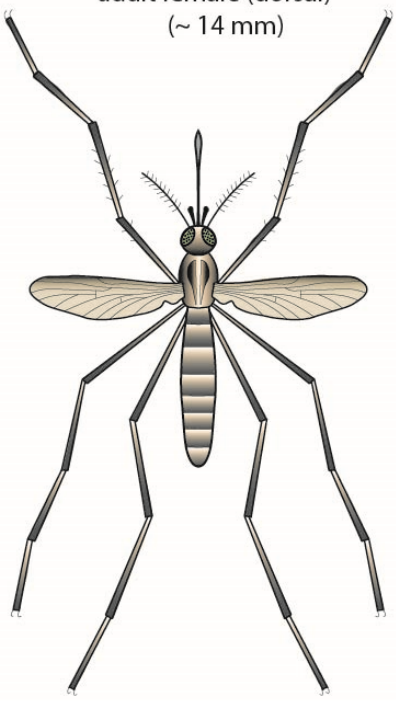
Diptera
(flies)

Diptera: Nematocera: Culicidae (mosquitoes)

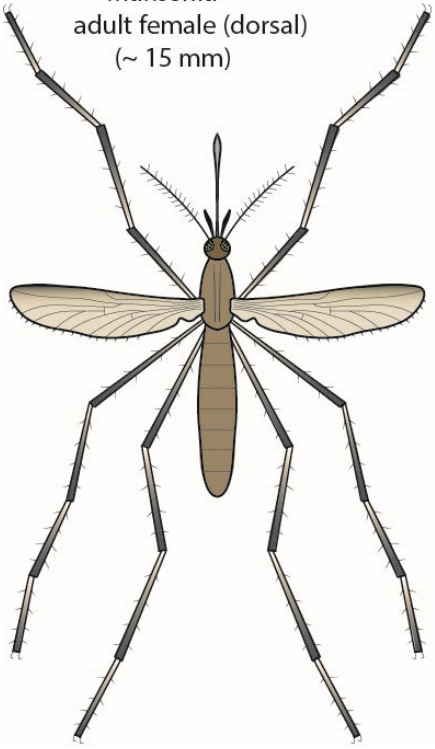
Culex
adult female (dorsal)
(~ 15 mm)



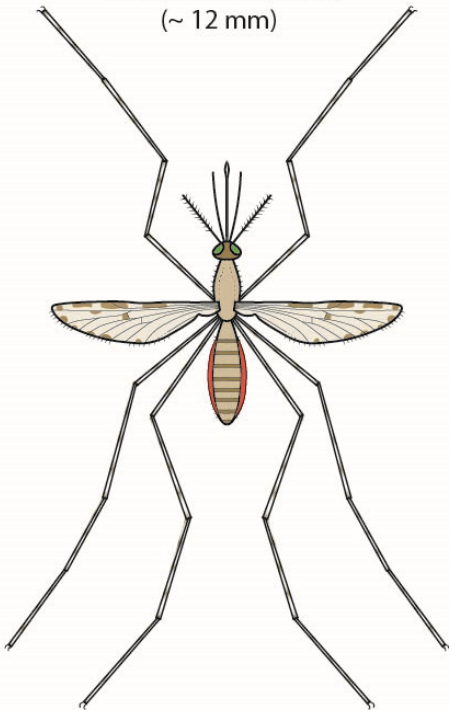
Aedes
adult female (dorsal)
(~ 14 mm)



Mansonia
adult female (dorsal)
(~ 15 mm)



Anopheles
adult female (dorsal)
(~ 12 mm)



Diptera: Nematocera: miscellaneous families (midges, black flies, sand flies)

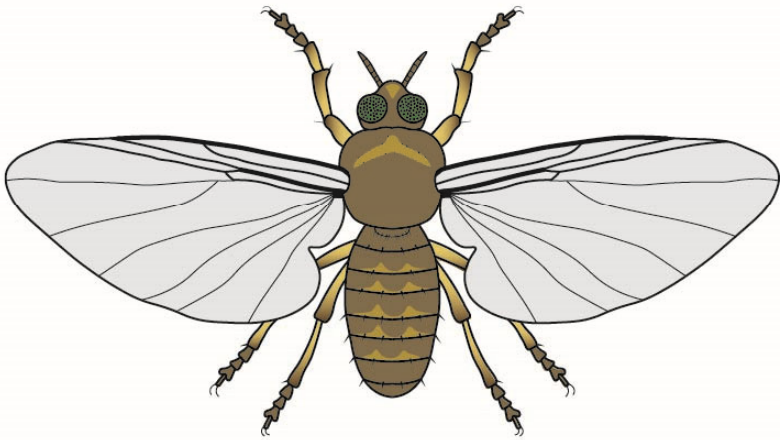
Culicoides

adult female (dorsal)
(~ 2 mm)



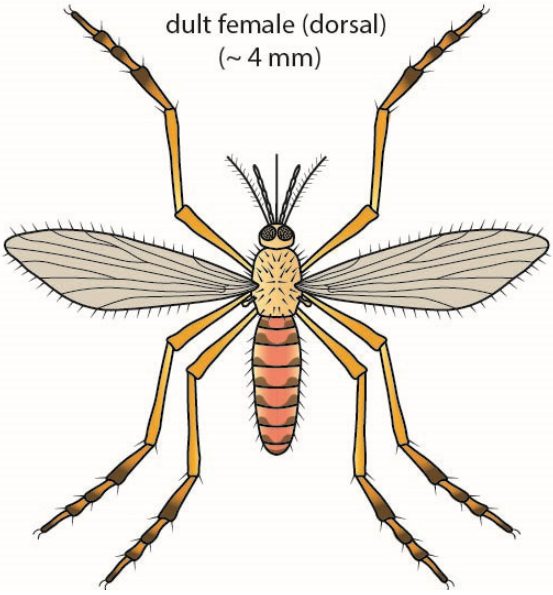
Simulium

adult female (dorsal)
(~ 4 mm)



Phlebotomus

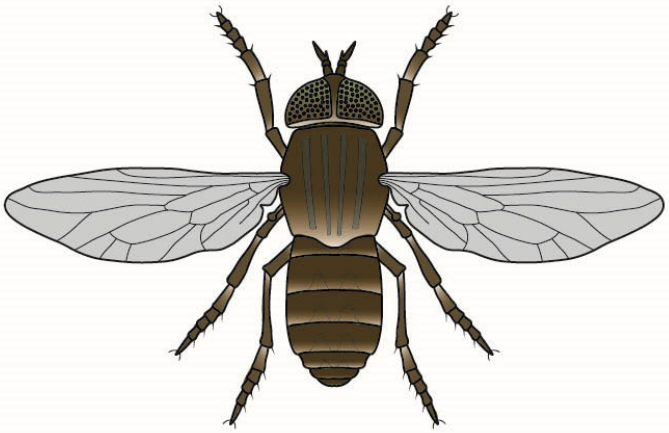
dult female (dorsal)
(~ 4 mm)



Diptera: Tabanomorpha

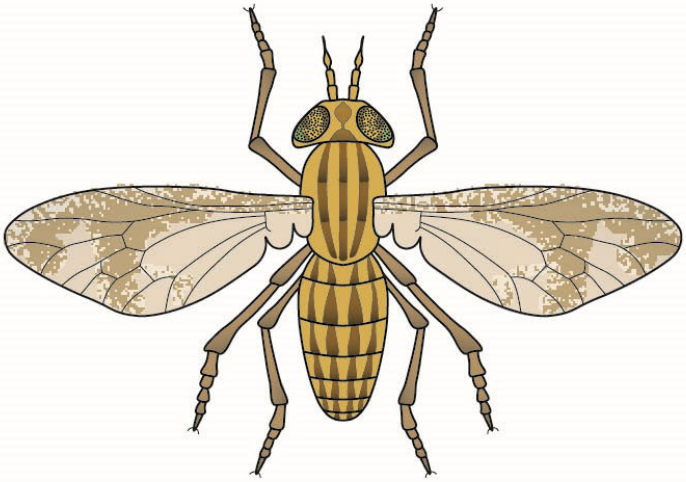
Tabanus

adult female (dorsal)
(~ 30 mm)



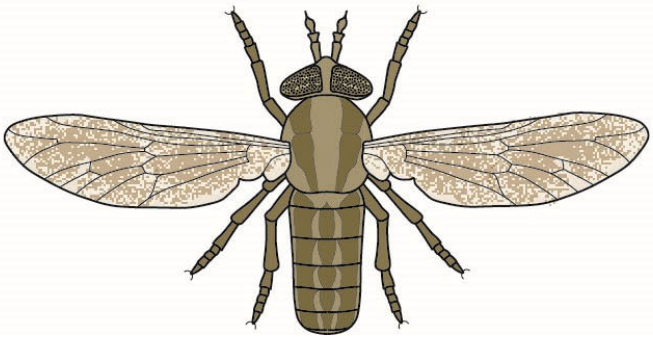
Chrysops

adult female (dorsal)
(~ 30 mm)



Haematopota

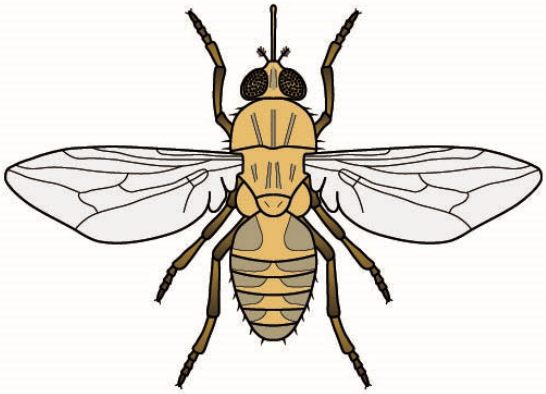
adult female (dorsal)
(~ 30 mm)



Diptera: Muscomorpha 1

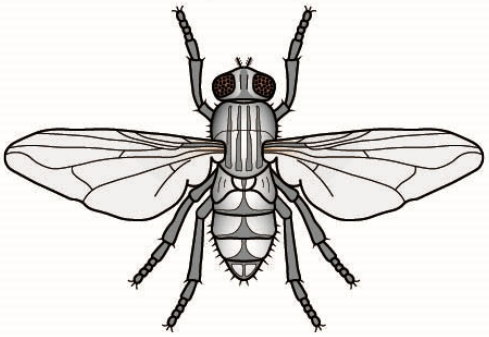
Glossina

adult female (dorsal)
(~ 10 mm)



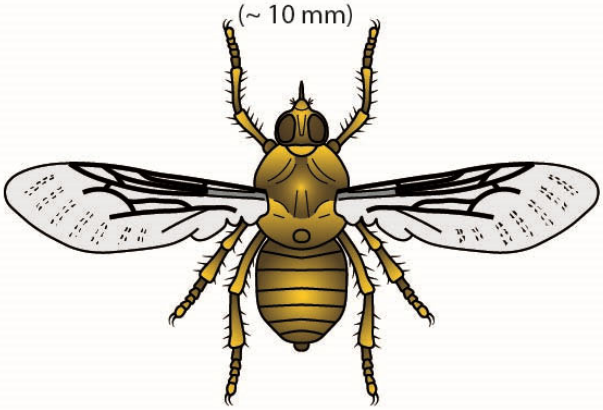
Musca

adult female (dorsal)
(~ 8 mm)



Hippobosca

adult female (dorsal)
(~ 10 mm)



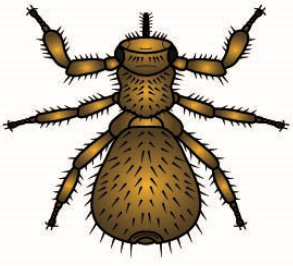
Stomoxys

adult female (dorsal)
(~ 8 mm)



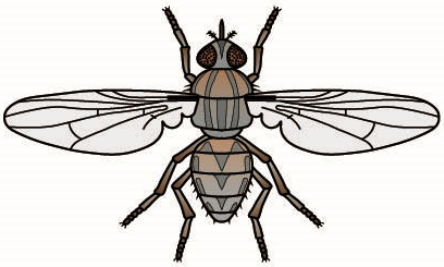
Melophagus

adult female (dorsal)
(~ 6 mm)



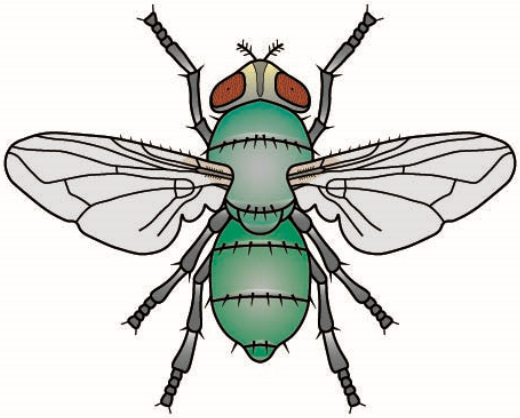
Haematobia

adult female (dorsal)
(~ 5 mm)

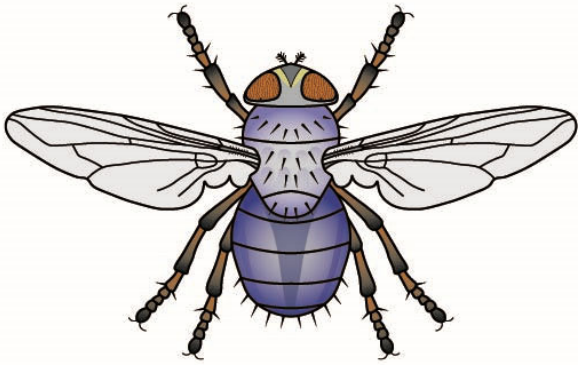


Diptera: Muscomorpha 2

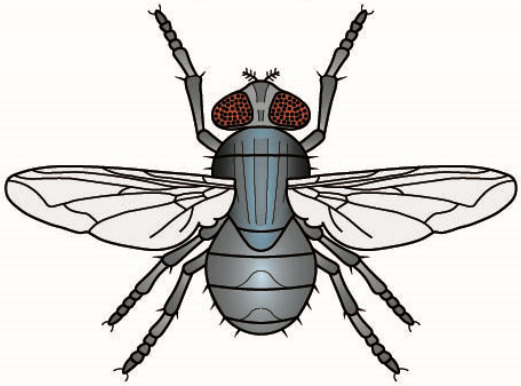
Lucilia
adult female (dorsal)
(~ 12 mm)



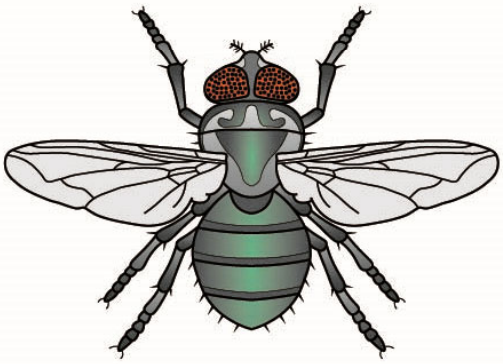
Calliphora
adult female (dorsal)
(~ 12 mm)



Cochliomyia
adult female (dorsal)
(~ 10 mm)



Chrysomya
adult female (dorsal)
(~ 10 mm)



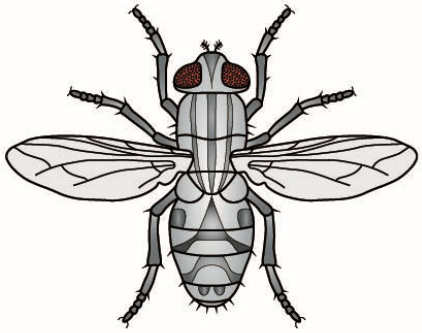
Cordylobia
adult female (dorsal)
(~ 8 mm)



Diptera: Muscomorpha 3

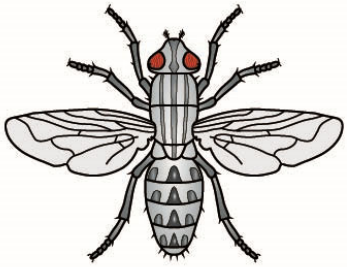
Sarcophaga

adult female (dorsal)
(~ 20 mm)



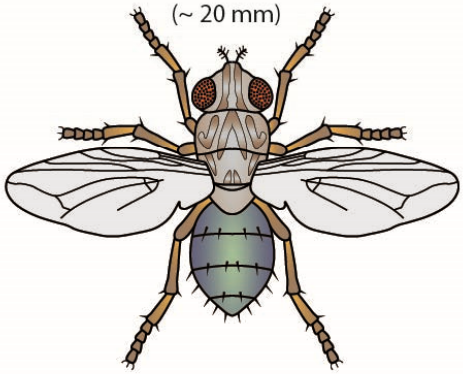
Wohlfahrtia

adult female (dorsal)
(~ 10 mm)



Dermatobia

adult female (dorsal)
(~ 20 mm)



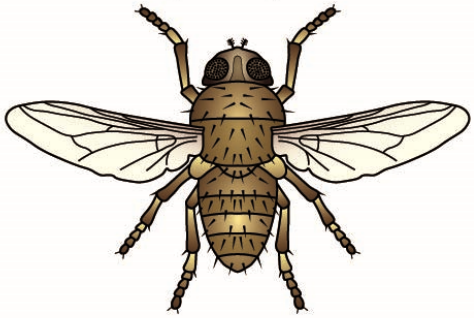
Oestrus

adult female (dorsal)
(~ 15 mm)



Hypoderma

adult female (dorsal)
(~ 15 mm)



Gasterophilus

adult female (dorsal)
(~ 15 mm)



Culex, Aedes, Mansonia
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Nematocerans include the culicids (mosquitoes), ceratopogonids (midges); simuliids (black flies) and psychodids (sand flies): only the females are parasitic and have piercing-sucking mouthparts. Culicids have elongated mouthparts adapted for piercing plants and animals. Male mosquitoes feed on plant nectar and juices, whereas females also feed on blood from vertebrate hosts to obtain nutrients for egg production. Eggs are laid in or near water and both the larval and pupal stages are aquatic and mobile. Four genera are of considerable biomedical importance, both culicine (*Culex*, *Aedes*, *Mansonia*) and anopheline (*Anopheles*) mosquitoes being voracious feeders and transmission vectors for other diseases. Adult culicine mosquitoes have transparent or speckled wings, short palps, rest with a flattened abdomen, usually lay eggs in rafts and the larvae have siphons. Mosquito bites are responsible for blood loss, annoyance, inflammation and hypersensitivity reactions. Around 835 *Culex* spp., 950 *Aedes* spp. and 27 *Mansonia* spp. have been described worldwide, with particular species implicated in the transmission of arboviruses, avian malaria, filarial nematodes and canine heartworm.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Nematocera (midges/mosquitoes, long filamentous antennae, aquatic larvae/pupae)
Family:	Culicidae (mosquitoes, elongate mouthparts form proboscis, slender wings with scales on veins/margins)
Subfamily:	Culicinae (scutellum with trilobed posterior margin, scaly abdomen, larva with prominent air-tube)
Genus:	*Culex* (parasitic on skin of mammals/birds)
Genus:	*Aedes* (parasitic on skin of mammals/birds)
Genus:	*Mansonia* (parasitic on skin of mammals/birds)
Species:	various species annoy vertebrate hosts, cause blood loss and dermal lesions, and transmit other diseases

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders

are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Nematocera comprises small slender flies that are 'thread-horned' i.e. they possess long filamentous antennae composed of many articulating segments (= nemato-cera). Adults have long narrow wings (with many branching veins) and specialized mouthparts (short or long) with a protective sheath (labium and labellae) protecting feeding stylets (labrum, mandibles, maxillae and hypopharynx) and flanked by 4-5 segmented palps (usually pendulous but slender in mosquitoes). Many species have aquatic life-cycles (larval/pupal stages associated with water) and all undergo complete metamorphosis whereby adults eclose from puparia through longitudinal slits (rather than circular caps like Cyclorrapha). The suborder contains 7 infraorders: Axymyiomorpha (larvae in decomposing wood); Bibionomorpha (gnats, lovebugs); Blephariceromorpha (mountain midges); Culicomorpha (mosquitoes, midges, black flies); Psychodomorpha (moth flies); Ptychopteromorpha (primitive crane flies); and Tipulomorpha

(crane flies). The infraorder Culicomorpha contains 2 superfamilies: Chironomoidea (biting, non-biting and trickle midges, black flies); and Culicoidea (midges, mosquitoes). The superfamily Culicoidea contains 4 families: Chaoboridae (phantom midges); Corethrellidae (frog-biting midges); Dixidae (meniscus midges); and Culicidae (mosquitoes). The family Culicidae are characterized by adults with thin elongate bodies with long mouthparts forming a conspicuous forward-projecting proboscis, slender wings with scales covering wing veins and at least 10 veins reaching the wing margins, and long filamentous antennae (males with plumose aristae, females with fewer shorter hairs). Several thousand mosquito species have been described in around 70 genera in 3 subfamilies: Anophelinae with 3 genera (*Anopheles, Bironella, Chagasia*); Toxorhynchitinae with 1 genus (*Toxorhynchites*); and Culicinae with 9 tribes and over 30 genera (including *Aedes, Culex*, *Mansonia*); with another 15 unplaced genera and 5 fossil genera.

Subfamily	Genera*	Preferred hosts	Site	Transmission
Culicinae	*Culex* (*Cx.*)	mammals, birds	skin	free-flying adults seek hosts
	Aedes (*Ae.*)	mammals, birds	skin	free-flying adults seek hosts
	Mansonia (*Ma.*)	mammals, birds	skin	free-flying adults seek hosts
Anophelinae	*Anopheles* (*An.*)	mammals, birds	skin	free-flying adults seek hosts

*Genus name given with internationally-recognized 2-letter abbreviation.

Culicine mosquitoes are characterized by adults having a scutellum with a trilobed posterior margin, a scaly abdomen and larval stages with prominent air-tubes. When resting, adult culicine mosquitoes do not raise their abdomens in the air. The adult females of some species are ectoparasitic and feed on the blood of vertebrate hosts. Generally, mosquitoes are not highly host specific but will feed preferentially on certain hosts. Female mosquitoes may feed on humans, domesticated animals (cattle, horses, goats, etc), birds (incl. chickens), wild mammals (such as deer and rabbits), reptiles (snakes and lizards) and amphibians (frogs and toads). Mosquitoes are attracted to their prey by carbon-dioxide expelled in respiration. In the tribe Culicini, members of the genus *Culex* (syn. *Phytotelmatomyia, Sirivanakarnius*) have medium-sized brown bodies and wings with prominent veins and light narrow scales. Over 835 species have been described in 26 subgenera. Most *Culex* spp. prefer domestic and wild birds over humans and livestock, although some species target larger animals such as pigs and cattle. In the tribe Aedini, members of the genus *Aedes* (syn. *Bohartius, Coetzeemyia, Cornetius, Heteraspidion, Huangmyia, Lepidotomyia, Mukwaya, Reinertia, Xyele, Zoromorphus*) have distinctive black and white markings on their bodies and legs, and wings with prominent veins and light narrow scales. Over 950 species have been described in some 80 subgenera. Unlike most other mosquitoes, they are active and bite only during the daytime, particularly early in the morning and in the evening just before dusk. In the tribe Mansoniini, members of the genus *Mansonia* (syn. *Panoplites*) are big black or brown mosquitoes with speckles on their wings and legs. Some 27 species have been described, most classified into 2 subgenera). These mosquitoes breed in ponds and lakes containing certain types of floating water plants (such as water lettuce and water hyacinths). Adult *Culex*, *Aedes* and *Mansonia* mosquitoes cause considerable annoyance to many animal species and humans, with mosquito swarms capable of causing significant blood loss from individuals. Moreover, adult mosquitoes are very effective vectors for blood-borne infectious diseases caused by various viral, bacterial, protozoal and nematode pathogens, including yellow fever, dengue, encephalitis, canine heartworm, lymphatic filariasis (leading to elephantiasis) and malaria (in animals but not humans) (summarized below).

Mosquito species (regional exemplars)	Hosts	Vectorial capacity	Distribution
Aedes			
Ae. aegypti, africanus, albopictus, bromeliae, cordellieri, furcifer, luteocephalus, metallicus, opok, polynesiensis, pseudoscutellaris, rotumae, scutellaris, taylori, vittatus	primates (incl. humans), rodents, ungulates	togaviruses (Chikungunya, Ross River), flaviviruses (yellow fever, dengue)	Eurasia, Africa, Americas, Australasia
Ae. circumluteolus, mcintoshi	ungulates	flaviviruses (Wesselsbron)	Africa
Ae. vexans	humans, pigs, lagomorphs	bunyaviruses (Tahyna)	Eurasia
Ae. futunae, polynesiensis, pseudoscutellaris, tabu, tongae, upolensis	humans, rodents	togaviruses (Ross River); filarial nematodes (*Wuchereria*)	Asia
Ae. albifasciatus	mammals, birds	togaviruses (western equine encephalomyelitis)	Americas
Aedes spp.	mammals, birds	haemoprotozoa (avian malaria); filarial nematodes (*Dirofilaria*)	cosmopolitan
Culex			
Cx. bitaeniorhynchus, fuscocephala, gelidus, pallens, pseudovishnui, quinquefasciatus, sitiens, tritaeniorhynchus, vishnui	humans, pigs, birds	flaviviruses (Japanese encephalitis); filarial nematodes (*Wuchereria*)	Asia

Cx. annulirostris, bitaeniorhynchus	humans, rodents	togaviruses (Ross River), flaviviruses (Murray Valley encephalitis); leporivirus (myxoma); filarial nematodes (*Wuchereria*)	Australasia
Cx. pipiens, theileri	humans, ungulates	bunyaviruses (Rift Valley fever)	Africa
Cx. cedecei, nigripalpus, ocossa, parocossa, taeniopus, tarsalis	humans, birds, horses, lagomorphs, rodents, bats	togaviruses (eastern, western and Venezuelan equine encephalomyelitis), bunyaviruses (California encephalitis)	Americas
Cx. molestus, pallens, quinquefasciatus	humans	filarial nematodes (*Wuchereria*)	Americas, Africa, Asia
Cx. nigripalpis, pipiens, quinquefasciatus, tarsalis, univittatus	humans, birds	togaviruses (Sindbis), flaviviruses (St Louis encephalitis, West Nile))	cosmopolitan
Culex spp.	mammals, birds, reptiles	haemoprotozoa (malaria) filarial nematodes (*Dirofilaria*)	cosmopolitan
Mansonia			
Ma. annulata, bonneae, dives, indiana, uniformis	humans	filarial nematodes (*Wuchereria, Brugia*)	Asia
Ma. titillans	humans, equids, rodents	togaviruses (Venezuelan equine encephalomyelitis); filarial nematodes (*Wuchereria*)	Americas

Full species lists (compilations of several databases)

***Aedes* species**	**Subgenus**
Ae. abnormalis	*Aedimorphus*
Ae. aboriginis	*Ochlerotatus*
Ae. abserratus	*Ochlerotatus*
Ae. aculeatus	*Ochlerotatus*
Ae. adami	*Catageiomyia*
Ae. adersi	*Diceromyia*
Ae. aegypti	*Stegomyia*
Ae. aenigmaticus	*Ochlerotatus*
Ae. aerarius	*Aedimorphus*
Ae. africanus	*Stegomyia*
Ae. agastyai	*Tewarius*
Ae. agrihanensis	*Stegomyia*
Ae. aitkeni	*Protomacleaya*
Ae. akkeshiensis	*Ochlerotatus*
Ae. albescens	*Rusticoidus*
Ae. albicosta	*Neomelaniconion*
Ae. albifasciatus	*Ochlerotatus*
Ae. albilabris	*Rampamyia*
Ae. albineus	*Ochlerotatus*
Ae. albiradius	*Neomelaniconion*
Ae. alboannulatus	*Dobrotworskyius*
Ae. alboapicus	*Protomacleaya*
Ae. albocephalus	*Polyleptiomyia*
Ae. albocinctus	*Hopkinsius*
Ae. albodorsalis	*Aedimorphus*
Ae. albolateralis	*Downsiomyia*
Ae. albolineatus	*Scutomyia*
Ae. albomarginatus	*Pseudarmigeres*
Ae. alboniveus	*Downsiomyia*
Ae. albonotatus	*Howardina*
Ae. albopictus	*Stegomyia*
Ae. alboscutellatus	*Aedimorphus*
Ae. albotaeniatus	*Danielsia*
Ae. albothorax	*Neomelaniconion*
Ae. alboventralis	*Aedimorphus*

Ae. alcasidi	*Stegomyia*
Ae. alektorovi	*Bruceharrisonius*
Ae. alexandrei	*Aedes*
Ae. alius	*Gilesius*
Ae. allotecnon	*Howardina*
Ae. alocasicola	*Finlaya*
Ae. alongi	*Bothaella*
Ae. aloponotum	*Ochlerotatus*
Ae. alorensis	*Stegomyia*
Ae. alternans	*Mucidus*
Ae. alticola	Unassigned
Ae. amabilis	*Protomacleaya*
Ae. amaltheus	*Stegomyia*
Ae. amateuri	*Ochlerotatus*
Ae. ambreensis	*Ochlerotatus*
Ae. ambremontis	*Paulianius*
Ae. amesii	*Lorrainea*
Ae. ananae	*Finlaya*
Ae. andamanensis	Unassigned
Ae. andersoni	*Ochlerotatus*
Ae. andrewsi	*Stegomyia*
Ae. anggiensis	*Patmarksia*
Ae. angustivittatus	*Ochlerotatus*
Ae. angustus	*Stegomyia*
Ae. annandalei	*Stegomyia*
Ae. annulipes	*Ochlerotatus*
Ae. annulirostris	*Christophersiomyia*
Ae. antipodeus	*Ochlerotatus*
Ae. aobae	*Stegomyia*
Ae. apicoannulatus	*Elpeytonius*
Ae. apicoargenteus	*Stegomyia*
Ae. arborealis	*Howardina*
Ae. arboricolus	*Scutomyia*
Ae. argenteitarsis	*Patmarksia*
Ae. argenteopunctatus	*Catageiomyia*
Ae. argenteoscutellatus	*Aedimorphus*

Ae. argenteoventralis	*Pseudarmigeres*
Ae. argenteus	Unassigned
Ae. argyrites	*Howardina*
Ae. argyronotum	*Patmarksia*
Ae. argyrothorax	*Protomacleaya*
Ae. arundinariae	Unassigned
Ae. ashworthi	*Halaedes*
Ae. assamensis	*Phagomyia*
Ae. atactavittatus	*Ochlerotatus*
Ae. atlanticus	*Ochlerotatus*
Ae. atropalpus	*Georgecraigius*
Ae. aurantius	*Mucidus*
Ae. auratus	*Ochlerotatus*
Ae. aureolineatus	*Howardina*
Ae. aureostriatus	*Bruceharrisonius*
Ae. auridorsum	*Molpemyia*
Ae. aurifer	*Ochlerotatus*
Ae. aurimargo	*Leptosomatomyia*
Ae. aurites	*Howardina*
Ae. aurivittatus	*Howardina*
Ae. auronitens	Unassigned
Ae. aurotaeniatus	*Belkinus*
Ae. aurovenatus	*Neomelaniconion*
Ae. australiensis	Unassigned
Ae. australis	*Halaedes*
Ae. avistylus	*Finlaya*
Ae. axitiosus	*Downsiomyia*
Ae. bahamensis	*Howardina*
Ae. baisasi	*Geoskusea*
Ae. bambiotai	*Aedimorphus*
Ae. bambusae	*Stegomyia*
Ae. bambusicolus	*Scutomyia*
Ae. bananea	*Diceromyia*
Ae. bancoi	*Aedimorphus*
Ae. bancroftianus	*Protomacleaya*
Ae. banksi	*Collessius*
Ae. barnardi	*Hopkinsius*
Ae. barraudi	*Paraedes*
Ae. becki	*Geoskusea*
Ae. bedfordi	*Catageiomyia*
Ae. behningi	*Ochlerotatus*
Ae. bejaranoi	*Ochlerotatus*
Ae. bekkui	*Edwardsaedes*
Ae. belleci	*Neomelaniconion*
Ae. bequaerti	*Neomelaniconion*
Ae. bergerardi	*Neomelaniconion*
Ae. berlandi	*Ochlerotatus*
Ae. berlini	*Protomacleaya*
Ae. bertrami	*Protomacleaya*
Ae. bevisi	*Aedimorphus*
Ae. bhutanensis	Unassigned
Ae. bicristatus	*Rusticoidus*
Ae. bimaculatus	*Ochlerotatus*
Ae. biocellatus	Unassigned
Ae. biskraensis	*Ochlerotatus*
Ae. biunguiculatus	*Nyctomyia*
Ae. blacklocki	*Stegomyia*
Ae. bogotanus	*Ochlerotatus*
Ae. boharti	*Scutomyia*
Ae. bolensis	*Neomelaniconion*
Ae. boneti	*Bifidistylus*

Ae. bonneae	*Paraedes*
Ae. bougainvillensis	*Finlaya*
Ae. braziliensis	*Protomacleaya*
Ae. breedensis	*Ochlerotatus*
Ae. brelandi	*Protomacleaya*
Ae. brevis	*Howardina*
Ae. brevitibia	*Alanstonea*
Ae. brevivittatus	*Howardina*
Ae. britteni	Unassigned
Ae. bromeliae	*Stegomyia*
Ae. brownscutumus	*Bothaella*
Ae. brucei	*Paulianius*
Ae. brunhesi	*Zavortinkius*
Ae. brygooi	*Zavortinkius*
Ae. buenaventura	*Protomacleaya*
Ae. burgeri	*Protomacleaya*
Ae. burjaticus	*Ochlerotatus*
Ae. burnetti	*Finlaya*
Ae. burnsi	*Stegomyia*
Ae. burpengaryensis	*Ochlerotatus*
Ae. busckii	*Howardina*
Ae. butleri	Unassigned
Ae. buxtoni	*Patmarksia*
Ae. caballus	*Ochlerotatus*
Ae. cacharanus	*Finlaya*
Ae. cacozelus	*Ochlerotatus*
Ae. caecus	*Aedimorphus*
Ae. calabyi	*Macleaya*
Ae. calcariae	*Ochlerotatus*
Ae. calceatus	*Stegomyia*
Ae. caliginosus	*Aedimorphus*
Ae. calumnior	*Ochlerotatus*
Ae. campana	*Protomacleaya*
Ae. campestris	*Ochlerotatus*
Ae. camptorhynchus	*Ochlerotatus*
Ae. canadensis	*Ochlerotatus*
Ae. cancricomes	*Cancraedes*
Ae. candidoscutellum	Unassigned
Ae. cantans	*Ochlerotatus*
Ae. cantator	*Ochlerotatus*
Ae. capensis	*Albuginosus*
Ae. carteri	*Neomelaniconion*
Ae. cartroni	*Skusea*
Ae. casali	*Protomacleaya*
Ae. caspius	*Ochlerotatus*
Ae. cataphylla	*Ochlerotatus*
Ae. cavaticus	*Isoaedes*
Ae. cavernicola	*Borichinda*
Ae. celebicus	*Lorrainea*
Ae. centropunctatus	*Aedimorphus*
Ae. chamboni	*Catageiomyia*
Ae. chaussieri	*Stegomyia*
Ae. chelli	*Ochlerotatus*
Ae. chemulpoensis	*Stegomyia*
Ae. cherrapunjiensis	*Hulecoeteomyia*
Ae. chionodes	*Christophersiomyia*
Ae. chionotum	*Protomacleaya*
Ae. christophersi	*Bruceharrisonius*
Ae. chrysolineatus	*Hulecoeteomyia*
Ae. chrysoscutus	*Paraedes*
Ae. chungi	*Jihlienius*

Ae. churchillensis	*Ochlerotatus*
Ae. ciliaris	Unassigned
Ae. cinereus	*Aedes*
Ae. circumluteolus	*Neomelaniconion*
Ae. clelandi	*Ochlerotatus*
Ae. clintoni	*Patmarksia*
Ae. clivis	*Ochlerotatus*
Ae. cogilli	*Phagomyia*
Ae. collessi	*Paraedes*
Ae. coluzzii	*Ochlerotatus*
Ae. comitatus	*Ochlerotatus*
Ae. communis	*Ochlerotatus*
Ae. condolescens	*Ochlerotatus*
Ae. contiguus	*Stegomyia*
Ae. continentalis	*Ochlerotatus*
Ae. cooki	*Stegomyia*
Ae. cordellieri	*Diceromyia*
Ae. corneti	*Stegomyia*
Ae. coulangesi	*Paulianius*
Ae. cozi	*Cornetius*
Ae. cozumelensis	*Howardina*
Ae. craggi	*Stegomyia*
Ae. crassiforceps	*Neomelaniconion*
Ae. cretinus	*Stegomyia*
Ae. crinifer	*Ochlerotatus*
Ae. croceus	*Finlaya*
Ae. crossi	Unassigned
Ae. culiciformis	*Pseudoskusea*
Ae. culicinus	*Aedimorphus*
Ae. cumminsii	*Aedimorphus*
Ae. cunabulanus	*Ochlerotatus*
Ae. curtipes	*Cancraedes*
Ae. cyprioides	*Ochlerotatus*
Ae. cyprius	*Ochlerotatus*
Ae. daggyi	*Geoskusea*
Ae. dahlae	*Ochlerotatus*
Ae. dahuricus	*Aedes*
Ae. daitensis	*Stegomyia*
Ae. daliensis	*Geoskusea*
Ae. dalzieli	*Aedimorphus*
Ae. daryi	*Protomacleaya*
Ae. dasyorrhus	*Lorrainea*
Ae. davidi	*Aedimorphus*
Ae. deboeri	*Stegomyia*
Ae. deccanus	*Phagomyia*
Ae. decticus	*Ochlerotatus*
Ae. deficiens	*Ochlerotatus*
Ae. demeilloni	*Stegomyia*
Ae. denderensis	*Stegomyia*
Ae. dendrophilus	*Stegomyia*
Ae. dentatus	*Aedimorphus*
Ae. derooki	*Patmarksia*
Ae. deserticola	*Jarnellius*
Ae. desmotes	*Stegomyia*
Ae. detritus	*Ochlerotatus*
Ae. dialloi	*Catageiomyia*
Ae. diantaeus	*Ochlerotatus*
Ae. diazi	*Protomacleaya*
Ae. dissimilierodes	*Kenknightia*
Ae. dissimilis	*Kenknightia*
Ae. dmitryi	*Aedes*

Ae. dobodurus	*Patmarksia*
Ae. dobrotworskyi	*Finlaya*
Ae. domesticus	*Aedimorphus*
Ae. doonii	*Bruceharrisonius*
Ae. dorsalis	*Ochlerotatus*
Ae. dorseyi	*Downsiomyia*
Ae. dufouri	*Ochlerotatus*
Ae. duplex	*Ochlerotatus*
Ae. dupreei	*Ochlerotatus*
Ae. durbanensis	*Aedimorphus*
Ae. dybasi	*Stegomyia*
Ae. dzeta	*Ochlerotatus*
Ae. ealaensis	*Stegomyia*
Ae. eatoni	Unassigned
Ae. ebogoensis	*Aedimorphus*
Ae. echinus	*Dahliana*
Ae. ecuadoriensis	*Howardina*
Ae. edgari	*Ochlerotatus*
Ae. edwardsi	*Stegomyia*
Ae. eidsvoldensis	*Ochlerotatus*
Ae. elchoensis	*Macleaya*
Ae. eldridgei	*Bothaella*
Ae. eleanorae	*Howardina*
Ae. ellinorae	*Neomelaniconion*
Ae. elsiae	*Collessius*
Ae. embuensis	*Hopkinsius*
Ae. epactius	*Georgecraigius*
Ae. eritreae	*Aedimorphus*
Ae. esoensis	*Aedes*
Ae. ethiopiensis	*Stegomyia*
Ae. eucephalaeus	*Ochlerotatus*
Ae. euedes	Unassigned
Ae. euiris	*Ochlerotatus*
Ae. euplocamus	*Ochlerotatus*
Ae. excrucians	*Ochlerotatus*
Ae. explorator	Unassigned
Ae. falabreguesi	*Catageiomyia*
Ae. fascipalpis	*Diceromyia*
Ae. feegradei	*Phagomyia*
Ae. fengi	*Luius*
Ae. ferinus	*Mucidus*
Ae. fijiensis	*Finlaya*
Ae. filicis	*Catageiomyia*
Ae. fimbripes	*Geoskusea*
Ae. fitchii	*Ochlerotatus*
Ae. flavescens	*Ochlerotatus*
Ae. flavicollis	*Diceromyia*
Ae. flavifrons	*Ochlerotatus*
Ae. flavimargo	*Neomelaniconion*
Ae. flavipennis	*Finlaya*
Ae. flavopictus	*Stegomyia*
Ae. fluviatilis	*Georgecraigius*
Ae. fontenillei	*Neomelaniconion*
Ae. formosensis	*Hulecoeteomyia*
Ae. fowleri	*Aedimorphus*
Ae. franciscoi	*Petermattinglyius*
Ae. franclemonti	*Finlaya*
Ae. fraseri	*Stegomyia*
Ae. freycinetiae	*Finlaya*
Ae. fryeri	*Coetzeemyia*
Ae. fulgens	*Zavortinkius*

Ae. fulvithorax	*Howardina*
Ae. fulvus	*Ochlerotatus*
Ae. fumidus	*Lorrainea*
Ae. furcifer	*Diceromyia*
Ae. fuscinervis	*Neomelaniconion*
Ae. fuscipalpis	*Finlaya*
Ae. fuscitarsis	*Finlaya*
Ae. futunae	*Stegomyia*
Ae. gabriel	*Protomacleaya*
Ae. gaffigani	*Kenknightia*
Ae. gahnicola	*Finlaya*
Ae. galindoi	*Protomacleaya*
Ae. galloisi	*Stegomyia*
Ae. galloisioides	*Stegomyia*
Ae. ganapathi	*Downsiomyia*
Ae. gandaensis	*Stegomyia*
Ae. gandarai	*Polyleptiomyia*
Ae. gani	*Finlaya*
Ae. gardnerii	*Stegomyia*
Ae. geminus	*Aedes*
Ae. geniculatus	*Dahliana*
Ae. geoffroyi	*Zavortinkius*
Ae. geoskusea	*Levua*
Ae. gibbinsi	*Aedimorphus*
Ae. gilcolladoi	*Dahliana*
Ae. gilli	*Himalaius*
Ae. gilliesi	*Albuginosus*
Ae. gombakensis	*Christophersiomyia*
Ae. gonguoensis	*Jihlienius*
Ae. gouldi	*Aedimorphus*
Ae. grabhami	*Howardina*
Ae. gracilelineatus	Unassigned
Ae. grahamii	*Mucidus*
Ae. grantii	*Stegomyia*
Ae. grassei	*Paulianius*
Ae. greenii	*Bruceharrisonius*
Ae. grenieri	*Catageiomyia*
Ae. gressitti	*Finlaya*
Ae. griffithi	*Ayurakitia*
Ae. grjebinei	*Pseudalbuginosus*
Ae. grossbecki	*Ochlerotatus*
Ae. guamensis	*Stegomyia*
Ae. guatemala	*Howardina*
Ae. gubernatoris	*Phagomyia*
Ae. guerrero	*Howardina*
Ae. gurneri	*Pseudarmigeres*
Ae. gurneyi	*Stegomyia*
Ae. gutzevichi	*Ochlerotatus*
Ae. hakanssoni	*Stegomyia*
Ae. hakusanensis	*Ochlerotatus*
Ae. hancocki	*Vansomerenis*
Ae. hansfordi	*Stegomyia*
Ae. harbachi	*Kenknightia*
Ae. harinasutai	*Downsiomyia*
Ae. harperi	*Danielsia*
Ae. harrisoni	*Ochlerotatus*
Ae. harveyi	*Hulecoeteomyia*
Ae. hastatus	*Ochlerotatus*
Ae. hatorii	*Collessius*
Ae. haworthi	*Albuginosus*
Ae. hebrideus	*Stegomyia*

Ae. heischi	*Stegomyia*
Ae. helenae	*Bothaella*
Ae. hendersoni	*Protomacleaya*
Ae. hensilli	*Stegomyia*
Ae. hesperonotius	*Ochlerotatus*
Ae. heteropus	*Protomacleaya*
Ae. hexodontus	*Ochlerotatus*
Ae. hirsuta	*Paulianius*
Ae. hirsutus	*Aedimorphus*
Ae. hodgkini	*Ochlerotatus*
Ae. hogsbackensis	*Stegomyia*
Ae. hoguei	*Stegomyia*
Ae. hokkaidensis	*Ochlerotatus*
Ae. hollandius	*Patmarksia*
Ae. hollingsheadi	*Finlaya*
Ae. holocinctus	*Aedimorphus*
Ae. homoeopus	*Protomacleaya*
Ae. hoogstraali	*Scutomyia*
Ae. hopkinsi	*Catageiomyia*
Ae. horotoi	*Finlaya*
Ae. horrescens	*Stegomyia*
Ae. hortator	*Sallumia*
Ae. huangae	*Zavortinkius*
Ae. hui	*Finlaya*
Ae. humeralis	*Macleaya*
Ae. hungaricus	*Ochlerotatus*
Ae. hurlbuti	*Bruceharrisonius*
Ae. hylaius	*Neomelaniconion*
Ae. ibis	*Christophersiomyia*
Ae. idanus	*Protomacleaya*
Ae. idjenensis	*Downsiomyia*
Ae. impatibilis	*Scutomyia*
Ae. imperfectus	*Ochlerotatus*
Ae. impiger	*Ochlerotatus*
Ae. implicatus	*Ochlerotatus*
Ae. impostor	*Protomacleaya*
Ae. imprimens	*Edwardsaedes*
Ae. inaequalis	*Howardina*
Ae. incomptus	*Ochlerotatus*
Ae. increpitus	*Ochlerotatus*
Ae. indonesiae	*Cancraedes*
Ae. inermis	*Downsiomyia*
Ae. inexpectatus	*Ochlerotatus*
Ae. infirmatus	*Ochlerotatus*
Ae. ingrami	*Hopkinsius*
Ae. inquinatus	*Phagomyia*
Ae. insolens	*Catageiomyia*
Ae. insolitus	*Protomacleaya*
Ae. intermedius	*Ochlerotatus*
Ae. interruptus	*Zavortinkius*
Ae. intrudens	*Ochlerotatus*
Ae. ioliota	*Howardina*
Ae. irritans	*Catageiomyia*
Ae. iwi	*Phagomyia*
Ae. iyengari	*Petermattinglyius*
Ae. jacobinae	*Ochlerotatus*
Ae. jambulingami	Unassigned
Ae. jamesi	*Aedimorphus*
Ae. jamoti	*Neomelaniconion*
Ae. japonicus	*Hulecoeteomyia*
Ae. jorgi	*Ochlerotatus*

Ae. josephinae	*Finlaya*
Ae. josiahae	*Stegomyia*
Ae. jugraensis	*Hulecoeteomyia*
Ae. juppi	*Ochlerotatus*
Ae. kabaenensis	*Geoskusea*
Ae. kanarensis	*Dendroskusea*
Ae. kapretwae	*Albuginosus*
Ae. karooensis	*Aedimorphus*
Ae. karwari	*Kenknightia*
Ae. kasachstanicus	*Ochlerotatus*
Ae. katherinensis	*Stegomyia*
Ae. keefei	Unassigned
Ae. keniensis	*Stegomyia*
Ae. kennethi	*Albuginosus*
Ae. kenyae	*Stegomyia*
Ae. kesseli	*Stegomyia*
Ae. khazani	*Phagomyia*
Ae. kiangsiensis	*Phagomyia*
Ae. kivuensis	*Stegomyia*
Ae. kleini	*Bothaella*
Ae. knabi	*Protomacleaya*
Ae. knighti	*Finlaya*
Ae. kochi	*Finlaya*
Ae. kohkutensis	*Cancraedes*
Ae. kolhapuriensis	Unassigned
Ae. kompi	*Protomacleaya*
Ae. koreicoides	Unassigned
Ae. koreicus	*Hulecoeteomyia*
Ae. krombeini	*Stegomyia*
Ae. krymmontanus	*Rusticoidus*
Ae. kummi	*Pseudarmigeres*
Ae. lacteus	*Downsiomyia*
Ae. laffooni	*Scutomyia*
Ae. laguna	*Jarnellius*
Ae. lamborni	*Bifidistylus*
Ae. lambrechti	*Skusea*
Ae. lamelliferus	*Lorrainea*
Ae. langata	*Stegomyia*
Ae. laniger	*Mucidus*
Ae. laoagensis	*Finlaya*
Ae. lasaensis	*Ochlerotatus*
Ae. lauriei	Unassigned
Ae. ledgeri	*Stegomyia*
Ae. leei	*Howardina*
Ae. leesoni	*Aedimorphus*
Ae. leonis	*Downsiomyia*
Ae. lepchanus	*Danielsia*
Ae. lepidonotus	*Rusticoidus*
Ae. lepidus	*Ochlerotatus*
Ae. leptolabis	*Aedimorphus*
Ae. lerozeboomi	*Kenknightia*
Ae. leucarthrius	*Aedimorphus*
Ae. leucomelas	*Ochlerotatus*
Ae. leucomeres	*Kenknightia*
Ae. lewelleni	*Finlaya*
Ae. lewnielseni	*Protomacleaya*
Ae. lilii	*Stegomyia*
Ae. lineatopennis	*Neomelaniconion*
Ae. linesi	*Ochlerotatus*
Ae. litoreus	*Downsiomyia*
Ae. littlechildi	*Macleaya*

Ae. litwakae	*Kenknightia*
Ae. lokojoensis	*Catageiomyia*
Ae. longifilamentus	*Ochlerotatus*
Ae. longiforceps	*Geoskusea*
Ae. longipalpis	*Zavortinkius*
Ae. longirostris	*Rhinoskusea*
Ae. longiseta	*Aedimorphus*
Ae. lophoventralis	*Phagomyia*
Ae. lorraineae	*Howardina*
Ae. lottei	*Catageiomyia*
Ae. lowisii	*Aedimorphus*
Ae. lucianus	*Mucidus*
Ae. lunulatus	*Geoskusea*
Ae. luridus	*Neomelaniconion*
Ae. luteifemur	*Ochlerotatus*
Ae. luteocephalus	*Stegomyia*
Ae. luteolateralis	*Neomelaniconion*
Ae. luteostriatus	*Vansomerenis*
Ae. luteus	*Finlaya*
Ae. luzonensis	*Kenknightia*
Ae. macdougalli	*Collessius*
Ae. macfarlanei	*Collessius*
Ae. macintoshi	*Ochlerotatus*
Ae. mackerrasi	*Patmarksia*
Ae. macmillani	*Macleaya*
Ae. madagascarensis	*Paulianius*
Ae. maehleri	*Stegomyia*
Ae. maffii	*Finlaya*
Ae. malayensis	*Stegomyia*
Ae. malikuli	*Stegomyia*
Ae. mallochi	Unassigned
Ae. mamoedjoensis	*Cancraedes*
Ae. manhi	*Bothaella*
Ae. mansouri	*Aedimorphus*
Ae. mariae	*Acartomyia*
Ae. marinkellei	*Howardina*
Ae. marshallensis	*Stegomyia*
Ae. marshallii	*Albuginosus*
Ae. martineti	*Ochlerotatus*
Ae. martinezi	*Howardina*
Ae. mascarensis	*Stegomyia*
Ae. masculinus	*Cancraedes*
Ae. masoalensis	*Aedimorphus*
Ae. masseyi	*Stegomyia*
Ae. mathioti	*Aedimorphus*
Ae. mathisi	Unassigned
Ae. mattinglyi	*Aedimorphus*
Ae. mattinglyorum	*Stegomyia*
Ae. maxgermaini	*Stegomyia*
Ae. mcdonaldi	*Ochlerotatus*
Ae. mcintoshi	*Neomelaniconion*
Ae. medialis	*Huaedes*
Ae. mediolineatus	*Aedimorphus*
Ae. mediopunctatus	*Stegomyia*
Ae. mediovittatus	*Gymnometopa*
Ae. medleri	*Finlaya*
Ae. mefouensis	*Diceromyia*
Ae. melanimon	*Ochlerotatus*
Ae. melanopterus	*Phagomyia*
Ae. menoni	*Paraedes*
Ae. meprai	*Ochlerotatus*

Ae. mercurator	*Ochlerotatus*
Ae. meronephada	*Catatassomyia*
Ae. mesostictus	Unassigned
Ae. metallicus	*Stegomyia*
Ae. metoecopus	*Protomacleaya*
Ae. michaelikati	*Pseudarmigeres*
Ae. mickevichae	*Stegomyia*
Ae. micropterus	*Dendroskusea*
Ae. microstictus	*Catageiomyia*
Ae. mikrokopion	*Downsiomyia*
Ae. milleri	*Ochlerotatus*
Ae. milsoni	*Dobrotworskyius*
Ae. minutus	*Catageiomyia*
Ae. mitchellae	*Ochlerotatus*
Ae. mixtus	*Catageiomyia*
Ae. mjobergi	*Downsiomyia*
Ae. mohani	*Downsiomyia*
Ae. moloiensis	*Macleaya*
Ae. monetus	*Zavortinkius*
Ae. monocellatus	Unassigned
Ae. monotrichus	*Neomelaniconion*
Ae. montanus	*Rampamyia*
Ae. montchadskyi	*Ochlerotatus*
Ae. monticola	*Jarnellius*
Ae. moucheti	*Skusea*
Ae. mpusiensis	*Stegomyia*
Ae. mubiensis	*Aedes*
Ae. mucidus	*Mucidus*
Ae. muelleri	*Lewnielsenius*
Ae. multiplex	*Pseudoskusea*
Ae. muroafcete	*Stegomyia*
Ae. mutilus	*Catageiomyia*
Ae. mzooi	*Zavortinkius*
Ae. natalensis	*Peudarmigeres*
Ae. nataliae	*Aedes*
Ae. natronius	*Aedimorphus*
Ae. neoafricanus	*Stegomyia*
Ae. neogalloisi	*Stegomyia*
Ae. neogeorgianus	*Finlaya*
Ae. neopandani	*Stegomyia*
Ae. nevadensis	*Ochlerotatus*
Ae. ngong	*Albuginosus*
Ae. nigerrimus	*Mucidus*
Ae. nigrescens	Unassigned
Ae. nigricephalus	*Aedimorphus*
Ae. nigrinus	*Ochlerotatus*
Ae. nigripes	*Ochlerotatus*
Ae. nigrithorax	*Ochlerotatus*
Ae. nigrocanus	*Ochlerotatus*
Ae. nigromaculis	*Ochlerotatus*
Ae. nigropterus	*Neomelaniconion*
Ae. nigrorhynchus	*Hulecoeteomyia*
Ae. nigrostriatus	*Aedimorphus*
Ae. ningheensis	*Collessius*
Ae. niphadopsis	*Ochlerotatus*
Ae. nipponicus	*Downsiomyia*
Ae. nippononiveus	*Downsiomyia*
Ae. nishikawai	*Downsiomyia*
Ae. nivalis	*Ochlerotatus*
Ae. niveoides	*Downsiomyia*
Ae. niveoscutum	*Protomacleaya*

Ae. niveus	*Downsiomyia*
Ae. njombiensis	*Stegomyia*
Ae. normanensis	*Ochlerotatus*
Ae. notoscriptus	*Rampamyia*
Ae. novalbitarsis	*Patmarksia*
Ae. novalbopictus	*Stegomyia*
Ae. novoniveus	*Downsiomyia*
Ae. nubilus	*Ochlerotatus*
Ae. nummatus	*Tewarius*
Ae. nyasae	*Hopkinsius*
Ae. nyounae	*Catageiomyia*
Ae. oakleyi	*Aedimorphus*
Ae. obturbator	*Ochlerotatus*
Ae. occidentalis	*Dobrotworskyius*
Ae. oceanicus	*Finlaya*
Ae. ochraceus	*Aedimorphus*
Ae. okinawanus	Unassigned
Ae. oligopistus	*Ochlerotatus*
Ae. omorii	*Downsiomyia*
Ae. opok	*Stegomyia*
Ae. orbitae	*Aedimorphus*
Ae. oreophilus	Unassigned
Ae. osornoi	*Howardina*
Ae. ostentatio	*Paraedes*
Ae. ovazzai	*Aedimorphus*
Ae. pachyurus	*Aedimorphus*
Ae. pagei	*Paraedes*
Ae. painei	Unassigned
Ae. palauensis	*Stegomyia*
Ae. palawanicus	*Cancraedes*
Ae. pallidostriatus	*Aedimorphus*
Ae. pallirostris	Unassigned
Ae. palmarum	*Patmarksia*
Ae. palpalis	*Neomelaniconion*
Ae. pampangensis	*Aedimorphus*
Ae. panchgangee	Unassigned
Ae. pandani	*Stegomyia*
Ae. papago	*Abraedes*
Ae. papuensis	*Patmarksia*
Ae. paradissimilis	*Kenknightia*
Ae. patersoni	*Ochlerotatus*
Ae. patriciae	*Stegomyia*
Ae. paullusi	*Stegomyia*
Ae. pecori	*Kenknightia*
Ae. pectinatus	*Ochlerotatus*
Ae. pecuniosus	*Molpemyia*
Ae. peipingensis	Unassigned
Ae. pembaensis	*Skusea*
Ae. penghuensis	*Cancraedes*
Ae. pennai	*Ochlerotatus*
Ae. perdita	*Aedes*
Ae. periskelatus	*Dendroskusea*
Ae. perkinsi	*Ochlerotatus*
Ae. pernotatus	*Stegomyia*
Ae. perplexus	*Stegomyia*
Ae. perryi	*Geoskusea*
Ae. pertinax	*Ochlerotatus*
Ae. perventor	*Sallumia*
Ae. pexus	*Downsiomyia*
Ae. phaecasiatus	*Ochlerotatus*
Ae. phaeonotus	*Ochlerotatus*

Ae. phillipi	*Zavortinkius*
Ae. phoeniciae	*Acartomyia*
Ae. phyllolabis	*Catageiomyia*
Ae. pia	*Stegomyia*
Ae. pillaii	*Rhinoskusea*
Ae. pingpaensis	*Edwardsaedes*
Ae. pionips	*Ochlerotatus*
Ae. pipersalatus	*Aedimorphus*
Ae. plagosus	Unassigned
Ae. platylepidus	*Scutomyia*
Ae. plumiferus	*Phagomyia*
Ae. podographicus	*Protomacleaya*
Ae. pogonurus	*Neomelaniconion*
Ae. poicilius	*Finlaya*
Ae. pollinctor	*Zavortinkius*
Ae. polynesiensis	*Stegomyia*
Ae. portonovoensis	*Rhinoskusea*
Ae. postspiraculosus	*Pseudoskusea*
Ae. poweri	*Stegomyia*
Ae. procax	*Ochlerotatus*
Ae. prominens	*Phagomyia*
Ae. protolepis	Unassigned
Ae. provocans	*Rusticoidus*
Ae. pseudalbolineatus	*Scutomyia*
Ae. pseudalbopictus	*Stegomyia*
Ae. pseudoafricanus	*Stegomyia*
Ae. pseudodominicii	*Howardina*
Ae. pseudonigeria	*Stegomyia*
Ae. pseudoniveus	*Downsiomyia*
Ae. pseudonormanensis	*Ochlerotatus*
Ae. pseudonummatus	*Tewarius*
Ae. pseudoscutellaris	*Stegomyia*
Ae. pseudotaeniatus	*Collessius*
Ae. pseudotarsalis	*Catageiomyia*
Ae. pubescens	*Aedimorphus*
Ae. pulchrithorax	*Vansomerenis*
Ae. pulchriventer	*Gilesius*
Ae. pulcritarsis	*Ochlerotatus*
Ae. pullatus	*Ochlerotatus*
Ae. pulverulentus	*Indusius*
Ae. punctifemoris	*Aedimorphus*
Ae. punctipes	*Petermattinglyius*
Ae. punctocostalis	*Neomelaniconion*
Ae. punctodes	*Ochlerotatus*
Ae. punctor	*Ochlerotatus*
Ae. punctothoracis	*Catageiomyia*
Ae. purpuraceus	*Ochlerotatus*
Ae. purpureifemur	*Ochlerotatus*
Ae. purpureipes	*Kompia*
Ae. purpureus	*Molpemyia*
Ae. purpuriventris	*Ochlerotatus*
Ae. quadripunctis	*Mucidus*
Ae. quadrivittatus	*Howardina*
Ae. quasiferinus	*Mucidus*
Ae. quasirubithorax	Unassigned
Ae. quasirusticus	*Rusticoidus*
Ae. quasiscutellaris	*Stegomyia*
Ae. quasiunivittatus	*Aedimorphus*
Ae. quinquelineatus	*Rampamyia*
Ae. ramachandrai	*Dendroskusea*
Ae. ramirezi	*Aztecaedes*

Ae. ratcliffei	*Ochlerotatus*
Ae. raymondi	*Ochlerotatus*
Ae. reali	*Catageiomyia*
Ae. refiki	*Rusticoidus*
Ae. reginae	*Dendroskusea*
Ae. reinerti	*Hulecoeteomyia*
Ae. rempeli	*Ochlerotatus*
Ae. reubenae	*Tewarius*
Ae. rhungkiangensis	*Stegomyia*
Ae. rhyacophilus	*Ochlerotatus*
Ae. rickenbachi	*Aedimorphus*
Ae. rimandoi	Unassigned
Ae. riparioides	*Ochlerotatus*
Ae. riparius	*Ochlerotatus*
Ae. riversi	*Stegomyia*
Ae. rizali	*Hulecoeteomyia*
Ae. roai	Unassigned
Ae. robinsoni	*Stegomyia*
Ae. rodhaini	*Paulianius*
Ae. rossicus	*Aedes*
Ae. rotanus	*Stegomyia*
Ae. rotumae	*Stegomyia*
Ae. rubiginosus	Unassigned
Ae. rubrithorax	*Dobrotworskyius*
Ae. rupestris	*Dobrotworskyius*
Ae. rusticus	*Rusticoidus*
Ae. ruwenzori	*Stegomyia*
Ae. sagax	*Ochlerotatus*
Ae. saimedres	*Stegomyia*
Ae. saipanensis	*Stegomyia*
Ae. sallumae	*Ochlerotatus*
Ae. samoanus	*Finlaya*
Ae. sampi	*Stegomyia*
Ae. sandrae	*Protomacleaya*
Ae. saperoi	*Downsiomyia*
Ae. sapiens	*Ochlerotatus*
Ae. sasai	*Aedes*
Ae. savoryi	*Tanakaius*
Ae. saxicola	*Hulecoeteomyia*
Ae. scanloni	*Diceromyia*
Ae. scapularis	*Ochlerotatus*
Ae. scatophagoides	*Mucidus*
Ae. schicki	*Protomacleaya*
Ae. schizopinax	*Ochlerotatus*
Ae. schlosseri	*Finlaya*
Ae. schroederi	*Protomacleaya*
Ae. schtakelbergi	*Ochlerotatus*
Ae. schwetzi	*Stegomyia*
Ae. scutellaris	*Stegomyia*
Ae. scutellatum	*Ochlerotatus*
Ae. scutoscriptus	*Stegomyia*
Ae. seampi	*Stegomyia*
Ae. seatoi	*Stegomyia*
Ae. sedaensis	*Ochlerotatus*
Ae. segermanae	*Stegomyia*
Ae. semlikiensis	*Aedimorphus*
Ae. senyavinensis	*Aedimorphus*
Ae. seoulensis	*Hopkinsius*
Ae. septemstriatus	*Howardina*
Ae. serafini	*Ochlerotatus*
Ae. sergievi	*Ochlerotatus*

Ae. serratus	*Ochlerotatus*
Ae. sexlineatus	*Howardina*
Ae. seychellensis	*Polylepidomyia*
Ae. shannoni	*Ochlerotatus*
Ae. shehzadae	*Downsiomyia*
Ae. sherki	*Hulecoeteomyia*
Ae. shortti	*Collessius*
Ae. sibiricus	*Stegomyia*
Ae. sierrensis	*Jarnellius*
Ae. silvestris	*Ochlerotatus*
Ae. simanini	*Ochlerotatus*
Ae. simlensis	*Himalaius*
Ae. simplex	*Cancraedes*
Ae. simpsoni	*Stegomyia*
Ae. simulans	*Elpeytonius*
Ae. sinensis	*Downsiomyia*
Ae. sinkiangensis	*Ochlerotatus*
Ae. sintoni	Unassigned
Ae. smithburni	*Catageiomyia*
Ae. soleatus	*Stegomyia*
Ae. sollicitans	*Ochlerotatus*
Ae. solomonis	*Finlaya*
Ae. sorsogonensis	*Finlaya*
Ae. spencerii	*Ochlerotatus*
Ae. spilotus	*Ochlerotatus*
Ae. spinosipes	*Macleaya*
Ae. spinosus	*Howardina*
Ae. squamiger	*Ochlerotatus*
Ae. stanleyi	Unassigned
Ae. stenei	*Howardina*
Ae. stenoetrus	*Aedimorphus*
Ae. stenoscutus	*Catageiomyia*
Ae. stevensoni	*Phagomyia*
Ae. sticticus	*Ochlerotatus*
Ae. stigmaticus	*Ochlerotatus*
Ae. stimulans	*Ochlerotatus*
Ae. stokesi	*Albuginosus*
Ae. stonei	*Finlaya*
Ae. stoneorum	*Macleaya*
Ae. stramineus	*Ochlerotatus*
Ae. strelitziae	*Stegomyia*
Ae. stricklandi	*Ochlerotatus*
Ae. subalbirostris	*Ochlerotatus*
Ae. subalbitarsis	*Patmarksia*
Ae. subalbopictus	*Stegomyia*
Ae. subargenteus	*Stegomyia*
Ae. subauridorsum	Unassigned
Ae. subbasalis	*Dobrotworskyius*
Ae. subdentatus	*Aedimorphus*
Ae. subdiversus	*Rusticoidus*
Ae. subniveus	*Downsiomyia*
Ae. subtrichurus	*Rusticoidus*
Ae. sudanensis	*Mucidus*
Ae. suffusus	Unassigned
Ae. sumidero	*Protomacleaya*
Ae. surcoufi	*Ochlerotatus*
Ae. synchytus	*Ochlerotatus*
Ae. syntheticus	*Aedimorphus*
Ae. tabu	*Stegomyia*
Ae. taeniarostris	*Neomelaniconion*
Ae. taeniorhynchoides	*Aedimorphus*
Ae. taeniorhynchus	*Ochlerotatus*
Ae. tahoensis	*Ochlerotatus*
Ae. taiwanus	*Bruceharrisonius*
Ae. tarsalis	*Catageiomyia*
Ae. taufflebi	*Aedimorphus*
Ae. taylori	*Diceromyia*
Ae. teesdalei	*Albuginosus*
Ae. tehuantepec	*Protomacleaya*
Ae. terrens	*Protomacleaya*
Ae. thailandensis	*Paraedes*
Ae. thelcter	*Ochlerotatus*
Ae. theobaldi	*Ochlerotatus*
Ae. thibaulti	*Ochlerotatus*
Ae. thomsoni	*Christophersiomyia*
Ae. thorntoni	*Protomacleaya*
Ae. thurmanae	*Cancraedes*
Ae. timorensis	*Geoskusea*
Ae. tiptoni	*Paulianius*
Ae. togoi	*Tanakaius*
Ae. tongae	*Stegomyia*
Ae. tonkinensis	*Collessius*
Ae. tonkingi	*Mucidus*
Ae. tonsus	*Geoskusea*
Ae. tormentor	*Ochlerotatus*
Ae. tortilis	*Ochlerotatus*
Ae. toxopeusi	Unassigned
Ae. tremulus	*Macleaya*
Ae. treubi	*Alanstonea*
Ae. triceriatus	Unassigned
Ae. tricholabis	*Aedimorphus*
Ae. trichurus	*Rusticoidus*
Ae. trimaculatus	*Aedimorphus*
Ae. triseriatus	*Protomacleaya*
Ae. trivittatus	*Ochlerotatus*
Ae. trukensis	*Aedimorphus*
Ae. tsiliensis	Unassigned
Ae. tubbutiensis	*Dobrotworskyius*
Ae. tulagiensis	*Stegomyia*
Ae. tulliae	*Macleaya*
Ae. turneri	*Ochlerotatus*
Ae. tutuilae	*Finlaya*
Ae. unicinctus	*Jihlienius*
Ae. unidentatus	Unassigned
Ae. unilineatus	*Stegomyia*
Ae. upatensis	*Ochlerotatus*
Ae. upolensis	*Stegomyia*
Ae. usambara	*Stegomyia*
Ae. valeryi	*Aedes*
Ae. vanemdeni	*Howardina*
Ae. vanus	*Downsiomyia*
Ae. vargasi	*Protomacleaya*
Ae. variepictus	*Huaedes*
Ae. varipalpus	*Jarnellius*
Ae. varuae	*Stegomyia*
Ae. veeniae	*Caageiomyia*
Ae. ventrovittis	*Ochlerotatus*
Ae. versicolor	Unassigned
Ae. vexans	*Aedimorphus*
Ae. vigilax	*Ochlerotatus*
Ae. vinsoni	*Stegomyia*
Ae. vittatus	*Fredwardsius*

Ae. vittiger	*Ochlerotatus*
Ae. wadai	*Stegomyia*
Ae. w-album	*Stegomyia*
Ae. walkeri	*Howardina*
Ae. wallacei	*Finlaya*
Ae. wardangensis	*Halaedes*
Ae. wardi	*Rhinoskusea*
Ae. washinoi	*Ochlerotatus*
Ae. wasselli	Unassigned
Ae. watasei	*Phagomyia*
Ae. watteni	*Downsiomyia*
Ae. wattensis	*Macleaya*
Ae. wauensis	*Huaedes*
Ae. wellmanii	*Hopkinsius*
Ae. wendyae	*Catageiomyia*

Ae. whartoni	*Petermattinglyius*
Ae. whitmorei	*Howardina*
Ae. wigglesworthi	*Aedimorphus*
Ae. wilkersoni	*Kenknightia*
Ae. woodi	*Stegomyia*
Ae. yamadai	*Aedes*
Ae. yangambiensis	*Catageiomyia*
Ae. yunnanensis	*Hulecoeteomyia*
Ae. yvonneae	*Catageiomyia*
Ae. zammitii	*Acartomyia*
Ae. zavortinki	*Protomacleaya*
Ae. zethus	*Paulianius*
Ae. zoosophus	*Protomacleaya*

***Culex* species**	**Subgenus**
Cx. abnormalis	*Culex*
Cx. abominator	*Melanoconion*
Cx. abonnenci	*Melanoconion*
Cx. accelerans	*Aedinus*
Cx. acharistus	*Culex*
Cx. acrostichalis	*Eumelanomyia*
Cx. aculeatus	*Lophoceraomyia*
Cx. acutipalus	*Lophoceraomyia*
Cx. adairi	*Lasiosiphon*
Cx. adamesi	*Melanoconion*
Cx. adami	*Eumelanomyia*
Cx. adersianus	*Eumelanomyia*
Cx. aestivus	*Lophoceraomyia*
Cx. aikenii	Unassigned
Cx. airozai	*Phenacomyia*
Cx. akritos	*Melanoconion*
Cx. alani	*Culex*
Cx. albertianus	*Eumelanomyia*
Cx. albinensis	*Melanoconion*
Cx. albinervis	*Oculeomyia*
Cx. albipes	*Microculex*
Cx. albirostris	Unassigned
Cx. albiventris	*Eumelanomyia*
Cx. alcocki	*Melanoconion*
Cx. aliciae	*Melanoconion*
Cx. alienus	*Culex*
Cx. alinkios	*Melanoconion*
Cx. alis	*Culex*
Cx. alogistus	*Melanoconion*
Cx. alorensis	*Lophoceraomyia*
Cx. alphus	Unassigned
Cx. amaniensis	*Eumelanomyia*
Cx. amazonensis	*Aedinus*
Cx. ameliae	*Culex*
Cx. americanus	Unassigned
Cx. amitis	*Melanoconion*
Cx. andersoni	*Culex*
Cx. andreanus	*Eumelanomyia*
Cx. andricus	*Melanoconion*
Cx. anduzei	*Carrollia*
Cx. anips	*Melanoconion*
Cx. annulioris	*Oculeomyia*

Cx. annulirostris	*Culex*
Cx. annuliventris	*Culex*
Cx. annulus	*Culex*
Cx. anoplicitus	*Melanoconion*
Cx. antennatus	*Culex*
Cx. antillummagnorum	*Micraedes*
Cx. antunesi	*Carrollia*
Cx. aphylactus	*Microculex*
Cx. aphyllus	*Melanoconion*
Cx. apicalis	*Neoculex*
Cx. apicinus	*Culex*
Cx. apicopilosus	Unassigned
Cx. aquarius	*Culex*
Cx. arawak	*Micraedes*
Cx. arbieeni	*Maillotia*
Cx. arboricolus	*Melanoconion*
Cx. archegus	*Culex*
Cx. argenteopunctatus	*Culex*
Cx. arizonensis	*Neoculex*
Cx. articularis	*Culex*
Cx. asteliae	*Culex*
Cx. astridianus	*Culex*
Cx. atracus	*Lophoceraomyia*
Cx. atratus	*Melanoconion*
Cx. atriceps	*Culex*
Cx. aurantapex	*Oceleomyia*
Cx. aureonotatus	*Melanoconion*
Cx. aureus	*Microculex*
Cx. australicus	*Culex*
Cx. avianus	*Maillotia*
Cx. axillicolus	*Acallyntrum*
Cx. azurini	*Culiciomyia*
Cx. azymus	*Microculex*
Cx. babahoyensis	*Carrollia*
Cx. bahamensis	*Culex*
Cx. bahiensis	*Melanoconion*
Cx. bahri	*Culiciomyia*
Cx. bailyi	*Culiciomyia*
Cx. baisasi	*Eumelanomyia*
Cx. bamborum	*Anoedioporpa*
Cx. bandoengensis	*Lophoceraomyia*
Cx. banksensis	*Culex*
Cx. barkerii	*Lophoceraomyia*

Cx. barraudi	*Culex*
Cx. barrinus	*Culiciomyia*
Cx. bastagarius	*Melanoconion*
Cx. batesi	*Melanoconion*
Cx. becki	*Lophoceraomyia*
Cx. bejaranoi	*Melanoconion*
Cx. belemensis	*Anoedioporpa*
Cx. belkini	*Acallyntrum*
Cx. bengalensis	*Lophoceraomyia*
Cx. bequaerti	*Melanoconion*
Cx. bergi	*Lophoceraomyia*
Cx. bernardi	*Lophoceraomyia*
Cx. beta	*Culex*
Cx. bhutanensis	Unassigned
Cx. bicki	*Acallyntrum*
Cx. bickleyi	*Culex*
Cx. bicornutus	*Lophoceraomyia*
Cx. bidens	*Culex*
Cx. bifoliolatus	*Melanoconion*
Cx. bigoti	Unassigned
Cx. bihaicolus	*Carrollia*
Cx. bihamatus	*Culex*
Cx. bilineatus	Unassigned
Cx. binigrolineatus	*Acallyntrum*
Cx. biscaynensis	*Micraedes*
Cx. bisulcatus	*Micraedes*
Cx. bitaeniorhynchus	*Oculeomyia*
Cx. boharti	*Neoculex*
Cx. bokorensis	*Eumelanomyia*
Cx. bolii	*Lophoceraomyia*
Cx. boninensis	*Sirivanakarnius*
Cx. bonneae	*Culex*
Cx. bonnei	*Carrollia*
Cx. bougainvillensis	*Acallyntrum*
Cx. brachiatus	*Melanoconion*
Cx. brami	*Culex*
Cx. brenguesi	*Eumelanomyia*
Cx. brethesi	*Culex*
Cx. breviculus	*Tinolestes*
Cx. brevipalpis	*Eumelanomyia*
Cx. brevipalpus	*Lophoceraomyia*
Cx. brevispinosus	*Culex*
Cx. browni	*Anoedioporpa*
Cx. brumpti	*Culex*
Cx. bukavuensis	*Culex*
Cx. buxtoni	*Lophoceraomyia*
Cx. cairnsensis	Unassigned
Cx. calabarensis	*Eumelanomyia*
Cx. calopus	Unassigned
Cx. calurus	*Culex*
Cx. cambournaci	*Culiciomyia*
Cx. campilunati	*Eumelanomyia*
Cx. camposi	*Culex*
Cx. canaanensis	*Anoedioporpa*
Cx. cantans	Unassigned
Cx. capensis	Unassigned
Cx. carcinophilus	*Melanoconion*
Cx. carcinoxenus	*Culex*
Cx. caribeanus	*Melanoconion*
Cx. carioca	*Microculex*
Cx. carleti	*Culex*

Cx. carolinensis	*Lophoceraomyia*
Cx. castaneus	*Lophoceraomyia*
Cx. castelli	*Culex*
Cx. castor	*Eumelanomyia*
Cx. castrensis	*Eumelanomyia*
Cx. castroi	*Phytotelmatomyia*
Cx. cataractarum	*Eumelanomyia*
Cx. cauchensis	*Tinolestes*
Cx. caudatus	*Melanoconion*
Cx. caudelli	*Melanoconion*
Cx. cedecei	*Melanoconion*
Cx. ceramensis	*Culiciomyia*
Cx. cerqueirai	*Carrollia*
Cx. chaetoventralis	*Neoculex*
Cx. chaguanco	*Anoedioporpa*
Cx. changuinolae	*Melanoconion*
Cx. chauveti	*Eumelanomyia*
Cx. cheesmanae	*Neoculex*
Cx. cheni	*Culciomyia*
Cx. chidesteri	*Culex*
Cx. chitae	*Culex*
Cx. chorleyi	*Culex*
Cx. christiani	*Lophoceraomyia*
Cx. chryselatus	*Microculex*
Cx. chrysothorax	Unassigned
Cx. cinctellus	*Lophoceraomyia*
Cx. cinerellus	*Culiciomyia*
Cx. clarki	*Melanoconion*
Cx. clastrieri	*Aedinus*
Cx. coerulescens	*Lophoceraomyia*
Cx. collessi	*Lophoceraomyia*
Cx. columnaris	Unassigned
Cx. comatus	*Melanoconion*
Cx. commevynensis	*Melanoconion*
Cx. comminutor	*Melanoconion*
Cx. comorensis	*Culex*
Cx. comptus	Unassigned
Cx. confundior	*Melanoconion*
Cx. conservator	*Anoedioporpa*
Cx. consimilis	Unassigned
Cx. consolator	*Microculex*
Cx. conspirator	*Melanoconion*
Cx. contei	*Melanoconion*
Cx. coppenamensis	*Melanoconion*
Cx. corentynensis	*Melanoconion*
Cx. corniger	*Phenacomyia*
Cx. cornutus	*Oculeomyia*
Cx. coronator	*Culex*
Cx. corrigani	*Anoedioporpa*
Cx. cottlei	*Lophoceraomyia*
Cx. covagarciai	*Culex*
Cx. crassicomus	*Lophoceraomyia*
Cx. crassistylus	*Neoculex*
Cx. creole	*Melanoconion*
Cx. crinicauda	*Culex*
Cx. cristovaoi	*Melanoconion*
Cx. crowei	*Lophoceraomyia*
Cx. crybda	*Melanoconion*
Cx. cubiculi	*Lophoceraomyia*
Cx. cubitatus	*Lophoceraomyia*
Cx. cubuculi	Unassigned

Cx. curtipalpis	*Lophoceraomyia*
Cx. curvibrachius	*Culex*
Cx. cuyanus	*Culex*
Cx. cylindricus	*Lophoceraomyia*
Cx. damascenoi	*Anoedioporpa*
Cx. damnatorum (fossil)	Unassigned
Cx. daumastocampa	*Microculex*
Cx. davisi	*Microculex*
Cx. decens	*Culex*
Cx. declarator	*Culex*
Cx. decorator	Unassigned
Cx. delfinadoae	*Culiciomyia*
Cx. delpontei	*Melanoconion*
Cx. delys	*Culex*
Cx. demeilloni	*Culex*
Cx. demissus	*Lophoceraomyia*
Cx. derivator	*Neoculex*
Cx. deserticola	*Maillotia*
Cx. diamphidius	*Melanoconion*
Cx. diengensis	*Culex*
Cx. digoelensis	*Lophoceraomyia*
Cx. diplophyllum	*Culex*
Cx. dispectus	*Culiciomyia*
Cx. distinguendus	*Melanoconion*
Cx. dohenyi	*Culex*
Cx. dolichophyllus	*Melanoconion*
Cx. dolosus	*Culex*
Cx. douglasi	*Neoculex*
Cx. dubitans	*Microculex*
Cx. dumbletoni	*Neoculex*
Cx. dunni	*Melanoconion*
Cx. duplicator	*Culex*
Cx. dureti	*Melanoconion*
Cx. durhami	*Lophoceraomyia*
Cx. duttoni	*Culex*
Cx. dyius	*Melanoconion*
Cx. eastor	*Melanoconion*
Cx. eduardoi	*Culex*
Cx. educator	*Melanoconion*
Cx. edwardsi	*Culex*
Cx. egcymon	*Melanoconion*
Cx. eknomios	*Melanoconion*
Cx. eldridgei	*Belkinomyia*
Cx. elephas	*Melanoconion*
Cx. elevator	*Melanoconion*
Cx. ellinorae	Unassigned
Cx. elongatus	*Microculex*
Cx. eminentia	*Lophoceraomyia*
Cx. ensiformis	*Melanoconion*
Cx. epanastasis	*Melanoconion*
Cx. epidesmus	*Oceleomyia*
Cx. epirus	Unassigned
Cx. equinoxialis	*Melanoconion*
Cx. erethyzonfer	*Micraedes*
Cx. erikae (fossil)	Unassigned
Cx. ernanii	*Melanoconion*
Cx. ernsti	*Melanoconion*
Cx. erraticus	*Melanoconion*
Cx. erythrothorax	*Culex*
Cx. eukrines	*Lophoceraomyia*
Cx. europaeus	*Neoculex*

Cx. evansae	*Melanoconion*
Cx. fairchildi	*Melanoconion*
Cx. fasciatus	Unassigned
Cx. fasciolatus	Unassigned
Cx. fasyi	*Culex*
Cx. faurani	*Melanoconion*
Cx. femineus	*Eumelanomyia*
Cx. fergusoni	*Neoculex*
Cx. fernandezi	*Culex*
Cx. ferreri	*Melanoconion*
Cx. fimbriforceps	*Eumelanomyia*
Cx. flabellifer	*Melanoconion*
Cx. flavicornis	*Lophoceraomyia*
Cx. flavovirens	Unassigned
Cx. flavus (fossil)	Unassigned
Cx. flochi	*Melanoconion*
Cx. foliaceus	*Culex*
Cx. foliafer	*Melanoconion*
Cx. foliatus	*Eumelanomyia*
Cx. fragilis	*Culiciomyia*
Cx. fraudatrix	*Lophoceraomyia*
Cx. fulleri	*Lophoceraomyia*
Cx. furlongi	*Culiciomyia*
Cx. fuscicinctus	*Culiciomyia*
Cx. fuscocephala	*Culex*
Cx. gagnei	*Lophoceraomyia*
Cx. gairus	*Microculex*
Cx. galindoi	*Melanoconion*
Cx. galliardi	*Eumelanomyia*
Cx. galvaoi	*Melanoconion*
Cx. gameti	*Culex*
Cx. gamma	*Neoculex*
Cx. ganapathi	*Lophoceraomyia*
Cx. garcesi	*Melanoconion*
Cx. garciai	*Culex*
Cx. garioui	*Eumelanomyia*
Cx. gaudeator	*Microculex*
Cx. gaufini	*Neoculex*
Cx. gelidus	*Culex*
Cx. geminus	*Oculeomyia*
Cx. germaini	*Eumelanomyia*
Cx. gibbulus	*Lophoceraomyia*
Cx. giganteus	*Oculeomyia*
Cx. gilliesi	*Culiciomyia*
Cx. globocoxitus	*Culex*
Cx. glyptosalpinx	*Melanoconion*
Cx. gnomatos	*Melanoconion*
Cx. gossi	*Lophoceraomyia*
Cx. gracicornis	*Lophoceraomyia*
Cx. grahamii	*Culex*
Cx. grandiosus	Unassigned
Cx. gravitator	*Melanoconion*
Cx. grenieri	*Culiciomyia*
Cx. gressitti	*Lophoceraomyia*
Cx. guayasi	*Culex*
Cx. guedesi	*Melanoconion*
Cx. guerreroi	*Carrollia*
Cx. guiarti	*Culex*
Cx. guizhouensis	*Culex*
Cx. guttatus	Unassigned
Cx. guyanensis	*Aedinus*

Cx. habilitator	*Culex*
Cx. hackeri	*Eumelanomyia*
Cx. hainanensis	Unassigned
Cx. halifaxii	Unassigned
Cx. hamoni	*Eumelanomyia*
Cx. hancocki	*Culex*
Cx. harleyi	*Culiciomyia*
Cx. harrisoni	*Culiciomyia*
Cx. hayashii	*Eumelanomyia*
Cx. hedys	*Microculex*
Cx. helenae	*Eumelanomyia*
Cx. hepperi	*Phytotelmatomyia*
Cx. herrerai	*Melanoconion*
Cx. hewitti	*Lophoceraomyia*
Cx. hilli	*Lophoceraomyia*
Cx. hinglungensis	*Eumelanomyia*
Cx. hirtipalpis	*Lophoceraomyia*
Cx. hopkinsi	*Culex*
Cx. horridus	*Eumelanomyia*
Cx. hortensis	*Maillotia*
Cx. huangae	*Culex*
Cx. humilis	Unassigned
Cx. hurlbuti	*Lophoceraomyia*
Cx. hutchinsoni	*Culex*
Cx. idottus	*Melanoconion*
Cx. ikelos	*Melanoconion*
Cx. imitator	*Microculex*
Cx. impositor	*Lophoceraomyia*
Cx. impudicus	*Neoculex*
Cx. inadmirabilis	*Melanoconion*
Cx. inatomii	*Barraudius*
Cx. incognitus	*Culex*
Cx. incomptus	*Lophoceraomyia*
Cx. inconspicuosus	*Eumelanomyia*
Cx. inculus	*Lophoceraomyia*
Cx. indecorabilis	*Melanoconion*
Cx. inextricabilis	*Melanoconion*
Cx. infantulus	*Lophoceraomyia*
Cx. inflictus	*Culex*
Cx. infoliatus	*Carrollia*
Cx. infula	*Oculeomyia*
Cx. ingrami	*Culex*
Cx. inhibitator	*Melanoconion*
Cx. inimitabilis	*Microculex*
Cx. innovator	*Melanoconion*
Cx. inornatus	Unassigned
Cx. insequens	Unassigned
Cx. insigniforceps	*Carrollia*
Cx. insignis	*Eumelanomyia*
Cx. insularis	*Lophoceraomyia*
Cx. interfor	*Culex*
Cx. intermedius	*Microculex*
Cx. interrogator	*Culex*
Cx. intonsus	*Melanoconion*
Cx. intrincatus	*Melanoconion*
Cx. invidiosus	*Culex*
Cx. invocator	*Melanoconion*
Cx. iolambdis	*Melanoconion*
Cx. iphis	*Eumelanomyia*
Cx. iridescens	*Carrollia*
Cx. isabelae	*Melanoconion*

Cx. iyengari	*Culex*
Cx. jacksoni	*Culex*
Cx. jalisco	*Micraedes*
Cx. janitor	*Culex*
Cx. javanensis	*Culiciomyia*
Cx. jefferyi	*Eumelanomyia*
Cx. jenningsi	*Microculex*
Cx. jenseni	*Lophoceraomyia*
Cx. jocasta	*Melanoconion*
Cx. johni	*Neoculex*
Cx. johnnyi	*Melanoconion*
Cx. johnsoni	*Melanoconion*
Cx. josephineae	*Lophoceraomyia*
Cx. jubifer	*Melanoconion*
Cx. judaicus	*Neoculex*
Cx. kanyamwerima	*Eumelanomyia*
Cx. katezari	Unassigned
Cx. kaviengensis	*Lophoceraomyia*
Cx. kazanjii	*Melanoconion*
Cx. kesseli	*Culex*
Cx. khazani	*Eumelanomyia*
Cx. kilara	*Eumelanomyia*
Cx. kinabaluensis	*Oculeomyia*
Cx. kingianus	*Eumelanomyia*
Cx. kiriensis	*Eumelanomyia*
Cx. kompi	*Carrollia*
Cx. kowiroensis	*Lophoceraomyia*
Cx. kuhnsi	*Lophoceraomyia*
Cx. kukenan	*Microculex*
Cx. kummi	*Melanoconion*
Cx. kusaiensis	*Lophoceraomyia*
Cx. kyotoensis	*Culiciomyia*
Cx. lacertosus	*Melanoconion*
Cx. lactator	*Phenacomyia*
Cx. laffooni	*Lophoceraomyia*
Cx. lahillei	*Culex*
Cx. lairdi	*Lophoceraomyia*
Cx. lakei	*Lophoceraomyia*
Cx. lampangensis	*Culiciomyia*
Cx. lanei	*Microculex*
Cx. lanzaroi	Unassigned
Cx. laplantei	*Eumelanomyia*
Cx. lasiopalpis	*Lophoceraomyia*
Cx. laticinctus	*Culex*
Cx. laticlasper	*Culex*
Cx. latifoliatus	*Eumelanomyia*
Cx. latisquama	*Tinolestes*
Cx. latus	*Neoculex*
Cx. laureli	*Eumelanomyia*
Cx. lavatae	*Lophoceraomyia*
Cx. leei	*Lophoceraomyia*
Cx. leonardi	*Neoculex*
Cx. levicastilloi	*Culex*
Cx. liberiensis	*Culiciomyia*
Cx. limacifer	*Melanoconion*
Cx. lineatus	*Afroculex*
Cx. litoralis	*Culex*
Cx. litwakae	*Culex*
Cx. longicornis	*Oculeomyia*
Cx. longisetosus	Unassigned
Cx. longistylus	Unassigned

Cx. longitubus	Unassigned
Cx. lopesi	*Melanoconion*
Cx. lucaris	*Lophoceraomyia*
Cx. lucifugus	*Melanoconion*
Cx. lugens	Unassigned
Cx. luteopleurus	*Anoedioporpa*
Cx. luzonensis	*Oculeomyia*
Cx. lygrus	*Culex*
Cx. macdonaldi	*Lophoceraomyia*
Cx. macfiei	*Culiciomyia*
Cx. machadoi	*Phytotelmatomyia*
Cx. macrostylus	*Eumelanomyia*
Cx. maculatus	Unassigned
Cx. madininensis	*Melanoconion*
Cx. malariager (fossil)	Unassigned
Cx. malayensis	*Eumelanomyia*
Cx. malayi	*Eumelanomyia*
Cx. mammilifer	*Lophoceraomyia*
Cx. manusensis	*Eumelanomyia*
Cx. maplei	*Culiciomyia*
Cx. maracayensis	*Culex*
Cx. marksae	*Lophoceraomyia*
Cx. marquesensis	*Culex*
Cx. martinezi	*Melanoconion*
Cx. martinii	*Neoculex*
Cx. mattinglyi	*Culex*
Cx. mauesensis	*Culex*
Cx. maxi	*Culex*
Cx. maxinocca	*Melanoconion*
Cx. megafolius	*Eumelanomyia*
Cx. megaonychus	*Culiciomyia*
Cx. mesodenticulatus	*Melanoconion*
Cx. metempsytus	*Carrollia*
Cx. miaolingensis	*Eumelanomyia*
Cx. micolo	*Eumelanomyia*
Cx. microphyllus	*Microculex*
Cx. microtaeniata	Unassigned
Cx. mijanae	*Eumelanomyia*
Cx. millironi	*Neoculex*
Cx. milloti	*Culiciomyia*
Cx. milwardi	*Melanoconion*
Cx. mimeticus	*Culex*
Cx. mimuloides	*Culex*
Cx. mimulus	*Culex*
Cx. mindanaoensis	Unassigned
Cx. minjensis	*Lophoceraomyia*
Cx. minor	*Lophoceraomyia*
Cx. minutissimus	*Lophoceraomyia*
Cx. minutus	Unassigned
Cx. miraculosus	*Culex*
Cx. mirificus	*Culex*
Cx. misionensis	*Melanoconion*
Cx. miyagii	*Acallyntrum*
Cx. modestus	*Barraudius*
Cx. mohani	*Eumelanomyia*
Cx. molestus	Unassigned
Cx. mollis	*Culex*
Cx. mongiro	*Culiciomyia*
Cx. moucheti	*Kitzmilleria*
Cx. mulrennani	*Melanoconion*
Cx. mundulus	*Culex*
Cx. murrelli	*Culex*
Cx. muruae	*Lophoceraomyia*
Cx. musarum	*Culex*
Cx. muspratti	*Culiciomyia*
Cx. mutator	*Melanoconion*
Cx. nailoni	*Culiciomyia*
Cx. nakuruensis	*Culex*
Cx. navalis	*Lophoceraomyia*
Cx. neavei	*Culex*
Cx. nebulosus	*Culiciomyia*
Cx. neglectus	*Microculex*
Cx. nicaroensis	*Nicaromyia*
Cx. nicceriensis	*Melanoconion*
Cx. niger	*Lophoceraomyia*
Cx. nigricorpus	Unassigned
Cx. nigrimacula	Unassigned
Cx. nigripalpus	*Culex*
Cx. nigropunctatus	*Culiciomyia*
Cx. nilgiricus	Unassigned
Cx. ninagongoensis	*Culex*
Cx. novaeguineae	Unassigned
Cx. oblita	Unassigned
Cx. obscurus	*Acalleomyia*
Cx. ocellatus	Unassigned
Cx. ocossa	*Melanoconion*
Cx. oedipus	*Melanoconion*
Cx. okinawae	*Eumelanomyia*
Cx. olimpioi	*Melanoconion*
Cx. omani	*Culex*
Cx. orbostiensis	*Lophoceraomyia*
Cx. oresbius	*Eumelanomyia*
Cx. orfilai	*Melanoconion*
Cx. orientalis	*Culex*
Cx. originator	*Anoedioporpa*
Cx. ornatothoracis	*Culex*
Cx. orstom	*Eumelanomyia*
Cx. otachati	*Eumelanomyia*
Cx. ousqua	*Culex*
Cx. oweni	*Lophoceraomyia*
Cx. pacificus	*Culex*
Cx. pairoji	*Lophoceraomyia*
Cx. pajoti	*Culex*
Cx. palaciosi	*Melanoconion*
Cx. pallidiceps	*Acallyntrum*
Cx. pallidothorax	*Culiciomyia*
Cx. pallipes	Unassigned
Cx. palpalis	*Culex*
Cx. pandani	*Culiciomyia*
Cx. panocossa	*Melanoconion*
Cx. papuensis	*Culiciomyia*
Cx. paracrybda	*Melanoconion*
Cx. paraculeatus	*Lophoceraomyia*
Cx. paramaxi	*Culex*
Cx. patientiae	*Melanoconion*
Cx. pavlovskyi	*Melanoconion*
Cx. peccator	*Melanoconion*
Cx. pedicellus	*Neoculex*
Cx. pedroi	*Melanoconion*
Cx. penai	*Melanoconion*
Cx. perexiguus	*Culex*
Cx. pereyrai	*Melanoconion*

Cx. perfidiosus	*Culex*
Cx. perfuscus	*Culex*
Cx. peringueyi	*Maillotia*
Cx. perkinsi	*Acallyntrum*
Cx. perplexus	*Culex*
Cx. perryi	*Lophoceraomyia*
Cx. pervigilans	*Culex*
Cx. petersi	*Lophoceraomyia*
Cx. peytoni	*Lophoceraomyia*
Cx. phangngae	*Eumelanomyia*
Cx. philipi	*Culex*
Cx. philippinensis	*Culex*
Cx. phlabistus	*Melanoconion*
Cx. phlogistus	*Melanoconion*
Cx. pholeter	*Lophoceraomyia*
Cx. phyllados	*Melanoconion*
Cx. pifanoi	*Melanoconion*
Cx. pilifemoralis	*Lophoceraomyia*
Cx. pilosus	*Melanoconion*
Cx. pinarocampa	*Culex*
Cx. pipiens	*Culex*
Cx. plectoporpe	*Melanoconion*
Cx. pleuristriatus	*Microculex*
Cx. plicatus	*Culex*
Cx. pluvialis	*Eumelanomyia*
Cx. poicilipes	*Oculeomyia*
Cx. portesi	*Melanoconion*
Cx. postspiraculosus	*Neoculex*
Cx. productus	*Melanoconion*
Cx. propinquus	*Culex*
Cx. prosecutor	*Culex*
Cx. protorhinus (fossil)	Unassigned
Cx. pruina	*Culex*
Cx. psatharus	*Melanoconion*
Cx. pseudoandreanus	*Eumelanomyia*
Cx. pseudojanthinosoma	*Culex*
Cx. pseudomelanoconia	*Neoculex*
Cx. pseudopruina	*Culex*
Cx. pseudornatus	*Lophoceraomyia*
Cx. pseudorubithoracis	*Lophoceraomyia*
Cx. pseudosinensis	*Oculeomyia*
Cx. pseudostigmatosoma	*Culex*
Cx. pseudosubaequalis	Unassigned
Cx. pseudovishnui	*Culex*
Cx. pulicarius	Unassigned
Cx. pulidoi	*Microculex*
Cx. pullus	*Culiciomyia*
Cx. punctiscapularis	Unassigned
Cx. pusillus	*Barraudius*
Cx. putumayensis	*Melanoconion*
Cx. quadrifoliatus	*Melanoconion*
Cx. quadripalpis	*Lophoceraomyia*
Cx. quasiguiarti	*Culex*
Cx. quasihibridus	*Melanoconion*
Cx. quasioriginator	*Anoedioporpa*
Cx. quettensis	*Maillotia*
Cx. quinquefasciatus	*Culex*
Cx. quintetti	*Eumelanomyia*
Cx. quiquefasciatus	Unassigned
Cx. quitensis	*Culex*
Cx. rabanicolus	*Melanoconion*
Cx. rabelloi	*Melanoconion*
Cx. rachoui	*Melanoconion*
Cx. raghavanii	*Lophoceraomyia*
Cx. rajah	*Culiciomyia*
Cx. rajaneeae	*Lophoceraomyia*
Cx. ramakrishnii	*Culiciomyia*
Cx. ramalingami	*Culiciomyia*
Cx. rausseoi	*Carrollia*
Cx. reducens	*Microculex*
Cx. reevesi	*Neoculex*
Cx. reginae	*Microculex*
Cx. reidi	*Lophoceraomyia*
Cx. rejector	*Microculex*
Cx. renatoi	*Phytotelmatomyia*
Cx. reptans	Unassigned
Cx. restrictor	*Anoedioporpa*
Cx. restuans	*Culex*
Cx. ribeirensis	*Melanoconion*
Cx. richardgarciai	*Eumelanomyia*
Cx. richei	*Eumelanomyia*
Cx. richeti	*Barraudius*
Cx. rima	*Eumelanomyia*
Cx. riojanus	*Culex*
Cx. romeroi	Unassigned
Cx. ronderosi	*Melanoconion*
Cx. rooti	*Melanoconion*
Cx. rorotaensis	*Melanoconion*
Cx. roseni	*Culex*
Cx. rotoruae	*Culex*
Cx. rubensis	*Neoculex*
Cx. rubinotus	*Eumelanomyia*
Cx. rubithoracis	*Lophoceraomyia*
Cx. ruthae	*Culiciomyia*
Cx. ryukyensis	*Culiciomyia*
Cx. ryukyuanus	*Eumelanomyia*
Cx. sacchettae	*Melanoconion*
Cx. salinarius	*Culex*
Cx. salisburiensis	*Maillotia*
Cx. saltanensis	*Culex*
Cx. samoaensis	*Oculeomyia*
Cx. sandrae	*Micraedes*
Cx. sangengluoensis	*Lophoceraomyia*
Cx. saramaccensis	*Melanoconion*
Cx. sardinerae	*Melanoconion*
Cx. sasai	*Culiciomyia*
Cx. scanloni	*Culiciomyia*
Cx. scheuberi	*Culex*
Cx. schicki	*Micraedes*
Cx. schilfgaardei	*Lophoceraomyia*
Cx. schwetzi	*Culex*
Cx. scimitar	*Culex*
Cx. scottii	*Culex*
Cx. sechani	*Culex*
Cx. secundus	*Carrollia*
Cx. secutor	*Culex*
Cx. sedlacekae	*Lophoceraomyia*
Cx. selai	*Eumelanomyia*
Cx. selangorensis	*Oculeomyia*
Cx. seldeslachtsi	*Culex*
Cx. semibrunneus	*Culiciomyia*
Cx. seniori	*Lophoceraomyia*

Cx. serratimarge	*Melanoconion*
Cx. seyrigi	*Maillotia*
Cx. shanahani	*Lophoceraomyia*
Cx. shebbearei	*Culiciomyia*
Cx. shoae	*Culex*
Cx. shopei	*Microculex*
Cx. silvai	*Melanoconion*
Cx. simplicicornis	*Eumelanomyia*
Cx. simpliciforceps	*Eumelanomyia*
Cx. simpsoni	*Culex*
Cx. simulator	*Melanoconion*
Cx. sinaiticus	*Culex*
Cx. sinensis	*Oculeomyia*
Cx. singhbhumensis	Unassigned
Cx. singuawaensis	*Lophoceraomyia*
Cx. siphanulatus	*Microculex*
Cx. sitiens	*Culex*
Cx. solitarius	*Culex*
Cx. solomonis	*Lophoceraomyia*
Cx. soperi	*Carrollia*
Cx. spathifurca	*Culiciomyia*
Cx. spathulatus	*Melanoconion*
Cx. spec	Unassigned
Cx. sphinx	*Culex*
Cx. spiculostylus	*Culiciomyia*
Cx. spiculosus	*Lophoceraomyia*
Cx. spinifer	Unassigned
Cx. spinosus	*Culex*
Cx. spissipes	*Melanoconion*
Cx. squamosus	*Oculeomyia*
Cx. starckeae	*Oculeomyia*
Cx. steffani	*Lophoceraomyia*
Cx. stellatus	*Eumelanomyia*
Cx. stenolepis	*Culex*
Cx. stercoreus	Unassigned
Cx. stigmatosoma	*Culex*
Cx. stonei	*Microculex*
Cx. striatipes	*Culex*
Cx. subaequalis	*Culiciomyia*
Cx. submarginalis	*Lophoceraomyia*
Cx. suborientalis	Unassigned
Cx. subrima	*Eumelanomyia*
Cx. subsalisburiensis	*Maillotia*
Cx. sumatranus	*Lophoceraomyia*
Cx. summorosus	*Culex*
Cx. sunyaniensis	*Eumelanomyia*
Cx. surinamensis	*Culex*
Cx. sursumptor	*Melanoconion*
Cx. sutili	*Microculex*
Cx. symbletos	*Melanoconion*
Cx. szemaoensis	*Lophoceraomyia*
Cx. taeniopus	*Melanoconion*
Cx. tamsi	*Culex*
Cx. tanzaniae (fossil)	Unassigned
Cx. tarsalis	*Culex*
Cx. tatoi	*Culex*
Cx. tauffliebi	*Eumelanomyia*
Cx. tecmarsis	*Melanoconion*
Cx. telesilla	*Culex*
Cx. tenagius	*Culex*
Cx. tenuipalpis	*Eumelanomyia*

Cx. terebor	*Melanoconion*
Cx. termi	*Culiciomyia*
Cx. territans	*Neoculex*
Cx. terzii	*Culex*
Cx. thalassius	*Culex*
Cx. theileri	*Culex*
Cx. theobaldi	*Melanoconion*
Cx. thriambus	*Culex*
Cx. thurmanorum	*Culiciomyia*
Cx. tianpingensis	*Culex*
Cx. tigripes	Unassigned
Cx. toroensis	*Culex*
Cx. torrentium	*Culex*
Cx. tournieri	*Melanoconion*
Cx. toviiensis	*Culex*
Cx. tramazayguesi	*Allimanta*
Cx. traubi	*Lophoceraomyia*
Cx. tricuspis	*Culiciomyia*
Cx. trifidus	*Melanoconion*
Cx. trifilatus	*Culex*
Cx. trifoliatus	*Culex*
Cx. trigeminatus	*Melanoconion*
Cx. trilobulatus	*Melanoconion*
Cx. trisetosus	*Melanoconion*
Cx. tritaeniorhynchus	*Culex*
Cx. tsengi	*Culex*
Cx. tuberis	*Lophoceraomyia*
Cx. umbripes	*Culex*
Cx. uncinatus	*Eumelanomyia*
Cx. unicornis	*Melanoconion*
Cx. uniformis	*Lophoceraomyia*
Cx. univittatus	*Culex*
Cx. urichii	*Carrollia*
Cx. usquatissimus	*Culex*
Cx. usquatus	*Culex*
Cx. vagans	*Culex*
Cx. vansomereni	*Culex*
Cx. variatus	*Lophoceraomyia*
Cx. variegatus	Unassigned
Cx. vattieri	*Eumelanomyia*
Cx. vaxus	*Melanoconion*
Cx. vectensis (fossil)	Unassigned
Cx. ventrilloni	*Culex*
Cx. versabilis	*Lophoceraomyia*
Cx. verutus	*Culex*
Cx. vexillifer	*Melanoconion*
Cx. vicinus	*Culex*
Cx. vidali	*Melanoconion*
Cx. vinckei	*Eumelanomyia*
Cx. virgultus	Unassigned
Cx. viridis	Unassigned
Cx. viridiventer	*Culiciomyia*
Cx. vishnui	*Culex*
Cx. vomerifer	*Melanoconion*
Cx. vulgaris	Unassigned
Cx. walukasi	*Lophoceraomyia*
Cx. wamanguae	*Lophoceraomyia*
Cx. wannonii	*Carrollia*
Cx. wansoni	*Eumelanomyia*
Cx. wardi	*Lophoceraomyia*
Cx. watti	*Culex*

Cx. wepsterae	*Melanoconion*
Cx. weschei	*Culex*
Cx. whartoni	*Lophoceraomyia*
Cx. whitei	*Culex*
Cx. whitmorei	*Culex*
Cx. whittingtoni	*Culex*
Cx. wigglesworthi	*Eumelanomyia*
Cx. wilfredi	*Lophoceraomyia*
Cx. wilsoni	*Carrollia*
Cx. winchesteri (fossil)	Unassigned
Cx. winkleri	*Lophoceraomyia*
Cx. worontzowi	*Microculex*
Cx. xenophobus	*Microculex*
Cx. yaoi	*Culiciomyia*
Cx. ybarmis	*Melanoconion*
Cx. yeageri	*Eumelanomyia*
Cx. yojoae	*Culex*
Cx. zeteki	*Melanoconion*
Cx. zombaensis	*Culex*

***Mansonia* species**	**Subgenera**
Ma. africana	*Mansonioides*
Ma. amazonensis	*Mansonia*
Ma. annulata	*Mansonioides*
Ma. annulifera	*Mansonioides*
Ma. bonneae	*Mansonioides*
Ma. cerqueirai	*Mansonia*
Ma. chagasi	*Mansonia*
Ma. dives	*Mansonioides*
Ma. dyari	*Mansonia*
Ma. flaveola	*Mansonia*
Ma. fonsecai	*Mansonia*
Ma. humeralis	*Mansonia*
Ma. iguassuensis	*Mansonia*
Ma. indiana	*Mansonioides*
Ma. indubitans	*Mansonia*
Ma. leberi	*Mansonia*
Ma. martinii (fossil)	Unassigned
Ma. melanesiensis	*Mansonioides*
Ma. papuensis	*Mansonioides*
Ma. pessoai	*Mansonia*
Ma. pseudotitillans	*Mansonia*
Ma. septempunctata	*Mansonioides*
Ma. suarezi	*Mansonia*
Ma. titillans	*Mansonia*
Ma. uniformis	*Mansonioides*
Ma. varivestita (fossil)	Unassigned
Ma. wilsoni	*Mansonia*

Parasite morphology: Mosquitoes have four developmental stages: eggs, larvae (four instars), pupae, and adults (or imagos). Adult mosquitoes lay ellipsoidal eggs 1-4 mm in length on the surface of freshwater sources. The outer eggshell (chorion) often has intricate surface structures in specific patterns, and *Culex* eggs have a cup-shaped corolla at one end. *Aedes* spp. lay single eggs without lateral floats, *Culex* spp. lay clusters of up to 300 eggs in floating rafts, and *Mansonia* spp. lay star-shaped clusters in floating rafts. Mosquito larvae (wrigglers or wigglers) have dark tubular bodies with a small rounded head, globular thorax and elongate segmented abdomen. The head has chewing mouthparts with an anterior mouth brush, 2 lateral antennae and 2 eyes comprised of clusters of lateral ocelli. The thorax is often highly setate and the abdomen terminates in 2 lateral branches, one being the anal segment with long setae in conspicuous brushes and the other being a barrel-shaped siphon containing respiratory spiracles (air tubes) (absent in anopheline larvae). The wrigglers swim to the water surface at frequent intervals to breathe through the posterior siphon by adopting a head-down angled posture (whereas anopheline larvae lay parallel to the water surface). The larvae moult four times, and at the fourth instar may reach a length of almost 13 mm. Mosquito pupae (tumblers) have comma-shaped bodies with the head and thorax fused to form a cephalothorax with the abdomen curled underneath. Developing appendages of the adult head and thorax may be observed within the cephalothorax which also contains an air pocket for buoyancy. The dorsal mesothorax bears a pair of respiratory tubes (air trumpets) and the abdomen terminates in a pair of paddle-like projections. Adult mosquitoes are small winged insects with slender bodies up to 15 mm long, elongate mouthparts, thin legs and narrow wings. Their bodies are covered with scales, setae and fine hairs which give distinctive marking for each species. *Aedes* spp. have distinctive black and white markings on their legs and bodies, *Culex* spp. are often covered with brown-black scales giving them a dark appearance, and *Mansonia* spp. are dark brown-black with speckles on their wings and legs. The body is divided into 3 conspicuous regions: a rounded head; an oval thorax; and an elongate segmented abdomen. When at rest, adult culicine mosquitoes do not raise their abdomens in the air (whereas anopheline mosquitoes do). The head bears 2 large fronto-lateral compound eyes (each with hundreds of ommatidial lenses), 2 long filamentous segmented antennae (plumose in males and pilose in females), 2 sensory maxillary palps (short in females and long brush-like in males) (in contrast, female anopheline mosquitoes have long palps) and complex piercing-sucking mouthparts forming a long forward-projecting proboscis (often as long as the head and thorax combined). The proboscis consists of a delicate labium forming a protective sheath for the other stylet-like mouthparts (fascicle comprising labrum, mandibles, hypopharynx and maxillae) and ends in 2 small sensory labella. The mandibles (with pointed tips) and maxillae (with serrated tips) are used to puncture skin, and then the labrum (with curled edges) fits together with the mandibles to form a tubular food canal while the hypopharynx forms a salivary canal. In female mosquitoes, the mouthparts are used to draw up blood from vertebrate hosts or sugar solutions from plants, while in males, the mandibles and maxillae have atrophied so they cannot pierce skin. Food is taken up by the muscular cibarial and pharyngeal pumps into the tubular oesophagus where dilute fluids (plant sugars) are shunted for temporary storage into saccular diverticula (ventral diverticulum often called the crop) whereas nutrient-rich foods (blood) are routed through the proventricular valve to the tubular midgut (for digestion), hindgut (connected to Malpighian excretory tubules), bulbous rectum and terminal anus. The thorax has 2 pairs of respiratory spiracles and is covered by a rigid scutum with a posterior lobe-like scutellum and distinctive bristles (setae absent from prespiracular area for *Aedes* and *Mansonia*,

and absent from both prespiracular and postspiracular areas for *Culex*). Dorsally, the thorax is the point of attachment for a pair of slender membranous wings with small squamae framed by prominent veins (distinctive pattern of costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu) and anal (A) primary veins and branches, with at least 10 veins reaching the wing margins). The wing veins and posterior wing margin are covered with narrow scales, light in colour for *Aedes* and *Culex*, and speckled (mixed light and dark) for *Mansonia* (but never with patches of dark scales like anophelines). A small pair of club-like halteres (highly reduced hindwings) are also present posteriorly and are thought to help stabilize flight. Ventrally, the thorax gives rise to 3 pairs of long thin legs, each consisting of 5 segments (coxa, trochanter, femur, tibia and tarsus) with the terminal tarsi carrying 2 claws and pulvilli surrounding a central pad (empodium). The claws on the forelegs may be simple (*Culex* females), toothed (*Culex* males, *Aedes* males and females) or lacking spurs (*Mansonia*), and the pulvilli may be large (*Culex*), small (*Aedes*, some *Mansonia*) or absent (some *Mansonia*). The abdomen is clearly segmented and capable of massive expansion (to accommodate large meals and developing eggs) due to membranous areas between each set of tergites and sternites. The posterior abdomen may be pointed (*Aedes*) or blunt (*Culex*, *Mansonia*) and is often densely covered with scales (patterned in *Aedes*, not so in *Culex*). Typically, 7 pairs of spiracles are found along the edges of the abdomen segments, and paired gonads are located within the posterior abdomen. The terminal abdominal segments are often modified by genital structures (ventral gonopores, female postgenital lobes (cerci), and male terminalia (including claspers)). Mature males have 2 testes with tubular vas deferens leading to a seminal vesicle (with lateral accessory glands) connected to a tubular ejaculatory duct that discharges through a retractable aedeagus (penis). Female mosquitoes have 2 ovaries (with polytrophic ovarioles) whose ducts unite to form a common oviduct connected to the gonopore via a genital chamber associated with spermathecae (for sperm storage) and small accessory glands.

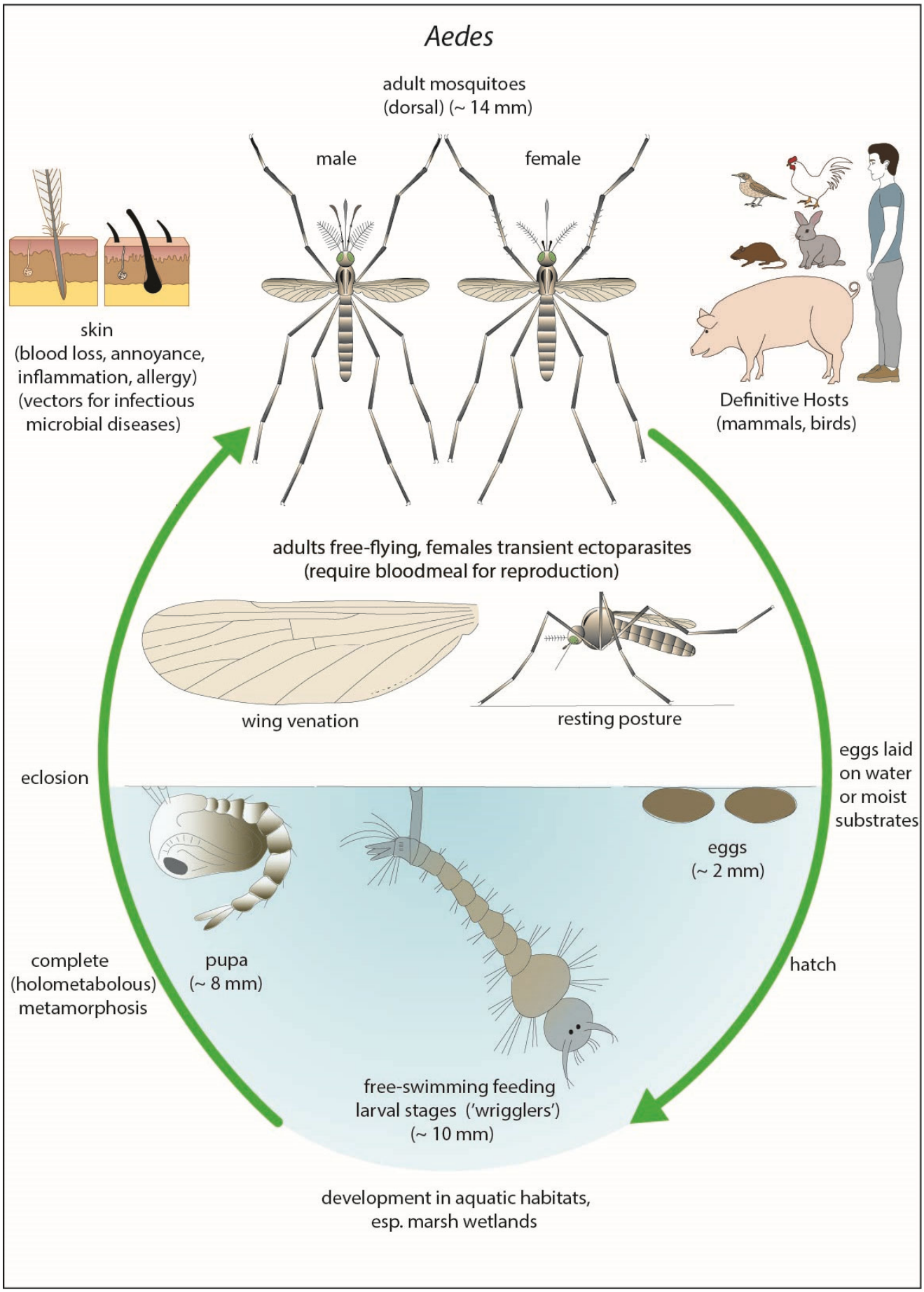
Site of infection: All developmental stages are free-living with eggs, larvae and pupae occurring in aquatic habitats and adult mosquitoes flying free over terrestrial habitats. Larval instars feed on organic material in water by filtering or gathering suspended material, scraping or shredding material from substrates and plants, and some species even prey on small aquatic invertebrates. Pupae are non-feeding stages undergoing metamorphosis from grub-like stages to winged insects. Adult mosquitoes of both sexes may feed on sugary solutions (plant nectar) to derive energy for growth and flight, but only female mosquitoes feed on blood from vertebrate hosts (bloodmeal required for sexual maturation and reproduction). Females may feed on a wide variety of hosts (mammals, birds, reptiles, amphibians) that are locally available, although many species have strong host preferences for particular host species (especially ungulates, carnivores, rodents and birds). *Aedes* spp. feed preferentially on small to large mammals (including cattle, sheep, horses and humans) as well as nesting and foraging birds and small reptiles. *Culex* spp. feed mostly on birds but may attack livestock, humans and some reptiles. *Mansonia* spp. feed predominantly on birds and some mammals (including humans). Most species are nocturnal feeders and the greatest biodiversity (species richness) occurs in tropical and subtropical regions followed by temperate zones.

Pathogenesis: Mosquitoes are painful and persistent biters – females may feed several times from the same or different hosts. Female mosquitoes probe host surfaces with their palps and proboscis and then penetrate the skin with their long fascicle of stylets which exsheath from the covering labium. They can penetrate many skin types (thick, thin, dry, moist, scaly), even through light coverings of matted hair, feathers and clothing. They feed on blood from dermal capillary beds, aided by injecting saliva containing potent chemicals that negatively affect vascular constriction, blood clotting, platelet aggregation, angiogenesis and immunity (universally, hematophagous arthropod saliva contains at least one anticlotting, one anti-platelet, and one vasodilatory substance). Mosquito bites become inflamed, characterised by localised rubor (redness), calor (heat), tumor (swelling) and dolor (itching). The bite itself then resolves spontaneously and has few serious consequences to the host unless an allergic reaction results. Some hosts become hypersensitive to mosquito bites and may exhibit immediate reactions within minutes (caused by type I hypersensitivity evident as wheal-and-flare skin inflammation) or delayed reactions occurring 1-2 days later (due to type IV hypersensitivity evident as erythematous lesions caused by cellular immune responses). Some hosts may even develop papular dermatitis with cutaneous oedema, epidermal ulceration, crusting, and alopecia. Mosquitoes are persistent nuisances to their vertebrates hosts which can become highly annoyed and irritated expending significant energy in aversion behaviours to escape predation. Livestock under persistent attack may fail to feed efficiently and exhibit poor growth, lowered weight gain and reduced milk production. In favourable seasons (suitable habitats and conducive climates), mosquito swarms can become so dense that their cumulative feeding may cause significant blood loss, resulting in transient anaemia. Bite sites can be prone to secondary bacterial infections, particularly if the skin is abraded through self-trauma (biting, scratching, rubbing). In addition to acting as voracious parasites in their own right, mosquitoes may also act as biological vectors for the transmission of many infectious diseases; notably those caused by viruses (esp. togaviruses, flaviviruses and bunyaviruses, collectively known as “arbo-viruses” (= arthropod-borne viruses)), protozoa (especially haemosporidia causing malaria*) and nematodes (filarial worms). Mosquitoes are not known to act as biological vectors for bacteria, although some mosquito species have been found to mechanically transfer bacterial species causing tularaemia and anthrax. Epidemiological and experimental studies have revealed *Culex* spp. to be efficient transmitters of yellow fever, West Nile virus, avian malaria, canine heartworm, *Setaria* filarial nematodes, and human lymphatic filariasis (caused by *Wuchereria bancrofti*). *Aedes* spp. transmit yellow fever, dengue, Zika virus, equine encephalitis virus, avian malaria, canine heartworm, and human lymphatic filariasis (caused by *W. bancrofti*), while *Mansonia* spp. transmit human lymphatic filariasis (caused by *W. bancrofti* and *Brugia* species). [*Note that the *Plasmodium* spp. causing malaria in humans are transmitted exclusively by anopheline mosquitoes, while culicine mosquitoes may act as vectors for *Plasmodium* spp. infecting birds, reptiles and some non-human mammals].

Developmental cycle and mode of transmission: Adult mosquitoes are free-flying whereas eggs, larvae and pupae are aquatic. The rate of development and longevity of the aquatic stages depends largely on prevailing environmental conditions, each stage usually taking several days but taking longer (several weeks) in more temperate regions (eggs and/or larvae of some species even overwintering). Female mosquitoes are oviparous and lay eggs in stagnant water or on moist substrates, anywhere from marsh wetlands (esp. *Aedes*) to organically-enriched standing waters (esp. *Culex*) and floating plants (*Mansonia*), including natural reservoirs (terrestrial and arboreal) and even temporary water-filled containers (such as plastic buckets). They are generally absent from large lakes and fast-flowing streams and rivers. Eggs are laid either singly (*Aedes*) or in clusters gathered together into floating rafts (*Culex*, *Mansonia*). Eggs immersed in water often hatch within 24 hours whereas those attached to neighbouring substrates may survive for several weeks to months until sufficient water stimulates hatching. Emergent larvae are free-swimming and feed on organic detritus and aquatic micro-organisms using elaborate mouth structures to filter/gather suspended material, scrape/shred material from substrates or prey on aquatic micro-organisms. Culicine larvae hang suspended head-down from the water surface and breathe through prominent air tubes emerging from a lateral siphon (in contrast, anopheline larvae lie parallel to the water surface and breathe through posterior spiracles). Larvae pass through 4 instars over 3-20 days depending on the species and water temperature. The last larval stage forms a non-feeding pupal stage in which metamorphosis to an adult occurs over 1-7 days. The pupae usually remain at the water surface and breathe air using prothoracic respiratory siphons, but they can be highly mobile when disturbed. Adult mosquitoes emerge from the pupal case onto the surface of the water or adjacent substrates where they rest until their bodies dry and harden. When resting, culicine mosquitoes typically hold their abdomens parallel to the substrate with their proboscis angled down (in contrast, anopheline mosquitoes hold their proboscis and abdomen in line, oblique to the substrate). Both male and female mosquitoes feed on sugar solutions derived from plants (notably nectar) and mating may occur within 24 hours of emergence. However, the females of most species are anautogenous and require a bloodmeal from a vertebrate host to complete their gonotrophic cycles, although some species are autogenous and may complete their first cycle without feeding on blood. Most mosquitoes feed on hosts at dusk or dawn (crepuscular) or during the night (nocturnal), although some *Aedes* spp. are day-biters. They find hosts using a range of olfactory, visual, thermal and tactile cues (especially, carbon dioxide, lactic acid, octenol, dark/contrasting and moving objects, body warmth, air currents). Some species readily entering dwellings for blood meals (endophagic) and to rest (endophilic). Culicine mosquitoes are generally weak fliers and do not move far, rarely flying over 1-2 km. Adults live from a week or two to several months, depending on the species, gender, season and environmental conditions. Culicine species are usually most abundant during warm summer months.

Differential diagnosis: Host reactions to mosquito bites are nonspecific and vary in onset, duration and severity. Most attacks go unnoticed by the host, although some individual mosquitoes may be observed before, during or after feeding. Hypersensitive individuals may develop dermatitis with persistent wheals and urticaria. The identification of mosquito species relies on the capture and microscopic examination of adults for characteristic morphological features (notably wing scale patterns and length of palps). A variety of molecular biological techniques have endeavored to detect specific gene sequences in mosquito extracts following polymerase chain reaction (PCR) amplification in order to identify possible sources of bloodmeals, indicate phylogenetic relationships between different mosquitoes, and detect infectious micro-organisms carried by mosquitoes.

Treatment and control: There are currently no direct treatments for mosquito bites, apart from providing symptomatic relief using corticosteroids, antihistamines and anti-pruritic lotions, especially in allergic patients. Various insecticides have been developed to kill adult mosquitoes, most being available as aerosol sprays containing organophosphates (coumaphos, chlorfenvinphos, diazinon, dioxathion, fenchlorvos, malathion, phosmet, stirofos, trichlorfon), carbamates or pyrethrins (permethrin, cyfluthrin, cypermethrin). Some formulations may also be incorporated into dust-bags or impregnated into eartags which can also be attached to animal collars or halters. Various traps have been developed to bait and immobilize or electrocute flying insects, and a range of insect repellents are available as sprays or lotions, including those containing diethyltoluamide (DEET). Many control programs have been based on spraying structures with insecticides exhibiting long-lasting residual activity, but their success has been compromised by the emergence of insecticide resistance by mosquito populations. Adopting behaviours to avoid mosquito contact have long been used in the management of human and animal populations, particularly housing individuals indoors (houses, barns, stables), installing barriers (doors and windows with screens, bed nets) and covering exposed skin (preferably with clothing impregnated with insect repellents). Reducing mosquito larvae populations has proven very successful, mainly by eliminating potential breeding sites (swamps, ditches, puddles, etc) and spraying water sources with chemicals to kill, smother or starve larvae. Some measure of biological control has also been achieved by using natural predators (mosquito fish and dragonflies) to reduce larval populations, using natural pathogens (microsporan parasites and *Wolbachia* bacteria) to reduce mosquito fitness, and releasing sterilized males or transgenically modified mosquitoes. Many countries have proactively adopted multiple forms of mosquito control into their public health management programs in attempts to curb the transmission of the many devastating infectious diseases carried by mosquitoes.

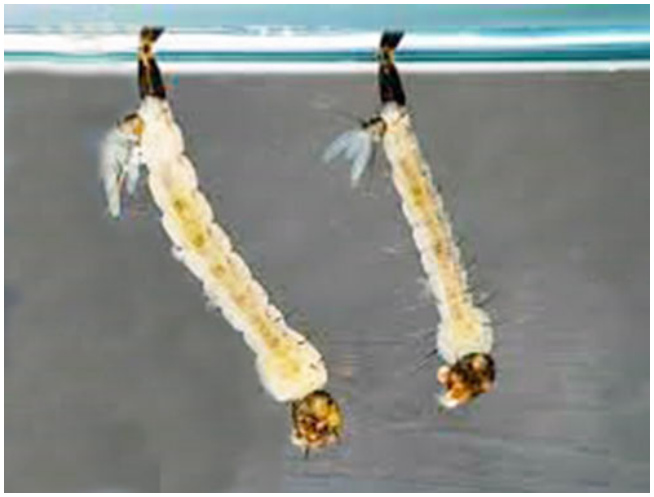

Aedes
adult mosquitoes
(dorsal) (~ 14 mm)
male
female
skin
(blood loss, annoyance,
inflammation, allergy)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, birds)
adults free-flying, females transient ectoparasites
(require bloodmeal for reproduction)
wing venation
resting posture
eclosion
eggs laid
on water
or moist
substrates
eggs
(~ 2 mm)
complete
(holometabolous)
metamorphosis
pupa
(~ 8 mm)
hatch
free-swimming feeding
larval stages ('wrigglers')
(~ 10 mm)
development in aquatic habitats,
esp. marsh wetlands



Aedes adult



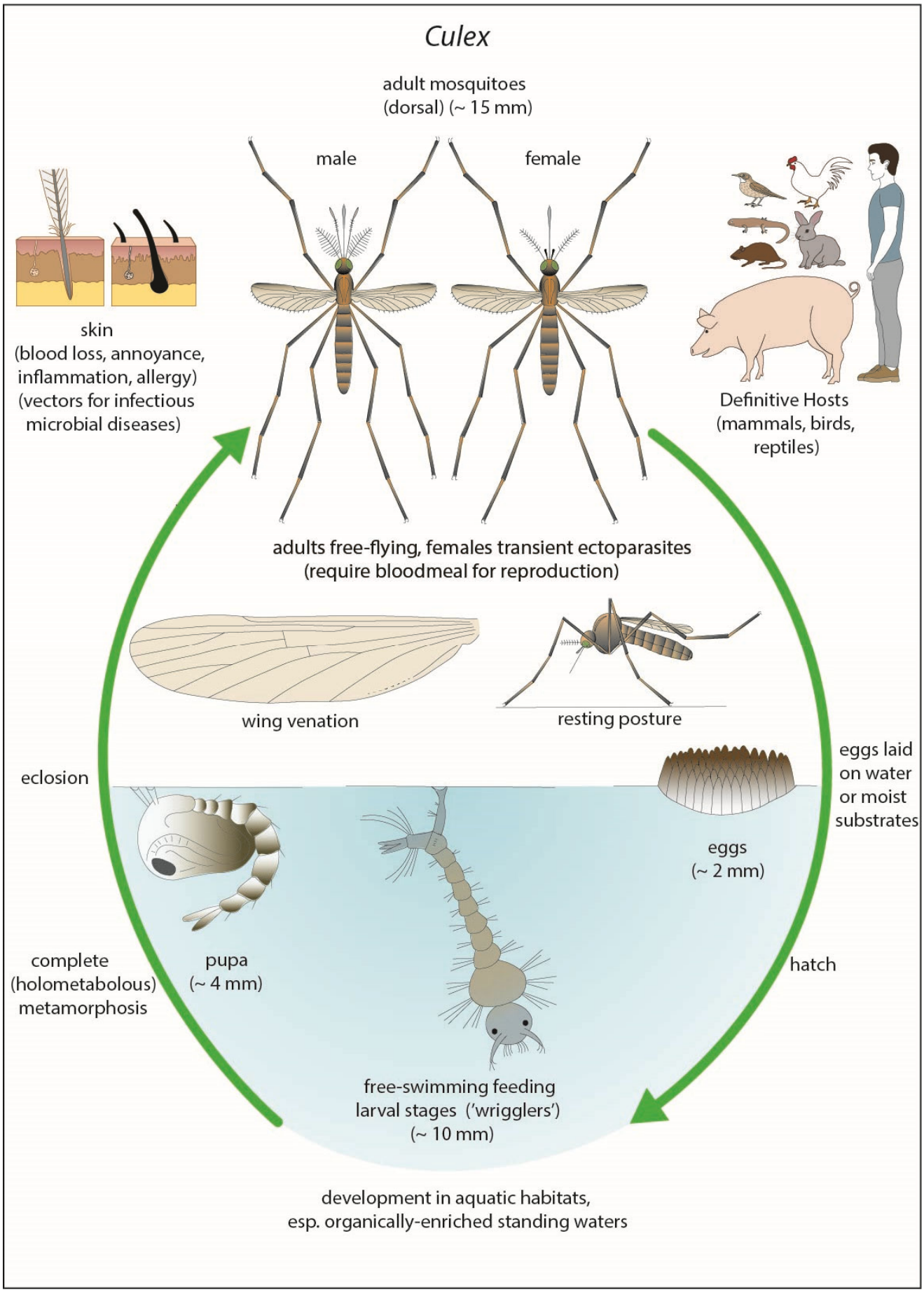
Aedes eggs



Aedes larvae

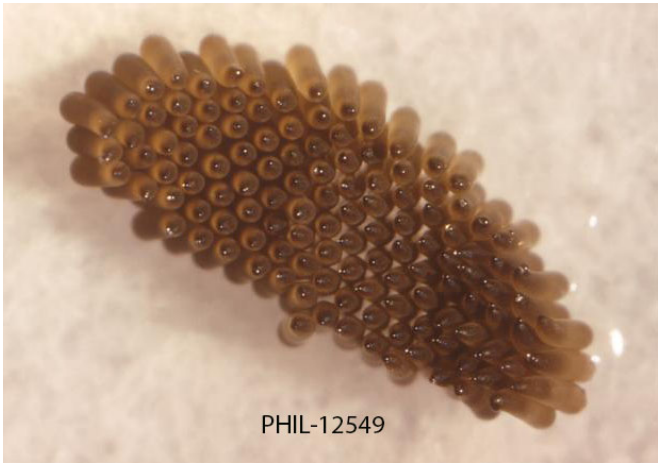


Aedes pupa


Culex
adult mosquitoes
(dorsal) (~ 15 mm)
male
female
skin
(blood loss, annoyance,
inflammation, allergy)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, birds,
reptiles)
adults free-flying, females transient ectoparasites
(require bloodmeal for reproduction)
wing venation
resting posture
eclosion
eggs laid
on water
or moist
substrates
eggs
(~ 2 mm)
complete
(holometabolous)
metamorphosis
pupa
(~ 4 mm)
hatch
free-swimming feeding
larval stages ('wrigglers')
(~ 10 mm)
development in aquatic habitats,
esp. organically-enriched standing waters



Culex adult



Culex eggs

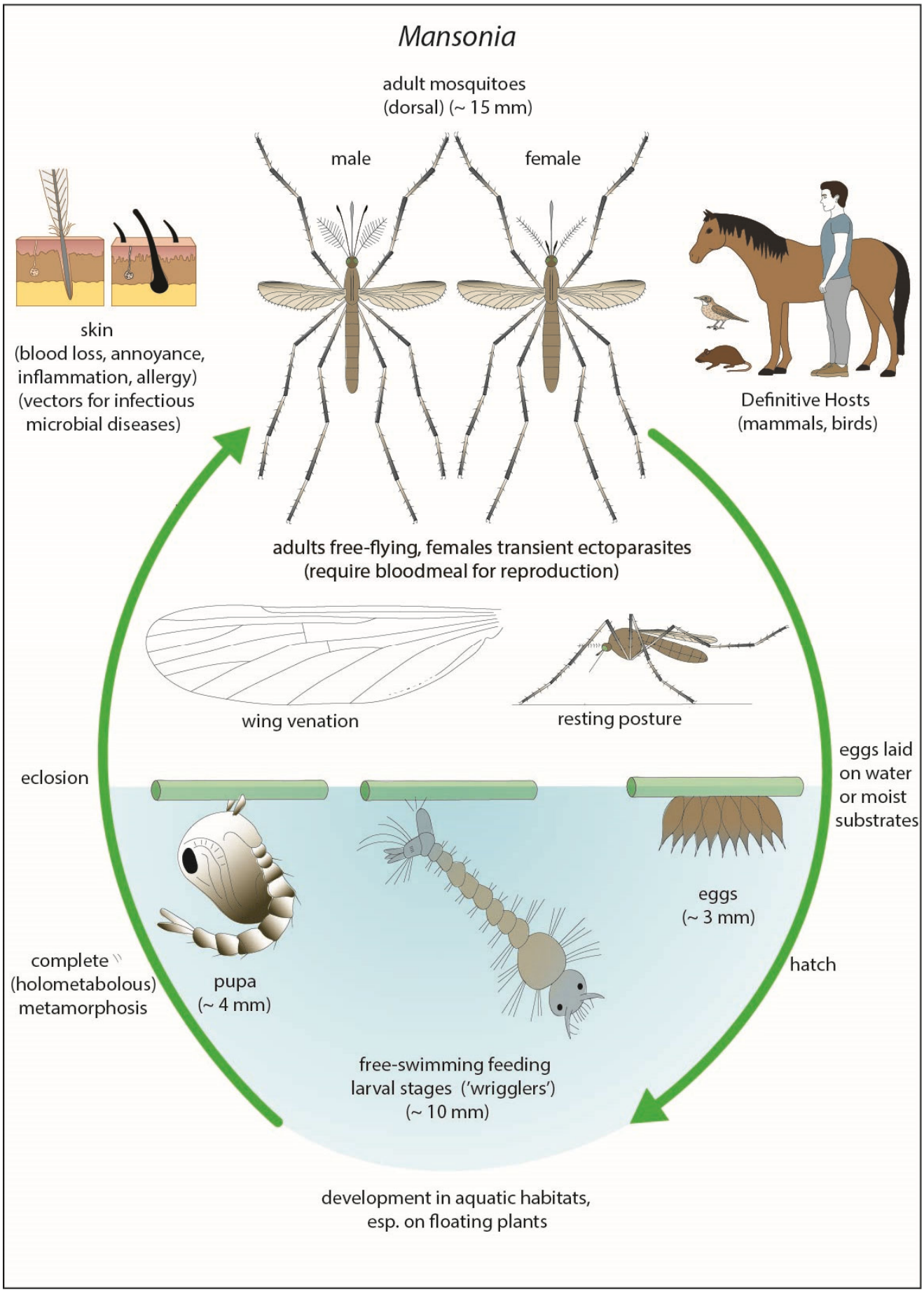


Culex larvae



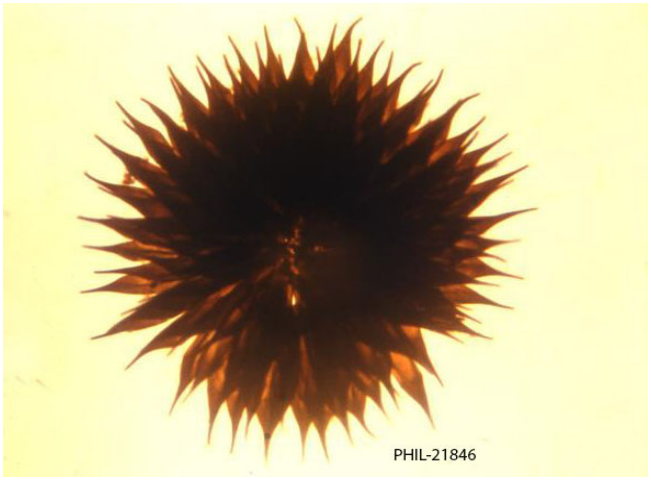
Culex pupae

Mansonia


adult mosquitoes
(dorsal) (~ 15 mm)
male
female
skin
(blood loss, annoyance,
inflammation, allergy)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, birds)
adults free-flying, females transient ectoparasites
(require bloodmeal for reproduction)
wing venation
resting posture
eclosion
eggs laid
on water
or moist
substrates
eggs
(~ 3 mm)
hatch
complete
(holometabolous)
metamorphosis
pupa
(~ 4 mm)
free-swimming feeding
larval stages ('wrigglers')
(~ 10 mm)
development in aquatic habitats,
esp. on floating plants



Mansonia adult



Mansonia adult



Mansonia adult



Mansonia adult

Anopheles
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Nematocerans include the culicids (mosquitoes), ceratopogonids (midges); simuliids (black flies) and psychodids (sand flies): only the females are parasitic and have piercing-sucking mouthparts. Culicids have elongated mouthparts adapted for piercing plants and animals. Male mosquitoes feed on plant nectar and juices, whereas females also feed on blood from vertebrate hosts to obtain nutrients for egg production. Eggs are laid in or near water and both the larval and pupal stages are aquatic and mobile. Four genera are of considerable biomedical importance, both culicine (*Culex*, *Aedes*, *Mansonia*) and anopheline (*Anopheles*) mosquitoes being voracious feeders and transmission vectors for other diseases. Adult anopheline mosquitoes have spotted wings, long palps, rest with a raised abdomen, lay single eggs with floats and their larvae lack siphons. Bites by female mosquitoes are responsible for blood loss, annoyance, inflammation and hypersensitivity reactions. There are approximately 495 *Anopheles* spp. worldwide, with up to 100 species implicated in the transmission of malaria, arboviruses, filarial nematodes and canine heartworm.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Nematocera (midges/mosquitoes, long filamentous antennae, aquatic larvae/pupae)
Family:	Culicidae (mosquitoes, elongate mouthparts form proboscis, slender wings with scales on veins/margins)
Subfamily:	Anophelinae (scutellum rounded or straight, abdominal sternites lack scales, larva lacks air-tube)
Genus:	*Anopheles* (parasitic on skin of mammals/birds)
Species:	various species annoy vertebrate hosts, cause blood loss and dermal lesions, and transmit other diseases

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Nematocera comprises small slender flies that are 'thread-horned' i.e. they possess long filamentous antennae composed of many articulating segments (= nemato-cera). Adults have long narrow wings (with many branching veins) and specialized mouthparts (short or long) with a protective sheath (labium and labellae) protecting feeding stylets (labrum, mandibles, maxillae and hypopharynx) and flanked by 4-5 segmented palps (usually pendulous but slender in mosquitoes). Many species have aquatic life-cycles (larval/pupal stages associated with water) and all undergo complete metamorphosis whereby adults eclose from puparia through longitudinal slits (rather than circular caps like Cyclorrapha). The suborder contains 7 infraorders: Axymyiomorpha (larvae in decomposing wood); Bibionomorpha (gnats, lovebugs); Blephariceromorpha (mountain midges); Culicomorpha (mosquitoes, midges, black flies); Psychodomorpha (moth flies); Ptychopteromorpha (primitive crane flies); and Tipulomorpha (crane flies). The infraorder Culicomorpha contains 2 superfamilies: Chironomoidea (biting, non-biting and trickle midges, black flies); and Culicoidea (midges, mosquitoes). The superfamily Culicoidea contains 4 families: Chaoboridae (phantom midges); Corethrellidae (frog-biting midges); Dixidae (meniscus midges); and Culicidae (mosquitoes). The family Culicidae are characterized

by adults with thin elongate bodies with long mouthparts forming a conspicuous forward-projecting proboscis, slender wings with scales covering wing veins and at least 10 veins reaching the wing margins, and long filamentous antennae (males with plumose aristae, females with fewer shorter hairs). Several thousand mosquito species have been described in around 70 genera in 3 subfamilies: Anophelinae with 3 genera (*Anopheles, Bironella, Chagasia*); Toxorhynchitinae with 1 genus (*Toxorhynchites*); and Culicinae with 9 tribes and over 30 genera (including *Aedes, Culex*, *Mansonia*); with another 15 unplaced genera and 5 fossil genera.

Subfamily	Genera*	Preferred hosts	Site	Transmission
Culicinae	*Culex* (*Cx.*)	mammals, birds	skin	free-flying adults seek hosts
	Aedes (*Ae.*)	mammals, birds	skin	free-flying adults seek hosts
	Mansonia (*Ma.*)	mammals, birds	skin	free-flying adults seek hosts
Anophelinae	*Anopheles* (*An.*)	mammals, birds	skin	free-flying adults seek hosts

*Genus name given with internationally-recognized 2-letter abbreviation.

Anopheline mosquitoes are characterized by adults having a rounded or straight scutellum, abdominal sternites lacking scales, and larval stages without air-tubes. Members of the genus *Anopheles* (syn. *Baimaia*) are found near water throughout the world, except Antarctica. They are mainly distributed around equatorial and tropical regions, but can be found in cooler climates. In many areas, they are found in close association with human populations due to activities such as deforestation and irrigation which displace or extend suitable habitats. Female *Anopheles* mosquitoes feed on many mammalian species, including humans, domestic and wild animals. They are not exclusively human (anthropophilic) or animal (zoophilic) and most mosquito species are host preferential rather than host specific. Their biting behaviour may cause considerable annoyance to their hosts, sometimes exacerbated by host inflammation and hypersensitivity. Over 495 *Anopheles* spp. have been described in 8 subgenera, with a growing number of species proving to be highly efficient vectors for the transmission of various blood-borne diseases in animals and humans, particularly those caused by arbo-viruses (= arthropod-borne viruses), haemoprotozoa and filarial nematodes, including encephalitis syndromes, canine heartworm, lymphatic filariasis (leading to elephantiasis) and malaria (in both animals and humans) (summarized below).

***Anopheles* species (regional exemplars)**	**Hosts**	**Vectorial capacity**	**Distribution**
An. atroparvus, claviger, hispaniola, labranchiae, messeae, pattoni, sacharovi, sinensis	humans	haemoprotozoa (malaria)	Europe
An. albimanus, albitarsis, allopha, aquasalis, argyritarsis, aztecus, bellator, braziliensis, cruzii, darlingi, freeborni, pseudopunctipennis, punctimacula, punctipennis, quadrimaculatus, nuneztovari	humans, primates	haemoprotozoa (malaria), filarial nematodes (*Wuchereria*)	Americas
An. arabiensis, bwambae, christyi, funestus, gambiae, hispaniola, melas, merus, moucheti, multicolor, nili, paulini, pharoensis, sergenti	humans	haemoprotozoa (malaria); filarial nematodes (*Wuchereria*)	Africa
An. gambiae, funestus	mammals, humans	togaviruses (O'nyong-nyong)	Africa
An. cinctus, dureni, marchadyi, smithi	rodents	haemoprotozoa (malaria)	Africa, Asia
An. annularis, culicifacies, dirus, fluviatilis, maculatus, minimus, nigerrimus, pulcherrimus, sacharovi, stephensi, superpictus, tesselatus	humans	haemoprotozoa (malaria)	Central Asia
An. aconitus, anthropophagus, balabacensis, campestris, candidiensis, dirus, donaldi, elegans, flavirostris, hackeri, introlatus, kweiyangensis, letifer, leucophryus, ludlowae, maculatus, minimus, nigerrimus, pattoni, philippinensis, sinensis, subpictus, sundiacus, vagus, whartoni	humans, primates	haemoprotozoa (malaria); filarial nematodes (*Wuchereria*)	Asia
An. anthropophagus, barbirostris, campestris, donaldi, kweiyangensis, nigerrimus, sinensis	humans	filarial nematodes (*Brugia*)	Asia
An. annulipes, bancrofti, farauti, karwari, koliensis, punctulatus, subpictus	humans	leporivirus (myxoma); haemoprotozoa (malaria); filarial nematodes (*Wuchereria*)	Australasia
An. crucians, punctipennis	mammals	filarial nematodes (*Dirofilaria*)	cosmopolitan

Full species list (compilation of several on-line databases)

***Anopheles* species**	**Subgenus**
An. aberrans	*Anopheles*
An. acaci	*Anopheles*
An. acanthotorynus	*Stethomyia*
An. aconitus	*Cellia*
An. africanus	Unassigned
An. ahomi	*Anopheles*
An. ainshamsi	*Cellia*
An. aitkenii	Unassigned
An. albertoi	*Nyssorhynchus*
An. albimanus	*Nyssorhynchus*
An. albitarsis	*Nyssorhynchus*
An. albotaeniatus	*Anopheles*
An. algeriensis	*Anopheles*
An. alongensis	*Anopheles*
An. amharicus	*Cellia*
An. amictus	*Cellia*
An. anchietai	*Anopheles*
An. annandalei	*Anopheles*
An. annularis	*Cellia*
An. annulatus	Unassigned
An. annulipalpis	*Anopheles*
An. annulipes	*Cellia*
An. anomalophyllus	*Nyssorhynchus*
An. anthropophagus	Unassigned
An. antunesi	*Nyssorhynchus*
An. apicimacula	*Anopheles*
An. apoci	*Cellia*
An. aquasalis	*Nyssorhynchus*
An. arabiensis	*Cellia*
An. arboricola	*Anopheles*
An. ardensis	*Cellia*
An. argenteolobatus	*Cellia*
An. argyritarsis	*Nyssorhynchus*
An. argyropus	*Anopheles*
An. arnoulti	Unassigned
An. artemievi	*Anopheles*
An. arthuri	*Nyssorhynchus*
An. aruni	*Cellia*
An. asiatica	*Lophomyia*
An. asiaticus	*Anopheles*
An. atacamensis	*Nyssorhynchus*
An. atratipes	*Anopheles*
An. atroparvus	*Anopheles*
An. atropos	*Anopheles*
An. aurirostris	*Cellia*
An. austenii	*Cellia*
An. auyantepuiensis	*Kerteszia*
An. azaniae	*Cellia*
An. azevedoi	*Cellia*
An. aztecus	*Anopheles*
An. baezai	*Anopheles*
An. baileyi	*Anopheles*
An. baimaii	*Cellia*
An. baisasi	*Cellia*
An. balabacensis	*Cellia*
An. balerensis	*Anopheles*
An. bambusicolus	*Kerteszia*
An. bancroftii	Unassigned
An. barberellus	*Cellia*
An. barberi	*Anopheles*
An. barbirostris	*Anopheles*
An. barbumbrosus	*Anopheles*
An. barianensis	*Anopheles*
An. beklemishevi	*Anopheles*
An. belenrae	*Anopheles*
An. bellator	*Kerteszia*
An. benarrochi	*Nyssorhynchus*
An. bengalensis	*Anopheles*
An. berghei	*Cellia*
An. bervoetsi	*Cellia*
An. boliviensis	*Kerteszia*
An. borneensis	*Anopheles*
An. brachypus	Unassigned
An. bradleyi	*Anopheles*
An. braziliensis	*Nyssorhynchus*
An. brevipalpis	*Anopheles*
An. brevirostris	*Anopheles*
An. brohieri	*Cellia*
An. brucei	*Cellia*
An. brumpti	*Cellia*
An. brunnipes	*Cellia*
An. bulkleyi	*Anopheles*
An. bustamentei	*Anopheles*
An. buxtoni	*Cellia*
An. bwambae	*Cellia*
An. calderoni	*Anopheles*
An. caliginosus	*Anopheles*
An. cameroni	*Cellia*
An. campestris	*Anopheles*
An. canorii	*Stethomyia*
An. carnevalei	*Cellia*
An. caroni	*Cellia*
An. carteri	*Cellia*
An. chiriquiensis	*Anopheles*
An. chodukini	*Anopheles*
An. christyi	*Cellia*
An. cinctus	*Cellia*
An. cinereus	Unassigned
An. claviger	*Anopheles*
An. clowi	*Cellia*
An. colledgei	*Anopheles*
An. collessi	*Anopheles*
An. coluzzii	*Cellia*
An. comorensis	*Cellia*
An. concolor	*Anopheles*
An. confusus	*Cellia*
An. corethroides	*Anopheles*
An. costai	*Anopheles*
An. costalis	Unassigned
An. courdurieri	Unassigned
An. coustani	*Anopheles*
An. cracens	*Cellia*
An. crawfordi	*Anopheles*
An. cristatus	*Cellia*
An. cristipalpis	*Cellia*
An. crucians	*Anopheles*
An. cruzii	*Kerteszia*
An. crypticus	*Anopheles*
An. cucphuongensis	*Anopheles*

An. culicifacies	*Cellia*
An. culiciformis	*Anopheles*
An. culifacies	Unassigned
An. cydippis	*Cellia*
An. daciae	*Anopheles*
An. dancalicus	*Cellia*
An. darlingi	*Nyssorhynchus*
An. daudi	*Cellia*
An. deaneorum	*Nyssorhynchus*
An. deemingi	*Cellia*
An. demeilloni	*Cellia*
An. diluvialis	*Anopheles*
An. dirus	*Cellia*
An. dispar	*Cellia*
An. dissidens	*Anopheles*
An. distinctus	*Cellia*
An. domicolus	*Cellia*
An. dominicanus (fossil)	Unassigned
An. donaldi	*Anopheles*
An. dravidicus	*Cellia*
An. dthali	*Cellia*
An. dualaensis	*Cellia*
An. dunhami	*Nyssorhynchus*
An. dureni	*Cellia*
An. earlei	*Anopheles*
An. eiseni	Unassigned
An. ejercitoi	*Anopheles*
An. elegans	*Cellia*
An. engarensis	*Anopheles*
An. eouzani	*Cellia*
An. epiroticus	*Cellia*
An. erepens	*Cellia*
An. erythraeus	*Cellia*
An. ethiopicus	*Cellia*
An. evandroi	*Anopheles*
An. evansae	*Nyssorhynchus*
An. faini	*Cellia*
An. farauti	*Cellia*
An. fausti	*Anopheles*
An. filipinae	*Cellia*
An. flavicosta	*Cellia*
An. flavirostris	*Cellia*
An. fluminensis	*Anopheles*
An. fluviatilis	*Cellia*
An. fontinalis	*Cellia*
An. forattinii	*Anopheles*
An. fragilis	*Anopheles*
An. franciscanus	*Anopheles*
An. franciscoi	*Anopheles*
An. freeborni	*Anopheles*
An. freetownensis	*Cellia*
An. freyi	*Anopheles*
An. funestus	*Cellia*
An. fuscicolor	*Anopheles*
An. fuscivenosus	*Cellia*
An. gabaldoni	*Anopheles*
An. gabonensis	*Cellia*
An. galvaoi	*Nyssorhynchus*
An. gambiae	*Cellia*
An. garnhami	Unassigned
An. georgianus	*Anopheles*

An. gibbinsi	Unassigned
An. gigas	*Anopheles*
An. gilesi	*Lophopodomyia*
An. goeldii	*Nyssorhynchus*
An. gomezdelatorrei	*Lophopodomyia*
An. gonzalezrinconesi	*Kerteszia*
An. grabhamii	*Anopheles*
An. gracilis	Unassigned
An. grassei	*Cellia*
An. greeni	*Cellia*
An. grenieri	*Cellia*
An. griveaudi	*Cellia*
An. guarani	*Nyssorhynchus*
An. guarao	*Anopheles*
An. hackeri	*Cellia*
An. hailarensis	*Anopheles*
An. halophylus	*Nyssorhynchus*
An. hamoni	*Cellia*
An. hancocki	*Cellia*
An. hargreavesi	*Cellia*
An. harperi	*Cellia*
An. harrisoni	*Cellia*
An. hectoris	*Anopheles*
An. heiheensis	*Anopheles*
An. hermsi	*Anopheles*
An. hervyi	*Cellia*
An. hilli	*Cellia*
An. hinesorum	*Cellia*
An. hodgkini	*Anopheles*
An. homunculus	*Kerteszia*
An. hughi	*Cellia*
An. hunteri	*Anopheles*
An. hyrcanus	*Anopheles*
An. implexus	*Christya*
An. incognitus	*Cellia*
An. indefinitus	*Cellia*
An. ininii	*Nyssorhynchus*
An. insulaeflorum	*Anopheles*
An. intermedius	Unassigned
An. interruptus	*Anopheles*
An. introlatus	*Cellia*
An. inundatus	*Anopheles*
An. irenicus	*Cellia*
An. jacobi	Unassigned
An. jamesii	*Cellia*
An. janconnae	*Nyssorhynchus*
An. jebudensis	*Cellia*
An. jeyporiensis	*Cellia*
An. judithae	*Anopheles*
An. karwari	*Cellia*
An. keniensis	*Cellia*
An. kiangsuensis	Unassigned
An. kingi	*Cellia*
An. kleini	*Anopheles*
An. kochi	*Cellia*
An. kokhani	*Cellia*
An. kolambuganensis	*Cellia*
An. koliensis	*Cellia*
An. kompi	*Stethomyia*
An. konderi	*Nyssorhynchus*
An. koreicus	*Anopheles*

An. kosiensis	*Cellia*
An. kweiyangensis	*Anopheles*
An. kyondawensis	*Baimaia*
An. labranchiae	*Anopheles*
An. lacani	*Cellia*
An. laneanus	*Kerteszia*
An. lanei	*Nyssorhynchus*
An. latens	*Cellia*
An. leesoni	*Cellia*
An. lepidotus	*Kerteszia*
An. lesteri	*Anopheles*
An. letabensis	*Cellia*
An. letifer	*Anopheles*
An. leucosphyrus	*Cellia*
An. lewisi	*Anopheles*
An. liangshanensis	*Anopheles*
An. limosus	*Cellia*
An. lindesayi	Unassigned
An. listeri	*Cellia*
An. litoralis	*Cellia*
An. lloreti	*Cellia*
An. longipalpis	*Cellia*
An. longirostris	*Cellia*
An. lounibosi	*Cellia*
An. lovettae	*Cellia*
An. ludlowae	Unassigned
An. lungae	*Cellia*
An. lutzii	*Nyssorhynchus*
An. macarthuri	*Cellia*
An. machardyi	*Cellia*
An. maculatus	*Cellia*
An. maculipalpis	*Cellia*
An. maculipennis	*Anopheles*
An. maculipes	*Anopheles*
An. majidi	*Cellia*
An. malefactor	*Anopheles*
An. maliensis	*Cellia*
An. manalangi	*Anopheles*
An. mangyanus	*Cellia*
An. marajoara	*Nyssorhynchus*
An. marshallii	*Cellia*
An. marteri	*Anopheles*
An. martinius	*Anopheles*
An. mascarensis	*Cellia*
An. mattogrossensis	*Anopheles*
An. maverlius	*Anopheles*
An. medialis	Unassigned
An. mediopunctatus	*Anopheles*
An. melanoon	*Anopheles*
An. melas	*Cellia*
An. menglangensis	*Anopheles*
An. meraukensis	*Cellia*
An. merus	*Cellia*
An. messeae	*Anopheles*
An. millecampsi	*Cellia*
An. milloti	*Cellia*
An. minimus	*Cellia*
An. minor	*Anopheles*
An. minutus	Unassigned
An. mirans	*Cellia*
An. moghulensis	*Cellia*

An. montanus	*Anopheles*
An. mortiauxi	*Cellia*
An. moucheti	Unassigned
An. mousinhoi	*Cellia*
An. multicinctus	*Cellia*
An. multicolor	*Cellia*
An. murphyi	*Cellia*
An. namibiensis	*Anopheles*
An. natalensis	*Cellia*
An. nataliae	*Cellia*
An. neivai	*Kerteszia*
An. nemophilous	*Cellia*
An. neomaculipalpus	*Anopheles*
An. nero	Unassigned
An. nigerrimus	*Anopheles*
An. nigritarsis	*Nyssorhynchus*
An. nilgiricus	*Anopheles*
An. nili	*Cellia*
An. nimbus	*Stethomyia*
An. nimpe	*Anopheles*
An. nitidus	*Anopheles*
An. nivipes	*Cellia*
An. njombiensis	*Cellia*
An. noniae	*Anopheles*
An. notanandai	*Cellia*
An. notleyi	*Cellia*
An. novaguinensis	*Cellia*
An. nuneztovari	*Nyssorhynchus*
An. obscurus	*Anopheles*
An. occidentalis	*Anopheles*
An. oiketorakras	*Lophopodomyia*
An. okuensis	*Christya*
An. omorii	*Anopheles*
An. oreios	*Cellia*
An. oryzalimnetes	*Nyssorhynchus*
An. oswaldoi	*Nyssorhynchus*
An. ovengensis	*Cellia*
An. pallidus	*Cellia*
An. palmatus	*Anopheles*
An. paltrinierii	*Cellia*
An. paludis	*Anopheles*
An. pampanai	*Cellia*
An. papuensis	*Anopheles*
An. parangensis	*Cellia*
An. parapunctipennis	Unassigned
An. parensis	*Cellia*
An. parvus	*Myzorhynchella*
An. pattoni	*Cellia*
An. pauliani	*Cellia*
An. peditaeniatus	*Anopheles*
An. perplexens	*Anopheles*
An. persiensis	*Anopheles*
An. peryassui	*Anopheles*
An. petragnani	*Anopheles*
An. peytoni	*Anopheles*
An. pharoensis	*Cellia*
An. philippinensis	*Cellia*
An. pholidotus	*Kerteszia*
An. pictipennis	*Nyssorhynchus*
An. pilinotum	*Anopheles*
An. pinjaurensis	*Anopheles*

An. plumbeus	*Anopheles*
An. pollicaris	*Anopheles*
An. powderi	*Anopheles*
An. powelli	*Anopheles*
An. prachongae	*Anopheles*
An. pretoriensis	*Cellia*
An. pristinus	Unassigned
An. pseudobarbirostris	*Anopheles*
An. pseudojamesi	*Cellia*
An. pseudomaculipes	*Anopheles*
An. pseudopictus	*Anopheles*
An. pseudopunctipennis	Unassigned
An. pseudosinensis	*Anopheles*
An. pseudostigmaticus	*Anopheles*
An. pseudosundaicus	*Cellia*
An. pseudotibiamaculatus	*Lophopodomyia*
An. pseudowillmori	*Cellia*
An. pujutensis	*Cellia*
An. pulcherrimus	*Cellia*
An. pullus	*Anopheles*
An. punctimacula	*Anopheles*
An. punctipennis	*Anopheles*
An. punctulatus	*Cellia*
An. pursati	*Anopheles*
An. quadriannulatus	*Cellia*
An. quadrimaculatus	*Anopheles*
An. rachoui	*Anopheles*
An. radama	*Cellia*
An. rageaui	*Cellia*
An. rampae	*Cellia*
An. ranci	*Cellia*
An. rangeli	*Nyssorhynchus*
An. recens	*Cellia*
An. reidi	*Anopheles*
An. rennellensis	*Cellia*
An. rhodesiensis	*Cellia*
An. riparis	*Cellia*
An. rivulorum	*Cellia*
An. rodhaini	*Cellia*
An. rollai	*Kerteszia*
An. rondoni	*Nyssorhynchus*
An. roperi	*Anopheles*
An. rottensis (fossil)	Unassigned
An. roubaudi	*Cellia*
An. ruarinus	*Cellia*
An. rufipes	*Cellia*
An. sacharovi	*Anopheles*
An. saeungae	*Anopheles*
An. salbaii	*Cellia*
An. samarensis	*Anopheles*
An. sanctielii	*Nyssorhynchus*
An. saperoi	Unassigned
An. saungi	*Cellia*
An. sawadwongporni	*Cellia*
An. sawyeri	*Nyssorhynchus*
An. scanloni	*Cellia*
An. schueffneri	*Cellia*
An. schwetzi	*Cellia*
An. separatus	*Anopheles*
An. seretsei	*Cellia*
An. sergentii	Unassigned
An. seydeli	*Cellia*
An. shannoni	*Anopheles*
An. similissimus	*Anopheles*
An. sinensis	*Anopheles*
An. sineroides	*Anopheles*
An. sintoni	*Anopheles*
An. sintonoides	*Anopheles*
An. smaragdinus	*Anopheles*
An. smithii	*Cellia*
An. soalalaensis	*Anopheles*
An. solomonis	*Cellia*
An. somalicus	*Cellia*
An. splendidus	*Cellia*
An. squamifemur	*Lophopodomyia*
An. squamosus	*Cellia*
An. stephensi	*Cellia*
An. stigmaticus	*Anopheles*
An. stookesi	*Cellia*
An. striatus	*Nyssorhynchus*
An. stricklandi	*Anopheles*
An. strodei	*Nyssorhynchus*
An. subpictus	*Cellia*
An. sulawesi	*Cellia*
An. sumatranus	*Anopheles*
An. sundaicus	*Cellia*
An. superpictus	*Cellia*
An. swahilicus	*Cellia*
An. symesi	*Anopheles*
An. takasagoensis	*Cellia*
An. tasmaniensis	*Anopheles*
An. tchekedii	*Cellia*
An. tenebrosus	*Anopheles*
An. tessellatus	Unassigned
An. theileri	*Cellia*
An. theobaldi	*Cellia*
An. thomasi	*Stethomyia*
An. tibiamaculatus	*Anopheles*
An. tigertti	*Anopheles*
An. torresiensis	*Cellia*
An. triannulatus	*Nyssorhynchus*
An. trinkae	*Nyssorhynchus*
An. turkhudi	Unassigned
An. umbrosus	*Anopheles*
An. upemba	Unassigned
An. vagus	*Cellia*
An. vanderwulpi	*Anopheles*
An. vaneedeni	*Cellia*
An. vanhoofi	*Cellia*
An. vanus	*Anopheles*
An. vargasi	*Lophopodomyia*
An. varuna	*Cellia*
An. vernus	*Cellia*
An. veruslanei	*Anopheles*
An. vestitipennis	*Anopheles*
An. vietnamensis	*Anopheles*
An. vinckei	*Cellia*
An. vulgaris	Unassigned
An. walkeri	*Anopheles*
An. walravensi	*Cellia*
An. watsonii	*Cellia*
An. wejchoochotei	*Anopheles*

An. wellcomei	Unassigned
An. wellingtonianus	*Anopheles*
An. whartoni	*Anopheles*
An. willmorei	*Cellia*
An. wilsoni	Unassigned

An. xelajuensis	*Anopheles*
An. xui	*Anopheles*
An. yaeyamaensis	Unassigned
An. ziemanni	*Anopheles*

Parasite morphology: Mosquitoes form four developmental stages: eggs, larvae (four instars), pupae and adults (imagos). Eggs appear as brown ellipsoidal bodies 1-4 mm in length with a pair of lateral floats for buoyancy. They occur singly on the water surface and are not collected into flotation rafts like many culicine species. Mosquito larvae (wrigglers or wigglers) have dark tubular bodies with a small rounded head, globular thorax and elongate segmented abdomen. The head has chewing mouthparts with an anterior mouth brush, 2 lateral antennae and 2 eyes comprised of clusters of lateral ocelli. The thorax is often highly setate and the abdomen terminates in a short plate bearing respiratory spiracles (unlike the air tubes (respiratory siphon) of culicine larvae) and a lateral anal segment with long setae in conspicuous brushes. The wrigglers swim to the water surface at frequent intervals to breathe through their posterior spiracles by floating parallel to the water surface (not head-down like culicine larvae). Four larval stages are formed - all being similar in morphology but becoming successively larger (first stage larvae measure up to 1.5 mm in length and fourth stage larvae up to 8-10 mm). Mosquito pupae (tumblers) are comma-shaped when viewed from the side, translucent and about 3.5 mm in length. The head and thorax are merged into a large cephalothorax with the abdomen curving underneath. Pupae breathe through a pair of respiratory trumpets on the cephalothorax. Adult *Anopheles* mosquitoes are small winged insects with slender bodies up to 12 mm long, elongate mouthparts, thin legs and narrow wings. Their bodies are covered with scales, setae and fine hairs which give distinctive marking for each species. Anopheline mosquitoes commonly have brown to grey bodies and often have spotted wings. The body is divided into a small rounded head, a globular thorax, and a long segmented abdomen. When at rest, anopheline mosquitoes hold their abdomen in the air in line with their proboscis, both forming an acute angle to the substrate (whereas culicine mosquitoes rest with their abdomen more or less parallel to the substrate but at an angle to their proboscis). The head has 2 large compound eyes consisting of hundreds of ommatidial lenses wrapped around the front and sides, with long filamentous segmented antennae arising between the eyes (pilose in females and plumose in males). Both male and female anopheline mosquitoes have 2 elongate anterior palps, almost as long as the proboscis (unlike culicine mosquitoes whose females have short palps). The palps in male anophelines are also broadened (clubbed) at their tips (not clubbed in culicines). The long anterior proboscis (often as long as the head and thorax combined) contains complex piercing-sucking mouthparts consisting of a delicate labium (with terminal labella) forming a protective sheath for the other stylet-like mouthparts (fascicle comprising labrum, pair of mandibles, hypopharynx and pair of maxillae). The mandibles (with pointed tips) and maxillae (with serrated tips) are used to puncture skin, and then the labrum (with curled edges) fits together with the mandibles to form a tubular food canal, while the hypopharynx forms a salivary canal. Female mosquitoes use their mouthparts to feed on blood from vertebrate hosts or sugar solutions from plants, whereas males do not feed on blood as their mandibles and maxillae have atrophied and cannot pierce skin. Liquid food is ingested with the aid of muscular cibarial and pharyngeal pumps into the tubular oesophagus. Dilute fluids (plant sugars) are shunted for temporary storage into saccular diverticula (ventral diverticulum often called the crop) whereas nutrient-rich foods (blood) are routed through the proventricular valve to the tubular midgut (for digestion), hindgut (connected to Malpighian excretory tubules), bulbous rectum and terminal anus. The thorax has 2 pairs of respiratory spiracles and is covered by a rigid scutum with a posterior scutellum and conspicuous bristles (setae absent from prespiracular and postspiracular areas). Dorsally, the thorax is the point of attachment for a pair of slender membranous wings with small squamae framed by prominent veins (distinctive pattern of costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu) and anal (A) primary veins and branches). The wings often appear spotted due to patches of dark and light scales (whereas the wings of culicine mosquitoes usually appear light). The posterior thorax also contains a small pair of club-like halteres (highly reduced hindwings thought to help stabilize flight). Ventrally, the thorax gives rise to 3 pairs of long thin legs, each consisting of 5 segments (coxa, trochanter, femur, tibia and tarsus) with the terminal tarsi carrying 2 claws (pulvilli absent) surrounding a central pad (empodium). The abdomen is clearly segmented and capable of massive expansion (to accommodate large meals and developing eggs) due to membranous areas between each set of tergites and sternites. The posterior abdomen may be pointed or blunt depending on the species and abdominal scales are absent. Typically, 7 pairs of spiracles are found along the edges of the abdomen segments, and paired gonads are located within the posterior abdomen. The terminal abdominal segments are often modified by genital structures (ventral gonopores, female postgenital lobes (cerci), and male terminalia (including claspers)). Mature males have 2 testes with tubular vas deferens leading to a seminal vesicle (with lateral accessory glands) connected to a tubular ejaculatory duct that discharges through a retractable aedeagus (penis). Female mosquitoes have 2 ovaries (with polytrophic ovarioles) whose ducts unite to form a common oviduct connected to the gonopore via a genital chamber associated with spermathecae (for sperm storage) and small accessory glands.

Site of infection: Pre-adult developmental stages of mosquitoes occur in aquatic habitats. Larvae feed on organic material in water by filtering or gathering suspended material, scraping or shredding material from substrates and plants, and some species even prey on small aquatic invertebrates. Pupae are non-feeding aquatic stages which undergo metamorphosis to form winged adults. All adult mosquitoes are free-flying and move about their environments seeking food sources and mates. Both male and female *Anopheles* mosquitoes are able to feed on natural sugars from flowers and rotting fruits. However, females are also haematophagous (blood-feeding) ectoparasites on vertebrate hosts. Blood provides an iron-rich protein source necessary for the production of eggs. Mosquitoes are attracted to hosts by carbon dioxide plumes and other breath chemicals, body odours and heat. Bite sites are related to convection currents around their hosts: when standing, they will bite around the foot or heel region, but if lying down, they will

bite any body part close to the ground, including the torso. Many *Anopheles* spp. bite during the night (nocturnal) when their host sleeps, other species are active at dawn or dusk (crepuscular), and some will enter dwellings to feed (endophagic) and rest (endophilic). They may feed on a wide variety of sympatric vertebrate hosts (mammals, birds and reptiles), although many species have strong preferences for particular host species (especially ungulates, carnivores, rodents and birds). *Anopheles* spp. are distributed throughout the world, being particularly numerous in tropical and subtropical regions but also inhabiting cool temperate zones.

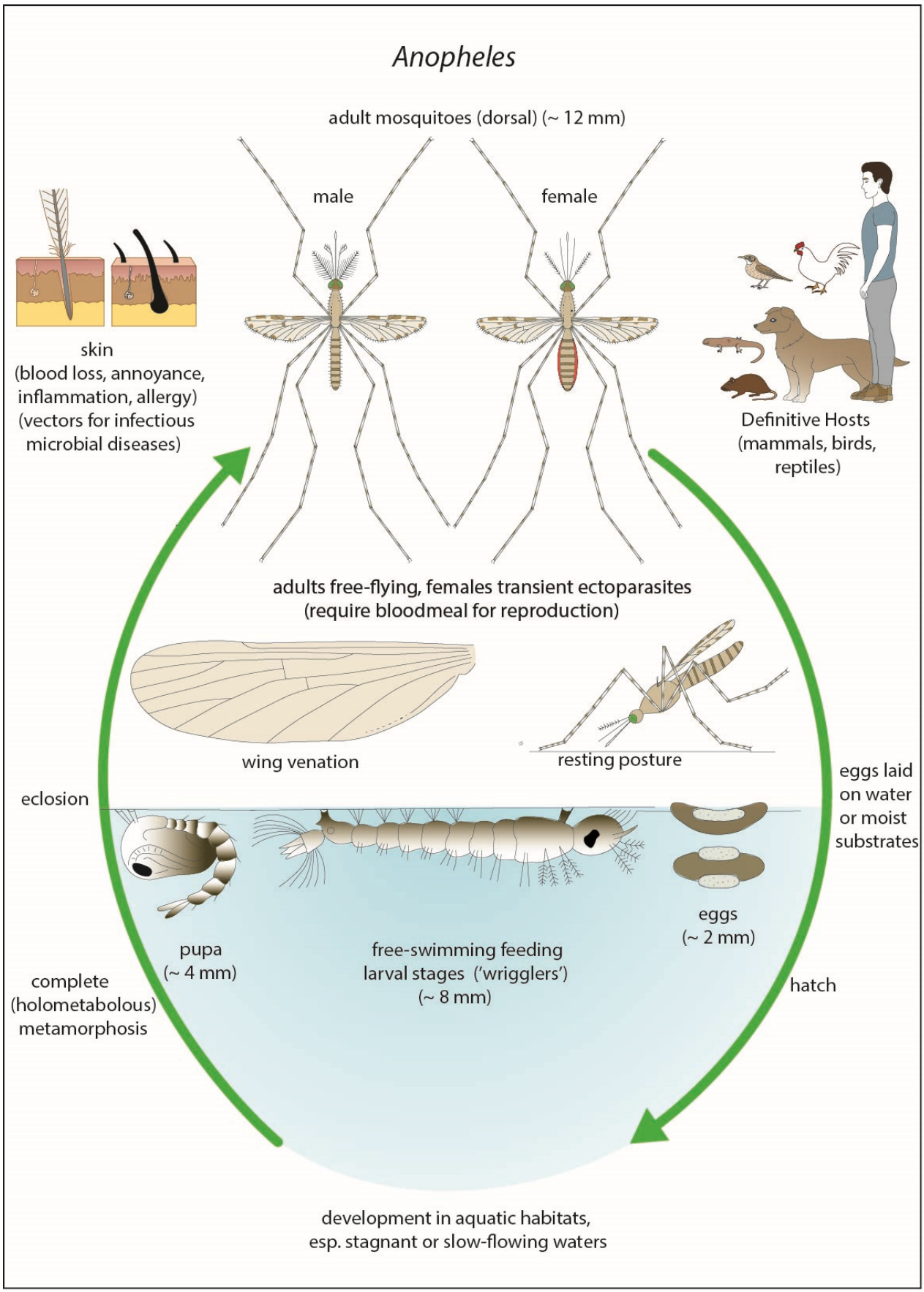
Pathogenesis: Female mosquitoes use their proboscis to pierce the skin of vertebrate hosts, penetrate small blood vessels and inject saliva before and during blood-feeding. Mosquito saliva contains several potent vaso-active chemicals with anti-coagulant, anti-platelet and vasodilatory activities. Initial exposure to mosquitoes often elicits little reaction, but subsequent bites show inflammatory reactions involving reddened (erythematous) papules and wheals around the puncture site. Bites may elicit itching sensation (pruritus) which induce scratching and may lead to secondary infections. Severely affected animals may develop papular dermatitis with cutaneous oedema, epidermal ulceration, crusting, and alopecia. Mosquito swarms can cause significant blood loss (anaemia) as well as considerable irritation and annoyance (biting stress) leading to risky and energetic aversion behaviours. Domestic livestock may be distracted from feeding and exhibit poor growth with lowered weight gains and reduced milk production. Repeated and persistent attack can result in hypersensitivity (immediate type I and/or delayed type IV) and severe allergic reactions (Skeeter syndrome), sometimes with unusual local or systemic effects such as angioedema, urticaria, wheezing, skin rashes and anaphylaxis. *Anopheles* mosquitoes also act as biological vectors for various infectious diseases, particularly viruses (incl. togaviruses, flaviviruses and bunyaviruses, collectively known as "arbo-viruses" (= arthropod-borne viruses)), protozoa (especially haemosporidians causing malaria) and nematodes (filarial worms). Various *Anopheles* spp. have been found to be highly efficient vectors for the transmission of viruses causing infectious equine anaemia, equine encephalitis and rabbit myxomatosis, nematodes causing canine heartworm (*Dirofilaria*) and human lymphatic filariasis (*Wuchereria* and *Brugia* spp.), and haemosporidia causing some mammalian, avian and reptilian malaria (note that anopheline mosquitoes are the sole vectors for the *Plasmodium* spp. causing human malaria]. Curiously, *Anopheles* spp. are not known to act as biological vectors for bacteria, although some species have been shown to be capable of mechanically transferring some bacterial species causing tularaemia and anthrax.

Developmental cycle and mode of transmission: Adult mosquitoes are efficient flyers and they actively seek hosts using chemotactic mechanisms, especially homing in on carbon dioxide plumes from expired breath. They can fly up to a few kilometres in their 2-3 week life-span, though females stay close to water sources to lay eggs. Females may deposit anywhere from 50-200 eggs per oviposition on the water surface, and the eggs have characteristic lateral floats that prevent them from sinking. The eggs hatch in 1-4 days releasing larvae which feed on organic material (detritus and micro-organisms) in stagnant or slow-flowing waters (pools, ponds, puddles, flooded tree-holes and even temporary water-filled containers). Anopheline larvae lie parallel to the water surface and breathe through pair of spiracles at the posterior end of the abdomen (while culicine larvae hang suspended from the water surface and breathe through prominent air tubes). The larvae develop through 4 instars over 3-20 days depending on environmental conditions, particularly water temperature and availability of larval food sources. The final larval instar then forms a non-feeding pupa in which to undergo complete metamorphosis. The pupae remain at the water surface breathing air using prothoracic respiratory siphons, but they can be highly mobile if disturbed. Pupation is completed within 1-7 days when the pupal case splits to release the adult which rests on nearby objects to harden its cuticle and inflate its wings. Adults then fly about their environments feeding on nectar and plant juices. Mating often occurs within 24 hours of emergence, but females are anautogenous and require bloodmeals from vertebrate hosts to complete their gonotrophic cycles and produce eggs. Females can bite multiple times and may take up to 3 bloodmeals before resting for several days prior to laying eggs.

Differential diagnosis: The visual detection of mosquitoes in the process of feeding is often not possible due to their nocturnal and transient feeding habits. Any resultant host reactions to bites are nonspecific and frequently delayed in onset. Capturing mosquitoes (by spraying or trapping) allows for their microscopic examination (using a magnifying lens or microscope) and identification. *Anopheles* species can be distinguished from other mosquito genera by the presence of black and white scales on their wings, the length of their palps being equal to the proboscis, and the elevated angle of their abdomens when resting (rather than being parallel to the resting surface). In some cases, serological tests for host antibodies to *Anopheles*-specific salivary proteins can be used to diagnose previous contact and the state of host immunity, especially in allergic or immunocompromised patients. A range of molecular biological techniques using polymerase chain reaction (PCR) amplification of specific gene sequences have been used on mosquito extracts to identify putative sources of bloodmeals, infer phylogenetic relationships between mosquito taxa, and also detect infectious micro-organisms carried by mosquitoes.

Treatment and control: There are currently no direct treatments for mosquito bites, apart from providing symptomatic relief using corticosteroids, antihistamines and anti-pruritic lotions, especially in allergic patients. Various insecticides have been developed to kill adult mosquitoes, most containing organophosphates (dioxathion, fenchlorvos), organophosphonates (chlorfenvinphos, trichlorfon), monothiophosphates (coumaphos, diazinon), dithiophosphates (malathion, phosmet), carbamates or pyrethrum and its derivatives (permethrin, cyfluthrin, cypermethrin). Various formulations may be used as aerosol and/or topical sprays, dust-bags or

impregnated into eartags which can also be affixed to animal collars and halters. Several traps have been developed to bait and immobilize or electrocute flying insects, and various insect repellents are available as sprays or lotions, notably those containing diethyltoluamide (DEET). Many control programs have been based on the indoor residual spraying of insecticides but their success has been compromised by the emergence of insecticide resistance by mosquito populations. Barriers can be used to separate mosquitoes from their hosts, including installing window screens, screening beds with impregnated nets, and covering exposed skin with clothing. Reducing mosquito larvae populations has proven very successful, mainly by eliminating potential breeding sites (swamps, ditches, puddles, etc) and spraying water sources with chemicals to kill, smother or starve larvae. Some measure of biological control has also been achieved by using natural predators (mosquito fish and dragonflies) to reduce larval populations, using natural pathogens (microsporan parasites and *Wolbachia* bacteria) to reduce mosquito fitness, and releasing sterilized males or transgenically modified mosquitoes. Many countries have adopted multiple methods of mosquito control in public health programs in attempts to curb the transmission of mosquito-borne infectious diseases.


Anopheles
adult mosquitoes (dorsal) (~ 12 mm)
male
female
skin
(blood loss, annoyance, inflammation, allergy)
(vectors for infectious microbial diseases)
Definitive Hosts
(mammals, birds, reptiles)
adults free-flying, females transient ectoparasites
(require bloodmeal for reproduction)
wing venation
resting posture
eclosion
eggs laid on water or moist substrates
pupa
(~ 4 mm)
free-swimming feeding larval stages ('wrigglers')
(~ 8 mm)
eggs
(~ 2 mm)
complete (holometabolous) metamorphosis
hatch
development in aquatic habitats,
esp. stagnant or slow-flowing waters



Anopheles adult



Anopheles egg



Anopheles larva head



Anopheles pupa

Culicoides
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Nematocerans include the culicids (mosquitoes), ceratopogonids (midges); simuliids (black flies) and psychodids (sand flies): only the females are parasitic and have piercing-sucking mouthparts. Ceratopogonids are very small but fierce flies known as biting midges. They have thoracic humps and narrow spotted wings. Many are daytime feeders, some crepuscular and others nocturnal, but all prefer still conditions as they do not cope well with winds. Most species feed on insects or cold-blooded animals, and only a few on mammals. Larvae develop in a range of conditions, mangroves, swamps, freshwater bodies, moist soils and animal dung. Female *Culicoides* spp. feed on humans and animals and are known to transmit viruses (bluetongue), protozoa (haemosporidia) and helminths (filarial nematodes).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class: Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder: Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order: Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder: Nematocera (midges/mosquitoes, long filamentous antennae, aquatic larvae/pupae)
Family: Ceratopogonidae (midges/sand flies, narrow spotted wings)
Genus: *Culicoides* (parasitic on skin of mammals/birds)
Species: various species cause pruritus, hypersensitivity

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission

Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Nematocera comprises small slender flies that are 'thread-horned' i.e. they possess long filamentous antennae composed of many articulating segments (= nemato-cera). Adults have long narrow wings (with many branching veins) and specialized mouthparts (short or long) with a protective sheath (labium and labellae) protecting feeding stylets (labrum, mandibles, maxillae and hypopharynx) and flanked by 4-5 segmented palps (usually pendulous but slender in mosquitoes). Many species have aquatic life-cycles (larval/pupal stages associated with water) and all undergo complete metamorphosis whereby adults eclose from puparia through longitudinal slits (rather than circular caps like Cyclorrapha). The suborder contains 7 infraorders: Axymyiomorpha (larvae in decomposing wood); Bibionomorpha (gnats, lovebugs); Blephariceromorpha (mountain midges); Culicomorpha (mosquitoes, midges, black flies); Psychodomorpha (moth flies); Ptychopteromorpha (primitive crane flies); and Tipulomorpha (crane flies). While small 'midges' have been further classified into several different groups, most are saprophages or detritivores, but several groups do contain representatives that bite vertebrate hosts in order to feed on blood. The infraorder Culicomorpha contains 2 superfamilies: Chironomoidea (biting, non-biting and trickle midges, black flies); and Culicoidea (meniscus midges, phantom midges, frog-biting midges, and mosquitoes).

The superfamily Chironomoidea contains 4 families: Ceratopogonidae (biting midges), Chironomidae (non-biting midges), Simuliidae (black flies), and Thaumaleidae (trickle midges). Members of the family Ceratopogonidae are readily distinguished by their small size, humped thorax, small head with long filamentous hairy antennae with 14-15 visible segments, short mouthparts, 5-segmented palps, short stout legs, and mottled hairy wings with forked medial veins and less than 8 veins reaching the wing margin. Over 6,000 ceratopogonid species have been described in over 100 genera in 4 subfamilies: Dasyheleinae with 1 genus; Leptoconopinae with 2 genera; Forcipomyiinae with 2 genera; and Ceratopogoninae with 6 tribes and 101 genera (including *Culicoides*); as well as several unplaced genera and over 20 fossil genera. In particular, the latter 3 subfamilies contain species that feed on vertebrate blood, with those belonging to 4 genera (*Austroconops, Leptoconops, Forcipomyia* and *Culicoides*) being notorious as annoying pests of humans and domestic animals, as well as acting as vectors for several infectious diseases (viruses, protozoa and helminths). Members of the genus *Culicoides* (syn. *Conopoides, Marksomyia, Padrosia, Remmia, Sensiculicoides*) are characterized by small biting midges with humped bodies and narrow spotted wings. Over 1,300 species have been described in 27 subgenera, many of them reported to feed on birds and mammals. Biting midges have been attributed many common names around the world attesting to their minute size and aggravating bites; including no-see-ums, punkies, five-o's, no-no's, brulot, knotts, kuiki, jejenes, maruins, makunagi, nukaka, nyung noi, agas, merutu, merotoe as well as moose flies and sand flies (but distinct from phlebotomine sand flies).

***Culicoides* species (regional exemplars)**	**Host preferences**	**Clinical signs (+ vectorial capacity)**	**Distribution**
C. bolitinos, brevitarsis, fulvus, gulbenkiani, histrio, imicola, impunctatus, insignis, milnei, nebeculosus, obsoletus, pulicaris, pungens, sibirica, sonorensis, variipennis, victoriae	domestic and wild mammals, some birds	annoyance, pruritus, hypersensitivity (equine dermatitis, bunyaviruses, reoviruses, rhabdoviruses, onchocerciasis, avian haemoproteid infection)	cosmopolitan
C. adersi, austeni, grahamii, inornatipennis	primates, incl. humans	annoyance, pruritus, hypersensitivity (hepatocystosis, mansonellosis)	Africa
C. denningi, furens, melanura, occidentalis, stelifer, venustus	domestic and wild mammals, incl. horses	annoyance, pruritus, hypersensitivity (eastern equine encephalitis)	North America
C. arboricola, crepuscularis, edeni, , haematopus, hinmani, knowltoni, sphagnemensis, stilobezzioides	birds, esp. passeriforms and galliforms	annoyance (avian haemoproteid infection)	North America
C. barbosai, diabolicus, paraensis, phlebotomus	primates, incl. humans	annoyance, hypersensitivity (mansonellosis, bunyaviruses)	South America
C. dycei, marksi, oxystoma, peregrinus, robertsi, wadai	domestic and wild mammals, and marsupials	annoyance, pruritus, hypersensitivity (bluetongue virus, onchocerciasis, reoviruses)	Australia
C. arakawae, circumscriptus, guttifer, schultzei	birds, esp. chickens	annoyance (avian leucocytozoonosis)	Asia

Full species list (compilation of several on-line data-bases)

***Culicoides* species**	**Subgenus**
C. abbreviatipennis (fossil)	Unassigned
C. abchazicus	*Avaritia*
C. acanthostoma	*Trithecoides*
C. accraensis	Unassigned
C. achkamalicus	*Oecacta*
C. achrayi	*Oecacta*
C. acotylus	*Oecacta*
C. actoni	*Avaritia*
C. adamskii	Unassigned
C. adersi	Unassigned
C. africanus	Unassigned
C. agamus (fossil)	Unassigned
C. agas	Unassigned
C. aitkeni	*Glaphiromyia*
C. alachua	*Avaritia*
C. alahialinus	*Oecacta*
C. alaskensis	*Beltranmyia*
C. alatavicus	*Oecacta*
C. alazanicus	*Oecacta*
C. albibasis	*Trithecoides*
C. albicans	*Oecacta*
C. albifascia	Unassigned
C. albipennis	Unassigned
C. albomacula	*Selfia*
C. albomotatus	Unassigned
C. albopunctatus	Unassigned
C. alboscutatus	*Trithecoides*
C. albosparsus	Unassigned
C. albovenosus	Unassigned

C. alexanderi	Unassigned
C. alexandrae	*Oecacta*
C. algecirensis	Unassigned
C. algeriensis	*Oecacta*
C. alishenensis	Unassigned
C. allantothecus	*Trithecoides*
C. almeidae	*Culicoides*
C. almirantei	*Oecacta*
C. alpicola	Unassigned
C. alpigenus	*Fastus*
C. altaicus	*Oecacta*
C. alticola	Unassigned
C. alvarezi	*Selfia*
C. amamiensis	*Culicoides*
C. amaniensis	Unassigned
C. amazonicus	Unassigned
C. ambericus (fossil)	*Oecacta*
C. ameliae	Unassigned
C. amossovae	*Oecacta*
C. anadyriensis	Unassigned
C. analis	Unassigned
C. andicola	*Avaritia*
C. andinus	*Oecacta*
C. andrewsi	*Culicoides*
C. angkaensis	*Culicoides*
C. angolensis	Unassigned
C. annandalei	*Avaritia*
C. annettae	*Hoffmania*
C. annosus (fossil)	Unassigned
C. annuliductus	Unassigned
C. anophelis	*Trithecoides*
C. antefurcatus	*Selfia*
C. antennalis	Unassigned
C. anthropophygas	*Sinocoides*
C. antilleanus (fossil)	*Oecacta*
C. antunesi	*Selfia*
C. aomoriensis	Unassigned
C. aquilinus	*Oecacta*
C. aquilonius (fossil)	Unassigned
C. arabiensis	Unassigned
C. aragaoi	Unassigned
C. arakanae	*Beltranmyia*
C. arboreus	*Oecacta*
C. arboricola	*Amossovia*
C. archboldi	*Oecacta*
C. ardentissimus	Unassigned
C. ardleyi	Unassigned
C. arenarius	Unassigned
C. arenicola	*Oecacta*
C. aricola	Unassigned
C. arizonensis	*Drymodesmyia*
C. arnaudi	*Oecacta*
C. arschanicus	Unassigned
C. arubae	Unassigned
C. asiaticus	*Oecacta*
C. atchleyi	Unassigned
C. atelis	Unassigned
C. aterinervis	*Culicoides*
C. atratus (fossil)	Unassigned
C. atripennis	*Oecacta*
C. aureus	*Oecacta*
C. austeni	Unassigned
C. austerus (fossil)	Unassigned
C. australiensis	Unassigned
C. austropalpalis	*Oecacta*
C. austroparaensis	Unassigned
C. autumnalis	*Culicoides*
C. avilaensis	*Oecacta*
C. azerbajdzhanicus	*Oecacta*
C. azureus	*Oecacta*
C. bachmanni	Unassigned
C. bahrainensis	Unassigned
C. baisasi	*Trithecoides*
C. bajensis	Unassigned
C. bakeri	*Drymodesmyia*
C. balsapambensis	*Oecacta*
C. balticus (fossil)	*Oecacta*
C. bambusicola	*Oecacta*
C. bancrofti	Unassigned
C. barbosai	*Oecacta*
C. barnetti	*Trithecoides*
C. barrosmachadoi	Unassigned
C. barthi	*Oecacta*
C. bassetorum	Unassigned
C. baueri	*Diphaomyia*
C. bayano	Unassigned
C. beaveri	Unassigned
C. beckae	*Amossovia*
C. bedfordi	Unassigned
C. begueti	*Oecacta*
C. belgicus	Unassigned
C. belkini	Unassigned
C. benarrochi	*Selfia*
C. bergi	*Diphaomyia*
C. bermudensis	*Beltranmyia*
C. bernardae	Unassigned
C. beybienkoi	*Oecacta*
C. biarcuatus	Unassigned
C. bickleyi	Unassigned
C. bicolor (fossil)	Unassigned
C. bicornus	Unassigned
C. biestroi	Unassigned
C. bifasciatus	Unassigned
C. bifidus (fossil)	Unassigned
C. bigeminus	*Avaritia*
C. biguttatus	*Silvaticulicoides*
C. bilobatus	Unassigned
C. bimaculatus	*Glaphiromyia*
C. birabeni	*Oecacta*
C. biscapus	Unassigned
C. bisignatus	Unassigned
C. bisolis	Unassigned
C. blantoni	*Diphaomyia*
C. bodemensis	Unassigned
C. bodemheimeri	Unassigned
C. bolitinos	*Avaritia*
C. boliviensis	Unassigned
C. boophagus	*Avaritia*
C. boormani	Unassigned
C. borinqueni	*Drymodesmyia*
C. bottimeri	*Wirthomyia*
C. bougainvillae	Unassigned

C. boydi	*Avaritia*
C. brachcordylus	Unassigned
C. brasilianus	*Glaphiromyia*
C. bredini	*Selfia*
C. brevifrontis	*Beltranmyia*
C. brevipalpis	*Avaritia*
C. brevitarsis	Unassigned
C. bricenoi	*Selfia*
C. brinchangensis	*Hoffmania*
C. brodzinskyi (fossil)	*Oecacta*
C. bromophilus	Unassigned
C. brookmani	*Selfia*
C. brosseti	Unassigned
C. brownei	*Hoffmania*
C. brucei	Unassigned
C. brunnicans	*Oecacta*
C. bubalus	*Culicoides*
C. buettikeri	Unassigned
C. buhetoensis	*Monoculicoides*
C. bulbostylus	*Oecacta*
C. bullus (fossil)	Unassigned
C. bundyensis	Unassigned
C. bunrooensis	*Oecacta*
C. burylovi	*Oecacta*
C. butleri	*Drymodesmyia*
C. bwambanus	Unassigned
C. bychowskyi	*Oecacta*
C. byersi	*Drymodesmyia*
C. cacticolus	*Drymodesmyia*
C. calcaratus	*Haemophoructus*
C. caldasi	Unassigned
C. calexicanus	Unassigned
C. californiensis	*Amossovia*
C. caliginosus	*Oecacta*
C. calloti	Unassigned
C. cambodiensis	*Culicoides*
C. cameronensis	Unassigned
C. cameroni	*Groganomyia*
C. camicasi	Unassigned
C. camposi	*Oecacta*
C. canadensis (fossil)	Unassigned
C. cancer	*Oecacta*
C. cancrisocius	Unassigned
C. capillosus	Unassigned
C. capricorniae	Unassigned
C. caprilesi	*Oecacta*
C. carbonelli	Unassigned
C. caridei	*Oecacta*
C. carpenteri	*Oecacta*
C. carpophilus	*Hoffmania*
C. carri (fossil)	Unassigned
C. carsiomelas	*Oecacta*
C. casei (fossil)	Unassigned
C. castillae	*Oecacta*
C. cataneii	*Oecacta*
C. catharinae	*Pontoculicoides*
C. caucaensis	*Oecacta*
C. caucoliberensis	*Oecacta*
C. causeyi	*Oecacta*
C. cavaticus	Unassigned
C. ceranowiczi (fossil)	Unassigned

C. certus	*Avaritia*
C. ceylanicus	Unassigned
C. chacoensis	Unassigned
C. chagyabensis	Unassigned
C. changbaiensis	Unassigned
C. charadraeus	*Oecacta*
C. charrua	Unassigned
C. chateaui	Unassigned
C. chaverrii	*Anilomyia*
C. chazeaui	Unassigned
C. cheahi	Unassigned
C. chengduensis	Unassigned
C. cheni	Unassigned
C. chewaclae	Unassigned
C. chiopterus	*Avaritia*
C. chitinosus	*Oecacta*
C. choochotei	*Culicoides*
C. chrysonotus	*Anilomyia*
C. cilipes	Unassigned
C. cinereus	Unassigned
C. circumbasalis	Unassigned
C. circumscriptus	*Beltranmyia*
C. citroneus	Unassigned
C. claggi	Unassigned
C. clarkei	Unassigned
C. clastrier	*Oecacta*
C. clavipalpis	Unassigned
C. cleaves	Unassigned
C. clintoni	Unassigned
C. coarctatus	Unassigned
C. cochisensis	*Amossovia*
C. cockerellii	*Culicoides*
C. combinothecus	Unassigned
C. commatis	*Selfia*
C. comosioculatus	*Oecacta*
C. comparis	*Avaritia*
C. concatervans	*Trithecoides*
C. confusus	Unassigned
C. congolensis	Unassigned
C. copiosus	*Drymodesmyia*
C. coracinus	Unassigned
C. cordiformis	Unassigned
C. cordiger	Unassigned
C. corneti	Unassigned
C. corniculus	Unassigned
C. cornutus	Unassigned
C. coronalis	Unassigned
C. corsis	*Oecacta*
C. corsoni	Unassigned
C. corti	Unassigned
C. costalis	Unassigned
C. coutinhoi	*Glaphiromyia*
C. covagarciai	*Anilomyia*
C. crassipilosus	*Oecacta*
C. crassus	Unassigned
C. crepuscularis	*Beltranmyia*
C. crescentris	*Selfia*
C. crucifer	*Oecacta*
C. cuiabai	Unassigned
C. culiciphagus	Unassigned
C. cummingi	Unassigned

C. cunctans	Unassigned
C. cuniculus	Unassigned
C. cylindratus	*Culicoides*
C. daedaloides	*Selfia*
C. daedalus	Unassigned
C. dalessandroi	Unassigned
C. damnosus	Unassigned
C. dampfi	*Selfia*
C. darlingtonae	*Oecacta*
C. dasyheleiformis (fossil)	*Oecacta*
C. dasyophus	*Oecacta*
C. dasyops	Unassigned
C. davidi	*Hoffmania*
C. daviesi	*Selfia*
C. davisi	Unassigned
C. deanei	Unassigned
C. debilipalpis	*Haematomyidium*
C. décor	*Anilomyia*
C. definitus	*Avaritia*
C. defoliarti	*Diphaomyia*
C. dekeyseri	Unassigned
C. delfinadoae	*Avaritia*
C. dellapei	*Haematomyidium*
C. delta	*Culicoides*
C. dendriticus	*Oecacta*
C. dendrophilus	*Oecacta*
C. denisae	*Oecacta*
C. denisoni	Unassigned
C. denningi	*Selfia*
C. dentatus	Unassigned
C. denticulatus	Unassigned
C. derisor	*Oecacta*
C. desertorum	*Beltranmyia*
C. desytoculus	Unassigned
C. dewulfi	*Avaritia*
C. diabolicus	*Glaphiromyia*
C. diamouanganai	Unassigned
C. dicrourus	*Oecacta*
C. diffusus	*Hoffmania*
C. digitalis	*Monoculicoides*
C. dikhros	Unassigned
C. dingriensis	*Oecacta*
C. diplus	Unassigned
C. discrepans	*Oecacta*
C. dispar	Unassigned
C. dispersus	*Oecacta*
C. distinctipennis	Unassigned
C. distinctus	Unassigned
C. diversus	Unassigned
C. divisus	*Hoffmania*
C. doeringae	Unassigned
C. dominicanus	*Anilomyia*
C. donajil	*Oecacta*
C. downesi	Unassigned
C. duartei	Unassigned
C. dubiosum	Unassigned
C. dubitatus	Unassigned
C. dubius	*Culicoides*
C. duddingstoni	*Oecacta*
C. dukinensis	Unassigned
C. dumdumi	*Culicoides*

C. dungunensis	*Trithecoides*
C. dunhuaensis	*Jilinocoides*
C. dunni	*Selfia*
C. duodenarius	*Meijerehelea*
C. dureti	Unassigned
C. dutoiti	Unassigned
C. dycei	Unassigned
C. dzhafarovi	*Oecacta*
C. eadsi	*Haematomyidium*
C. edeni	*Diphaomyia*
C. efferus	*Anilomyia*
C. effusus	*Culicoides*
C. elbeli	*Trithecoides*
C. eldridgei	Unassigned
C. elemae	*Amossovia*
C. elizabethae	Unassigned
C. elongatulus (fossil)	Unassigned
C. elongatus	Unassigned
C. elutus	*Culicoides*
C. enderleini	Unassigned
C. engubandei	Unassigned
C. eoselficus (fossil)	Unassigned
C. equatoriensis	*Oecacta*
C. erairai	*Oecacta*
C. eremicus	Unassigned
C. erikae	*Diphaomyia*
C. eriodendroni	Unassigned
C. esakii	Unassigned
C. espinolai	Unassigned
C. estevezae	Unassigned
C. eublepharus	*Oecacta*
C. eupurus	Unassigned
C. evansi	*Diphaomyia*
C. excavatus	Unassigned
C. expalleus	*Monoculicoides*
C. exspectator	Unassigned
C. fadzili	Unassigned
C. faghihi	*Oecacta*
C. fagineus	*Culicoides*
C. farri	*Anilomyia*
C. fascipennis	*Oecacta*
C. felippebauerae	*Mataemyia*
C. fernandezi	*Oecacta*
C. fernandoi	*Hoffmania*
C. ferreyrai	Unassigned
C. festivipenis	*Oecacta*
C. fieldi	*Oecacta*
C. filamentis	Unassigned
C. filarifer	*Glaphiromyia*
C. filicinus	*Avaritia*
C. filiductus	Unassigned
C. filipalpis (fossil)	Unassigned
C. firuzae	*Oecacta*
C. flavescens	*Trithecoides*
C. flavidorsalis	Unassigned
C. flavimaculinotalis	Unassigned
C. flavipes	Unassigned
C. flavipulicaris	*Culicoides*
C. flavirostris	Unassigned
C. flaviscriptus	Unassigned
C. flaviscutatus	*Trithecoides*

C. flaviscutellaris	*Trithecoides*
C. flavisomum	Unassigned
C. flavitibialis	*Trithecoides*
C. flavivenula	*Glaphiromyia*
C. flavus	Unassigned
C. flinti	Unassigned
C. flochabonnenci	*Oecacta*
C. florenciae	*Oecacta*
C. floridensis	Unassigned
C. flukei	*Amossovia*
C. fluminensis	Unassigned
C. flumineus	Unassigned
C. fluvialis	*Oecacta*
C. fluviatilis	*Selfia*
C. foleyi	*Oecacta*
C. footei	*Diphaomyia*
C. forattinii	*Oecacta*
C. fordae	*Trithecoides*
C. fossicola	Unassigned
C. fossilis (fossil)	Unassigned
C. foxi	*Glaphiromyia*
C. fragmentum	Unassigned
C. franclemonti	Unassigned
C. franklini	*Hoffmania*
C. freeborni	*Culicoides*
C. frohnei	*Culicoides*
C. fukienensis	Unassigned
C. fukudai	Unassigned
C. fulbrighti	Unassigned
C. fulvithorax	Unassigned
C. fulvus	Unassigned
C. furcillatus	*Oecacta*
C. furens	*Oecacta*
C. furensoides	*Oecacta*
C. fuscicaudae	Unassigned
C. fuscus	Unassigned
C. gabaldoni	*Oecacta*
C. galindoi	*Oecacta*
C. galliardi	Unassigned
C. gambiae	Unassigned
C. garciai	*Avaritia*
C. gedanensis (fossil)	Unassigned
C. gejgelensis	*Oecacta*
C. gemellus	*Haemophoructus*
C. geminus	Unassigned
C. gentilis	*Haemophoructus*
C. gentiloides	*Haemophoructus*
C. geocheloneoides	*Tokunagahelea*
C. germanus	*Oecacta*
C. gewertzi	*Trithecoides*
C. giganteus	Unassigned
C. gigas	*Monoculicoides*
C. ginesi	*Oecacta*
C. glabellus	*Oecacta*
C. glabrior	*Oecacta*
C. gladysae	Unassigned
C. gluchovae	*Beltranmyia*
C. glushchenkoae	*Avaritia*
C. gorgasi	*Oecacta*
C. gornostaevae	Unassigned
C. gouldi	*Trithecoides*
C. gracilior (fossil)	Unassigned
C. gracilipes	*Oecacta*
C. grahamii	Unassigned
C. grandensis	*Monoculicoides*
C. grandibocus (fossil)	Unassigned
C. gregsoni	*Culicoides*
C. grenieri	Unassigned
C. griffithi	*Avaritia*
C. griseidorsum	*Oecacta*
C. griseolus	Unassigned
C. grisescens	*Culicoides*
C. guadeloupensis	*Oecacta*
C. guangxiensis	*Jilinocoides*
C. guarani	Unassigned
C. guerrai	*Oecacta*
C. guineensis	Unassigned
C. gulbenkiani	Unassigned
C. gutsevichi	*Oecacta*
C. guttatus	*Glaphiromyia*
C. guttifer	*Meijerehelea*
C. guttipennis	*Amossovia*
C. guyanensis	*Oecacta*
C. gymnopterus	*Haemophoructus*
C. haematopotus	*Diphaomyia*
C. haitiensis	Unassigned
C. halonostictus	*Beltranmyia*
C. hamiensis	Unassigned
C. hanae	*Oecacta*
C. haranti	*Oecacta*
C. hasegawai	*Avaritia*
C. hawsi	Unassigned
C. hayakawai	*Avaritia*
C. hayesi	*Anilomyia*
C. hegneri	*Meijerehelea*
C. heliconiae	*Glaphiromyia*
C. heliophilus	*Oecacta*
C. helveticus	*Monoculicoides*
C. hengduanshanensis	Unassigned
C. henryi	Unassigned
C. herero	Unassigned
C. hermani	*Avaritia*
C. heteroclits	*Oecacta*
C. hewitti	Unassigned
C. hieroglyphicus	*Selfia*
C. hildae	Unassigned
C. hildebrandoi	Unassigned
C. himalayae	Unassigned
C. hinmani	*Drymodesmyia*
C. hinnoi	*Trithecoides*
C. hirstus	Unassigned
C. hirsutus	Unassigned
C. hirtipennis	*Culicoides*
C. hirtulus	*Avaritia*
C. hispanicolus (fossil)	*Oecacta*
C. histrio	*Meijerehelea*
C. hitchcocki	Unassigned
C. hoffmani	*Oecacta*
C. hoffmanioides	*Haemophoructus*
C. hoguei	Unassigned
C. hokkaidoensis	Unassigned
C. holcus	Unassigned

C. hollandiensis	Unassigned
C. hollensis	*Beltranmyia*
C. homochorus	*Beltranmyia*
C. homotomus	*Monoculicoides*
C. hondurensis	*Culicoides*
C. hornsbyensis	Unassigned
C. hortensis	Unassigned
C. horticola	*Oecacta*
C. huambensis	Unassigned
C. huayingensis	Unassigned
C. huberti	*Trithecoides*
C. huffi	Unassigned
C. hui	*Avaritia*
C. hulinensis	Unassigned
C. humeralis	*Trithecoides*
C. husseyi	Unassigned
C. hyalinus	Unassigned
C. hylas	*Glaphiromyia*
C. hypsipyles	Unassigned
C. ibericus	*Pontoculicoides*
C. ibriensis	Unassigned
C. ichesi	Unassigned
C. ignacioi	*Glaphiromyia*
C. iliensis	*Oecacta*
C. imicola	*Avaritia*
C. imitador	*Oecacta*
C. imperceptus	*Avaritia*
C. impunctatus	*Culicoides*
C. impusilloides	Unassigned
C. indecorus	Unassigned
C. indianus	*Culicoides*
C. inexploratus	Unassigned
C. inflatipalpalis	Unassigned
C. infulatus	Unassigned
C. innoxius	*Culicoides*
C. inornatithorax	*Trithecoides*
C. insignipennis	*Culicoides*
C. insignis	*Hoffmania*
C. insinuatus	*Oecacta*
C. insolatus	*Drymodesmyia*
C. insulanus	Unassigned
C. insularis	*Oecacta*
C. interrogatus	Unassigned
C. inthanonensis	*Oecacta*
C. inyoensis	*Diphaomyia*
C. iphthimus	Unassigned
C. iranicus	*Oecacta*
C. iriartei	*Culicoides*
C. irregularis	Unassigned
C. irwini	Unassigned
C. isechnoensis	*Meijerehelea*
C. isioloensis	Unassigned
C. jacksoni	*Selfia*
C. jacobsoni	*Avaritia*
C. jamaicensis	*Drymodesmyia*
C. jamesi	*Selfia*
C. jamnbacki	Unassigned
C. japonicus	*Beltranmyia*
C. javae	Unassigned
C. javanicus	Unassigned
C. jefferyi	Unassigned

C. jianfenglingensis	Unassigned
C. jimmiensis	*Culicoides*
C. jonesi	*Drymodesmyia*
C. jouberti	Unassigned
C. jucundus (fossil)	Unassigned
C. juddi	*Avaritia*
C. jumineri	*Oecacta*
C. jurbergi	*Diphaomyia*
C. jurensis	*Oecacta*
C. jurutiensis	*Haematomyidium*
C. kaimosiensis	Unassigned
C. kaluginae (fossil)	Unassigned
C. kampa	*Haematomyidium*
C. kamrupi	*Pontoculicoides*
C. kanagai	Unassigned
C. kangdingewnsis	*Fastus*
C. karagiensis	*Oecacta*
C. karajevi	*Oecacta*
C. karakumensis	*Oecacta*
C. karenensis	Unassigned
C. kasimi	*Oecacta*
C. kayi	*Marksomyia*
C. kelantanensis	*Avaritia*
C. kelinensis	Unassigned
C. kepongensis	*Avaritia*
C. kerichoensis	Unassigned
C. kettlei	*Haematomyidium*
C. kibatiensis	Unassigned
C. kibunensis	Unassigned
C. kinabaluensis	*Hoffmania*
C. kinari	*Haemophoructus*
C. kingi	*Oecacta*
C. kirbyi	Unassigned
C. kirgizicus	*Oecacta*
C. kirinensis	*Culicoides*
C. kisangkini	*Haemophoructus*
C. klossi	*Culicoides*
C. knowltoni	*Beltranmyia*
C. kobae	Unassigned
C. kolymbiensis	Unassigned
C. komarovi	Unassigned
C. konmiaoensis	*Sinocoides*
C. koreensis	*Beltranmyia*
C. korossoensis	Unassigned
C. kotonkan	Unassigned
C. krameri	Unassigned
C. kribiensis	Unassigned
C. krombeini	Unassigned
C. kucheensis	Unassigned
C. kugitangi	*Oecacta*
C. kumbaensis	Unassigned
C. kurensis	*Oecacta*
C. kusaiensis	Unassigned
C. kuscheli	Unassigned
C. kyotoensis	*Avaritia*
C. kyushuensis	Unassigned
C. labis	Unassigned
C. lacustris	Unassigned
C. lahontan	*Culicoides*
C. laimargus	Unassigned
C. lamborni	Unassigned

C. landauae	*Oecacta*
C. lanei	*Oecacta*
C. langeroni	*Oecacta*
C. lansangensis	*Culicoides*
C. lanyuensis	*Culicoides*
C. laoensis	*Trithecoides*
C. lasaensis	Unassigned
C. latifrons	Unassigned
C. latifrontis	*Oecacta*
C. latipennis	Unassigned
C. laurae (fossil)	Unassigned
C. leanderensis	Unassigned
C. leechi	Unassigned
C. leei	Unassigned
C. lenae	*Oecacta*
C. lenti	Unassigned
C. leoni	*Oecacta*
C. leopoldoi	*Oecacta*
C. leucostictus	Unassigned
C. lichyi	*Oecacta*
C. lieni	*Oecacta*
C. liliputanus (fossil)	Unassigned
C. limai	*Oecacta*
C. limonensis	*Oecacta*
C. lini	Unassigned
C. linleyi	Unassigned
C. lisicarruni	Unassigned
C. liubaensis	*Beltranmyia*
C. liui	*Culicoides*
C. liukueiensis	Unassigned
C. lobatoi	Unassigned
C. loisae	*Silvaticulicoides*
C. longicercus	*Trithecoides*
C. longicollis	*Monoculicoides*
C. longior	Unassigned
C. longipalpis	*Culicoides*
C. longipennis	*Oecacta*
C. longiporus	Unassigned
C. longiradialis	Unassigned
C. longirostris	Unassigned
C. lopesi	*Oecacta*
C. lophortygis	Unassigned
C. loughnani	*Drymodesmyia*
C. loxodontis	*Avaritia*
C. luganicus	*Oecacta*
C. luglani	Unassigned
C. lulianchengi	Unassigned
C. lutealaris	*Anilomyia*
C. luteolus	*Trithecoides*
C. luteoventus	*Culicoides*
C. lutzi	*Glaphiromyia*
C. lyrinotatus	*Oecacta*
C. maai	*Avaritia*
C. macclurei	*Avaritia*
C. macfiei	*Trithecoides*
C. macieli	*Oecacta*
C. macintoshi	Unassigned
C. mackerrasi	Unassigned
C. macrostigma	*Oecacta*
C. maculatus	*Avaritia*
C. maculipennis	*Haemophoructus*
C. maculiscutellaris	Unassigned
C. maculitibialis	*Trithecoides*
C. madagascarensis	Unassigned
C. magnificus	*Beltranmyia*
C. magnipalpis	*Oecacta*
C. magnipictus	Unassigned
C. magnithecalis	*Meijerehelea*
C. magnus	Unassigned
C. majorinus	Unassigned
C. malariologiensis	Unassigned
C. malayae	*Culicoides*
C. malevillei	*Oecacta*
C. mamaensis	Unassigned
C. mammalicolus (fossil)	Unassigned
C. manchuriensis	*Beltranmyia*
C. manikumari	*Trithecoides*
C. marcleti	*Oecacta*
C. marginalis	Unassigned
C. marginatus	Unassigned
C. marginus	Unassigned
C. margipictus	Unassigned
C. marinkellei	*Culicoides*
C. maritime	*Oecacta*
C. marksi	Unassigned
C. marmoratus	Unassigned
C. marshi	*Anilomyia*
C. martinezi	*Oecacta*
C. martyrius	*Haematomyidium*
C. maruim	*Glaphiromyia*
C. mathisi	Unassigned
C. matsuzawai	*Trithecoides*
C. mayeri	Unassigned
C. mcdonaldi	Unassigned
C. mcdowelli	Unassigned
C. mckeeveri	*Diphaomyia*
C. mcmillani	Unassigned
C. megacanthus (fossil)	Unassigned
C. meijerei	Unassigned
C. melanesiae	Unassigned
C. melleus	Unassigned
C. mellipes	*Haemophoructus*
C. menghaiensis	Unassigned
C. menglaensis	Unassigned
C. meridionalis	Unassigned
C. mesghalii	*Oecacta*
C. metagonatus	*Anilomyia*
C. micheli	Unassigned
C. micromaculatus	Unassigned
C. midorensis	*Oecacta*
C. miharai	*Oecacta*
C. mihunensis	*Jilinocoides*
C. mikros	*Tokunagahelea*
C. milnei	Unassigned
C. minasensis	Unassigned
C. minimaporus	*Jilinocoides*
C. minimus	*Avaritia*
C. minipalpis	*Avaritia*
C. minutunculus	Unassigned
C. minutus	Unassigned
C. miocenicus (fossil)	Unassigned
C. miombo	*Avaritia*

C. mirsae	*Oecacta*
C. mirzaevi	*Pontoculicoides*
C. mississippiensis	*Beltranmyia*
C. miuntissimus	*Oecacta*
C. mohave	Unassigned
C. mojingaensis	*Oecacta*
C. molestior	Unassigned
C. molestus	Unassigned
C. mollis	Unassigned
C. molotovae	Unassigned
C. mongolensis	*Oecacta*
C. monicae	*Anilomyia*
C. monocylichnus	*Trithecoides*
C. monoensis	Unassigned
C. monothecalis	Unassigned
C. montanus	*Avaritia*
C. monticola	*Oecacta*
C. moreensis	Unassigned
C. moreli	Unassigned
C. morisitai	*Oecacta*
C. mortivallis	Unassigned
C. motoensis	Unassigned
C. moucheti	Unassigned
C. mukerjii	*Diphaomyia*
C. mulrennani	*Silvaticulicoides*
C. multifarious	Unassigned
C. multifidous	*Beltranmyia*
C. multimaculatus	Unassigned
C. multinotatae	Unassigned
C. multipunctatus	*Selfia*
C. murphyi	Unassigned
C. murrayi	*Avaritia*
C. murtalai	Unassigned
C. musajevi	*Beltranmyia*
C. muscicola	Unassigned
C. mykytowyczi	Unassigned
C. mystacinus	Unassigned
C. nagarzensis	Unassigned
C. nairobiensis	Unassigned
C. nampui	*Trithecoides*
C. namulus	Unassigned
C. nanellus	Unassigned
C. nanpingensis	Unassigned
C. nanus	Unassigned
C. narrabeenensis	Unassigned
C. nasuensis	Unassigned
C. nattaiensis	Unassigned
C. navaiae	*Beltranmyia*
C. nayabazari	*Avaritia*
C. neavei	Unassigned
C. neghmei	*Oecacta*
C. neoangolensis	Unassigned
C. neofagineus	*Culicoides*
C. neomelanesiae	Unassigned
C. neomontanus	*Culicoides*
C. neopalpalis	Unassigned
C. neoparaensis	*Oecacta*
C. neopulicaris	*Culicoides*
C. neoschultzei	Unassigned
C. nevilli	Unassigned
C. newsteadi	*Culicoides*
C. nibleyi	*Oecacta*
C. nielamensis	Unassigned
C. niger	*Oecacta*
C. nigeriae	Unassigned
C. nigrigenus	*Anilomyia*
C. nigripennis	Unassigned
C. nigripes	*Avaritia*
C. nigritus	Unassigned
C. nigroannulatus	*Culicoides*
C. nigrosignatus	Unassigned
C. nigrus	Unassigned
C. nilogenus	Unassigned
C. nilophilus	Unassigned
C. niphanae	*Avaritia*
C. nipponensis	*Culicoides*
C. nitens	*Haemophoructus*
C. nivosus	Unassigned
C. nobrei	Unassigned
C. nocivus	Unassigned
C. noshaquensis	*Oecacta*
C. notatus	Unassigned
C. novaguineanus	Unassigned
C. novairelandi	Unassigned
C. novamexicanus	Unassigned
C. nubeculosus	*Monoculicoides*
C. nudipalpis	*Avaritia*
C. nudipennis	*Oecacta*
C. nukabirensis	Unassigned
C. nunomemoguri	*Oecacta*
C. nuntius	Unassigned
C. nupurius	*Avaritia*
C. nyakini	*Haemophoructus*
C. nyungnoi	*Trithecoides*
C. obesus (fossil)	Unassigned
C. obnoxius	*Oecacta*
C. obscuratus (fossil)	Unassigned
C. obsoletus	*Avaritia*
C. obuncus (fossil)	Unassigned
C. occidentalis	*Monoculicoides*
C. ochraceimaculatus	*Beltranmyia*
C. ochraceipennis	*Beltranmyia*
C. ochrothorax	Unassigned
C. octosignatus	Unassigned
C. oculatus	Unassigned
C. ocumarensis	*Glaphiromyia*
C. odai	Unassigned
C. odiatus	*Oecacta*
C. odiosus	Unassigned
C. okazawai	Unassigned
C. oklahomensis	*Amossovia*
C. olyslageri	Unassigned
C. omogensis	*Oecacta*
C. onderstepoortensis	Unassigned
C. onoi	*Oecacta*
C. oregonensis	Unassigned
C. orescius	*Oecacta*
C. orestes	*Hoffmania*
C. orientalis	*Avaritia*
C. orjuelai	*Avaritia*
C. ornatus	Unassigned
C. ostroushkoae	*Silvaticulicoides*

C. ousairani	*Amossovia*
C. ovalis	Unassigned
C. owyheensis	Unassigned
C. oxianus	*Beltranmyia*
C. pabloi	Unassigned
C. pachymerus	*Oecacta*
C. padusae	*Culicoides*
C. paksongi	*Trithecoides*
C. palauensis	Unassigned
C. palawanensis	Unassigned
C. pallidicornis	*Oecacta*
C. pallidimaculosus	Unassigned
C. pallidizonatus	Unassigned
C. pallidothorax	Unassigned
C. pallidus	*Oecacta*
C. palmerae	Unassigned
C. palpalis	*Hoffmania*
C. palpifer	*Trithecoides*
C. palpisimilis	*Avaritia*
C. pamiricus	*Oecacta*
C. pampaensis	Unassigned
C. pampangensis	Unassigned
C. pampoikilus	Unassigned
C. panamensis	*Drymodesmyia*
C. pancensis	Unassigned
C. pangkorensis	*Avaritia*
C. papillatus	Unassigned
C. papilliger	Unassigned
C. papuensis	Unassigned
C. parabarnetti	*Trithecoides*
C. parabubalus	*Hoffmania*
C. paradisionensis	Unassigned
C. paraensis	Unassigned
C. paraflavescens	*Trithecoides*
C. paragarciai	Unassigned
C. parahumeralis	*Trithecoides*
C. paraignacioi	*Hoffmania*
C. paraimpunctatus (fossil)	Unassigned
C. paraliui	*Culicoides*
C. paramalayae	*Hoffmania*
C. parapiliferus	Unassigned
C. parararipalpis	*Trithecoides*
C. parascopus	Unassigned
C. parauapebensis	Unassigned
C. parroti	*Monoculicoides*
C. parvimaculatus	Unassigned
C. parviscriptus	Unassigned
C. parvulus	Unassigned
C. pastus	*Avaritia*
C. patulipalpis	*Oecacta*
C. paucienfuscatus	*Oecacta*
C. paulipictus	Unassigned
C. pechumani	*Avaritia*
C. pecosensis	*Amossovia*
C. peculiaris	*Diphaomyia*
C. pelilioensis	Unassigned
C. pellucidus	Unassigned
C. pendleburyi	*Trithecoides*
C. pentamaculatus	*Oecacta*
C. perakensis	Unassigned
C. peregrinus	*Culicoides*
C. perettii	Unassigned
C. perornatus	Unassigned
C. peruvianus	Unassigned
C. petersi	Unassigned
C. petronius	*Oecacta*
C. phaeonotus	*Oecacta*
C. phlebotomus	*Macfiella*
C. photophilus	Unassigned
C. picadoae	Unassigned
C. pichindensis	Unassigned
C. pictellum	Unassigned
C. pictilis	*Avaritia*
C. pictipennis	*Oecacta*
C. picturatus	*Oecacta*
C. pifanoi	*Oecacta*
C. pikongkoi	*Haemophoructus*
C. piliferus	Unassigned
C. pilosipennis	Unassigned
C. pilosus	*Drymodesmyia*
C. platiradius	Unassigned
C. plaumanni	*Hoffmania*
C. poikilonotus	*Drymodesmyia*
C. polynesiae	Unassigned
C. polypori	*Hoffmania*
C. polystictus	*Selfia*
C. pongsomiensis	*Oecacta*
C. popayanensis	*Anilomyia*
C. poperonghensis	*Oecacta*
C. posoensis	Unassigned
C. praesignis	Unassigned
C. pretoriensis	Unassigned
C. profundus	Unassigned
C. prolixipalpis	*Meijerehelea*
C. propinquus	*Oecacta*
C. propriipennis	*Oecacta*
C. prussicus (fossil)	Unassigned
C. pseudocordiger	Unassigned
C. pseudocrescentis	Unassigned
C. pseudodiabolicus	*Hoffmania*
C. pseudoheliconiae	Unassigned
C. pseudoheliophilus	*Oecacta*
C. pseudolangeroni	Unassigned
C. pseudopallidipennis	Unassigned
C. pseudopallidus	*Oecacta*
C. pseudopalpalis	*Avaritia*
C. pseudoreticulatus	Unassigned
C. pseudosalinarius	Unassigned
C. pseudostigmatus	Unassigned
C. pseudoturgidus	*Avaritia*
C. pulchellus	Unassigned
C. pulchripennis	*Oecacta*
C. pulicaris	Unassigned
C. pumilus	Unassigned
C. puncticeps	Unassigned
C. puncticollis	*Monoculicoides*
C. punctithorax	Unassigned
C. pungens	*Avaritia*
C. pungobovis	Unassigned
C. puracensis	*Avaritia*
C. puripennis	*Oecacta*
C. purus	Unassigned

C. pusilloides	*Avaritia*
C. pusillus	*Avaritia*
C. pycnostictus	Unassigned
C. pygmaeus	Unassigned
C. qabdoensis	Unassigned
C. qinghaiensis	Unassigned
C. qiongzhongensis	Unassigned
C. quadratus	*Culicoides*
C. quadrisignatus	Unassigned
C. quadrivittatus	Unassigned
C. quaiparaensis	*Oecacta*
C. quatei	*Avaritia*
C. quaterifasciatus	Unassigned
C. queenslandae	Unassigned
C. quinquelineatus	Unassigned
C. quinquermaculatus	Unassigned
C. rabauli	Unassigned
C. rachoui	*Oecacta*
C. radicitus	*Avaritia*
C. radiomaculatus	Unassigned
C. rageaui	Unassigned
C. rangeli	*Oecacta*
C. raposoensis	Unassigned
C. raripalpis	*Trithecoides*
C. rariradialis	*Haemophoructus*
C. rarus	*Meijerehelea*
C. ravus	Unassigned
C. reconditus	*Oecacta*
C. recurvus	*Culicoides*
C. reevesi	*Haematomyidium*
C. remerki	Unassigned
C. remotus	Unassigned
C. reticulatus	*Oecacta*
C. rhizophorensis	Unassigned
C. rhombus	Unassigned
C. ribeiroi	Unassigned
C. riebi	Unassigned
C. riethi	*Monoculicoides*
C. riggsi	Unassigned
C. riouxi	*Oecacta*
C. ritzei	*Oecacta*
C. robini	Unassigned
C. rochemus	Unassigned
C. rodriguezi	*Oecacta*
C. ronderosae	*Diphaomyia*
C. rostratus	*Anilomyia*
C. roswelli	Unassigned
C. rugulithecus	*Trithecoides*
C. ruiliensis	Unassigned
C. ruizi	*Hoffmania*
C. rutilis	Unassigned
C. ryckmani	*Drymodesmyia*
C. saboyae	Unassigned
C. sabroskyi	Unassigned
C. saevanicus	*Oecacta*
C. saevus	*Pontoculicoides*
C. sahariensis	*Oecacta*
C. saintjusti	*Hoffmania*
C. sajanicus	*Oecacta*
C. salebrosus	Unassigned
C. salihi	Unassigned

C. salinarius	*Beltranmyia*
C. saltaensis	Unassigned
C. saltonensis	*Culicoides*
C. samoensis	Unassigned
C. sanguisuga	*Avaritia*
C. saninensis	*Oecacta*
C. sanmartini	Unassigned
C. santanderi	Unassigned
C. santonicus	*Oecacta*
C. sarawakensis	*Trithecoides*
C. saundersi	Unassigned
C. scanloni	Unassigned
C. schramae	Unassigned
C. schultzei	Unassigned
C. scopus	*Glaphiromyia*
C. scoticus	*Avaritia*
C. segnis	*Oecacta*
C. seimi	*Avaritia*
C. sejfadinei	*Pontoculicoides*
C. selangorensis	*Avaritia*
C. sellersi	Unassigned
C. semicircum	Unassigned
C. semimaculatus	*Oecacta*
C. sensillatus	*Oecacta*
C. septemmaculatus	Unassigned
C. sergenti	*Oecacta*
C. shahgudiani	*Oecacta*
C. shaklawensis	*Oecacta*
C. shermani	Unassigned
C. shimoniensis	Unassigned
C. shortti	*Oecacta*
C. siamensis	*Avaritia*
C. sibiricus	*Beltranmyia*
C. sibiricus (fossil)	Unassigned
C. sierrensis	*Culicoides*
C. sigaensis	*Avaritia*
C. sigmoidus	Unassigned
C. signatus	Unassigned
C. sikkimensis	*Avaritia*
C. silverstrii	Unassigned
C. similis	Unassigned
C. simulans	Unassigned
C. simulator	*Oecacta*
C. sinanoensis	*Avaritia*
C. sitiens	*Drymodesmyia*
C. slovacus	*Pontoculicoides*
C. smeei	Unassigned
C. snowi	Unassigned
C. sogdianus	*Oecacta*
C. sommermanae	*Culicoides*
C. sonorensis	*Monoculicoides*
C. sordidellus	*Culicoides*
C. sousadiasi	Unassigned
C. speciosus (fossil)	*Oecacta*
C. sphagnumensis	*Beltranmyia*
C. sphenostylus (fossil)	Unassigned
C. spiculae	*Haemophoructus*
C. spinifer	Unassigned
C. spinosus	*Silvaticulicoides*
C. spinoverbosus	Unassigned
C. spinulosus	Unassigned

C. spurius	*Oecacta*
C. stagetus	Unassigned
C. stanicicus	*Oecacta*
C. stellifer	*Oecacta*
C. stepicola	*Oecacta*
C. stercorarius	Unassigned
C. stigma	*Monoculicoides*
C. stigmalis	*Selfia*
C. stigmaticus	Unassigned
C. stilobezzioides	*Wirthomyia*
C. stonei	Unassigned
C. suarezi	*Avaritia*
C. subfagineus	Unassigned
C. subfasciipennis	*Oecacta*
C. subflavescens	*Trithecoides*
C. subgedanensis (fossil)	Unassigned
C. subgedanicus (fossil)	Unassigned
C. subimmaculatus	Unassigned
C. sublettei	*Silvaticulicoides*
C. subltifrontis	*Oecacta*
C. submagnesianus	Unassigned
C. subneglectus	*Oecacta*
C. suborientalis	*Avaritia*
C. subpalpifer	*Trithecoides*
C. subpunctatus	Unassigned
C. subravus	Unassigned
C. subschultzei	Unassigned
C. subsylvarum	*Oecacta*
C. succineus (fossil)	*Oecacta*
C. succivarius (fossil)	*Oecacta*
C. suiyangensis	*Avaritia*
C. sumatrae	*Culicoides*
C. superfluthecus	Unassigned
C. superfulvus	Unassigned
C. suspectus	Unassigned
C. swaminathi	*Oecacta*
C. sylvarum	*Oecacta*
C. sylvicola	Unassigned
C. tadzhikistanicus	*Oecacta*
C. tahemanensis	*Culicoides*
C. taimyricus (fossil)	Unassigned
C. taiwanensis	Unassigned
C. talgariensis	*Oecacta*
C. tamada	*Trithecoides*
C. tamaensis	Unassigned
C. tamboensis	*Oecacta*
C. taonanensis	*Monoculicoides*
C. tarapaca	Unassigned
C. tatebeae	Unassigned
C. tauffiebi	Unassigned
C. tauricus	*Pontoculicoides*
C. tavaresi	Unassigned
C. tawauensis	*Haemophoructus*
C. tayulingensis	Unassigned
C. tbilisicus	*Oecacta*
C. tentorius	*Oecacta*
C. tenuifasciatus	*Hoffmania*
C. tenuilosus	*Oecacta*
C. tenuipalpis	*Trithecoides*
C. tenuipennis (fossil)	Unassigned
C. tenuistylus	*Selfia*
C. teretipalpis	Unassigned
C. testudinalis	Unassigned
C. tetrathyris	*Oecacta*
C. thurmanae	*Avaritia*
C. tianmushanensis	Unassigned
C. tiaratus	*Oecacta*
C. tibetensis	*Avaritia*
C. tidwelli	*Hoffmania*
C. tienhsiangensis	Unassigned
C. tissoti	Unassigned
C. tobaensis	*Avaritia*
C. tohokuensis	*Oecacta*
C. tokunagai	*Oecacta*
C. tonmai	*Trithecoides*
C. tororensis	Unassigned
C. tororoensis	Unassigned
C. torreyae	*Haematomyidium*
C. torridus	*Drymodesmyia*
C. towadaensis	*Culicoides*
C. toyamaruae	*Beltranmyia*
C. transferrans	*Oecacta*
C. translucens	Unassigned
C. translucens	Unassigned
C. trapidoi	Unassigned
C. travassosi	*Hoffmania*
C. travisi	Unassigned
C. triallantionis	*Trithecoides*
C. triangulatus	*Oecacta*
C. trichopis	Unassigned
C. trifasciellus	Unassigned
C. trifidus	Unassigned
C. trilineatus	*Oecacta*
C. trimaculipennis	*Hoffmania*
C. trinidadensis	*Hoffmania*
C. tripallidus	Unassigned
C. trisignatus	Unassigned
C. tristanii	Unassigned
C. tristriatulus	*Culicoides*
C. tritenuifasciatus	Unassigned
C. trivittatus	*Oecacta*
C. trizonatus	Unassigned
C. tropicalis	Unassigned
C. trouilleti	Unassigned
C. truncatus (fossil)	Unassigned
C. truncorum	*Oecacta*
C. tsutaensis	Unassigned
C. tuamsombooni	*Oecacta*
C. tugaicus	*Oecacta*
C. tunkinensis	Unassigned
C. turanicus	*Oecacta*
C. turgidus	*Avaritia*
C. tuttifrutti	*Avaritia*
C. tyrrelli (fossil)	Unassigned
C. ukrainensis	*Oecacta*
C. uncistylus	Unassigned
C. undentaris	*Oecacta*
C. unetensis	Unassigned
C. unicolor	Unassigned
C. unicus	*Haemophoructus*
C. uniradialis	*Oecacta*
C. univittatus	*Oecacta*

C. uruguayensis	Unassigned
C. usingeri	*Silvaticulicoides*
C. ustinovi	*Oecacta*
C. utahensis	Unassigned
C. utowana	Unassigned
C. vagus	Unassigned
C. variatus	Unassigned
C. variifrons	*Oecacta*
C. variipennis	*Monoculicoides*
C. venezulensis	*Oecacta*
C. ventralis (fossil)	Unassigned
C. venustus	*Hoffmania*
C. verbosus	Unassigned
C. verecundus	*Hoffmania*
C. vetustus	Unassigned
C. vexans	*Oecacta*
C. vicinus	Unassigned
C. victoriae	Unassigned
C. vidourlensis	*Oecacta*
C. villosipennis	*Amossovia*
C. vitreipennis	*Oecacta*
C. vitshumbiensis	Unassigned
C. vomensis	Unassigned
C. wadai	*Avaritia*
C. walkeri	Unassigned
C. wandashanensis	Unassigned
C. wansoni	Unassigned
C. wardi	Unassigned
C. waringi	Unassigned
C. wenzeli	Unassigned
C. werneri	Unassigned
C. williamsi	Unassigned
C. willistoni	*Macfiella*
C. williwilli	Unassigned
C. wirthi	Unassigned
C. wirthomyia	*Drymodesmyia*
C. wisconsiensis	Unassigned
C. wisconsinensis	*Beltranmyia*
C. wokei	*Oecacta*
C. wuyiensis	Unassigned
C. xanifer	*Hoffmania*
C. xanthoceras	Unassigned
C. xanthogaster	Unassigned
C. xinjiangensis	Unassigned
C. xuguitensis	Unassigned
C. yamii	*Culicoides*
C. yanbianensis	Unassigned
C. yankari	Unassigned
C. yasumatsui	Unassigned
C. yemenensis	Unassigned
C. yoosti (fossil)	Unassigned
C. yoshimurai	Unassigned
C. youngi	Unassigned
C. yuchihensis	*Culicoides*
C. yui	*Oecacta*
C. yukonensis	*Culicoides*
C. yunanensis	Unassigned
C. zentae	*Marksomyia*
C. zhogolevi	*Oecacta*
C. zikaensis	Unassigned
C. zuluensis	Unassigned
C. zumbadoi	Unassigned

Parasite morphology: Ceratopogonid midges form 4 different types of developmental stages: eggs; larvae; pupae; and adults. The eggs are small (250-500 μm long), cylindrical to crescent-shaped, initially white in colour but gradually darkening to brown, and covered with minute projections. The larvae and long and slender with tubular segmented bodies ranging up to 2-5 mm in length. They have a small dark yellow to brown head capsule possessing mouthparts with non-opposable mandibles that move vertically or partially rotate to scrape, tear and seize items. The buccal cavity has a complex sclerotized epipharynx with pharyngeal combs. The cylindrical body is translucent white with 12 segments and no appendages except for 4 pairs of caudal setae. There are 4 larval instars which depend on cutaneous respiration (most lack spiracles) and osmoregulation via narrow bifid anal papillae (everted sporadically through the anus when alive but usually retracted in preserved specimens). Pupae are light brown in colour and have elongate conical bodies up to 2-3 mm long. The broader anterior end has a pair of short prothoracic respiratory horns with numerous tiny spiracular openings at their tips. The long body appears segmented as details of the internal developmental stages are visible, including developing adult appendages and cuticular features such as tubercles, spines and setae. Adult midges are small winged insects usually 1.0-2.5 mm long (some up to 4 mm) with grey to brown (sometimes black) bodies with an iridescent sheen. They have 3 distinct body parts: a small conical head, a humped thorax and an ovoid abdomen. The head has 2 large well-developed compound eyes, 2 elongate filamentous antennae (basal scape, enlarged pedicel containing Johnston's organ, and 13 flagellomeres) and forward-projecting biting/piercing mouthparts (well developed in females, particularly in blood-sucking species, but reduced in males). The stylet-like mouthparts are contained in a short proboscis (sheath formed by labium with terminal labella) and consist of an upper labrum-epipharynx, a pair of blade-like mandibles (with teeth along the inner edges), a pair of curved lacinae (maxillae) and a ventral hypopharynx (with a longitudinal groove along which saliva flows during feeding). The mouthparts are flanked by maxillary palps each with 5 segments, the third segment being enlarged and bearing specialized sensilla in a sensory pit. The alimentary tract consists of a tubular oesophagus leading to a globular proventriculus where dilute fluids (e.g. plant sugars) may be shunted for storage into a saccular diverticulum (crop) whereas nutrient-rich foods (e.g. blood) are routed to the tubular midgut (for digestion) with waste passing through the hindgut (connected to Malpighian excretory tubules), rectum (with expandable ampulla) and terminal anus. The globular thorax is often black spotted and the dorsal scutum appears humped over the head with a distinct set of small humeral pits along the anterior edge. The thorax bears 2 pairs of respiratory spiracles (anterior mesothoracic pair and posterior metathoracic pair) and often contains small bristles. The dorsal thorax gives rise to a pair of elongate narrow wings which appear hairy and mottled (spotted) due to distinct patterns of tiny setae (macro- and micro-trichia) on the wing surface (rather than pigment). The wing membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), anal (A)] with distinct patterns (notably forked M veins, R-M cross-veins present, and 2 radial cells present). At rest, the wings are

folded over each other and held flat on abdomen. The second pair of wings in all dipteran flies are highly reduced to a pair of posterior knob-like halteres used to stabilize flight. The ventral thorax gives rise to 3 pairs of short stout legs, each with 5 segments (coxa, trochanter, femur, tibia, and tarsus), the latter carrying a pair of claws surrounding a central empodium. The ovoid abdomen has 11 segments and 7 pairs of dorso-lateral spiracles. The terminal segments are modified by the presence of ventral genital plates and ducts and external genital appendages (female ovipositor, male claspers). Males have 2 testes connected by tubular vas deferens to a seminal vesicle (with lateral accessory glands) leading to an ejaculatory duct with a terminal bulb located beneath the genital plate housing the retractable copulatory aedeagus. Females have 2 ovaries (with polytrophic ovarioles) connected by oviducts to a globular uterus, often with associated spermatheca and accessory glands, leading to the vulva.

Site of infection: Only adult female midges of some *Culicoides* spp. are transient blood-feeders on vertebrate hosts. They typically have a narrow range of preferred hosts in tropical regions, but will feed on other available hosts in cooler temperate regions. Many species appear to feed primarily on mammals, whereas others feed preferentially on birds, reptiles or amphibians. A small range of species have been found to bite humans, domestic animals (esp. cattle, sheep and horses), smaller ground-dwelling mammals, poultry and aviary birds. Some species have also been found to exhibit site preferences, some (such as *C. brevitarsis*) feeding along the dorsal mid-line, while others (such as *C. marksi*) feed on the legs and belly. All other developmental stages (eggs, larvae and pupae) are free-living in aquatic or semi-aquatic habitats (ranging from ponds to bogs to decaying organic material).

Pathogenesis: Although midges have shorter mouthparts than mosquitoes, they inflict more painful bites by using their cutting mandibles to puncture/lacerate the host skin causing blood to seep into surrounding tissues. Female midges are pool feeders and imbibe this blood through a food canal formed by the other mouthparts and the pumping action of strong pharyngeal muscles. During feeding, they inject saliva containing vasoactive compounds with anti-coagulant, anti-platelet and vasodilatory properties. Midge bites may cause significant fly worry to their hosts, especially when conditions favour population explosions leading to dense swarms. Animals become stressed, irritated and annoyed and may exhibit extravagant avoidance behaviours resulting in energy expenditure, biting stress and reduced grazing leading to decreased productivity and self-trauma predisposing to secondary infections. Lesions may develop at bite sites with papule formation, inflammation and pruritus. Many individuals may also develop hypersensitivity reactions (both immediate and delayed) after repeated exposure to midge salivary components. Some humans develop reactive papules with intense pruritus which may last for days, whereas some animals may develop severe papular dermatitis which lasts for weeks. Horses may develop a condition known as ‘sweet itch’ or ‘Queensland itch’ with intense irritation, papules, ulceration, crusting, scaling, severe pruritus, lichenification, hyperpigmentation, excoriation and alopecia, exacerbated by self-trauma (rubbing, scratching). Lesions may be present dorsally or ventrally, particularly along the back, withers and base of the tail. Horses of all breeds and sexes may be affected, usually annually when conditions favour midge swarms. Biting midges have been shown to act as both biological and mechanical vectors for various infectious diseases, particularly arthropod-borne (arbo-) viruses, including bunyaviruses (causing Crimean-Congo haemorrhagic fever, Oropouche, Shuni and Dugbe in humans and cattle, and a range of conditions in wildlife), reoviruses (causing African horse sickness, bluetongue in livestock, epizootic haemorrhagic fever in deer, and a number of regional specific conditions in livestock), and rhabdoviruses (causing bovine ephemeral fever). Biting midges also transmit filarial nematodes (causing mansonellosis in humans and onchocerciasis in animals), and haemosporidia (causing leucocytozoonosis and haemoproteid lesions in birds).

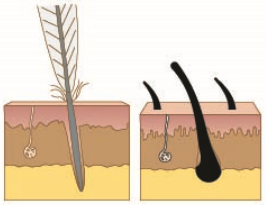
Developmental cycle and mode of transmission: Biting midges are free-living insects for their entire life-cycles, but the female adult stages of some species are transient ectoparasites biting vertebrate hosts and feeding on their blood to obtain nutrients for egg production. Like all dipteran insects, midges undergo complete metamorphosis whereby grub-like larvae undergo pupation and transform into winged adults. Gravid females are oviparous and oviposit eggs in batches in a wide range of aquatic and semi-aquatic habitats extending from the tropics to subpolar regions. The eggs hatch in 2-7 days releasing vermiform segmented larvae which live, feed and develop in their moist environments. Larvae have been found in open waters (including standing or slow-flowing saline and freshwater ponds, streams and river margins), water-logged or damp earth (freshwater and tidal marshes, mangroves, swamps, bogs, peats, mud holes and wet soil) and decaying organic material (tree holes and other cavities in wood, rotting cacti, decaying vegetation, and animal dung). The species *C. brevitarsis* develops mainly in cattle dung. The larvae of some species are good swimmers with a distinctive serpentine side-to-side thrashing motion in water, some browse over wet or submerged substrates, while others burrow into moist semi-solid substrates. *Culicoides* larvae prefer organically-enriched substrates where they feed opportunistically on detritus and particulate material, including micro-organisms (bacteria, fungi, algae, diatoms, protozoa) and small invertebrates (rotifers, oligochaetes, nematodes, insect larvae). The larvae grow and moult through 4 instars over 2-6 weeks, although many species may extend that period for up to a year when they overwinter as larvae for several months, or when larvae become dormant during hot summer months. Pupation usually occurs in spring or early summer, when fourth larval instars form pupal cases in which to undergo metamorphosis to adults over 3-10 days. Pupae occur near the surface of water bodies or moist substrates so they can respire through their anterior prothoracic horns. Male midges often emerge just before females and mating usually occurs in swarms (coincident with synchronous/seasonal development). Both males and females may feed on nectar from flowering plants, but the females of some species are anautogenous and require a bloodmeal from a vertebrate hosts before they can lay eggs (although some species are autogenous and emerge with enough nutrients to undergo at least the first gonotrophic cycle). Females seek hosts using chemical and thermal cues (odours and warmth) and they usually feed at 3-4 day intervals on mammals, birds, reptiles and even other invertebrates. Different *Culicoides* spp. may exhibit some degree of host specificity or at least host

preferences (e.g. *C. brevitarsis* feeds primarily on cattle, while *C. imicola* feeds mainly on horses). Most female midges only undergo 2-3 gonotrophic cycles after feeding, with egg development taking 3-10 days before oviposition in moist environments. Females may lay from 25-450 eggs over their life-spans, which may be as brief as 2-7 weeks but may be extended for several months (possibly 2 years?) in colder subpolar regions. The females of most species feed in the early morning or late afternoon (crepuscular activity) although some may feed overnight (nocturnal). Feeding is also more prevalent and frequent during overcast or dull humid weather. Many environmental factors have been found to influence midge flight activity, including temperature, humidity, light intensity, lunar cycles, barometric pressure and wind velocity, but adult midges are generally not strong fliers and are found close to aquatic/semi-aquatic habitats suitable for larvae. Geographic and ecological factors have been used to recognize regionally-specific species-groups, with 'maritime' species being significant pests to humans and coastal developments (many having painful bites, even through standard mosquito nets), and several 'peri-urban' and 'rural' species negatively impacting livestock industries.

Differential diagnosis: Clinical signs observed in vertebrates are not sufficiently characteristic to facilitate diagnosis as dermal lesions and inflammation may be attributed to many ectoparasites. Likewise, the assessment of clinical parameters is non-specific, with haematological examination often revealing peripheral eosinophilia, and histopathological examination of skin biopsies generally demonstrating eosinophilic perivascular dermatitis. While the development of papular dermatitis in hosts exhibiting seasonal or protracted irritation around twilight hours may be suggestive of feeding activity, diagnosis depends on direct observation of biting midges which is often difficult due to their small size, cryptic behaviour and extreme host avoidance behaviours. Differential diagnosis relies on the capture of feeding midges using baits or nets for subsequent microscopic examination and identification. Immunodiagnostic techniques have been used to detect host reactions to midge antigens in intradermal skin tests, and molecular biological techniques have been used to detect gene sequences from various *Culicoides* spp. following polymerase chain reaction (PCR) amplification (notably those midge species implicated in the transmission of viral diseases).

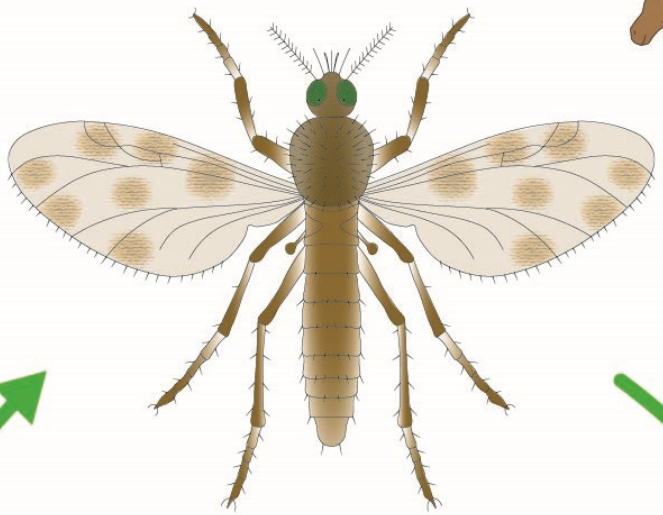
Treatment and control: Hosts exhibiting clinical signs of biting midge infestations may be treated with insecticides to discourage and suppress biting activity (topical formulations such as sprays, pour-ons, creams, dusts, or impregnated eartags applied to ears, collars or halters). Many conventional insecticides have proven effective against biting midges; including organophosphates (coumaphos, chlorfenvinphos, diazinon, dioxathion, fenchlorvos, malathion, phosmet, stirofos, trichlorfon) and pyrethroids (permethrin, cyfluthrin, cypermethrin). Severely affected hosts may also require supportive therapy in the form of systemic glucocorticoids and antihistamines to alleviate inflammation and hypersensitivity reactions. A range of management practices have been adopted to avoid biting midges, notably by moving people or livestock indoors at twilight, closing or screening doors and windows, and covering bare skin preferably with cloth treated with insect repellents (such as diethyltoluamide, DEET). However, such efforts are not always appropriate or effective, given that some midge species follow hosts indoors, others are small enough to move through conventional screen meshes, and some are able to bite through thin clothing. The application of insecticides with good residual activity to indoor areas (particularly midge resting places) has met with limited success as has the use of traps or baits containing attractants and insecticides, often simply due to the huge numbers of midges occurring in seasonal swarms. Similarly, attempts to treat breeding or congregation sites with insecticides have met with limited success. Adulticides delivered in mists or fogs often require regular (weekly) applications as they disperse unevenly and are unsuitable in windy conditions. Larvicides applied to water sources, wet grounds and manure simply lack coverage over the numerous and diverse habitats utilized by midge larvae (aquatic and semi-aquatic) and may also have undesirable ecological impacts (killing non-target species, upsetting natural cycles). Nonetheless, every effort should be made where possible to eliminate midge breeding sites by removing dung, rotting vegetable matter, maintaining water reticulation systems, regularly flushing ponds and irrigation channels, draining standing waters, and even discing wet soils.

Culicoides



skin
(annoyance, pruritus, inflammation, allergy)
(vectors for infectious microbial diseases)

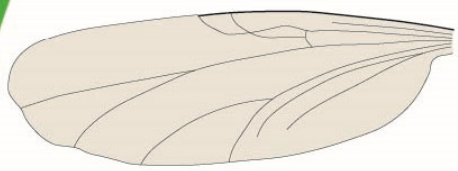
adult female
(dorsal) (~ 2 mm)



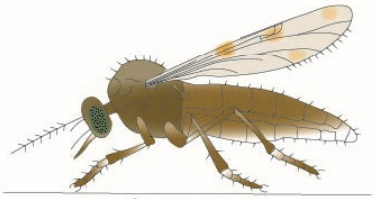


Definitive Hosts
(mammals, birds)

adults free-flying, females transient ectoparasites
(require bloodmeal for reproduction)



wing venation



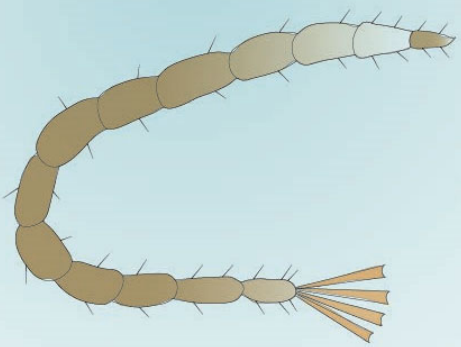
resting posture

eclosion

eggs laid in moist areas

pupa
(~ 2.5 mm)







egg
(~ 350 µm)

complete (holometabolous) metamorphosis

hatch

free-living feeding larva
(~ 3 mm)

development in semi-aquatic to aquatic habitats,
incl. mangroves, swamps, moist soils, animal dung, freshwater bodies



Culicoides adult



Culicoides eggs



Culicoides larva



Culicoides pupa

Simulium
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Nematocerans include the culicids (mosquitoes), ceratopogonids (midges); simuliids (black flies) and psychodids (sand flies): only the females are parasitic and have piercing-sucking mouthparts. Simuliids are small black flies (or buffalo gnats) with humped backs and broad unadorned wings (not patterned or hairy). Larval development requires flowing oxygenated waters such as streams and rivers. Adults have cutting mouthparts and their bites are painful making them significant annoying pests of livestock. Females feed on a variety of mammals and birds, with most species demonstrating some degree of host specificity. Anthropophilic *Simulium* species may cause hypersensitivity reactions in humans (black fly fever) and transmit filarioid nematodes of the genus *Onchocerca*, including the species causing river blindness in Africa.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Nematocera (midges/mosquitoes, long filamentous antennae, aquatic larvae/pupae)
Family:	Simuliidae (small black flies/buffalo gnats, characteristic humped backs, wings not patterned or hairy)
Genus:	*Simulium* (parasitic on skin of mammals/birds)
Species:	various species cause annoyance and allergic reactions in livestock (and vector other diseases)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran	Biodiversity	Parasitic	Status	Pathogenesis*	Disease

families		stages			transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Nematocera comprises small slender flies that are 'thread-horned' i.e. they possess long filamentous antennae composed of many articulating segments (= nemato-cera). Adults have long narrow wings (with many branching veins) and specialized mouthparts (short or long) with a protective sheath (labium and labellae) protecting feeding stylets (labrum, mandibles, maxillae and hypopharynx) and flanked by 4-5 segmented palps (usually pendulous but slender in mosquitoes). Many species have aquatic life-cycles (larval/pupal stages associated with water) and all undergo complete metamorphosis whereby adults eclose from puparia through longitudinal slits (rather than circular caps like Cyclorrapha). The suborder contains 7 infraorders: Axymyiomorpha (larvae in decomposing wood); Bibionomorpha (gnats, lovebugs); Blephariceromorpha (mountain midges); Culicomorpha (mosquitoes, midges, black flies); Psychodomorpha (moth flies); Ptychopteromorpha (primitive crane flies); and Tipulomorpha (crane flies). Many species are free-living detritivores but some have adapted to bite vertebrate hosts in order to feed on blood. The infraorder Culicomorpha contains 2 superfamilies: Chironomoidea (biting, non-biting and trickle midges, black flies); and Culicoidea (meniscus midges, phantom midges, frog-biting midges, and mosquitoes). The superfamily Chironomoidea contains 4 families: Ceratopogonidae (biting midges), Chironomidae (non-biting midges), Simuliidae (black flies), and Thaumaleidae (trickle midges).

Members of the family Simuliidae are commonly known as black flies (sometimes called buffalo gnats as well as turkey gnats, jejens, coffee flies, and even 'sand flies') but they are not always black in colour. They are distinguished more by their humped thorax, broad non-hairy wings (with veins thickened anteriorly and less than 8 veins reaching the wing margin), short non-hairy antennae (usually with 11 rounded segments), long 5-segmented palps extending beyond the proboscis, and the first abdominal tergite possessing a basal scale fringed with hairs. Over 2,000 species have been described in around 30 genera in 3 subfamilies: Parasimulinae with 1 genus; Prosimulinae with 2 genera; and Simuliinae with 30 genera (including *Simulium*); plus 8 unplaced genera and 7 fossil genera. *Simulium* spp. have a cosmopolitan distribution and are prevalent in areas where flowing water is present (required for larval/pupal stages). Many black fly species are anautogenous as female flies need to feed on vertebrate blood to produce eggs. Collectively, black flies feed on an extensive range of vertebrates (mammals and birds), although some species have strong preferences for particular hosts (often reflected in their common names). The genus *Simulium* (syn. *Asiosimulium, Bakerina, Choporus, Simulia*) contains over 1,700 species, many classified in 60 subgenera. Around 200 species are considered to be significant biting pests of domestic animals and humans, as well as acting as vectors for the transmission of several pathogenic infectious diseases, including onchocerciasis (causing nodular lesions in animals and humans, and river blindness in humans), viral encephalitis and stomatitis in domestic livestock, and leucocytozoonosis in poultry.

***Simulium* species (regional exemplars)**	**Host preferences**	**Clinical signs (+ vectorial capacity)**	**Distribution**
S. bovis, callidum, colombaschense, damnosum, equinum, erythrocephalum, exiguum, kurenze, melatum, metallicum, neavei, ochraceum, ornatum, vorax, woodi	domestic and wild mammals (esp. ungulates), including humans	annoyance, pruritus, allergy, petechial haemorrhages (onchocerciasis, myxomatosis)	cosmopolitan
S. arcticum, pecuarum, rostratum, truncate, tuberostum, venustum, verecundum, vittatum	domestic and wild mammals (esp. ungulates, some carnivores, lagomorphs)	annoyance, pruritus, allergy, petechial haemorrhages	Holarctic
S. adersi, anatinum, angustitarse, aureum, johannseni, meridionale, ruggelsi, slossonae	birds (esp. galliforms, anseriforms), some domestic and wild mammals	annoyance, pruritus, allergy, petechial haemorrhages, anaemia (leucocytozoonosis, eastern encephalitis virus)	Holarctic

Full species list (compilation of several on-line data-bases)

***Simulium* species**	**Subgenus**
S. abadii	*Gomphostilbia*
S. abatanense	*Simulium*
S. abbreviatum	*Simulium*
S. aberrans	*Nevermannia*
S. acarayense	*Xenosimulium*
S. acmerium	*Nevermannia*
S. acontum	*Simulium*
S. acostai	*Simulium*
S. acrotrichum	*Simulium*
S. acutum	*Hellichiella*
S. adamsoni	*Inseliellum*
S. adelaideae	*Inseliellum*
S. adersi	*Meilloniellum*
S. adleri	*Gomphostilbia*
S. admixtum	*Inseliellum*
S. adolfolutzi	*Ectemnaspi*
S. adornatum	*Obuchovia*
S. adsonense	*Hebridosimulium*
S. adventicium	*Simulium*
S. aemulum	*Simulium*
S. aeneifacies	*Simulium*
S. aequifurcatum	*Psaroniocompsa*
S. aestivum	*Nevermannia*
S. africanum	*Metomphalus*
S. afronuri	*Phoretomyia*
S. akopi	*Cnetha*
S. akouense	*Metomphalus*
S. alajense	*Simulium*
S. alatum	*Nevermannia*
S. albanense	*Ectemnaspi*
S. albellum	*Obuchovia*
S. alberti	*Simulium*
S. albicinctum	*Pternaspatha*
S. albilineatum	*Pternaspatha*
S. albivirgulatum	*Metomphalus*
S. albopictum	*Xenosimulium*
S. alcocki	*Pomeroyellum*
S. alfurense	*Wallacellum*
S. alidae	Unassigned
S. alienigenum	*Morops*
S. alirioi	*Psilopelmia*
S. alizadei	*Montisimulium*
S. allaeri	*Pomeroyellum*
S. almae	*Psilocnetha*
S. alpinum	*Montisimulium*
S. altayense	*Gomphostilbia*
S. amazonicum	*Cerqueirellum*
S. ambigens	*Freemanellum*
S. ambiguum	*Simulium*
S. ambonense	*Gomphostilbia*
S. ambositrae	*Xenosimulium*

S. ammosovi	*Nevermannia*
S. amurense	*Nevermannia*
S. anaimense	*Ectemnaspi*
S. anamariae	*Psaroniocompsa*
S. anatinum	*Hellichiella*
S. anatolicum	*Hebridosimulium*
S. anchistinum	*Simulium*
S. anduzei	*Simulium*
S. anggiense	*Morops*
S. angrense	*Psaroniocompsa*
S. angulistylum	*Gomphostilbia*
S. angustatum	*Nevermannia*
S. angusticorne	*Nevermannia*
S. angustifilum	*Simulium*
S. angustifrons	*Nevermannia*
S. angustifurca	*Wilhelmia*
S. angustipes	*Eusimulium*
S. angustitarse	*Nevermannia*
S. annae	*Eusimulium*
S. annulatum	*Pternaspatha*
S. annuliforme	*Hellichiella*
S. annulitarse	*Schoenbaueria*
S. annulum	*Hellichiella*
S. antenusi	*Psilopelmia*
S. antibrachium	*Nevermannia*
S. antillarum	*Psilopelmia*
S. antlerum	*Morops*
S. antonii	*Ectemnaspi*
S. anustipes	*Eusimulium*
S. aokii	*Simulium*
S. apoense	*Gomphostilbia*
S. appalachiense	*Simulium*
S. apricarium	*Simulium*
S. arabicum	*Nevermannia*
S. arakawae	*Simulium*
S. aranti	*Phosterodoros*
S. arboreum	*Simulium*
S. arcabucense	Unassigned
S. arcticum	*Simulium*
S. arctium	*Hellichiella*
S. arenicola	*Eusimulium*
S. arfakense	*Morops*
S. argentatum	*Xenosimulium*
S. argenteostriatum	*Simulium*
S. argentipes	*Simulium*
S. argentipile	*Eusimulium*
S. argentiscutum	*Cerqueirellum*
S. argus	*Psilozia*
S. argyreatum	*Simulium*
S. argyrocinctum	*Simulium*
S. arisanum	*Simulium*
S. arlecchinum	*Inseliellum*
S. armeniacum	*Eusimulium*
S. armoricanum	*Nevermannia*
S. arnoldi	*Metomphalus*
S. aropaense	*Morops*
S. arpiense	*Eusimulium*
S. arpiense	*Montisimulium*
S. artum	*Nevermannia*
S. asakoae	*Gomphostilbia*
S. asishi	*Simulium*

S. aspericorne	*Nevermannia*
S. asperum	*Gomphostilbia*
S. assadovi	*Montisimulium*
S. asulcatum	*Montisimulium*
S. atlanticum	*Dexomyia*
S. atlasicum	*Simulium*
S. atratoides	*Gomphostilbia*
S. atratum	*Gomphostilbia*
S. atrum	*Simulium*
S. atyophilum	*Lewisellum*
S. audreyae	*Pomeroyellum*
S. aureliani	*Pomeroyellum*
S. aureofulgens	*Simulium*
S. aureohirtum	*Nevermannia*
S. aureonigrum	*Morops*
S. aureosimile	*Nevermannia*
S. aureum	*Eusimulium*
S. auricoma	*Obuchovia*
S. auristriatum	*Pomeroyellum*
S. australe	*Nevermannia*
S. avilae	*Morops*
S. awashense	*Pomeroyellum*
S. ayrozai	*Hearlea*
S. azerbaidzhanicum	*Eusimulium*
S. azorense	*Eusimulium*
S. baatori	*Eusimulium*
S. babai	*Nevermannia*
S. babuyanense	*Gomphostilbia*
S. bachmanni	*Pternaspatha*
S. baetiphilum	*Phoretomyia*
S. baffinense	*Hellichiella*
S. baforti	*Nevermannia*
S. baglungense	*Gomphostilbia*
S. bagmaticum	Unassigned
S. bahense	*Simulium*
S. baiense	*Inaequalium*
S. baimaii	Unassigned
S. baisasae	*Gomphostilbia*
S. balcanicum	*Wilhelmia*
S. baliemense	*Morops*
S. baltazarae	*Simulium*
S. balteatum	*Boreosimulium*
S. banahauense	*Simulium*
S. banaticum	*Simulium*
S. banauense	*Gomphostilbia*
S. banksi	*Hebridosimulium*
S. banluangense	*Gomphostilbia*
S. bannaense	*Gomphostilbia*
S. bansonae	*Morops*
S. barabense	*Hellichiella*
S. baracorne	*Simulium*
S. barbatipes	*Pternaspatha*
S. barnesi	*Simulium*
S. barraudi	*Simulium*
S. barretti	*Gomphostilbia*
S. bartangum	*Montisimulium*
S. bataksense	*Gomphostilbia*
S. batoense	*Gomphostilbia*
S. bayakorum	*Pomeroyellum*
S. beaupertuyi	*Inaequalium*
S. beaupertuyi	*Simulium*

S. beiwanense	*Eusimulium*
S. beltukovae	*Nevermannia*
S. benjamini	*Xenosimulium*
S. benquetense	*Simulium*
S. bequaerti	*Pomeroyellum*
S. berberum	*Simulium*
S. berghei	*Freemanellum*
S. bergi	*Simulium*
S. beringovi	*Argentisimulium*
S. berneri	*Phoretomyia*
S. bertrandi	*Nevermannia*
S. bezzii	*Simulium*
S. biakense	*Morops*
S. biancoi	*Nevermannia*
S. bicolense	*Gomphostilbia*
S. bicoloratum	*Psilopelmia*
S. bicorne	*Nevermannia*
S. bicorne	*Nevermannia*
S. bicornutum	*Ectemnaspi*
S. bidentatum	*Simulium*
S. bifenestratum	*Chirostilbia*
S. bifila	*Byssodon*
S. biforaminiferum	*Simulium*
S. bifurcatum	*Gomphostilbia*
S. bimaculatum	*Simulium*
S. binuanense	*Gomphostilbia*
S. bipunctatum	*Psilopelmia*
S. biseriatum	*Obuchovia*
S. bishopi	*Simulium*
S. bisnovem	*Anasolen*
S. biuxinisa	*Hemicnetha*
S. bivittatum	*Psilopelmia*
S. blacklocki	*Pomeroyellum*
S. blancasi	*Eremulium*
S. blantoni	*Notolepria*
S. bobpetersoni	*Psilopelmia*
S. bogusium	*Inseliellum*
S. boldstemta	*Nevermannia*
S. bonaerense	*Pomeroyellum*
S. bonninense	*Eusimulium*
S. bordai	*Pternaspatha*
S. borneoense	*Nevermannia*
S. borunicornutum	Unassigned
S. botulibranchium	*Xenosimulium*
S. botulus	*Morops*
S. bovis	*Metomphalus*
S. brachium	*Nevermannia*
S. brachyantherum	*Eusimulium*
S. brachyarthrum	*Schoenbaueria*
S. brachycladum	*Hellichiella*
S. brachystylum	*Montisimulium*
S. bracteatum	*Eusimulium*
S. brandti	*Morops*
S. bravermani	*Wilhelmia*
S. brevicorne	*Montisimulium*
S. brevidens	*Nevermannia*
S. brevifile	*Obuchovia*
S. brevifurcatum	*Pomeroyellum*
S. brevilabrum	*Gomphostilbia*
S. brevipar	*Simulium*
S. brevitarse	*Nevermannia*
S. brevitruncatum	*Gomphostilbia*
S. bricenoi	*Hemicnetha*
S. bronchiale	*Simulium*
S. brunhesi	Unassigned
S. brunneum	*Nevermannia*
S. bryopodium	*Nevermannia*
S. buckleyi	*Nevermannia*
S. bucolicum	*Gomphostilbia*
S. buettikeri	*Wilhelmia*
S. buisseti	*Edwardsellum*
S. buissoni	*Inseliellum*
S. bujakovi	*Boophthora*
S. bukovskii	*Simulium*
S. bulbiferum	*Nevermannia*
S. bulbosum	*Montisimulium*
S. bulla	*Simulium*
S. bullatum	*Simulium*
S. burchi	*Hearlea*
S. burgeri	*Nevermannia*
S. burmense	*Nevermannia*
S. burtoni	*Gomphostilbia*
S. bustosi	*Simulium*
S. butwalense	*Gomphostilbia*
S. buxtoni	*Byssodon*
S. cabrerai	*Wallacellum*
S. caesariatum	*Inseliellum*
S. cagayanense	*Gomphostilbia*
S. caledonense	*Nevermannia*
S. callidum	*Psilopelmia*
S. callipygium	*Hebridosimulium*
S. canadense	*Hearlea*
S. candelabrum	*Nevermannia*
S. canescens	Unassigned
S. cangshanense	*Eusimulium*
S. canlaonense	*Simulium*
S. canonicola	*Nevermannia*
S. caohaiense	*Odagmia*
S. capricorne	*Hearlea*
S. caprii	*Pternaspatha*
S. carbunculum	*Nevermannia*
S. carinatum	*Wallacellum*
S. carolinae	*Hearlea*
S. carpathicum	*Nevermannia*
S. carthusiense	*Nevermannia*
S. castaneum	*Inseliellum*
S. cataractarum	*Inseliellum*
S. catariense	*Pomeroyellum*
S. catleyi	*Gomphostilbia*
S. caucasicum	*Simulium*
S. cauchense	*Coscaroniellum*
S. caudisclerum	*Nevermannia*
S. cavum	*Metomphalus*
S. celebesense	*Wallacellum*
S. celsum	*Simulium*
S. centrale	*Gomphostilbia*
S. cerqueirai	Unassigned
S. cerradense	*Coscaroniellum*
S. cervicornutum	*Pomeroyellum*
S. cervus	*Morops*
S. ceylonicum	*Gomphostilbia*
S. chainarongi	*Simulium*

S. chairuddini	*Nevermannia*
S. chaliowae	*Simulium*
S. chamlongi	*Simulium*
S. chaowaense	*Gomphostilbia*
S. chaquense	*Cerqueirellum*
S. cheesmanae	*Inseliellum*
S. chelevini	*Boophthora*
S. chelevini	*Schoenbaueria*
S. cheni	*Eusimulium*
S. chenzhouense	*Nevermannia*
S. cheongi	*Gomphostilbia*
S. chiangmaiense	*Simulium*
S. chiharuae	*Hellichiella*
S. chilianum	*Xenosimulium*
S. chiriquiense	*Hearlea*
S. chitoense	*Nevermannia*
S. chlorum	*Simulium*
S. cholodkovskii	*Simulium*
S. chomustachi	*Gomphostilbia*
S. chongqingense	*Gomphostilbia*
S. chongqingense	*Simulium*
S. choochotei	*Simulium*
S. chovdica	*Nevermannia*
S. chowettani	Unassigned
S. chowi	*Montisimulium*
S. christophersi	*Simulium*
S. chromatinum	*Simulium*
S. chromocentrum	*Simulium*
S. chubarevae	*Nevermannia*
S. chumporense	*Gomphostilbia*
S. chungi	*Simulium*
S. chutteri	*Metomphalus*
S. claricentrum	Unassigned
S. clarkei	*Hellichiella*
S. clarki	*Xenosimulium*
S. clarum	*Psilopelmia*
S. clathrinum	*Morops*
S. clavibranchium	*Inaequalium*
S. clavum	*Morops*
S. clibanarium	*Inseliellum*
S. coalitum	*Pomeroyellum*
S. coarctatum	*Simulium*
S. codreanui	*Nevermannia*
S. colasbelcouri	*Metomphalus*
S. colombaschense	*Simulium*
S. concavustylum	*Eusimulium*
S. concludium	*Inseliellum*
S. confusum	*Simulium*
S. congareenarum	*Hellichiella*
S. conicum	*Nevermannia*
S. connae	*Inseliellum*
S. consimile	*Simulium*
S. continii	*Obuchovia*
S. contractum	*Simulium*
S. contrerense	*Hearlea*
S. conundrum	*Simulium*
S. copleyi	*Phoretomyia*
S. corbis	*Simulium*
S. cormonsi	*Ectemnaspi*
S. corniferum	*Nevermannia*
S. corpulentum	*Simulium*

S. costalimai	*Simulium*
S. costaricense	*Xenosimulium*
S. costatum	*Nevermannia*
S. cotabatoense	*Simulium*
S. cotopaxi	*Pternaspatha*
S. courtneyi	*Daviesellum*
S. couverti	*Nevermannia*
S. covagarciai	*Simulium*
S. covagarciai	Unassigned
S. craigi	*Nevermannia*
S. crassicaulum	*Nevermannia*
S. crassifilum	*Simulium*
S. crassimanum	*Simulium*
S. crassum	*Hellichiella*
S. cremnosi	*Simulium*
S. crenobium	*Nevermannia*
S. cristalinum	*Hemicnetha*
S. cristatum	*Morops*
S. croaticum	*Simulium*
S. crocinum	*Simulium*
S. crosskeyi	*Metomphalus*
S. croxtoni	*Nevermannia*
S. cruszi	*Simulium*
S. cryophilum	*Nevermannia*
S. cuasiexiguum	*Notolepria*
S. cuasisanguineum	*Cerqueirellum*
S. cuneatum	*Cerqueirellum*
S. curriei	*Hellichiella*
S. curvans	*Nevermannia*
S. curvastylum	*Gomphostilbia*
S. curvistyle	*Simulium*
S. curvitarse	*Simulium*
S. curvum	*Gomphostilbia*
S. dahestanicum	*Wilhelmia*
S. dailekhense	*Simulium*
S. daisense	*Simulium*
S. dalmati	*Hearlea*
S. daltanhani	Unassigned
S. damascenoi	*Psaroniocompsa*
S. damingense	*Simulium*
S. damnosum	*Edwardsellum*
S. dandrettai	*Psilopelmia*
S. danense	*Metomphalus*
S. danijari	*Montisimulium*
S. darjeelingense	*Gomphostilbia*
S. dasguptai	*Nevermannia*
S. davaoense	*Gomphostilbia*
S. dawaense	*Metomphalus*
S. deagostinii	*Pternaspatha*
S. debacli	*Simulium*
S. debegene	*Freemanellum*
S. decafile	*Montisimulium*
S. decafiliatum	*Montisimulium*
S. decimatum	*Simulium*
S. decimfiliatum	*Montisimulium*
S. decollectum	*Nevermannia*
S. decolletum	Unassigned
S. decorum	*Simulium*
S. decuplum	*Gomphostilbia*
S. definitum	*Simulium*
S. defoliarti	*Simulium*

S. degrangei	*Simulium*
S. dehnei	*Hemicnetha*
S. dekeyseri	*Chirostilbia*
S. delatorrei	*Hearlea*
S. delfinadoae	*Simulium*
S. delizhanense	*Nevermannia*
S. delponteianum	*Cerqueirellum*
S. demutaense	*Morops*
S. dendrofilum	*Schoenbaueria*
S. denistylum	*Gomphostilbia*
S. dentatum	*Simulium*
S. dentaturum	*Nevermannia*
S. dentulosum	*Anasolen*
S. deserticola	*Simulium*
S. desertorum	*Simulium*
S. desirei	Unassigned
S. diamantinum	*Pternaspatha*
S. diaznajerai	*Xenosimulium*
S. diceros	*Phoretomyia*
S. dieguerense	*Edwardsellum*
S. digitatum	*Simulium*
S. digrammicum	*Simulium*
S. dinellii	*Psilopelmia*
S. discrepans	*Simulium*
S. disneyi	*Morops*
S. distinctum	*Chirostilbia*
S. diversibranchium	*Inaequalium*
S. dixiense	*Phosterodoros*
S. djafarovi	*Nevermannia*
S. djallonense	*Pomeroyellum*
S. djebaglense	*Montisimulium*
S. dogieli	*Hellichiella*
S. doipuiense	*Simulium*
S. dojeycorium	*Inseliellum*
S. dola	*Gomphostilbia*
S. dolini	*Argentisimulium*
S. dolomitense	*Nevermannia*
S. donovani	*Eusimulium*
S. downsi	*Psilopelmia*
S. dubitskii	*Phoretodagmia*
S. duboisi	*Nevermannia*
S. dudgeoni	*Gomphostilbia*
S. dugesi	*Psilopelmia*
S. dukei	*Phoretomyia*
S. dumogaense	*Simulium*
S. dunfellense	*Nevermannia*
S. dunhuangense	*Wilhelmia*
S. duodecimcornutum	*Montisimulium*
S. duodecimum	*Pomeroyellum*
S. duodenicornium	*Thyrsopelma*
S. duolongum	*Gomphostilbia*
S. duplex	*Hellichiella*
S. dureti	*Pternaspatha*
S. dussertorum	*Inseliellum*
S. dycei	*Morops*
S. earlei	*Hemicnetha*
S. egregium	*Simulium*
S. ekomei	*Pomeroyellum*
S. ela	*Gomphostilbia*
S. elatum	*Nevermannia*
S. elburnum	*Nevermannia*

S. elongatum	*Simulium*
S. emarginatum	*Hellichiella*
S. emiliae	*Obuchovia*
S. empascae	*Chirostilbia*
S. empopomae	*Freemanellum*
S. encisoi	*Psilozia*
S. englundi	*Inseliellum*
S. eouzani	*Metomphalus*
S. ephemerophilum	*Simulium*
S. ephippioidum	*Simulium*
S. epistum	*Gomphostilbia*
S. equinum	*Wilhelmia*
S. erectum	*Nevermannia*
S. erimoense	*Eusimulium*
S. erythrocephalum	*Boophthora*
S. escomeli	*Psilopelmia*
S. estevezi	*Hearlea*
S. ethelae	*Hearlea*
S. ethiopiense	*Lewisellum*
S. euryadminiculum	*Hellichiella*
S. euryplatamum	*Eusimulium*
S. evelynae	*Morops*
S. evenhuisi	*Inseliellum*
S. evillense	*Pomeroyellum*
S. exasperans	*Inseliellum*
S. excisum	*Hellichiella*
S. exiguum	*Notolepria*
S. exile	*Simulium*
S. eximium	*Simulium*
S. exulatum	*Eusimulium*
S. faheyi	*Morops*
S. falcoe	*Nevermannia*
S. falculatum	*Hemicnetha*
S. fallisi	*Hellichiella*
S. fangense	*Nevermannia*
S. fanjingshanense	*Gomphostilbia*
S. fararae	*Inseliellum*
S. farcimine	*Morops*
S. fenestratum	*Simulium*
S. ferganicum	*Simulium*
S. feuerborni	*Nevermannia*
S. fibrinflatum	*Phosterodoros*
S. fidum	*Gomphostilbia*
S. fimbriatum	*Morops*
S. fionae	Unassigned
S. flaveolum	*Simulium*
S. flavicans	*Simulium*
S. flavidum	*Simulium*
S. flavigaster	*Simulium*
S. flavinotatum	*Nevermannia*
S. flavipes	*Nevermannia*
S. flavipictum	*Xenosimulium*
S. flavoantennatum	*Schoenbaueria*
S. flavocinctum	*Gomphostilbia*
S. flavum	*Simulium*
S. flexibranchium	*Eusimulium*
S. florae	*Nevermannia*
S. floresense	*Gomphostilbia*
S. fluviatile	*Nevermannia*
S. fontanum	*Simulium*
S. fontinale	*Nevermannia*

S. fontium	*Nevermannia*
S. forcipatum	*Simulium*
S. fossatiae	*Inseliellum*
S. fragai	*Metomphalus*
S. freemani	*Hemicnetha*
S. friederichsi	*Gomphostilbia*
S. friedlanderi	*Chirostilbia*
S. frigidum	*Simulium*
S. fucense	*Nevermannia*
S. fujianense	*Simulium*
S. fuliginis	*Pomeroyellum*
S. fulvipes	*Simulium*
S. furcillatum	*Ectemnaspi*
S. furculatum	*Nevermannia*
S. fuscatum	Unassigned
S. fuscicorne	*Nevermannia*
S. fuscinerve	*Nevermannia*
S. fuscitarse	*Simulium*
S. fuscopilosum	*Simulium*
S. fuscum	*Simulium*
S. futaense	*Metomphalus*
S. fuzhouense	*Simulium*
S. gabaldoni	*Psilopelmia*
S. gabovae	*Simulium*
S. gagiduense	*Morops*
S. gallinum	*Inseliellum*
S. galloprovinciale	*Obuchovia*
S. ganalesense	*Xenosimulium*
S. gariepsense	*Afrosimulium*
S. garmsi	*Pomeroyellum*
S. garniense	*Nevermannia*
S. gatchaliani	*Simulium*
S. geigyi	*Pomeroyellum*
S. gejgelense	*Nevermannia*
S. germuense	*Wilhelmia*
S. ghoomense	*Montisimulium*
S. gibense	*Metomphalus*
S. giganteum	*Hemicnetha*
S. gilleti	*Pomeroyellum*
S. gimpuense	*Gomphostilbia*
S. glatthaari	*Nevermannia*
S. globosum	*Simulium*
S. goeldii	*Xenosimulium*
S. goinyi	*Lewisellum*
S. gokarnaense	*Simulium*
S. golani	*Wilhelmia*
S. gombakense	*Morops*
S. gomphocorne	*Nevermannia*
S. gonzalezherrejoni	*Psilopelmia*
S. gonzalezi	*Notolepria*
S. gorokae	*Morops*
S. gouldingi	*Nevermannia*
S. gracile	*Nevermannia*
S. gracilipes	*Crosskeyellum*
S. gravelyi	*Simulium*
S. grenieri	Unassigned
S. gribae	*Simulium*
S. griseicolle	*Byssodon*
S. griseifrons	*Simulium*
S. grisescens	*Simulium*
S. griseum	*Psilopelmia*

S. griveaudi	*Xenosimulium*
S. grossifilum	*Simulium*
S. guamense	*Inseliellum*
S. guaporense	*Psaroniocompsa*
S. guerrerense	*Hemicnetha*
S. guerreroi	*Xenosimulium*
S. guianense	*Trichodagmia*
S. guimari	*Eusimulium*
S. guniki	*Gomphostilbia*
S. gurneyae	*Simulium*
S. gusevi	*Simulium*
S. gutsevitshi	*Byssodon*
S. guttatum	*Pomeroyellum*
S. gviletense	*Montisimulium*
S. gyas	*Metomphalus*
S. gyorkosae	*Gomphostilbia*
S. hackeri	*Simulium*
S. hadiae	*Gomphostilbia*
S. haematopotum	*Psilopelmia*
S. hagai	*Morops*
S. hailuogouense	*Montisimulium*
S. halmaheraense	*Morops*
S. hargreavesi	*Metomphalus*
S. harrisoni	*Pomeroyellum*
S. haysi	*Phosterodoros*
S. hechti	*Simulium*
S. hectorvargasi	*Pternaspatha*
S. heishuiense	*Montisimulium*
S. heldsbachense	*Gomphostilbia*
S. hematophilum	*Simulium*
S. hemicyclium	*Gomphostilbia*
S. henanense	*Nevermannia*
S. hengshanense	*Simulium*
S. heptapotamicum	*Byssodon*
S. heptaspicae	*Anasolen*
S. herreri	*Pternaspatha*
S. hessei	*Freemanellum*
S. hibernale	*Simulium*
S. hiemale	*Simulium*
S. hieroglyphicum	*Hemicnetha*
S. hightoni	*Lewisellum*
S. himalayense	*Simulium*
S. hinmani	*Hemicnetha*
S. hiroshii	*Gomphostilbia*
S. hirsutilateris	*Freemanellum*
S. hirsutum	*Meilloniellum*
S. hirticranium	*Inseliellum*
S. hirtinerve	*Simulium*
S. hirtipannum	*Simulium*
S. hirtipupa	*Xenosimulium*
S. hispaniola	*Simulium*
S. hispidum	*Inseliellum*
S. hissetteum	*Pomeroyellum*
S. hoffmanni	*Xenosimulium*
S. hoiseni	*Gomphostilbia*
S. hongpingense	*Simulium*
S. horacioi	*Simulium*
S. horococchuspi	*Pternaspatha*
S. horokaense	*Simulium*
S. howletti	*Simulium*
S. huaimorense	*Gomphostilbia*

S. huairayacu	*Trichodagmia*
S. huangshanense	*Simulium*
S. huemul	*Pternaspatha*
S. hukaense	*Inseliellum*
S. humerosum	*Simulium*
S. hunanense	*Gomphostilbia*
S. hunteri	*Simulium*
S. ibarakiense	*Nevermannia*
S. ibariense	*Simulium*
S. ibericum	*Obuchovia*
S. ibleum	*Nevermannia*
S. ichnusae	*Cnetha*
S. ifugaoense	*Morops*
S. ignescens	*Ectemnaspi*
S. iguazuense	*Xenosimulium*
S. imerinae	*Xenosimulium*
S. immortale	*Simulium*
S. impar	*Nevermannia*
S. impukane	*Pomeroyellum*
S. inaequale	*Inaequalium*
S. incanum	Unassigned
S. incertum	*Xenosimulium*
S. incognitum	*Simulium*
S. incrustatum	*Pomeroyellum*
S. indicum	*Himalayum*
S. indicum	*Wilhelmia*
S. inermum	*Gomphostilbia*
S. infenestrum	*Simulium*
S. infernale	*Psilozia*
S. inflatum	*Montisimulium*
S. innocens	*Hellichiella*
S. inornatum	*Morops*
S. intermedium	*Simulium*
S. inthanonense	*Gomphostilbia*
S. inuitkiense	*Morops*
S. iphias	*Xenosimulium*
S. iracouboense	*Psilopelmia*
S. irayense	*Morops*
S. irianense	*Morops*
S. iriartei	*Aspathia*
S. iridescens	*Simulium*
S. itaunense	*Trichodagmia*
S. itelmenica	*Nevermannia*
S. ituriense	*Pomeroyellum*
S. ivashchenkoi	*Schoenbaueria*
S. ivdelense	*Schoenbaueria*
S. iwahigense	*Simulium*
S. iwatense	*Simulium*
S. izuense	*Nevermannia*
S. jacobsi	*Psilopelmia*
S. jacumbae	*Simulium*
S. jacuticum	*Simulium*
S. jaimeramirezi	*Ectemnaspi*
S. jani	*Simulium*
S. janzeni	*Simulium*
S. janzi	*Metomphalus*
S. japonicum	*Simulium*
S. jasgulemum	*Montisimulium*
S. jayapuraense	*Morops*
S. jefersoni	*Chirostilbia*
S. jeffreyi	*Simulium*

S. jenningsi	*Phosterodoros*
S. jerezense	*Psilopelmia*
S. jeteri	*Thyrsopelma*
S. jianjinshanense	*Montisimulium*
S. jieyangense	*Gnus*
S. jilinense	*Eusimulium*
S. jilinense	*Nevermannia*
S. jimmaense	*Metomphalus*
S. jinbianense	*Gomphostilbia*
S. jnabsium	*Inseliellum*
S. jobbinsi	*Simulium*
S. joculator	*Boreosimulium*
S. johannae	*Pomeroyellum*
S. johannseni	*Hellichiella*
S. johnfrumi	*Hebridosimulium*
S. johnsoni	*Hearlea*
S. jolyi	*Hebridosimulium*
S. jomsomense	*Eusimulium*
S. jonesi	*Phosterodoros*
S. josephi	*Morops*
S. joyae	*Inseliellum*
S. juarezi	*Hearlea*
S. jugatum	*Simulium*
S. jujuyense	*Psaroniocompsa*
S. junkumae	*Gomphostilbia*
S. juxtacrenobium	*Nevermannia*
S. juxtadamnosum	*Edwardsellum*
S. kabanayense	*Psilopelmia*
S. kachvorjanae	*Simulium*
S. kaffaense	Unassigned
S. kainantuense	*Morops*
S. kaiti	*Morops*
S. kalimerahense	*Gomphostilbia*
S. kambaitense	*Nevermannia*
S. kamimurai	*Gomphostilbia*
S. kamtshadalicum	Unassigned
S. kamtshaticum	*Simulium*
S. kanchaveli	*Simulium*
S. kapuri	*Simulium*
S. karasuae	*Obuchovia*
S. karenkoense	*Simulium*
S. kariyai	*Hellichiella*
S. karzhantavicum	*Nevermannia*
S. kaszabi	*Eusimulium*
S. katangae	*Nevermannia*
S. katoi	*Simulium*
S. kauntzeum	*Anasolen*
S. kawagishii	*Morops*
S. kawamurae	*Simulium*
S. kazahstanicum	*Eusimulium*
S. keenani	*Hemicnetha*
S. keiseri	*Nevermannia*
S. keningauense	*Simulium*
S. kenyae	*Pomeroyellum*
S. keravatense	*Gomphostilbia*
S. kerei	*Morops*
S. kerisorum	*Simulium*
S. kerzhneri	*Montisimulium*
S. kiangaraense	Unassigned
S. kietaense	*Morops*
S. kiewfinense	*Gomphostilbia*

S. kilibanum	*Edwardsellum*
S. kinabaluense	*Simulium*
S. kingundense	*Metomphalus*
S. kipengere	*Edwardsellum*
S. kirgisorum	*Montisimulium*
S. kiritshenkoi	*Simulium*
S. kisoense	*Simulium*
S. kitetense	*Edwardsellum*
S. kivuense	*Lewisellum*
S. klonganense	*Gomphostilbia*
S. knidirii	*Rubzovia*
S. kobayashii	*Montisimulium*
S. koidzumii	*Byssodon*
S. kokodae	*Morops*
S. kolakaense	*Gomphostilbia*
S. kompi	*Simulium*
S. konakovi	*Simulium*
S. konkourense	*Edwardsellum*
S. konoi	*Nevermannia*
S. kozlovi	*Simulium*
S. krebsorum	*Simulium*
S. krombeini	*Gomphostilbia*
S. krymense	*Eusimulium*
S. kuandianense	*Eusimulium*
S. kugartsuense	*Nevermannia*
S. kugitangi	*Nevermannia*
S. kuingingiense	*Gomphostilbia*
S. kumboense	*Phoretomyia*
S. kurense	*Simulium*
S. kurganense	*Montisimulium*
S. kurilense	*Simulium*
S. kurtaki	*Nevermannia*
S. kuznetzovi	*Nevermannia*
S. kwangoense	*Metomphalus*
S. kyushuense	*Simulium*
S. labellei	*Psilopelmia*
S. laciniatum	*Hebridosimulium*
S. lagunaense	*Gomphostilbia*
S. lahillei	*Trichodagmia*
S. lakei	*Phosterodoros*
S. lalokiense	*Morops*
S. lama	*Wilhelmia*
S. lamachi	*Rubzovia*
S. lampangense	*Simulium*
S. landonoense	*Simulium*
S. laneportoi	*Chirostilbia*
S. langtangense	*Simulium*
S. languidum	*Byssodon*
S. laoshanstum	*Gomphostilbia*
S. laplandica	*Odagmia*
S. larvipilosum	*Nevermannia*
S. larvispinosum	*Hearlea*
S. lassmanni	*Simulium*
S. laterale	*Simulium*
S. latifile	*Nevermannia*
S. latigonium	*Nevermannia*
S. latilobus	*Simulium*
S. latimentum	*Simulium*
S. latipes	*Hellichiella*
S. latipollex	*Edwardsellum*
S. latistylum	*Simulium*

S. latitarsus	*Simulium*
S. lawnhillense	*Morops*
S. laxum	*Simulium*
S. leberrei	*Pomeroyellum*
S. ledongense	*Simulium*
S. lehi	*Gomphostilbia*
S. leigongshanense	*Eusimulium*
S. lekhaniense	*Nevermannia*
S. leonense	*Edwardsellum*
S. leopoldense	*Inaequalium*
S. lepnevae	*Gomphostilbia*
S. letabum	*Metomphalus*
S. letense	*Nevermannia*
S. letrasense	*Psilopelmia*
S. lewisi	*Psilopelmia*
S. leytense	*Simulium*
S. liberiense	*Pomeroyellum*
S. lidiae	*Nevermannia*
S. lididae	*Cnetha*
S. lilianae	*Morops*
S. liliwense	*Morops*
S. lilotense	*Nevermannia*
S. limay	*Pternaspatha*
S. limbatum	*Psaroniocompsa*
S. linduense	*Simulium*
S. lineatum	*Wilhelmia*
S. lineothorax	*Simulium*
S. lingziense	*Eusimulium*
S. liriense	*Simulium*
S. litoreum	*Gomphostilbia*
S. litshkense	*Montisimulium*
S. littopyga	*Inseliellum*
S. lividum	Unassigned
S. llutense	*Pternaspatha*
S. lobatoi	Unassigned
S. loeiense	*Gomphostilbia*
S. loerchae	Unassigned
S. lonchatum	*Simulium*
S. lonckei	*Inseliellum*
S. longifiliatum	*Montisimulium*
S. longipalpe	*Simulium*
S. longipes	*Nevermannia*
S. longirostre	*Morops*
S. longistylatum	*Shewellomyia*
S. longitarse	*Eusimulium*
S. longithallum	*Psilopelmia*
S. longitruncum	*Gomphostilbia*
S. longitruncum	*Gomphostilbia*
S. longplatum	*Simulium*
S. longshengense	*Gomphostilbia*
S. longtanstum	*Nevermannia*
S. lorense	*Simulium*
S. lotii	*Inseliellum*
S. lourencoi	*Psaroniocompsa*
S. loutetense	*Nevermannia*
S. loveridgei	*Nevermannia*
S. luadiense	*Edwardsellum*
S. luchoi	*Pternaspatha*
S. lucyae	*Hebridosimulium*
S. ludingens	*Nevermannia*
S. lugense	Unassigned

S. luggeri	*Phosterodoros*
S. luliangense	*Montisimulium*
S. lumbwanum	*Phoretomyia*
S. lundstromi	*Nevermannia*
S. lunduense	*Simulium*
S. luppovae	*Nevermannia*
S. lurauense	*Gomphostilbia*
S. luridum	*Simulium*
S. lurybayae	*Xenosimulium*
S. lushanense	*Simulium*
S. lushanense	Unassigned
S. lutzi	*Xenosimulium*
S. lutzianum	*Ectemnaspi*
S. luzonicum	*Gomphostilbia*
S. machadoi	*Edwardsellum*
S. mackerrasorum	*Morops*
S. maculatum	*Byssodon*
S. maehongsonense	*Gomphostilbia*
S. maelanoiense	*Gomphostilbia*
S. maenoi	*Simulium*
S. maertensi	*Edwardsellum*
S. maewongense	*Gomphostilbia*
S. mafuluense	*Morops*
S. magnum	*Xenosimulium*
S. makartshenkovi	*Gomphostilbia*
S. makilingense	*Wallacellum*
S. maklarini	*Simulium*
S. malaibaense	*Simulium*
S. malardei	*Inseliellum*
S. malayense	*Simulium*
S. malinoense	*Simulium*
S. malukuense	*Morops*
S. malyschevi	*Gnus*
S. mamasaense	*Gomphostilbia*
S. manadoense	*Gomphostilbia*
S. manbucalense	*Morops*
S. manense	*Freemanellum*
S. mangabeirai	*Psilopelmia*
S. mangasepi	*Gomphostilbia*
S. manokwariense	*Morops*
S. manooni	*Simulium*
S. manuselaense	*Morops*
S. maraaense	*Inseliellum*
S. maranguapense	*Inaequalium*
S. marathrumi	*Psaroniocompsa*
S. margaritae	*Obuchovia*
S. margaritatum	*Inaequalium*
S. mariavulcanoae	*Inaequalium*
S. maritimum	*Eusimulium*
S. marlieri	*Phoretomyia*
S. marocanum	*Obuchovia*
S. marquezi	*Simulium*
S. marsicanum	*Nevermannia*
S. masabae	*Anasolen*
S. masilauense	*Simulium*
S. maskeyae	*Simulium*
S. mataverense	*Inseliellum*
S. matokoense	*Morops*
S. matteabranchium	*Simulium*
S. mauense	*Psilopelmia*
S. maximum	*Simulium*

S. mayuchuspi	*Ectemnaspi*
S. mayumbense	*Pomeroyellum*
S. mazzottii	*Psilopelmia*
S. mcmahoni	*Pomeroyellum*
S. meadowi	*Gomphostilbia*
S. mediaxisus	*Simulium*
S. mediocoloratum	*Simulium*
S. mediodentatum	*Simulium*
S. mediovittatum	*Psilopelmia*
S. medusaeforme	*Metomphalus*
S. meigeni	*Nevermannia*
S. melanocephalum	*Phoretomyia*
S. melanopus	*Simulium*
S. melatum	*Morops*
S. mellah	Unassigned
S. menchacai	*Hearlea*
S. mendiense	*Morops*
S. mengense	*Edwardsellum*
S. mengi	*Gomphostilbia*
S. menglaense	*Simulium*
S. merga	*Montisimulium*
S. meridionale	*Byssodon*
S. merops	*Pomeroyellum*
S. merritti	*Nevermannia*
S. mesasiaticum	*Simulium*
S. mesodontium	*Inseliellum*
S. metallicum	*Simulium*
S. metatrsale	*Gomphostilbia*
S. metecontae	Unassigned
S. meyerae	*Psilopelmia*
S. miblosi	*Gomphostilbia*
S. microbranchium	*Hearlea*
S. microlepidum	*Edwardsellum*
S. middlemissae	*Inseliellum*
S. mie	*Nevermannia*
S. milloti	*Nevermannia*
S. minahasaense	*Nevermannia*
S. minangkabaum	*Simulium*
S. mindanaoense	*Gomphostilbia*
S. mindoroense	*Gomphostilbia*
S. mindoroense	*Simulium*
S. minji	*Morops*
S. minuanum	*Psaroniocompsa*
S. minus	*Hellichiella*
S. minusculum	*Cerqueirellum*
S. minuticorpus	*Cnetha*
S. minutum	*Nevermannia*
S. miyagii	*Gomphostilbia*
S. modicum	*Nevermannia*
S. mogii	*Gomphostilbia*
S. molliculum	*Simulium*
S. mongolense	Unassigned
S. mongolicum	*Simulium*
S. montiblense	*Gomphostilbia*
S. monticola	*Simulium*
S. monticoloides	*Simulium*
S. montium	*Montisimulium*
S. montshadskii	*Nevermannia*
S. morae	*Simulium*
S. morisonoi	*Nevermannia*
S. morsitans	*Simulium*

S. motoyukii	*Morops*
S. moucheti	*Phoretomyia*
S. moultoni	*Nevermannia*
S. moxiense	*Montisimulium*
S. muangpanense	*Gomphostilbia*
S. multiclavulatum	*Pomeroyellum*
S. multidentatum	*Cnetha*
S. multifurcatum	*Simulium*
S. multistriatum	*Simulium*
S. mumfordi	*Inseliellum*
S. munumense	*Gomphostilbia*
S. murmanum	*Simulium*
S. murvanidzei	*Nevermannia*
S. mussauense	*Morops*
S. mutucuna	*Xenosimulium*
S. mysterium	*Hellichiella*
S. nacojapi	*Simulium*
S. nahimi	*Cerqueirellum*
S. nakanoi	*Simulium*
S. nakhonense	*Simulium*
S. namdanense	*Gomphostilbia*
S. namense	*Gomphostilbia*
S. nami	*Gomphostilbia*
S. nanoiense	*Gomphostilbia*
S. nanthaburiense	*Gomphostilbia*
S. nanum	*Simulium*
S. napuense	*Gomphostilbia*
S. narcaeum	*Nevermannia*
S. natalense	*Metomphalus*
S. naturale	*Nevermannia*
S. neavei	*Lewisellum*
S. nebulicola	*Simulium*
S. nebulosum	*Hellichiella*
S. negativum	*Simulium*
S. neireti	*Xenosimulium*
S. nemorale	*Pternaspatha*
S. nemorivagum	*Montisimulium*
S. nemuroense	*Simulium*
S. neornatipes	*Nevermannia*
S. neoviceps	*Inseliellum*
S. nepalense	*Gomphostilbia*
S. netteli	*Psilopelmia*
S. ngabogei	*Anasolen*
S. nganganum	*Edwardsellum*
S. ngouense	*Metomphalus*
S. nicholsoni	*Morops*
S. nigricorne	*Hearlea*
S. nigricoxum	*Simulium*
S. nigrifacies	*Simulium*
S. nigrifemur	*Xenosimulium*
S. nigrimana	*Trichodagmia*
S. nigripilosum	*Simulium*
S. nigristrigatum	*Pternaspatha*
S. nigritarse	*Nevermannia*
S. nigrofemoralum	*Gomphostilbia*
S. nigrofusipes	*Eusimulium*
S. nigrogilvum	*Himalayum*
S. nigrum	*Schoenbaueria*
S. niha	*Simulium*
S. nikkoense	*Simulium*
S. nilesi	*Psilopelmia*

S. nilgiricum	*Simulium*
S. nili	*Anasolen*
S. nishijimai	*Simulium*
S. nitidithorax	*Simulium*
S. nobile	*Simulium*
S. nodosum	*Simulium*
S. noelleri	*Simulium*
S. norfolkense	*Nevermannia*
S. norforense	*Morops*
S. noroense	*Morops*
S. notatum	*Psilopelmia*
S. notiale	*Phosterodoros*
S. notoense	*Hellichiella*
S. novemarticulatum	*Gomphostilbia*
S. novigracile	*Eusimulium*
S. novolineatum	*Simulium*
S. nubis	*Simulium*
S. nudifrons	*Simulium*
S. nudipes	*Morops*
S. nujiangense	*Simulium*
S. nunesdemelloi	Unassigned
S. nuneztovari	*Psilopelmia*
S. nuneztovari	*Psilopelmia*
S. nuwakotense	*Gomphostilbia*
S. nyaense	*Pomeroyellum*
S. nyanzense	*Nevermannia*
S. nyasalandicum	*Lewisellum*
S. nyssa	*Phosterodoros*
S. obesum	*Xenosimulium*
S. obichingoum	*Montisimulium*
S. obikumbense	*Simulium*
S. oblongum	*Asiosimulium*
S. ochoai	*Psilopelmia*
S. ochraceum	*Psilopelmia*
S. ochrescentipes	Unassigned
S. ocreastylum	*Montisimulium*
S. octofiliatum	*Montisimulium*
S. octospicae	*Anasolen*
S. oculatum	*Morops*
S. odontostylum	*Montisimulium*
S. ogatai	*Gomphostilbia*
S. ogonukii	*Wallacellum*
S. oguamai	*Pomeroyellum*
S. oitanum	*Simulium*
S. okinawaense	*Gomphostilbia*
S. oligocenicum (fossil)	*Hellichiella*
S. oligotuberculatum	*Nevermannia*
S. olimpicum	*Psilopelmia*
S. olonicum	*Hellichiella*
S. omorii	*Simulium*
S. omutaense	*Gomphostilbia*
S. onoi	Unassigned
S. onum	*Montisimulium*
S. opunohuense	*Inseliellum*
S. orbitale	*Trichodagmia*
S. oresti	*Chelocnetha*
S. ornatipes	*Nevermannia*
S. ornatum	*Simulium*
S. orsovae	*Nevermannia*
S. oshimaense	Unassigned
S. oshimanum	*Simulium*

S. ovazzae	*Lewisellum*
S. oviceps	*Inseliellum*
S. oviedoi	*Xenosimulium*
S. oyapockense	*Cerqueirellum*
S. ozarkense	*Simulium*
S. padangense	*Gomphostilbia*
S. pahangense	*Daviesellum*
S. palauense	*Inseliellum*
S. palawanense	*Simulium*
S. pallidicranium	*Inseliellum*
S. pallidofemur	*Simulium*
S. pallidum	*Simulium*
S. palmatum	*Simulium*
S. palmeri	*Pomeroyellum*
S. palniense	*Simulium*
S. palopoense	*Simulium*
S. palustre	*Simulium*
S. pamahaense	*Morops*
S. panamense	*Psilopelmia*
S. pandanophilum	*Edwardsellum*
S. pangunaense	*Morops*
S. pankumuense	*Hebridosimulium*
S. papaveroi	*Xenosimulium*
S. papuense	*Morops*
S. paracarolinae	*Hearlea*
S. paracorniferum	*Nevermannia*
S. paradisium	*Hebridosimulium*
S. paraequinum	*Wilhelmia*
S. paraguayense	*Notolepria*
S. parahiyangum	*Gomphostilbia*
S. parahiyangum	*Gomphostilbia*
S. paralongipalpe	Unassigned
S. paraloutetense	*Nevermannia*
S. paramorsitans	*Simulium*
S. paranense	*Xenosimulium*
S. paranubis	*Simulium*
S. parapusillum	*Schoenbaueria*
S. parargyreatum	*Simulium*
S. parawaterfallum	*Simulium*
S. parimaense	Unassigned
S. parmatum	*Boreosimulium*
S. parnassum	*Simulium*
S. parrai	*Simulium*
S. parvulum	*Simulium*
S. parvum	*Simulium*
S. pathrushevae	*Nevermannia*
S. patrushevae	*Schoenbaueria*
S. pattoni	*Gomphostilbia*
S. patzicianense	*Simulium*
S. paucicuspis	*Eusimulium*
S. pauliani	*Pomeroyellum*
S. pautense	*Ectemnaspi*
S. pavlovskii	*Simulium*
S. paynei	*Hemicnetha*
S. pegalanense	*Gomphostilbia*
S. peggyae	*Morops*
S. pekingense	*Wilhelmia*
S. penai	*Eremulium*
S. penobscotense	*Phosterodoros*
S. pentaceros	*Metomphalus*
S. peregrinum	*Gomphostilbia*

S. perflavum	*Psilopelmia*
S. perforatum	*Nevermannia*
S. perlucidulum	*Nevermannia*
S. perplexum	*Trichodagmia*
S. pertinax	*Chirostilbia*
S. peskovi	*Montisimulium*
S. petersoni	*Simulium*
S. petropoliense	*Xenosimulium*
S. phapeungense	*Gomphostilbia*
S. phayaoense	*Simulium*
S. philippianum	*Xenosimulium*
S. philippii	*Pternaspatha*
S. philipponi	Unassigned
S. phluktainae	Unassigned
S. pichi	*Pternaspatha*
S. pichoni	*Inseliellum*
S. pictipes	*Shewellomyia*
S. pifanoi	*Ectemnaspi*
S. pilosum	*Eusimulium*
S. pindiense	*Wilhelmia*
S. pingxianensis	*Gomphostilbia*
S. pintoi	*Trichodagmia*
S. piperi	*Simulium*
S. piscicidium	*Simulium*
S. pitasawatae	*Gomphostilbia*
S. pitense	*Simulium*
S. planipuparium	*Nevermannia*
S. platytarse	*Simulium*
S. plumbeum	*Edwardsellum*
S. podostemi	*Phosterodoros*
S. pohaense	*Morops*
S. polare	*Simulium*
S. politum	*Nevermannia*
S. polyprominulum	*Montisimulium*
S. pontinum	*Simulium*
S. popowae	*Obuchovia*
S. posticatum	*Simulium*
S. pothigaiense	*Simulium*
S. praelargum	*Nevermannia*
S. prafiense	*Morops*
S. prayongi	*Gomphostilbia*
S. proctorae	*Inseliellum*
S. prodexargenteum	*Pternaspatha*
S. prominentum	*Simulium*
S. promorsitans	*Simulium*
S. pseudequinum	*Wilhelmia*
S. pseudoamazonicum	*Cerqueirellum*
S. pseudoantillarum	*Psilopelmia*
S. pseudocallidum	*Psilopelmia*
S. pseudocallidum	*Psilopelmia*
S. pseudocorium	*Inseliellum*
S. pseudoexiguum	*Inaequalium*
S. pseudonearcticum	*Byssodon*
S. pseudopusillum	*Schoenbaueria*
S. puaense	*Gomphostilbia*
S. pufauense	*Inseliellum*
S. pugetense	*Nevermannia*
S. puigi	*Simulium*
S. pukaengense	*Simulium*
S. pulanotum	*Simulium*
S. pulchripes	*Simulium*

S. pulchrum	*Pternaspatha*
S. puliense	*Simulium*
S. pullus	*Simulium*
S. pulverulentum	*Hemicnetha*
S. purii	*Nevermannia*
S. purosae	*Morops*
S. pusillum	*Schoenbaueria*
S. putre	*Xenosimulium*
S. qianense	*Simulium*
S. qiaolaoense	*Nevermannia*
S. qinghaiense	*Wilhelmia*
S. qingshuiense	*Nevermannia*
S. qingxilingense	*Wilhelmia*
S. qini	Unassigned
S. qinlingense	*Nevermannia*
S. qiongzhouense	*Nevermannia*
S. quadratum	*Boreosimulium*
S. quadrifidum	*Coscaroniellum*
S. quadrifila	*Wilhelmia*
S. quadristrigatum	*Psaroniocompsa*
S. quadrivittatum	*Psilopelmia*
S. quasidecolletum	*Nevermannia*
S. quasifrenum	*Simulium*
S. quattuordecimfiliatum	*Montisimulium*
S. quatturodecimfilum	*Montisimulium*
S. quebecense	*Nevermannia*
S. quechuanum	*Pternaspatha*
S. quilleverei	Unassigned
S. quinquefiliatum	*Simulium*
S. quinquestriatum	*Simulium*
S. racenisi	*Simulium*
S. ramosum	*Simulium*
S. ramulosum	*Simulium*
S. ranauense	*Simulium*
S. rangeli	*Notolepria*
S. rangiferinum	*Schoenbaueria*
S. ransikiense	*Morops*
S. raohense	*Nevermannia*
S. rappae	*Xenosimulium*
S. rappae	*Xenosimulium*
S. rashidi	*Simulium*
S. rasyani	*Edwardsellum*
S. ratekholaense	*Simulium*
S. raunsimnae	*Morops*
S. raybouldi	*Nevermannia*
S. rayohense	*Gomphostilbia*
S. rebunense	*Nevermannia*
S. recurvum	*Wallacellum*
S. reginae	*Eusimulium*
S. remissum	*Simulium*
S. remotum	*Simulium*
S. rendalense	*Hellichiella*
S. repertum	*Edwardsellum*
S. reptans	*Simulium*
S. resimum	*Wallacellum*
S. retusum	*Simulium*
S. rezvoi	*Simulium*
S. rheophilum	*Simulium*
S. rhodesinese	*Anasolen*
S. rhopaloides	*Gomphostilbia*
S. rickenbachi	*Phoretomyia*

S. riograndense	*Chirostilbia*
S. rithrogenophila	*Phoretodagmia*
S. rithrogenophilum	*Simulium*
S. rivasi	*Xenosimulium*
S. riverai	*Morops*
S. rivierei	*Inseliellum*
S. rivosecchii	*Nevermannia*
S. rivosecchii	*Simulium*
S. robynae	*Psilopelmia*
S. rodhaini	*Pomeroyellum*
S. romanai	*Ectemnaspi*
S. roquemayu	*Ectemnaspi*
S. roraimense	*Cerqueirellum*
S. rorotaense	*Psilopelmia*
S. rosemaryae	*Gomphostilbia*
S. roslihashimi	*Gomphostilbia*
S. rothfelsi	Unassigned
S. rotifilis	*Simulium*
S. rotundatum	*Simulium*
S. rotundum	*Pomeroyellum*
S. rounae	*Morops*
S. ruandae	*Metomphalus*
S. rubescens	*Nevermannia*
S. rubicundulum	*Hemicnetha*
S. rubiginosum	*Psilopelima*
S. rubrithorax	*Hemicnetha*
S. rubroflavifemur	*Simulium*
S. rubtzovi	*Simulium*
S. rubzovium	*Schoenbaueria*
S. rudnicki	*Simulium*
S. rufibasis	*Simulium*
S. ruficorne	*Nevermannia*
S. rufithorax	*Nevermannia*
S. rugglesi	*Simulium*
S. ruizi	*Simulium*
S. rurutuense	*Inseliellum*
S. rutherfoordi	*Nevermannia*
S. sabahense	*Simulium*
S. saccai	*Hellichiella*
S. saccatum	*Simulium*
S. sacculiferum	*Nevermannia*
S. saihoense	*Morops*
S. sakhalinum	*Montisimulium*
S. sakishimaense	*Simulium*
S. salazarae	*Morops*
S. salebrosum	*Simulium*
S. saliceti	*Nevermannia*
S. salinum	*Eusimulium*
S. samarkandica	*Schoenbaueria*
S. samboni	*Psilopelmia*
S. sanctipauli	*Edwardsellum*
S. sandyi	*Simulium*
S. sangrense	*Wilhelmia*
S. sanguineum	*Cerqueirellum*
S. santomi	*Pomeroyellum*
S. saradzhoense	*Montisimulium*
S. sarawakense	*Gomphostilbia*
S. sasai	*Nevermannia*
S. sastscheri	*Simulium*
S. satsumense	*Eusimulium*
S. savici	*Simulium*

S. saxosum	*Simulium*
S. schamili	*Simulium*
S. schevyakovi	*Montisimulium*
S. schizolomum	*Eusimulium*
S. schizostylum	*Montisimulium*
S. schmidtmummi	*Psaroniocompsa*
S. schoenemanni	*Pternaspatha*
S. schoutedeni	*Pomeroyellum*
S. schwetzi	*Pomeroyellum*
S. scutellatum	*Xenosimulium*
S. scutistriatum	*Hemicnetha*
S. sechani	*Inseliellum*
S. segusina	*Obuchovia*
S. selwynense	*Morops*
S. semushini	*Simulium*
S. senile	*Nevermannia*
S. septentrionale	*Simulium*
S. seramense	*Simulium*
S. sergenti	*Wilhelmia*
S. serranum	*Chirostilbia*
S. serratum	*Gomphostilbia*
S. setsukoae	*Simulium*
S. sexafile	*Simulium*
S. sexiens	*Meilloniellum*
S. sextuplum	*Gomphostilbia*
S. shadini	*Montisimulium*
S. shandongense	*Nevermannia*
S. shangchuanense	*Simulium*
S. shannonae	*Inseliellum*
S. shanxiense	*Simulium*
S. sheilae	*Gomphostilbia*
S. shennongjiaense	*Simulium*
S. sherwoodi	*Gomphostilbia*
S. sheveligiense	*Montisimulium*
S. shevtshenkovae	*Simulium*
S. shewellianum	*Ectemnaspi*
S. shiraki	*Simulium*
S. shoae	*Anasolen*
S. shogakii	*Gomphostilbia*
S. siamense	*Gomphostilbia*
S. sicuani	*Ectemnaspi*
S. silvaticum	*Eusimulium*
S. silvestre	*Nevermannia*
S. simianshanense	*Eusimulium*
S. simile	*Pternaspatha*
S. simoffi	*Simulium*
S. simplex	*Nevermannia*
S. simulacrum	*Simulium*
S. simulans	*Simulium*
S. singgihi	*Gomphostilbia*
S. singtamense	*Simulium*
S. siolii	*Psaroniocompsa*
S. sirbanum	*Edwardsellum*
S. sirimonense	*Nevermannia*
S. slossonae	*Simulium*
S. smarti	*Hemicnetha*
S. snowi	*Phosterodoros*
S. sofiani	*Gomphostilbia*
S. solarii	*Hemicnetha*
S. solomonense	*Morops*
S. songense	*Gomphostilbia*

S. sonkulense	*Montisimulium*
S. sorongense	*Morops*
S. soubrense	*Edwardsellum*
S. souzalopesi	*Xenosimulium*
S. speculiventre	*Nevermannia*
S. spilmani	*Simulium*
S. spinibranchium	*Chirostilbia*
S. spinifer	*Psilopelmia*
S. spinosibranchium	*Wallacellum*
S. spinulicorne	*Freemanellum*
S. spiroi	*Hebridosimulium*
S. splendidum	*Simulium*
S. spoonatum	*Simulium*
S. squamosum	*Edwardsellum*
S. stackelbergi	*Montisimulium*
S. standfasti	*Morops*
S. starmuhlneri	*Nevermannia*
S. steatopygium	*Hebridosimulium*
S. stellatum	Unassigned
S. stelliferum	*Pternaspatha*
S. stenophallum	*Simulium*
S. stevensoni	*Tetisimulium*
S. strelkovi	*Nevermannia*
S. striatum	*Simulium*
S. strigidorsum	*Pternaspatha*
S. striginotum	*Chirostilbia*
S. suarezi	*Psilopelmia*
S. suarezi	*Psilopelmia*
S. subatrum	*Simulium*
S. subclavibranchium	*Inaequalium*
S. subcostatum	*Nevermannia*
S. subexiguum	*Notolepria*
S. subgriseum	*Nevermannia*
S. sublonckei	*Inseliellum*
S. subnigrum	*Inaequalium*
S. subornatoides	*Simulium*
S. subpallidum	*Xenosimulium*
S. subpalmatum	*Simulium*
S. subparadisium	*Hebridosimulium*
S. subpusillum	*Schoenbaueria*
S. subratai	*Nevermannia*
S. subtile	*Simulium*
S. subvariegatum	*Simulium*
S. suchariti	*Simulium*
S. suchitrae	*Asiosimulium*
S. sulawesiense	*Gomphostilbia*
S. sumapazense	*Grenieriella*
S. sumatraense	*Gomphostilbia*
S. sumatraense	*Simulium*
S. sundaicum	*Gomphostilbia*
S. supercilium	*Hebridosimulium*
S. suplidoi	*Simulium*
S. surachaii	*Montisimulium*
S. sutebense	*Morops*
S. sutheppuiense	*Gomphostilbia*
S. suzukii	*Simulium*
S. syafruddini	*Gomphostilbia*
S. synanceium	*Eusimulium*
S. synanceium	*Gomphostilbia*
S. syriacum	*Obuchovia*
S. sytshevskiae	*Montisimulium*

S. taalense	*Simulium*
S. tachengense	*Tetisimulium*
S. tafae	*Morops*
S. tafulaense	*Morops*
S. tahanense	*Gomphostilbia*
S. tahitiense	*Inseliellum*
S. taipei	*Eusimulium*
S. taipokauense	*Simulium*
S. taishanense	*Montisimulium*
S. taiwanicum	*Simulium*
S. takae	*Morops*
S. takahasii	*Wilhelmia*
S. takense	*Simulium*
S. talassicum	*Wilhelmia*
S. tallaferroae	*Xenosimulium*
S. tamorense	*Simulium*
S. tanae	*Titanopteryx*
S. tanae	Unassigned
S. tandrokum	Unassigned
S. tanetchowi	Unassigned
S. tani	*Simulium*
S. tarbagataicum	*Simulium*
S. tarnogradskii	*Simulium*
S. tarsale	*Hemicnetha*
S. tarsatum	*Hemicnetha*
S. tashikulganense	*Gomphostilbia*
S. tatianae	*Montisimulium*
S. tatopaniense	*Simulium*
S. taulingense	*Nevermannia*
S. tauricum	*Nevermannia*
S. taxodium	*Phosterodoros*
S. taylori	*Metomphalus*
S. teerachanense	*Gomphostilbia*
S. temascalense	*Hearlea*
S. tenerificum	*Eusimulium*
S. tentaculum	*Pomeroyellum*
S. tenuatum	*Simulium*
S. tenuipes	*Eremulium*
S. tenuistylum	*Gomphostilbia*
S. tenuitarse	*Nevermannia*
S. tenuitarse	*Simulium*
S. tergospinosum	*Psaroniocompsa*
S. teruamanga	*Inseliellum*
S. tescorum	*Simulium*
S. thailandicum	*Simulium*
S. thienemanni	*Simulium*
S. thungchangense	*Gomphostilbia*
S. thyolense	*Edwardsellum*
S. tianchi	*Nevermannia*
S. timondavidi	*Nevermannia*
S. timorense	*Simulium*
S. titarense	*Simulium*
S. tjanschanicum	*Simulium*
S. tjidodense	*Nevermannia*
S. tobetsuense	*Simulium*
S. tokachiense	*Boreosimulium*
S. tokarense	*Gomphostilbia*
S. tolimaense	*Ectemnaspi*
S. tolongoinae	*Nevermannia*
S. tomae	*Gomphostilbia*
S. tomentosum	*Simulium*

S. tomohonense	*Simulium*
S. tondewandouense	*Metomphalus*
S. tongbaishanense	*Wilhelmia*
S. torautense	*Gomphostilbia*
S. tormentor	*Simulium*
S. torresianum	*Morops*
S. tosariense	*Nevermannia*
S. toubkal	*Nevermannia*
S. touffeum	*Metomphalus*
S. townsendi	*Trichodagmia*
S. transbaikalicum	*Schoenbaueria*
S. transcaspicum	*Obuchovia*
S. transiens	*Parabyssodon*
S. travassosi	*Inaequalium*
S. travisi	*Psilopelmia*
S. triangustum	*Simulium*
S. tricorne	*Simulium*
S. tricrenum	*Nevermannia*
S. tridens	*Byssodon*
S. trifasciatum	*Simulium*
S. triglobus	*Simulium*
S. trilineatum	*Simulium*
S. trirugosum	*Gomphostilbia*
S. trisphaerae	*Byssodon*
S. trivittatum	*Psilopelmia*
S. trombetense	Unassigned
S. trukense	*Inseliellum*
S. truncatum	*Simulium*
S. truncatum	*Simulium*
S. tsharae	*Hemicnetha*
S. tsheburovae	*Hellichiella*
S. tshernovskii	*Schoenbaueria*
S. tshuni	*Argentisimulium*
S. tuberculum	*Hebridosimulium*
S. tuberosum	*Simulium*
S. tuenense	*Gomphostilbia*
S. tulshii	*Simulium*
S. tumidum	*Gomphostilbia*
S. tumninum	*Gnus*
S. tumpaense	*Simulium*
S. tumulosum	*Simulium*
S. tumum	*Gomphostilbia*
S. tunja	*Ectemnaspi*
S. turgaicum	*Wilhelmia*
S. tuyense	*Wallacellum*
S. uaense	*Inseliellum*
S. ubiquitum	*Simulium*
S. uchidai	*Nevermannia*
S. uemotoi	*Nevermannia*
S. ufengense	*Simulium*
S. ulyssesi	*Coscaroniellum*
S. uncum	*Simulium*
S. underhilli	*Phosterodoros*
S. undulatum	*Hebridosimulium*
S. unicornutum	*Pomeroyellum*
S. unum	*Gomphostilbia*
S. upikae	*Simulium*
S. urbanum	*Nevermannia*
S. urubambanum	*Xenosimulium*
S. urundiense	*Meilloniellum*
S. usovae	*Hellichiella*

S. ussovae	*Hemicnetha*
S. valparaiense	*Simulium*
S. vampirum	*Simulium*
S. vamprium	*Simulium*
S. vangilsi	*Pomeroyellum*
S. vantshi	*Rubzovia*
S. vantshum	*Montisimulium*
S. varians	*Xenosimulium*
S. varicorne	*Gomphostilbia*
S. variegatum	*Simulium*
S. veltistshevi	*Wilhelmia*
S. velutinum	*Eusimulium*
S. venator	*Psilopelmia*
S. venezuelense	*Cerqueirellum*
S. ventricum (fossil)	Unassigned
S. venustum	*Simulium*
S. veracruzanum	*Psilopelmia*
S. verecundum	*Simulium*
S. vernum	*Nevermannia*
S. vershininae	*Simulium*
S. versicolor	*Obuchovia*
S. versicolor	*Xenosimulium*
S. vidanoi	*Nevermannia*
S. vigintifile	*Simulium*
S. vilhenai	*Edwardsellum*
S. violator	*Eusimulium*
S. violovitshi	*Montisimulium*
S. virgatum	*Hemicnetha*
S. visayaense	*Gomphostilbia*
S. vischarvi	*Gomphostilbia*
S. visuti	*Simulium*
S. vitile	*Nevermannia*
S. vittatum	*Psilozia*
S. voilense	*Simulium*
S. voltae	*Anasolen*
S. vorax	*Metomphalus*
S. vulcanoae	*Psilopelmia*
S. vulgare	*Simulium*
S. wakrisense	*Morops*
S. walterwittmeri	*Pternaspatha*
S. wambanum	*Edwardsellum*
S. wamenae	*Morops*
S. wanchaii	*Asiosimulium*
S. wangxianense	*Nevermannia*
S. wantoatense	*Morops*
S. watanabei	*Simulium*
S. waterfallum	*Simulium*
S. watetoense	*Morops*
S. weiningense	*Eusimulium*
S. weisiense	*Montisimulium*
S. weji	*Simulium*
S. wellmanni	*Metomphalus*
S. weyeri	*Pomeroyellum*
S. whartoni	*Gomphostilbia*
S. wilhelmlandae	*Morops*
S. wirthi	*Hemicnetha*
S. wolffhuegeli	*Psilopelmia*
S. woodi	*Lewisellum*
S. wulaofengense	*Montisimulium*
S. wulindongense	*Nevermannia*
S. wutaishanense	*Tetisimulium*
S. wuzhishanense	*Simulium*
S. wygodzinskyorum	*Grenieriella*
S. wygoi	*Simulium*
S. wyomingense	*Nevermannia*
S. xanthinum	*Simulium*
S. xanthogastrum	*Simulium*
S. xiaodaoense	*Tetisimulium*
S. xiaolongtanense	*Simulium*
S. xinbinense	*Nevermannia*
S. xingyiense	*Wilhelmia*
S. xinzhouense	*Montisimulium*
S. yacuchuspi	*Pternaspatha*
S. yadongense	*Simulium*
S. yaeyamaense	*Gomphostilbia*
S. yahense	*Edwardsellum*
S. yamayaense	*Nevermannia*
S. yemenense	*Meilloniellum*
S. yepocapense	*Hemicnetha*
S. yokotense	*Simulium*
S. yonagoense	*Boophthora*
S. yonakuniense	*Wallacellum*
S. yongi	*Simulium*
S. yuanbaoshanense	*Gomphostilbia*
S. yuleae	*Morops*
S. yunnanense	*Gomphostilbia*
S. yuntaiense	*Montisimulium*
S. yuphae	*Simulium*
S. yushangense	*Nevermannia*
S. zairense	*Phoretomyia*
S. zakhariense	*Nevermannia*
S. zaporojae	*Chelocnetha*
S. zempoalense	*Psilopelmia*
S. zephyrus	*Boreosimulium*
S. zetterstedti	*Simulium*
S. zhangjiajiense	*Nevermannia*
S. zhiltzovae	*Nevermannia*
S. zombaense	*Metomphalus*
S. zonatum	*Gomphostilbia*

Parasite morphology: Like all dipteran insects, *Simulium* spp. form 4 different types of morphological stages during their life-cycle: eggs; larvae; pupae; and adults. Eggs measure from 100-500 µm in length and are oval to triangular in shape with rounded edges. They are creamy-white in colour when deposited but darken to brown within 24 hours. They have a glutinous outer layer and a smooth inner shell, sometimes containing a subapical micropyle. Larvae develop through 5-11 instars which gradually increase in size up to 5-15 mm long. They have elongated cylindrical creamy-brown bodies with 2 distinctive stubby prolegs (one thoracic and one terminal abdominal) facilitating attachment to underwater substrates using rows of tiny hooks that enmesh with silk spun from adjacent glands. They have hardened head capsules with a small dorsal tubercle (egg burster), lateral eyespots, a pair of 4-segmented

antennae and anterior mouths with opposable toothed mandibles that move pincer-like in a horizontal plane. Most species possess a prominent pair of anterior labral fans used for filter feeding, although some species lack these fans and use their mouthparts to scrape food from substrates. Early instars usually rely on cuticular respiration, but later instars develop posterior gills and mature larvae are distinguished by the presence of black gill spots on the thorax. Pupae are enclosed in dark-coloured conical silken cocoons 2-4 mm long which are attached to substrates by their pointed posterior ends. Simuliid pupae are readily identifiable by the presence of long branched or filamentous respiratory gills protruding from their blunted anterior ends. The pupae resemble adult stages with all appendages held close to the body. Adult black flies have small squat bodies 1-5 mm long (a few species up to 10 mm) with a characteristically humped thorax and broad wings. Despite their name, they are not always black with colouration but may range to grey, brown and even yellow-orange. They have small rounded heads with large compound eyes meeting at the midline in males (holoptic) but separate in females (dichoptic). They have a single pair of short bead-like antennae, each comprising a basal scape, pedicel and then 7-9 rounded flagellomeres lacking setae. The head has a short thick downward-directed proboscis flanked by a longer pair of maxillary palps (5-segmented) present in both sexes. The mouthparts (pair of mandibles, pair of maxillae, labrum and hypopharynx) are sheathed within the labium when not in use. Most piercing stylets are serrated or toothed in blood-feeding females but not in males. The ventral hypopharynx bears a longitudinal groove along which saliva flows during feeding. The alimentary tract consists of a tubular oesophagus leading to a globular proventriculus (with saccular diverticula) ultimately routed to the digestive midgut, then the hindgut (with excretory Malpighian tubules), rectum (with expandable ampulla) and terminal anus. The thorax is generally ovoid with a characteristic dorsal convex arch or hump. The scutum usually lacks setae and bristles but many species display coloured patterns of pigmentation. The mesothorax bears one pair of short broad wings, either smoky opaque or hyaline but never patterned, hairy or scaly. The wing membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] which are thickened along the anterior margin and have a large anal lobe. Like other dipteran flies, the second pair of wings are highly reduced to a pair of posterior knob-like halteres used to stabilize flight. The ventral thorax is the point of attachment for 3 pairs of short hairless legs, each composed of 5 segments (coxa, trochanter, femur, tibia, tarsus) with the latter bearing tarsal claws that are either unarmed or toothed (in species feeding on mammals) or equipped with a thumb-like lobe (in species feeding on birds). The abdomen is ovoid and segmented, most without setae except for the first abdominal tergite being modified to form a prominent basal scale fringed with fine hairs. The abdominal covering is membranous, notably in females to accommodate significant expansion after bloodmeals. The abdomen typically has 7 pairs of lateral spiracles for respiration and the terminal segments are highly modified by external genitalia (ventral genital ducts, male claspers, female ovipositor). Males possess 2 testes connected by vas deferens to a seminal vesicle (with lateral accessory glands) leading to a tubular ejaculatory duct with a terminal bulb near the retractable copulatory aedeagus. Females have 2 ovaries (with polytrophic ovarioles) joined by tubular oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva.

Site of infection: Black flies are free-living insects with aquatic developmental stages and free-flying adults which feed on plant sugars, although adult female flies of some species must also feed on vertebrate blood in order to produce eggs. These transient ectoparasites feed on a wide variety of mammalian and avian hosts, most species being stenoxenous and feeding on closely-related animals, both domestic and wild. Most blood-feeding black flies target bare unprotected skin with little or no hair, notably around the face, ears, neck, abdomen, legs and ankles, with some even attempting to crawl into facial orifices. Several species also exhibit some site specificity, where those that transmit *Onchocerca* to humans in Africa biting the lower limbs and trunk, while those in the Americas preferentially bite the scalp and upper body.

Pathogenesis: Female black flies are telmophagous (pool feeders) as they use their mouthparts to cut the skin and rupture capillaries causing blood to pool in the tissues from where it is sucked up using muscular pharyngeal pumps. They are determined feeders that are not easily interrupted and typically remain feeding over several minutes until satiated, often ingesting their own weight in blood. The saliva they inject at bite sites contains powerful chemicals with anticoagulant, vasodilatory, analgesic and even anaesthetic properties. Host pathological responses may be divided into 3 stages: local trauma to bites; progressive allergic responses to salivary components; and diminished health and productivity due to cumulative host stress. Feeding flies cause structural damage to cutaneous tissues resulting in focal lesions with erythema, haematoma and wheal formation, petechial haemorrhages, ulceration, blood loss, oedematous swellings, dermatitis, and pruritus which can persist for days. Clinical consequences appear to more severe in young ungulates and nestling birds. Mass attacks by fly swarms have also been associated with sudden death characterized by acute stress, general petechial haemorrhages, anaemia, oedema of the larynx and abdominal wall, and sometimes acute toxemia and anaphylactic shock. Bites can be painful to the host resulting in considerable fly worry and biting-stress (annoyance, irritation) precipitating unusual avoidance behaviours (recumbency, quivering, fleeing, even stampedes) and self-trauma (due to biting, scratching, and rubbing) which may predispose wounds to secondary bacterial infections. Hosts may become distracted from feeding, grooming and mating and demonstrate reduced productivity (reduced growth, poor weight gain or even weight loss, lower milk production and decreased egg production). Individuals with prolonged exposure to biting flies may also develop allergic reactions to salivary components (both immediate and delayed hypersensitivity), sometimes causing a systemic illness known as black fly fever characterized by headaches, nausea, vomiting, fever, lethargy, adenitis, localized dermatitis and occasionally asthmatic responses. In addition to being significant biting and nuisance pests to humans and livestock, many *Simulium* spp. may act as biological vectors for infectious diseases caused by viruses (eastern equine encephalitis, vesicular stomatitis in cattle, horses and pigs), protists (leucocytozoonosis and trypanosomiasis in poultry, some waterfowl and raptors) and

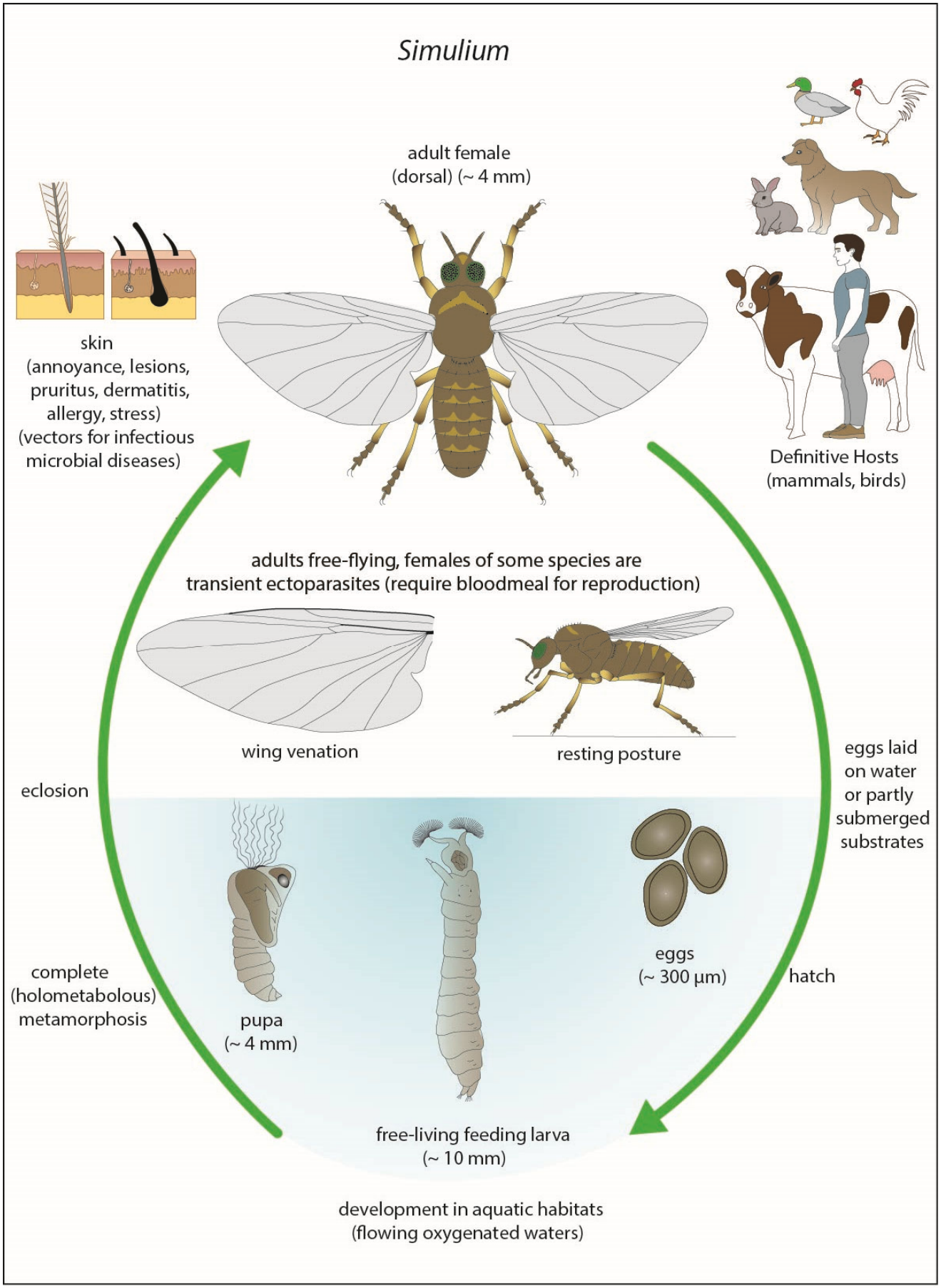
filarial nematodes (mansonellosis and onchocerciasis, including the species *Onchocerca volvulus* causing river blindness in humans in Africa).

Developmental cycle and mode of transmission: Black flies undergo holometabolous (complete) metamorphosis whereby grub-like larvae transform in pupal cocoons to form winged adults. Egg deposition, larval development and pupation take place in aquatic environments, specifically in flowing water whether it be a trickling stream or raging river. Gravid females are oviparous and lay eggs on partially submerged substrates (stones, vegetation) or on the water surface, often in batches of 150-600 eggs although some species oviposit individual eggs. The eggs usually hatch in 2-12 days although this can be delayed for several weeks for many species due to unfavourable conditions (some species over-winter as eggs, while others may over-summer). The eggs of several species have also been shown to survive in moist sand along dried waterways for up to 2 years and then hatch *en masse* following flooding. Emergent larvae attach themselves to vegetation or rocks in flowing water using silken threads and small hooks on their prolegs. They are essentially sedentary although they can change their site of attachment to downstream locations if food becomes scarce or oxygen levels drop. Most species filter feed on detritus and micro-organisms using their labral fans, while other species living in pristine environments (such as glacial melt-waters) have lost their fans and scrape substrates for food. The larvae (and pupae) remain in flowing currents rather than stagnant waters as they require oxygenated water for respiration and survival. The kinetics of larval development depends on the species, prevailing environmental conditions (particularly temperature) and food availability. Most species moult through 5-11 larval instars (average 6-7) over a period of several weeks, but sometimes extended up to 1 year (some species over-winter as larvae). The final larval instar spins a conical cocoon with the narrow end attached to shallow submerged objects and the open end with the highly branched or filamentous respiratory gills facing downstream. Pupation generally takes 3-10 days and the immature adult emerges rising to the surface in a bubble of air. Adults emerge during the daytime, with males usually emerging first and then waiting to mate with emergent females, sometimes in swarms. Both males and females feed on plant nectar to derive energy. Not all species are blood-feeders and their females are obligatorily autogenous and may complete ovarian (gonotrophic) cycles (maturation of egg batches) using internal energy reserves. However, the females of other species are anautogenous and do require bloodmeals to produce eggs, completing each gonotrophic cycle 2-10 days after feeding. These species are therefore transient haematophagous ectoparasites on a range of vertebrate hosts. They often aggregate in trees along waterways and emerge in dense swarms when hosts become available. Females use a variety of senses to find hosts; particularly olfactory (exhaled carbon dioxide, body odours), thermal (body temperature), visual (size, shape, colour) and tactile (skin texture) cues. Black flies are moderate fliers and generally require low wind speed, although they can disperse for kilometres when wind-assisted. Most hosts that are bitten live close to running water and are attacked during the day in the outdoors (exophilic). Female flies live for 3-4 weeks and lay eggs in batches of 150-600 eggs but they usually only complete 2-4 gonotrophic cycles before dying. The duration of the entire life-cycle depends largely on the climate in which the fly species live, with many in cold regions being univoltine and only completing a single generation annually, many in temperate regions being multivoltine and completing around 7 generations annually while those in the tropics may complete up to 20 generations annually.

Differential diagnosis: Clinical signs exhibited by hosts (dermal lesions, inflammation and pruritus) are nonspecific and may be attributed to a range of aetiological agents (ectoparasites, microbes, allergic and other skin conditions). Nevertheless, black fly bites (and even black fly fever) may be suspected in affected hosts with relevant temporal and spatial histories (seasonal afflictions in proximity to flowing water). Diagnosis is dependent on the direct observation of biting flies but this can be difficult in nervous animals shying away from small flies. While black flies may be captured using baits or nets, their identification is difficult as many species are morphologically indistinguishable. Entomologists often resort to more holistic approaches to species identification and examine characteristics of aquatic pre-adult stages (eggs, larvae and pupae), but still refer to species ‘groups’ or ‘complexes’ in recognition of the potential existence of cryptic, sibling or cyto-species. Genetic karyotyping studies have detected unique banding patterns on polytene chromosomes from larval silk glands, and molecular biological studies on adult flies (particularly those implicated in the transmission of river blindness) are beginning to discover signature sequences in nuclear and mitochondrial genes amplified by polymerase chain reaction (PCR).

Treatment and control: Humans suffering from adverse reactions to black fly bites may be treated symptomatically with anti-inflammatory and antipruritic lotions or creams, as well as antibiotics for secondary infections as required. Those experiencing severe allergic reactions (including black fly fever) may require hospitalization and systemic treatment with glucocorticoids and antihistamines to alleviate hypersensitivity responses. Over the last few decades, a range of topical insecticides have been applied to animals in attempts to reduce the frequency of attack. Early studies reported good success using the organochlorine dichlorodiphenyltrichloroethane (DDT) but it has been discontinued due to rapid development of resistance as well as undesirable effects on non-target species. Subsequent studies reported successes with other organochlorides (methoxychlor), organophosphates (temephos, malathion) and insect growth regulators (triazines), but most were not selective and had negative impacts on non-target species. Intensively-farmed livestock have responded well to treatment with macrocyclic lactones (ivermectin as pour-ons or impregnated in eartags) and oils, greases or salves laced with repellents (permethrins, and even turpentine) applied to susceptible sites (particularly ears). Aerial and ground fogging with DDT and permethrin products have been used to kill free-flying adults in the environment, as well as larvae in aquatic habitats, but such measures have largely been abandoned due to ecological concerns and the recent development of alternative larvicidal treatments. Great success has been reported when spraying the environment with the entomopathogenic bacterium *Bacillus thuringiensis* var. *israelensis* whose endotoxins kill black fly larvae by disrupting the

integrity of their midguts. Many countries have adopted control programmes involving spraying bacterial suspensions by hand or aircraft to a wide variety of waterways. Other attempts at biological control have evaluated mermithid nematodes, microsporidia, chytrid fungi and several viruses as parasites and pathogens of black flies. Some control has been achieved by reducing the suitability of potential breeding habitats by the physical removal of attachment sites in water (esp. trailing vegetation) and engineering irrigation systems to avoid fast currents (installing ponds and periodically manipulating water levels to expose larvae). Several animal management practices can also be used to reduce the incidence of fly attack, including housing animals indoors or building covered shelters as black flies do not venture inside darkened cooler areas or buildings. Insecticides and repellents can also be sprayed on surfaces or coverings around doors and windows. People may also adopt higher levels of personal protection, staying indoors during peak biting times (mornings and evenings), covering-up (wearing light-coloured clothing with gathered cuffs and collars, even wearing fine-mesh head-nets to avoid swarms when working outside) and using insect repellents (applying natural or synthetic chemicals to the skin or clothing). While many studies have shown that the repellent diethyltoluamide (DEET) may be used safely on humans, it should not by sprayed on animals as it may be toxic if ingested by licking, and several studies have suggested that it may not repel some *Simulium* species.


Simulium
adult female
(dorsal) (~ 4 mm)
skin
(annoyance, lesions,
pruritus, dermatitis,
allergy, stress)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, birds)
adults free-flying, females of some species are
transient ectoparasites (require bloodmeal for reproduction)
wing venation
resting posture
eclosion
eggs laid
on water
or partly
submerged
substrates
complete
(holometabolous)
metamorphosis
pupa
(~ 4 mm)
eggs
(~ 300 µm)
hatch
free-living feeding larva
(~ 10 mm)
development in aquatic habitats
(flowing oxygenated waters)



Simulium adult



Simulium eggs



Simulium larva



Simulium pupa

Phlebotomus, Lutzomyia
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Nematocerans include the culicids (mosquitoes), ceratopogonids (midges); simuliids (black flies) and psychodids (sand flies): only the females are parasitic and have piercing-sucking mouthparts. Psychodids include the phlebotomine sand flies, which have characteristically hairy bodies and wings. Adults have cutting mandibles and females feed on plant juices and blood by pool-feeding (telmophagy). They parasitize reptiles, amphibians, birds and mammals, incl. humans. Eggs are laid near decomposing material as the larvae require organic debris on which to feed. Both Old World genera (*Phlebotomus*) and New World/American genera (*Lutzomyia*) are anthropophilic and known to transmit protozoa (leishmaniasis), bacteria (Carrions' disease) and viruses (sand fly fever).

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Nematocera (midges/mosquitoes, long filamentous antennae, aquatic larvae/pupae)
Family:	Psychodidae (moth flies/sand flies, incl. phlebotomines, characteristically hairy bodies and wings)
Genus:	*Phlebotomus* (parasitic on skin of mammals/birds)
Genus:	*Lutzomyia* (parasitic on skin of mammals/birds)
Species:	various species cause irritation, pruritus, wheals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic	Biodiversity	Parasitic	Status	Pathogenesis*	Disease transmission

dipteran families		stages			
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Nematocera comprises small slender flies that are 'thread-horned' i.e. they possess long filamentous antennae composed of many articulating segments (= nemato-cera). Adults have long narrow wings (with many branching veins) and specialized mouthparts (short or long) with a protective sheath (labium and labellae) protecting feeding stylets (labrum, mandibles, maxillae and hypopharynx) and flanked by 4-5 segmented palps (usually pendulous but slender in mosquitoes). Many species have aquatic life-cycles (larval/pupal stages associated with water) and all undergo complete metamorphosis whereby adults eclose from puparia through longitudinal slits (rather than circular caps like Cyclorrapha). The suborder contains 7 infraorders: Axymyiomorpha (larvae in decomposing wood); Bibionomorpha (gnats, lovebugs); Blephariceromorpha (mountain midges); Culicomorpha (mosquitoes, midges, black flies); Psychodomorpha (moth flies); Ptychopteromorpha (primitive crane flies); and Tipulomorpha (crane flies). Many species are free-living detritivores but some have adapted to bite vertebrate hosts in order to feed on blood. The infraorder Psychodomorpha contains 3 superfamilies: Anisopodoidea (wood gnats), Psychodoidea (moth flies), and Scatopsoidea (dung midges). The superfamily Psychodoidea contains the single family Psychodidae which are collectively and commonly known as moth flies, but includes free-living drain flies, sink flies, filter flies, sewer flies/gnats, as well as haematophagous 'sand flies'. Psychodid flies have small narrow hairy bodies, large black eyes, long filamentous antennae, long mouthparts with 5-segmented

palps, long legs and long narrow pointed and hairy wings with numerous parallel veins running to the wing margins. Over 3,000 psychodid species have been described in over 150 genera in 5 subfamilies: 3 subfamilies containing non-biting flies (namely, Bruchomyiinae with 3 genera; Psychodinae with 104 genera; Trichomyiinae with 1 genus); and 2 subfamilies containing biting flies (Sycoracinae with 2 genera, and Phlebotominae with 27 genera (including *Lutzomyia* and *Phlebotomus*)); with another 12 unplaced genera and 3 fossil genera.

The broad usage of the term 'sand fly' has been a source of some confusion as it has been applied not only to phlebotomines, but sometimes also to quite different flies, notably black flies (family Simuliidae) and biting midges (family Ceratopogonidae). Phlebotomine sand flies have characteristically hairy bodies, well-developed mandibles, long cylindrical antennal segments, and hairy wings (with 2 longitudinal wing veins between radial and medial forks) typically held sloping upwards (trough-like) when at rest. They are found throughout the world, especially in tropical and subtropical regions, with many taxa being confined to either the Old World (Africa, Asia) e.g. *Phlebotomus* and *Sergentomyia,* or the New World (Americas) e.g. *Lutzomyia, Brumptomia,* and *Warileya*. The genus *Phlebotomus* (syn. *Cyniphes, Flebotomus, Haemasson*) contains almost 140 species, most classified in 13 subgenera; while the genus *Lutzomyia* (syn. *Fransaia*, *Lutziola*) contains over 440 species, most classified in 19 subgenera. Adult flies may feed on a wide range of material, including nectar from plants and detritus in moist environments, sewage and decaying organic matter, but the females of most sand fly species are anautogenous and require a bloodmeal from a vertebrate host for their ovaries to complete their development (although some species are autogenous and may complete the first gonotrophic cycle without taking blood). While some species are anthropophilic and will feed on humans, most are zoophilic and feed on an extensive range of animals (domestic and wild mammals, birds, reptiles and amphibians. A growing number of species have gained notoriety as vectors for the transmission of viral, bacterial and protozoal diseases, notably *Leishmania* spp. responsible for cutaneous, mucocutaneous and visceral leishmaniasis in mammals (including humans).

Sand fly species (regional exemplars)	**Host preferences**	**Clinical signs (Vectorial capacity)**	**Distribution**
Phlebotomus aculeatus, alexandri, ansarii, duboscqi, guggisbergi, longipes, papatasi, pedifer, rossi, salehi, sergenti	mammals: primates (incl. humans); rodents (murids, sciurids), carnivores (canids), hyraxes; occasionally birds	irritation, wheals (Old World cutaneous leishmaniasis, sand fly fever virus, Chandipura virus)	Old World (Eurasia, Africa)
P. alexandri, argentipes, ariasi, caucasicus, celiae, chinensis, kandelakii, langeroni, longicuspis, longiductus, martini, neglectus, orientalis, perfiliewi, pernicosus, smirnovi, tobbi, transcaucasicus, vansomerenae	mammals: primates (incl. humans); rodents (murids), carnivores (canids), occasionally bovids	irritation, wheals (Old World visceral leishmaniasis, sand fly fever virus,)	Old World (Eurasia, Africa)
Lutzomyia anduzei, anthophora, ayacuchensis, ayrozai, carrerai, christopheri, diabolica, flaviscutellata, gomezi, hartmanni, intermedia, lichyi, llanosmartini, migonei, nuneztovari, olmeca, ovallesi, panamensis, paraensis, peruensis, pessoai, reducta, spinicrassa, squamiventris, townsendi, shannoni, trapidoi, trinidadensis, ubiquitalis, umbratilis, verrucarum, wellcomei, whitmani, ylephiletor, youngi, yucamensis	mammals: primates (incl. humans), bradypodids (sloths), didelphids (opossums), cingulates (armadillos, anteaters), carnivores (canids, felids, herpestids, procyonids, hystricids), equids, rodents (capromyids, dasyproctids, echimyids, heteromyids, murids, sciurids), occasionally artiodactyls (cattle, sheep, pronghorns, swine), some birds	irritation, wheals (New World cutaneous leishmaniasis, bartonellosis, sandfly fever virus, vesicular stomatitis virus, Changuinola fever virus)	New World (Americas)
L. antunesi, cruzi, evansi, longipalpis	domestic and wild mammals: primates (incl. humans), canids, opossums	irritation, wheals (New World visceral leishmaniasis)	New World (Central and South America)

Full species list (compilation of several on-line data-bases)

***Phlebotomus* species**	**Subgenus**
P. aculeatus	*Larroussius*
P. acuminatus	*Australophlebotomus*
P. alexandri	*Paraphlebotomus*
P. andrejevi	*Paraphlebotomus*
P. angustus	*Adlerius*
P. ansarii	*Synphlebotomus*
P. argentipes	*Euphlebotomus*
P. ariasi	*Larroussius*
P. ashfordi	*Larroussius*

P. asperulus	*Idiophlebotomus*
P. autumnalis	*Euphlebotomus*
P. balcanicus	*Adlerius*
P. barguesae	*Euphlebotomus*
P. berentiensis	*Madaphlebotomus*
P. bergeroti	*Phlebotomus*
P. betisi	*Larroussius*
P. boucheti	*Idiophlebotomus*
P. brevifilis	*Australophlebotomus*
P. brevifiloides	*Australophlebotomus*
P. brevis	*Adlerius*
P. buccinator	*Australophlebotomus*
P. burneyi	*Larroussius*
P. canaaniticus	*Larroussius*
P. caucasicus	*Paraphlebotomus*
P. caudatus	*Euphlebotomus*
P. celiae	*Synphlebotomus*
P. chabaudi	*Paraphlebotomus*
P. chadlii	*Larroussius*
P. chinensis	*Adlerius*
P. chiyankiensis	*Anaphlebotomus*
P. colabaensis	*Anaphlebotomus*
P. comatus	*Adlerius*
P. davidi	*Adlerius*
P. dispar	*Idiophlebotomus*
P. duboscqi	*Phlebotomus*
P. dycei	*Australophlebotomus*
P. economidesi	*Transphlebotomus*
P. eleanorae	*Synphlebotomus*
P. elgonensis	*Larroussius*
P. erebicola	*Idiophlebotomus*
P. fantalensis	*Larroussius*
P. fengi	*Adlerius*
P. fertei	*Madaphlebotomus*
P. fontenillei	*Madaphlebotomus*
P. fortunatarum	*Abonnencius*
P. frondifer	*Idiophlebotomus*
P. galilaeus	*Larroussius*
P. gemetchi	*Paraphlebotomus*
P. gibiensis	*Larroussius*
P. gigas	*Spelaeophlebotomus*
P. gouldi	*Euphlebotomus*
P. grimmi	Unassigned
P. grovei	*Synphlebotomus*
P. guggisbergi	*Larroussius*
P. halepensis	*Adlerius*
P. hoepplii	*Anaphlebotomus*
P. huberti	*Anaphlebotomus*
P. ilami	*Larroussius*
P. jacusieli	*Paraphlebotomus*
P. kabulensis	*Adlerius*
P. kandelakii	*Larroussius*
P. katangensis	*Synphlebotomus*
P. kazeruni	*Paraphlebotomus*
P. keshishiani	*Larroussius*
P. kiangsuensis	*Euphlebotomus*
P. kyreniae	*Adlerius*
P. langeroni	*Larroussius*
P. lengi	*Larroussius*
P. longicuspis	*Larroussius*
P. longiductus	*Adlerius*

P. longipes	*Larroussius*
P. mackerrasi	*Australophlebotomus*
P. maduloae	Unassigned
P. major	*Larroussius*
P. martini	*Synphlebotomus*
P. mascittii	*Larroussius*
P. mascomai	*Euphlebotomus*
P. mesghalii	*Euphlebotomus*
P. minteri	*Spelaeophlebotomus*
P. mireillae	*Paraphlebotomus*
P. mongolensis	*Paraphlebotomus*
P. multihamata	Unassigned
P. nadimi	*Euphlebotomus*
P. naqbenius	*Adlerius*
P. neglectus	*Larroussius*
P. newsteadi	*Synphlebotomus*
P. notteghemae	Unassigned
P. notus	*Larroussius*
P. nuri	*Paraphlebotomus*
P. orientalis	*Larroussius*
P. papatasi	*Phlebotomus*
P. papuensis	*Australophlebotomus*
P. pedifer	*Larroussius*
P. perfiliewi	*Larroussius*
P. perniciosus	*Larroussius*
P. pexopharynx	*Australophlebotomus*
P. philippinensis	*Euphlebotomus*
P. pholetor	*Idiophlebotomus*
P. pungens (fossil)	Unassigned
P. riouxi	*Paraphlebotomus*
P. rodhaini	*Anaphlebotomus*
P. rossi	*Synphlebotomus*
P. rousettus	*Anaphlebotomus*
P. rupester	*Adlerius*
P. saevus	*Paraphlebotomus*
P. salangensis	*Adlerius*
P. salehi	*Phlebotomus*
P. saltiae	*Synphlebotomus*
P. sanctijohani	*Anaphlebotomus*
P. sejunctus	*Idiophlebotomus*
P. sergenti	*Paraphlebotomus*
P. sichuanensis	*Adlerius*
P. sikandraensis	*Synphlebotomus*
P. simici	*Adlerius*
P. sinensis	Unassigned
P. smirnovi	*Larroussius*
P. somaliensis	*Larroussius*
P. stantoni	*Anaphlebotomus*
P. stellae	*Idiophlebotomus*
P. sundarai	Unassigned
P. syriacus	*Larroussius*
P. taylori	*Synphlebotomus*
P. teshi	*Idiophlebotomus*
P. tobbi	*Larroussius*
P. transcaucasicus	*Larroussius*
P. trifilis	*Australophlebotomus*
P. tubifer	*Idiophlebotomus*
P. tumenensis	*Euphlebotomus*
P. turanicus	*Adlerius*
P. vansomerenae	*Synphlebotomus*
P. vaomalalae	*Madaphlebotomus*

P. vaseti	Unassigned
P. vetus (fossil)	Unassigned
P. vincenti	*Madaphlebotomus*
P. wellingsae	*Idiophlebotomus*
P. yunshengensis	*Euphlebotomus*
P. zulrfagarensis	*Adlerius*

***Lutzomyia* species**	**Subgenus**
L. abonnenci	*Psathyromyia*
L. absonodonta	*Micropygomyia*
L. abunaensis	Unassigned
L. acostai	*Trichophoromyia*
L. adamsi	*Helcocyrtomyia*
L. aldafalcaoae	Unassigned
L. alencari	*Lutzomyia*
L. almerioi	*Lutzomyia*
L. alphabetica	Unassigned
L. amarali	*Lutzomyia*
L. amazonensis	*Psychodopygus*
L. amilcari	Unassigned
L. ancashensis	*Lutzomyia*
L. andersoni	Unassigned
L. andina	Unassigned
L. anduzei	*Nyssomyia*
L. antezanai	Unassigned
L. anthophora	*Dampfomyia*
L. antioquiensis	Unassigned
L. antunesi	*Nyssomyia*
L. apache	*Helcocyrtomyia*
L. appendiculata	Unassigned
L. aquilonia	*Coromyia*
L. aragaoi	Unassigned
L. araracuarensis	*Lutzomyia*
L. arevaloi	Unassigned
L. arthuri	*Psychodopygus*
L. atroclavata	*Micropygomyia*
L. atulapai	*Dampfomyia*
L. aulari	Unassigned
L. auraensis	*Trichophoromyia*
L. ayacuchensis	*Helcocyrtomyia*
L. ayrozai	*Psychodopygus*
L. baculus	Unassigned
L. bahiensis	Unassigned
L. baityi	Unassigned
L. barrettoi	Unassigned
L. battistinii	*Lutzomyia*
L. begonae	*Evandromyia*
L. beltrani	*Coromyia*
L. beniensis	*Trichophoromyia*
L. bernalei	*Psychodopygus*
L. bettinii	*Trichophoromyia*
L. bianchigalatiae	*Pintomyia*
L. bibinae	*Nyssomyia*
L. bicolor	*Nyssomyia*
L. bicornuta	*Lutzomyia*
L. bifoliata	*Lutzomyia*
L. bispinosa	*Psychodopygus*
L. blancasi	*Helcocyrtomyia*
L. boliviana	Unassigned
L. borgmeieri	Unassigned
L. botella	*Helcocyrtomyia*
L. bourrouli	*Evandromyia*
L. brachiphallus	*Evandromyia*
L. brachipyga	*Trichophoromyia*
L. brandaoi (fossil)	*Lutzomyia*
L. brasiliensis	Unassigned
L. brazilorum (fossil)	Unassigned
L. breviducta	Unassigned
L. brisolai	Unassigned
L. bursiformis	Unassigned
L. caballeroi	*Helcocyrtomyia*
L. caceresi	Unassigned
L. cajamarcensis	*Pifanomyia*
L. calcarata	*Pressatia*
L. californica	*Micropygomyia*
L. caligata	*Lutzomyia*
L. callipyga	Unassigned
L. caminoi	Unassigned
L. campbelli	*Psathyromyia*
L. campograndensis	Unassigned
L. camposi	*Pressatia*
L. capixaba	Unassigned
L. caprina	*Viannamyia*
L. carmelinoi	Unassigned
L. carpenteri	Unassigned
L. carrerai	*Psychodopygus*
L. carvalhoi	*Lutzomyia*
L. castanea	*Helcocyrtomyia*
L. castanheirai	*Trichophoromyia*
L. castilloi	*Psathyromyia*
L. castroi	*Lutzomyia*
L. cavernicola	*Lutzomyia*
L. cayennensis	*Micropygomyia*
L. ceferinoi	*Helcocyrtomyia*
L. cellulana	*Trichophoromyia*
L. cerqueirai	*Evandromyia*
L. cerradincola	Unassigned
L. chagasi	*Psychodopygus*
L. chassigneti	Unassigned
L. chavinensis	Unassigned
L. chiapanensis	*Micropygomyia*
L. chotensis	Unassigned
L. choti	*Pressatia*
L. christenseni	*Pintomyia*
L. christophei	Unassigned
L. cipoensis	*Lutzomyia*
L. cirrita	*Helcocyrtomyia*
L. claustrei	*Psychodopygus*
L. clitella	*Trichophoromyia*
L. columbiana	Unassigned
L. complexa	*Psychodopygus*
L. conviti	*Trichopygomyia*
L. corossoniensis	*Psychodopygus*
L. correalimai	Unassigned
L. cortelezzii	Unassigned

L. corumbaensis	Unassigned
L. costalimai	Unassigned
L. coutinhoi	Unassigned
L. cratifer	*Psathyromyia*
L. cruciata	*Lutzomyia*
L. cruzi	*Lutzomyia*
L. ctenidophora	*Micropygomyia*
L. cubensis	Unassigned
L. cultellata	*Psathyromyia*
L. damascenoi	*Pintomyia*
L. dasymera	*Psathyromyia*
L. dasypodogeton	*Trichopygomyia*
L. davisi	*Psychodopygus*
L. deleoni	*Coromyia*
L. delpozoi	Unassigned
L. dendrophyla	*Psathyromyia*
L. deorsa	Unassigned
L. depaquiti	*Trichopygomyia*
L. derelicta	Unassigned
L. dereuri	Unassigned
L. diabolica	*Lutzomyia*
L. diazi	Unassigned
L. digitata	*Lutzomyia*
L. disiuncta	Unassigned
L. disneyi	*Coromyia*
L. dispar	*Lutzomyia*
L. dodgei	*Dampfomyia*
L. douradoi	*Psychodopygus*
L. dreisbachi	*Lutzomyia*
L. dubitans	Unassigned
L. duncanae	*Pressatia*
L. dunhami	*Trichophoromyia*
L. duppyorum	*Micropygomyia*
L. durani	*Micropygomyia*
L. dysponeta	*Pressatia*
L. echinatopharynx	*Lutzomyia*
L. edentula	*Nyssomyia*
L. edwardsi	Unassigned
L. elegans	*Trichopygomyia*
L. emberai	Unassigned
L. equatorialis	*Pressatia*
L. erwindonaldoi	*Helcocyrtomyia*
L. eurypyga	*Trichophoromyia*
L. evandroi	Unassigned
L. evangelistai	*Lutzomyia*
L. evansi	Unassigned
L. fairchildi	*Psychodopygus*
L. fairtigi	*Psychodopygus*
L. falcaorum	Unassigned
L. falcata	*Lutzomyia*
L. falquetoi	*Lutzomyia*
L. fariasi	*Viannamyia*
L. farilli	*Micropygomyia*
L. ferreirana	Unassigned
L. ferroae	*Trichopygomyia*
L. firmatoi	Unassigned
L. fischeri	*Pintomyia*
L. flabellata	*Lutzomyia*
L. flaviscutellata	*Nyssomyia*
L. flochi	*Trichophoromyia*
L. fluviatilis	*Sciopemyia*
L. fonsecai	Unassigned
L. forattinii	*Lutzomyia*

L. fraihai	*Nyssomyia*
L. furcata	*Viannamyia*
L. galatiae	*Helcocyrtomyia*
L. gaminarai	*Lutzomyia*
L. gantieri	*Trichopygomyia*
L. gasparviannai	*Lutzomyia*
L. gaucha	*Lutzomyia*
L. geniculata	*Psychodopygus*
L. georgii	*Evandromyia*
L. gibba	*Trichophoromyia*
L. gibsoni	*Pintomyia*
L. goiana	Unassigned
L. gomezi	*Lutzomyia*
L. gonzaloi	*Helcocyrtomyia*
L. gorbitzi	*Migonemyia*
L. grimaldii	*Lutzomyia*
L. gruta	Unassigned
L. guatemalensis	*Psathyromyia*
L. guderiani	*Helcocyrtomyia*
L. guilvardae	*Pifanomyia*
L. guyanensis	*Psychodopygus*
L. hardisoni	*Micropygomyia*
L. hartmanni	*Helcocyrtomyia*
L. hermanlenti	*Lutzomyia*
L. hernandezi	*Nyssomyia*
L. herreri	*Helcocyrtomyia*
L. hirsute	*Psychodopygus*
L. howardi	*Trichophoromyia*
L. huacalquensis	Unassigned
L. ignacioi	Unassigned
L. imperatrix	*Helcocyrtomyia*
L. incasica	*Trichophoromyia*
L. inflata	Unassigned
L. infraspinosa	*Evandromyia*
L. infusca	*Helcocyrtomyia*
L. ininii	*Trichophoromyia*
L. inornata	*Nyssomyia*
L. inpai	*Evandromyia*
L. insolita	*Dampfomyia*
L. intermedia	*Nyssomyia*
L. inusitata	Unassigned
L. ischnacantha	*Lutzomyia*
L. ischyracantha	*Lutzomyia*
L. isopsi	Unassigned
L. isovespertilionis	*Coromyia*
L. killicki	*Psychodopygus*
L. killickorum (fossil)	Unassigned
L. kirigetiensis	*Helcocyrtomyia*
L. kuscheli	*Pintomyia*
L. lainsoni	*Psychodopygus*
L. lanei	*Lutzomyia*
L. larensis	*Helcocyrtomyia*
L. legerae	*Lutzomyia*
L. lenti	*Barrettomyia*
L. leohidalgoi	*Dampfomyia*
L. leonidasdeanei	*Psychodopygus*
L. lerayi	*Psathyromyia*
L. lewisi	*Micropygomyia*
L. lichyi	*Lutzomyia*
L. limafalcaoae	Unassigned
L. llanosmartinsi	*Psychodopygus*
L. lloydi	*Psychodopygus*
L. longiflocosa	Unassigned

L. longipalpis	*Lutzomyia*
L. longipennis	Unassigned
L. longispina	*Trichopygomyia*
L. lopesi	*Trichophoromyia*
L. loretonensis	*Trichophoromyia*
L. luisleoni	*Psychodopygus*
L. lutziana	*Psathyromyia*
L. machupicchu	Unassigned
L. maesi	*Tricholateralis*
L. majuscula	Unassigned
L. mamedei	*Pressatia*
L. manciola	Unassigned
L. mangabeirana	Unassigned
L. maracayensis	Unassigned
L. maranonensis	*Pifanomyia*
L. marinkellei	*Lutzomyia*
L. maripaensis	*Psychodopygus*
L. martinezi	*Trichopygomyia*
L. maruaga	Unassigned
L. matiasi	Unassigned
L. matosi	*Psychodopygus*
L. meirai	*Trichophoromyia*
L. melloi	*Trichophoromyia*
L. microps	*Sciopemyia*
L. micropyga	*Micropygomyia*
L. migonei	*Migonemyia*
L. minasensis	*Micropygomyia*
L. misionensis	Unassigned
L. mollinedoi	Unassigned
L. monstruosa	*Evandromyia*
L. monticolus	Unassigned
L. monzonensis	*Helcocyrtomyia*
L. moralesi	Unassigned
L. moucheti	Unassigned
L. munaypata	Unassigned
L. nadiae	Unassigned
L. naftalekatzi	Unassigned
L. napoensis	*Trichophoromyia*
L. nematoducta	*Sciopemyia*
L. nemorosa	*Trichophoromyia*
L. nevesi	Unassigned
L. nicaraguensis	*Psychodopygus*
L. nociva	*Nyssomyia*
L. nocticola	*Psychodopygus*
L. noguchii	*Helcocyrtomyia*
L. novoae	Unassigned
L. nuneztovari	Unassigned
L. octavioi	*Trichophoromyia*
L. odax	Unassigned
L. oliveirai	*Micropygomyia*
L. olmeca	*Nyssomyia*
L. omagua	*Trichophoromyia*
L. oppidana	*Helcocyrtomyia*
L. oresbia	Unassigned
L. orestes	Unassigned
L. osornoi	*Helcocyrtomyia*
L. oswaldoi	Unassigned
L. ottolinai	Unassigned
L. ovallesi	Unassigned
L. pabloi	*Trichophoromyia*
L. pacae	Unassigned
L. pajoti	*Nyssomyia*
L. paleotownsendi (fossil)	*Lutzomyia*
L. paleotrichia (fossil)	*Lutzomyia*
L. pallidithorax	*Helcocyrtomyia*
L. panamensis	*Psychodopygus*
L. paraensis	*Psychodopygus*
L. parimaensis	*Psychodopygus*
L. pascalei	Unassigned
L. pastazaensis	*Trichophoromyia*
L. paterna (fossil)	Unassigned
L. pelloni	*Lutzomyia*
L. pennyi	*Sciopemyia*
L. perezi	Unassigned
L. permira	*Dampfomyia*
L. peruensis	*Helcocyrtomyia*
L. pescei	*Helcocyrtomyia*
L. pessoai	*Pintomyia*
L. pestanai	*Psathyromyia*
L. petari	*Lutzomyia*
L. petropolitana	Unassigned
L. pia	Unassigned
L. piedraferroi	Unassigned
L. pilosa	Unassigned
L. pinna	*Trichopygomyia*
L. pinottii	*Evandromyia*
L. pisuquia	Unassigned
L. ponsi	Unassigned
L. pradobarrientosi	Unassigned
L. pratti	Unassigned
L. preclara	*Sciopemyia*
L. pseudolongipalpis	Unassigned
L. punctigeniculata	*Psathyromyia*
L. pusilla	Unassigned
L. quadrispinosa	*Micropygomyia*
L. quasitownsendi	Unassigned
L. quechua	Unassigned
L. quillabamba	Unassigned
L. quinquefer	Unassigned
L. rabelloi	Unassigned
L. ramirezi	Unassigned
L. rangeliana	Unassigned
L. ratcliffei	*Trichopygomyia*
L. readyi	*Trichophoromyia*
L. reburra	*Trichophoromyia*
L. reclusa	*Helcocyrtomyia*
L. recurva	*Psychodopygus*
L. reducta	*Nyssomyia*
L. reinerti	*Trichophoromyia*
L. renei	*Lutzomyia*
L. richardwardi	*Nyssomyia*
L. rispaili	*Helcocyrtomyia*
L. robusta	*Pifanomyia*
L. rondoniensis	*Trichopygomyia*
L. rorotaensis	Unassigned
L. rosabali	*Dampfomyia*
L. rostrans	*Trichophoromyia*
L. ruii	*Trichophoromyia*
L. runoides	Unassigned
L. rupicola	Unassigned
L. saccai	Unassigned
L. sallesi	Unassigned
L. saltuosa	*Trichophoromyia*
L. samueli	Unassigned
L. sanguinaria	*Helcocyrtomyia*
L. saulensis	Unassigned

L. sauroida	Unassigned
L. scaffi	*Psathyromyia*
L. schreiberi	*Micropygomyia*
L. scorzai	*Helcocyrtomyia*
L. sericea	Unassigned
L. serrana	Unassigned
L. servulolimai	*Sciopemyia*
L. shannoni	*Psathyromyia*
L. shawi	*Nyssomyia*
L. sherlocki	*Lutzomyia*
L. singularis	Unassigned
L. sinuosa	*Trichophoromyia*
L. sipani	*Evandromyia*
L. soccula	*Psathyromyia*
L. sordellii	*Sciopemyia*
L. souzacastroi	*Psathyromyia*
L. souzalopesi	*Lutzomyia*
L. spathotrichia	*Lutzomyia*
L. spinicrassa	Unassigned
L. squamiventris	*Psychodopygus*
L. steatopyga	*Coromyia*
L. stewarti	*Helcocyrtomyia*
L. strictivilla	*Helcocyrtomyia*
L. suapiensis	Unassigned
L. sylvicolus	*Nyssomyia*
L. tanyopsis	*Psathyromyia*
L. tarapacaensis	*Evandromyia*
L. tejadai	*Helcocyrtomyia*
L. teratodes	*Evandromyia*
L. termitophila	Unassigned
L. texana	*Lutzomyia*
L. thula	*Psychodopygus*
L. tihuiliensis	Unassigned
L. tocaniensis	Unassigned
L. toroensis	Unassigned
L. torrealbai	Unassigned
L. torresi	Unassigned
L. tortura	*Helcocyrtomyia*
L. torvida	Unassigned
L. townsendi	Unassigned
L. trapidoi	*Nyssomyia*
L. triacantha	*Pressatia*
L. trichopyga	*Trichopygomyia*
L. trinidadensis	Unassigned
L. triramula	*Trichopygomyia*
L. trispinosa	*Pressatia*
L. tuberculata	*Viannamyia*
L. turelli	*Trichopygomyia*
L. ubiquitalis	*Trichophoromyia*
L. umbratilis	*Nyssomyia*
L. undulata	*Psathyromyia*
L. valderramai	Unassigned
L. vargasi	*Helcocyrtomyia*
L. vattierae	*Sciopemyia*
L. velascoi	*Trichophoromyia*
L. venezuelensis	*Micropygomyia*
L. verrucarum	Unassigned
L. vesicifera	*Coromyia*
L. vespertilionis	*Coromyia*
L. vexator	*Helcocyrtomyia*
L. viannamartinsi	*Trichophoromyia*
L. vindicator	*Helcocyrtomyia*
L. viriosa	*Coromyia*
L. volcanensis	*Psathyromyia*
L. vonatzingeni	*Lutzomyia*
L. wagleyi	*Trichopygomyia*
L. walkeri	Unassigned
L. waltoni	*Nyssomyia*
L. wattsi	*Helcocyrtomyia*
L. wellcomei	*Psychodopygus*
L. whitmani	*Nyssomyia*
L. wilkersoni	*Trichophoromyia*
L. williamsi	Unassigned
L. wilsoni	Unassigned
L. wirthi	*Micropygomyia*
L. witoto	*Trichopygomyia*
L. xerophila	*Lutzomyia*
L. yasuniensis	*Psychodopygus*
L. yencanensis	*Micropygomyia*
L. ylephiletor	*Nyssomyia*
L. youngi	Unassigned
L. yuilli	*Nyssomyia*
L. zeledoni	*Coromyia*

Parasite morphology: Phlebotomine sand flies form 4 different types of morphological stages during their developmental cycles: eggs; larvae (4 instars); pupae; and adults (males and females). Eggs are elliptical measuring 300-400 x 90-100 μm with rounded ends and one side not as convex as the other. They are pale cream-yellow in colour when laid but darken to amber-brown within 12 hours. The eggs have fine surface markings evident as ellipses, polygons, ridges or pits. Larvae develop through 4 maggot-like stages (L1-4) characterized by the possession of dark or black head capsules, grey-yellow-white segmented bodies (with lateral and dorsal clavate setae) and distinctive elongate caudal setae (1 pair in L1 and 2 pairs in L2-4). Phlebotomine larval segments do not have dorsal sclerites like members of the subfamily Psychodinae. Newly-hatched larvae (L1) measure from 0.5-0.6 mm long and have a protuberance (egg burster) on the dorsal head capsule, while L2-4 have gradually increased in size to 3-5 mm long and do not have egg bursters. The head has short antennae, lateral eyespots, and short chewing mouthparts comprising a labrum, maxillae and dentate mandibles opposing a plate-like serrate mentum. The larvae have prothoracic and caudal spiracles and each abdominal segment has a short ventral proleg. Just prior to pupation, L4 turn white as they evacuate their gut contents. Pupae are 2-4 mm long and club shaped with the head and thorax curved backwards and the posterior retaining the L4 exuvia which is attached vertically to the substrate. The pupae are obtect, with developing eyes, antennae, legs and wings visible (closely appressed to the body). The prothorax has a pair of short tube-like respiratory organs and the abdomen is highly setate. Pupae are pale creamy-white in colour, but darken to brown-orange prior to eclosion. Adult flies have small narrow grey-brown-yellow bodies measuring 2-5 mm long that characteristically have ‘moth-like’ hairy features. The head is small and elongate, with 2 large black compound eyes, no ocelli, and a pair of long slender filiform antennae (12-16 segments) covered with short setae (each segment also bearing a whorl of long setae).

Phlebotomine flies have a beak-like proboscis with piercing-sucking mouthparts directed downwards and at least as long as the head. The proboscis is flanked by long recurved palps (5 segments) with scattered setae (the longest palpal segment is the third in *Lutzomyia* and the fifth in *Phlebotomus*). In females, the mouthparts consist of lanceolate stylets (labrum, paired dentate mandibles, paired dentate maxillae, and hypopharynx) which are held in a fleshy labium when not in use. In males, the mouthparts are weakly developed, contain few or no teeth, and mandibles are not present. Ingested foods travel through a tubular oesophagus to a globular proventriculus with saccular diverticula and then passed to the tubular gut (midgut for digestion, hindgut with Malpighian excretory tubules, rectum with expandable ampulla, and terminal anus). The thorax possesses a distinctive ventral hump which is densely covered with long thin setae. The dorsal scutum bears 2 large ovate-elliptical wings which are typically held erect over the thorax when at rest. The wings have a thick covering of small hairs and the wing membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] with most running parallel (particularly those between R and M forks) and cross-veins only found in the inner third. Like all dipteran flies, a second pair of wings are found along the posterior thorax but are highly reduced to a pair of knob-like halteres used to stabilize flight. The ventral thorax gives rise to 6 stilt-like legs, each with 5 segments (coxa, trochanter, femur, tibia, and tarsus) terminating in a pair of small claws with a central pad. The elliptical abdomen contains 6-8 segments which are also covered with long thin setae. The abdomen usually has 7 pairs of lateral spiracles, and the terminal segments are modified by external genitalia (genital plates with ducts opening ventrally, females with anal recti and ovipositors, males with caudal claspers). Males have 2 testes connected by vas deferens to a seminal vesicle (with lateral accessory glands) leading to the ejaculatory duct and retractable copulatory aedeagus. Females have 2 ovaries (with polytrophic ovarioles) joined by oviducts to a globular uterus, often with associated spermatheca and accessory glands, leading to the vulva and caudal ovipositor.

Site of infection: Female phlebotomine sand flies are haematophagous and take bloodmeals from vertebrate hosts, including mammals (esp. humans, domestic and companion animals, wild ungulates and rodents), birds (poultry, aviary birds, and ground-dwelling birds), reptiles (snakes and lizards) and some amphibians. Sand flies vary in their host specificities, with some species being euryxenous and feeding opportunistically on available hosts, while others are stenoxenous and feed on several, often closely-related, hosts. A few species feed preferentially (sometimes exclusively) on birds or bats. Many species are anthropophilic and will feed on humans, but they are also zoophilic and feed on animals. Sand flies bite exposed skin, often on limb extremities (hands/feet, ankles/wrists) but also on hairless or sparsely-covered areas (face, nose, lips, eyelids, ears, neck and tail). They are unable to bite through clothing. All pre-adult developmental stages (eggs, larvae and pupae) are free-living in humid terrestrial environments.

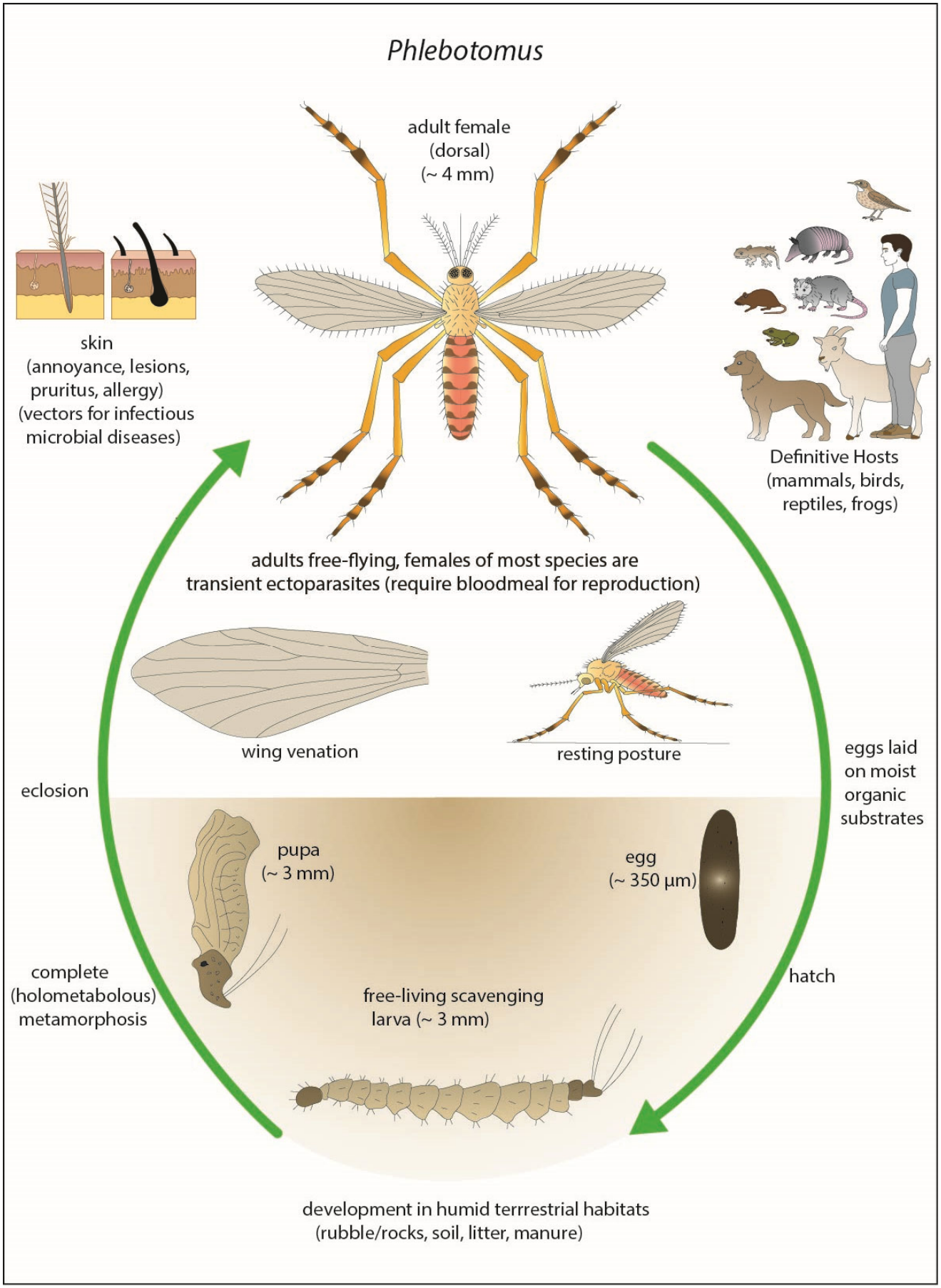
Pathogenesis: Adult female flies are annoying biting pests that often probe and bite repeatedly before feeding to repletion. They use their scissor-like mandibles to cut the skin and underlying blood vessels while their toothed maxillae hold onto the sides of the wound to keep the mouthparts in place. Sand flies are telmophagous (pool feeders) and feed on blood haemorrhaging into the wound using a food canal formed between the anterior labrum and posterior hypopharynx, the latter also having a groove for the injection of saliva into the wound. Sand fly saliva has been shown to contain many vaso-active compounds to assist feeding, including spreading agents (hyaluronidase), vasodilators and anticoagulants. While sand flies rarely feed in large numbers, their bites are sharp and painful causing intense irritation to the host for the duration of feeding (up to 3 minutes if not disturbed). Most species are crepuscular and nocturnally active and therefore interfere with sleep by waking hosts or keeping them awake. Bite sites become apparent as red-pink papules (2-3 mm in diameter, 0.5 mm high) which remain prominent for 4-5 days. The inflammation is often accompanied by intense pruritus causing further agitation and frustration, particularly in children. Self-trauma due to scratching may exacerbate wounds, making them susceptible to secondary bacterial infections. Initial bites typically induce sensitization to salivary components, so that subsequent bites result in allergic reactions (immediate and delayed hypersensitivity) with transient erythema, hives, swelling of the eyelids or lips, blistered papules that discharge serum, and occasionally systemic reactions including fever, nausea and debility. Eventually, most hosts experiencing long-term chronic exposure become desensitized and no longer develop hypersensitivity reactions. Many sand fly species have also gained notoriety as very efficient biological vectors for transmission of infectious diseases, particularly those caused by viruses (Pappataci or sand fly fever in rodents and primates, Changuinola fever in sloths, Chandipura in hedgehogs, vesicular stomatitis in ungulates and wildlife), bacteria (bartonellosis or Carrion's disease in humans) and protozoa (notably, *Leishmania* spp. causing disfiguring and deadly cutaneous, mucocutaneous and visceral leishmaniasis in humans and some animals).

Developmental cycle and mode of transmission: Sand flies undergo complete metamorphosis whereby eggs hatch grub-like larvae which transform in pupae to free-flying adults. Gravid females typically lay eggs in small batches (30-100) in damp and cool terrestrial environments where decaying organic material is present: including crevices in moist soil, rocks and rubble; forest litter, around tree roots, hollows and crotches; manure; animal structures (burrows, dens, nests, even termite mounds) and man-made structures (houses, sheds, cellars, toilets, barns, stables, and wells). The eggs hatch in 4-20 days and the emergent larvae are free-living scavengers feeding on organic debris, such as decaying plant material, fungi, microorganisms and faeces. Four larval stages occur over 20-60 days, but in cold climates, some species exhibit developmental quiescence (diapause) as eggs or larvae which may last up to a year in unfavourable conditions. The final larval instars form pupae which undergo metamorphosis over 5-10 days, longer in cooler climates. Adult flies emerge and both sexes feed on plant nectar, sap and honeydew. The females of most species, however, are anautogenous and require one or more blood meals to complete each gonotrophic cycle. A few species are autogenous and may complete the first cycle without a bloodmeal, but need one for subsequent cycles. Mating may occur before or after blood-

feeding. Females lay eggs approximately 4-10 days after feeding, and they can then return for another bloodmeal to undergo another ovarian cycle within 48-72 hours. Adult flies rest in moist and dark refugia (walls, cracks, tree trunks, caves, burrows) during the day and emerge to feed at night, dawn or dusk. *Phlebotomus* spp. feed mainly on mammals in savannah and desert areas, while *Lutzomyia* spp. feed on mammals and reptiles in damper forested areas. Female flies use a variety of visual, chemical, thermal and tactile sensors to seek hosts, often entering houses apparently attracted by light. Sand flies walk with a distinctive hesitating movement and have limited powers of flight. They fly noiselessly and horizontally to ground in characteristic short hops (several cm) when wind speeds are low (flight impeded when wind speed is >5 kph). Many species only disperse 100-200 m from their breeding sites, rarely ranging up to 2 km even over several days. Adult dispersal is usually not wind-assisted as they remain in their refugia and do not fly in windy conditions. Some neotropical species have been found to move vertically between the forest floor and canopy, with a flight range of 200-500 m. Most adult flies live for several (2-6) weeks, and the entire life-cycle may be completed in as little as 21-60 days depending on species, temperature, humidity, photoperiod, food availability, but can be extended up to a year in species which undergo egg/larval diapause ((many Palaearctic species have 2 generations per year).

Differential diagnosis: Clinical signs exhibited by humans and animals are not specific enough to facilitate diagnosis, as painful bites, rosy papules and pruritus may be caused by a range of ectoparasites. Diagnosis is best afforded by the direct demonstration of sand flies at bite sites, that is, small, hairy, silent, hopping flies with distinctively upwardly-pointed wings (forming a vertical 'V') when at rest. Differential diagnosis is achieved by microscopically examining flies captured by means of suction tubes, adhesive papers, light traps, or baits both from hosts and resting areas (smoke, insect repellants and even feather dusters may be used to flush flies from cryptic resting sites). The identification of phlebotomine species is difficult and clearing adult specimens and examining internal structures (notably mouthparts and genitalia). Phlebotomine species have also been identified from environmental samples (soil and litter) following the extraction of larvae using Berlese funnels, sieving and floatation techniques as well as waiting for adults to emerge from pupae. More recently, molecular biological techniques have been used to characterize phlebotomine species (particularly those involved in the transmission of leishmaniasis) by polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA) and mitochondrial (cytochrome) gene sequences.

Treatment and control: Sand fly bites in humans can be treated with topical anti-inflammatory, antipruritic and antiseptic formulations to provide symptomatic relief and prevent secondary infections. Systemic glucocorticoids and antihistamines may also be required in individuals experiencing severe allergic and hypersensitivity reactions. A range of insecticides have been administered to animals as sprays, pour-ons or systemic formulations to protect them against sand fly bites, including organochlorines (such as dichlorodiphenyltrichloroethane (DDT)), organophosphates (malathion), carbamates (carbaryl), natural and synthetic pyrethrins (cyhalothrin, permethrin, cypermethrin, cyfluthrin, etofenprox) and chloronicotinyles (imidacloprid). Insecticides with good residual activity have also been used to treat indoor fixtures where sand flies may rest, including walls, ceilings, doors, window frames and screens. Personal protection may be afforded by covering bare skin with clothing, using insect repellents (permethrin, diethymethylbenzamide (DEET), piperidene, neem oil) on skin and/or clothing, and using mosquito coils to generate insecticidal smoke indoors (pyrethroids mixed with slow-burning filler). Attempts to use insecticides to treat potential breeding sites (moist terrestrial habitats) have met with limited success due to their widespread, diverse and often inaccessible locations. In addition, sand fly populations rapidly developed resistance to DDT and it was discontinued in most countries (also due to significant toxicity and environmental concerns). Increasing resistance has been reported against various pyrethroids. Several studies have reported moderate successes using insecticide-treated sugar/fruit baits to attract flies, while a few studies have used male pheromones to attract females to insecticidal baits. Various countries advocate the use of indoor barriers in the form of fine-mesh nets and screens, preferably impregnated with insect repellents or insecticides as sand flies may pass through coarse untreated barriers. Successful control or mitigation programmes also rely on the elimination of potential breeding and resting sites, through building maintenance (repairing cracks in structures, removing rubble heaps and termite mounds, relocating storage piles), improved hygiene (clearing dumps and organic refuse), vegetation control (remove plants used as food sources, sometime regions resorting to local deforestation, introduce plants toxic to sand flies such as *Bougainvillea, Ricinus* and *Solanum* spp.,) and change animal management practices (temporary relocation of livestock, reposition camps to dry ground, favour windy areas, cull reservoir hosts, notably canids and rodents).


Phlebotomus
adult female
(dorsal)
(~ 4 mm)
skin
(annoyance, lesions,
pruritus, allergy)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, birds,
reptiles, frogs)
adults free-flying, females of most species are
transient ectoparasites (require bloodmeal for reproduction)
wing venation
resting posture
eclosion
eggs laid
on moist
organic
substrates
pupa
(~ 3 mm)
egg
(~ 350 µm)
complete
(holometabolous)
metamorphosis
hatch
free-living scavenging
larva (~ 3 mm)
development in humid terrrestrial habitats
(rubble/rocks, soil, litter, manure)



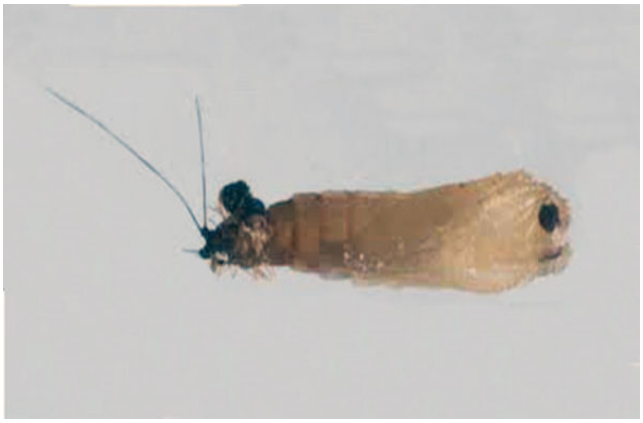
Phlebotomus adult



Phlebotomus eggs



Phlebotomus larva



Phlebotomus pupa

Tabanus, Chrysops, Haematopota
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Tabanomorphans have semiaquatic life cycles where eggs laid on vegetation overhanging mud or shallow water hatch into large predaceous larvae. The adults are large robust flies and include the tabanids (known variously as horse flies, deer flies, doctor flies, clegs or March flies). Most species are not host specific, but exhibit host preferences for different mammalian hosts. Females have slashing-sponging mouthparts to pierce the skin and feed on pools of blood (telmophagy). They are daytime feeders and have painful bites causing significant host annoyance. Various *Chrysops* and *Tabanus* spp. may also act as mechanical or biological vectors for protozoans (trypanosomes), helminths (filarial nematodes), bacteria (anaplasmosis, anthrax) and viruses (hog cholera, equine swamp fever).

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))
Family:	Tabanidae (large stout horse/deer/March flies, often brightly coloured, painful bite, daytime feeders)
Genus:	*Tabanus* (parasitic on skin of mammals)
Genus:	*Chrysops* (parasitic on skin of mammals)
Genus:	*Haematopota* (parasitic on skin of mammals)
Species:	various species cause irritation

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Tabanomorpha form pupae from which adults eclose through a longitudinal slit (not a circular cap like Muscomorpha), adults with stout bodies, bulbous faces, short 3-segmented antennae (= brachycera) often bearing feather-like aristae, palps with 2 segments, wings with enlarged thoracic squamae, and semi-aquatic life cycles where eggs laid on vegetation overhanging mud or shallow water hatch into large predaceous larvae with head capsules sclerotized anteriorly (incomplete posteriorly). Two main superfamilies have been recognized: Tabanoidea (horse and deer flies), and Rhagionoidea (snipe flies and an assortment of small affiliated families). Four families are recognized within the

superfamily Tabanoidea, namely, Athericidae (ibis flies), Oreoleptidae (rare mountain fly), Pelecorhynchidae (rare 'snipe' flies) and Tabanidae (horse flies), all apparently united by the presence of a venom canal in larval mandibles.

The family Tabanidae contains stout flies with large eyes, the third antennal segment containing 4-8 sections, palps containing an enlarged second segment, wings where the vein R4+5 forks to form large Y across the wing tip, and feet with 3 pads. Over 4,300 tabanid species have been described in over 130 genera classified in 3-5 subfamilies. The family Tabanidae conventionally contains 3 subfamilies: Pangoniinae (long-tongued horse flies with ocelli, and an antennal flagellum bearing 8 annuli), Chrysopsinae (deer flies or banded horse flies with an antennal flagellum bearing a basal plate and 4 annuli and whose females have a shining callus on the frons), and Tabaninae (horse flies lacking ocelli and without spurs on their hind-tibia). Some authorities have added another 2 subfamilies, the Adersiinae (with a single genus) and the Scepcidinae (with 2 genera), but molecular phylogenetic studies have not supported their inclusion. The subfamily Tabaninae contains 54 genera, most classified within 3 tribes: Diachlorini with 33 genera; Haematopotini with 4 genera (including *Haematopota*); Tabanini with 11 genera (including *Tabanus*); and another 6 unplaced genera.

The genus *Tabanus* (syn. *Alliomma, Astigmatophthalmus, Bellaria, Brachypsalidia, Callotabanus, Chelommia, Chelotabanus, Gymnochela, Hybostraba, Lophotabanus, Macrocormus, Neotabanus, Odontotabanus, Phyrta, Straba, Styporhamphis, Taeniotabanus*) is characterized by adult flies with clear wings (sometimes dark or banded), 5-segmented antennal flagellum, and legs lacking apical spurs on their tibia. Over 1,440 *Tabanus* spp. have been described, many classified into 4 subgenera. The genus *Haematopota* (syn. *Austenia, Chrysopota, Chrysozona, Haematopata, Haematopoda, Holcoceria, Parahaematopota, Potisa, Ricardomsia, Sterrhocera, Tylopelma*) contains over 550 species of flies characterized by mottled wings, and 4-segmented antennal flagellum. The subfamily Chrysopsinae contains 17 genera classified in 3 tribes: Bouvieromyiini with 7 genera; Chrysopsini with 5 genera (including *Chrysops*); and Rhinomyzini with 5 genera. The genus *Chrysops* (syn. *Chrysopsis, Euops, Heterochrysops, Neochrysops, Psilochrysops, Psylochrysops)* is characterized by flies with wings possessing a dark costal region and a single dark broad transverse band, 5-segmented antennal flagellum, and legs with small apical spurs on their tibia (often hidden by hairs). Over 300 *Chrysops* spp. have been described, many classified into 4 subgenera. While tabanids are cosmopolitan in distribution, many species vary in their host specificity, regional and seasonal occurrence, often bearing common names reflecting their proclivities, such as horse flies, deer flies, March flies, doctor flies, and clegs. Females have slashing-sponging mouthparts to pierce the skin and feed on pools of blood (telmophagy). They are daytime feeders and have painful bites causing significant annoyance to their hosts.

Tabanid flies (regional exemplars)	**Host preferences**	**Clinical signs (Vectorial capacity)**	**Distribution**
Tabanus (horse flies) (e.g. *T. atratus, bovinus, lineola, nigrovittatus, par, punctifer, quinquevittatus, similis, sulcifrons, taeniola, thoracinus*)	wild and domestic animals, humans	irritation (anthrax, pasteurellosis, trypanosomiasis, anaplasmosis, loasis)	worldwide
Chrysops (deer flies) (e.g. *C. caecutiens, dimidiata, discalis, siacea*)	wild and domestic animals, humans	irritation (pasteurellosis, trypanosomiasis, loasis)	worldwide
Haematopota (clegs) (e.g. *H. americana, brucei, brunnescens, patellicornis, pluvialis*)	wild and domestic animals, humans	irritation (anthrax, pasteurellosis, trypanosomiasis, anaplasmosis, loasis)	worldwide, except Australia

Full species list (compilation of several on-line data-bases)

***Tabanus* species**	**Subgenus**
T. aaptus	Unassigned
T. aar	*Tabanus*
T. abactor	*Tabanus*
T. abaculus	*Tabanus*
T. abaurantiacus	*Tabanus*
T. abauristriatus	*Tabanus*
T. abbasalis	*Tabanus*
T. abbreviatus	*Tabanus*
T. abditus	*Tabanus*
T. abdominalis	*Tabanus*
T. abiens	Unassigned
T. abscondens	*Tabanus*
T. acallosus	*Tabanus*
T. acallus	*Tabanus*
T. accensus	Unassigned
T. accipiter	Unassigned
T. acer	Unassigned
T. acuminaris	*Tabanus*
T. acutus	*Tabanus*
T. adiastolus	Unassigned
T. admelanopygus	Unassigned
T. administrans	*Tabanus*
T. advena	Unassigned
T. aegrotus	*Tabanus*
T. aeneus	Unassigned

T. agnoscibilis	*Tabanus*
T. agrestis	Unassigned
T. aidini	Unassigned
T. alatocinereus	Unassigned
T. albicans	Unassigned
T. albicinctus	*Tabanus*
T. albicuspis	Unassigned
T. albifacies	Unassigned
T. albifrons	Unassigned
T. albilinea	Unassigned
T. albinus	*Agelanius*
T. albipes	Unassigned
T. albiscutellus	*Tabanus*
T. albitibialis	Unassigned
T. albitriangulatis	*Tabanus*
T. albocapillus	Unassigned
T. albocirculus	Unassigned
T. albocostatus	*Tabanus*
T. albocreus	Unassigned
T. albofasciatus	*Tabanus*
T. albopunctatus	*Tabanus*
T. albosetosus	Unassigned
T. algeriensis	Unassigned
T. altermaculatus	*Tabanus*
T. alticola	*Tabanus*
T. alumnus	Unassigned
T. alvarengai	Unassigned
T. amaenus	*Tabanus*
T. amamiensis	Unassigned
T. amapaensis	Unassigned
T. americanus	*Tabanus*
T. amoenatus	*Tabanus*
T. anabates	*Tabanus*
T. anatolicus	Unassigned
T. andamanensis	Unassigned
T. andamanicus	*Tabanus*
T. andersoni	Unassigned
T. angustifrons	Unassigned
T. angustilimbatus	*Tabanus*
T. angustipalpis	*Tabanus*
T. angustistriatus	*Tabanus*
T. angustitriangularis	Unassigned
T. angustiventer	*Tabanus*
T. angustofrons	Unassigned
T. angustus	Unassigned
T. aniptus	Unassigned
T. annamensis	*Tabanus*
T. annamiticus	*Tabanus*
T. annamitus	*Tabanus*
T. anomalus	*Tabanus*
T. ansarii	Unassigned
T. antarcticus	Unassigned
T. antennarum	Unassigned
T. anthrax	Unassigned
T. antunesi	Unassigned
T. apicalis	Unassigned
T. appendicifer	Unassigned
T. approximatus	Unassigned
T. aquilus	Unassigned
T. arabicus	Unassigned

T. aranti	*Tabanus*
T. arbucklei	Unassigned
T. arctus	Unassigned
T. ardalus	*Tabanus*
T. ardens	*Tabanus*
T. arenicolor	Unassigned
T. arenivagus	Unassigned
T. arfaai	Unassigned
T. argentatus	Unassigned
T. argenteomaculatus	Unassigned
T. argenteus	Unassigned
T. argentifrons	Unassigned
T. argentisignatus	*Tabanus*
T. argentivittatus	Unassigned
T. arisanus	*Tabanus*
T. armeniacus	Unassigned
T. armenicus	Unassigned
T. arnaudi	Unassigned
T. atamuradovi	Unassigned
T. ater	Unassigned
T. atratoides	Unassigned
T. atratus	*Tabanus*
T. atrimaculatus	*Tabanus*
T. atrimanus	Unassigned
T. atripilosus	*Tabanus*
T. atripunctatus	*Tabanus*
T. atrisignatus	*Tabanus*
T. atristylatus	Unassigned
T. atriventer	*Tabanus*
T. atrohirtus	*Tabanus*
T. atropathenicus	Unassigned
T. atropilosus	Unassigned
T. attenuatus	*Tabanus*
T. attenuis	*Tabanus*
T. aublanti	*Tabanus*
T. audyi	*Tabanus*
T. aurantium	Unassigned
T. aurepiloides	Unassigned
T. aurepilus	Unassigned
T. auribundus	*Tabanus*
T. auricingulatus	*Tabanus*
T. auricircus	Unassigned
T. aurifer	*Tabanus*
T. auriflammus	*Tabanus*
T. aurilineatus	*Tabanus*
T. auripilosus	*Tabanus*
T. auripunctatus	Unassigned
T. aurisegmentatus	*Tabanus*
T. aurisetosus	*Tabanus*
T. aurisparsus	*Tabanus*
T. auristriatus	*Tabanus*
T. auriventer	*Tabanus*
T. auriventralis	Unassigned
T. aurivittatus	Unassigned
T. aurora	Unassigned
T. aurotestaceus	*Tabanus*
T. australicus	Unassigned
T. autumnalis	Unassigned
T. avittatus	*Tabanus*
T. bactrianus	Unassigned

T. baguiensis	*Tabanus*
T. bakeri	*Tabanus*
T. balabacensis	*Tabanus*
T. ballmeri	Unassigned
T. baohaii	Unassigned
T. baojiensis	Unassigned
T. barbarus	Unassigned
T. barbatus	Unassigned
T. barclayi	Unassigned
T. barnesi	*Tabanus*
T. basalis	*Tabanus*
T. bashiri	Unassigned
T. basilaris	Unassigned
T. bellus	*Agelanius*
T. beneficus	Unassigned
T. bequaertianus	Unassigned
T. beshkentica	Unassigned
T. besti	Unassigned
T. bewanensis	Unassigned
T. biannularis	*Tabanus*
T. biatripunctatus	*Tabanus*
T. bicoloratus	*Tabanus*
T. bifarius	Unassigned
T. bifloccus	Unassigned
T. bigoti	*Tabanus*
T. biguttatus	Unassigned
T. bilateralis	*Tabanus*
T. billingtoni	Unassigned
T. bilorus	Unassigned
T. bimini	Unassigned
T. birdiei	*Tabanus*
T. birmanicus	*Tabanus*
T. bishoppi	*Tabanus*
T. biswasi	Unassigned
T. bivari	Unassigned
T. boharti	*Tabanus*
T. bombayensis	*Tabanus*
T. borealoriens	Unassigned
T. borniensis	*Tabanus*
T. boroumandi	Unassigned
T. boueti	Unassigned
T. bovinus	Unassigned
T. brancoi	Unassigned
T. brassofortei	Unassigned
T. brevicallus	*Tabanus*
T. brevifrons	Unassigned
T. brevitrianguliferus	Unassigned
T. brevittatus	Unassigned
T. briani	Unassigned
T. brincki	Unassigned
T. brochei	*Bellardia*
T. brodeni	Unassigned
T. bromiolus	Unassigned
T. bromius	Unassigned
T. brumpti	Unassigned
T. brunneicollis	Unassigned
T. brunneocallosus	Unassigned
T. brunneothorax	Unassigned
T. brunneus	Unassigned
T. brunnicolor	*Tabanus*
T. brunnipennis	*Tabanus*
T. brunnipes	*Tabanus*
T. brunniventer	*Tabanus*
T. bubali	*Tabanus*
T. bubalophilus	*Tabanus*
T. bubbermani	*Tabanus*
T. bucolicus	*Tabanus*
T. budda	Unassigned
T. budongoensis	Unassigned
T. burgeri	*Tabanus*
T. burmanensis	*Tabanus*
T. caduceus	Unassigned
T. caeculus	Unassigned
T. caenosus	*Tabanus*
T. caerulescens	*Tabanus*
T. calabyi	Unassigned
T. calcarius	Unassigned
T. calens	*Tabanus*
T. calidus	*Tabanus*
T. caligneus	Unassigned
T. callogaster	Unassigned
T. cambodianus	*Tabanus*
T. cambodiensis	*Tabanus*
T. camelarius	Unassigned
T. campechianus	Unassigned
T. campestris	Unassigned
T. candidus	*Tabanus*
T. canipalpis	Unassigned
T. canipus	*Tabanus*
T. canus	Unassigned
T. capelai	Unassigned
T. castancus	Unassigned
T. castaneoventris	Unassigned
T. casteetus	Unassigned
T. castellanus	Unassigned
T. catenatus	*Tabanus*
T. caucasius	Unassigned
T. cayensis	*Tabanus*
T. cazieri	*Tabanus*
T. cementus	Unassigned
T. centroafricanus	Unassigned
T. cepuricus	*Tabanus*
T. cervinus	Unassigned
T. ceylonicus	Unassigned
T. chalcothrix	Unassigned
T. charrua	Unassigned
T. chekiangensis	Unassigned
T. cheliopterus	*Tabanus*
T. chenfui	Unassigned
T. chentangensis	Unassigned
T. chicoi	Unassigned
T. chinensis	Unassigned
T. chloropsis	*Tabanus*
T. choiseulensis	Unassigned
T. chosenensis	Unassigned
T. choumarae	Unassigned
T. christophi	Unassigned
T. chrysogaster	*Tabanus*
T. chrysoleucus	Unassigned
T. chrysurinus	Unassigned

T. chrysurus	Unassigned
T. cincta	Unassigned
T. cinerescens	Unassigned
T. cingulatus	Unassigned
T. cinnamoneus	*Tabanus*
T. circumalbatus	*Tabanus*
T. circumseptus	*Agelanius*
T. citripilosus	*Tabanus*
T. claripennis	Unassigned
T. claritibialis	Unassigned
T. clenchi	Unassigned
T. cnemidotus	*Tabanus*
T. cneus	Unassigned
T. coarctatus	*Tabanus*
T. cohaerens	Unassigned
T. colchidicus	Unassigned
T. colombensis	*Tabanus*
T. columbus	Unassigned
T. combustus	Unassigned
T. comitans	Unassigned
T. commixtus	*Tabanus*
T. comosus	Unassigned
T. concolor	Unassigned
T. concurrens	Unassigned
T. conformis	Unassigned
T. confucius	Unassigned
T. confusiens	*Tabanus*
T. congoicola	Unassigned
T. congoiensis	Unassigned
T. conicus	*Tabanus*
T. coniformis	Unassigned
T. coninckae	*Tabanus*
T. conius	*Tabanus*
T. consanguineus	*Tabanus*
T. conspicuus	Unassigned
T. conterminus	*Tabanus*
T. copemani	Unassigned
T. coquilletti	Unassigned
T. corax	Unassigned
T. cordiger	Unassigned
T. cordigeroides	Unassigned
T. coreanus	Unassigned
T. corone	Unassigned
T. corpulentus	Unassigned
T. corrigata	Unassigned
T. craverii	*Tabanus*
T. crocitinctipennis	*Tabanus*
T. crocodilinus	Unassigned
T. crosskeyi	Unassigned
T. cruzesilvai	Unassigned
T. cubensis	*Taeniotabanus*
T. cuculus	Unassigned
T. cuisancei	Unassigned
T. curticornis	Unassigned
T. curtus	Unassigned
T. cuspidatus	Unassigned
T. cyclops	*Tabanus*
T. cyclopus	Unassigned
T. cylindricallosus	*Tabanus*
T. cylindrocallus	Unassigned

T. cymatophorus	*Tabanus*
T. daedalus	*Tabanus*
T. daishojii	Unassigned
T. daohaoi	Unassigned
T. darimonti	Unassigned
T. darlingtoni	Unassigned
T. davidsoni	Unassigned
T. decipiens	Unassigned
T. decoratus	*Tabanus*
T. defilippii	*Tabanus*
T. demellonis	*Tabanus*
T. denshamii	Unassigned
T. denticulatus	Unassigned
T. despectus	*Agelanius*
T. destructus	*Tabanus*
T. dietrichi	*Tabanus*
T. dimidiatus	Unassigned
T. discifer	Unassigned
T. discors	Unassigned
T. discrepans	*Tabanus*
T. discus	Unassigned
T. dissimilis	*Tabanus*
T. distinctus	Unassigned
T. ditaenia	Unassigned
T. divaricatus	*Agelanius*
T. diversifrons	*Tabanus*
T. diversus	Unassigned
T. dives	Unassigned
T. divisus	Unassigned
T. divulsus	Unassigned
T. dolini	Unassigned
T. dominicanus	Unassigned
T. dominus	Unassigned
T. donaldsoni	Unassigned
T. doreicus	Unassigned
T. dorsifer	*Tabanus*
T. dorsifloccus	Unassigned
T. dorsiger	Unassigned
T. dorsivitta	Unassigned
T. dorsobimaculatus	Unassigned
T. dorsomaculatus	Unassigned
T. dorsonotatus	*Tabanus*
T. dubius	Unassigned
T. duckei	Unassigned
T. dunni	Unassigned
T. dzhafarovi	Unassigned
T. eadsi	*Tabanus*
T. easteetus	Unassigned
T. effilatanus	*Tabanus*
T. effilatus	*Tabanus*
T. eggeri	Unassigned
T. ekor	Unassigned
T. eldridgei	Unassigned
T. elongatus	*Tabanus*
T. enanus	Unassigned
T. enderleini	*Tabanus*
T. endymion	*Tabanus*
T. equalis	*Tabanus*
T. equicinctus	*Tabanus*
T. erebus	Unassigned

T. erythraeus	*Tabanus*
T. euphanes	*Tabanus*
T. eurycerus	*Tabanus*
T. eurytopus	Unassigned
T. exagens	Unassigned
T. excelsus	*Tabanus*
T. exclusus	Unassigned
T. exilipalpis	*Tabanus*
T. exoticus	*Tabanus*
T. explicatus	*Tabanus*
T. expulsus	Unassigned
T. extricans	Unassigned
T. factiosus	*Tabanus*
T. faini	Unassigned
T. fairchildi	*Tabanus*
T. falviscutellus	*Tabanus*
T. fasciatus	Unassigned
T. fascius	*Tabanus*
T. felderi	*Tabanus*
T. femoralis	Unassigned
T. ferrugineus	Unassigned
T. fijianus	Unassigned
T. filipjevi	Unassigned
T. firmus	Unassigned
T. flammeus	Unassigned
T. flaviannulatus	*Tabanus*
T. flavicapitis	Unassigned
T. flavicornis	*Tabanus*
T. flavicoxa	Unassigned
T. flavimarginatus	*Tabanus*
T. flavimedius	*Tabanus*
T. flavioculatus	*Tabanus*
T. flavipennis	Unassigned
T. flavipilosus	*Tabanus*
T. flavipus	*Tabanus*
T. flaviscutellatus	*Tabanus*
T. flaviscutellus	*Tabanus*
T. flavissimus	*Tabanus*
T. flavistriatus	*Tabanus*
T. flavitibiatus	*Tabanus*
T. flavitriangularis	*Tabanus*
T. flavivittatus	*Tabanus*
T. flavohirtus	*Tabanus*
T. flavothorax	*Tabanus*
T. flexilis	*Tabanus*
T. flocculus	Unassigned
T. fontinalis	*Tabanus*
T. formosiensis	*Tabanus*
T. fortis	Unassigned
T. fossilis (fossil)	Unassigned
T. fragai	Unassigned
T. fraseri	Unassigned
T. fratellus	Unassigned
T. fraternus	Unassigned
T. frondosus	*Tabanus*
T. fronto	*Tabanus*
T. fujianensis	Unassigned
T. fulcifrons	Unassigned
T. fullo	Unassigned
T. fulvicallus	*Tabanus*
T. fulvicapillus	Unassigned
T. fulvicinctus	*Tabanus*
T. fulvifasciatus	Unassigned
T. fulviger	Unassigned
T. fulvilateralis	Unassigned
T. fulvilinearis	*Tabanus*
T. fulvilineis	*Tabanus*
T. fulvilineus	Unassigned
T. fulvimedioides	Unassigned
T. fulvimedius	Unassigned
T. fulvissimus	*Tabanus*
T. fulvulus	*Tabanus*
T. fumeus	*Tabanus*
T. fumidus	Unassigned
T. fumifer	*Tabanus*
T. fumipennis	*Tabanus*
T. fumomarginatus	Unassigned
T. funebris	Unassigned
T. furunculigenus	Unassigned
T. furunculus	*Tabanus*
T. furvicaudus	Unassigned
T. fuscibarbus	*Tabanus*
T. fuscicauda	*Tabanus*
T. fuscicornis	*Tabanus*
T. fuscicostatus	*Tabanus*
T. fuscifrons	*Tabanus*
T. fuscipleuris	Unassigned
T. fuscithorax	*Tabanus*
T. fusciventer	*Tabanus*
T. fuscofasciatus	Unassigned
T. fuscomaculatus	*Tabanus*
T. fuscomarginatus	Unassigned
T. fusconervosus	*Tabanus*
T. fuscopunctatus	*Tabanus*
T. fuscotibialis	Unassigned
T. fuscoventris	Unassigned
T. fuscus	Unassigned
T. fuzhouensis	Unassigned
T. fuzouensis	Unassigned
T. galloisi	Unassigned
T. geminus	Unassigned
T. geniculatus	*Tabanus*
T. geographicus	Unassigned
T. gertrudae	*Tabanus*
T. gertudae	*Tabanus*
T. gibensis	Unassigned
T. gigas	Unassigned
T. gilanus	*Tabanus*
T. gilingilensis	Unassigned
T. gilvellus	*Tabanus*
T. gilvilineis	*Tabanus*
T. gilvus	*Tabanus*
T. gladiator	*Tabanus*
T. glaucomaculis	*Tabanus*
T. glauconotatus	*Tabanus*
T. glaucopis	Unassigned
T. glaucus	Unassigned
T. golovi	Unassigned
T. gonghaiensis	Unassigned
T. gracilicornis	Unassigned

T. gracilis	*Tabanus*
T. grandicaudus	Unassigned
T. grandis	Unassigned
T. granti	*Tabanus*
T. gratus	Unassigned
T. gressitti	Unassigned
T. griseifacies	*Tabanus*
T. griseilineis	*Tabanus*
T. griseinus	Unassigned
T. griseipalpis	*Tabanus*
T. griseithorax	*Tabanus*
T. griseoscutellatus	*Tabanus*
T. grunini	Unassigned
T. guapiensis	Unassigned
T. guatemalanus	Unassigned
T. guineensis	Unassigned
T. guizhouensis	Unassigned
T. guizhouensis	Unassigned
T. guttatus	Unassigned
T. guyanensis	Unassigned
T. guyonae	Unassigned
T. gymnorhynchus	Unassigned
T. gyruchus	Unassigned
T. haemagogus	Unassigned
T. haimovitchae	Unassigned
T. hainanensis	Unassigned
T. haitiensis	Unassigned
T. hakkariensis	Unassigned
T. hamoni	Unassigned
T. hashemi	Unassigned
T. hauseri	Unassigned
T. haysi	Unassigned
T. hedlundi	Unassigned
T. hellenicus	Unassigned
T. helvinus	Unassigned
T. herbertensis	Unassigned
T. herculeanus	Unassigned
T. hinellus	*Tabanus*
T. hipparionis (fossil)	Unassigned
T. hirsutus	Unassigned
T. hirtipalpis	*Tabanus*
T. hirtistriatus	*Tabanus*
T. hirtitibia	Unassigned
T. hisarensis	Unassigned
T. hispanicus	Unassigned
T. hispanus	Unassigned
T. hispidus	Unassigned
T. hissaricus	Unassigned
T. hoang	Unassigned
T. holtzianus	Unassigned
T. honestus	Unassigned
T. hongchowensis	*Tabanus*
T. hongchowoides	Unassigned
T. hongkongiensis	*Tabanus*
T. hoogstraali	*Tabanus*
T. hottentotta	Unassigned
T. howdeni	*Tabanus*
T. huangshanensis	Unassigned
T. humboldti	Unassigned
T. humilis	Unassigned

T. humillimus	*Tabanus*
T. humiloides	Unassigned
T. hybridus	*Tabanus*
T. hypomacros	*Tabanus*
T. hyugaensis	Unassigned
T. ianthinus	Unassigned
T. iber	Unassigned
T. ichiokai	Unassigned
T. ictericus	*Tabanus*
T. idulis	Unassigned
T. ignobilis	*Tabanus*
T. ilchanii	Unassigned
T. ilharcoi	Unassigned
T. illustris	Unassigned
T. imitans	*Tabanus*
T. immanis	*Tabanus*
T. immixtus	*Tabanus*
T. imparicallosus	*Tabanus*
T. impertinens	Unassigned
T. importunus	Unassigned
T. impurus	Unassigned
T. inaensis	Unassigned
T. inaequannulatus	Unassigned
T. inaequisignatus	*Tabanus*
T. incisus	Unassigned
T. incohaerens	Unassigned
T. inconspicuus	Unassigned
T. incultus	*Tabanus*
T. indecisus	Unassigned
T. indianus	*Tabanus*
T. indicus	Unassigned
T. indifferens	*Tabanus*
T. indiscriminatus	*Tabanus*
T. indistinctus	Unassigned
T. indosinensis	*Tabanus*
T. indrae	Unassigned
T. infans	Unassigned
T. infestans	Unassigned
T. infestus	Unassigned
T. inflatipalpis	*Tabanus*
T. ingens	*Tabanus*
T. inhambanensis	Unassigned
T. inifromis	*Tabanus*
T. innotabilis	Unassigned
T. inobservatus	*Tabanus*
T. inscitus	Unassigned
T. insecutor	Unassigned
T. insidiator	*Tabanus*
T. insignis	Unassigned
T. internus	Unassigned
T. invalidus	*Tabanus*
T. isis	Unassigned
T. itaituba	Unassigned
T. ixion	*Tabanus*
T. iyoensis	Unassigned
T. jacobarius	Unassigned
T. jacobi	*Tabanus*
T. jadini	Unassigned
T. javanus	*Tabanus*
T. jeanae	Unassigned

T. jigongshanensis	Unassigned
T. jigongshanoides	Unassigned
T. jigonshanensis	Unassigned
T. jilamensis	Unassigned
T. jinghongensis	Unassigned
T. jinhuai	Unassigned
T. johannesi	Unassigned
T. johnburgeri	Unassigned
T. johnsoni	*Tabanus*
T. joidus	*Tabanus*
T. joshii	Unassigned
T. jucundus	*Tabanus*
T. justorius	*Tabanus*
T. kabuensis	Unassigned
T. kaburagii	Unassigned
T. kakhyenensis	*Tabanus*
T. kamengensis	Unassigned
T. karaosus	Unassigned
T. karenkoensis	*Tabanus*
T. katoi	Unassigned
T. kermani	Unassigned
T. kesseli	*Tabanus*
T. khalafi	*Tabanus*
T. khasiensis	*Tabanus*
T. kiangsuensis	Unassigned
T. kingi	Unassigned
T. kinoshitai	Unassigned
T. kisliuki	*Tabanus*
T. konis	*Tabanus*
T. kotoshoensis	*Tabanus*
T. krombeini	Unassigned
T. kumaonensis	Unassigned
T. kumrakomensis	Unassigned
T. kunmingensis	Unassigned
T. kwangsinensis	Unassigned
T. kwatta	Unassigned
T. kwiluensis	Unassigned
T. lacajaensis	Unassigned
T. lacustris	*Tabanus*
T. laetetinctus	Unassigned
T. laevigatus	Unassigned
T. laleani	Unassigned
T. lamiensis	Unassigned
T. lanatus	Unassigned
T. laotianus	*Tabanus*
T. larvatus	Unassigned
T. lateralbus	*Tabanus*
T. lateralis	Unassigned
T. laterina	Unassigned
T. laticeps	Unassigned
T. laticinctus	*Tabanus*
T. laticornis	Unassigned
T. laticornis	*Tabanus*
T. laticorpus	*Tabanus*
T. latifascies	*Tabanus*
T. lavandoni	Unassigned
T. laverani	Unassigned
T. leclercqi	Unassigned
T. leleani	Unassigned
T. lenticulatus	Unassigned

T. lenticuloides	Unassigned
T. lentis	Unassigned
T. lentisignatus	*Tabanus*
T. leucocnematus	*Tabanus*
T. leucohirtus	*Tabanus*
T. leucomelas	*Tabanus*
T. leucopogon	*Tabanus*
T. leucostomus	Unassigned
T. levantinus	Unassigned
T. leveri	Unassigned
T. lewisi	Unassigned
T. liangshanensis	Unassigned
T. ligatus	Unassigned
T. lijiangensis	Unassigned
T. limbatineuris	*Tabanus*
T. limbithorax	Unassigned
T. limitatus	*Tabanus*
T. limushanensis	Unassigned
T. lineataenia	Unassigned
T. lineifrons	Unassigned
T. lineola	*Tabanus*
T. lingfengi	Unassigned
T. litigiosus	Unassigned
T. liventipes	Unassigned
T. loczyi	*Tabanus*
T. longibasalis	*Tabanus*
T. longicornutus	*Tabanus*
T. longinquus	Unassigned
T. longipennis	Unassigned
T. longistylus	Unassigned
T. longiusculus	*Tabanus*
T. longus	*Tabanus*
T. loukashkini	Unassigned
T. lubutuensis	Unassigned
T. lucidulus	Unassigned
T. lucifer	*Tabanus*
T. lufirensis	Unassigned
T. luizae	Unassigned
T. lunatus	Unassigned
T. lushanensis	*Tabanus*
T. lutzi	Unassigned
T. luzonensis	*Tabanus*
T. lyneborgi	Unassigned
T. macdonaldi	*Tabanus*
T. macer	*Tabanus*
T. macfarlanei	*Tabanus*
T. machadoi	Unassigned
T. macilentus	Unassigned
T. mackerrasi	Unassigned
T. macquarti	Unassigned
T. macrocerus	Unassigned
T. maculicornis	Unassigned
T. maculifrons	Unassigned
T. maculinevris	Unassigned
T. maculipennis	*Tabanus*
T. maculosus	*Tabanus*
T. madoerensis	*Tabanus*
T. maedai	Unassigned
T. maerens	Unassigned
T. maini	Unassigned

T. maiombensis	Unassigned
T. major	Unassigned
T. makimurae	Unassigned
T. malayensis	*Tabanus*
T. maliensis	Unassigned
T. mandarinus	*Tabanus*
T. manipurensis	*Tabanus*
T. marginalis	*Tabanus*
T. marginatus	Unassigned
T. marginenevris	Unassigned
T. marianii	Unassigned
T. marmoratus	Unassigned
T. marmorosus	Unassigned
T. martini	Unassigned
T. martinii	Unassigned
T. masamitsui	Unassigned
T. mateusi	Unassigned
T. matosi	Unassigned
T. matsumotoensis	Unassigned
T. matsuzawai	Unassigned
T. matutinimordicus	Unassigned
T. maurus	Unassigned
T. mazzottii	*Tabanus*
T. mediatrimaculatus	*Tabanus*
T. medionotatus	Unassigned
T. meghalayensis	Unassigned
T. meihuashanensis	Unassigned
T. melanocerus	*Tabanus*
T. melanogaster	Unassigned
T. melanognathus	*Tabanus*
T. mendossai	Unassigned
T. mengdingensis	Unassigned
T. menoensis	Unassigned
T. mentitus	*Tabanus*
T. meraukensis	Unassigned
T. meridionalis	Unassigned
T. merychippi (fossil)	Unassigned
T. mesnili	Unassigned
T. mesogaeus	Unassigned
T. mesquitelai	Unassigned
T. mexicanus	Unassigned
T. mianjangalensis	Unassigned
T. miki	Unassigned
T. miles	Unassigned
T. mimus	Unassigned
T. mindanensis	*Tabanus*
T. miniatus	Unassigned
T. minimus	*Tabanus*
T. minor	Unassigned
T. minshanensis	Unassigned
T. minuscularius	Unassigned
T. minusculus	Unassigned
T. mishanensis	Unassigned
T. mistshenkoi	Unassigned
T. mitidjensis	Unassigned
T. miyajima	Unassigned
T. miyakei	*Tabanus*
T. moderator	*Tabanus*
T. modestus	Unassigned
T. moerens	Unassigned

T. mofidii	Unassigned
T. mogollon	*Tabanus*
T. molestus	*Tabanus*
T. monchai	Unassigned
T. mongolensis	Unassigned
T. monilifer	Unassigned
T. monocallosus	Unassigned
T. monoculus	Unassigned
T. monoensis	*Tabanus*
T. monokini	*Tabanus*
T. monomiensis	Unassigned
T. monops	Unassigned
T. monotaeniatus	*Tabanus*
T. monotaxis	Unassigned
T. montiasiaticus	Unassigned
T. morbosus	*Tabanus*
T. mordax	Unassigned
T. moreli	Unassigned
T. morio	Unassigned
T. morsitans	Unassigned
T. mossambicensis	Unassigned
T. motuoensis	Unassigned
T. mouchai	Unassigned
T. mucronatus	Unassigned
T. mularis	*Tabanus*
T. multicinctus	*Tabanus*
T. murdochi	Unassigned
T. muruensis	Unassigned
T. muscoides	*Tabanus*
T. mutatus	Unassigned
T. namdaphaicus	*Tabanus*
T. namibiensis	Unassigned
T. nanpingensis	Unassigned
T. nantae	Unassigned
T. napaensis	*Tabanus*
T. nartshukae	Unassigned
T. neavei	Unassigned
T. nebulosus	Unassigned
T. nefarius	*Tabanus*
T. nefas	Unassigned
T. neglectus	Unassigned
T. negritos	*Tabanus*
T. nematocallus	Unassigned
T. nemocallosus	*Tabanus*
T. nemoralis	Unassigned
T. neoindianus	*Tabanus*
T. neotriangularis	Unassigned
T. neovestitus	Unassigned
T. nepalensis	*Tabanus*
T. nephodes	*Tabanus*
T. nereus	Unassigned
T. nexus	*Tabanus*
T. nicobarensis	*Tabanus*
T. nigeriensis	Unassigned
T. nigra	Unassigned
T. nigrabdominis	Unassigned
T. nigrefronti	*Tabanus*
T. nigrescens	*Tabanus*
T. nigrhinus	*Tabanus*
T. nigricaudus	Unassigned

T. nigrifascies	Unassigned
T. nigrifeminibus	Unassigned
T. nigrifer	Unassigned
T. nigrihinus	*Tabanus*
T. nigrimaculatus	Unassigned
T. nigrimanus	Unassigned
T. nigrimordicus	Unassigned
T. nigrinus	*Tabanus*
T. nigripes	*Tabanus*
T. nigrita	Unassigned
T. nigriventris	Unassigned
T. nigrofemoratus	Unassigned
T. nigrostriatus	Unassigned
T. nigrotectus	*Tabanus*
T. nigrovittatus	*Tabanus*
T. nilakinus	*Tabanus*
T. nipponicus	Unassigned
T. niveinotatus	Unassigned
T. noctuinus	*Tabanus*
T. noncallosus	Unassigned
T. nondescriptus	Unassigned
T. notatus	Unassigned
T. novaescotiae	*Tabanus*
T. nyasae	Unassigned
T. nyctops	Unassigned
T. obconicus	*Tabanus*
T. obesus	Unassigned
T. obliquemaculatus	Unassigned
T. obscuratus	Unassigned
T. obscurefumatus	Unassigned
T. obscurehirtus	Unassigned
T. obscurestigmatus	Unassigned
T. obscurestriatus	Unassigned
T. obscurilineatus	Unassigned
T. obscurior	Unassigned
T. obscurus	Unassigned
T. obsolescens	Unassigned
T. obsoletimaculus	Unassigned
T. obsoletus	Unassigned
T. obtusipalpis	Unassigned
T. obumbratus	Unassigned
T. occidentalis	*Tabanus*
T. ochroater	*Tabanus*
T. ochroceras	*Tabanus*
T. ochrogaster	*Tabanus*
T. ochros	*Tabanus*
T. octulus	Unassigned
T. okinawanoides	Unassigned
T. okinawanus	*Tabanus*
T. oknos	*Tabanus*
T. oldroydi	*Tabanus*
T. olivaceiventris	Unassigned
T. oliviventris	Unassigned
T. oliviventroides	Unassigned
T. olsufjevi	Unassigned
T. olympius	Unassigned
T. omeishanensis	Unassigned
T. omnirobustus	Unassigned
T. onoi	Unassigned
T. opalescens	Unassigned

T. oppugnator	Unassigned
T. optatus	*Tabanus*
T. opulentus	Unassigned
T. orbicallus	*Tabanus*
T. orbis	Unassigned
T. oreophilus	Unassigned
T. orientalis	*Tabanus*
T. orientis	*Tabanus*
T. orphnos	Unassigned
T. otsurui	Unassigned
T. ovazzai	Unassigned
T. oviventris	*Tabanus*
T. oxybeles	Unassigned
T. oxyceratus	*Tabanus*
T. pachypalpus	Unassigned
T. paganus	Unassigned
T. palauensis	Unassigned
T. palawanensis	*Tabanus*
T. pallidepectoratus	*Tabanus*
T. pallidescens	*Tabanus*
T. pallidifacies	Unassigned
T. pallidipectoratus	Unassigned
T. pallidipes	Unassigned
T. pallidiscutum	*Tabanus*
T. pallidiventer	*Tabanus*
T. pallipennis	Unassigned
T. palpalis	Unassigned
T. palpinus	*Tabanus*
T. papuensis	Unassigned
T. par	Unassigned
T. parabactrianus	*Tabanus*
T. parabrunneus	*Tabanus*
T. parabuddha	Unassigned
T. parachinensis	Unassigned
T. parachrysater	Unassigned
T. paradiversifrons	Unassigned
T. paradoxus	Unassigned
T. paraflavimarginatus	Unassigned
T. parafuscomaculatus	*Tabanus*
T. parahippi (fossil)	Unassigned
T. parahybridus	*Tabanus*
T. paraichiokai	Unassigned
T. parallelifrons	*Tabanus*
T. paralleliventer	*Tabanus*
T. pararubidus	Unassigned
T. pararufiventris	*Tabanus*
T. parasexcinctus	Unassigned
T. parawuyishanensis	Unassigned
T. parimmixtus	*Tabanus*
T. particaecus	Unassigned
T. particolor	*Tabanus*
T. partitus	Unassigned
T. parvicallosus	Unassigned
T. parvidentatus	Unassigned
T. parviformus	Unassigned
T. passosi	Unassigned
T. patriarchus	Unassigned
T. pauper	*Tabanus*
T. paviei	Unassigned
T. pazukii	Unassigned

T. pechumani	Unassigned
T. pellucidus	Unassigned
T. pellus	*Tabanus*
T. penai	Unassigned
T. pendleburyi	*Tabanus*
T. pengquensis	Unassigned
T. perakiensis	*Tabanus*
T. perelegans	Unassigned
T. perileucus	Unassigned
T. persimilis	Unassigned
T. pertinens	Unassigned
T. peruvianus	Unassigned
T. petiolatus	*Tabanus*
T. petiscai	Unassigned
T. philippinensis	*Tabanus*
T. piceiventris	Unassigned
T. picicalosus	Unassigned
T. pictiventris	*Tabanus*
T. pingxiangensis	Unassigned
T. planus	Unassigned
T. platensis	Unassigned
T. platycerus	Unassigned
T. pleskei	Unassigned
T. pluto	Unassigned
T. pollinosus	Unassigned
T. polygonus	Unassigned
T. polyphemus	Unassigned
T. portschinskii	Unassigned
T. postactus	Unassigned
T. praematurus	*Tabanus*
T. praepilatus	Unassigned
T. praepositus	Unassigned
T. praeteritus	Unassigned
T. pratti	*Tabanus*
T. prefulventer	Unassigned
T. primitivus	Unassigned
T. principis	Unassigned
T. priscoides	*Tabanus*
T. pristinus	Unassigned
T. procallosus	Unassigned
T. productus	Unassigned
T. promesogaeus	Unassigned
T. prometheus	Unassigned
T. propinquus	Unassigned
T. provincialis	*Tabanus*
T. proximus	*Tabanus*
T. pruinosus	*Tabanus*
T. prunicolor	Unassigned
T. pseudoannularis	Unassigned
T. pseudocingulatus	*Agelanius*
T. pseudoculus	Unassigned
T. pseudogratus	Unassigned
T. pseudoliviventris	Unassigned
T. pseudolunatus	Unassigned
T. pseudonebulosus	Unassigned
T. pseudothoracinus	Unassigned
T. ptolemaeanus	Unassigned
T. pubescens	Unassigned
T. pugiunculus	Unassigned
T. puillomaculatus	Unassigned

T. pullulus	Unassigned
T. pullus	Unassigned
T. pulvifer	Unassigned
T. pumilus	*Tabanus*
T. punctifer	*Tabanus*
T. punctipleura	Unassigned
T. puncturius	Unassigned
T. pungens	*Tabanus*
T. pusillus	*Tabanus*
T. puteus	*Tabanus*
T. qinlingensis	Unassigned
T. quadrifocus	Unassigned
T. quadriguttatus	Unassigned
T. quadrisignatus	Unassigned
T. quadritriangularis	*Tabanus*
T. quaesitus	*Tabanus*
T. quatei	*Tabanus*
T. quatuornotatus	Unassigned
T. queenslandii	Unassigned
T. quinarius	Unassigned
T. quinquecinctus	*Tabanus*
T. quinquepunctatus	Unassigned
T. quinquetriangularis	*Tabanus*
T. quinquevittatus	*Tabanus*
T. quirinus	Unassigned
T. rageaui	Unassigned
T. rallus	Unassigned
T. rectilineatus	*Tabanus*
T. rectus	Unassigned
T. recusans	Unassigned
T. reducens	*Tabanus*
T. regularis	Unassigned
T. reinwardtii	*Tabanus*
T. remotus	Unassigned
T. restrepoensis	Unassigned
T. rhinargus	*Tabanus*
T. rhizonshine	*Tabanus*
T. rhizophorae	Unassigned
T. ricardae	Unassigned
T. rixator	Unassigned
T. riyadhae	Unassigned
T. rockefelleri	*Tabanus*
T. rosarioi	Unassigned
T. rosselensis	Unassigned
T. rossi	*Tabanus*
T. rothschildi	Unassigned
T. roubaudi	*Tabanus*
T. rousselii	Unassigned
T. rubicundulus	*Tabanus*
T. rubicundus	*Tabanus*
T. rubidaceus	Unassigned
T. rubidoides	*Tabanus*
T. rubidus	*Tabanus*
T. rubiginosus	*Tabanus*
T. rubioi	Unassigned
T. rubiventris	Unassigned
T. rubricauda	Unassigned
T. rubripes	Unassigned
T. rubriscutatus	*Tabanus*
T. rubriventris	Unassigned

T. rubudoides	Unassigned
T. rufescens	Unassigned
T. ruficoloratus	*Tabanus*
T. rufidens	Unassigned
T. rufimedius	*Tabanus*
T. rufioloratus	*Tabanus*
T. rufipes	Unassigned
T. rufiscutellatus	*Tabanus*
T. rufiventris	Unassigned
T. rufofrater	*Tabanus*
T. rufus	Unassigned
T. ruoqiangensis	Unassigned
T. rupinae	Unassigned
T. rupium	Unassigned
T. russatoides	Unassigned
T. russatus	Unassigned
T. rusticatus	Unassigned
T. ryukyuensis	*Tabanus*
T. sabuletoroides	Unassigned
T. sabuletorum	Unassigned
T. sackeni	*Tabanus*
T. safavii	Unassigned
T. sagax	*Tabanus*
T. sagittipalpis	*Tabanus*
T. samarensis	*Tabanus*
T. samawangensis	Unassigned
T. samoensis	Unassigned
T. sandersoni	Unassigned
T. sannio	Unassigned
T. sanyaensis	Unassigned
T. sapporoensis	Unassigned
T. sapporoenus	Unassigned
T. sarbazensis	Unassigned
T. sarmentoi	Unassigned
T. sasai	Unassigned
T. sauteri	*Tabanus*
T. saxicolus	Unassigned
T. scaralus	Unassigned
T. schadei	Unassigned
T. schiva	Unassigned
T. scholae	Unassigned
T. schurmansi	*Tabanus*
T. schwardti	Unassigned
T. scutellus	*Tabanus*
T. searsi	*Tabanus*
T. secedens	Unassigned
T. secundus	Unassigned
T. selene	Unassigned
T. selousi	Unassigned
T. selvaticus	*Tabanus*
T. semenovi	Unassigned
T. semiargenteus	Unassigned
T. semicircularis	Unassigned
T. semirufus	*Tabanus*
T. separatus	Unassigned
T. sepiensis	*Tabanus*
T. sepikensis	Unassigned
T. sequens	Unassigned
T. sericiventris	Unassigned
T. serus	*Tabanus*
T. servillei	*Tabanus*
T. severini	Unassigned
T. sexcinctus	*Tabanus*
T. sextriangulus	Unassigned
T. shaanxiensis	Unassigned
T. shannonellus	Unassigned
T. shantungensis	Unassigned
T. shelkovnikovi	Unassigned
T. shennongjianensis	Unassigned
T. shikokuensis	Unassigned
T. shyamarupi	*Tabanus*
T. siamensis	*Tabanus*
T. siassensis	Unassigned
T. sibsagarensis	Unassigned
T. siccus	Unassigned
T. sidneyensis	Unassigned
T. siebersi	*Tabanus*
T. sierrensis	*Tabanus*
T. signatipennis	Unassigned
T. signatus	Unassigned
T. signifer	*Tabanus*
T. significans	*Tabanus*
T. silvanus	Unassigned
T. similis	*Tabanus*
T. simplicissimus	*Tabanus*
T. simpsoni	Unassigned
T. sinewitensis	Unassigned
T. sinicus	*Tabanus*
T. skarduensis	Unassigned
T. smirnovi	Unassigned
T. soembawensis	*Tabanus*
T. sorbillans	Unassigned
T. soubiroui	*Tabanus*
T. sowi	Unassigned
T. sparus	*Tabanus*
T. spec	Unassigned
T. speciosus	*Tabanus*
T. spectabilis	Unassigned
T. speculum	*Tabanus*
T. sphinx	*Tabanus*
T. splendens	Unassigned
T. spodopteroides	Unassigned
T. spodopterus	Unassigned
T. stabilis	Unassigned
T. stackelbergiellus	Unassigned
T. statzi (fossil)	Unassigned
T. stekhoveni	*Tabanus*
T. stenocephalus	Unassigned
T. sticticolis	Unassigned
T. stonei	*Tabanus*
T. strangmannii	Unassigned
T. striatus	*Tabanus*
T. strigimaculus	Unassigned
T. strix	Unassigned
T. stueberi	Unassigned
T. stygius	*Tabanus*
T. subbasalis	Unassigned
T. subcaeruleus	Unassigned
T. subcallosus	Unassigned
T. subcamipus	*Tabanus*

T. subcanipus	*Tabanus*
T. subcinerascens	*Tabanus*
T. subcinerescens	Unassigned
T. subcinnamoneus	Unassigned
T. subcohaerens	Unassigned
T. subcordiger	*Tabanus*
T. subcrassus	Unassigned
T. subfemoralis	*Tabanus*
T. subflavicornis	*Tabanus*
T. subfurvicaudus	Unassigned
T. subhirtus	*Tabanus*
T. subhybridus	*Tabanus*
T. subimmanis	*Tabanus*
T. subjoidus	*Tabanus*
T. sublongus	*Tabanus*
T. submacilentus	Unassigned
T. submalayensis	Unassigned
T. subniger	*Tabanus*
T. suboblongus	Unassigned
T. suboliviventris	Unassigned
T. subparadoxus	Unassigned
T. subpulliomaculatus	Unassigned
T. subrecusans	Unassigned
T. subruber	*Tabanus*
T. subrubidus	*Tabanus*
T. subrussatus	Unassigned
T. subsabuletorum	Unassigned
T. subsimilis	Unassigned
T. subsinerascens	*Tabanus*
T. subviolaceus	Unassigned
T. succurvus	*Tabanus*
T. sudeticus	Unassigned
T. sufis	*Tabanus*
T. sugens	Unassigned
T. sulcifrons	*Tabanus*
T. sulfurescens	*Tabanus*
T. sumatrensis	*Tabanus*
T. superjumentarius	*Tabanus*
T. surifer	Unassigned
T. swiridowi	Unassigned
T. symmetrus	Unassigned
T. syriacus	Unassigned
T. systenus	Unassigned
T. szechenyianus	*Tabanus*
T. sziladyi	*Tabanus*
T. taeniatus	Unassigned
T. taeniellus	*Tabanus*
T. taeniola	Unassigned
T. taiensis	Unassigned
T. taipingensis	Unassigned
T. taiwanus	Unassigned
T. talyshi	Unassigned
T. tambaensis	Unassigned
T. tamthaiorum	Unassigned
T. tangi	Unassigned
T. tardinotus	Unassigned
T. taygetus	Unassigned
T. teishengi	Unassigned
T. tenasserimi	*Tabanus*
T. tendeiroi	Unassigned

T. tenebrosus	*Tabanus*
T. tenens	*Tabanus*
T. tenuicornis	Unassigned
T. tenuifrons	*Tabanus*
T. tenuipalpis	Unassigned
T. tenuis	Unassigned
T. tenuistria	Unassigned
T. tephrodes	Unassigned
T. teraiensis	*Tabanus*
T. tergestinus	Unassigned
T. terminalis	Unassigned
T. terterjani	Unassigned
T. testaceiventris	Unassigned
T. testaceus	Unassigned
T. tetropsis	*Tabanus*
T. texanus	*Tabanus*
T. thellus	Unassigned
T. thermarum	Unassigned
T. thiemeana	Unassigned
T. thoracinus	Unassigned
T. thurmani	*Tabanus*
T. tianyui	Unassigned
T. tienmuensis	*Tabanus*
T. tientsinensis	Unassigned
T. tiluensis	*Tabanus*
T. tinctipennis	Unassigned
T. tinctothorax	*Tabanus*
T. tinctus	Unassigned
T. titoi	Unassigned
T. tokaraensis	Unassigned
T. tokunoshimaensis	Unassigned
T. tonglai	*Tabanus*
T. toshiokai	Unassigned
T. toumanoffi	*Tabanus*
T. townsendi	Unassigned
T. townsvilli	Unassigned
T. transversus	Unassigned
T. traubi	*Tabanus*
T. trememberensis	Unassigned
T. triangularis	Unassigned
T. trianguliger	Unassigned
T. triangulum	Unassigned
T. triceps	Unassigned
T. tricoloratus	*Tabanus*
T. tricolorus	Unassigned
T. trifasciatus	Unassigned
T. trigonus	Unassigned
T. trijunctus	*Tabanus*
T. trilineatus	Unassigned
T. trimaculatus	*Tabanus*
T. trinominatus	*Tabanus*
T. tripurensis	*Tabanus*
T. triquetrornatus	Unassigned
T. tristichus	Unassigned
T. tristis	*Tabanus*
T. trivittatus	Unassigned
T. tuberculatus	*Tabanus*
T. tumidicallus	Unassigned
T. tumiscapens	*Tabanus*
T. tunicatus	Unassigned

T. turbidus	*Tabanus*
T. umbrinus	Unassigned
T. umbripennis	Unassigned
T. undulans	*Tabanus*
T. unicinctus	Unassigned
T. unicus	Unassigned
T. unifasciatus	Unassigned
T. unifasciens	*Tabanus*
T. uniformis	*Tabanus*
T. unilineatus	Unassigned
T. unipunctatus	Unassigned
T. unisignatus	*Tabanus*
T. unistriatus	Unassigned
T. univentris	*Tabanus*
T. ustus	Unassigned
T. vagus	Unassigned
T. vanleeuweni	Unassigned
T. varelai	Unassigned
T. variabilis	Unassigned
T. varians	Unassigned
T. varicolor	*Tabanus*
T. variegatus	Unassigned
T. varipes	Unassigned
T. variventris	Unassigned
T. vaseyi	Unassigned
T. vectensis (fossil)	Unassigned
T. velutinus	Unassigned
T. ventriflavimarginatus	*Tabanus*
T. venustus	*Tabanus*
T. vernus	Unassigned
T. vestitus	Unassigned
T. veterinarius	Unassigned
T. vibex	Unassigned
T. vicinus	Unassigned
T. violaceus	*Tabanus*
T. virgulatus	*Tabanus*
T. viridis	Unassigned
T. vittiger	Unassigned
T. vivax	*Tabanus*
T. vix	*Tabanus*
T. wallacei	*Tabanus*
T. weiheensis	Unassigned
T. weiningensis	Unassigned
T. wellmanii	Unassigned
T. wenzeli	*Tabanus*
T. weyrauchi	Unassigned
T. wiedemanni	*Tabanus*
T. wilkersoni	Unassigned
T. williamsii	Unassigned
T. wilpattuensis	Unassigned
T. wilsoni	*Tabanus*
T. wokei	Unassigned
T. woollastoni	Unassigned
T. wuyishanensis	Unassigned
T. wuzhishanensis	Unassigned
T. wyndhamensis	Unassigned
T. xanthocorus	Unassigned
T. xanthogaster	Unassigned
T. xanthoimus	*Tabanus*
T. xanthomelas	Unassigned
T. xanthos	Unassigned
T. xanti	*Tabanus*
T. xenorhynchus	Unassigned
T. xerodes	Unassigned
T. xuezhongi	Unassigned
T. xuthopogon	Unassigned
T. xuthus	*Tabanus*
T. yablonicus	Unassigned
T. yadongensis	Unassigned
T. yaeyamaensis	Unassigned
T. yakuensis	Unassigned
T. yanbaruensis	Unassigned
T. yao	Unassigned
T. yarchus	Unassigned
T. yasujensis	Unassigned
T. yishanensis	Unassigned
T. yoneyamai	Unassigned
T. yoshimotoi	Unassigned
T. yucatanus	Unassigned
T. yulensis	Unassigned
T. yunnanensis	Unassigned
T. zancala	*Tabanus*
T. zayaensis	Unassigned
T. zayasi	*Taeniotabanus*
T. zayuensis	Unassigned
T. zebrinus	*Tabanus*
T. zeirii	Unassigned
T. zhongpingi	Unassigned
T. zimini	Unassigned
T. zodiacus	Unassigned
T. zoster	*Tabanus*
T. zoulouensis	Unassigned
T. zunmingi	Unassigned
T. zythicolor	*Tabanus*

***Chrysops* species**	**Subgenus**
C. abaptistus	Unassigned
C. abatus	Unassigned
C. abavius	*Chrysops*
C. aberrans	*Chrysops*
C. additus	Unassigned
C. aeneus	*Chrysops*
C. aestuans	*Chrysops*
C. affinis	*Chrysops*
C. alajuelensis	Unassigned
C. albicinctus	Unassigned
C. alleni	Unassigned
C. alter	Unassigned
C. altivagus	*Chrysops*
C. amazon	*Chrysops*
C. angaricus	*Chrysops*
C. angolensis	Unassigned
C. anthrax	*Chrysops*

C. aprugnus	Unassigned
C. argentinus	Unassigned
C. armeniensis	*Petersenichrysops*
C. asbestos	*Chrysops*
C. ater	*Chrysops*
C. atlanticus	*Chrysops*
C. atrivittatus	Unassigned
C. auroguttatus	Unassigned
C. austeni	Unassigned
C. australis	Unassigned
C. balzaphire	*Chrysops*
C. basalis	*Chrysops*
C. beameri	*Chrysops*
C. berta	Unassigned
C. bicolor	Unassigned
C. bifasciatus	Unassigned
C. bifurcatus	Unassigned
C. bimaculosus	Unassigned
C. bishoppi	*Chrysops*
C. bistellatus	*Chrysops*
C. bivittatus	Unassigned
C. boliviensis	Unassigned
C. bonariensis	Unassigned
C. brevifascius	Unassigned
C. brimleyi	*Chrysops*
C. brucei	Unassigned
C. brunneus	*Chrysops*
C. bulbicornis	Unassigned
C. buxtoni	*Petersenichrysops*
C. caecutiens	Unassigned
C. calidus	Unassigned
C. callidus	*Chrysops*
C. calogaster	Unassigned
C. calopterus	Unassigned
C. calvus	*Chrysops*
C. canifrons	*Chrysops*
C. carbonarius	*Chrysops*
C. centurionis	Unassigned
C. cervulus	Unassigned
C. chaharicus	*Chrysops*
C. chiefengensis	*Chrysops*
C. chiriquensis	Unassigned
C. chusanensis	Unassigned
C. ciliaris	Unassigned
C. cincticornis	*Chrysops*
C. clavicornis	*Chrysops*
C. coloradensis	*Chrysops*
C. compactus	*Petersenichrysops*
C. concavus	*Chrysops*
C. connexus	*Chrysops*
C. coquilletti	*Chrysops*
C. costaricensis	Unassigned
C. costatus	Unassigned
C. croceus	Unassigned
C. crucians	Unassigned
C. cuclux	*Chrysops*
C. currani	Unassigned
C. cursim	*Chrysops*
C. dacne	*Chrysops*
C. dampfi	*Chrysops*
C. dawsoni	*Chrysops*
C. decipiens	Unassigned
C. delicatulus	*Chrysops*
C. deqenensis	Unassigned
C. designatus	Unassigned
C. dimidiatus	Unassigned
C. dimmocki	*Chrysops*
C. discalis	*Chrysops*
C. dispar	Unassigned
C. dissectus	*Chrysops*
C. dissimilis	*Chrysops*
C. distinctipennis	Unassigned
C. divaricatus	*Chrysops*
C. divisus	*Chrysops*
C. dixianus	*Chrysops*
C. dorsopunctus	*Chrysops*
C. dorsovittatus	*Chrysops*
C. dubiens	Unassigned
C. ecuadorensis	Unassigned
C. excitans	*Chrysops*
C. facialis	*Chrysops*
C. fairchildi	Unassigned
C. fasciatus	Unassigned
C. fascipennis	*Chrysops*
C. fixissimus	Unassigned
C. flavescens	Unassigned
C. flavidus	*Chrysops*
C. flavipennis	Unassigned
C. flavipes	*Chrysops*
C. flaviscutellatus	Unassigned
C. flaviventris	Unassigned
C. flavocinctus	Unassigned
C. flavoscutellatus	Unassigned
C. flinti	Unassigned
C. floridanus	Unassigned
C. formosus	Unassigned
C. frazari	Unassigned
C. frigidus	*Chrysops*
C. frontalis	Unassigned
C. fuliginosus	*Chrysops*
C. fulvaster	*Chrysops*
C. fulvistigma	*Chrysops*
C. funebris	Unassigned
C. furcatus	*Chrysops*
C. fusciapex	Unassigned
C. fuscipennis	Unassigned
C. fuscomarginalis	Unassigned
C. geminatus	*Chrysops*
C. godinhoi	Unassigned
C. gracilis	Unassigned
C. grandis	Unassigned
C. griseicollis	Unassigned
C. gutipennis	Unassigned
C. hamatus	*Petersenichrysops*
C. harmani	*Chrysops*
C. hinei	*Chrysops*
C. hirsuticallus	*Chrysops*
C. hubbardi	Unassigned
C. hyalinus	*Liochrysops*
C. hyalipennis	*Turanochrysops*

C. idlani	Unassigned
C. ifasi	*Chrysops*
C. impunctus	Unassigned
C. incisuralis	Unassigned
C. incisus	Unassigned
C. inconspicuus	Unassigned
C. indianus	Unassigned
C. indus	*Chrysops*
C. infernalis	Unassigned
C. inflaticornis	Unassigned
C. insulensis	Unassigned
C. intrudens	Unassigned
C. italicus	*Chrysops*
C. japonicus	*Chrysops*
C. laetus	Unassigned
C. langi	Unassigned
C. laniger	Unassigned
C. lateralis	*Chrysops*
C. laticeps	Unassigned
C. latifasciatus	*Chrysops*
C. latifrons	*Chrysops*
C. latitibialis	Unassigned
C. leucospilus	Unassigned
C. liaoningensis	*Chrysops*
C. longicornis	Unassigned
C. longirostris	Unassigned
C. lugens	Unassigned
C. luteopennis	*Chrysops*
C. lutzi	Unassigned
C. macquarti	*Chrysops*
C. madagascarensis	Unassigned
C. maerens	Unassigned
C. magnificus	Unassigned
C. makerovi	*Chrysops*
C. marmoratus	Unassigned
C. matilei	Unassigned
C. mauritanicus	*Chrysops*
C. maximus	Unassigned
C. melaenus	Unassigned
C. melicharii	*Chrysops*
C. mexicanus	Unassigned
C. mitis	*Chrysops*
C. mlokosiewiczi	Unassigned
C. moechus	*Chrysops*
C. molestus	Unassigned
C. montanus	*Chrysops*
C. mutatus	*Chrysops*
C. neavei	Unassigned
C. neobrasiliensis	Unassigned
C. niger	*Chrysops*
C. nigribimbo	*Chrysops*
C. nigricorpus	Unassigned
C. nigripes	*Chrysops*
C. nigriventris	Unassigned
C. nigrobasalis	Unassigned
C. noctifer	*Chrysops*
C. obliquefasciatus	Unassigned
C. obsoletus	*Chrysops*
C. okavangoensis	Unassigned
C. olivaceus	Unassigned
C. omissus	Unassigned
C. oxianus	*Chrysops*
C. pachycerus	Unassigned
C. pachycnemius	Unassigned
C. pallidefemoratus	Unassigned
C. pallidiventris	*Chrysops*
C. pallidulus	Unassigned
C. papuensis	Unassigned
C. paradesignata	Unassigned
C. paraguayensis	Unassigned
C. parallelogrammus	*Chrysops*
C. parvifascius	Unassigned
C. parvulus	*Chrysops*
C. passosi	*Chrysops*
C. patricia	Unassigned
C. pauliani	Unassigned
C. pechumani	*Chrysops*
C. pellucidus	Unassigned
C. perpensus	Unassigned
C. pertinax	Unassigned
C. peruvianus	Unassigned
C. petersi	Unassigned
C. pettigrewi	Unassigned
C. philipi	Unassigned
C. pikei	*Chrysops*
C. piresi	*Chrysops*
C. potanini	*Chrysops*
C. proclivis	*Chrysops*
C. provocans	*Chrysops*
C. pseudofuscipennis	Unassigned
C. pudicus	*Chrysops*
C. pusillulus	Unassigned
C. reicherti	*Chrysops*
C. relictus	*Chrysops*
C. renjifoi	Unassigned
C. reticulatus	Unassigned
C. ricardoae	*Chrysops*
C. rossi	Unassigned
C. rufipes	*Chrysops*
C. sackeni	*Chrysops*
C. sandyi	Unassigned
C. scalaratus	Unassigned
C. seguyi (fossil)	Unassigned
C. sejunctus	*Chrysops*
C. semiignitus	*Chrysops*
C. separatus	*Chrysops*
C. sepulcralis	*Chrysops*
C. sequax	*Chrysops*
C. shermani	*Chrysops*
C. signifer	Unassigned
C. silaceus	Unassigned
C. silviaris	Unassigned
C. silvifacies	Unassigned
C. sinensis	Unassigned
C. sordidus	Unassigned
C. soror	Unassigned
C. srilankensis	Unassigned
C. stackelbergi	*Turanochrysops*
C. stackelbergiellus	*Chrysops*
C. stekhoveni	Unassigned

C. stimulans	Unassigned
C. stonei	*Chrysops*
C. streptobalius	Unassigned
C. striatulus	*Chrysops*
C. striatus	*Chrysops*
C. suavis	*Chrysops*
C. subcaecutiens	*Chrysops*
C. surdus	*Chrysops*
C. szechuanensis	*Chrysops*
C. tardus	Unassigned
C. tarimi	Unassigned
C. terminalis	Unassigned
C. thailandensis	Unassigned
C. tibialis	Unassigned
C. tidwelli	*Chrysops*
C. translucens	Unassigned
C. trifarius	Unassigned
C. trisignatus	Unassigned
C. tristis	Unassigned
C. tumidicornis	Unassigned
C. turanicus	*Chrysops*
C. univittatus	*Chrysops*
C. unizona	Unassigned

C. upsilon	*Chrysops*
C. uruguayensis	Unassigned
C. validus	*Chrysops*
C. vargus	Unassigned
C. varians	Unassigned
C. variegatus	*Chrysops*
C. venezuelensis	Unassigned
C. venus	*Chrysops*
C. viduatus	*Chrysops*
C. vietnamensis	Unassigned
C. violovitshi	*Chrysops*
C. virgulatus	*Chrysops*
C. vittatus	*Chrysops*
C. weberi	Unassigned
C. wileyae	*Chrysops*
C. willistoni	Unassigned
C. woodi	Unassigned
C. yamaguchii	*Chrysops*
C. yunnanensis	Unassigned
C. zahrai	Unassigned
C. zayasi	Unassigned
C. zinzalus	*Chrysops*

***Haematopota* species**
H. abacis
H. abatrata
H. abbreviata
H. aberdarensis
H. abyssinica
H. achlys
H. adami
H. adusta
H. albalinea
H. albicapilla
H. albihalter
H. albihirta
H. albimanica
H. albimedia
H. albiocrea
H. albofasciatipennis
H. algira
H. aliena
H. alluaudi
H. alticola
H. altimontana
H. alyta
H. amala
H. americana
H. amicoi
H. ampla
H. angolensis
H. angustifrons
H. angustisegmentata
H. annandalei
H. annulipes
H. anomala
H. antennata

H. aquilina
H. areei
H. argentipes
H. arioi
H. arrabidaensis
H. assamensis
H. athlyna
H. atomaria
H. atrata
H. atriventer
H. atropathenica
H. aurescens
H. avida
H. ayresi
H. bactriana
H. badia
H. bantuana
H. barombi
H. barri
H. barrosi
H. bashanensis
H. bealesi
H. bedfordi
H. benoisti
H. bequaerti
H. beringeri
H. bicolor
H. bigoti
H. biguttata
H. biharensis
H. bilineata
H. biorbis
H. bipunctata
H. biroi

H. bistrigata
H. bizonata
H. borneana
H. bowdeni
H. brevicornis
H. brevis
H. brucei
H. brulli
H. brunnescens
H. brunnicornis
H. brunnipennis
H. brunnipes
H. brutsaerti
H. bullatifrons
H. burgeri
H. burmanica
H. burtoni
H. burtti
H. caenofrons
H. camicasi
H. cana
H. canapicalis
H. casca
H. caseiroi
H. caspica
H. castaneiventer
H. castroi
H. champlaini
H. chekiangensis
H. chengyongi
H. chinensis
H. chongoroiensis
H. chvalai
H. ciliatipes
H. cilipes
H. cingalensis
H. cingulata
H. circina
H. circumscripta
H. clarkana
H. claudinae
H. coalescens
H. cognata
H. comodoliacis
H. completa
H. concentralis
H. concurrens
H. coninckae
H. contracta
H. coolsi
H. copemanii
H. cordigera
H. coronata
H. corrigata
H. corsoni
H. crassicornis
H. crassicrus
H. crassitibia
H. crewei
H. cristata

H. crossi
H. crudelis
H. cruneta
H. csikii
H. cynthiae
H. darjeelingensis
H. daveyi
H. decora
H. degenensis
H. delicta
H. delozi
H. demeilloni
H. demellonis
H. denshamii
H. desertorum
H. dissimilis
H. distincta
H. divisapex
H. dolondoloensis
H. dubiosa
H. dukei
H. duplicata
H. duttoni
H. echma
H. edax
H. elegans
H. elephantina
H. enriquei
H. ensifer
H. epoptica
H. equina
H. equitibiata
H. erlangshanensis
H. erythromera
H. eugeniae
H. evanescens
H. excipula
H. exiguicornuta
H. faini
H. fairchildi
H. famicis
H. fariai
H. fasciata
H. fasciatapex
H. fenestralis
H. ferruginea
H. festiva
H. fiadeiroi
H. flavicornis
H. flavipuncta
H. fletcheri
H. fonsecai
H. fontesi
H. formosana
H. fradei
H. fraterna
H. fukienensis
H. fulva
H. fulvipes
H. fumigata

H. furians
H. furtiva
H. furva
H. fusca
H. fuscicornis
H. fuscolimbata
H. fuscomarginata
H. gabuensis
H. gallica
H. gallii
H. gamae
H. germaini
H. giganticornuta
H. glenni
H. gobindai
H. gracai
H. gracilicornis
H. gracilis
H. graeca
H. grahami
H. grandis
H. grandvauxi
H. gregoryi
H. greniere
H. gressitti
H. griseicoxa
H. guacangshanensis
H. guangxiensis
H. guineensis
H. hainani
H. hakusanensis
H. hanzhogensis
H. hardyi
H. harpax
H. hastata
H. hedini
H. helviventer
H. hennauxi
H. heptagramma
H. hieroglyphica
H. hikosanensis
H. hindostani
H. hirsuta
H. hirsuticornis
H. hirsutitarsus
H. hirta
H. holtmanni
H. horrida
H. hostilis
H. howarthi
H. imbrium
H. immaculata
H. inconspicua
H. incrassicornis
H. indiana
H. infernalis
H. inflaticornis
H. ingluviosa
H. innominata
H. inornata

H. insidiatrix
H. intermedia
H. intrincata
H. irregularis
H. irritans
H. irrorata
H. italica
H. jacobsoni
H. javana
H. jellisoni
H. jianzhongi
H. jiri
H. johnburtoni
H. kansuensis
H. kashmirensis
H. katangaensis
H. kaulbacki
H. kemali
H. keralaensis
H. kerri
H. kivuensis
H. knekidis
H. koryoensis
H. kouzuensis
H. krombeini
H. lacessens
H. lambi
H. lamborni
H. lamottei
H. lancangjiangensis
H. lasiops
H. lata
H. latebricola
H. lathami
H. latifascia
H. laverani
H. leclercqui
H. lepointei
H. lewisi
H. libera
H. limai
H. limbata
H. lineata
H. lineola
H. lineota
H. litoralis
H. lobatoi
H. longa
H. longeantennata
H. longipennis
H. lukiangensis
H. lunai
H. lunulata
H. machadoi
H. maculata
H. maculiplena
H. maculosifacies
H. magnifica
H. malabarica
H. malacrizi

H. malayensis
H. malefica
H. mangkamensis
H. marakuetana
H. marceli
H. marginata
H. marthae
H. masseyi
H. matherani
H. matosi
H. megaera
H. meglaensis
H. melloi
H. mendesi
H. mendossaorum
H. mengdingensis
H. menglaensis
H. mephista
H. meteorica
H. microcera
H. mingqingi
H. minuscula
H. minuscularia
H. mlanjensis
H. mokanshanensis
H. molesta
H. montana
H. monteiroi
H. monticola
H. montisdraconis
H. mordax
H. mordens
H. moreli
H. mouchai
H. mouzinhoi
H. mukteswarensis
H. nagashimai
H. nasuensis
H. nathani
H. neavei
H. nefanda
H. nefandoides
H. nepalensis
H. newtoni
H. nigriantenna
H. nigricans
H. nigricolor
H. nigrifrons
H. nigripennis
H. nigrita
H. nigrocinerea
H. nigrofusca
H. nitidifacies
H. nobilis
H. nobrei
H. nocens
H. nociva
H. noxialis
H. nubilis
H. obscura

H. obsoleta
H. ocellata
H. ocelligera
H. ochracea
H. okui
H. oldroydi
H. olsufjevi
H. omeishanensis
H. oporina
H. orba
H. ovazzai
H. pachycera
H. paisanai
H. palancaensis
H. pallens
H. pallida
H. pallidimarginata
H. pallidipennis
H. pallidula
H. pandazisi
H. paratruncata
H. pardalina
H. partifascia
H. passosi
H. patellicornis
H. pattoni
H. paucipunctata
H. paulettae
H. pavlovskii
H. pearsoni
H. pechumani
H. pekingensis
H. pellucida
H. pendleburyi
H. pereirai
H. perplexa
H. personata
H. pertinens
H. perturbans
H. peusi
H. philipi
H. picea
H. picta
H. pilosifemura
H. pinguicornis
H. pinicola (fossil)
H. piresi
H. pisinna
H. pluvialis
H. pollinantenna
H. pottsi
H. pratasi
H. procyon
H. prolixa
H. przewalskii
H. pseudolusitanica
H. pseudomachadoi
H. pulchella
H. punctifera
H. punctulata

H. pungens
H. pygmaea
H. qilianshanensis
H. qionghaiensis
H. quadrifenestrata
H. quartaui
H. quathlambia
H. qui
H. rabida
H. rafaeli
H. rara
H. recurrens
H. remota
H. restricta
H. ribeirorum
H. rohtakensis
H. roralis
H. rotundata
H. rubens
H. rubida
H. rubidicornis
H. rufipennis
H. rufula
H. ruwenzorii
H. sabiensis
H. saccae
H. saegeri
H. salomae
H. sanguinaria
H. saravanensis
H. sauli
H. scanloni
H. schmidi
H. schoutedeni
H. scutellaris
H. scutellata
H. semiclara
H. serranoi
H. sewelli
H. seydeli
H. shinonagai
H. sica
H. sidamensis
H. sikkimensis
H. similis
H. sinensis
H. sineroides
H. singarensis
H. singularis
H. sobrina
H. sofalensis
H. sparsa
H. spectabilis
H. spenceri
H. sphaerocallus
H. splendens
H. stackelbergi
H. stimulans
H. stonei
H. striata

H. subcylindrica
H. subirrorata
H. subkoryoensis
H. subturkestanica
H. sumelae
H. surugaensis
H. tabanula
H. taciturna
H. takensis
H. tamerlani
H. taunggyiensis
H. tchivinguiroensis
H. teixeirai
H. tenasserimi
H. tendeiroi
H. tenuicrus
H. tenuis
H. tessellata
H. theobaldi
H. thurmanorum
H. tiomanensis
H. tonkiniana
H. torquens
H. torrevillasi
H. tosta
H. touratieri
H. toyamensis
H. transiens
H. travassosdiasi
H. triatipennis
H. tuberculata
H. tumidicornis
H. turkestanica
H. ugandae
H. unicolor
H. u-nigrum
H. unizonata
H. ustulata
H. valadonis
H. variantennata
H. varifrons
H. vassali
H. veigasimonis
H. vexans
H. vexativa
H. vicentei
H. vicina
H. vieirai
H. vilhenai
H. vimoli
H. virgatipennis
H. vittata
H. volneri
H. vulcan
H. vulnerans
H. vulnifica
H. whartoni
H. willistoni
H. wittei
H. wuzhishanensis

H. yanggangi	*H. zambeziaca*
H. yongpingi	*H. zengjiani*
H. yungani	*H. zombaensis*
H. yunnanensis	*H. zophera*
H. yunnanoides	*H. zuluensis*

Parasite morphology: Tabanid flies form 4 different types of morphological stages during their development: eggs; larvae (6-13 instars); pupae; and adults (males and females). Eggs are large and elongate (1-3 mm long), elliptical-cylindrical with rounded ends, and initially creamy white but darken to brown-black within several hours. Upon hatching, the eggs release fusiform segmented larvae which moult through 6-13 instars gradually growing up to 15-30 mm long (a few species grow up to 60 mm). Most stages are creamy-white with dark bands on each segment, although some species are green-brownish or appear mottled due to species-specific pigmentation patterns. The larvae have small incomplete (partially sclerotized) head capsules with a pair of 3-jointed antennae and strong curved mandibles. The abdominal segments have lateral and ventral warty outgrowths known as pseudopods (3 pairs in Chrysopinae, 4 pairs in Tabaninae). The pseudopods are intermediate in size in semi-aquatic species (represented by most tabanids), short in terrestrial species, but longer and dentate in the few species adapted to fully aquatic habitats. The larvae breathe through a posterior dorsal respiratory siphon and the anal segment has an enigmatic pear-shaped vesicle (Graber's organ). The final larval instar forms a cylindrical pupa, rounded anteriorly and tapering posteriorly, measuring up to 20-30 mm long. Pupae are glossy brown in appearance and have a rigid anterior cephalothorax covering, 7 flexible abdominal segments (most bearing marginal setae), and several pairs of caudal spine-like tubercles (known as pupal asters). Details of the internal morphological features of the developing adult are visible through the pupal case, including the head, thoracic and abdominal segments, with wings and legs closely appressed to the body. Adult tabanids are large robust stout flies (5-30 mm long) with big coloured eyes, prominent antennae, pendulous palps, broad wings with marginal Y-shaped veins, and feet with 3 pads. They have a covering of fine setae imparting a slightly furry appearance, particularly over the head and thorax, but their bodies do not have large bristle-like setae (commonly found on muscid and calliphorid flies). Tabanids may be readily differentiated into horse flies (Tabaninae) or deer flies (Chrysopinae) on basis of several characters. Horse flies are larger (10-30 mm) and have dark bodies (brown-black, sometimes green-blue, often with stripes of pale patches) while deer flies are smaller (5-11 mm) and have lighter bodies (yellow-orange to grey, with striped abdomens). Both have large compound eyes that are brightly coloured appearing iridescent in life (green-brown with horizontal stripes in *Tabanus*, green-red with zigzag bands in *Haematopota*, and gold-green with spots in *Chrysops*). The eyes are separated by a frons in females (dichoptic) but touch medially in males (holoptic). Small ocelli are also present in deer flies but vestigial or absent in horse flies. Both have prominent antennae projecting forwards, but those in horse flies are shorter, The antennae are composed of 3 segments of symmetric (*Haematopota*) or asymmetric (*Tabanus*, *Chrysops*) shape: a basal scape; middle pedicel; and an elongate anterior flagellum (base enlarged in *Tabanus*) with multiple pseudosegments (flagellomeres) separated by small annulations (3 in *Haematopota*, 4 in *Chrysops* and *Tabanus*). The first flagellomere is thicker in all genera, and bears a lateral horn-like projection in *Tabanus* spp. The head contains a stout ventral proboscis formed by a fleshy labium (with terminal sensory labella) containing a bundle of 6 chitinous stylets used for feeding. The stylets include a pair of flat saw-like mandibles and a pair of narrow toothed file-like maxillae used to lacerate tissues, together with a rigid hypopharynx to deliver saliva and a large labellum to sponge up fluids. These slashing-sponging mouthparts are well developed in female flies which feed on blood, but are highly reduced in males which only feed on nectar and plant exudates. The mouthparts are flanked by 2 maxillary palps, each consisting of 2 segments with the base of the apical segment being enlarged and often appearing bulbous. The alimentary tract consists of a tubular oesophagus leading to a globular proventriculus (with saccular diverticula (or crop) where dilute fluids may be shunted for temporary storage) connected to a tubular midgut (for digestion), hindgut (with excretory Malpighian tubules), rectum (with expandable ampulla) and terminal anus. The globular thorax is covered by a tough scutum with a posterior lobe-like scutellum and bears 2 pairs of thoracic respiratory spiracles. The dorsal thorax gives rise to a pair of broad membranous forewings (clear, cloudy or spotted in *Tabanus*, mottled in *Haematopota*, and banded in *Chrysops*) with membranes supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)], with the radial veins R4+5 forking to form a large 'Y' at the wing tip. When at rest, flies hold their wings partly folded over the abdomen. The basal lobe (calypter) covers the hindwings which are highly reduced to small knob-like halteres used to stabilize flight (2 pairs of wings characteristic for all 'Di-ptera'). Adults have 3 pairs of stout dark legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) with spurs present on the mid-tibiae (in *Tabanus* and *Haematopota*) or hind-tibiae (in *Chrysops*). All legs terminate in tarsi with 2 claws and 3 pads (2 pulvilli and a central pad-like empodium). The ellipsoidal abdomen is segmented (often with distinct marks or bands separating segments) and typically possesses 7 pairs of lateral respiratory spiracles. The terminal abdominal segments are modified by external genitalia (genital plates, claspers and ovipositors). Males have 2 testes connected by vas deferens to a seminal vesicle (with accessory glands) leading to the tubular ejaculatory duct and retractable copulatory aedeagus. Females have 2 ovaries (with polytrophic ovarioles) joined by oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva and ovipositor.

Site of infection: Pre-adult developmental stages occur in semi-aquatic or aquatic (rarely terrestrial) habitats, whereas adult flies are free-flying and feed to plants sugars. Female flies of many species, however, are haematophagous and must feed on blood in order to produce eggs. They are therefore transient ectoparasites of vertebrate hosts, feeding mainly on large mammals, principally ungulates. While their regional common names (such as horse flies, deer flies, buffalo flies, moose flies, elephant flies) suggests that

they may be host specific, most tabanid species are stenoxenous (feeding on closely-related hosts) and opportunistic (feeding on locally available hosts). Tabanids have been observed to feed on smaller mammals (carnivores, rodents), birds (waterfowl, corvids), and sometimes reptiles (lizards, turtles). *Tabanus* spp. (commonly known as horse flies, some as greenheads or bluetail flies) feed mainly on livestock as well as wild artiodactyls and perissodactyls, sometimes on humans. Most species feed preferentially on the legs and lower ventral bodies of their hosts, while others feed along the flanks, midline, head or neck. *Haematopota* spp. (known as horse flies, cleg flies or simply clegs) feed mostly on cattle and other livestock (particularly along the belly and crutch), and will bite humans (mainly on the wrists or bare legs). *Chrysops* spp. (known as deer flies, yellow flies, June flies, or stouts) feed readily on cervids, bovids, equids and frequently attack humans, typically biting the upper body, head, and shoulders.

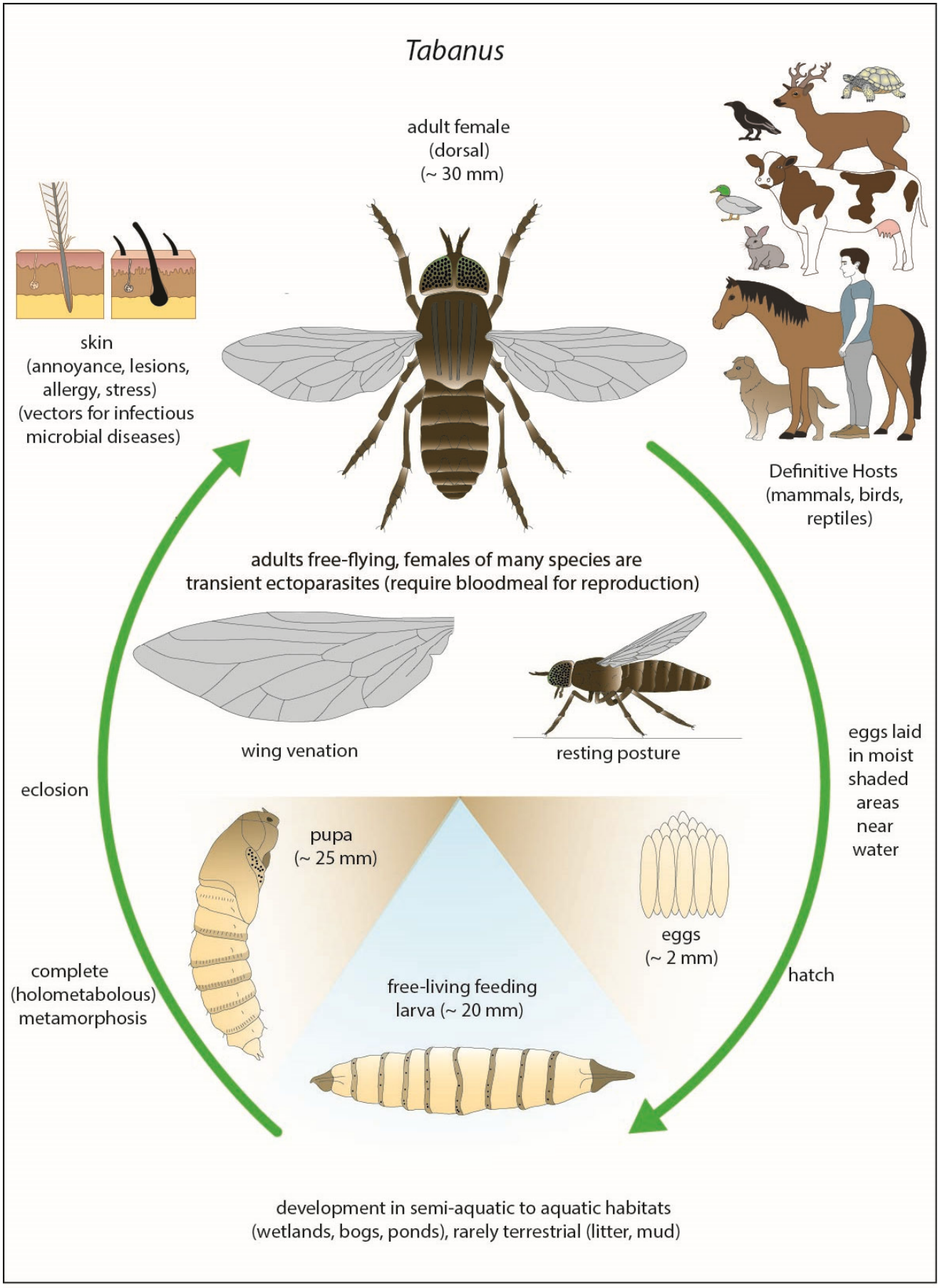
Pathogenesis: Female tabanids are large aggressive flies with painful bites resulting in considerable annoyance, dermal lesions and sometimes allergic reactions, all contributing to poor productivity in their hosts. Most horse and deer flies are noisy buzzing fliers (although clegs fly noiselessly) and their persistent efforts to feed cause great host consternation and disturbance. Female flies have well-developed slashing-sponging mouthparts, using their scissor-like and saw-like stylets to lacerate dermal tissues and then sponging up blood pooling in the wound (process known as telmophagy). During feeding, they inject saliva containing various vaso-active compounds, notably anticoagulants. The resultant bites are deep and painful, resulting in the formation of pruritic papules and wheals, which may become haemorrhagic, ulcerative and necrotic with crust formation. Some hosts develop immediate and/or delayed hypersensitivity to fly saliva with allergic reactions observed in humans including hives, urticaria, dizziness, weakness, difficulty in breathing, wheezing and angioedema (swelling around the eyes or lips). Depending on the species and size of the flies, they may imbibe 20-700 mg of blood per meal which can lead to significant blood loss, sometimes manifest as anaemia. Hosts under attack often exhibit unusual avoidance behaviours to fly worry, gregarious hosts sometimes forming tightly-packed groups protecting their heads in the centre (herding defence) while solitary hosts may lash out or take flight. Animals may attempt to lick, bite or scratch pruritic bite sites, sometimes leading to self-trauma and worsening lesions prone to secondary infections. Distracted animals do not feed efficiently and demonstrate decreased performance, reduced weight gain (sometimes weight loss), reduced milk production, and even hide damage. While flies are often brushed off due to their painful bites, they are remarkably resilient to swatting and their persistence in feeding on available hosts provides ideal opportunities for the transmission of infectious diseases. Horse and deer flies may act as biological or mechanical vectors where micro-organisms either develop within the flies or are simply carried on contaminated mouthparts. Tabanid flies have been shown to act as efficient vectors for viruses (causing equine infectious anaemia, bovine leukemia, and hog cholera), bacteria (causing anaplasmosis, tularemia, pasteurellosis and anthrax in livestock), protozoa (causing trypanosomiasis (nagana and surra) and besnoitiosis in ungulates) and helminths (filaroid nematodes causing dirofilariasis in marsupials, arterial elaeophorosis in deer, and loasis in humans).

Developmental cycle and mode of transmission: Like all dipterans, tabanid flies undergo complete metamorphosis where grub-like larvae transform into flying adults in pupae. Gravid female flies are oviparous and lay batches of 100-1,000 eggs in a single mass, most horse flies stacking eggs pyramidally in 3-4 tiers, while most deer flies lay eggs in a single layer. Eggs are deposited in moist shady environments on the undersides of plants and rocks usually overhanging or emerging from water. They hatch after 2-12 days depending on species, location and temperature (faster at higher temperatures). The emergent larvae drop to the moist substrate beneath and moult once, apparently without feeding, before moving into the substrate for further development. The larvae of most species are semi-aquatic in lentic-lotic habitats (mud or saturated vegetation in marshes, wetlands, bogs and along pond or stream margins) although some species are terrestrial (in pockets of wet soil in meadows or leaf litter in forests). *Chrysops* spp. develop in particularly wet locations, whereas *Tabanus* spp. prefer moist habitats. Larvae feed on decaying organic material, detritus and algae, but are also predatory and carnivorous (sometimes cannibalistic) feeding on a range of invertebrates, including annelids and the larvae of other insects (chironomid midges, crane flies) and arthropods. Developing larvae moult through 6-13 instars over periods ranging from 0.5-3.0 years, depending on species, geographic location and environmental conditions (development prolonged in cold, dry or other unfavourable conditions). In spring, the final larval instars move to drier soil near the ground surface above the waterline and form pupae from which adult flies emerge 7-21 days later. Males usually emerge first and wait for females for mating, often in swarms generally at landmarks such as hilltops. Both males and females feed on nectar and pollen of flowers (some species being important pollinators of particular flowers). However, the females of most species are anautogenous and require bloodmeals to complete ovarian (gonotrophic) cycles (egg production), although some species appear to be autogenous and may complete one or several cycles without blood-feeding. Females take large bloodmeals from vertebrates and eggs are produced 3-6 days after feeding. Tabanids are most abundant during the warmer months of the year and they are strong and agile fliers capable of dispersing for kilometres. Females hunt for hosts during the daytime using a range of olfactory, visual, thermal and tactile senses, particularly expired carbon dioxide, movement, body temperature and surface texture. Female *Chrysops* even appear to be attracted by smoke from residences. Adult flies live for 2-4 weeks and the entire life cycle may be completed several times a year in the tropics (multivoltine) or once a year in temperate regions (univoltine). Tabanids are widespread throughout the world but are absent in polar regions and have patchy island distributions. Provided moist areas are locally available for breeding, tabanids occupy diverse habitats ranging from deserts to alpine meadows (up to 3,000 metres).

Differential diagnosis: Clinical signs exhibited by hosts (pruritic papules, wheals) are relatively nonspecific and may be attributable to a variety of ectoparasites or skin conditions. Diagnosis is often afforded by the observation of large (often noisy) flies delivering painful bites, assisted by capturing specimens for microscopic examination. Flies may also be captured from the environment using

traps baited with chemical attractants. Tabanid identification is based mostly on adult morphological characters of the head, wing venation, and sometimes the last abdominal segment. Recent molecular biological studies have been used to characterize tabanid species (especially those involved in disease transmission) following polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA) and mitochondrial (cytochrome) gene sequences.

Treatment and control: Humans bitten by horse and deer flies may seek symptomatic relief by washing bite sites with cold water or applying cold compresses, and using topical or systemic antihistamines and glucocorticoids to alleviate pruritus and inflammation. Animals may be treated with insecticidal sprays, dusts, pour-ons or eartags containing organophosphates (coumaphos, chlorfenvinphos, diazinon, dioxathion, fenchlorvos, malathion, phosmet, stirofos, trichlorfon) or pyrethrins (permethrin, cyfluthrin, cypermethrin), but their efficacy is usually limited due to the short residence time of flies on hosts (several minutes per meal with days in between) and variable emergence of many different species over time and space. The treatment of the immediate environment with residual insecticides, mostly pyrethroids, has provided some short-term relief in some intensively-grazed areas, but aerial applications (sprays, mists and fogs) dissipate quickly and may have untoward ecological impacts. The diversity and abundance of potential breeding sites also precludes the widespread application of insecticides which are ineffective against larval and pupal stages buried in soils. Nevertheless, the removal of aquatic vegetation and leaf litter has been shown to assist population control, as has periodically changing water levels in ponds and irrigation channels (alternately drying out larvae and flooding pupae). Animal management practices designed to limit attack rates include building shelters for livestock (flies avoid shaded places), housing animals indoors in daylight during peak fly season (flies are diurnal), avoiding pasture-forest ecotones, and using fly traps (curtain, box, canopy) baited with chemical attractants (carbon dioxide, octenol) and moving shapes (notably, black ball suspended beneath ‘Manitoba’ traps). Ecological studies have identified various parasites (fungi, nematodes, tachinid flies) and predators (wasps, hornets, dragonflies, birds) of tabanid developmental stages, but few attempts at biological control have been made.


Tabanus
adult female
(dorsal)
(~ 30 mm)
skin
(annoyance, lesions,
allergy, stress)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, birds,
reptiles)
adults free-flying, females of many species are
transient ectoparasites (require bloodmeal for reproduction)
wing venation
resting posture
eggs laid
in moist
shaded
areas
near
water
eclosion
pupa
(~ 25 mm)
eggs
(~ 2 mm)
complete
(holometabolous)
metamorphosis
free-living feeding
larva (~ 20 mm)
hatch
development in semi-aquatic to aquatic habitats
(wetlands, bogs, ponds), rarely terrestrial (litter, mud)



Tabanus adult



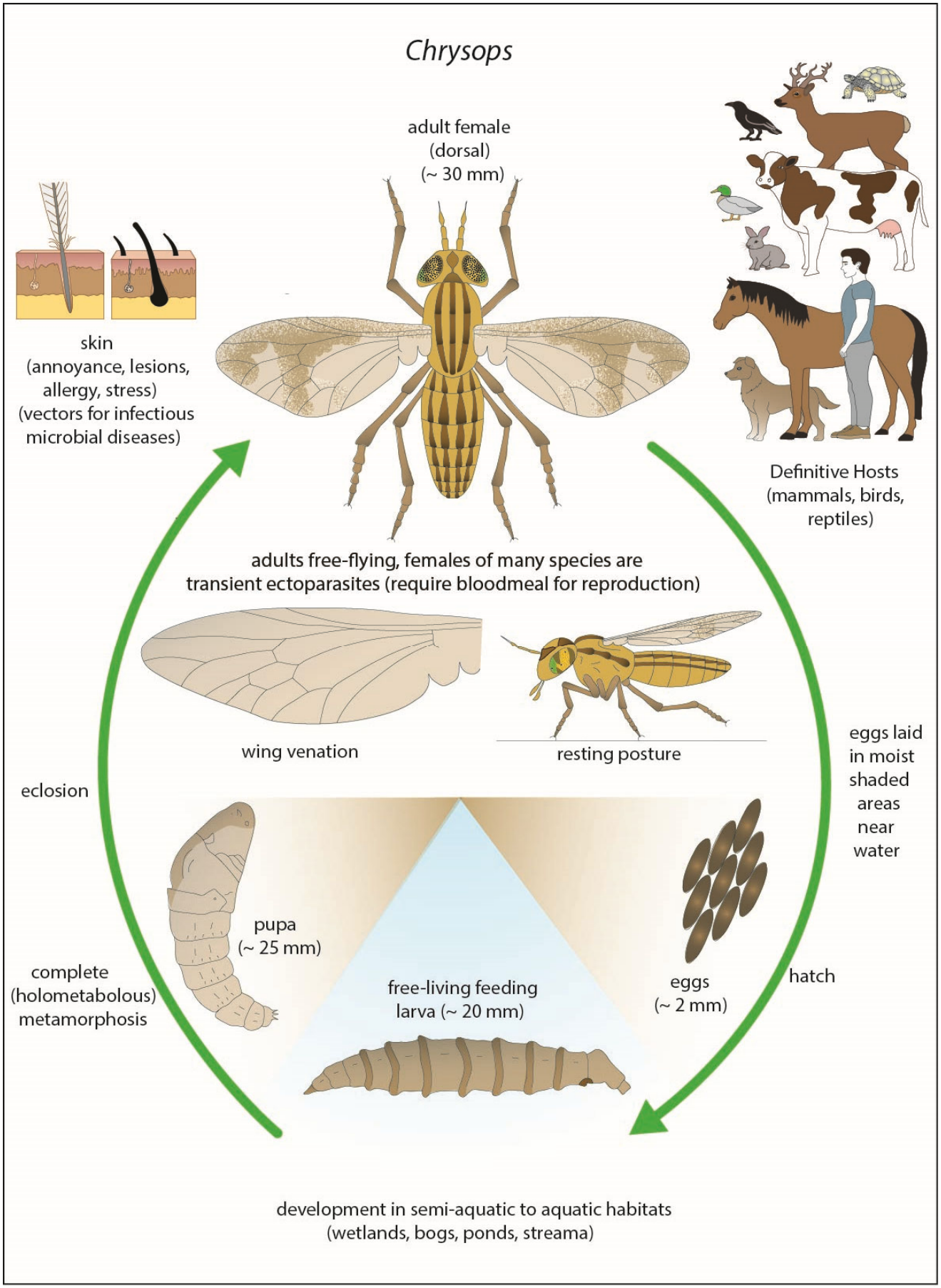
Tabanus eggs



Tabanus larva

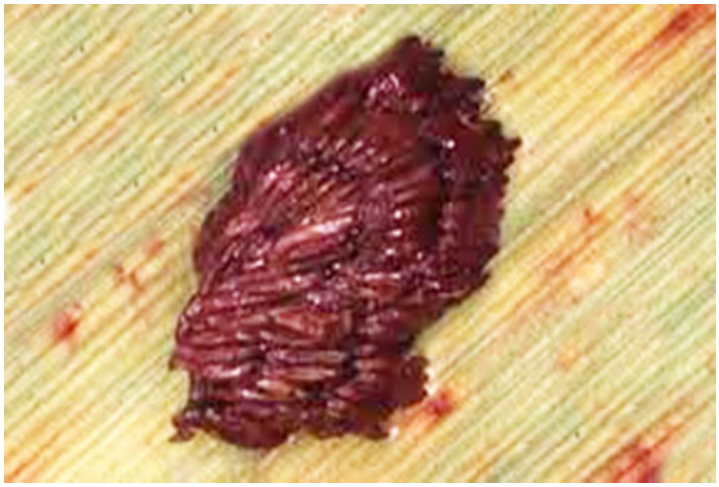


Tabanus pupa


Chrysops
adult female
(dorsal)
(~ 30 mm)
skin
(annoyance, lesions,
allergy, stress)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, birds,
reptiles)
adults free-flying, females of many species are
transient ectoparasites (require bloodmeal for reproduction)
wing venation
resting posture
eggs laid
in moist
shaded
areas
near
water
eclosion
pupa
(~ 25 mm)
complete
(holometabolous)
metamorphosis
free-living feeding
larva (~ 20 mm)
eggs
(~ 2 mm)
hatch
development in semi-aquatic to aquatic habitats
(wetlands, bogs, ponds, streama)



Chrysops adult



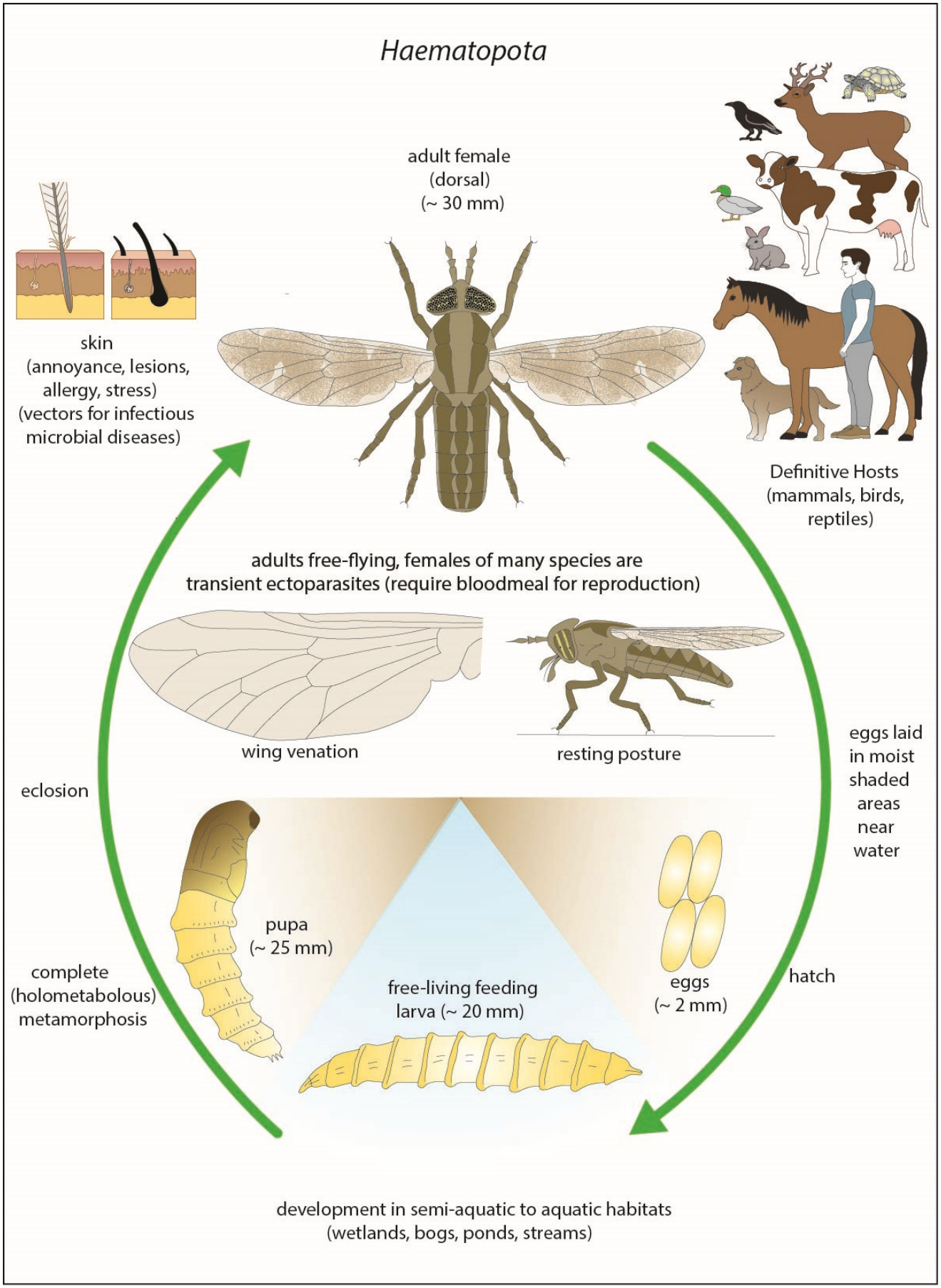
Chrysops eggs



Chrysops larva



Chrysops pupa


Haematopota
adult female
(dorsal)
(~ 30 mm)
skin
(annoyance, lesions,
allergy, stress)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, birds,
reptiles)
adults free-flying, females of many species are
transient ectoparasites (require bloodmeal for reproduction)
wing venation
resting posture
eggs laid
in moist
shaded
areas
near
water
eclosion
pupa
(~ 25 mm)
eggs
(~ 2 mm)
hatch
complete
(holometabolous)
metamorphosis
free-living feeding
larva (~ 20 mm)
development in semi-aquatic to aquatic habitats
(wetlands, bogs, ponds, streams)

	
Haematopota adult	*Haematopota* adult

Glossina
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Glossinids (tsetse flies) have biting mouthparts and the base of the proboscis is bulbous. Both sexes are daytime blood-feeders on a variety of animals. Females are larviparous and pupiparous, depositing developed larvae in loose dry soil to undergo pupation. The sole genus *Glossina* only occurs in sub-Saharan Africa, and most species have been shown to transmit trypanosomes to animals (nagana) and humans (sleeping sickness).

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha **(**Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Superfamily:	Hippoboscoidea (pupa-bearers)
Family:	Glossinidae (tsetse flies, biting mouthparts, characteristic proboscis bulb, both sexes blood-feeders)
Genus:	*Glossina* (parasitic on skin of mammals)
Species:	various species cause irritation, pruritus, hypersensitivity

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora (containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the

halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases). The superfamily Hippoboscoidea contains 4 families: Glossinidae (tsetse flies); Hippoboscidae (louse flies); Nycteribiidae (bat flies); and Streblidae (bat flies).

The family Glossinidae comprises the tsetse flies which are not dorso-ventrally flattened and have prominent biting mouthparts with a long bulbous proboscis embraced by long palps, antennal arista with short feathery hairs on the dorsal side only, and wings with uncrowded veins and a hatchet-shaped discal medial cell. Adult flies of both sexes feed on blood from a range of wild and domestic mammals (including humans), birds, and reptiles throughout sub-Saharan Africa. The single genus *Glossina* contains 23 species that have been allocated to 3 species-groups (now considered subgenera): the '*mortisans* group' (subgenus *G.* (*Glossina*)) occurring throughout East Africa and feeding mainly on savannah-dwelling mammals; the '*fusca* group' (subgenus *G.* (*Austenia*)) occurring throughout West and Central Africa feeding mainly on forest-dwelling animals; and the '*palpalis* group' (subgenus *G.* (*Nemorhina*)) being widespread throughout Africa in riverine and lacustrine environments and feeding mainly on local reptiles and mammals. A range of species are notorious for the transmission of haemoprotozoal trypanosomes causing serious diseases in domestic animals (nagana in cattle) and humans (sleeping sickness).

***Glossina* species**	**Hosts***	**Clinical signs [vectorial capacity]**	**Distribution**
Subgenus*: G.* (*Austenina*) ['*fusca* group'] (forest habitats)			
G. brevipalpis	Primates: hominid (human); Artiodactyla: bovid (cattle, buffalo, sheep, goat, eland, roan antelope, waterbuck, bushbuck, duiker), giraffid (giraffe), hippopotamid (hippopotamus), suid (warthog, bushpig); Proboscidea: elephantid (elephant); Perissodactyla: rhinocerotid (rhinoceros); Carnivora: hyaenid (hyena); Rodentia: hystricid (porcupine); Sauria: varanid (monitor); Aves (unspecified birds)	irritation [trypanosomiasis]	Central, East and South Africa
G. frezili	Artiodactyla: bovid (cattle)	irritation	Central Africa
G. fusca (incl. subspp. *congolensis, fusca*)	Artiodactyla: bovid (cattle, buffalo, waterbuck, bushbuck, duiker), suid (bushpig, red river hog); Proboscidea: elephantid (elephant); Tubulidentata: orycteropodid (aardvark); Rodentia: hystricid (porcupine)	irritation [trypanosomiasis]	West, Central and East Africa
G. fuscipleuris	Primates: hominid (human), cercopithecid (baboon), Artiodactyla: bovid (cattle, buffalo, bushbuck), hippopotamid (hippopotamus), suid (warthog, bushpig, giant forest hog)	irritation [trypanosomiasis]	Central and East Africa
G. haningtoni	Artiodactyla: bovid (cattle)	irritation	West and Central Africa
G. longipennis	Primates: hominid (human); Artiodactyla: bovid (buffalo), giraffid (giraffe), suid (warthog); Perissodactyla: rhinocerotid (rhinoceros); Proboscidea: elephantid (elephant); Tubulidentata: orycteropodid (aardvark); Carnivora: canid (dog), felid (cat), hyaenid (hyena); Struthioniformes: struthionid (ostrich)	irritation [trypanosomiasis]	East Africa
G. medicorum	Artiodactyla: bovid (cattle, bushbuck)	irritation	West, Central and East Africa
G. nashi	Artiodactyla: bovid (cattle)	irritation	Central and South Africa
G. nigrofusca (incl. subspp. *nigrofusca, hopkinsi*)	Primates: hominid (human); Artiodactyla: bovid (cattle, bushbuck), suid (pig); Rodentia: hystricid (porcupine)	irritation [trypanosomiasis]	West, Central and East Africa
G. schwetzi	Artiodactyla: bovid (cattle)	irritation	Central and South Africa
G. severini	Artiodactyla: bovid (cattle)	irritation	Central Africa
G. tabaniformis	Primates: hominid (human); Artiodactyla: bovid (cattle,	irritation	West, Central and

	buffalo, sheep, goat, bushbuck, duiker), suid (pig, warthog, bushpig, red river hog); Perissodactyla: equid (donkey); Rodentia: hystricid (porcupine); Sauria: varanid (monitor)	[trypanosomiasis]	South Africa
G. vanhoofi	Artiodactyla: bovid (cattle)	irritation	Central Africa
Subgenus*: G.* (*Glossina*) ['*morsitans* group'] (savannah habitats)			
G. austeni	Primates: hominid (human); Artiodactyla: suid (warthog, bushpig), bovid (cattle, buffalo, sheep, goat, eland, kudu, bushbuck, duiker, suni), hippopotamid (hippopotamus); Proboscidea: elephantid (elephant); Rodentia: hystricid (porcupine)	irritation [trypanosomiasis]	East and South Africa
G. longipalpis	Primates: hominid (human, chimpanzee); Artiodactyla: suid (warthog, bushpig), bovid (cattle, buffalo, bushbuck, duiker); Proboscidea: elephantid (elephant); Tubulidentata: orycteropodid (aardvark); Rodentia: hystricid (porcupine); Aves (unspecified birds)	irritation [trypanosomiasis]	West and Central Africa
G. morsitans (incl. subspp. *centralis, morsitans, submorsitans*)	Primates: hominid (human, chimpanzee), cercopithecid (baboon); Artiodactyla: suid (pig, warthog, bushpig), bovid (cattle, buffalo, sheep, goat, eland, roan antelope, sable antelope, kudu, waterbuck, hartebeest, impala, bushbuck, reedbuck, gazelle, duiker, oribi, puku), giraffid (giraffe), hippopotamid (hippopotamus); Perissodactyla: equid (donkey, zebra), rhinocerotid (rhinoceros); Proboscidea: elephantid (elephant); Carnivora: canid (dog), felid (cat), hyaenid (hyena); Tubulidentata: orycteropodid (aardvark); Rodentia: hystricid (porcupine); Aves (unspecified birds); Reptilia (unspecified reptiles)	irritation [trypanosomiasis]	West, Central, East and South Africa
G. pallidipes	Primates: hominid (human, chimpanzee); Artiodactyla: suid (warthog, bushpig), bovid (cattle, buffalo, sheep, goat, eland, roan antelope, oryx, kudu, waterbuck, wildebeest, hartebeest, impala, bushbuck, reedbuck, gazelle, duiker), giraffid (giraffe), hippopotamid (hippopotamus); Perissodactyla: equid (donkey), rhinocerotid (rhinoceros); Proboscidea: elephantid (elephant); Carnivora: felid (cat), hyaenid (hyena); Rodentia: hystricid (porcupine); Sauria: varanid (monitor); Aves (unspecified birds); Reptilia (unspecified reptiles)	irritation [trypanosomiasis]	West, Central, East and South Africa
G. swynnertoni	Primates: hominid (human, chimpanzee), cercopithecid (baboon); Artiodactyla: suid (warthog, bushpig), bovid (cattle, buffalo, sheep, goat, eland, roan antelope, kudu, waterbuck, hartebeest, topi, impala, bushbuck, reedbuck, gazelle, duiker, steenbok), giraffid (giraffe), hippopotamid (hippopotamus); Perissodactyla: rhinocerotid (rhinoceros); Proboscidea: elephantid (elephant); Carnivora: canid (dog), felid (cat), hyaenid (hyena); Tubulidentata: orycteropodid (aardvark); Aves (unspecified birds); Reptilia (unspecified reptiles)	irritation [trypanosomiasis]	East Africa
Subgenus*: G.* (*Nemorhina*) ['*palpalis* group'] (riverine habitats)			
G. caliginea	Primates: hominid (human)	irritation [trypanosomiasis]	West and Central Africa
G. fuscipes (incl. subspp. *fuscipes, martinii, quanzensis*)	Primates: hominid (human, chimpanzee), cercopithecid (baboon); Artiodactyla: suid (pig, warthog, bushpig), bovid (cattle, buffalo, sheep, goat, waterbuck, bushbuck), hippopotamid (hippopotamus); Carnivora: canid (dog); Suliformes: phalacrocoracid (cormorant); Sauria: varanid (monitor); Serpentes (unspecified snake); Testudines (unspecified tortoise)	irritation [trypanosomiasis]	West, Central, East and South Africa
G. pallicera (incl. subspp. *pallicera, newsteadi*)	Primates: hominid (human); Artiodactyla: suid (pig), bovid (sheep, goat, bushbuck); Rodentia: hystricid (porcupine); Anura (unspecified amphibians)	irritation [trypanosomiasis]	West and Central Africa
G. palpalis (incl. subspp. *gambiensis, palpalis*)	Primates: hominid (human, chimpanzee), cercopithecid (baboon); Artiodactyla: suid (pig, warthog, bushpig), bovid (cattle, buffalo, sheep, goat, roan antelope, wildebeest, hartebeest, bushbuck, duiker, oribi), hippopotamid	irritation [trypanosomiasis]	West, Central and South Africa

	(hippopotamus); Perissodactyla: equid (donkey); Proboscidea: elephantid (elephant); Carnivora: canid (dog), felid (cat); Suliformes: phalacrocoracid (cormorant); Sauria: varanid (monitor); Crocodilia: crocodylid (crocodile)		
G. tachinoides	Primates: hominid (human, chimpanzee), cercopithecid (baboon); Artiodactyla: suid (pig, warthog), bovid (cattle, buffalo, sheep, goat, roan antelope, waterbuck, bushbuck, duiker), hippopotamid (hippopotamus); Carnivora: canid (dog), felid (cat); Rodentia: hystricid (porcupine); Suliformes: phalacrocoracid (cormorant); Sauria: varanid (monitor); Crocodilia: crocodylid (crocodile); Serpentes (unspecified snake); Aves (unspecified birds)	irritation [trypanosomiasis]	West, Central and East Africa

*Host records include observations of tsetse flies feeding on natural, experimental and bait hosts, as well as host groups identified by molecular analyses of tsetse bloodmeals.

Parasite morphology: Tsetse flies form 4 different types of developmental stages (eggs, larvae, pupae and adults) but the eggs and larvae develop within the uterus of adult female flies. Eggs develop one at a time in the uterus and are ovoid in shape and around 1.6 mm long. A first stage larva (L1) emerges using an anterior labral tooth to break the egg chorion. The larva is supported against the ridged uterine wall by a membranous choriothete and secretions from the milk glands pool around the larval mouth to be ingested. Larvae are ellipsoidal cream-yellow segmented stages with a pair of respiratory lobes developing at the posterior end and gradually darkening to black. Larvae develop through 3 instars (L1-3), initially measuring around 1.8 mm but growing up to 7-8 mm in length. Mature L3 deposited on soil by gravid females burrow into the substrate and form a puparium by hardening of the tegument before moulting to form a pupa. These stages measure 5-7 mm long and are ovoid with distinctive posterior lobes. Following metamorphosis, winged adult flies emerge from pupae. Adult tsetse flies have narrow bodies that are not dorso-ventrally flattened and vary in colour from yellow-brown to brown-black. Adults range in size from 5-15 mm in length, depending on species, although those belonging to different groups often overlap: e.g. 8-11 mm long for *palpalis* group (generally recognized by dark brown hindtarsi), 7-10 mm for *morsitans* group (with striped dorsal abdomen); 9-12 mm for *fusca* group (with dark wings and long narrow palpi); the latter often including a *brevipalpis* subgroup measuring 10-14 mm (with pale wings and short palpi). The body of the adult fly has 3 conspicuous tagma: a small head, ovoid thorax, and conical abdomen. Both sexes have broad triangular heads with frontal ptilinal sutures (like all muscoids), 2 large brown-red compound eyes well separated laterally, short feathery antennae and prominent forward-projecting mouthparts. Each antenna is composed of 3 dissimilar segments: a short basal scape; a square middle pedicel; and a longer rectangular and curved apical flagellum characteristically with a large dorsal bristle (arista) with 17-29 short dorsal feathery (branched) setae (hairs). The mouthparts are evident as a long rigid proboscis embraced by pair of long palps. The proboscis has a unique swollen bulbous base and is composed of 2 elongate stylets (labrum and hypopharynx) protected ventrally by a rigid labium which has apical labella armed with teeth. When feeding, the labrum and hypopharynx form a food canal and the hypopharynx also contains a hollowed groove to deliver saliva into the bite site. Blood is sucked up by the strong muscular pharynx into the tubular oesophagus leading to a globular proventriculus with associated crop. The proventriculus secretes a peritrophic membrane that lines and protects the digestive midgut which contains endosymbiotic enterobacteria which are essential for vitamin B metabolism (flies without bacterial symbiotes cannot complete reproduction). Digestive waste is passed to the hindgut (connected to Malpighian excretory tubules), rectum and terminal anus. The large thorax is covered by a dorsal scutum that is usually dull light brown-grey with dark mottled patterns. The thorax has distinctive patterns of setation: all species having a hypopleuron without rows of stout setae, whereas the pteropleuron bears a few strong bristles in the *fusca* group, but only contains setulose hairs in the *palpalis* and *morsitans* groups. Additionally, the hairs fringing the thoracic squamae in the *fusca* group are numerous and curly (imparting a woolly appearance), while those in the *palpalis* and *morsitans* groups are not curly but have a neat fringe-like appearance. The mesothorax bears a pair of membranous wings that are hyaline to dusky depending on the species. Wing membranes supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] characteristically with the M vein curving anteriorly to form a distinctive hatchet-shaped discal cell. At rest, the wings are folded flat and scissor like over the abdomen. Like all Diptera, tsetse flies have a second pair of wings that are highly reduced to knob-like halteres used to stabilize flight. Tsetse flies are also identified as calyptrate flies in that they have posterobasal wing lobes (calypters) that cover the halteres. The ventral thorax gives rise to 3 pairs of legs, each with 5 segments (coxa, trochanter, femur, tibia, and tarsus), with the latter having 5 tarsomeres terminating in 2 claws and 2 small pads (pulvilli). The legs vary considerably in colouration, but all segments of the hind-tarsi are dark brown-black in the *palpis* group, whereas only the distal segments are dark in the *morsitans* group. The abdomen is globular, often wider than long, and the membranous segments are highly expandable being able to accommodate large bloodmeals. The abdomen is often dull light brown-grey and usually marked by conspicuous dark stripes or patches imparting a mottled appearance. The terminal abdominal segments bear external genitalia that differentiates males (with a prominent dorsal button-like hypopygium) and females (without hypopygium, but with larvipositor). Males have 2 testes connected by vas deferens to a seminal vesicle leading to a tubular ejaculatory duct. The hypopygium contains an extendable phallosome and 2 pairs of copulatory claspers (superior claspers long in *fusca* group, medium in *palpis* group, and short in *morsitans* group). Females have 2 ovaries (but each with only 2 ovarioles) that are joined to oviducts forming a common duct that expands to form a uterus that accommodates one embryo at a time. The uterus, with associated spermatheca (for sperm storage) and branched accessory (milk) glands, leads to the vulva and the tip of the abdomen is elongated to form a larvipositor.

Site of infection: Adult tsetse flies are ectoparasitic and both female and male flies feed on host blood, usually biting areas where the skin is soft (neck, ears, face, feet, ankles, legs, wrists, arms). Different tsetse species have preferred hosts (particularly suids and bovids), but may feed on other hosts in the vicinity (such as elephants, hippopotamuses, porcupines, aardvarks, primates (including humans), some reptiles and birds), yet steadfastly avoiding others (e.g. zebras and wildebeest). Biological and ecological differences have been used to assign all *Glossina* spp. to 3 species-groups (now considered subgenera): the '*mortisans* group' (subgenus *G.* (*Glossina*)) feeding mainly on savannah-dwelling mammals (especially artiodactyls such as buffalo, bushbuck, kudu, duiker, springbok, giraffe, warthogs, bushpigs, rhinoceros); the '*fusca* group' (subgenus *G.* (*Austenia*)) feeding mainly on forest-dwelling animals (bushbuck, buffalo, cattle, giraffe, rhinoceros, elephant, hippopotamus, bushpig, river hog, porcupine, aardvark and even ostrich); and the '*palpalis* group' (subgenus *G.* (*Nemorhina*)) feeding mainly on reptiles (crocodiles, water monitors) and mammals (bushbuck, oxen, smaller mammals, humans) visiting watering sources.

Pathogenesis: Feeding tsetse flies first probe host skin with their stout proboscis, and then use labellar teeth on the end of the labium to penetrate the skin and lacerate dermal tissues with strong back-and-forth movements of the head. Ruptured capillaries haemorrhage into the wound and flies suck up pooled blood through a food canal formed by the labrum and hypopharynx. Feeding is aided by the injection of saliva containing anticoagulants via a hypopharyngeal groove. Both sexes feed every 4-5 days and they engorge in 1-10 minutes unless disturbed and imbibe up to 0.03 ml of blood (which doubles or triples their unfed body weight). Heavy infestations may cause blood loss severe enough to manifest as anaemia, but most attacks are not so severe. Tsetse bites are painful due to the traumatic structural damage and ensuing inflammation with bite sites becoming red, swollen and itchy. This causes significant discomfort to the host which may resort to licking, scratching or rubbing behaviours to seek relief, sometimes resulting in self-trauma exacerbating wounds and making them susceptible to secondary bacterial infections. Inflammatory lesions slowly dissipate over days but can remain tender for several weeks. Livestock subject to intermittent and constant attack may exhibit considerable fly-worry and biting-stress leading to reduced feeding efficiency, decreased performance and loss of productivity in terms of meat and milk production. Individual hosts may also develop allergic reactions to fly saliva components, with both immediate and delayed hypersensitivity reactions, and sometimes anaphylaxis, occurring after repeated bites. In Africa, tsetse flies are notorious as biological vectors for haemoprotozoan parasites, notably *Trypanosoma* spp. that cause nagana in cattle and sleeping-sickness in humans. Tsetse flies have been instrumental in limiting the establishment and development of livestock industries on the African continent, as most introduced ungulates are highly susceptible to trypanosomiasis while native wildlife are largely trypanotolerant and act as reservoirs of infection for domestic animals.

Trypanosomiasis	**Hosts**	**Main *Glossina* vectors**
Trypanosoma brucei gambesiense (West African sleeping sickness)	humans	*G. fuscipes, palpalis, tachinoides*
Trypanosoma brucei rhodesiense (East African sleeping sickness)	humans, cattle, antelopes	*G. morsitans, pallidipes, swynnertoni*
Trypanosoma brucei (nagana)	domestic animals, antelopes, warthog, lion, hyena	*G. fuscipes, longipalpis, morsitans, palpalis, pallidipes, tachinoides*
Trypanosoma vivax (nagana, souma)	domestic animals, antelopes, giraffe, warthog, zebra, lion	*G. morsitans* group*, fuscipes, palpalis, tachinoides, vanhoofi*
Trypanosoma suis	pigs, warthog	*G. brevipalpis, vanhoofi*
Trypanosoma congolense	domestic animals, antelopes, giraffe, bushpig, elephant, zebra, lion, hyena	*G. morsitans* group*, brevipalpis, fuscipes, palpalis, tachinoides, vanhoofi*
Trypanosoma simiae	pig, warthog, camel, cattle, horse	*G. austeni, brevipalpis, fusca, fuscipleuris, longipalpis, morsitans, pallidipes, palpalis, tabaniformis, tachinoides, vanhoofi*
Trypanosoma uniforme	domestic animals, antelopes, giraffe	*G. fuscipes, palpalis*

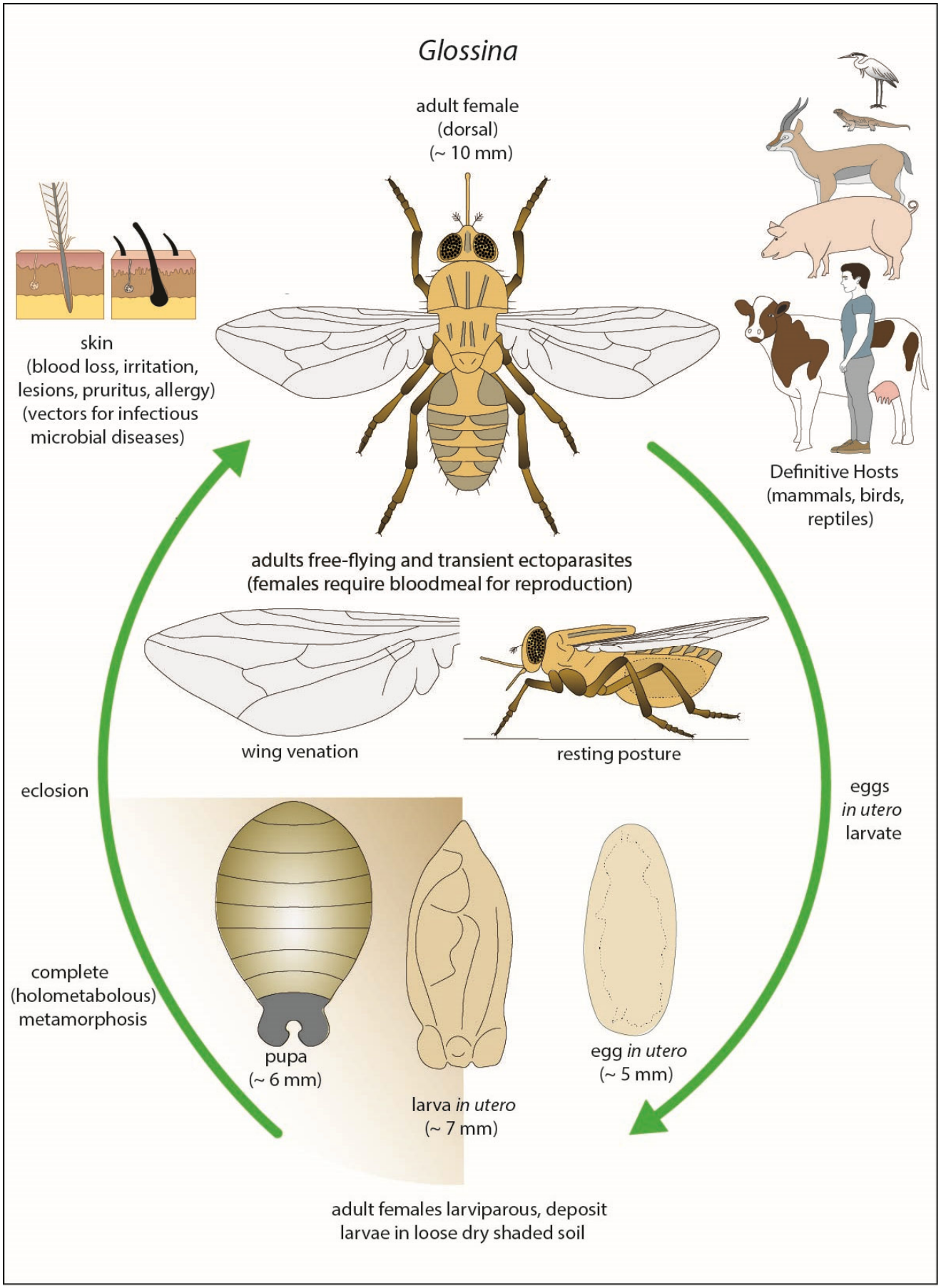
Developmental cycle and mode of transmission: Tsetse flies undergo holometabolous (complete) metamorphosis, whereby grub-like larvae transform in pupae into winged adults. Their cycle, however, differs from many flies in that females retain single eggs in the uterus where they hatch and moult through 3 larval stages (L1-3) before being laid. Larvae are sequestered in pouches against the uterine wall and nourished by milk gland secretions. This reproductive behaviour is described as adenotrophic viviparity (= "gland-fed, live-birth") with female flies being larviparous and birthing mature L3 (although a few texts state that females are pupiparous as they only release larva they are ready to pupate). During a gonotrophic cycle, eggs are released one at a time from the ovary (from alternate ovaries in subsequent cycles) and fertilized in the oviduct with sperm stored from previous matings. The egg is retained in the common oviduct which is expanded posteriorly to form the uterus. Embryogenesis occurs over 1-4 days and the resultant L1 then hatches using an egg tooth to rupture the egg wall. The larva is retained in the uterus in a membranous pouch where it respires through unique posterior polypneustic lobes and fed on secretions from specialized maternal accessory (milk)

glands. The larvae grow and moult to L2 in 1-2 days and then to L3 in 2-5 days. Mature L3 grow so large that they occupy and grossly distend the abdomen. Some 7-12 days after fertilization, female flies deposit (larviposit) the solitary mature L3 on loose sandy soil shaded by trees or other vegetation. Larvae are negatively phototactic and positively thigmotactic and immediately burrow 15-25 mm below the soil surface to form an immobile puparium by hardening of the integument. Several hours to days later, moulting occurs within the puparial case to form a true pupa. Pupation generally takes 30 days but may be extended for another 3-7 weeks in adverse environmental conditions. Adult flies eclose from pupae through a circular puparial cap using an eversible inflatable head pouch (ptilium). Teneral adults push their way to the surface of the ground to rest before taking flight. Both male and female flies feed exclusively on vertebrate blood, and it generally takes several days and a few bloodmeals before the fly cuticle hardens and the thoracic flight muscles fully develop. Obtaining nutrition from bloodmeals is assisted by enterobacterial symbionts in the midgut (*Wigglesworthia* in bacteriocytes), the symbiosis being mutualistic (obligatory for fly nutrition and fecundity). [Note that other bacterial endosymbionts also occur (*Sodalis* in various tissues, and *Wolbachia* mainly in reproductive tissues) but are not essential for fly survival]. Female flies are sexually receptive soon after emergence, but males require several bloodmeals before they become fertile. During mating, sperm is transferred in a spermatophore and stored in female spermathecae (females are fertile for life after a single mating, but they often mate more than once). Males mate once or twice and only live for 2-3 weeks. Females are anautogenous and require bloodmeals in order to complete their gonotrophic (ovarian) cycles. While females usually live for 20-40 days, sometimes up to 3-4 months, they generally only produce 2-3 offspring during their life-times. Adult tsetse flies search for hosts for only a few hours during the day flying up to 1 km, and spend the remaining time sheltering in shaded places such as trees or bushes. They are attracted to their hosts mainly by chemical (esp. expired carbon dioxide) then visual (shapes, contrasting colours, movement) cues, and are able to follow odour plumes upwind for 100-200 m before zeroing in on hosts. Flies vary in their seasonal abundance, often coinciding with the availability of hosts, but may not be present throughout the whole year. Their geographic distribution in so-called fly belts differs according to species; with those in the *fusca* group inhabiting forest ecosystems along coastal West Africa and Central Africa; those of the *mortisans* group distributed throughout inland savannah regions adjacent to coastal forests (often in close association with herds of herbivores migrating over African plains), and those of the *palpalis* group found along rivers, lakes and streams throughout East, Central and West Africa.

Differential diagnosis: Clinical signs exhibited by humans and animals bitten by tsetse flies are nonspecific (painful pruritic lesions) and may be attributable to other ectoparasites (including stable flies, horse flies, and clegs). Diagnosis is generally made by direct observation of feeding tsetse flies, and confirmed by capturing specimens for microscopic examination and identification. At rest, tsetse flies fold their wings flat one over the other over the abdomen, while other flies hold their wings in different attitudes. Under magnifying lenses, the wings of tsetse flies possess a distinctive hatchet-shaped discal cell not found in any other flies. Tsetse flies also have a prominent forward-projecting proboscis and feathery drooping antennae. The differentiation of tsetse species is based on a range of small morphological differences, particularly involving patterns of setation and colouration of various body parts. Various biochemical and genetic techniques have been used to characterize tsetse fly species, including matrix-assisted laser desorption/ionisation (MALDI) spectroscopy and isoenzyme electrophoresis. More recently, molecular biological techniques have been applied not only to the identification of tsetse bloodmeals but also to the characterization and phylogeny of tsetse fly species, particularly those acting as vectors for trypanosomes, or those hosting enterobacterial symbionts. Polymerase chain reaction (PCR) protocols have been used to amplify nuclear and mitochondrial gene sequences, with genomic databases being established from hybridization and fingerprinting studies.

Treatment and control: Fly bites may be treated using topical or systemic anti-inflammatory and anti-pruritic preparations to alleviate symptoms, antihistamines to moderate allergic reactions, and even antiseptics and antibiotics to prevent or curtail secondary infections. Most treatment and control programmes target adult tsetse flies as they are the only parasitic stages (even carrying eggs and larvae to term), whereas free-living pupae are encysted in soil. Insecticides have basically been used in 4 different ways: as topical or systemic preparations to treat livestock at risk; as aerial preparations to kill flying adults in the environment; as residual sprays to treat fly resting sites on vegetation; and as killing agents in traps and baits. Studies have reported variable successes with most insecticide groups: including inorganic metal-based formulations (sulphur, arsenate and copper compounds), organochlorines (dichlorodiphenyltrichloroethane (DDT), lindane, dieldrin, endosulfan), organophosphates (fenitrothion, iodofenphos, tetrachlovinphos, naled, crotoxyphos, chlorfenvinphos, fenthion, pirimetaphos, azamethiphos), carbamates (carbaryl, methylcarbamate, bendiocarb, propoxur), pyrethroids (deltamethrin, resmethrin, bioresmethrin, cismethrin, permethrin, cypermethrin, dimethylcyclopropanecarboxylates) and macrocyclic lactones (spinosad); with endosulfan, dieldrin and deltamethrin proving particularly effective. No appreciable insecticide resistance has been reported in tsetse fly populations, but treatment programmes have changed over decades due to environmental concerns about some compounds (particularly DDT which has now largely been discontinued). Many insecticides used to treat livestock do not have long-lasting activity, so they need to be reapplied at regular intervals, although some pyrethroids have good residual activity and need only be used once (effectively transforming animals into live baits). It is to be remembered that these insecticides are not deterrents or repellents and do not prevent fly bites, but flies coming into contact with therapeutic doses on the skin or in the blood have reduced vigour and survival, thus depleting local populations. Unfortunately, attempts to treat wild animals, acting as reservoir hosts for both tsetse flies and trypanosomes, have largely proven ineffective due to the sheer numbers involved, their wide dispersed distributions and their relative inaccessibility. Various aerial-based programmes have been developed to disperse insecticides into the environment as aerosols in space sprays, using thermal exhaust or rotary atomiser equipment in helicopters or fixed-wing aircraft. Spraying may only be carried out in suitable meterological conditions (avoiding wind and rain) and is generally ineffective in forested terrains. Other problems have

been encountered with spray composition (many need to be emulsified in oil), incorrect droplet sizes (dissipate when too small, fall to ground or only on top of vegetation when too big), variable residual activity (many need to be regularly reapplied) and environmental concerns (untoward impacts on local ecosystems, particularly involving water, thus caution is required when targeting riverine tsetse species). Many African countries have adopted ground-based spraying programmes where insecticides with good residual activity are applied to sites where flies rest (teneral adults rest on shady soil, mature adults rest underneath leaves, twigs and branches of trees, bushes and other vegetation). Hand-spraying may be done on foot using knap-sacks or from vehicles using mechanized broadcasters. Comparative studies demonstrated that the selective application of sprays to soil and vegetation in hot-spots around villages, pens and water sources often had greater effect that indiscriminate spraying. Various ingenious traps and baits have been developed that use chemical and visual attractants (carbon dioxide, shapes and colours imitating ungulates) to lure tsetse flies onto surfaces treated with residual insecticides. Good success has been reported in small areas using blue-black cloth soaked in pyrethroids and mounted on box frames, but they generally require costly maintenance particularly during rainy/stormy seasons. Other efforts to control fly populations near villages and farms involved habitat destruction (by clearing land) and excluding reservoir hosts (by fencing or culling), but despite initial benefits these strategies have been discontinued due to increasing concerns regarding the conservation of wildlife and ecosystems. Promising results have been achieved by releasing cultured male flies that have been sterilized by irradiation or chemical means, but they were sometimes not competitive enough for mates to markedly reduce fly populations. Humans may enhance their personal protection by wearing thicker clothing (neutral-coloured long-sleeved shirts and pants), applying insect repellents to bare skin and clothing (although most have proven poorly effective against tsetse), installing fly screens and bed nets in households, and changing work patterns to avoid flies during the hottest part of the day when they seek shelter in forests, bushlands and riverine vegetation (exposure to flies is directly linked to certain activities like forestry and fishing). Future studies may also explore methods for the biological control of tsetse flies using natural predators or pests, which include wasps, ants, bombyliids and beetles that kill pupae, as well as spiders, dragonflies, assassin flies and wasps that prey on adult flies. Many countries across Africa utilize multiple integrated approaches to control tsetse flies to curb the ravages of human and animal trypanosomiases, with education programmes helping to raise public awareness and participation.


Glossina
adult female
(dorsal)
(~ 10 mm)
skin
(blood loss, irritation,
lesions, pruritus, allergy)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, birds,
reptiles)
adults free-flying and transient ectoparasites
(females require bloodmeal for reproduction)
wing venation
resting posture
eclosion
eggs
in utero
larvate
complete
(holometabolous)
metamorphosis
pupa
(~ 6 mm)
larva in utero
(~ 7 mm)
egg in utero
(~ 5 mm)
adult females larviparous, deposit
larvae in loose dry shaded soil



Glossina adults



Glossina adult



Glossina adult



Glossina adult

Melophagus
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Hippoboscids (louse flies) are unusual in being dorsoventrally flattened with a soft leathery abdomen. Both sexes have piercing mouthparts and suck blood from mammals and birds. Most are permanent ectoparasites using strong claws on their feet to cling to hairs or feathers. Females are larviparous and pupiparous, depositing developed larvae on the host to attach and undergo pupation. Infestations by *Melophagus* and *Hippobosca* spp. have been associated with unthriftiness in sheep and other mammals.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Superfamily:	Hippoboscoidea (pupa-bearers
Family:	Hippoboscidae (flat/louse flies, leathery abdomen, piercing mouthparts, strong claws on feet)
Genus:	*Melophagus* (parasitic on skin/fleece of sheep)
Species:	various species cause anaemia, reduced productivity

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders

are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora

(containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases).

The superfamily Hippoboscoidea contains 4 families: Glossinidae (tsetse flies); Hippoboscidae (louse flies); Nycteribiidae (bat flies); and Streblidae (bat flies). The family Hippoboscidae contains dorsoventrally flattened flies with piercing mouthparts, leathery abdomens and strong claws on their feet. These 'flat' flies may be wingless or have wings with veins crowded into the leading half of wing. Members are often found as ectoparasites on many species on wild birds, although some infest ungulates, including domestic livestock. Over 200 species have been described in over 20 genera classified into 1-3 subfamilies. Usually, one subfamily is recognized (Hippoboscinae) albeit with 4 tribes: Hippoboscini with 2 genera (including *Hippobosca*), Lipoptenini with 2 genera (including *Melophagus*), Olfersiini with 3 genera, and Ornithomyini with 6 genera, with another 10 unplaced genera. Alternatively, some authorities have placed parasites of birds into the separate subfamily Ornithomyinae, and melophagine parasites of artiodactyls into the subfamily Melophaginae (or Lipopteninae).

Tribe	Genera	Hosts	Site	Transmission
Hippoboscini	*Hippobosca*	equids, bovids	skin	direct
Lipotenini	*Melophagus*	bovids, cervids	skin	direct

The genus *Melophagus* (syn. *Mellophagus*, *Melophaga*) contains 8 species that mainly parasitize artiodactyls (cloven-hoofed animals), particularly in temperate zones around the world. Early workers recognized 2 'species groups' (elevated tentatively to subgenera *M.* (*Melophagus*) and *M.* (*Dorcadophagus*)) on the basis of morphological differences in adult sclerotization, setation and palpi, but it is not yet known whether they are supported by molecular characterization studies. These dipteran ectoparasites are unusual in that they are wingless and have leathery integuments (somewhat resembling ticks). They spend their entire lives on their hosts whereby viviparous females produce mature larvae which almost immediately undergo pupation. Transmission between hosts is by close body contact. Keds have been introduced to most parts of the world where domestic sheep are kept. Infestations were previously more widespread and abundant but contemporary treatment and control programs have proven particularly effective.

***Melophagus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
Species group 'a' (tentatively subgenus *M.* (*Dorcadophagus*))				
M. antilopes	Artiodactyla: bovid (goitered gazelle)	skin		Asia
M. rupicaprinus	Artiodactyla: bovid (chamois, alpine ibex)	skin		Europe
Species group 'b'(tentatively subgenus *M.* (*Melophagus*))				
M. ovinus (sheep ked) (syn. *Hippobosca bolivianus, fera, montanus, ovinus*) (incl. subspp. *ovinus, himalayae*)	Artiodactyla: bovid (cattle, European bison, yak, sheep, bighorn sheep, Dall sheep, argali, goat, alpine ibex, chamois, Mongolian gazelle), cervid (hog deer); Lagomorpha: leporid (rabbit); Carnivora: canid (dog, red fox); Primates: hominid (human)	skin (neck, shoulders, belly)	irritation, anaemia, wool loss, cockle (vector for ovine trypanosomiasis, eperythrozoonosis)	worldwide, esp. temperate zones
Ungrouped				
M. dyspnoetus	Artiodactyla: bovid (Siberian ibex)	skin		Russia
M. grunini	?	skin		Kazakhstan
M. kamtshaticus	Artiodactyla: bovid (bighorn sheep)	skin		Russia
M. kaukasikus	?	skin		Russia
M. pantholopsus	Artiodactyla: bovid (Tibetan antelope)	skin		China

Parasite morphology: *Melophagus* spp. form 4 different types of developmental stages (eggs, larvae, pupae and adults) but only the latter 2 are found on hosts as the eggs and larvae develop *in utero* within female keds. Developing eggs appear as single cream-coloured inclusions measuring around 1.1 x 0.3 mm. Developing larvae appear as ovoid stages that are nourished by maternal milk gland secretions and grow through 3 instars (L1-3) to measure up to 4 mm long. Mature L3 (sometimes called prepupa) are laid by females and immediately harden forming barrel-shaped puparia 3-4 mm long that are initially creamy-yellow with a dark posterior respiratory plate, but they darken uniformly to red-brown within hours. The enclosed stage forms a pupa which appears as an

amorphous gel-like blob while undergoing metamorphosis into an adult fly. Adult keds are readily identifiable as wingless louse flies with dorsoventrally-flattened bodies measuring 4-8 mm long. They are grey-reddish brown in colour, covered with many setae (short bristly hairs), have a soft leathery abdomen and 6 long clawed legs. The body has 3 conspicuous tagma: a short head fixed to the broad flattened thorax; and a large ovoid abdomen with inconspicuous segments. The head is short and broad with 2 small lateral brown compound eyes (more setae on inner orbit in species group 'b' than 'a'), broad interantennal frons lacking ocelli, small immovable antennae located in deep rimmed pits and bearing few setae, and a forward-projecting proboscis flanked by long palps (longer in species group 'b' than 'a'). The proboscis strongly sclerotized and its base is partly retracted into a ventral head pouch when not in use while the distal portion is concealed within the palpal sheath. The proboscis contains piercing-sucking stylet-like mouthparts well adapted for feeding from blood vessels (process known as solenophagy) using the long thin labium (with terminal dentate labella) to cut the skin and the labrum and hypopharynx coming together to form a food channel for sucking. Blood is sucked up using strong pharyngeal muscles and passes through a tubular oesophagus to a globular proventriculus with an associated saccular crop. The digestive midgut apparently does not possess a peritrophic matrix but does contain endosymbiotic enterobacteria within bacteriocytes and a small granular bacteriome. Waste is passed through the hindgut (with excretory Malpighian tubules) to the rectum and terminal anus. The thorax has a shield-like dorsal scutum but completely lacks wings (apterous), as both the forewings and halteres are absent (unique to the genus *Melophagus* as other hippoboscid taxa have forewings, albeit some transiently, and stumpy halteres). The ventral thorax is the point of attachment for 3 pairs of long stout legs, each composed of 5 segments (coxa, trochanter, robust femur, flattened tibia, and tarsus), with the tarsi terminating in a pair of large toothed and recurved claws with prominent basal heels. The abdomen is bulbous, soft and leathery without distinct segments, although some species may have 1-2 tergal plates (species group 'a') while they are absent in others (species group 'b'). The abdomen is highly setate and contains pairs of lateral respiratory spiracles. The posterior end of female keds often appears flattened with a terminal asetate plate, while hind-end of male keds is rounded. Males have 2 testes connected to a seminal vesicle leading to a tubular ejaculatory duct and terminal copulatory apparatus (with retractable phallosome and claspers). Females have 2 ovaries connected by oviducts to a common duct expanding posteriorly to form a uterus that accommodates one embryo at a time. The uterus, with associated spermatheca (for sperm storage) and branched accessory (milk) glands, leads to the vulva in the terminal genital plate.

Site of infection: Adult keds and their pupae occur in the pelage (fleece, coat) of their mammalian hosts, principally sheep and related bovid artiodactyls. They are most commonly found under the neck, shoulders and ventral belly (ribs to breech), and contrary to popular belief, they do not undertake daily or seasonal migration between sites. Keds may occasionally be found in other closely-attending mammals, notably the ears of sheep-dogs (herding or guardian dogs) and on human skin (especially shepherds).

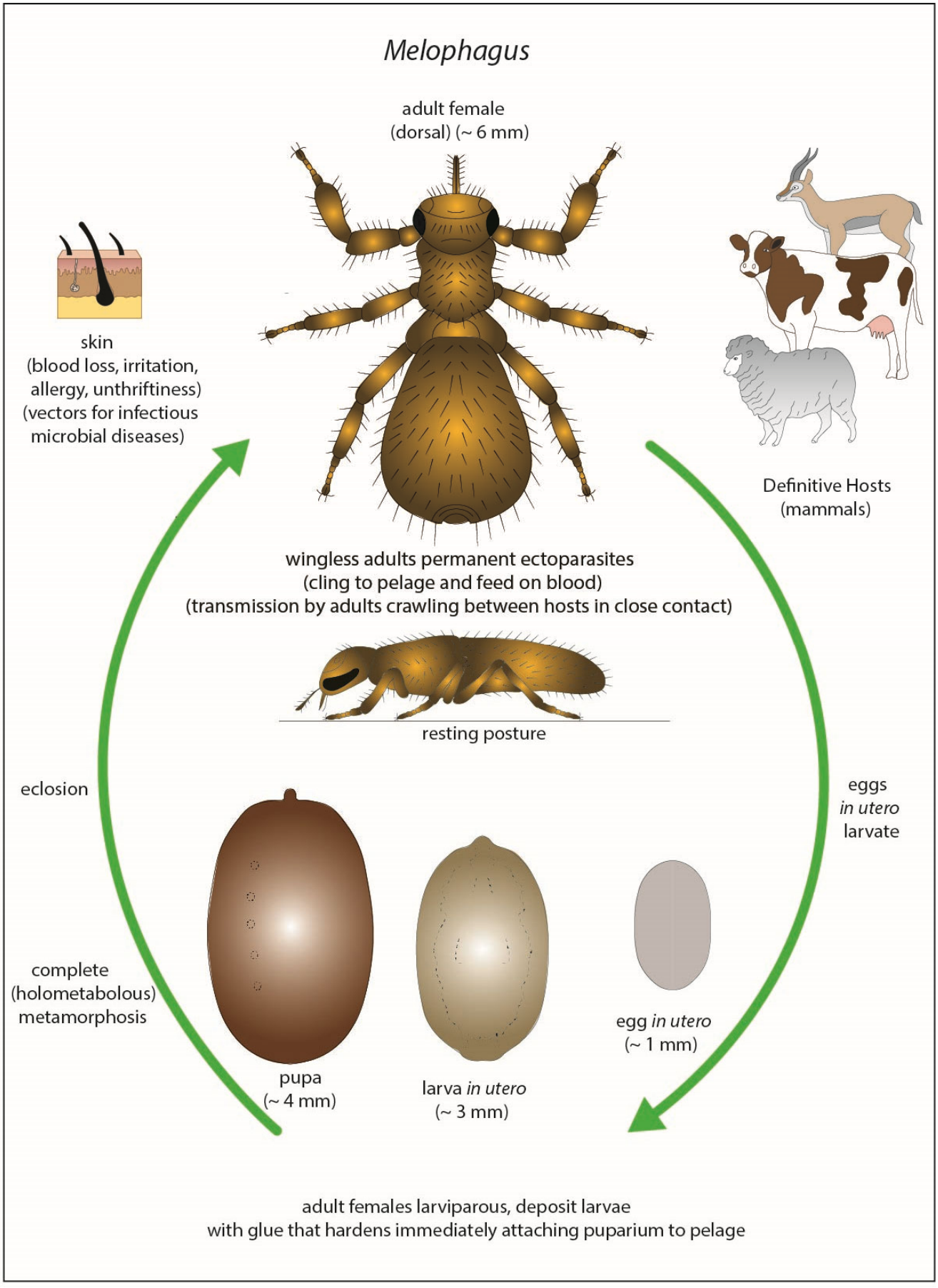
Pathogenesis: *Melophagus* spp. are sedentary wingless flies that feed on vertebrate hosts by piercing the skin with their mouthparts and sucking blood. Both male and female flies feeding every 24-36 hours, engorging over 5-10 minutes from blood vessels near bases of wool/hair follicles. Ked bites cause irritation, inflammation and pruritus, resulting in animals seeking relief by biting, scratching or rubbing afflicted areas, usually leading to self-trauma with loss and damage of wool (depilation, broken fibres). The fleece becomes thin, ragged and dirty with permanent brown dicolouration caused by ked faeces leading to down-graded value. Blemishes at bite sites may be exacerbated by allergic dermatitis reactions leading to ridged defects in sheepskins (called cockle or rib cockle) evident as scattered dense brown nodules that significantly reduces hide value for both grain and suede leather production. Host immune responses to persistent attack include cellular infiltration and vasoconstriction to reduce dermal capillary flow, but these responses may also contribute to poorer wool growth and reduced quality. Infested animals suffer biting-stress and do not feed well with resultant unthriftiness, loss of condition, weight loss and reduced wool growth, particularly in lambs and pregnant ewes. Heavy infestations may also result in blood loss severe enough to manifest as anaemia, especially in lambs. *Melophagus* spp. are traditionally not renowned for the transmission of infectious diseases, as they are generally confined to the same individual hosts for multiple generations. Biological studies have shown that they may transmit the nonpathogenic haemoprotozoan *Trypanosoma melophagium* via stercorarian transmission, and experimental studies found they may carry blue-tongue virus although there is little evidence to suggest they are natural vectors. More recently, molecular studies have detected gene sequences from various bacteria (*Acinetobacter*, *Rickettsia* (spotted fever group), *Bartonella*, *Anaplasma* and even *Borrelia burgdorferi sensu lato*), protozoa (*Theileria ovis*) and viruses (Border disease virus) in keds from around the world, but their involvement in disease transmission remains speculative.

Developmental cycle and mode of transmission: Like all dipteran flies, keds undergo complete metamorphosis whereby grub-like larvae form pupae in which they transform into adult flies. However, unlike most Diptera, larval development occurs *in utero* (rather than in aquatic or terrestrial habitats), and all stages occur on vertebrate hosts (adults are wingless and stay on hosts). Female keds do not lay eggs but produce them one at a time and retain them in the reproductive tract where they embryonate using yolk reserves. After 1-2 days, larvae emerge from the eggs and are retained in the uterus where they are nourished by secretions from special milk glands over 7-8 days. These secretions also facilitate the vertical transmission of endosymbiotic bacteria, some being ubiquitous and obligate (essential) for ked survival (*Arsenophonus*) while others appear to facultative (including *Sodalis*, *Bartonella* and *Wolbachia* spp.). The larvae develop through 3 instars (L1-3) before mature L3 which have ceased to feed (also called prepupae) are birthed. This type of reproduction is known as adenotrophic viviparity and the female flies are larviparous (not pupiparous as suggested by early works). Prepupae are deposited (larviposited) on the fleece covered with a secretion that hardens on drying and glues the puparium to wool above the skin (*Melophagus* is the only hippoboscid to glue puparia to their hosts, as those of other hippoboscids

are deposited, or drop, on bedding or the ground). The prepupa forms a true pupa within 6-12 hours or parturition, and complete pupation takes 19-23 days in summer, 20-36 days in winter, but up to 45 days in more adverse conditions. Young adult keds then emerge and both sexes begin feeding on host blood. Teneral females (whose cuticles have not yet hardened) may mate within several days of eclosion, and a single mating may provide enough sperm for her lifetime (stored internally in spermathecae), but most mate several times when multiple males are present. Gravid females may produce their first larvae after 12-14 days, and then subsequent larvae every 7-8 days. Male keds live for 2-3 months while females live for 4-6 months and may produce 10-12 larvae (sometimes up to 20) in their lifetime. The whole life-cycle may be completed in as little as 5 weeks, but generally takes longer, especially in cooler months. Transmission from host-to-host occurs by direct body contact and the transfer of adult keds, rather than by contamination of the surrounding environment. Indeed, keds that fall from hosts only live only a few days and are not highly mobile. Most transmission occurs during periods on intimate host contact, particularly from ewes to suckling lambs. Keds have been observed to move to the surface of the fleece in response to increasing temperatures, possibly aided by increased host motility accompanying flocking behaviour. In temperate regions, ked numbers and transmission peaks around winter, particularly when sheep are gathered together for feeding or shelter.

Differential diagnosis: Infestations may be suspected in animals exhibiting irritability, unthriftiness and damaged wool, but dermal lesions indicative of feeding sites are cryptic and hidden beneath the fleece. Subsequent physical examination may reveal patchy discolouration of the wool (due to ked faeces) and occasional small red-brown ‘dirt’ granules (pupae). Definitive diagnosis, however, is afforded by the direct detection of adult keds on the skin or in the fleece, particularly around the ribs. Specimens should be collected for microscopic examination and identification, particularly since keds are often erroneously referred to as tick-like or louse-like. Adult keds are identified by their unique appearance as flat hairy 6-legged wingless flies. Recent studies have applied molecular biological techniques to the characterization of ked species following the polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA) gene sequences as well as mitochondrial genome analyses.

Treatment and control: A wide range of insecticides have been used to treat infestations in livestock, including inorganic metal-based pesticides, organophosphates (such as coumaphos, malathion, diazinon), chloronicotinyles (imidacloprid), pyrethroids (pyrethrin), and macrocyclic lactones (ivermectin). Treatment is highly effective against adult keds, but not against encased pupae, so treatment needs to be repeated 24-28 days later, or the insecticide used needs to have residual activity of several weeks. Most modern treatments used to control sheep lice are also effective against ked infestations, especially those containing ivermectin or pyrethrin. Shearing sheep has been found to remove many adults and pupae (up to 75%), so it is highly beneficial to shear sheep before treatment, particularly before lambing. Insecticides may be applied as topical or systemic preparations, such as dips, sprays, dusts or spot-ons, and care should be taken to ensure topical applications penetrate the fleece. Many countries have developed highly successful control programmes for sheep ked and have eradicated, or almost eradicated, infestations in commercial sheep flocks. Routine monitoring, annual treatments, stock movement restrictions and quarantine measures have been used in many programmes, but are now often no longer considered necessary.


Melophagus
adult female
(dorsal) (~ 6 mm)
skin
(blood loss, irritation,
allergy, unthriftiness)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals)
wingless adults permanent ectoparasites
(cling to pelage and feed on blood)
(transmission by adults crawling between hosts in close contact)
resting posture
eclosion
eggs
in utero
larvate
complete
(holometabolous)
metamorphosis
pupa
(~ 4 mm)
larva in utero
(~ 3 mm)
egg in utero
(~ 1 mm)
adult females larviparous, deposit larvae
with glue that hardens immediately attaching puparium to pelage



Melophagus adult female



Melophagus adult male



Melophagus pupa

Hippobosca
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Hippoboscids (louse flies) are unusual in being dorsoventrally flattened with a soft leathery abdomen. Both sexes have piercing mouthparts and suck blood from mammals and birds. Most are permanent ectoparasites using strong claws on their feet to cling to hairs or feathers. Females are larviparous and pupiparous, depositing developed larvae on the host to attach and undergo pupation. Infestations by *Melophagus* and *Hippobosca* spp. have been associated with unthriftiness in sheep and other mammals.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Superfamily:	Hippoboscoidea (pupa-bearers)
Family:	Hippoboscidae (flat/louse flies, leathery abdomen, piercing mouthparts, strong claws on feet)
Genus:	*Hippobosca* (parasitic on skin of mammals)
Species:	various species cause irritation

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders

are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora (containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal

suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases).

The superfamily Hippoboscoidea contains 4 families: Glossinidae (tsetse flies); Hippoboscidae (louse flies, some called forest flies, keds or iron flies); Nycteribiidae (bat flies); and Streblidae (bat flies). The family Hippoboscidae contains dorsoventrally flattened flies with piercing mouthparts, leathery abdomens and strong claws on their feet. These 'flat' or 'louse' flies may be wingless or have wings with veins crowded into the leading half of wing. Members are often found as ectoparasites on many species on wild birds, although some infest ungulates, including domestic livestock. Over 200 species have been described in over 20 genera classified into 1-3 subfamilies. Usually, one subfamily is recognized (Hippoboscinae) albeit with 4 tribes: Hippoboscini with 2 genera (including *Hippobosca*), Lipoptenini with 2 genera (including *Melophagus*), Olfersiini with 3 genera, and Ornithomyini with 6 genera), with another 10 unplaced genera. Alternatively, some authorities have placed parasites of birds into the separate subfamily Ornithomyinae, and melophagine parasites of artiodactyls into the subfamily Melophaginae (or Lipopteninae).

Tribe	Genera	Hosts	Site	Transmission
Hippoboscini	*Hippobosca*	equids, bovids	skin	direct
Lipotenini	*Melophagus*	bovids, cervids	skin	direct

The genus *Hippobosca* (syn. *Hippoboscus, Hyppobosca*) contains 7 species of louse flies which are blood feeders commonly infesting cattle and horses around the world. Early workers recognized 3-4 'species groups' on the basis of various differences in adult body morphology, principally involving wings, genitals, abdominal plates and setation. Even though all members of this genus retain their wings, adult flies live almost permanently on their hosts, often in clusters on body parts with little to no hair (e.g. perineum, udders, ventrum). If disturbed, they may fly away but will return very quickly to the same or adjacent hosts. Infestations are a common cause of fly worry which may interfere with livestock production.

***Hippobosca* species**	**Hosts**	**Clinical signs**	**Distribution**
Species group 'a'			
H. equina (syn. *H. taurina*) (horse louse fly, forest fly)	Perissodactyla: equid (horse, donkey, mule); Artiodactyla: bovid (cattle, buffalo, sheep, goat), camelid (camel), cervid (red deer); Lagomorpha: leporid (rabbit); Carnivora: canid (dog); Rodentia: caviid (guinea pig); Primates: hominid (human); Accipitriformes: accipitrid (northern goshawk); Columbiformes: columbid (pigeon); Pelecaniformes: ardeid (grey heron)	irritation (vector for equine piroplasmosis, bovine trypanosomiasis, Q fever, rickettsioses, avian haemoproteids)	worldwide (esp. Eurasia, Africa)
H. fulva (syn. *H. martinaglia*)	Artiodactyla: bovid (Kirk's dik-dik, steenbok, Cape grysbok, duiker, impala, Grant's gazelle, Lichtenstein's hartebeest, harnessed bushbuck)	irritation	Africa
H. longipennis (syn. *H. canina, capensis, cunicosa, fossulata, francilloni, orientalis*) (dog fly, dog louse fly)	Carnivora: canid (dog, pariah dog, dhole, African wild dog, jackal, red fox, bat-eared fox), felid (cat, African wildcat, cheetah, serval, lion, leopard, lynx), herpestid (mongoose), hyaenid (spotted hyena , striped hyena), mustelid (badger), viverrid (African civet, mongoose); Artiodactyla: bovid (cattle, antelope, duiker, Kirk's dik-dik), cervid (roe deer); Perissodactyla: equid (mule); Primates: hominid (human); Aves (unspecified birds)	irritation	Africa, Eurasia
Species group 'b'			
H. camelina (syn. *H. bactriana, dromedarina*) (camel fly)	Artiodactyla: camelid (camel, dromedary); Perissodactyla: equid (horse); Primates: hominid (human)	irritation	Africa, Middle-East
Species group 'c'			
H. hirsuta	Artiodactyla: bovid (waterbuck, puku)	irritation	Africa

H. rufipes (syn. *H. albomuculata, albonotata, camelopardalis*) (cattle louse fly)	Artiodactyla: bovid (cattle, hartebeest, black wildebeest, blue wildebeest, springbok, steenbok, korrigum, gemsbok, eland), giraffid (giraffe); Perissodactyla: equid (horse, donkey, Burchell's zebra); Carnivora: canid (dog); Primates: hominid (human)	irritation	Africa
H. variegata (syn. *H. aegyptiaca, bipartita, calopsis, maculata, sudanica*) (horse louse fly)	Perissodactyla: equid (horse, donkey, mule); Artiodactyla: bovid (cattle, water buffalo), camelid (camel, dromedary); Carnivora: canid (dog); Aves (unspecified birds)	irritation	Africa, Asia

*The species *H. struthionis* described from ostriches has been transferred to the genus *Struthiobosca,* and the species *H. vespertilionis* described from bats has been synonymized with *Strebla wiedemanni.*

Parasite morphology: *Hippobosca* spp. form 4 different types of developmental stages (eggs, larvae, pupae and adults), but they are unusual flies in that the eggs and larvae develop *in utero* within female flies. Eggs develop one at a time in the uterus and appear as translucent creamy ovoid stages around 1mm long. The emergent larvae are retained in the uterus and grow through 3 instars (L1-3) while being nourished on secretions from maternal accessory (milk) glands. The larvae grow up to 4-5 mm long and appear as creamy white-yellow ellipsoidal stages with a dark spot on the body. When L3 cease feeding, they are known as prepupae and are deposited (larviposited) by the female into the external environment. They form a puparium and rapidly darken to black as the encased stage forms a pupa and undergoes metamorphosis to an adult fly. Early studies recognized 3 *Hippobosca* species groups primarily on the basis of morphological differences in adult terminalia, setation, sclerotization and wing venation (with complexity generally increasing through groups 'a', 'b' and 'c'), but it is not yet known whether these groups are supported by molecular characterization studies. Adults are robust shiny brown-black flies, often with yellowish spots marking their dorsoventrally flattened bodies. They range in length from 2-12 mm depending on species, and are sparsely haired and have 2 well-developed forewings. The body has 3 conspicuous tagma: a rounded head; a stout globular thorax; and an expandable ovoid abdomen. The head is not broader than long, and is highly movable, being held clear of the thorax by a short neck. The head bears 2 large brown eyes located laterally and widely separated by the interantennal frons without ocelli. There are 2 small and immovable antennae located in deep rimmed pits, and a pair of stout palps extend forwards and downwards usually forming a sheath around the proboscis. The strongly sclerotized proboscis has piercing-sucking mouthparts for cutting skin and feeding from blood vessels (solenophagy). An elongate labium is the principal piercing structure and has terminal labella armed with teeth. Two long stylets (labrum and hypopharynx) come together when feeding to form a food channel, the latter also having a gutter for the flow of saliva. Blood sucked up by the muscular pharynx is delivered to a tubular oesophagus leading to a globular proventriculus (with saccular crop) before opening into the digestive midgut (without peritrophic matrix), hindgut (with excretory Malpighian tubules), rectum and anus. The midgut contains endosymbiotic bacteria (*Arsenophonus*) within bacteriocytes that may be essential for fly nutrition and survival (while other bacteria, such as *Wolbachia,* detected in other tissues are apparently facultative). The broad thorax is not markedly flattened and is covered by a dorsal scutum with rounded or square shoulders and a posterior lobe-like scutellum. The prothoracic respiratory spiracles open dorsolaterally, and anterior to the points of attachment of the 2 long broad wings, which overlap to cover the abdomen when at rest. Members of the genus *Hippobosca* are permanently winged, unlike some other hippoboscids which shed their wings on finding a host (especially species on birds) or completely lack wings (like *Melophagus*). The wing membranes are supported by 6 primary wing veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] crowded anteriorly (including 2 cross-veins) but trailing posteriorly (without a closed anal cell). The wings appear tinted grey-red and are distinctly crenulated with posterior lobes including a broad alula and distinct calypters covering the stumpy halteres (highly reduced hindwings). The ventral thorax bears 3 pairs of stout hairy legs, each composed of 5 segments (small coxa and trochanter, enlarged femur, flattened tibia, and terminal tarsus), with the latter bearing a pair of large simple claws and pad-like pulvilli. The ovoid-ellipsoid abdomen lacks conspicuous segments and many species also lack dorsal sclerites [species group 'a' with 3 median tergal plates; species group 'b' with 1 plate in males, none in females; species group 'c' lacking plates], The abdomen is covered by a soft flexible integument allowing for gross distention during feeding and larval development. Adult reproductive organs are located in posterior abdomen with genital ducts opening terminally. Males have 2 testes connected by vas deferens to a seminal vesicle leading to a tubular ejaculatory duct and terminal copulatory apparatus (with retractable phallosome and claspers) [species groups 'a' and 'c' with slender rod-like claspers, species group 'b' with thicker curved claspers]. Females have 2 ovaries (with few ovarioles) connected to a common oviduct expanding posteriorly to form a uterus that accommodates one embryo at a time. The uterus, with associated spermatheca (for sperm storage) and branched accessory (milk) glands, leads to the vulva in the terminal genital plate.

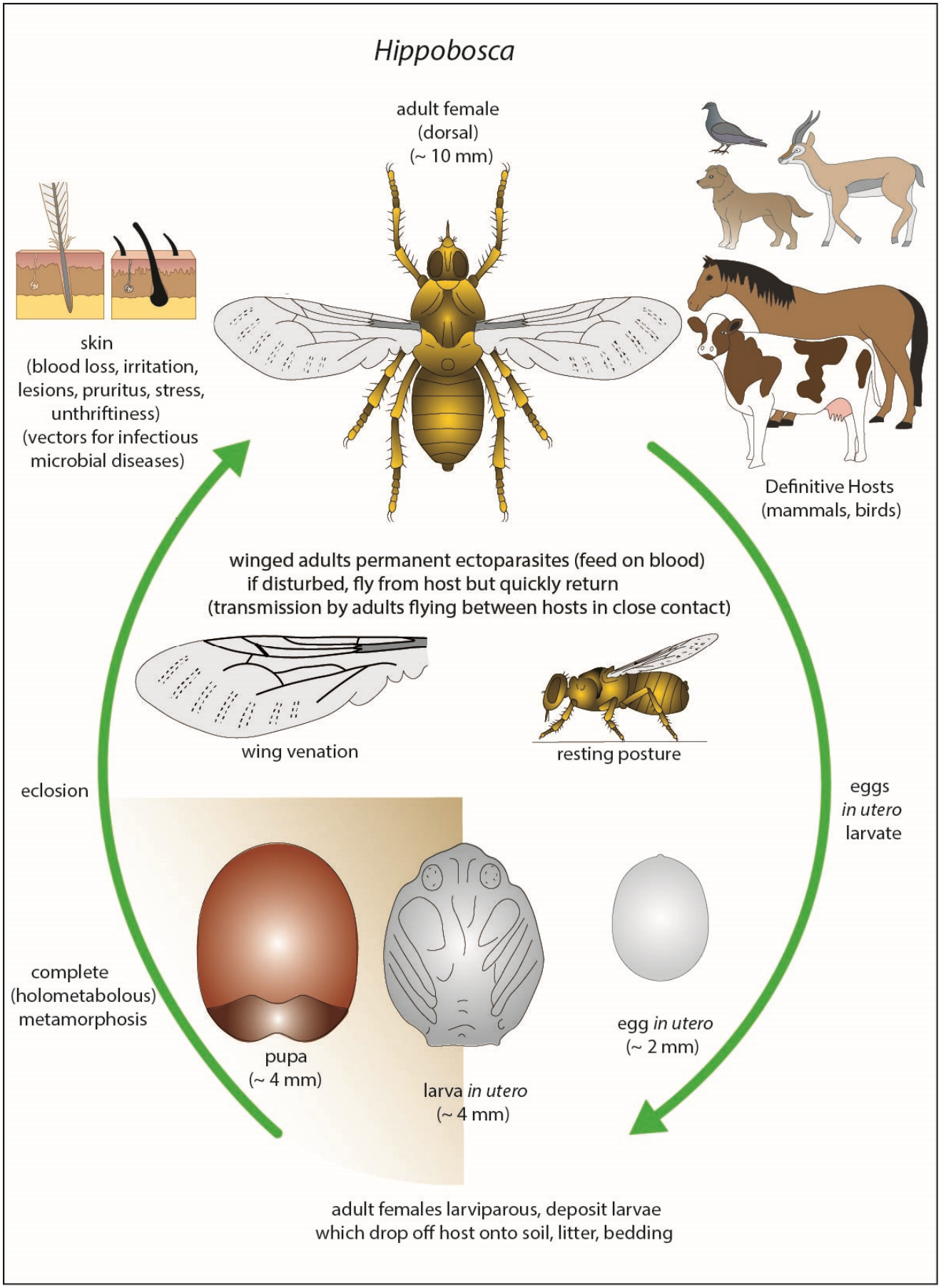
Site of infection: *Hippobosca* spp. occur predominantly on mammals (ungulates and carnivores) with some species occasionally biting humans, and a few species rarely infesting birds (raptors, pigeons, heron) (cf. many other hippoboscids occur predominantly on birds). They are obligate ectoparasites and must feed on vertebrate blood in order to survive and reproduce. Adult flies stay in close contact with their hosts and rapidly return or seek nearby hosts if disturbed. Many species are stenoxenous (infest closely-related hosts), but most have strong host preferences either for horses, cattle or carnivores (canids and felids). They feed and rest mostly under the tail around the perineum, between the hindlegs on the inner thigh, around the pubis and genitalia, around the udders in cattle, and sometimes around the head, often places where they are least disturbed by host grooming.

Pathogenesis: Louse flies are haematophagous and both sexes feed on vertebrate blood several times a day with bloodmeals lasting up to 15 minutes. If disturbed, flies quickly resume feeding until replete. Their mouthparts are well adapted to blood-feeding and they use their labium with terminal dentate labella to pierce the skin and then the labrum and hypopharynx form a food canal to suck blood as well as inject saliva containing anticoagulant properties. While flies take small volumes of blood, they feed repeatedly and heavy infestations can lead to significant blood loss, sometimes manifest in anaemia. Fly bites are quite painful and cause traumatic skin lesions, inflammation and pruritus. Hosts exhibit considerable irritation (often called fly worry or biting stress) and resort to behaviours to seek relief from itchy bite sites. They may lick, bite or scratch affected areas, but often rub them against hard objects (walls, trees, fences), sometimes resulting in self-trauma, thus exacerbating wounds and opening them to secondary bacterial or screw-worm infections. Animals may also twitch their tails and limbs nervously, and vigorous stamping by horses has been linked to leg injuries. Animals are distracted from efficient feeding and may exhibit decreased performance, reduced weight gain and even weight loss sometimes leading to emaciation. Individual animals may occasionally develop anaphylactic reactions apparently due to hypersensitivity to fly saliva. Louse flies generally remain in contact with individual hosts and are therefore not renowned for the transmission of infectious diseases. Nevertheless, some louse fly species have been shown to act as vectors for haemoprotozoan parasites (avian haemoproteids (only *Haemoproteus,* as *Parahaemoproteus* are transmitted by ceratopogonid biting midges), nonpathogenic bovine trypanosomes (*Trypanosoma theileri*), bacteria (equine piroplasmosis, Q fever, rickettsioses and bartonellosis in ruminants) and helminths (filarial nematodes in mammals and birds, incl. *Dipetalonema dracunculoides* in dogs and hyenas).

Developmental cycle and mode of transmission: Louse flies live almost permanently on their host, often in clusters on body parts with little to no hair. Transmission between hosts is achieved by adults flying from one host to another, often to those in close proximity, although the adults are good fliers. *Hippobosca* spp. do not shed their wings after finding a host, unlike some other hippoboscids. Like all Diptera, they undergo complete metamorphosis whereby grub-like larvae transform in pupal cases into adult flies. However, unlike most other flies, female louse flies do not lay eggs but retain their eggs one at a time in their reproductive tracts where they release larvae that are nurtured for 3-8 days through 3 instars (L1-3) on secretions from specialized accessory (milk) glands. Female flies only give birth to mature L3 which have ceased feeding (often known as prepupae). This type of reproduction is known as adenotrophic viviparity, and the females are considered to be larviparous (recent texts referring to them as macro-larviparous) as they deposit prepupa which immediately form puparia. Prepupae may be deposited on or off hosts, but they are not glued to hairs (like *Melophagus*) and drop off onto the ground, bedding, nests or roosts. In many species, females fly to adjacent substrates and deposit prepupae in sheltered places in animal holding facilities, in soil cracks and crevices, in humus or debris, and underneath plants near plant roots. The prepupal tegument hardens almost immediately forming a puparium in which pupations occurs over 15-20 days, but up to 142 days for some species in cooler environments. Adult flies emerge and seek hosts on which to feed and mate. Without bloodmeals, flies do not survive off hosts for more then 1-2 weeks. Both sexes may live for up to 4-5 months, but males usually die sooner. Females may produce from 5-15 offspring in their lifetimes. Most species prefer warm sunny weather and are most abundant during summer months.

Differential diagnosis: The diagnosis of infestations on clinical grounds is extremely difficult due to the cryptic nature of the flies and the non-specificity of host reactions to fly bites. Diagnosis is generally afforded by close observation of hosts exhibiting fly worry and the direct detection of louse flies biting body parts, mainly under the tail and between the hind legs. Flies may be captured by suction, nets or baits for microscopic examination and identification. Recent molecular biological studies have been used to characterize species and determine phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear (28S ribosomal DNA, caspase-activated Dnase (CAD)) and mitochondrial (16S ribosomal DNA, cytochrome c oxidase subunit 1) gene sequences.

Treatment and control: Because louse flies stay in close contact with their hosts when resting on the skin in between bloodmeals, infestations on domestic livestock, pets and zoo animals are readily treated with both topical and systemic insecticides. These have included organochlorines (methoxychlor), organophosphates (coumaphos, chlorfenvinphos, malathion, diazinon), synthetic pyrethroids (cypermethrin, deltamethrin, permethrin), carbamates (carbaryl) and arylpyrazoles (fipronil), although macrocyclic lactones appear to be limited in effect at their usual therapeutic doses. The most common and effective treatments currently used for mammals and birds involve monthly spraying with fipronil or deltamethrin, or treatment of animals and their housing with carbaryl-sulphur dust formulations. Some measure of prevention has been achieved by the regular grooming of hosts, probably due to the sustained disturbance of fly populations rather than making feeding and resting sites less hospitable. Because pupation generally occurs in soil and debris in the immediate environment, frequently changing bedding and nesting materials and removing organic wastes will help eliminate deposited pupae and prevent re-infestations.


Hippobosca
adult female
(dorsal)
(~ 10 mm)
skin
(blood loss, irritation,
lesions, pruritus, stress,
unthriftiness)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals, birds)
winged adults permanent ectoparasites (feed on blood)
if disturbed, fly from host but quickly return
(transmission by adults flying between hosts in close contact)
wing venation
resting posture
eclosion
eggs
in utero
larvate
complete
(holometabolous)
metamorphosis
pupa
(~ 4 mm)
larva in utero
(~ 4 mm)
egg in utero
(~ 2 mm)
adult females larviparous, deposit larvae
which drop off host onto soil, litter, bedding



Hippobosca adults



Hippobosca adult



Hippobosca pupa

Musca
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Muscid flies include many non-biting and biting genera, the former being nuisances and the latter being blood-feeders. Most species are synanthropic (closely associated with humans) and they breed in all types of organic waste. Two subfamilies are recognized: muscines (house flies, bush flies, face flies) with sucking mouthparts adapted to feeding on decaying organic matter; and stomoxines (stable flies, horn/buffalo flies) with elongate biting mouthparts adapted to blood feeding. House flies (*Musca* spp.) have been shown to serve as mechanical vectors for an extraordinary range of infectious diseases in humans, most being enteric diseases occasioned by faecal contamination.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Muscidae (house/bush/stable/buffalo flies, nuisance flies, synanthropic (associated with human activity))
Subfamily:	Muscinae (with sucking mouthparts adapted to feeding on decaying organic matter)
Genus:	*Musca* (pests of mammals)
Species:	various species cause annoyance

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders

are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 divisions: the Schizophora

(containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases).

The superfamily Muscoidea contains 4 families: Muscidae (house flies), Fanniidae (latrine flies), Scathophagidae (dung flies) and Anthomyiidae (anthomyiid flies). The family Muscidae contains robust flies with plumose aristae and wings where vein A2 is not strongly curved (unlike latrine flies). The family contains both free-living flies, some of which are nuisance pests of livestock and humans, as well as blood-sucking flies feeding on vertebrates. Over 4,200 species have been described in some 190 genera classified into 9-10 subfamilies: Achanthipterinae, Azeliinae, Coenosiinae, Cyrtoneurininae, Dichaetomyiinae, Muscinae, Mydaeinae, Phaoniinae, and Reinwardtiinae; with another 58 unplaced genera and several fossil genera. Alternatively, some authorities recognize 2 tribes (Muscini and Stomoxyini) in the subfamily Muscinae, some have elevated the tribe Stomoxyini to subfamily status (Stomoxinae), while others have demoted the subfamilies Azeliinae and Reinwardtiinae to tribes (Azelini and Reinwardtiini) in the subfamily Muscinae].

Subfamily	Genera	Hosts	Site	Transmission
Muscinae (with sponging mouthparts)	*Musca*	mammals,	nonparasitic	nonparasitic
Stomoxinae (with biting mouthparts)	*Stomoxys*	mammals	skin	direct
	Haematobia	bovines	skin	direct

The subfamily Muscinae contains many species of free-living flies that feed on decaying organic matter, some feeding on secretions from animals. The subfamily contains 17-22 genera (including *Musca*) which are nuisance flies to various animal and human populations around the world as well as mechanical (and sometimes biological) vectors for various infectious diseases (including mastitis, conjunctivitis, anthrax, enteric bacteria/viruses, and helminths). The genus *Musca* (syn. *Byomya*, *Eumusca*, *Plaxemya*) contains over 150 species classified in 10 subgenera. They have been afforded many common names often associated with behavioural or ecological traits, including house-fly, face-fly, bazaar-fly, or bush-fly. Adults feed by sponging up wet secretions at the mouth, nostrils, eyes, teats, or the edges of wounds, some species using a ring of prestomal teeth at the end of the labellum to scrape the skin surface to yield exudates. They annoy a wide variety of domestic and wild animals, sometimes causing bizarre avoidance behaviours that may result in self-trauma but also deplete energy reserves and interfere with feeding. Many species are also synanthropic and exploit food and habitats created by human activities, notably agriculture, housing, garbage and waste disposal.

***Musca* species (regional exemplars)**	**Host preferences**	**Clinical signs (vectorial capacity)**	**Distribution**
M. autumnalis (face fly)	wild and domestic animals (esp. cattle, sheep, goats, pigs, horses, camels), humans	annoyance (mechanical vectors for keratoconjunctivitis (pink eye)) (intermediate hosts of *Parafilaria* and *Thelazia*)	Eurasia, Africa, North America
M. crassirostris	wild and domestic animals, humans	annoyance (mechanical vectors for mastitis, conjunctivitis, anthrax, enteric bacteria/viruses, helminth eggs)	Mediterranean
M. domestica (house fly, typhoid fly)	wild and domestic animals (esp. cattle, sheep, goats, pigs, horses, camels), humans	annoyance (mechanical vectors for mastitis, conjunctivitis, anthrax, enteric bacteria/viruses, helminth eggs) (intermediate hosts for nematodes *Habronema*/*Raillietina* spp.)	worldwide
M. sorbens (bazaar fly)	wild and domestic animals (esp. cattle, sheep, goats, pigs, horses, camels), humans	annoyance (mechanical vectors for conjunctivitis, enteric bacteria/viruses)	Africa, Orient
M. vetustissima	wild and domestic animals (esp.	annoyance	Australia, Africa

(bush fly)	cattle, sheep, goats, pigs, horses, camels), humans	(mechanical vectors for conjunctivitis, enteric bacteria/viruses)	

Full species list (compilation of several on-line data-bases)

***Musca* species**	**Subgenus**
M. aethiops	*Eumusca*
M. afra	*Byomya*
M. albina	*Lissosterna*
M. alpesa	*Philaematomyia*
M. amita	*Eumusca*
M. arcuata	Unassigned
M. asiatica	Unassigned
M. ausus	Unassigned
M. bakeri	*Viviparomusca*
M. bezzii	*Viviparomusca*
M. bicolor	Unassigned
M. biseta	*Byomya*
M. bohemica	Unassigned
M. cadaverum	Unassigned
M. calieva	Unassigned
M. calleva	*Musca*
M. capensis	*Byomya*
M. carinata	Unassigned
M. cassara	*Byomya*
M. chibcha	Unassigned
M. chingaza	Unassigned
M. ciliata	Unassigned
M. conducens	*Byomya*
M. confiscata	*Byomya*
M. confluo	Unassigned
M. conica	Unassigned
M. continua	Unassigned
M. convexifrons	*Viviparomusca*
M. costalis	Unassigned
M. costata	Unassigned
M. craggi	*Eumusca*
M. crassipes	Unassigned
M. crassirostris	*Philaematomyia*
M. cuprea	Unassigned
M. curpraria	Unassigned
M. curviforceps	*Musca*
M. dasyops	*Byomya*
M. divisa	Unassigned
M. doclea	Unassigned
M. domestica	*Musca*
M. dorsalis	Unassigned
M. dorsomaculata	Unassigned
M. dubia	Unassigned
M. elatior	*Philaematomyia*
M. embera	Unassigned
M. emdeni	Unassigned
M. equinoactialis	Unassigned
M. ethiopica	*Byomya*
M. fasciata	Unassigned
M. femorata	Unassigned
M. fergusoni	Unassigned
M. flavicans	Unassigned
M. fletcheri	*Eumusca*
M. formosana	*Viviparomusca*
M. freedmani	*Byomya*
M. fuscipennis	Unassigned
M. gabonensis	Unassigned
M. harpyia	Unassigned
M. hebes	Unassigned
M. heidiae	*Eumusca*
M. hervei	*Eumusca*
M. hirsute	Unassigned
M. hugonis	*Byomya*
M. hydropica	Unassigned
M. iguaque	Unassigned
M. illingworthi	*Viviparomusca*
M. incerta	Unassigned
M. inferior	*Ptilolepis*
M. interrupta	Unassigned
M. katios	Unassigned
M. khofarae	Unassigned
M. laemica	Unassigned
M. lamosca	Unassigned
M. larvipara	*Viviparomusca*
M. lasiopa	*Eumusca*
M. lasiophthalma	*Byomya*
M. leucocephala	Unassigned
M. liberia	*Byomya*
M. lindneri	*Byomya*
M. lothari	*Eumusca*
M. lucidula	*Byomya*
M. lusoria	*Eumusca*
M. maculipennis	Unassigned
M. magdalena	Unassigned
M. malaisei	*Setimusca*
M. mallochi	Unassigned
M. matilia	Unassigned
M. meruensis	*Philaematomyia*
M. moneta	Unassigned
M. munroi	*Eumusca*
M. negriabdomina	Unassigned
M. neustriae	Unassigned
M. nevilli	*Eumusca*
M. nora	Unassigned
M. obscura	Unassigned
M. osiris	*Plaxemya*
M. patersoni	*Eumusca*
M. pattoni	*Byomya*
M. pellucens	Unassigned
M. picea	Unassigned
M. pijao	Unassigned
M. pilifacies	*Plaxemya*
M. pilosa	Unassigned
M. placida	Unassigned
M. planiceps	*Byomya*

M. polisma	Unassigned
M. polita	Unassigned
M. porce	Unassigned
M. procedo	Unassigned
M. pseudocorvina	*Eumusca*
M. quimbaya	Unassigned
M. rapax	Unassigned
M. recedans	Unassigned
M. recurro	Unassigned
M. redians	Unassigned
M. rubripes	Unassigned
M. ruficrus	Unassigned
M. rufiventris	Unassigned
M. santoshi	*Pseudosetimusca*
M. scutellaris	Unassigned
M. segmentaria	Unassigned
M. seniorwhitei	*Eumusca*
M. setulosa	*Eumusca*
M. somalorum	*Eumusca*
M. sorbens	*Byomya*
M. spangleri	*Byomya*
M. spec	Unassigned
M. splendens	*Viviparomusca*
M. stabulans	Unassigned
M. striatacta	Unassigned
M. stuckenbergi	Unassigned
M. suffusa	Unassigned
M. sumapaz	Unassigned
M. sutagao	Unassigned
M. tahitiensis	Unassigned
M. tempestatum	*Byomya*
M. tempestiva	*Byomya*
M. terraereginae	Unassigned
M. tibetana	*Plaxemya*
M. transvaalensis	*Byomya*
M. turbida	Unassigned
M. ugandae	*Eumusca*
M. varia	Unassigned
M. ventrosa	*Byomya*
M. vermileo	Unassigned
M. vespasianus	Unassigned
M. vetustissima	Unassigned
M. vicina	Unassigned
M. villeneuvii	*Eumusca*
M. violacea	Unassigned
M. vitripennis	*Byomya*
M. wittweri	*Byomya*
M. xanthomelaena	Unassigned
M. xanthomelas	*Eumusca*

Parasite morphology: Muscid flies form 4 different types of morphological stages during their developmental cycles: namely, eggs, larvae (3 instars), pupae and adults (male and female). *Musca* eggs are creamy white and typically elongate-ellipsoid measuring from 1-3 mm long, most being concave dorsally with 2 ribs forming hatching pleats, and some with a short anterior respiratory stalk (e.g. *Musca autumnalis*). Larval stages (known as maggots) are creamy white-yellow and have elongate segmented bodies with a pointed anterior end and a blunted posterior end (whereas oestroid larvae are more cylindrical). Larvae develop through 3 instars (L1-3) growing up to 7-12 mm long. The head bears an anterior mouth with mouth hooks but is otherwise highly reduced lacking eyes and with minute papilla-like antennae. The head lacks a sclerotized capsule but is supported internally by a sclerotized cephalo-pharyngeal skeleton. Larvae do not have legs, but the 8 abdominal segments have ventral patches of tiny transverse spines forming creeping welts. All larvae breathe using respiratory spiracles: one anterior pair (absent in L1) located laterally on the first thoracic segment (and apparent as small branched tubercles); and a second larger posterior pair located dorsally on caudal abdominal plates (each consisting of a sclerotized peripheral ring (peritreme), 2-3 straight-sinuous slit-like openings for gas exchange (2 slits in L1-2, and 3 slits in L3) and an ecdysal scar from a previous moult). In muscid larvae the slits slant towards the midline, while in sarcophagids the slits slant away from the midline [in contrast to oestrid larvae which have porous plates]. When L3 mature, the tegument contracts and hardens to form a cylindrical barrel-shaped puparium measuring from 2-8 mm long, varying in colour from white-yellow to red-brown and sometimes black, usually darkening with age. Inside the puparium, a pupa forms leaving larval structures (spiracles and cephalo-pharyngeal skeleton) embedded in the puparial case. Adults are brownish grey-black flies 5-10 mm long, often with dark longitudinal stripes on the thorax (called vittae) and dark spots on abdomen. Their bodies have 3 conspicuous tagma: a short broad head, stout thorax and ellipsoidal abdomen. The head possesses both a ptilinal suture and facial lunule (like all Muscoidea and Oestroidea, but unlike other calyptrates), 2 large red-brown compound eyes located laterally and separated by a frons bearing 3 small ocelli, and a distinctive pair of anterior antennae (each composed of a small basal scape and a club-like pedicel from which emerges a bilaterally-plumose arista (single undivided flagellum bearing fine setae)). All *Musca* spp. are liquid feeders that have sponging rather than biting mouthparts that project downwards and are flanked by strong oral bristles (vibrissae). The proboscis consists of 3 major elements: a basal rostrum flanked by short setate palps; a cylindrical haustellum housing an anterior labrum, slender hypopharynx and sheath-like labium; and a terminal 2-lobed labellum lined with prestomal teeth and pseudotracheae (rows of fine setae). Liquids ingested by strong pharyngeal muscular action (cibarial pump) pass into a tubular oesophagus and proventriculus leading to the digestive midgut. Dilute fluids like plant sugars may be shunted for temporary storage into a saccular diverticulum, the contents of which may be regurgitated and reingested to aid evaporation. Waste material passes through the hindgut (with excretory Malpighian tubules) to the rectum (with expandable ampulla) and terminal anus. Fly specks that collect on feeding and resting sites therefore consist of both fly vomit and faeces. The pyriform thorax is usually dull with 2-4 dark longitudinal stripes, 2 pairs of respiratory spiracles (anterior mesothoracic and posterior metathoracic), and a bare hypopleuron (without bristles or setae in muscids). The mesothorax bears 2 long wings, with membranes supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)], with vein A1 vanishing before reaching the wing margin, vein A2 not strongly curved (unlike latrine flies), and vein M1 having a sharp forward bend. Like all Diptera, the hindwings are highly reduced to a pair of stumpy halteres used to stabilize flight. Like other calyptrate flies, the halteres are covered by calypters

(posterobasal wing lobes), but only the Muscoidea and Oestroidea have a bulbous greater ampulla below the wing base. The ventral thorax is the point of attachment for 3 pairs of legs: each consisting of 5 segments (coxa, trochanter, femur, tibia, and tarsus); and each terminating in a pair of claws with 2 pads (pulvilli) surrounding several central bristles (empodium). The abdomen is often dull yellow-brown, sometimes with a longitudinal dark band, sometimes chequered light-dark patterns, and sometimes with lighter yellow sides. Segmentation is often reduced from 10-12 to as few as 5 visible segments due to posterior segments being modified by terminalia (anal cerci in both sexes, claspers and retractable aedeagus in males, tubular telescopic ovipositor in females). Males have 2 testes with vas deferens leading to a seminal vesicle (with lateral accessory glands) and a tubular ejaculatory duct connected to the aedeagus in the genital pouch. Females have 2 ovaries joined by oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva and posterior ovipositor.

Site of infection: *Musca* spp. are non-biting filth flies that feed on liquids and suspensions both off hosts (plants nectar, honeydew) and on hosts (surface secretions (sweat, tears, snot, saliva), excreta (urine, faeces) and wounds). Their favoured feeding sites are moist areas due to discharges around the eyes, nose, mouth, lips, perineum, vulva, and preputium or urethral process of the penis. They are not highly host specific but will feed opportunistically from a range of vertebrate hosts. However, many species are attracted to large mammals as sources of food as well as faeces for oviposition, and have attained many regional common names suggesting some degree of site or host specificity (such as face fly, house fly, bazaar fly, bush fly).

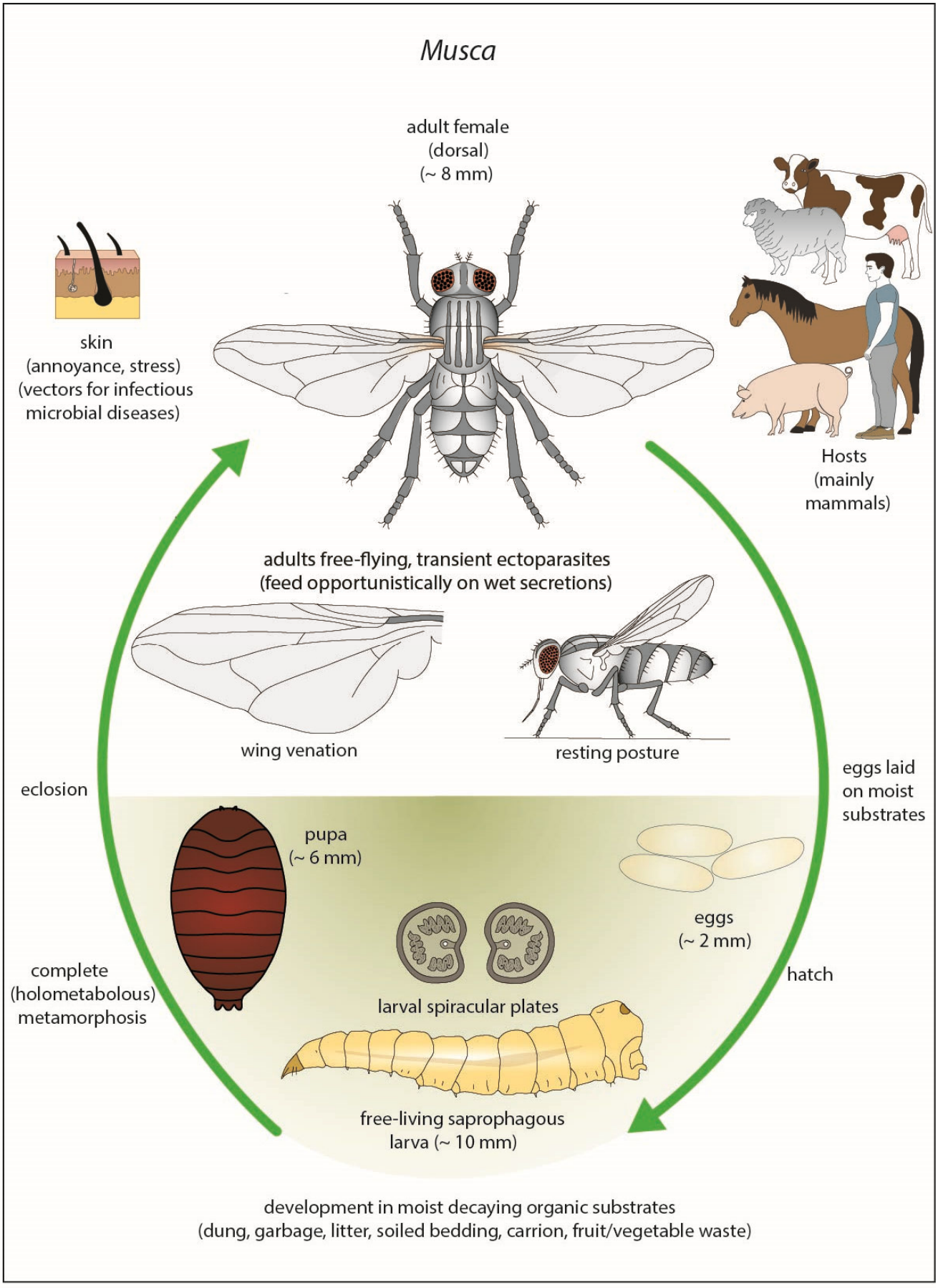
Pathogenesis: Adult flies scavenge on host surface secretions using their sponging mouthparts, essentially by a process of salivating, scrubbing and sucking (they do not penetrate skin). The labellum is opened out and pressed against the substrate releasing saliva laden with enzymes. The labellum is then opened and closed to scarify food into the saliva, with the resultant suspension being drawn along the pseudotracheae into the food canal. They will feed on sweat, tears, lachrymal secretions, snot, saliva, mucus, and serous exudates (sometimes even blood but only if it is seeping from wounds). When not feeding, they will rest on solid structures which become speckled with fly spots (vomit and faeces). Filth flies are usually considered to be minor nuisances causing annoyance to their hosts, but dense clusters may cause severe irritation and disturbance (fly worry) resulting in energy-consuming avoidance behaviours (swatting, shaking, twitching) and reduced feeding efficiency with lowered weight gain and decreased performance. Several species have occasionally been associated with secondary myiases when their larvae invade host tissues, notably undressed wounds, eyes with excessive lacrimation, urogenitalia associated with urine-soaked clothing, and even the gastro-intestinal tract (when larvae are either ingested in contaminated food or undergo retro-infection through the anus when attracted by faecal soiling). Filth flies have been implicated in the transmission of many infectious diseases, predominantly by acting as mechanical vectors (or paratenic transport hosts) for various bacteria, viruses, protozoa and helminths, either by carrying infectious stages on their surfaces (hairy feet, bodies and mouthparts) or by passing them in vomitus or faeces. Transmission may occur by direct skin contact or by food and drink contamination. Filth flies live and breed in or near dung heaps and other decomposing materials, so they have frequently been found to transmit enteric pathogens causing diarrhoea (including bacillary and amoebic dysentery, salmonellosis, shigellosis, escherichiosis, typhoid, cholera, cryptosporidiosis, giardiasis, hepatitis A, Cocksackie virus, and enteric cytopathogenic human orphan (ECHO) viruses) as well as tuberculosis, trachoma eye disease and pyogenic cocci in humans, and anthrax, mastitis and keratoconjunctivitis (pink-eye) in cattle. Several species have also been found to carry the eggs or larvae of several helminths, including nematodes (*Ascaris, Enterobius, Trichuris* in humans*, Habronema, Draschia, Thelazia* and *Parafilaria* in ungulates) and cestodes *(Hymenolepis, Raillietina* and *Choanotaenia* in mammals and birds).

Developmental cycle and mode of transmission: Muscid flies exhibit holometabolous development where grub-like larvae undergo complete metamorphosis in pupae to form adult winged flies. Females are oviparous and lay eggs in batches of 50-150 eggs every 2-5 days under ideal conditions (smaller batches for face flies, and longer intervals in colder conditions). The eggs are deposited in a wide variety of decaying organic substrates, so long as they are moist enough to support aerobic microbial fermentation. Substrates common around human habitations and livestock enclosures include animal dung, manure piles, open privies, garbage dumps, rotting feedstuffs, soiled bedding, poultry litter, carrion, and fruit and vegetable wastes. Different *Musca* spp. may show some habitat preferences, such as *M. autumnalis* and *M. vetustissima* for cattle dung, while others, including *M. domestica,* lay eggs in any decaying material. Eggs hatch within 12 hours releasing larvae which are saprophagous and feed by filtering bacteria, yeasts and other small suspended particles in the semi-liquid habitats (cf. larvae of other muscid genera may also be facultative predators). Larvae grow through 3 instars (L1-3) over 3-5 days before the mature L3 burrows into the adjacent ground and forms a puparium containing a pupa. Pupation generally takes from 2-6 days, but may be longer (20 days or more) in colder conditions. Some species may also over-winter in the pupal stage, with adults only emerging with warmer weather. Adults eclose from pupae through a circular cap (and not through a longitudinal slit like Nematocera and other Brachycera). Adult flies are strong fliers and most species are active during daylight hours preferring direct sunshine over shaded enclosures, although anthropophilic species will invade households and barns. The adults locate food sources using chemical and visual senses (olfaction and sight) and feed to obtain nutrients for survival and reproduction. The females of most species are anautogenous and require protein meals to complete their first gonotrophic (ovarian) cycles. Mating takes place after males resting on vantage points intercept passing females which then store enough sperm to remain fertile for life. Eggs are produced over several days and oviposited in batches, before the next gonotrophic cycle begins. Adult flies live for around 14 days, although some species may overwinter as adults in sheltered hibernacula such as tree bark or building crevices. The whole life-cycle may be completed in as little as 7-10 days, but usually takes longer (40-50 days) at lower temperatures. Most species are multivoltine and have multiple generations each

year, up to 12 in temperate regions, but up to 20 in tropical regions. Nonetheless, most species exhibit seasonal patterns in abundance which coincide with warm moist conditions suitable for larval habitats.

Differential diagnosis: Infestations by nuisance filth flies may be evident by the disturbance caused by flies alighting on moist areas of skin (around eyes, mouth and perineum), but can only be confirmed by capturing adults for microscopic examination and identification. On the rare occasions when larval myiases may be attributed to filth flies, diagnosis has been made by careful examination of larval instars for their key morphological characteristics. Molecular biological techniques have been used to characterize species and examine phylogenetic relationships following the amplification by polymerase chain reaction (PCR) of nuclear and mitochondrial genes - indeed the complete genomes have been sequenced for several *Musca* spp.

Treatment and control: Animals may be protected from some fly worry by the topical application (sprays, dusts, some pour-ons) of various insecticides (organochlorines, organophosphates, pyrethroids), although they are often limited in effect as filth flies spend little time in contact with their hosts. Many insecticides do not have long-lasting activity and need to be applied regularly, while those with long residual activity may be used not only on animals but also on fly resting places in the immediate environment (building walls, ceilings and fixtures). The most effective formulations appear to be sprays combining the pyrethroid permethrin with synergists (piperonyl butoxide, bicycloheptene dicarboximide) and repellents (diethyltoluamide, DEET). There are mounting concerns about the over-use of insecticides in the environment due to the potential for the emergence of insecticide-resistance as well as their persistence and detrimental impacts on natural ecosystems. Adult flies may also be killed in closed spaces by knockdown aerosols, sticky traps, light traps, and insecticide baits (using sugar or pheromone attractants). Fly repellents (such as diethyltoluamide, DEET) may also be used for personal protection, either applied directly to the skin or onto clothing. Indoor enclosures can also be protected by erecting barriers (screens, curtains and nets) around entry points, and individuals may be protected by covering bare skin with long-sleeved clothing and wearing fly veils or other headwear with fly deterrents (dangling strings). Controlling filth fly populations is of enormous public health significance as they may transmit so many infectious diseases, but regrettably basic sanitation, waste management, and animal husbandry practices are often not of high enough standard in many rural and peri-urban situations, and are severely compromised in times of drought, flood, famine and war. The removal of free-standing organic waste (human and animal faeces, manure piles, rotting vegetable matter, garbage) will reduce available larval habitats and help manage fly populations. The use of chemical larvicides on organic waste is often discouraged due to environmental concerns and their potential effects on the many natural predators, parasitoids and parasites of fly larvae and pupae (including mites, beetles, wasps and other flies). Many countries utilize integrated pest management strategies involving improved sanitation, farm and household management, food and milk hygiene, and the judicious use of insecticides and repellents. Education campaigns designed to make populations aware of food, water, animal and personal hygiene may assist in reducing the transmission of infectious diseases.


Musca
adult female
(dorsal)
(~ 8 mm)
skin
(annoyance, stress)
(vectors for infectious
microbial diseases)
Hosts
(mainly
mammals)
adults free-flying, transient ectoparasites
(feed opportunistically on wet secretions)
wing venation
resting posture
eclosion
eggs laid
on moist
substrates
pupa
(~ 6 mm)
eggs
(~ 2 mm)
complete
(holometabolous)
metamorphosis
hatch
larval spiracular plates
free-living saprophagous
larva (~ 10 mm)
development in moist decaying organic substrates
(dung, garbage, litter, soiled bedding, carrion, fruit/vegetable waste)



Musca adult



Musca adult



Musca eggs



Musca larva



Musca larval spiracles



Musca pupae

Stomoxys
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Muscid flies include many non-biting and biting genera, the former being nuisances and the latter being blood-feeders. Most species are synanthropic (closely associated with humans) and they breed in all types of organic waste. Two subfamilies are recognized: muscines (house flies, bush flies, face flies) with sucking mouthparts adapted to feeding on decaying organic matter; and stomoxines (stable flies, horn/buffalo flies) with elongate biting mouthparts adapted to blood feeding. Stable flies (*Stomoxys* spp.) attack humans and domestic animals, having serious impacts on tourism, cattle productivity and horse performance. They may also transmit a range of viral, bacterial, protozoal and helminth infections.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Muscidae (house/bush/stable/buffalo flies, nuisance flies, synanthropic (associated with human activity))
Subfamily:	Stomoxinae (with elongate biting mouthparts adapted to blood feeding)
Genus:	*Stomoxys* (parasitic on skin of mammals)
Species:	various species cause annoyance, allergy

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding

on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora

(containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases).

The superfamily Muscoidea contains 4 families: Muscidae (house flies), Fanniidae (latrine flies), Scathophagidae (dung flies) and Anthomyiidae (anthomyiid flies). The family Muscidae contains robust flies with plumose aristae and wings where vein A2 is not strongly curved (unlike latrine flies). The family contains both free-living flies, some of which are nuisance pests of livestock and humans, as well as blood-sucking flies feeding on vertebrates. Over 4,200 species have been described in some 190 genera classified into 9-10 subfamilies: Achanthipterinae, Azeliinae, Coenosiinae, Cyrtoneurininae, Dichaetomyiinae, Muscinae, Mydaeinae, Phaoniinae, and Reinwardtiinae; with another 58 unplaced genera and several fossil genera. Alternatively, some authorities recognize 2 tribes (Muscini and Stomoxyini) in the subfamily Muscinae, while others have elevated the tribe Stomoxyini to subfamily status (Stomoxinae).

Subfamily	Genera	Hosts	Site	Transmission
Muscinae (with sponging mouthparts)	*Musca*	mammals	nonparasitic	nonparasitic
Stomoxinae (with biting mouthparts)	*Stomoxys*	mammals	skin	direct
	Haematobia	bovines	skin	direct

The subfamily Stomoxinae contains 4 genera (*Haematobia*, *Haematobosca*, *Stygeromyia* and *Stomoxys*) although some authorities have merged the genus *Haematobosca* (and the former genus *Lyperosia*) with *Haematobia*. These flies have elongate biting mouthparts adapted to blood feeding on domestic animals and wildlife. The genus *Stomoxys* (syn. *Stomoxis*) contains 18 species of stable flies that feed mainly on the legs and ears of horses, cattle and some companion animals (dogs). Adult flies inflict irritating bites resulting in significant annoyance to their hosts, and allergic individuals may develop papular skin lesions. Various species have been implicated as vectors in the transmission of infectious diseases, including anthrax, viral anaemia, surra (trypanosomiasis) and nematode granulomas (summer sores).

***Stomoxys* species**	Hosts	Clinical signs	Distribution
S. bengalensis (syn. *S. oblongopunctatus*)	Artiodactyla: bovid (cattle), traps*	annoyance	Asia
S. boueti	Artiodactyla: bovid (buffalo); traps		Africa
S. calcitrans (syn. *S. aculeata, aurifacies, bouffardi, chrysocephala, claripennis, cunctans, cybira, dira, flavescens, geniculata, griseiceps, hovas, infesta, inimica, korogwensis, libatrix, minuta, nebulosa, occidentis, parasita, plurinota, praecox, pungens, rubifrons, soudanense, sugillatrix, tessellata, vulnerans*) (stable fly)	Artiodactyla: bovid (cattle, buffalo, sheep, goat), camelid (camel), cervid (deer), suid (pig); Perissodactyla: equid (horse, donkey); Lagomorpha: leporid (rabbit); Carnivora: canid (dog), felid (cat); Rodentia; Murid (rats); Primates: hominid (human), cercopithecid (monkeys); traps	annoyance, allergy (vector for trypanosomiases, anthrax, fungi, nematodes (*Habronema, Draschia*))	worldwide
S. indica (syn. *S. discalis, hastata, latipennis, limbata, pratti, pusilla, triangulais*)	Artiodactyla: bovid (cattle), traps	annoyance	Asia
S. inornata (syn. *S. rodhainica*)	Artiodactyla: bovid (cattle, buffalo), traps, dung	annoyance	Africa
S. luteola (syn. *S. ochrosoma*)	traps		Africa
S. nigra (incl. subspp. *nigra*, *bilineatus*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat); Perissodactyla: equid	annoyance (mechanical vector for	Africa

(syn. *S. bouvieri, clara, doryphora, glauca, griseola, halophila, lafonti, schoutedeni, sexvittata*)	(horse, donkey); Primates: hominid (human); traps	trypanosomiasis (nagana, surra))	
S. ochrosoma (syn. *S. flavida*)	Artiodactyla: bovid (cattle, buffalo), traps	annoyance	Africa
S. omega (incl. subspp. *omega, wigglesworthi*)	Artiodactyla: bovid (cattle, buffalo), traps, dung	annoyance	Africa
S. pallida (syn. *S. neavi*)	Artiodactyla: bovid (antelope); traps		Africa
S. pulla	traps		Asia
S. sitiens (syn. *S. dubitalis, separabilis*)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse, donkey); Primates: hominid (human); traps, dung	annoyance	Asia, Africa
S. stigma	traps		Africa
S. taeniata (syn. *S. brunnipes, intermedia, sellata*)	Artiodactyla: bovid (cattle, buffalo), traps, dung	annoyance (mechanical vector for trypanosomiasis (surra))	Africa
S. transvittata	dung		Africa
S. uruma	Artiodactyla: bovid (cattle, water buffalo); traps		Asia
S. varipes	traps		Africa
S. xanthomelas	Artiodactyla: bovid (cattle), traps, dung	annoyance	Africa

*Many studies report the collection of adult flies using odour-baited traps (in villages, farms and forests); or the emergence of adult flies from organic waste or animal dung collected from the environment.

Several other species have been reassigned to other genera: including *S. asiliformis* (now *Syneches muscarius*); *S. flava* (now *Fischeria bicolor*)*; S. humeralis* (now *Toxotarsus humeralis*)*; S. morio* (now *Hyperalonia morio morio*)*; and S. stimulans* (now *Haematobia* (*Haematobosca*) *stimulans*).

Parasite morphology: Stable flies (*Stomoxys* spp.) form 4 types of morphological developmental stages: eggs, larvae, pupae and adults. The eggs are white and have an elongate sausage shape measuring around 1 mm in length with one curved side and the other straight and bearing a longitudinal groove (hatching pleat). Larvae (known as maggots) have soft cream-coloured bodies that taper from the pointed anterior end to the blunted posterior end (oestroid larvae are more cylindrical). They develop through 3 instars (L1-3) growing from 1mm up to 11-12 mm in length. The body is segmented and lacks a sclerotized head capsule but has an internal cephalopharyngeal skeleton. The anterior mouth bears mouthhooks which are small in L1-2, but large and bill-shaped in L3. The segments lack bristles and legs but have ventral patches of small spines forming creeping welts. The larvae breathe using 2 pairs of respiratory spiracles: a small pair of anterior tubercle-like spiracles (absent in L1); and a larger pair of dark caudal spiracles, each appearing as a simple hole in L1, as 2 short stout non-sinuous slits on a weakly-pigment plate in L2, and as 3 longer sinuous slits on a heavily-pigmented sclerotized plate (peritreme) in L3. The caudal spiracles of *Stomoxys* spp. are further characterized by being subtriangular in shape and widely separated (compared to those in other muscid larvae). Mature L3 form barrel-like puparia 4-6 mm long by contraction and hardening of the tegument which gradually darkens to reddish-brown in colour. A pupa is formed inside which undergoes metamorphosis to form a winged adult which ecloses through a circular cap (like all Cyclorrhapha) rather than a longitudinal slit (like Nematocera and other Brachycera). Adult stable flies have small grey bodies 4-10 mm long, with 4 dark longitudinal stripes on the thorax and 3-7 circular black spots on the abdomen. Adults often have a thin or dense covering of fine setae (sometimes referred to as 'pollinosity'). They have 3 conspicuous body tagma: a globular head; pyriform thorax; and ovate abdomen. The large mobile head bears both a ptilinal suture and facial lunule (like other Muscoidea and Oestroidea, but unlike other calyprate flies) and 2 large brown well-developed compound eyes located laterally and separated by a frontal frons with 3 small ocelli. Adults have a pair of unique antennae that lie in an anterior groove in the head. The antennae are composed of 3 dissimilar segments, comprising a short basal scape, a longer pendulous pedicel, and a single plumose dorsal arista (bristle-like flagellum with short setae on the dorsal surface only). *Stomoxys* spp. are blood-feeders and have piercing-sucking mouthparts that are conspicuous as a stout proboscis projecting forwards when not in use. The proboscis is flanked by 2 short strap-like palps whose inner surfaces are not grooved (palps longer and grooved internally in *Haematobia*). The mouthparts comprise a small basal rostrum supporting a rigid haustellum that contains a hardened labium as a piercing structure, with the terminal labella reduced but armed with large sharp sclerotized teeth (replacing the pseudotracheae in sponging muscine flies). Once the host skin is cut, the labium is inserted into the wound and the contained labrum and hypopharynx come together to form a food canal. Blood is sucked up by the muscular pharynx (acting as a cibarial pump) and delivered to the tubular oesophagus and proventriculus (with associated storage diverticula) before being digested in the midgut with waste passed through the hindgut (with excretory Malpighian tubules) to the terminal anus. The thorax is covered by a rigid scutum which is grey with 4 prominent dark stripes (called vittae). Thoracic plates vary in their patterns of setation with stout bristles lacking on the anterior sternopleuron, hypopleuron, notopleuron (setulose in *Haematobosca*)

and propleuron (sometimes setulose in *Haematobosca*). The mesothorax sports a pair of stout wings with wing membranes supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] with vein A1 vanishing before the wing margin, vein M1 curving evenly towards the margin, and the discal cell having a symmetrical trapezoidal shape. Like all Diptera, the hindwings are highly reduced to a pair of knob-like halteres used to stabilize flight. The halteres are covered by posterobasal wing lobes (calypters) that distinguish all calyptrate flies. The ventral thorax gives rise to 3 pairs of legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus), and all ending in a pair of claws flanking 2 pads (pulvilli) and several central bristles (empodium). The short broad abdomen is darker dorsally than ventrally and the first few segments have several (3-7) dark grey-black circular spots giving them a mottled pattern. The number of visible segments is generally reduced to 5 (from 10-12) because the posterior segments are modified by terminalia (anal cerci in both sexes, retractable copulatory aedeagus and claspers in males, cylindrical telescoping ovipositor in females). Males have 2 testes connected by vas deferens to a seminal vesicle (with lateral accessory glands) and a tubular ejaculatory duct leading to the aedeagus in the genital pouch. Females have 2 ovaries joined to oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva and ovipositor.

Site of infection: Flies belonging to the genus *Stomoxys* are commonly called stable flies, but they are also known variously as beach flies, dog flies, lawn-mower flies and even biting house flies. The adults feed on blood from a small range of vertebrate hosts, mostly feeding on ungulates (horses, cattle, buffalo) but they will readily attack companion animals (dogs, cats), wildlife (deer, rabbits, rats) and even humans. Large animals are usually attacked on the legs, flanks, back and belly, while smaller animals are bitten around the face, ears, neck and legs. Stable flies now have a cosmopolitan distribution and are found on all continents except Antarctica, their dispersal aided by frequent livestock translocations.

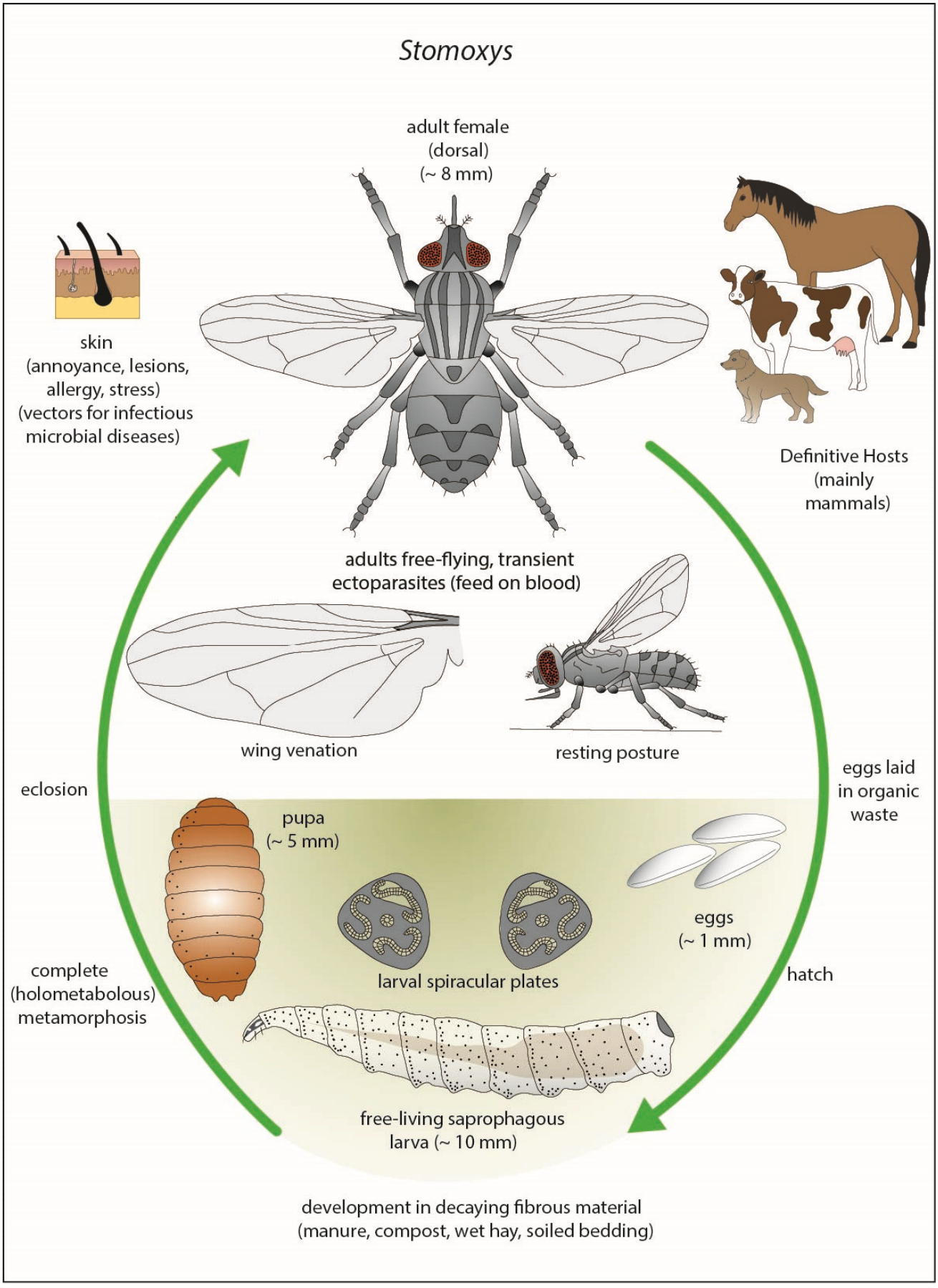
Pathogenesis: Stable flies are haematophagous and both sexes feed on vertebrate blood taking small blood meals once or several times a day (feeding lasting for a few minutes if undisturbed). They feed by cutting the skin with toothed mouthparts and then inserting stylets that couple together to form a tube to suck blood from dermal capillaries as well as deliver fly saliva. Fly bites are very painful and distressing to the host, resulting in intense irritation and disturbance (fly worry, biting stress) with livestock adopting aversive behaviours (swatting, stamping, kicking, bunching) that make them difficult to handle (muster, groom, milk). Hosts are disturbed from feeding which leads to decreased performance and productivity losses (poor weight gain, reduced milk yield). The bites cause traumatic skin damage with small punctate lesions evident as papules 5-10 mm in diameter with a small central scab. Host inflammatory responses result in welts with swelling that may cause hair covering the lesion to become raised. Hosts may attempt to relieve accompanying pruritus by biting, scratching or rubbing affected areas which can lead to self-trauma exacerbating wounds and opening them to secondary infections. Fly bites around the face and ears can lead to erythema, exudation and crust formation, including ear-edge dermatoses in dogs. While stable flies may engorge on blood up to 3 times their own body weight, most species do not attack in swarms dense enough to cause blood loss severe enough to manifest as anaemia. Stable flies are not renowned as vectors for the transmission of infectious diseases, although studies have shown they may transmit some trypanosomiases (sleeping sickness in humans, nagana in horses, cattle, sheep and goats, surra in horses and dogs, and mal de caderas in horses, cattle, sheep and goats), possibly equine infectious anaemia (retrovirus), and act as intermediate hosts for spirurid nematodes (*Habronema* and *Draschia*) producing summer sores in horses. Recent studies have also shown that several species of stable flies may act as hosts for a diverse array of acarine mites (5 families of Mesostigmata, 2 families of Prostigmata, and 4 families of Astigmata) which attach to external body surfaces. The significance of infestations is unknown, even though one genus (*Trichotrombidium*) is known to be an obligate parasitic mite of Muscidae, while most other mites were apparently opportunistic passengers engaged in phoretic transfer (paratenic transport) between vertebrate hosts.

Developmental cycle and mode of transmission: Muscid flies exhibit holometabolous development where eggs hatch grub-like larvae which undergo pupation to transform into winged adults. Female flies are oviparous and may lay up to 500-1,000 eggs in batches of 25-30 deposited in dung or decaying organic matter. The eggs hatch in 4-5 days releasing larvae which feed, grow and moult through 3 developmental instars (L1-3) over 12-13 days depending on the temperature (longer in colder conditions, with some over-wintering as larvae in temperate regions). The larvae develop best in decaying fibrous substrates such as manure, soiled straw bedding, wet hay, silage, compost, algal mats, moist grass clippings, and mounds of decaying vegetation (including sugarcane bagasse, beet pulp and peanut hulls from processing plants). The larvae are saprophagous and feed on vegetable matter and micro-organisms including bacteria, yeasts and algae (in comparison, the larvae of some other muscid genera may also be facultative predators). Pupation then occurs in the same habitat, but often at the periphery where the soil is drier. Mature L3 cease feeding and form puparia by contraction and hardening of the tegument. A pupa forms inside and undergoes metamorphosis to an adult over a period of 6-26 days depending on temperature (longer in colder conditions). Teneral adults eclose from pupae and after a short period for their cuticle and wings to harden, they fly in search of hosts on which to feed. They are strong fliers and persistent in their efforts to feed on vertebrates. Both males and females feed exclusively on host blood, and females are anautogenous and require bloodmeals to complete gonotrophic (ovarian) cycles. Mating occurs shortly after eclosion when males perch on substrates to intercept passing females. After mating, females store enough sperm to remain fertile for life and they may produce 50-100 eggs in each ovarian cycle. Adults generally live for 1-2 months in cooler weather, but only 3-4 weeks in hotter weather. Most species are multivoltine and form multiple generations each year, the number being dependent on the prevailing climatic conditions in different geographic locations. Breeding may occur continuously in tropical and subtropical regions, but may be confined to warm seasons in

colder temperate regions. Stable flies are generally most abundant in summer and autumn, and can often be observed resting in sunny locations (on trees, fences, barns, houses) seeking hosts or mates, or digesting bloodmeals. Adult flies are active during the day and prefer direct sunlight but will follow animals into the shade, including entering buildings.

Differential diagnosis: Most attacks by stable flies are indicated by the searing pain accompanying their persistent attempts to bite and feed. However, the resultant skin lesions are not pathognomic and may be attributable to other ectoparasites. Diagnosis is usually confirmed by capturing feeding flies (by hand, nets or baits) and identifying them by close examination (aided by magnifying glasses). Stable flies are superficially similar in appearance to house flies but are slightly smaller and have a distinctive stiletto-like proboscis (for biting) while house flies have smaller stouter mouthparts (for sponging). Modern molecular biological studies have been conducted to characterize species and determine their phylogenetic relationships, mostly following polymerase chain reaction (PCR) amplification of nuclear and mitochondrial gene sequences, although the whole genome of *S. calcitrans* has been completed.

Treatment and control: If required, stable fly bites may be treated topically with anti-inflammatory, analgesic and antiseptic preparations, or systemically with corticosteroids and antihistamines, to alleviate irritation and pruritus. Agitated or distressed animals (mostly horses) may require tranquilisers. Animals may be protected from stable flies to some degree by the topical application (sprays, dusts, some pour-ons, impregnated ear-tags) of chemical insecticides, such as organochlorines, organophosphates and pyrethroids. Many preparations do not last long on hosts and need to be regularly re-applied to achieve protection. Some preparations have longer residual activities and may be used to treat animals or to spray resting sites where flies congregate, such as barnyard fences, stalls, and walls. Insecticides should not be used indiscriminately to lessen the chances of the development of insecticidal resistance and to mitigate their detrimental effects as they accumulate in the environment. Aerosol space-sprays have been used to kill adult flies in intensive-husbandry situations (stables, dairies, feedlots) but they are not effective in windy conditions, and droplet sizes need to be small enough for adequate dispersal. Chemical fly repellents (such as DEET) have also been used directly on hosts on sparsely-haired sites or in closed quarters to deter stable flies. The use of fly traps, electric grids and baits have not proven particularly effective against blood-feeding stable flies. Animal and farm management practices may be modified to protect stock from fly bites as well as to control fly populations by reducing available larval habitats. The use of fly barriers (doors, screens, curtains, nets) may protect indoor spaces, and animals may be housed during periods of peak fly activity. Every effort should be made to eliminate potential breeding sites for larvae by managing organic waste through improved hygiene and better sanitation (including dung removal, disposal of soiled bedding, periodically turning compost piles, avoiding accumulations of grass cuttings and other vegetation, storing feedstuffs high and dry, and cleaning up spilled feed). Several studies have begun to investigate methods for biological control, particularly using dung beetles to reduce larval habitats, and parasitoids (wasps and beetles) which reproduce in stable fly larvae and/or pupae.


Stomoxys
adult female
(dorsal)
(~ 8 mm)
skin
(annoyance, lesions,
allergy, stress)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mainly
mammals)
adults free-flying, transient
ectoparasites (feed on blood)
wing venation
resting posture
eclosion
eggs laid
in organic
waste
pupa
(~ 5 mm)
eggs
(~ 1 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
hatch
free-living saprophagous
larva (~ 10 mm)
development in decaying fibrous material
(manure, compost, wet hay, soiled bedding)



Stomoxys adult



Stomoxys eggs



Stomoxys larva



Stomoxys larval spiracles



Stomoxys pupa

Haematobia
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Muscid flies include many non-biting and biting genera, the former being nuisances and the latter being blood-feeders. Most species are synanthropic (closely associated with humans) and they breed in all types of organic waste. Two subfamilies are recognized: muscines (house flies, bush flies, face flies) with sucking mouthparts adapted to feeding on decaying organic matter; and stomoxines (stable flies, horn/buffalo flies) with elongate biting mouthparts adapted to blood feeding. Horn flies (*Haematobia* spp.) are significant pests of cattle throughout the world and they may also transmit bovine mastitis and filarial nematodes.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Muscidae (house/bush/stable/buffalo flies, nuisance flies, synanthropic (associated with human activity))
Subfamily:	Stomoxinae (with elongate biting mouthparts adapted to blood feeding)
Genus:	*Haematobia* (parasitic on skin of bovines)
Species:	various species cause annoyance

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders

are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora

(containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases).

The superfamily Muscoidea contains 4 families: Muscidae (house flies), Fanniidae (latrine flies), Scathophagidae (dung flies) and Anthomyiidae (anthomyiid flies). The family Muscidae contains robust flies with plumose aristae and wings where vein A2 is not strongly curved (unlike latrine flies). The family contains both free-living flies, some of which are nuisance pests of livestock and humans, as well as blood-sucking flies feeding on vertebrates. Over 4,200 species have been described in some 190 genera classified into 9-10 subfamilies: Achanthipterinae, Azeliinae, Coenosiinae, Cyrtoneurininae, Dichaetomyiinae, Muscinae, Mydaeinae, Phaoniinae, and Reinwardtiinae [some authorities recognize 2 tribes (Muscini and Stomoxyini) in the subfamily Muscinae, while others have elevated the latter tribe to subfamily status (Stomoxinae)].

Subfamily	Genera	Hosts	Site	Transmission
Muscinae (with sponging mouthparts)	*Musca*	mammals,	nonparasitic	nonparasitic
Stomoxinae (with biting mouthparts)	*Stomoxys*	mammals	skin	direct
	Haematobia	bovines	skin	direct

The subfamily Stomoxinae contains 4 genera: *Haematobia*, *Haematobosca*, *Stygeromyia* and *Stomoxys* - although some authorities have merged the genus *Haematobosca* with *Haematobia*. These flies have elongate biting mouthparts adapted to blood feeding on a wide variety of mammalian hosts, especially cattle and buffalo in both tropical and temperate regions. In particular, the buffalo fly (*H. exigua*) and the horn fly (*H. irritans*) cause significant fly worry in their hosts, papular skin lesion in allergic individuals, and act as vectors for the transmission of filarial nematodes and possibly protozoal theileriosis.

Fly species	Hosts	Clinical signs	Distribution
Haematobia (syn. *Glossinella*, *Haemathobia*, *Haphospatha*, *Hoematobia*, *Lyparosia*, *Lyperosia, Priophora, Siphona*)			
H. exigua (syn. *H. irritans exigua, australis, flavohirta*) (buffalo fly)	Artiodactyla: bovid (cattle, water buffalo, bison), camelid (camel), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig)	irritation, blood loss (vector for *Stephanofilaria*)	Asia, Australia
H. irritans (syn. *H. cornicula, pungens, serrata, tibialis, Lyperosia irritans, meridionalis, rufifrons, weissi, Conops irritans*) (horn fly)	Artiodactyla: bovid (cattle, water buffalo, bison, sheep, goat), camelid (camel), suid (pig); Perissodactyla: equid (horse, donkey); Carnivora: canid (dog); Primates: hominid (human)	irritation, blood loss (vector for *Stephanofilaria, Parabronema, Habronema*)	Eurasia, North Africa, North America, Australia
H. meridiana	Artiodactyla: giraffid (giraffe), suid (warthog)	irritation	Africa
H. minuta (syn. *H. longipalpis, potrix, Lyperosia*)	Artiodactyla: bovid (cattle, buffalo, water buffalo, tiang); Perissodactyla: equid (horse); Primates: hominid (human)	irritation, blood loss (vector for *Stephanofilaria*)	Africa
H. shillingsi	Perissodactyla: rhinocerotid (black rhinoceros)	irritation	Africa
H. spinigera	Artiodactyla: bovid (cattle, buffalo), giraffid (giraffe); Perissodactyla: equid (zebra)	irritation	Africa
H. thirouxi (incl. subspp. *potans, thirouxi*) (syn. *H. hirudo*)	Artiodactyla: bovid (cattle, buffalo, sheep, impala, korrigum); Perissodactyla: equid (horse, Burchell's zebra,), rhinocerotid (black rhinoceros); Carnivora: canid (dog); Primates: hominid (human)	irritation	Africa
H. titillans (syn. *H. thirouxi titillans, bovina, equina, latirostris, scolopax*)	Artiodactyla: bovid (cattle, sheep, goat), camelid (camel); Perissodactyla: equid (horse)	irritation (vector for *Stephanofiliaria, Parabronema*)	Asia

Haematobosca (syn. *Bdellia*, *Bdellolarynx*, *Haematobina*, *Lyperosiops*, more recently synonymized with *Haematobia* by various authorities)			
Hb. aberrans	traps*, buffalo farm		Asia
Hb. alcis (= *crassipalpis*)	Artiodactyla: cervid (moose)	irritation	Holarctic
Hb. atripalpis (syn. *Hb. perturbans*)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse, donkey)	(vector for *Parafilaria*)	Palearctic
Hb. augustifrons	traps		Africa
Hb. aurata	traps		Africa
Hb. croceicornis	traps		West Africa
Hb. decipiens	traps		Europe
Hb. evecta	traps		Europe
Hb. hirtifrons	traps		Africa
Hb. kangwagyei	traps		Africa
Hb. latifrons (syn. *Hb. mallochi*)	Artiodactyla: bovid (cattle, buffalo)		Africa
Hb. praedatrix	traps		Africa
Hb. sanguinolenta (syn. *Bdellolarynx, Haematobia aculeata, caraboa, chinensis, nudinervis, rufipes, Siphona carabao, Stomoxys chinensis*)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse, donkey)	irritation	Asia, Africa
Hb. squalida (syn. *Hb. lutosa*)	Artiodactyla: bovid (cattle, buffalo), traps		Africa
Hb. stimulans (syn. *Hb. melanogaster, ferox, geniculata, vernalis, ryszardi, Siphona*) (large horn fly, large meadow bite fly)	Artiodactyla: bovid (cattle, water buffalo), cervid (elk); Perissodactyla: equid (horse); Primates: hominid (human)	irritation, blood loss (vector for *Stephanofilaria, Setaria*)	Palearctic, Central Asia
Hb. trivittata	traps		Eurasia
Hb. uniseriata	traps; Artiodactyla: suid (warthog)		South Africa
Hb. wooffi	Artiodactyla: bovid (cattle, buffalo)		Africa
Hb. zuluensis	traps		South Africa

*Collections made from environment using traps or nets for adult flies.

Parasite morphology: *Haematobia* and *Haematobosca* spp. form 4 different types of morphological stages: eggs; larvae; pupae; and adults. Eggs are ovoid, but concave on one side and convex on the other, measuring around 1mm long and appear white, yellow or tan when laid but darken to a reddish brown. Larvae (known as maggots) have white elongate tapered bodies, with an anterior pointed end bearing the head and a posterior blunted end bearing dark dorsal spiracular plates (oestroid larvae are more cylindrical). They develop through 3 instars (L1-3) growing from 1.5 mm up to 7 mm in length. Larvae lack a sclerotized head capsule but they have an internal cephalopharyngeal skeleton bearing mouthhooks (small and rounded in L1-2 and large and bill-shaped in L3). They have 12 body segments and are legless, but they have patches of tiny spines on ventral abdominal segments forming creeping welts. They breathe using 2 pairs of respiratory spiracles: a small anterior pair (absent in L1) apparent as branched tubercles; and larger posterior pair evident as simple holes in L1 and as 3 sinuous slits with an ecdysal scar on a pigmented plate (peritreme) in L2-3. In muscid larvae, the spiracular slits slant towards the midline, while those in sarcophagid larvae slant away from midline (in contrast, oestrid larvae have porous spiracular plates). Mature L3 form barrel-shaped puparia 3-4 mm long by contraction and hardening of the tegument which gradually darkens from white to reddish-brown. Inside, a pupa is formed which undergoes metamorphosis to form a winged adult which ecloses through a circular cap (like all Cyclorrhapha) rather than a longitudinal slit (like Nematocera and other Brachycera). Adult flies range in size from 3-6 mm long and have brown-grey to black shiny bodies with a dense covering of fine setae (sometimes referred to as pollinosity) which is grey-olive in *Haematobia* spp. and yellow-black in Haematobosca spp. They have 3 conspicuous body tagma: a rounded head; stout pyriform thorax; and ovate abdomen. The head has both a ptilinal suture and facial lunule (like other Muscoidea and Oestroidea, but unlike other calyprate flies) and 2 large red-brown compound eyes located laterally and separated by a frontal frons with 3 small ocelli. A pair of unique reddish-brown antennae lie in an anterior groove on the frons, each antenna composed of 3 dissimilar segments, comprising a short basal scape, a longer pendulous pedicel, and a single plumose dorsal arista (bristle-like flagellum) with short setae on the dorsal surface for *Haematobia* but on the dorsal and ventral surfaces for *Haematobosca.* Adult flies are biting blood-feeding species and have piercing-sucking mouthparts projecting forwards as a single proboscis when not in use. The proboscis is flanked by a pair of grey-yellow palps that are as long as

the proboscis and strap-like with grooves on the internal surfaces (cf. biting Stomoxys flies have shorter non-grooved palps). The mouthparts consist of a small basal rostrum supporting a rigid haustellum with a hardened labium and terminal labella armed with large sharp sclerotized teeth (replacing the pseudotracheae in sponging muscine flies). Once the host skin is cut by the labella, the labium is inserted into the wound and the contained labrum and hypopharynx come together to form a food canal. Blood is ingested using strong pharyngeal muscles and routed through the tubular oesophagus and proventriculus (with associated storage diverticula) before being digested in the midgut with waste passed through the hindgut (with excretory Malpighian tubules) to the terminal anus. The thorax is covered by a hard brown scutum with 2 parallel dark stripes running dorsally just behind the head. The thoracic plates vary in their patterns of setation, the hypopleuron lacking a row of stout setae, and the notopleuron and propleuron bare in *Haematobia* (like *Stomoxys*) or setulose in *Haematobosca*. The mesothorax sports a pair of stout shiny wings that are held flat over the abdomen at rest, but held at an angle to the body when feeding to form a reflective angular shape. Wing membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] with vein A1 vanishing before the wing margin, vein M1 curving evenly towards the margin, and the discal cell having a symmetrical trapezoidal shape. Like all Diptera, the hindwings are highly reduced to a pair of knob-like halteres used to stabilize flight. The halteres are covered by posterobasal wing lobes (calypters) that distinguish all calyptrate flies. The ventral thorax gives rise to 3 pairs of legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus), and all ending in a pair of claws flanking 2 pads (pulvilli) and several central bristles (empodium). The abdomen does not have marked dorsal patterns of pigmentation (like Stomoxys) and the number of visible segments is generally reduced to 5 (from 10-12) because the posterior segments are modified by terminalia (anal cerci in both sexes, retractable copulatory aedeagus and claspers in males, cylindrical telescoping ovipositor in females). Males have 2 testes connected by vas deferens to a seminal vesicle (with lateral accessory glands) and a tubular ejaculatory duct leading to the aedeagus in the genital pouch. Females have 2 ovaries joined to oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva and ovipositor.

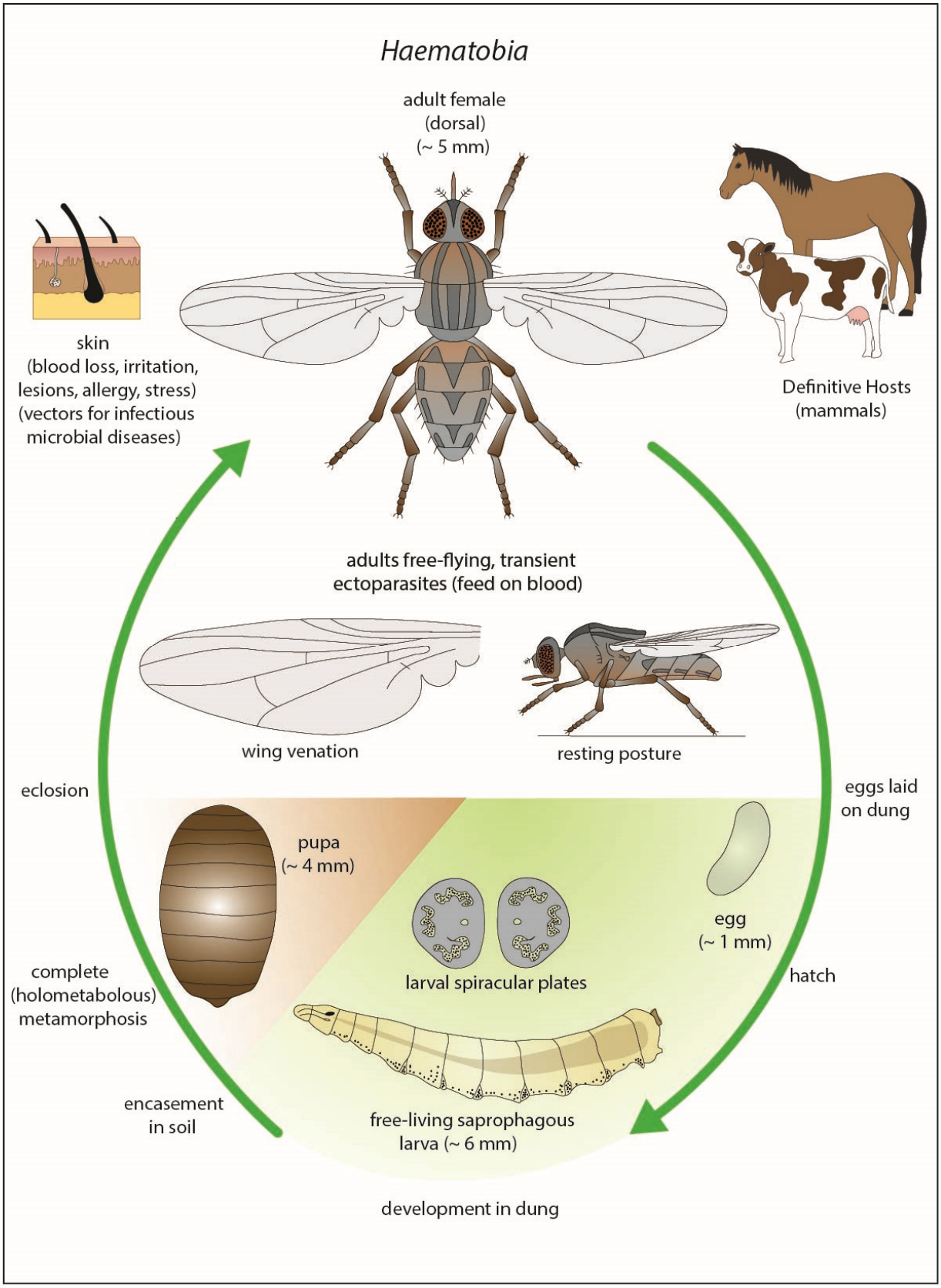
Site of infection: Adult flies are obligatory ectoparasites that must feed on vertebrate blood to complete their life-cycles. Buffalo and horn flies feed primarily on blood from bovid hosts (especially cattle and buffalo), but they may feed opportunistically on other hosts, notably larger ungulates, and sometimes humans. Adult flies prefer short-haired dark-coloured hosts, apparently for ease of access to the skin as well as for camouflage against predators. Horn flies (*H. irritans*) were originally given their common name because they cluster around the horns, but both horn flies and buffalo flies (*H. exigua*) often congregate on areas least likely to be disturbed (neck, belly, thighs, shoulders, flanks and back). Horn flies remain in contact with their hosts both day and night, resting with their heads down (cf. stable flies rest with their heads up), while *Haematobosca stimulans* spend less time resident on their hosts. Adult flies have been observed to be most abundant on short-haired bulls, followed by steers, cows and then calves. Females flies leave their hosts usually only as long as it takes to deposit eggs in manure where the larvae develop.

Pathogenesis: These biting flies are haematophagous and both sexes use their piercing-sucking mouthparts to feed on vertebrate blood, males feed up to 20 times a day while females feed up to 40 times daily. Adult flies tend to associate with individual hosts or a small numbers of hosts within a herd, and populations of several thousand flies may occur on individual hosts. Flies move around the body of the host apparently to regulate temperature and avoid wind and rain, often relocating to the belly during the hottest parts of the day. An individual fly may consume 10-21 µl of blood per day, so heavy infestations can cause significant blood loss resulting in anaemia, particularly in young animals. Adult flies use their labellar teeth to cut the skin and then insert their labium into the wound. The labrum and hypopharynx come together to form a food canal through which the flies suck blood from dermal capillaries as well as to inject saliva containing anticoagulant properties. Flies repeatedly insert, withdraw and re-insert their mouthparts several times during feeding, which causes considerable trauma, pain and irritation. Bites are evident as inflamed erythematous papules with a central puncture wound. These lesions can persist for several days and become scabs covered with dried exudates. The wounds are intensely pruritic, and hosts seek to relieve the itch by biting, scratching or rubbing affected regions, which may cause self-trauma and open ulcerative wounds susceptible to secondary infections, even attracting other flies. Persistent attack often leads to ventral, and sometimes periorbital, dermatitis in horses and cattle. Dermal lesions may be severe enough to cause cosmetic defects in tanned and dyed leather. Some individual hosts become allergic to fly saliva and develop hypersensitivity reactions with severe dermatitis, oedema, thickened scaly skin, alopecia and wet eczema around bites (such individuals are often culled from herds to improve herd resistance). Animals subject to sustained fly-worry exhibit many aversive behaviours (licking backs, twitching flanks, swishing tails, stamping feet, kicking at belly, standing in water) which sometimes makes them difficult to handle (muster, groom, treat). They become distracted from feeding and exhibited productional losses due to decreased weight gain, reduced milk production, poor reproductive performance and damaged hides. It has been estimated that as few as 30 buffalo flies or 12 horn flies may reduce weight gain in cattle, and producers consider infestations in excess of 100-200 flies sufficient grounds to commence treatment. These biting flies are not major vectors for the transmission of infectious microbial diseases because they spend so much of their lives on individual, or only a few, hosts. Horn flies have been shown to act as intermediate hosts for the spirurid nematode *Stephanofilaria stilesi* which can cause granular dermatitis in cattle. They may act as mechanical vectors for summer mastitis caused by bacteria (*Staphylococcus aureus* and others) and possibly several other bacterial infections (*Salmonella enterica, Staphylococcus saprophyticus, Morganella morganii, Serratia marcescens*). Buffalo flies have been found to act as intermediate hosts for various nematodes (*Stephanofilaria, Setaria, Parafilaria, Habronema*) causing crusted skin lesions in cattle. Molecular screening studies have returned positive results for *Theileria orientalis* in buffalo flies, but their involvement in transmission is unknown.

Developmental cycle and mode of transmission: Like all dipterans, these flies undergo holometabolous (complete) metamorphosis as their grub-like larval stages transform in pupae into winged adult flies. They are commonly known as dung biting flies as they breed in dung and feed by biting hosts to suck blood. Gravid female flies leave their hosts temporarily to oviposit 12-30 eggs almost exclusively in crevices or under edges (away from light) of undisturbed dung pats, sometimes on adjacent blades of grass. The dung is usually fresh (within minutes of host defaecation) and invariably from cattle or buffalo (dung from horses, sheep and other large mammals is not suitable). The eggs hatch in 12-24 hours releasing first stage larvae (L1) which burrow into nutrient-rich areas in the faeces and feed on bacteria. They develop through 2 more larval instars (L2-3) over 4-8 days before burrowing downwards away from the crust towards the soil. Mature L3 form puparia by hardening of the tegument and the enclosed pupae transform into winged adult flies over 5-8 days, although pupation may be delayed for several days or weeks depending on environmental conditions (horn fly pupae may over-winter in some temperate regions leading to synchronized emergence and fly swarms). Adult flies eclose from pupae and fly free in the environment during the day seeking hosts on which to feed (they do not survive more than a few days without a host). Once a suitable host is located, adult flies rarely leave the host unless to mate or lay eggs (although *Haematobosca* spp. spend less time on hosts than *Haematobia* spp.). Their reproductive organs mature over several days and mating commences. Both male and female flies feed on blood but females are anautogenous and require bloodmeals to complete their gonotrophic (ovarian) cycles. Females produce eggs 3-4 days after feeding and they may lay 80-100 eggs (sometimes up to 400) in their life-times. Adult flies only live for 1-3 weeks and their whole life-cycle may be completed in 10-14 days in optimal environmental conditions, but the cycle may be extended for several weeks in cooler weather (larvae do not hatch at temperatures below 11°C). Transmission from host-to-host occurs when newly-hatched adults search for hosts (sometimes flying up to 10 km), when female flies return to different hosts after laying eggs, and when flies transfer between hosts in close contact (at herding, mustering, mating, milking, etc.). Fly reproduction is continuous and most populations are multivoltine with multiple generations occurring each year (fewer in colder regions). Infestations appear seasonal and flies are more abundant in summer and autumn. Haematobia spp. occur in most cattle-producing regions around the world and their geographic distribution in temperate regions is often restricted to those with warmer winters (frosts kill over-wintering pupae).

Differential diagnosis: Infestations in livestock may be suspected on the basis of clinical signs (behavioural changes, skin lesions) and history (seasonal occurrence), but are readily confirmed by direct observation and identification of biting flies (small grey-black flies with thoracic stripes, overlapping wings and prominent proboscis with long palps). Other fly species associated with cattle may need to be discounted, such as stable flies, face flies and even house flies. Adult flies can be collected for examination by swatting, spraying, netting or trapping. A range of molecular biological techniques have been used to characterize species and populations following polymerase chain reaction (PCR) amplification of fly DNA (random amplified polymorphic DNA (RAPD), nuclear genes (ribosomal DNA), mitochondrial genes (cytochrome c oxidase) and even the whole genome for the horn fly). Other molecular characterization studies are investigating the diversity of bacteria associated with flies, including endosymbionts.

Treatment and control: Skin severely affected by fly bites may be treated on individual animals with topical or systemic glucocorticoids, antihistamines, antiseptics and antibiotics to relieve clinical signs (inflammation, pruritus) and combat secondary infections. Many producers resort to culling allergic cattle to improve herd resistance, but taking care not to confuse diagnoses (similar sores may be caused by other unrelated pathogens). Infestations on livestock may be combated using conventional and modern insecticides, applied as sprays, dips, dusts, pour-ons, impregnated tags, injectable or oral medications. Successful treatments have included a range of organochlorines, organophosphates, pyrethroids, carbamates, and macrocyclic lactones, but resistance to some insecticides in the first 3 categories have emerged in fly populations. Insecticides with longer residual activities have proven efficacious against persistent fly populations and the use of fly repellents (such as DEET) assists treatment. Treatment of the environment with residual insecticides has limited effect as flies reside on the hosts rather than on nearby substrates, and the treatment of dung pats is discouraged as insecticides may kill natural predators, parasitoids and parasites of flies. Several studies have shown that cattle given methoprene (topical, injectable or sustained-release boluses) produce dung pats that partially inhibit egg hatching and/or pupal eclosion, thus reducing fly populations. Alternatively, potential breeding sites may be reduced by improving pasture hygiene through dung removal, dung spreading, or introducing dung beetles. Fly traps may also be used around mustering or watering points where stock are trained to walk through darkened veiled tunnels which dislodges flies near sticky, insecticidal or electric baits. Recent studies on biological control have shown some promise with the identification of some predatory beetles, ants, wasps and other muscid larvae that kill larval and/or pupal stages, and observations that the bacterial insecticide *Bacillus thurigiensis* was highly toxic against larvae.


Haematobia
adult female
(dorsal)
(~ 5 mm)
skin
(blood loss, irritation,
lesions, allergy, stress)
(vectors for infectious
microbial diseases)
Definitive Hosts
(mammals)
adults free-flying, transient
ectoparasites (feed on blood)
wing venation
resting posture
eclosion
eggs laid
on dung
pupa
(~ 4 mm)
egg
(~ 1 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
hatch
encasement
in soil
free-living saprophagous
larva (~ 6 mm)
development in dung



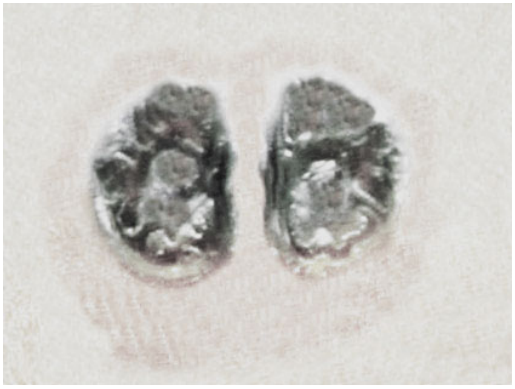
Haematobia adults



Haematobia adult



Haematobia larva



Haematobia adult

Lucilia, Calliphora
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Calliphorids (blow flies) are not parasitic as adults but their larvae help destroy carcasses and may cause traumatic cutaneous myiases (flystrike, screwworm infestation) in live mammals. Adult flies are large and often metallic in colour. Eggs laid on hosts release larvae which may penetrate the skin to feed on subcutaneous tissues. Most species are facultative invaders causing primary, secondary or tertiary strike, although several (notably screwworms) are obligate parasites. Larvae of *Lucilia* and *Calliphora* species are primary or secondary facultative invaders and cause serious flystrike in domestic livestock.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Calliphoridae (blow flies, often metallic, larvae cause myiases (flystrike/screwworm infestation))
Genus:	*Lucilia* (primary) (parasitic on skin/subcutaneous tissues of mammals)
Genus:	*Calliphora* (secondary) (parasitic on skin/subcutaneous tissues of mammals)
Species:	various species cause myiasis (flystrike) in sheep)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders

are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora

(containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases). Several superfamilies contain species whose larvae feed on the flesh of vertebrate hosts, mostly when dead (carrion) but sometimes when still living (causing fly-strike). Oestroid and muscoid larvae are well-adapted for living in moist organic substrates ranging from wet faeces to carrion to living flesh.

The superfamily Oestroidea contains large flies that are not dorsoventrally flattened, their wing veins are not crowded, and the discal medial cell of the wings widens gradually. The superfamily contains 7 families: Calliphoridae (blow flies, written as two words to distinguish them from other fly-like insects with compound names such as dragonflies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Calliphoridae is characterized by blow flies with metallic iridescent bodies (blue-black, violet-blue, green), strong bristles, well-developed mouthparts and antennae, and weak post-scutellum. The family contains over 1,100 species of blow flies, carrion flies, bluebottles, greenbottles and cluster flies which help destroy carcases, although many species have been implicated in larval myiasis ('flystrike') in living animals. Most invasions are facultative (opportunistic) causing primary, secondary or tertiary flystrike (categorized according to whether they initiate strike or occur later), although several species (notably screwworms) are obligate parasites whose larvae must develop in flesh. The larvae of most blow fly species are not selective feeders and they exhibit broad host specificity, usually for mammals, occasionally birds and less commonly amphibians and reptiles. Myiasis-causing flies have been found worldwide, particularly in temperate and tropical regions with large domestic livestock populations, but also in cooler regions where wildlife abound. Some 75 genera have been described in 11 subfamilies: Ameniinae, Aphyssurinae, Auchmeromyiinae, Calliphorinae, Chrysomyinae, Helicoboscinae, Melanomyinae, Mesembrinellinae, Phumosinae, Rhiniinae and Toxotarsinae, with another 14 unplaced genera and several fossil genera. The subfamily Chrysomyinae comprises blow flies distinguished by setose stem veins, while members of the subfamily Calliphorinae are characterized by adult flies bearing wings with bare stem veins.

Family	Genera	Hosts	Strike	Myiasis*
Calliphoridae	*Lucilia*	mammals	primary	Facultative (AU, CU, GI, NP, TR, UG)
	Calliphora	mammals	secondary	Facultative (AU, CU, GI, NP, TR, UG)
	Cochliomyia	mammals	primary, secondary	Facultative or obligate (TR)
	Chrysomya	mammals	primary, secondary	Facultative or obligate (TR)
	Cordylobia	mammals	primary	Obligate (CU, TR)

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

Five tribes are recognized in the subfamily Calliphorinae (namely, Bengaliini, Calliphorini, Luciliini, Melanodexiini, and Polleniini); with the tribe Calliphorini (bristly lower calypter, bare suprasquamal ridge) containing 18 genera (including *Calliphora*) and the tribe Luciliini (bare lower calypter, setate suprasquamal ridge) containing 5 genera (including *Lucilia*). The genus *Lucilia* (syn. *Acrophagella, Argoracrites, Bufolucilia, Caesariceps, Chaetophaenicia, Dasylucilia, Phaenicia*) contains over 260 species, with some classified in 4 subgenera but most remaining unassigned. Many species are known commonly as green bottle flies due to the metallic coppery-green thorax and abdomen of adults, although some species may be bronze to blue in colour. The genus *Calliphora* (syn. *Abonesia, Acronesia, Acrophaga, Steringomyia, Stobbeola*) contains almost 150 species with most classified in 12 subgenera, although 30 species remain unplaced. Many species appear as blue or brown bottle flies with a grey thorax and honey-coloured abdomen, but the colour variation of species ranges from black-grey through brown to blue-green. The larvae of several calliphorine species parasitize the dermal tissues of live mammalian hosts, causing fly-strike which is costly to livestock industries, in terms of lost production and expensive treatment and prevention. Many primary strike flies belong to the genus *Lucilia* (esp. *L. cuprina, L. sericata*) while many secondary or tertiary strike flies belong to the genera *Calliphora* (incl. *C. stygia, C. augur, C. albifrontalis, C. vicina*)

Calliphorid fly species	Hosts	Location	Clinical signs	Distribution

Tribe: *Luciliini* (bare lower calypter, setate suprasquamal ridge)				
L. cuprina (greenbottle fly, Australian sheep blow fly)	carrion, plus live sheep, other wild and domestic animals, human	skin	primary facultative myiasis (irritation, lesions, distress, anaemia, toxaemia, anorexia)	worldwide
L. sericata (European greenbottle fly)	sheep, other wild and domestic mammals, birds, lizards, human	skin	primary facultative myiasis (irritation, lesions, distress, anaemia, toxaemia, anorexia) (plus mechanical vectors for *Mycobacterium*)	worldwide
Tribe: Calliphorini (bristly lower calypter, bare suprasquamal ridge)				
C. albifrontalis (Western Australian brown blow fly)	carrion, plus live sheep, other wild and domestic animals	skin	secondary or tertiary facultative myiasis (lesions)	Australasia
C. augur (lesser brown blow fly, blue-bodied blow fly)	carrion, plus live sheep, other wild and domestic animals	skin	secondary or tertiary facultative myiasis (lesions)	Australasia
C. nociva (syn. *C. dubia*) (lesser brown blow fly)	carrion, plus live sheep, other wild and domestic animals	skin	secondary or tertiary facultative myiasis (lesions)	Australasia
C. stygia (syn. *C. laemica*) (large brown blow fly, eastern golden-haired blow fly)	carrion, plus live sheep, other wild and domestic animals	skin	secondary, sometimes primary, facultative myiasis (lesions)	Australasia
C. vicina (syn. *C. erythrocephala*) (bluebottle fly)	carrion, plus wild and domestic animals	skin	secondary facultative myiasis (lesions)	worldwide
C. vomitoria (bluebottle fly)	carrion, plus wild and domestic animals	skin	secondary facultative myiasis (lesions)	worldwide

Full species list (compilation of several on-line data-bases)

***Lucilia* species**	**Subgenus**
L. adisoemartoi	Unassigned
L. aestuans	Unassigned
L. affinis	Unassigned
L. agilis	Unassigned
L. albofasciata	Unassigned
L. albofusca	Unassigned
L. amoena	Unassigned
L. ampullacea	Unassigned
L. andrewsi	Unassigned
L. angustifrons	Unassigned
L. angustifrontata	Unassigned
L. appendicifera	*Sinolucilia*
L. ardens	Unassigned
L. arrogans	Unassigned
L. arvensis	Unassigned
L. aurata	Unassigned
L. aureovultu	Unassigned
L. azurea	Unassigned
L. basalis	Unassigned
L. basifera	Unassigned
L. bazini	*Lucilia*
L. benigna	Unassigned
L. bicolor	Unassigned
L. bismarckensis	Unassigned
L. blanda	Unassigned

L. bufonivora	*Bufolucilia*
L. caerulea	Unassigned
L. caeruleiviridis	Unassigned
L. caerulescens	Unassigned
L. caesar	*Lucilia*
L. caesarina	Unassigned
L. caesarion	Unassigned
L. caesia	Unassigned
L. calidula	Unassigned
L. calviceps	Unassigned
L. campestris	Unassigned
L. carbunculus	Unassigned
L. chini	*Bufolucilia*
L. chrysella	Unassigned
L. chrysigastris	Unassigned
L. chrysis	Unassigned
L. cinctella	Unassigned
L. claviceps	Unassigned
L. cluvia	Unassigned
L. coccinea	Unassigned
L. coelestis	Unassigned
L. coeruleifrons	Unassigned
L. coeruleiviridis	Unassigned
L. cognata	Unassigned
L. consobrins	Unassigned
L. cornicina	Unassigned

L. corusca	Unassigned
L. cuprea	Unassigned
L. cuprina	Unassigned
L. cyanea	Unassigned
L. cyanella	Unassigned
L. cylindrica	Unassigned
L. deceptor	Unassigned
L. decora	Unassigned
L. delicatula	Unassigned
L. deses	Unassigned
L. diffusa	Unassigned
L. dimidiata	Unassigned
L. discolor	Unassigned
L. diversa	Unassigned
L. dives	Unassigned
L. docilis	Unassigned
L. dolosa	Unassigned
L. dorsalis	Unassigned
L. dulcis	Unassigned
L. elegans	Unassigned
L. elongata	Unassigned
L. erythraea	Unassigned
L. exilis	Unassigned
L. eximia	Unassigned
L. facialis	Unassigned
L. fastuosa	Unassigned
L. fausta	Unassigned
L. favilla	Unassigned
L. fayeae	Unassigned
L. fernandica	Unassigned
L. fervida	Unassigned
L. flagrans	Unassigned
L. flammea	Unassigned
L. flammula	Unassigned
L. flaviceps	Unassigned
L. flavidipennis	Unassigned
L. flavipalpis	Unassigned
L. floralis	Unassigned
L. foetida	Unassigned
L. fulgens	Unassigned
L. fulges	Unassigned
L. fulgida	Unassigned
L. fulvicornis	Unassigned
L. fulvifrons	Unassigned
L. fulvipes	Unassigned
L. fulvocothurnata	Unassigned
L. fumicosta	Unassigned
L. fuscanipennis	Unassigned
L. fuscipalpis	Unassigned
L. gemma	Unassigned
L. gemula	Unassigned
L. germana	Unassigned
L. glabrata	Unassigned
L. graphita	Unassigned
L. gratiosa	Unassigned
L. gressitti	Unassigned
L. hainanensis	*Lucilia*
L. hilaris	Unassigned
L. hirsutula	*Phaenicia*
L. hominivorax	Unassigned

L. hyacinthina	Unassigned
L. ibis	Unassigned
L. ignea	Unassigned
L. ignita	Unassigned
L. illustris	Unassigned
L. impatiens	Unassigned
L. incisuralis	Unassigned
L. inclyta	Unassigned
L. indica	Unassigned
L. infernalis	Unassigned
L. ingenua	Unassigned
L. insignis	Unassigned
L. insignita	Unassigned
L. inventrix	Unassigned
L. japuhybensis	Unassigned
L. juvenis	Unassigned
L. labialis	Unassigned
L. laetatoria	Unassigned
L. laevis	Unassigned
L. lenis	Unassigned
L. lepida	Unassigned
L. libera	Unassigned
L. ligurriens	Unassigned
L. limbata	Unassigned
L. limpidpennis	Unassigned
L. littoralis	Unassigned
L. locuples	Unassigned
L. lucigerens	Unassigned
L. luteicornis	Unassigned
L. magnicornis	Unassigned
L. magnifica	Unassigned
L. maialis	Unassigned
L. marginalis	Unassigned
L. marginata	Unassigned
L. meigenii	Unassigned
L. metallica	Unassigned
L. mexicana	Unassigned
L. micans	Unassigned
L. mirifica	Unassigned
L. modesta	Unassigned
L. modica	Unassigned
L. nigriceps	Unassigned
L. nigrifrons	Unassigned
L. nigrocoerulea	Unassigned
L. nitida	Unassigned
L. nitidula	Unassigned
L. notata	Unassigned
L. nuptialis	Unassigned
L. obscurella	Unassigned
L. obscuripalpis	Unassigned
L. ochricornis	Unassigned
L. ovatrix	Unassigned
L. pallescens	Unassigned
L. pallipes	Unassigned
L. papuensis	Unassigned
L. paraensis	Unassigned
L. parphyrina	Unassigned
L. pauperata	Unassigned
L. peronii	Unassigned
L. peruviana	Unassigned

L. pilosa	*Phaenicia*
L. pilosiventris	*Phaenicia*
L. pinguis	Unassigned
L. pionia	Unassigned
L. polita	Unassigned
L. porphyrina	Unassigned
L. praestans	Unassigned
L. prasina	Unassigned
L. pratensis	Unassigned
L. pretiosa	Unassigned
L. princeps	Unassigned
L. problematica	Unassigned
L. prompta	Unassigned
L. propinqua	Unassigned
L. pruinosa	Unassigned
L. pubescens	Unassigned
L. pulchella	Unassigned
L. pulverulenta	Unassigned
L. pumicea	Unassigned
L. purpurea	Unassigned
L. purpurescens	Unassigned
L. pyrochroa	Unassigned
L. pyrois	Unassigned
L. pyropus	Unassigned
L. quieta	Unassigned
L. rectinevris	Unassigned
L. regalis	*Phaenicia*
L. retroversa	Unassigned
L. rhodocera	Unassigned
L. rica	Unassigned
L. richardsi	*Phaenicia*
L. rognesi	Unassigned
L. rostrellum	Unassigned
L. rubicornis	Unassigned
L. rubrella	Unassigned
L. ruficeps	Unassigned
L. rufifacies	Unassigned
L. rutila	Unassigned
L. salazarae	Unassigned
L. sapphirea	Unassigned
L. scintilla	Unassigned
L. scutellaris	Unassigned
L. sericata	Unassigned
L. setosa	Unassigned
L. shansiensis	*Phaenicia*
L. shenyangensis	*Lucilia*
L. silvarum	Unassigned
L. sinensis	Unassigned
L. snyderi	Unassigned
L. socialis	Unassigned
L. solers	Unassigned
L. soror	Unassigned
L. spectabilis	Unassigned
L. spekei	Unassigned
L. spinicosta	Unassigned
L. stackelbergi	Unassigned
L. subtilis	Unassigned
L. sumptuosa	Unassigned
L. taiwanica	Unassigned
L. taiyanensis	*Phaenicia*
L. tenera	Unassigned
L. tepida	Unassigned
L. teres	Unassigned
L. terraenovae	Unassigned
L. thatuna	Unassigned
L. thoracica	Unassigned
L. timorensis	Unassigned
L. tomentosa	Unassigned
L. umbrosa	Unassigned
L. urens	Unassigned
L. vaga	Unassigned
L. valida	Unassigned
L. varipalpis	Unassigned
L. varipes	Unassigned
L. venusta	Unassigned
L. vernalis	Unassigned
L. viatrix	Unassigned
L. vicina	Unassigned
L. violacea	Unassigned
L. violacina	Unassigned
L. virgo	Unassigned
L. viridana	Unassigned
L. viridescens	Unassigned
L. viridifrons	Unassigned
L. viridis	Unassigned
L. viridula	Unassigned
L. viridulans	Unassigned
L. viva	Unassigned
L. vulgata	Unassigned
L. woodi	Unassigned

***Calliphora* species**	**Subgenus**
C. abina	*Acronesia*
C. alaskensis	*Acronesia*
C. albifrontalis	*Neocalliphora*
C. aldrichia	*Acronesia*
C. algira	Unassigned
C. alpina	*Acrophaga*
C. anana	*Acronesia*
C. antennatis	Unassigned
C. antipodes	Unassigned
C. antojuanaee	Unassigned
C. arta	*Eucalliphora*
C. aruspex	*Paracalliphora*
C. assimilis	Unassigned
C. atripalpis	*Calliphora*
C. augur	*Paracalliphora*
C. auriventris	Unassigned
C. australica	Unassigned
C. axata	*Paracalliphora*
C. bezzii	Unassigned

C. brunibarbis	Unassigned
C. bryani	*Oceanocalliphora*
C. cadaverum	Unassigned
C. calcedoniae	Unassigned
C. calliphoroides	*Triceratopyga*
C. canimicans	*Australocalliphora*
C. centralis	*Paracalliphora*
C. chinghaiensis	*Acrophaga*
C. clarki	Unassigned
C. clausa	Unassigned
C. clementei	Unassigned
C. collini	*Acronesia*
C. coloradensis	Unassigned
C. croceipalpis	Unassigned
C. dasyophthalma	Unassigned
C. deflexa	Unassigned
C. dichromata	*Paracalliphora*
C. dispar	Unassigned
C. dubia	*Paracalliphora*
C. echinosa	*Acronesia*
C. elliptica	Unassigned
C. erectiseta	*Calliphora*
C. espiritusanta	*Paracalliphora*
C. eudypti	Unassigned
C. fallax	*Paracalliphora*
C. flavicauda	Unassigned
C. floccosa	Unassigned
C. forresti	*Paracalliphora*
C. franzi	*Acrophaga*
C. fulviceps	*Paracalliphora*
C. fulvicoxa	*Paracalliphora*
C. fuscipennis	Unassigned
C. fuscofemorata	*Australocalliphora*
C. genarum	Unassigned
C. gilesi	*Paracalliphora*
C. grahami	*Aldrichina*
C. gressitti	*Paracalliphora*
C. grisescens	Unassigned
C. grunini	Unassigned
C. hasanuddini	*Paracalliphora*
C. hilli	*Paracalliphora*
C. himalayana	Unassigned
C. icela	Unassigned
C. insignis	Unassigned
C. io	Unassigned
C. irazuana	Unassigned
C. javanica	*Paracalliphora*
C. kanoi	*Paracalliphora*
C. kermadeca	*Paracalliphora*
C. lata	*Calliphora*
C. latifrons	Unassigned
C. leucosticta	*Paracalliphora*
C. lilaea	Unassigned
C. livida	Unassigned
C. loewi	*Calliphora*
C. lopesi	Unassigned
C. lordhowensis	*Australocalliphora*
C. macleayi	*Paracalliphora*
C. maestrica	Unassigned
C. majuscula	Unassigned

C. malayana	*Paracalliphora*
C. maritima	*Paracalliphora*
C. maryfullerae	Unassigned
C. melinda	Unassigned
C. metallica	Unassigned
C. minor	Unassigned
C. mogii	Unassigned
C. montana	*Acronesia*
C. morticia	Unassigned
C. mumfordi	*Paracalliphora*
C. neohortonaa	Unassigned
C. neozelandica	Unassigned
C. nigribarbis	*Calliphora*
C. nigrithorax	*Neocalliphora*
C. nociva	Unassigned
C. norfolka	*Paracalliphora*
C. nothocalliphoralis	Unassigned
C. noumea	Unassigned
C. ochracea	*Neocalliphora*
C. onesioidea	*Australocalliphora*
C. papua	Unassigned
C. papuensis	*Paracalliphora*
C. paradoxa	*Triceratopyga*
C. pattoni	*Calliphora*
C. perida	Unassigned
C. peruviana	Unassigned
C. phacoptera	Unassigned
C. plebeia	Unassigned
C. popoffana	*Acronesia*
C. porphyrina	*Paracalliphora*
C. praepes	Unassigned
C. prosternalis	Unassigned
C. psudovomitoria	Unassigned
C. pubescens	Unassigned
C. quadrimaculata	*Neocalliphora*
C. robusta	Unassigned
C. rohdendorfi	*Calliphora*
C. rostrata	Unassigned
C. ruficornis	Unassigned
C. rufipalpis	Unassigned
C. rufipes	Unassigned
C. salivaga	*Paracalliphora*
C. simulata	*Paracalliphora*
C. sinensis	*Calliphora*
C. splendens	*Calliphora*
C. splendida	Unassigned
C. stelviana	Unassigned
C. sternalis	Unassigned
C. stygia	*Neocalliphora*
C. stylifera	*Steringomyia*
C. subalpina	*Acrophaga*
C. tasmanensis	Unassigned
C. tasmaniae	Unassigned
C. terraenovae	Unassigned
C. testaceifacies	Unassigned
C. tianshanica	*Calliphora*
C. toxopeusi	*Papuocalliphora*
C. triseta	Unassigned
C. uralensis	Unassigned
C. varifrons	*Paracalliphora*

C. vicina	*Calliphora*
C. viridescens	Unassigned
C. viridiventris	Unassigned
C. vomitoria	*Calliphora*

C. xanthura	*Paracalliphora*
C. yezoana	Unassigned
C. zaidamensis	*Calliphora*

Parasite morphology: Blow flies form 4 different types of developmental stages: eggs, larvae (three instars), pupae and adults. Eggs appear as creamy-yellow ovoid-oblong bodies (~ 1 mm long) deposited in clusters. Larvae (commonly called maggots) have elongated cylindrical white-cream opaque bodies that grow through 3 developmental instars (L1-3) from 5-20 mm in length. They have reduced head capsules but possess distinctive cephalopharyngeal skeletons with a pair of anterior darkened rasping mouthhooks. They respire through spiracles, an anterior pair, each with 7-10 openings; and a posterior pair, each with one (*Lucilia*) or 2 (*Calliphora*) internal projections and 3 slanting oval slits in a sclerotized plate called a peritreme (in contrast, oestrid larvae have flat porous plates). The body has 12 conspicuous segments, often bearing segmental belts of small rounded projections (tubercles) giving it a 'screw-like' appearance (Oestroidea are distinguished from Muscoidea by larvae possessing rudimentary armature). Pupae are formed inside the exoskeleton of the last larval instar and appear as ellipsoidal creamy-brown cocoons (10-14 mm long) with barely visible transverse striations. The pupae are cyclorrhaphous with an anterior circular seam that forms an exit aperture. Calliphorid blow flies have robust bodies that are not dorsoventrally flattened, are distinctively coloured and adorned with characteristic patterns of setae (chaetotaxy). They are small-medium sized flies (measuring 8-14 mm in length) with metallic iridescent bodies (blue-black, violet-blue, green or bronze) and strong bristles (Oestroidea are distinguished from Muscoidea by the presence of bristles on the thoracic meron). *Lucilia* spp. are often referred to as green bottle flies due to their metallic coppery-green thorax and abdomen, although some species may be blue to bronze in colour. Different species are often distinguished by colour variations, e.g. *L. cuprina* and *L. sericata* are differentiated by the green and black colouration of the femurs on their front legs. *Calliphora* spp. are usually blue or brown bottle flies with a grey thorax and honey-coloured abdomen, but the colour variation of species ranges from black-grey through brown-copper to blue-green. Colour variation can also be used to distinguish species: e.g. *Ca. stygia* has a brownish chequered abdomen, *Ca. augur* has a bright blue longitudinal band on its abdomen and *Ca. dubia* has a darker blue band on the abdomen. Adults have 3 conspicuous body parts: a big round head; stout thorax; and pyriform abdomen. The head possesses both a ptilinal suture and facial lunule (like Muscoidea, but unlike other calyptrate flies), 2 large brown compound eyes (well separated in females and close together in males), and 2 well-developed short pendulous antennae, each composed of 3 dissimilar segments: a small basal scape; a club-like pedicel with a complete dorsal seam; and a large dorsal bristle (arista) that is bilaterally plumose (feathery) [oestroid and muscoid flies distinguished from other calyptrates by possessing antennae with aristae]. Calliphorids have well-developed sponging-sucking mouthparts to feed on liquids, but do not have piercing elements as they do not bite hosts and do not feed on blood. The ventral proboscis comprises a basal rostrum flanked by short palps, a cylindrical haustellum housing an anterior labrum, slender hypopharynx and sheath-like labium; and a terminal sponging labellum. Liquids ingested with the aid of pharyngeal muscles pass into a tubular oesophagus and proventriculus (with associated diverticula) and then to the digestive midgut, hindgut (with excretory Malpighian tubules), rectum and terminal anus. The thorax is covered by a scutum with a continuous mid-dorsal suture and a small post-scutellum. The scutum contains stout bristle-like setae, including a vertical row on the meron (lacking on muscoid flies), a row on the hypopleuron, and 3 postsutural dorsocentral pairs (in *Lucilia*). The mesothorax bears 2 narrow clear wings with wing membranes uncrowded and supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)]. Calliphorine flies have bare stem veins, M veins angled sharply upwards near the outer margin, and the discal medial cell widening gradually. The wings have prominent hind lobes (calypters or squamae), with *Calliphora* spp. having a bristly lower calypter and bare suprasquamal ridge, while *Lucilia* spp. have a bare lower calypter and a setate suprasquamal ridge. Like all Diptera, the hindwings have been greatly reduced to knobby halteres (used to stabilize flight), covered by the calypters (in all calyptrates). Oestroid and muscoid flies are further distinguished from other calyptrates by the presence of bulbous swellings (greater ampulla) below the wing base. The ventral thorax gives rise to 3 pairs of long thin legs, each composed of 5 segments (coxa, trochanter, femur, tibia, tarsus) and terminating in a pair of claws with pad-like pulvilli surrounding a central bristle (empodium). The pyriform abdomen usually has 5 conspicuous segments with lateral respiratory spiracles and terminalia specific for each gender (aedeagus and claspers for males, ovipositor for females). Males have 2 testes connected by vas deferens to a seminal vesicle (with lateral accessory glands) leading to a tubular ejaculatory duct and retractable copulatory aedeagus with claspers located near the genital pouch. Females have 2 ovaries joined by oviducts to a globular uterus (with associated spermatheca and accessory glands) opening to the vulva with a cylindrical telescoping ovipositor.

Site of infection: These blow flies are facultative parasites, particularly of sheep, and sometimes other domestic animals. Adult flies cause no direct harm but the larval stages emerging from eggs laid next to the skin invade host tissues, causing myiasis. Eggs are laid in batches of 50-250 on carrion or on moist wounds or the soiled wet fleece of live animals, causing body, breech, tail, poll (head) or pizzle strike depending on where emergent larvae invade cutaneous tissues. Some species may also invade body orifices, such as orbital, nasal, aural and anal passages, urogenital tracts and even the umbilical cords of newborns. Body strike is found commonly around the shoulders and along the back, and has been associated with bacterial dermatophilosis and pseudomonal fleece rot. In Merino sheep, breech and tail strike commonly occur due to the excessive wrinkled skin of the hindquarters that becomes fouled with faeces and urine.

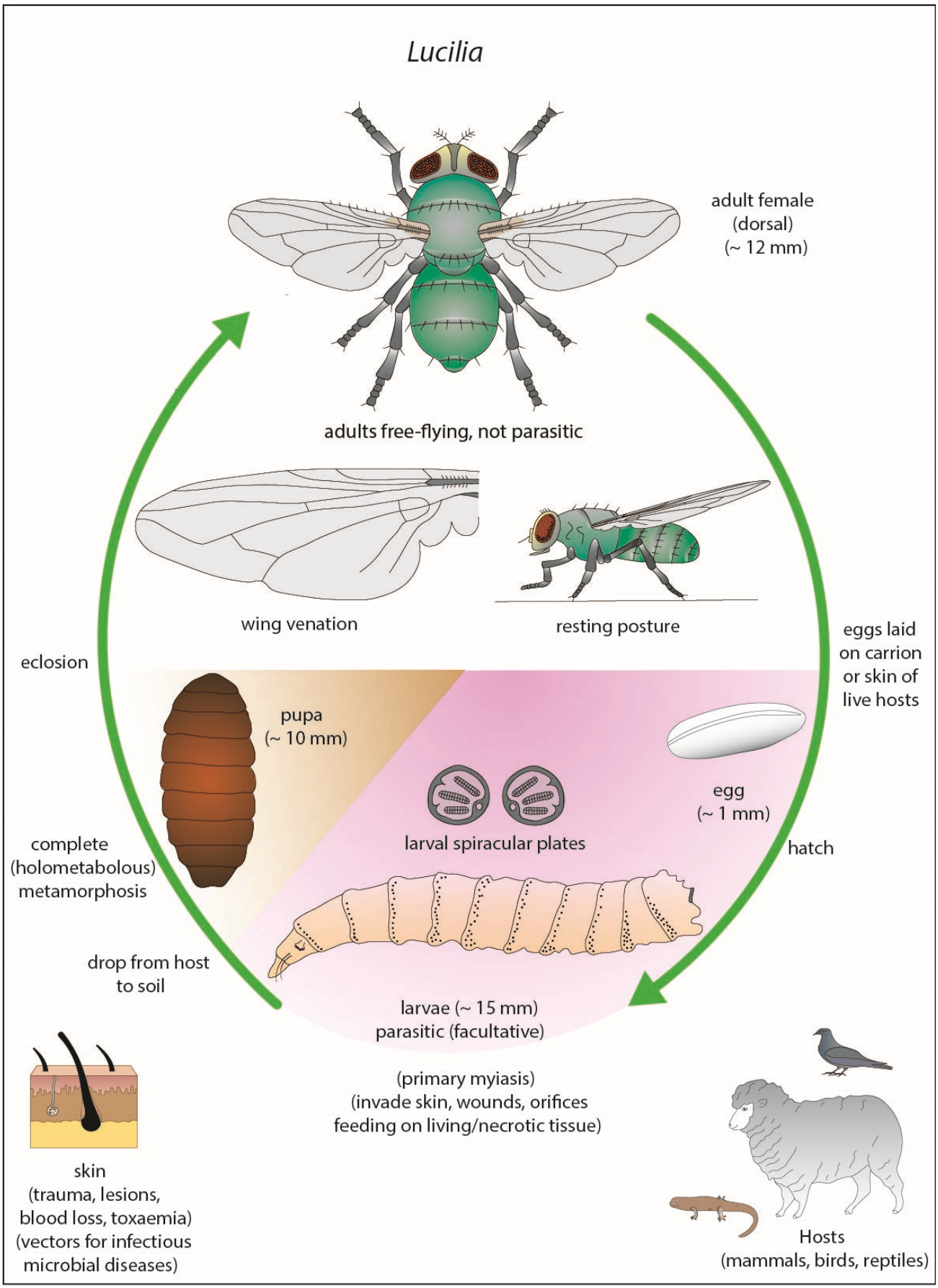
Pathogenesis: Some myiasis-causing fly species are obligate parasites and can only complete their development using a living host. The majority, however, are facultative parasites and can develop in both living and dead organic material. They comprise primary facultative species (such as *Lucilia* spp.), which can initiate myiasis but also live as saprophages in decaying organic matter or carcases, and secondary facultative species (such as *Calliphora* spp.), which live normally as saprophages and cannot initiate myiasis but can secondarily invade pre-existing infestations. Flies are attracted to soiled pelage (fur, hair, wool), pungent wounds and chronic nasopharyngeal and urogenital infections. Various odours appear to act as chemo-attractants, especially those associated with decomposing organic matter, but also including those produced by bacteria causing fleece rot or dermatophilosis on rain-soaked animals. Gravid females lay eggs on or around wounds (due to trauma, castration, tail-docking, de-horning, navels) and orifices (nostrils, eyes, mouth, ears, anus, vagina), areas that are moist and contain proteinaceous material for the emergent larvae. Fly strike may cause superficial or invasive tissue lesions, with considerable trauma, pain, stress, anaemia, and in severe cases, an acute and potentially fatal toxaemia due to ammonia excreted by the larvae. Facultative myiasis usually involves masses of maggots which can result in death of the host either directly (expanding invasive lesions) or indirectly (predisposing host to disease or predation). Obligate myiasis usually involve fewer larvae but they can be more invasive leading to deeper lesions. In both instances, larvae invade necrotic or living tissue causing traumatic cutaneous myiasis. Three larval instars develop over 4-6 days and they cause great suffering by feeding directly on host tissues. Maggots secrete proteolytic enzymes and tear at the tissues with strong oral hooks resulting in extensive lesions. Initially, larvae may feed superficially on skin and exudates or on necrotic tissue, but in crowded conditions they may feed on live healthy tissue in order to survive and continue their development. Larvae burrow into tissue headfirst, with their caudal spiracles exposed near the surface. Once replete, mature larvae drop from the host to the ground to form pupae. Single infestations by a few larvae may be well tolerated by the host, sometimes being covert producing few clinical signs and healing well without complications. Heavier or multiple infestations, however, can be extremely debilitating causing significant irritation and distress resulting in the host rapidly losing condition becoming anorexic, dull and depressed. Animals may chew, scratch or rub affected areas, resulting in cavernous painful lesions with progressive ulceration, necrosis and haemorrhage. Other primary, secondary and even tertiary blow flies are attracted to existing lesions resulting in prolonged infestations and expansive lesions. The amount of tissue damage is dependent on the cumulative duration of infestations and the numbers of maggots present. The severity of disease (myiasis) varies considerably depending on the sites of infestation and the extent of tissue invasion. Subcutaneous lesions may become so deep that they involve internal organs resulting in a wide range of clinical signs, including fever, anaemia, dyspnoea, renal dysfunction, cardiac signs and toxaemia, which may prove fatal around 2 weeks after initial infestation. Lesions are also predisposed to secondary bacterial infections, with toxaemia ranging from pyaemia to septicaemia.

Developmental cycle and mode of transmission: Blow flies have holometabolous developmental cycles involving the complete metamorphosis of vermiform larvae through a non-feeding pupa stage to form winged adults. Adult flies are free-flying and both sexes require water and carbohydrates for energy which they obtain from honeydew and juices from flowering plants. Most blow flies are anautogenous in that the females require a protein meal (usually from nectar or decaying organic matter) to complete oogenesis (egg maturation). Calliphorid flies are oviparous, females laying eggs after searching for suitable sites for oviposition; being attracted to carrion or moist body areas with putrefactive odours and protein exudates due to wounds, skin conditions (such as dermatitis) or pelage soiled with urine or faeces (especially dags on sheep). They lay batches of 50-250 eggs several times over 2-3 weeks, usually towards the end of the day to prevent their desiccation by prolonged exposure to sunlight. The eggs hatch after 6-24 hours although it may take longer in colder conditions. Emergent larvae begin to feed immediately on host tissue and they undergo two moults, one after 12-18 hours and another some 30-60 hours later. The first larval instars are highly susceptible to desiccation and are not capable of penetrating unbroken skin. The second and third instars are able to abrade skin with their oral hooks and they produce enzymes that break down the skin causing serous exudates. The larvae of some blow fly species also exhibit predatory behaviour and may feed on larvae of other species. After 3-6 days of feeding, replete larvae leave the host, drop to the ground and burrow into the topsoil or leaf litter where they shrink and harden to form non-feeding pupae. Pupation may be completed in 3-7 days or be delayed for several weeks by colder conditions. Adult blow flies are ready to mate several days after emergence and the fertilized females produce eggs over 2-3 weeks. The whole life-cycle (egg-to-egg) may be completed within 2-6 weeks, particularly warm humid regions. Blow fly populations exhibit seasonal fluctuations in their numbers and activity in response to prevailing climatic conditions and the availability of susceptible hosts. *L. cuprina* is more prevalent in warm-temperate and subtropical regions, while *L. sericata* is more prevalent in cool-temperate regions. Fly numbers typically increase during spring as temperature and humidity rise, but decrease during colder months. Pre-pupae can over-winter in the soil, resulting in their synchronized emergence and fly swarms in spring. Hot dry summers reduce fly numbers significantly unless sufficient rainfall occurs. Flystrike is worse in many agricultural areas when neonates (lambs, calves, foals) are abundant as they are more susceptible to infestation, particularly when wounded during castrating, branding, dehorning or shearing. The incidence of fly strike is also greater in animals with wet fleeces due to persistent rainfall. Infestations may spread within host populations and over time and space because female flies usually attack more than one host and larvae dropping from ambulatory hosts pupate in the soil over wide areas.

Differential diagnosis: Myiases are diagnosed on the basis of clinical signs and the detection and identification of larvae in lesions (sores, wounds, ulcers, furuncles). Physical examination of wounds can be aided by medical imaging technologies (such as ultrasound) to help differentiate lesions due to other aetiological agents (such as tungiasis, leishmaniasis, onchocerciasis, tropical ulcers, abscesses, pyogenic infections, adenopathy, cellulitis, furunculosis, and subcutaneous cysts). The larvae of most blow fly genera can be differentiated on the basis of their size, shape and appearance as well as the arrangement of their posterior spiracles. The spiracles of blow fly larvae have straight slits compared to sinuous slits in house fly larvae. The peritreme (outer perimeter) of

the spiracles is entire in primary strike flies and broken in secondary strike flies. It is thin in *Lucilia* spp. and thick in *Calliphora* spp. First stage larvae have one slit, second stage larvae have 2 slits and third stage larvae have 3 slits. The identification of individual species is often confounded by their similar morphology, so if required, live larvae extracted from the host may be maintained in the laboratory on meat or a synthetic medium to pupate and develop into an adult fly, which can then be identified by their distinctive morphological features. Several attempts have been made to develop less-demanding diagnostic tests using immunological assays for larval excretory-secretory (ES) products and other antigenic preparations, but they are confined to research laboratories. Molecular biological techniques have been used to genotypically characterize flies and larvae by polymerase chain reaction (PCR) amplification of specific gene sequences; including nuclear 16S ribosomal RNA, 18S ribosomal RNA, mitochondrial 12S DNA, cytochrome oxidase I and II, transfer RNA and NADH dehydrogenase.

Treatment and control: Four major approaches are used to control myiases: therapeutic intervention (wound treatment); chemoprophylaxis (periodic applications of insecticides); minimizing predisposing conditions (stock husbandry and management); and reducing fly populations (environmental management). Medical cases rely on prompt surgical interventions and debridement to extract larvae from wounds using tweezers, forceps or needles. Patients may require supportive anti-inflammatory, antiseptic and antibiotic therapy to counter symptoms and complications. Occlusive coverings of oily creams/dressings (petroleum jelly, lanolin, liquid paraffin, mineral oil, vegetable oil, beeswax, sometimes nail polish, adhesive tape, butter, chewing gum) have been used to suffocate larvae before their removal, and stringent antiseptics (hydrogen peroxide, chloroform) may entice larvae to exit wounds or body orifices (some early remedies involved using raw meat poultices). Standard veterinary practice for flystruck animals relies on the use of topical dressings or systemic insecticides that target larvae. Early formulations containing creosote, eucalyptus oil, paraffin, phenol and others were painted directly onto wounds mixed with resinous tar, while next generation formulations incorporated a wide range of insecticidal organochlorides and organophosphates into topical powders, pastes and sprays. However, significant problems were encountered with drug toxicity and flies developing resistance to organochlorides (especially DDT) and organophosphates (many are now banned as dips although some are still available as dressings). More recently, topical formulations of pyrethroids (permethrin, cypermethrin, deltamethrin) and spinosyns (spinosad) as well as systemic applications of salicylanilides (closantel) and macrocyclic lactones (notably ivermectin, doramectin) have been used to treat myiases with great effect. Domestic livestock are usually treated prophylactically to prevent infestations using organophosphorous and pyrethroid insecticides which persist in the pelage for up to 10 weeks. These formulations may be applied by whole body plunge dipping, jetting or shower sprays, taking care to maintain correct insecticide concentrations. In sheep, long greasy wool may act as a barrier to chemical treatment so many farmers often treat after shearing. Some insect growth regulators (cyromazine, dicyclanil) have given good protection as single pour-on applications but only when used in timely fashion before anticipated challenge. Ear tags impregnated with organophosphates or pyrethroids have been used with good effect, mainly on cattle. Spinosad and ivermectin can also be given as jetting treatments, the latter also being available as an injectable or in the form of an intra-ruminal controlled-release bolus. Domestic animals should be regularly inspected during fly season, and infested individuals should be isolated and treated. Various livestock management procedures have been developed to prevent strike, such as dagging (removing faecally-soiled wool), crutching (shearing wool around breech), tail docking (amputation) and mulesing (removing hindquarter skin folds). Infections by gastrointestinal helminths should also be controlled to prevent diarrhoeal wetting of perineal wool. Certain breeds of sheep are more susceptible to strike because the wool and skin are too easily wetted with urine or remain wet after rain. Breeding plain-bodied sheep with fewer wrinkles and barer breech areas reduces the problem of fly strike. Many blow fly species multiply in carrion so every effort should be made to remove and destroy carcases in the field. Shallow burying may not be effective as some larvae have been found to burrow through metres of loose soil. Several studies have used carcases treated with insecticides and chemo-attractants as baited traps for fly control, but large-scale control would pose many logistic problems. Good results have been obtained in controlling other insect populations by releasing irradiated sterile males bred in the laboratory to compete for wild-type mates, but the best results were obtained in small confined areas with low population densities. More recently, a good case has been made for developing a vaccine for flystrike. Acquired resistance has been well documented in sheep and studies on passive immunity have shown that antibodies from previously infested sheep have conferred some protection to recipient animals by reducing larval growth. Several studies have subsequently reported larval growth inhibition in animals vaccinated with antigenic extracts from the larval peritrophic membrane of *L. cuprina,* but studies are on-going. Lastly, mention must be made of two alternate applications involving blow fly larvae. Several species (including *L. sericata*) have been used for ‘maggot debridgement (debridement) therapy’ to treat humans with non-healing wounds (pressure ulcers, venous stasis ulcers, diabetic foot wounds, postsurgical wounds) whereby sterile laboratory-reared maggots were used to clean wounds by preferentially feeding on dead necrotic tissue. In forensic entomology, calliphorid flies have also been used to provide information about the time of host death (post-mortem interval) based on the kinetics and dynamics of their larval activity.

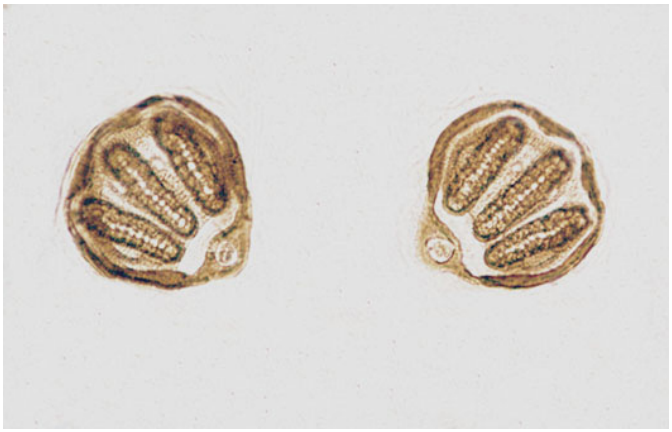

Lucilia
adult female
(dorsal)
(~ 12 mm)
adults free-flying, not parasitic
wing venation
resting posture
eggs laid
on carrion
or skin of
live hosts
eclosion
pupa
(~ 10 mm)
egg
(~ 1 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
hatch
drop from host
to soil
larvae (~ 15 mm)
parasitic (facultative)
(primary myiasis)
(invade skin, wounds, orifices
feeding on living/necrotic tissue)
skin
(trauma, lesions,
blood loss, toxaemia)
(vectors for infectious
microbial diseases)
Hosts
(mammals, birds, reptiles)



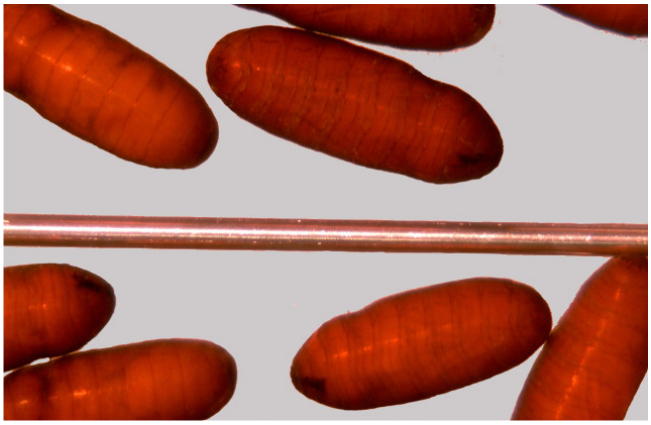
Lucilia adult



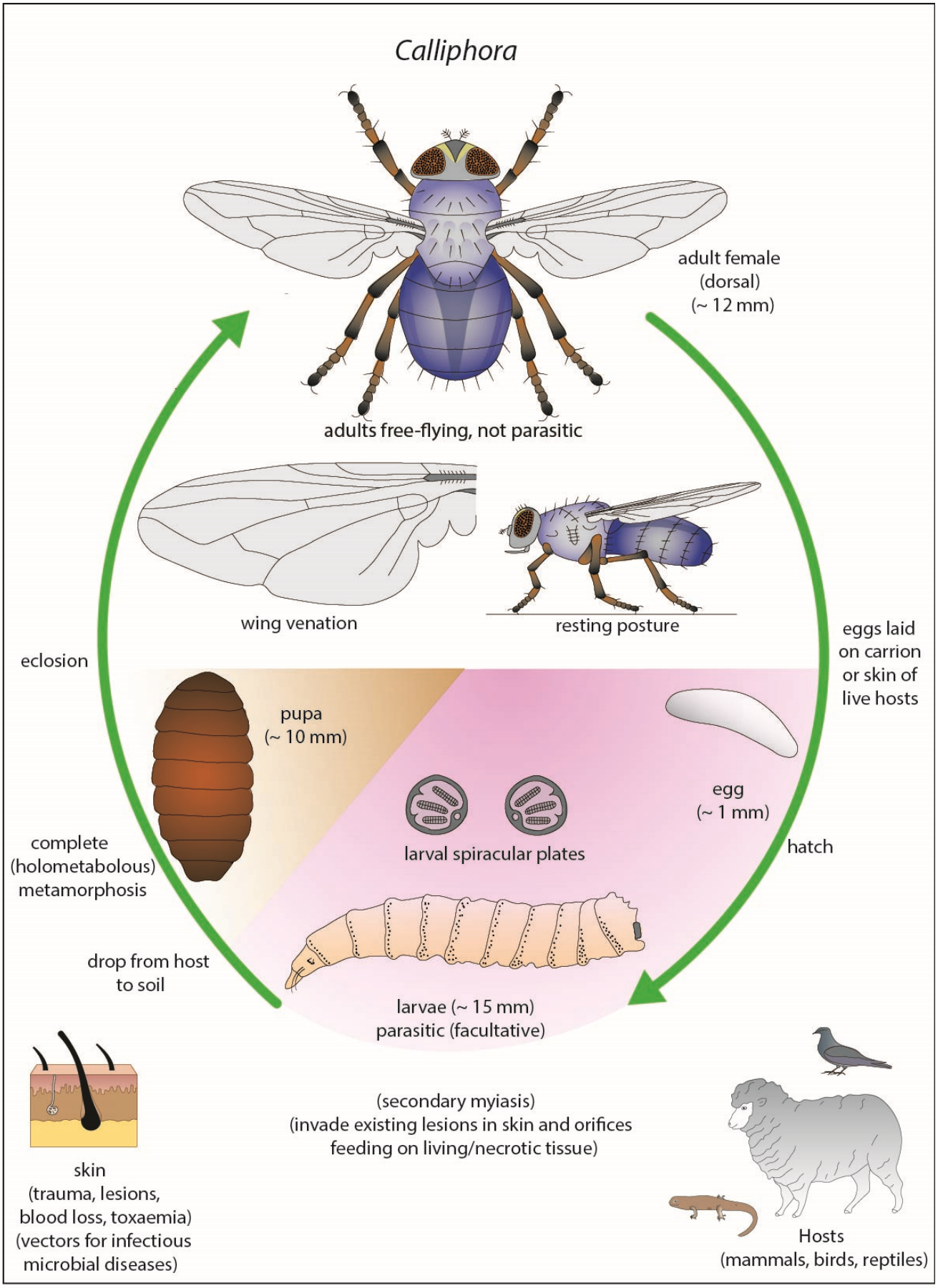
Lucilia larvae



Lucilia larval spiracles



Lucilia pupae


Calliphora
adult female
(dorsal)
(~ 12 mm)
adults free-flying, not parasitic
wing venation
resting posture
eggs laid
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drop from host
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parasitic (facultative)
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(invade existing lesions in skin and orifices
feeding on living/necrotic tissue)
skin
(trauma, lesions,
blood loss, toxaemia)
(vectors for infectious
microbial diseases)
Hosts
(mammals, birds, reptiles)



Calliphora adult



Calliphora eggs



Calliphora larvae



Calliphora larval spiracles

Cochliomyia*, *Chrysomya
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Calliphorids (blow flies) are not parasitic as adults but their larvae help destroy carcasses and may cause traumatic cutaneous myiases (flystrike, screwworm infestation) in live mammals. Adult flies are large and often metallic in colour. Eggs laid on hosts release larvae which may penetrate the skin to feed on subcutaneous tissues. Most species are facultative invaders causing primary, secondary or tertiary strike, although several (notably screwworms) are obligate parasites. Larvae of *Cochliomyia* (primary screwworm) and *Chrysomya* (Old World screwworm) enter through mucous membranes and wounds in a range of mammals and cause serious life-threatening lesions.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Calliphoridae (blow flies, often metallic, larvae cause myiases (flystrike/screwworm infestation))
Genus:	*Cochliomyia* (primary screwworm) (parasitic on skin/subcutaneous tissues of mammals)
Genus:	*Chrysomya* (Old World screwworm) (parasitic on skin/subcutaneous tissues of mammals)
Species:	various species cause myiases in animals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera (‘true’ flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders

are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora

(containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases). Several superfamilies contain species whose larvae feed on the flesh of vertebrate hosts, mostly when dead (carrion) but sometimes when still living (causing fly-strike). Oestroid and muscoid larvae are well-adapted for living in moist organic substrates ranging from wet faeces to carrion to living flesh.

The superfamily Oestroidea contains large flies that are not dorsoventrally flattened, their wing veins are not crowded, and the discal medial cell of the wings widens gradually. The superfamily contains 7 families: Calliphoridae (blow flies, written as two words to distinguish them from other fly-like insects with compound names such as dragonflies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Calliphoridae is characterized by blow flies with metallic iridescent bodies (blue-black, violet-blue, green), strong bristles, well-developed mouthparts and antennae, and weak post-scutellum. The family contains over 1,100 species of blow flies, carrion flies, bluebottles, greenbottles and cluster flies which help destroy carcases, although many species have been implicated in larval myiasis ('flystrike') in living animals. Most invasions are facultative (opportunistic) causing primary, secondary or tertiary flystrike (categorized according to whether they initiate strike or occur later), although several species (notably screwworms) are obligate parasites whose larvae must develop in flesh. The larvae of most blow fly species are not selective feeders and they exhibit broad host specificity, usually for mammals, occasionally birds and less commonly amphibians and reptiles. Myiasis-causing flies have been found worldwide, particularly in temperate and tropical regions with large domestic livestock populations, but also in cooler regions where wildlife abound. Some 75 genera have been described in 11 subfamilies: Ameniinae, Aphyssurinae, Auchmeromyiinae, Calliphorinae, Chrysomyinae, Helicoboscinae, Melanomyinae, Mesembrinellinae, Phumosinae, Rhiniinae and Toxotarsinae, with another 14 unplaced genera and several fossil genera. The subfamily Chrysomyinae comprises blow flies distinguished by setose stem veins, and 2 tribes are recognized : Chrysomyini with 8 genera (including *Chrysomya* and *Cochliomyia*); and Phormiini with 6 genera.

Family	Genera	Hosts	Strike	Myiasis*
Calliphoridae	*Lucilia*	mammals	primary	Facultative (AU, CU, GI, NP, TR, UG)
	Calliphora	mammals	secondary	Facultative (AU, CU, GI, NP, TR, UG)
	Cochliomyia	mammals	primary, secondary	Facultative or obligate (TR)
	Chrysomya	mammals	primary, secondary	Facultative or obligate (TR)
	Cordylobia	mammals	primary	Obligate (CU, TR)

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

Several genera in the subfamily Chrysomyinae have medical and veterinary significance as larval stages cause debilitating myiases (notably *Chrysomya, Cochliomyia, Compsomyiops, Phormia, Protophormia, Protocalliphora*). The genus *Chrysomya* (syn. *Achoetandrus, Ceylonomyia, Chrysomja, Crysomya, Pycnosoma, Pycnosomops*) contains 38 species recorded as carrion-feeders or as obligate or facultative invaders of domestic animals and humans, including the notorious screwworms and the bird-nest blow flies. Several species commonly cause facultative fly strike in sheep around the world (e.g. *Ch. rufifacies, Ch. micropogon* (*mallochi*) and *Ch. varipes* renowned as secondary strike flies), while one species (the Old World screwworm *Ch. bezziana*) causes obligate myiasis in animals and humans, usually invading through wounds. Several species have proven to be important in forensic science as their proclivities for corpses and their regular life cycles allow investigators to retrospectively predict time of death. The genus *Cochliomyia* contains 4 species, with their screwworm larvae infesting numerous animal species, including humans, throughout the American tropics. Different species feed either on living tissue (e.g. the primary or New World screwworm *Co. hominivorax*) or necrotic tissue (e.g. the secondary screwworm *Co. macellaria*).

Parasite species	Hosts	Location	Clinical signs (vectorial capacity)	Distribution
Cochliomyia				
Co. aldrichi	Mammalia (various domestic and	skin	necrophagous,	Americas

	wild animals, plus carrion)	(wounds)	secondary facultative myiasis	
Co. hominivorax (syn. *Callitroga americana*) (New World screwworm, American screwworm, primary screwworm)	Artiodactyla: bovid (cattle, sheep, goat), suid (pig); Perissodactyla: equid (horse); Carnivora: canid (dog); Primates: hominid (human); Mammalia (other wild and domestic animals)	skin (orifices, wounds)	obligate myiasis [cavernous lesion, liquefaction, necrosis, haemorrhage]	Americas
Co. macellaria (syn. *Co. violacea*) (secondary screwworm)	Artiodactyla: bovid (cattle, sheep, goat), suid (pig); Perissodactyla: equid (horse); Carnivora: canid (dog); Primates: hominid (human); Mammalia (other domestic animals and wildlife, plus carrion)	skin (wounds)	secondary facultative myiasis [forensic applications] (mechanical vectors for botulism in birds, salmonellosis, poliomyelitis and swine influenza)	Americas
Co. minima	Mammalia (various domestic and wild animals, plus carrion)	skin (wounds)	necrophagous, primary or secondary facultative myiasis	Americas
Chrysomya				
Ch. albiceps (syn. *Ch. indica, Compsomyia flaviceps*) (hairy-maggot blow fly)	Mammalia (various domestic and wild animals); carrion (pig, rat)	skin	necrophagous, secondary facultative myiasis [forensic applications]	Africa, Mediterranean, Americas
Ch. bezziana (Old World screwworm)	Artiodactyla: bovid (cattle, sheep); Perissodactyla: equid (horse, donkey); Carnivora: canid (dog); Primates: hominid (human); Mammalia (other domestic and wild animals)	skin (orifices, wounds)	obligate myiases [cavernous lesions, liquefaction, necrosis, haemorrhage]	tropical Africa, Asia, India
Ch. cabrerai	traps			South-East Asia
Ch. chani	carrion (monkey, pig, rabbit, incl. human cadavers)		necrophagous	South-East Asia
Ch. chloropyga (syn. *Ch. costata, dejeanii, epanalepsis, lalandii, sensua, soror, trygaea*)	Artiodactyla: bovid (sheep); carrion (pig, impala), dung		necrophagous, secondary facultative myiasis	Africa
Ch. defixa	Mammalia (native animals)			Southeast Asia
Ch. flavifrons (syn. *Ch. fulvipes)*	traps			Australia
Ch. fulvicruris	traps			Europe
Ch. greenbergi	traps			Indonesia
Ch. incisuralis	traps			Australia
Ch. inclinata (syn. *Ch. grienieri, roubaudi, tellinii*)	Primates: hominid (human); Rodentia: murid (cane rat); carrion		necrophagous, secondary facultative myiasis	Africa
Ch. latifrons	traps			Australia
Ch. laxifrons	traps			Africa
Ch. marginalis (syn. *Ch. regalis*)	Artiodactyla: bovid (cattle) impala); carrion (pig); dung	skin (wounds)	necrophagous, secondary facultative myiasis	Africa, Central Asia
Ch. megacephala (syn. *Ch. duvaucelii, gratiosa*) (Oriental latrine fly)	Mammalia (various domestic and wild animals); carrion (pig)	skin	necrophagous, secondary facultative myiasis [forensic applications] (mechanical vector for enteric pathogens)	worldwide
Ch. micropogon (syn. *Ch. mallochi p.p.*) (steel blue blow fly)	Mammalia (various domestic and wild animals); carrion	skin	necrophagous, secondary facultative myiasis	Australia
Ch. nigripes	carrion (incl. human cadavers), traps			Australasia

Ch. norrisi	traps			New Guinea
Ch. oumeensis	traps			Africa
Ch. pachymera	traps			Madagascar
Ch. pacifica	traps			Pacific
Ch. phaonis	carrion		necrophagous [forensic applications]	Central Asia
Ch. pinguis (syn. *Ch. nigriceps*)	carrion (incl. human cadavers)		necrophagous	Eurasia
Ch. polymita (syn. *Ch. atrifrons*)	traps			Africa
Ch. putoria	carrion (pig); dung		necrophagous (mechanical vector for enteric bacteria)	Americas, Africa
Ch. rufifacies (syn. *Ch. pingi*) (secondary green blow fly, green hairy-maggot blow fly)	Artiodactyla: bovid (cattle, sheep); Carnivora: canid (fox), mustelid (badger); Mammalia (various domestic and wild animals); carrion	skin	necrophagous, secondary facultative myiasis [forensic applications]	Australasia, Orient, Americas
Ch. sabroskyi	traps			New Guinea
Ch. saffranea (syn. *Ch. mallochi p.p.*)	traps			Australasia
Ch. samarensis	traps			Philippines
Ch. schoenigi	traps			Philippines
Ch. semimetallica	dung, carrion		necrophagous	Australasia
Ch. sulcifrons (syn. *Ch. noonadan*)	traps			Australasia
Ch. tagulai	traps			New Guinea
Ch. thanomthini	traps			South-East Asia
Ch. vanemdeni	traps			Africa
Ch. varipes (syn. *Ch. annulipes*) (small hairy-maggot blow fly)	Mammalia (various domestic and wild animals); carrion, dung	skin	necrophagous, secondary facultative myiasis	Australia, Pacific
Ch. villeneuvi	Primates: hominid (human cadaver)		necrophagous [forensic applications]	Asia
Ch. yayukae	traps			Indonesia

*Adult flies collected from environment using traps or nets.

Parasite morphology: These blow flies form 4 different types of morphological stages during their development: eggs; larvae (3 instars); pupae; and adults (males and females). Eggs are white-cream in colour and elongate measuring 1.0-1.5 mm long with a tapered end at one side. They are oviposited in loose or overlapping clusters on the edges of wounds or body orifices. Larvae (commonly called maggots) are cream in colour and have cylindrical bodies narrowing anteriorly (cf. muscoid larvae are more tapering). They develop through 3 larval instars (L1-3) and grow up to 15-17 mm in length. They have 12 segments, most with a band of small dark spines encircling the body giving the larva a threaded screw-like appearance (hence the common name of screwworm). Some species have smooth bodies between the bands of spines, while others may have fleshy tubercles projecting from segments (e.g. *Ch. bezziana* has 10 or more spines around the spiracular area, while *Co. macellaria* with spines in V-shape at the anal protuberance). The larvae lack sclerotized head capsules, but they have an internal cephalopharyngeal skeleton bearing rasping mouthhooks. All larvae breathe using 2 sets of respiratory spiracles: a small anterior pair which are brown to orange in colour (pigmentation extending to tracheal trunks in *Co. hominivorax* but not *Co. macellaria*) and have 7-10 openings (*Cochliomya*) or 4-13 openings (*Chrysomya*); and a larger posterior pair evident as caudal plates, each with an incomplete sclerotized periphery (peritreme) and 3 large oval slits (in contrast, oestrid larvae have porous spiracular plates). Mature L3 form puparia which are light to dark brown in colour, ellipsoidal measuring 9-11 x 3-4 mm and have a few circular body segments. The appendages of the enclosed pupae are visible externally and are held closely appressed to body. Adult flies eclose through a circular cap (like all Cyclorrhapha) and not through a longitudinal slit (like Nematocera and Brachycera). Calliphorid flies are large measuring up to 8-12 mm long and have stout setate bodies characteristically metallic green to bluish-green (like polished metal). *Cochliomyia* spp. are usually blue-green to violet-green with 3 prominent black longitudinal stripes on the thorax, while *Chrysomya* spp. have shiny blue-black to blue-green bodies with 2 faint dark stripes on the thorax and narrow dark bands along the posterior margins of the abdominal segments. Different species may be distinguished by variations in their colouring and ornamentation, e.g. *Ch. rufifacies* has a black band on each abdominal segment, while *Ch. varipes* has black and yellow banded legs. Adult flies have 3 conspicuous tagma: a large rounded head; a stout shield-like thorax; and a pyriform abdomen. The head often bears a pale face (yellow for *Chrysomya*, yellow-orange to red for *Cochliomyia*) with both a ptilinal suture and a facial lunule (like all Muscoidea and Oestroidea but unlike other calypterate flies). The head also has 2 large well-developed compound eyes that are usually red-brown to orange in

colour (closer together in males than females) and 2 short pendulous antennae, each composed of 3 dissimilar segments: a short basal scape, a club-like pedicel with a complete dorsal seam, and a single large dorsal bristle (arista) that is bilaterally plumose (setae on both sides). Adult calliphorids have well-developed sponging mouthparts to feed on liquids, but they do not bite hosts and do not feed on blood. The ventral proboscis comprises a basal rostrum flanked by short palps, a cylindrical haustellum with a sheath-like labium housing an anterior labrum and a slender hypopharynx; and a terminal sponging labellum. Ingested liquids pass through the tubular oesophagus to the globular proventriculus (with saccular diverticulum) then into the digestive midgut, hindgut (with excretory Malpighian tubules), rectum and terminal anus. The thorax is covered by a shield-like scutum with a small posterior lobe (scutellum). The dorsal scutum contains either long dense setae (*Cochliomyia*) or short sparse setae (*Chrysomya*) as well as stout bristles, including a vertical row on the meron (lacking on muscoid flies), and a stout row on the hypopleuron. The mesothorax gives rise to 2 lateral narrow wings which are usually clear (glassy in the case of *Ch. bezziana*) and sometimes with coloured basicosta (e.g. brown for *Co. hominivorax* and yellow for *Co. macellaria*). Wing membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] with chrysomine flies having setate stem veins (not bare like calliphorine) and M veins that angle sharply upwards near the wing margin. The wings have prominent hind lobes (calypters, squamae) with setae on their dorsal surfaces. Like other dipterans, the hindwings have been highly reduced to small club-like halteres used to stabilize flight. Like all calyptrates, the halteres are covered by the calypters. Oestroid and muscoid flies are further distinguished from other calyptrates by the presence of bulbous swellings (greater ampulla) below the wing base. The ventral thorax is the point of attachment for 3 pairs of long thin dark legs, each composed of 5 segments (coxa, trochanter, femur, tibia, tarsus), all terminating in 2 claws with pad-like pulvilli surrounding a central bristle (empodium). The abdomen is segmented and tapered posteriorly, ending in pointed terminalia (male aedeagus, female ovipositor). Males have 2 testes with vas deferens connecting to a seminal vesicle (with lateral accessory glands) leading to the tubular ejaculatory duct and retractable copulatory aedeagus and claspers. Females have 2 ovaries linked by oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva and a cylindrical telescoping ovipositor.

Site of infection: Adult flies are not parasitic on animals, but female flies lay their eggs near damaged skin or body orifices and the emergent larvae invade host tissues. Many species are necrophagous in carrion, while some may invade the tissues of living animals causing primary or secondary myiases (fly strike). Several *Chrysomya* spp. cause facultative (secondary) fly strike in ruminants around the world, and one species (*Ch. bezziana,* the Old World screwworm) is notorious for causing obligate myiasis in animals and humans in Africa, India and Asia. *Cochliomyia* spp. are primary or secondary invaders in the tissues of numerous animal species, including humans, throughout the American tropics. One species (the New World (American) screwworm *Co. hominivorax*) causes obligate (primary) myiasis in living tissues, while other species (e.g. *Co. macellaria*) cause facultative (secondary) myiasis in necrotic tissue. Screwworm flies are not highly host specific and the adult flies lay their eggs at the edges of wounds (cuts, scratches, bites, shearing, dehorning, castration, umbilicus) or orifices (nostrils, mouth, eyes, ears, anus, vagina) of many animal species, including domestic animals, wildlife and sometimes humans.

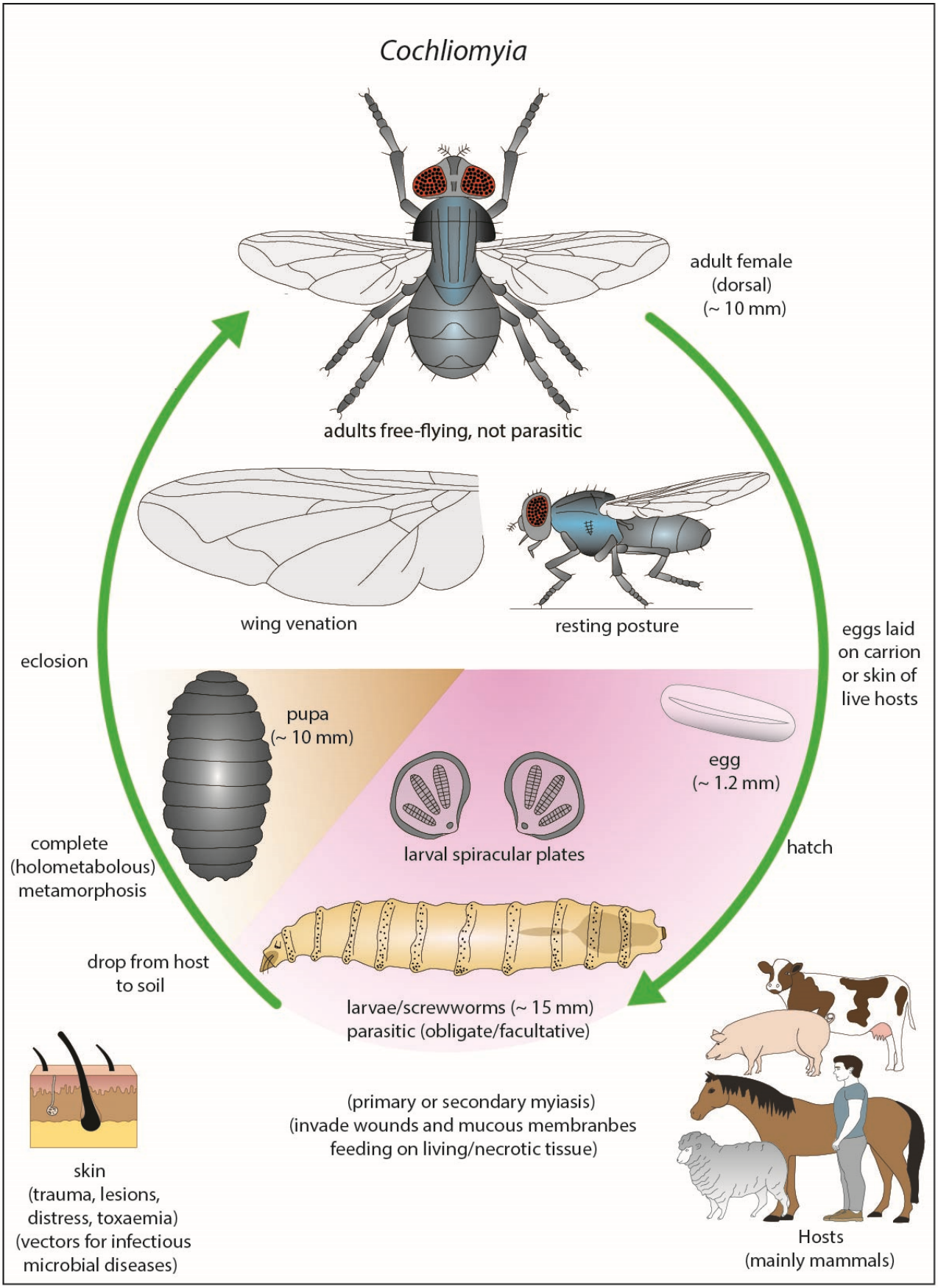
Pathogenesis: Larvae of these blow flies are commonly called screwworms as they burrow headfirst into host flesh and resemble woodwork screws. The larvae require protein-rich foods from animal tissues to complete their development, but they cannot penetrate intact skin. Instead, they invade through wounds or orifices causing cutaneous myiasis. Larvae hatching from one batch of eggs laid by a female fly near a minor skin wound may lead to an expanding lesion packed with several hundred maggots. The larvae feed using their hook-like mouthparts to scrape at host tissues dislodging fragments that are bathed in larval salivary enzymes and sucked up as a nutrient soup. The extent of tissue damage is dependent on the duration and intensity of infestation. Larvae often feed gregariously burrowing into the flesh causing pocket-like lesions that are not solely confined to superficial cutaneous regions, but may become cavernous and involve internal organs. Feeding maggots cause severe pain and distress to the host, eliciting a range of aversive and defensive behaviours (biting, scratching, rubbing, swatting, twitching, galloping, etc.) which are not only energy expensive but may also further open wounds to secondary infections. Untreated, lesions often worsen with progressive necrosis, ulceration, haemorrhage and liquefaction resulting in fluid leakage and purulent pungent odours (often attracting other myiasis-producing flies). Although mature and replete larvae leave host wounds to pupate, infestations are usually not synchronous but involve continuous or successive waves of developing larvae and the cumulative tissue damage is often irreversible. Animals become depressed, anorexic, lose condition, and may die (from dehydration, toxaemia/septicaemia, and various organ failures). In endemic regions, it is essential that any traumatic wounds in livestock due to natural causes (fighting, thorns, bites and disease) or husbandry practices (shearing, tagging, branding, dehorning, tail-docking, crutching, mulseing, castration) be treated as soon as practicable to reduce the incidence of life-threatening myiasis. Female flies are attracted to wounds not only to oviposit eggs but also to feed on exudates and liquids. Several screwworm species have been implicated as mechanical vectors for various microbial diseases, including botulism in birds, salmonellosis, poliomyelitis and swine influenza.

Developmental cycle and mode of transmission: Blow flies undergo holometabolous development where grub-like larvae metamorphose in pupae into winged adults. Female flies are oviparous and may lay 50-400 eggs every 2-4 days on the edges of wounds or body orifices, either in single masses (e.g. *Co. macellaria*) or in overlapping rows (e.g. *Co. hominivorax*). The eggs hatch within 12-24 hours releasing larvae which invade moist host tissues and commence feeding. Larvae develop through 3 instars (L1-3) over 4-12 days, burrowing deeper into host tissues. When L3 become mature and replete with food, they cease feeding and migrate out of the wound dropping to the ground as prepupal stages. They burrow into the topsoil (often beneath leaves and organic

debris) and form puparia by contraction and hardening of their teguments. Pupae form within and undergo metamorphosis to adult stages over several weeks. Pupation may take anywhere from 7-60 days depending on prevailing environmental conditions (longer in colder weather, some species over-wintering as pupae in temperate regions). Teneral adult flies eclose through circular caps and after a short resting period to dry and harden their cuticles, they fly in search of mates and hosts. Adult flies are generally strong fliers and may travel more than 20 km seeking food and mates. Males become sexually mature within 1 day while females mature over 3-4 days. Males feed on plant liquids (such as flower nectar) and they often linger near flowering shrubs to intercept females. Males mate aggressively and frequently, while females usually only mate once but store enough sperm to remain fertile for life. Females are attracted by moisture and odours from wounds on vertebrate hosts and they feed on exudates and fluids near wounds. Most species (including *Co. hominivorax* and most *Ch. bezziana* strains) are autogenous and do not require protein meals to complete gonotrophic (ovarian) cycles and produce eggs. However, others (such as *Co. macellaria* and a few *Ch. bezziana* strains) may be anautogenous and do require additional nutrients in order to produce their first eggs. Female flies live for 1-3 weeks and may produce over 1,000 eggs in their life-times. The whole life-cycle may be completed in warm tropical regions in as little as 3 weeks, but may be extended for several months in cooler temperate regions (when pupae over-winter).

Differential diagnosis: Infestations are provisionally diagnosed by the direct observation of penetrating cutaneous lesions containing fly larvae feeding head-down on host tissues. Diagnoses are confirmed by the collection and identification of larvae on the basis of their morphological characteristics, especially spiracle and tracheal morphology, pigmentation, and armature (setation). It is advisable to collect larvae from deep within the wound to increase the chances of collecting mature stages, and to kill larvae in boiling water prior to fixation for ease of observation. In case of doubt, larvae can be cultured in the laboratory on meat or synthetic medium until they mature, pupate and transform to adult flies. Immunodiagnostic studies have also been conducted to detect host immune responses to larval excretory-secretory (ES) antigens, and monoclonal antibodies have been developed to differentiate screwworm species in enzyme-linked immunosorbent assays (ELISA). Modern molecular biological studies have now been developed to characterize species and examine phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear (28S ribosomal DNA, internal transcribed spacers, elongation factor-1 alpha) and mitochondrial (cytochrome c oxidase I) gene sequences.

Treatment and control: Screwworm infestations require urgent medical intervention as they will often progressively worsen and become life-threatening. Wounds should be thoroughly cleansed with antiseptics, necrotic tissue debrided (under local anaesthesia for penetrating wounds) and larvae extracted by surgical removal, suffocation or insecticide treatment. Patients may require supportive therapy, including analgesics, anti-inflammatories, antibiotics and rehydration. Larvae can be smothered by covering their spiracles with occlusive dressings (oily creams or salves, such as petroleum jelly, lanolin, paraffin or mineral oil, beeswax, and sometimes nail polish, adhesive tape, chewing gum, butter) and they can sometimes be coaxed from wounds using stringent antiseptics (hydrogen peroxide, chloroform in vegetable oil). It is now more usual practice to treat wounds with larvicidal insecticides, which have been variously applied as impregnated dressings, smears, tars, pour-ons, sprays, dips, suspensions, gels, powders and dusts, as well as oral or injectable systemic preparations. Early formulations containing creosote, eucalyptus oil, paraffin, phenol and others were painted directly onto wounds mixed with resinous tar, while next generation formulations incorporated a wide range of insecticidal organochlorides (such as dichloro-diphenyl-trichloroethane (DDT), lindane) and organophosphates (such as coumaphos, diazinon) into topical powders, pastes and sprays. However, significant problems were encountered with drug toxicity and flies developing resistance to organochlorides (especially DDT) and organophosphates (many are now banned as dips although some are still available as dressings). More recently, topical formulations of pyrethroids (permethrin, cypermethrin, deltamethrin) and spinosyns (spinosad) as well as systemic applications of salicylanilides (closantel) and macrocyclic lactones (notably ivermectin, doramectin) have been used to treat myiases with great effect. Domestic livestock may be protected for up to 10 weeks using insecticides with good residual activity (organophosphates and pyrethroids applied topically or via impregnated eartags), and some insect growth regulators (cyromazine, dicyclanil) have given protection for up to 8 weeks. Macrocyclic lactones are available as injectable, pour-on or oral medications or in the form of a controlled-release intra-ruminal bolus. In addition to chemotherapy and chemoprophylaxis, other strategies can be used to prevent and control myiases, mainly by minimizing predisposing conditions (stock husbandry and management); and reducing fly populations (environmental management). Livestock should be subject to regular health surveillance and quarantine so that wounds can be quickly detected and treated promptly. Various husbandry practices may be adopted to prevent screwworm infestation, including regular dagging and crutching (clipping soiled wool/hair around the perineum), tail docking (amputation) and Mules' operation (removal of skin folds around breech). Attention should also be paid to wounds associated with ear-tagging, dehorning, branding, castration and even the umbilical cord stump of newborns. Many blow fly species have been shown to multiply in carrion so every effort should be made to remove and destroy carcases in the field. Several studies have used carcases treated with chemo-attractants and insecticides as baited traps for fly control, but large-scale programmes pose many logistic problems. Good results have been obtained in controlling (and even eradicating) screwworm populations in several Central American regions by releasing sterile (irradiated) males bred in the laboratory to compete for mates. Many interventions can be used to great effect in intensive agricultural systems, but are less appropriate for extensive systems and for wildlife management. Reservoirs of natural infestations may persist in wild animal populations in pockets of inaccessible areas, so further land clearance and utilization needs to account for sporadic encounters. Several recent studies have also examined the possibility of developing a vaccine for screwworm infestations. Animals vaccinated with larval extracts (esp. peritrophic membranes) showed reduced larval growth and increased larval mortality upon challenge, but the underlying mechanisms of protection remain to be determined.


Cochliomyia
adult female
(dorsal)
(~ 10 mm)
adults free-flying, not parasitic
wing venation
resting posture
eggs laid
on carrion
or skin of
live hosts
eclosion
pupa
(~ 10 mm)
egg
(~ 1.2 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
hatch
drop from host
to soil
larvae/screwworms (~ 15 mm)
parasitic (obligate/facultative)
(primary or secondary myiasis)
(invade wounds and mucous membranbes
feeding on living/necrotic tissue)
skin
(trauma, lesions,
distress, toxaemia)
(vectors for infectious
microbial diseases)
Hosts
(mainly mammals)



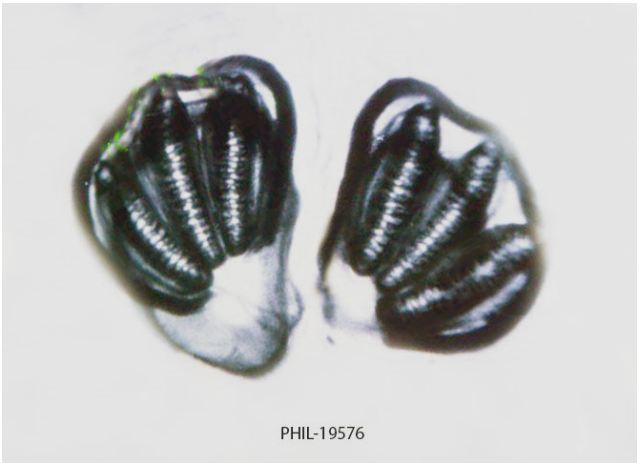
Cochliomyia adult



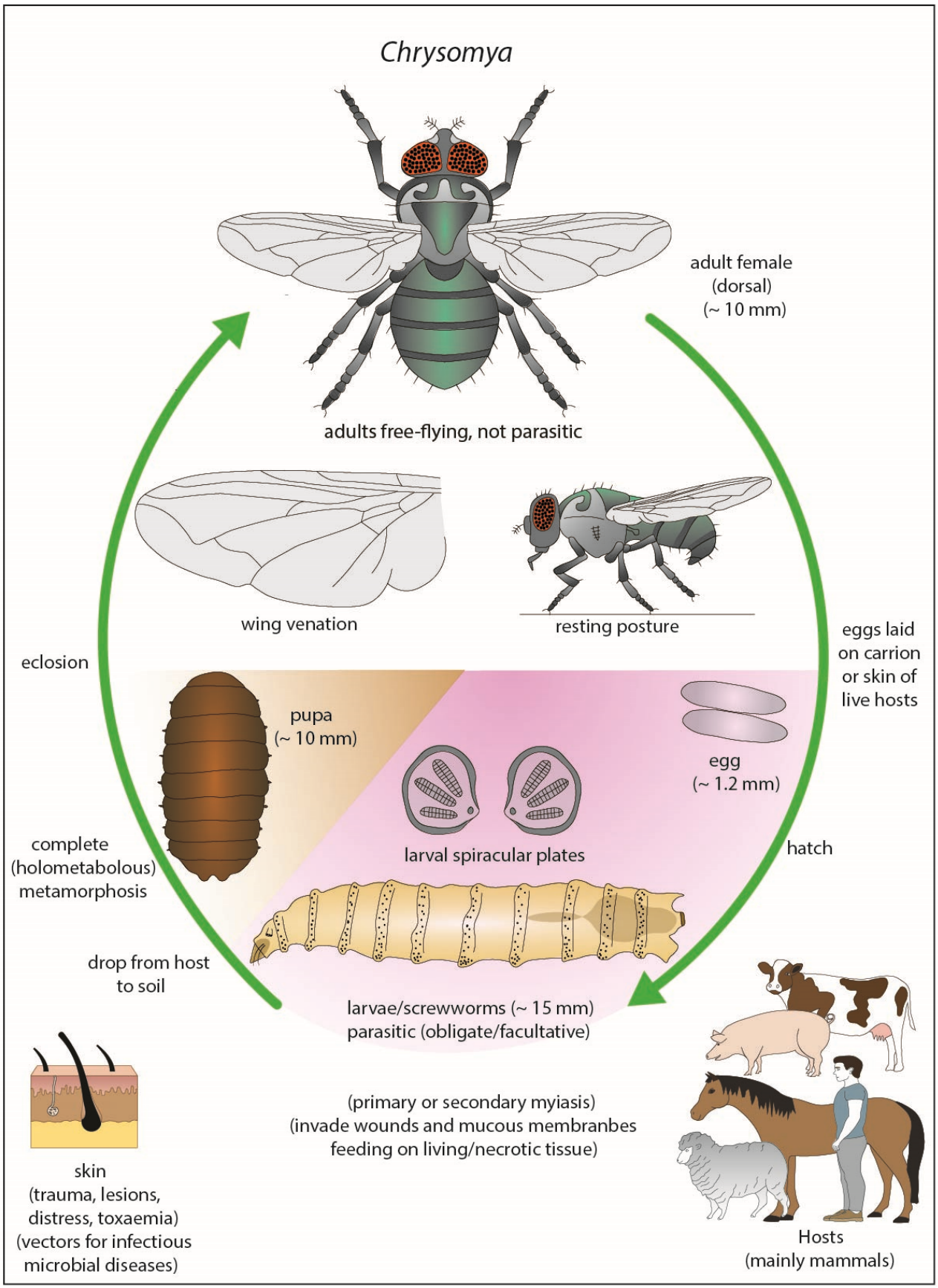
Cochliomyia eggs



Cochliomyia larva



Cochliomyia larval spiracles


Chrysomya
adult female
(dorsal)
(~ 10 mm)
adults free-flying, not parasitic
wing venation
resting posture
eggs laid
on carrion
or skin of
live hosts
eclosion
pupa
(~ 10 mm)
egg
(~ 1.2 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
hatch
drop from host
to soil
larvae/screwworms (~ 15 mm)
parasitic (obligate/facultative)
(primary or secondary myiasis)
(invade wounds and mucous membranbes
feeding on living/necrotic tissue)
skin
(trauma, lesions,
distress, toxaemia)
(vectors for infectious
microbial diseases)
Hosts
(mainly mammals)



Chrysomya adult



Chrysomya eggs



Chrysomya larvae



Chrysomya pupa

Cordylobia
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Calliphorids (blow flies) are not parasitic as adults but their larvae help destroy carcasses and may cause traumatic cutaneous myiases (flystrike, screwworm infestation) in live mammals. Adult flies are large and often metallic in colour. Eggs laid on hosts release larvae which may penetrate the skin to feed on subcutaneous tissues. Most species are facultative invaders, although several are obligate parasites. Larvae of the tumbu fly *Cordylobia* invade the skin of mammals and cause obligate furuncular myiases.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Calliphoridae (blow flies, often metallic, larvae cause myiases (flystrike/screwworm infestation))
Genus:	*Cordylobia* (tumbu fly) (parasitic on skin/subcutaneous tissues of mammals)
Species:	various species cause obligate furuncular myiases

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora (containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the

halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases). Several superfamilies contain species whose larvae feed on the flesh of vertebrate hosts, mostly when dead (carrion) but sometimes when still living (causing fly-strike). Oestroid and muscoid larvae are well-adapted for living in moist organic substrates ranging from wet faeces to carrion to living flesh.

The superfamily Oestroidea contains large flies that are not dorsoventrally flattened, their wing veins are not crowded, and the discal medial cell of the wings widens gradually. The superfamily contains 7 families: Calliphoridae (blow flies, written as two words to distinguish them from other fly-like insects with compound names such as dragonflies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Calliphoridae is characterized by blow flies with metallic iridescent bodies (blue-black, violet-blue, green), strong bristles, well-developed mouthparts and antennae, and weak post-scutellum. The family contains over 1,100 species of blow flies, carrion flies, bluebottles, greenbottles and cluster flies which help destroy carcases, although many species have been implicated in larval myiasis ('flystrike') in living animals. Most invasions are facultative (opportunistic) causing primary, secondary or tertiary flystrike (categorized according to whether they initiate strike or occur later), although several species (notably screwworms) are obligate parasites whose larvae must develop in flesh. The larvae of most blow fly species are not selective feeders and they exhibit broad host specificity, usually for mammals, occasionally birds and less commonly amphibians and reptiles. Myiasis-causing flies have been found worldwide, particularly in temperate and tropical regions with large domestic livestock populations, but also in cooler regions where wildlife abound. Some 75 genera have been described in 11 subfamilies: Ameniinae, Aphyssurinae, Auchmeromyiinae, Calliphorinae, Chrysomyinae, Helicoboscinae, Melanomyinae, Mesembrinellinae, Phumosinae, Rhiniinae and Toxotarsinae, with another 14 unplaced genera and several fossil genera. According to various authorities, the subfamily Auchmeromyiinae contains 7-11 genera (including *Cordylobia*). The larvae of most genera appear to be obligate parasites on a range of hosts, some on vertebrates (rodents, ruminants, carnivores and primates) and others on invertebrates (notably ant and termite nests).

Family	Genera	Hosts	Strike	Myiasis*
Calliphoridae	*Lucilia*	mammals	primary	Facultative (AU, CU, GI, NP, TR, UG)
	Calliphora	mammals	secondary	Facultative (AU, CU, GI, NP, TR, UG)
	Cochliomyia	mammals	primary, secondar	Facultative or obligate (TR)
	Chrysomya	mammals	primary, secondary	Facultative or obligate (TR)
	Cordylobia	mammals	primary	Obligate (CU, TR)

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The genus *Cordylobia* (syn. *Stasisia, Neocordylobia*) contains 3 species whose adults feed on organic matter ranging from rotting fruit and vegetables to animal faeces, while their larvae are endoparasitic in the dermal tissues of mammals where they cause temporary myiases. Individual larvae cause furuncular (boil-like) lesions superficially in the skin with small opening through which they breath using their posterior spiracles, each characteristically with 3 curved slits surrounded by a peritreme. Tumbu fly larvae have been found in rodents, carnivores (dogs, cats), wild bovids (esp. antelope) and domestic livestock in tropical areas of sub-Saharan Africa. Humans may be accidentally infected, particularly during the wet season when moist soil (and even clothes) are desirable sites for oviposition, with emergent larvae penetrating any skin in contact.

Cordylobia* species	Hosts	Location	Clinical signs	Distribution
C. anthropophaga (syn. *C. grunbergi, murium, Ochromyia*) (tumbu fly, mango fly, putzi fly, skin maggot fly, Cayor worm)	Primates: hominid (human); Artiodactyla: bovid (livestock, antelope); Rodentia: caviid (guinea pig); Carnivora: canid (dog); other domestic and wild animals	skin	obligate myiases (painful swelling, pruritus, serous exudate)	sub-Saharan Africa
C. rodhaini	Primates: hominid (human),	skin	obligate myiases	tropical

(syn. *C. ebadiana, Stasisia*) (Lund's fly)	cercopithecid (mona monkey); Rodentia: nesomyid (Gambian pouched rat); Artiodactyla: bovid (bay duiker, blue duiker, grey duiker, black-fronted duiker); other wild and domestic animals		(painful swelling, pruritus, serous exudate)	Africa
C. ruandae	Rodentia: murid (woodland thicket rat); Artiodactyla: bovid (ruminants)	skin	obligate myiasis	Africa

*Various authorities have transferred the nominal species *C. roubaudi* and *C. praegrandis* to the genera *Neocordylobia* and *Pachychoeromyia* respectively.

Parasite Morphology: *Cordylobia* spp. form 4 different types of morphological stages during their developmental cycles: namely, eggs; larvae (3 instars); pupae (inside puparia); and adults (males and females). The eggs are creamy-yellow in colour and ovoid to banana-shaped measuring 0.8-1.0 mm long. Larvae have stout cylindrical white-yellow bodies with a narrow pointed anterior end and a broader truncated posterior end. They develop through 3 instars (L1-3) growing from 1 mm up to 15-33 mm in length depending on species (L3 of *C. anthropophaga* grow up to 11-15 x 5 mm, while those of *C. rodhani* grow up to 17-33 x 8 mm). Larvae lack sclerotized head capsules but have an internal cephalopharyngeal skeleton with rasping mouthparts (2 hook-shaped labial sclerites). The body has 12 segments without obvious fleshy processes but covered with small sharp cuticular spines (denser on last 5 segments). The spines are usually dark yellow-brown to black, directed backwards, and single toothed. All larvae breathe through 2 pairs of respiratory spiracles: a small anterior pair, each with finger-like processes forming of an irregular clump of openings; and a larger posterior pair located caudal circular plates, each with a weakly sclerotized perimeter (peritreme) framing 3 serpentine slits which are curved in L3 of *C. anthropophaga* and sinuous in *C. rodhani* (L1 only have 1 slit) [in comparison, oestrid larvae form flat porous spiracular plates]. Mature L3 form barrel-shaped puparia 6-12 mm long, cocoons that contain pupae whose developing appendages are visible externally. Adults eclose through circular caps (like all Cyclorrhapha) and not through longitudinal slits (like Nematocera and Brachycera). Adult tumbu flies have stout compact bodies 7-15 mm long, which are not metallic-coloured (like other blow flies) but are dull yellow-brown or red-brown. The head, thorax and legs are often yellow, and the thorax may also have 2 broad blue-grey dorsal stripes or diffuse patches. Both sexes are similar in appearance (males slightly smaller) and their bodies have many long thick setae in the form of bristles. They have 3 distinct body tagma: a large oval head, thick thorax, and tapering abdomen. The head possesses both a ptilinal suture and facial lunule (like other Oestroidea and Muscoidea, but unlike other calypterate flies), 2 well-developed large dark compound eyes separated by a small frons, and 2 distinctive antennae, each composed of 3 dissimilar segments: a short basal scape; a club-like pedicel with a complete dorsal seam; and an anterior flagellum composed of a single bristle-like arista that is bilaterally plumose (setae on both sides). Fly mouthparts are of the sponging type and do not have piercing elements (adults are not blood-feeders). The mouthparts are contained within a stout downward-directed proboscis flanked by short club-like palps. The proboscis comprises a short rostrum, a longer cylindrical haustellum (with sheath-like labium housing an anterior labrum and a slender hypopharynx) and a flattened terminal sponging labellum. Liquid foods pass through a tubular oesophagus to a globular proventriculus (with saccular diverticulum) then into the digestive midgut, hindgut (with excretory Malpighian tubules), rectum and terminal anus. The thorax is covered by a sclerotized scutum with a posterior lobe-like scutellum. The dorsal surface bears numerous small setae and a small number of larger bristle-like setae, including a vertical row on the meron (lacking on muscoid flies), 3 pairs of dorsocentral bristles, and hypopleural and pteropleural bristles more ventrally located than the presutural bristle. The mesothorax gives rise to 2 narrow clear-brown wings with membranes supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)]. Tumbu flies have bare stem veins and the lobes along the hind-edge of the wings (calypters or squamae) lack setae. Like all dipterans, the hindwings have been highly reduced to small knob-like halteres used to stabilize flight. Like other calyptrate flies, the halteres are covered by the calypters. However, only oestroid and muscoid flies possess bulbous swellings (greater ampulla) below the wing base. Ventrally, the thorax bears 3 pairs of legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus), all terminating in a pair of claws with pad-like pulvilli surrounding a central bristle (empodium). The segmented abdomen is usually pyriform in shape tapering to a narrow rounded posterior. The visible segments contain lateral spiracles and the posterior segments are usually modified by terminal genital structures (male aedeagus and claspers, female ovipositor). Males have 2 testes connected by vas deferens to a seminal vesicle (with lateral accessory glands) which opens to a tubular ejaculatory duct and retractable copulatory aedeagus. Females with 2 ovaries joined by oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva and telescoping cylindrical ovipositor.

Site of Infection: Adult flies are free-flying and feed on rotting fruits, vegetables, animal faeces and sometimes carrion. The larvae, however, are obligate parasites that require vertebrate hosts for their development. Larvae infect dogs, cats, rodents and wild bovids (especially antelope) in tropical areas of sub-Saharan Africa, humans sometimes becoming accidentally infected. Larvae penetrate the skin and develop directly under the cuticle, most commonly around the feet, buttocks, lower back, waist and backs of the arms (although they may occur elsewhere). When replete, mature larvae drop from the host to pupate in the soil.

Pathogenesis: Eggs laid on or near host skin release first-stage larvae (L1) which can rapidly penetrate the skin upon contact, often unnoticed by the host. Individual larvae then feed on cutaneous tissues causing furuncular (boil-like) lesions (rather than abraded

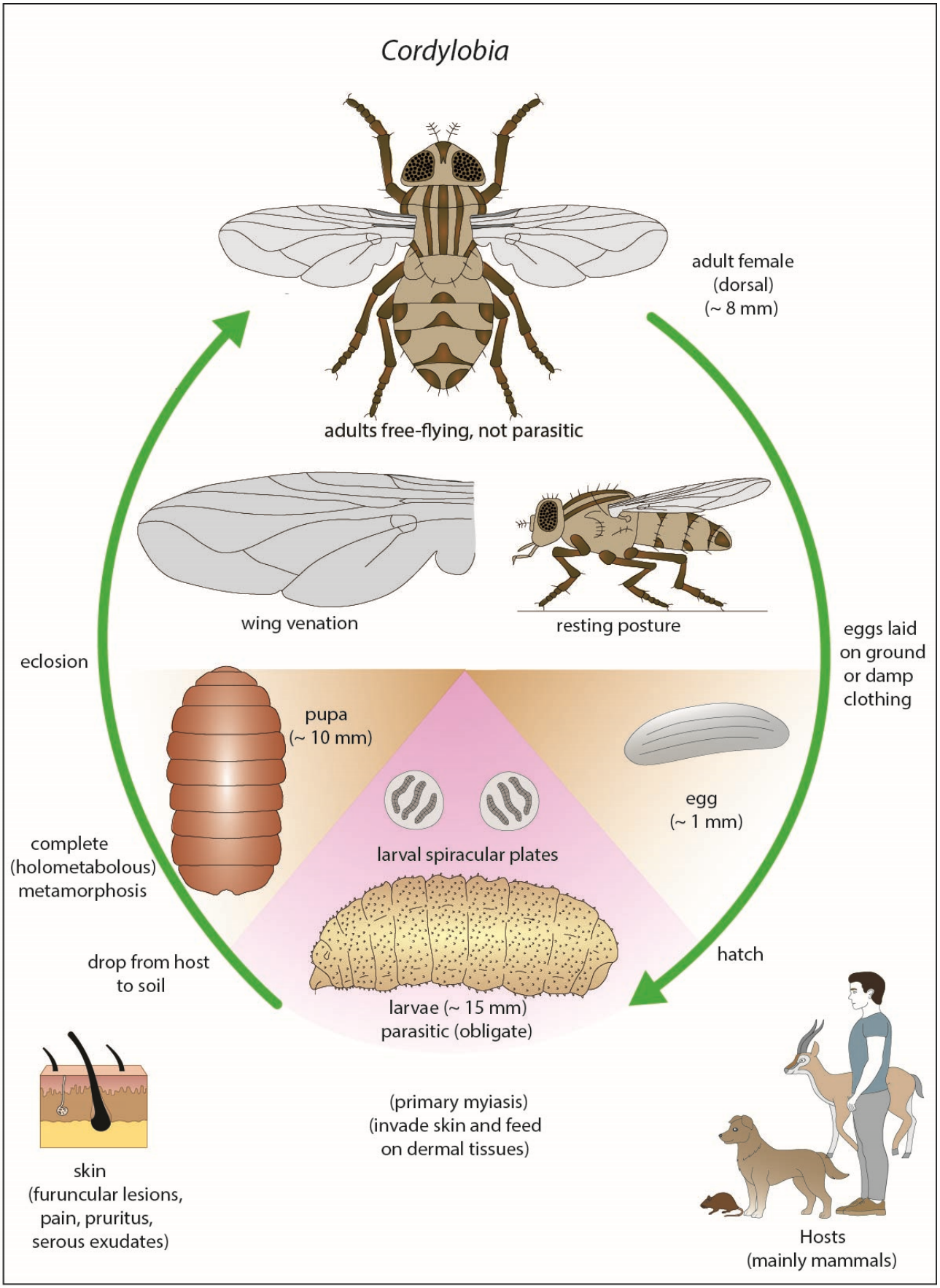
expanding lesions like other blow fly larvae, or cavernous lesions like screwworms). The larvae feed, grow and develop through another 2 instars (L2-3) over 1-2 weeks. *C. anthropophaga* larvae develop parallel to the surface of the skin while *C. rodhaini* larvae develop perpendicularly. When replete, mature L3 then exit the host wounds and drop to the ground to pupate. Skin lesions often begin as small sores with erythema surrounding a central puncture site and mild intermittent pruritus developing over 1-2 days. They are often superficial in location and maintain a central opening 2-3 mm in diameter through which the larvae respire using their posterior spiracles. The lesions then develop over several days into painful boil-like furuncles growing up to 15-35 mm in diameter. The 'boils' appear as micro-abscesses becoming surrounded by host inflammatory responses, tissue granulation, and fibrosis. They begin oozing fluids which is a combination of interstitial fluid, serum, blood, immune cells (eosinophils, lymphocytes), tissue debris and larval waste products. Larvae may even be seen protruding from advanced wounds and the sensation of movement within the papules is common. Lesions become red, swollen, pruritic, and tender to touch with pain ranging from periodic stinging to intense throbbing. Systemic effects are usually not noted, although host inflammation to multiple lesions may be accompanied by regional lymphadenopathy and fever. Many patients become distressed and agitated, and some develop malaise and insomnia. In most hosts, larvae do not migrate into deeper tissues, and pain ceases upon exit of the larvae with lesions healing and scarring over weeks but often retaining traces of the central puncture for months. Curiously, secondary bacterial infections of lesions are uncommon, apparently due to the bacteriostatic activity of larval gut secretions. However, there have been reports of bacterial (commonly *Staphylococcus aureus*) and fungal infections exacerbating wounds, sometimes with fever and septicaemia. Hosts may also develop septic or anaphylactic shock if larvae are damaged during inept attempts at removal. Fatalities have been reported in infested dogs, particularly small breeds with thin soft skin that are susceptible to multiple attacks. Larvae may cause significant oedema or may penetrate to deeper tissues. In endemic regions, rats are preferred hosts and may carry larger numbers of larvae than humans and dogs, often with fatal consequences.

Developmental cycle and mode of transmission: Tumbu flies exhibit holometabolous (complete) metamorphosis in that grub-like larval stages transform in pupae into winged adult insects. Both male and female flies are free-flying and feed on liquids and organic matter from decaying fruits, vegetables, faeces and carrion. Females are oviparous and lay eggs in batches of 100-300 in the morning or evening on dry shaded ground (particularly sandy ground contaminated with urine, faeces or sweat) or on damp or soiled clothing or bed linen. The eggs hatch in 7-20 days releasing first-stage larvae (L1) which adhere to substrates (sand grains or clothing) and remain viable for 2-15 days, depending on conditions (longer in moist conditions). The L1 lie in wait for a host and react rapidly to vibrations and sudden increases in temperature and carbon dioxide. Larvae coming into contact with exposed host skin attach and rapidly penetrate unbroken skin using their oral hooks. Humans often become infected by sleeping on the bare ground, walking over soil with bare feet, or coming into contact with contaminated clothing or bedding (soiled items or those hung out to dry). Once through the skin, larvae do not wander but feed on cutaneous and subcutaneous tissues creating a shallow furuncle (sometimes called a warble). The larvae develop through 3 instars over 7-15 days and they breathe through their caudal spiracles through the central punctum in each wound. When replete, mature L3 cease feeding and leave the host as prepupal stages falling to the ground and burying themselves in surface debris. They form puparia by contraction and hardening of the tegument and the enclosed pupae transform into adults over 10-26 days. Adult flies feed and mate soon after emergence, being most active in the cooler evening or morning but resting in darker places during the day and night (unless attracted to artificial lights). Female flies live for 2-3 weeks and may produce in excess of 500 eggs in their life-times. The whole life-cycle may be completed in 1-2 months, but generally takes longer in cooler regions, flies being most abundant in the wet season.

Differential Diagnosis: Infestations by tumbu fly larvae should be suspected in individuals spending time in endemic areas who have developed non-healing skin lesions that persist for 1-2 weeks and begin discharging exudates from a central punctum. Accompanying signs may include pruritus, tenderness, recurrent pain and sensations of movement within the lesion. Diagnoses are confirmed by the direct observation of larvae within wounds, their removal by forceps or incision, and their identification by examination of their morphological features (particularly spiracles, setae, and mouth hooks). Diagnosis may also be facilitated by rearing larvae in the laboratory on meat or synthetic media until they pupate and release adult flies for examination. Furuncular lesions may also be examined using medical imaging technologies, notably ultrasound and radiography. Modern molecular biological techniques have been used to confirm diagnoses, characterize species and examine phylogenetic relationships by polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA) and mitochondrial (cytochrome c oxidase) gene sequences.

Treatment and Control: Because mature larvae exit the host wound after 1-2 weeks to pupate in soil, most infestations are considered to be transient and self-limiting. However, the pain and psychological distress associated with furuncular myiases often predicates medical intervention. Larvae can be removed from lesions by careful manipulation with tweezers or probes, but they are sometimes difficult to extract due to their bulbous bodies and tegumental spines. Some clinicians inject boils with lidnocaine and epinephrine to help flush out larvae. As last resort, larvae can be removed surgically under local anaesthesia with incision and debridement of the wound, taking care to extract the whole larva as any remaining fragments may cause severe inflammation and granulomas. Treating wounds with insecticides is discouraged as dying or dead larvae can also cause serious inflammatory reactions. Patients are usually given supportive therapies in the form of analgesics, anti-inflammatories, antiseptics, antibiotics and rehydration. Prior to removal, larvae may be smothered by covering the central punctum and spiracles with occlusive dressings of viscous materials (including petroleum jelly, mineral or vegetable oil, liquid paraffin, beeswax, and sometimes butter, nail polish,

adhesive tape and chewing gum). Larvae move closer to the surface and become torpid making them easier to manipulate. Medical imaging technologies can be used to assist precise localization of foreign bodies, notably ultrasonic examination. The prevention of infestations is based around breaking transmission cycles, either by killing adult flies, by limiting the exposure of hosts to infective larvae, and by denying flies access to alternative breeding sites. Residual insecticides and repellents can be used on humans and animals at risk, as well as on potential resting places in the immediate environment. Barriers, screens and nets can be used to provide fly-free housing and sleeping quarters. People should refrain from sleeping on the ground and beds should not be in direct contact with soil. Covered shoes should be worn, even when crossing sandy soils. Improved sanitary and laundry practices should be used to clean and dry clothing (including swimwear) and bedding. Efforts should be made to remove standing faeces, piles of organic debris and any carcases, as they attract flies for feeding and oviposition. Lastly, attempts should be made to control rodents in communities, as they contribute greatly to sylvatic cycles for tumbu flies.


Cordylobia
adult female
(dorsal)
(~ 8 mm)
adults free-flying, not parasitic
wing venation
resting posture
eggs laid
on ground
or damp
clothing
eclosion
pupa
(~ 10 mm)
egg
(~ 1 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
drop from host
to soil
hatch
larvae (~ 15 mm)
parasitic (obligate)
(primary myiasis)
(invade skin and feed
on dermal tissues)
skin
(furuncular lesions,
pain, pruritus,
serous exudates)
Hosts
(mainly mammals)



Cordylobia adult



Cordylobia larva

Sarcophaga
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Sarcophagids (flesh flies) have large checkered bodies but are not parasitic as adults. Most species are larviparous and normally breed in carrion, but the female will deposit larvae on invertebrate and vertebrate hosts to become facultative parasites. Larvae of *Sarcophaga* spp. cause furuncular myiases in domestic animals and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Sarcophagidae (flesh flies, not metallic, breed in excrement/carrion/decomposing organic matter)
Genus:	*Sarcophaga* (parasitic on skin/subcutaneous tissues of mammals)
Species:	various species cause furuncular myiases

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora (containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without

covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases). Several superfamilies contain species whose larvae feed on the flesh of vertebrate hosts, mostly when dead (carrion) but sometimes when still living (causing fly-strike). Oestroid and muscoid larvae are well-adapted for living in moist organic substrates ranging from wet faeces to carrion to living flesh.

The superfamily Oestroidea is characterized by large flies that are not dorsoventrally flattened, their wing veins are not crowded, and the discal medial cell of the wings widens gradually. The superfamily contains 7 families: Calliphoridae (blow flies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Sarcophagidae contains over 2,500 species whose adults are not metallic in colour (like the blow flies) and whose larvae feed on decomposing organic matter (including excrement and carrion) and sometimes the dermal tissues of living vertebrates. Flesh flies have well-developed mouthparts, dull grey bodies with strong bristles and 3 black stripes on the scutum and spots on the abdomen. Around 108 genera have been described and classified into 3 subfamilies: Miltogramminae (parasitoids of arthropods), Paramacronychiinae (including *Wohlfahrtia*), and Sarcophaginae (including *Sarcophaga*).

Family	Genera	Hosts	Strike	Myiasis*
Sarcophagidae	*Sarcophaga*	mammals	secondary, primary	Facultative or accidental (AU, CU, GI, TR)
	Wohlfahrtia	mammals, birds	primary	Obligate, facultative (CU, TR)

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; TR = traumatic.

The genus *Sarcophaga* (syn. *Bulbostyla, Caledonicesa, Devriesia, Erichsonia, Heteronychia, Lehrera, Listeria, Pierretia*) contains well over 1,000 species classified into 157 subgenera (although some subgenera may subsequently prove to be distinct genera). Most species form adults with conspicuous red compound eyes that exhibit sexual dimorphism (eyes set further apart in females than in males). The larvae typically feed on decaying meat (including bacteria and other small organisms living on carrion), although some breed in dung and others are parasitoids of caterpillars (including pest species in forests and orchards). Although most *Sarcophaga* spp. are entirely free living, the larvae of several species have been found as facultative parasites of domestic animals and humans, causing temporary myiases, e.g. *S. haemorrhoidalis* is a typical carrion fly but its larvae may infest living animals.

***Sarcophaga* species (regional exemplars)**	Hosts	Location	Clinical signs (vectorial capacity)	Distribution
S. africa (syn. *S. geogina, nurus, Mesothryia madagascarensis*)	mammals (humans, livestock, carrion), gastropods (snails)	skin	facultative myiasis	worldwide
S. aldrichi (friendly fly, large flesh fly)	insects (forest tent caterpillars)	flesh	parasitoid	North America
S. bullata (grey flesh fly)	mammals (carrion)	flesh	necrophagous [forensic applications]	Nearctic
S. carnaria (syn. *S. variegata*) (cryptic worm flesh fly)	mammals (carrion, dung), gastropods (snails), annelids (earthworms)	flesh	necrophagous, parasitoid	Europe
S. crassipalpis	mammals (livestock)	skin wounds	facultative myiasis [laboratory applications]	worldwide
S. haemorrhoidalis (syn. *Bercaea cruentata*) (red-tailed flesh fly)	mammals (humans, livestock, wildlife)	skin, gut, rectum, nasal passages, ears	facultative myiases [forensic applications] (enteric bacteria, tapeworms, polio)	worldwide
S. subvicina (lesser worm flesh fly)	mammals (livestock, carrion)	flesh	facultative myiasis	Palearctic

Species list (compilation of several on-line data-bases)

***Sarcopohaga* species**	**Subgenus**
S. abramovi	*Heteronychia*
S. absurda	*Uroxanthisca*
S. acrophila	*Bercaeopsis*
S. adhamae	*Liosarcophaga*
S. adriatica	*Sarcophaga*
S. adusta	*Afrothyrsocnema*
S. adzharica	*Liosarcophaga*
S. aegyptica	*Liosarcophaga*
S. aenigma	*Aethiopisca*
S. aenigmoides	Unassigned
S. afra	*Aethiopisca*
S. africa	*Bercaea*
S. agnata	*Helicophagella*
S. agrestis	Unassigned
S. aheria	*Xanthopterisca*
S. airosalis	*Bulbostyla*
S. alba	*Leucomyia*
S. albiceps	*Parasarcophaga*
S. alcicornis	*Lioproctia*
S. aldabrae	*Afrothyrsocnema*
S. aldrichi	*Varirosellea*
S. alina	*Beziella*
S. allisoni	*Liosarcophaga*
S. alpha	*Sarcorohdendorfia*
S. alpina	*Sarcophaga*
S. altitudinis	*Helicophagella*
S. ambon	*Lioproctia*
S. amica	*Phallosphaera*
S. amicoides	*Phallosphaera*
S. amita	*Heteronychia*
S. amplicercus	*Liosarcophaga*
S. anaces	*Krameromyia*
S. anastrenua	*Heteronychia*
S. anatolica	*Heteronychia*
S. anchoriformis	*Robineauella*
S. ancilla	*Heteronychia*
S. ancilloides	*Heteronychia*
S. andaluciana	*Pandelleana*
S. andamanensis	*Sarcosolomonia*
S. angarosinica	*Liosarcophaga*
S. angelicae	*Heteronychia*
S. aniyai	*Sinonipponia*
S. annandalei	*Lioproctia*
S. antilope	*Sarcorohdendorfia*
S. apsuarum	*Sarcophaga*
S. aquila	Unassigned
S. arabari	*Sarcosolomonia*
S. arachnivora	*Baranovisca*
S. aratrix	*Rosellea*
S. arcipes	*Heteronychia*
S. argyrostoma	*Liopygia*
S. arizonica	Unassigned
S. armenica	*Heteronychia*
S. arnaudiella	*Kanoa*
S. arno	*Bercaea*
S. asahinai	*Myorhina*
S. assamensis	*Pandelleisca*
S. assimilis	*Sarcorohdendorfia*
S. atavina	*Heteronychia*
S. aureicrania	*Torgopampa*
S. aureifacies	*Sarcorohdendorfia*
S. aureolata	*Lioproctia*
S. aurescens	*Lioproctia*
S. auricauda	*Liosarcophaga*
S. auriecrania	*Torgopampa*
S. aurifrons	*Taylorimyia*
S. aurora	*Johnsonimima*
S. austenii	*Salemmyia*
S. australis	*Asceloctella*
S. bachmayeri	*Sarcophaga*
S. bainbriggei	*Pandelleisca*
S. bajkalensis	*Heteronychia*
S. balanina	*Heteronychia*
S. ballardi	*Pandelleisca*
S. bancroftorum	Unassigned
S. bangkokensis	*Kanomyia*
S. banksi	*Baranovisca*
S. baoxingensis	*Bellieriomima*
S. baranoffi	*Sarcophaga*
S. baranovi	*Sarcosolomonia*
S. barioensis	*Phallosphaera*
S. barracloughiana	*Nyikamyia*
S. baruai	Unassigned
S. basiseta	*Lioproctia*
S. basuto	*Cyclophalla*
S. batangomyia	*Philiphaga*
S. batissa	*Curranea*
S. batissoides	*Beziella*
S. baudeti	*Pandelleisca*
S. beameri	*Bercaeopsis*
S. bechuanae	*Liopygia*
S. beckiana	*Rosellea*
S. beeri	*Wohlfahrtiopsis*
S. beesoni	*Lioproctia*
S. belanovskyi	*Heteronychia*
S. belgiana	*Thyrsocnema*
S. bellae	*Boettcheriola*
S. bellowi	*Hyperacanthisca*
S. benaci	*Heteronychia*
S. benefactor	*Uroxanthisca*
S. bengalensis	*Boettcherisca*
S. beninella	Unassigned
S. benshiensis	*Pierretia*
S. berberina	Unassigned
S. bergi	*Sarcophaga*
S. beta	*Sarcorohdendorfia*
S. bezziana	*Heteronychia*
S. bezzii	*Johnstonimyia*
S. bicolor	*Bercaeopsis*
S. bidentata	*Sarcorohdendorfia*
S. bifrons	*Sarcorohdendorfia*
S. bihami	*Bellieriomima*
S. birganjensis	Unassigned

S. bishoppi	*Wohlfahrtiopsis*
S. bivittata	*Johnsonimima*
S. bodenheimeri	*Yerohama*
S. boettcheri	*Heteronychia*
S. booersiana	*Afrosarcophaga*
S. borneensis	*Pseudothyrsocnema*
S. borodorf	Unassigned
S. brachiata	Unassigned
S. braueri	*Sarcorohdendorfia*
S. braunsi	*Prionophalla*
S. brevicornis	*Liosarcophaga*
S. brevigaster	Unassigned
S. budapestana	*Heteronychia*
S. bulamatadi	*Uroxanthisca*
S. bulgarica	*Heteronychia*
S. bullata	*Neobellieria*
S. burungae	*Bercaea*
S. bushmenia	*Liosarcophaga*
S. buxtoni	*Sarcosolomonia*
S. cabrerai	*Boettcherisca*
S. cadyi	*Bulbostyla*
S. caerulescens	*Robineauella*
S. caledonia	Unassigned
S. calicifera	*Uroxanthisca*
S. canadensis	*Neosarcophaga*
S. cantrelli	*Baranovisca*
S. caraormana	*Pandelleola*
S. carinata	*Bercaeopsis*
S. carnaria	*Sarcophaga*
S. carolinensis	*Sarcosolomonia*
S. castellana	*Afrothyrsocnema*
S. catharosa	Unassigned
S. caudagalli	*Pseudothyrsocnema*
S. cavagnaroi	*Tolucamyia*
S. cavangarei	*Kozlovea*
S. cepelaki	*Heteronychia*
S. cetu	*Kozlovea*
S. chaetoneura	Unassigned
S. chalcura	*Sarcosolomonia*
S. chambaensis	*Sarcosolomonia*
S. chapini	*Heteronychia*
S. cheesmanae	*Sinonipponia*
S. choudhuryi	*Liosarcophaga*
S. choudhuryi	Unassigned
S. chrysotelus	Unassigned
S. cineria	Unassigned
S. circa	*Sarcosolomonia*
S. cirrhura	*Sarcorohdendorfia*
S. citellivora	*Neobellieria*
S. clarahenae	*Heteronychia*
S. claripalpis	Unassigned
S. claviger	Unassigned
S. clavus	*Sarcorohdendorfia*
S. cockerellae	*Mehria*
S. coei	*Robineauella*
S. cognata	*Liosarcophaga*
S. collessi	*Sarcosolomonia*
S. concreata	*Sinonipponia*
S. condona	*Xanthopterisca*
S. confusa	*Sarcosolomonia*

S. congesta	*Sarcophaga*
S. consanguinea	*Heteronychia*
S. conwayae	Unassigned
S. cooleyi	*Neobellieria*
S. corsicana	*Thyrsocnema*
S. crassimargo	*Helicophagella*
S. crassipalpis	*Liopygia*
S. crinita	*Sarcosolomonia*
S. crinitula	*Pseudothyrsocnema*
S. crispina	*Lipoptilocnema*
S. crispula	*Lipoptilocnema*
S. croatica	*Sarcophaga*
S. croca	*Heteronychia*
S. cruenata	*Bercaea*
S. cuautla	*Bulbostyla*
S. cucullans	*Discachaeta*
S. cultellata	*Liopygia*
S. currani	*Aethiopisca*
S. curva	*Liopygia*
S. curvicercus	Unassigned
S. curvifemoralis	*Heteronychia*
S. cuthbertsoni	*Phallosarcophaga*
S. cygnocercus	*Cornexcisia*
S. cyrtophorae	Unassigned
S. czernyi	*Macabiella*
S. daciana	Unassigned
S. dahliana	*Phalacrodiscus*
S. dambriensis	Unassigned
S. danxomeia	Unassigned
S. darwiniana	*Sarcorohdendorfia*
S. dasguptai	*Thyrsocnema*
S. daurica	*Robineauella*
S. davidsonii	*Arachnidomyia*
S. decisa	Unassigned
S. delicata	*Spatulapica*
S. demeilloni	*Afrothyrsocnema*
S. depressifrons	*Heteronychia*
S. desaii	*Sarcorohdendorfia*
S. desertorum	*Heteronychia*
S. destructor	*Phytosarcophaga*
S. dewulfi	*Paraethiopisca*
S. dimidiatipes	*Poecilometopa*
S. diminuta	*Bellieriomima*
S. dingaani	*Liopygia*
S. dinuzului	*Beziella*
S. discifera	Unassigned
S. disneyi	Unassigned
S. disputata	*Sarcophaga*
S. dissimilis	*Heteronychia*
S. distincta	Unassigned
S. diurpaneia	Unassigned
S. djakonovi	*Robineauella*
S. dreyfusi	*Ahavanella*
S. dromafricana	*Xanthopterisca*
S. dukoicus	*Leucomyia*
S. dumoga	Unassigned
S. dux	*Liosarcophaga*
S. dysderci	*Uroxanthisca*
S. edwardsi	Unassigned
S. edwardsiana	*Aethianella*

S. ehrlichi	*Zombanella*
S. einsteiniella	*Pterolobomyia*
S. elanis	*Bercaeopsis*
S. elegantipes	*Xanthopterisca*
S. elhawagryi	Unassigned
S. elongata	*Neosarcophaga*
S. emdeni	*Liosarcophaga*
S. emeishanensis	*Pterosarcophaga*
S. emmrichi	*Embulinkisa*
S. emmrichiana	*Liosarcophaga*
S. emuensis	*Sarcorohdendorfia*
S. enderleini	*Heteronychia*
S. eos	*Beziella*
S. erecta	*Beziella*
S. erlangeri	*Transvaalomyia*
S. esthera	*Discachaeta*
S. eta	*Liosarcophaga*
S. etoshana	*Nesbittia*
S. evagorata	*Heteronychia*
S. evelynae	*Liosarcophaga*
S. evenhuisi	*Liosarcophaga*
S. exuberans	*Liosarcophaga*
S. fabea	*Sarcosolomonia*
S. fani	*Myorhina*
S. fanigalia	*Pseudothyrsocnema*
S. fattigi	*Bercaeopsis*
S. fattigina	*Bulbostyla*
S. fatua	*Johnstonimyia*
S. fedtshenkoi	*Stackelbergeola*
S. fenchihuensis	Unassigned
S. feralis	*Liosarcophaga*
S. fergusonina	*Sarcorohdendorfia*
S. fernandae	Unassigned
S. ferox	*Heteronychia*
S. filia	*Heteronychia*
S. filiola	*Heteronychia*
S. fimbricauda	*Liosarcophaga*
S. flagellifera	*Rohdendorfisca*
S. flavibarbis	*Liopygia*
S. flavibasis	*Poecilometopa*
S. flavifemorata	*Parasarcophaga*
S. flexuosa	*Hoa*
S. footei	*Bercaeopsis*
S. forceps	*Liosarcophaga*
S. formosensis	*Boettcherisca*
S. fortisa	*Bercaeopsis*
S. freedmani	*Beziella*
S. freidbergi	*Xanthopterisca*
S. freyi	*Prionophalla*
S. froggatti	*Sarcorohdendorfia*
S. fulvipes	Unassigned
S. furcadorsalis	*Uroxanthisca*
S. furcata	*Sarcorohdendorfia*
S. furcoides	*Uroxanthisca*
S. furutonensis	*Nudicerca*
S. fuscipennis	*Scotathyrsia*
S. futilis	*Iranihindia*
S. gabrielei	*Heteronychia*
S. gadiriana	*Xanthopterisca*
S. galileana	*Stackelbergeola*

S. gallica	*Heteronychia*
S. galmuda	*Boettcherella*
S. gambiensis	*Liosarcophaga*
S. ganselene	Unassigned
S. ganura	*Fijimyia*
S. garbo	*Liosarcophaga*
S. geari	*Heteronychia*
S. genuforceps	*Bellieriomima*
S. georgiana	*Wohlfahrtiopsis*
S. germaini	*Uroxanthisca*
S. gertrudae	*Aethiopisca*
S. ghaiae	*Sarcorohdendorfia*
S. giganta	*Heteronychia*
S. gigas	*Rosellea*
S. globicauda	*Afrothyrsocnema*
S. globovesica	*Bellieriomima*
S. gnu	*Afrothyrsocnema*
S. gomezbustilloi	*Leclercqiomyia*
S. goodhopeia	*Liosarcophaga*
S. gorodkovi	*Helicophagella*
S. gorokaensis	*Johnstonimyia*
S. graciliforceps	*Bellieriomima*
S. gracilior	Unassigned
S. gracilis	*Neosarcophaga*
S. graeca	*Heteronychia*
S. granulata	*Mimarhopocnemis*
S. gravelyi	*Phallosphaera*
S. grenieri	*Heteronychia*
S. gresiventris	*Pandelleisca*
S. gressitti	*Alisarcophaga*
S. grueti	*Stackelbergeola*
S. grunini	*Robineauella*
S. guezoia	Unassigned
S. guillarmodi	*Heteronychia*
S. guyanensis	*Mehria*
S. haemorrhoa	*Heteronychia*
S. haemorrhoides	*Heteronychia*
S. hai	*Sarcosolomonia*
S. hainanensis	*Sinonipponia*
S. hainanna	*Rosellea*
S. hakusana	*Takanoa*
S. hamoni	*Liosarcophaga*
S. harinasutai	*Sarcosolomonia*
S. harpax	*Liosarcophaga*
S. hautieri	Unassigned
S. helanshanensis	*Heteronychia*
S. helenae	*Heteronychia*
S. helicivora	*Bercaeopsis*
S. hellenica	*Heteronychia*
S. henania	*Asiopierretia*
S. hennigi	*Sarcophaga*
S. henryi	*Sarcorohdendorfia*
S. heptapotamica	*Heteronychia*
S. hera	*Liopygia*
S. hervebazini	*Sinonipponia*
S. hesterna	*Bercaeopsis*
S. highlandica	*Boettcherisca*
S. hinei	*Mehria*
S. hinglungensis	*Liosarcophaga*
S. hiromui	*Sarcorohdendorfia*

S. hirsuta	Unassigned
S. hirticrus	*Helicophagella*
S. hirtipes	*Parasarcophaga*
S. hokurikuensis	*Nihonea*
S. hollandia	*Sarcorohdendorfia*
S. hongheensis	*Sarcosolomonia*
S. horii	*Bellieriomima*
S. horti	*Sarcorohdendorfia*
S. hortobagyensis	*Helicophagella*
S. houghi	*Mehria*
S. howensis	*Sarcorohdendorfia*
S. hozawai	*Horiisca*
S. huangshanensis	*Robineauella*
S. hugoi	Unassigned
S. hui	*Pandelleisca*
S. hunti	*Liosarcophaga*
S. idmais	*Liosarcophaga*
S. idonea	*Bercaeopsis*
S. ikat	*Sarcorohdendorfia*
S. ikedai	*Sarcorohdendorfia*
S. imbecilla	*Pseudodiscachaeta*
S. imita	*Lioproctia*
S. imitatrix	*Sarcorohdendorfia*
S. immaculata	Unassigned
S. impatiens	*Sarcorohdendorfia*
S. inaequalis	*Bercaea*
S. incisilobata	*Thyrsocnema*
S. indica	*Pseudothyrsocnema*
S. inducta	*Uroxanthisca*
S. indusa	*Sarcorohdendorfia*
S. inextricata	*Sarcorohdendorfia*
S. ingwavumae	*Afrothyrsocnema*
S. inhacaensis	*Liosarcophaga*
S. inopinata	*Helicophagella*
S. insula	*Pandelleisca*
S. insularis	*Pandelleana*
S. invaria	*Boettcherisca*
S. inzi	*Liosarcophaga*
S. inzoides	*Liosarcophaga*
S. ironalis	*Bulbostyla*
S. irrequieta	*Sarcorohdendorfia*
S. ismailiana	*Liosarcophaga*
S. isorokui	Unassigned
S. israeliana	*Golania*
S. iulicida	*Pierretia*
S. iwuensis	*Pandelleisca*
S. jacobi	*Liosarcophaga*
S. jacobsoni	*Liosarcophaga*
S. jamesi	*Iranihindia*
S. jamila	*Sokotriella*
S. japonica	*Robineauella*
S. jaroschevskyi	*Liosarcophaga*
S. javana	*Robineauella*
S. javanica	*Boettcherisca*
S. javi	*Sinonipponia*
S. jeanleclercqi	*Sarcophaga*
S. johnsoni	*Wohlfahrtiopsis*
S. josephi	*Bellieriomima*
S. juliaetta	*Neosarcophaga*
S. juncta	*Liosarcophaga*

S. jupalnica	*Sarcophaga*
S. kadeisi	*Beziella*
S. kagaensis	*Bellieriomima*
S. kaimaraensis	*Fengia*
S. kairatuensis	*Pseudothyrsocnema*
S. kalabariana	*Pterolobomyia*
S. kanekoi	*Amamia*
S. kanoi	*Liosarcophaga*
S. kanoiana	*Liosarcophaga*
S. kaplani	*Sarcophaga*
S. kappa	*Johnstonimyia*
S. karachiensis	Unassigned
S. karakoncolos	*Hadroxena*
S. karna	Unassigned
S. karnyi	*Boettcherisca*
S. kataphygionis	*Heteronychia*
S. kaushanensis	*Sarcosolomonia*
S. kawayuensis	*Pandelleisca*
S. kayaensis	*Asiopierretia*
S. keegani	*Phallantha*
S. keiseri	*Prionophalla*
S. kempi	*Harpagophalla*
S. kentejana	*Thyrsocnema*
S. keresophalla	*Yerohama*
S. kericho	*Poecilometopa*
S. kerteszi	*Heteronychia*
S. kesseli	*Wohlfahrtiopsis*
S. keziviana	*Myorhina*
S. khasiensis	*Rosellea*
S. kikuyana	*Mauritiella*
S. kirgizica	*Liosarcophaga*
S. kisangani	*Uroxanthisca*
S. kitaharai	*Liosarcophaga*
S. kiyokoae	Unassigned
S. kladosoides	Unassigned
S. klinzigi	*Anthostilophalla*
S. klinzigiana	*Hochiella*
S. kobachidzei	*Heteronychia*
S. kobayashii	*Liosarcophaga*
S. koehleri	Unassigned
S. kohla	*Liosarcophaga*
S. koimani	*Boettcherisca*
S. komi	*Sinonipponia*
S. konakovi	*Phallosphaera*
S. kopetdaghica	*Robineauella*
S. kovatschevitchi	*Liosarcophaga*
S. kozlovi	*Heteronychia*
S. krathonmai	*Boettcherisca*
S. kugleri	*Pandelleana*
S. kunonis	*Heteronychia*
S. kupangensis	*Sarcosolomonia*
S. kurahashii	*Phallosphaera*
S. lacrymans	*Heteronychia*
S. lageniharpes	*Pierretia*
S. lanei	*Lipoptilocnema*
S. langi	*Prionophalla*
S. lanna	*Mehria*
S. lasiostyla	Unassigned
S. lederbergi	*Heteronychia*
S. lednicensis	*Heteronychia*

S. leechi	*Prionophalla*
S. lehmanni	Unassigned
S. lejlekensis	*Heteronychia*
S. lekebai	*Parasarcophaga*
S. lhasae	*Pseudothyrsocnema*
S. libera	*Neobellieria*
S. liberia	*Scotathyrsia*
S. liberiphaga	*Sarconimba*
S. limbata	*Heteronychia*
S. limbatella	Unassigned
S. limela	*Callostuckenbergia*
S. limpopoensis	*Liopygia*
S. lincta	*Johnstonimyia*
S. lindae	*Arachnidomyia*
S. lindneriana	*Uroxanthisca*
S. lingulata	*Bellieriomima*
S. lini	*Bellieriomima*
S. litsingeri	*Mehria*
S. littoralis	*Hardyella*
S. liukiuensis	*Liosarcophaga*
S. lomagundica	*Prionophalla*
S. lombokensis	*Sarcosolomonia*
S. londti	*Nuzzaciella*
S. londtiana	*Liosarcophaga*
S. longanota	*Dasysceloctis*
S. longestylata	*Notoecus*
S. longicornuta	*Cornexcisia*
S. longifilia	*Sarcorohdendorfia*
S. longisterna	*Neobellieria*
S. longistylata	*Pseudothyrsocnema*
S. lopesi	*Baliisca*
S. lorengauensis	*Pandelleisca*
S. lorosa	*Mehria*
S. lothianensis	*Kozlovea*
S. louisianensis	*Bercaeopsis*
S. luabae	*Liosarcophaga*
S. lubaia	*Mitumbana*
S. lucentina	*Spatulapica*
S. lunigera	*Myorhina*
S. lushainensis	*Thyrsocnema*
S. luzonensis	*Liosarcophaga*
S. lypai	*Liosarcophaga*
S. maai	*Sarcosolomonia*
S. mababiensis	*Liosarcophaga*
S. macroauriculata	*Parasarcophaga*
S. macromembrana	*Heteronychia*
S. macrura	*Helicophagella*
S. maculata	*Helicophagella*
S. maculigaster	*Amharomyia*
S. maculipennis	*Dasysceloctis*
S. maculosa	Unassigned
S. madeirensis	*Liosarcophaga*
S. madrasiola	*Sarconandia*
S. magensi	*Phallanthisca*
S. magnifica	*Sarcorohdendorfia*
S. major	Unassigned
S. malaitensis	Unassigned
S. malgache	*Uroxanthisca*
S. mandelania	*Sabiella*
S. mantiae	*Seniorwhitea*

S. maramureshana	Unassigned
S. marcelleclercqi	*Sarcophaga*
S. marcosgarciae	*Liosarcophaga*
S. mariobezzii	*Sarcosolomonia*
S. maritima	*Liosarcophaga*
S. marshalli	*Liosarcophaga*
S. martellata	*Iranihindia*
S. martellatoides	*Iranihindia*
S. masaiana	*Curranea*
S. matilei	*Sarcophaga*
S. mauritiana	*Lioplacella*
S. maxima	*Sarcorohdendorfia*
S. mazaliana	*Xanthopterisca*
S. mazuella	*Liosarcophaga*
S. mazurmovitshi	*Heteronychia*
S. mcgoughi	*Heteronychia*
S. mediterranea	*Heteronychia*
S. mefouensis	*Beziella*
S. megafilosia	*Sarcorohdendorfia*
S. mehadiensis	*Stackelbergeola*
S. meiofilosia	*Sarcorohdendorfia*
S. melania	*Pierretia*
S. melanura	*Helicophagella*
S. membranijuxta	*Hoa*
S. membranocorporis	*Pterosarcophaga*
S. menadensis	Unassigned
S. menelika	*Anthostilophalla*
S. mersinensis	Unassigned
S. metopina	*Heteronychia*
S. metzgeri	*Phallosphaera*
S. midnaporensis	*Lioproctia*
S. mimobasalis	*Sarcorohdendorfia*
S. mimobrevicornis	Unassigned
S. mimoris	*Bercaeopsis*
S. minima	*Heteronychia*
S. minor	*Phallocheira*
S. minutissima	*Mehria*
S. misera	*Parasarcophaga*
S. mishnania	*Yerohama*
S. moldavica	*Sarcophaga*
S. momba	*Liopygia*
S. monodia	*Liosarcophaga*
S. monospila	*Liosarcophaga*
S. monserrati	*Liosarcophaga*
S. monspellensia	*Heteronychia*
S. mont	*Sarcorohdendorfia*
S. montana	*Sarcorohdendorfia*
S. montiblensis	Unassigned
S. monticola	*Bercaeopsis*
S. montivaga	*Afrothyrsocnema*
S. moravica	*Sarcophaga*
S. morenita	*Heteronychia*
S. morosa	*Bercaeopsis*
S. mossambica	*Heteronychia*
S. mouchajosefi	*Sarcophaga*
S. moucheti	*Liosarcophaga*
S. mulaba	*Liosarcophaga*
S. multicolor	*Lioproctia*
S. multivillosa	*Sarcorohdendorfia*
S. munroi	*Xanthopterisca*

S. munronis	*Nesbittia*
S. musashinensis	*Sinonipponia*
S. musitali	*Afrothyrsocnema*
S. mutesa	Unassigned
S. mutila	*Heteronychia*
S. namaquensis	*Prionophalla*
S. namibia	*Liosarcophaga*
S. nanpingensis	*Liosarcophaga*
S. nanula	*Heteronychia*
S. natalensis	*Liosarcophaga*
S. nathani	*Boettcherisca*
S. naumanni	*Rosellea*
S. nearctica	*Robineauella*
S. neglecta	*Phallosarcophaga*
S. nemoralis	*Mehria*
S. nepalensis	*Boettcherisca*
S. neuweileri	*Liosarcophaga*
S. nevoi	*Pseudothyrsocnema*
S. nicobarensis	*Pseudothyrsocnema*
S. niculescui	*Thyrsocnema*
S. nigribasicosta	*Dinemomyia*
S. nigricaudata	*Heteronychia*
S. nigridorsalis	Unassigned
S. nigriventris	*Myorhina*
S. nihbadella	*Xanthopterisca*
S. nipponensis	*Heteronychia*
S. nitidiventris	*Poecilophalloides*
S. nodosa	*Liosarcophaga*
S. nomita	*Curranea*
S. noonganensis	*Bellieriomima*
S. nostalgica	*Spatulapica*
S. notabilis	*Lioproctia*
S. notatipennis	*Scotathyrsia*
S. novella	*Helicophagella*
S. noverca	*Helicophagella*
S. novercoides	*Helicophagella*
S. nubica	*Afrothyrsocnema*
S. nuzzacii	Unassigned
S. obvia	*Heteronychia*
S. occidentalis	*Neosarcophaga*
S. occulta	*Sarcosolomonia*
S. octomaculata	*Poecilometopa*
S. offecta	*Neobellieria*
S. oharai	*Malawithyrsia*
S. oitana	*Pterophalla*
S. okaliana	*Helicophagella*
S. okazakii	*Kanoa*
S. olsoufjevi	*Mehria*
S. omari	Unassigned
S. omikron	*Sarcorohdendorfia*
S. ontariensis	*Bercaeopsis*
S. opata	*Harpagophylloides*
S. optata	*Malliophalla*
S. ora	*Helicophagella*
S. orientalis	*Seniorwhitea*
S. ornatijuxta	Unassigned
S. oshimensis	*Phallonychia*
S. ostindicae	*Fengia*
S. otiophalla	*Kalshovenella*
S. owadai	Unassigned

S. pachyura	*Helicophagella*
S. pagensis	*Sarcophaga*
S. paineiana	*Lioproctia*
S. palavae	Unassigned
S. palestinensis	*Liosarcophaga*
S. panaya	*Pseudothyrsocnema*
S. panchganiensis	*Harpagophalla*
S. pandellei	*Heteronychia*
S. pandifera	Unassigned
S. panormi	Unassigned
S. papaii	*Sinonipponia*
S. papuensis	*Sarcosolomonia*
S. par	*Liopygia*
S. paralina	*Beziella*
S. parallela	*Bercaeopsis*
S. paramonovi	*Stackelbergeola*
S. paramulaba	*Liosarcophaga*
S. parasurcoufi	*Bercaea*
S. pattoni	*Lioproctia*
S. pauciseta	*Heteronychia*
S. paularnaudi	*Macabiella*
S. paulina	*Bercaeopsis*
S. peckae	*Heteronychia*
S. penicillata	*Heteronychia*
S. pennopluma	*Liosarcophaga*
S. peregrina	*Boettcherisca*
S. perisi	*Perisimyia*
S. perissa	*Neosarcophaga*
S. persica	*Iranihindia*
S. perspicax	*Neosarcophaga*
S. peshelicis	*Kozlovea*
S. petrovae	*Heteronychia*
S. phallosoma	*Liosarcophaga*
S. pharaonis	*Liosarcophaga*
S. phoenicopterus	*Seniorwhitea*
S. picibasicosta	*Robineauella*
S. piciventris	*Sarcorohdendorfia*
S. pingi	*Pandelleisca*
S. piva	*Sarcorohdendorfia*
S. platariae	*Thyrsocnema*
S. pleomenda	*Bercaeopsis*
S. pleskei	*Liosarcophaga*
S. plotnikovi	*Heteronychia*
S. plutus	*Uroxanthisca*
S. polistensis	*Neobellieria*
S. polita	Unassigned
S. polystylata	*Pandelleisca*
S. pomeroyi	*Beziella*
S. pongola	*Hochiella*
S. pontica	*Heteronychia*
S. porrecta	*Heteronychia*
S. portschinskyi	*Liosarcophaga*
S. praedatrix	*Sarcorohdendorfia*
S. praedo	Unassigned
S. praelibera	*Baranovisca*
S. praerupta	*Kermalia*
S. pratti	*Bercaeopsis*
S. preussi	*Cercosarcophaga*
S. princeps	*Seniorwhitea*
S. promiscua	*Liosarcophaga*

S. propinqua	*Lioplacella*
S. prosballiina	*Lioproctia*
S. protuberans	*Pandelleana*
S. proxima	*Heteronychia*
S. pseudobenaci	*Heteronychia*
S. pseudoscoparia	*Robineauella*
S. pseudosubulata	*Bellieriomima*
S. pterygota	*Bellieriomima*
S. pubicornis	*Neosarcophaga*
S. pudongensis	*Beziella*
S. pulla	*Thyrsocnema*
S. pumila	*Heteronychia*
S. punctipennis	*Poecilometopa*
S. purpurascens	Unassigned
S. pusana	*Sarcorohdendorfia*
S. pyrenaica	*Sarcophaga*
S. quinqueramosa	Unassigned
S. quinquestrigata	*Heteronychia*
S. quoi	*Heteronychia*
S. rabunensis	*Bercaeopsis*
S. rageaui	*Beziella*
S. rayssae	*Drakensbergiana*
S. recta	*Heteronychia*
S. recurvata	*Myorhina*
S. redux	*Liosarcophaga*
S. reedi	*Anthostilophalla*
S. regularis	*Xanthopterisca*
S. reicostae	*Helicophagella*
S. reposita	*Baranovisca*
S. resnikae	*Pandelleola*
S. retrostylata	*Rossikenya*
S. rhynchura	*Sarcorohdendorfia*
S. robustispinosa	Unassigned
S. rohdendorfi	*Liosarcophaga*
S. rohdendorfia	*Sarcosolomonia*
S. rohdendorfiana	*Robineauella*
S. romanica	*Sarcophaga*
S. rondaniana	*Heteronychia*
S. rosellei	*Helicophagella*
S. rosellensis	*Heteronychia*
S. rozkosnyi	Unassigned
S. ruficornis	*Liopygia*
S. rufipes	Unassigned
S. ruticilla	Unassigned
S. sabae	*Liosarcophaga*
S. sabiensis	*Liopygia*
S. sabroskyi	*Bercaeopsis*
S. sachsae	*Drakensbergiana*
S. safaria	Unassigned
S. sakharovae	*Afrothyrsocnema*
S. salemiana	*Liosarcophaga*
S. salerensis	*Heteronychia*
S. salkhit	*Liosarcophaga*
S. samia	*Scotathyrsia*
S. santosdiasi	*Liopygia*
S. santospintosi	*Mediterranisca*
S. sapitwana	*Malawixia*
S. saprianovae	*Lioproctia*
S. saputaraensis	*Ziminisca*
S. sarezia	*Helicophagella*

S. sarraceniae	*Bercaeopsis*
S. sarracenioides	*Liosarcophaga*
S. sarupi	*Liosarcophaga*
S. sawainensis	*Alisarcophaga*
S. sayersi	*Liosarcophaga*
S. schineri	*Heteronychia*
S. schnabli	*Heteronychia*
S. schoemani	*Seniorwhitea*
S. schrameli	*Tolucamyia*
S. schuetzei	*Kramerea*
S. schusteri	*Sarcophaga*
S. scopariiformis	*Liosarcophaga*
S. seagoi	*Bercaeopsis*
S. sedlaceki	*Sarcosolomonia*
S. selene	*Uroxanthisca*
S. semenovi	*Ziminisca*
S. semimarginalis	*Liosarcophaga*
S. seniorwhitei	*Sarcorohdendorfia*
S. separata	*Sarcorohdendorfia*
S. septentrionalis	*Boettcherisca*
S. serbica	*Sarcophaga*
S. serrata	*Hosarcophaga*
S. serratocudo	*Sarcorohdendorfia*
S. setifacies	*Sarcosolomonia*
S. setinervis	*Heteronychia*
S. sexpunctata	*Mehria*
S. seychellica	*Afrothyrsocnema*
S. shermani	*Liosarcophaga*
S. shimbana	*Liosarcophaga*
S. shinolopia	*Pseudothyrsocnema*
S. shinonagai	*Sarcosolomonia*
S. shirakii	*Phallanthisca*
S. shiritakaensis	*Liosarcophaga*
S. shnitnikovi	*Heteronychia*
S. shoniella	*Liosarcophaga*
S. shresthai	*Sarcosolomonia*
S. shuxia	*Bellieriomima*
S. sichotealini	*Phallantha*
S. sicilia	*Heteronychia*
S. siciliae	*Pandelleana*
S. siciliana	*Heteronychia*
S. siciliensis	*Heteronychia*
S. siganella	*Batissophalla*
S. sigilla	*Tolucamyia*
S. sigma	*Liosarcophaga*
S. silbergliedi	*Mehria*
S. silvai	*Prionophalla*
S. sima	*Bercaeopsis*
S. similis	*Pandelleisca*
S. simplex	*Poseidonimyia*
S. simulatrix	*Liosarcophaga*
S. simultaneousa	Unassigned
S. sinuata	*Sarcotachinella*
S. sisyphus	*Sisyhelicobia*
S. sistuliformis	*Bellieriomima*
S. slameckovae	*Kramerella*
S. slovaca	*Heteronychia*
S. smarti	*Sinonipponia*
S. smirnovi	*Heteronychia*
S. smithi	*Pierretia*

S. smithiana	*Heteronychia*
S. snyderi	*Bercaeopsis*
S. socrus	*Myorhina*
S. solitaria	*Thyrsocnema*
S. solomonica	*Liosarcophaga*
S. sororcula	*Myorhina*
S. sororia	*Salemea*
S. sorror	Unassigned
S. souzalopesi	*Baliisca*
S. spangleri	*Beziella*
S. spatulifera	*Heteronychia*
S. spatuliformis	*Bellieriomima*
S. spilargyra	*Liosarcophaga*
S. spilogaster	*Poecilometopa*
S. spinifera	*Lioproctia*
S. spinigera	*Sarcorohdendorfia*
S. spinipenis	Unassigned
S. spinosa	*Pseudothyrsocnema*
S. stackelbergi	*Bellieriomima*
S. stanleyiana	Unassigned
S. statuta	*Neosarcophaga*
S. sternalis	*Liosarcophaga*
S. strenua	*Heteronychia*
S. stricklandi	*Sarcosolomonia*
S. strumiana	*Liosarcophaga*
S. struthioides	*Pandelleana*
S. stuckenbergi	*Seniorwhitea*
S. stuckenbergiana	*Petuniophalla*
S. stygia	*Beziella*
S. stylata	*Sarcorohdendorfia*
S. subaenescens	*Mehria*
S. subdiscalis	*Liosarcophaga*
S. subdistinguenda	*Afrothyrsocnema*
S. subharpax	*Liosarcophaga*
S. subulata	*Bellieriomima*
S. subvicina	*Sarcophaga*
S. sudanica	*Dolichophalla*
S. sudiai	*Bercaeopsis*
S. suffa	Unassigned
S. suffusa	*Liopygia*
S. suhaylia	*Yemeniella*
S. sumbaensis	*Lioproctia*
S. sumunensis	*Sarcosolomonia*
S. sundaensis	*Sarcorohdendorfia*
S. superba	*Chrysosarcophaga*
S. surcoufi	*Liopygia*
S. surda	*Zumptiopsis*
S. susainathani	*Sarcosolomonia*
S. sushkini	*Stackelbergeola*
S. susteriana	Unassigned
S. suthep	*Rosellea*
S. sutilis	*Bercaeopsis*
S. sympaestria	*Liosarcophaga*
S. synia	*Sarcosolomonia*
S. taenionota	*Parasarcophaga*
S. tainanensis	Unassigned
S. taiwanensis	*Lioproctia*
S. taka	*Pandelleisca*
S. takahasii	*Bellieriomima*
S. talomoensis	*Boettcherisca*

S. talonata	*Harpagophalla*
S. tangerensis	*Heteronychia*
S. tanzaniae	*Liopygia*
S. tanzaniella	*Sabakia*
S. tarsata	*Bercaeopsis*
S. taurica	*Heteronychia*
S. telengai	*Heteronychia*
S. tenuicornis	*Bellieriomima*
S. tenuiforceps	*Heteronychia*
S. tephroides	Unassigned
S. tephrura	*Fijimyia*
S. teretirostris	*Liosarcophaga*
S. teskeyi	*Mandalania*
S. tetona	*Bercaeopsis*
S. tetra	*Bercaeopsis*
S. tetrix	*Heteronychia*
S. tewfiki	*Seniorwhitea*
S. thailandica	*Robineauella*
S. thalhammeri	*Heteronychia*
S. thatuna	*Neosarcophaga*
S. theodori	*Pandelleisca*
S. theseus	*Harpagophylloides*
S. thinhi	*Pierretia*
S. thirionae	*Heteronychia*
S. tibialis	*Liosarcophaga*
S. timorensis	*Boettcherisca*
S. todiscoae	Unassigned
S. torvida	*Lioproctia*
S. trabzonensis	*Sarcophaga*
S. transpyrenaica	*Thyrsocnema*
S. transvaalensis	*Curranea*
S. travassosi	*Arachnidomyia*
S. tricolor	*Heteronychia*
S. trifulcata	*Sarcosolomonia*
S. triplasia	*Neobellieria*
S. triplex	*Sarcorohdendorfia*
S. tristylata	*Pandelleisca*
S. tsengi	*Sugiyamamyia*
S. tshernovi	*Kozlovea*
S. tshernovi	*Sarcosolomonia*
S. tsinanensis	*Heteronychia*
S. tsintaoensis	*Mehria*
S. tsushimae	*Liosarcophaga*
S. tuberosa	*Liosarcophaga*
S. tulagiensis	*Sarcosolomonia*
S. tunisiae	*Heteronychia*
S. tupada	Unassigned
S. turana	*Heteronychia*
S. turkanella	*Pterolobomyia*
S. uamensis	*Curranea*
S. uemotoi	*Robineauella*
S. ugamskii	*Asiopierretia*
S. ukrainica	*Sarcophaga*
S. uliginosa	*Liosarcophaga*
S. uncicurva	*Heteronychia*
S. uncus	*Sarcorohdendorfia*
S. unguitigris	*Parasarcophaga*
S. uniseta	*Bellieriomima*
S. urceola	*Sarcorohdendorfia*
S. ussuriensis	*Liosarcophaga*

S. utilis	*Wohlfahrtiopsis*
S. vachai	*Heteronychia*
S. vadoni	*Liosarcophaga*
S. vagans	*Heteronychia*
S. vancouverensis	*Neosarcophaga*
S. vanrienbeecki	*Beziella*
S. vansoni	*Afrothyrsocnema*
S. vanuatu	Unassigned
S. variabilis	*Sarcorohdendorfia*
S. variegata	*Sarcophaga*
S. versatilis	*Sarcosolomonia*
S. vervesi	*Kozlovea*
S. vicaria	*Beziella*
S. vicina	*Heteronychia*
S. vietnamensis	Unassigned
S. vietnamica	*Liosarcophaga*
S. villa	*Chaetophalla*
S. villeneuveana	*Heteronychia*
S. villeneuvei	*Myorhina*
S. villipes	*Mindanaoa*
S. villisterna	*Sarcorohdendorfia*
S. violovitshi	*Heteronychia*
S. vitilevensis	Unassigned
S. vockerothi	*Durbanella*
S. voluptus	*Liosarcophaga*
S. vorax	Unassigned
S. wagneri	*Liosarcophaga*
S. wahisi	*Heteronychia*
S. walayari	*Robineauella*
S. wallenbergi	*Sarcophaga*
S. walshi	*Liosarcophaga*
S. weberi	*Devriesia*
S. wetzeli	*Liosarcophaga*
S. weyeri	*Prionophalla*
S. whitneyi	*Sarcorohdendorfia*
S. wiesenthali	Unassigned
S. wrangeliensis	*Neosarcophaga*
S. wujiangiana	*Sarcorohdendorfia*
S. wumengia	*Sarcorohdendorfia*
S. wyatti	*Pierretia*
S. xizangensis	*Tuberomembrana*
S. yaanensis	*Bellieriomima*
S. yadvashemia	*Braunsiella*
S. yelangiops	*Phallosphaera*
S. yonahaensis	*Takaraia*
S. yorkii	*Liosarcophaga*
S. yuwanensis	Unassigned
S. yvorei	*Liosarcophaga*
S. zaitzevi	*Iranihindia*
S. zarudnyi	*Stackelbergeola*
S. zeta	*Sarcorohdendorfia*
S. zhelochovtzevi	*Heteronychia*
S. zhouquensis	*Bellieriomima*
S. ziegleri	*Xanthopterisca*
S. zimba	Unassigned
S. zuli	*Boettcherisca*
S. zuluensis	*Afrothyrsocnema*
S. zulunata	*Xanthopterisca*
S. zumpti	*Hyperacanthisca*
S. zumptiana	*Sarcophaga*

Parasite morphology: *Sarcophaga* spp. form 4 different types of morphological stages during their developmental cycles: eggs (in utero); larvae (3 instars); pupae (in puparia); and adult flies (male and female). The eggs are retained by female flies within uterine pouches where they embryonate and grow to 0.5-3.5 x 0.1-0.8 mm. They hatch within the uterus releasing larvae which are deposited (larviposited) in the external environment. Larvae have elongated cylindrical white-yellow bodies that are stout in the middle (more robust than blow fly larvae), taper anteriorly to a narrow mouth and are truncated posteriorly. They develop through 3 instars (L1-3) growing from 1-5 mm long up to 20 mm depending on the species. They lack a sclerotized head capsule (although the first segment may sometimes be sclerotized dorsally) and they have an internal cephalopharyngeal skeleton with paired mandibles that are strong and curved like a hook. Sarcophaginae larvae usually lack a labral sclerite, but in some cases, a small triangular plate may be located between the mandibles. The body segments have conspicuous bands of small spines (absent in muscoid larvae), and the hindmost segment has an anal opening located on a posteroventral lobe with lateral tubercles. Larvae breathe using 2 pairs of respiratory spiracles: a small anterior pair, each consisting of a short branched stalk resembling a fan (absent in L1); and a larger caudal pair, each forming a plate recessed in a deep cavity (unique to flesh flies) surrounded by 8-12 tubercles (dorsal ones often sclerotized with toothed processes, ventral ones often covered in nipple-like projections). The spiracular plates are bound by an incomplete sclerotized peripheral ring (peritreme) and have 3 straight vertical slits (2 slits in L1) slanted away from the midline (slits in muscid larvae slant towards the midline, while oestrid larvae have porous plates often without slits). Mature L3 form cylindrical-oval (barrel-shaped) puparia measuring 5-10 mm long that are initially creamy brown in colour but darken to red-brown with age. The enclosed pupa undergoes metamorphic transformation into a winged adult fly which ecloses through a circular cap (like all Cyclorrhapha) rather than longitudinal slits (like Brachycera and Nematocera). Adult sarcophagids are medium-large in size ranging from 4-23 mm in length depending on the species (e.g. *S. haemorrhoidalis* adults are 7-14 mm long, while those of *S. bullata* are 8-17 mm long). *Sarcophaga* spp. do resemble blow flies but are not metallic in colour, and have dull grey-black bodies with 3 longitudinal thoracic stripes and a checkered (tessellated) pattern of dark rectangles on the abdomen. Their bodies have long thick bristle-like setae as well as shorter finer setae. Adults have 3 conspicuous tagma: an oval head; a narrow thorax; and a robust abdomen. The head is often pale ashen grey in colour and has 2 well-developed red compound eyes (set further apart in females than males). Both a ptilinal suture and facial lunule are present (similar to other Oestroidea and Muscoidea, but unlike other calyptrates). The head is adorned with long bristles on the genae (cheeks) and females have 2 orbital bristles (absent in males). There are 2 anterior antennae, each composed of 3 dissimilar segments: a short basal scape; a club-like pedicel with a complete dorsal seam; and an anterior flagellum comprising a large dorsal bristle (arista) that is plumose (feather-like) only at its base (unlike calliphorids whose arista are plumose their entire lengths). Adult flies have sponging

mouthparts that lack piercing elements (adults are not blood-feeders). The mouthparts are contained within a short ventral proboscis flanked by small club-like palps. The proboscis consists of a short rostrum, a tubular haustellum (with a labial sheath holding an anterior labrum and a slender hypopharynx), and a flattened terminal sponging labellum. Ingested foods are routed through a tubular oesophagus to the globular proventriculus (with saccular diverticula) and then on to the midgut (for digestion), hindgut (with excretory Malpighian tubules), rectum and terminal anus. The thorax is covered by a shield-like scutum but lacks a post-scutellum (hind lobe). A prominent row of black bristles occurs on the hypopleuron to either side of the thorax, and another row is found just under the wing base (these presence of these 2 sets of bristles distinguishes sarcophagids from muscids). *Sarcophaga* spp. also have 4 (rather than 2-3) notopleural bristles, 3 sternopleural bristles, and vertical row of bristles on meron (lacking on muscoid flies). The mesothorax gives rise to a pair of narrow clear wings whose wing membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] with the M vein bending towards the leading edge. Like all dipterans, the hindwings have been reduced to small club-like halteres used to stabilize flight. Like all calyptrates, the halteres are covered by posterobasal wing lobes (calypters). Flesh flies also have bulbous swellings (greater ampullae) below their wing bases. The ventral thorax bears 3 pairs of long black legs, each composed of 5 segment (coxa, trochanter, femur, tibia, and tarsus) and terminating in a pair of claws with large pad-like pulvilli. The middle tibia is bare while the hind-tibia is setate with a fringe of short setae or irregularly-placed long setae. The abdomen is ovoid with dorsal segments displaying unique tessellated colour patterns and lateral spiracles. The terminal segments are modified by genital structures which provide key features used to identify sarcophagid genera. Males have 2 testes connected by vas deferens to a seminal vesicle (with lateral accessory glands) leading to a tubular ejaculatory duct and copulatory aedeagus and claspers that are often bright red in colour. Females have 2 ovaries with oviducts leading to a globular uterus (with associated spermatheca and accessory glands). Eggs are retained in expanded bilobed uterine pouches until they hatch and the larvae are birthed through a terminal larvipositor.

Site of infection: Adult flesh flies are free-living and attracted to decomposing organic matter where females deposit larvae. Many species breed in carrion, thus deserving their genus name (*Sarcophaga* literally meaning 'meat-eater') as well as their common name (flesh fly). Some species may also breed in dung, and others are internal parasites (parasitoids) of other insects (especially caterpillars). Several carrion-feeding species may also opportunistically cause facultative cutaneous myiases in live animals when larvae invade wounds or soiled pelage (coat), notably *S. haemorrhoidalis*. Some animals may also acquire gastro-intestinal infestations when they accidentally ingest fly-blown food. Larval myiases have been found in domestic animals, pets, and wildlife as well as in humans, with some fly species adapting well to human habitations and being attracted indoors by faecal odours.

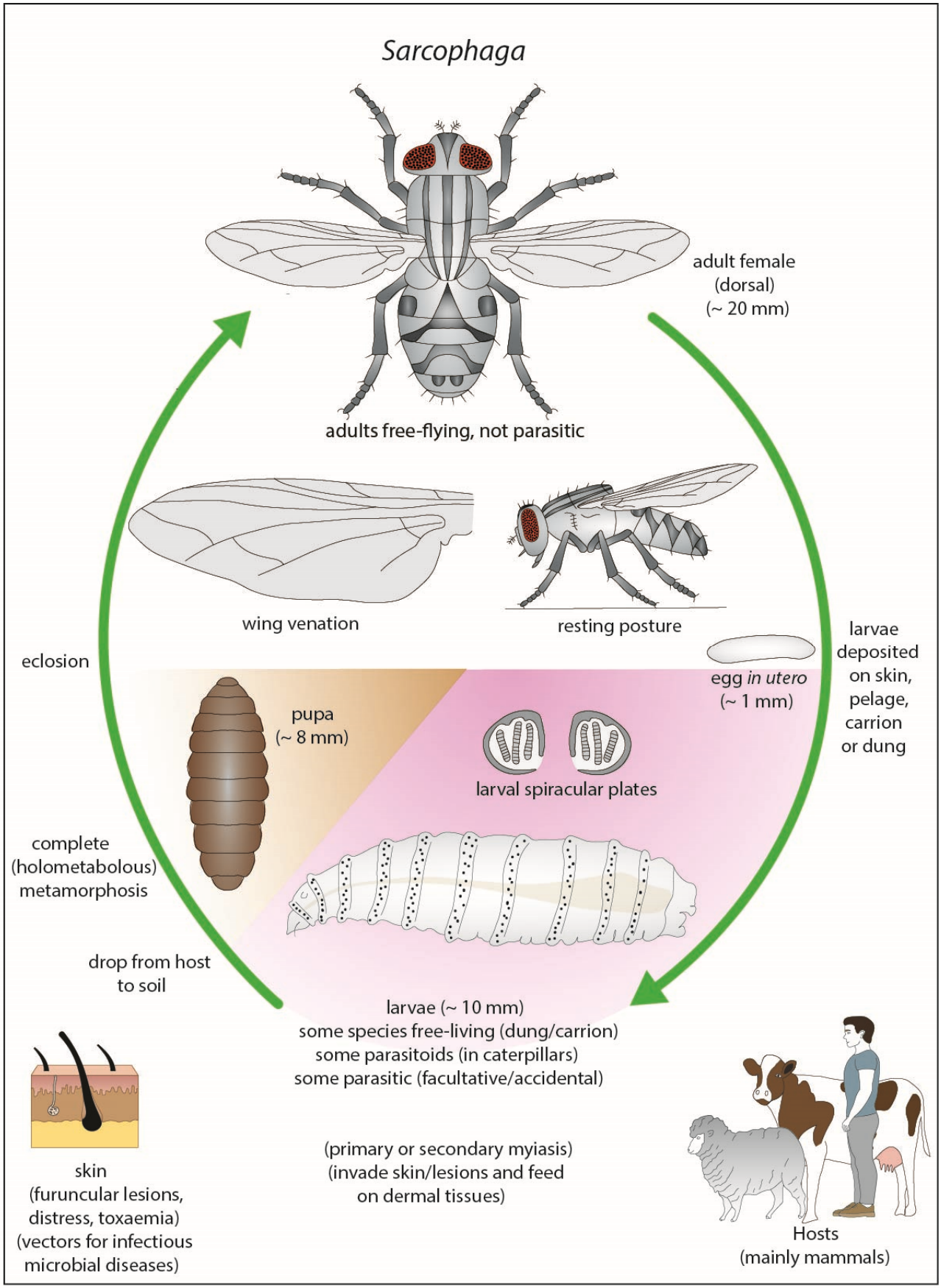
Pathogenesis: Vertebrate hosts may acquire larval infestations when gravid female flies deposit larvae near wounds or soiled coats. The larvae feed on necrotic or dead flesh using their rasping and tearing mandibles, mostly being confined to superficial regions. Most infestations result in furuncular (boil-like) dermal lesions containing a few larvae which breathe through a common central punctum (puncture point or pore). Furuncles develop over several days as larvae feed and are evident as pustules surrounded by inflamed tissue with variable pruritus. Infestations are often considered self-limiting as mature larvae leave the hosts and drop to the ground to pupate. Some hosts do not seem bothered by a few small lesions, but multiple and more severe lesions may cause marked distress. Animals often attempt to relieve clinical signs by biting, scratching or rubbing affected areas which can result in self-trauma and open wounds to secondary bacterial infections. Other sites of infestation have been reported in companion animals, including auricular myiasis (on the outer ear), and aural myiasis (with ear discharge, otalgia and itching). A growing number of cases have also been reported involving gastro-intestinal myiasis in carnivores, and humans, when larvae have been ingested with contaminated meat although they resolve quickly when larvae are excreted with faeces. Because adult flesh flies come into contact with carrion and faeces (some species being particularly attracted to human food and filth), they may act as mechanical vectors for the transmission of various infectious diseases, particularly enteric bacteria which may be carried on the fly body, legs or mouthparts to animal or human food or open sores. *S. haemorrhoidalis* has also been found to carry polio virus.

Developmental cycle and mode of transmission: Flesh flies exhibit holometabolous development whereby grub-like larvae transform in pupae into winged adult flies. Female flies are not oviparous and do not lay eggs. Instead, they retain fertilized eggs in uterine pouches until they produce larvae. Females are viviparous as they give birth to live larvae. Females use their larvipositors to deposit several larvae at a time head-first on decaying organic material (carrion and dung) and sometimes near wounds or soiled coats on live animals. The larvae burrow into the substrate to feed and grow through 3 instars (L1-3) over 3-7 days. They are voracious and will eat almost anything of animal origin that they encounter, including the larvae of other insects (caterpillars, grasshoppers, beetles, other flies) and even snails. Indeed, sarcophagid larvae are larger than those of most other wound-colonizing flies, and often out-compete other species. When replete, mature L3 cease feeding and exit the wound dropping to the ground. They burrow into the soil and form puparia by contraction and hardening of their tegument. The enclosed pupae undergo pupation over 1-2 weeks, but this can be extended in cooler climatic conditions in temperate regions (some species hibernating or over-wintering as pupae). Adult flies emerge and after a short resting period to harden their cuticles and wings, they fly in search of food, mates and larviposition sites. Female flies live for 15-21 days and may produce 30-200 larvae in that time. The whole life-cycle may be completed in as little as 23 days, but is often takes up to 34 days or longer in cooler conditions. While adults may feed on plant sugars (flower nectar, sap), many species are strongly attracted to animal remains in both early and late stages of decomposition, even flying through extreme weather conditions to reach carrion (sarcophagids are often the first flies to colonize cadavers). Some may also opportunistically invade wounds and soiled coats on live animals. Other species are attracted to dung and are routinely

found around compost piles and latrine pits. Even other species invade the tissues of insect larvae (notably caterpillars) as parasitoids or cleptoparasitoids where they complete their larval development by consuming the host. Adult flies prefer sunlight over shaded conditions and are more abundant worldwide in regions with warm climates and during warmer months.

Differential diagnosis: The diagnosis of myiases due to flesh fly larvae is difficult on clinical grounds as many aetiological agents (including other fly species) may cause similar cutaneous lesions. Diagnoses are therefore made by the direct detection, collection and identification of sarcophagid larvae from wounds. Species-specific identification is difficult and recourse is sometimes made to the cultivation of larvae on meat or synthetic media until they pupate and release adult flies for examination. More recently, molecular biological techniques have been used to identify species and examine their phylogenetic relationships by polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA) and mitochondrial (cytochrome oxidase I and II) gene sequences.

Treatment and control: Fly strike wounds should be treated as soon as practicable to minimize their impact on the host and prevent secondary infections. Wounds should be cleansed with antiseptics and attempts made to remove the maggots, either using tweezers, flushing with lidnocaine and/or epinephrine, or by surgical incision, debridement and extraction under local anaesthesia. Larvae may be made more compliant to extraction by smothering them with occlusive dressings that are oil-based (petroleum jelly, mineral or vegetable oils, liquid paraffin, butter, beeswax, and even nail polish, adhesive tape, or chewing gum) or contain insecticidal chemicals (organochlorines, organophosphates, or pyrethroids). Care should be taken not to damage larvae to prevent inflammation, and patients should be given supportive therapy in the form of analgesics, anti-inflammatories, antibiotics and rehydration solutions. The prevention of fly strike revolves around prophylactic insecticidal treatments, establishing barriers between hosts and gravid female flies, and reducing fly populations by eliminating breeding sites. Insecticides with good residual activity may be used on livestock, particularly after management procedures that involve inflicting wounds (branding, dehorning, castration, tailing). Housing facilities may be improved to separate livestock from humans, with window and door screens used to exclude adult flies. Every effort should be made eliminate potential breeding sites for flies by proper disposal of carcases (burn, bury) and improving sanitation (remove faeces). Flesh flies have also been used for forensic applications, as they are usually the first flies to locate and colonize human corpses. Determining the duration of larval developmental stages under different environmental conditions has allowed forensic investigators to calculate the approximate time of infestation (and thereby infer the approximate time of death).


Sarcophaga
adult female
(dorsal)
(~ 20 mm)
adults free-flying, not parasitic
wing venation
resting posture
larvae
deposited
on skin,
pelage,
carrion
or dung
egg in utero
(~ 1 mm)
eclosion
pupa
(~ 8 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
drop from host
to soil
larvae (~ 10 mm)
some species free-living (dung/carrion)
some parasitoids (in caterpillars)
some parasitic (facultative/accidental)
(primary or secondary myiasis)
(invade skin/lesions and feed
on dermal tissues)
skin
(furuncular lesions,
distress, toxaemia)
(vectors for infectious
microbial diseases)
Hosts
(mainly mammals)



Sarcophaga adult



Sarcophaga eggs



Sarcophaga larvae



Sarcophaga pupae

Wohlfahrtia
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Sarcophagids (flesh flies) have large checkered bodies but are not parasitic as adults. Most species are larviparous and normally breed in carrion, but the female will deposit larvae on invertebrate and vertebrate hosts to become facultative parasites. Larvae of *Wohlfahrtia* spp. cause obligate myiases typified by invasive cavernous lesions in livestock, and humans.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Sarcophagidae (flesh flies, not metallic, breed in excrement/carrion/decomposing organic matter)
Genus:	*Wohlfahrtia* (parasitic on skin/subcutaneous tissues of mammals)
Species:	various species cause myiases

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora (containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small

squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases). Several superfamilies contain species whose larvae feed on the flesh of vertebrate hosts, mostly when dead (carrion) but sometimes when still living (causing fly-strike). Oestroid and muscoid larvae are well-adapted for living in moist organic substrates ranging from wet faeces to carrion to living flesh.

The superfamily Oestroidea is characterized by large flies that are not dorsoventrally flattened, their wing veins are not crowded, and the discal medial cell of the wings widens gradually. The superfamily contains 7 families: Calliphoridae (blow flies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Sarcophagidae contains over 2,500 species whose adults are not metallic in colour (like the blow flies) and whose larvae feed on decomposing organic matter (including excrement and carrion) and sometimes the dermal tissues of living vertebrates. Flesh flies have well-developed mouthparts, dull grey bodies with strong bristles and 3 black stripes on the scutum and spots on the abdomen. Around 108 genera have been described and classified into 3 subfamilies: Miltogramminae (parasitoids of arthropods), Paramacronychiinae (including *Wohlfahrtia*), and Sarcophaginae (including *Sarcophaga*).

Family	Genera	Hosts	Strike	Myiasis*
Sarcophagidae	*Sarcophaga*	mammals	secondary, primary	Facultative or accidental (AU, CU, GI, TR)
	Wohlfahrtia	mammals, birds	primary	Obligate, facultative (CU, TR)

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; TR = traumatic.

The genus *Wohlfahrtia* (syn. *Afrowohlfahrtia, Bracia, Disjunctio, Eubracia, Hemibracia, Pandellea, Paraphyto, Wohfartia*) contains 27 species which have been described as parasitoids of insects (orthoptera), necrophages of carrion or as facultative (occasionally obligate) parasites of warm-blooded vertebrates, predominantly artiodactyls (sheep, goats, cattle, camels), perissodactyls (horses), some carnivores (dogs) and occasionally humans and even poultry. They are large flies with bristly bodies, spotted abdomens and long black legs. Vertebrates become infected when gravid female flies deposit larvae near wounds or body orifices resulting in tissue invasion and furuncular myiasis.

***Wohlfahrtia* species**	**Hosts**	**Clinical signs**	**Distribution**
W. africana	trapped*		Africa
W. aschersoni	trapped		Africa
W. atra (syn. *Sinotibetomyia curvifemura*)	trapped		Asia
W. balassogloi	carrion	necrophagous	Asia
W. bella	trapped	facultative myiasis	Africa, Eurasia
W. brevicornis	trapped		China
W. brunnipalpis	carrion	necrophagous	Africa
W. cheni	trapped		Asia
W. erythrocera	Orthoptera (grasshoppers), carrion	parasitoid, necrophagous	Africa, Central Asia
W. euvittata	Orthoptera (locusts)	parasitoid	Africa
W. fedtschenkoi	carrion	necrophagous	Eurasia
W. grunini	trapped		Eurasia
W. ilanramoni	trapped		Eurasia
W. indigens (syn. *W. aethiopica, triquetra*)	trapped, carrion	necrophagous, facultative myiasis	Africa, Eurasia
W. intermedia	carrion	necrophagous	Eurasia
W. magnifica (syn. *W. hirtiparafacialis*) (spotted flesh fly, Wohlfahrt's wound myiasis fly)	Artiodactyla: bovid (cattle, sheep, goat) camelid (camel), suid (pig); Perissodactyla: equid (horse); Carnivora: canid (dog); Primates: hominid (human); Galliformes (poultry): other wild and domestic animals	obligate myiases (cavernous lesions, liquefaction, necrosis, haemorrhage)	Eurasia, Africa

W. monegrosensis	trapped		Europe
W. nuba (syn. *W. longicorpuris, volucris*) (flesh fly)	Artiodactyla: camelid (camel); Primates: hominid (human); other wild and domestic animals, carrion	necrophagous, secondary facultative myiasis (deepening lesions) [forensic applications]	Africa, Eurasia
W. pachytyli	Orthoptera (locusts); Artiodactyla: bovid (cattle)	parasitoid, facultative myiasis	Africa
W. pavlovskyi	carrion	necrophagous	Eurasia
W. seguyi	trapped		Africa
W. smarti	trapped		Africa
W. spinisternum	trapped		China
W. stackelbergi	carrion	necrophagous	Eurasia
W. trina	trapped, carrion	facultative myiasis	Africa, Eurasia
W. vigil (syn. *W. meigenii, opaca*) (grey flesh fly, fox maggot)	Carnivora: canid (dog, fox, silver fox), felid (cat), mustelid (mink, ferret); Lagomorpha: leporid (rabbit, cottontail); Rodentia: cricetid (meadow vole); Mammalia (other wild and domestic animals); Primates: hominid (human); Anseriformes: anatid (ducklings); Anura (unspecified frogs, toads)	necrophagous, facultative myiasis (furuncular)	Holarctic
W. villeneuvi (syn. *W. musiva*)	carrion	necrophagous	Eurasia, Africa

*Adult flies caught in traps or larvae deposited in flesh baits.

Parasite morphology: *Wohlfahrtia* spp. form 4 types of morphological stages during their development: namely, eggs (*in utero*), larvae (3 instars), pupae (in puparia), and adult flies (male and female). The eggs are retained in bilobed expansions of the uterus in female flies where they embryonate and hatch to release larvae. Female flies are viviparous and birth live larvae. The larvae (known as maggots) have cylindrical cream-yellow bodies that taper anteriorly to a narrow head and are truncated posteriorly. They develop through 3 larval instars (L1-3) and grow from 4-5 mm up to 20 mm in length. They do not have a sclerotized head capsule but have an internal cephalopharyngeal skeleton bearing 2 curved mandibles. Their bodies have 12 conspicuous segments, most with distinct segmental bands of small spines (muscoid larvae lack body spines). Larvae breathe using 2 pairs of respiratory spiracles, a small anterior pair located laterally on segment 2, and a larger posterior pair located caudally in deep pits on segment 12. The anterior spiracles appear as small branched fans, while the caudal spiracles appear as plates with an incomplete perimeter (peritreme) surrounding 3 oval slits slanted away from the midline (muscid larvae have slits slanted towards the midline, while oestrid larvae have porous spiracular plates). Mature L3 form barrel-shaped puparia 8-10 mm long which are initially creamy-yellow in colour but slowly darken to red-brown as they age. The enclosed pupae undergo metamorphosis to form a winged adult fly which emerges through a circular pupal cap (like all Cyclorrhapha). Adult flies are relatively large measuring 6-10 mm in length and they resemble house flies but do not have metallic-coloured bodies. Instead, they have dulled dark bristly bodies with prominent thoracic stripes and abdominal spots. Adults have 3 body tagma: an oval head, slender thorax, and stout abdomen. The head has both a ptilinal suture and facial lunule (like other Oestroidea and Muscoidea, but unlike other calyptrates), 2 well-developed red-brown compound eyes located laterally (closer together in males than females), 2-5 postsutural dorsocentral bristles, but bare cheeks (setate in *Sarcophaga*). Adults have 2 anterior flagella, each consisting of 3 dissimilar segments: a short basal scape; a club-like pedicel with a complete dorsal seam; and an anterior flagellum comprising a single large dorsal bristle (arista) without any setae. The mouthparts are located on a ventral proboscis flanked by short club-like palps. Flies have sponging mouthparts without piercing elements (adults are not blood-feeders). The proboscis comprises a short rostrum, a longer cylindrical haustellum (with a sheath-like labium framing an anterior labrum and a slender hypopharynx) and a flattened terminal sponging labellum. Ingested food is directed through a tubular oesophagus to a globular proventriculus (with saccular diverticula) and then passed into the midgut (for digestion), hindgut (with excretory Malpighian tubules), rectum and terminal anus. The thorax is covered by a shield-like scutum but lacks a posterior lobe-like scutellum. There are 2 sets of bristles on each side of the thorax and under the wings (lacking in muscid flies), 4 notopleural bristles, and a vertical row of bristles on the thoracic meron (present in all oestroid flies, but lacking on muscoid flies). The mesothorax gives rise to 2 clear membranous wings whose membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)], with costal spine being as long as the r-m crossvein, and the M vein curving sharply up towards the outer leading edge. The hindwings have been highly reduced to a pair of small club-like halteres used to stabilize flight (like all Diptera), and the halteres are covered by posterior wing lobes (like all calyptrates). Flesh flies also have bulbous swellings (greater ampullae) beneath their wing bases. The ventral thorax is the point of attachment for 3 pairs of long black legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) and all terminating in 2 claws and large pad-like pulvilli. The segmented abdomen has distinctive patterns of black median and lateral spots (median ones partially coalescing) and the terminal segments are modified by genital structures (male aedeagus and claspers, female larvipositor). Male flies have 2 testes linked by vas deferens to a seminal vesicle (with lateral accessory glands) that leads to a tubular ejaculatory duct and retractable

copulatory aedeagus. Female flies have 2 ovaries joined by oviducts to a globular uterus (with associated spermatheca and accessory glands). Fertilized eggs are retained in expanded bilobed uterine pouches and larvae are birthed through a terminal telescoping larvipositor.

Site of infection: Adult *Wohlfahrtia* flesh flies are not parasitic on hosts, but females produce larvae which can invade host tissues. The larvae of some *Wohlfahrtia* spp. are internal parasitoids of insects (particularly grasshoppers), while others are necrophages of carrion and sometimes facultative (occasionally obligate) parasites of warm-blooded vertebrates. In particular, larvae of the Old World species *W. magnifica* and the New World species *W. opaca* and *W. vigil* may initiate cutaneous myiasis as primary (obligate) invaders. Infestations have been recorded predominantly in artiodactyls (sheep, goats, cattle, camels), perissodactyls (horses), some carnivores (dogs) and occasionally humans and even poultry. Larvae have been found mostly in association with wounds or host orifices, including the mouth, nose, eye, ear, perineum and genitalia, but have occasionally been detected elsewhere on the body.

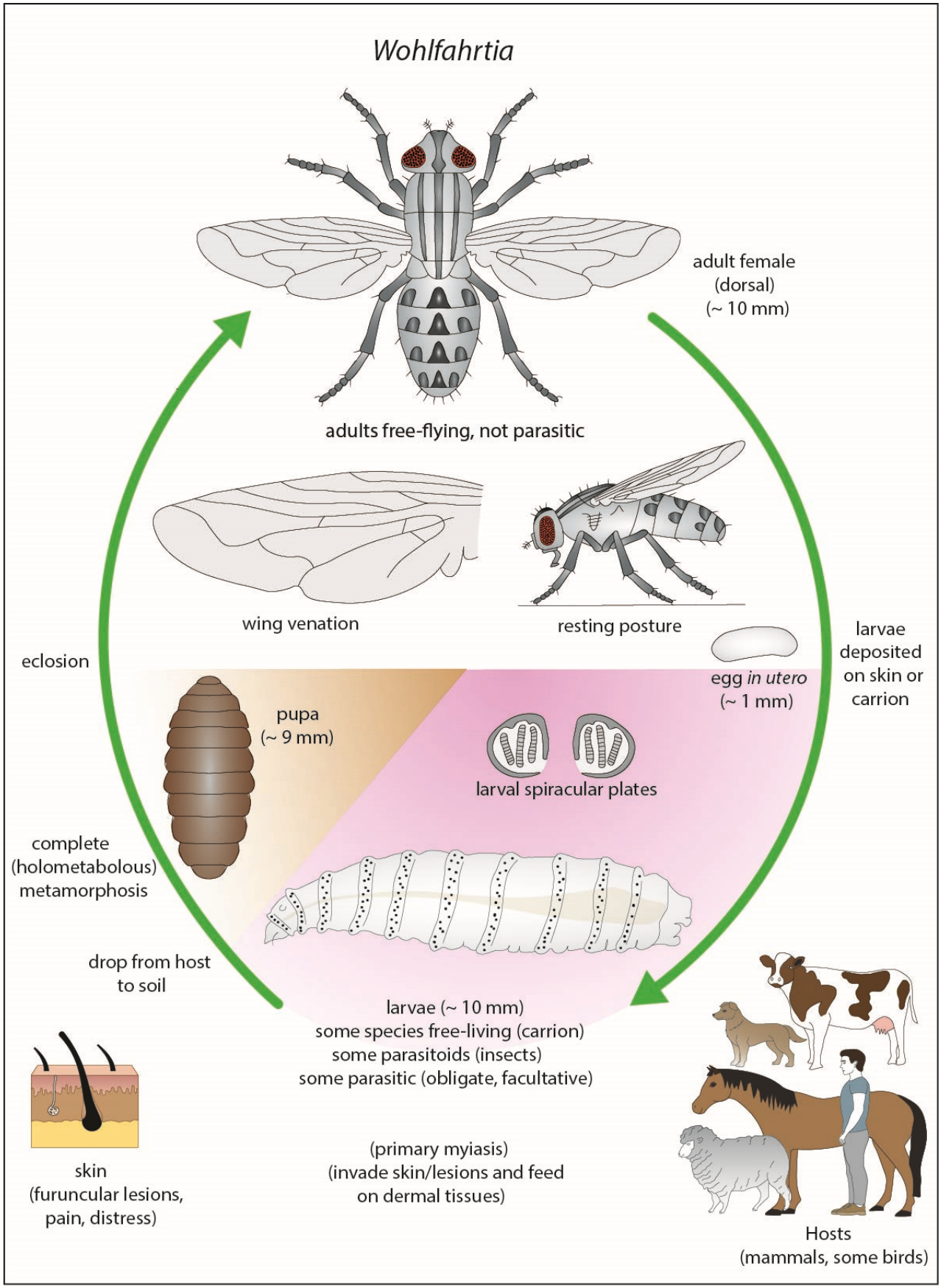
Pathogenesis: Female flies are strongly attracted to flesh but they are not blood or tissue feeders. Instead, they deposit (larviposit) larvae on carrion or on fresh wounds and scratches and moist body openings on live animals. The larvae invade cutaneous tissues using their rasping-cutting mouthparts, on occasion even penetrating thin unbroken skin. The larvae burrow into subcutaneous tissues to feed and grow through 2 more larval instars. They usually cause furuncular (boil-like) lesions, sometimes abscesses, containing one or a few larvae which breathe through a central punctum (pore or puncture point) in the pustule. Occasionally, they may cause more expansive lesions packed with larvae (similar to those caused by screwworm larvae). After approximately one week, mature larvae leave the wounds and drop to the ground to pupate. The pain and stress associated with cutaneous lesions may be severe, with animals becoming distressed and often attempting to relieve the irritation by biting, scratching or rubbing lesions. This may result in self-trauma exacerbating wounds making them haemorrhagic, necrotic and open to secondary bacterial infections. Animals may become anorexic, weakened, and lose condition resulting in production losses in livestock, and sometimes succumb to heavy infestations. Humans rarely become infested, although even a few larvae in ectopic locations (particularly nasal passages) can have serious clinical consequences.

Developmental cycle and mode of transmission: Like all Diptera, flesh flies exhibit holometabolous development where grub-like larvae undergo complete metamorphosis in pupae to form winged adult insects. However, unlike most other flies, *Wohlfahrtia* spp. are not oviparous and do not lay eggs. Instead, they are viviparous and give birth to first-stage larvae (L1) which develop in eggs retained in uterine pouches. Gravid female flies deposit several larvae head-first through their larvipositor onto carrion, or near host wounds or orifices on live animals. The larvae feed on flesh for 4-8 days and grow through another 2 larval instars (L2-3). When replete, mature L3 leave the wounds and drop to the ground. They burrow into the soil and form puparia by contraction and hardening of their teguments. Pupae develop inside the cases and transform over 4-12 days into adults (although pupation can be delayed in cooler condition, with some species in temperate regions over-wintering as pupae). Adult flies emerge from pupae through circular caps and after a brief period of rest to harden their cuticles, they fly in search of food and mate 3-4 days after eclosion. Adult flies feed on plant liquids (nectar and sap) but are attracted to flesh for larviposition. Female flies deposit 6-16 larvae at a time and may produce 120-170 larvae over their 35-40 day lifespans. The entire life-cycle may be completed in 4-6 weeks, but generally takes longer in cooler conditions. In most endemic regions, infestations occur seasonally with the incidence being highest over summer. Epidemiological studies in several countries also indicate considerable annual variation in incidence with some years having massive outbreaks for undetermined reasons.

Differential diagnosis: The differential diagnosis of cutaneous myiases on clinical grounds and history is difficult due to the nonspecificity of signs and symptoms and the large number of possible aetiological agents (especially other fly species which may cause myiasis). Infestations are conventionally diagnosed by the detection and collection of larvae from wounds, and their identification on the basis of their morphological characteristics (notably, oral hooks, segmental bands and spiracles, all of which are more prominent on mature larvae). On occasion, larvae may also be cultivated in the laboratory on meat or synthetic media until they pupate and release winged adults for identification. A range of molecular biological studies have been used to identify and characterize species by polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA) and mitochondrial (cytochrome oxidase I and II) gene sequences.

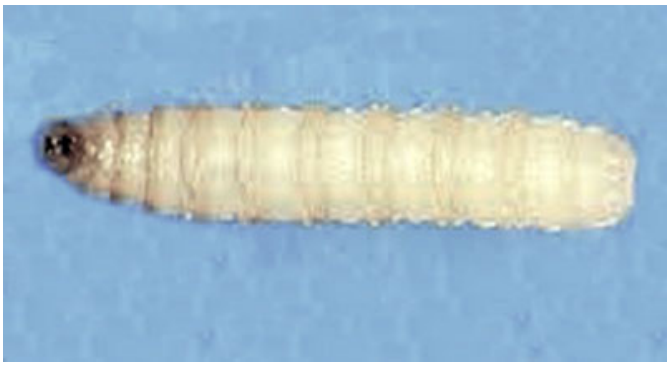
Treatment and control: Wounds infested with maggots are best treated promptly using antiseptic techniques to cleanse and debride wounds. Larvae may be extracted by using tweezers or forceps, by flushing with lidnocaine and epinephrine, or by surgical excision and extraction under local anaesthesia. Larvae may also be made more amenable to extraction by smothering their spiracles with occlusive dressings of oils or fats (such as petroleum jelly, mineral or vegetable oil, liquid paraffin, beeswax, butter, pork fat, and sometimes nail polish, adhesive tape, or chewing gum). Supportive therapy with analgesics, anti-inflammatories, antibiotics, and rehydration may be given to alleviate symptoms and counter secondary infections. Care should be taken not to damage larvae during extraction to prevent inflammatory responses to larval fragments. A number of ready-to-use dressings containing insecticides are also available in most countries for treating wounds either therapeutically or prophylactically after shearing, branding, tagging, dehorning, tailing or castration. Insecticides may be applied as powders, sprays, salves or compression dressings containing

organochlorines (lindane), organophosphates (diazinon, chlorpyrifos, trichlorfon), carbamates (carbaryl, propoxur) or synthetic pyrethroids (permethrin, cypermethrin, deltamethrin). Insecticides with good residual activity may also be used to protect livestock and companion animals against flesh flystrike, including pour-on insect growth regulators (dicyclanil, cyromazine) and some systemic macrocyclic lactones (doramectin, although ivermectin and moxidectin are often ineffective). Efforts to control other blood-sucking parasites (ticks, mites, fleas, lice and other flies) often reduce the incidence of flesh fly myiasis, as *Wohlfahrtia* flies are often attracted to wounds caused by these parasites. The prevention of infestations is based around breaking transmission cycles by killing adult flies (with aerosol insecticides), restricting their access to hosts (through better housing with window and door screens) and eliminating potential breeding sites (through improved sanitation, removal of faeces, disposal of carcases). Individuals working in endemic regions during fly season may benefit from applying insecticides or repellents to skin or clothing, and by maintaining personal hygiene. Several studies have been conducted on the use of *W. nuba* for ‘maggot therapy’ for treating ragged infected wounds in humans, as this species feeds only on necrotic flesh (similar to *Lucilia sericata*).


Wohlfahrtia
adult female
(dorsal)
(~ 10 mm)
adults free-flying, not parasitic
wing venation
resting posture
larvae
deposited
on skin or
carrion
egg in utero
(~ 1 mm)
eclosion
pupa
(~ 9 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
drop from host
to soil
larvae (~ 10 mm)
some species free-living (carrion)
some parasitoids (insects)
some parasitic (obligate, facultative)
(primary myiasis)
(invade skin/lesions and feed
on dermal tissues)
skin
(furuncular lesions,
pain, distress)
Hosts
(mammals, some birds)



Wohlfahrtia adult



Wohlfahrtia larva



Wohlfahrtia pupa

Dermatobia
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Oestrids (bot flies) are large hairy flies but they are not parasitic as adults. Their larvae (bots) are obligatory endoparasites in the integumentary, respiratory or digestive tracts of animals, and they exhibit a high degree of host specificity. Four subfamilies are recognized: cuterebrines (skin bots), oestrines (head maggots), gasterophilines (stomach bots) and hypodermatines (cattle grubs/warbles). Cuterebrine larvae of *Dermatobia* spp. cause cutaneous myiases in many warm-blooded animals, including humans. Their life cycle is unusual in that adult flies lay eggs on carrier insects, mosquitoes and other flies, which then transfer them to vertebrate hosts.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Oestridae (large hairy bot flies, third larval stage or bot resemble small sausages, larvae cause myiases)
Subfamily:	Cuterebrinae (skin bot flies)
Genus:	*Dermatobia* (parasitic on skin of cattle/humans)
Species:	various species cause cutaneous myiases

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders

are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora

(containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases). Several superfamilies contain species whose larvae feed on the flesh of vertebrate hosts, mostly when dead (carrion) but sometimes when still living (causing fly-strike). Oestroid and muscoid larvae are well-adapted for living in moist organic substrates ranging from wet faeces to carrion to living flesh.

The superfamily Oestroidea is characterized by relatively large flies that are not dorsoventrally flattened, their wing veins are not crowded, and the discal medial cell of the wings widens gradually. The superfamily contains 7 families: Calliphoridae (blow flies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Oestridae (bot flies, also known as warble flies, heel flies, gad flies) form large hairy adult flies with bulbous heads, small antennae, rudimentary mouthparts, and wings with subcostal veins running parallel to the costa before joining it. Females produce eggs which hatch by discarding an anterodorsal cap, releasing vermiform larvae which are endoparasitic in the tissues (skin, digestive tract or respiratory passages) of vertebrates. The first larval instars have thorn-like spines encircling several segments, while second and third instars have ecdysal (moulting) scars around their spiracular plates (characteristic for the family Oestridae). Over 150 species have been described in some 25 genera in 5 subfamilies: Cephenemyiinae (deer bot flies), Cuterebrinae (New World skin bot flies), Gasterophilinae (stomach bot flies), Hypodermatinae (Old World skin bot flies, warble flies), and Oestrinae (nose and throat bot flies); with one unplaced genus and 3 fossil genera. Representative genera of veterinary significance are tabulated below:

Oestrid subfamily	Genera	Hosts	Strike	Myiasis*
Cuterebrinae (New World skin bot flies)	*Dermatobia*	cattle, humans	primary	Obligate (CU)
Oestrinae (nose and throat bot flies)	*Oestrus*	sheep	primary	Obligate (OC, NP)
Hypodermatinae (Old World skin bot flies, cattle grubs, ox warbles, heel flies)	*Hypoderma*	cattle	primary	Obligate (CU)
Gasterophilinae (stomach bot flies)	*Gasterophilus*	equines	primary	Obligate (GI)

*type of myiasis: CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular.

The subfamily Cuterbrinae contains 2 genera (*Cuterebra, Dermatobia*) of New World skin bot flies whose larvae parasitize the skin of mammals and some birds. The genus *Dermatobia* contains a single species, *D. hominis* (known as the tropical or American warble fly, human bot fly, or torsalo). The flies have an unusual life-cycle in that females attach their eggs to other live mammalophilic arthropods which act as porters or transporter vectors delivering the eggs to the skin of vertebrate hosts (process also called phoretic transfer or paratenic transport). *Dermatobia* eggs have been shown to be vectored by over 40 species of mosquitoes and muscoid flies, as well as one species of tick. Vertebrate hosts have included humans, wild and domestic animals, companion animals, poultry and aviary birds. *Dermatobia* larvae released from hatched eggs invade subcutaneous tissues causing distress, furuncular lesions, reduced productivity and damaged hides. The flies are restricted in their distribution to the evergreen tropical forests of South and Central America as they require humid conditions for egg survival and moist soil for pupal development.

***Dermatobia* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
D. hominis (human bot fly, tropical warble fly, Torsalo, berne, ura, nuche)	Primates: hominid (human), cercopithecid (various monkeys); Carnivora: canid (dog), felid (cat); Artiodactyla: bovid (cattle, buffalo, sheep, goat); Perissodactyla: equid (horse); Galliformes: phasianid (turkey); Piciformes: ramphastid (toucan); and others	skin (wounds)	obligate myiasis (suppurative swellings, severe pain)	Central and South America

Parasite morphology: *Dermatobia hominis* forms 4 different types of morphological stages during its development: eggs; larvae; pupae; and adults. The eggs are ovoid, curved dorsally and flattened ventrally, measuring around 1.0 x 0.5 mm. They are creamy yellow to brown in colour, soft-shelled with a highly sculptured outer chorion, and have a well-developed anterodorsal cap (operculum). Larvae (commonly called bots) grow through 3 instars (L1-3), increasing in size from 1.0-1.5 mm up to 18-24 mm long. They have segmented bodies that are initially white (L1), then change to creamy-yellow (L2-3) and finally darken to brown-black (mature L3). The larvae have distinctive shapes, L1 being drumstick-shaped with elongate thin posterior segments, L2 becoming more robust, and L3 becoming cylindrical-pyriform with thickened body segments that taper posteriorly. The bots lack a sclerotized head capsule, but possess an internal cephalopharyngeal skeleton with large rasping mouthparts (vertically-biting mandibles). The tegumental surface is armed with black thorn-like backward-facing spines that encircle anterior segments, as well as a progressively denser covering of smaller flat plate-like spines (oestrine larvae have few spines, while muscoid larvae lack spines). Larvae breathe through 2 pairs of respiratory spiracles: small inconspicuous anterior spiracles that appear flower-like; and larger posterior spiracles located on a caudal plate that is not surrounded by a distinct peritreme and has 2 sets of 3 parallel slits (calliphorid larvae have 3 slits surrounded by a peritreme, and other oestrid larvae have porous spiracular plates). L2 and L3 also possess ecdysal (moulting) scars around their spiracular plates (characteristic for Oestridae). Pupae are similar in appearance to L3, being ellipsoidal and measuring 20-25 x 5-7 mm, but they are much darker in colour ranging from dark brown to black. Pupae are obtect with faint transverse striations, appendages and spines externally visible, and often exhibiting prominent anterior spiracles (which become everted during pupation). Adult flies eclose through circular caps (like all Cyclorrhapha) rather than through longitudinal slits (like Nematocera, and Brachycera). Adults appear as large hairy flies with stout bodies measuring 10-20 mm long by 4-5 mm wide. They are covered in small setae but generally lack stout bristles. They have a striking bee-like appearance, with yellow-orange heads and legs contrasting with the blue-black thorax and abdomen. Their heads are bulbous and possess both a ptilinal suture and facial lunule (like Muscoidea and Oestroidea but unlike other calypterate flies). The side of the head is broad and pale and contains large orange compound eyes separated by a frons (eyes closer together in males than females) with another 3 simple eyes (ocelli) located on the top of the head. Adults have 2 small antennae located within facial pits, each antenna consisting of 3 dissimilar segments: a short basal scape; a club-like pedicel with a complete dorsal seam; and an anterior flagellum comprising of large dorsal bristle (arista) that is plumose (setate) on the outer side only (arista bare in Oestrinae and Hypodermatinae). Adult flies have vestigial mouthparts and do not feed (similar to other oestrid flies); living instead on reserves built up as voracious larvae. Likewise, their alimentary tract is vestigial but may function to regulate water. The thorax is covered by a shield-like scutum with a posterior lobe-like scutellum. The thorax has a sparse covering of short setae and a vertical row of bristles on the meron (lacking on muscoid flies). The mesothorax has a twice-bent suture and bears a pair of narrow brown wings whose membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)], with Sc veins running parallel to the C vein, and the M vein extending directly to the outermost wing. Like all Diptera, the hindwings have been highly reduced to stumpy halteres used to stabilize flight. Like all calyptrate flies, the halteres are covered by hindlobes of the forewings (called squamae or calypters) which are bare (asetate) and large (in all oestrids except gasterophilines). Like all Oestroidea and Muscoidea, adult flies also have bulbous swellings (greater ampulla) underneath the wing bases. The ventral thorax gives rise to 3 pairs of long stout coloured legs, each consisting of 5 segments (coxa, trochanter, femur, tibia, and tarsus) and terminating in a pair of claws with pad-like pulvilli surrounding a central bristle (empodium). The abdomen is often metallic coloured and covered with fine hair. The segments bear lateral spiracles and the terminal segments are modified by genital structures (female pseudovipositor, male aedeagus and claspers). Males have 2 testes joined by vas deferens to a seminal vesicle (with lateral accessory glands) leading to a tubular ejaculatory duct and copulatory aedeagus. Females have 2 ovaries connected by oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva and the terminal elongated pseudovipositor.

Site of infection: *Dermatobia* larvae are obligate parasites in the skin of warm-blooded vertebrates. They exhibit a broad host specificity, unlike other oestrid flies which have a narrow specificity for a small range of hosts. Infestations have been reported in primates (incl. humans), ungulates (cattle, sheep, goats, equines), carnivores (cats, dogs), and some poultry and aviary birds. They are most commonly encountered in cattle, dogs and humans. Larvae invade subcutaneous layers of the skin at any exposed sites, commonly on the legs, arms, scalp and back. arms, legs, back and scalp. On rare occasions, they have also been found associated with the eyes, mouth, nose and genitalia. Adult flies are not parasitic, but females waylay and pressgang other live arthropods (mosquitoes, muscoid flies and even ticks) into serving as transport vectors for their eggs. The eggs are attached to external surfaces of these vectors who then deliver them to vertebrates when they feed.

Pathogenesis: First-stage larvae (L1) hatched from eggs are able to penetrate vertebrate host skin either by burrowing through intact skin or through hair follicles, insect bites or other pre-existing lesions. The larvae feed using their sclerotized mouthparts to tear and rasp host tissues resulting in the development of a small (2-3 mm) elevated erythematous papule within 24 hours. L1 do not migrate away from the point of entry but they may move deeper into subcutaneous, and sometimes underlying muscular, tissue as they develop through another 2 instars (this is in contrast to other oestrid larvae which migrate away from their point of entry to mature in other tissues). The papule indurates and grows over several weeks into a furuncular (boil-like) lesion up to 10-35 mm in diameter and 5-10 mm high. Furuncles are like micro-abscesses as they are surrounded by granulation tissue (acute and chronic inflammatory cells) and fibrosis. The larvae live in these encapsulated pockets (often referred to as warbles) and create a small central hole (punctum or pore) to the surface through which they breathe and excrete waste. Warbles are evident as non-healing lesions that may suppurate and weep serosanguinous or seropurulent fluids with intermittent bleeding and fetid odours. They may persist for 6-10

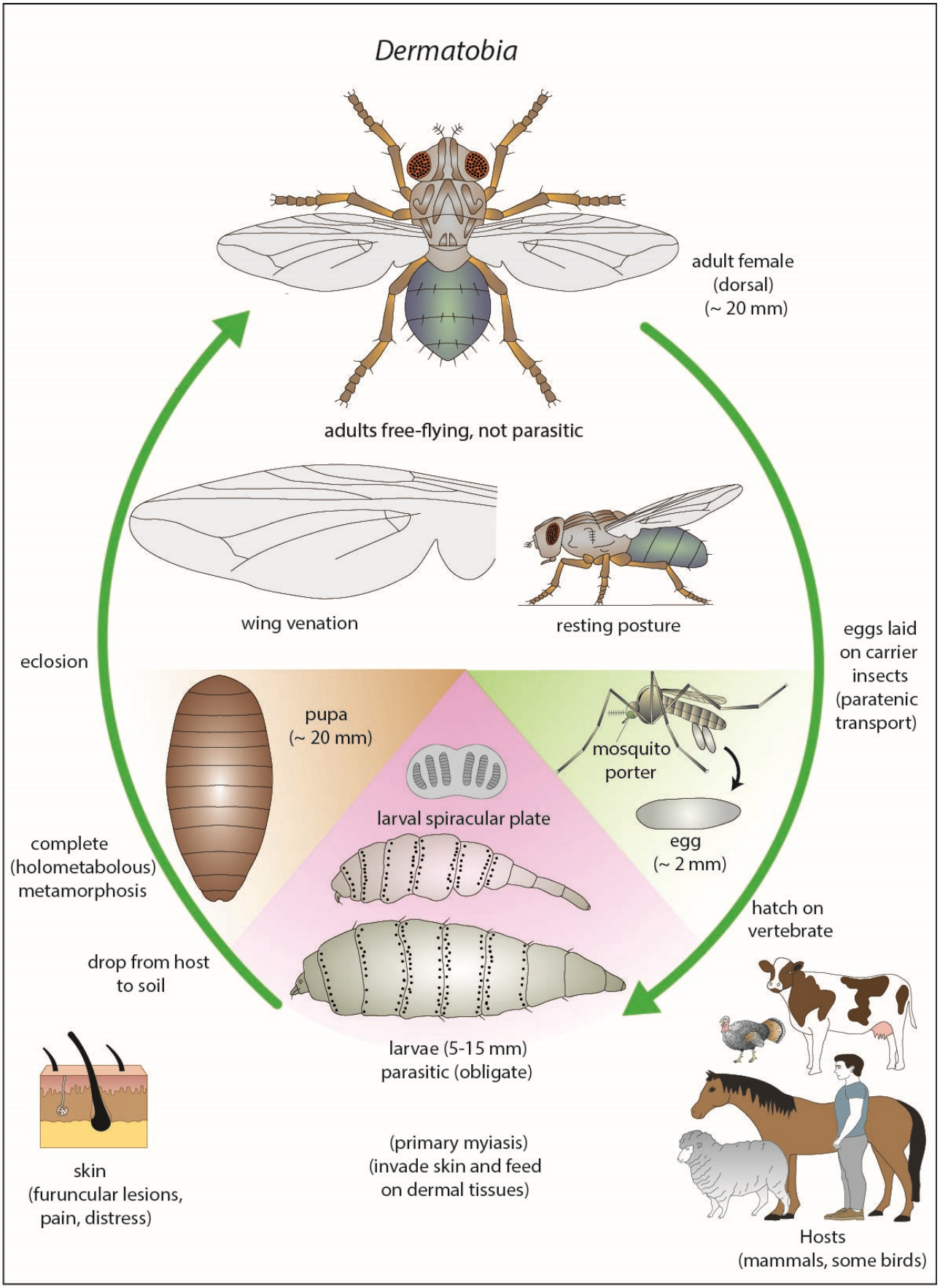
weeks, and sometimes last for up to 3 months. Hosts often become distressed and experience severe acute pain with inflammation and pruritus. Patients may describe a creeping or crawling sensation under the skin, particularly when lesions are covered. Some develop systemic signs such as headache and regional lymphadenopathy. Despite the invasive nature of the wounds, few patients develop secondary bacterial infections which is thought to be due to the bacteriostatic action of larval secretions. When replete, mature L3 move to the surface of the furuncles and leave the wounds dropping to the ground to pupate. Lesions generally resolve spontaneously without overt scarring following removal or emergence of the larvae. On rare occasions, larvae have been associated with eye lesions (opthalmomyiasis), nasal lesions (rhinomyiasis), genital lesions (vaginal myiasis), and even brain lesions (cerebral myiasis where larvae have burrowed through fontanelles in the skull of an infant). In Central America, these bot flies cause a significant problem in cattle (known colloquially as 'warbles'), with reduced meat and milk production and damage to hides.

Developmental cycle and mode of transmission: The life-cycle of bot flies involves holometabolous development in that grub-like larvae undergo complete metamorphic transformation in pupae into winged adults. The adult flies are free-flying but do not feed or seek vertebrate hosts on which to lay eggs. Instead, the females have adopted a unique means of ensuring their eggs come into contact with vertebrate hosts. They capture other blood-feeding arthropod ectoparasites and deposit small batches of 6-30 eggs on their external surfaces (abdomen and legs), securing them with water-resistant adhesive secretions. These arthropods are then released and continue their own cycles which involves locating and feeding on blood from vertebrates. The bot fly eggs embryonate over 5-15 days and are triggered to hatch while the arthropod is feeding in response to increased temperature and moisture levels associated with vertebrate hosts. The released larvae come into contact with vertebrate skin and burrow into subcutaneous tissues ultimately causing furuncular lesions. Because the eggs are effectively passively carried to vertebrates, the arthropods are considered to be mechanical transport vectors (porters) for the bot flies. This process is known variously as paratenic transport or phoretic transfer. *Dermatobia* eggs have been shown to be vectored by over 40 species of mosquitoes (mostly day-biting culicids), filth flies (muscids), blow flies (calliphorids), horse flies (tabanids) and even some hard ticks (ixodids). The use of numerous types of transporter vectors, each with different host specificities, is thought to contribute to the broad host range of *Dermatobia* for mammals and birds. Similarly, *Dermatobia* infestations are not site specific, but will occur on any skin available to the porter. On occasion, when gravid female bot flies cannot find a porter, eggs have been shown to be oviposited on vegetation or clothes hung outside to dry, and the larvae emerge if they come into contact with vertebrate hosts. Larvae usually penetrate the skin within one hour but are able to survive for several days before entry. They develop in subcutaneous tissues and do not wander to other sites to mature (unlike other oestrid larvae which migrate extensively). The larvae develop through 3 instars (L1-3) over 4-8 weeks, but may sometimes persist up to 10-18 weeks. Mature L3 then emerge from the wounds, drop to the ground and burrow into the soil forming puparia by hardening of their teguments. Pupation varies considerably in duration, ranging from 3-18 weeks depending on prevailing environmental conditions (longer in cooler climates). Cuterebrine bot flies in temperate zones typically over-winter as diapausing pupae (while other oestrids over-winter as larvae in their hosts). Adult flies emerge from the pupae and take flight in search of mates and arthropod hosts for their eggs. Adults do not feed but live on energy stores accumulated as larvae. Female flies are autogenous and may produce eggs soon after emergence and mating. Adults live for 4-9 days and females may produce up to 800 eggs in their lifetimes. *D. hominis* requires high relative humidity for eggs to survive and moist soil for pupae to develop. Infestations are generally restricted to the humid tropical forests in Central and South America, occurring along margins of cool moist secondary forests in hilly and lowland regions (including abundant coffee plantations).

Differential diagnosis: Infestations may be suspected on the basis of clinical grounds (painful furuncular lesions, warbles) and patient history (residence of travel to endemic regions). However, furuncles are often misdiagnosed as infected arthropod bites, abscesses or tropical ulcers in travelers returning from endemic countries. Diagnosis is made by the direct detection of larvae within wounds, their collection (by careful extraction) and their identification based on morphological characters (notably, spiracles, mouth hooks and tegumental spines). Medical imaging technologies may be used to assist the discrimination of larvae within wounds, usually ultrasonography. Modern molecular biological techniques have been used to characterize isolates by polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA) and mitochondrial (cytochrome oxidase) gene sequences.

Treatment and control: It is recommended that furuncular wounds be treated and larvae extracted to prevent secondary infections (by bacteria or other fly larvae), abscess formation, cellulitis, regional lymphadenopathy, malaise and fever. Larvae may be removed by careful manipulation with forceps, tweezers or even venom extraction syringes, but the bots are difficult to extract due to their bulbous bodies and backwardly-facing spines. Occlusive dressings are often used to cover the central pores in the warbles through which the larvae breathe using their posterior spiracles. This brings the larvae closer to the surface and may suffocate them so they are easier to extract. A range of oil- or fat-based dressings have been used, including petroleum jelly, vaseline, mineral or vegetable oil, liquid paraffin, beeswax, bacon fat, butter, and even chewing gum, adhesive tape, fingernail polish and raw meat poultices. The central punctum usually needs to be enlarged and lidnocaine and epinephrine can be flushed into the wound to cause local contraction. In many cases, the wound may need to be incised and debrided under local anaesthesia to remove the larvae, taking care not to damage them as residual fragments may cause inflammatory and/or allergic reactions. Recent studies have indicated that the application of macrocyclic lactones (avermectin, ivermectin) to wounds in awkward or inaccessible sites resulted in the spontaneous emigration of *D. hominis* bots. More typically, chemical insecticides are used prophylactically to prevent infestations in livestock and pets by targeting the haematophagous arthropod porters of bot fly eggs, as well as the emergent larvae. Conventional insecticides may be applied as topical sprays, dips, pour-ons or impregnated tags, including organochlorines (toxaphene, dichloro-

diphenyl-trichloroethane (DDT), lindane), organophosphates (crufomate, trichlorfon, fenthion), and salicylanilides (closantel), although topical or systemic applications of macrocyclic lactones (ivermectin, abamectin, doramectin) are now widely used. Insecticides should be applied at regular intervals depending on their residual activity and duration of protection. Humans working in endemic regions may benefit by applying insect repellents (such as diethyltoluamide (DEET)) to skin or clothing, wearing long-sleeved clothing, ironing clothing that has been hung outside to kill any deposited eggs, and erecting barriers (screens, curtains, nets) around living and sleeping quarters. Maintaining good hygiene and the prompt treatment of any wounds with stringent antiseptics or alcohol will assist in the prevention of infestations.

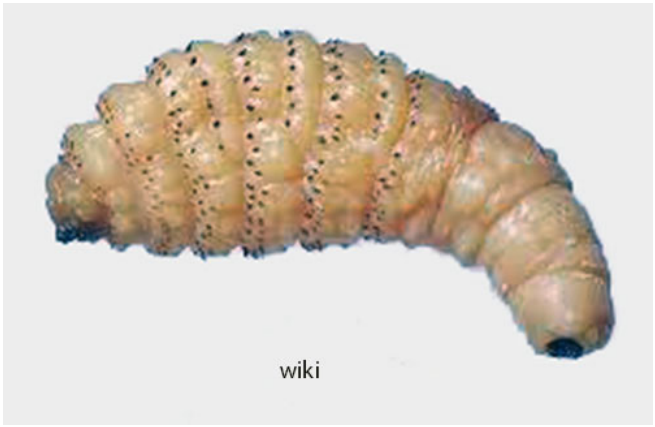

Dermatobia
adult female
(dorsal)
(~ 20 mm)
adults free-flying, not parasitic
wing venation
resting posture
eggs laid
on carrier
insects
(paratenic
transport)
eclosion
pupa
(~ 20 mm)
mosquito
porter
larval spiracular plate
egg
(~ 2 mm)
complete
(holometabolous)
metamorphosis
hatch on
vertebrate
drop from host
to soil
larvae (5-15 mm)
parasitic (obligate)
skin
(furuncular lesions,
pain, distress)
(primary myiasis)
(invade skin and feed
on dermal tissues)
Hosts
(mammals, some birds)



Dermatobia adult



Dermatobia young larva



Dermatobia mature larva



Dermatobia pupa

Oestrus
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Oestrids (bot flies) are large hairy flies but they are not parasitic as adults. Their larvae (bots) are obligatory endoparasites in the integumentary, respiratory or digestive tracts of animals, and they exhibit a high degree of host specificity. Four subfamilies are recognized: cuterebrines (skin bots), oestrines (head maggots), gasterophilines (stomach bots) and hypodermatines (cattle grubs/warbles). Oestrine larvae of *Oestrus* spp. develop in the nasal passages and sinuses of hoofed animals causing considerable pain.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Oestridae (large hairy bot flies, third larval stage or bot resemble small sausages, larvae cause myiases)
Subfamily:	Oestrinae (head maggots)
Genus:	*Oestrus* (parasitic in nasal sinuses of sheep)
Species:	various species cause nasopharyngeal myiases

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders

are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora

(containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases). Several superfamilies contain species whose larvae feed on the flesh of vertebrate hosts, mostly when dead (carrion) but sometimes when still living (causing fly-strike). Oestroid and muscoid larvae are well-adapted for living in moist organic substrates ranging from wet faeces to carrion to living flesh.

The superfamily Oestroidea is characterized by relatively large flies that are not dorsoventrally flattened, their wing veins are not crowded, and the discal medial cell of the wings widens gradually. The superfamily contains 7 families: Calliphoridae (blow flies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Oestridae (bot flies, also known as warble flies, heel flies, gad flies) form large hairy adult flies with bulbous heads, small antennae, rudimentary mouthparts, and wings with subcostal veins running parallel to the costa before joining it. Females produce eggs which hatch by discarding an anterodorsal cap, releasing vermiform larvae which are endoparasitic in the tissues (skin, digestive tract or respiratory passages) of vertebrates. The first larval instars have thorn-like spines encircling several segments, while second and third instars have ecdysal (moulting) scars around their spiracular plates (characteristic for the family Oestridae). Over 150 species have been described in some 25 genera in 5 subfamilies: Cephenemyiinae (deer bot flies), Cuterebrinae (New World skin bot flies), Gasterophilinae (stomach bot flies), Hypodermatinae (Old World skin bot flies, warble flies), and Oestrinae (nose and throat bot flies); with one unplaced genus and 3 fossil genera. Representative genera of veterinary significance are tabulated below:

Oestrid subfamily	Genera	Hosts	Strike	Myiasis*
Cuterebrinae (New World skin bot flies)	*Dermatobia*	cattle, humans	primary	Obligate (CU)
Oestrinae (nose and throat bot flies)	*Oestrus*	sheep	primary	Obligate (OC, NP)
Hypodermatinae (Old World skin bot flies, cattle grubs, ox warbles, heel flies)	*Hypoderma*	cattle	primary	Obligate (CU)
Gasterophilinae (stomach bot flies)	*Gasterophilus*	equines	primary	Obligate (GI)

*type of myiasis: CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular.

The subfamily Oestrinae contains 9 genera (*Cephenemyia, Cephalopina, Gedoelstia, Kirkioestrus, Oestrus, Pharyngobolus, Pharyngomyia, Rhinoestrus, Tracheomyia*); all being viviparous flies that deposit or forcibly eject packets of larvae onto the muzzle or eyes of vertebrate hosts. The larvae migrate into the nasal cavities and may cause nasopharyngeal myiases. The genus *Oestrus* (syn. *Aestrus, Cephalemya, Cephalemyia, Cephalomyia, Estrus, Oestreus*) contains 8 species that infect domestic livestock (especially sheep and goats) as well as some wild ungulates (antelope, deer) and occasionally animals and people in close contact (such as sheep dogs, shepherds, farmers). Infections are usually temporary as the third stage larvae leave their hosts to undergo pupation in the soil. Nasal and throat bots are cosmopolitan in distribution, and are widespread throughout Africa and central Asia.

Oestrus* species	Hosts	Location	Clinical signs	Distribution
O. aureoargentatus (syn. *O. regalis*)	Artiodactyla: bovid (sable antelope, roan antelope, topi, tsessebe, hartebeest, Lichtenstein's hartebeest, blue wildebeest)	nasal passages	obligate myiasis	Africa
O. caucasicus (incl. *O. gvozdevi*)	Artiodactyla: bovid (ibex, Pyrenean ibex, Siberian ibex, Caucasian tur)	nasal passages	obligate myiasis	Central Asia
O. curvicauda	Perissodactyla: equid (horse)	nasal passages	obligate myiasis	Europe
O. dubitatus	Artiodactyla: bovid (blue wildebeest)	nasal passages	obligate myiasis	Africa
O. halensis	Artiodactyla: bovid (sheep)	nasal passages	obligate myiasis	Europe
O. macdonaldi (syn. *O. bassoni*)	Artiodactyla: bovid (hartebeest)	nasal passages	obligate myiasis	Africa

O. ovis (syn. *O. argalis, perplexus*) (sheep nasal bot)	Artiodactyla: bovid (sheep, Lacaune sheep, argali, bighorn, goat, ibex), camelid (camel), cervid (white-tailed deer); Carnivora: canid (dog); Primates: hominid (human)	nasal passages, eyes	obligate myiasis (nasal discharge, sneezing)	worldwide
O. variolosus (syn. *O. bertrandi, disjunctus, interruptus*)	Artiodactyla: bovid (topi, tsessebe, bontebok, hartebeest, Lichtenstein's hartebeest, sable antelope, gemsbok, blue wildebeest)	nasal passages	obligate myiasis	Africa

*The species *O. cervi* and *O. elaphi* described from deer have been transferred by most authorities to the genus *Cephenemyia*

Parasite morphology: *Oestrus* spp. form 4 different types of developmental stages: eggs (*in utero*); larvae (3 instars); pupae (in puparia); and adults (males and females). Eggs appear as elongate bodies approximately 1 mm long which are surrounded by thin translucent shells and are retained within the uterus of female flies. The eggs hatch releasing larvae which are subsequently birthed by larviposition. The larvae (called bots, sometimes grubs) are robust, cylindrical tapering at both ends, and become somewhat flattened ventrally as they mature. They develop through 3 instars (L1-3) growing from 1-2 mm to 12-20 mm and then up to 20-35 mm in length. They are initially white in colour but become yellow-brown with dark transverse bands on each segment (they do not become completely black like Hypodermatinae and Cuterebrinae). The segmented body lacks fleshy projections but bears numerous small spines mostly clustered together in ventral patches on most segments (unlike muscoid larvae which lack spines). Larvae lack sclerotized head capsules but have internal cephalopharyngeal skeletons with prominent rasping mouthparts containing well-developed dark curved mandibles (oral hooks). The caudal segment also bears 2 sets of 10-11 posterior hooks (crochets) located on terminal protuberances. The larvae respire through posterior spiracles located on 2 caudal black circular plates (not indented) with numerous openings (pores) arranged in radial ray patterns (in contrast, cuterebrine larvae have plates with 3 slits containing numerous openings, while calliphorid larvae have plates with 3 slits surrounded by a sclerotized peritreme). In *Oestrus* spp., anterior spiracles are absent or obscure, posterior spiracles on L1 are rudimentary, those on L2 have <100 pores, and those on L3 have >100 pores. Plates on L2 and L3 also encloses a button-like ecdysal (moulting) scar which is characteristic for most Oestridae. Mature L3 leave the host and form puparia which are robust dark-brown barrel-shaped bodies 20-30 mm long. The enclosed pupae transform into adult flies which eclose through circular caps (like all Cyclorrhapha) and not through longitudinal slits (like Nematocera and Brachycera). Adults are large heavy-bodied flies 10-19 mm long with grey-brown bodies that appear mottled due to patchy coverings of short brown hairs (but lacking stout bristles). They have bulbous broad heads flattened front-to-back that are dull yellow in colour but randomly covered with black glossy pits. Their heads possess both a ptilinal suture and facial lunule (like other Oestroidea and Muscoidea, but unlike other calyptrate flies). They have 2 small yellowish compound eyes located laterally and separated by a large frons with small wart-like protuberances (tubercles), and 2 small antennae sunken into pits on the face, each composed of 3 dissimilar segments: a short basal scape; a club-like pedicel with a complete dorsal seam; and an anterior flagellum comprising a single large slender bristle (arista) which is bare (like those of Hypodermatinae, but unlike those of Cuterebrinae which are plumose). Adult flies have small and inconspicuous mouthparts, reduced to small knobs and lacking palps. Adult flies do not feed but live on energy stores acquired as larvae. The alimentary tract is also rudimentary, but may possibly be used for water uptake and fluid regulation. The thorax is covered by a shield-like scutum with a posterior lobe-like scutellum bearing small black tubercles. The dorsal scutum often bears four black parallel stripes composed of tiny hairs. Like other oestroid flies, there is a vertical row of bristles on the thoracic meron (lacking on muscoid flies). The mesothorax bears one pair of small clear wings whose membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)], with the Sc vein running parallel to the C vein, and the M vein not reaching the wing margin directly but joining the R vein. Similar to all Diptera, the hindwings have been reduced to small club-like halteres used to stabilize flight. The halteres are covered by posterobasal lobes of the forewings (squamma or calypters) which are typically large in oestrids (except gasterophilines). Adults also have bulbous swellings (greater ampullae) below their wing bases like other oestrids. The ventral thorax is the point of attachment for 3 pairs of short robust yellow hairy legs, each composed of 5 segments (coxa, trochanter, femur, tibia, and tarsus) with the tarsal portions covered with strong bristles and all legs terminating in a pair of claws with pad-like pulvilli surrounding a central bristle (empodium). The segmented abdomen usually appears globular with a shiny integument lightly covered in hairs. The terminal segments are modified by genital structures, including a copulatory aedeagus in males and a cylindrical telescoping larvipositor in females. Male flies have 2 testes with vas deferens leading to a seminal vesicle (with lateral accessory glands) feeding into a tubular ejaculatory duct linked to the aedeagus and claspers. Female fliers have 2 ovaries connected by oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva and terminal larvipositor.

Site of infection: Adult nasal bot flies are not parasitic and they simply do not feed. They are free-flying and gravid females search for suitable hosts on which to deposit larvae, usually by forcibly ejecting packets of larvae onto the muzzle or eyes. The larval stages are obligate parasites and can only complete their development in the upper respiratory passages of a small range of artiodactylan hosts, including domestic livestock (sheep and goats) as well as some wild ungulates (antelope and deer). The larvae exhibit high site specificity (tissue tropism) for the nasopharynx, nasal passages and sinuses, although they may sometimes invade the brain, gums and lungs. Occasionally, first-stage larvae may infest animals and humans in close contact with livestock (such as shepherds and sheep dogs), being found in nasal cavities, frontal sinuses, mouth, pharynx, gums, conjunctival sac, cornea, and ears, but they are unable to develop further.

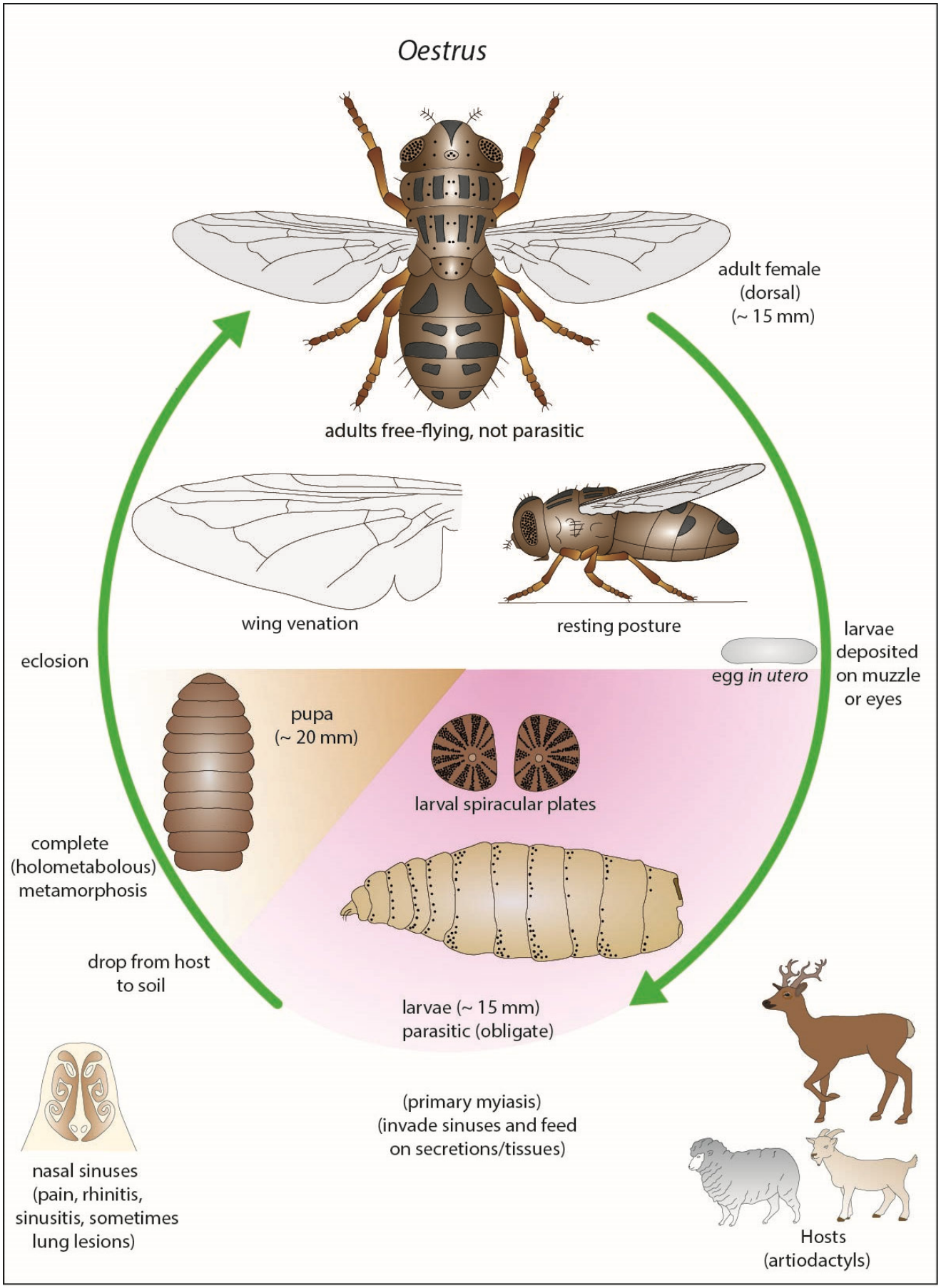
Pathogenesis: Despite the morbid spectre often associated with nasopharyngeal myiasis, clinical signs are rarely encountered in natural hosts. Sheep often do not exhibit overt signs of infestation, and nasal bot populations generally self-regulate with only around 10 larvae completing development per host. Nonetheless, pathological changes may occur in 4 successive phases: fly worry associated with larviposition; rhinitis caused by first-stage larvae (L1); sinusitis caused by subsequent larvae (L2-3); and lung lesions due to errant larvae. Sheep often react to hovering flies attempting to larviposit and they develop avoidance behaviours to protect their faces from flies, gathering together in tightly-packed groups with their noses dug into the fleece of their neighbours, standing with their heads downcast in clumps of vegetation, or taking refuge in windswept areas. Sheep resume grazing when flies become inactive at dawn and dusk. Over time, sheep may exhibit transient reductions in production parameters due to disturbed grazing and the stress associated with fly worry. Other ungulates (goats, deer) have different browsing/grazing habits and react less to adult flies. Rhinitis develops after larviposition when first-stage larvae (L1) crawl over the mucosa of the nasal passages feeding on mucus and desquamated cells using their mouth hooks and excretory/secretory (ES) products with proteolytic activity. This initially causes a profuse discharge of clear mucus that subsequently becomes mucopurulent and tinged with blood streaks (petechial haemorrhages due to larval mouth hooks and spines). The resultant parasitic rhinitis is characterized by sticky mucoid nasal discharges (sometimes haemorrhagic) with squamous metaplasia and catarrhal inflammation. The volume of nasal discharge is not directly correlated to the intensity of infestation (number of larvae) but appears to be influenced by individual host susceptibility and concomitant infections (worsened by bacterial and/or viral infections). Nasal discharges can become caked with dust in hot dry regions or cause straw, hay and other material to adhere to the nose causing discomfort, distress and breathing difficulties with sneezing, nose rubbing, head shaking, and sometimes stamping of the feet. Affected animals also resort to mouth-breathing which interferes with feeding (grazing and rumination) leading to loss of appetite, emaciation and sometimes death. Sinusitis occurs when larvae enter the frontal sinuses via the ethmoid process and begin feeding on mucus and epithelial cell materials as they grow and develop through another 2 instars (L2-3). Host tissues become inflamed with epithelial changes and copious mucus production. Nasal discharges may persist with a continuation of discomfort, breathing difficulties and altered feeding habits that may impair health and productivity. Clinical signs may also be exacerbated in some individual hosts which develop hypersensitivity responses to larval ES products. When mature, L3 re-enter the nasal passages and exit the host to pupate on the ground. Expulsion generally occurs by bouts of sneezing (often violently) with head shaking and animals seeking support by leaning against structures (trees, posts, walls). Any larvae dying in the sinuses may lead to allergic and inflammatory responses, bacterial infection and septic sinusitis. Lung lesions may also develop when larvae pass down the trachea to lung tissues as well as when purulent discharges are inhaled resulting in lung abscesses and/or interstitial pneumonia. Occasionally, larvae may penetrate the olfactory mucosa and enter the brain causing ataxia, circling and head-pressing. Infestations may also develop in humans and dogs working in close contact with livestock when flies larviposit on them but the larvae usually do not develop beyond L1. Infestations have been associated with transient nasopharyngeal myiasis (larvae in nasal passages, sinuses, pharynx), oral myiasis (mouth, gums) or opthalmomyiasis (conjunctiva and cornea) – the latter being most common and usually manifest as acute conjunctivitis.

Developmental cycle and mode of transmission: These bot flies exhibit holometabolous development in that grub-like larvae undergo complete metamorphosis in pupae transforming into winged adults. Females flies are not oviparous (do not lay eggs) but are viviparous or ovoviviparous (birth live larvae). Eggs are retained within the uterus of female flies where they embryonate and produce first-stage larvae (L1). These larvae are deposited (larviposited) in batches of 3-35 in jets of viscous uterine fluid forcibly ejected from females hovering (often without landing) into the nose or eyes of suitable vertebrate hosts. The larvae are positively thermotactic, negatively phototactic and negatively geotactic and quickly crawl into the nose, mouth, eyes and migrate to the nasal cavities to feed. After several weeks, the larvae migrate to the frontal sinuses or pharyngeal regions where they continue to feed and develop through another 2 instars (L2-3). The time taken for larvae to complete their development is highly variable, and may extend up to 9 months in regions with colder climates. Most oestrid larvae overwinter in their hosts (except the cuterebrines which typically overwinter as diapausing pupae). Mature L3 then return to the nasal passages and are expelled from the host via sneezing (often in energetic bouts). The larvae burrow into the ground (1-10 cm deep) under rocks, stones or vegetation and arch their bodies forming puparia by contraction and hardening of the teguments. The encased pupae develop into an adult over 3-9 weeks depending on environmental conditions (longer in cooler conditions). Adult flies emerge and take flight seeking mates and hosts (for larviposition) using a range of olfactory, visual and thermal cues (plumes of respiratory carbon dioxide, body shapes, colours, temperature and moisture). Male flies gather at aggregation sites (usually prominent hilltops) to intercept passing females for mating. Adult flies do not feed (but may take up water) and they only live for 2-4 weeks. Females may produce 100-600 larvae in their life-times, larvipositing during the hottest part of the day. Flies are most active during hot dry summer months so most infestations are considered seasonal. However, flies may be able to complete 2 generations each year in some subtropical regions.

Differential diagnosis: Nasal bot fly infestations may be suspected on clinical grounds (especially rhinitis/sinusitis, sticky mucus, sneezing) but definitive diagnosis depends on the recovery of larvae for close examination. This is often problematic as the larvae are confined to inaccessible sites (nasal passages and sinuses) for months. Occasionally, larvae may be recovered after severe sneezing attacks, but often they are only detected at necropsy. Examination of clinical parameters may reveal elevated levels of mast cells and eosinophils. Medical imaging technologies may be used to assist diagnoses in individual animals by the detection of soft tissue masses within nasal passages and sinuses. Several immunoserological tests (immunodiffusion, indirect haemagglutination tests and enzyme-linked immunosorbent assays) have been developed to detect specific host antibodies against larval somatic

antigens, but they are not broadly available. Molecular biological techniques have also been used to identify and characterize larvae following polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA) and mitochondrial (cytochrome oxidase I and II) gene sequences.

Treatment and control: Infestations in humans are generally treated by manually or surgically removing larvae where possible, although the larvae do not develop further and die. Supportive therapy is best provided in the form of analgesics, anti-inflammatories, antihistamines and antibiotics to alleviate symptoms and prevent secondary infections. The treatment of livestock is rarely warranted, but clinical infestations are treated using chemical insecticides that may be applied systemically (oral, injectable, sustained-release bolus or pour-ons) so that therapeutic levels may reach the mucosa of nasal passages and sinuses harbouring larvae. Several systemic organophosphates (e.g. trichlorfon) were originally used, but they have now been superseded by salicylanilides (rafoxanide, closantel, nitroxinil) and macrocyclic lactones (ivermectin, doramectin, moxidectin, abamectin) which are highly active against all larval stages. The prevention of infestations revolves around environmental management practices to reduce pupae populations (by seasonally burning pastures and tall grasses) and animal management practices to protect them from questing flies (by stock rotation to pastures beyond the flight range of adult flies). Several attempts have been made to develop vaccines against nasal bot flies. Vaccination with larval extracts and proteins (including serine proteases) did not induce significant protection in sheep, while several salivary gland extracts appeared to be immunogenic. Preliminary studies have also explored several avenues for biological control, involving the release of sterile male flies, and the aerosol application of suspensions of the bacterium *Bacillus thuringiensis* which contain natural insecticides. There are many logistic problems preventing the widespread application of these programs, as larvae cannot be cultured (pupae must be recovered for irradiation), and aerosol sprays must be delivered in confined indoor spaces. At present, no insect repellents have been found to be effective against nasal bot flies.


Oestrus
adult female
(dorsal)
(~ 15 mm)
adults free-flying, not parasitic
wing venation
resting posture
larvae
deposited
on muzzle
or eyes
egg in utero
eclosion
pupa
(~ 20 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
drop from host
to soil
larvae (~ 15 mm)
parasitic (obligate)
(primary myiasis)
(invade sinuses and feed
on secretions/tissues)
nasal sinuses
(pain, rhinitis,
sinusitis, sometimes
lung lesions)
Hosts
(artiodactyls)



Oestrus adult



Oestrus larva



Oestrus larval spiracles



Oestrus pupa

Hypoderma
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Oestrids (bot flies) are large hairy flies but they are not parasitic as adults. Their larvae (bots) are obligatory endoparasites in the integumentary, respiratory or digestive tracts of animals, and they exhibit a high degree of host specificity. Four subfamilies are recognized: cuterebrines (skin bots), oestrines (head maggots), gasterophilines (stomach bots) and hypodermatines (cattle grubs/warbles). Larvae of *Hypoderma* spp. migrate in the tissues of cattle and deer, sometimes horses and humans, eventually forming lesions in the lumbar skin resulting in decreased productivity and damaged hides.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Oestridae (large hairy bot flies, third larval stage or bot resemble small sausages, larvae cause myiases)
Subfamily:	Hypodermatinae (cattle grubs, ox warbles, heel flies)
Genus:	*Hypoderma* (parasitic in subcutaneous tissues of cattle)
Species:	various species cause cutaneous myiases

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera (‘true’ flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders

are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora

(containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases). Several superfamilies contain species whose larvae feed on the flesh of vertebrate hosts, mostly when dead (carrion) but sometimes when still living (causing fly-strike). Oestroid and muscoid larvae are well-adapted for living in moist organic substrates ranging from wet faeces to carrion to living flesh.

The superfamily Oestroidea is characterized by relatively large flies that are not dorsoventrally flattened, their wing veins are not crowded, and the discal medial cell of the wings widens gradually. The superfamily contains 7 families: Calliphoridae (blow flies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Oestridae (bot flies, also known as warble flies, heel flies, gad flies) form large hairy adult flies with bulbous heads, small antennae, rudimentary mouthparts, and wings with subcostal veins running parallel to the costa before joining it. Females produce eggs which hatch by discarding an anterodorsal cap, releasing vermiform larvae which are endoparasitic in the tissues (skin, digestive tract or respiratory passages) of vertebrates. The first larval instars have thorn-like spines encircling several segments, while second and third instars have ecdysal (moulting) scars around their spiracular plates (characteristic for the family Oestridae). Over 150 species have been described in some 25 genera in 5 subfamilies: Cephenemyiinae (deer bot flies), Cuterebrinae (New World skin bot flies), Gasterophilinae (stomach bot flies), Hypodermatinae (Old World skin bot flies, warble flies), and Oestrinae (nose and throat bot flies); with one unplaced genus and 3 fossil genera. Representative genera of veterinary significance are tabulated below:

Oestrid subfamily	Genera	Hosts	Strike	Myiasis*
Cuterebrinae (New World skin bot flies)	*Dermatobia*	cattle, humans	primary	Obligate (CU)
Oestrinae (nose and throat bot flies)	*Oestrus*	sheep	primary	Obligate (OC, NP)
Hypodermatinae (Old World skin bot flies, cattle grubs, ox warbles, heel flies)	*Hypoderma*	cattle	primary	Obligate (CU)
Gasterophilinae (stomach bot flies)	*Gasterophilus*	equines	primary	Obligate (GI)

*type of myiasis: CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular.

The subfamily Hypodermatinae contains 9 genera classified in 2 tribes: Hyperdermatini (genera *Hypoderma, Oestroderma, Oestromyia, Pallasiomyia, Pavlovskiata, Portschinskia, Przhevalskiana, Strobiloestrus*); and Ochotonini (genus *Ochotonia*). These large flies are oviparous, landing briefly on hosts to deposit eggs from which larvae hatch to invade subcutaneous tissues causing elevated furuncular boil-like lesions (commonly called warbles). Such behaviour has led to a variety of common names, including warble flies, cattle grubs or wolves, heel flies, bomb flies, and gad flies. The genus *Hypoderma* (syn. *Epidermella, Kneiffiella, Locelliderma, Neokneiffia, Pycnodon, Schizochorella*) contains 76 species, several allocated to 2 subgenera, but most species remain unassigned. Warble flies are significant pests to cattle and other livestock industries, particularly throughout Europe and the Americas.

***Hypoderma* species (regional exemplars)**	**Host preferences**	**Location**	**Clinical signs**	**Distribution**
Subgenus *H.* (*Hypoderma*)				
H. bovis (warble fly, northern cattle grub)	Artiodactyla: bovid (cattle, bison, musk ox, sheep); Perissodactyla: equid (horse); Primates: hominid (human)	subcutaneous tissues, spinal canal	obligate myiasis (annoyance (gad), fluid-filled swellings (warbles), damaged hides, illthrift)	Eurasia, Americas, Africa
H. lineatum (warble fly, common cattle grub, heel fly)	Artiodactyla: bovid (cattle, sheep); Perissodactyla: equid (horse); Primates: hominid (human)	subcutaneous tissues, oesophagus	obligate myiasis (bloat, faulty regurgitation, warbles, damaged hides)	Eurasia, Americas, Africa
Subgenus *H.* (*Oedemagena*)				

H. tarandi (reindeer warble fly, reindeer grub)	Artiodactyla: cervid (reindeer, caribou), bovid (musk ox)	subcutaneous tissues, spinal canal	obligate myiasis (warbles)	Holarctic
Unassigned species				
H. actaeon	Artiodactyla: cervid (red deer, roe deer)	subcutaneous tissues	obligate myiasis (warbles)	Asia
H. diana (warble fly)	Artiodactyla: cervid (roe deer, red deer), bovid (mouflon, argali)	subcutaneous tissues, spinal canal	obligate myiasis (warbles)	Holarctic
H. sinense	Artiodactyla: bovid (cattle, yak)	subcutaneous tissues	obligate myiasis (warbles)	Holarctic

Full species list (compilation of several on-line data-bases)

***Hypoderma* species**	**Subgenus**
H. aceris	Unassigned
H. actaeon	Unassigned
H. agapanthi	Unassigned
H. ageratum (now *Przhevalskiana silenis*)	Unassigned
H. albofasciatum	Unassigned
H. alborubrum	Unassigned
H. allicinum	Unassigned
H. allii	Unassigned
H. alpinum	Unassigned
H. aquilinum	Unassigned
H. asphodeli	Unassigned
H. berberidis	Unassigned
H. bidwillii	Unassigned
H. bihospitum	Unassigned
H. borneense	Unassigned
H. bovis	*Hypoderma*
H. campanulatum	Unassigned
H. capreola	Unassigned
H. caricis	Unassigned
H. carinatum	Unassigned
H. commune	Unassigned
H. conigenum	Unassigned
H. cookianum	Unassigned
H. cordylines	Unassigned
H. corni	Unassigned
H. crossi (now *Przhevalskiana silenis*)	Unassigned
H. cuspidatum	Unassigned
H. desertorum	Unassigned
H. diana	Unassigned
H. dryadis	Unassigned
H. dundasicum	Unassigned
H. epilobii	Unassigned
H. eucalypti	Unassigned
H. euphorbiae	Unassigned
H. ferulae	Unassigned
H. filicina	Unassigned
H. gaultheriae	Unassigned
H. handelii	Unassigned
H. hansbroughii	Unassigned
H. hederae	Unassigned
H. ilicinum	Unassigned
H. insulare	Unassigned
H. junipericola	Unassigned
H. labiorum-aurantiorum	Unassigned
H. leschenaultii	Unassigned
H. liliense	Unassigned
H. linderae	Unassigned
H. lineatum	*Hypoderma*
H. mexicanum	Unassigned
H. minteri	Unassigned
H. mirabile	Unassigned
H. moschiferi	Unassigned
H. nitidum	Unassigned
H. obtectum	Unassigned
H. paralinderae	Unassigned
H. patholopsum	Unassigned
H. qinghaiense	Unassigned
H. qinlingense	Unassigned
H. rhododendri-mariesii	Unassigned
H. rostrupii	Unassigned
H. rubi	Unassigned
H. rufilabrum	Unassigned
H. sabinae	Unassigned
H. shimanense	Unassigned
H. shiqii	Unassigned
H. siculum	Unassigned
H. sigmoideum	Unassigned
H. sinensis	Unassigned
H. smilacicola	Unassigned
H. stephanandrae	Unassigned
H. sticheri	Unassigned
H. tarandi	*Oedemagena*
H. thujae	Unassigned
H. tillandsiae	Unassigned
H. tunicatum	Unassigned
H. urniforme	Unassigned
H. versicolor	Unassigned
H. viburni	Unassigned

Parasite morphology: *Hypoderma* spp. form 4 different types of morphological stages during their development: namely, eggs; larvae; pupae; and adults. Eggs are thin elongate stages 1.0-1.2 mm long with a smooth creamy white-yellow to light grey-brown chorion. They are affixed to hairs with glue and small terminal clasps and hatch through an anterodorsal slit-like cap (not an operculum). Larvae (commonly known as bots, sometimes grubs and wolves associated with warbles) have thick robust cylindrical bodies tapering anteriorly. They develop through 3 larval instars (L1-3) growing over several months from 1-2 mm long up to 27-30 mm and are initially white but gradually darken to black at maturity. They lack sclerotized head capsules but have internal cephalopharyngeal skeletons bearing mouthhooks. The segmented body does not have any fleshy projections, but the larvae have thorn-like spines (absent on muscoid larvae). On L1, the spines encircle several anterior segments and form a sparse but uniform covering along the body. On L2, the spines are stouter and broader, with small groups of smooth spines occurring over body (denser anteriorly) imparting a glassy appearance. On L3, the cuticles appear granular and reticulated, becoming flattened dorsally and developing 3 longitudinal rows of tubercular ridges. The spines form prominent rows on the leading and trailing edges of the thoracic and abdominal segments. The spines are flat and blade-shaped with single points (sometimes 2), and are usually facing backwards although there are small groups facing forwards on cephalic and terminal segments. Larvae respire through 2 caudal spiracular plates (anterior spiracles absent or obscure). The plates are flat and shaped like incomplete (open) rings (unlike calliphorid larvae which have plates with 3 slits surrounded by a peritreme). *Hypoderma* spp. have porous plates (with over 100 small pores) and are initially opaque white but darken to grey in mature larvae. The ring-like plates in L2 and L3 also surround central button-like ecdysal (moulting) scars (*H. bovis* having a narrow funnel-like channel to the central button, while *H. lineatum* has a broad channel). Mature L3 form barrel-shaped puparia by contraction and hardening of their teguments which darken to dark brown or black. The enclosed pupae are obtect with barely visible appendages (including a concavity forming behind the cranium) and adults eclose through circular caps (like all Cyclorrhapha) and not through longitudinal slits (like Nematocera and Brachycera). Adults are large robust flies 10-15 mm long with dark bodies covered with bands of small dense yellow-orange hairs (resembling bumble bees), but lacking bristles. Their head are bulbous (short but broad, flattened front-to-back) and possess both a ptilinal suture and facial lunule (like all calyptrates). The facial region is covered with dense hairs and 2 small compound eyes are located laterally separated by a large frons. They have 2 small antennae sunken into facial pits, each antenna comprised of 3 dissimilar segments: a small basal scape; a club-like pedicel with a complete dorsal seam; and an anterior flagellum composed of single large bristle (arista) which is bare (plumose in cuterebrines). The mouthparts are small and vestigial lacking palps as the adults do not feed. The alimentary tract is also rudimentary although it may be used for water uptake and regulation. The stout thorax is covered by convex scutum with a posterior lobe-like scutellum. It has a dense covering of small hairs and a vertical row of longer hairs on the thoracic meron. The mesothorax gives rise to a pair of long narrow clear wings, whose membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)], with the Sc vein running parallel to the C vein, the first R vein lacking a hump at the Sc break, and the M vein extending all the way to the leading edge of the wing. Like all Diptera, the hindwings have been reduced to small knob-like halteres thought to stabilize flight. Like all calyptrates, the halteres are covered by posterior lobes of the forewings (called calypters or squamae), which are large in all oestrids (except gasterophilines). The ventral thorax bears 3 pairs of short robust hairy legs, each consisting of 5 segments (coxa, trochanter, femur, tibia, and tarsus), and all ending in a pair of claws with pad-like pulvilli surrounding a central bristle (empodium). The segmented abdomen is globular-pyriform, covered with small hairs, possesses lateral spiracles and the terminal segments are modified by genital structures (male aedeagus and claspers, females ovipositor). Males have 2 testes joined by vas deferens to a seminal vesicle (with lateral accessory glands) leading to the tubular ejaculatory duct and copulatory aedeagus. Females have 2 ovaries with oviducts leading to a globular uterus (with associated spermatheca and accessory glands) opening to the vulva and telescoping ovipositor.

Site of infection: The Hypodermatinae are known as the New World skin bot flies, but the adult flies are not parasitic and do not even feed. The larvae, on the other hand, are obligate endoparasites and can only complete their life-cycles in live hosts. They primarily infest ungulates (cattle, sheep, deer, horses) and have become significant pests to cattle industries, particularly throughout Europe and the Americas. Female flies oviposit on hairs and skin on the legs and flanks and the emergent larvae invade skin penetrating to subcutaneous tissues. The larvae then migrate through host tissues to specific locations where they reside for months. Different species showing high tissue tropism (site specificity) for the oesophageal submucosa (*H. lineatum*) or epidural fat in the spinal cord (*H. bovis*). Larvae then return to subcutaneous tissues, primarily along the dorsal mid-line, and form furuncular lesions (called warbles). Larvae may also infest humans in close contact with cattle, being found in the back, neck, legs and occasionally in the eye or spinal cord.

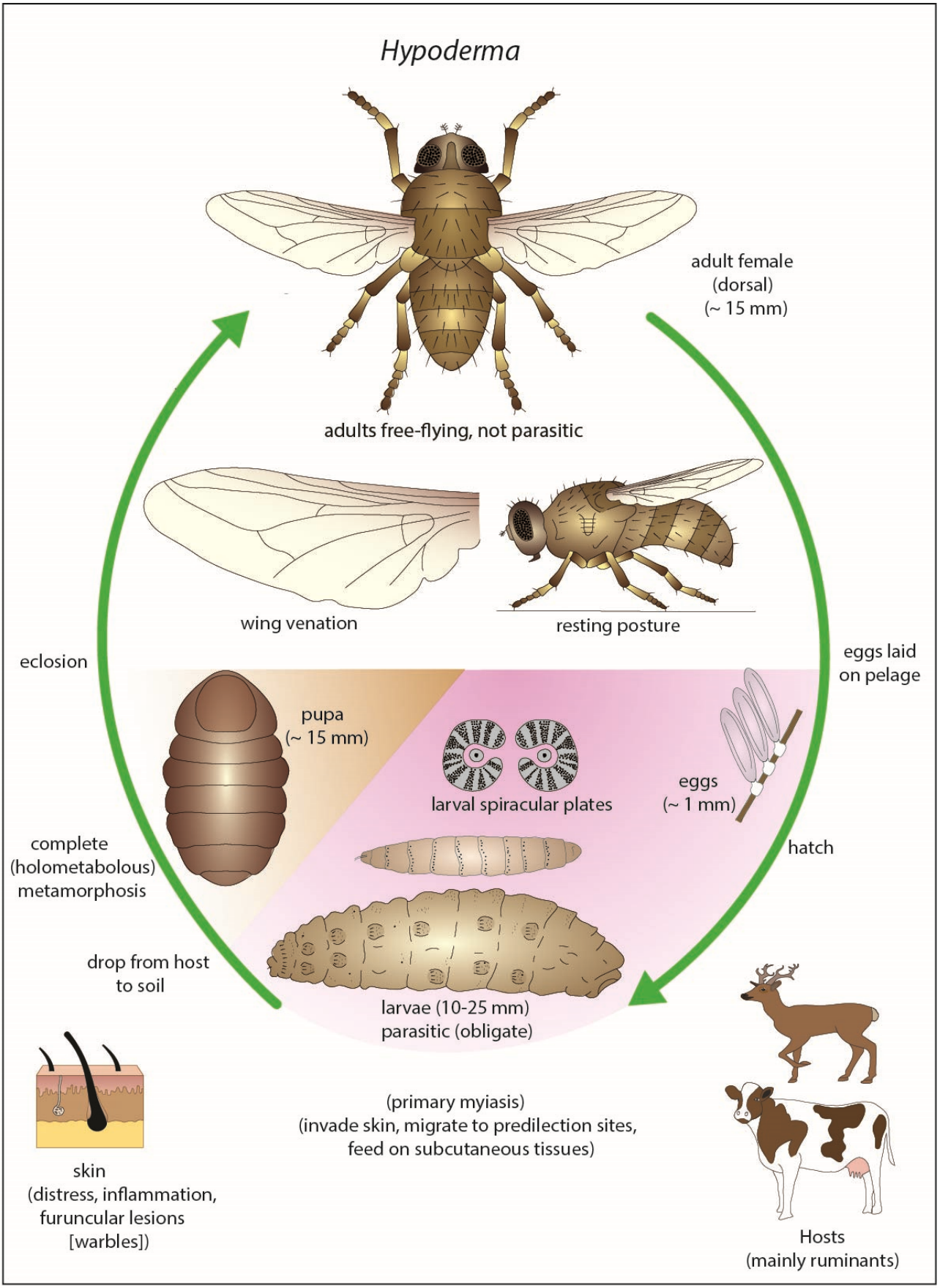
Pathogenesis: *Hypoderma* spp. may cause disease in 3 successive phases: firstly, when adult flies worry cattle when ovipositing; secondly, when larvae invade tissues causing a migratory myiasis; and lastly, when mature larvae cause furuncular myiasis (known as warbles, cattle grubs or wolves); although there are usually no symptoms until the appearance of the granulomatous subdermal furuncles. Gravid female flies approach hosts with a characteristic buzzing noise and are recognized by cattle instantly, frightening them into headlong flights of panic to escape, usually with their tails held erect. This avoidance behaviour is called gadding (hence the alternative common name for adults as gad flies), and it may lead self-injury from collisions with obstacles (fences, trees, etc.). Cattle may also defensively kick up their hooves to discourage ovipositing flies (hence another common name for adults as heel flies). Female flies are very persistent and dart in to land briefly on the host for oviposition (earning them another common name as bomb flies). Animals under constant attack show significant stress from fly worry and their interrupted feeding may cause production losses (reduced weight gain and milk yield). The stress may also impair innate inflammatory and specific immunity in animals making them more susceptible to secondary bacterial and viral infections. Eggs successfully attached to host hairs hatch

releasing first-stage larvae (L1) which immediately burrow beneath the skin via hair follicles using their mouth hooks and secretions of proteolytic enzymes (serine proteases). Skin penetration sometimes causes small lesions and some unease but they rapidly disappear. L1 move away from the site of penetration by migrating through connective tissues and muscles causing migratory myiasis typified by mechanical tissue damage with necrosis, inflammation, eosinophilic infiltrates and oedema (worsening after repeated infestations). Larvae migrate to deeper host tissues where they reside for several months (over-wintering). The larvae of different fly species have specific routes and destinations of migration, and the attendant pathologies differ. *H. bovis* migrates along nerve tracts to reach the spinal cord and then over-winters in the epidural connective tissues and fat around the lumbar and thoracic vertebrae. Dying or dead larvae in the spinal canal provoke strong inflammatory responses which may cause temporary but prolonged paralysis. In contrast, *H. lineatum* migrates along connective tissue between muscular fascial planes to overwinter in the submucosa of oesophagus. Their migration routes are often characterized by yellowish-green gelatinous deposits due to massive infiltrates of eosinophils. After winter, the larvae resume their migration moving to subcutaneous tissues along the backs of their bovid hosts. Here they feed and moult twice causing furuncular (boil-like) granulomas (lesions known as warbles). These large fluid-filled nodular swellings may grow up to 30 mm in diameter and they have a central puncture point (punctum or pore) through which the larvae breathe using their caudal spiracles. The lesions are often painful and may cause considerable damage to hides due to inflammation, oedema, and puncture points, as well as tissue necrosis due to secondary bacterial infections with purulent discharges. The adjacent and underlying flesh may also become green and gelatinous due to massive eosinophilic infiltrates (known as butchers jelly) that require trimming from carcases. Production losses include reduced weight gains and milk yields, higher rates of carcase rejections and condemnations, and damaged hides that cannot be used for leather. Larvae that are accidentally ruptured or die within furuncles may cause severe anaphylactic reactions and even death. Infestations vary in intensity with many hosts harbouring a few larvae but a few hosts harbouring several hundred larvae. Heavier infestations occur in young animals (presumably indicating the development of partial protective immunity in older animals) and in male animals. Humans (particularly children) may become accidentally infected by larvae which penetrate the skin and wander causing visible sinuous inflamed tracks with irritation and pruritus (subdermal or dermal creeping myiasis). Larvae may persist for months causing severe pain, fever, discomfort, skin allergies, eosinophilia and even skin warbles on the neck and shoulders. Occasionally, larvae may migrate into the eye causing ocular myiasis with pain, nausea, restlessness, swelling of the eyelids, dislocation of the lens, retinal perforation and sometimes blindness.

Developmental cycle and mode of transmission: Skin bot flies undergo complete (holometabolous) metamorphosis whereby grub-like larvae undergo pupation transforming into winged adult flies. Female flies are oviparous and land briefly on hosts to attach eggs to hair shafts using adhesive secretions and clasping structures where they are protected from dislodgement, grooming and desiccation. Eggs may be oviposited singly on hairs over the rump (H. bovis) or in rows of 6-15 eggs on hairs on the legs (*H. lineatum*). The eggs hatch in 2-7 days releasing first-stage larvae (L1) that are positively thermotactic and penetrate hair follicles within 6 hours of hatching. L1 burrow into subcutaneous connective tissues and migrate to the submucosal connective tissue of the oesophagus (*H. lineatum*) or thoraco-lumbar spinal canal (*H. bovis*) where they reside for 3-8 months (typically over-wintering in these locations). All oestrid larvae overwinter in their hosts (except the cuterebrines which overwinter as diapausing pupae). In spring, L1 leave their resting places and resume migration moving to the dorsal midline and forming palpable swelling (warbles). The larvae create holes in the centre of the furuncular lesions so they can breathe using their posterior spiracles. They continue to feed and moult twice over 4-11 weeks forming L2 and then L3. In early spring, mature L3 cease feeding and form prepupal stages which enlarge the central punctum and exit the warble falling to the ground to pupate. They actively burrow into the soil beneath grass or leaf litter and form puparia. The enclosed pupae undergo metamorphosis into adults with pupation taking 2-10 weeks, depending on the climate and soil temperature (longer in colder conditions, and not at all in wet conditions). Winged adult flies emerge but do not seek food sources as they do not feed. Instead, they fly about searching for mates and suitable hosts for oviposition. Male flies gather at aggregation points along dry stream beds or roadways in small valleys (not on hilltops like Oestrinae). They perch on shrubs or tall grasses to intercept passing females. After mating, females may undertake long flights searching for hosts (some species chase reindeer up to 600 km), being attracted to increased concentrations of carbon dioxide. Adult flies only live for around one week, but females may produce up to 300-800 eggs in that time. They are most active on sunny days in warm weather and are univoltine with one generation per year (over-wintering as L1 in hosts).

Differential diagnosis: Infestations in livestock may be strongly suspected when hosts exhibit gadding behaviour during fly season, when fly eggs are found on host hairs, when hosts exhibit transient inflammatory tracts with high eosinophilia, and when they finally develop furuncular lesions (warbles). Infestations in humans living near cattle may be suspected when they develop eosinophilia together with myalgias, migratory swellings, pleuritis, pericarditis and furunculosis, recurrent eyelids swellings or conjunctivitis. Definitive diagnosis is made by the direct detection of larvae in lesions, confirmed by their collection and identification (characteristic morphology, especially of spiracles and spines). If required, mature larvae can be allowed to pupate in the laboratory and the emergent flies identified. Medical imaging technologies can be used to examine lesions in inaccessible or cryptic locations, looking for granulomas containing soft tissue masses. Several immunodiagnostic tests (complement fixation tests, indirect haemagglutination tests, enzyme-linked immunosorbent assays) have been developed to detect specific host antibodies against larval excretory/secretory (ES) products, often allowing infestations to be detected well before the formation of warbles. Molecular biological techniques have also been used to facilitate diagnosis and characterize species following polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA, serine proteases (hypodermins A, B and C)) and mitochondrial (cytochrome oxidase I and II) gene sequences.

Treatment and control: Infestations in humans are usually treated by removing the larvae from host tissues, cleaning and dressing the wounds and giving supportive therapies in the form of analgesics, anti-inflammatories, and even antibiotics. Larvae can sometimes be gently manipulated from wounds using tweezers or forceps, sometimes aided by flushing furuncles with lidnocaine and epinephrine, but usually surgery is required to enlarge the central pore so the larvae can be extracted intact. Occlusive dressings of oily or fatty materials (petroleum jelly, liquid paraffin, mineral or vegetable oils, beeswax, butter, and even chewing gum, sticky tape and nail polish) may be used to cover the wounds (especially the respiratory pores) thus coaxing the larvae to the surface and smothering them for ease of extraction. Care must be taken not to lacerate the larvae as residual fragments may provoke severe allergic reactions, including anaphylaxis. Similarly, larvae may also be manually or surgically removed from warbles in cattle, but livestock are usually treated with topical or systemic insecticides. The timing of treatment, however, is critical, as the use of systemic drugs before warbles are formed may cause the death of first-stage larvae residing in the oesophagus or spinal cord, with the resultant inflammation causing a range of clinical conditions (dysphagia, paresis, paralysis, ataxia, etc). The efficacy of conventional organochlorines (such as lindane) and organophosphates (such as trichlorphon or fenthion) may be reduced once larvae have formed granulomatous warbles. Caution must also be exercised as the sudden release of material from dying or dead larvae may cause allergic reactions. Animals are now more usually treated with less toxic systemic macrocyclic lactones (ivermectin, moxidectin, doramectin, abamectin, eprinomectin) which are effective against all larval stages and cause the spontaneous expulsion of larvae from warbles. Two treatments are recommended in endemic regions, the first in autumn (targeting first-stage larvae before they reach their over-wintering sites in the oesophagus or spinal cord) and the second in spring (targeting second and third stage larvae forming warbles). Several studies have also attempted to treat wildlife by using baits or salt licks treated with macrocyclic lactones. There appears to be a strong case for the development of a vaccine, as cattle develop a strong protective immunity against infestation after natural exposure. Experimental vaccination with larval extracts and proteins (hypodermins, serine proteases) has been shown to induce some protection as evidenced by increased larval mortality. Several attempts have been made to reduce fly populations in some isolated regions by the release of sterile (irradiated) male flies, but there are currently no efficient techniques for rearing enough flies in the laboratory. Preventive measures generally revolve around protecting livestock from flystrike by prophylactic treatments (topical insecticides), providing protective shelters (flies prefer bright light and avoid shaded areas), pasture rotation (moving stock away from areas where flies pupate), restricting livestock translocations and conducting regular health surveillance.


Hypoderma
adult female
(dorsal)
(~ 15 mm)
adults free-flying, not parasitic
wing venation
resting posture
eclosion
eggs laid
on pelage
pupa
(~ 15 mm)
larval spiracular plates
eggs
(~ 1 mm)
complete
(holometabolous)
metamorphosis
hatch
drop from host
to soil
larvae (10-25 mm)
parasitic (obligate)
(primary myiasis)
(invade skin, migrate to predilection sites,
feed on subcutaneous tissues)
skin
(distress, inflammation,
furuncular lesions
[warbles])
Hosts
(mainly ruminants)



Hypoderma adult



Hypoderma eggs



Hypoderma larva



Hypoderma adult

Gasterophilus
(insect: dipteran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Insects are hexapods with three pairs of uniramous legs, three tagmata (head, thorax, abdomen), ectognathous mouthparts with whole-limb mandibles, and one pair of antennae. Diptera (true flies) have two pairs of wings, but the hindwings are reduced to stabilizing halteres. All species are holometabolans and exhibit complete metamorphosis whereby vermiform larval stages undergo pupation and transform into free-flying adults. Several major parasitic groups are recognized: nematocerans (small slender bodies, long filamentous antennae, narrow wings) and brachycerans (larger bodies, short stout antennae, broad wings); the latter being divided into the Tabanomorpha (larval head capsule sclerotized) and the Muscomorpha (larval head not sclerotized, circular-seamed (cyclorrhaphous) pupae). Muscomorphans include the glossinids (tsetse flies), hippoboscids (louse flies), muscids (house flies), calliphorids (blow flies), sarcophagids (flesh flies) and oestrids (bot flies); all with sponging or biting mouthparts. These flies are either ectoparasitic with adults biting hosts (former three groups) or endoparasitic with vermiform larvae developing in host tissues (latter three groups). Oestrids (bot flies) are large hairy flies but they are not parasitic as adults. Their larvae (bots) are obligatory endoparasites in the integumentary, respiratory or digestive tracts of animals, and they exhibit a high degree of host specificity. Four subfamilies are recognized: cuterebrines (skin bots), oestrines (head maggots), gasterophilines (stomach bots) and hypodermatines (cattle grubs/warbles). Gasterophiline larvae of *Gasterophilus* spp. develop from ingested eggs and attach to the mucosal surface of the gastrointestinal tract of horses where they may overwinter.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Hexapoda (three tagmata, three pairs uniramous legs, whole-limb mandibles, Malpighian tubules)
Class:	Insecta (ectognathous mouthparts (bases lie outside head capsule), single pair antennae, many with wings)
Superorder:	Holometabola (Endopterygota) (young do not resemble adults, pupae, with internally developing wings)
Order:	Diptera (true flies, single pair of forewings, hindwings modified into halteres, vermiform larvae)
Suborder:	Brachycera (tabanid/March flies, short stout antennae often with aristae, telmophagy)
Infraorder:	Muscomorpha (Cyclorrhapha) (flies, cyclorrhaphous (circular-seamed) pupae, larval head not sclerotized)
Division:	Schizophora (head with frontal suture (lunule))
Section:	Calyptratae (calypters cover halteres)
Family:	Oestridae (large hairy bot flies, third larval stage or bot resemble small sausages, larvae cause myiases)
Subfamily:	Gasterophilinae (stomach bots)
Genus:	*Gasterophilus* (parasitic in stomach of equines)
Species:	various species cause stomatitis, ulceration

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Insects are hexapods with six legs, three distinct body parts, two antennae and mouthparts with whole-limb mandibles. Insects are the most biodiverse group on the planet, with millions of species described in numerous taxa. Notorious ectoparasitic species belong to four orders in two superorders: the Hemipterodea (Exopterygota) containing the orders Hemiptera (bugs) and Phthiraptera (lice); and the Holometabola (Endopterygota) containing the orders Siphonaptera (fleas) and Diptera ('true' flies). Flies are small winged holometabolans that undergo complete (holometabolous) metamorphosis with vermiform larvae undergoing pupation in silk cocoons. Thousands of dipteran species have been described throughout the world, most being free-living saprophages (detritivores) but some being parasitic either as adults biting and feeding on hosts (often haematophagous) or producing larvae that invade host tissues (condition known as myiasis). Two major suborders

are recognized: the Nematocera (with small bodies, long filamentous antennae, narrow wings and aquatic larvae and pupae); and the Brachycera (with large bodies, short stout antennae often with aristae and broad wings).

Major parasitic dipteran families	Biodiversity	Parasitic stages	Status	Pathogenesis*	Disease transmission
Suborder: Nematocera (small midges/mosquitoes, thread-horned with long filamentous segmented antennae (= nemato-cera), aquatic life-cycles (larval/pupal stages associated with water), female adults require blood meal before they can lay eggs) (34 families)					
Culicidae (mosquitoes)	3 subfamilies, 70 genera, 3,500 species	adult ♀	obligate	blood-sucking	viral, protozoal, helminth
Psychodidae (moth flies, sand flies)	5 subfamilies, 150 genera, 3,000 species	adult ♀	obligate	blood-feeding	viral, bacterial, protozoal
Simuliidae (black flies)	3 subfamilies, 30 genera, 2,000 species	adult ♀	obligate	blood-feeding	protozoal, helminth
Ceratopogonidae (biting midges)	4 subfamilies, 110 genera, 6,000 species	adult ♀	obligate	blood-feeding	viral, protozoal, helminth
Suborder: Brachycera (large tabanid/March flies, with stout and fewer antennal segments (= brachy-cera), antennae often with aristae, females with slashing-sponging mouthparts to pierce skin and feed on pool of blood (telmophagy)) (120 families)					
Infraorder: Tabanomorpha (larval head capsule incomplete posteriorly (only anterior parts sclerotized))					
Tabanidae (horse flies, deer flies)	3-5 subfamilies, 133 genera, 4,300 species	adult ♀ [+ larvae]	obligate [accidental]	blood-feeding [GI, UG, TR myiasis]	viral, bacterial, protozoal, helminth
Infraorder: Muscomorpha (Cyclorrhapha) (aristate antennae, setose bodies, cyclorrhaphous pupa)					
Section: Calyptratae (calypters cover halteres)					
Superfamily: Muscoidea (synanthropic flies)					
Muscidae (house flies, stable flies)	9-10 subfamilies, 190 genera, 4,200 species	adult ♀, ♂ [+ larvae]	obligate [accidental]	biting, blood-feeding [CU, GI, TR myiasis]	bacterial, helminth
Superfamily: Oestroidea (cause larval myiases) (6 families)					
Calliphoridae (blow flies)	11 subfamilies, 75 genera, 1,100 species	larvae	facultative, obligate	CU, GI, NP, AU, UG TR, myiasis	-
Sarcophagidae (flesh flies)	3 subfamilies, 108 genera, 2,500 species	larvae	facultative, obligate	TR, GI, CU myiasis	-
Oestridae (bot flies, warble flies)	5 subfamilies, 25 genera, 150 species	larvae	obligate	CU, GI, NP, OC myiasis	-
Superfamily: Hippoboscoidea (pupa-bearers)					
Glossinidae (tsetse flies)	1 genus, 3 species-groups, 25 species	adult ♀, ♂	obligate	blood	protozoal
Hippoboscidae (louse flies, keds)	1-3 subfamilies, 21 genera, 212 species	adult ♀, ♂	obligate	blood	viral, protozoal, helminth

*type of myiasis: AU = auricular; CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular; TR = traumatic; UG = uro-genital.

The suborder Brachycera contains 6 infraorders: Asilomorpha (bee flies, robber flies, spider flies), Muscomorpha (previously suborder Cyclorrhapha) (house flies, blow flies, fruit flies), Stratiomyomorpha (soldier flies), Tabanomorpha (horse, deer and snipe flies), Vermileonomorpha (wormlions) and Xylophagomorpha (awl flies); all of which vary considerably in their morphological and biological characteristics. Members of the infraorder Muscomorpha differ from the others in that they form cyclorrhaphous (circular-seamed) pupae (adults eclose through a circular cap rather than a longitudinal slit), larvae without sclerotized heads, and adults with short pendulous 3-segmented antennae (the third segment often bearing feather-like aristae), palps with a single segment, and feet with 2 pads. Collectively, 15 superfamilies have been classified into 2 Divisions: the Schizophora

(containing flies whose heads bear a frontal ptilinial suture and sclerotized lunule); and the Aschiza (hover flies lacking a frontal suture and lunule). Within the Schizophora, 2 sections are recognized: the Calypterae (comprising flies with calypters covering the halteres, large squamae, a strong thoracic suture and well-defined grooves on the antennal pedicels); and the Acalypterae (without covering calypters, small squamae, a weak thoracic suture and no pedicel grooves). Calyptratae flies are divided into 3 superfamilies: Muscoidea (synanthropic flies with well-developed sponging mouthparts for feeding on decaying organic material or biting mouthparts for blood-feeding, most females being oviparous (egg-layers)); Hippoboscoidea (louse flies and tsetse flies with elongate biting mouthparts for blood-feeding, female flies formerly regarded as pupa-bearers and placed in group Pupipara (now defunct) as they have since been shown to birth mature larvae (considered to be prepupae)); and Oestroidea (blow flies, bot flies and flesh flies whose larvae are endoparasitic and cause myiases). Several superfamilies contain species whose larvae feed on the flesh of vertebrate hosts, mostly when dead (carrion) but sometimes when still living (causing fly-strike). Oestroid and muscoid larvae are well-adapted for living in moist organic substrates ranging from wet faeces to carrion to living flesh.

The superfamily Oestroidea is characterized by relatively large flies that are not dorsoventrally flattened, their wing veins are not crowded, and the discal medial cell of the wings widens gradually. The superfamily contains 7 families: Calliphoridae (blow flies); Oestridae (bot flies); Polleniidae (cluster flies); Rhinophoridae (woodlouse flies); Sarcophagidae (flesh flies); Tachinidae (parasitic flies); and Ulurumyiidae (McAlpine's fly). The family Oestridae (bot flies, also known as warble flies, heel flies, gad flies) form large hairy adult flies with bulbous heads, small antennae, rudimentary mouthparts, and wings with subcostal veins running parallel to the costa before joining it. Females produce eggs which hatch by discarding an anterodorsal cap, releasing vermiform larvae which are endoparasitic in the tissues (skin, digestive tract or respiratory passages) of vertebrates. The first larval instars have thorn-like spines encircling several segments, while second and third instars have ecdysal (moulting) scars around their spiracular plates (characteristic for the family Oestridae). Over 150 species have been described in some 25 genera in 5 subfamilies: Cephenemyiinae (deer bot flies), Cuterebrinae (New World skin bot flies), Gasterophilinae (stomach bot flies), Hypodermatinae (Old World skin bot flies, warble flies), and Oestrinae (nose and throat bot flies); with one unplaced genus and 3 fossil genera. Representative genera of veterinary significance are tabulated below:

Oestrid subfamily	Genera	Hosts	Strike	Myiasis*
Cuterebrinae (New World skin bot flies)	*Dermatobia*	cattle, humans	primary	Obligate (CU)
Oestrinae (nose and throat bot flies)	*Oestrus*	sheep	primary	Obligate (OC, NP)
Hypodermatinae (Old World skin bot flies, cattle grubs, ox warbles, heel flies)	*Hypoderma*	cattle	primary	Obligate (CU)
Gasterophilinae (stomach bot flies)	*Gasterophilus*	equines	primary	Obligate (GI)

*type of myiasis: CU = cutaneous; GI = gastro-intestinal; NP = naso-pharyngeal; OC = ocular.

The subfamily Gasterophilinae contains 5 genera classified in 4 tribes: Cobboldiini (genus *Cobboldia*), Gasterophilini (*Gasterophilus*, *Gyrostigma*), Neocuterebrini (*Neocuterebra*), and Rutteniini (*Ruttenia*). These large flies lay eggs which hatch larvae that invade the gastro-intestinal tracts of herbivores (wild and domestic ungulates). The genus *Gasterophilus* (syn. *Enteromyia, Enteromyza, Gastrophilus, Gastrus, Haemorrhoestrus, Rhinogastrophilus, Stomachobia, Progastrophilus*) contains 9 species whose larvae infect stomach and duodenum particularly of equids (horses, donkeys, mules, zebras), but also some large African wildlife (elephants, rhinoceroses) and occasionally other smaller domestic animals (e.g. deer, dogs, rabbits) and sometimes humans. These stomach bot flies are endemic in Palaearctic and Afrotropical regions, but those infecting horses have been spread around the world by numerous equine translocations. Humans become infected accidentally by ovipositing flies or by larval transfer when nuzzling pet or work horses.

Gasterophilus species	Hosts	Location	Clinical signs	Distribution
G. flavipes (syn. *Oestrus*)	Perissodactyla: equid (donkey)	stomach	obligate myiasis	Eurasia
G. haemorrhoidalis (syn. *G. duodenalis, pallens, pseudohaemorrhoidalis, salutiferus, Oestrus*) (throat horse bot, lip bot, rectal horse bot)	Perissodactyla: equid (horse, Przewalski's horse, ass, donkey, mule, Burchell's zebra, mountain zebra); dubious record in Artiodactyla: cervid (reindeer)	buccal mucosa, tongue, stomach, duodenum, rectum	obligate myiasis (stomatitis, ulceration, anorexia)	worldwide
G. inermis (syn. *Gastrus*)	Perissodactyla: equid (horse, Przewalski's horse, ass,	buccal mucosa, rectum	obligate myiasis (stomatitis,	Eurasia, Africa

(unarmed horse bot)	Burchell's zebra)		ulceration, anorexia)	
G. intestinalis (syn. *G. equi, magnicornis, Oestrus bengalensis, equi p.p., gastricus p.p., gastrophilus, schwabianus*) (common horse bot, armed horse bot)	Perissodactyla: equid (horse, Przewalski's horse, donkey, ass, mule)	buccal mucosa, tongue, stomach	obligate myiasis (stomatitis, ulceration, anorexia)	worldwide
G. meridionalis (syn. *Oestrus*) (non-spotted zebra bot)	Perissodactyla: equid (Burchell's zebra)	stomach	obligate myiasis	Africa
G. nasalis (syn. *G. albescens, clarkii, crossi, jumentarum, Gastrus subjacens, Oestrus equi p.p., fasciculosus, gastricus p.p., nasalis, salutaris, stomachinus, veterinus*) (nose horse bot, Linnaeus' horse bot)	Perissodactyla: equid (horse, Przewalski's horse, donkey, ass, Burchell's zebra); dubious records in Artiodactyla: bovid (cattle, sheep, goat)	buccal mucosa, tongue, stomach, duodenum	obligate myiasis (stomatitis, ulceration, anorexia)	worldwide
G. nigricornis (syn. *G. viridis, Gastrus*) (broad-bellied horse bot)	Perissodactyla: equid (horse, Przewalski's horse, donkey, ass)	buccal mucosa, tongue, stomach, duodenum	obligate myiasis (stomatitis, ulceration, anorexia)	Asia, Middle-East
G. pecorum (syn. *G. gammeli, hammeli, selysi, vulpecula, Gastrus ferruginatus, jubarum, lativentris, Oestrus vituli*) (dark-winged horse bot)	Perissodactyla: equid (horse, Przewalski's horse, donkey, ass, Burchell's zebra, Persian onager)	buccal mucosa, oesophagus, stomach	obligate myiasis (stomatitis, ulceration, anorexia)	Eurasia, Africa
G. ternicinctus (syn. *G. gedoelsti*)	Perissodactyla: equid (Burchell's zebra)	stomach	obligate myiasis	Africa

Parasite morphology: *Gasterophilus* spp. form 4 different types of morphological developmental stages: eggs, larvae, pupae and adults. The eggs are elongate and ellipsoidal measuring 1-2 mm long and are either white-yellow (e.g. G. intestinalis) or brown-black (e.g. *G. nasalis, G. haemorrhoidalis*). They are attached to host hairs by an attachment organ (either short and caudal, or elongate and ventral) and have a subterminal operculum (anterodorsal cap). Larvae (commonly called bots, or sometimes grubs) are initially fusiform but become cylindrical, with a narrow anterior head and a robust body tapering gradually to a truncated posterior. They are also initially white but turn red-orange (e.g. *G. intestinalis*) to yellow-green (e.g. *G. nasalis*) in color. They develop through 3 larval instars (L1-3) growing in size from 1-2 mm to 14-20 mm when mature. Larvae do not have any fleshy projections but they bear numerous body spines with blunt or sharp tips (muscoid larvae lack spines). The spines are pointed backwards and are arranged in 1-3 rows (one row in *G. nasalis*, and 2 rows in *G. intestinalis* and *G. haemorrhoidalis*) concentrated in bands at the edges of segments. The head is small (usually retracted) and lacks a sclerotized head capsule but has an internal cephalopharyngeal skeleton with prominent rasping mouthparts (mouth hooks). Larvae breathe using 2 pairs of respiratory spiracles: an small anterior pair that are often obscure (sometimes visible as small bunches of protruding tissue); and a larger posterior pair apparent as flat oval plates located within deep depressions in the caudal segment, Each plate with 3 elongate openings (2 on L1) that are characteristically curved (with a mid-elbow) in gasterophilines (other oestrid larvae form porous spiracular plates, while calliphorid larvae form plates with 3 slits surrounded by a peritreme). Mature larvae form puparia that are similar in size, shape and ornamentation to mature L3, but are somewhat shrivelled in appearance and dark brown-black in colour. The enclosed pupae transform into winged adults which eclose through a circular cap (like all Cyclorrhapha) and not through longitudinal slits (like Nematocera and Brachycera). Adult flies are large (11-15 mm long) with yellow to dark-brown bodies (resembling bumble-bees) covered dorsally with dense yellow-brown hairs and laterally with creamy-white hairs (but lacking stout bristles). Their bodies have 3 conspicuous tagma: a broad head; globular thorax; and ellipsoidal abdomen. The heads are bulbous (broad but flattened front-to-back), covered with smooth velvety hairs, and possess both a ptilinal suture and facial lunule (like other Oestroidea and Muscoidea, but unlike other calyptrates). They have a pair of large brown compound eyes located laterally and separated by a large frons. They possess a pair of short anterior antennae, each composed of 3 dissimilar segments: a short basal scape; a short club-like pedicel; and an anterior flagellum composed of long slender tapered bristle (arista) which is bare (without setae but with small sparse microtrichia). The ventral mouthparts are small and non-functional (adults do not feed) with vestigial palps and proboscis evident as small yellow-brown knobs. The alimentary tract is rudimentary and may possibly be used for water regulation. The thorax is covered by a scutum with posterior lobe-like scutellum, both covered with fine dense setae forming transverse dark bands. A single

vertical row of bristles is located on the thoracic meron (like other oestroids, but lacking on muscoid flies). The mesothorax bears one pair of wings with dark patches. The wing membranes are supported by 6 primary veins [costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A)] with Sc veins running parallel to the C vein, dm-cu cross-veins absent, and the M vein extending to the outer trailing edge of the wing. Like all Diptera, a second pair of wings have been highly reduced to small club-like halteres thought to be used to stabilize flight. Like all calyptrate flies, the halteres are covered by hindlobes of the forewings (known as squammae or calypters), which in this case are small (other oestrids have large calypters). Similar to other oestrids, gasterophilines have bulbous swellings (greater ampulla) located beneath their wing bases. The ventral thorax gives rise to 3 pairs of long hairy legs, each comprised of 5 segments (coxa, trochanter, femur, tibia, and tarsus) and all terminating in a pair of claws with pad-like pulvilli surrounding a central bristle (empodium). The segmented abdomen is covered with fine dense setae arranged in light-dark patches, often appearing tricoloured with white hairs located on anterior segments, black hairs on middle segments and dark yellow hairs on posterior segments. Male flies have 2 testes connected by vas deferens to a seminal vesicle (with lateral accessory glands) leading to a tubular ejaculatory duct and retractable copulatory aedeagus and claspers. Female flies have 2 ovaries joined by oviducts to a globular uterus (with associated spermatheca and accessory glands) leading to the vulva. Females have a strong protuberant ovipositor that is often held curved beneath the abdomen and mistaken for a sting.

Site of infection: Adult flies are not parasitic but free-living and free-flying. Females flies do seek vertebrate hosts, not to feed upon, but rather to deposit eggs on hair shafts. The emergent larvae are obligate endoparasites and can only complete their development after invading the gastro-intestinal tracts of equids (horses, donkeys, mules and even some zebra). First-stage larvae (L1) invade the oral mucosa and tongue and then migrate down the alimentary tract where L2 and L3 attach to the lining of the stomach (*G. intestinalis*), the anterior duodenum (*G. nasalis*) or the rectum (*G. haemorrhoidalis*). Some accidental infestations have been reported in humans in close contact with horses when L1 burrow into the skin causing sinuous tracks before dying.

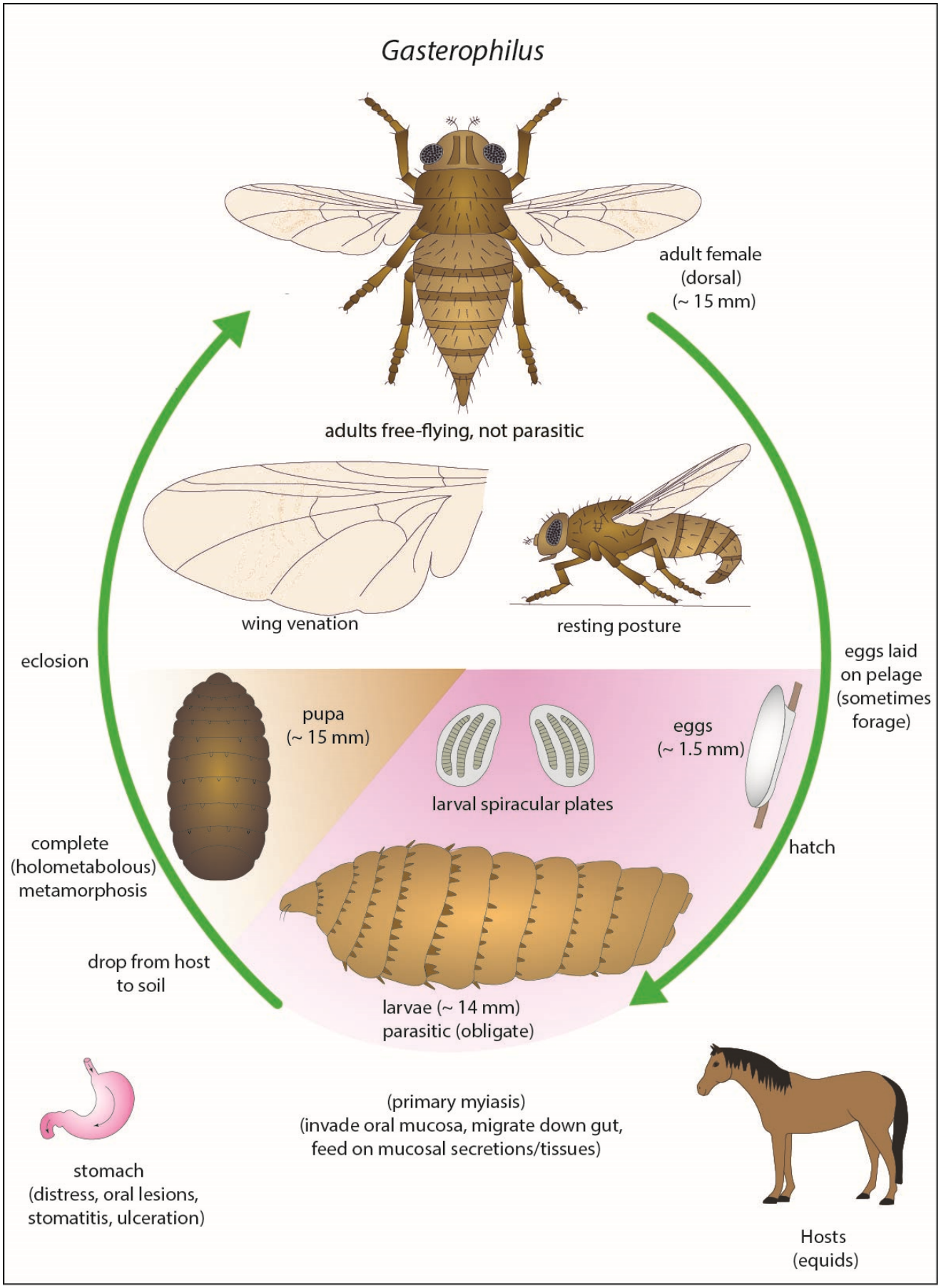
Pathogenesis: Despite the macabre spectre of having fly larvae residing within the gut, most infestations are well tolerated by hosts and clinical signs are rarely seen. Most equids appear to tolerate burdens of around 100 bots without apparent ill effects. Nonetheless, some pathology may be observed in 3 successive phases: firstly when ovipositing flies cause fly worry, secondly when invading L1 penetrate oral tissues; and thirdly when maturing larvae attach to the gut mucosa. Gravid female flies hover near their intended hosts and dart in to deposit eggs on hairs around the face, forelegs and belly. This hovering and dive-bombing behaviour may disturb some animals and cause aversive behaviours including panicky headlong flight (gadding) sometimes resulting in self-wounding. Female flies may also chase galloping horses and deposit eggs when they halt. The degree of fly worry varies for different fly species, with nearly all horse breeds reacting to *G. nasalis*, while usually only thoroughbreds and not draft breeds react to *G. intestinalis.* Eggs adhering to hairs may also irritate horses which then attempt to groom by licking (which in many instances stimulates the eggs to hatch). Larvae entering the mouth bury themselves in the buccal mucosa, gums and tongue where they may wander for around 28 days causing irritation, inflammation, excessive salivation and sometimes ulceration. Those penetrating the gums near molar teeth can cause pain upon mastication with chewing problems leading to loss of appetite and poor growth. Lesions are also prone to secondary bacterial infection, with the development of necrotic and pustular pockets and loosened teeth. Larvae then migrate down the gastro-intestinal tract taking up residence in specific locations, feeding on host tissues and secretions and developing through another 2 larval instars (L2-3). These stages typically attach to the mucosal lining of the stomach, duodenum and/or rectum, and remain immobile for 9-12 months (over-wintering inside their equid hosts). Their presence often does not cause any clinical signs, although a non-specific syndrome of unthriftiness, poor coat, mild colic and poor appetite has been ascribed to bot infestations. Large numbers of developing larvae have been associated with local inflammation, chronic gastritis, colic, epithelial sloughing, nodular mucosal proliferation, squamous cell tumours, obstructions, ulcerative erosions and abscesses, sometimes with stomach perforation, peritonitis and anaemia. Infestations with *G. pecorum* have also been associated with swallowing difficulties and obstructions (due to oesophageal inflammation, constriction and muscular hypertrophy), and those by *G. haemorrhoidalis* may occasionally cause rectal prolapse. Humans in close contact with horses may become accidentally infected when L1 invade the skin or eyes causing cutaneous myiasis (sinuous inflamed tracks, termed creeping myiasis) and ocular myiasis (irritation, conjunctivitis, corneal abrasions). Such infections are generally transient as the L1 cannot develop further in humans and usually die.

Developmental cycle and mode of transmission: Like all Diptera, these bot flies exhibit holometabolous development where eggs hatch grub-like larvae that undergo complete metamorphosis in pupae to form winged adults. Female flies are oviparous and attach eggs to hair shafts on equids, mostly around the face (*G. nasalis* under the chin, *G. haemorrhoidalis* on the nose, lips and mouth) but also on the forelegs, belly, shoulders, flanks and mane (*G. intestinalis*). Alternatively, a few species (e.g. *G. pecorum*) do not deposit eggs on hosts but attach them to plant leaves and stems liable to be consumed as forage. The eggs embryonate over 5-10 days and then hatch spontaneously (e.g. *G. nasalis* and *G. haemorrhoidalis*) or when licked (e.g. *G. intestinalis*) or when ingested with forage (e.g. *G. pecorum*). In moist conditions, eggs on forage may stay dormant for months until ingested. Hatching releases L1 that either crawl to the mouth or are ingested (crawling appears to stimulate host licking). They then penetrate the anterior end of the tongue, the buccal mucosa or the gums at interdental spaces. L1 wander in these tissues for approximately 28 days before moving to the stomach (nonglandular portion) and intestines (anterior duodenum or rectum) to mature. They moult to L2 just before or after arrival in the gut and then moult to L3 after approximately 5 weeks. Altogether, larvae may reside in hosts for up to 9-12 months, typically over-wintering in the host like other oestrid species (except the cuterebrines which overwinter as diapausing pupae). In late winter or

early spring, mature L3 detach from the mucosa, pass through the intestines and exit the host with faeces. They burrow into the ground and form puparia by contraction and hardening of the integument. The enclosed pupae then transform into adults with pupation taking 3-10 weeks depending on the temperature (longer in colder conditions). Adult flies emerge from pupae and fly about searching for mates and hosts for their larvae (adult do not feed). Males fly to aggregation points (high ground) and wait to intercept passing females. Fertilized females are strong fliers and may fly long distances seeking hosts for oviposition using olfactory and visual senses. They have short lifespans and only live for 10-14 days, but can lay 150-1,000 eggs in that period (up to 2,500 for *G. pecorum* which deposits eggs on forage). Adult flies are active in summer during the daytime (usually early afternoon in warm sunny weather) and they are univoltine producing only one generation each year. They have a very broad distribution around the world, having been translocated to many countries with their equine hosts. Humans become infected accidentally either by ovipositing flies or by larval transfer when grooming or nuzzling pet or work horses.

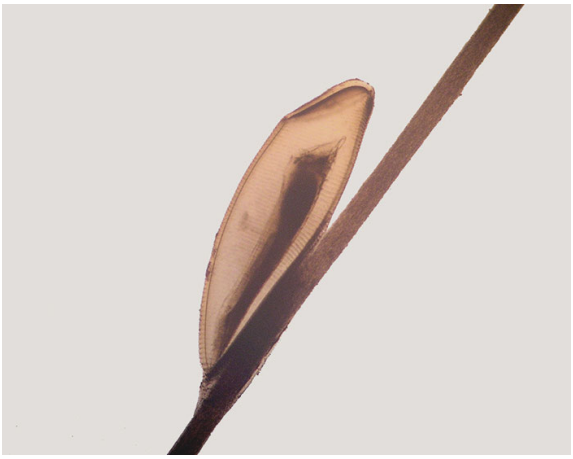
Differential diagnosis: Most infestations are asymptomatic or remain subclinical and go undiagnosed. Even when clinical signs occur (unthriftiness, poor coat, mild colic, poor appetite), they are very non-specific and may be attributed to other aetiological agents or disease conditions. Infestations may be suspected when adult bot flies are observed bothering animals, or when fly eggs are detected on hairs around the face and legs. Diagnosis is made by the direct detection of larvae and their identification on the basis of their structural characteristics. However, the only stages accessible antemortem are L1 in mouth lesions and mature L3 freshly excreted in faeces. The detection of larvae developing in the oesophagus, stomach or intestines is generally made incidentally at postmortem. Clinicians have often resorted to using endoscopic techniques on particularly valuable horses to detect larvae attached to mucosal surfaces, but biopsies are not recommended as foreign material may leak into the circulation provoking allergic responses. Immunoserological tests (enzyme-linked immunosorbent assays) have been developed to detect specific host antibodies against larval extracts, with the advantage that cryptic infestations may be detected as larvae over-winter in hosts. A variety of molecular biological techniques have been used to characterize bot fly species, usually after polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA, haemoglobin-1) and mitochondrial (cytochrome oxidase I and II) gene sequences.

Treatment and control: Chemical insecticides are routinely used for chemotherapy and chemoprophylaxis, with a wide variety of formulations available as liquids, gels, pastes, boluses, feed additives, pour-ons, or injectables. Topical insecticides may be used regularly during fly season to discourage oviposition or kill emergent L1, but they are less effective against larvae already residing with the gastro-intestinal tract. Systemic insecticides may be used to kill bots in the buccal cavity as well as in the gastro-intestinal tract, with treatments usually conducted during autumn or early winter (after the first frost has killed the adult flies). Good efficacy has been reported for organochlorines (lindane, dichlorodiphenyltrichloroethane (DDT)), organophosphates (trichlorfon, chlorpyrifos, chlorfenvinphos, coumaphos, diazinon) but particularly for macrocyclic lactones (avermectins) which are highly effective against all larval stages. It is recommended that drugs be used selectively and judiciously to forestall the development of drug resistance (particularly to the avermectins which are also used to control helminthiases in horses). It has been noted that routine grooming during fly season can greatly reduce the incidence of myiasis, as fly eggs can be trimmed off hairs or dislodged using fine-toothed combs, and washing with warm water containing an insecticide can induce eggs to hatch and kill emergent larvae. Animal handlers should also practice good hygiene and adopt personal protective measures; including wearing insect repellents on skin and clothing, wearing rubber gloves when grooming animals, and refraining from nuzzling or kissing horses. It is also important to adopt good sanitation practices to remove and dispose of faeces which may contain mature L3 and prepupae. Horse faeces should be transported off-site so the mature larvae do not burrow into the surrounding soil to pupate.


Gasterophilus
adult female
(dorsal)
(~ 15 mm)
adults free-flying, not parasitic
wing venation
resting posture
eclosion
eggs laid
on pelage
(sometimes
forage)
pupa
(~ 15 mm)
eggs
(~ 1.5 mm)
larval spiracular plates
complete
(holometabolous)
metamorphosis
hatch
drop from host
to soil
larvae (~ 14 mm)
parasitic (obligate)
(primary myiasis)
(invade oral mucosa, migrate down gut,
feed on mucosal secretions/tissues)
stomach
(distress, oral lesions,
stomatitis, ulceration)
Hosts
(equids)



Gasterophilus adult



Gasterophilus egg



Gasterophilus larvae



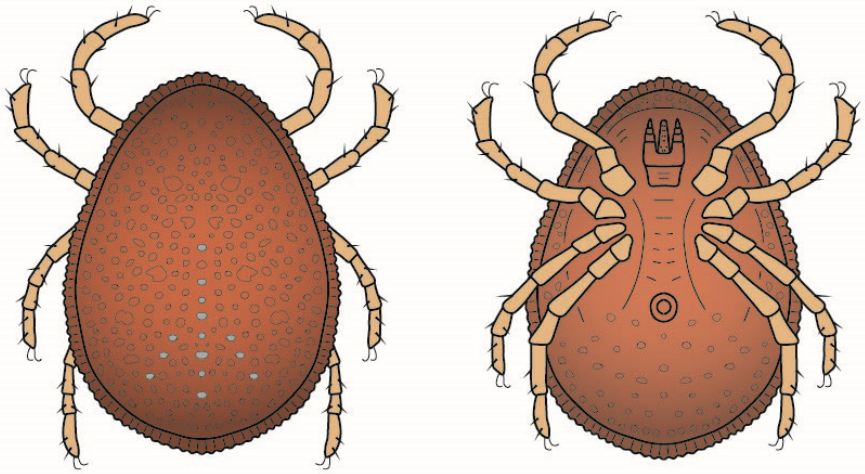
Gasterophilus adult

Ixodida
(ticks)

Acari: Metastigmata: Argasidae

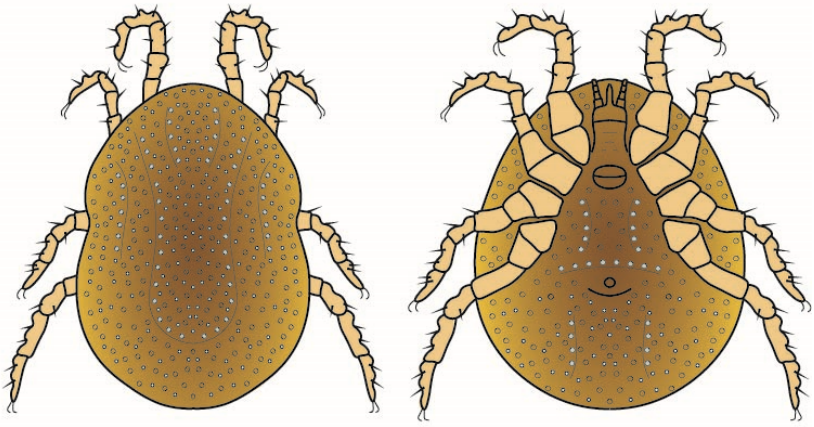
Argas
adults (~ 10 mm)

dorsal ventral



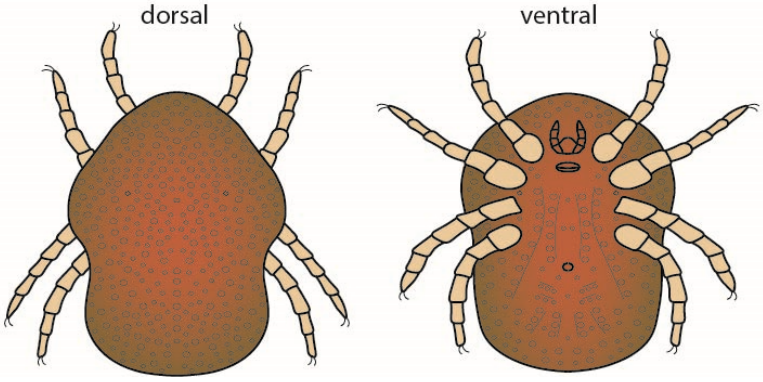
Ornithodorus
adults (~ 10 mm)

dorsal ventral

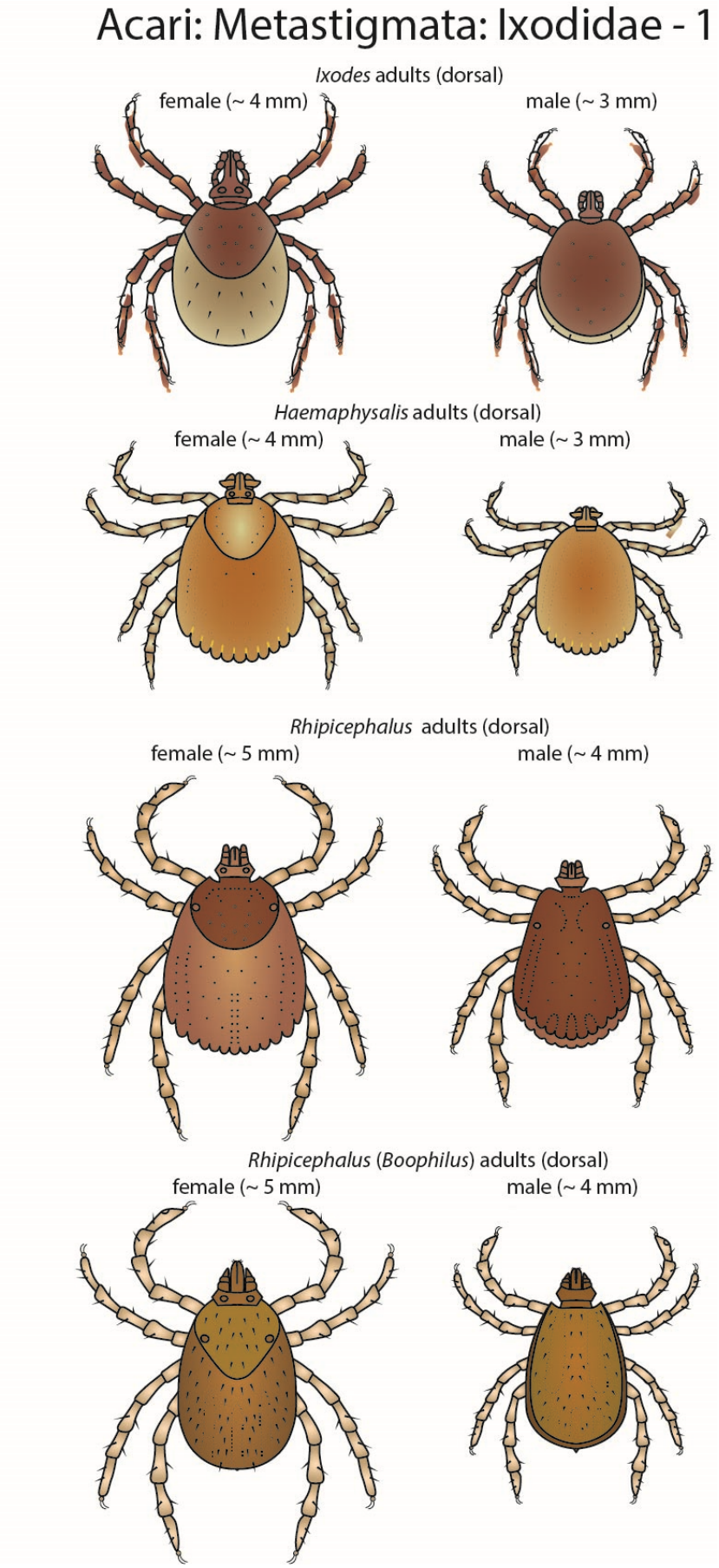


Otobius
adults (~ 8 mm)

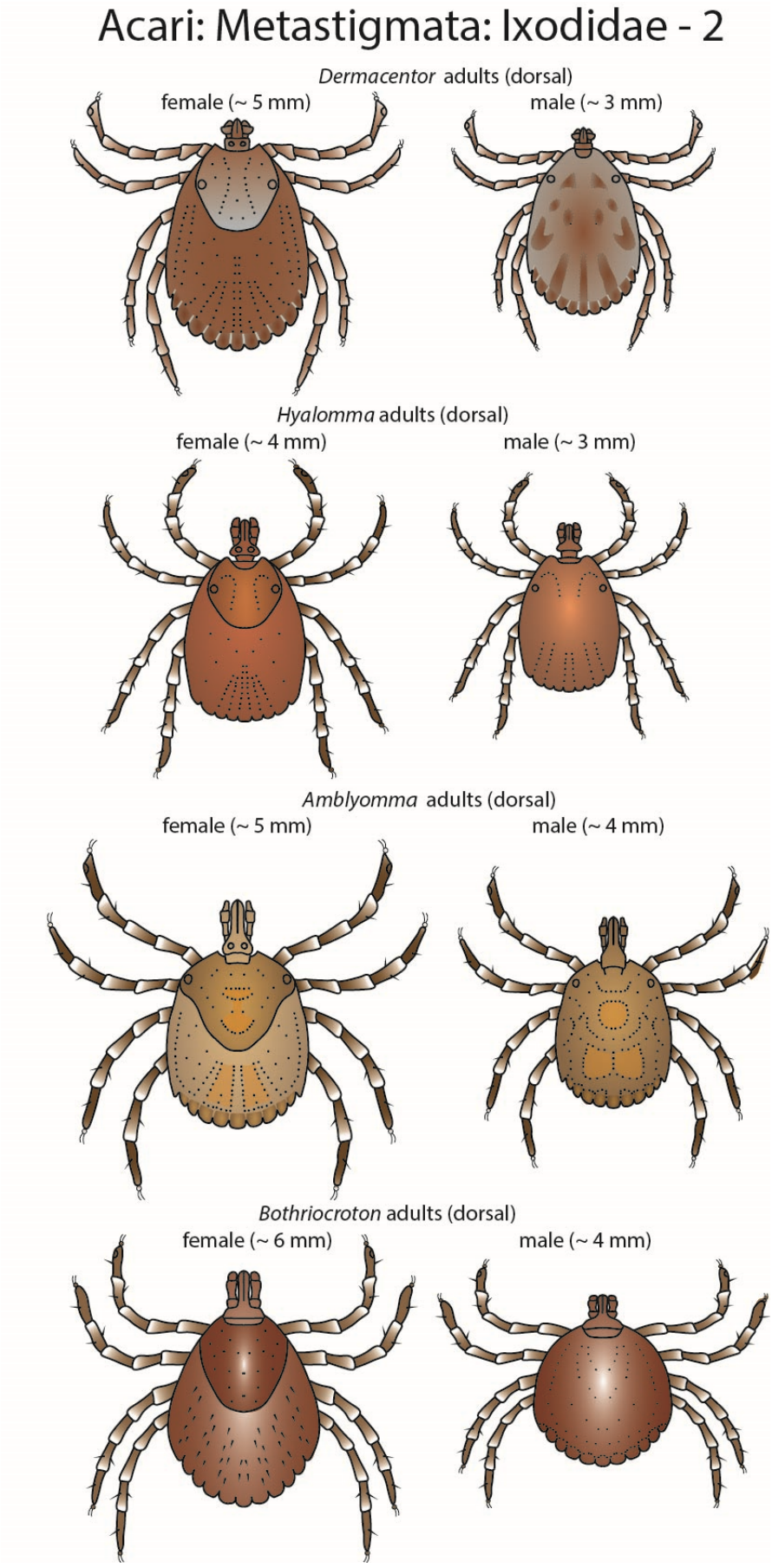
dorsal ventral



Acari: Metastigmata: Ixodidae - 1



Acari: Metastigmata: Ixodidae - 2



Argas
(arachnid: tick)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ticks have respiratory stigmata posterior to their legs. They are obligate blood-feeding ectoparasites on vertebrate hosts and their hypostomes are toothed and exposed. Two families are recognized: Argasidae and Ixodidae, known as soft and hard ticks, respectively. Argasids have soft leathery bodies lacking a dorsal scutum and the capitulum is covered by the body. They are transient feeders on mammals and birds and have multi-host life-cycles, spending the majority of time hiding in cracks/crevices/soil in the surrounding environment, especially nests and dens. Infestations by *Argas* spp. on domestic birds may cause irritation, anaemia and paralysis as well as transmit bacterial and viral diseases.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on capitulum)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Ixodida (Metastigmata) (ticks, macroscopic, stigmata posterior to legs, hypostome toothed, ectoparasites)
Family: Argasidae (soft ticks, lack dorsal scutum, capitulum covered by body, hide in cracks/crevices)
Genus: *Argas* (parasitic on skin of birds)
Species: various species cause irritation and anaemia in chickens

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial

Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on capitulum) [34 superfamilies]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs (behind coxae III or IV); and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Ticks are further characterized by macroscopic bodies with an exposed ventral hypostome (toothed with backwardly-directed barbs), chelicerae with only 2 joints, long legs with free articulated coxae (not fused to the body wall) and tarsi I each bearing a complex sensory pit (Haller's organ). They are obligate blood-sucking parasites which feed on terrestrial vertebrates (mammals, birds, reptiles and some amphibians) as larvae, nymphs and adults with 1-, 2- or 3-host life-cycles. Almost 1,000 tick species have been classified within some 20 genera from numerous wild and domesticated animals around the world. Two main families are recognized: the Argasidae containing ~200 species of 'soft' ticks with flexible leathery cuticles, ventral capitula, short feeding times (< 1 hour) and long life-spans (up to 20 years); and the Ixodidae containing ~800 species of 'hard' ticks with rigid dorsal scutal plates, anterior capitula, long feeding times (hours to days) and shorter life-span (2-6 years). Basic characteristics of representative genera considered in this resource are tabulated below.

Genus	**Capitulum**				**Idiosoma**				**Usual no. of hosts**
	location	**basis capitulum**	**mouth-parts**	**palps**	**integument**	**festoons**	**eyes**	**male ventral plates**	

Argasidae (soft ticks with leathery cuticle, stigmata between coxae III)									
Argas	ventral	triangular	short	leg-like	stippled with lateral suture	absent	absent	absent	>3
Ornithodorus	ventral	rectangular	short	leg-like	mamillated	absent	usually absent	absent	>3
Otobius	ventral	rectangular	short	leg-like	spinose (nymphs), granulated (adult)	absent	absent	absent	1
Ixodidae (hard ticks with sclerotized dorsal plate (scutum), stigmata behind coxae IV)									
Prostriata (anal groove anterior)									
Ixodes	anterior	triangular	long	long	inornate	absent	absent	present	3
Metastriata (anal groove posterior)									
Amblyomma	anterior	rectangular	long	long	ornate	present	present	indistinct	3
(*Aponomma*)	anterior	rectangular	long	long	often ornate	present	absent	absent	3
Rhipicephalus	anterior	hexagonal	short	medium	some ornate	present	present	present	3
(*Boophilus*)	anterior	hexagonal	short	short	inornate	absent	present	present	1
Dermacentor	anterior	rectangular	short	medium	often ornate	present	present	absent	3
Haemaphysalis	anterior	rectangular	short	short	inornate	present	absent	absent	3
Hyalomma	anterior	rectangular	long	long	inornate	present	present	present	2
Bothriocroton	anterior	pentagonal	long	long	ornate	present	absent	absent	3

The family Argasidae contains 5 subfamilies (Antricolinae, Argasinae, Nothoaspisinae, Ornithodorinae, Otobinae) which vary in morphology, biology, host range and specificity. Members of the subfamily Argasinae have dorsoventrally flattened bodies with roughly-stippled integuments whose dorsal and ventral surfaces meet to form distinct lateral suture-like margins. All motile developmental stages are transient ectoparasites, often emerging nocturnally from host nests or residences to feed. A small number of taxa have been identified within the subfamily, but their taxonomic ranks vary according to different authorities (being recognized as separate genera, or as subgenera in the genus *Argas*). Consensus opinion recognizes 3 genera (*Argas*, *Ogadenus* and *Reticulinasus*) from a range of avian hosts as well as small mammals such as bats and rodents. Around 74 *Argas* spp. belonging to 5 subgenera (*A.* (*Argas*), *A.* (*Carios*), *A.* (*Chiropterargas*), *A.* (*Persicargas*) and *A.* (*Secretargas*)) have been described mostly from birds and bats around the world, particularly in areas with dry (even arid) climates. Most species are not strictly host specific (oioxenous), but can feed opportunistically on related hosts, such as other birds (stenoxenous), and sometimes even on non-related hosts, such as rodents and occasionally humans (euryxenous). The fowl tick, *A. persicus*, is cosmopolitan in distribution and infestations may cause significant problems in domestic poultry, particularly in birds kept in aged timber structures where developmental stages may sequester in cracks and crevices.

***Argas* species**	**Hosts**	**Clinical signs**	**Distribution**
A. (*Persicargas*) *abdussalami*	Accipitriformes: accipitrid (white-rumped vulture); Columbiformes: columbid (pigeon, cote); Galliformes: phasianid (chicken, nests)		Pakistan
A. aequalis (syn. *Ornithodorus*)	host unknown		Africa
A. (*Chiropterargas*) *afghanistaniensis*	Chiroptera: rhinopomatid (greater mouse-tailed bat)		Afghanistan
A. (*Argas*) *africolumbae*	Columbiformes: columbid (speckled pigeon); Pelecaniformes: threskiornithid (southern bald ibis); Passeriformes: hirundinid (rock martin)		Africa
A. (*Carios*) *aragaoi* (syn. *Ornithodorus*)	Rodentia: cricetid (yellowish rice rat)		South America
A. (*Persicargas*) *arboreus*	Accipitriformes: accipitrid (martial eagle); Galliformes: phasianid (chicken); Gruiformes: gruid (black crowned crane); Passeriformes: corvid (pied crow, hooded crow); Pelecaniformes: ardeid (western cattle egret); pelecanid (pink-backed pelican)		Egypt
A. (*Argas*) *assimilis*	Passeriformes: hirundinid (red-rumped swallow)		Asia
A. (*Carios*) *australiensis*	host unknown, collected from bat-infested house		Australia
A. (*Argas*) *beijingensis*	Columbiformes: columbid (rock dove)		China
A. beklemischevi	Accipitriformes: accipitrid (Egyptian vulture)		Europe
A. (*Chiropterargas*) *boueti*	Chiroptera: emballonurid (naked-rumped tomb bat, Egyptian tomb bat), hipposiderid (trident bat), megadermatid (heart-nosed bat), molossid (Egyptian free-tailed bat, European free-tailed bat), nycterid (Egyptian		Mediterranean

	slit-faced bat), pteropodid (Egyptian fruit bat), rhinolophid (greater horseshoe bat, lobed horseshoe bat, Geoffroy's horseshoe bat, Mehely's horseshoe bat, Bokhara horseshoe bat, Arabian horseshoe bat), rhinopomatid (greater mouse-tailed bat, lesser mouse-tailed bat, Egyptian mouse-tailed bat), vespertilionid (desert long-eared bat, Christie's long-eared bat, Kuhl's pipistrelle, Christmas Island pipistrelle, white-winged serotine); Primates: hominid (human)		
A. brevipes	Falconiformes: falconid (American kestrel); Passeriformes: hirundinid (violet-green swallow), troglodytid (cactus wren); Piciformes: picid (gilded flicker, Mearn's woodpecker, ant-eating woodpecker); Strigiformes: strigid (ferruginous pygmy owl, eastern screech owl)		North America
A. brumpti	Artiodactyla: suid (desert warthog); Hyracoidea: procaviid (rock hyrax, yellow-spotted rock hyrax); Rodentia: hystricid (crested porcupine), murid (grey spiny mouse, eastern spiny mouse, Cairo spiny mouse, house mouse), caviid (guinea pig); Lagomorpha: leporid (rabbit); Carnivora: herpestid (meerkat), felid (lion) Primates: hominid (human); Sauria: agamid (spiny agama, ocellated spinytail, rock agama), gerrhosaurid (giant plated lizard), phyllodactylid (white-spotted wall gecko); Columbiformes: columbid (pigeon); Galliformes: numidid (helmeted guineafowl); Passeriformes: passerid (sparrow)	lesions (potential vector for saurian hepatozoonosis)	Africa
A. bureschi	Rodentia: sciurid (European ground squirrel, nest)		Europe
A. (Carios) capensis	Charadriiformes: larid (red-billed gull, brown noddy, sooty tern); Procellariiformes: procellariid (black-winged petrel, Kermadec petrel, little shearwater); Phaethontiformes: phaethontid (red-tailed tropicbird); Suliformes: phalacrocoracid (spotted shag), sulid (Australasian gannet); Gruiformes: rallid (spotless crake)		New Zealand
A. (*Chiropterargas*) *ceylonensis*	Chiroptera: emballonurid (black-bearded tomb bat, cave)		Sri Lanka
A. columbarum	Columbiformes: columbid (pigeon); Primates: hominid (human)		Europe
A. coniceps	Passeriformes: passerid (house sparrow)		Europe
A. (*Chiropterargas*) *confusus*	Chiroptera: emballonurid (naked-rumped tomb bat, Egyptian tomb bat), hipposiderid (trident bat), miniopterid (Natal long-fingered bat, small bent-winged bat), molossid (lappet-eared free-tailed bat, Egyptian free-tailed bat), nycterid (Egyptian slit-faced bat), rhinolophid (greater horseshoe bat), rhinopomatid (Egyptian mouse-tailed bat), vespertilionid (desert long-eared bat, Kuhl's pipistrelle, yellow bat, Cape serotine, thick-eared bat); Rodentia: dipodid (Euphrates jerboa)		Africa
A. (*Argas*) *cooleyi*	Accipitriformes: cathartid (California condor); Passeriformes: hirundinid (cliff swallow); Strigiformes: strigid (northern barred owl)		North America
A. (*Chiropterargas*) *cordiformis*	Chiroptera: nycterid (Egyptian slit-faced bat)		Africa
A. cucumerinus	host unknown, collected from soil		South America
A. (*Argas*) *dalei*	Strigiformes: strigid (burrowing owl)		South America
A. (*Carios*) *daviesi*	Chiroptera: vespertilionid (eastern forest bat)		Australia
A. (*Carios*) *dewae*	Chiroptera: rhinolophid (smaller horseshoe bat), vespertilionid (Gould's wattled bat, large-eared pied bat, lesser long-eared bat, eastern forest bat, eastern false pipistrelle)		Australia
A. (*Argas*) *dulus*	Passeriformes: bombycillid (palmchat, nest)		Central America
A. (*Secretargas*) *echinops*	Afrosoricida: tenrecid (lesser hedgehog tenrec)		Madagascar
A. (*Argas*) *falco*	Falconiformes: falconid (Nankeen kestrel, nest)		Australia

A. (*Persicargas*) *giganteus*	Galliformes: odontophorid (Gambel's quail); Passeriformes: corvid (pinyon jay, Tamaulipas crow), mimid (curve-billed thrasher, crissal thrasher, Bendire's thrasher, sage thrasher, parid (mountain chickadee), passerellid (fox sparrow, white-crowned sparrow, eastern towhee, canyon towhee, Abert's towhee, dark-eyed junco); Strigiformes: strigid (eastern screech owl, burrowing owl)		North America
A. (*Persicargas*) *gilcolladoi*	Accipitriformes: accipitrid (Griffon vulture)		Europe
A. (*Carios*) *gujaratensis*	Chiroptera: vespertilionid (greater Asiatic yellow bat)		India
A. hermanni (incl. subspp. *latus, macrostigmatus, vulgaris*)	Columbiformes: columbid (pigeon, rock dove); Coraciiformes: coraciid (European roller); Falconiformes: falconid (lanner falcon); Passeriformes: corvid (hooded crow, brown-necked raven, fan-tailed raven); Strigiformes: strigid (little owl); Suliformes: phalacrocoracid (European shag); Chiroptera: vespertilionid (desert long-eared bat)	(possible vector for borreliosis, arboviruses, Tunis, Quaranfil, Chenuda and West Nile viruses)	Europe
A. (*Argas*) *himalayensis*	Galliformes: phasianid (snow partridge)		Nepal
A. hoogstraali	Sauria: oplurid (Anzamala Madagascar swift, Cuvier's Madagascar swift, Dumeril's Madagascar swift, Grandidier's Madagascar swift)		Madagascar
A. (*Carios*) *hoogstraali* [name preoccupied, as above]	Chiroptera: emballonurid (long-winged tomb bat)		India
A. (*Carios*) *indicus*	Chiroptera: molossid (Egyptian free-tailed bat)		India
A. (*Argas*) *japonicus*	Passeriformes: hirundinid (lesser striated swallow, common house martin); Artiodactyla: bovid (cattle)	(possible vector for rickettsiosis and anaplasmosis)	Asia
A. (*Persicargas*) *keiransi*	Falconiformes: falconid (Chimango caracara)		South America
A. (*Argas*) *lagenoplastis*	Passeriformes: hirundinid (Australian fairy martin)		Australia
A. latus	Columbiformes: columbid (rock dove, European turtle dove); Coraciiformes: coraciid (European roller); Passeriformes: corvid (fan-tailed raven)		Central Asia
A. (*Argas*) *lowryae*	Falconiformes: falconid (Nankeen kestrel)		Australia
A. (*Carios*) *macrodermae*	Chiroptera: megadermatid (ghost bat)		Australia
A. (*Argas*) *macrostigmatus*	Siluriformes: phalacrocoracid (crested cormorant)		Europe
A. magnus	Columbiformes: columbid (rock dove); Galliformes: phasianid (chicken)		South America
A. (*Argas*) *monachus*	Psittaciformes: psittacid (monk parakeet)		South America
A. (*Argas*) *monolakensis*	Charadriiformes: larid (California gull); Primates: hominid (human)	(possible vector for Q fever)	North America
A. (*Argas*) *moreli*	hosts unknown, collected from infested house		South America
A. (*Argas*) *neghmei*	Galliformes: phasianid (chicken); Columbiformes: columbid (dovecotes); Lagomorpha: leporid (rabbit); Primates: hominid (human)	pruritus	South America
A. (*Persicargas*) *nullarborensis*	Passeriformes: corvid (little crow)		Australia
A. passerinus	Passeriformes: passerid (sparrow, nest)		China
A. (*Persicargas*) *persicus* (syn. *A. chinche, mauritianus, miniatus, minutus*) (fowl tick, chicken tick, adobe tick, blue bug)	Accipitriformes: accipitrid (golden eagle, eastern imperial eagle, martial eagle, white-rumped vulture, black kite, Swainson's hawk, Eurasian sparrowhawk, long-legged buzzard, pallid harrier), cathartid (black vulture, turkey vulture), pandionid (osprey), sagittariid (secretary bird); Anseriformes: anatid (duck, mallard, cinnamon teal, goose); Bucerotiformes: upupid (Eurasian hoopoe); Columbiformes: columbid (pigeon, rock dove, laughing dove, spotted dove, European turtle dove, Oriental turtle dove, mourning dove); Coraciiformes: coraciid (European roller), meropid (European bee-eater); Cuculiformes: cuculid (greater roadrunner, rufous-vented ground	irritation, anaemia, toxicosis, paralysis (vector for borreliosis, fowl spirochaetosis, aegyptianellosis, anaplasmosis, Crimean-Congo haemorrhagic fever, Kyasanur forest disease)	worldwide

	cuckoo); Falconiformes: falconid (saker falcon, common kestrel, lesser kestrel, red-footed falcon); Galliformes: numidid (helmeted guineafowl, Transvaal guineafowl), phasianid (chicken, red junglefowl, turkey, California valley quail, Gambel's quail, rock partridge, pheasant); Gruiformes: gruid (wattled crane, black crowned crane); Passeriformes: alaudid (Calandra lark), corvid (pied crow, rook, western jackdaw, white-necked raven, black-headed jay, Eurasian magpie, black-billed magpie), emberizid (red-headed bunting), fringillid (canary), hirundinid (barn swallow), icterid (western meadowlark), laniid (great grey shrike), passerid (house sparrow, Spanish sparrow, Eurasian tree sparrow, rock sparrow), passerellid (golden-crowned sparrow), sturnid (common starling, rosy starling, pale-winged starling), turdid (mistle thrush); Pelecaniformes: ardeid (common heron, grey heron, cattle egret), pelecanid (pelican), threskiornithid (Hadada ibis); Piciformes: picid (great spotted woodpecker, European green woodpecker); Psittaciformes: psittacid (monk parakeet); Strigiformes: strigid (short-eared owl, little owl, Eurasian eagle-owl, brown fish owl, western screech owl); Struthioniformes: struthionid (ostrich); Suliformes: anhingid (snakebird); Artiodactyla: bovid (cattle, goat), suid (pig); Lagomorpha: leporid (European rabbit, Texas jack rabbit); Rodentia: cricetid (grey dwarf hamster, European hamster), heteromyid (chisel-toothed kangaroo-rat), murid (African grass rat, black rat, Turkestan rat, mouse); Carnivora: canid (dog); Primates: hominid (human); Anura: bufonid (common toad)		
A. pipistrellae (syn. *A. fischeri*)	Chiroptera: hipposiderid (Greggory's trident leaf-nosed bat), vespertilionid (common pipistrelle, Kuhl's pipistrelle, Savi's pipistrelle, lesser Papuan pipistrelle, Japanese house bat)		Egypt, Asia
A. (*Argas*) *polonicus*	Columbiformes: columbid (rock dove); Primates: hominid (human)	itchy lesions	Europe
A. pusillus	Chiroptera: vespertilionid (lesser Asiatic yellow bat, Temminck's bat, brown pipistrelle, Japanese house bat); Primates: hominid (human)		Asia
A. (*Persicargas*) *radiatus*	Galliformes: phasianid (chicken)		North America
A. (*Argas*) *reflexus* (syn. *Ixodes columbae*) (pigeon tick)	Accipitriformes: accipitrid (eagle, long-legged buzzard, black kite), cathartid (California condor); Anseriformes: anatid (Muscovy duck, goose); Apodiformes: apodid (swift); Cathartiformes: cathartid (condor); Columbiformes: columbid (blue hill pigeon, rock dove, stock dove, European turtle dove); Coraciiformes: coraciid (European roller); Falconiformes: falconid (Lanner falcon); Galliformes: numidid (helmeted guineafowl), phasianid (chicken, turkey, rock partridge); Passeriformes: corvid (hooded crow, western jackdaw, brown-necked raven, fan-tailed raven), hirundinid (cliff swallow, barn swallow, common house martin, Eurasian crag martin), laniid (brown shrike, woodchat shrike), muscicapid (bluethroat, common rock thrush), passerid (house sparrow, Spanish sparrow, tree sparrow, rock sparrow); Strigiformes: strigid (eastern screech owl, little owl); Artiodactyla: bovid (harnessed bushbuck); Perissodactyla: equid (horse); Eulipotyphla: erinaceid (long-eared hedgehog); Rodentia: cricetid (hamster), murid (great gerbil); Chiroptera: vespertilionid (Asian long-tailed bat); Carnivora: felid (cat); Primates: hominid (human)	irritation, anaemia, toxicosis (vector for borreliosis, fowl spirochaetosis, aegyptianellosis, West Nile virus, Chenuda virus, Quaranfil virus)	Europe, Asia, Africa
A. (*Persicargas*) *ricei*	Accipitriformes: cathartid (black vulture, turkey vulture, roosts)		North America

A. (*Persicargas*) *robertsi*	Anseriformes: anatid (lesser whistling teal, ruddy shelduck, Eurasian teal, garganey); Ciconiiformes: ciconiid (stork, Asian openbill); Cuculiformes: cuculid (Asian koel); Galliformes: phasianid (chicken); Passeriformes: corvid (jungle crow), sturnid (pied myna, Javan myna, black-collared myna); Pelecaniformes: ardeid (cattle egret, great egret, little egret, intermediate egret, grey heron, pied heron, black-crowned night heron, African heron, Javan pond heron), pelecanid (grey pelican), threskiornithid (Oriental white ibis, Australian white ibis, glossy ibis); Psittaciformes: cacatuid (galah); Siluriformes: anhingid (Oriental darter), phalacrocoracid (great cormorant, pygmy cormorant, little black cormorant, little pied cormorant, little cormorant); Strigiformes: strigid (Indian scops owl, spotted owlet)		Australia
A. sanchezi	Columbiformes: columbid (mourning dove, turtle dove); Galliformes: phasianid (chicken, turkey)		North America
A. (*Carios*) *sinensis*	Chiroptera: vespertilionid (Japanese house bat)		China
A. (*Carios*) *sonenshinei*	Chiroptera: vespertilionid (Dormer's bat)		India
A. (*Persicargas*) *streptopelia*	Columbiformes: columbid (European turtle dove)		Cyprus
A. striatus	Passeriformes: ploceid (sociable weaver, nest)		Africa
A. (*Persicargas*) *theilerae*	Accipitriformes: accipitrid (white-backed vulture, nest)		Africa
A. (*Secretargas*) *transgariepinus* (syn. *A. kochi*)	Chiroptera: rhinolophid (greater horseshoe bat), rhinopomatid (Egyptian mouse-tailed bat, lesser mouse-tailed bat), vespertilionid (serotine bat, meridional serotine, Savi's pipistrelle, Nathusius's pipistrelle, grey long-eared bat, desert long-eared bat, Christie's long-eared bat, greater mouse-eared bat, whiskered bat, Geoffroy's bat); Primates: hominid (human)	(possible vector for rickettsioses)	Mediterranean
A. transverse	host unknown, collected from vegetation		Galapagos Islands
A. (*Argas*) *tridentatus*	Passeriformes: passerid (house sparrow)		Europe
A. (Carios) vespertilionis (short-legged bat tick)	Chiroptera: emballonurid (naked-rumped tomb bat, Egyptian tomb bat, yellow-bellied sheath-tailed bat, Pel's pouched bat), hipposiderid (trident bat, great roundleaf bat), miniopterid (common bent-wing bat, pale bent-wing bat), molossid (European free-tailed bat, Egyptian free-tailed bat, eastern free-tailed bat), noctilionid (lesser bulldog bat); nycterid (Egyptian slit-faced bat), rhinolophid (greater horseshoe bat, lesser horseshoe bat, Blasius's horseshoe bat, Geoffroy's horseshoe bat, Mehely's horseshoe bat, Mediterranean horseshoe bat), rhinopomatid (lesser mouse-tailed bat, greater mouse-tailed bat, Egyptian mouse-tailed bat), pteropodid (Egyptian fruit bat), vespertilionid (western barbastelle, serotine bat, meridional serotine, banana serotine, Cape serotine, northern bat, common pipistrelle, Alashanian pipistrelle, Savi's pipistrelle, Kuhl's pipistrelle, Madeira pipistrelle, Nathusius's pipistrelle, Soprano pipistrelle, lesser Papuan pipistrelle, Japanese house bat, Moloney's mimic bat, Alcathoe bat, Bechstein's bat, Brandt's bat, Daubenton's bat, Geoffroy's bat, Gould's wattled bat, Natterer's bat, lesser mouse-eared bat, greater mouse-eared bat, pond bat, northern bat, whiskered bat, greater noctule bat, lesser noctule, common noctule, desert long-eared bat, brown long-eared bat, grey long-eared bat, Christie's long-eared bat, Gaisler's long-eared bat, Ruppell's broad-nosed bat, parti-coloured bat); Carnivora: canid (dog); Primates: hominid (human); Galliformes: phasianid (chicken); Piciformes: picid (European green woodpecker); Procellariiformes: procellariid (Yelkouan shearwater)	pruritus (possible vector for rickettsioses, ehrlichiosis, borreliosis, babesiosis, bat nairoviruses and flaviviruses)	Middle-East

A. victoriensis	Galliformes: phasianid (chicken)		Australia
A. vulgaris (syn. *A. delicatus*)	Accipitriformes: accipitrid (long-legged buzzard, Egyptian vulture); Anseriformes: anatid (ruddy shelduck); Columbiformes: columbid (rock dove, pigeon); Coraciiformes: coraciid (European roller); Galliformes: phasianid (chukar partridge); Passeriformes: corvid (rook, western jackdaw), hirundinid (barn swallow), muscicapid (Finsch's wheatear), passerid (house sparrow, rock sparrow), sturnid (common starling); Strigiformes: strigid (little owl); Primates: hominid (human)		Europe
A. (*Persicargas*) *walkerae* (chicken tick, fowl tampan)	Galliformes: phasianid (chicken, turkey); Struthioniformes: struthionid (ostrich)	irritation, anaemia, paralysis (vector for borreliosis, aegyptianellosis)	Africa
A. (*Chiropterargas*) *wilsoni*	Chiroptera: rhinopomatid (greater mouse-tailed bat)		India
A. (*Persicargas*) *zumpti*	Accipitriformes: accipitrid (Cape vulture)		Africa

Parasite morphology: Argasid ticks form 4 different types of morphological stages during their developmental cycles: namely, eggs; larvae (one instar); nymphs (2-7 instars); and adults (male and female). The eggs are spherical to oval in shape measuring around 0.5 mm long and are usually clustered together in large masses. They are initially light orange in colour but gradually turn grey just before hatching. Larvae have dorsoventrally-flattened ovate bodies measuring around 0.75 mm in length. They are covered by a leathery tan cuticle with irregular dark markings and characteristically have 6 long thin legs. Larvae lack stigmata and tracheae as respiration and water loss occurs direct through the tegument. Nymphs also have dorsoventrally-flattened ovate bodies but they characteristically have 8 long thin legs. They develop through several (2-7) nymphal instars growing in size up to 4 mm in length. Most stages are brown, orange or black in colour and have irregular dark markings. Nymphs possess a pair of respiratory openings (stigmata) usually surrounded by a circular-oval plate. Adult ticks have oval bodies 4-15 mm long when viewed dorsally. They are covered by unsclerotized leathery cuticles with wrinkled roughened surfaces due to the presence of fine irregular folds with numerous tiny button-like protuberances with central pit (in contrast, ixodid ticks have sclerotized dorsal plates). The dorsal and ventral surfaces meet to form a distinct lateral margin or suture composed of irregular quadrangular plates or cells (not present in *Ornithodorus*). Unfed ticks have dorsoventrally-flattened discoid bodies, whereas engorged ticks become swollen and rounded. The body is usually yellow-brown in colour in unfed ticks, but turns reddish-brown or slaty blue after bloodmeals. All ticks have 2 main parts, the head (capitulum) and the body (idiosoma). In argasids, the capitulum is hidden in a ventral depression (camerostome) underneath the anterior idiosoma and is not visible in dorsal view, whereas the capitulum in ixodid ticks projects forwards and is visible dorsally. It also lacks porose areas which are present on the dorsal surfaces of ixodid females. The capitulum comprises the basis capitulum (integumental ring encircling mouthparts) and the gnathosoma (feeding structure comprising 2 palps, 2 chelicerae and toothed hypostome). The mouthparts are adapted for piercing skin and sucking blood, and are small relative to the size of the body. The palps are sensory structures that move laterally and do not enter skin when feeding (ticks lack antennae). Each palp has 4 segments of equal length (unlike ixodids where they are not equal), although the last segment may appear slightly smaller as it is located in a recess in segment 3 and fitted with small setae. The chelicerae are specialized appendages used for cutting the skin of the host enabling soft ticks to reach down to dermal capillaries. They have 2 segments and are tubular with long curved shafts in spinose sheaths, ending in 2 cutting digits with recurved teeth/denticles. The chelicerae have a horizontal cutting action, ripping and tearing flesh to form a small pool of blood. The hypostome is then inserted into the blood pool to facilitate feeding as well as anchoring the tick to the host. The hypostome is an extension of the basis capitulum and is dentate (with retrograde denticles) and may be notched apically (e.g. *A. persicus*) or not (e.g. *A. reflexus*). The alimentary tract consists of a tubular buccal canal (formed dorsally by the chelicerae and ventrally by the hypostome), paired salivary glands (like clusters of grapes), muscular sucking pharynx (with pharyngeal valve), short tubular oesophagus, large saccular midgut (sometimes called stomach or ventriculus) with several pairs of looped or branched diverticula (caeca) with excretory elements (Malpighian tubules and coxal glands), then a short tube to the vesicular rectal sac (replacing the hindgut in ticks) and subterminal ventral anus. The idiosoma lacks hard sclerotized plates (only present on ixodids) and consists of an anterior podosoma (with legs and genital pore) and a posterior opisthosoma (area behind coxae bearing spiracles and anus). Argasids have small respiratory spiracular plates (stigmata) located between coxae III and IV (whereas ixodids have large spiracular plates behind coxae IV). The podosoma bears 8 long slender legs, each with 6 segments (coxae, trochanter, femur, patella (genu), tibia, and tarsus) and all ending in a pair of claws without pad-like pulvilli (present in ixodids). The coxae lack spur-like projections (present in ixodids) and the dorsal tarsus I has a unique sensory apparatus (Haller's organ) with an anterior pit and posterior capsule (used for odour, temperature, light and mechanical sensation). Argasids generally show limited sexual dimorphism, although females are able to engorge to several times the size of males and they have wider genital apertures. Females have a single saccular ovary (grape-like when gravid) with paired tubular oviducts (with distal ampulla) leading to a common uterus (with associated accessory glands) opening to the vagina (with cervical and vestibular regions). The cervical region acts as a receptaculum seminis and the vestibular vagina actively prolapses during oviposition. The genital aperture consists of a transverse slit (wider than long) surrounded by a prominent fold and connected to special Gene's organs which produce waxy egg coatings during oviposition. Males have 2 testes connected by tubular vas efferentia to a common vas deferens with a large

multilobed accessory gland leading to the ejaculatory duct. The genital aperture is circular to crescent-shaped without an apron and without external genitalia. Males produce spermatophores (packets of spermatids) which are grasped by his chelicerae and placed under the genital operculum of females.

Site of infection: Larvae, nymphs and adult argasid ticks are temporary ectoparasites of birds and mammals. Over 70 *Argas* spp. have been described from birds belonging to 17 passeriform and 34 non-passeriform families (including terrestrial and water birds, fowl and birds of prey), mammals belonging to 29 families (rodents, bats, carnivores, ungulates and humans), 4 lizard families and one toad family. While many species appear to have preferred feeding sites, such as on the breast or under the wings of birds, they generally feed opportunistically and rapidly before dropping off into the surrounding environment (particularly nests, burrows, caves and other resting sites). Argasids may bite humans on exposed areas such as legs and arms.

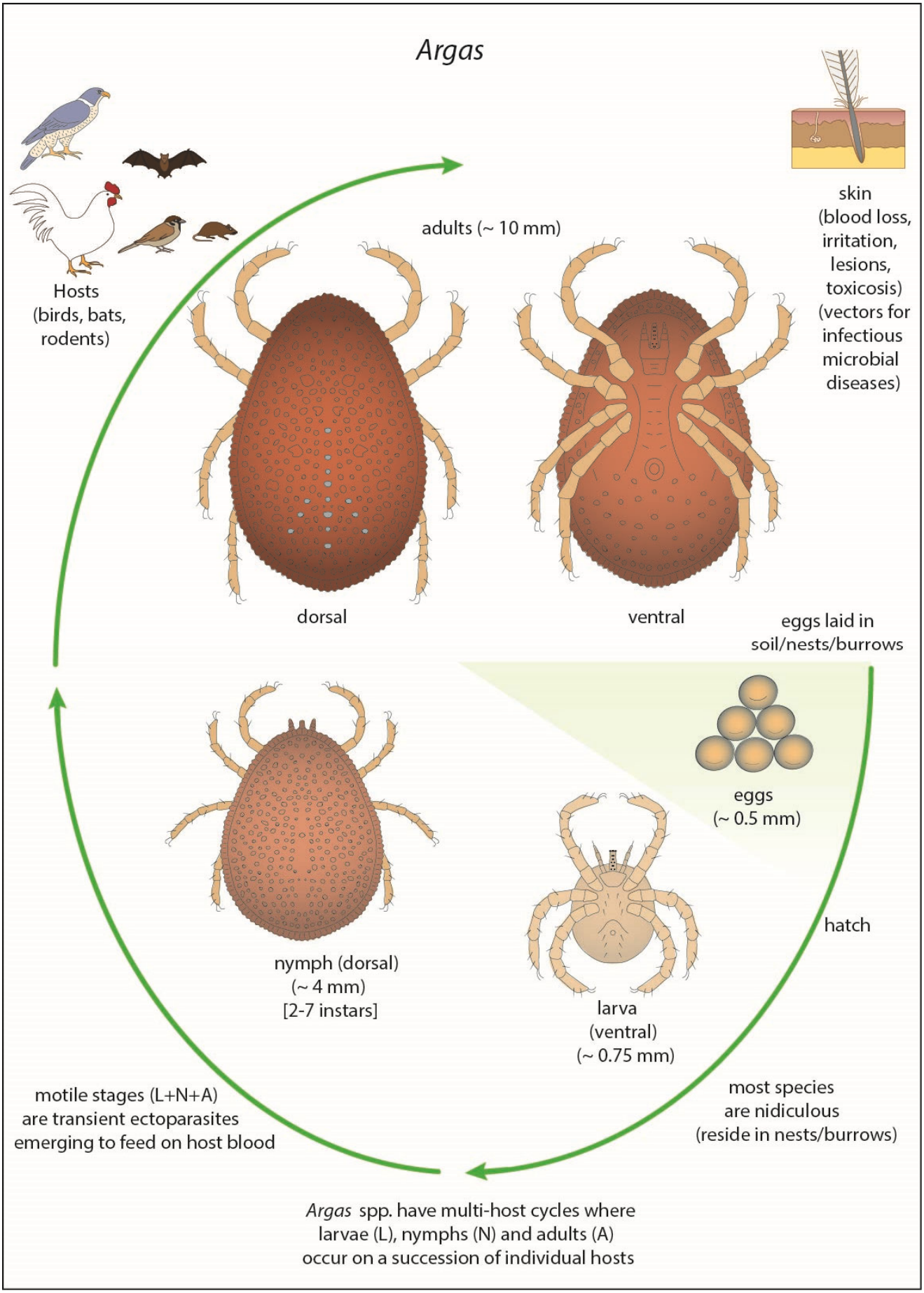
Pathogenesis: All motile stages of *Argas* spp. are haematophagous parasites which use their chelicerae to cut into host skin forming blood pools into which they insert their hypostomes to suck blood (feeding process known as telmophagy). Larvae, nymphs and adult ticks do not attach firmly to the host like ixodid ticks do, but rather feed quickly (usually < one hour) and then detach to drop off the host (although the larvae of some species may stay on hosts for longer periods). Many argasid bites are painless and go unnoticed as the ticks inject saliva containing analgesic properties as well as cytolytic, anticoagulant, vasodilatory and vascular permeability activities. During feeding, the ticks may regurgitate excess fluids back into the host, and argasids have special secretory coxal glands that aid in fluid regulation. Bite sites often become irritated and inflamed with pruritus (itching), oedema (fluid build-up), and erythema (redness of skin). Small granulomas may develop at feeding sites as they become infiltrated by host inflammatory cells (esp. eosinophils) and surrounded by fibrotic reactions. Heavy infestations may cause restlessness and unthriftiness with weakness, reduced weight gain (sometimes emaciation), reduced egg production, and anaemia, sometimes severe enough as to prove fatal. Lesions may be more severe in some individual hosts which exhibit hypersensitivity reactions to tick saliva, and heavy infestations (particularly by larvae) have been associated with toxicosis and partial paralysis in domestic fowl. Argasid ticks biting humans have been associated with a range of vague symptoms, including headaches, dizziness, sweating, chills, and anaphylaxis. Because the feeding stages constantly move on and off hosts, they are efficient vectors for the transmission of various infectious diseases; particularly bacterial causing avian spirochaetosis (*Borrelia anserina*) and anaplasmosis (*Aegyptianella pullorum*). Molecular screening studies have also detected numerous other micro-organisms with unproven pathogenicity in ticks from wild and domestic birds: including bacteria in the genera *Anaplasma*, *Bartonella*, *Borrelia*, *Coxiella*, *Ehrlichia*, *Francisella*, *Rickettsia* and *Rickettsiella*; viruses belonging to the families Flaviviridae, Orthomyxoviridae, Orthonairoviridae, Phenuiviridae and Reoviridae; and the haemoprotozoan genera *Babesia* and *Hemolivia.*

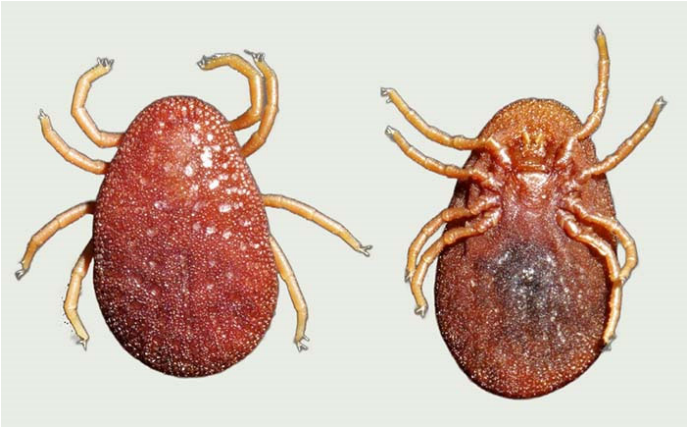
Developmental cycle and mode of transmission: Like all ticks, *Argas* spp. exhibit incomplete (hemimetabolous) metamorphosis whereby eggs hatch larvae which moult through several nymphal stages before forming adults. They have multi-host life-cycles as each developmental stage is a temporary ectoparasite feeding on the blood of a succession of hosts. They do not attach permanently but drop off after each bloodmeal and rest in the surrounding environment. Most species are nidicolous and occur in nests, dens, burrows or host resting areas. The ticks can survive for long periods without feeding (weeks or months), even under harsh dry conditions. They have long life-spans and can persist within seasonal breeding areas from year to year, but are able to complete multiple generations each year when conditions are favourable and when suitable hosts are readily available (as occurs with domestic poultry). Gravid female ticks lay eggs off their hosts in nests and burrows where they hatch in several days releasing 6-legged larvae. The larvae can survive for months without feeding but they must eventually locate a host to feed on blood in order to develop further (in contrast, *Ornithodorus* larvae do not feed; whereas adult *Otobius* do not feed). Of all the *Argas* developmental stages, larvae stay on hosts the longest feeding over several (4-10) days. When replete, the larvae drop off the hosts into the surrounding environment where they moult into first-stage 8-legged nymphs over several days. The nymphs can also survive for many weeks without feeding but they also require bloodmeals in order to develop further. Nymphs feed rapidly (within an hour) and then drop off their hosts and moult into second-stage nymphs. Argasid species form multiple nymphal instars, ranging from 2 up to 7 (whereas ixodid ticks only form one). All instars feed rapidly on hosts and then drop off to moult in the nest/burrow. The final nymphal instars moult to form adult ticks (male or female) which are usually nocturnal feeders, emerging from cracks and crevices in nests or burrows to feed on resting or sleeping hosts before returning to their shelters to avoid daylight desiccation. Adults have been shown to travel long distances (kilometres) searching for hosts and they can survive without feeding for long periods (up to 2 years) by entering diapause. Ticks feed periodically on hosts and become sexually mature, although mating and egg laying occurs off hosts in sheltered environments. Argasids may mate multiple times (whereas ixodid ticks mate only once) and females usually lay batches of 25-200 eggs after bloodmeals. Females may lay up to several thousand eggs during her lifetime. The entire life-cycle (egg-to-egg) may be completed in as little as 30 days but more often takes 100-130 days in warm humid conditions, so ticks may rapidly become abundant, particularly in intensive poultry facilities. Infestations in wild animals, however, often appear seasonally as ticks are able to survive in breeding sites that are frequented only annually by hosts. Argasids are more common in dry conditions, including deserts, especially when hosts construct nests or burrows with copious shelters.

Differential diagnosis: While infestations may be suspected on the basis of clinical grounds (skin lesions, anaemia, unthriftiness), other ectoparasites or disease processes may cause similar symptoms/signs. Infestations are usually detected by the direct

observation of tick developmental stages (larvae, nymphs and/or adults) feeding on hosts, although most stages feed nocturnally and transiently. Examination of host resting sites (nests, roosts and burrows) may reveal marked contamination by tick scat (black faecal deposits) and tick stages may be found amongst nesting/bedding materials. Diagnoses are best confirmed by the microscopic examination and identification of captured specimens by their morphological characteristics. Molecular biological techniques have been used to characterize species and infer phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear (18S and 28S ribosomal RNA, internal transcribed spacer regions 1 and 2) and mitochondrial (12S and 16S ribosomal RNA, cytochrome c oxidase subunit I) gene sequences.

Treatment and control: Infestations by individual ticks may be countered by physical removal of the tick using fine surgical instruments (forceps, tweezers, needles) or a range of specially-designed plastic devices (tick keys, lassos, tweezers, twists or V-shaped tools). Care should be taken not to crush or squeeze the ticks (which can force salivary and gut contents into wounds) and gentle pressure should be applied so as to not rip out their mouthparts (leaving them embedded can exacerbate lesions). While many folklore remedies suggest that different oily, stringent or volatile chemicals applied to the backs of attached ticks may help in their removal (including mineral oil, eucalyptus oil, peppermint oil, soap, rubbing alcohol, nail polish, chloroform, vinegar, lemon juice, baking soda, vaseline, petroleum jelly, heated probes or hot extinguished matches), such treatment may also cause them to regurgitate or secrete material back into the hosts. A wide range of acaricides have been developed for the treatment of tick infestations in livestock, available as ointments, emulsions, powders, dusts, dips, sprays, showers, footbaths, drenches, injections, or as pour-on or spot-on applications. A range of self-treatment devices have also been developed to treat wildlife or extensively-farmed animals, including medicated nesting materials, bait boxes, rubbing posts or rollers, and supplementary feed bins. Many early preparations required multiple applications as they exhibited limited penetration into host plumage or pelage or had poor efficacy against some developmental stages. However, more modern formulations have longer-lasting residual activity and are available in slow-release formulations or as systemic applications. Successful treatments have been reported using arsenical preparations, kerosene emulsions, organochlorines (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (dioxathion, fenchlorphos), organophosphonates (chlorfenvinphos, dichlorvos, tetrachlorvinphos, trichlorfon), monothiophosphates (chlorpyrifos, coumaphos, cythioate, diazinon, fenthion, propetamphos), dithiophosphates (malathion, phosmet), carbamates (carbaryl), pyrethroids (permethrin, flumethrin, deltamethrin, decamethrin, cypermethrin, cyprothrin), formamidines (amitraz), macrocyclic lactones (ivermectin, selamectin), phenylpyrazole (fipronil), chloronicotinyl (imidacloprid), isoxazolines (afoxolaner, fluralaner), natural products (rotenone) and some insect growth regulators or chitin synthesis inhibitors (methoprene, pyriproxyfen). Some acaricide resistance has been found in tick populations against arsenic compounds, some organochlorines and organophosphates, pyrethroids and formamidines. It is recommended that acaricides be used strategically during peak seasons as well as intermittently or in rotation to avoid the further development of drug resistance. Treatment protocols are also best used in integrated tick management strategies, involving environmental management (spraying sheds with residual acaricides, removing litter, clearing vegetation), livestock management (avoid overstocking, grazing management with pasture/pen rotation/spelling), regular health surveillance (screening, culling, quarantine), vermin control (using barriers, traps, baits) and wildlife management (by fencing, hunting, trapping or diverting migration routes).


Argas
Hosts
(birds, bats,
rodents)
skin
(blood loss,
irritation,
lesions,
toxicosis)
(vectors for
infectious
microbial
diseases)
adults (~ 10 mm)
dorsal
ventral
eggs laid in
soil/nests/burrows
eggs
(~ 0.5 mm)
hatch
larva
(ventral)
(~ 0.75 mm)
nymph (dorsal)
(~ 4 mm)
[2-7 instars]
most species
are nidiculous
(reside in nests/burrows)
motile stages (L+N+A)
are transient ectoparasites
emerging to feed on host blood
Argas spp. have multi-host cycles where
larvae (L), nymphs (N) and adults (A)
occur on a succession of individual hosts



Argas adults



Argas adult female and eggs



Argas larva



Argas nymphs

Ornithodorus
(arachnid: tick)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ticks have respiratory stigmata posterior to their legs. They are obligate blood-feeding ectoparasites on vertebrate hosts and their hypostomes are toothed and exposed. Two families are recognized: Argasidae and Ixodidae, known as soft and hard ticks, respectively. Argasids have soft leathery bodies lacking a dorsal scutum and the capitulum is covered by the body. They are transient feeders on mammals and birds and have multi-host life-cycles, spending the majority of time hiding in cracks/crevices in the surrounding environment, especially nests and dens. Infestations by sand tampans (*Ornithodorus* spp.) occur on a wide range of mammalian hosts; some species causing allergy, toxicosis and paralysis as well as transmitting viral, bacterial and protozoal diseases.

Classification:
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on capitulum)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Ixodida (Metastigmata) (ticks, macroscopic, stigmata posterior to legs, hypostome toothed, ectoparasites)
Family: Argasidae (soft ticks, lack dorsal scutum, capitulum covered by body, hide in cracks/crevices)
Genus: *Ornithodorus* (parasitic on skin of mammals)
Species: various species cause anaemia and toxicosis in mammals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial

Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on capitulum) [34 superfamilies]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs (behind coxae III or IV); and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Ticks are further characterized by macroscopic bodies with an exposed ventral hypostome (toothed with backwardly-directed barbs), chelicerae with only 2 joints, long legs with free articulated coxae (not fused to the body wall) and tarsi I each bearing a complex sensory pit (Haller's organ). They are obligate blood-sucking parasites which feed on terrestrial vertebrates (mammals, birds, reptiles and some amphibians) as larvae, nymphs and adults with 1-, 2- or 3-host life-cycles. Almost 1,000 tick species have been classified within some 20 genera from numerous wild and domesticated animals around the world. Two main families are recognized: the Argasidae containing ~200 species of 'soft' ticks with flexible leathery cuticles, ventral capitula, short feeding times (< 1 hour) and long life-spans (up to 20 years); and the Ixodidae containing ~800 species of 'hard' ticks with rigid dorsal scutal plates, anterior capitula, long feeding times (hours to days) and shorter life-span (2-6 years). Basic characteristics of representative genera considered in this resource are tabulated below.

Genus	**Capitulum**				**Idiosoma**				**Usual no. of hosts**
	location	**basis capitulum**	**mouth-parts**	**palps**	**integument**	**festoons**	**eyes**	**male ventral plates**	

Argasidae (soft ticks with leathery cuticle, stigmata between coxae III)									
Argas	ventral	triangular	short	leg-like	stippled with lateral suture	absent	absent	absent	>3
Ornithodorus	ventral	rectangular	short	leg-like	mamillated	absent	usually absent	absent	>3
Otobius	ventral	rectangular	short	leg-like	spinose (nymphs), granulated (adult)	absent	absent	absent	1
Ixodidae (hard ticks with sclerotized dorsal plate (scutum), stigmata behind coxae IV)									
Prostriata (anal groove anterior)									
Ixodes	anterior	triangular	long	long	inornate	absent	absent	present	3
Metastriata (anal groove posterior)									
Amblyomma	anterior	rectangular	long	long	ornate	present	present	indistinct	3
(*Aponomma*)	anterior	rectangular	long	long	often ornate	present	absent	absent	3
Rhipicephalus	anterior	hexagonal	short	medium	some ornate	present	present	present	3
(*Boophilus*)	anterior	hexagonal	short	short	inornate	absent	present	present	1
Dermacentor	anterior	rectangular	short	medium	often ornate	present	present	absent	3
Haemaphysalis	anterior	rectangular	short	short	inornate	present	absent	absent	3
Hyalomma	anterior	rectangular	long	long	inornate	present	present	present	2
Bothriocroton	anterior	pentagonal	long	long	ornate	present	absent	absent	3

The family Argasidae contains 5 subfamilies (Antricolinae, Argasinae, Nothoaspisinae, Ornithodorinae, Otobinae) which vary in morphology, biology, host range and specificity. Members of the subfamily Ornithodorinae have flat discoid bodies with a roughened mamillated integument but lacking distinct lateral margins. Two genera (*Alectorobius* and *Ornithodorus*) have been described as haematophagous ectoparasites on mammalian and avian hosts around the world. Members of the genus *Ornithodorus* (syn. *Ornithodoros*) are often nidicolous with 2 nymphal stages and adult ticks feeding on animals inhabiting nests, roosts, burrows and dens (larval stages develop within eggs and do not feed). Around 120 *Ornithodorus* spp. have been described from domestic and wild animals, sometimes in association with skin lesions and blood loss. Several species have been allocated to 7 subgenera (*O.* (*Alectorobius*), *O.* (*Alveonasus*), *O.* (*Ornithodorus*), *O.* (*Pavlovskyella*), *O.* (*Proknekalia*), *O.* (*Reticulinasus),* and *O.* (*Subparmatus*)), but the majority remain unplaced. In the few species whose life-cycles are known, the ticks appear to have a reasonably broad host specificity with nymphs and adults feeding intermittently on a small range of sympatric host species, often those sharing sandy habitats (hence the common name for many species as 'sand tampans'). Several species have also been shown to be efficient vectors for the transmission of viral and bacterial infectious diseases in livestock, especially relapsing fevers, Q fever and swine fever.

***Ornithodorus* species**	**Hosts**	**Clinical signs**	**Distribution**
O. acinus (syn. *Argas*)	host unknown, collected from caves		Africa
O. (*Pavlovskyella*) *alactagalis*	Carnivora: canid (fox), mustelid (European badger); Eulipotyphla: erinaceid (long-eared hedgehog); Rodentia: cricetid (European hamster, dwarf hamster, water vole), dipodid (small five-toed jerboa), murid (house mouse, jird, fat sand rat); Primates: hominid (human); Galliformes: phasianid (chicken); Sauria (unspecified lizard); Anura: bufonid (European green toad, burrow)	(vector for spirochaetosis, relapsing fever borreliosis)	Europe
O. (*Alectorobius*) *amblus* (syn. *Argas*)	Charadriiformes: larid (Inca tern); Pelecaniformes: pelecanid (Peruvian brown pelican); Sphenisciformes: spheniscid (Humboldt penguin); Suliformes: phalacrocoracid (red-legged cormorant, Guanay cormorant), sulid (Peruvian booby, blue-footed booby); Primates: hominid (human)	inflammation, pruritus	South America
O. anduzei	host unknown, collected from bat cave		South America
O. antiquus	fossil (amber)		Central America
O. apertus	Artiodactyla: suid (warthog, burrows); Rodentia: hystricid (porcupines, burrows)		Africa
O. aquilae	Accipitriformes: accipitrid (golden eagle, ferruginous hawk); Falconiformes: falconid (prairie falcon, American kestrel)		North America
O. arenicolous	Eulipotyphla: erinaceid (long-eared hedgehog); Rodentia: ctenodactylid (common gundi), murid (fat sand rat, Shaw's jird, lesser Egyptian gerbil); Sauria: agamid (Egyptian spiny-tailed lizard), varanid (unspecified monitor lizard)		Egypt
O. (*Pavlovskyella*)	Rodentia: murid (great gerbil, red-tailed gerbil); Carnivora:	(vector for	Central Asia

asperus (syn. *O. verrucosus*)	canid (wolf, jackal, fox), mustelid (badger); Primates: hominid (human); Bucerotiformes: upupid (hoopoe); Coraciiformes: coraciid (roller); Galliformes: phasianid (chicken); Passeriformes: sturnid (starling); Testudines: testudinid (unspecified tortoise); Sauria: agamid (agama); Serpentes: colubrid (grass snake), viperid (blunt-nosed viper)	borreliosis)	
O. atacamensis	Sauria: liolaemid (tree iguana), teiid (dwarf tegu)		South America
O. azteci	Chiroptera: emballonurid (lesser dog-like bat), mystacinid (short-tailed bat), noctilionid (lesser bulldog bat), phyllostomid (Aztec fruit-eating bat, Cuban fruit-eating bat, Jamaican fruit-eating bat, Waterhouse's leaf-nosed bat, Tome's sword-nosed bat, common vampire bat)		Central America
O. batuensis	Chiroptera: hipposiderid (diadem leaf-nosed bat), pteropodid (cave nectar bat, dusky fruit bat, western naked-backed fruit bat, Sulawesi rousette, Geoffroy's rousette, Leschenault's rousette, Lucas's short-nosed fruit bat), vespertilionid (narrow-winged pipistrelle, Temminck's bat)		South-East Asia
O. brasiliensis (mouro tick)	Artiodactyla: tayassuid (collared peccary); Carnivora: canid (dog), mephitid (Molina's hog-nosed skunk); Cingulata: dasypodid (southern long-nosed armadillo); Primates: hominid (human)	irritation, lesions, toxicosis	South America
O. brodyi	Chiroptera: emballonurid (proboscis bat), mormoopid (Parnell's mustached bat), phyllostomid (great fruit-eating bat, Aztec fruit-eating bat, Jamaican fruit-eating bat, big-eared woolly bat, Seba's short-tailed bat, Sowell's short-tailed bat, fringe-lipped bat, common vampire bat), vespertilionid (black myotis)		Central America
O. (*Alveonasus*) *buettikeri*	hosts unknown		Oman
O. (*Alectorobius*) *camicasi*	Chiroptera: pteropodid (Egyptian fruit bat)		Africa
O. (*Alveonasus*) *canestrinii* (syn. *Argas*)	Artiodactyla: bovid (sheep, goat, cattle, gazelle); Rodentia: caviid (guinea pig), murid (great gerbil); Galliformes: phasianid (chukar partridge)		Central Asia
O. (*Alectorobius*) *capensis* (seabird soft tick)	Anseriformes: anatid (duck); Charadriiformes: alcid (ancient murrelet), larid (western gull, silver gull, red-billed gull, black-tailed gull, kelp gull, Hermann's gull, common tern, sooty tern, spectacled tern, roseate tern, white tern, sandwich tern, greater crested tern, royal tern, common noddy, black noddy, brown noddy, blue noddy, lesser noddy), scolopacid (spotted sandpiper, ruddy turnstone); Galliformes: phasianid (chicken); Gruiformes: rallid (spotless crake); Pelecaniformes: pelecanid (brown pelican), threskiornithid (roseate spoonbill); Phaethontiformes: phaethontid (red-tailed tropicbird); Procellariiformes: diomedeid (black-footed albatross, Laysan albatross), hydrobatid (Markham's storm petrel), oceanitid (Polynesian storm petrel), procellariid (black-winged petrel, Bonnin petrel, Bulwer's petrel, Kermadec petrel, Phoenix petrel, little shearwater, streaked shearwater, wedge-tailed shearwater, Christmas shearwater); Strigiformes: strigid (burrowing owl); Suliformes: fregatid (lesser frigatebird, great frigatebird), phalacrocoracid (spotted shag, European shag, Brandt's cormorant), sulid (brown booby, masked booby, red-footed booby, Australasian gannet); Sphenisciformes: spheniscid (little penguin, Jackass penguin, African penguin); Lagomorpha: leporid (rabbit); Primates: hominid (human); Sauria: iguanid (marine iguana); Testudines: cheloniid (green sea turtle)	irritation (vector for Soldado virus, possibly West Nile virus, rickettsioses, Q fever)	Australia
O. (*Alectorobius*) *casebeeri*	Rodentia: cricetid (big-eared climbing rat, Stirton's deer mouse)		Central America
O. carvernicolous	Chiroptera: phyllostomid (pale spear-nosed bat, fringe-lipped bat, greater round-eared bat, Pallas's long-tongued bat, Seba's short-tailed bat, Geoffroy's tailless bat, flat-faced fruit-eating		South America

	bat)		
O. cerradoensis	Rodentia: caviid (Brazilian guinea pig), echimyid (punare)		South America
O. (*Alectorobius*) *cheikhi*	Charadriiformes: larid (tern nesting sites)		North Africa
O. (*Alectorobius*) *chironectes*	Didelphimorphia: didelphid (water opossum); Rodentia: cricetid (hispid cotton rat)		Central America
O. (*Reticulinasus*) *chiropterphila*	Chiroptera: rhinolophid (rufous horseshoe bat)		India
O. cholodkovskyi	Chiroptera: rhinolophid (greater horseshoe bat); Rodentia: murid (unspecified rodent burrows)		Central Asia
O. (*Alectorobius*) *clarki*	Chiroptera: mormoopid (big naked-backed bat, Davy's naked-backed bat)		Central America
O. (*Alectorobius*) *collocaliae*	Apodiformes: apodid (cave swiftlet)		Indonesia
O. compactus	Testudines: testudinid (leopard tortoise, geometric tortoise, angulate tortoise, serrated tortoise, tent tortoise, Greek tortoise, great padloper, speckled padloper)		Africa
O. concanensis	Chiroptera: molossid (Mexican free-tailed bat), vespertilionid (big brown bat, tricolored bat, cave myotis, Townsend's big-eared bat); Accipitriformes: accipitrid (golden eagle, red-tailed hawk); Falconiformes: falconid (prairie falcon); Passeriformes: hirundinid (cave swallow, cliff swallow)		North America
O. (*Alectorobius*) *coniceps*	Anseriformes: anatid (ruddy shelduck, common scoter); Apodiformes: apodid (house swift); Charadriiformes: larid (Pallas's gull, common tern, sandwich tern, roseate tern); Columbiformes: columbid (domestic pigeon, wood pigeon, African rock pigeon, rock dove); Galliformes: phasianid (chicken); Passeriformes: hirundinid (swallow, crag martin), passerid (house sparrow, rock sparrow); Pelecaniformes: pelecanid (Dalmatian pelican); Suliformes: phalacrocoracid (great cormorant); Artiodactyla: bovid (sheep); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig), murid (mouse); Chiroptera: vespertilionid (Kuhl's pipistrelle); Primates: hominid (human)	irritation (vector for avian spirochaetosis, Baku virus, possibly West Nile virus)	Mediterranean
O. coprophilus (now *Antricola*)	Chiroptera: phyllostomid (Waterhouse's leaf-nosed bat) plus several collections from bat guano		North America
O. (Ornamentum) coriaceus (pajaroello tick)	Artiodactyla: bovid (cattle, sheep), cervid (white-tailed deer, black-tailed deer, mule deer); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Rodentia: cricetid (deermouse), murid (mouse, rat), sciurid (squirrel, chipmunk); Primates: (unspecified monkey), hominid (human); Galliformes: phasianid (chicken); Passeriformes: hirundinid (cliff swallow)	painful bite, irritation [plus vector for African swine fever, epizootic bovine abortion)]	Americas
O. cyclurae	Sauria: iguanid (Cuban rock iguana)		Cuba
O. darwini	Sauria: iguanid (marine iguana, Galapagos land iguana)		Galapagos Islands
O. davisi	Rodentia: cricetid (yellowish rice rat)		South America
O. (*Alveonasus*) *delanoei* (syn. *Argas*)	Rodentia: caviid (guinea pig), hystricid (crested porcupine); Eulipotyphla: erinaceid (long-eared hedgehog)		Central Asia
O. (Alectorobius) denmarki	Charadriiformes: larid (common noddy, brown noddy, black tern, sooty tern, unspecified gull nests); Suliformes: sulid (brown booby)		North America
O. dugesi	Rodentia: cricetid (white-throated woodrat, nest); Artiodactyla: suid (pig); Chiroptera (unspecified bat); Primates: hominid (human)	(vector for African swine fever)	Americas
O. dunni	Chiroptera: noctilionid (lesser bulldog bat); Rodentia: caviid (guinea pig), murid (white rat)		Central America
O. dusbabeki	Chiroptera: molossid (velvety free-tailed bat, black mastiff bat, Pallas's mastiff bat), noctilionid (greater bulldog bat), phyllostomid (Jamaican fruit bat), vespertilionid (big brown bat)		Cuba
O. (Alectorobius)	Chiroptera: emballonurid (gray sac-winged bat, lesser dog-		Americas

dyeri	like bat), mormoopid (Parnell's moustached bat), phyllostomid (fringe-lipped bat, lesser long-nosed bat, Waterhouse's leaf-nosed bat, California leaf-nosed bat, Cozumelan golden bat), vespertilionid (fish-eating bat)		
O. eboris (syn. *Argas*)	Rodentia: hystricid (porcupine, burrow)		Africa
O. echimys	Rodentia: echimyid (speckled spiny tree-rat)		South America
O. (Alectorobius) elongatus	host unknown, recovered from crate		Central America
O. eptesicus	Chiroptera: vespertilionid (Argentine brown bat)		South America
O. eremicus	Rodentia: cricetid (deer mouse)		North America
O. (*Pavlovskyella*) *erraticus* (species complex incl. *O. costalis, kairouanensis, marocanus, merionesi, normandi, occidentalis, rupestris, sonrai, Argas erraticus*) (European soft tick, sand tampan)	Artiodactyla: bovid (cattle, sheep, goat), suid (pig, boar); Carnivora: canid (Egyptian red fox); Eulipotyphla: erinaceid (long-eared hedgehog), soricid (African giant shrew); Rodentia: cricetid (golden hamster), hystricid (crested porcupine), murid (house mouse, common spiny mouse, fat sand rat, African grass rat, black rat, pleasant gerbil, pygmy gerbil, slender gerbil, Cheesman's gerbil, Harwood's gerbil, Sundevall's jird, Shaw's jird), nesomyid (Gambian pouched rat), sciurid (striped ground squirrel, burrow); Chiroptera (unspecified bat); Primates: hominid (human); Sauria: agamid (Egyptian spiny-tail lizard), scincid (common skink), varanid (Nile monitor); Serpentes: viperid (puff adder); Anura: bufonid (western leopard toad, Berber toad, African toad, European green toad); Passeriformes: acrocephalid (tree warbler), muscicapid (unspecified chat); Strigiformes: strigid (burrowing owl, little owl)	irritation (vector for Q fever, borreliosis (tick-borne relapsing fever) and African swine fever)	Europe, Africa, Middle East
O. faccinii	Anura: bufonid (ornate forest toad), cycloramphid (rock river frog)		South America
O. (*Reticulinasus*) *faini*	Chiroptera: pteropodid (Egyptian fruit bat, Leschenault's rousette)		Africa
O. foleyi (syn. *Argas*)	Artiodactyla: bovid (zebu, goat), camelid (dromedary); Primates: hominid (human)		Africa
O. (Alectorobius) fonsecai	Chiroptera: emballonurid (lesser dog-like bat), phyllostomid (Seba's short-tailed bat, fringe-lipped bat, common vampire bat)		South America
O. (Alectorobius) furcosus	Artiodactyla: suid (pig); Rodentia: caviid (guinea pig), murid (rat); Lagomorpha: leporid (rabbit); Primates: hominid (human); Columbiformes: columbid (pigeon)	(possible vector for borreliosis and Mexican spotted fever)	South America
O. galapagensis	Sauria: iguanid (marine iguana), tropidurid (Galapagos lava lizard); Passeriformes: thraupid (small ground finch)		Galapagos Islands
O. graingeri	Chiroptera: megadermatid (vampire bat), nycterid (Egyptian slit-faced bat), rhinolophid (horseshoe bat); Rodentia: hystricid (porcupine); Primates: hominid (human)		Africa
O. (Alectorobius) grenieri	Rodentia: nesomyid (Malagasy giant rat, burrow)		Madagascar
O. guaporensis	host unknown, collected from bat roosts		South America
O. (*Ornamentum*) *gurneyi* (syn. *Argas*) (kangaroo soft tick)	Diprotodontia: macropodid (red kangaroo, eastern grey kangaroo, common wallaroo); Rodentia: murid (rat, mouse); Lagomorpha: leporid (rabbit); Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Carnivora: canid (dog); Primates: hominid (human); Sauria: agamid (bearded dragon), scincid (sleepy lizard)	irritation (vector for Q fever)	Australia
O. (Alectorobius) hadiae	Chiroptera: pteropodid (Geoffroy's rousette, greenish naked-backed fruit bat, lesser short-nosed fruit bat)		Indonesia
O. hasei (syn. *Argas*)	Chiroptera: emballonurid (sac-winged bat), molossid (velvety free-tailed bat, black mastiff bat, dwarf dog-faced bat, Mato Grosso dog-faced bat), mormoopid (ghost-faced bat, Davy's naked-backed bat), noctilionid (lesser bulldog bat, greater bulldog bat), phyllostomid (flat-faced fruit-eating bat, stripe-headed round-eared bat, pygmy round-eared bat, little yellow-shouldered bat, Salvin's big-eyed bat, great fruit-eating bat,		South America

	dwarf little fruit bat, Antillean fruit-eating bat, Jamaican fruit bat, Miller's long-tongued bat, greater spear-nosed bat, Orinoco sword-nosed bat, striped hairy-nosed bat, brown tent-making bat, fringe-lipped bat, common vampire bat), vespertilionid (black myotis, cave myotis, solver-tipped myotis, Thomas's big-eared brown bat, tiny yellow bat); Rodentia: cricetid (northern grass mouse)		
O. hermsi (sand tampan)	Rodentia: cricetid (eastern deer mouse), murid (canyon mouse, bushy-tailed wood rat, desert wood rat), sciurid (western chipmunk, American red squirrel, golden-mantled ground squirrel, tree squirrel); Chiroptera: vespertilionid (mouse-eared bat); Primates: hominid (human); Passeriformes: turdid (bluebird), tyrannid (Say's phoebe); Piciformes: picid (unspecified woodpecker)	irritation (vector for borreliosis (relapsing fever) and African swine fever)	North America
O. (*Ornithodorus*) *huajianensis*	Rodentia: sciurid (Tarbagan marmot)		China
O. (*Ornithodorus*) *indica*	Artiodactyla: cervid (Indian muntjac)		India
O. jerseyi	fossil (amber)		Central America
O. (Alectorobius) jul	host unknown, collected from bat cave		South America
O. (Alectorobius) kelleyi	Chiroptera: molossid (Mexican free-tailed bat), vespertilionid (big brown bat, little brown bat, pallid bat, tricolored bat, canyon bat, eastern small-footed myotis, western small-footed myotis, California myotis, Rafinesque's big-eared bat); Rodentia: caviid (guinea pig), murid (white rat); Primates: hominid (human)		North America
O. (Alectorobius) knoxjonesi	Chiroptera: emballonurid (gray sac-winged bat)		Central America
O. (*Alectorobius*) *kohlsi* (syn. O. *boliviensis*)	Chiroptera: molossid (velvety free-tailed bat, Sinaloan mastiff bat), vespertilionid (black myotis); Primates: hominid (human)		South America
O. lahillei	Sauria: teiid (dwarf tegu); Serpentes: colubrid (Chilean green racer)		South America
O. (*Alectorobius*) *lahorensis* (syn. *Argas*) (sand tampan)	Artiodactyla: bovid (sheep, argali, goat, Afghan urial, cattle), camelid (camel); Perissodactyla: equid (horse, donkey); Rodentia: caviid (guinea pig), murid (mouse); Lagomorpha: leporid (European hare); Carnivora: canid (dog); Primates: hominid (human); Galliformes: phasianid (chicken) (2-host cycle)	irritation, anaemia, toxicosis, paralysis (vector for brucellosis, Q fever, tularemia, anaplasmosis, piroplasmosis, Persian relapsing fever)	Eurasia
O. (*Pavlovskyella*) *macmillani*	Diprotodontia: phalangerid (common brushtail possum); Psittaciformes: cacatuid (galah); Strigiformes: strigid (southern boobook owl, morepork)		Australia
O. (*Reticulinasus*) *madagascariensis*	Chiroptera: pteropodid (cave-inhabiting fruit bats)		Madagascar
O. (*Subparmatus*) *marinkellei*	Chiroptera: mormoopid (big naked-backed bat, Wagner's mustached bat, Parnell's mustached bat)		South America
O. (*Alectorobius*) *maritimus*	Charadriiformes: alcid (common murre, razor-billed auk), larid (common tern, roseate tern, sandwich tern, herring gull, yellow-legged gull, black-legged kittiwake); Pelecaniformes: ardeid (little egret); Suliformes: phalacrocoracid (great cormorant, European shag); Primates: hominid (human)	irritation, weight loss, reduced growth (vector for Soldado virus)	Europe
O. (*Alectorobius*) *marmosae*	Didelphimorphia: didelphid (Robinson's mouse opossum); Rodentia: cricetid (climbing mouse)		South America
O. (Alectorobius) microlophi	Sauria: tropidurid (four-banded Pacific iguana, Atacamen Pacific iguana)		South America
O. mimon	Chiroptera: phyllostomid (striped hairy-nosed bat), vespertilionid (big-eared brown bat, Brazilian brown bat, Argentine brown bat, diminutive serotine); Didelphimorphia: didelphid (white-eared opossum, agile gracile opossum, Paraguayan fat-tailed mouse opossum); Rodentia: cricetid		South America

	(small-footed bristly mouse); Primates: hominid (human); Passeriformes: dendrocolaptid (straight-belled woodcreeper, narrow-billed woodcreeper, buff-throated woodcreeper), thraupid (grey-headed tanager)		
O. montensis	Anura: bufonid (terrestrial toad)		South America
O. (*Subparmatus*) *mormoops*	Chiroptera: mormoopid (leaf-chinned bat), phyllostomid (Waterhouse's leaf-nosed bat)		Central America
O. moubata (syn. *Argas*) (sand tampan, eyeless tampan, hut tampan, African tampan)	Artiodactyla: bovid (cattle, sheep, goat, Lichtenstein's hartebeest, waterbuck), giraffid (giraffe), suid (pig, common warthog, desert warthog); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig), hystricid (Cape porcupine), murid (mouse), nesomyid (Gambian pouched rat); Tubulidentata: orycteropodid (aardvark); Pholidota: manid (ground pangolin); Carnivora: canid (dog), felid (cat, lion); Chiroptera: pteropodid (straw-coloured fruit bat); Primates: cercopithecid (guenon), hominid (human); Galliformes: phasianid (chicken, turkey); Sauria: chamaeleonid (chameleon), gekkonid (tropical house gecko), gerrhosaurid (black-lined plated lizard); Serpentes: viperid (puff adder, rhombic night adder, blunt-nosed viper); Testudines: testudinid (greater padloper, serrated tortoise, tent tortoise)	irritation (vector for borreliosis (African relapsing fever), aegyptianellosis, spirochaetosis, trypanosomes, African swine fever, Q fever)	Africa, Middle East
O. (*Alectorobius*) *muesebecki*	Suliformes: sulid (masked booby); Primates: hominid (human)		Africa
O. (Alectorobius) multisetosus	Chiroptera: pteropodid (bare-backed fruit bat, greenish naked-backed fruit bat)		Indonesia, New Guinea
O. (Alectorobius) natalinus	Chiroptera: natalid (Gervais's funnel-eared bat)		Cuba
O. nicollei	Carnivora: canid (dog, coyote); Rodentia: cricetid (Allen's wood rat, swamp rat), sciurid (squirrel); Primates: hominid (human); Serpentes: viperid (sidewinder, Florida diamond-back rattlesnake)		Mexico
O. normandi	Rodentia: murid (Shaw's jird, rat); Primates: hominid (human)	(vector for borreliosis)	South America
O. octodontus	Rodentia: octodontid (common degu)		South America
O. (Alectorobius) papuensis	Chiroptera: pteropodid (bare-backed fruit bat, greenish naked-backed fruit bat, common tube-nosed fruit bat, cave nectar bat)		Indonesia
O. parkeri (syn. *O. wheeleri*) (sand tampan)	Rodentia: cricetid (deer mouse, southern grasshopper mouse, pack rat, sagebrush vole), heteromyid (chisel-toothed kangaroo rat), mustelid (weasel), sciurid (white-faced prairie dog, marmot, golden-mantled ground squirrel, California ground squirrel, Columbian ground squirrel, Richardson's ground squirrel, least chipmunk); Lagomorpha: leporid (cottontail, black-tailed jackrabbit, hare); Carnivora: canid (kit fox), mustelid (weasel); Primates: hominid (human); Strigiformes: strigid (burrowing owl); Testudines: testudinid (desert tortoise)	irritation, allergic reactions [plus vectors for borreliosis (relapsing fever), Rocky Mountain spotted fever, African swine fever]	Africa, Europe, North America
O. (*Alveonasus*) *peringueyi*	Passeriformes: hirundinid (cliff swallow)		Africa
O. (*Alveonasus*) *peusi*	Passeriformes: hirundinid (red-rumped swallow), sittid (western rock nuthatch)		Africa
O. (Alectorobius) peruvianus	Chiroptera: molossid (velvety free-tailed bat), phyllostomid (long-tongued bat, common vampire bat)		South America
O. (Alectorobius) piriformis	Chiroptera: miniopterid (common bentwing bat), pteropodid (Leschenault's rousette)		India
O. porcinus (syn. *O. moubata porcinus*) (incl. subspp. *avivora, domestica, porcinus*) (eyed tampan)	Artiodactyla: bovid (cattle, zebu), suid (pig, bushpig, warthog); Rodentia: hystricid (porcupine); Tubulidentata: orycteropodid (aardvark); Pholidota: manid (ground pangolin); Carnivora: canid (dog), felid (cat); Primates: hominid (human); Galliformes: phasianid (chicken)	irritation [plus vectors for African swine fever]	Africa, Europe

O. (Alectorobius) procaviae	Hyracoidea: procaviid (rock hyrax)		Middle-East
O. (Alectorobius) pteropteryx	Chiroptera: emballonurid (lesser dog-like bat)		South America
O. puertoricensis	Rodentia: cricetid (swamp rat), echimyid (Guyenne spiny rat), murid (brown rat, black rat); Lagomorpha: leporid (forest cottontail); Carnivora: felid (cat), herpestid (mongoose); Primates: hominid (human): Galliformes: phasianid (chicken); Strigiformes: strigid (burrowing owl)		Central America
O. quilinensis	Rodentia: cricteid (central leaf-eared mouse)		South America
O. (*Reticulinasus*) *rennellensis*	Chiroptera: pteropodid (Solomon's naked-backed fruit bat)		Solomon Islands, New Guinea
O. rietcorreai	Rodentia: caviid (rock cavy)		South America
O. (*Alectorobius*) *rioplatensis*	Carnivora: mephitid (Molina's hog-nosed skunk); Rodentia: caviid (cavy), cricteid (naked-soled conyrat, rice rat); Sauria: liolaemid (James's tree iguana, high mountain lizard), phyllodactylid (Uruguay marked gecko)		South America
O. (*Alectorobius*) *rondoniensis*	Chiroptera (unspecified bat, caves)		South America
O. (*Alectorobius*) *rossi*	Chiroptera: phyllostomid (greater long-nosed bat, California leaf-nosed bat, Waterhouse's leaf-nosed bat, yellow-shouldered bat, long-tongued bat), vespertilionid (big brown bat, canyon bat)		North America
O. rostratus (syn. *O. nattereri*)	Artiodactyla: bovid (cattle, goat), suid (pig), tayassuid (peccary); Rodentia: murid (mouse); Lagomorpha: leporid (rabbit); Carnivora: canid (dog); Primates: hominid (human)	pruritus (vector for rickettsiosis and possibly Q fever)	South America
O. rudis (syn. *O. venezuelensis*) (sand tampan)	Rodentia: dasyproctid (agouti), murid (mouse, rat); Primates: hominid (human); Galliformes: phasianid (chicken) and other unspecified bird nests	irritation (vector for borreliosis (relapsing fever))	Americas
O. salahi	Chiroptera: pteropodid (Egyptian rousette)		Egypt
O. saraivai	Anura: cycloramphid (Boraceia button frog)		South America
O. savignyi (syn. *Argas, A. schinzii, O. morbillosus, pavimentosus*) (sand tampan, eyed tampan)	Artiodactyla: bovid (cattle, buffalo, sheep, goat), camelid (camel), cervid (deer), giraffid (giraffe), suid (pig); Perissodactyla: equid (horse), rhinocerotid (rhinoceros); Carnivora: canid (dog), felid (lion); Primates: cercopithecid (crab-eating macaque), hominid (human); Galliformes: phasianid (chicken, turkey)	irritation, allergic reactions, toxicosis, paralysis (vector for Alkhurma haemorrhagic fever)	Africa, Middle East, India
O. (Alectorobius) sawaii	Procellariiformes: procellariid (streaked shearwater)		Japan
O. (Alectorobius) setosus	Chiroptera: molossid (broad-eared bat), mormoopid (Parnell's mustached bat, Wagner's mustached bat)		Americas
O. (*Reticulinasus*) *solomonis*	Chiroptera: pteropodid (unspecified flying fox, cave)		Solomon Islands
O. (Alectorobius) sparnus (syn. *Otobius*)	Rodentia: cricetid (desert woodrat, bushy-tailed woodrat, eastern deer mouse, canyon mouse, pinyon mouse, northern grasshopper mouse), heteromyid (long-tailed pocket mouse); Artiodactyla: cervid (unspecified deer)		North America
O. (*Alectorobius*) *spheniscus*	Sphenisciformes: spheniscid (Humboldt penguin); Primates: hominid (human)		South America
O. (Alectorobius) stageri	Chiroptera: molossid (Mexican free-tailed bat), vespertilionid (cave myotis, pallid bat); Primates: hominid (human)		Americas
O. steini (syn. *Argas*, *Carios*)	Chiroptera: pteropodid (cave nectar bat, Sulawesi rousette, Geoffroy's rousette, Leschenault's rousette, western naked-backed fruit bat, dusky fruit bat)		Asia
O. tabajara	Rodentia: caviid (rock cavy)		South America
O. (*Alectorobius*) *tadaridae*	Chiroptera: molossid (free-tailed bat)		Cuba
O. (*Alectorobius*) *talaje*	Artiodactyla: bovid (cattle), camelid (llama, guanaco), suid (pig), tayassuid (collared peccary); Perissodactyla: equid	(vector for borreliosis)	Americas

(syn. *Argas, A. coniceps)*	(horse); Rodentia: caviid (Spix's yellow-toothed cavy, rock cavy), cricetid (hispid cotton rat, Brazilian pygmy rice rat, terraced rice rat, Amazon marsh rat, white-throated woodrat, eastern woodrat, Southern Plains woodrat, pack rat, vesper mouse, cane mouse), echimyid (common punare, white-spined Atlantic spiny rat, Ihering's Atlantic spiny rat), heteromyid (Ord's kangaroo rat, desert kangaroo rat, hispid pocket mouse), murid (brown rat, black rat, mouse), nesomyid (Gambian pouched rat), sciurid (California ground squirrel, Mexican ground squirrel, round-tailed ground squirrel); Didelphimorphia: didelphid (southern opossum, white-eared opossum, gray short-tailed opossum); Carnivora: canid (dog), felid (cat); Chiroptera: vespertilionid (tropical big-eared brown bat, brown long-eared bat); Primates: atelid (mantled howler monkey), cebid (Colombian white-faced capuchin, squirrel monkey), cercopithecid (rhesus macaque), hominid (human); Charadriiformes: larid (brown noddy, sooty tern, Pallas's gull); Galliformes: phasianid (chicken); Passeriformes: furnariid (plain thornbird); Pelecaniformes: pelecanid (Dalmatian pelican); Sphenisciformes: spheniscid (little penguin, African penguin); Strigiformes: strigid (burrowing owl); Suliformes: phalacrocoracid (great cormorant), sulid (blue-footed booby); Sauria: lacertid (unspecified lizard); Serpentes: boid (boa, rainbow boa), pythonid (reticulated python)		
O. tartakovskyi	Rodentia: cricetid (hamster, Afghan vole), dipodid (small five-toed jerboa, northern three-toed jerboa, Bobrinski's jerboa, Severtzov's jerboa), hystricid (crested porcupine), murid (great gerbil, red-tailed gerbil, Libyan jird, Persian jird, Tamarisk jird, midday jird, short-tailed bandicoot rat), sciurid (yellow ground squirrel, red-cheeked ground squirrel, long-clawed ground squirrel); Eulipotyphla: erinaceid (long-eared hedgehog); Lagomorpha: ochotonid (Afghan pika); Carnivora: canid (red fox, jackal), mustelid (steppe polecat, marbled polecat, least weasel); Primates: hominid (human); Anseriformes: anatid (common shelduck); Passeriformes: passerid (house sparrow); Strigiformes: strigid (little owl); Testudines: testudinid (Mediterranean tortoise, Russian tortoise, steppe turtle); Anura: bufonid (European green toad); Sauria: agamid (steppe agama), anguid (European glass lizard), gekkonid (frog-eyed gecko), lacertid (reticulate racerunner), varanid (desert monitor); Serpentes: boid (dwarf sand boa), viperid (Halys pit viper)	(vector for borreliosis)	Russia
O. (*Pavlovskyella*) *tholozani* (syn. *O. crassi, p*apillipes, *Argas*) (sand tampan)	Artiodactyla: bovid (cattle, zebu, sheep, goat), camelid (Bactrian camel); Eulipotyphla: erinaceid (hedgehog); Rodentia: caviid (guinea pig), cricetid (golden hamster), hystricid (crested porcupine), murid (fat sand rat, great gerbil, Libyan jird, spiny mouse); Lagomorpha: leporid (rabbit); Carnivora: canid (dog, jackal, fox), mustelid (European badger); Chiroptera: rhinopomatid (mouse-tailed bat); Primates: hominid (human) and unspecified monkey; Columbiformes: columbid (rock pigeon), Galliformes: phasianid (chicken); Sauria: gekkonid (unspecified gecko)	irritation [plus vector for Persian relapsing fever, possibly Q fever, borreliosis, West Nile virus, Karshi virus, Kyasanur forest disease virus]	Africa, Eurasia
O. (*Alectorobius*) *tiptoni*	Chiroptera: noctilionid (greater bulldog bat)		South America
O. transversus	Testudines: testudinid (Galapagos giant tortoise)		Galapagos Islands
O. (*Alectorobius*) *turicata* (syn. *Argas, O. americanus, venezuelensis*) (sand tampan,	Artiodactyla: bovid (cattle, sheep), camelid (llama, guanaco), cervid (deer), suid (pig), tayassuid (collared peccary); Perissodactyla: equid (horse); Eulipotyphla: talpid (mole); Rodentia: cricetid (pack rat, Southern Plains woodrat, northern grasshopper mouse), geomyid (tuza), heteromyid (kangaroo rat), murid (rat), sciurid (Fisher ground squirrel,	irritation, toxicosis, allergies [plus vectors for Q fever, borreliosis (relapsing fever), and African swine	North America

relapsing fever tick)	California ground squirrel, spotted ground squirrel, thirteen-lined ground squirrel, black-tailed prairie dog); Lagomorpha: leporid (rabbit, black-tailed jackrabbit, desert cottontail); Primates: hominid (human); Strigiformes: strigid (burrowing owl); Testudines: testudinid (gopher tortoise, desert tortoise, yellow-marginated tortoise), emydid (western box turtle), Anura: ranid (gopher frog); Serpentes: viperid (unspecified rattlesnake)	fever]	
O. (Alectorobius) tuttlei	Rodentia: dasyproctid (agouti); Perissodactyla: tapirid (South American tapir)		South America
O. (*Proknekalia*) *vansomereni* (syn. *Argas*)	Passeriformes: hirundinid (lesser striped swallow, red-rumped swallow), muscicapid (mocking cliff chat)		Africa
O. viguerasi	Chiroptera: mormoopid (Peter's ghost-faced bat, Davy's naked-backed bat, sooty mustached bat, Parnell's mustached bat), phyllostomid (Cuban fruit-eating bat, Cuban flower bat)		Cuba
O. xerophylus	Rodentia: cricetid (central leaf-eared mouse)		South America
O. yumatensis	Chiroptera: phyllostomid (great fruit-eating bat, Aztec fruit-eating bat, Jamaican fruit bat, Waterhouse's leaf-nosed bat, common vampire bat), vespertilionid (cave myotis, southern myotis, Yuma myotis, tricolored bat, Mexican big-eared bat, Rafinesque's big-eared bat, Townsend's big-eared bat); Primates: hominid (human)		North America
O. (*Alectorobius*) *yunkeri*	Charadriiformes: larid (spectacled tern); Procellariiformes: diomedeid (waved albatross); Sphenisciformes: spheniscid (Galapagos penguin); Suliformes: phalacrocoracid (flightless cormorant), sulid (blue-footed booby); Sauria: iguanid (marine iguana, beach); Carnivora: otariid (Galapagos sea lion, beach)		Galapagos Islands
O. zumpti	Carnivora: herpestid (yellow mongoose); Rodentia murid (four-striped grass mouse, rock rat, Saunder's vlei rat, Indian gerbil)		Africa

Parasite morphology: Sand tampans, *Ornithodorus* spp., form 4 different types of morphological stages during their development: eggs; larvae; nymphs; and adults. Eggs are oval-spherical measuring around 0.5 mm long and are surrounded by a translucent brown-red waxy layer. Larvae have subglobular bodies measuring 0.5-0.9 mm in length and they are covered by a tan-brown smooth cuticle. They have 6 pale tan-coloured legs attached to the anterior half of the body and protruding beyond the lateral margins. They have anterior mouthparts that also project beyond the body margin. Larvae lack respiratory stigmata and tracheae as respiration and water regulation occurs through the tegument. Nymphs have ovate-ellipsoidal dorsoventrally-flattened bodies when unfed, but become swollen and subglobular when engorged. *Ornithodorus* spp. have 4-7 nymphal instars growing up to 3-7 mm long depending on the species. They are usually tan-dark brown in colour and sometimes have dark irregular patterns. The cuticle appears rough in texture due to the presence of numerous small tubercles or mammillae (rounded bumps), sometimes with tiny reticulated folds. Nymphs have a pair of respiratory stigmata often surrounded by circular-oval plates and they typically have 8 long thin tan legs projecting beyond the anterior lateral margins of the body. The heads of early nymphal instars, particularly unfed stages, may be visible in dorsal view, but those of mature and engorged instars are usually located underneath the idiosoma and are not seen dorsally. Adult ticks have sac-like globular bodies that appear partially flattened when unfed but become dorsally convex when engorged. They typically have rounded or pyriform profiles, but the dorsal and ventral surfaces meet without forming a lateral margin or suture (whereas a suture is present in *Argas* spp.). They range in size from 4-15 mm long and are covered by unsclerotized leathery cuticles with wrinkled roughened surfaces due to the presence of numerous small rounded raised areas (mammillae), sometimes with fine irregular folds (in contrast, ixodid ticks have sclerotized dorsal plates). Adults may be grey, tan, orange, dark brown and even light red in colour, many pale species often turning blue to dark red after feeding. Most species are inornate but several species are ornate and have areas with pale reticulated cuticular patterns. All ticks have 2 main tagma, the head (capitulum) and the body (idiosoma). In argasids, the capitulum is hidden in a ventral depression (camerostome) underneath the anterior idiosoma and is not visible in dorsal view (whereas that of ixodid ticks projects forwards and is visible dorsally). It lacks porose areas which are present on the dorsal surfaces of ixodid females. The capitulum consists of the basis capitulum (integumental ring encircling mouthparts) and the gnathosoma (feeding structure comprising 2 palps, 2 chelicerae and toothed hypostome). The mouthparts are small relative to body size but are well adapted for piercing skin and sucking blood. The sensory palps move laterally and do not enter the skin when feeding (ticks lack antennae). Each palp has 4 segments of equal length (unlike ixodids where they are not equal), although the last segment may appear slightly smaller as it is located in a recess in segment 3 and fitted with small setae. The specialized chelicerae are used for cutting the skin of the host enabling soft ticks to reach down to dermal capillaries. The chelicerae have 2 segments and are tubular with long curved shafts in spinose sheaths, ending in 2 cutting digits with recurved teeth. They have a horizontal cutting action, ripping and tearing flesh to form a small pool of blood. The hypostome is

then inserted into the blood pool to facilitate feeding as well as anchoring the tick to the host. The hypostome is an extension of the basis capitulum and is dentate with backward-facing teeth. The alimentary tract consists of an anterior buccal canal (formed dorsally by the chelicerae and ventrally by the hypostome), paired salivary glands (like clusters of grapes), muscular pharynx (with pharyngeal valve), tubular oesophagus, large saccular midgut (stomach or ventriculus) with several pairs of branched diverticula (caeca) with excretory elements (Malpighian tubules and coxal glands) with a short tube leading to the vesicular rectal sac (analogue of hindgut in ticks) and subterminal ventral anus. The idiosoma lacks hard sclerotized plates (only present on ixodids) and consists of an anterior podosoma (with legs and genital pore) and a posterior opisthosoma (area behind coxae bearing spiracles and anus). Argasids have small respiratory spiracular plates (stigmata) located between coxae III and IV (whereas ixodids have large spiracular plates behind coxae IV). Most species lack eyes, but a few species have simple eyes located laterally in supracoxal folds (e.g. *O. savignyi* and *O. coriaceus*). The podosoma bears 8 long slender legs, each with 6 segments (coxae, trochanter, femur, patella (genu), tibia, and tarsus) often bearing distinct humps and all ending in a pair of claws without pad-like pulvilli (present in ixodids). The coxae lack spur-like projections (present in ixodids) and the dorsal tarsus I has a unique sensory apparatus (Haller's organ) with an anterior pit and posterior capsule (used for odor, temperature, light and mechanical sensation). Argasids generally show limited sexual dimorphism, although females are able to engorge to several times the size of males and they have wider genital apertures. Females have a single saccular ovary (grape-like when gravid) with paired tubular oviducts (with distal ampulla) leading to a common uterus (with associated accessory glands) opening to the vagina (with cervical and vestibular regions). The cervical region acts as a receptaculum seminis and the vestibular vagina actively prolapses during oviposition. The genital aperture consists of a transverse slit (wider than long) surrounded by a prominent fold and connected to special Gene's organs which produce waxy egg coatings during oviposition. Males have 2 testes connected by tubular vas efferentia to a common vas deferens with a large multilobed accessory gland leading to the ejaculatory duct. The genital aperture is circular to crescent-shaped without an apron and without external genitalia. Males produce spermatophores (packets of spermatids) which are grasped by his chelicerae and placed under the genital operculum of females.

Site of infection: Nymphs, adults and sometimes larvae of *Ornithodorus* spp. are ectoparasitic on a range of vertebrate hosts, including mammals (belonging to 60 families in 14 orders, including ungulates, marsupials, small herbivores, carnivores, bats, rodents, primates), birds (belonging to 11 passeriform and 27 non-passeriform families in 18 orders, including seabirds, shorebirds, waterbirds, fowl, birds of prey), reptiles (13 lizard families, 4 snake families, 3 tortoise families) and amphibians (3 frog/toad families). The parasites crawl onto hosts to feed on blood and then drop off into the surrounding environment, many species burrowing into sandy soil and others being nidicolous (dwelling in nest/burrows). Ticks have often been found feeding on hosts in sites that are difficult to groom (such as the head, neck and belly) but they may also occur more widespread on other body regions (legs, shoulders, flanks and under the wings of birds).

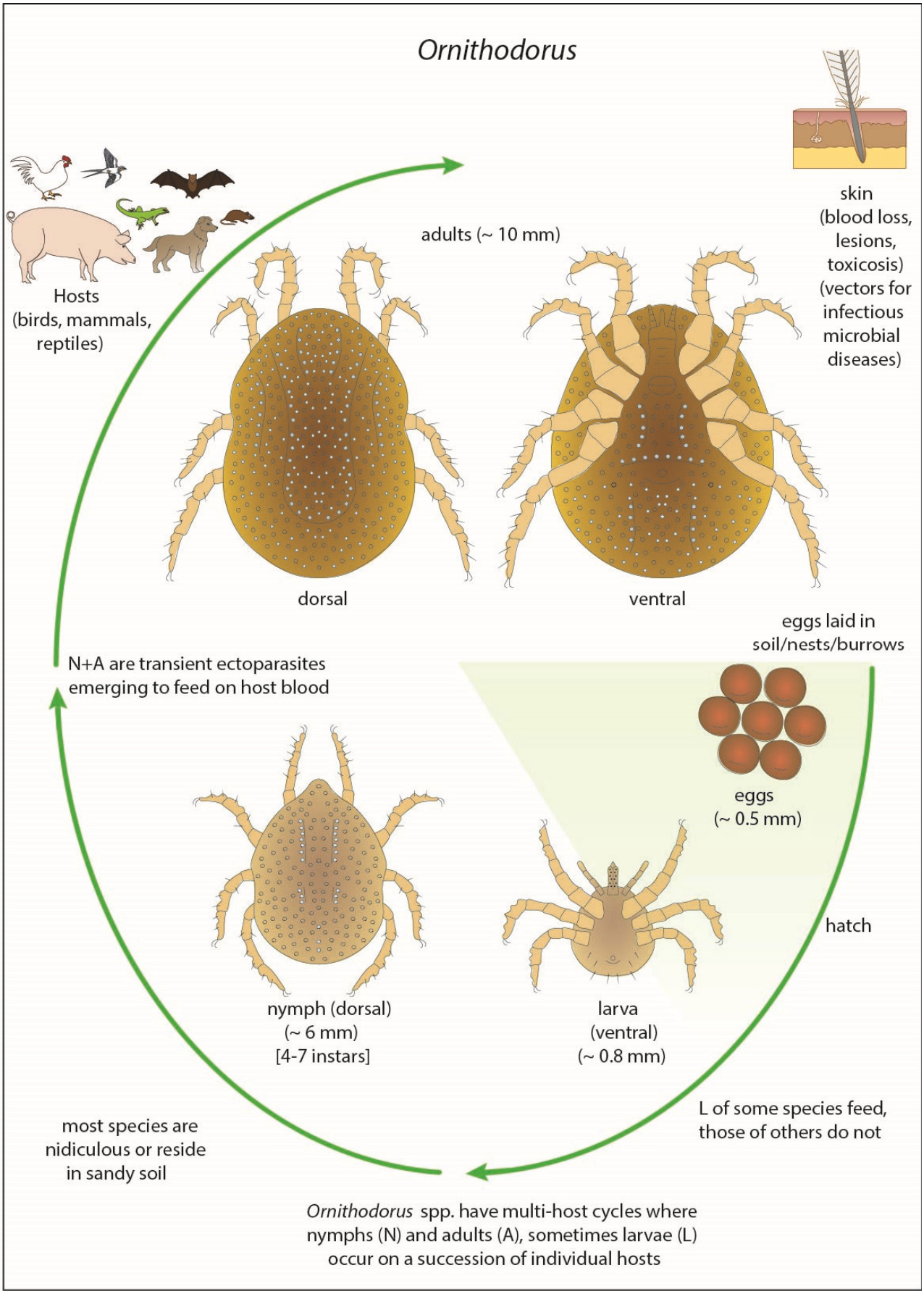
Pathogenesis: Sand tampans are haematophagous and use their piercing/sucking mouthparts to cut the skin of the host and suck blood from pools of blood forming in the dermis (process known as telmophagy). Even though ticks feed transiently and feeding times are short (around 30 minutes), their bites can be painful and cause considerable irritation with tissue trauma, inflammation (erythema, oedema), pruritus, and occasional focal haemorrhages and necrosis. During feeding, ticks inject saliva containing various vasoactive compounds with cytolytic, anticoagulant, vasodilatory, and vascular permeability activities, and the saliva of some species is also thought to contain analgesic compounds. Individual hosts may develop allergic or hypersensitivity reactions to salivary compounds, which exacerbates skin lesions and exaggerates host responses. Some species (e.g. *O. savignyi* and *O. lahorensis*) may even cause signs of paralysis in domestic livestock, not from any neurotoxic components in saliva but from toxicosis reactions involving rashes, tracheopharyngeal compression and muscle weakness. Infested animals may suffer severe biting stress, particularly tethered or housed animals. They may attempt to groom affected areas by licking, preening, biting or scratching, sometimes leading to self-trauma which can lead to open wounds susceptible to secondary bacterial infections. Heavy infestations may also cause significant blood loss manifest as anaemia, which can sometimes be fatal. Domestic livestock may not feed efficiently with consequential meat and/or milk production losses. The ticks may also act as efficient vectors (biological and/or mechanical) for the transmission of infectious diseases caused by arboviruses (including African swine fever virus), bacteria (various *Borrelia* spp. causing relapsing fever, *Brucella* spp. causing brucellosis, *Coxiella* sp. causing Q fever, *Francisella* sp. causing tularaemia, *Pajaroellobacter* sp. causing epizootic bovine abortion) and haemoprotozoans (*Theileria* spp. causing piroplasmosis).

Developmental cycle and mode of transmission: Like all ticks, *Ornithodorus* spp. undergo incomplete (hemimetabolous) metamorphosis whereby eggs hatch larvae which moult through several nymphal stages to form adults. They have multi-host life-cycles as the feeding stages are transient ectoparasites that suck blood from a succession of hosts and rest in the surrounding environment between feeds. Gravid female ticks lay eggs in small batches in sandy soil or sheltered spaces in host nests or burrows. Depending on environmental conditions, the eggs hatch in 7-30 days (longer in drier conditions) releasing small 6-legged larvae. There is only one larval stage which is quite hardy and may survive for months in the environment. Studies on different tick species vary in whether the larvae feed or not: those of most species (e.g. *O. moubata*) are thought not to feed before moulting; while those of several species (e.g. *O. turicata*) have been observed to feed rapidly (15-30 minutes) before dropping off and moulting; and those of a few species (e.g. *O. puertoricensis*) have been found to feed for extended periods (several days) before detaching and moulting. Larvae moult to form 8-legged nymphs which develop through 4-7 instars (whereas ixodid ticks only form one nymphal instar).

Nymphs may survive for weeks without feeding but each instar requires a bloodmeal before dropping off the host to moult to the next stage. The final nymphal instars moult to form adult ticks, which may also survive for weeks in the environment before locating hosts on which to feed. Both males and females feed on blood, typically rapidly (minutes to hours) and periodically for their whole lifespans, although intervals between bloodmeals may be months. Adults are extremely hardy and may survive even in harsh conditions up to 5-7 years without feeding. Mature ticks do not mate on hosts, and argasids may mate multiple times (whereas ixodids usually only mate once). Females undergo multiple gonotrophic cycles and lay small batches (15-130) of eggs after feeding, producing several hundred to over one thousand eggs in their lifetimes. Many *Ornithodorus* spp. are nidicolous and inhabit protected niches in nests (in cliffs, burrows, on the ground and some in trees) or in caves, dens, hides and habitual resting places. Some are endophilic and may infest indoor spaces in barns, stables, houses and even crevices in stone and clay walls and fences. Other species burrow into litter and loose soil frequented by hosts, often sandy resting places under shady trees or rock overhangs. A few species (e.g. *O. savignyi*) are hunter ticks and actively seek hosts by scuttling along ground when stimulated by host vibrations, heat or odours (including pheromones produced by resident ticks). A couple of species that parasitize livestock (*O savignyi* and *O coriaceus*) are also unique in that they have simple eyes and rest near ground level in shaded areas where animals rest and sleep. Most species are nocturnal feeders on hosts in tropical and subtropical regions, including steppes, semideserts and regions with long dry seasons.

Differential diagnosis: Infestations may be indicated on clinical grounds by the occurrence of painful and pruritic skin lesions sometimes associated with anaemia. However, a variety of other aetiological agents may cause similar disease syndromes, including other arthropods, infectious micro-organisms and some other pathologies (especially inflammatory and allergic conditions). Diagnoses are generally made by the direct observation of tick stages biting hosts, even though such stages are often transient feeders. Ticks are best identified by microscopic examination of specimens collected from the host plumage or pelage. More recently, molecular biological techniques have been used to identify and characterize species following the polymerase chain reaction (PCR) amplification of nuclear (18S and 28S ribosomal DNA, internal transcribed spacer regions 1 and 2) and mitochondrial (12S and 16S ribosomal DNA, cytochrome c oxidase subunit I) gene sequences.

Treatment and control: Opportunistic or incidental infestations detected on individual hosts may be treated by physically removing ticks using fine surgical instruments (tweezers, forceps) or special removal devices (twists, loops/lassos, tick keys or V-shaped tools). Ticks should be removed gently without crushing to avoid squeezing saliva and gut contents back into wounds, and without tearing to avoid leaving fragments embedded in wounds causing inflammatory reactions. Some clinicians have reported moderate successes removing ticks using chemical sprays (freezing agents or pyrethroid acaricides), but traditional folklore remedies using stringent or volatile chemicals applied to the backs of ticks may do more harm than good as distressed or dying ticks may regurgitate or release toxic or pro-inflammatory materials. Individual hosts may require supportive chemotherapies to combat pain, pruritus, inflammation and possible secondary bacterial infections. Livestock and companion animals are more usually treated using a range of acaricidal chemicals, including arsenical preparations, organochlorines (dichloro-diphenyl-trichloroethane (DDT, lindane), organophosphates (dioxathion, fenchlorphos), organophosphonates (chlorfenvinphos, dichlorvos, tetrachlorvinphos, trichlorfon), monothiophosphates (chlorpyrifos, coumaphos, cythioate, diazinon, fenthion, propetamphos), dithiophosphates (malathion, phosmet), carbamates (carbaryl), pyrethroids (permethrin, flumethrin, deltamethrin, decamethrin, cypermethrin, cyprothrin), formamidines (amitraz), macrocyclic lactones (ivermectin, selamectin), phenylpyrazole (fipronil), chloronicotinyl (imidacloprid), isoxazolines (afoxolaner, fluralaner), natural products (rotenone) and some insect growth regulators or chitin synthesis inhibitors (methoprene, pyriproxyfen). Treatments may be applied topically or systemically via a range of modalities, including emulsions, sprays, showers, dips, footbaths, dusts, powders, drenches, injections, pour-ons, spot-ons, impregnated collars or tags, medicated supplementary feeds, or using self-treatment devices (bait boxes, rubbing posts or rollers, and treated nesting materials). Regrettably, there are growing reports of tick populations developing resistance to various arsenic compounds, organochlorines, organophosphates, pyrethroids and formamidines, so it is recommended that acaricides be used strategically (only when needed) and in cyclic rotation to avoid further resistance problems. Animals often require periodic re-treatment as ticks can survive in the surrounding environment for long periods. Some formulations with long-lasting residual activity have also been used against resting stages in local environments, notably around households, farms, military bases, and recreational areas. Various preventive measures may also be adopted to break transmission cycles by enhanced health surveillance (screening programmes, quarantine, culling), grazing management (avoid overstocking, pasture rotation, pasture spelling/resting, clearing vegetation (cut, slash, burn, plough), stabling), and wildlife management (exclusion of reservoir hosts by barriers, trapping or hunting, vermin control, diversion of habitual migration routes, and encouraging grooming species such as oxpeckers).


Ornithodorus
skin
(blood loss,
lesions,
toxicosis)
(vectors for
infectious
microbial
diseases)
adults (~ 10 mm)
Hosts
(birds, mammals,
reptiles)
dorsal
ventral
eggs laid in
soil/nests/burrows
N+A are transient ectoparasites
emerging to feed on host blood
eggs
(~ 0.5 mm)
hatch
nymph (dorsal)
(~ 6 mm)
[4-7 instars]
larva
(ventral)
(~ 0.8 mm)
L of some species feed,
those of others do not
most species are
nidiculous or reside
in sandy soil
Ornithodorus spp. have multi-host cycles where
nymphs (N) and adults (A), sometimes larvae (L)
occur on a succession of individual hosts



Ornithodorus adult dorsal



Ornithodorus adult ventral

Otobius
(arachnid: tick)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ticks have respiratory stigmata posterior to their legs. They are obligate blood-feeding ectoparasites on vertebrate hosts and their hypostomes are toothed and exposed. Two families are recognized: Argasidae and Ixodidae, known as soft and hard ticks, respectively. Argasids have soft leathery bodies lacking a dorsal scutum and the capitulum is covered by the body. They are transient feeders on mammals and birds and have multi-host life-cycles, spending the majority of time hiding in cracks/crevices in the surrounding environment, especially nests and dens. Infestations by *Otobius* spp. occur in the ears of domestic animals and rabbits, causing inflammation and eliciting scratching trauma.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on capitulum)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Ixodida (Metastigmata) (ticks, macroscopic, stigmata posterior to legs, hypostome toothed, ectoparasites)
Family: Argasidae (soft ticks, lack dorsal scutum, capitulum covered by body, hide in cracks/crevices)
Genus: *Otobius* (parasitic in ears of mammals)
Species: various species cause inflammation and lesions in the ears of domestic animals and rabbits

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial

Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on capitulum) [34 superfamilies]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs (behind coxae III or IV); and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Ticks are further characterized by macroscopic bodies with an exposed ventral hypostome (toothed with backwardly-directed barbs), chelicerae with only 2 joints, long legs with free articulated coxae (not fused to the body wall) and tarsi I each bearing a complex sensory pit (Haller's organ). They are obligate blood-sucking parasites which feed on terrestrial vertebrates (mammals, birds, reptiles and some amphibians) as larvae, nymphs and adults with 1-, 2- or 3-host life-cycles. Almost 1,000 tick species have been classified within some 20 genera from numerous wild and domesticated animals around the world. Two main families are recognized: the Argasidae containing ~200 species of 'soft' ticks with flexible leathery cuticles, ventral capitula, short feeding times (< 1 hour) and long life-spans (up to 20 years); and the Ixodidae containing ~800 species of 'hard' ticks with rigid dorsal scutal plates, anterior capitula, long feeding times (hours to days) and shorter life-span (2-6 years). Basic characteristics of representative genera considered in this resource are tabulated below.

Genus	**Capitulum**				**Idiosoma**				**Usual no. of hosts**
	location	**basis capitulum**	**mouth-parts**	**palps**	**integument**	**festoons**	**eyes**	**male ventral plates**	

Argasidae (soft ticks with leathery cuticle, stigmata between coxae III)									
Argas	ventral	triangular	short	leg-like	stippled with lateral suture	absent	absent	absent	>3
Ornithodorus	ventral	rectangular	short	leg-like	mamillated	absent	usually absent	absent	>3
Otobius	ventral	rectangular	short	leg-like	spinose (nymphs), granulated (adult)	absent	absent	absent	1
Ixodidae (hard ticks with sclerotized dorsal plate (scutum), stigmata behind coxae IV)									
Prostriata (anal groove anterior)									
Ixodes	anterior	triangular	long	long	inornate	absent	absent	present	3
Metastriata (anal groove posterior)									
Amblyomma	anterior	rectangular	long	long	ornate	present	present	indistinct	3
(*Aponomma*)	anterior	rectangular	long	long	often ornate	present	absent	absent	3
Rhipicephalus	anterior	hexagonal	short	medium	some ornate	present	present	present	3
(*Boophilus*)	anterior	hexagonal	short	short	inornate	absent	present	present	1
Dermacentor	anterior	rectangular	short	medium	often ornate	present	present	absent	3
Haemaphysalis	anterior	rectangular	short	short	inornate	present	absent	absent	3
Hyalomma	anterior	rectangular	long	long	inornate	present	present	present	2
Bothriocroton	anterior	pentagonal	long	long	ornate	present	absent	absent	3

The family Argasidae contains 5 subfamilies (Antricolinae, Argasinae, Nothoaspisinae, Ornithodorinae, Otobinae) which vary in morphology, biology, host range and specificity. Members of the subfamily Otobinae have flattened bodies with spinose integuments but lacking distinct lateral margins. They are unusual argasid ticks in that only the early developmental stages (larvae and nymphs) are parasitic in the ear canals of individual hosts while the resultant adult stages are not parasitic and do not feed. Only one genus (*Otobius*) has been described with 2 species, one (*O. megnini*) reported from a range of domestic and wild mammals, and another (*O. lagophilus*) being restricted to rabbits. Infestations have been associated with inflammation and blockages of the ear canals, with consequential behavioural disorders resulting in self-trauma, ulcerations and secondary infections.

***Otobius* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
O. lagophilus (rabbit ear tick)	Lagomorpha: leporid (white-tailed jackrabbit, black-tailed jackrabbit, desert jackrabbit, desert cottontail, mountain cottontail, hare), ochotonid (American pika); Rodentia: cricetid (canyon mouse, southern grasshopper mouse), sciurid (Townsend's ground squirrel); Carnivora: felid (cat); Perissodactyla: equid (donkey); Chiroptera: vespertilionid (pallid bat); Passeriformes: alaudid (horned lark) (1-host cycle)	ears (larval and nymphal stages)	irritation, inflammation, waxy exudate, scratching trauma (vector for Colorado tick fever, Rocky Mountain spotted fever)	North America
O. megnini (syn. *Argas*, *Ornithodorus*) (spinose ear tick)	Carnivora: canid (dog, coyote), felid (cat, lion); Artiodactyla: antilocaprid (pronghorn), bovid (cattle, zebu, sheep, mountain sheep, bighorn sheep, goat, mountain goat), camelid (camel, llama, alpaca), cervid (white-tailed deer, black-tailed deer, mule deer, elk), suid (pig); Perissodactyla: equid (horse, donkey, mule), tapirid (Baird's tapir); Lagomorpha: leporid (rabbit, black-tailed jackrabbit, cottontail, hare); Primates: hominid (human); Struthioniformes: struthionid (ostrich) (1-host cycle)	ears (larval and nymphal stages)	irritation, inflammation, otitis, waxy exudate, scratching trauma, ulceration, paralysis (suspected vector for Q fever)	Americas, India, Africa, Australia

Parasite morphology: *Otobius* spp. form 4 different types of developmental stages; namely eggs; larvae; nymphs (2 instars); and adults. The eggs are small spherical to ovoid stages ranging in size from 0.2-0.8 mm long and from brown to red in colouration. Larvae are small round stages measuring 2-3 mm in length and are often tan in colour, sometimes with darker reticulated patterns, but becoming red when feeding on blood. They have a conspicuous gnathosoma (head) with forward-protruding mouthparts, and a larger rounded idiosoma (body) with 6 long thin ventral legs. Larvae lack stigmata and tracheae as respiration and fluid regulation occurs through the cuticle. Nymphs are larger ovate to ellipsoidal stages which usually have a grey-brown mottled appearance, but become red-black when feeding. There are 2 nymphal instars which grow up to 7-10 mm long when fed. The mouthparts are usually hidden in dorsal view being located ventrally underneath the anterior rim of the idiosoma. The cuticle is leathery (lacking sclerotized plates like ixodid ticks) and is distinctly spinose with numerous small spines. Nymphs have 8 pale long legs, each ending in a pair of

claws. They have a pair of lateral respiratory openings (stigmata) often surrounded by a circular-oval stigmatal plate, but nymphs lack genital openings. In larvae and nymphs, the piercing/sucking mouthparts are functional and consist of 2 palps, 2 chelicerae and a toothed hypostome. The palps are sensory and do not enter the skin when feeding (ticks lack antennae). The chelicerae are specialized cutting structures with long curved shafts with dentate terminal digits which rip and tear host flesh to form small blood pools. The toothed hypostome is inserted into the blood pool to facilitate feeding as well as anchoring the tick to the host. The chelicerae and hypostome form a food (buccal) canal to imbibe blood and inject saliva. Blood is sucked up by a muscular pharynx (with pharyngeal valve) and delivered to a saccular midgut with branched diverticula (caeca) and excretory Malpighian tubules. Adult ticks have ellipsoidal bodies that appear moderately dorso-ventrally flattened and have with rounded anterior and posterior margins. They range in colour from beige-brown-black and usually measure 5-8 mm in length. The gnathosoma (head) is small and not visible in dorsal view as it is located underneath the anterior edge of the large idiosoma (body). The cuticular covering is leathery (lacking sclerotized plates like ixodid ticks) and there is no distinct lateral suture or margin between the dorsal and ventral surfaces (whereas *Argas* spp. have distinct lateral margins). The integument is granulated and usually appears speckled with tiny pore-like discs and larger shrinkage indentations. Adults have rudimentary non-functional mouthparts located ventrally between a pair of 4-segmented sensory palps. The mouthparts have small chelicerae and highly reduced hypostomes without teeth (adults do not feed). They also have rudimentary alimentary tracts with a tubular foregut, saccular midgut and vesicular rectal sac. The idiosoma comprises an anterior podosoma (bearing legs and genital pore) and a posterior opisthosoma (area behind coxae bearing respiratory stigmata and anal aperture). Adults have 8 pale stout jointed legs, each composed of 6 segments (coxae, trochanter, femur, patella (genu), tibia, and tarsus) and all terminating in a pair of claws without pad-like pulvilli. The coxae lack spurs (present in ixodids) and the dorsal tarsus I has a sensory structure (Haller's organ) used to detect odour, temperature and tactile stimuli. Like other argasids, *Otobius* spp. have small respiratory spiracular plates located between coxae III and IV (whereas ixodids have larger spiracular plates behind coxae IV). Male and female ticks show little external sexual dimorphism although gravid females are generally larger and their genital aperture is slit-like (rather than crescent-shaped like males). Females have a single saccular ovary with paired oviducts leading to a common uterus (with lateral accessory glands). The uterus opens to the vagina which has a short cervical region (acting as a receptaculum seminis) and a vestibular regions (capable of prolapsing during oviposition). The genital pore appears as a transverse slit (wider than long) surrounded by a prominent fold (apron). Males have paired testes with vas efferentia joining to form a common vas deferens (with multilobed accessory glands) leading to the ejaculatory duct and genital pore. Males produce packets of spermatids (spermatophores) which are transferred to the genital operculum of females.

Site of infection: *Otobius* spp. are unusual ticks as their adult stages are free living and do not feed on hosts, whereas their larval and nymphal stages are ectoparasitic on a small range of mammalian hosts and a few bird species. They are commonly known as spinose ear ticks because of their spiny cuticles and their predilection for the ear canals. Infestations have been recorded on lagomorphs, small carnivores, ungulates, rodents, bats, humans, and occasionally on land birds.

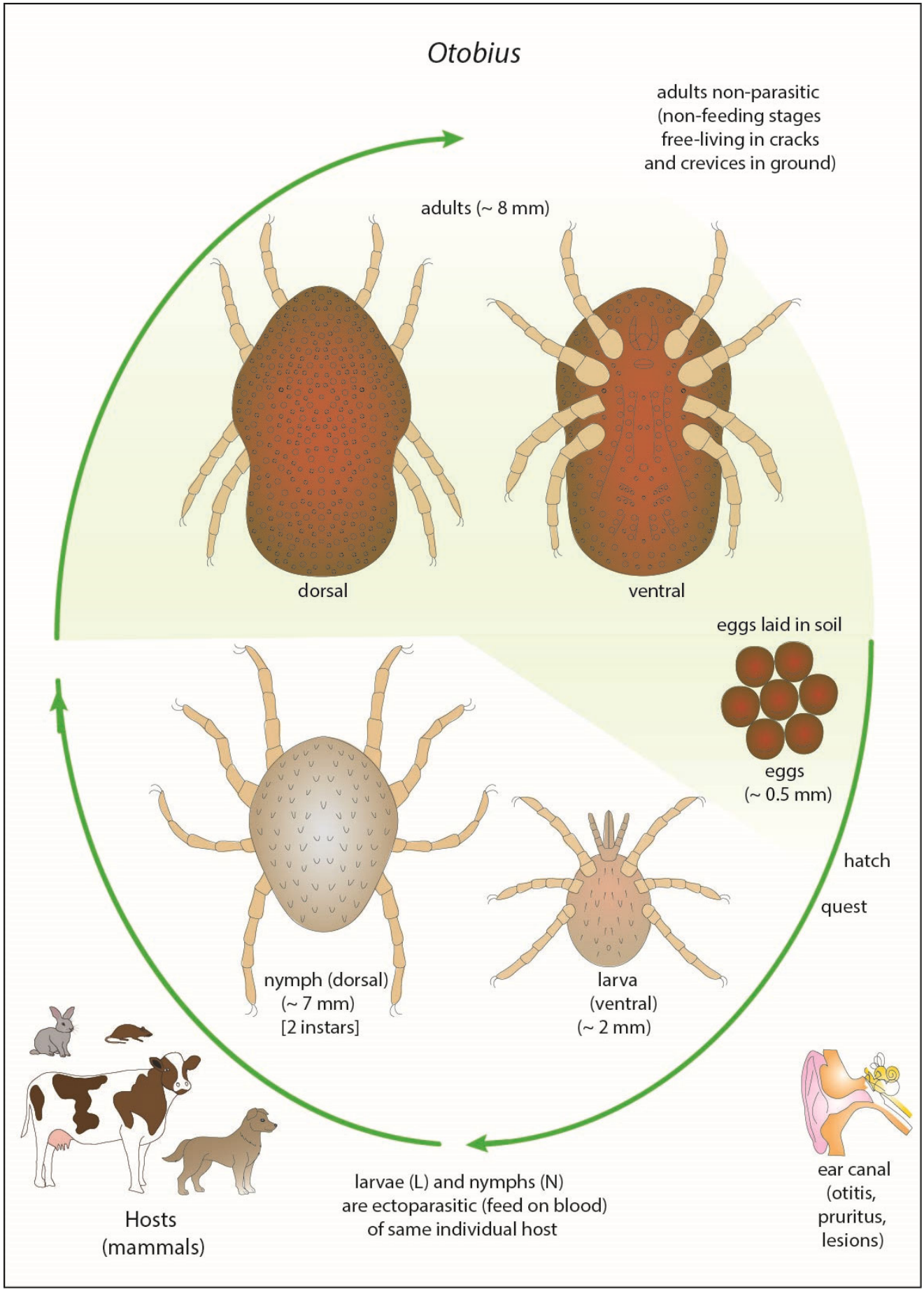
Pathogenesis: Larvae and nymphs are haematophagous ectoparasites that use their cutting/sucking mouthparts to feed on blood from the highly vascular areas of the ear canals. They do not suck blood directly from vessels, but use their cutting chelicerae to create blood pools on which they feed (process known as telmophagy). Larvae and both nymphal stages feed repeatedly but do not become grossly engorged. Bites are painful causing severe irritation to the ear canals with inflammation, fibrosis and pruritus developing over several days (condition known as otoacariasis or parasitic otitis). During feeding, larvae and nymphs inject saliva containing vaso-active compounds (including anticoagulants and vasodilators) which may also elicit allergic or hypersensitivity reactions in certain hosts, leading to further irritation and inflammation. Infestations may cause ear canker or otitis externa with frequent head tilting or shaking, scratching and rubbing, muscle spasms, discoloured or waxy discharges, unpleasant smells, and sometimes perforation of the ear drums. Heavy infestations may cause anaemia, reduced feeding efficiency with anorexia and weight loss (particularly during winter), and some animals (notably cattle and horses) may show nervous disorders (suggestive of tick toxicosis or paralysis) with head-heavy stances, lack of muscle coordination, myotonia, convulsions, collapse and death. Bite sites may also become ulcerated and susceptible to invasion by secondary bacterial infections and fly larvae (screw-worm myiases) resulting in otitis media, otitis interna, and encephalitis with fatal consequences. These ear ticks are also suspected of being vectors for a range of infectious diseases, including coxiellosis (Q fever), tularaemia, Rocky Mountain spotted fever and Colorado tick fever, but their role in natural transmission remains to be determined.

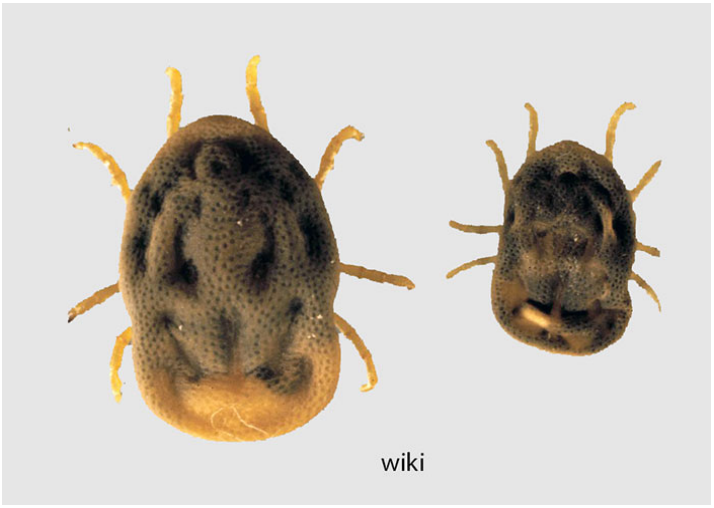
Developmental cycle and mode of transmission: Spinose ear ticks undergo incomplete (hemimetabolous) metamorphosis whereby eggs hatch into larvae which moult into nymphs and then adults. These ticks are unusual, however, in that the adult ticks are free-living whereas the larval and nymphal stages are ectoparasitic in the ear canals of individual hosts (thus categorizing them as having 1-host life-cycles). Gravid female ticks lay eggs in clusters in cracks and crevices on the ground where they hatch in 2-8 weeks releasing 6-legged larvae. The larvae crawl up vegetation and other vertical substrates (rocks, walls, fences) and quest for hosts, not by pursuing them but by waiting for them to brush past. Larvae are able to survive for extended periods (up to 2 months) in the external environment. Once they crawl onto a host, they migrate to the ears and attach to skin in the grooves and folds of the ear canal and feed on blood intermittently for 5-10 days (in comparison, *Argas* larvae also feed on blood, while *Ornithodorus* larvae do not). Larvae then moult *in situ* to form nymphs which develop through 2 instars over several weeks. Reports differ as to whether first-stage nymphs feed or do not feed before moulting in 7-10 days to second-stage nymphs, whereas second-stage nymphs have been reported to feed periodically for 1-7 months, particularly over winter and spring. Nymphs then leave the ears of their hosts and

crawl out onto the ground to hide in cracks/crevices, under rocks/litter and sometimes under tree bark. They moult to form adult ticks which mature over 1-6 weeks depending on environmental conditions (longer in colder regions). The adults are free-living non-feeding stages that may survive for almost 2 years (they apparently absorb water from the atmosphere to survive). Adult mate on the ground where males constantly seek females. After mating, females begin to produce eggs after 6-29 days and they may lay batches of 100-250 eggs for several weeks to months, producing up to 1,500 eggs in their life-times. The whole life-cycle may be completed in as little as 2-4 months, although most regions report only 2 generations per year, often coinciding with warmer weather with low-moderate humidity (including arid and semi-arid environments).

Differential diagnosis: Infestations are usually not diagnosed on clinical grounds as many aetiological agents may cause ear canker or otitis externa. Otoscopic examination of the ear canal may reveal small inflamed nodules, bite sites and sometimes feeding ticks. It is more usual to use cotton swabs or blunt forceps to remove waxy exudates which are then examined for the presence of larvae and nymphs. Tick feeding stages may be identified by their unique morphological characteristics (e.g. the spines on *O. megnini* nymphs are more numerous and thicker anteriorly than posteriorly whereas those of *O. lagophilus* are similar in size and number, the hypostome of *O. megnini* has 4 pairs of ventral teeth while that of *O. lagophilus* only has 3 pairs). Molecular biological techniques have been used to characterize species following polymerase chain reaction (PCR) amplification of nuclear rRNA (18S and 28S ribosomal RNA, internal transcribed spacers 1 and 2) and mitochondrial (12S and 16S ribosomal RNA, cytochrome c oxidase subunit I, nicotinamide adenine dinucleotide dehydrogenase subunit 5) gene sequences.

Treatment and control: Although some individual stages (usually large second-stage nymphs) may be physically removed from the external meatus using tweezers/forceps and gentle pressure, most feeding stages are too small or located too deep in the ear canal to be accessible. Attempts to irrigate or flush the ear canals (ear lavage) are often unsuccessful as feeding stages are firmly attached and often covered in hard waxy exudates. Infestations are usually treated with chemical acaricides either applied topically or systemically as dusts/powders, oils/sprays, spot-on or pour-ons, impregnated collars/tags, or as oral or injectable formulations. Successful treatments of feeding stages have been reported using arsenical preparations, organochlorines (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (coumaphos, chlorfenvinphos, chlorpyrifos, diazinon, dichlorvos, dioxathion, fenchlorphos, malathion, phosmet, propetamphos, trichlorfon), pyrethroids (cypermethrin, cyprothrin, decamethrin, deltamethrin, flumethrin, permethrin), carbamates (carbaryl), formamidines (amitraz), phenylpyrazole (fipronil) and macrocyclic lactones (ivermectin, abamectin), although systemic formulations may be ineffective against non-feeding stages (such as first-stage nymphs) so repeated treatments may be necessary. Ticks infesting human ears have been removed by treating with pine oil containing chlordane, or mixture of pine oil and cottonseed oil. Control programmes should also target free-living stages to prevent re-infestations, so acaricides with long-lasting residual activity (some organochlorines, organophosphates and pyrethroids) may be used as dusts or sprays to treat the surrounding environment (particularly animal housing and human habitations). Other preventive measures may be used to break transmission cycles through improvements to hygiene (cleaning holding facilities, destroying contaminated bedding), health surveillance (regular screening, quarantine, culling), animal management (avoid overstocking, pasture rotation, moving habitual camps), wildlife control (exclusion by barriers, trapping or hunting) and personal protection (applying repellents such as diethyltoluamide (DEET) to the skin or clothing).


Otobius
adults non-parasitic
(non-feeding stages
free-living in cracks
and crevices in ground)
adults (~ 8 mm)
dorsal
ventral
eggs laid in soil
eggs
(~ 0.5 mm)
hatch
quest
nymph (dorsal)
(~ 7 mm)
[2 instars]
larva
(ventral)
(~ 2 mm)
Hosts
(mammals)
larvae (L) and nymphs (N)
are ectoparasitic (feed on blood)
of same individual host
ear canal
(otitis,
pruritus,
lesions)



Otobius adults



Otobius adult



Otobius larva



Otobius nymph

Ixodes
(arachnid: tick)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ticks have respiratory stigmata posterior to their legs. They are obligate blood-feeding ectoparasites on vertebrate hosts and their hypostomes are toothed and exposed. Two families are recognized: Argasidae and Ixodidae, known as soft and hard ticks, respectively. Ixodids have hard bodies with a dorsal scutum (shield-shaped plate) and the capitulum is not covered by the body. Larvae, nymphs and adults attach and feed on host blood, their life-cycles involving one, two or three hosts depending on whether moulting occurs on or off the host. Some 650 species of hard ticks infest mammals, birds and reptiles. Infestations by *Ixodes* spp. are common three-host ticks on a range of domestic and wild mammals and birds; most causing irritation and inflammation, some causing toxicoses and paralysis, and many transmitting viral, bacterial and protozoal infectious diseases.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on capitulum)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Ixodida (Metastigmata) (ticks, macroscopic, stigmata posterior to legs, hypostome toothed, ectoparasites)
Family: Ixodidae (hard ticks, with dorsal scutum, capitulum projects anteriorly, attach and feed on 1, 2 or 3 hosts)
Genus: *Ixodes* (parasitic on skin of mammals/birds)
Species: various species cause irritation, dermatitis, toxicosis or paralysis in domestic and wild animals, incl. humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					

Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on capitulum) [34 superfamilies]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs (behind coxae III or IV); and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Ticks are further characterized by macroscopic bodies with an exposed ventral hypostome (toothed with backwardly-directed barbs), chelicerae with only 2 joints, long legs with free articulated coxae (not fused to the body wall) and tarsi I each bearing a complex sensory pit (Haller's organ). They are obligate blood-sucking parasites which feed on terrestrial vertebrates (mammals, birds, reptiles and some amphibians) as larvae, nymphs and adults with 1-, 2- or 3-host life-cycles. Almost 1,000 tick species have been classified within some 20 genera from numerous wild and domesticated animals around the world. Two main families are recognized: the Argasidae containing ~200 species of 'soft' ticks with flexible leathery cuticles, ventral capitula, short feeding times (< 1 hour) and long life-spans (up to 20 years); and the Ixodidae containing ~800 species of 'hard' ticks with rigid dorsal scutal plates, anterior capitula, long feeding times (hours to days) and shorter life-span (2-6 years). Basic characteristics of representative genera considered in this resource are tabulated below.

Genus	**Capitulum**				**Idiosoma**				**Usual**
	location	**basis**	**mouth-**	**palps**	**integument**	**festoons**	**eyes**	**male**	**no. of**

		capitulum	parts					ventral plates	hosts
Argasidae (soft ticks with leathery cuticle, stigmata between coxae III)									
Argas	ventral	triangular	short	leg-like	stippled with lateral suture	absent	absent	absent	>3
Ornithodorus	ventral	rectangular	short	leg-like	mamillated	absent	usually absent	absent	>3
Otobius	ventral	rectangular	short	leg-like	spinose (nymphs), granulated (adult)	absent	absent	absent	1
Ixodidae (hard ticks with sclerotized dorsal plate (scutum), stigmata behind coxae IV)									
Prostriata (anal groove anterior)									
Ixodes	anterior	triangular	long	long	inornate	absent	absent	present	3
Metastriata (anal groove posterior)									
Amblyomma (*Aponomma*)	anterior	rectangular	long	long	ornate	present	present	indistinct	3
	anterior	rectangular	long	long	often ornate	present	absent	absent	3
Rhipicephalus (*Boophilus*)	anterior	hexagonal	short	medium	some ornate	present	present	present	3
	anterior	hexagonal	short	short	inornate	absent	present	present	1
Dermacentor	anterior	rectangular	short	medium	often ornate	present	present	absent	3
Haemaphysalis	anterior	rectangular	short	short	inornate	present	absent	absent	3
Hyalomma	anterior	rectangular	long	long	inornate	present	present	present	2
Bothriocroton	anterior	pentagonal	long	long	ornate	present	absent	absent	3

The family Ixodidae contains 6 subfamilies (Amblyomminae, Bothriocrotoninae, Haemaphysalinae, Hyalomminae, Ixodinae and Rhipicephalinae) which vary in their morphology, biology, host ranges and specificity. [Note that some taxonomic authorities have merged the subfamilies Rhipicephalinae and Hyalomminae, while others have subsequently assigned the subfamilies Amblyomminae and Rhipicephalinae into the new family Amblyommidae, predominantly on the basis of molecular phylogenetic studies]. Hard ticks had previously been divided into 2 groups: the Prostriata (with the anal groove anterior to the anus) and the Metastriata (anal groove absent or posterior to anus). The Prostriata essentially comprises the subfamily Ixodinae with over 230 species assigned to the single extant genus *Ixodes* [plus one fossil genus (*Cornupalpatum*)], while the Metastriata contains members of the remaining subfamilies with over 600 species classified into 18 genera. The subfamily Ixodinae comprises prostriate inornate ticks lacking eyes and festoons, but whose males possess sclerotized ventral plates. All *Ixodes* spp. are ectoparasitic on small to large mammals or birds as 3-host ticks (larvae, nymphs and adults parasitizing different individual hosts). Ticks are often named after a particular host (e.g. dog tick) but they are generally not strictly host-specific, but rather host-preferential, attempting to feed on many passing animal species. Larvae tend to feed on small hosts (usually rodents, birds), nymphs on mid-sized hosts (rodents, omnivores, birds) and adults on mid-sized to large hosts (carnivores, herbivores). A total of 15 subgenera of *Ixodes* have been recognized on the basis of tick morphology (especially the form of Haller's organ, palps, hypostome, spurs, sternal plates, porose areas), host occurrence and geographic distribution.

***Ixodes* subgenera**	**Common hosts**	**Number of species recorded in each zoogeographic region**					
		Nearctic (North America)	Palearctic (Eurasia)	Ethiopian (Africa)	Neotropical (South America)	Oriental (India, SE Asia)	Australian (Australia, New Guinea)
I. (*Ixodes*) [=*I.* (*Trichotoixodes*)]	mammals, birds, reptiles	14	21	8	24	12	
I. (*Pholeoixodes*) [=*I.* (*Ixodiopsis*)]	mammals, birds	18	21		3		
I. (*Afrixodes*)	mammals, birds			42		2	
I. (*Partipalpiger*)	mammals		1			1	
I. (*Exopalpiger*)	mammals		1	1	3		4
I. (*Endopalpiger*)	marsupials, monotremes, rodents						7
I. (*Coxixodes*)	monotremes						1
I. (*Sternalixodes*)	mammals						9
I. (*Alloixodes*)	rodents				1		
I. (*Haemixodes*)	rodents				1		
I. (*Eschatocephalus*) [=*I.* (*Pomerantzevella*)]	bats		3	4		3	3
I. (*Lepidixodes*)	bats			1		1	

I. (*Ceratixodes*)	seabirds	1	1		1	1	1
I. (*Multidentatus*)	birds	2	1	5	1	1	9
I. (*Scaphixodes*)	birds	2	7			1	

The subgenera *Ixodes* (*Ceratixodes*), *I.* (*Scaphixodes*) and *I.* (*Multidentatus*) are common on coastal birds on most continents, *I.* (*Eschatocephalus*) and *I.* (*Lepidixodes*) are found on bats throughout the world, *I.* (*Alloixodes*) and *I.* (*Haemixodes*) are confined to rodents in South America, *I.* (*Endopalpiger*)*, I.* (*Coxixodes*) and *I.* (*Sternalixodes*) are found on marsupials and monotremes in Australia and New Guinea, *I.* (*Afrixodes*) occur mostly on native animals and birds in Africa, several *I.* (*Exopalpiger*) and *I.* (*Partipalpiger*) species infest mammals on most continents, except North America, while the most speciose subgenera *I.* (*Ixodes*) and *I.* (*Pholeoixodes*) are found on mammals, birds and reptiles throughout the world, except Australia. Various species are notorious as opportunistic ectoparasites of domestic animals and humans (e.g. *I. ricinus* in Europe, *I ovatus* and *I. persulcatus* in Japan and Russia, *I. scapularis* and *I. pacificus* in North America, and *I. holocyclus* in Australia); some causing tick paralysis in susceptible hosts (e.g. *I. holocyclus, I. cornuatus, I. rubicundus*), and others transmitting infectious microbial diseases (e.g. *I. ricinus, I. pacificus, I. scapularis*).

***Ixodes* species (* = type species for subgenus)**	**Host range**	**Clinical signs**	**Distribution**
I. abrocomae	Rodentia: abrocomid (Bennett's chinchilla rat), cricetid (long-haired grass mouse, olive grass mouse, yellow-rumped leaf-eared mouse)		South America
I. (*Endopalpiger*) *acer*	Dasyuromorphia: dasyurid (New Guinean quoll); Diprotodontia: petaurid (long-fingered triok); Peramelemorphia: peramelid (striped bandicoot, kalubu bandicoot, Raffray's bandicoot); Rodentia: murid (squirrel-toothed rat)		New Guinea
I. acanthoglossi	Monotremata: tachyglossid (western long-beaked echidna)		New Guinea
I. (*Ixodes*) *acuminatus* (syn. *I. dorriensmithi*) (southern rodent tick)	Rodentia: cricetid (short-tailed field vole, bank vole, Guernsey vole), glirid (garden dormouse), murid (house mouse, yellow-necked mouse, striped field mouse, wood mouse, brown rat); Eulipotyphla: erinaceid (European hedgehog, northern white-breasted hedgehog), soricid (crowned shrew, pygmy shrew, lesser white-toothed shrew), talpid (mole); Carnivora: canid (dog, gray wolf, red fox), felid (cat), mustelid (badger, marten, ferret, least weasel, European mink); Primates: hominid (human); Accipitriformes: accipitrid (common buzzard); Galliformes: phasianid (red partridge); Passeriformes: turdid (common blackbird)	(possible vector for borrelioses)	Europe
I. (*Ixodes*) *acutitarsus* (syn. *I. gigas, laevis*)	Artiodactyla: bovid (cattle, zebu, yak, buffalo, bharal, goral, mithun, sheep, goat, Japanese serow), cervid (dwarf musk deer), suid (pig, wild boar); Rodentia: cricetid (vole), murid (house mouse), sciurid (ground squirrel); Eulipotyphla: soricid (shrew); Carnivora: canid (dog), felid (unspecified), ursid (unspecified bears); Primates: hominid (human); Passeriformes: corvid (red-billed blue magpie), timaliid (unspecified)		Eurasia
I. aequalis	Rodentia: sciurid (California ground squirrel)		North America
I. (*Ixodes*) *affinis*	Artiodactyla: bovid (cattle), cervid (white-tailed deer, red brocket, gray brocket); Perissodactyla: equid (horse); Eulipotyphla: soricid (southern short-tailed shrew); Didelphimorphia: didelphid (Virginia opossum, Robinson's mouse opossum); Rodentia: cricetid (woodrat, Peruvian cotton rat, long-whiskered rice rat, cotton mouse), murid (rat, mouse), sciurid (eastern gray squirrel); Carnivora: canid (dog), felid (bobcat, jaguar, cougar, ocelot, Florida panther), procyonid (raccoon, white-nosed coati), ursid (spectacled bear); Primates: hominid (human); Accipitriformes: cathartid (black vulture); Passeriformes: cardinalid (northern cardinal), furnariid (red-billed scythe bill), mimid (brown thrasher), parulid (golden-crowned warbler, white-rimmed warbler), passerellid (white-throated sparrow, saffron-billed sparrow, eastern towhee), thraupid (white-lined tanager, orange-headed tanager), troglodytid (house wren, Carolina wren), turdid (American robin, creamy-bellied thrush, rufous-bellied thrush); Sauria: teiid (unspecified whiptail)	trauma, irritation, dermatitis	Americas
I. (*Afrixodes*) *albignaci*	Afrosoricida: tenrecid (Talazac's shrew tenrec); Rodentia: murid (black rat)		Madagascar

I. (*Exopalpiger*) *alluaudi*	Eulipotyphla: soricid (greater red musk shrew, Hildegarde's shrew, Jackson's shrew); Afrotheria: macroscelid (elephant shrew); Afrosoricida: chrysochlorid (golden mole); Rodentia: bathyergid (Cape mole-rat), murid (four-striped grass mouse, delectable soft-furred mouse, Southern African vlei rat, Grant's gerbil, Lobengula's gerbil), spalacid (mole-rat); Lagomorpha: leporid (hare)		Africa
I. amarali	Didelphimorphia: didelphid (gray short-tailed opossum, pygmy short-tailed opossum, white-eared opossum, northern red-sided opossum, Amazonian red-sided opossum); Rodentia: cricetid (montane grass mouse, hairy-tailed bolo mouse, blackish grass mouse, Atlantic forest climbing mouse, terraced rice rat, large-headed rice rat, black-footed pygmy rice rat, small-eared pygmy rice rat, Brazilian pygmy rice rat, marsh rat), echimyid (hairy Atlantic spiny rat), murid (black rat, brown rat)		South America
I. (*Multidentatus*) *amersoni*	Charadriiformes: larid (fairy tern); Pelecaniformes: sulid (red-footed booby); Procellariiformes: procellariid (white-headed petrel)		Pacific Islands, New Zealand
I. ampullaceus	Rodentia: nesomyid (Gambian pouched rat)		Africa
I. (*Sternalixodes*) *anatis*	Anseriformes: anatid (mallard, Pacific black duck, giant Canada goose); Apterygiformes: apterygid (North Island brown kiwi, southern brown kiwi); Gruiformes: rallid (buff weka); Carnivora: felid (cat faeces)		Australasia
I. (*Exopalpiger*) *andinus*	Rodentia: cricetid (Peruvian vesper mouse, Darwin's leaf-eared mouse?)		South America
I. angulatus incertae sedis	Eulipotyphla: erinaceid (Amur hedgehog)		China
I. (*Pholeoixodes*) *angustus*	Eulipotyphla: soricid (common shrew, slender shrew, long-tailed shrew, long-clawed shrew, Olympic shrew, Trowbridge shrew, Laxmann's shrew, Siberian large-toothed shrew, Eurasian least shrew, Eurasian pygmy shrew, wandering shrew, northern short-tailed shrew), talpid (mole, American shrew-mole, hairy-tailed mole); Didelphimorphia: didelphid (common opossum, white-eared opossum); Rodentia: aplodontid (mountain beaver), cricetid (small-toothed harvest mouse, western harvest mouse, zempoaltepec, deer mouse, brush mouse, canyon mouse, pinyon mouse, white-footed mouse, southern plains woodrat, bushy-tailed woodrat, dusky-footed woodrat, Alfaro's rice rat, long-tailed vole, eastern meadow vole, California vole, Guatemalan vole, Townsend's vole, grey red-backed vole, southern red-backed vole, northern red-backed vole, heather vole, montane vole, tundra vole, southern bog lemming), geomyid (gopher, Columbian pocket gopher), heteromyid (pocket mouse, chisel-toothed kangaroo rat), murid (mouse, striped field mouse, large Japanese field mouse, black rat, brown rat, bushy-tailed woodrat), sciurid (American red squirrel, western gray squirrel, solver gray squirrel, soft-haired squirrel, ground squirrel, Columbian ground squirrel, Douglas ground squirrel, northern flying squirrel, white-tailed antelope squirrel, eastern chipmunk, least chipmunk, cliff chipmunk, Siberian chipmunk, Townsend chipmunk, cascades chickadee squirrel, redwood chickaree squirrel), sminthid (long-tailed birch mouse), zapodid (western jumping mouse, woodland jumping mouse, Pacific jumping mouse); Lagomorpha: leporid (black-tailed jackrabbit, cottontail rabbit, snowshoe hare), ochotonid (American pika, alpine pika); Carnivora: canid (dog, gray fox), felid (cat), procyonid (raccoon, ringtail); Chiroptera: vespertilionid (little brown bat); Primates: hominid (human); Passeriformes: emberizid (bunting)	trauma, irritation, dermatitis (vector for Lyme disease)	North America
I. annulatus	Artiodactyla: cervid (white-tailed deer)		North America
I. (*Exopalpiger*) *antechini*	Dasyuromorphia: dasyurid (eastern quoll, yellow-footed antechinus, dusky antechinus, brown antechinus, swamp antechinus, fat-tailed dunnart, slender-tailed dunnart); Procellariiformes: procellariid (fairy prion)		Australia
I. (*Ixodes*) *apronophorus* (syn. *I. apronatus,*	Artiodactyla: suid (pig); Rodentia: castorid (Eurasian beaver), cricetid (common vole, bank vole, tundra vole, northern red-backed vole, short-tailed field vole, narrow-headed vole, European water	(vector for Omsk haemorrhagic	Eurasia

pari)	vole, grey dwarf hamster, European hamster, muskrat), dipodid (great jerboa), echimyid (nutria), murid (striped field mouse, yellow-necked mouse, wood mouse, Eurasian harvest mouse, brown rat), sciurid (red squirrel, spotted giant flying squirrel, Siberian chipmunk); Eulipotyphla: soricid (common shrew, Eurasian pygmy shrew, Mediterranean water shrew, Eurasian water shrew); Lagomorpha: leporid (hare), Carnivora: canid (dog, red fox); Primates: hominid (human); Columbiformes: columbid (collared dove); Gruiformes: rallid (spotted crake); Passeriformes: fringillid (brambling), motacillid (white- wagtail), muscicapid (unspecified), parid (great tit), turdid (common blackbird); Serpentes: viperid (unspecified)	fever virus and possibly tularemia, babesiosis, encephalitis virus)	
I. aptericola	Apterygiformes: apterygid (southern brown kiwi)		New Zealand
I. apteridis	Apterygiformes: apterygid (North Island brown kiwi, southern brown kiwi)		New Zealand
I. arabukiensis	Carnivora: herpestid (bushy-tailed mongoose)		Africa
I. (*Pholeoixodes*) *arboricola* (syn. *I. dryadis, passericola, strigicola*) (tree-hole tick)	Rodentia: murid (mouse, yellow-necked mouse); Carnivora: canid (dog); Chiroptera: vespertilionid (common noctule); Charadriiformes: burhinid (stone-curlew); Columbiformes: columbid (dove); Falconiformes: falconid (peregrine falcon); Galliformes: phasianid (chicken); Passeriformes: acrocephalid (reed warbler), certhiid (Eurasian treecreeper), corvid (jackdaw), fringillid (European greenfinch, bullfinch), hirundinid (sand martin), muscicapid (European robin, pied flycatcher, spotted flycatcher, collared flycatcher, isabelline wheatear, common redstart, black redstart), parid (great tit, European crested tit, Eurasian blue tit, marsh tit, willow tit, coal tit), passerid (house sparrow, rock sparrow, Eurasian tree sparrow, white-winged snowfinch), phylloscopid (willow warbler), sittid (Eurasian nuthatch), sturnid (common starling), sylviid (Eurasian blackcap), troglodytid (wren), turdid (common blackbird); Piciformes: picid (great spotted woodpecker); Strigiformes: strigid (western barn owl, little owl, tawny owl)	trauma, irritation (possible vector for borreliosis, rickettsioses, encephalitis virus)	Africa, Eurasia, North America
I. (*Ixodes*) *arebiensis*	host unknown, collected from vegetation		Africa
I. ariadnae	Chiroptera: vespertilionid (brown long-eared bat, greater mouse-eared bat, lesser mouse-eared bat, pond bat, Alcathoe bat, Bechstein's bat, Daubenton's bat, Geoffroy's bat, Natterer's bat)		Europe
I. (*Ixodes*) *arvicolae*	Rodentia: cricetid (European water vole), echimyid (nutria), murid (house mouse, wood mouse): Eulipotyphla: soricid (lesser white-toothed shrew)		Europe
I. asanumai	Squamata: lacertid (green grass lizard); scincid (Japanese five-lined skink, Ousima skink); Carnivora: canid (dog)		Japan
I. (*Eschatocephalus*) *audyi*	Rodentia: murid (mountain giant Sunda rat)		Asia
I. (*Afrixodes*) *aulacodi*	Artiodactyla: bovid (black duiker, Maxwell's duiker, royal antelope, harnessed bushbuck); Eulipotyphla: soricid (Oriental shrew); Rodentia: hystricid (brush-tailed porcupine), murid (Rudd's mouse, gerbil), nesomyid (Gambian pouched rat), thryonomyid (greater cane rat); Carnivora: herpestid (Egyptian mongoose), viverrid (African civet); Galliformes: numidid (helmeted guineafowl); Passeriformes: cisticolid (white-chinned prinia)		Africa
I. (*Afrixodes*) *auriculaclongae*	Rodentia: murid (mouse, brush-furred mouse, southern multimammate mouse, black rat); Eulipotyphla: soricid (unspecified shrew)		Africa
I. (*Multidentatus*) *auritulus* (syn. *I. thoracicus*)	Accipitriformes: accipitrid (bald eagle); Apodiformes: apodid (white-throated swift); Charadriiformes: lariid (kelp gull, New Zealand Antarctic tern), scolopacid (South Island snipe, Antipodes snipe, Subantarctic snipe), stercorariid (brown skua, South polar skua); Columbiformes: columbid (ruddy ground dove); Falconiformes: falconid (striated caracara); Galliformes: cracid (horned guan, rusty-margined guan), odontophorid (spotted wood quail), phasianid (ruffed grouse, blue grouse, willow grouse, dusky grouse); Gruiformes: rallid (western weka, Stewart Island weka);	trauma (possible vector for borreliosis)	Americas, Africa, Australia, New Zealand

	Passeriformes: acanthizid (Tasmanian scrubwren), artamid (black currawong), callaeid (South Island saddleback), certhiid (Eurasian treecreeper), conopophagid (rufous gnateater), corvid (American crow, Steller's jay), emberizid (uniform finch, buff-throated warbling finch, black-and-rufous warbling finch, mourning sierra-finch, greenish yellow-finch, double-collared seedeater, slender-billed finch), fringillid (pale-naped brushfinch, slaty brushfinch, purple finch), furnariid (thorn-tailed rayadito, canebrake groundcreeper, blackish cinclodes, buff-winged cinclodes, dark-bellied cinclodes, white-throated treerunner, rufous-capped spinetail, Spix's spinetail, buff-browed foliage-gleaner, white-chinned thistletail, rufous hernero, sharp-tailed streamcreeper, freckle-breasted thornbird), icterid (Austral blackbird, long-tailed meadowlark), motacillid (pipit), parulid (white-rimmed warbler, golden-crowned warbler, masked yellowthroat, ovenbird), passerellid (pale-naped brushfinch, slaty brushfinch, volcano junco, Shufeldt's junco, dark-eyed junco, rufous-collared sparrow, savannah sparrow, fox sparrow, Kodiak fox sparrow), passerid (sparrow, song sparrow, rusty song sparrow), petroicid (western yellow robin), rhinocryptid (tapaculo), rhinocryptid (unspecified tapalco), thamnophilid (variable antshrike, rufous-capped antshrike), thraupid (scarlet-bellied mountain tanager, golden-crowned tanager, lacrimose mountain tanager, blue-and-yellow tanager, blue-and-black tanager, black-goggled tanager, blue-capped tanager, diademed tanager, white-sided flowerpiercer, slaty flowerpiercer, uniform finch, gray-throated warbling finch, buff-throated warbling finch, black-and-rufous warbling finch, greenish yellow finch, slender-billed finch, pardusco, mourning sierra finch, golden-billed saltator, double-collared seedeater), troglodytid (house wren, bay wren, timberline wren, moustached wren, bay wren, Santa Marta wren), turdid (black-billed nightingale-thrush, white-necked thrush, creamy-bellied thrush, mountain thrush, Austral thrush, sooty thrush, Andean slaty thrush, rufous-bellied thrush, varied thrush), tyrannid (white-crested elaenia, velvety black tyrant, mottle-cheeked tyrannulet); Pelecaniformes: ardeid (black-crowned night heron), Piciformes: picid (Andean flicker); Procellariiformes: diomedeid (wandering albatross, Atlantic yellow-nosed albatross, black-browed albatross, Gibson's albatross), oceanitid (black-bellied storm petrel, white-faced storm petrel), pelecanoidid (Magellanic diving petrel), procellariid (sooty shearwater, flesh-footed shearwater, Buller's shearwater, Hutton's shearwater, grey petrel, soft-plumaged petrel, great-winged petrel, common diving petrel, Kerguelen petrel, fairy prion, broad-billed prion, fulmar prion, Antarctic prion); Psittaciformes: nestorid (South Island kaka), strigopid (kakapo); Sphenisciformes: spheniscid (king penguin, Snares penguin, little penguin, yellow-eyed penguin); Tinamiformes: tinamid (Andean tinamou); Rhynchocephalia: sphenodontid (tuatara); Carnivora: otariid (New Zealand sea lion); Rodentia: cricetid (olive montane mouse, forest small rice rat, Tome's rice rat, meadow vole), sciurid (golden-mantled ground squirrel, yellow-bellied marmot, woodchuck)		
I. (*Endopalpiger*) *australiensis*	Artiodactyla: bovid (cattle), suid (pig); Diprotodontia: macropodid (quokka), potoroid (long-nosed potoroo, boodie, woylie); Carnivora: canid (dog); Primates: hominid (human)		Australia
I. (*Pholeoixodes*) *baergi*	Passeriformes: hirundinid (cliff swallow); Primates: hominid (human)		North America
I. (*Afrixodes*) *bakeri*	Eulipotyphla: soricid (swamp musk shrew, forest shrew); Macroscelidea: macroscelidid (elephant shrew); Rodentia: murid (African vlei rat)		Africa
I. (*Pholeoixodes*) *bakonyensis*	Carnivora: mustelid (European badger)		Europe
I. (*Pholeoixodes*) *banksi*	Rodentia: castorid (American beaver), cricetid (muskrat); Carnivora: mustelid (North American river otter); Primates: hominid (human)	trauma, irritation,	North America

		dermatitis (plus vector for tularemia)	
I. barkeri	Monotremata: tachyglossid (short-beaked echidna)		Australia
I. (*Afrixodes*) *bedfordi*	Rodentia: murid (African vlei rat, four-striped mouse)		Africa
I. bengalensis	Sauria (varanid (Bengal monitor)		India
I. (*Scaphixodes*) *berlesei*	Apodiformes: apodid (Pacific swift); Columbiformes: columbid (rock dove); Falconiformes: falconid (common kestrel, gyrfalcon); Passeriformes: emberizid (unspecified), cariliid (unspecified), corvid (red-billed chough, Daurian jackdaw, western jackdaw), muscicapid (blue rock-thrush, northern wheatear, white-winged redstart, black redstart), passerid (unspecified), sturnid (starling), turdid (unspecified)		Palearctic
I. (*Ixodes*) *bequaerti*	Passeriformes: emberizid (unspecified), malurid (red-winged fairywren), thraupid (blue-black grassquit), turdid (unspecified thrush); Trogoniformes: trogonid (collared trogon, resplendent quetzal)		Central America
I. bimaculatus (syn. *I. hippopotamensis, Hyalomma hippopotamense, Amblyomma hippopotami*) (now *Cosmiomma hippopotamensis*)	Artiodactyla: hippopotamid (hippopotamus)		Africa
I. birmanensis	Testudines: geomyid (Indian black turtle), testudinid (elongated tortoise)		Africa, Asia
I. (*Ixodes*) *bivari*	Lagomorpha: leporid (rabbit)		Europe
I. bocatorensis	Lagomorpha: cuniculid (lowland paca); Rodentia: dasyproctid (red-rumped agouti, Central American agouti); Pilosa: bradypodid (pale-throated sloth), cyclopedid (silky anteater), myrmecophagid (southern tamandua); Perissodactyla: tapirid (South American tapir)		South America
I. (*Ixodes*) *boliviensis* (syn. *I. bicornis*)	Artiodactyla: bovid (cattle), cervid (white-tailed deer); Perissodactyla: equid (horse, mule), tapirid (Baird's tapir); Didelphimorphia: didelphid (common opossum); Rodentia: erethizontid (Mexican hairy dwarf porcupine), sciurid (unspecified squirrel); Carnivora: canid (dog, bush dog, fox), felid (cat, jaguar, cougar), procyonid (raccoon, white-nosed coati, South American coati), ursid (spectacled bear); Primates: hominid (human); Galliformes: cracid (great curassow), phasianid (pheasant)		Americas
I. (*Afrixodes*) *brewsterae*	Carnivora: felid (unspecified), herpestid (marsh mongoose, Egyptian mongoose)		Africa
I. (*Afrixodes*) *browningi*	Rodentia: murid (brush-furred mouse, soft-furred mouse), sciurid (sun squirrel, red-legged sun squirrel, Thomas's rope squirrel)		Africa
I. (*Afrixodes*) *brumpti*	Hyracoidea: procaviid (yellow-spotted rock hyrax)		Africa
I. (*Ixodes*) *brunneus* (syn. *I. bifurcatus*)	Accipitriformes: accipitrid (golden eagle); Anseriformes: anatid (greylag goose); Columbiformes: columbid (mourning dove, lemon dove); Galliformes: odontophorid (bobwhite quail), phasianid (turkey); Gruiformes: rallid (corn crake); Piciformes: rhampastid (toucan); Passeriformes: bombycillid (cedar waxwing), cardinalid (black-headed grosbeak, western tanager), corvid (blue jay, coast jay, Eurasian jay, Steller's jay), emberizid (common reed bunting), fringillid (house finch, purple finch, hawfinch, American goldfinch, European greenfinch, brambling), hirundinid (barn swallow, violet-green swallow), icterid (red-winged blackbird, meadowlark, common grackle, purple grackle), laniid (island shrike), mimid (brown thrasher, grey catbird), motacillid (meadow pipit, tree pipit, white-browed wagtail), muscicapid (European robin, whinchat, European stonechat), parid (great tit), parulid (ovenbird), passerellid (dark-eyed junco, slate-coloured junco, field sparrow, white-throated sparrow, golden-crowned sparrow, white-crowned sparrow, song	lesions, paralysis	Americas

	sparrow, fox sparrow, eastern towhee, white-eyed towhee), passerid (house sparrow, chipping sparrow, Eurasian tree sparrow, Italian sparrow), pycnonotid (brown-eared bulbil), regulid (goldcrest), sittid (Eurasian nuthatch), Sturnid (starling), thraupid (masked crimson tanager), troglodytid (winter wren, Carolina wren), turdid (blackbird, red-winged blackbird, eastern bluebird, American robin, true thrush, hermit thrush, song thrush, Andean slaty thrush, ring ouzel); Rheiformes: rheid (greater rhea); Strigiformes: strigid (barred owl); Rodentia: cricetid (marsh rice rat), sciurid (eastern gray squirrel); Carnivora: felid (cat); Microbiotheria: microbiotherid (colocolo opossum); Primates: hominid (human)		
I. calcarhebes	Rodentia: murid (Natal multimammate mouse)		Africa
I. (*Scaphixodes*) *caledonicus* (northern bird tick)	Apodiformes: apodid (common swift); Charadriiformes: alcid (Atlantic puffin), larid (black-legged kittiwake); Columbiformes: columbid (dove, pigeon); Falconiformes: falconid (peregrine falcon, gyrfalcon, kestrel); Passeriformes: corvid (jackdaw, hooded crow, common raven), fringillid (crossbill), muscicapid (common redstart, black redstart, blue rock thrush), sturnid (starling); Procellariiformes: procellariid (northern fulmar)		Palearctic
I. californicus	Artiodactyla: bovid (cattle, goat), cervid (black-tailed deer, elk); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit, mountain cottontail, hare); Rodentia: caviid (guinea pig), cricetid (long-tailed vole, white-footed mouse), murid (house mouse, rat), sciurid (ground squirrel); Carnivora: canid (dog, American red fox, gray fox), felid (cat); Primates: hominid (human); Galliformes: phasianid (chicken, grouse); Passeriformes: mimid (crissal thrasher); Strigiformes: strigid (burrowing owl); Sauria: anguid (alligator lizard), phrynosomatid (western fence lizard)		North America
I. (*Ixodes*) *candavius*	Artiodactyla: bovid (goat)		Australia
I. (*Pholeoixodes*) *canisuga* (syn. *I. barbarossae, latirostris, melicola, sciuricola, vulpicola, vulpinus, autumnalis vulpis*) (dog tick)	Artiodactyla: bovid (sheep), cervid (red deer, muntjac), suid (pig); Perissodactyla: equid (horse, mule); Lagomorpha: leporid (rabbit), ochotonid (Daurian pika); Eulipotyphla: erinaceid (European hedgehog, northern white-breasted hedgehog); Rodentia: sciurid (tarbagan marmot, long-tailed marmot, squirrel, ground squirrel); Carnivora: canid (dog, golden jackal, red fox), felid (cat), herpestid (small Asian mongoose), mustelid (European badger, pine marten, ferret, mink); Passeriformes: corvid (western jackdaw), hirundinid (sand martin), parid (Eurasian blue tit, great tit), passerid (house sparrow, tree sparrow), sittid (Eurasian nuthatch), sturnid (common starling); Strigiformes: strigid (little owl)	trauma, pruritus, dermatitis, alopecia, anaemia (plus vector for babesiosis, theileriosis)	Eurasia
I. (*Alloixodes*) *capromydis**	Rodentia: echimyid (Desmarest's hutia)	trauma	Cuba
I. catarinensis	Carnivora: felid (cat); Didelphimorphia: didelphid (woolly mouse opossum); Rodentia: cricetid (Paraguayan rice rat)		South America
I. (*Afrixodes*) *catherinei*	Lagomorpha: leporid (scrub hare)		Africa
I. (*Afrixodes*) *cavipalpus*	Artiodactyla: bovid (cattle, sheep, goat, korrigum, klipspringer, waterbuck, reedbuck, steenbok, Kirk's dikdik, steenbok, common duiker, bay duiker, Lichtenstein's hartebeest, Thomson's gazelle); Lagomorpha: leporid (hare); Eulipotyphla: erinaceid (South African hedgehog); Carnivora: canid (dog, side-striped jackal), felid (cat, African wildcat, lion, leopard), herpestid (slender mongoose), viverrid (common genet, rusty-spotted genet, African civet, Congo civet); Primates: cercopithecid (yellow baboon, moustached guenon), hominid (human)		Africa
I. (*Afrixodes*) *ceylonensis*	Artiodactyla: bovid (cattle); Eulipotyphla: soricid (Asian house shrew); Rodentia: herpestid (ruddy mongoose), murid (black rat, bandicoot rat, Indian bush rat, Blanford's rat, little Indian field mouse), sciurid (jungle palm squirrel); Carnivora: felid (leopard cat, jungle cat), herpestid (ruddy mongoose); Primates: cercopithecid (bonnet macaque); Passeriformes: alaudid (unspecified lark)	(possible vector for Kyasanur Forest disease)	Sri Lanka
I. (*Pholeoixodes*) *chilensis*	Chiroptera: vespertilionid (Chilean myotis)		South America

I. chiropterorum	Chiroptera: miniopterid (common bent-wing bat), rhinolophid (greater horseshoe bat), vespertilionid (Natterer's bat)		Europe
I. chordeilis	Caprimulgiformes: caprimulgid (common nighthawk)		North America
I. (*Afrixodes*) *colasbelcouri*	Afrosoricida: tenrecid (tailless tenrec); Eulipotyphla: (soricid (shrew); Rodentia: murid (roof rat, black rat), nesomyid (unspecified rat)		Madagascar
I. (*Eschatocephalus*) *collaris*	Chiroptera: hipposiderid (Pomona roundleaf bat), rhinolophid (interme4diate horseshoe bat)		Asia
I. (*Scaphixodes*) *collocaliae*	Apodiformes: apodid (white-rumped swiftlet)		Australasia
I. columnae	Rodentia: cricetid (red-backed vole), murid (large Japanese field mouse, small Japanese field mouse), sciurid (red squirrel, Japanese squirrel, Japanese giant flying squirrel); Lagomorpha: leporid (rabbit); Primates: hominid (human); Galliformes: phasianid (ring-necked pheasant, Swinhoe's pheasant); Piciformes: picid (unspecified woodpecker); Passeriformes: alcippeid (grey-cheeked fulvetta), cettid (yellow-bellied bush warbler), emberizid (black-faced bunting), muscicapid (snowy-browed flycatcher, white-browed bush robin), paradoxornithid (vinous-throated parrotbill), turdid (pale thrush), zosteropid (Taiwan yuhina)		Palearctic
I. (*Pholeoixodes*) *conepati*	Rodentia: sciurid (rock squirrel); Carnivora: mephitid (skunk, hog-nosed skunk), procyonid (ringtail)		North America
I. (*Sternalixodes*) *confusus*	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Diprotodontia: macropodid (unspecified wallaby); Carnivora: felid (cat); Aves (unspecified)		New Guinea
I. (*Pholeoixodes*) *cookei* (syn. *I. cruciarius*)	Artiodactyla: bovid (cattle, sheep); Didelphimorphia: didelphid (common opossum, Virginia opossum); Eulipotyphla: soricid (masked shrew, American water shrew); Lagomorpha: leporid (eastern cottontail); Rodentia: cricetid (deer mouse, eastern meadow vole), erethizontid (North American porcupine), geomyid (pocket gopher), hystricid (unspecified porcupine), murid (brown rat, field mouse, northern golden mouse), sciurid (groundhog, prairie dog, marmot, pallid yellow-bellied woodchuck, southern woodchuck, rock squirrel, brown ground squirrel, fox squirrel, gray squirrel, thirteen-lined ground squirrel), zapodid (meadow jumping mouse); Carnivora: canid (dog, coyote, American red fox, gray fox), castorid (American beaver), felid (cat, bobcat, cougar), mephitid (striped skunk, spotted skunk, Rio Grande spotted skunk, Florida skunk), mustelid (North American river otter, long-tailed weasel, short-tailed weasel, least weasel, ferret, American mink, European mink, American badger, fisher, marten, stoat), phocid (unspecified seal), procyonid (common raccoon, eastern raccoon, ringtail), viverrid (civet); Primates: hominid (human); Strigiformes: strigid (snowy owl); Passeriformes: emberizid (unspecified bunting), turdid (American robin)	trauma, irritation, dermatitis (vector for Powassan encephalitis, tularemia, spotted fever, borreliosis (Lyme disease), filarioid nematode (*Ackertia marmotae*))	Americas
I. (*Ixodes*) *cooleyi*	Rodentia: ctenomyid (tuco-tuco)		South America
I. (*Ixodes*) *copei*	Passeriformes: mimid (northern mockingbird), turdid (white-eyed thrush)		Central America
I. (*Sternalixodes*) *cordifer**	Dasyuromorphia: dasyurid (unspecified); Diprotodontia: petaurid (striped possum), phalangerid (southern common cuscus, northern common cuscus, white cuscus, Sulawesi bear cuscus), macropodid (unspecified wallaby); Rodentia: murid (Pacific rat, marmoset xanthurus rat); Primates: tarsiid (Dian's tarsier, Lariang tarsier); Gruiformes: rallid (unspecified rail); Passeriformes: acanthazid (unspecified peep-warbler, unspecified scrub-wren), cnemophilid (silken satinbird, velvet satinbird), locustellid (malia, chestnut-backed bush warbler), meliphagid (unspecified honeyeater), muscicapid (rufous-throated flycatcher), oriolid (pitohui), pachycephalid (unspecified whistler), paradisaeid (short-tailed paradigalla), petroicid (Australasian robin), rhipidurid (unspecified fantail), turdid (unspecified bubbling thrush), zosteropid (white-eye)	trauma	Australasia
I. coreensis	Carnivora: canid (Korean raccoon dog)		Asia
I. (*Exopalpiger*)	Galliformes (unspecified quail)		South America

cornuae			
I. (*Sternalixodes*) *cornuatus* (Tasmanian paralysis tick, southern paralysis tick)	Artiodactyla: bovid (cattle, sheep); Diprotodontia: macropodid (common wallaroo, Tasmania pademelon, kangaroo, wallaby), phalangerid (common brushtail possum), phascolarctid (koala), potoroid (Tasmania bettong), vombatid (common wombat); Peramelemorphia: peramelid (southern brown bandicoot, eastern barred bandicoot); Rodentia: murid (black rat, bush rat, swamp rat, house mouse); Carnivora: canid (dog), felid (cat); Primates: hominid (human); Passeriformes: acanthizid (Tasmanian scrubwren), artamid (black currawong, grey butcherbird), pachycephalid (grey shrike-thrush)	trauma, toxicosis, paralysis	Australia
I. (*Afrixodes*) *corwini*	Carnivora: canid (dog), felid (cat), herpestid (common slender mongoose, Cape gray mongoose), mustelid (African clawless otter), viverrid (common genet, Cape genet)		Africa
I. (*Ixodes*) *cuernavacensis*	Apodiformes: apodid (white-naped swift)		North America
I. (*Afrixodes*) *cumulatimpunctatus**	Artiodactyla: bovid (royal antelope, harnessed bushbuck, bongo, oribi, bay duiker, black duiker, zebra duiker, Maxwell's duiker), suid (red river hog), tragulid (water chevrotain); Eulipotyphla: soricid (unspecified shrew); Pholidota: manid (African black-bellied pangolin); Hyracoidea: procaviid (western tree hyrax); Rodentia: hystricid (African brush-tailed porcupine), murid (typical striped grass mouse, delectable soft-furred mouse, rusty-bellied brush-furred rat, marsh rat, Indian gerbil), nesomyid (Gambian pouched rat), sciurid (fire-footed rope squirrel), thryomomyid (greater cane rat); Carnivora: felid (leopard), herpestid (marsh mongoose, common kusimanse), viverrid (African civet); Primates: cercopithecid (Diana monkey), hominid (chimpanzee); Cuculiformes: cuculid (Senegal coucal); Galliformes: numidid (plumed guineafowl, black guineafowl), Passeriformes: turdid (Fraser's rufous thrush)	trauma, irritation	Africa
I. (*Pholeoixodes*) *dampfi*	Rodentia: geomyid (pocket gopher)		North America
I. (*Pholeoixodes*) *danyi*	Carnivora: canid (fox)		Europe
I. (*Ixodes*) *daveyi*	Artiodactyla: bovid (buffalo); Proboscidea: elephantid (elephant); Hyracoidea: procaviid (hyrax); Columbiformes: columbid (lemon dove); Musophagiformes: musophagid (purple-crested turaco, Rwenzori turaco); Passeriformes: cisticolid (croaking cisticola), ploceid (red-billed quelea), turdid (olive thrush)		Africa
I. (*Afrixodes*) *dawesi*	Afrosoricida: potamogalid (giant otter shrew, Ruwenzori otter shrew), tenrecid (tenrec)		Africa
I. (*Sternalixodes*) *dendrolagi*	Diprotodontia: macropodid (Matchie's tree-kangaroo)		New Guinea
I. (*Ixodes*) *dentatus*	Artiodactyla: bovid (sheep); Didelphimorphia: didelphid (opossum); Lagomorpha: leporid (eastern cottontail, New England cottontail, European rabbit, swamp rabbit, snowshoe hare); Rodentia: cricetid (muskrat, meadow vole, deer mouse, white-footed mouse), murid (golden harvest mouse, brown rat, cotton rat), sciurid (American red squirrel, Douglas squirrel, groundhog); Carnivora: procyonid (common raccoon); Primates: hominid (human); Galliformes: odontophorid (bobwhite quail); Passeriformes: cardinalid (northern cardinal), corvid (blue jay), icterid (common grackle), mimid (brown thrasher), parid (tufted titmouse), passerellid (song sparrow, swamp sparrow, fox sparrow, field sparrow, white-throated sparrow, white-crowned sparrow, dark-eyed junco, eastern towhee), passerid (house sparrow), troglodytid (Carolina wren), turdid (hermit thrush, Swainson's thrush)	trauma, irritation, dermatitis (vector for Lyme disease, Connecticut virus, spotted fever, tularemia)	North America
I. (*Ixodes*) *dicei*	Lagomorpha: leporid (Dice's cottontail)		Costa Rica
I. didelphis	Didelphimorphia: didelphid (brown four-eyed opossum, white-eared opossum, Brazilian opossum); Rodentia: caviid (guinea pig), murid (mouse)		South America
I. diversicoxalis	Rodentia: cricteid (social vole), murid (house mouse, wood mouse);		Central Asia

	Eulipotyphla: soricid (greater white-toothed shrew)		
I. (*Ixodes*) *diversifossus*	Artiodactyla: bovid (cattle); Lagomorpha: leporid (hare, mountain cottontail, jack rabbit, black-tailed jack rabbit, Washington jack rabbit); Rodentia: cricetid (woodrat), sciurid (Townsend's chipmunk); Carnivora: procyonid (common raccoon); Galliformes: odontophorid (bobwhite quail); Passeriformes: passerellid (fox sparrow)		North America
I. (*Afrixodes*) *djaronensis*	Carnivora: viverrid (large spotted genet, mongoose)		Africa
I. (*Ixodes*) *domerguei*	Passeriformes: ploceid (nelicourvi weaver), vangid (common newtonia)		Madagascar
I. donarthuri	Artiodactyla: bovid (common duiker, southern reedbuck)		Africa
I. downsi	Chiroptera: phyllostomid (Geoffroy's tailless bat); Caprimulgiformes: steatornithid (oilbird)		Central America
I. (*Afrixodes*) *drakensbergensis*	Artiodactyla: bovid (cattle, goat, eland)		Africa
I. (*Ixodes*) *eadsi*	Rodentia: heteromyid (Mexican spiny pocket mouse), cricetid (white-footed mouse, hispid cotton rat), murid (house mouse, fulvous harvest mouse), sciurid (chipmunk); Eulipotyphla: soricid (shrew)		North America
I. eastoni	Rodentia: cricetid (southern red-backed vole, long-tailed vole, eastern meadow vole, bushy-tailed woodrat, eastern deer mouse), dipodid (unspecified), sciurid (least chipmunk), zapodid (meadow jumping mouse); Eulipotyphla: soricid (common shrew)		North America
I. (*Multidentatus*) *eichorni* (syn. *I. mindanensis*)	Coraciiformes: alcedinid (kingfisher); Galliformes: phasianid (red junglefowl); Passeriformes: turdid (Norfolk thrush); Primates: hominid (human)		Australasia
I. eidmanni	Rodentia: nesomyid (Gambian pouched rat)		Africa
I. eldaricus	Rodentia: cricetid (grey dwarf hamster), murid (Cairo spiny mouse, house mouse, wood mouse, field mouse, mouse-like hamster, Persian jird, short-tailed bandicoot rat); Eulipotyphla: soricid (bicolored shrew); Carnivora: canid (red fox), felid (jungle cat); Chiroptera: rhinolophid (horseshoe bat); Charadriiformes: larid (gull); Galliformes: phasianid (common partridge, rock partridge, grey partridge, chukar partridge); Passeriformes: alaudid (lark), cettid (Cetti's warbler), corvid (crow), emberizid (red-headed bunting), fringillid (finch), locustellid (common grasshopper warbler), motacillid (tree pipit, tawny pipit), muscicapid (common redstart, Eversmann's redstart, European robin), passerid (house sparrow, saxaul sparrow), prunellid (dunnock), sittid (nuthatch), sturnid (common starling), sylviid (whitethroat), turdid (common blackbird, song thrush, black-throated thrush); Strigiformes: strigid (owl)		Central Asia
I. (*Afrixodes*) *elongatus*	Macroscelidea: macroscelidid (short-snouted elephant shrew); Rodentia: murid (black rat, southern multimammate mouse, Natal multimammate mouse, red veld rat, creek rat); Eulipotyphla: soricid (shrew)		Africa
I. (*Multidentatus*) *eudyptidis* (syn. *I. intermedius, neumanni, praecoxalis*)	Anseriformes: anatid (unspecified duck); Charadriiformes: larid (silver gull, kelp gull, red-billed gull, black-backed gull, whiskered tern, black-fronted tern, Antarctic tern, Caspian tern), Pelecaniformes: threskiornithid (royal spoonbill); Procellariiformes: diomedeid (northern royal albatross, northern Buller's albatross, Chatham albatross), pelecanoidid (common diving petrel), procellariid (white-headed petrel, soft-plumaged petrel, Cook's petrel, Providence petrel, fairy prion); Sphenisciformes: spheniscid (yellow-eyed penguin, little penguin, Fiordland penguin); Suliformes: phalacrocoracid (great cormorant, spotted shag), sulid (northern gannet, Australasian gannet); Strigiformes: tytonid (Tasmanian masked owl); Rodentia: murid (mouse)		Australia, New Zealand
I. euplecti	Passeriformes: cisticolid (rattling cisticola, croaking cisticola), fringillid (yellow-fronted canary), malaconotid (black-crowned tchagra), motacillid (tree pipit), muscicapid (northern wheatear), ploceid (yellow-mantled widowbird, yellow bishop, yellow-crowned		Africa

	bishop, black bishop, black-winged red bishop, Baglafecht weaver), pycnonotid (yellow-throated leaflove), turdid (African thrush, Abyssinian ground thrush)		
I. (*Afrixodes*) *evansi*	Artiodactyla: bovid (harnessed bushbuck)		Africa
I. exaratus	Chiroptera: vespertilionid (parti-coloured bat, western barbastelle)		Europe
I. exilipes	Sauria: lacertid (ocellated lizard)		Africa
I. (*Exopalpiger*) *fecialis*	Dasyuromorphia: dasyurid (yellow-footed antechinus, dusky antechinus, brown antechinus, fawn antechinus, fat-tailed dunnart, slender-tailed dunnart, tiger quoll, western quoll, eastern quoll, Tasmanian devil), myrmecobiid (numbat); Peramelemorphia: peramelid (northern brown bandicoot, southern brown bandicoot, long-nosed bandicoot); Diprotodontia: macropodid (unspecified wallaby), phalangerid (brushtail possum), potoroid (unspecified); Rodentia: murid (mouse, black rat, bush rat, dusky field rat, pale field rat, , Australian swamp rat, fawn-footed mosaic-tailed rat); Perissodactyla: equid (horse); Carnivora: canid (dog), felid (cat); Primates: hominid (human)		Australia
I. (*Ixodes*) *festai* (syn. *I. thompsoni*)	Eulipotyphla: erinaceid (European hedgehog); Lagomorpha: leporid (European rabbit); Rodentia: glirid (garden dormouse, Maghreb garden dormouse), murid (black rat, wood mouse, Algerian mouse, Barbary striped grass mouse, North African gerbil), sciurid (red squirrel); Carnivora: canid (red fox), mustelid (common weasel); Galliformes: phasianid (chukar, Barbary partridge); Passeriformes: turdid (blackbird, thrush); Strigiformes: strigid (little owl); Sauria: agamid (Bibron's agama), lacertid (sand lizard, Algerian sand racer), scincid (ocellated skink, Algerian skink)		Africa
I. (*Pholeoixodes*) *filippovae* (syn. *I. crenulatus p.p.*)	Rodentia: sciurid (marmots)		Eurasia
I. (*Ixodes*) *fossulatus*	Artiodactyla: bovid (cattle); Carnivora: canid (dog)		Asia, South America
I. frequens	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Primates: hominid (human)		Japan
I. (*Ixodes*) *frontalis* (syn. *I. pallipes, pari, sturni*)	Accipitriformes: accipitrid (Harris's hawk); Anseriformes: anatid (greylag goose); Charadriiformes: haematopodid (unspecified oystercatcher); Columbiformes: columbid (unspecified dove); Falconiformes: falconid (common kestrel); Galliformes: phasianid (common quail); Gruiformes: rallid (corncrake, water rail); Passeriformes: acrocephalid (Eurasian reed warbler, great reed warbler), alaudid (woodlark), certhiid (treecreeper), cettid (Cetti's warbler), corvid (Eurasian magpie, Eurasian jay, Steller's jay, rook), emberizid (pine bunting, common reed bunting, yellowhammer), fringillid (European goldfinch, European greenfinch, chaffinch, hawfinch, brambling, bullfinch, linnet, redpoll, black rosy finch), laniid (red-backed shrike, brown shrike), locustellid (Savi's warbler), motacillid (tree pipit, meadow pipit, white wagtail), muscicapid (European robin, common redstart, black redstart, spotted flycatcher, red-breasted flycatcher, whinchat, European stonechat, common nightingale, thrush nightingale, bluethroat), parid (great tit, long-tailed tit, marsh tit, willow tit, coal tit, blue tit), passerid (house sparrow, tree sparrow, rock sparrow), phylloscopid (willow warbler, chiffchaff), prunellid (dunnock), reguliid (goldcrest), remizid (Eurasian penduline tit), sittid (Eurasian nuthatch), sturnid (starling), sylviid (barred warbler, Eurasian blackcap, Sardinian warbler, common whitethroat, lesser whitethroat), thraupid (masked crimson tanager), troglodytid (Eurasian wren), turdid (common blackbird, fieldfare, redwing, ring ouzel, song thrush, isabelline wheatear, hermit thrush); Piciformes: picid (great spotted woodpecker); Strigiformes: strigid (unspecified owl); Carnivora: mustelid (badger, marten); Primates: hominid (human)	(possible vector for arboviruses, borrelioses, anaplasmosis)	Palearctic
I. (*Ixodes*) *fuscipes*	Artiodactyla: bovid (cattle), cervid (brown brocket, little red		South America

(syn. *I. aragaoi*)	brocket); Perissodactyla: equid (horse); Didelphimorphia: didelphid (short-tailed opossum, northern three-striped opossum, yellow-sided opossum, big lutrine opossum); Pilosa: myrmecophagid (southern tamandua); Rodentia: cricetid (Azara's grass mouse, Parana grass mouse, black-footed pygmy rice rat, lesser Wilfred's mouse), cuniculid (paca), dasyproctid (red-rumped agouti), sciurid (Brazilian squirrel); Carnivora: canid (dog), felid (cougar, ocelot); Passeriformes: furnariid (freckle-breasted thornbird, buff-browed foliage-gleaner, black-billed scythe bill, lesser woodcreeper), parulid (white-browed warbler, golden-crowned warbler), thamnophilid (dusky-tailed antbird), thraupid (ruby-crowned tanager, black-goggled tanager), turdid (white-necked thrush, rufous-bellied thrush)		
I. fuscomaculatus	Serpentes: boid (common boa)		South America
I. (*Afrixodes*) *fynbosensis*	Rodentia: murid (four-striped grass mouse); Eulipotyphla: soricid (shrew); Carnivora: canid (dog)		Africa
I. (*Ixodes*) *galapagoensis*	Rodentia: cricetid (Galapagos rice rat)		Galapagos Islands
I. garhwalicus	Artiodactyla: bovid (sheep)		India
I. (*Exopalpiger*) *ghilarovi*	Rodentia: cricetid (grey dwarf hamster, European snow vole, Caucasian snow vole, Daghestan pine vole), murid (yellow-necked mouse); Eulipotyphla: soricid (Radde's shrew)		Russia
I. (*Ixodes*) *gibbosus*	Artiodactyla: bovid (cattle, sheep, goat), camelid (camel); Perissodactyla: equid (horse); Eulipotyphla: erinaceid (hedgehog); Lagomorpha: leporid (hare); Carnivora: canid (dog); Primates: hominid (human); Passeriformes: turdid (blackbird)		Palearctic
I. (*Endopalpiger*) *giluwensis*	Rodentia: murid (eastern white-eared giant rat, squirrel-toothed rat, Rothschild's woolly rat)		New Guinea
I. globulosus	Rodentia: hystricid (staple-tailed porcupine)		Asia
I. (*Exopalpiger*) *goliath*	Rodentia: murid (eastern white-eared giant rat)		New Guinea
I. (*Ixodes*) *granulatus*	Rodentia: cricetid (Mexican deer mouse, Chapman's rice rat), murid (house mouse, striped field mouse, pencil-tailed tree mouse, black rat, greater bandicoot rat, mountain spiny rat, Bartel's spiny rat, Rajah spiny rat, Whitehead's spiny rat, Annandale's rat, ricefield rat, unicoloured rice rat, grey tree rat, dark-tailed tree rat, long-tailed giant rat, Edward's long-tailed giant rat, Polynesian rat, yellow-breasted rat, mountain giant Sunda rat, Muller's giant Sunda rat, Malaysian wood rat, Manipur white-toothed rat, Bartel's rat, Musschenbroek's Sulawesi maxomys, Hoffman's Sulawesi rat), sciurid (gray-bellied squirrel, black-striped squirrel, gray squirrel, plantain squirrel, Anderson's squirrel, Low's squirrel, Pallas's squirrel, Prevost's squirrel, three-striped ground squirrel, Bornean mountain ground squirrel, northern palm squirrel, Javanese flying squirrel, least pygmy squirrel, giant squirrel, shrew-faced squirrel, Asian red-cheeked squirrel, slender squirrel); Eulipotyphla: erinaceid (short-tailed gymnure), soricid (moonrat, Malayan shrew, Oriental shrew); Scandentia: ptilocercid (pen-tailed treeshrew), tupaiid (common treeshrew, northern treeshrew, mountain treeshrew, Sumatran treeshrew, Bornean smooth-tailed treeshrew, Horsfield's treeshrew); Carnivora: felid (tiger), herpestid (mongoose); Primates: hominid (human); Sauria: scincid (little brown skink); Passeriformes: corvid (red-billed blue magpie), emberizid (black-faced bunting), sittid (Eurasian nuthatch), sylviid (unspecified warbler), timaliid (unspecified babbler), turdid (blackbird, pale thrush)		Eurasia
I. gregsoni	Carnivora: felid (cat), mustelid (mink, fisher, American marten)		North America
I. (*Ixodes*) *guatemalensis*	Rodentia: cricetid (big deer mouse), sciurid (red-bellied squirrel, Mexican gray squirrel); Eulipotyphla: soricid (Goodwin's broad-clawed shrew); Carnivora: mustelid (long-tailed weasel)		Central America
I. (*Ixodes*) *guernseyensis*	Rodentia: cricetid (bank vole)		Europe
I. (*Scaphixodes*) *gussevi*	Passeriformes: passerid (rock sparrow)		Central Asia

I. happinus	Artiodactyla: bovid (cattle)		Japan
I. hayashii	Carnivora: canid (dog)		Japan
I. (*Pholeoixodes*) *hearlei*	Rodentia: sciurid (pine squirrel, Streator's red squirrel, fox squirrel, golden-mantled ground squirrel, Tahoe chipmunk); Carnivora: procyonid (common raccoon)		North America
I. heathi	Diprotodontia: burramyid (mountain pygmy possum)		Australia
I. (*Afrixodes*) *heinrichi*	Passeriformes: macrosphenid (moustached grass warbler)		Africa
I. (*Pholeoixodes*) *hexagonus** (syn. *I. erinaceus, reduvius, sexpunctatus, crenulatus p.p.*) (hedgehog tick)	Artiodactyla: bovid (cattle, sheep, argali, goat, oryx), suid (pig, wild boar); Perissodactyla: equid (horse, donkey); Didelphimorphia: didelphid (opossum); Eulipotyphla: erinaceid (European hedgehog, northern white-breasted hedgehog, long-eared hedgehog), soricid (common shrew, pygmy shrew), talpid (European mole); Lagomorpha: leporid (European rabbit, mountain hare, desert hare, tolai hare, European hare, Chinese hare), ochotonid (Daurian pika); Rodentia: cricetid (grey dwarf hamster, European hamster, Chinese hamster, winter white dwarf hamster, northern mole vole, common vole, narrow-headed vole), dipodid (great jerboa, Mongolian five-toed jerboa), echimyid (coypu), geomyid (pocket gopher), glirid (garden dormouse, hazel dormouse, European edible dormouse), heterocephalid (mole rat), hystricid (crested porcupine), murid (house mouse, wood mouse, Eurasian harvest mouse, brown rat, black rat, short-tailed bandicoot rat, great gerbil), sciurid (red squirrel, eastern grey squirrel, little ground squirrel, golden-mantled ground squirrel, speckled ground squirrel, thirteen-lined ground squirrel, relict ground squirrel, Altai marmot, European ground squirrel, Daurian ground squirrel, long-tailed marmot, gray marmot, Bobak marmot, Menzbier's marmot, Tarbagan marmot, groundhog), sminthid (southern birch mouse, Tien Shan birch mouse); Carnivora: canid (dog, common raccoon dog, jackal, red fox, corsac fox), felid (cat, wildcat, ocelot), herpestid (Egyptian mongoose), mephitid (striped skunk), mustelid (European badger, Eurasian otter, stoat, least weasel, ferret, European polecat, steppe polecat, marbled polecat, European mink, beech marten, stone marten, European pine marten); Primates: hominid (human); Charadriiformes: charadriid (golden plover, European golden plover), scolopacid (ruff); Columbiformes: columbid (rock dove, common wood pigeon), Coraciiformes: coraciid (European roller), meropid (European bee-eater), Falconiformes: falconid (common kestrel, lesser kestrel); Galliformes: phasianid (common quail, grey partridge, rock partridge, chukar partridge); Gruiformes: rallid (corncrake); Passeriformes: acrocephalid (sedge warbler), alaudid (Eurasian skylark), corvid (red-billed chough), emberizid (rock bunting, yellowhammer), fringillid (common linnet, common chaffinch), hirundinid (sand martin), motacillid (tawny pipit, meadow pipit, pied wagtail), muscicapid (European robin, Siberian blue robin, collared flycatcher, pied flycatcher, isabelline wheatear, northern wheatear, common redstart, African stonechat), parid (great tit, Eurasian blue tit), passerid (house sparrow, rock sparrow, Eurasian tree sparrow), phylloscopid (common chiffchaff, willow warbler), prunellid (dunnock), regulid (common firecrest), sittid (western rock nuthatch), sturnid (common starling, rosy starling), sylviid (Eurasian blackcap, common whitethroat), troglodytid (Eurasian wren), turdid (common blackbird, song thrush, fieldfare); Strigiformes: strigid (little owl, swamp owl)	trauma, pruritus, dermatitis (plus vector for borreliosis, babesiosis, theileriosis, Russian encephalitis virus)	Eurasia, Africa, North America
I. (*Ixodes*) *himalayensis*	Rodentia: murid (mouse); Eulipotyphla: soricid (shrew)		India
I. (*Sternalixodes*) *hirsti* (Hirst's marsupial tick)	Diprotodontia: macropodid (western grey kangaroo, eastern grey kangaroo, red-necked wallaby, brush-tailed rock wallaby, red-necked pademelon, swamp wallaby), potoroid (brush-tailed bettong, long-nosed potoroo), petaurid (common ringtail possum, eastern ringtail possum), phalangerid (common brushtail possum, short-eared brushtail possum, Tasmanian brush-tailed possum),		Australia

	phascolarctid (koala); Carnivora: canid (dog), felid (cat); Rodentia: murid (bush rat, black rat); Passeriformes: acanthizid (striated thornbill, brown thornbill, white-bowed scrubwren), meliphagid (New Holland honeyeater, crescent honeyeater, tawny-crowned honeyeater, brown-headed honeyeater), muscicapid (scarlet robin), pardalotid (spotted pardalote)		
I. (*Pholeoixodes*) *holdenriedi*	Rodentia: geomyid (Botta's pocket gopher)		North America
I. (*Sternalixodes*) *holocyclus* (Australian paralysis tick, eastern paralysis tick)	Artiodactyla: bovid (cattle, sheep, goat), camelid (camel), cervid (deer), suid (pig); Perissodactyla: equid (horse); Dasyuromorphia: dasyurid (yellow-footed antechinus, tiger quoll, brush-tailed phascogale, slender-tailed dunnart); Peramelemorphia: peramelid (northern brown bandicoot, southern brown bandicoot, long-nosed bandicoot); Diprotodontia: macropodid (black-striped wallaby, red-necked wallaby, Godman's rock-wallaby, brush-tailed rock-wallaby, swamp wallaby, red-legged pademelon, red kangaroo, Lumholtz's tree kangaroo), petaurid (striped possum, sugar glider), phalangerid (short-eared possum, common brushtail possum); phascolarctid (koala), potoroid (rufous rat-kangaroo, northern bettong), vombatid (wombat); Monotremata: tachyglossid (short-beaked echidna); Lagomorpha: leporid (rabbit); Rodentia: caviid (guinea pig), murid (house mouse, brown rat, black rat, cane-field rat, dusky field rat, pale field rat, bush rat, rakali, fawn-footed mosaic-tailed rat, Papua grassland mosaic-tailed rat, giant white-tailed rat, naked-tail rat), sciurid (red squirrel, red-tailed squirrel); Carnivora: canid (dog, dingo), felid (cat); Chiroptera: pteropodid (spectacled flying-fox), vespertilionid (little bat); Primates: hominid (human); Anseriformes: anatid (duck); Cuculiformes: cuculid (unspecified cuckoo); Galliformes: phasianid (chicken, turkey); Psittaciformes: psittaculid (crimson rosella); Passeriformes: acanthizid (yellow-throated scrubwren, white-browed scrubwren), artamid (pied butcherbird, Australian magpie, Lord Howe currawong), corvid (Australian raven), meliphagid (unspecified honeyeater), pittid (noisy pitta), ptilonorhynchid (bowerbird); Psittaciformes: psittacid (crimson rosella)	trauma, toxicosis, paralysis (plus vector for Q fever, Queensland tick typhus)	Eastern Australia
I. (*Ixodes*) *hoogstraali*	Rodentia: murid (king jird)		Arabia
I. (*Scaphixodes*) *howelli*	Passeriformes: hirundinid (cliff swallow), fringillid (gray-crowned rosy finch); Falconiformes: falconid (prairie falcon)		North America
I. (*Ixodes*) *hyatti* (syn. *I. ochotonarius*)	Lagomorpha: ochotonid (Royle's pika, Moupin pika); Rodentia: murid (mouse)		Nepal, Pakistan
I. (*Endopalpiger*) *hydromyidis*	Rodentia: murid (rakali, sooty beaver-rat, bush rat, black rat)		Australia
I. imperfectus	Didelphimorphia: didelphid (Chaco fat-tailed opossum)		South America
I. inopinatus	Artiodactyla: bovid (cattle, sheep); Carnivora: canid (red fox); Serpentes: lamprophiid (Cape sand snake), Sauria: lacertid (Algerian sand racer), varanid (mangrove monitor)		Eurasia, Africa
I. (*Ceratixodes*) *jacksoni*	Suliformes: phalacrocoracid (spotted shag)	trauma	Australasia
I. japonensis	Artiodactyla: bovid (cattle, sheep), cervid (barking deer, Indian muntjac); Perissodactyla: equid (mule); Eulipotyphla: erinaceid (European hedgehog), soricid (greater white-toothed shrew), talpid (Japanese mole); Lagomorpha: leporid (rabbit, mountain hare; Scandentia: tupaiid (common treeshrew); Rodentia: cricetid (Bedford's red-backed vole, Japanese grass vole, red vole), heteromyid (California pocket mouse), murid (brown rat, Japanese house mouse, small Japanese field mouse, large Japanese field mouse), sciurid (ground squirrel); Carnivora: canid (dog, common raccoon dog), felid (cat), mustelid (Japanese weasel), ursid (giant panda); Primates: hominid (human)		Asia
I. (*Ixodes*) *jellisoni*	Rodentia: cricetid (canyon mouse), geomyid (pocket gopher), heteromyid (long-tailed pocket mouse, California pocket mouse, agile kangaroo rat, California kangaroo rat), sciurid (ground		North America

	squirrel); Carnivora: canid (dog), felid (cat); Primates: hominid (human)		
I. (*Exopalpiger*) *jonesae*	Rodentia: cricetid (soft-furred Oldfield mouse, forest small rice rat); Paucituberculata: caenolestid (Tate's shrew opossum)		South America
I. juvenis	Sauria: leiocephalid (unspecified iguana/curlytail)		South America
I. (*Pholeoixodes*) *kaiseri*	Carnivora: canid (red fox, desert fox), felid (jungle cat, African wildcat), hyaenid (striped hyena), mustelid (European badger); Eulipotyphla: erinaceid (European hedgehog); Rodentia: hystricid (Indian crested porcupine)		Eurasia, Africa
I. (*Pholeoixodes*) *kangdingensis*	Carnivora: mustelid (Siberian weasel)		China
I. (*Ixodes*) *kashmiricus*	Artiodactyla: bovid (cattle, sheep, goat); Rodentia: murid (house mouse, Turkestan rat), sciurid (flying squirrel); Carnivora: canid (dog); Primates: hominid (human); Sauria: agamid (rock agama)		Eurasia
I. (*Ixodes*) *kazakstani*	Artiodactyla: bovid (cattle); Eulipotyphla: soricid (long-tailed shrew); Lagomorpha: leporid (Tolai hare); Rodentia: cricetid (common vole, European snow vole, grey dwarf hamster), glirid (forest dormouse), murid (house mouse, wood mouse, midday jird, Tamarisk jird, great gerbil), sminthid (birch mouse); Primates: hominid (human); Galliformes: phasianid (rock partridge, ring-necked pheasant)		Central Asia
I. kelloggi	Passeriformes: corvid (Steller's jay), turdid (unspecified thrush)		North America
I. kempi	Rodentia: sciurid (red-bellied tree squirrel)		India
I. (*Multidentatus*) *kerguelensis*	Procellariiformes: diomedeid (wandering albatross), oceanitid (white-faced storm petrel), procellariid (grey petrel, soft-plumaged petrel, white-chinned petrel, Kerguelen petrel, Providence petrel, broad-billed prion, fairy prion, Antarctic prion, sooty shearwater, short-tailed shearwater, flesh-footed shearwater, common diving petrel, South Georgia diving petrel); Sphenisciformes: spheniscid (unspecified penguin); Psittaciformes: strigopid (kakapo)		Australia, New Zealand
I. (*Pholeoixodes*) *kingi* (syn. *I. pratti*) (rotund tick)	Rodentia: cricetid (desert woodrat, bushy-tailed woodrat, western harvest mouse, northern grasshopper mouse, southern grasshopper mouse, canyon mouse, pinyon mouse, cactus mouse, deer mouse, montane vole, sagebrush vole), geomyid (northern pocket gopher, Botta's pocket gopher, Mazama pocket gopher, Wyoming pocket gopher), heteromyid (little pocket mouse, long-tailed pocket mouse, Oregon pocket mouse, Great Basin pocket mouse, dark kangaroo mouse, chisel-toothed kangaroo rat, Merriam's kangaroo rat, Ord's kangaroo rat, Richardson's kangaroo rat), sciurid (black-tailed prairie dog, white-tailed prairie dog, Mexican prairie dog, Utah prairie dog, Gunninson's prairie dog, woodchuck, rock squirrel, Richardson's red squirrel, golden-mantled ground squirrel, Columbian ground squirrel, Wyoming ground squirrel, Richardson's ground squirrel, Townsend's ground squirrel, Uinta ground squirrel, white-tailed antelope squirrel, least chipmunk, cliff chipmunk, yellow-bellied marmot, pallid yellow-bellied woodchuck); Lagomorpha: leporid (cottontail, desert cottontail, mountain cottontail, rabbit, black-tailed jackrabbit), ochotonid (American pika); Carnivora: canid (dog, wolf, coyote, red fox, kit fox), felid (cat, bobcat), mephitid (striped skunk, western spotted skunk, eastern spotted skunk, hog-nosed skunk), mustelid (American badger, California badger, mink, black-footed ferret, long-tailed weasel), procyonid (common raccoon, ringtail); Serpentes: colubrid (striped whipsnake)	trauma, irritation, dermatitis (possible vector for tularemia)	North America
I. (*Multidentatus*) *kohlsi*	Charadriiformes: larid (greater crested tern, fairy tern); Sphenisciformes: spheniscid (little penguin); Suliformes: phalacrocoracid (black-faced cormorant), sulid (Australasian gannet); Procellariiformes: procellariid (short-tailed shearwater); Primates: hominid (human)		Australia
I. (*Lepidixodes*) *kopsteini** (syn. *I. paradoxus*) (Kopstein's bat tick)	Chiroptera: emballonurid (Theobald's tomb bat), molossid (white-striped free-tailed bat, northern free-tailed bat, little free-tailed bat, wrinkle-lipped free-tailed bat, Malayan free-tailed bat, Angolan free-tailed bat, hairless bat), vespertilionid (long-eared bat)	trauma, irritation	Africa, Asia, Australia

I. (*Ixodes*) *kuntzi*	Rodentia: murid (black rat, Coxing's white-bellied rat, Oldfield white-bellied rat, Taiwan field mouse), sciurid (Pallas's squirrel, Swinhoe's striped squirrel, red giant flying squirrel, red-and-white giant flying squirrel, Taiwan flying squirrel); Passeriformes: muscicapid (unspecified flycatcher), sittid (Eurasian nuthatch), timaliid (unspecified babbler), turdid (unspecified thrush)		Taiwan
I. (*Pholeoixodes*) *lagodechiensis*	Strigiformes: strigid (tawny owl)		Central Asia
I. lagotis	Rodentia: chinchillid (plains viscacha, northern viscacha)		South America
I. (*Ixodes*) *laguri*	Rodentia: cricetid (common vole, social vole, narrow-headed vole, bank vole, European water vole, European snow vole, European pine vole, Major's pine vole, golden hamster, grey dwarf hamster, Evermann's hamster, Ciscaucasian hamster, European hamster, Turkish hamster, steppe lemming), glirid (European edible dormouse), murid (house mouse, wood mouse, mound-building mouse, striped field mouse, Black Sea field mouse, Ural field mouse, Eurasian harvest house, great gerbil, Mongolian gerbil, Tristram's jird, brown rat, water rat), sciurid (yellow ground squirrel, speckled ground squirrel, little ground squirrel, red-cheeked ground squirrel, European ground squirrel, bobak marmot), sminthid (northern birch mouse, southern birch mouse); Eulipotyphla: erinaceid (long-eared hedgehog, European hedgehog), soricid (lesser white-toothed shrew); Lagomorpha: leporid (European hare), ochotonid (steppe pika); Carnivora: canid (dog, red fox), felid (cat), mustelid (steppe polecat, marbled polecat, European polecat, least weasel, European pine marten); Primates: hominid (human); Passeriformes: alaudid (Eurasian skylark)		Europe
I. laridis	Charadriiformes: larid (white-fronted tern, Caspian tern, silver gull, kelp gull); Pelecaniformes: threskiornithid (royal spoonbill); Procellariiformes: diomedeid (northern royal albatross, northern Buller's albatross, Chatham albatross), procellariid (white-headed petrel); Suliformes: phalacrocoracid (great cormorant, spotted shag, Otago shag), sulid (Australasian gannet)	lesions, possibly paralysis	Australia, New Zealand
I. (*Ixodes*) *lasallei*	Rodentia: cuniculid (lowland paca), dasyproctid (black agouti, red-rumped agouti, Central American agouti); Didelphimorphia: didelphid (woolly mouse opossum); Carnivora: felid (ocelot)		South America
I. (*Afrixodes*) *latus*	Artiodactyla: bovid (cattle); Rodentia: sciurid (black-and-red bush squirrel); Hyracoidea: procaviid (hyrax)		Africa
I. (*Multidentatus*) *laysanensis**	Anseriformes: anatid (Hawaiian duck); Charadriiformes: larid (sooty tern, greater crested tern, brown noddy), scolopacid (ruddy turnstone); Passeriformes: drepanidid (Hawaiian honeycreeper), fringillid (finch), sturnid (starling); Phaethontiformes: phaethontid (red-tailed tropicbird); Procellariiformes: diomedeid (black-footed albatross, Laysan albatross), procellariid (wedge-tailed shearwater); Suliformes: fregatid (great frigatebird), sulid (red-footed booby, masked booby); Primates: hominid (human)	trauma	Pacific Islands
I. (*Afrixodes*) *lemuris*	Primates: cheirogaleid (unspecified mouse lemur), lemurid (red-fronted lemur); Rodentia: murid (unspecified rodent)		Madagascar
I. (*Afrixodes*) *lewisi*	Artiodactyla: bovid (cattle, buffalo, sheep, common eland, harnessed bushbuck, common duiker, red forest duiker, Kirk's dik-dik, bongo), giraffid (giraffe); Hyracoidea: procaviid (hyrax); Carnivora: canid (dog), felid (unspecified)		Africa
I. lindbergi	Primates: hominid (human)		Himalayas
I. lisphilus	Rodentia: sciurid (Japanese squirrel)		Japan
I. (*Pholeoixodes*) *lividus* (syn. *I. hirundinicola, plumbeus*)	Coraciiformes: alcedinid (kingfisher), meropid (bee-eater); Passeriformes: alaudid (Eurasian skylark), hirundinid (common house martin, sand martin), muscicapid (redstart), parid (tit), passerid (Eurasian tree sparrow), sturnid (common starling), turdid (common blackbird); Rodentia: murid (wood mouse); Carnivora: canid (dog); Chiroptera: vespertilionid (common pipistrelle)	anaemia (possible vector for rickettsioses, borreliosis, encephalitis virus, West Nile virus)	Palearctic
I. longiscutatus	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Rodentia:		South America

	caviid (montane guinea pig, Brazilian guinea pig), cricetid (Altiplano grass mouse, dark bolo mouse, yellow pygmy rice rat, black-footed pygmy rice rat, long-nosed hocicudo, Waterhouse's swamp rat)		
I. (*Ixodes*) *loricatus* (syn. *I. coxaefurcatus*)	Didelphimorphia: didelphid (common opossum, big-eared opossum, white-eared opossum, agile gracile opossum, big lutrine opossum, water opossum, brown four-eyed opossum, gray-and-black four-eyed opossum, gray four-eyed opossum, southeastern four-eyed opossum, yellow-sided opossum, red-sided short-tailed opossum, long-nosed short-tailed opossum, northern three-striped opossum, woolly mouse opossum, Linnaeus's mouse opossum); Cingulata: dasypodid (nine-banded armadillo); Rodentia: caviid (guinea pig), cricetid (Azara's grass mouse, vesper mouse, Cariri climbing mouse, unspecified cane mouse, russet rice rat, terraced rice rat, large-headed rice rat, yellow pygmy rice rat, black-footed pygmy rice rat, web-footed marsh rat, Argentine swamp rat, Waterhouse's swamp rat, red hocicudo, long-nosed hocicudo), cuniculid (lowland paca), murid (house, black rat, brown rat); Carnivora: procyonid (South American coati); Primates: atelid (Geoffroy's spider monkey)		South America
I. (*Afrixodes*) *loveridgi*	Rodentia: nesomyid (southern giant pouched rat)		Africa
I. (*Ixodes*) *luciae*	Artiodactyla: cervid (brown brocket); Didelphimorphia: didelphid (common opossum, white-eared opossum, big lutrine opossum, brown-eared woolly opossum, bare-tailed woolly opossum, woolly mouse opossum, white-bellied woolly mouse opossum, Mexican mouse opossum, Linnaeus's mouse opossum, Robinson's mouse opossum, Tschudi's slender opossum, brown four-eyed opossum, northern red-sided opossum, southern red-sided opossum, Anderson's four-eyed opossum, gray four-eyed opossum, grayish mouse opossum, buff-bellied fat-tailed mouse opossum, Cinderella fat-tailed mouse opossum); Eulipotyphla: soricid (shrew); Rodentia: cricetid (vesper mouse, Sumichrast's vesper rat, western Amazonian oryzomys, unicolored rice rat, bicolored arboreal rice rat, small-eared pygmy rice rat, marsh rice rat, Yungas rice rat, Pittier's crab-eating rat, cotton rat, short-tailed cane mouse), cuniculid (lowland paca), echimyid (spiny rat); Carnivora: canid (dog)		Africa, South America
I. (*Ixodes*) *lunatus*	Rodentia: murid (black rat), nesomyid (lowland red forest rat, white-bellied nesomys); Afrosoricida: tenrecid (tenrec, greater hedgehog tenrec, Dobson's shrew tenrec)		Madagascar
I. (*Endopalpiger*) *luxuriosus**	Dasyuromorphia: dasyurid (New Guinean quoll); Peramelemorphia: peramelid (white-lipped bandicoot, striped bandicoot, Raffray's bandicoot); Diprotodontia: macropodid (tree kangaroo, small dorcopsis, pademelon), petaurid (long-fingered triok), phalangerid (Stein's cuscus), pseudocheirid (coppery ringtail possum); Monotremata: tachyglossid (echidna); Rodentia: murid (Rothschild's woolly rat, eastern white-eared giant rat, black-tailed mosaic-tailed rat, mountain mosaic-tailed rat, giant white-tailed rat, moss forest rat, Stein's rat)	trauma	Australasia
I. (*Afrixodes*) *macfarlanei*	Artiodactyla: bovid (yellow-backed duiker); Carnivora: viverrid (Cape genet)		Africa
I. (*Ixodes*) *malayensis*	Scandentia: tupaiid (common treeshrew)		Asia
I. (*Pholeoixodes*) *marmotae*	Rodentia: cricetid (bushy-tailed woodrat, deer mouse), erethizontid (North American porcupine), sciurid (woodchuck, yellow-bellied marmot, golden-mantled ground squirrel, Columbian ground squirrel, Richardson's ground squirrel, Uinta ground squirrel); Passeriformes: hirundinid (sand martin)		North America
I. (*Pholeoixodes*) *marxi*	Artiodactyla: bovid (unspecified); Lagomorpha: leporid (black-tailed jackrabbit, snowshoe hare); Eulipotyphla: soricid (shrew); Rodentia: cricetid (vole, deer mouse, white-footed mouse), sciurid (eastern chipmunk, least chipmunk, eastern grey squirrel, American red squirrel, northern flying squirrel); Carnivora: canid (dog, fox), felid (cat), mustelid (weasel), procyonid (raccoon); Primates: hominid (human); Passeriformes (unspecified)	(vector for Powassan virus)	North America

I. maskelli	Procellariiformes: diomedeid (wandering albatross)		New Zealand
I. maslovi	host unknown, collected from vegetation		Russia
I. (*Afrixodes*) *matopi*	Artiodactyla: bovid (goat, klipspringer); Hyracoidea: procaviid (rock hyrax, yellow-spotted rock hyrax); Lagomorpha: leporid (red rock hare)		Africa
I. megathyreus	Carnivora: canid (dog); Eulipotyphla: erinaceid (European hedgehog)		Europe
I. mellinus	Carnivora: mustelid (European badger)		Europe
I. (*Ixodes*) *mexicanus*	Passeriformes: emberizid (unspecified bunting), passerellid (yellow-eyed junco), troglodytid (spotted wren, cactus wren)		North America
I. (*Afrixodes*) *microgalei*	Afrosoricida: tenrecid (pygmy shrew tenrec, shrew-toothed shrew tenrec, Dobson's shrew tenrec)		Madagascar
I. (*Ixodes*) *minor* (syn. *I. bishoppi*)	Rodentia: cricetid (woodrat, hispid cotton rat, eastern rice rat, Boquete rice rat, Mexican deer mouse, Florida mouse, vesper mouse), murid (house mouse, rat), sciurid (woodchuck, eastern gray squirrel); Lagomorpha: leporid (eastern cottontail); Carnivora: mephitid (eastern spotted skunk); Passeriformes: passerellid (eastern towhee), troglodytid (house wren), turdid (ruddy-capped nightingale-thrush)		Americas
I. (*Afrixodes*) *minutae*	Rodentia: murid (southern multimammate mouse)		Africa
I. (*Endopalpiger*) *mirzai*	Dasyuromorphia: dasyurid (three-striped dasyure); Peramelemorphia: peramelid (striped bandicoot); Galliformes: megapodid (wattled brush turkey)		New Guinea
I. (*Scaphixodes*) *mitchelli*	Galliformes: phasianid (Himalayan monal, snow partridge)		Nepal
I. (*Ixodes*) *monospinosus*	Artiodactyla: bovid (unspecified), cervid (deer); Rodentia: cricetid (vole), murid (mouse); Eulipotyphla: talpid (mole); Carnivora: ursid (bear); Primates: hominid (human)		Palearctic
I. (*Ixodes*) *montoyanus*	Artiodactyla: cervid (northern pudu, brocket deer); Carnivora: procyonid (western mountain coati)		South America
I. (*Afrixodes*) *moreli*	Artiodactyla: bovid (harnessed bushbuck, bay duiker, black duiker, red-flanked duiker, zebra duiker, Maxwell's duiker, royal antelope, suni); Rodentia: thryonomyid (greater cane rat); Carnivora: felid (leopard), nandiniid (African palm civet), viverrid (African civet)		Africa
I. moscharius	Artiodactyla: moschid (dwarf musk deer)		China
I. (*Ixodes*) *moschiferi* (syn. *I. rangtangensis*)	Artiodactyla: moschid (Siberian musk deer, alpine musk deer, dwarf musk deer)		Nepal, China
I. mossambicensis	Rodentia: thryonomyid (greater cane rat)		Africa
I. (*Afrixodes*) *muniensis*	Artiodactyla: bovid (goat, bushbuck, bay duiker, blue duiker, black duiker, black-fronted duiker, red-flanked duiker, Maxwell's duiker, harnessed bushbuck, royal antelope, forest antelope, Bate's dwarf antelope, bongo), giraffid (giraffe), suid (pig, red river hog); Hyracoidea: procaviid (western tree hyrax); Rodentia: murid (Rudd's mouse), nesomyid (Gambian pouched rat), sciurid (Gambian sun squirrel), thryonomyid (greater cane rat); Carnivora: canid (dog), felid (cat, leopard), herpestid (common kusimanse), viverrid (African civet); Primates: hominid (human)		Africa
I. (*Ixodes*) *muris* (mouse tick)	Artiodactyla: cervid (white-tailed deer); Rodentia: cricetid (eastern meadow vole, montane vole, meadow mouse, muskrat, deer mouse, white-footed mouse), murid (mouse, brown rat), sciurid (eastern gray squirrel, eastern chipmunk), zapodid (meadow jumping mouse, woodland jumping mouse); Eulipotyphla: soricid (common shrew, long-tailed shrew, northern short-tailed shrew, Arctic shrew, Say's least shrew, American water shrew); Lagomorpha: leporid (eastern cottontail, Mearn's cottontail); Carnivora: canid (dog, American red fox), felid (cat), mephitid (striped skunk), procyonid (raccoon); Primates: hominid (human); Charadriiformes: larid (gull), scolopacid (sandpiper); Galliformes: odontophorid (bobwhite), phasianid (fowl); Passeriformes: corvid (blue jay), emberizid (bunting), icterid (blackbird), mimid (gray catbird, brown thrasher), parulid (yellowthroat, northern waterthrush, mourning warbler, black-and-white warbler, blue-winged warbler, Tennessee warbler),	trauma, irritation, dermatitis (plus vector for theileriosis, babesiosis)	North America

	passerellid (song sparrow, swamp sparrow, white-throated sparrow, eastern towhee), troglodytid (house wren, Carolina wren), turdid (Swainson's thrush, American robin, veery)		
I. (*Multidentatus*) *murreleti*	Charadriiformes: alcid (Scripp's murrelet, Guadalupe murrelet)		North America
I. myospalacis	Rodentia: spalacid (Chinese zokor)		China
I. (*Afrixodes*) *myotomys*	Carnivora: felid (cat, caracal); Rodentia: murid (bush vlei rat, bush Karoo rat)		Africa
I. (*Sternalixodes*) *myrmecobii*	Dasyuromorphia: myrmecobiid (numbat); Diprotodontia: potoroid (woylie); Perissodactyla: equid (horse); Carnivora: canid (dog), felid (cat): Primates: hominid (human)		Australia
I. (*Afrixodes*) *nairobiensis*	Artiodactyla: bovid (unspecified), suid (desert warthog); Eulipotyphla: soricid (white-toothed shrew); Rodentia: murid (black rat, East African creek rat, rock rat, grass rat, Creel groove-toothed swamp rat, tropical vlei rat, Abyssinian grass rat, Namaqua rock rat, typical striped grass mouse, southern multimammate mouse, Natal multimammate mouse); Carnivora: canid (dog), herpestid (mongoose), viverrid (African civet)		Africa
I. (*Afrixodes*) *nchisiensis*	Rodentia: murid (Abyssinian grass rat); Eulipotyphla: soricid (Oriental shrew); Macroscelidea: macroscelidid (four-toed elephant shrew)		Africa
I. (*Ixodes*) *nectomys*	Rodentia: cricetid (western Amazonian nectomys)		South America
I. (*Ixodes*) *neotomae*	Rodentia: cricetid (dusky-footed woodrat, desert woodrat, muskrat, deer mouse), heteromyid (kangaroo rat); Lagomorpha: leporid (brush rabbit, volcano rabbit, black-tailed jackrabbit, desert cottontail, La Jolla jackrabbit, hare); Carnivora: canid (dog, gray fox)		North America
I. (*Afrixodes*) *neitzi*	Artiodactyla: bovid (mountain reedbuck, impala)		Africa
I. (*Afrixodes*) *nesomys*	Rodentia: nesomyid (pouched rat)		Africa
I. neuquenensis	Microbiotheria: microbiotheriid (monito del monte (little bush monkey), Panchos's monito del monte)		South America
I. nicolasi	Artiodactyla: bovid (cattle)		Africa
I. (*Ixodes*) *nipponensis*	Artiodactyla: bovid (cattle, goat), cervid (water deer, Siberian roe deer), suid (boar); Perissodactyla: equid (horse); Eulipotyphla: soricid (Asian house shrew, lesser Ryuka shrew), talpid (Ussuri mole); Lagomorpha: leporid (mountain hare, Japanese hare); Rodentia: cricetid (deer mouse), murid (mouse, black rat, Ryuku mouse), sciurid (Siberian chipmunk); Carnivora: canid (dog, raccoon dog), felid (cat, leopard cat), mustelid (Asian badger, Siberian weasel), ursid (bear); Primates: hominid (human); Passeriformes: emberizid (black-faced bunting), motacillid (wagtail, Pechora pipit), phylloscopid (dusky warbler), sylviid (babbler), turdid (eyebrowed thrush, pale thrush); Sauria: lacertid (Amur grass lizard, mountain grass lizard), scincid (Tsushima ground skink)	(possible vector for anaplasmosis, borreliosis)	Asia
I. (*Ixodes*) *nitens*	Rodentia: murid (Maclear's rat)		Christmas Island
I. nodulipes	Chiroptera: vespertilionid (parti-coloured bat, western barbastelle)		Europe
I. (*Pholeoixodes*) *nuttalli*	Rodentia: chinchillid (southern viscacha, northern viscacha)		South America
I. (*Ixodes*) *nuttallianus* (syn. *I. muntiaci, ricinoides*)	Artiodactyla: bovid (cattle, yak, goral, buffalo, sheep, serow, goat), cervid (swamp deer, Indian muntjac), moschid (musk deer); Carnivora: canid (dog)		Eurasia
I. (*Ixodes*) *occultus*	Rodentia: cricetid (unspecified hamster), murid (great gerbil, midday jird, Libyan jird, house mouse), sciurid (yellow ground squirrel); Eulipotyphla: soricid (lesser white-toothed shrew, piebald shrew); Carnivora: mustelid (least weasel, mountain weasel, marbled polecat); Serpentes: viperid (Amur viper)		Central Asia
I. (*Pholeoixodes*) *ochotonae*	Lagomorpha: ochotonid (American pika); Rodentia: cricetid (bushy-tailed woodrat, deer mouse, canyon mouse, pinyon mouse, red-backed vole, meadow vole, heather vole), geomyid (northern pocket		Americas

	gopher), sciurid (cliff chipmunk, pine squirrel, golden-mantled ground squirrel, Uinta ground squirrel, white-tailed antelope squirrel); Carnivora: canid (gray fox)		
I. ochotonarius	Lagomorpha: ochotonid (Moupin pika)		China
I. (*Afrixodes*) *okapiae*	Artiodactyla: giraffid (okapi)		Africa
I. (*Afrixodes*) *oldi*	Artiodactyla: bovid (cattle, black duiker); Eulipotyphla: soricid (Oriental shrew); Pholidota: manid (long-tailed pangolin); Macroscelidea: macroscelidid (elephant shrew); Rodentia: heterocephalid (mole rat), murid (forest rat, sub-Saharan pygmy mouse), nesomyid (Gambian pouched rat), sciurid (grey squirrel, African bush squirrel); Carnivora: canid (dog), felid (cat, leopard), herpestid (marsh mongoose, long-haired mongoose, Egyptian mongoose), viverrid (common genet, rusty-spotted genet, African civet); Primates: cercopithecid (mona monkey, spot-nosed monkey)		Africa
I. orbiculatus	Rodentia: sciurid (fox squirrel)		North America
I. (*Coxixodes*) *ornithorhynchi** (platypus tick)	Monotremata: ornithorhynchid (platypus)	trauma	Australia
I. (*Partipalpiger*) *ovatus**	Artiodactyla: bovid (cattle, zebu, zhum, buffalo, sheep, goat, goral, serow), cervid (Indian muntjac, chital, tufted deer, dwarf musk deer, alpine musk deer); Perissodactyla: equid (horse); Rodentia: cricetid (Royle's high mountain vole), murid (house mouse, little Himalayan rat, chestnut rat); Lagomorpha: leporid (Japanese hare, mountain hare), ochotonid (Royle's pika); Eulipotyphla: soricid (house shrew, brown-toothed shrew, Sikkim large-clawed shrew), talpid (mole); Scandentia: tupaiid (treeshrew); Carnivora: canid (dog, red dog, golden jackal), felid (wildcat, leopard cat), mustelid (Siberian weasel), ursid (giant panda), viverrid (Asian palm civet); Primates: hominid (human); Galliformes: phasianid (kalij pheasant); Passeriformes: emberizid (bunting)	trauma, irritation, dermatitis (plus vector for theileriosis, borreliosis)	Asia, Japan
I. ozarkus	Artiodactyla: cervid (deer); Carnivora: canid (dog), procyonid (raccoon); Primates: hominid (human)		North America
I. (*Ixodes*) *pacificus* (western black-legged tick)	Artiodactyla: bovid (cattle, sheep, goat), cervid (Columbian black-tailed deer); Perissodactyla: equid (horse, mule); Lagomorpha: leporid (cottontail, jackrabbit, snowshoe hare); Didelphimorphia: didelphid (Virginia opossum); Eulipotyphla: soricid (vagrant shrew), talpid (North American mole, northern broad-footed mole, coast mole); Rodentia: cricetid (dusky-footed woodrat, desert woodrat, deer mouse, brush mouse, canyon mouse, cactus mouse, pinyon mouse, western harvest mouse, California vole), heteromyid (long-tailed pocket mouse, California pocket mouse, Great Basin pocket mouse), murid (mouse, rat), sciurid (cliff chipmunk, northern flying squirrel, western gray squirrel, pine squirrel, Douglas's squirrel, chickaree, California ground squirrel), zapodid (jumping mouse); Carnivora: canid (dog, wolf, coyote, gray fox), felid (cat, wildcat, bobcat, cougar), mustelid (American mink, long-tailed weasel), procyonid (raccoon); Primates: hominid (human); Galliformes: phasianid (California quail, grouse); Passeriformes: corvid (California scrub jay, magpie), emberizid (unspecified bunting), passerellid (rufous-crowned sparrow, chipping sparrow, golden-crowned sparrow, dark-eyed junco), troglodytid (unspecified wren); Sauria: anguid (northern alligator lizard, southern alligator lizard), phrynosomatid (blue-bellied lizard, sagebrush lizard, Great Basin fence lizard), teiid (whiptail lizard); Serpentes: colubrid (north-western garter snake)	trauma, irritation, tick paralysis (vector for borreliosis (incl. Lyme disease), tularemia, *Babesia*-like organisms, spotted fever, anaplasmosis, ehrlichiosis, encephalitis)	North America
I. (*Multidentatus*) *paranaensis*	Apodiformes: apodid (biscutate swift, sooty swift, great dusky swift, white-collared swift)		South America
I. (*Ixodes*) *pararicinus*	Artiodactyla: bovid (cattle), cervid (brown brocket), tayassuid (collared peccary); Perissodactyla: equid (horse); Didelphimorphia: didelphid (sepia short-tailed opossum, buff-bellied fat-tailed mouse opossum); Rodentia: cricetid (large vesper mouse, fecund vesper mouse, destructive pygmy rice rat); Carnivora: canid (dog); Chiroptera: phyllostomid (common vampire bat); Passeriformes:		South America

	corvid (plush-crested jay), emberizid (saffron-billed sparrow, rufous-collared sparrow, stripe-headed brush-finch, yellow-striped brush-finch, red pileated finch), furnariid (buff-browed foliage-gleaner), parulid (brown-capped whitestart, two-banded warbler), passerellid (saffron-billed sparrow, white-browed brushfinch, yellow-striped brushfinch), thraupid (red pileated finch), troglodytid (house wren), turdid (creamy-bellied thrush, rufous-bellied thrush, Andean slaty thrush)		
I. parvirostris	Suliformes: phalacrocoracid (pelagic cormorant)		Japan
I. (*Ixodes*) *pavlovskyi* (incl. subspp. *pavlovskyi*, *occidentalis*)	Artiodactyla: bovid (cattle); Eulipotyphla: erinaceid (hedgehog), soricid (common shrew, bicolored shrew); Lagomorpha: leporid (rabbit), ochotonid (pika); Rodentia: cricetid (common vole, grey red-backed vole, northern red-backed vole), murid (striped field mouse, wood mouse, house mouse), sciurid (Siberian chipmunk), sminthid (Altai birch mouse); Carnivora: canid (dog), procyonid (raccoon); Primates: hominid (human); Anseriformes: anatid (unspecified duck); Columbiformes: columbid (blue hill pigeon); Galliformes: phasianid (hazel grouse, western capercaillie); Gruiformes: rallid (corn crake); Passeriformes: corvid (carrion crow), emberizid (yellowhammer, pine bunting), fringillid (European goldfinch, common rosefinch), motacillid (tree pipit), muscicapid (common redstart), sturnid (common starling), sylviid (common whitethroat), turdid (fieldfare)	trauma (vector for tick-borne encephalitis, Kemerovo virus, Lyme disease)	Eurasia
I. (*Multidentatus*) *percavatus*	Charadriiformes: alcid (puffin), larid (herring gull); Procellariiformes: diomedeid (Atlantic yellow-nosed albatross), oceanitid (black-bellied storm petrel), procellariid (short-tailed shearwater, blue petrel, common diving petrel, South Georgia diving petrel); Sphenisciformes: spheniscid (little penguin); Passeriformes: turdid (Tristan thrush)		islands in Atlantic and Indian oceans
I. (*Ixodes*) *peromysci*	Rodentia: cricetid (eastern deer mouse), murid (mouse); Sauria: anguid (glass lizard)		North America
I. (*Ixodes*) *persulcatus* (taiga tick)	Artiodactyla: bovid (cattle, sheep, argali, goat), camelid (camel), cervid (elk, red deer, roe deer, sika deer, Manchurian wapiti, moose), moschid (Siberian musk deer), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit, desert hare, mountain hare, Tolai hare, Manchurian hare), ochotonid (alpine pika, northern pika, large-eared pika); Eulipotyphla: erinaceid (European hedgehog, Amur hedgehog), soricid (common shrew, long-clawed shrew, greater white-toothed shrew, lesser white-toothed shrew, Siberian large-toothed shrew, Arctic shrew, Eurasian water shrew, Eurasian least shrew, pygmy shrew, Eurasian pygmy shrew, Pacific shrew, Laxmann's shrew, Ussuri shrew), talpid (European mole, Ussuri mole); Rodentia: cricetid (muskrat, common vole, bank vole, reed vole, tundra vole, narrow-headed vole, Japanese grass vole, Maximowicz's vole, short-tailed field vole, grey red-backed vole, northern red-backed vole, silver mountain vole, European pine vole, European water vole, Tien Shan forest vole, northern mole vole, grey dwarf hamster, European hamster, Chinese striped hamster, giant rat-headed hamster, wood lemming, steppe lemming), glirid (forest dormouse), murid (house mouse, striped field mouse, Eurasian harvest mouse, small Japanese field mouse, large Japanese field mouse, yellow-necked mouse, wood mouse, black rat, brown rat, great gerbil), sciurid (Siberian chipmunk, gray marmot, red squirrel, Siberian flying squirrel), sminthid (northern birch mouse, long-tailed birch mouse, Altai birch mouse, Tianshan birch mouse); Carnivora: canid (dog, wolf, dhole, common raccoon dog, red fox), felid (cat, Eurasian lynx, leopard, snow leopard, tiger), mustelid (European badger, yellow-throated marten, pine marten, steppe polecat, stoat, least weasel, Siberian weasel), ursid (brown bear); Primates: hominid (human); Accipitriformes: accipitrid (besra, Eurasian sparrowhawk, common buzzard, hen harrier, Montagu's harrier); Bucerotiformes: upupid (Eurasian hoopoe); Charadriiformes: scolopacid (Eurasian woodcock, Swinhoe's snipe,	trauma (vector for babesiosis, theileriosis, anaplasmosis, borreliosis (incl. Lyme disease), ehrlichiosis, tick-borne encephalitis, Omsk haemorrhagic fever, Russian spring-summer viral encephalitis)	Eurasia

	green sandpiper); Columbiformes: columbid (hill pigeon, common wood pigeon, European turtle dove, Oriental turtle dove); Cuculiformes: cuculid (common cuckoo, Himalayan cuckoo, Malaysian hawk-cuckoo); Falconiformes: falconid (common kestrel); Galliformes: phasianid (chicken, common quail, hazel grouse, black grouse, wood grouse, rock partridge, chukar partridge, green pheasant, western capercaillie); Gruiformes: rallid (corn crake, wood hen); Passeriformes: acrocephalid (great reed warbler, thick-billed warbler, Blyth's reed warbler, Oriental reed warbler, marsh warbler), alaudid (Eurasian skylark), campephagid (rosy minivet), cardinalid (scarlet grosbeak), cettid (Asian stubtail), corvid (azure-winged magpie, Eurasian magpie, hooded crow, western jackdaw, Eurasian jay, Siberian jay, spotted nutcracker), emberizid (yellow-breasted bunting, meadow bunting, chestnut bunting, black-faced bunting, yellow-throated bunting, white-capped bunting, chestnut-eared bunting, pine bunting, rustic bunting, common reed bunting, Tristram's bunting, yellowhammer), fringillid (brambling, bullfinch, chaffinch, hawfinch, European goldfinch, common rosefinch, Siberian long-tailed rosefinch, common redpoll, red crossbill), hirundinid (sand martin), icterid (meadowlark), laniid (red-backed shrike, brown shrike, great grey shrike, tiger shrike), locustellid (river warbler, lanceolated warbler, common grasshopper warbler, Gray's grasshopper warbler, Pallas's grasshopper warbler), motacillid (tree pipit, olive-backed pipit, white wagtail, grey wagtail, western yellow wagtail), muscicapid (red-flanked bluetail, black-headed chat, Siberian rubythroat, rufous-tailed robin, Siberian blue robin, spotted flycatcher, blue-and-white flycatcher, grey streaked flycatcher, Asian brown flycatcher, Mugimaki flycatcher, Burmese paradise flycatcher, common nightingale, thrush nightingale, common redstart, Daurian redstart, European robin, bluethroat, northern wheatear, whinchat, African stonechat), parid (great tit, marsh tit, black-capped chickadee), passerid (house sparrow, tree sparrow), phylloscopid (dusky warbler, willow warbler, wood warbler, Arctic warbler, common chiffchaff), prunellid (mountain accentor, dunnock), reguliid (goldcrest), sittid (Eurasian nuthatch), sturnid (common starling, white-cheeked starling, Daurian starling), sylviid (common whitethroat, lesser whitethroat, garden warbler), troglodytid (Eurasian wren), turdid (common blackbird, song thrush, black-throated thrush, red-throated thrush, fieldfare, Amami ground thrush, grey-backed thrush, little thrush, Naumann's thrush, Siberian thrush, eyebrowed thrush, pale thrush, mistle thrush); Piciformes: picid (black woodpecker, great spotted woodpecker, lesser spotted woodpecker, white-backed woodpecker, grey-headed woodpecker, hairy woodpecker, Eurasian three-toed woodpecker, Eurasian wryneck); Strigiformes: strigid (short-eared owl); Suliformes: phalacrocoracid (great cormorant); Sauria: lacertid (sand lizard, viviparous lizard)		
I. (*Ixodes*) *petauristae* (syn. *I. kerri*)	Artiodactyla: cervid (chital), tragulid (Indian spotted chevrotain); Eulipotyphla: soricid (Asian house shrew); Rodentia: hystricid (Indian crested porcupine), murid (black rat, Blanford's rat), sciurid (Indian giant squirrel, Indian giant flying squirrel); Carnivora: canid (dhole), felid (leopard); Primates: hominid (human)		India, Sri Lanka
I. phascolomys	Diprotodontia: vombatid (common wombat)		Australia
I. (*Scaphixodes*) *philipi*	Procellariiformes: hydrobatid (band-rumped storm petrel), procellariid (streaked shearwater)		Japan
I. (*Afrixodes*) *pilosus* (russet tick, bush tick)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, roan antelope, impala, harnessed bushbuck, waterbuck, southern reedbuck, grey rhebok, steinbock, grysbok, Lichtenstein's hartebeest, gwape, nyala, suni, oribi, klipspringer, common duiker, blue duiker, red forest duiker, Thomson's gazelle), suid (pig, warthog); Perissodactyla: equid (horse, donkey, mule); Eulipotyphla: erinaceid (South African hedgehog); Macroscelidea: macroscelidid (elephant shrew); Lagomorpha: leporid (scrub hare, Natal red rock hare); Rodentia:	trauma, irritation, dermatitis, anaemia, paralysis	South Africa

	sciurid (squirrel); Carnivora: canid (dog, black-backed jackal, bat-eared fox), felid (cat, caracal, serval, African wildcat, leopard, lion), viverrid (civet); Chiroptera; rhinolophid (Geoffroy's horseshoe bat); Primates: hominid (human); Passeriformes: cisticolid (Levaillant's cisticola), ploceid (yellow-crowned bishop)		
I. (*Endopalpiger*) *planiscutatus*	Rodentia: murid (moss-forest rat)		New Guinea
I. (*Ixodes*) *pomerantzi*	Lagomorpha: leporid (common tapeti, eastern cottontail, Chiapas cottontail, Dice's cottontail)		South America
I. (*Pholeoixodes*) *pomerantzevi*	Rodentia: cricetid (reed vole, grey red-backed vole, northern red-backed vole), murid (striped field mouse, large Japanese field mouse, brown rat), sciurid (Siberian chipmunk); Eulipotyphla: erinaceid (European hedgehog, Amur hedgehog), soricid (common shrew, Siberian chipmunk); Carnivora: canid (dog, red fox)		Russia
I. pospelovae	Chiroptera: miniopterid (common bentwing bat), vespertilionid (lesser mouse-eared bat)		Europe
I. praematurus	Passeriformes: timaliid (babbler), turdid (ground thrush), zosteropid (white-eye)		Timor
I. (*Exopalpiger*) *priscicollaris**	Dasyuromorphia: dasyurid (unspecified phascogale)	trauma, irritation	New Guinea
I. (*Afrixodes*) *procaviae*	Hyracoidea: procaviid (southern tree hyrax, rock hyrax); Artiodactyla: suid (warthog)		Africa
I. prokopjevi	Eulipotyphla: erinaceid (Daurian hedgehog)		Eurasia
I. pseudorasus	Artiodactyla: bovid (cattle, buffalo, royal antelope, pygmy antelope, harnessed bushbuck, black-fronted duiker, suni, bongo), giraffid (okapi), suid (red river hog); Hyracoidea: procaviid (tree hyrax); Rodentia: nesomyid (Gambian pouched rat); Carnivora: canid (dog), felid (leopard, lion), herpestid (mongoose), viverrid (genet, African civet); Primates hominid (human); Cuculiformes: cuculid (white-browed coucal)		Africa
I. pterodromae	Procellariiformes: diomedeid (wandering albatross), procellariid (soft-plumaged petrel, Kerguelen petrel, common diving petrel, Antarctic prion, short-tailed shearwater, flesh-footed shearwater, sooty shearwater); Sphenisciformes: spheniscid (penguin); Carnivora: felid (cat)		Africa, Australia
I. punctulatus	Artiodactyla: cervid (roe deer)		Europe
I. (*Afrixodes*) *radfordi*	Rodentia: murid (black rat)		India
I. (*Afrixodes*) *rageaui*	Primates: cercopithecid (grivet, moustached guenon, blue monkey), hominid (human)		Africa
I. (*Afrixodes*) *randrianasoloi*	Afrosoricida: tenrecid (tenrec); Rodentia: murid (black rat)		Africa
I. (*Afrixodes*) *rasus*	Artiodactyla: bovid (cattle, buffalo, sheep, goat, royal antelope, brown antelope, Bate's dwarf antelope, blue duiker, red forest duiker, black duiker, black-fronted duiker, white-bellied duiker, yellow-backed duiker, Maxwell's duiker, bushbuck, impala, suni, bongo), cervid (African water chevrotain), giraffid (okapi), suid (pig, bushpig, red river hog, desert warthog); Macroscelidea: macroscelidid (giant elephant shrew); Eulipotyphla: soricid (bicolored shrew, African giant shrew, Cretan shrew); Hyracoidea: procaviid (southern tree hyrax, western tree hyrax); Pholidota: manid (tree pangolin); Lagomorpha: leporid (African savanna hare); Rodentia: hystricid (African brush-tailed porcupine), murid (black rat, gray brush-furred rat, yellow-spotted brush-furred rat, groove-toothed rat, Creek groove-toothed swamp rat, Abyssinian grass rat, African grass rat, Guinean grass rat, African marsh rat, tropical vlei rat, house mouse, pygmy mouse, typical striped grass mouse, Peter's striped mouse, Temminck's mouse, Guinea multimammate mouse, gracile tateril, slender gerbil), nesomyid (Gambian pouched rat, Emin's pouched rat, giant forest rat), spalacid (Rwanda African mole-rat), thryonomyid (greater cane rat); Carnivora: canid (dog), felid (leopard, serval), herpestid (Cape genet, slender mongoose, marsh mongoose, large gray mongoose, white mongoose, Egyptian	trauma, irritation	Africa

	mongoose, common kusimanse), viverrid (African civet, African palm civet); Primates: cercopithecid (grey-cheeked mangabey, red-tailed monkey, moustached guenon, greater spot-nosed monkey, western red colobus, olive baboon), hominid (chimpanzee, human); Cuculiformes: cuculid (unspecified cuckoo); Galliformes: numidid (plumed guineafowl, black guineafowl), phasianid (double-spurred spurfowl); Passeriformes: turdid (Fraser's rufous thrush)		
I. (*Ixodes*) *redikorzevi* (syn. *I. transcaucasicus hystrix*)	Eulipotyphla: erinaceid (long-eared hedgehog, European hedgehog, southern white-breasted hedgehog, northern white-breasted hedgehog, Syrian long-eared hedgehog), soricid (common shrew, bicolored shrew, greater white-toothed shrew, lesser white-toothed shrew, piebald shrew, Eurasian water shrew, Radde's shrew), talpid (blind mole); Lagomorpha: leporid (Cape hare, European hare, tolai hare), ochotonid (Afghan pika); Rodentia: cricetid (grey dwarf hamster, European hamster, steppe lemming, common vole, montane water vole, short-tailed field vole, Gunther's vole, Robert's snow vole, social vole, Major's pine vole), glirid (forest dormouse), murid (house mouse, hillock mouse, European mouse, striped field mouse, steppe field mouse, eastern broad-toothed field mouse, Black Sea field mouse, wood mouse, Cairo spiny mouse, Ural field mouse, Eurasian harvest mouse, black rat, brown rat, Turkestan rat, African grass rat, short-tailed bandicoot rat, Libyan jird, Persian jird, Shaw's jird, Tamarisk jird, Tristram's jird, great gerbil), sciurid (European ground squirrel, little ground squirrel, long-clawed ground squirrel, Caucasian squirrel), spalacid (Middle East blind mole-rat); Carnivora: canid (dog, red fox, golden jackal), mustelid (marbled polecat, steppe polecat, least weasel, ferret, European badger), sciurid (marmot); Chiroptera: vespertilionid (unspecified bat); Primates: hominid (human); Anseriformes: anatid (red-breasted merganser); Charadriiformes: charadriid (European golden plover); Columbiformes: columbid (rock dove); Coraciiformes: coraciid (European roller); Galliformes: phasianid (common quail, rock partridge, mountain partridge, Daurian partridge, ring-necked pheasant); Gruiformes: rallid (water rail); Otidiformes: otidid (great bustard); Passeriformes: alaudid (crested lark, Calandra lark), corvid (jay, Eurasian magpie), emberizid (common reed bunting, corn bunting, rock bunting), fringillid (hawfinch), laniid (shrike), motacillid (tawny pipit, meadow pipit), muscicapid (thrush nightingale, European robin, northern wheatear, western black-eared wheatear, variable wheatear, African stonechat), parid (great tit), passerid (house sparrow, rock sparrow), phylloscopid (common chiffchaff, greenish warbler), sturnid (common starling), turdid (common blackbird, black-throated thrush, red-throated thrush, Siberian thrush, song thrush, fieldfare); Pterocliformes: pteroclid (black-bellied sandgrouse); Strigiformes: strigid (short-eared owl); Sauria: anguid (European glass lizard), lacertid (sand lizard, European green lizard, Balkan wall lizard); Serpentes: colubrid (steppe rat snake), viperid (Siberian pit viper); Testudines: emydid (unspecified tortoise)	irritation, allergy, toxemia	Central Asia
I. (*Afrixodes*) *rhabdomysae*	Rodentia: murid (four-striped grass mouse), nesomyid (pouched rat); Eulipotyphla: soricid (unspecified shrew); Macroscelidea: macroscelidid (elephant shrew)		Africa
I. (*Ixodes*) *ricinus** (syn. *I. fodiens, fuscus, lacertae, nigricans, pustularum, rufus, sciuri, variegatus*) (castor bean tick, sheep tick, common European tick)	Artiodactyla: bovid (cattle, zebu, water buffalo, European bison, sheep, mouflon, goat, mountain goat, Bezoar ibex, chamois, oryx), camelid (camel), cervid (red deer, maral, roe deer, sika deer, fallow deer, muntjac, water deer, black-tailed deer, white-tailed deer, brocket deer, moose), suid (pig, wild boar); Perissodactyla: equid (horse, donkey, mule); Lagomorpha: leporid (European rabbit, brush rabbit, eastern cottontail, mountain cottontail, black-tailed jackrabbit, Colorado desert jackrabbit, European hare, mountain hare, blue hare, brown hare); Eulipotyphla: erinaceid (northern white-breasted hedgehog, southern white-breasted hedgehog, long-eared hedgehog, European hedgehog), soricid (common shrew,	trauma, anaemia, paralysis (plus vectors for babesiosis, theileriosis, anaplasmosis, Q-fever, ehrlichiosis, louping-ill virus, rickettsial	Eurasia, Africa, Australia

	bicolored shrew, Laxmann's shrew, Radde's shrew, Eurasian water shrew, Mediterranean water shrew, alpine shrew, pygmy shrew, Eurasian pygmy shrew, lesser white-toothed shrew, greater white-toothed shrew), talpid (European mole, broad-footed mole); Didelphimorphia: didelphid (Virginia opossum, large American opossum); Rodentia: cricetid (common vole, bank vole, short-tailed field vole, tundra vole, social vole, European water vole, European snow vole, alpine pine vole, European pine vole, Major's pine vole, Tatra pine vole, grey dwarf hamster, European hamster, Eversmann's hamster, cotton mouse, white-footed mouse, Oldfield mouse, steppe lemming, muskrat, big-eared woodrat, swamp rice rat), dipodid (great jerboa, William's jerboa), echimyid (coypu), glirid (dormouse, garden dormouse, hazel dormouse, forest dormouse, European edible dormouse), heteromyid (spiny pocket mouse), murid (black rat, brown rat, house mouse, meadow mouse, striped field mouse, Ural field mouse, Black Sea field mouse, yellow-necked mouse, Eurasian harvest mouse, wood mouse), sciurid (red squirrel, eastern gray squirrel, western grey squirrel, Siberian chipmunk, Caucasian squirrel, Siskiyou chipmunk, little ground squirrel, speckled ground squirrel, European ground squirrel, California ground squirrel), sminthid (northern birch mouse), spalacid (lesser blind mole-rat); Carnivora: canid (dog, raccoon dog, wolf, timber wolf, coyote, Arctic fox, red fox, gray fox), castorid (Eurasian beaver), felid (cat, wildcat, bobcat, Florida bobcat, cougar, puma, jaguar, leopard, ocelot), mephitid (striped skunk), mustelid (European badger, European pine marten, stone marten, beech marten, least weasel, stoat, European polecat, steppe polecat, ferret, otter, European mink), procyonid (raccoon), ursid (brown bear), viverrid (common genet); Chiroptera: rhinolophid (lesser horseshoe bat, greater horseshoe bat), vespertilionid (whiskered bat); Primates: hominid (human); Accipitriformes: accipitrid (common buzzard, European honey buzzard, red kite, black kite, Eurasian sparrowhawk, northern goshawk, golden eagle, lesser spotted eagle); Anseriformes: anatid (mallard, duck, greylag goose, common pochard, red-crested pochard); Apodiformes: apodid (common swift); Bucerotiformes: upupid (Eurasian hoopoe); Caprimulgiformes: caprimulgid (Eurasian nightjar); Charadriiformes: charadriid (northern lapwing, European golden plover), larid (common gull, black-headed gull), scolopacid (Eurasian curlew, Eurasian woodcock, common snipe, ruff); Ciconiiformes: ciconiid (white stork); Columbiformes: columbid (stock dove, rock dove, Eurasian collared dove, European turtle dove, common wood pigeon); Cuculiformes: cuculid (common cuckoo); Falconiformes: falconid (common kestrel, saker falcon, merlin, Eurasian hobby); Galliformes: phasianid (chicken, turkey, rock partridge, grey partridge, red grouse, black grouse, hazel grouse, common quail, common pheasant, ring-necked pheasant, western capercallie, black francolin, willow ptarmigan); Gruiformes: gruid (crane), rallid (rail, Eurasian coot, corn crake, spotted crake); Passeriformes: acrocephalid (marsh warbler, sedge warbler, icterine warbler, great reed warbler, Eurasian reed warbler), aegithalid (long-tailed tit), alaudid (woodlark, Eurasian skylark, crested lark), bombycillid (Bohemian waxwing), cardinalid (cardinal), certhiid (Eurasian treecreeper), corvid (common raven, carrion crow, hooded crow, rook, western jackdaw, Eurasian jay, Crimean jay, Eurasian magpie, spotted nutcracker), emberizid (rock bunting, corn bunting, Ortolan bunting, yellowhammer), fringillid (canary, European goldfinch, European greenfinch, Eurasian bullfinch, hawfinch, common chaffinch, brambling, common linnet, redpoll, red crossbill, Eurasian siskin), hirundinid (barn swallow, sand martin, house martin), laniid (red-backed shrike, brown shrike), locustellid (river warbler, grasshopper warbler), motacillid (meadow pipit, water pipit, tree pipit, tawny pipit, Pechora pipit, grey wagtail, pied	fever, staphylococcal pyaemia, borreliosis (incl. Lyme disease), tick-borne encephalitis, spring-summer encephalitis)	

	wagtail, white wagtail, western yellow wagtail, eastern yellow wagtail), muscicapid (common nightingale, thrush nightingale, northern wheatear, pied wheatear, fieldfare, European robin, common redstart, black redstart, whinchat, African stonechat, pied flycatcher, spotted flycatcher, collared flycatcher, bluethroat), oriolid (Eurasian golden oriole), parid (European crested tit, great tit, willow tit, Eurasian blue tit, coal tit, marsh tit, black-capped chickadee), passerellid (towhee), passerid (house sparrow, Spanish sparrow, Eurasian tree sparrow), phylloscopid (common chiffchaff, willow warbler, wood warbler, greenish warbler), prunellid (dunnock), regulid (goldcrest, common firecrest), sittid (Eurasian nuthatch), sturnid (common starling), sturnid (common starling), sylviid (Eurasian blackcap, garden warbler, common whitethroat, lesser whitethroat, barred warbler, Sardinian warbler), thraupid (Diuca finch), troglodytid (Eurasian wren), turdid (common blackbird, true thrush, Austral thrush, redwing, ring ouzel, song thrush, mistle thrush, fieldfare), tyrannid (grey shrike-tyrant); Piciformes: picid (Eurasian wryneck, European green woodpecker, great spotted woodpecker, middle spotted woodpecker, lesser spotted woodpecker, Eurasian three-toed woodpecker); Podicipediformes: podicipedid (grebe); Strigiformes: strigid (long-eared owl, short-eared owl, tawny owl, swamp owl, barn owl, Eurasian eagle-owl, burrowing owl); Sauria: anguid (southern alligator lizard), crotaphytid (collared lizard), lacertid (sand lizard, Algerian sand racer, rock lizard, viviparous lizard, European green lizard, ocellated lizard, common wall lizard, Italian wall lizard, Crimean wall lizard, Madeiran wall lizard, Caucasus emerald lizard), phrynosomatid (western fence lizard), scincid (red-headed skink); Serpentes: colubrid (four-lined snake, grass snake, smooth snake, spotted whip snake), viperid (meadow viper, steppe viper); Testudines: testudinid (Greek tortoise)		
I. (*Multidentatus*) *rothschildi* (syn. *I. diomedeae*)	Charadriiformes: alcid (guillemot, Atlantic puffin), larid (European herring gull); Procellariiformes: diomedeid (yellow-nosed albatross), procellariid (Manx shearwater); Suliformes: phalacrocoracid (European shag)		Americas
I. (*Ixodes*) *rotundatus*	Rodentia: spalacid (unspecified mole-rat); Artiodactyla: bovid (bushbuck)		Africa
I. (*Afrixodes*) *rubicundus* (Karoo paralysis tick)	Artiodactyla: bovid (cattle, sheep, goat, springbok, grysbok, bontebok, grey rhebok, steenbok, eland, mountain reedbuck, Grant's gazelle, antelope), camelid (camel), cervid (deer), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (Natal red rock hare, Smith's red rock hare, scrub hare, Cape hare, red rock rabbit); Macroscelidea: macroscelidid (rock elephant shrew, Cape elephant shrew); Hyracoidea: procaviid (hyrax); Rodentia: murid (Namaqua rock rat), nesomyid (pouched rat); Carnivora: canid (dog, red jackal, black-backed jackal), felid (cat, black-footed cat, South African wildcat, caracal), hyaenid (aardwolf); Passeriformes: alaudid (lark), ploceid (weaver)	trauma, toxicosis, paralysis	South Africa
I. (*Pholeoixodes*) *rubidis*	Didelphimorphia: didelphid (unspecified opossum); Rodentia: myocastorid (coypu); Carnivora: canid (gray fox), mephitid (striped hog-nosed skunk), mustelid (tayra, long-tailed weasel), procyonid (raccoon, ringtail, northern olingo, ring-tailed coati)		North America
I. (*Pholeoixodes*) *rugicollis* (syn. *I. cornutus*)	Carnivora: canid (dog, red fox), felid (cat), mustelid (stoat, marten, beech marten, European polecat, European pine marten)		Central Asia
I. (*Pholeoixodes*) *rugosus*	Rodentia: cricteid (dusky-footed woodrat), sciurid (squirrel); Didelphimorphia: didelphid (opossum); Carnivora: canid (dog, coyote, gray fox), felid (bobcat), mephitid (striped skunk, western spotted skunk, California spotted skunk), mustelid (long-tailed weasel), procyonid (raccoon)		North America
I. (*Ixodes*) *sachalinensis*	Lagomorpha: leporid (mountain hare)		Russia
I. (*Ixodes*) *scapularis*	Artiodactyla: bovid (cattle, American bison, sheep, goat), camelid	trauma,	North America

(syn. *I. dammini*) (black-legged tick, shoulder tick, deer tick)	(camel), cervid (white-tailed deer, elk), suid (pig), tayassuid (collared peccary); Perissodactyla: equid (horse, mule); Didelphimorphia: didelphid (common opossum, Virginia opossum); Eulipotyphla: soricid (northern short-tailed shrew); Rodentia: cricetid (white-footed mouse, deer mouse, harvest mouse, Oldfield mouse, hispid cotton rat, pack rat, muskrat, marsh rice rat, eastern meadow vole, beach vole), erethizontid (porcupine), murid (mouse, brown rat, rice rat), sciurid (eastern chipmunk, eastern gray squirrel, red squirrel, fox squirrel, woodchuck); Lagomorpha: leporid (marsh rabbit, eastern cottontail, white-sided jackrabbit, hare); Carnivora: canid (dog, wolf, coyote, red fox, American red fox, gray fox), felid (cat, bobcat, Florida bobcat, Florida panther, ocelot), mephitid (striped skunk, eastern spotted skunk), mustelid (fisher, New York weasel), procyonid (raccoon); Chiroptera: vespertilionid (big brown bat); Primates: hominid (human); Accipitriformes: accipitrid (red-tailed hawk); Columbiformes: columbid (mourning dove); Galliformes: odontophorid (northern bobwhite), phasianid (chicken, ruffed grouse, quail, turkey); Gruiformes: gruid (sandhill crane); Passeriformes: corvid (blue jay, raven), fringillid (rose-breasted grosbeak, American goldfinch), icterid (brown-headed cowbird, common grackle), mimid (gray catbird, brown thrasher), muscicapid (common redstart), oriolid (Baltimore oriole), parulid (common yellowthroat, myrtle warbler, ovenbird), passerellid (song sparrow, swamp sparrow, white-throated sparrow, eastern towhee, junco), sturnid (common starling), turdid (American robin, hermit thrush); Sauria: anguid (eastern glass lizard), phrynosomatid (eastern fence lizard), scincid (little brown skink, broadhead skink, common five-lined skink); Testudines: emydid (unspecified tortoise)	irritation (vector for babesiosis, theileriosis, borreliosis (incl. Lyme disease), human granulocytic ehrlichiosis, anaplasmosis, tularemia, spotted fever, Powassan virus)	
I. (*Afrixodes*) *schillingsi*	Rodentia: cricetid (white-footed mouse), murid (black rat, crested rat), sciurid (unspecified squirrel); Hyracoidea: procaviid (hyrax); Primates: cercopithecid (Samango monkey, king colobus, mantled guereza, moustached guenon), galagid (brown greater galago), hominid (human)		Africa
I. (*Ixodes*) *schulzei*	Rodentia: cricetid (montane grass mouse, russet rice rat, scaly-footed water rat, yellow pygmy rice rat, black-footed pygmy rice rat); Passeriformes: muscicapid (Kalahari scrub robin)		South America, Africa
I. (*Pholeoixodes*) *sculptus*	Artiodactyla: bovid (sheep, goat), cervid (white-tailed deer); Perissodactyla: equid (horse); Lagomorpha: leporid (Mearn's cottontail, white-tailed jackrabbit, hare), ochotonid (American pika); Eulipotyphla: talpid (eastern mole); Didelphimorphia: didelphid (opossum); Rodentia: cricetid (dusky-footed woodrat, deer mouse, white-footed mouse, long-tailed vole, montane vole, western heather vole), dipodid (San Bernardino kangaroo rat), geomyid (brown pocket gopher, plains pocket gopher, northern pocket gopher, Botta's pocket gopher, Illinois pocket gopher), heteromyid (little pocket mouse), murid (mouse), sciurid (Merriam's chipmunk, black-tailed prairie dog, white-tailed prairie dog, Gunninson's prairie dog, Utah prairie dog, rock squirrel, golden-mantled ground squirrel, spotted ground squirrel, striped ground squirrel, thirteen-lined ground squirrel, Belding ground squirrel, California ground squirrel, Colorado ground squirrel, Columbian ground squirrel, Franklin's ground squirrel, Richardson's ground squirrel, Uinta ground squirrel, Wyoming ground squirrel, white-tailed antelope squirrel, yellow-bellied marmot), zapodid (western jumping mouse); Carnivora: canid (dog, red fox, gray fox), felid (cat, wildcat), mephitid (eastern spotted skunk, western spotted skunk, striped skunk), mustelid (American badger, long-tailed weasel), procyonid (raccoon), viverrid (civet); Primates: hominid (human); Galliformes: odontophorid (quail); Passeriformes: corvid (blue jay), turdid (thrush)		
I. scuticrenatus	Didelphimorphia: didelphid (opossum)		North America
I. (*Scaphixodes*) *semenovi*	Falconiformes: falconid (common kestrel); Passeriformes: corvid (red-billed chough), hirundinid (common house martin), passerid		Central Asia

	(white-winged snowfinch), prunellid (alpine accentor)		
I. (*Haemixodes*) *serrafreirei*	Rodentia (unspecified species)		South America
I. shahi	Lagomorpha: ochotonid (Royle's pika); Rodentia: murid (house mouse)		Nepal
I. shinchikuensis	Carnivora: canid (dog)		Taiwan
I. (*Partipalpiger*) *siamensis*	Rodentia: murid (Gairdner's shrewmouse); Eulipotyphla: soricid (Chinese mole shrew)		Asia
I. sigalasi	Charadriiformes: charadriid (northern lapwing); Passeriformes: turdid (blackbird)		Europe
I. sigelos	Rodentia: abrocomid (Bennett's chinchilla rat), cricetid (long-haired grass mouse, olive grass mouse, highland grass mouse, Spegazzini's grass mouse, drylands vesper mouse, Andean long-clawed mouse, western Patagonian laucha, Patagonian chinchilla mouse, southern big-eared mouse, yellow-rumped leaf-eared mouse, long-tailed pygmy rice rat, bunny rat), murid (brown rat), octodontid (Chilean rock rat, common degu)		South America
I. (*Scaphixodes*) *signatus* (syn. *I. arcticus*)	Charadriiformes: alcid (common murre), larid (black-tailed gull); Passeriformes: fringillid (mountain finch), turdid (Siberian thrush); Procellariiformes: procellariid (northern fulmar); Suliformes: phalacrocoracid (great cormorant, pelagic cormorant, Brandt's cormorant); Carnivora: otariid (northern fur seal)		Americas, Europe
I. (*Ixodes*) *silvanus*	Passeriformes: furnariid (sooty-fronted spinetail, buff-browed foliage-gleaner), parulid (two-banded warbler), passerellid (yellow-striped brushfinch, rufous-collared sparrow), thraupid (orange-headed tanager), tityrid (crested becard), turdid (rufous-bellied thrush, Andean slaty thrush)		South America
I. (*Eschatocephalus*) *simplex* (syn. *I. chiropterum*)	Chiroptera: miniopterid (common bentwing bat, little bentwing bat, Natal long-fingered bat), rhinolophid (greater horseshoe bat, smaller horseshoe bat, eloquent horseshoe bat, Geoffroy's horseshoe bat), vespertilionid (greater mouse-eared bat, eastern long-fingered bat, Alcathoe bat, Cape hairy bat, common pipistrelle, unspecified vesper bat); Afrosoricida: potamogalid (giant otter shrew); Rodentia: murid (mouse)	(possible vector for chiropteran piroplasmosis)	Australia, Eurasia, Africa
I. (*Ixodes*) *sinaloa*	Rodentia: cricetid (marsh rice rat, long-tailed rice rat, Alfaro's rice rat, Coues's rice rat, Sumichrast's harvest mouse, Mexican deer mouse), heteromyid (painted spiny pocket mouse, Salvin's spiny pocket mouse); Didelphimorphia: didelphid (grayish mouse opossum)		North America
I. sinensis	Artiodactyla: bovid (cattle, buffalo, sheep), cervid (white-tailed deer); Lagomorpha: leporid (hare); Rodentia: murid (mouse); Carnivora: canid (dog), felid (cat, leopard); Primates: hominid (human); Galliformes: phasianid (fowl)	(possible vector for rickettsioses)	China
I. (*Afrixodes*) *soarimalalae*	Afrosoricida: tenrecid (Cowman's shrew tenrec)		Madagascar
I. (*Pholeoixodes*) *soricis*	Eulipotyphla: soricid (common shrew, vagrant shrew, dusky shrew, northern montane shrew, Trowbridge's shrew), talpid (shrew-mole, broad-footed mole, Townsend's mole); Rodentia: cricetid (gray-tailed vole, Townsend's vole, North American deer mouse), geomyid (northern pocket gopher); Primates: hominid (human)		North America
I. (*Eschatocephalus*) *spiculae*	Chiroptera: (unspecified bat)		Africa
I. (*Afrixodes*) *spinae*	Hyracoidea: procaviid (rock hyrax); Rodentia: not specified; Passeriformes: fringillid (unspecified finch), motacillid (tree pipit), ploceid (southern red bishop)		Africa
I. (*Ixodes*) *spinicoxalis*	Rodentia: murid (red tree rat, white-bellied rat, narrow-tailed white-bellied rat), sciurid (black-striped squirrel); Scandentia: tupaiid (Horsfield's treeshrew); Eulipotyphla: soricid (Oriental shrew); Carnivora: mephitid (Sunda stink badger), mustelid (yellow-throated marten, Malayan glutton), viverrid (Asian palm civet); Passeriformes: muscicapid (flycatcher), pittid (pitta)		Indonesia
I. (*Ixodes*) *spinipalpis*	Rodentia: cricetid (bushy-tailed woodrat, dusky-footed woodrat, desert woodrat, Mexican woodrat, deer mouse, cactus mouse,		North America

	pinyon mouse, western harvest mouse, groove-toothed harvest mouse, northern grasshopper mouse, California vole), heteromyid (little pocket mouse, long-tailed pocket mouse, Merriam's kangaroo rat), murid (rat), sciurid (ground squirrel, pine squirrel, Douglas's squirrel, chipmunk); Eulipotyphla: soricid (common shrew, vagrant shrew); Lagomorpha: leporid (volcano rabbit, brush rabbit, jackrabbit, cottontail, hare), ochotonid (American pika); Carnivora: canid (dog), mustelid (weasel); Primates: hominid (human); Passeriformes: corvid (Florida scrub jay, Eurasian magpie), emberizid (bunting), mimid (gray catbird), parulid (orange-crowned warbler), passerellid (song sparrow, golden-crowned sparrow, Lincoln's sparrow, eastern towhee, dark-eyed junco), troglodytid (wren), turdid (hermit thrush, varied thrush)		
I. spinosus	Rodentia: cuniculid (lowland paca), dasyproctid (agouti, green acouchi)		South America
I. (*Endopalpiger*) *steini*	Dasyuromorphia: dasyurid (speckled dasyure)		New Guinea
I. (*Endopalpiger*) *stellae*	Dasyuromorphia: dasyurid (New Guinea quoll); Peramelemorphia: peramelid (striped bandicoot)		New Guinea
I. (*Ixodes*) *stilesi* (syn. *I. elegans*)	Artiodactyla: cervid (pudu); Rodentia: cricetid (long-tailed pygmy rice rat)		South America
I. sturni	Passeriformes: sturnid (common starling)		Europe
I. (*Pholeoixodes*) *stromi*	Rodentia: cricetid (common vole, bank vole, silver mountain vole, timber vole, narrow-headed vole, grey red-backed vole, gray dwarf hamster), murid (wood mouse, Turkestan rat); Eulipotyphla: soricid (unspecified shrew); Lagomorpha: ochotonid (large-eared pika); Carnivora: mustelid (unspecified weasel); Passeriformes: emberizid (red-headed bunting), muscicapid (white-winged redstart)		Central Asia
I. (*Pholeoixodes*) *subterraneus*	Columbiformes: columbid (European turtle dove); Coraciiformes: coraciid (European roller); Falconiformes: falconid (lesser kestrel); Galliformes: phasianid (fowl); Passeriformes: alaudid (crested lark), corvid (Eurasian magpie), fringillid (European goldfinch), passerid (house sparrow, Eurasian tree sparrow), sturnid (common starling, rosy starling, turdid (red-throated thrush); Strigiformes: strigid (owl)		Palearctic
I. succineus	fossil (amber)		Europe
I. sulcatus	Passeriformes: alaudid (brown lark), emberizid (yellowhammer), fringillid (bullfinch), sittid (Eurasian nuthatch)		Europe
I. (*Pholeoixodes*) *taglei*	Artiodactyla: cervid (pudu)		South America
I. taiwanensis	Artiodactyla: cervid (sambar deer), suid (wild boar); Carnivora: canid (dog), felid (cat)		Asia
I. (*Ixodes*) *tamaulipas*	Rodentia: sciurid (Deppe's squirrel)		North America
I. (*Ixodes*) *tancitarius*	Rodentia: cricetid (groove-toothed harvest mouse, unspecified deer mouse)		North America
I. (*Ixodes*) *tanuki*	Artiodactyla: cervid (sika deer); Rodentia: cricetid (grey red-backed vole, Smith's vole), murid (large Japanese field mouse); Carnivora: canid (Japanese raccoon dog), felid (cat), mustelid (mountain weasel, Siberian weasel, yellow-throated marten, Japanese badger), procyonid (raccoon)		Eurasia
I. (*Ixodes*) *tapirus*	Perissodactyla: tapirid (mountain tapir, Baird's tapir)		South America
I. (*Endopalpiger*) *tasmani* (common marsupial tick)	Dasyuromorphia: dasyurid (agile antechinus, yellow-footed antechinus, dusky antechinus, Tasmanian dusky antechinus, western quoll, tiger quoll, brush-tailed phascogale, white-footed dunnart, common dunnart, Tasmanian devil); Diprotodontia: burramyid (Tasmanian pygmy possum, lesser pygmy possum); macropodid (red-necked wallaby, Pearson Island rock-wallaby, Tasmanian pademelon, red-legged pademelon), petaurid (Leadbeater's possum), phalangerid (short-eared brushtail possum, Tasmanian brushtail possum, common brushtail possum), phascolarctid (koala), potoroid (eastern bettong, long-nosed potoroo), pseudocheirid (greater glider, yellow-bellied glider, sugar glider, green ringtail possum, common ringtail possum), vombatid (common wombat); Peramelemorphia: peramelid (northern brown bandicoot, southern brown bandicoot,		Australia

	eastern barred bandicoot, long-nosed bandicoot); Monotremata: tachyglossid (short-beaked echidna); Lagomorpha: leporid (European rabbit); Rodentia: murid (broad-toothed rat, giant white-tailed rat, fawn-footed melomys, rakali, long-tailed mouse, canefield rat, dusky field rat, bush rat, swamp rat, brown rat, black rat, white-footed rabbit-rat); Perissodactyla: equid (horse); Carnivora: canid (dog), felid (cat); Primates: hominid (human)		
I. (*Ixodes*) *tatei*	Carnivora: canid (red fox)		Middle-East
I. (*Scaphixodes*) *tauricus*	Suliformes: phalacrocoracid (European shag)		Central Asia
I. (*Ixodes*) *tecpanensis*	Rodentia: geomyid (giant pocket gopher)		Central America
I. tenuirostris	Rodentia: cricetid (common vole, bank vole, red-backed vole, field vole, short-tailed field vole, water vole, European water vole), murid (house mouse, wood mouse, Eurasian harvest mouse, brown rat); Eulipotyphla: soricid (common shrew, Eurasian pygmy shrew), talpid (European mole); Galliformes: phasianid (pheasant)		Europe
I. tertiarius	fossil		North America
I. (*Pholeoixodes*) *texanus*	Didelphimorphia: didelphid (common opossum, Virginia opossum); Lagomorpha: leporid (eastern cottontail, hare); Rodentia: cricetid (vole), murid (rat), sciurid (fox squirrel, pine squirrel, tree squirrel, eastern gray squirrel, American red squirrel, California gray squirrel, Richardson's Columbian squirrel, golden-mantled ground squirrel, yellow-bellied marmot, pallid yellow-bellied marmot, Tahoe chipmunk, southern woodchuck); Carnivora: canid (dog, gray fox, kit fox), felid (cat, bobcat), mephitid (striped skunk, western spotted skunk), mustelid (American badger, long-tailed weasel, short-tailed weasel, Arizona weasel, mink, new marten, fisher, stoat, American mink), procyonid (raccoon, ringtail, cacomistle), viverrid (civet); Primates: hominid (human)	trauma, irritation, dermatitis (vector for babesiosis, spotted fever)	North America
I. (*Ixodes*) *theilerae*	Passeriformes: hirundinid (barn swallow), platysteirid (Cape batis), ploceid (red-billed quelea, Cape weaver), sturnid (wattled starling), turdid (olive thrush)		Africa
I. theodori	Primates: hominid (human)		Israel
I. (*Afrixodes*) *thomasae*	Artiodactyla: bovid (suni); Eulipotyphla: soricid (shrew); Rodentia: murid (Abyssinian grass rat, tropical vlei rat, mouse, Natal multimammate mouse); Cuculiformes: cuculid (coucal); Passeriformes: malaconotid (black-crowned tchagra), ploceid (weaver)		Africa
I. (*Ixodes*) *tiptoni*	Rodentia: sciurid (red-tailed squirrel)		Central America
I. (*Ixodes*) *tovari*	Artiodactyla: bovid (cattle, goat); Lagomorpha: leporid (black-tailed jackrabbit, desert cottontail, hare); Rodentia: heteromyid (Ord's kangaroo rat); Passeriformes: emberizid (unspecified bunting), icterid (western meadowlark), passerellid (black-throated sparrow)		North America
I. (*Afrixodes*) *transvaalensis*	Rodentia: murid (Namaqua rock rat)		Africa
I. (*Exopalpiger*) *trianguliceps* (syn. *I. nivalis, Endopalpiger heroldi*)	Eulipotyphla: erinaceid (European hedgehog), soricid (common shrew, Eurasian pygmy shrew, Eurasian least shrew, alpine shrew, Arctic shrew, Caucasian shrew, Laxmann's shrew, Taiga shrew, Eurasian water shrew, Etruscan shrew, Mediterranean water shrew, lesser white-toothed shrew, Siberian large-toothed shrew, Caucasian pygmy shrew), talpid (European mole, Altai mole); Rodentia: cricetid (common vole, bank vole, meadow vole, tundra vole, social vole, short-tailed field vole, silvery mountain vole, grey red-backed vole, northern red-backed vole, narrow-headed vole, European water vole, European snow vole, alpine pine vole, European pine vole, Major's pine vole, Tatra pine vole, long-clawed mole vole, grey dwarf hamster, European hamster, wood lemming), echimyid (nutria), glirid (forest dormouse, hazel dormouse), murid (black rat, brown rat, Turkestan rat, water rat, house mouse, striped field mouse, Ural field mouse, forest mouse, wood mouse, yellow-necked mouse, Eurasian harvest mouse), sciurid (red squirrel, grey squirrel,	trauma, irritation (vector for anaplasmosis, and possibly borreliosis)	Europe

	Siberian chipmunk), sminthid (northern birch mouse); Lagomorpha: leporid (rabbit, hare); Perissodactyla: equid (horse); Carnivora: canid (fox), mustelid (least weasel, mottled polecat); Chiroptera: vespertilionid (big brown bat); Primates: hominid (human); Galliformes: phasianid (fowl); Passeriformes: corvid (crow), emberizid (yellowhammer), fringillid (finch); motacillid (tree pipit), turdid (blackbird); Piciformes: picid (great spotted woodpecker); Strigiformes: strigid (tawny owl); Sauria: lacertid (sand lizard, viviparous lizard)		
I. (*Sternalixodes*) *trichosuri* (possum tick)	Diprotodontia: macropodid (unspecified), phalangerid (common brushtail possum, Tasmanian brushtail possum), potoroid (eastern bettong); Peramelemorphia: peramelid (southern brown bandicoot); Rodentia: murid (black rat, bush rat, Australian swamp rat); Passeriformes: acanthizid (Tasmanian scrubwren)		Australia
I. (*Ixodes*) *tropicalis*	Rodentia: cricetid (golden Oldfield mouse, Tome's rice rat), echimyid (Bolivian bamboo rat); Didelphimorphia: didelphid (common opossum)		South America
I. (*Ixodes*) *turdus*	Rodentia: murid (large Japanese field mouse); Eulipotyphla: erinaceid (European hedgehog); Primates: hominid (human); Galliformes: phasianid (Chinese bamboo partridge); Strigiformes: strigid (owl); Passeriformes: cisticolid (singing cisticola, plain prinia), cettid (Korean bush warbler), emberizid (meadow bunting, yellow-throated bunting, black-faced bunting, Tristram's bunting), fringillid (hawfinch, brambling), motacillid (olive-backed pipit), muscicapid (red-flanked bluetail), pycnonotid (brown-eared bulbul), phylloscopid (western crowned warbler, dusky warbler), turdid (common blackbird, true thrush, song thrush, brown-headed thrush, grey-backed thrush, eyebrowed thrush, pale thrush, scaly thrush)		Palearctic
I. (*Afrixodes*) *ugandanus*	Artiodactyla: bovid (harnessed bushbuck, yellow-backed duiker, Maxwell's duiker); Hyracoidea: procaviid (yellow-spotted rock hyrax); Rodentia: nesomyid (Gambian pouched rat), thryonomyid (greater cane rat); Carnivora: herpestid (slender mongoose, large grey mongoose), viverrid (rusty-spotted genet, civet); Primates: cercopithecid (moustached guenon), lorisid (potto); Cuculiformes: cuculid (white-browed coucal)		Africa
I. (*Afrixodes*) *uilenbergi*	Afrosoricida: tenrecid (mole-like rice tenrec, highland streaked tenrec, shrew-toothed shrew tenrec, Dobson's shrew tenrec)		Madagascar
I. (*Afrixodes*) *uncus*	Afrosoricida: tenrecid (shrew-toothed shrew tenrec, Dobson's shrew tenrec)		Madagascar
I. (*Scaphixodes*) *unicavatus** (cormorant tick)	Charadriiformes: alcid (puffin); Falconiformes: falconid (gyrfalcon); Passeriformes: motacillid (European rock pipit, water pipit); Procellariiformes: diomedeid (wandering albatross); Siluriformes: phalacrocoracid (great cormorant, black cormorant, European shag)	trauma	Europe
I. (*Ceratixodes*) *uriae** (syn. *I. borealis, fimbriatus, hirsutis, putus*) (seabird tick)	Anseriformes: anatid (Campbell teal); Charadriiformes: alcid (common murre, thick-billed murre, razorbill, large-billed guillemot, black guillemot, Atlantic puffin), chionid (black-faced sheathbill), haematopodid (blackish oystercatcher), larid (black-legged kittiwake, herring gull, kelp gull, glaucous gull, glaucous-winged gull, black-backed southern gull, dolphin gull, Antarctic tern), scolopacid (curlew), stercorarid (great skua, brown skua); Passeriformes: fringillid (crossbill), hirundinid (sand martin), muscicapid (wheatear), sturnid (starling); Procellariiformes: diomedeid (wandering albatross, Antipodean albatross, Atlantic yellow-nosed albatross, Buller's albatross, Campbell albatross, Gibson's albatross, Salvin's albatross, southern royal albatross, northern royal albatross, grey-headed albatross, black-browed albatross, shy albatross, white-capped albatross, light-mantled albatross, sooty albatross), hydrobatid (northern storm petrel), procellariid (southern giant petrel, northern giant petrel, white-headed petrel, grey petrel, diving petrel, Kerguelen petrel, Cape petrel, Antarctic prion, fairy prion, sooty shearwater, Hutton's shearwater, Mank's shearwater, northern fulmar); Sphenisciformes: spheniscid (little penguin, yellow-eyed penguin, chinstrap penguin,	trauma, irritation (plus vector for borreliosis, possibly arboviruses, reoviruses, bunyaviruses and flaviviruses)	circumpolar

	king penguin, Adelie penguin, gentoo penguin, Magellanic penguin, Fiordland penguin, eastern rockhopper penguin, southern rockhopper penguin, macaroni penguin, snares penguin, crested penguin, erect-crested penguin, royal penguin); Suliformes: phalacrocoracid (black-faced cormorant, neotropic cormorant, spotted shag, rock shag, New Zealand king shag, Imperial shag, Auckland shag, Campbell shag, Kerguelen shag, Macquarie shag, Otago shag), sulid (booby, Australasian gannet, northern gannet); Carnivora: mustelid (otter); Rodentia: murid (rat, mouse); Primates: hominid (human)		
I. (*Haemixodes*) *uruguayensis**	Rodentia: cricetid (yellow pygmy rice rat, Waterhouse's swamp rat, grass mouse)	trauma	South America
I. (*Afrixodes*) *vandicus*	Artiodactyla: bovid (duiker); Macroscelidea: macroscelidid (black-and-rufous elephant shrew); Carnivora: canid (dog), felid (leopard), herpestid (marsh mongoose), viverrid (civet); Primates: hominid (human)		Africa
I. (*Ixodes*) *venezuelensis*	Didelphimorphia: didelphid (common opossum, gray four-eyed opossum, sepia short-tailed opossum, northern red-sided opossum, Mexican mouse opossum); Rodentia: cricetid (Alfaro's rice water rat, Costa Rican dusky rice rat, Talamancan rice rat, Tome's rice rat, short-tailed cane mouse, forest small rice rat, woodland Oldfield mouse, Mexican deer mouse, buff-bellied climbing mouse, Panamanian climbing rat), dasyproctid (red-rumped agouti, red acouchi, green acouchi), echimyid (Guyenne spiny rat, Tome's spiny rat), heteromyid (forest spiny pocket mouse, Trinidad spiny pocket mouse), murid (house mouse), sciurid (North Amazon red squirrel)		South America
I. (*Ixodes*) *ventalloi* (syn. *I. thompsoni*) (rabbit tick)	Lagomorpha: leporid (European rabbit, European hare); Eulipotyphla: erinaceid (European hedgehog, North African hedgehog), soricid (greater white-toothed shrew); Rodentia: glirid (garden dormouse), hystricid (crested porcupine), murid (black rat, brown rat, wood mouse, Barbary striped grass mouse, Algerian mouse, North African gerbil), sciurid (red squirrel); Carnivora: canid (dog, red fox), felid (cat, Iberian lynx), herpestid (Egyptian mongoose), mustelid (European badger, least weasel, beech marten); viverrid (common genet); Primates: hominid (human); Galliformes: phasianid (red-legged partridge, chukar partridge, ring-necked pheasant); Gruiformes: rallid (water rail); Strigiformes: strigid (little owl, long-eared owl, short-eared owl), tytonid (barn owl); Passeriformes: corvid (Eurasian magpie), turdid (common blackbird, fieldfare); Sauria: agamid (North African rock agama), lacertid (Algerian sand racer), scincid (many-scaled cylindrical skink, Algerian orange-tailed skink)	(possible vector for Q fever, rickettsioses, anaplasmosis, Eyach and Erve viruses)	Europe
I. (*Eschatocephalus*) *vespertilionis** (syn. *I. flavipes, longipes*)	Chiroptera: emballuronid (sheath-tailed bat), hipposiderid (Sundevall's roundleaf bat), miniopterid (common bentwing bat, little bentwing bat, pale bentwing bat, Natal long-fingered bat), rhinolophid (greater horseshoe bat, lesser horseshoe bat, eastern horseshoe bat, Blasius's horseshoe bat, Geoffroy's horseshoe bat, Mediterranean horseshoe bat), vespertilionid (greater mouse-eared bat, lesser mouse-eared bat, brown long-eared bat, whiskered bat, pond bat, common noctule, serotine bat, long-fingered bat, western barbastelle, Bechstein's bat, Cape hairy bat, Daubenton's bat, Geoffroy's bat, common pipistrelle, Kuhl's pipistrelle, Nathusius's pipistrelle, Natterer's bat); Carnivora: canid (dog); Primates: hominid (human)	trauma (possible vectors for bartonellosis, babesiosis)	Europe, Asia, Africa, Australia
I. (*Exopalpiger*) *vestitus* (numbat tick)	Dasyuromorphia: dasyurid (western quoll), myrmecobiid (numbat); Serpentes: elapid (eastern brown snake), pythonid (unspecified python)		Australia
I. (*Endopalpiger*) *victoriensis*	Diprotodontia: potoroid (long-footed potoroo), pseudocheirid (common ringtail possum), vombatid (common wombat)		Australia
I. viperarum	Serpentes: viperid (unspecified viper)		Europe
I. (*Afrixodes*) *walkerae*	Carnivora: herpestid (water mongoose), viverrid (rusty-spotted genet); Galliformes: numidid (crested guineafowl); Passeriformes:		Africa

	turdid (olive thrush)		
I. (*Ixodes*) *werneri*	Rodentia: murid (Palawan spiny rat, chestnut white-bellied rat), Scandentia: tupaiid (treeshrew)		Philippines
I. (*Pholeoixodes*) *woodi*	Rodentia: cricetid (eastern woodrat, southern plains woodrat, bushy-tailed woodrat, Mexican woodrat, hispid cotton rat, deer mouse, white-footed mouse), geomyid (pocket gopher), heteromyid (kangaroo rat), sciurid (Mexican ground squirrel); Eulipotyphla: soricid (Crawford's gray shrew); Carnivora: mephitid (striped skunk, spotted skunk), procyonid (common raccoon); Primates: hominid (human); Passeriformes: tyrannid (western kingbird)		North America
I. woyliei	Diprotodontia: potoroid (woylie); Peramelemorphia: peramelid (quenda), thylacomyid (greater bilby)		Australia
I. (*Endopalpiger*) *zaglossi*	Monotremata: tachyglossid (western long-beaked echidna)		Indonesia
I. (*Afrixodes*) *zairensis*	Eulipotyphla: soricid (greater red musk shrew)		Africa
I. (*Multidentatus*) *zumpti*	Procellariiformes: diomedeid (sooty albatross, Atlantic yellow-nosed albatross), procellariid (great shearwater, prion, diving petrel)		Africa

Parasite morphology: *Ixodes* spp. form 4 different types of developmental stages; eggs; larvae; nymphs; and adults. The eggs are small shiny-brown ovoid stages measuring up to 0.5 mm long and are often clustered together in large sticky masses. Emergent larvae (also known as seed ticks or pepper ticks) have ovate dorso-ventrally flattened bodies measuring less than 1 mm in length and are usually yellow-brown in colour. The idiosoma (body) has a hardened (sclerotized) pentagonal dorsal plate (scutum) located anteriorly while the remainder of the body has a rounded oval margin. Larvae have 3 pairs of long jointed legs located ventrally on the anterior idiosoma. The capitulum (head) is visible in dorsal view as a forward projection and has a gnathosoma with 2 palps flanking the mouthparts (comprising 2 chelicerae and a central toothed hypostome). Larvae lack respiratory stigmata, tracheae and genital pores. Nymphs have ovate flattened bodies with a conspicuous capitulum bearing mouthparts and an idiosoma with an anterior dorsal scutum. Nymphs are generally larger and darker in colour than larvae, measuring up to 2 mm long and ranging from brown to black, but often with a lighter posterior idiosoma, sometimes patterned. They characteristically have 4 pairs of long jointed legs attached ventrally, and a pair of respiratory openings (stigmata) surrounded by oval plates located behind the fourth pair of basal coxae. Like larvae, nymphs lack genital pores. Adult ticks have round dorso-ventrally flattened bodies that range in length from 2-4 mm when unfed, but females may become ovoid and swell to 10-20 mm in diameter when engorged. Most species are brown to reddish brown in colour, sometimes grey-black. Adults are clearly divided into 2 parts: a small anterior capitulum (head) and a larger posterior sac-like idiosoma (body). The capitulum projects forwards and is visible from above (whereas that of argasid ticks is ventral and not visible). It consists of the basis capitulum (integumental ring encircling mouthparts) and the gnathosoma (feeding structure comprising 2 palps, 2 chelicerae and toothed hypostome). In females, the basis capitulum also has 2 dorsal porose areas (absent in argasids) which are used to water-proof eggs. *Ixodes* spp. have long mouthparts (not short like *Rhipicephalus*/*Boophilus*, *Dermacentor*, *Haemaphysalis*) that are mounted on short triangular basis capituli (not rectangular like *Amblyomma*/*Aponomma*, *Dermacentor*, *Haemaphysalis*, *Hyalomma*, nor hexagonal like *Rhipicephalus*/*Boophilus*, nor pentagonal like *Bothriocroton*). The palps are club-like sensory structures that move laterally and do not enter the skin when the tick is feeding. They are long (not short like *Rhipicephalus*/*Boophilus*, *Dermacentor*, and *Haemaphysalis*) and are composed of 4 unequal segments; the second segment being tapered at its base, and the fourth segment being greatly reduced and bearing chemoreceptor sensillae. The chelicerae are cutting structures used horizontally to rip and tear the flesh to form small pools of blood. They have 2 segments and are tubular with long curved shafts in spinose sheaths, and terminate in 2 cutting digits with recurved teeth. The central hypostome is an extension of the basis capitulum and is dentate with backward-facing teeth. It is inserted into the blood pool to facilitate feeding as well as to anchor the tick to its host. During feeding, the chelicerae and hypostome form the buccal canal to inject saliva and suck blood. The alimentary tract consists of a muscular pharynx (with pharyngeal valve), tubular oesophagus, large saccular midgut with branched diverticula (caeca) and excretory Malpighian tubules, a vesicular rectal sac (analogue of hindgut in ticks) and subterminal ventral anus. *Ixodes* spp. are prostriate ticks in that they possess an inverted U-shaped anal groove extending anteriorly and enclosing the anus, whereas all other ixodid genera are metastriate ticks and have a posterior anal groove. All ixodids are hard ticks with chitinized dorsal plates (scutum) which are absent in soft argasid ticks. The scutum covers the whole back of males (= conscutum) but only the anterior portion of females (often becoming obscured following engorgement). *Ixodes* spp. are inornate and have plain dorsal surfaces without coloured patterns (not ornate like *Amblyomma*/*Aponomma*, *Bothriocroton*, and some *Rhipicephalus* and *Dermacentor* spp.), without marginal notches or festoons (present in all other ixodid genera, except *Boophilus*), and without pigmented 'eyes' (present in *Amblyomma*, *Rhipicephalus*/*Boophilus*, *Dermacentor* and *Hyalomma*). The ventral idiosoma gives rise to 4 pairs of long jointed legs, each with 6 segments (coxae, trochanter, femur, patella (genu), tibia and tarsus) and all terminating in a pair of claws with a pad-like pulvillus (pulvillus absent or rudimentary in argasids). The legs are generally paler in colour than the body, but they lack conspicuous pale rings or markings (present on *Amblyomma* and *Hyalomma*). The first pair of legs have a special sensory structure (Haller's organ) on the dorsal tarsus which is used to detect temperature, odour and tactile stimuli. Ixodid coxae also have spurs (absent in argasids) with *Ixodes* spp. typically having a single large internal spur on coxae I. Adults have a pair of respiratory stigmata with large plates located behind coxae IV (whereas the stigmata in argasids are located between coxae III). *Ixodes* spp. exhibit marked sexual dimorphism, particularly with respect to body size (females are larger,

especially after feeding), mouthparts (longer in females), dorsal scutum (complete covering on males, partial covering on females), ventral plates (on males only) and porose areas on the basis capitulum (on females only). Males have flat sclerotized plates covering much of their ventral surface: including an anal plate (around the subterminal anus), 2 adanal plates (either side of the anus), a large median plate (between the anus and the midbody gonopore), 2 epimeral plates (lateral to the median plate and containing the spiracles), and a pregenital plate (anterior to the gonopore). These plates are absent in most other ixodid genera (*Aponomma*, *Dermacentor*, *Haemaphysalis*, and *Bothriocroton*) and reduced in number in others (*Rhipicephalus*). Males have 2 tubular testes with vas efferentia fusing to form a common vas deferens (large multilobed accessory glands) leading to the ejaculatory duct and gonopore (genital opening) which is situated ventrally around the midbody and has an anterior sclerotized flap (genital apron). Males produce packets of spermatids (spermatophores) which are transferred to the genital operculum of females. Females have a single saccular ovary (becoming grape-like when gravid) with paired oviducts joined to a common uterus (with tubular accessory glands that help coat eggs) opening to a vagina with a saccular cervical region (acting as a receptaculum seminis) and a vestibular region (capable of prolapsing during oviposition). The female gonopore (genital opening) is located ventrally around the midbody and is U- or V-shaped with marginal folds and an anterior genital apron. Females also have special glands (Gene's organ) located near the gnathosoma-idiosoma junction which produce waxy coatings for eggs as they emerge during oviposition.

Site of infection: Larval, nymphal and adult ticks are obligate but transient ectoparasites that attach to the skin of their hosts. *Ixodes* spp. often have broad host ranges (euryxenous or stenoxenous) and infest multiple mammalian, avian and/or reptilian hosts. Different life-cycle stages may also occur on different animal species, with larvae often found on small terrestrial hosts, nymphs being found on a wider range of sympatric hosts, and adults also infesting larger vertebrates. *Ixodes* spp. have been reported on mammals belonging to 102 families in 25 orders (including herbivores, omnivores and carnivores), birds belonging to 64 passerine families and 57 non-passerine families in 29 orders (including seabirds, shore birds, waterfowl, forest birds, terrestrial birds and some birds of prey) and reptiles belonging to 8 lizard families, 6 snake families and 3 tortoise families. Most species have preferred (predilection) sites of attachment on different hosts, often involving cryptic areas among skin folds which are difficult for hosts to groom. Ticks on humans often move to the head behind the ears, or attach to the skin under tight-fitting clothing (such as elasticized waist-bands). Animals are generally infested by larvae on the belly, legs and groin, by nymphs on the head, forelegs, brisket and shoulders, and by adults on the neck, shoulders, face and ears.

Pathogenesis: Ixodid ticks are haematophagous ectoparasites causing traumatic tissue damage, inflammation, hypersensitivity, anaemia, production losses, toxicoses and paralysis as well as transmitting infectious diseases. When attaching to a new host, ticks use their chelicerae in a ripping and tearing motion to cut a channel in the skin resulting in the formation of a small pool of blood and fluid into which they insert their hypostomes, thus forming a tubular food channel through which saliva is injected and blood is ingested. This feeding process is known as telmophagy (pool feeding), as distinct from solenophagy (sucking direct from blood vessels) as practised by other ectoparasites (e.g. mosquitoes). Feeding ticks also concentrate their blood meals by secreting (regurgitating) host-derived fluids back into the host. Hard ticks attach and feed gradually over 2-14 days as they must grow new cuticle to accommodate their blood meals. Their hypostomes have recurved teeth which serve as anchors and many species secrete a cement-like substance from their salivary glands to aid attachment, thereby usually creating a sterile abscess-like feeding site. Tick saliva also contains numerous chemicals to assist feeding (anticoagulant and antihaemostatic substances) as well as to suppress rejection by the host (anti-inflammatory compounds and immunomodulatory proteins and lipids). Paradoxically, when ticks detach after feeding, the salivary components they leave behind are antigenic and stimulate inflammation and granuloma formation. Nonetheless, host reactions to tick bites vary considerably. Many bites are painless and the hosts do not even notice them. However, tick mouthparts often penetrate to the dermis resulting in haemorrhage, collagen degeneration, focal necrosis and sometimes local hypersensitivity with papule and wheal formation. Bites may therefore cause discomfort, local irritation, erythema (redness), oedema (swelling), pruritus (itching), alopecia, papular dermatitis, sores, ulcers and sometimes burning sensations, rash, headache and fever. Small local granulomatous reactions consisting of mixed inflammatory cells (neutrophils, lymphocytes, plasma cells) with fibrosis are common. Tick bites often become secondarily infected with bacteria, especially when ticks are forcibly removed leaving their mouthparts embedded in the skin, resulting in abscesses which may spread to the circulation causing bacteraemia and septicaemia. Ticks require substantial blood meals for moulting to the next developmental stage or for egg production. Larvae may ingest 11-17 times their pre-feeding weight while adult females may ingest 60-120 times their pre-feeding weight. Estimates of the blood volume consumed vary from 0.7-8.9 mL per female in some ixodid species. Heavy infestations may therefore result in significant blood loss and the host may become anaemic.

The salivary gland secretions of some *Ixodes* spp. (notably *I. holocyclus* and *I. cornuatus* in Australia and *I. rubicundus* in Africa) also contain neurotoxins which may cause a progressive flaccid ascending motor paralysis in susceptible hosts by inhibiting production of the neurotransmitter acetylcholine at neuromuscular junctions. The neurotoxins are released during feeding by larval, nymph and adult stages, but especially by engorging females. Clinical signs usually appear 3 days after attachment and worsen thereafter, first paralysing the legs, then the arms and finally the thorax and throat. Accompanying signs include delayed cardiac repolarization (long QT syndrome), pulmonary oedema, tracheopharyngeal compression, dysphonia, depressed gag and swallowing reflexes, aspiration pneumonia, pupil dilation, regurgitation or vomiting, dyspnoea, cyanosis, laboured respiration with a prolonged expiratory phase and expiratory grunt. Small susceptible animals may die from respiratory failure unless the ticks are removed, although their condition may continue to deteriorate for 48 hours after tick removal. A single engorging female tick may release enough neurotoxin to kill a dog or cat, or cause partial paralysis in an infant or small child. Several ticks may produce enough to kill

neonatal domestic animals, and heavy infestations may prove fatal to larger domestic animals. Host susceptibility to the neurotoxins varies considerably between species, with many native animals apparently being refractory to toxic effects, and thus acting as wildlife reservoirs for infestations. In endemic areas, some hosts may also acquire transient resistance, as evidenced by reductions in engorgement success, egg production and hatching and increased tick mortality. Resistant hosts often develop cutaneous granulocytic reactions around bite sites, with subsequent degranulation and histamine release inhibiting feeding success. Both specific humoral and cell-mediated immune responses have been demonstrated in infested hosts, but their role in the acquisition of any protection is unknown, especially since ticks have been shown to be able to modulate or suppress host immune responses. Nonetheless, tick paralysis responds well to treatment with antibodies contained in anti-serum raised in animals subject to repeated non-lethal challenge.

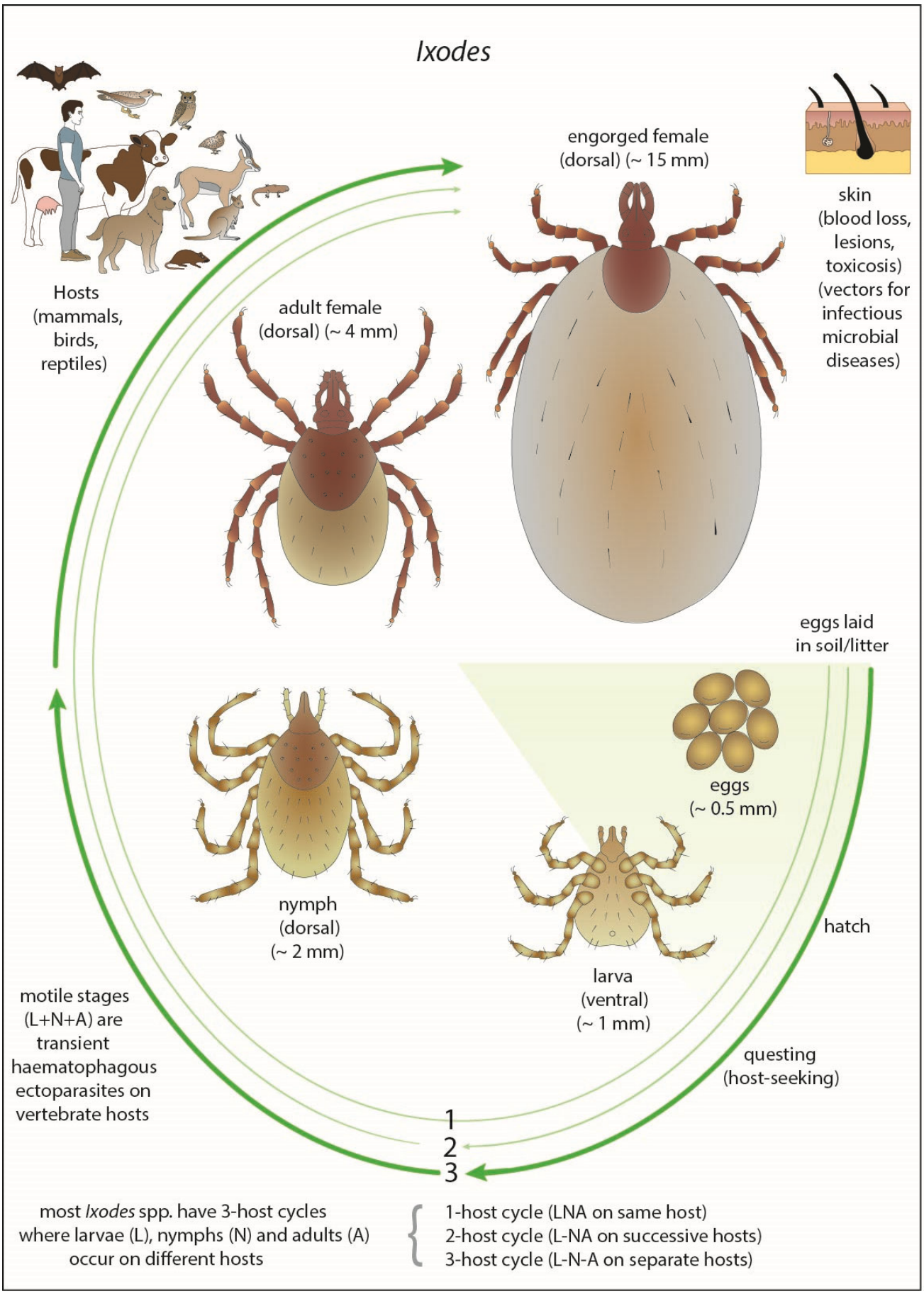
In addition to the direct effects of ticks on hosts, they also exert many indirect effects by acting as vectors (biological and/or mechanical) for the transmission of various infectious diseases. Their long life spans (years), frequent changing of hosts (3-host life-cycles), prolonged feeding (days to weeks), voracious appetites (large blood meals) and profuse secretory and excretory products (saliva, regurgitated fluids, faeces) make them efficient vectors for various viral, bacterial, protozoal and helminth infections. Many of these pathogens undergo trans-stadial transmission (from larva to nymph to adult ticks) while some also undergo transovarian transmission (from adult female ticks to their eggs). Pathogenic micro-organisms transmitted by ticks include: viruses causing tick-borne encephalitis, Powassan encephalitis, Omsk haemorrhagic fever, African swine fever and louping ill; rickettsial bacteria causing spotted fevers, tick typhus, anaplasmosis, ehrlichiosis and Q fever; coccobacilli causing tularemia; staphylococci causing pyaemia; spirochaetes causing Lyme disease; piroplasms causing babesiosis and theileriosis; and even the nematode *Ackertia* causing filariasis. The major vectors for tick-borne diseases in humans and domestic animals are *I. ricinus* and *I. persulcatus* in Eurasia and *I. scapularis* and *I. pacificus* in North America.

Developmental cycle and mode of transmission: Ticks actively seek hosts, not by pursuing them but by sedentary questing; i.e., climbing vegetation and waiting for hosts to brush past. Questing behaviour is influenced by changes in environmental temperature, humidity and day length. Ticks are prone to desiccation so they quest more actively when hydrated, and return to humid ground level when dehydrated. Body heat, movement, vibrations, visual images, odours and carbon dioxide act as stimuli for tick attachment to passing hosts. Ticks are found in wooded and forested regions of world, often near water sources where warm-blooded animals come to drink, or along trails, or on pastures. Many *Ixodes* spp. are nidicolous (nest-dwelling) and are closely associated with nests, hides, shelters or burrows of their small mammalian or bird hosts, or in nearby soil, leaf litter, bark or foliage. Once contact is made with a host, ticks migrate to suitable or preferred sites of attachment. Ticks exhibit hemimetabolous (incomplete) metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults (ixodid ticks only have 1 nymphal instar whereas argasids have 2-7 instars). Most *Ixodes* spp. have 3-host life-cycles whereby larvae, nymphs and adults all feed on different hosts for several days before dropping off the host to continue development. Eggs in the environment hatch when climatic conditions are suitable (warm and humid), usually from 40-110 days after being laid. Emergent hexapod larvae (known as seed, grass or pepper ticks) undergo 7-44 days of hardening before attaching to small hosts (rodents, birds) to feed for 4-6 days. Once replete, they detach and moult 19-41 days later in the environment to form octopod nymphs. The nymphs attach to mid-sized hosts (rodents, carnivores, birds) 5-30 days later and feed for 4-7 days. Replete nymphs then detach and moult 3-11 weeks later to form adults which become sexually mature soon thereafter. Male and female ticks may mate before or after attachment to mid-sized to large hosts (carnivores, herbivores, omnivores) 7-77 days later. Males feed very little on blood, instead they may attach to female ticks by piercing her cuticle and feeding on haemolymph. Attached females usually do not fully engorge on host blood unless they are inseminated and their ovaries become vitellogenic (although parthenogenesis has been observed in several tick species). Inseminated females feed for periods ranging from 6-30 days, becoming grossly enlarged during engorgement. When replete, the fecund females detach and lay eggs 11-20 days later in the environment in soil crevices, underneath leaf litter or on vegetation. Eggs are laid in cohesive masses of several thousand eggs at a rate of 20-200 eggs per day for 3-34 days. Female ixodid ticks die 1-2 days after egg production is completed, so they only undergo a single gonotrophic cycle (compared to multiple cycles for argasid ticks). The amount of time each stage spends in the environment (off-host) varies considerably according not only to host availability but also prevailing climatic conditions. In temperate and subpolar regions, tick activity is seasonal and influenced by ambient temperature, photoperiod and incident solar energy. Many species may undergo temporary diapause to survive adverse environmental conditions by lowering their metabolic rates, becoming inactive, delaying development or delaying oviposition. Larvae and nymphs are generally more active in autumn before over-wintering and forming adults which feed and breed during spring and early summer. In tropical regions where day length and temperature vary only slightly throughout the year, tick activity is influenced by the transition from the dry to the rainy season. Hard ticks have been found to live for 2-6 years, but the whole life-cycle is often completed within a year in tropical regions or within 2-3 years in more temperate colder regions.

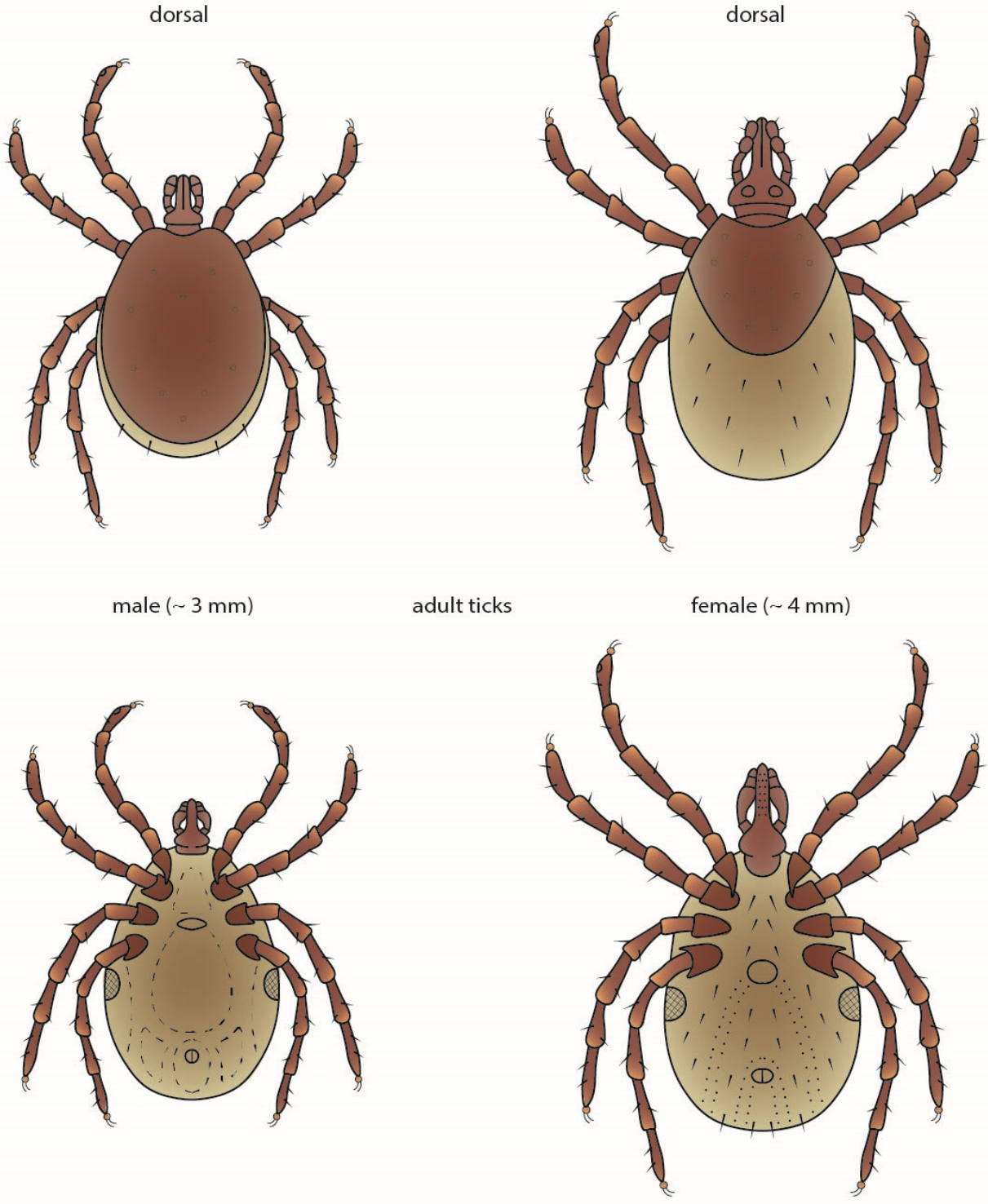
Differential diagnosis: Questing ticks may be recovered from the environment using baits (carbon dioxide from dry ice) or by dragging cloth strips or flags through vegetation. Infestations on hosts, however, are usually detected by finding feeding stages attached to the skin, especially large engorging females. Evidence of recent infestation may be seen at predilection sites as small inflamed nodules, sometimes accompanied by nonspecific pathophysiological changes (such as rash, fever, peripheral nerve dysfunction, respiratory difficulty, oesophageal dysfunction and hypertension). Nonetheless, differential diagnosis is performed by removing ticks and examining them microscopically for species-specific morphotypic characters. A range of dichotomous and polychotomous taxonomic keys are available to identify the different developmental stages (larvae, nymphs, males and females) of

most ixodid tick species. Protein electrophoresis and cuticular hydrocarbon analyses have been used to complement taxonomic studies, and molecular characterization studies have used polymerase chain reactions (PCR) to amplify specific gene sequences: including nuclear ribosomal RNA (18S, 28S, ITS1, ITS2) and mitochondrial RNA (12S, 16S), cytochrome c oxidase subunit 1 (cox1) and nicotinamide adenine dinucleotide dehydrogenase subunit 5 (pnad5).

Treatment and control: Individual ticks attached to hosts can be physically removed, preferably by sliding fine forceps/tweezers or special removal devices (tick keys, twists, loops/lassos, or V-shaped tools) under their mouthparts and then exerting gentle backwards pressure until the tick lets go. Excessive force should not be used to avoid squeezing tick contents into the wound as well as to avoid tearing out the mouthparts leaving them behind (in which case they should be surgically removed). It is advisable not to use heat, detergents or irritant solvents to treat ticks before removal as this may cause them to inject or regurgitate more material into the bite site. However, some studies have indicated that treating them with permethrin creams, pyrethroid sprays, chloroform, benzyl benzoate, bicarbonate of soda or freeze-drying them with ether-containing sprays may aid in their removal. People should exercise personal protection by covering exposed skin, tucking pants into boots or socks, applying insect repellents (containing permethrins, DEET or picaridan) to skin and clothing, and avoiding grassy areas and shrubs during active tick seasons. Routine skin inspection should be practiced especially for humans and animals most at risk (i.e. those regularly moving through bush vegetation). Various acaricides have proven effective for the treatment of animals when used as dips, sprays, pour-ons, slow-release collars or ear-tags, tablets, drenches, in-food medications or applied using devices associated with feeders or nesting materials. Domestic animals have been treated successfully with topical organophosphonates (chlorfenvinphos, dichlorvos, dioxathion, tetrachlorvinphos, trichlorfon), monothiophosphates (chlorpyrifos, coumaphos, diazinon, fenthion, propetamphos), dithiophosphates (malathion, phosmet), chlorinated hydrocarbons (DDT, lindane), neonicotinoids (imidacloprid), arsenical preparations, carbamates (carbaryl), pyrethroids (permethrin, deltamethrin, flumethrin, cyfluthrin, decamethrin, cypermethrin, alphamethrin), formamidines (amitraz), phenylpyrazoles (fipronil) as well as with parenteral macrocyclic lactones (ivermectin, selamectin), salicylanilide (closantel) and isoxazoline-substituted benzamide derivatives (fluralaner). Several studies have found treatment with insect growth regulators and hormones (methoprene, ecdysteroid mimics, juvenile hormones) disrupt tick development but these formulations are not widely available. There are mounting concerns about the development of resistance to acaricides in some tick populations with treatment failures being recorded with increasing frequency against arsenical compounds, organochlorines, organophosphates, pyrethroids and formamidines. To combat the development and spread of resistance, it is recommended that tick populations be checked for acaricidal resistance (by *in situ* or *in vitro* larval immersion, larval packet or adult immersion tests, immunoassays or genotypic screening) and that the major classes of acaricides (except organochlorines) be used in cyclic rotation or as co-formulations. The management of patients experiencing tick paralysis is based on tick removal, treatment with anti-serum and providing supportive care. Finding ticks on animals can be difficult and should include thorough visual and tactile examination of the whole body (including crevices and orifices), using grooming devices or clippers as required. Empirical treatment with an acaricide should also be provided to ensure any stages overlooked will be killed. Clinically-affected animals should be treated with anti-serum to neutralize circulating toxins, even after tick removal in mild or highly suspect cases (clinical signs often worsen for several days). A variety of management strategies have been developed for tick infestations of domestic animals but their efficacy is diminished in many instances by the persistence of ticks on wildlife reservoirs, especially in areas where wildlife and domestic stock constantly intermingle. Efforts should be taken to exclude wildlife from animal-holding facilities using barriers, traps, baits and other vermin control strategies. Pet owners should regularly inspect their animals for infestations, provide long-lasting prophylactic treatment and restrict their access to bush areas where ticks are endemic. Many states and countries have adopted legislature which restricts livestock movement into and from endemic areas and facilitates appropriate quarantine. Various management strategies (such as pasture rotation or spelling, clearing vegetation by cultivation/ploughing, cutting/slashing or prescribed burning) have also been used to minimize the transmission of infestations and reduce tick burdens on pastures. Several computerized mathematical prediction models have been developed to help schedule treatment times and other interventions based on multiple bionomic factors, including prevailing weather (temperature, moisture, rainfall), microclimate (photoperiod, circadian rhythms), macroclimate (seasons), vegetation (type, structure, density), geographic location (latitude, longitude, elevation), land-use and animal husbandry (cohorts, grazing history). Many native animal species are genetically resistant to heavy tick infestations. This is being exploited in cross-breeding programs e.g. *Bos indicus* (Zebu) cattle and Sanga breeds of *Bos taurus* cattle are more tick-resistant than European *Bos taurus* breeds. More recently, several experimental vaccination studies using salivary gland proteins (Salp25D and tHRF) and other metabolic extracts (subolesin) from *I. scapularis* have provided variable protection to laboratory and field animals exposed to homologous tick challenge. [Note that very successful results have been reported in vaccination studies using hidden gut antigens from a range of other ixodid tick spp. (notably *Boophilus microplus*, but also including *Rhipicephalus appendiculatus* and *Hyalomma anatolicum*)]. Many biological control options are also being investigated to reduce tick populations using predators, parasites and pests: including the use of parasitic chalcid wasps that oviposit in ixodid nymphs, seeding pastures with parasitic nematodes (*Steinernema*, *Heterorhabditis*) or entomopathogenic fungi (*Beauveria, Metarhizum*) that prey on tick stages; encouraging natural predators (such as oxpecker grooming birds); and growing plants which use structural or chemical deterrents to tick-questing behaviours.


Ixodes
Hosts (mammals, birds, reptiles)
engorged female (dorsal) (~ 15 mm)
skin (blood loss, lesions, toxicosis) (vectors for infectious microbial diseases)
adult female (dorsal) (~ 4 mm)
eggs laid in soil/litter
eggs (~ 0.5 mm)
nymph (dorsal) (~ 2 mm)
larva (ventral) (~ 1 mm)
hatch
questing (host-seeking)
motile stages (L+N+A) are transient haematophagous ectoparasites on vertebrate hosts
1
2
3
most *Ixodes* spp. have 3-host cycles where larvae (L), nymphs (N) and adults (A) occur on different hosts
1-host cycle (LNA on same host)
2-host cycle (L-NA on successive hosts)
3-host cycle (L-N-A on separate hosts)

Ixodes


dorsal
dorsal
male (~ 3 mm)
adult ticks
female (~ 4 mm)
ventral
ventral



Ixodes adult



Ixodes adult female, engorged



Ixodes adult female and eggs



Ixodes larva



Ixodes nymph



Ixodes paralysis tick on dog

***Rhipicephalus* (incl. *Boophilus*)**
(arachnid: tick)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ticks have respiratory stigmata posterior to their legs. They are obligate blood-feeding ectoparasites on vertebrate hosts and their hypostomes are toothed and exposed. Two families are recognized: Argasidae and Ixodidae, known as soft and hard ticks, respectively. Ixodids have hard bodies with a dorsal scutum (shield-shaped plate) and the capitulum is not covered by the body. Larvae, nymphs and adults attach and feed on host blood, their life-cycles involving one, two or three hosts depending on whether moulting occurs on or off the host. Some 650 species of hard ticks infest mammals, birds and reptiles. Infestations by *Rhipicephalus* (incl. *Boophilus*) spp. are common as 1, 2 or 3 host ticks on mammals; most species causing irritation and toxicosis, and many transmitting infectious diseases, notably piroplasm tick fevers to domestic livestock.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on capitulum)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Ixodida (Metastigmata) (ticks, macroscopic, stigmata posterior to legs, hypostome toothed, ectoparasites)
Family: Ixodidae (hard ticks, with dorsal scutum, capitulum projects anteriorly, attach and feed on 1, 2 or 3 hosts)
Genus: *Rhipicephalus* (incl. *Boophilus*) (parasitic on skin of mammals)
Species: various species causing skin lesions on livestock and transmitting tick fevers

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on capitulum) [34 superfamilies]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs (behind coxae III or IV); and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Ticks are further characterized by macroscopic bodies with an exposed ventral hypostome (toothed with backwardly-directed barbs), chelicerae with only 2 joints, long legs with free articulated coxae (not fused to the body wall) and a complex sensory pit (Haller's organ) on tarsus I. They are obligate blood-sucking parasites which feed on terrestrial vertebrates (mammals, birds, reptiles and some amphibians) as larvae, nymphs and adults with 1-, 2- or 3-host life-cycles. Almost 1,000 species have been classified within some 20 genera from numerous wild and domesticated animals around the world. Two main families are recognized: the Argasidae containing ~200 species of 'soft' ticks with flexible leathery cuticles, ventral capitula, short feeding times (< 1 hour) and long life-spans (up to 20 years); and the Ixodidae containing ~800 species of 'hard' ticks with rigid dorsal scutal plates, anterior capitula, long feeding times (hours to days) and shorter life-span (2-6 years). Basic characteristics of representative genera considered in this resource are tabulated below.

Genus	**Capitulum**				**Idiosoma**				**Usual no. of hosts**
	location	**basis capitulum**	**mouth-parts**	**palps**	**integument**	**festoons**	**eyes**	**male ventral**	

								plates	
Argasidae (soft ticks with leathery cuticle, stigmata between coxae III)									
Argas	ventral	triangular	short	leg-like	stippled with lateral suture	absent	absent	absent	>3
Ornithodorus	ventral	rectangular	short	leg-like	mamillated	absent	usually absent	absent	>3
Otobius	ventral	rectangular	short	leg-like	spinose (nymphs), granulated (adult)	absent	absent	absent	1
Ixodidae (hard ticks with sclerotized dorsal plate (scutum), stigmata behind coxae IV)									
Prostriata (anal groove anterior)									
Ixodes	anterior	triangular	long	long	inornate	absent	absent	present	3
Metastriata (anal groove posterior)									
Amblyomma	anterior	rectangular	long	long	ornate	present	present	indistinct	3
(*Aponomma*)	anterior	rectangular	long	long	often ornate	present	absent	absent	3
Rhipicephalus	anterior	hexagonal	short	medium	some ornate	present	present	present	3
(*Boophilus*)	anterior	hexagonal	short	short	inornate	absent	present	present	1
Dermacentor	anterior	rectangular	short	medium	often ornate	present	present	absent	3
Haemaphysalis	anterior	rectangular	short	short	inornate	present	absent	absent	3
Hyalomma	anterior	rectangular	long	long	inornate	present	present	present	2
Bothriocroton	anterior	pentagonal	long	long	ornate	present	absent	absent	3

The family Ixodidae contains 6 subfamilies (Amblyomminae, Bothriocrotoninae, Haemaphysalinae, Hyalomminae, Ixodinae and Rhipicephalinae) which vary in their morphology, biology, host ranges and specificity. [Note that some taxonomic authorities have merged the subfamilies Rhipicephalinae and Hyalomminae, while others have subsequently assigned the subfamilies Amblyomminae and Rhipicephalinae into the new family Amblyommidae, predominantly on the basis of molecular phylogenetic studies]. Hard ticks had previously been divided into 2 groups: the Prostriata (with the anal groove anterior to the anus) and the Metastriata (anal groove absent or posterior to anus). The Prostriata essentially comprises the subfamily Ixodinae with over 230 species assigned to the single extant genus *Ixodes* [plus one fossil genus (*Cornupalpatum*)], while the Metastriata contains members of the remaining subfamilies with over 600 species classified into 18 genera. The subfamily Rhipicephalinae contains 7 genera (*Anomalohimalaya*, *Cosmiomma*, *Dermacentor*, *Margaropus*, *Nosomma*, *Rhipicentor* and *Rhipicephalus*) and essentially comprises metastriate ticks (often ornate) with eyes and festoons and adult males have ventral plates. The genus *Rhipicephalus* is further characterized by short mouthparts with a hexagonal basis capitulum and short palps, long legs with bifurcate coxae I and tarsi IV bearing ventral hooks, and stigmatal plates having comma-shaped tail-like protrusions. Some 77 *Rhipicephalus* spp. have been described in mammalian hosts, including ungulates, carnivores and small ground-dwelling mammals. Most have 3-host life-cycles, but some have 2-host cycles. All species of the former genus *Boophilus* ('blue' ticks) have recently been transferred on the basis of molecular evidence to the genus *Rhipicephalus*, where they are recognized within a separate subgenus, *R.* (*Boophilus*), with more diverse characteristics (notably having 1-host life-cycles, being inornate, lacking festoons, having rounded stigmatal plates, ridged palps, and an inconspicuous anal groove). Several *Rhipicephalus* (and former *Boophilus*) spp. are notorious ectoparasites of domestic livestock and companion animals, causing health and production problems due to blood loss and toxicoses as well as transmitting a range of infectious diseases, especially tick fevers caused by the protozoan parasites *Babesia* and *Theileria* spp.

***Rhipicephalus* species**	**Hosts**	**Clinical signs**	**Distribution**
R. (*Boophilus*) *annulatus* (syn. *R. congolensis, I. bovis, dugesii, indentatus, Boophilus bovis*) (blue cattle tick, Texas cattle fever tick)	Artiodactyla: bovid (cattle, zebu, banteng, buffalo, water buffalo, bison, American buffalo, sheep, goat, giant eland, roan antelope, Coke's hartebeest), camelid (camel), cervid (white-tailed deer, rusa deer, sambar deer, spotted deer, muntjac), suid (pig, red river hog); Perissodactyla: equid (horse, donkey, mule); Lagomorpha: leporid (Baird's hare); Rodentia: dasyproctid (agouti), erethizontid (North American porcupine); Carnivora: canid (dog), felid (cat, lion); Primates: hominid (human); Galliformes: phasianid (fowl); Passeriformes: alaudid (lark), fringillid (chaffinch), sturnid (starling); Sauria: agamid (rock agama), lacertid (European green lizard) (1-host cycle)	trauma, irritation, anaemia (vector for babesiosis, anaplasmosis, rickettsioses)	Americas, Africa, Eurasia
R. appendiculatus (brown ear tick)	Artiodactyla: bovid (cattle, buffalo, forest buffalo, water buffalo, sheep, goat, puku, Gunther's dikdik, Kirk's dikdik, common duiker, blue duiker, bay duiker, red forest duiker, duikerbok, blesbok, eland, impala, lechwe, nyala, harnessed bushbuck, Cape bushbuck, waterbuck, reedbuck, mountain reedbuck, southern reedbuck, Bohor reedbuck, kudu, greater kudu, klipspringer, roan	trauma, toxaemia, toxicosis, sweating sickness, paralysis (vector	sub-Saharan Africa

	antelope, sable antelope, hartebeest, Coke's hartebeest, Lichtenstein's hartebeest, suni, Livingstone's suni, springbok, steenbuck, Ugandan kob, white-bearded gnu, common wildebeest, blue wildebeest, topi, Grant's gazelle, Thomson's gazelle, oribi, sitatunga, tsessebe***),*** camelid (camel), cervid (deer), giraffid (giraffe), suid (pig, bushpig, red river hog, giant forest hog, desert warthog); Perissodactyla: equid (horse, donkey, mule, Burchell's zebra, Grant's zebra), rhinocerotid (white rhinoceros, black rhinoceros); Proboscidea: elephantid (African elephant); Macroscelidea: macroscelidid (eastern rock elephant shrew, western rock elephant shrew, golden-rumped elephant shrew); Eulipotyphla: erinaceid (South African hedgehog); Hyracoidea: procaviid (rock hyrax, yellow-spotted rock hyrax); Pholidota: manid (Temminck's ground pangolin); Rodentia: hystricid (crested porcupine, African porcupine, Cape porcupine), murid (black rat, four-striped grass mouse, pygmy mouse, southern multimammate mouse, Natal multimammate mouse, Cape gerbil, southern African vlei rat, striped grass rat, brush-furred rat, swamp rat), pedetid (springhare), sciurid (red bush squirrel, African bush squirrel, Smith's bush squirrel, Cape ground squirrel), thryonomyid (large cane rat, greater cane rat); Lagomorpha: leporid (rabbit, hare, savannah hare, scrub hare, red rock hare, Natal red rock hare, Cape hare); Carnivora: canid (dog, hunting dog, African wild dog, black-backed jackal, side-striped jackal, bat-eared fox), felid (cat, African wildcat, serval, cheetah, leopard, lion), herpestid (meerkat, common slender mongoose, gray mongoose, banded mongoose, yellow mongoose, marsh mongoose, Egyptian mongoose, white-tailed mongoose), hyaenid (brown hyena, striped hyena, spotted hyena), mustelid (ratel, zorilla), viverrid (African civet, small spotted genet, large spotted genet, rusty-spotted genet); Primates: cercopithecid (grivet, guenon, Chacma baboon), galagid (brown greater galago), hominid (human, western gorilla); Coliiformes: coliid (white-backed mousebird); Coraciiformes: alcedinid (brown-hooded kingfisher); Galliformes: numidid (helmeted guineafowl), phasianid (chicken, common quail, crested francolin); Passeriformes: laniid (long-crested helmet shrike), passerid (yellow-throated bush sparrow), sturnid (Meve's glossy starling); Piciformes: lybiid (crested barbet), picid (golden-tailed woodpecker); Struthioniformes: struthionid (ostrich); Testudines (unspecified tortoise) (3-host cycle)	for theileriosis, ehrlichiosis, hepatozoonosis, rickettsial fever, Thogoto virus, Nairobi sheep disease)	
R. aquatilis	Artiodactyla: bovid (cattle, sitatunga); Carnivora: felid (lion, leopard)		Africa
R. arakeri	Rodentia: murid (rat, mouse)		India
R. armatus	Artiodactyla: bovid (sheep, Grant's gazelle); Perissodactyla: equid (donkey); Eulipotyphla: erinaceid (four-toed hedgehog); Lagomorpha: leporid (Cape hare); Rodentia: murid (northern pygmy gerbil); Carnivora: canid (dog, hunting dog, golden jackal, black-backed jackal, bat-eared fox), felid (African wildcat, caracal, lion, leopard, cheetah), hyaenid (spotted hyena, striped hyena), mustelid (zorilla); Primates: hominid (human); Otidiformes: otidid (kori bustard) (3-host cycle)		Africa
R. (*Rhipicephalus*) *arnoldi*	Artiodactyla: bovid (klipspringer); Perissodactyla: equid (mountain zebra); Hyracoidea: procaviid (rock hyrax); Macroscelidea: macroscelidid (rock elephant shrew); Lagomorpha: leporid (Cape hare, scrub hare, Jameson's red rock hare, Smith's red rock rabbit); Rodentia: murid (Tullberg's soft-furred mouse, four-striped grass mouse, field mouse); Carnivora: felid (caracal) (3-host cycle)		Africa
R. attenuatus	Perissodactyla: equid (horse)		Africa
R. aurantiacus	Artiodactyla: bovid (buffalo, forest buffalo, water buffalo), suid (red river hog); Primates: hominid (human)		Africa

R. (*Boophilus*) *australis* (Australian cattle tick)	Artiodactyla: bovid (cattle, zebu, Himalayan zebu, gayal, nilgai, water buffalo, sheep, goat), camelid (dromedary), cervid (muntjac), suid (pig); Perissodactyla: equid (horse); Carnivora: canid (dog), felid (cat); Primates: hominid (human); Passeriformes: passerid (sparrow) (1-host cycle)	(vector for babesiosis)	Australasia
R. (*Rhipicephalus*) *bequaerti*	Artiodactyla: bovid (cattle, buffalo, goat), suid (red river hog, forest hog, bushpig); Primates: hominid (human)		Africa
R. bergeoni	Artiodactyla: bovid (cattle, sheep, goat, mountain nyala, bushbuck, greater kudu), suid (pig); Perissodactyla: equid (horse); Carnivora: hyaenid (striped hyena)		Africa
R. boueti	Hyracoidea: procaviid (rock hyrax)		Africa
R. breviceps	Eulipotyphla: erinaceid (long-eared hedgehog, collared hedgehog); Rodentia: murid (Indian gerbil)		Pakistan
R. (*Digineus*) *bursa* (syn. *R. bilenus, lundbladi*)	Artiodactyla: bovid (cattle, zebu, water buffalo, sheep, Asiatic mouflon, goat, argali, kri-kri, harnessed bushbuck, mountain gazelle), camelid (dromedary), cervid (red deer, roe deer, sika deer, sambar deer, fallow deer), suid (pig, wild boar); Perissodactyla: equid (horse, donkey); Lagomorpha: leporid (European rabbit, European hare, Somalian hare, tolai hare); Eulipotyphla: erinaceid (European hedgehog, South African hedgehog); Rodentia: cricetid (bank vole, social vole, European hamster), glirid (garden dormouse), hystricid (crested porcupine), murid (rat, wood mouse, Tristram's jird), sciurid (red squirrel); Carnivora: canid (dog, red fox), felid (cat), mustelid (marbled polecat, ferret); Primates: hominid (human); Anseriformes: anatid (goose); Bucerotiformes: upupid (Eurasian hoopoe); Galliformes: phasianid (rock partridge); Passeriformes: corvid (rook), motacillid (tree pipit), muscicapid (isabelline wheatear), sturnid (common starling); Piciformes: picid (middle spotted woodpecker); Strigiformes: strigid (long-eared owl); Sauria: lacertid (sand lizard) (2-host cycle)	trauma, irritation (vector for babesiosis, theileriosis, anaplasmosis, ehrlichiosis, Q fever, Nairobi sheep disease virus, and possibly Crimean-Congo haemorrhagic fever virus)	sub-Saharan Africa, Europe
R. (*Boophilus*) *calcaratus* (syn. *Ixodes*) (blue tick)	Artiodactyla: bovid (cattle, buffalo, water buffalo, sheep, urial, goat, goitered gazelle), camelid (camel), cervid (red deer, Bactrian deer, Central Asian red deer, sika deer), suid (pig, wild boar); Perissodactyla: equid (horse, donkey); Lagomorpha: leporid (European hare); Eulipotyphla: erinaceid (hedgehog); Rodentia: murid (house mouse, short-tailed bandicoot rat), sciurid (red squirrel); Carnivora: canid (dog, red fox), felid (cat), ursid (brown bear); Galliformes: phasianid (partridge); Passeriformes: alaudid (Eurasian skylark, Calandra lark), corvid (magpie), passerid (Spanish sparrow); Sauria: lacertid (sand lizard, Caucasian agama) (1-host cycle)	trauma, irritation, anaemia (vector for babesiosis, anaplasmosis)	Eurasia, Africa
R. camicasi	Artiodactyla: bovid (cattle, sheep, goat, gerenuk, eland), camelid (camel), suid (warthog); Perissodactyla: equid (donkey, zebra, Grevy's zebra), Lagomorpha: leporid (Cape hare); Tubulidentata: orycteropid (aardvark); Carnivora: canid (dog, bat-eared fox), felid (cheetah) (3-host cycle)	(possible vector for anaplasmosis)	Africa
R. capensis (syn. *Boophilus, R. gertrudae*) (Cape brown tick)	Artiodactyla: bovid (cattle, zebu, buffalo, forest buffalo, sheep, goat, impala, eland, greater kudu, gemsbok, grey rhebok, sable antelope, Lichtenstein's hartebeest, black wildebeest, bontebok, springbok, reedbuck, sitatunga), cervid (deer), suid (pig, bushpig, red river hog, common warthog, desert warthog); Perissodactyla: equid (horse, donkey, mountain zebra), rhinocerotid (black rhinoceros); Macroscelidea: macroscelidid (western rock elephant shrew); Lagomorpha: leporid (scrub hare, Cape hare); Rodentia: glirid (African dormouse), hystricid (Cape porcupine), murid (hairy-footed gerbil, Cape gerbil, red veld rat, Namaqua rock rat, bush vlei rat, tropical vlei rat, South African vlei rat, bush Karoo rat, Namaqua rock mouse, four-striped grass mouse); Carnivora: canid (dog, side-striped jackal, black-headed jackal, bat-eared fox, Cape fox), felid (cat, caracal, lion, leopard, cheetah), hyaenid	trauma, irritation (vector for theileriosis, anaplasmosis)	Africa

	(aardwolf), viverrid (civet); Primates: cercopithecid (chacma baboon), hominid (human); Galliformes: numidid (guineafowl); Passeriformes: muscicapid (unspecified flycatcher), pycnonotid (unspecified bulbul); Sauria: varanid (Nile monitor); Testudines: testudinid (geometric tortoise) (3-host cycle)		
R. carnivoralis	Artiodactyla: bovid (cattle, zebu); Hyracoidea: procaviid (rock hyrax, yellow-spotted rock hyrax); Carnivora: canid (dog), felid (cheetah, lion, leopard), hyaenid (spotted hyena, striped hyena); Primates: hominid (human) (3-host cycle)		Africa
R. (*Boophilus*) *caudatus*	Artiodactyla: bovid (cattle, buffalo, water buffalo, sheep); Perissodactyla: equid (horse, mule); Carnivora: canid (dog)		Asia
R. complanatus	Artiodactyla: bovid (buffalo, harnessed bushbuck), suid (pig, warthog, bushpig, desert warthog, forest hog, red river hog); Rodentia: murid (Cameroon soft-furred mouse, Tullberg's soft-furred mouse); Carnivora: viverrid (civet); Primates: hominid (human)		Africa
R. compositus (syn. *R. ayeri*)	Artiodactyla: bovid (cattle, buffalo, forest buffalo, sheep, goat, roan antelope, eland, bushbuck, waterbuck, puku, Lichtenstein's hartebeest, sitatunga, common duiker, roan antelope), giraffid (giraffe, Masai giraffe), suid (pig, bushpig, giant forest hog, red river hog, desert warthog); Perissodactyla: equid (donkey), rhinocerotid (black rhinoceros); Proboscidea: elephantid (African bush elephant); Rodentia: murid (African grass rat, Abyssinian grass rat, swamp rat, Nile rat, greater creek rat, Jackson's soft-furred rat, jumping mouse); Carnivora: canid (dog), felid (lion, leopard, cheetah), viverrid (African civet); Primates: hominid (human) (3-host cycle)		Africa
R. confusus	Artiodactyla: bovid (buffalo, waterbuck, eland, sable antelope, roan antelope, common duiker, Lichtenstein's hartebeest), suid (pig, bushpig, red river hog, desert warthog); Perissodactyla: equid (horse); Carnivora: canid (dog)		Africa
R. cuspidatus	Artiodactyla: bovid (eland, red-fronted gazelle, oribi), suid (red river hog, desert warthog); Rodentia: hystricid (crested porcupine), thryonomyid (greater cane rat); Tubulidentata: orycteropodid (aardvark); Carnivora: canid (golden jackal), felid (serval, leopard), herpestid (banded mongoose, white-tailed mongoose, Egyptian mongoose), hyaenid (spotted hyena, striped hyena); Galliformes: phasianid (double-spurred francolin) (3-host cycle)		Africa
R. (*Boophilus*) *decoloratus* (syn. *Boophilus florae, scheepersi*) (African blue tick)	Artiodactyla: bovid (cattle, zebu, buffalo, water buffalo, sheep, goat, impala, eland, giant eland, harnessed bushbuck, greater kudu, sable antelope, roan antelope, royal antelope, hartebeest, Lichtenstein's hartebeest, dama gazelle, red-fronted gazelle, Grant's gazelle, blue wildebeest, gnu, nyala, tiang, impala, southern reedbuck, waterbuck, sitatunga, oryx, duiker, topi, springbok, blesbok, gemsbok, sassaby, korrigum), camelid (dromedary), giraffid (giraffe), suid (pig, bushpig, red river hog, warthog); Perissodactyla: equid (horse, donkey, mule, plains zebra, Burchell's zebra); Macroscelidea: macroscelidid (four-toed elephant shrew); Lagomorpha: leporid (rabbit, scrub hare); Rodentia: murid (multimammate mouse); Carnivora: canid (dog, African wild dog, black-backed jackal), felid (cat, lion, cheetah), herpestid (common slender mongoose); Primates: hominid (human): Charadriiformes: charadriid (three-banded plover); Galliformes: numidid (helmeted guineafowl, black guineafowl); Passeriformes: sturnid (common myna); Pelecaniformes: ardeid (cattle egret); Suliformes: phalacrocoracid (reed cormorant); Serpentes: pythonid (unspecified python); Testudines: testudinid (unspecified tortoise) (1-host cycle)	trauma, irritation, anaemia (vector for babesiosis, anaplasmosis, spirochaetosis, borreliosis)	sub-Saharan Africa

R. deltoideus	Artiodactyla: bovid (Grant's gazelle); Lagomorpha: leporid (hare); Otidiformes: otidid (Jackson's rufous-necked bustard); Struthioniformes: struthionid (ostrich)		Africa
R. distinctus (syn. *R. punctatus*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, impala, roan antelope, sable antelope, common duiker, red forest duiker, waterbuck, klipspringer, gerenuk, Kirk's dik-dik, steenbok, greater kudu, gemsbok, common eland, nyala, oribi, harnessed bushbuck, topi, hartebeest, Sharpe's grysbok, tsessebe), giraffid (giraffe), suid (bushpig, desert warthog); Perissodactyla: equid (horse, donkey, plains zebra, Burchell's zebra); Hyracoidea: procaviid (rock hyrax, southern tree hyrax, yellow-spotted rock hyrax); Macroscelidea: macroscelidid (rock elephant shrew); Eulipotyphla: soricid (shrew); Lagomorpha: leporid (savannah hare, European hare, Cape hare, Jameson's red rock rabbit, Smith's red rock rabbit); Rodentia: murid (Natal multimammate mouse, Namaqua rock mouse, swamp rat, bush Karoo rat, field mouse), pedetid (springhare); Carnivora: felid (African wildcat, caracal, lion, leopard), herpestid (yellow mongoose); Primates: hominid (human) (3-host cycle)		Africa
R. duttoni (Angolan brown ear tick)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, eland, impala, common duiker); Perissodactyla: equid (horse); Lagomorpha: leporid (savannah hare); Carnivora: canid (dog), viverrid (African civet); Otidiformes: otidid (black-bellied bustard) (3-host cycle)	otitis (vector for theileriosis)	Africa
R. dux (syn. *R. schwetzi*)	Artiodactyla: bovid (cattle, buffalo, forest buffalo, waterbuck), suid (pig, bushpig, red river hog, giant forest hog, desert warthog); Proboscidea: elephantid (African elephant); Primates: hominid (human)		Africa
R. erlangeri	Perissodactyla: equid (horse)		Africa
R. evertsi (incl. subspp. *evertsi*, *mimeticus*) (red-legged tick, red tick)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, eland, red hartebeest, Cape hartebeest, Coke's hartebeest, Jackson's hartebeest, Lichtenstein's hartebeest, Roosevelt's hartebeest, reedbuck, blue wildebeest, black wildebeest, sable antelope, roan antelope, dwarf antelope, blesbok, greater kudu, lesser kudu, Cape kudu, impala, steenbuck, common duiker, Cape duiker, blue duiker, red forest duiker, springbok, harnessed bushbuck, Cape bushbuck, Cape grysbok, Sharpe's grysbok, southern reedbuck, mountain reedbuck, waterbuck, bontebok, blesbok, grey rhebok, gemsbok, steenbok, Grant's gazelle, Thomson's gazelle, Isabella gazelle, gerenuk, oribi, kob, korrigum, tsessebe, sitatunga, Kirk's dik-dik, nilgai, nyala, fringe-eared oryx, tsessebe, topi, klipspringer, waterbuck kob, lechwe, puku), camelid (camel), giraffid (giraffe, southern giraffe), suid (pig, bushpig, desert warthog); Perissodactyla: equid (horse, donkey, mule, plains zebra, Burchell's zebra, Grant's zebra, Grevy's zebra, Hartmann's mountain zebra), rhinocerotid (white rhinoceros, black rhinoceros); Proboscidea: elephantid (African elephant); Macroscelidea: macroscelidid (rufous elephant shrew, short-snouted elephant shrew, round-eared elephant shrew); Hyracoidea: procaviid (rock hyrax, yellow-spotted rock hyrax); Rodentia: hystricid (crested porcupine, South African porcupine), murid (striped grass mouse, Namaqua rock mouse, tree rat, Abyssinian grass rat, red veld rat), nesomyid (Gambian pouched rat, short-tailed pouched mouse, fat mouse), pedetid (springhare, South African springhare), sciurid (Smith's bush squirrel, Huet's bush squirrel, unstriped ground squirrel), thryonomyid (greater cane rat); Lagomorpha: leporid (rabbit, Smith's red rock rabbit, European hare, scrub hare, savannah hare, Cape hare, Natal red rock hare); Carnivora: canid (dog, hunting dog, side-striped jackal, black-backed jackal), felid (cat, African wildcat, caracal, leopard, cheetah, lion), herpestid (meerkat, banded mongoose, marsh mongoose, common slender mongoose), hyaenid (aardwolf), mustelid (ratel), viverrid (African civet, genet); Primates: cercopithecid (Chacma baboon, yellow	trauma, irritation, paralysis (vector for babesiosis, theileriosis, anaplasmosis, borreliosis, spirochaetosis)	sub-Saharan Africa

	baboon, vervet monkey, colobus monkey), hominid (human); Accipitriformes: accipitrid (pale chanting goshawk); Coliiformes: coliid (white-backed mousebird); Galliformes: numidid (helmeted guineafowl), phasianid (crested francolin); Passeriformes: alaudid (red-capped lark), hirundinid (greater striped swallow), leiothrichid (arrow-marked babbler), malaconotid (brown-crowned tchagra), ploceid (red-billed quelea); Suliformes: phalacrocoracid (reed cormorant); Testudines: testudinid (leopard tortoise) (2-host cycle)		
R. exophthalmos	Artiodactyla: bovid (cattle, sheep, goat, impala, eland, springbok, gemsbok, steenbok, grey rhebok, mountain reedbuck, greater kudu), suid (pig, desert warthog); Perissodactyla: equid (horse, donkey, Burchell's zebra); Lagomorpha: leporid (scrub hare, Cape hare); Macroscelidea: macroscelidid (Cape elephant shrew, Smith's rock elephant shrew, short-eared elephant shrew); Rodentia: murid (Namaqua rock rat); Carnivora: canid (dog), felid (lion); Galliformes: phasianid (chicken) (3-host cycle)		Africa
R. follis	Artiodactyla: bovid (cattle, buffalo, sheep, black wildebeest, springbok, eland, bushbuck, greater kudu, gemsbok), giraffid (giraffe), suid (bushpig); Perissodactyla: equid (horse, mountain zebra); Rodentia: murid (four-striped grass mouse, swamp rat); Carnivora: canid (dog), felid (caracal, cheetah); Primates: hominid (human) (3-host cycle)		Africa
R. (*Pterygodes*) *fulvus*	Artiodactyla: bovid (sheep, Barbary sheep, goat), camelid (camel); Rodentia: ctenodactylid (common gundi), murid (northern pygmy gerbil); Primates: hominid (human)		Africa, Europe
R. (*Boophilus*) *geigyi*	Artiodactyla: bovid (cattle, sheep, tiang, kongoni); Carnivora: canid (dog), felid (cat); Primates: hominid (human) (1-host cycle)	(possible vector for babesiosis)	sub-Saharan Africa
R. glabroscutatus (syn. *R. glabroscutatum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, red hartebeest, black wildebeest, bontebok, blesbok, springbok, steenbok, gemsbok, grey rhebok, eland, greater kudu, common duiker, mountain reedbuck); Perissodactyla: equid (horse, mountain zebra); Hyracoidea: procaviid (rock hyrax); Lagomorpha: leporid (scrub hare, Smith's red rock rabbit); Rodentia: murid (fur-striped grass mouse), pedetid (springhare); Carnivora: canid (dog), felid (caracal); Primates: hominid (human); Galliformes: numidid (helmeted guineafowl) (2-host cycle)		Africa
R. gladiger	Artiodactyla: bovid (goat); Perissodactyla: equid (horse)		Africa
R. guilhoni	Artiodactyla: bovid (cattle, sheep, goat, kob, korrigum, red-fronted gazelle, roan antelope, sing-sing waterbuck), camelid (camel), giraffid (giraffe), suid (warthog); Perissodactyla: equid (horse, donkey); Lagomorpha: leporid (hare); Eulipotyphla: erinaceid (four-toed hedgehog); Rodentia: murid (gerbil, African grass rat, Nile rat), sciurid (striped ground squirrel); Carnivora: canid (dog, jackal, pale fox), felid (cat, African wildcat, caracal, serval), hyaenid (spotted hyena), mustelid (striped polecat), viverrid (African civet); Primates: hominid (human); Accipitriformes: accipitrid (martial eagle, white-backed vulture); Ciconiiformes: ciconiid (saddle-billed stork, Maribou stork); Galliformes: phasianid (red junglefowl); Otidiformes: otidid (Arabian bustard, Denham's bustard); Strigiformes: strigid (barn owl); Struthioniformes: struthionid (ostrich) (3-host cycle)	(possible vector for rickettsiosis, Q fever, Crimean-Congo haemorrhagic fever, Wad Medani and Ngoye viruses)	Africa
R. haemaphysaloides	Artiodactyla: bovid (cattle, gaur, zebu, buffalo, water buffalo, goat, sheep, goral, Nilgiri tahr, Himalayan tahr, serow), camelid (dromedary), cervid (chital deer, sambar deer, spotted deer, Indian muntjac), suid (pig, banded pig, Indian boar, Philippine warty pig); Perissodactyla: equid (horse, donkey, mule), rhinocerotid (Javan rhinoceros); Eulipotyphla: soricid (Asian house shrew, Anderson's		Indo-China

	shrew); Lagomorpha: leporid (Bengal hare, Indian hare, black-napped hare); Rodentia: hystricid (Malayan porcupine), murid (black rat, lesser bandicoot rat, greater bandicoot rat, soft-furred rat, Cutch rat, Blanford's rat, Indian bush rat, house mouse, flat-haired mouse, little Indian field mouse, Indian brown spiny mouse, Indian gerbil), sciurid (bobak marmot, jungle palm squirrel, Indian giant squirrel); Carnivora: canid (dog, dhole, wolf, golden jackal, red fox), felid (Asian golden cat, marbled cat, fishing cat, leopard, tiger, herpestid (Indian grey mongoose), mustelid (greater hog badger, European pine marten), ursid (sloth bear); Primates: cercopithecid (northern plains gray langur), hominid (human); Cuculiformes: cuculid (crow pheasant); Galliformes: phasianid (chicken, red junglefowl); Passeriformes: muscicapid (orange-breasted flycatcher), paradoxornithid (Oriental yellow-eyed babbler), turdid (brown-headed thrush) (3-host cycle)		
R. hilgerti	Carnivora: canid (variegated wolf)		Africa
R. humeralis	Artiodactyla: bovid (cattle, buffalo, sheep, goat, eland, bushbuck, waterbuck, Coke's hartebeest, Speke's gazelle), camelid (camel), suid (bushpig, warthog, Somali warthog); Perissodactyla: equid (donkey), rhinocerotid (black rhinoceros); Proboscidea: elephantid (African elephant); Rodentia: sciurid (unstriped ground squirrel); Carnivora: canid (dog, black-backed jackal, bat-eared fox, sand fox), felid (lion); Primates: cercopithecid (Hamadryas baboon), galagid (greater bushbaby), hominid (human); Accipitriformes: accipitrid (great sparrowhawk) (3-host cycle)		Africa
R. hurti	Artiodactyla: bovid (cattle, buffalo, eland, harnessed bushbuck, sitatunga, common duiker, roan antelope), giraffid (giraffe), suid (pig, bushpig, red river hog, warthog); Perissodactyla: rhinocerotid (black rhinoceros); Rodentia: murid (Angoni vlei rat); Carnivora: canid (dog, jackal), felid (lion, leopard), viverrid (genet); Primates: hominid (human) (3-host cycle)		Africa
R. interventus	Artiodactyla: bovid (cattle, sheep, topi, Grant's gazelle, oribi, Cape grysbok, bushbuck, unspecified antelope); Carnivora: canid (dog)		Africa
R. jeanneli	Artiodactyla: bovid (cattle, buffalo, sheep, goat, common eland, bongo, bushbuck, greater kudu, common duiker), suid (pig, wild boar, bushpig, forest hog, warthog); Perissodactyla: equid (horse, Burchell's zebra), rhinocerotid (black rhinoceros); Rodentia: murid (brush-furred rat, swamp rat), spalacid (East African mole-rat); Carnivora: canid (dog), felid (lion); Primates: hominid (human); Galliformes: phasianid (spurfowl) (3-host cycle)		Africa
R. kochi (syn. *R. mossambicus, neavei*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, eland, impala, harnessed bushbuck, waterbuck, southern reedbuck, Bohor reedbuck, greater kudu, fringe-eared oryx, roan antelope, sable antelope, suni, nyala, oribi, klipspringer, steenbok, common duiker, red forest duiker, yellow-backed duiker, blue wildebeest, Lichtenstein's hartebeest, Grant's gazelle, Thomson's gazelle, Kirk's dik-dik, Cape grysbok), camelid (camel), giraffid (Masai giraffe), suid (red river hog, bushpig, desert warthog); Proboscidea: elephantid (African elephant); Perissodactyla: equid (horse, donkey, plains zebra, Burchell's zebra), rhinocerotid (black rhinoceros); Lagomorpha: leporid (European hare, Cape hare, scrub hare, savannah hare); Macroscelidea: macroscelidid (four-toed elephant shrew); Rodentia: hystricid (Cape porcupine); Carnivora: canid (dog, side-striped jackal), felid (lion, leopard), viverrid (African civet); Primates: hominid (human); Galliformes: phasianid (yellow-necked spurfowl); Otidiformes: otidid (black-bellied bustard) (3-host cycle)		Africa
R. (*Boophilus*) *kohlsi*	Artiodactyla: bovid (cattle, sheep, goat), camelid (camel);		Middle-East

	Perissodactyla: equid (horse, mule) (1-host cycle)		
R. leporis	Artiodactyla: bovid (goat), cervid (red deer); Eulipotyphla: erinaceid (European hedgehog, desert hedgehog, Brandt's hedgehog, long-eared hedgehog); Lagomorpha: leporid (desert hare, tolai hare, Cape hare); Rodentia: dipodid (small five-toed jerboa), murid (great gerbil); Carnivora: canid (dog, wolf, golden jackal, red fox), mustelid (steppe polecat, marbled polecat) (3-host cycle)		Central Asia
R. longiceps	Artiodactyla: bovid (cattle, buffalo, klipspringer, gemsbok, Lichtenstein's hartebeest), giraffid (giraffe), suid (pig, warthog); Perissodactyla: rhinocerotid (rhinoceros)		Africa
R. longicoxatus (syn. *R. camelopardalis*	Artiodactyla: bovid (buffalo, sheep, goat, dik-dik), camelid (camel), giraffid (Masai giraffe), suid (bushpig, red river hog); Carnivora: canid (dog), felid (serval)		Africa
R. longus (syn. *R. cliffordi, falcatus, pseudolongus*)	Artiodactyla: bovid (cattle, zebu, buffalo, forest buffalo, sheep, goat, common eland, giant eland, impala, mountain nyala, bongo, waterbuck, sable antelope, roan antelope, blue wildebeest, Lichtenstein's hartebeest), suid (pig, bushpig, red river hog, forest hog, desert warthog); Perissodactyla: equid (horse, Burchell's zebra), rhinocerotid (black rhinoceros); Proboscidea: elephantid (African elephant); Tubulidentata: orycteropodid (aardvark); Lagomorpha: leporid (Cape hare); Macroscelidea: macroscelidid (elephant shrew); Rodentia: murid (typical striped grass mouse); Carnivora: canid (dog, African wild dog, side-striped jackal, bat-eared fox), felid (lion, leopard), herpestid (banded mongoose), hyaenid (spotted hyena); Primates: hominid (human); Charadriiformes: recurvirostrid (black-winged stilt) (3-host cycle)		Africa
R. lounsburyi	Artiodactyla: bovid (sheep, eland, black wildebeest, bontebok, grey rhebok, mountain reedbuck); Rodentia: murid (four-striped grass mouse); Carnivora: felid (caracal) (3-host cycle)		Africa
R. maculatus	Artiodactyla: bovid (cattle, buffalo, sheep, goat, eland, roan antelope, sable antelope, suni, oribi, waterbuck, southern reedbuck, bushbuck, eland, nyala, lesser kudu, greater kudu, common duiker, red forest duiker, blue wildebeest, Lichtenstein's hartebeest, impala), suid (pig, bushpig, red river hog, common warthog, desert warthog); Perissodactyla: equid (Burchell's zebra), rhinocerotid (black rhinoceros, white rhinoceros); Proboscidea: elephantid (African elephant, African bush elephant); Lagomorpha: leporid (scrub hare); Macroscelidea: macroscelidid (elephant shrew); Hyracoidea: procaviid (hyrax); Carnivora: felid (lion, cheetah, serval), hyaenid (spotted hyena), viverrid (African civet); Primates: hominid (human); Sauria: varanid (Nile monitor) (3-host cycle)		Africa
R. masseyi (syn. *R. tendeiroi*)	Artiodactyla: bovid (cattle, buffalo, sheep, impala, eland, nyala, harnessed bushbuck, greater kudu, sable antelope), suid (bushpig, red river hog, warthog); Perissodactyla: equid (horse, Burchell's zebra); Tubulidentata: orycteropodid (aardvark); Lagomorpha: leporid (hare); Rodentia: sciurid (Cape ground squirrel); Carnivora: canid (dog, Cape fox), felid (lion, leopard), herpestid (meerkat, yellow mongoose, marsh mongoose)		Africa
R. (*Boophilus*) *microplus* (syn. *Haemaphysalis micropla, Boophilus distans, fallax, intraoculatus, krijgsmani, longiscutatus, rotundiscutatus, sinensis, sharifi*)	Artiodactyla: bovid (cattle, banteng, gaur, zebu, buffalo, water buffalo, sheep, goat, sable antelope, black wildebeest, grey rhebok), camelid (camel), cervid (red deer, sambar deer, white-tailed deer, marsh deer, pampas deer, brown brocket, grey brocket, red brocket, chital, Philippine deer), suid (pig, wild boar), tayassuid (white-lipped peccary, collared peccary, Chacoan peccary); Perissodactyla: equid (horse, donkey), tapirid (South American tapir, Baird's tapir); Lagomorpha: leporid (rabbit, European hare); Rodentia: caviid (capybara), erethizontid (orange-spined hairy dwarf porcupine), murid (mouse); Diprotodontia: macropodid	trauma, irritation, anaemia (vector for babesiosis, anaplasmosis, borreliosis, Q fever)	Asia, Australia, Americas, Africa

(incl. clades A and B) (pantropical cattle tick, southern cattle tick, Asiatic blue tick) [note that the 'Australian cattle tick' has been renamed *R. australis*]	(wallaby, kangaroo); Didelphimorphia: didelphid (big-eared opossum); Pilosa: bradypodid (pale-throated sloth), myrmecophagid (giant anteater); Carnivora: canid (dog, dingo, maned wolf, pampas fox, hoary fox, gray fox, crab-eating fox), felid (cat, pampas cat, colocolo, ocelot, oncilla, jaguar, jaguarundi, cougar, lion), herpestid (small Indian mongoose), procyonid (South American coati); Chiroptera: phyllostomid (little yellow-shouldered bat); Primates: atelid (Colombian red howler), cercopithecid (Formosan rock macaque), hominid (human); Anura: bufonid (cane toad); Accipitriformes: accipitrid (roadside hawk); Falconiformes: falconid (yellow-headed caracara); Passeriformes: passerid (house sparrow); Pelecaniformes: ardeid (cattle egret) (1-host cycle)		
R. moucheti	Artiodactyla: bovid (cattle); Carnivora: canid (dog), viverrid (African civet); Primates: cercopithecid (common patas monkey) (3-host cycle)		Africa
R. muehlensi	Artiodactyla: bovid (cattle, buffalo, sheep, goat, bushbuck, roan antelope, sable antelope, nyala, impala, suni, reedbuck, steenbok, gemsbok, waterbuck, greater kudu, lesser kudu, gerenuk, common duiker, red forest duiker, Cape duiker, eland, harnessed bushbuck, Lichtenstein's hartebeest, Grant's gazelle), giraffid (giraffe), suid (bushpig, red river hog, warthog); Perissodactyla: equid (plains zebra), rhinocerotid (black rhinoceros, white rhinoceros); Proboscidea: elephantid (African elephant); Lagomorpha: leporid (scrub hare); Hyracoidea: procaviid (rock hyrax); Macroscelidea: macroscelidid (elephant shrew); Rodentia: sciurid (Smith's bush squirrel); Carnivora: canid (dog, black-backed jackal), felid (leopard), herpestid (common slender mongoose, white-tailed mongoose, lesser mongoose), hyaenid (hyena), viverrid (civet); Primates: hominid (human) (3-host cycle)		Africa
R. muhsamae	Artiodactyla: bovid (cattle, buffalo, sheep, goat, bushbuck, roan antelope, kob, oribi, Bohor reedbuck), suid (pig, red river hog, warthog); Perissodactyla: equid (horse, donkey); Rodentia: hystricid (crested porcupine), murid (Nile rat), sciurid (striped ground squirrel, Geoffroy's ground squirrel); Lagomorpha: leporid (hare); Carnivora: canid (dog, side-striped jackal), felid (lion, leopard), hyaenid (spotted hyena), mustelid (striped polecat), viverrid (African civet); Primates: hominid (human) (3-host cycle)		Africa
R. neumanni	Artiodactyla: bovid (sheep, goat, black wildebeest, springbok, gemsbok, grey rhebok, mountain reedbuck); Perissodactyla: equid (horse); Rodentia: murid (Namaqua rock mouse); Carnivora: canid (dog) (3-host cycle)		Africa
R. nitens	Artiodactyla: bovid (cattle, buffalo, sheep, goat, harnessed bushbuck, bontebok, springbok, grey rhebok), suid (warthog); Perissodactyla: equid (horse, mountain zebra); Lagomorpha: leporid (scrub hare); Carnivora: canid (dog, African wild dog); Galliformes: numidid (guineafowl) (3-host cycle)		Africa
R. oculatus	Artiodactyla: bovid (cattle, sheep, goat, impala, eland, kudu, springbok, gemsbok, steenbok, Cape bushbuck, Grant's gazelle, duiker, mountain reedbuck), giraffid (giraffe), suid (pig); Perissodactyla: equid (horse, donkey); Macroscelidea: macroscelidid (short-snouted elephant shrew); Lagomorpha: leporid (mountain hare, scrub hare, Cape hare, Smith's red rock rabbit); Rodentia: pedetid (springhare), murid (field mouse); Primates: hominid (human); Galliformes: numidid (helmeted guineafowl) (3-host cycle)		Africa
R. oreotragi	Artiodactyla: bovid (klipspringer)		Africa
R. phthirioides	Perissodactyla: equid (horse)		Africa

R. pilans	Artiodactyla: bovid (cattle, water buffalo, sheep, goat), cervid (Javan rusa, Timor deer, sambar deer), suid (pig); Perissodactyla: equid (horse); Eulipotyphla: soricid (house shrew, black-footed shrew, Sulawesi white-toothed shrew); Rodentia: murid (montane bunomys, greater bandicoot rat, Sulawesi rat, Oriental spiny rat, chestnut rat, ricefield rat, lesser moonrat, Malaysian field rat, Pacific rat, Tanezumi rat, black rat); Carnivora: canid (dog), felid (tiger), viverrid (common palm civet); Chiroptera: pteropid (Leschenault's rousette); Primates: hominid (human) (3-host cycle)		Asia
R. piresi	Artiodactyla: bovid (impala, nyala, suni, common duiker); Lagomorpha: leporid (scrub hare); Rodentia: sciurid (red bush squirrel, Smith's bush squirrel)		Africa
R. planus	Artiodactyla: bovid (cattle, buffalo, impala, waterbuck, common duiker), suid (pig, bushpig, red river hog, black forest hog, warthog); Proboscidea: elephantid (African elephant); Tubulidentata: orycteropid (aardvark); Lagomorpha: leporid (scrub hare, Cape hare); Rodentia: hystricid (crested porcupine, Cape porcupine), murid (Tullberg's soft-furred mouse, striped grass rat); Carnivora: canid (side-striped jackal); Primates: hominid (human) (3-host cycle)		Africa
R. plumbeus	Artiodactyla: bovid (cattle, sheep, goat), suid (pig); Perissodactyla: equid (horse, donkey, mule); Lagomorpha: leporid (rabbit, European hare); Eulipotyphla: erinaceid (European hedgehog); Carnivora: canid (dog), felid (cat); Charadriiformes: charadriid (European golden plover); Galliformes: phasianid (common partridge); Passeriformes: alaudid (crested lark, Eurasian skylark, Calandra lark), fringillid (common linnet, European goldfinch), motacillid (white wagtail, yellow wagtail, meadow pipit, tree pipit), muscicapid (wheatear, European stonechat)		Europe, North Africa
R. pomeranzevi	Lagomorpha: leporid (desert hare, tolai hare)		Central Asia
R. praetextatus	Artiodactyla: bovid (cattle, buffalo, sheep, goat, Coke's hartebeest, blue wildebeest, topi, dorcas gazelle, Grant's gazelle, Thomson's gazelle, steenbok, eland, nyala, bushbuck, greater kudu, common duiker, red forest duiker, sable antelope, gemsbok, Bohor reedbuck), camelid (camel), giraffid (giraffe), hippopotamid (hippopotamus), suid (pig, boar, bushpig, forest hog, warthog); Perissodactyla: equid (horse, donkey, Burchell's zebra, Grevy's zebra), rhinocerotid (black rhinoceros); Proboscidea: elephantid (African elephant); Eulipotyphla: erinaceid (Somali hedgehog); Tubulidentata: orycteropid (aardvark); Pholidota: manid (Temminck's ground pangolin); Lagomorpha: leporid (Cape hare); Rodentia: hystricid (crested porcupine), murid (four-striped grass mouse, striped grass rat, swamp rat, Nile rat, black-tailed gerbil), sciurid (unstriped ground squirrel); Carnivora: canid (dog, hunting dog, side-striped jackal, black-backed jackal, golden jackal, bat-eared fox), felid (cat, African wildcat, caracal, serval, lion, leopard, cheetah), herpestid (white-tailed mongoose, marsh mongoose), hyaenid (striped hyena, spotted hyena, aardwolf), viverrid (African civet, small spotted genet); Primates: cercopithecid (vervet monkey, baboon), hominid (human); Galliformes: phasianid (chicken) (3-host tick)	irritation, paralysis (vector for Nairobi sheep disease)	Africa
R. pravus (syn. *R. neavi*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, Bright's gazelle, Grant's gazelle, Soemmerring's gazelle, Thomson's gazelle, Waller's gazelle, harnessed bushbuck, waterbuck, sitatunga, kob, silver dik-dik, Kirk's dik-dik, Gunther's dik-dik, common duiker, bay duiker, red forest duiker, yellow-backed duiker, eland, gerenuk, impala, greater kudu, lesser kudu, nyala, gerenuk, oribi, fringe-eared oryx, East African oryx, korrigum, southern reedbuck, Bohor reedbuck, Coke's hartebeest, Jackson's hartebeest, Lichtenstein's hartebeest, Roosevelt's hartebeest, blue wildebeest, sable antelope, roan antelope, klipspringer, steenbok, gemsbok,		Africa

	dibatag, suni, steenbok, tsessebe), camelid (camel), giraffid (giraffe, Masai giraffe), suid (pig, red river hog, warthog); Perissodactyla: equid (horse, donkey, Burchell's zebra), rhinocerotid (black rhinoceros); Proboscidea: elephantid (African elephant); Eulipotyphla: erinaceid (four-toed hedgehog, Sudanese hedgehog); Tubulidentata: orycteropid (aardvark); Lagomorpha: leporid (scrub hare, red rock hare, European hare, Somalia hare, Cape hare, African savanna hare, Bunyoro rabbit); Macroscelidea: macroscelidid (dusky-footed elephant shrew, rufous elephant shrew, western rock elephant shrew, short-snouted elephant shrew, bushveld elephant shrew, four-toed elephant shrew); Hyracoidea: procaviid (rock hyrax); Rodentia: dipodid (jerboa), hystricid (Cape porcupine), murid (Namaqua rock rat, red rock rat, red veld rat, whistling rat, southern multimammate mouse, Natal multimammate mouse, field mouse), sciurid (unstriped ground squirrel, Cape ground squirrel, Smith's bush squirrel), thryonomyid (greater cane rat); Carnivora: canid (dog, golden jackal, black-backed jackal, bat-eared fox), felid (lion, leopard), herpestid (yellow mongoose), hyaenid (spotted hyena, striped hyena), viverrid (genet); Chiroptera: megadermatid (heart-nosed bat), vespertilionid (banana bat); Primates: cercopithecid (yellow baboon, olive baboon), hominid (human); Accipitriformes: accipitrid (great sparrowhawk), sagittariid (secretary bird); Charadriiformes: glareolid (three-banded courser); Otidiformes: otidid (black-bellied bustard, kori bustard); Passeriformes: hirundinid (banded martin), laniid (telephonus shrike), malaconotid (tropical boubou, southern tchagra); Struthioniformes: struthionid (ostrich); Suliformes: phalacrocoracid (reed cormorant); Testudines (unspecified tortoise) (3-host cycle)		
R. pulchellus (ivory-ornamented tick, zebra tick, yellow-backed tick)	Artiodactyla: bovid (cattle, buffalo, forest buffalo, sheep, goat, eland, impala, gnu, topi, dibatag, gemsbok, hartebeest, red hartebeest, Coke's hartebeest, blue wildebeest, black wildebeest, blackbuck, waterbuck, bushbuck, Grant's gazelle, Soemmerring's gazelle, Speke's gazelle, Thomson's gazelle, gerenuk, fringe-eared oryx, East African oryx, steenbok, lesser kudu, greater kudu, silver dik-dik, Gunther's dik-dik, red forest duiker, sable antelope), camelid (camel), giraffid (giraffe), suid (pig, bushpig, warthog); Perissodactyla: equid (horse, donkey, mule, plains zebra, Burchell's zebra, Grant's zebra), rhinocerotid (black rhinoceros); Proboscidea: elephantid (African elephant); Eulipotyphla: erinaceid (Somali hedgehog); Tubulidentata: orycteropid (aardvark); Lagomorpha: leporid (scrub hare, savannah hare, Cape hare, Ethiopian hare); Macroscelidea: macroscelidid (four-toed elephant shrew); Rodentia: caviid (guinea pig), murid (spiny mouse, black rat, Angoni vlei rat, southern multimammate mouse, black-tailed gerbil), sciurid (Huet's bush squirrel); Tubulidentata: orycteropodid (aardvark); Carnivora: canid (dog, hunting dog, black-backed jackal, bat-eared fox), felid (African wildcat, cheetah, leopard, lion), herpestid (slender mongoose, white-tailed mongoose), hyaenid (striped hyena, aardwolf), viverrid (small spotted genet, large spotted genet); Chiroptera: rhinopomatid (lesser mouse-tailed bat), vespertilionid (Cape serotine); Primates: cercopithecid (yellow baboon), hominid (human); Galliformes: phasianid (double-spurred francolin, yellow-necked francolin); Struthioniformes: struthionid (ostrich) (3-host cycle)	trauma, irritation (vector for theileriosis, babesiosis, trypanosomiasis, rickettsioses, Crimean-Congo haemorrhagic disease, Nairobi sheep disease, kajiado, kismayo, dugbe, Barbur)	Africa
R. (*Rhipicephalus*) *pumilio*	Artiodactyla: bovid (cattle, sheep, argali, goat, goitered gazelle, saiga antelope), camelid (camel), cervid (red deer, roe deer), suid (pig); Perissodactyla: equid (horse, donkey, onager); Eulipotyphla: erinaceid (long-eared hedgehog, Brandt's hedgehog); Lagomorpha: leporid (rabbit, European hare, desert hare, mountain hare, tolai hare, Yarkand hare), ochotonid (Pallas's pika); Rodentia: cricetid (flat-headed vole, narrow-headed vole, European snow vole,		Central Asia

	European water vole, Eversmann's hamster, European hamster, yellow steppe lemming), dipodid (small five-toed jerboa, northern three-toed jerboa), murid (house mouse, wood mouse, Black Sea field mouse, midday jird, Libyan jird, Tamarisk jird, great gerbil), sciurid (red-cheeked ground squirrel, yellow ground squirrel, little ground squirrel, relict ground squirrel, long-clawed ground squirrel); Carnivora: canid (dog, wolf, golden jackal, red fox), felid (cat, African wildcat), mustelid (European badger, least weasel, steppe polecat, marbled polecat); Primates: hominid (human); Accipitriformes: accipitrid (tawny eagle, shikra, black kite); Columbiformes: columbid (European turtle dove); Coraciiformes: coraciid (European roller); Galliformes: phasianid (grey partridge); Otidiformes: otidid (great bustard, little bustard); Passeriformes: acrocephalid (Blyth's reed warbler), alaudid (Eurasian skylark), corvid (rook, Eurasian magpie), laniid (red-tailed shrike, woodchat shrike), motacillid (white wagtail), muscicapid (isabelline wheatear, common nightingale, African stonechat), passerid (house sparrow), sturnid (common starling), sylviid (lesser whitethroat); Serpentes: viperid (Amur pit viper) (3-host cycle))		
R. (*Rhipicephalus*) *pusillus*	Artiodactyla: cervid (red deer), suid (pig); Eulipotyphla: erinaceid (Algerian hedgehog), soricid (greater white-toothed shrew); Lagomorpha: leporid (European rabbit); Rodentia: cricetid (muskrat), glirid (garden dormouse), murid (house mouse, orchard rat, Algerian mouse, brown rat); Carnivora: canid (dog, red fox, Iberian fox), felid (Eurasian lynx, Iberian lynx), mustelid (ferret, weasel, European badger), viverrid (genet); Primates: hominid (human); Strigiformes: strigid (unspecified owl) (3-host cycle)	(vector for rickettsiosis)	Eurasia
R. ramachandrai	Rodentia: murid (Indian gerbil, Indian desert gerbil, lesser bandicoot rat, sand-coloured rat, soft-furred field rat), sciurid (jungle striped squirrel); Carnivora: canid (dog, Bengal fox) (3-host cycle)		India
R. reichenowi	Artiodactyla: bovid (cattle, buffalo, waterbuck, oribi, steenbok, common duiker, nyala, Lichtenstein's hartebeest), suid (warthog, red river hog); Perissodactyla: equid (plains zebra); Tubulidentata: orycteropodid (aardvark); Rodentia: hystricid (Cape porcupine, Ethiopian crested porcupine); Carnivora: canid (side-striped jackal), felid (lion); Primates: hominid (human)		Africa
R. rhipicephali	Primates: hominid (human)		Africa
R. (*Rhipicephalus*) *rossicus*	Artiodactyla: bovid (cattle, water buffalo, sheep, goat, goitered gazelle), camelid (camel), cervid (red deer), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (European rabbit, mountain hare, European hare), ochotonid (Pallas's pika); Eulipotyphla: erinaceid (long-eared hedgehog, European hedgehog); Rodentia: cricetid (common vole, social vole, bank vole, European water vole, European hamster, Ciscaucasian hamster, grey dwarf hamster), dipodid (great jerboa), glirid (forest dormouse), murid (house mouse, yellow-necked mouse, wood mouse, Black Sea field mouse, brown rat, Tamarisk jird), sciurid (little ground squirrel, speckled ground squirrel, European ground squirrel, bobak marmot), sminthid (southern birch mouse); Carnivora: canid (dog, wolf, golden jackal, red fox), felid (cat, jaguar), mustelid (steppe polecat, marbled polecat, least weasel); Chiroptera: vespertilionid (serotine bat); Primates: hominid (human); Accipitriformes: accipitrid (common buzzard, western marsh harrier); Galliformes: phasianid (common quail); Passeriformes: alaudid (crested lark, Mediterranean short-toed lark), corvid (Eurasian magpie), emberizid (Ortolan bunting), fringillid (hawfinch), muscicapid (bluethroat), passerid (Eurasian tree sparrow); Sauria: lacertid (sand lizard, European green lizard); Testudines: testudinid (Greek tortoise) (3-host cycle)	(vector for tularemia, Crimean-Congo haemorrhagic fever and West Nile virus and possibly piroplasmosis and Q fever)	Eurasia

R. (*Rhipicephalus*) *sanguineus* (syn. *R. beccarii, brevicollis, limbatus, macropis, punctatissimus, rubicundus, rutilus, secundus, siculus, stigmaticus, sulcatus*) (brown dog tick, kennel tick)	Artiodactyla: bovid (cattle, zebu, buffalo, forest buffalo, water buffalo, sheep, Asiatic mouflon, goat, chamois, roan antelope, sable antelope, oribi, common eland, kob, impala, red hartebeest, Lichtenstein's hartebeest, common duiker, bay duiker, Maxwell's duiker, red forest duiker, waterbuck, southern reedbuck, korrigum, dama gazelle, dorcas gazelle, red-fronted gazelle, goitered gazelle, Arabian gazelle, Grant's gazelle, Thomson's gazelle, kudu, greater kudu, sitatunga, lechwe, klipspringer, fringe-eared oryx, gemsbok, steenbok, Bohor reedbuck, saiga antelope, harnessed bushbuck, kongoni, Gunther's dik-dik), camelid (dromedary, Bactrian camel), cervid (white-tailed deer, fallow deer), giraffid (giraffe**,** okapi), suid (pig, wild boar, red river hog, desert warthog, Philippine warty pig), tayassuid (peccary); Perissodactyla: equid (horse, donkey, mule, plains zebra), rhinocerotid (black rhinoceros), tapirid (South American tapir); Proboscidea: elephantid (elephant); Didelphimorphia: didelphid (white-eared opossum); Lagomorpha: leporid (Egyptian hare, Ethiopian hare, Togo hare, scrub hare, desert hare, mountain hare, grass hare, Cape hare, European hare, Indian hare, tolai hare, African savanna hare, European rabbit, Bunyoro rabbit, black-tailed jackrabbit, Jameson's red rock hare, common tapeti); Eulipotyphla: erinaceid (long-eared hedgehog, collared hedgehog, four-toed hedgehog, desert hedgehog, European hedgehog, northern white-breasted hedgehog, North African hedgehog, South African hedgehog, Sudanese hedgehog), soricid (greater white-toothed shrew, Asian house shrew); Macroscelidea: macroscelidid (four-toed elephant shrew, rufous elephant shrew, North African elephant shrew); Tubulidentata: orycteropodid (aardvark); Hyracoidea: procaviid (rock hyrax, yellow-spotted rock hyrax); Pholidota: manid (pangolin, Chinese pangolin); Pilosa: bradypodid (pale-throated sloth), myrmecophagid (northern tamandua, southern tamandua); Rodentia: caviid (capybara, guinea pig, Brazilian guinea pig, Patagonian mara), cricetid (common vole, silver mountain vole, social vole, Gunther's vole, grey dwarf hamster, European hamster, northern mole vole, meadow mouse), ctenodactylid (common gundi), dipodid (four-toed jerboa, greater Egyptian jerboa), hystricid (crested porcupine, Indian crested porcupine), murid (brown rat, black rat, Turkestan rat, short-tailed bandicoot rat, fat sand rat, unicoloured rice rat, yellow-breasted rat, African grass rat, Abyssinian grass rat, house mouse, Asian house mouse, fat mouse, typical striped grass mouse, four-striped grass mouse, yellow-necked mouse, steppe mouse, wood mouse, Tullberg's soft-furred mouse, eastern spiny mouse, Cairo spiny mouse, great gerbil, bushy-tailed gerbil, Anderson's gerbil, Cheesman's gerbil, Kemp's gerbil, lesser Egyptian gerbil, greater Egyptian gerbil, North African gerbil, Tarabul's gerbil, midday jird, Libyan jird, Shaw's jird, Sundevall's jird, Tamarisk jird, gracile tateril), nesomyid (Gambian pouched rat), petetid (springhare), sciurid (marmot, red squirrel, Gambian sun squirrel, Congo rope squirrel, long-clawed ground squirrel), thryonomyid (greater cane rat); Carnivora: canid (dog, African wild dog, wolf, variegated wolf, African wolf, coyote, golden jackal, silver jackal, black-backed jackal, side-striped jackal, bat-eared fox, crab-eating fox, red fox, pale fox, fennec fox, hoary fox, Cape fox, Ruppell's fox), felid (cat, marbled cat, fishing cat, African wildcat, jungle cat, cougar, lynx, serval, leopard, lion, jaguar, tiger, cheetah, caracal), herpestid (common slender mongoose, white-tailed mongoose, marsh mongoose, Egyptian mongoose), hyaenid (spotted hyena, striped hyena, brown hyena, aardwolf), mustelid (striped polecat, steppe polecat, marbled polecat, European polecat, European badger, lesser grison), procyonid (South American coati), ursid (sloth bear, brown bear), viverrid (common genet, rusty-spotted genet, Cape genet, African civet); Chiroptera: phyllostomid (common vampire bat); Primates: callitrichid (black-tailed	trauma, irritation, toxicosis, paralysis (vector for ehrlichiosis, babesiosis, hepatozoonosis, anaplasmosis, rickettsioses, Boutonneuse fever, Rocky Mountain spotted fever, Nairobi sheep disease)	worldwide

	marmoset, pied tamarin, Geoffroy's tamarin), cercopithecid (olive baboon, grivet, greater spot-nosed monkey, red monkey, patas monkey), galagid (brown greater galago, Senegal bushbaby, Zanzibar bushbaby), hominid (human); Accipitriformes: accipitrid (tawny eagle, martial eagle, grasshopper buzzard, long-legged buzzard, white-tailed hawk, black kite, hooded vulture, white-backed vulture, cinerous vulture, Griffon vulture, European honey buzzard), sagittariid (secretary bird); Bucerotiformes: bucerotid (white-thighed hornbill), upupid (Eurasian hoopoe); Columbiformes: columbid (rock dove, European turtle dove); Coraciiformes: coraciid (European roller), meropid (European bee-eater); Charadriiformes: burhinid (Eurasian stone curlew); Ciconiiformes: ciconiid (African openbill, Marabou stork, Abdim's stork); Coliiformes: coliid (mousebird); Columbiformes: columbid (ringed pigeon); Cuculiformes: cuculid (African emerald cuckoo, Senegal coucal); Falconiformes: falconid (common kestrel); Galliformes: phasianid (chicken, common quail, rock partridge, grey partridge); Otidiformes: otidid (white-bellied bustard, black-bellied bustard, greater bustard, lesser bustard, Arabian bustard, Kori bustard, Denham's bustard); Passeriformes: alaudid (red-capped lark, crested lark, woodlark, Eurasian skylark, Calandra lark), corvid (raven, rook, western jackdaw, Eurasian magpie), fringillid (common chaffinch), hirundinid (sand martin), icterid (Chopi blackbird), motacillid (white wagtail), muscicapid (western black-eared wheatear, isabelline wheatear, common redstart), passerid (house sparrow, Spanish sparrow), sturnid (common starling), thraupid (bananaquit); Pelecaniformes: scopid (hamerkop), threskiornithid (Hadada ibis); Pterocliformes: pteroclid (black-bellied sandgrouse); Strigiformes: strigid (little owl, striped owl, short-eared owl, Eurasian eagle-owl, Pharaoh eagle-owl); Struthioniformes: struthionid (ostrich, Masai ostrich, Somali ostrich); Serpentes: boid (boa), viperid (puff adder); Crocodilia: crocodylid (spectacled caiman); Testudines: testudinid (Greek tortoise) (3-host cycle)		
R. (*Pomerantzevia*) *scalpturatus*	host unknown, collected from environment		Asia
R. (*Rhipicephalus*) *schulzei*	Artiodactyla: bovid (cattle, sheep, goat, goitered gazelle, saiga antelope), camelid (camel), cervid (red deer), suid (pig); Perissodactyla: equid (horse, donkey); Lagomorpha: leporid (European hare, tolai hare), ochotonid (Pallas's pika); Eulipotyphla: erinaceid (long-eared hedgehog), soricid (lesser white-toothed shrew); Rodentia: cricetid (common vole, flat-headed vole, European water vole, northern mole vole, social vole, grey dwarf hamster, European hamster, Eversmann's hamster, steppe lemming), dipodid (great jerboa, small five-toed jerboa, northern three-toed jerboa, thick-tailed three-toed jerboa, dwarf fat-tailed jerboa), glirid (forest dormouse), murid (house mouse, striped field mouse, Eurasian harvest mouse, wood mouse, midday jird, Libyan jird, Tamarisk jird, great gerbil), sciurid (little ground squirrel, red-cheeked ground squirrel, large-toothed ground squirrel, long-tailed ground squirrel, yellow ground squirrel, russet ground squirrel, Tien Shan ground squirrel, European ground squirrel, long-clawed ground squirrel, bobak marmot), sminthid (southern birch mouse); Carnivora: canid (dog, wolf, golden jackal, red fox), felid (cat, lynx), mustelid (least weasel, European badger, steppe polecat, marbled polecat); Primates: hominid (human); Accipitriformes: accipitrid (steppe eagle, long-legged buzzard); Serpentes: colubrid (blotched rat snake) (3-host cycle)		Europe, Africa
R. sculptus	Artiodactyla: bovid (buffalo, roan antelope, sable antelope, hartebeest, waterbuck), giraffid (giraffe), suid (pig); Perissodactyla: equid (Burchell's zebra); Carnivora: canid (dog)		Africa, North America

	(3-host cycle)		
R. senegalensis	Artiodactyla: bovid (cattle, buffalo, sheep, goat, bongo, kanki, eland, common duiker, black duiker, bay duiker, red-flanked duiker, Maxwell's duiker, blue wildebeest, Lichtenstein's hartebeest, roan antelope, royal antelope, oribi, harnessed bushbuck, kob, Bohor reedbuck), giraffid (giraffe), suid (pig, red river hog, desert warthog); Perissodactyla: equid (horse), rhinocerotid (black rhinoceros); Proboscidea: elephantid (African elephant); Macroscelidea: macroscelidid (elephant shrew); Eulipotyphla: soricid (white-toothed shrew); Pholidota: manid (giant ground pangolin); Lagomorpha: leporid (Cape hare); Tubulidentata: orycteropodid (aardvark); Rodentia: herpestid (banded mongoose), hystricid (crested porcupine, African brush-tailed porcupine), murid (typical striped grass mouse, soft-furred rat, striped grass rat, gerbil), nesomyid (giant pouched rat), sciurid (African striped squirrel, Cuvier's tree squirrel), thryonomyid (greater cane rat); Carnivora: canid (dog, hunting dog, golden jackal), felid (lion, leopard), herpestid (banded mongoose), viverrid (small spotted genet, African civet); Primates: cercopithecid (spot-nosed monkey), hominid (human); Anseriformes: anatid (white-faced whistling duck) (3-host cycle)		Africa
R. serranoi	Artiodactyla: bovid (klipspringer); Hyracoidea: procaviid (rock hyrax, yellow-spotted rock hyrax, tree hyrax); Carnivora: felid (leopard)		Africa
R. simpsoni	Artiodactyla: bovid (buffalo, black duiker, red-flanked duiker, Maxwell's duiker, bushbuck, royal antelope, kob), suid (red river hog); Rodentia: hystricid (tufted-tailed porcupine, African brush-tailed porcupine, crested porcupine), murid (marsh rat, African grass rat), nesomyid (Gambian pouched rat), thryonomyid (greater cane rat, lesser cane rat); Carnivora: felid (leopard), viverrid (African civet); Primates: cercopithecid (Skye's monkey); Passeriformes: acrocephalid (African yellow warbler), viduid (village indigobird) (3-host cycle)		Africa
R. (*Rhipicephalus*) *simus* (syn. *R. longoides*, *perpulcher*, *shipleyi*) (glossy brown tick)	Artiodactyla: bovid (cattle, zebu, buffalo, sheep, goat, korrigum, dikdik, Gunther's dikdik, common duiker, red-flanked duiker, common eland, giant eland, Grant's gazelle, Thomson's gazelle, greater kudu, oribi, southern reedbuck, bohor reedbuck, bushbuck, harnessed bushbuck, waterbuck, roan antelope, sable antelope, steenbok, tiang, blue wildebeest, impala, nyala, lechwe, red hartebeest, Lichtenstein's hartebeest, bongo, topi, gemsbok, kob, klipspringer), camelid (dromedary), giraffid (giraffe), hippopotamid (hippopotamus), suid (pig, bushpig, forest hog, red river hog, South African river hog, common warthog, desert warthog); Perissodactyla; equid (horse, donkey, mule, plains zebra, Burchell's zebra), rhinocerotid (black rhinoceros, white rhinoceros); Proboscidea: elephantid (African elephant); Eulipotyphla: erinaceid (long-eared hedgehog, South African hedgehog), soricid (white-toothed shrew); Tubulidentata: orycteropodid (aardvark); Pholidota: manid (Temminck's ground pangolin); Lagomorpha: leporid (rabbit, Cape hare, African savanna hare, scrub hare); Macroscelidea: macroscelidid (short-snouted elephant shrew, four-toed elephant shrew, black-and-rufous elephant shrew); Hyracoidea: procaviid (rock hyrax); Rodentia: caviid (guinea pig), glirid (woodland dormouse, spectacled dormouse), hystricid (crested porcupine, Cape porcupine), murid (Abyssinian grass rat, African swamp rat, Karoo rat, groove-toothed swamp rat, rock rat, red veld rat, bush vlei rat, tropical vlei rat, Angoni vlei rat, South African vlei rat, Sloggett's vlei rat, gray brush-furred rat, African soft-furred rat, African grass rat, Namaqua rock rat, whistling rat, tree rat, house mouse, single-striped mouse, typical striped grass mouse, four-striped grass	trauma, irritation, paralysis (vector for babesiosis, anaplasmosis, rickettsioses)	Africa

	mouse, buffoon striped grass mouse, Griselda's striped grass mouse, Cameroon soft-furred mouse, Jackson's soft-furred mouse, Tullberg's soft-furred mouse, Namaqua rock mouse, southern multimammate mouse, Natal multimammate mouse, eastern spiny mouse, Cairo spiny mouse, African pygmy mouse, savannah gerbil, bushveld gerbil, Cape gerbil, Kemp's gerbil, savannah gerbil, king jird), nesomyid (South African pouched rat), pedetid (South African springhare), sciurid (striped ground squirrel, Cape ground squirrel, African striped squirrel, Kuhl's tree squirrel, Smith's bush squirrel), thryonomyid (greater cane rat); Carnivora: canid (dog, hunting dog, African wild dog, variegated wolf, African wolf, golden jackal, side-striped jackal, black-backed jackal, Cape fox, bat-eared fox), felid (cat, African wildcat, cheetah, leopard, lion, serval, caracal, tiger), herpestid (marsh mongoose, water mongoose, yellow mongoose, banded mongoose, white-tailed mongoose, meerkat), hyaenid (spotted hyena, striped hyena, brown hyena, aardwolf), mustelid (ratel, honey badger), viverrid (African civet, common genet, rusty-spotted genet, Cape genet); Chiroptera: rhinolophid (lesser horseshoe bat); Primates: cercopithecid (olive baboon, king colobus), galagid (brown greater galago), hominid (human); Galliformes: numidid (helmeted guineafowl), phasianid (chicken); Passeriformes: cisticolid (green-capped eremomela, rattling cisticola), estrildid (blue waxbill), malaconotid (black-backed puffback); Pelecaniformes: phalacrocoracid (reed cormorant); Sauria: scincid (African striped skink); Testudines: testudinid (Greek tortoise) (3-host cycle)		
R. supertritus (syn. *R. coriaceus*)	Artiodactyla: bovid (cattle, buffalo, goat, eland, giant eland, greater kudu, Coke's hartebeest, Lichtenstein's hartebeest, sable antelope, roan antelope, oribi, greater kudu, common eland, giant eland), giraffid (giraffe), suid (desert warthog); Perissodactyla: equid (horse, plains zebra, Burchell's zebra), rhinocerotid (rhinoceros); Hyracoidea: procaviid (rock hyrax); Rodentia: hystricid (South African porcupine); Carnivora: canid (dog, hunting dog), felid (lion), hyaenid (spotted hyena, striped hyena); Primates: hominid (human)		Africa
R. tetracornus	Eulipotyphla: soricid (Chinese mole shrew); Rodentia: cricetid (unspecified), murid (red spiny rat, Himalayan field rat, Gairdner's shrewmouse)		Asia
R. theileri	Artiodactyla: bovid (cattle, sheep); Eulipotyphla: erinaceid (South African hedgehog); Pholidota: manid (Temminck's ground pangolin); Rodentia: murid (Namaqua rock mouse), sciurid (Cape ground squirrel, Smith's bush squirrel); Carnivora: canid (dog, black-backed jackal, Cape fox), herpestid (yellow mongoose, meerkat) (3-host cycle)		Africa
R. tricuspis (syn. *R. glyphis*, *lunulatus*)	Artiodactyla: bovid (cattle, zebu, buffalo, forest buffalo, sheep, goat, oribi, tiang, roan antelope, sable antelope, hartebeest, red hartebeest, Jackson's hartebeest, Lelwel hartebeest, Lichtenstein's hartebeest, blue wildebeest, steenbok, korrigum, common duiker, red forest duiker, waterbuck, bushbuck, southern reedbuck, impala, gemsbok, greater kudu, Grant's gazelle, common eland, nyala, kob, tiang, kongoni, Sharpe's grysbok), camelid (camel), giraffid (giraffe), suid (pig, bushpig, forest hog, red river hog, warthog); Perissodactyla: equid (horse, plains zebra, Burchell's zebra), rhinocerotid (black rhinoceros); Eulipotyphla: erinaceid (South African hedgehog); Tubulidentata: orycteropodid (aardvark); Lagomorpha: leporid (rabbit, scrub hare, Cape hare); Rodentia: hystricid (crested porcupine), murid (four-striped grass mouse, Natal multimammate mouse, gray brush-furred rat, Namaqua rock rat), pedetid (South African springhare); Carnivora: canid (dog, African wild dog, Cape fox, side-striped jackal, black-backed jackal, bat-eared fox, Cape fox), felid (caracal, lion, leopard,		Africa

	serval), hyaenid (brown hyena, aardwolf), viverrid (African civet); Chiroptera: pteropodid (unspecified flying fox); Primates: hominid (human); Anseriformes: anatid (white-faced whistling duck); Gruiformes: rallid (red-knobbed coot); Otidiformes: otidid (black bustard, white-bellied bustard); Strigiformes: strigid (barn owl) (3-host cycle)		
R. (*Rhipicephalus*) *turanicus*	Artiodactyla: bovid (cattle, buffalo, water buffalo, sheep, argali, goat, goitered gazelle, Grant's gazelle, Thomson's gazelle, eland, greater kudu, common duiker, roan antelope, gemsbok, lechwe, saiga antelope), camelid (dromedary, camel), cervid (red deer, Bactrian deer), suid (pig, warthog); Perissodactyla: equid (horse, donkey, mule, Burchell's zebra, onager); Tubulidentata: orycteropid (aardvark); Lagomorpha: leporid (European rabbit, Corsican hare, European hare, Indian hare, Cape hare, scrub hare, desert hare, tolai hare); Eulipotyphla: erinaceid (northern white-breasted hedgehog, long-eared hedgehog, European hedgehog, Brandt's hedgehog, Indian hedgehog), soricid (greater white-toothed shrew, common European white-toothed shrew, Asian house shrew); Rodentia: cricetid (common vole, social vole, Afghan vole, Gunther's vole, European snow vole, European water vole, European hamster, grey dwarf hamster), dipodid (William's jerboa), glirid (European edible dormouse), hystricid (Indian crested porcupine), murid (house mouse, yellow-necked mouse, wood mouse, broad-toothed mouse, black rat, brown rat, Turkestan rat, lesser bandicoot rat, short-tailed bandicoot rat, great gerbil, Indian gerbil, Indian desert gerbil, Libyan jird, Persian jird, Tristam's jird, Tamarisk jird), sciurid (yellow ground squirrel, long-clawed ground squirrel, Indian palm squirrel, long-tailed marmot); Carnivora: canid (dog, wolf, red fox, corsac fox, Karaganka fox, golden jackal, side-striped jackal, black-backed jackal, red fox, bat-eared fox), felid (cat, jungle cat, black-footed cat, African wildcat, caracal, serval, cheetah, leopard, snow leopard, lion), herpestid (Egyptian mongoose), hyaenid (brown hyena, aardwolf), mustelid (Eurasian badger, steppe polecat, marbled polecat, least weasel, ferret), ursid (brown bear), viverrid (African civet, genet); Primates: cercopithecid (vervet monkey), hominid (human); Accipitriformes: accipitrid (short-toed snake-eagle, Wahlberg's eagle, black kite, white-headed vulture), sagittariid (secretary bird); Caprimulgiformes: caprimulgid (European nightjar); Charadriiformes: burhinid (Cape dikkop); Ciconiiformes: ciconiid (Marabou stork); Columbiformes: columbid (dove); Galliformes: phasianid (chicken); Otidiformes: otidid (black bustard, Denham's bustard); Passeriformes: alaudid (crested lark), corvid (rook), sturnid (rosy starling); Piciformes: picid (white-winged woodpecker); Strigiformes: strigid (marsh owl, Eurasian eagle-owl); Struthioniformes: struthionid (ostrich); Sauria: lacertid (Caucasus emerald lizard, multi-ocellated racerunner); Serpentes: viperid (puff adder) (3-host cycle)	(vector for babesiosis, theileriosis, hepatozoonosis, rickettsiosis)	Africa, Eurasia
R. walkerae	Artiodactyla: giraffid (giraffe)		Africa
R. warburtoni	Artiodactyla: bovid (cattle, sheep, goat, gemsbok); Lagomorpha: leporid (scrub hare, Cape hare, Smith's red rock rabbit); Macroscelidea: macroscelidid (rock elephant shrew); Carnivora: canid (dog), felid (African wildcat); Rodentia: murid (Namaqua rock mouse), pedetid (springhare); Primates: hominid (human); Passeriformes: alaudid (lark) (3-host cycle)	irritation, paralysis	Africa
R. zambeziensis (lowveld brown ear tick)	Artiodactyla: bovid (cattle, buffalo, goat, impala, greater kudu, blue wildebeest, klipspringer, steenbok, eland, nyala, bushbuck, common duiker, roan antelope, sable antelope), giraffid (giraffe), suid (bushpig, warthog); Perissodactyla: equid (horse, Burchell's zebra), rhinocerotid (white rhinoceros); Lagomorpha: leporid (scrub hare, Cape hare); Rodentia: hystricid (South African	trauma, irritation, anaemia (plus vectors for theileriosis, ehrlichiosis)	Africa

	porcupine), pedetid (springhare), sciurid (Smith's bush squirrel); Tubulidentata: orycteropodid (aardvark); Carnivora: canid (dog, hunting dog, black-backed jackal), felid (cat, cheetah, lion, leopard), herpestid (slender mongoose, marsh mongoose, banded mongoose, white-tailed mongoose), hyaenid (brown hyena, spotted hyena), viverrid (African civet); Primates: cercopithecid (vervet monkey), hominid (human); Galliformes: numidid (helmeted guineafowl), phasianid (chicken) (3-host cycle)		
R. ziemanni (syn. *R. cuneatus*)	Artiodactyla: bovid (cattle, zebu, buffalo, forest buffalo, sheep, goat, bongo, bushbuck, common duiker, bay duiker, blue duiker, black duiker, zebra duiker, yellow-backed duiker, red-flanked duiker, banded duiker, Maxwell's duiker, grysbok, oribi, giant eland, royal antelope), cervid (water chevrotain), giraffid (okapi), suid (pig, red river hog, warthog); Perissodactyla: rhinocerotid (black rhinoceros); Proboscidea: elephantid (African elephant); Hyracoidea: procaviid (rock hyrax, tree hyrax); Rodentia: hystricid (crested porcupine, tufted-tailed porcupine, African brush-tailed porcupine), thryonomyid (greater cane rat); Carnivora: canid (dog, jackal), felid (leopard, serval), mustelid (otter), viverrid (African civet); Primates: cercopithecid (baboon), hominid (human)		Africa
R. zumpti	Artiodactyla: bovid (cattle, buffalo, Lichtenstein's hartebeest, steenbok, waterbuck, nyala, oribi, greater kudu, common duiker), suid (bushpig, red river hog, desert warthog); Perissodactyla: equid (plains zebra, Burchell's zebra), rhinocerotid (black rhinoceros); Rodentia: hystricid (Cape porcupine); Carnivora: canid (dog), felid (lion), viverrid (African civet); Primates: hominid (human) (3-host cycle)		Africa

Parasite morphology: *Rhipicephalus* spp. (including *Boophilus* spp.) form 4 different types of morphological stages during their development: eggs; larvae; nymphs; and adults. Eggs are small orange-brown ovoid stages measuring around 0.4 mm in diameter. Larvae have ovate flattened bodies measuring 0.5-0.6 mm long. They are covered by toughened cuticles that are usually pale cream-brown in colour with a slightly darker posterior portion. They have conspicuous anterior heads (capitulum) with pointy palps flanking the central protruding mouthparts. The posterior sac-like body (idiosoma) has a hard chitinized plate (scutum) covering the antero-dorsal surface. Larvae are characterized by the possession of 3 pairs of long pale legs attached to the anterior ventral idiosoma, but they lack respiratory openings (stigmata) and tracheae. Nymphs have dorso-ventrally flattened bodies that are oval-elliptical in dorsal profile and measure 1.0-1.4 mm in length. They have a conspicuous orange-brown to red-brown dorsal scutum and the posterior idiosoma is usually cream-grey, sometimes with white patches. The anterior capitulum is visible and contains a pair of pointy palps projecting forwards. Nymphs typically have 8 long pale legs tipped with claws, and they possess a pair of lateral respiratory stigmata surrounded by oval plates. Adult ticks have ovate-pyriform bodies that are tapered anteriorly, flattened ventrally but convex dorsally (capable of marked distention during engorgement). Unfed ticks range in length from 2-6 mm, but engorged females may swell up to 8-20 mm long (members of the subgenus *R.* (*Boophilus*) are typically smaller, ranging from 2-3 mm long when unfed and 6-12 mm when engorged). Adults range in colour from creamy-brown to reddish-brown in colour, and they often darken to grey or brown-black after feeding. They have 2 conspicuous body tagma: a small anterior capitulum (head) visible from above (whereas that of argasids is ventral and not visible) and a larger saccular idiosoma (body). The capitulum comprises the basis capitulum (integumental ring encircling mouthparts) and the gnathosoma (feeding structures with palps, chelicerae and hypostome). The basis capitulum is hexagonal (not triangular, rectangular or pentagonal) and has distinct lateral projections (rounded in the subgenus *R.* (*Boophilus*)). Female ticks also have clusters of small pores (porose areas) on the dorsal surfaces (involved in waterproofing eggs during oviposition). The mouthparts project forwards and are short being similar in length to the basis capitulum. The palps are sensory structures that move laterally and do not enter the skin when feeding. They are short, often wider than long, and their segments may contain dorsal and lateral ridges (especially in the subgenus *R.* (*Boophilus*)). The chelicerae are tubular dentate structures that move horizontally to cut flesh forming small pools of blood. The barbed hypostome is inserted into the blood pool to facilitate feeding as well as to aid attachment. A food canal is formed by apposition of the dorsal chelicerae and ventral hypostome allowing blood to be ingested and saliva to be injected. The alimentary tract contains a muscular pharynx (with pharyngeal valve), tubular oesophagus (short tube), large saccular midgut (ventriculus) with lateral diverticula (caeca), short intestine (with excretory Malpighian tubules) leading to the posterior rectal sac. The anus is located ventrally near the midbody and contains a posterior (metastriate) anal groove, which is difficult to see in members of the subgenus *R.* (*Boophilus*) (in comparison, the genus *Ixodes* has an anterior (prostriate) anal groove). The idiosoma is covered by a hard waxy cuticle with a distinct sclerotized dorsal plate (scutum). The scutum almost completely covers males (= conscutum) but is confined to a smaller anterior circular-pyriform shield in females. The cuticle may also contain ridges and/or depressions depending on tick species (members of the subgenus *R.* (*Boophilus*) have 3 longitudinal grooves) as well as tiny surface folds, small punctuations (pores) and numerous setae. The scutum of most *Rhipicephalus* spp. is inornate (without coloured patterns), except for several species (*R. dux, humeralis,*

maculatus, pulchellus) which have lighter and darker patches. A pair of simple convex or flat eyes are present on the lateral margins of the scutum, but are difficult to observe in some species. The posterior margin of the idiosoma also bears a series of grooves or indentations (known as festoons) which are present in all species, except those belonging to the subgenus *R.* (*Boophilus*). The ventral idiosoma gives rise to 4 pairs of pale cream-yellow legs (without distinct pale rings) which are unequal in size, the second pair being the shortest and the fourth pair being the longest. The legs are well developed and consist of 6 segments (coxae, trochanter, femur, patella (genu), tibia, and tarsus) terminating in a pair of claws with a pad-like pulvillus (pulvillus absent or rudimentary in argasids). A distinctive feature of *Rhipicephalus* spp. is the presence of a pair of large external spurs on coxae I which impart a forked appearance (argasid coxae without spurs). In addition, tarsi IV have ventral hooks, and tarsi I have a dorsal sensory apparatus (Haller's organ) used to detect temperature, chemical and tactile stimuli. Adults possess a pair of respiratory openings with stigmatal plates located behind coxae IV, the plates bearing comma-shaped tail-like protrusions (in comparison, argasids have small stigmata located between coxae III). Adults display considerable sexual dimorphism, including differences in body size (females being larger, especially when engorged), in dorsal scutum size (males being covered, but not females), the presence of ventral plates (in males only) and the presence of specialized porose areas on the basis capitulum (on females only). Females have a single saccular ovary with paired oviducts joined to a common uterus (with accessory glands) opening to a bipartite vagina (cervical region acting as receptaculum seminis to store spermatophores, and vestibular region prolapsing during oviposition. The genital opening (gonopore) is located on the ventral midbody and is U- or V-shaped with marginal folds and an anterior sclerotized flap (genital apron). During oviposition, eggs pass through a special gland (Gene's organ) located near the gnathosoma-idiosoma junction which helps waterproof eggs. Males have pairs of flat sclerotized ventral plates (adanal and accessory plates) located either side of the subterminal anus (absent in the genera *Aponomma*, *Dermacentor*, *Haemaphysalis*, and *Bothriocroton,* but more extensive in the genus *Ixodes*). Adult males have paired tubular testes joined to a common vas deferens (with a multilobed accessory gland) leading to the ejaculatory duct. The gonopore is situated ventrally around the midbody and has an anterior genital apron, Males produce packets of spermatids (spermatophores) which are transferred to the genital operculum of females.

Site of infection: All motile developmental stages (larvae, nymphs, adults) are ectoparasitic on vertebrate hosts, with each successive stage usually found on a different host. Most species have 3-host life-cycles, although a few have 2-host life-cycles and all members of the subgenus *R.* (*Boophilus*) have one-host life-cycles. Infestations are generally found on multiple host species (broad euryxenous or stenoxenous host ranges), although different tick species tend to have host preferences for particular mammalian, avian and/or reptilian hosts. Infestations have been reported on mammals belonging to 55 families in 16 orders (including ungulates, insectivores, rodents, bats, carnivores, marsupials and primates), birds belonging to 22 passerine families and 28 non-passerine families in 20 orders (including water birds, terrestrial birds, forest birds, and some birds of prey), reptiles belonging to 4 lizard families, 4 snake families, one tortoise family and one crocodile family, and amphibians belonging to one toad family. While all ectoparasitic stages may migrate around the host body, some demonstrate preferred attachment/feeding sites (tissue tropism), particularly for areas of the body that are difficult for the host to groom. In heavy infestations, however, ticks can be found more widely distributed over the body. Larval stages seem to preferentially feed on softer skin found on the forelegs, thighs and flanks of their hosts, while nymphs and adults feed mainly around the belly, shoulders, neck, and when present, the ears, escutcheon, base of the tail, and between the toes.

Pathogenesis: Light infestations may be asymptomatic or subclinical, but heavier infestations may cause mild to severe disease with cutaneous lesions and systemic effects on their hosts. The severity of disease is dependent on numerous factors, including differences in tick pathogenicity (species/strain variations), host susceptibility (physiological and immunological status), the stage, duration and intensity of infestations, and the presence of concomitant infections. *Rhipicephalus* larvae, nymphs and adults are all obligate haematophagous parasites that use their mouthparts to cut into dermal tissues producing pools of blood which are ingested (feeding process known as telmophagy). All stages attach firmly to the skin of their hosts, usually creating a sterile abscess where they feed on lymph and whole blood. The volume of blood ingested by individual feeding stages may be small (< 1 ml), but engorging females may take up significantly more (up to 10 ml per tick). Heavy infestations therefore may cause enough blood loss to manifest as anaemia with prolonged infestations leading to jaundice. Infestations cause focal tissue trauma resulting in cutaneous lesions with irritation, inflammation, erythema, oedema, pruritus, necrosis and haemorrhages as well as haematoma and granuloma formation. During feeding, ticks inject saliva containing many vaso-active compounds, including those with analgesic, anticoagulant, vasodilatory, inflammatory, antigenic and even toxic properties. The glue or cement they use for attachment also contains compounds which stimulate inflammation and granuloma formation. Individual hosts may also suffer allergic or hypersensitivity reactions to foreign compounds, which leads to further inflammation and more severe lesions. Secretions from some tick species (e.g. *R. evertsi*) may also disrupt metabolic processes leading to liver damage and toxaemia, especially in young animals. Metabolic parameters affected include reductions in serum iron, cholesterol, phospholipids, albumin, alkaline phosphatase and amylase, as well as elevations in serum urea-nitrogen and gamma-globulins. Infested animals may develop fever with increases in water intake, urinary volume and faecal volume (both water and dry matter content). Infestations in livestock often cause their hosts considerable biting-stress (tick worry) leading to reduced productivity due to inefficient feeding with anorexia, poor growth with reduced weight gain or weight loss, and lowered milk production in dairy animals. Granulomatous skin lesions also damage hides resulting in reduced market value. The course of infestations is greatly influenced by both innate and acquired immune responses. Naive (previously unexposed) cattle often develop heavy infestations but then gradually acquire protective immunity (resistance) over several months which helps them survive repeated exposures. Tropical breeds of *Bos indicus* cattle develop greater resistance than European or British breeds of *Bos taurus* cattle. Paradoxically, cattle have also been shown to develop transient

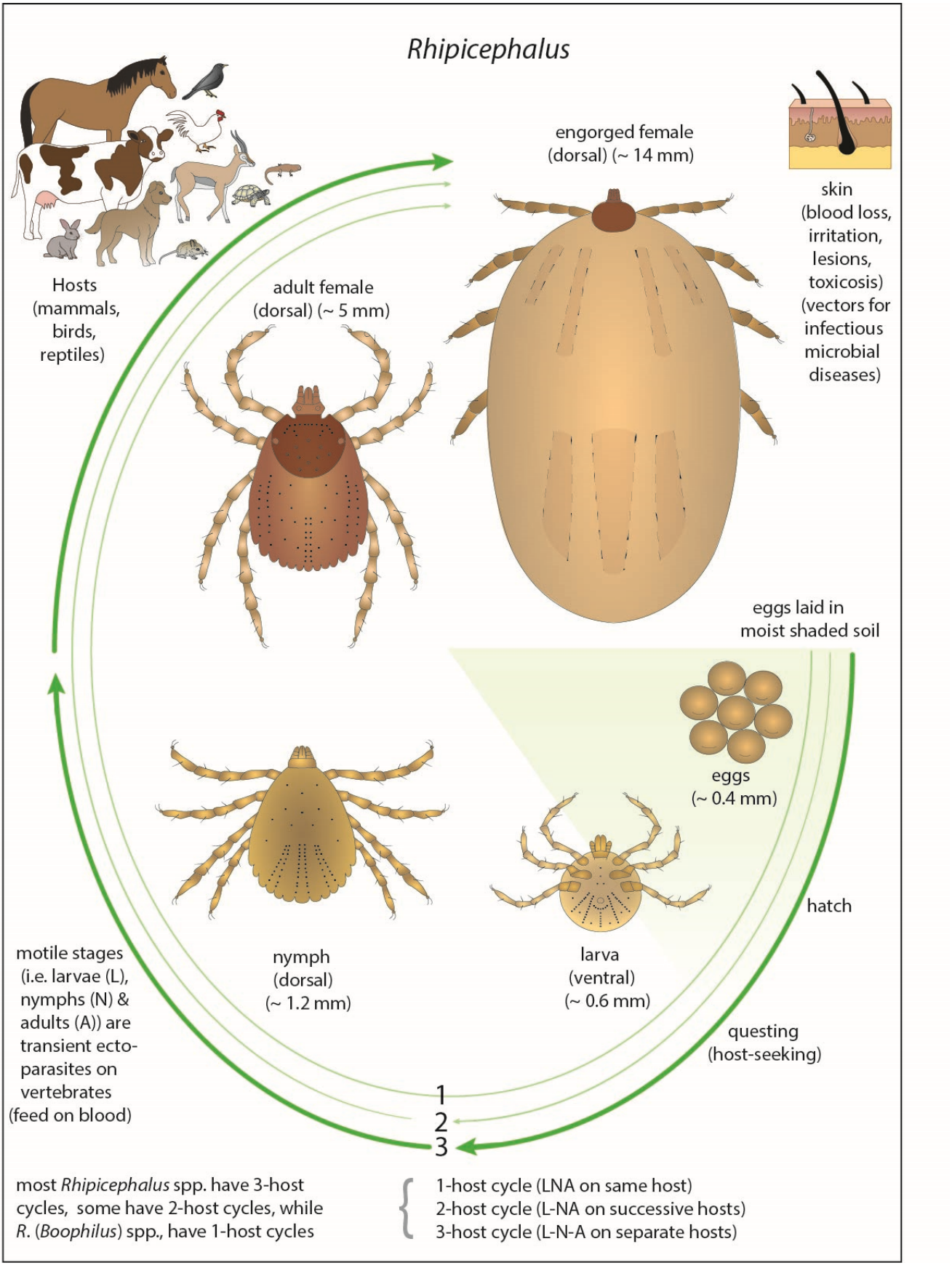
immunosuppression that favours tick survival and transmission. Experimental studies have shown that compounds in tick saliva (particularly prostaglandins) may inhibit both cellular and humoral host responses, as evidenced by depleted numbers of T and B lymphocytes in peripheral blood and reduced antibody responses. These enigmatic and complex interactions are prime examples of the ongoing evolutionary arm race between parasite pathogenicity and host immunity. Epidemiological and experimental studies have shown that many *Rhipicephalus* spp. act as efficient vectors for the transmission of various infectious microbial diseases. The ticks may act as mechanical vectors where microbes are passively transported between hosts, but many also act as biological vectors where microbial stages undergo amplification (growth and multiplication) in ticks, The microbes invariably undergo trans-stadial transmission (transfer between different metamorphic stages) and some even exhibit trans-ovarian transmission (vertical transfer from female adult ticks to eggs). Transmission may occur during feeding (via the injection of salivary secretions), during fluid regulation (via the regurgitation of excess gut fluids back into bite sites) or during waste elimination (via the excretion of materials from the hindgut and/or Malpighian tubules). *Rhipicephalus* spp. may transmit haemoprotozoan parasites causing theileriosis (East Coast fever) and babesiosis (tick fever), rickettsial bacteria causing anaplasmosis, rickettsiosis (spotted fever), ehrlichiosis, spirochaetes causing borreliosis (relapsing fever, Lyme disease), proteobacteria causing coxiellosis (Q fever) and orthonairoviruses causing Nairobi sheep disease. In particular, the species *R. sanguineus* (brown dog tick) acts as a vector for canine babesiosis caused by *Babesia canis* resulting in haemolytic anaemia and jaundice in dogs. Species belonging to the subgenus *R.* (*Boophilus*) (commonly known as blue ticks) are important vectors for bovine babesiosis (tick fever) caused by *Babesia bigemina* and *B. bovis* resulting in significant morbidity and mortality in cattle populations in tropical and subtropical regions.

Developmental cycle and mode of transmission: *Rhipicephalus* spp. undergo incomplete (hemimetabolous) metamorphosis whereby eggs hatch larvae that moult to nymphs and then adult ticks. Each developmental stage feeds once to repletion on blood from vertebrate hosts, usually a succession of 3 different hosts (sometimes 2), but those in the subgenus *R.* (*Boophilus*) only use one-host. Those with 3-host life-cycles drop off the host after feeding and moult to the next developmental stage in the external environment. The duration of the off-host stages varies considerably and are heavily influenced by prevailing environmental conditions (particularly temperature and relative humidity). Gravid female ticks lay large batches of eggs (hundreds to thousands) in moist shaded areas in soil and vegetation where they hatch in 14-42 days, although this may take up to 145 days when conditions are unfavourable (cold and dry). The emergent 6-legged larvae (known as seed ticks, grass ticks, or pepper ticks) take several days to harden and then ascend vegetation to quest for hosts (sedentary ambush strategy rather than actively hunting/pursuing hosts). They are able to sense various chemical, temperature and tactile stimuli associated with passing hosts and they actively wave their forelegs in the air when triggered by host odours (exhaled carbon dioxide, urinary ammonia), body heat, and vibrations (sound and movement). In suitable moist conditions, larvae may quest for hosts for between 20-240 days. They infest passing animals by crawling onto the skin where they probe for suitable feeding sites. Most species have preferred hosts, often small terrestrial vertebrates (mammals, birds and reptiles), and they are reluctant to feed on unusual hosts (as evidenced by protracted probing, taking small sample meals, dropping off and seeking alternative hosts). When hosts are suitable, the larvae attach to the skin and feed on blood over several days. When replete they drop off the host into the surrounding environment to digest their bloodmeals and moult into nymphs after 2-3 weeks. Like all ixodid ticks, they only form one nymphal instar (in contrast to argasid ticks which form between 2-7 nymphal instars). Nymphs also ascend vegetation to quest for hosts, many species showing some preferences for small mammals (particularly rodents) and birds. They are able to seek hosts for several days to months depending on environmental conditions. Having located a host, they crawl onto the skin, attach and feed on blood for several days. When replete, they drop off their hosts into the external environment to digest their bloodmeals and moult into adult ticks after 1-2 weeks. The adults wait for suitable conditions and then ascend vegetation to quest over several days to months for passing hosts, often larger vertebrates (including domestic and companion animals). Once attached, adults feed on blood for longer periods of time (one week or more) and are able to grow new cuticle to accommodate their larger bloodmeals. Ticks mature after feeding and usually mate on their hosts, with males seeking attached females to inseminate with spermatophores. Fertilized females then engorge on host blood, increasing markedly in size to become up to 100-120 times their pre-feeding weight. Once engorged, the females drop off into the immediate environment and soon begin to lay large batches of eggs (cumulatively totally 2,000-10,000) over several weeks before dying. Oviposition may be delayed for several weeks under adverse cold/dry environmental conditions, and some species are even thought to undergo developmental diapause in cold climates. The whole life-cycle of 3-host *Rhipicephalus* spp. may be completed in as little as 2 months under ideal conditions, so there are often several generations per year in tropical and subtropical regions. However, in temperate regions with well-defined wet and dry seasons, many species only have one generation per year. In colder regions, developmental stages may only be able to feed over summer months so there may be only one complete generation every 2-3 years. Members of the subgenus *R.* (*Boophilus*) have one-host life cycles that may be completed in 2-3 months in tropical regions and 6-9 months in subtropical to temperate regions. All developmental stages occur on the same host, with larvae and nymphs feeding for several days before moulting around one week later, and adults feeding for longer periods before mating. Males take small meals and may mate several times, even living detached from hosts for several months in cold conditions. There are even several reports of adult males feeding on haemolymph from female ticks. Fertilized females engorge with blood and drop off their hosts into the surrounding environment. They continue development for several days to weeks and then lay egg batches over 2-44 days. Most *Rhipicephalus* spp. show patchy aggregated distributions on livestock within and between farms in endemic regions, because female ticks oviposit large numbers of eggs in small areas leading to focal pasture contamination. All off-host developmental stages require moisture and shade to survive, so tick populations are usually greater on unimproved pastures with tussocky grasses and small bushes rather than on improved pastures. Infestations also abound on pastures with high stocking densities as more hosts come into contact with ticks and supply blood for their nutritional requirements.

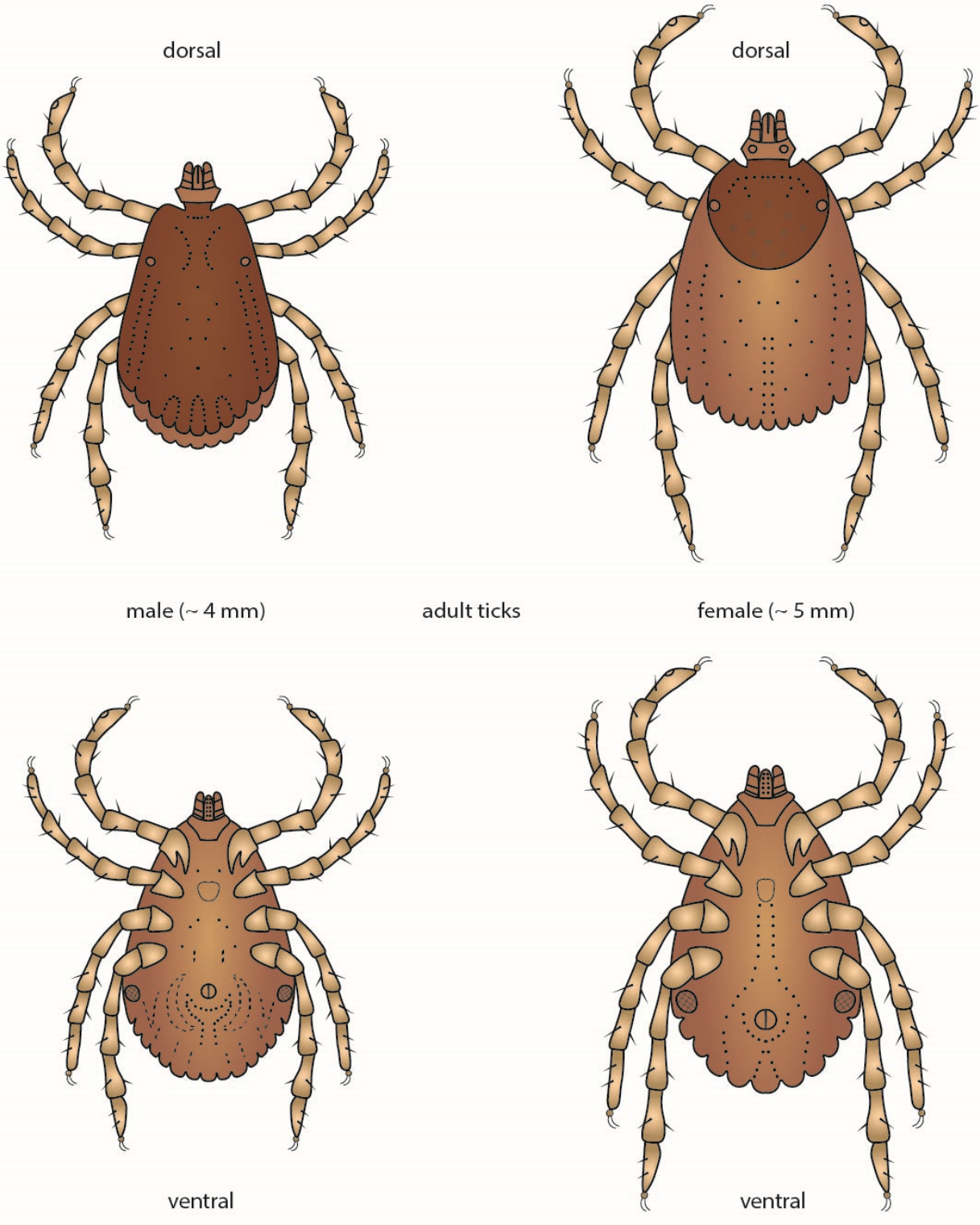
Differential diagnosis: It is difficult to diagnose infestations on the basis of symptomatology as other aetiological agents may cause similar skin lesions (especially other ectoparasites) and a range of diseases may involve haematological and biochemical perturbations manifest as anaemia, jaundice, toxicosis, anorexia and loss of condition. Infestations are generally diagnosed by the direct detection of ticks feeding on hosts. Specimens may be carefully removed using tweezers or special tick removal tools for microscopic examination. Samples may also be frozen or fixed in alcohol for subsequent molecular analyses (proteins or DNA). Engorged female ticks may be collected for acaricide resistance testing in egg hatch or larval development assays, and should be stored and transported in small bottles with moist wadding and ventilation holes small enough to prevent any hatched larvae from escaping. Ticks may be collected from pastures and surrounding environs using blanket drags or dry ice traps. Specimens may be identified to genus by their unique morphological characteristics, and there are dichotomous taxonomic keys which include most common species (although some identifications may be difficult due to pleomorphic variation between species, strains, stages and even regions). More recently, molecular biological techniques have been used to characterize species and infer phylogenetic relationships following the polymerase chain reaction (PCR) amplification of nuclear (18S and 28S ribosomal RNA, internal transcribed spacers 1 and 2) and mitochondrial (12S and 16S ribosomal RNA, cytochrome c oxidase subunit I, nicotinamide adenine dinucleotide dehydrogenase subunit 5) gene sequences.

Treatment and control: Incidental infestations on humans are usually treated by removing the offending ticks and providing symptomatic relief (analgesics, anti-pruritics, anti-histamines, anti-inflammatories, disinfectants and possibly antibiotics to prevent secondary bacterial infections in open wounds). Ticks should be gently removed using curved tweezers or special tick removal devices (tick twists, loops/lassos, keys or V-shaped tools) taking care not to squeeze or break them (to avoid forcing gut content and saliva into the wound or leaving behind fragments which exacerbate inflammation). If the tick mouthparts break off and remain in the wound, clinicians should endeavour to remove them surgically. Some success in encouraging ticks to drop off has been reported by applying freezing agents or pyrethroid acaricides directly to their backs, but damaged or dying ticks may also release compounds back into the host. People at risk may deter tick attack by using personal repellents (such as diethyltoluamide (DEET), permethrin, picaridin, eucalyptus oil) on their skin or clothing, wearing heavier clothing (boots, socks, light-coloured trousers and long-sleeved shirts with gathered or tucked cuffs), and avoiding bushy habitats. Livestock and companion animals are best treated (both therapeutically and prophylactically) with topical or systemic acaricides, which are available in a range of dips, baths, sprays, showers, emulsions, dusts, pour-ons, spot-ons, collars, impregnated eartags/tailtags, injections, drenches and tablets, some even being applied using self-treatment devices (rubbing posts/rollers, medicated supplementary feeds). Animals have been treated effectively using a range of acaricidal chemicals; including arsenical preparations, organochlorines (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (dioxathion, fenchlorphos), organophosphonates (chlorfenvinphos, dichlorvos, tetrachlorvinphos, trichlorfon), monothiophosphates (chlorpyrifos, coumaphos, cythioate, diazinon, fenthion, propetamphos), dithiophosphates (malathion, phosmet), carbamates (carbaryl), pyrethroids (permethrin, flumethrin, deltamethrin, decamethrin, cypermethrin, cyprothrin), formamidines (amitraz), macrocyclic lactones (ivermectin, selamectin), phenylpyrazoles (fipronil), chloronicotinyls (imidacloprid), isoxazolines (afoxolaner, fluralaner) as well as some natural products (rotenone) and some insect growth regulators or chitin synthesis inhibitors (methoprene, pyriproxyfen). Careful attention should be paid to drug contra-indications as some formulations are toxic or cause detrimental side-effects in certain animal species. While good results have been obtained with single treatments for ticks with one-host life-cycles, treating ticks with 2-host or 3-host cycles is more difficult as they require periodic re-treatment to negate re-infestation, although slow-release formulations or those with long-lasting residual activity may help reduce treatment frequency. The incorrect or over-usage of acaricides has led to the rapid development and spread of drug resistance, particularly against arsenical compounds, organochlorines, organophosphates, pyrethroids, formamidines and some macrocyclic lactones. Strategies to combat resistance include periodically cycling between acaricide groups, using co-formulations (cocktails), avoiding under-dosing, and regularly testing for resistance (using *in situ* or *in vitro* egg hatch, larval development or adult immersion tests). While resistance testing may be tedious and time-consuming, studies have begun to develop more rapid immunoassays or molecular screening tests. Producers are encouraged to adopt integrated tick management programmes involving health surveillance (screening, quarantine), strategic treatment (often to prevent a “spring rise”), animal management (avoid overstocking, culling, restricting movements), environmental control (cleaning holding facilities, applying residual acaricides), grazing management (pasture rotation, pasture spelling/resting, stabling, clearing vegetation), and controlling wildlife reservoirs (interrupt/divert migration routes, hunting, fencing, trapping, medicated supplementary feeds). A range of computerized prediction models have also been developed to assist producers, based on multiple bionomic factors, including climate (temperature, moisture, rainfall, photoperiod), location (latitude, longitude, elevation), vegetation type and structure, land use and animal husbandry. Epidemiological and experimental studies have shown that certain breeds of cattle have an innate genetic resistance to tick infestations. Indigenous *Bos indicus* breeds (Zebu, Brahman, Nelore, Mdulla, Iruga Red) are more resistant than introduced *Bos taurus* beef and dairy breeds (Hereford, Shorthorn, Simmental, Angus and Holstein-Friesian), and indigenous African *Bos taurus* breeds (N’dama, Sanga) are also resistant to ticks. Some tick-resistant breeds also seem to acquire better protective immunity to tick-borne diseases if exposed to them at an early age. Many successful programmes have been developed to produce tick-resistant cattle by cross-breeding, selecting resistant individuals and culling heavily-infested individuals. However, repeated culling of susceptible individuals or those with waning resistance appear to be necessary to maintain herd resistance over time. The nutrition status of the hosts may also influence the degree of resistance exhibited. Cattle given lucerne as a supplementary feed were more resistant to ticks that animals grazing only on native grasses, and their better nutrition allowed them to counter the effects of any developing anaemia. Variable successes have been reported in the control and prevention of tick infestations using vaccines derived from various tick extracts, notably concealed gut antigens (BM86 and BM95 from *R. microplus*, BA86 from *R. annulatus*) but also

including some salivary gland proteins (64TRP from *R. appendiculatus*) and other metabolic extracts (serpins from *R. appendiculatus*). Studies on biological control have explored the impact of various parasites, pests and predators on tick populations, including grooming birds (oxpeckers), pathogenic nematodes (*Steinernema* and *Heterorhabditis*), entomopathogenic fungi (*Beauveria* and *Metarhizum*), parasitic wasps and pasture manipulation using tropical legumes.

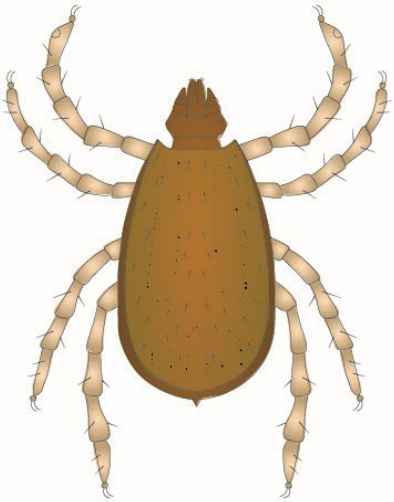

Rhipicephalus
Hosts
(mammals,
birds,
reptiles)
engorged female
(dorsal) (~ 14 mm)
skin
(blood loss,
irritation,
lesions,
toxicosis)
(vectors for
infectious
microbial
diseases)
adult female
(dorsal) (~ 5 mm)
eggs laid in
moist shaded soil
eggs
(~ 0.4 mm)
hatch
larva
(ventral)
(~ 0.6 mm)
nymph
(dorsal)
(~ 1.2 mm)
motile stages
(i.e. larvae (L),
nymphs (N) &
adults (A)) are
transient ecto-
parasites on
vertebrates
(feed on blood)
questing
(host-seeking)
1
2
3
most Rhipicephalus spp. have 3-host
cycles, some have 2-host cycles, while
R. (Boophilus) spp., have 1-host cycles
1-host cycle (LNA on same host)
2-host cycle (L-NA on successive hosts)
3-host cycle (L-N-A on separate hosts)

Rhipicephalus



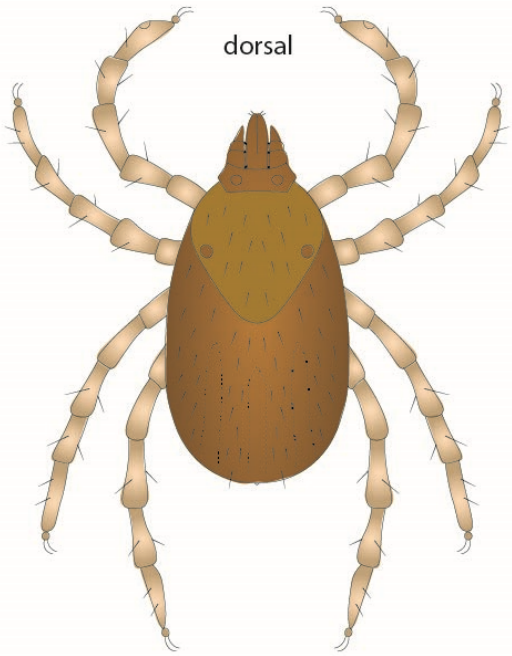
Rhipicephalus (*Boophilus*)

dorsal



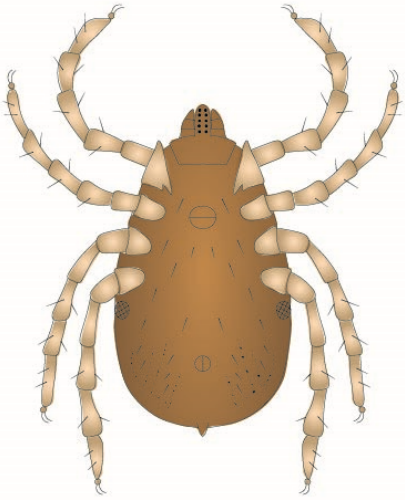
male (~ 4 mm)

dorsal

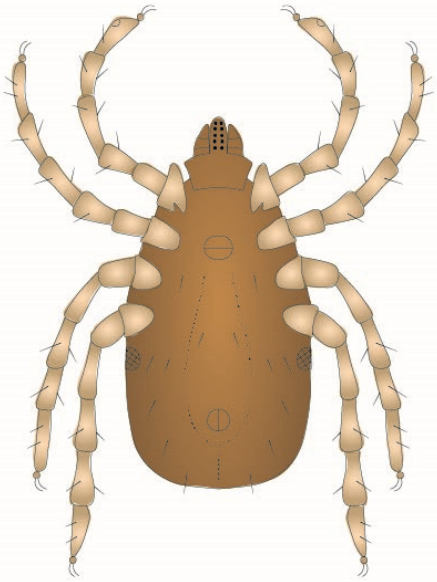


female (~ 5 mm)

adult ticks



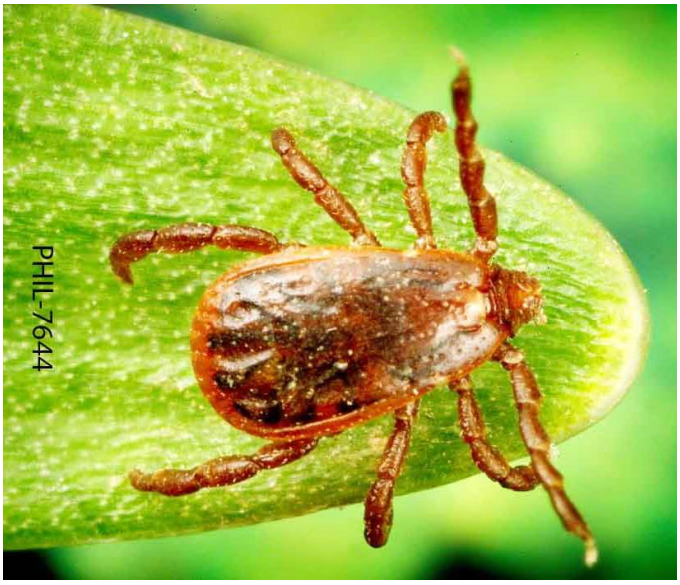
ventral



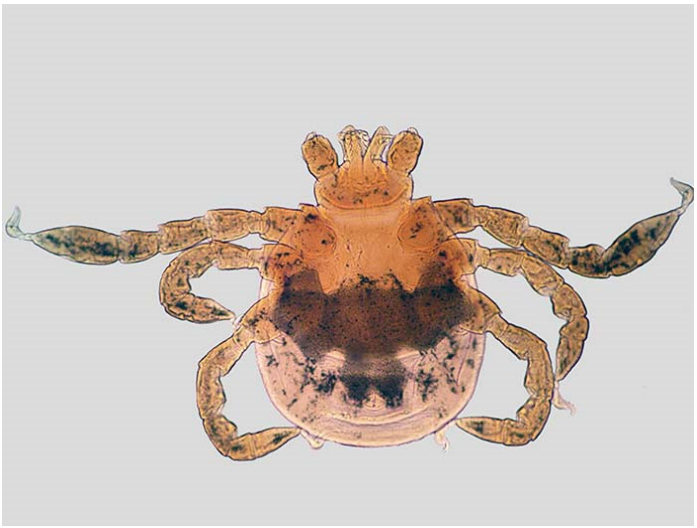
ventral



Rhipicephalus adults



Rhipicephalus adult



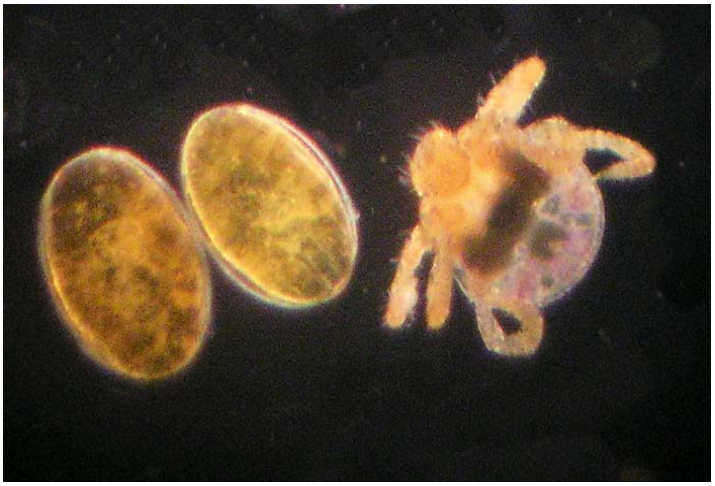
Rhipicephalus larva



Rhipicephalus adult



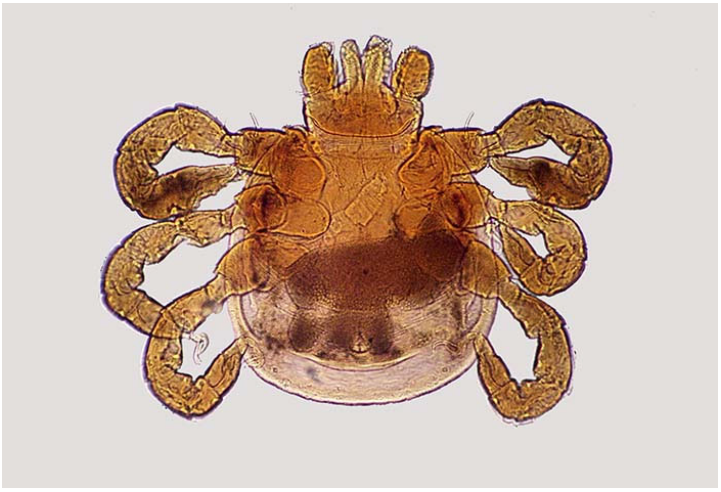
Rhipicephalus (*Boophilus*) adults



Rhipicephalus (*Boophilus*) eggs and larva



Rhipicephalus (*Boophilus*) larvae



Rhipicephalus (*Boophilus*) larva

Haemaphysalis
(arachnid: tick)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ticks have respiratory stigmata posterior to their legs. They are obligate blood-feeding ectoparasites on vertebrate hosts and their hypostomes are toothed and exposed. Two families are recognized: Argasidae and Ixodidae, known as soft and hard ticks, respectively. Ixodids have hard bodies with a dorsal scutum (shield-shaped plate) and the capitulum is not covered by the body. Larvae, nymphs and adults attach and feed on host blood, their life-cycles involving one, two or three hosts depending on whether moulting occurs on or off the host. Some 650 species of hard ticks infest mammals, birds and reptiles. Infestations by *Haemaphysalis* spp. occur as three-host ticks on a range of domestic and wild animals, causing local skin reactions and transmitting various infectious diseases.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on capitulum)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Ixodida (Metastigmata) (ticks, macroscopic, stigmata posterior to legs, hypostome toothed, ectoparasites)
Family: Ixodidae (hard ticks, with dorsal scutum, capitulum projects anteriorly, attach and feed on 1, 2 or 3 hosts)
Genus: *Haemaphysalis* (parasitic on skin of mammals)
Species: various species cause lesions on mammals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on capitulum) [34 superfamilies]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs (behind coxae III or IV); and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Ticks are further characterized by macroscopic bodies with an exposed ventral hypostome (toothed with backwardly-directed barbs), chelicerae with only 2 joints, long legs with free articulated coxae (not fused to the body wall) and a complex sensory pit (Haller's organ) on tarsus I. They are obligate blood-sucking parasites which feed on terrestrial vertebrates (mammals, birds, reptiles and some amphibians) as larvae, nymphs and adults with 1-, 2- or 3-host life-cycles. Almost 1,000 species have been classified within some 20 genera from numerous wild and domesticated animals around the world. Two main families are recognized: the Argasidae containing ~200 species of 'soft' ticks with flexible leathery cuticles, ventral capitula, short feeding times (< 1 hour) and long life-spans (up to 20 years); and the Ixodidae containing ~800 species of 'hard' ticks with rigid dorsal scutal plates, anterior capitula, long feeding times (hours to days) and shorter life-span (2-6 years). Basic characteristics of representative genera considered in this resource are tabulated below.

Genus	**Capitulum**				**Idiosoma**				**Usual no. of hosts**
	location	**basis capitulum**	**mouth-parts**	**palps**	**integument**	**festoons**	**eyes**	**male ventral plates**	

Argasidae (soft ticks with leathery cuticle, stigmata between coxae III)									
Argas	ventral	triangular	short	leg-like	stippled with lateral suture	absent	absent	absent	>3
Ornithodorus	ventral	rectangular	short	leg-like	mamillated	absent	usually absent	absent	>3
Otobius	ventral	rectangular	short	leg-like	spinose (nymphs), granulated (adult)	absent	absent	absent	1
Ixodidae (hard ticks with sclerotized dorsal plate (scutum), stigmata behind coxae IV)									
Prostriata (anal groove anterior)									
Ixodes	anterior	triangular	long	long	inornate	absent	absent	present	3
Metastriata (anal groove posterior)									
Amblyomma	anterior	rectangular	long	long	ornate	present	present	indistinct	3
(*Aponomma*)	anterior	rectangular	long	long	often ornate	present	absent	absent	3
Rhipicephalus	anterior	hexagonal	short	medium	some ornate	present	present	present	3
(*Boophilus*)	anterior	hexagonal	short	short	inornate	absent	present	present	1
Dermacentor	anterior	rectangular	short	medium	often ornate	present	present	absent	3
Haemaphysalis	anterior	rectangular	short	short	inornate	present	absent	absent	3
Hyalomma	anterior	rectangular	long	long	inornate	present	present	present	2
Bothriocroton	anterior	pentagonal	long	long	ornate	present	absent	absent	3

The family Ixodidae contains 6 subfamilies (Amblyomminae, Bothriocrotoninae, Haemaphysalinae, Hyalomminae, Ixodinae and Rhipicephalinae) which vary in their morphology, biology, host ranges and specificity. [Note that some taxonomic authorities have merged the subfamilies Rhipicephalinae and Hyalomminae, while others have subsequently assigned the subfamilies Amblyomminae and Rhipicephalinae into the new family Amblyommidae, predominantly on the basis of molecular phylogenetic studies]. Hard ticks had previously been divided into 2 groups: the Prostriata (with the anal groove anterior to the anus) and the Metastriata (anal groove absent or posterior to anus). The Prostriata essentially comprises the subfamily Ixodinae with over 230 species assigned to the single extant genus *Ixodes* [plus one fossil genus (*Cornupalpatum*)], while the Metastriata contains members of the remaining subfamilies with over 600 species classified into 18 genera. The subfamily Haemaphysalinae comprises metastriate inornate ticks with festoon but lacking eyes and ventral shields. Nine genera have been recognized (*Amblyocento*, *Anocento*, *Conocento*, *Dermacentor*, *Dermacentorites*, *Dermiomma*, *Haemalasto*, *Haemaphysalis* and *Puncticento*). [Note that all members of the former genus *Aponomma* have now been transferred to the genera *Amblyomma* or *Bothriocroton*]. The genus *Haemaphysalis* contains around 116 species of small ticks with short laterally-projecting palps, most species being classified with 9 subgenera: namely, *H.* (*Aboimisalis*), *H. (Aborphysalis*), *H. (Alloceraea*), *H. (Allophysalis*), *H. (Haemaphysalis*), *H. (Herpetobia*), *H. (Kaiseriana*), *H. (Ornithophysalis*), and H. (*Rhipistoma*). The majority are 3-host ticks of mammals, with several species considered to be significant veterinary pests causing skin lesions, anaemia, reduced production and sometimes toxicoses, paralysis and mortality in livestock and companion animals.

***Haemaphysalis* species**	**Hosts**	**Clinical signs**	**Distribution**
H. (*Aborphysalis*) *aborensis*	Artiodactyla: bovid (buffalo, yak, zhum), cervid (sambar deer, muntjac), moschid (musk deer), suid (Indian boar); Scandentia: tupaiid (common treeshrew); Rodentia: hystricid (crestless Himalayan porcupine); Carnivora: felid (tiger), mustelid (greater hog-badger); Primates: hominid (human); Galliformes: phasianid (chicken, red junglefowl); Passeriformes: parid (green-backed tit), turdid (pale thrush)		India
H. (*Kaiseriana*) *aciculifer*	Artiodactyla: bovid (cattle, buffalo, sheep, goat, oribi, red hartebeest, Roosevelt's hartebeest, common duiker, red forest duiker, tiang, Grant's gazelle, Thomson's gazelle, harnessed bushbuck, Cape bushbuck, southern reedbuck, Bohor reedbuck, waterbuck, kob, Ugandan kob, sitatunga, suni, kongoni), suid (warthog); Eulipotyphla: erinaceid (African hedgehog); Lagomorpha: leporid (Cape hare); Hyracoidea: procaviid (rock hyrax); Rodentia: murid (typical striped grass mouse, Tullberg's soft-furred mouse, soft-furred rat, rusty-bellied brush-furred rat, East African soft-furred mouse), sciurid (ground squirrel); Carnivora: canid (dog, black-backed jackal), felid (wildcat, serval, lion, leopard), herpestid (gray mongoose, banded mongoose, Egyptian mongoose), hyaenid (striped hyena), viverrid (African civet, large spotted genet); Galliformes: phasianid (fowl);		Africa

	Passeriformes: corvid (pied crow)		
H. (*Kaiseriana*) *aculeata*	Artiodactyla: bovid (cattle, buffalo), cervid (spotted deer), tragulid (Sri Lankan spotted chevrotain); Rodentia: murid (rat), hystricid (crested porcupine); Carnivora: felid (leopard), herpestid (ruddy mongoose); Primates: cercopithecid (bonnet macaque, northern plains gray langur), hominid (human); Cuculiformes: cuculid (greater coucal); Galliformes: phasianid (fowl); Passeriformes: muscicapid (Indian robin), pycnonotid (bulbul), sturnid (myna), timaliid (babbler)	(possible vector for Kyasanur Forest disease virus)	India, Sri Lanka
H. adleri	Artiodactyla: bovid (cattle), suid (pig); Carnivora: canid (golden jackal, red fox), felid (jungle cat, African wildcat), mustelid (marbled polecat)		Palearctic
H. africana	Cuculiformes: cuculid (Burchell's coucal)		Africa
H. ambigua	Artiodactyla: bovid (Japanese serow)		Eurasia
H. angorense	Perissodactyla: equid (donkey)		Europe
H. (*Kaiseriana*) *anomala*	Artiodactyla: bovid (cattle, buffalo, water buffalo, goat), cervid (sambar deer, Indian muntjac); Lagomorpha: leporid (rabbit); Rodentia: murid (black rat, soft-furred rat); Carnivora: canid (wolf), felid (leopard); Primates: hominid (human); Cuculiformes: cuculid (greater coucal); Galliformes: phasianid (chicken); Passeriformes: turdid (thrush) (3-host cycle)	(possible vector for Kyasanur Forest disease virus)	Indo-Asia
H. (*Kaiseriana*) *anomaloceraea*	host unknown, collected from vegetation		China
H. (*Rhipistoma*) *anoplus*	Rodentia: nesomyid (island mouse, red forest rat)		Madagascar
H. (*Alloceraea*) *aponommoides*	Artiodactyla: bovid (cattle, zebu, yak, zhum, buffalo, sheep, goat, serow), cervid (Indian muntjac), suid (wild boar); Perissodactyla: equid (horse); Eulipotyphla: soricid (broad-toothed shrew, Sikkim large-clawed shrew); Rodentia: cricetid (Royle's high mountain vole), murid (house mouse, chestnut rat, little Himalayan rat), sciurid (lesser giant flying squirrel); Carnivora: canid (dog), felid (cat), ursid (Asian black bear); Primates: hominid (human); Galliformes: phasianid (monal pheasant); Sauria (unspecified lizard)		India, Nepal
H. asiatica	Artiodactyla: suid (pig); Scandentia: tupaiid (common treeshrew); Rodentia: murid (rat), sciurid (Bersdmore's ground squirrel); Carnivora: canid (dog), felid (leopard cat, leopard), viverrid (Asian palm civet, Malayan civet, large Indian civet); Sauria: lacertid (multi-ocellated racerunner)		Asia
H. (*Aborphysalis*) *atheruri*	Rodentia: hystricid (Asiatic brush-tailed porcupine); Scandentia: tupaiid (treeshrew); Carnivora: canid (dog)		Malaysia
H. (*Kaiseriana*) *bancrofti* (syn. *H. meraukensis, novaeguineae*) (wallaby tick)	Diprotodontia: macropodid (allied rock-wallaby, short-eared rock-wallaby, Godman's rock-wallaby, brush-tailed rock-wallaby, bridled nailtail wallaby, agile wallaby, common wallaroo, black wallaroo, black-striped wallaby, tammar wallaby, western grey kangaroo, eastern grey kangaroo, whiptail wallaby, red-necked wallaby, swamp wallaby, red-necked pademelon, unspecified dorcopsis), potoroid (rufous bettong, long-nosed potoroo, woylie), petaurid (sugar glider), phalangerid (common brushtail possum), phascolarctid (koala), vombatid (common wombat), Dasyuromorphia: dasyurid (northern quoll, spotted-tailed quoll); Peramelemorphia: peramelid (northern brown bandicoot, southern brown bandicoot, long-nosed bandicoot, common spiny bandicoot, long-nosed spiny bandicoot), thylacomyid (greater bilby); Rodentia: murid (black rat, water rat); Artiodactyla: bovid (cattle, zebu, banteng, buffalo, sheep), cervid (red deer, sambar deer), suid (pig, boar); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Carnivora: canid (dog, dingo), felid (cat); Chiroptera: : pteropodid (broad-striped tube-nosed fruit bat), vespertilionid (eastern forest bat); Primates: hominid (human); Cuculiformes: cuculid (pheasant coucal); Gruiformes: rallid (rail); Passeriformes: artamid (Australian magpie)	trauma, irritation (vector for theileriosis)	Australia, New Guinea

	(3-host cycle)		
H. bandicota	Artiodactyla: bovid (cattle); Rodentia: murid (bandicoot rat); Scandentia: tupaiid (treeshrew); Carnivora: herpestid (mongoose)		Asia
H. (*Rhipistoma*) *bartelsi*	Rodentia: sciurid (red giant flying squirrel, spotted giant flying squirrel)		Indonesia
H. benedito	Artiodactyla: bovid (goat, mountain goat)		Europe
H. bequaerti	Hyracoidea: procaviid (rock hyrax, yellow-spotted rock hyrax)		Africa
H. (*Haemaphysalis*) *birmaniae*	Artiodactyla: bovid (cattle, zebu, yak, zhum, buffalo, water buffalo, goral, goat, antelope, serow, blackbuck), cervid (Indian muntjac, Reeve's muntjac, Indian sambar deer, chital deer), suid (bushpig); Perissodactyla: equid (horse); Lagomorpha: leporid (Indian hare); Pholidota: manid (pangolin); Rodentia: hystricid (Asiatic brush-tailed porcupine, Himalayan porcupine), murid (mouse); Carnivora: canid (dog), ursid (Asian black bear), viverrid (masked palm civet): Primates: hominid (human)		Asia
H. (*Kaiseriana*) *bispinosa* (bush tick)	Artiodactyla: bovid (cattle, zebu, buffalo, water buffalo, sheep, goat, Nilgiri tahr, red forest duiker), cervid (barking deer, water deer, sika deer, chital, muntjac, spotted deer, Sri Lankan axis deer, sambar deer, red deer, elk), suid (pig, Indian boar), tragulid (Sri Lankan spotted chevrotain); Perissodactyla: equid (horse, donkey, mule); Eulipotyphla: erinaceid (Indian hedgehog), soricid (Asian house shrew), talpid (mole); Peramelemorphia: peramelid (northern brown bandicoot); Diprotodontia: macropodid (common wallaroo, black-striped wallaby); Lagomorpha: leporid (European rabbit, mountain hare, black-naped hare, European hare, Indian hare); Rodentia: caviid (guinea pig), hystricid (crested porcupine), murid (house mouse, black rat, brown rat, soft-furred rat, Blanford's rat), sciurid (jungle palm squirrel); Carnivora: canid (dog, raccoon dog, Indian wolf, golden jackal, dhole), felid (cat, jungle cat, Asiatic wildcat, caracal, tiger, lion, leopard), herpestid (mongoose), hyaenid (striped hyena), ursid (sloth bear), mustelid (Japanese badger, stoat, European polecat), viverrid (common genet, masked palm civet, small Indian civet); Primates: cercopithecid (bonnet macaque, toque macaque, northern plains gray langur, black monkey), hominid (human); Accipitriformes: accipitrid (hawk); Anseriformes: anatid (mallard, Indian spot-billed duck); Charadriiformes: charadriid (plover); Coraciiformes: coraciid (Indian roller); Cuculiformes: cuculid (cuckoo); Galliformes: phasianid (chicken, red junglefowl, Sri Lankan junglefowl, turkey, ring-necked pheasant); Passeriformes: alaudid (Eurasian skylark), corvid (crow), leiothrichid (yellow-billed babbler), passerid (house sparrow), pittid (Indian pitta), pomatostomid (white-browed babbler), sturnid (starling), turdid (song thrush), vangid (common woodshrike); Psittaciformes: psittacid (parrot); Strigiformes: strigid (owl) (3-host cycle)	trauma, irritation (vector for babesiosis, theileriosis, and possibly Q fever, Kyasanur forest disease virus)	Australasia
H. (*Rhipistoma*) *bochkovi*	Carnivora: herpestid (marsh mongoose), mustelid (spotted-necked otter)		Africa
H. (*Kaiseriana*) *borneata*	Artiodactyla: cervid (sambar deer)		Malaysia
H. (*Ornithophysalis*) *bremneri*	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Diprotodontia: phalangerid (common brush-tailed possum); Aegotheliformes: aegothelid (Australian owlet-nightjar)		Australia
H. (*Rhipistoma*) *burkinae*	Lagomorpha: leporid (Cape hare); Carnivora: viverrid (rusty-spotted genet, Hausa genet)		Africa
H. calva	Artiodactyla: bovid (buffalo), cervid (muntjac), suid (boar); Carnivora: ursid (bear), viverrid (civet)		Asia
H. (*Rhipistoma*) *camicasi*	Eulipotyphla: erinaceid (four-toed hedgehog); Lagomorpha: leporid (Cape hare); Rodentia: murid (Bellier's striped grass mouse, multimammate mouse, Natal multimammate mouse, gerbil), nesomyid (Gambian pouched rat), sciurid (Gambian sun squirrel, striped ground squirrel); Carnivora: canid (African wild dog, wolf, golden jackal, pale fox), felid (wildcat, leopard), herpestid		Africa

	(common slender mongoose, banded mongoose, white-tailed mongoose, Egyptian mongoose, Gambian mongoose), mustelid (honey badger), viverrid (African civet, common genet, Hausa genet); Primates: galagid (Senegal bushbaby)		
H. (*Haemaphysalis*) *campanulata*	Artiodactyla: bovid (cattle), cervid (sambar deer); Perissodactyla: equid (horse); Lagomorpha: leporid (European rabbit); Rodentia: murid (black rat); Carnivora: canid (dog, wolf); Primates: hominid (human); Strigiformes: strigid (little owl)		Eurasia
H. (*Rhipistoma*) *canestrinii*	Lagomorpha: leporid (Burmese hare); Rodentia: murid (rat, mouse), sciurid (five-striped palm squirrel); Scandentia: tupaiid (treeshrew); Lagomorpha: leporid (hare); Carnivora: canid (Asiatic jackal, Bengal fox), felid (fishing cat, leopard cat, jungle cat, tiger, leopard), herpestid (small Indian mongoose), mustelid (hog-badger, ferret-badger), viverrid (large Indian civet, palm civet, small Taiwan civet); Primates: hominid (human); Cuculiformes: cuculid (greater coucal); Galliformes: phasianid (chicken, red junglefowl); Testudines: geoemydid (Indian black turtle), testudinid (elongated tortoise)		Eurasia
H. (*Aborphysalis*) *capricornis*	Artiodactyla: bovid (Sumatran serow)		Asia
H. caucasica	Artiodactyla: bovid (mouflon); Lagomorpha: leporid (desert hare, tolai hare, European hare); Eulipotyphla: erinaceid (European hedgehog); Rodentia: cricetid (grey dwarf hamster), murid (house mouse, wood mouse, Turkestan rat); Carnivora: canid (red fox, golden jackal), mustelid (beech marten, European badger, least weasel, ferret), ursid (bear); Primates: hominid (human); Bucerotiformes: upupid (Eurasian hoopoe); Galliformes: phasianid (common quail, grey partridge); Passeriformes: corvid (European jay), fringillid (common chaffinch), muscicapid (whinchat), turdid (blue rock thrush); Sauria: lacertid (regel lacertid, sand lizard, felseneidechse), scincid (Berber skink)		Central Asia
H. (*Kaiseriana*) *celebensis*	Artiodactyla: bovid (cattle, water buffalo, anoa), cervid (Javan rusa), suid (pig, Celebes warty pig); Perissodactyla: equid (horse); Rodentia: murid (Musschenbroek's Sulawesi maxomys, Pacific rat, Hoffmann's Sulawesi rat); Primates: hominid (human)		Indonesia
H. centropi	Accipitriformes: accipitrid (pied harrier); Cuculiformes: cuculid (lesser coucal, greater coucal); Galliformes: phasianid (red junglefowl); Passeriformes: pycnonotid (red-whiskered bulbul)		Asia
H. (*Aboimisalis*) *chordeilis*	Artiodactyla: bovid (cattle, sheep); Perissodactyla: equid (horse); Lagomorpha: leporid (cottontail, hare); Rodentia: geomyid (smooth-toothed pocket gopher), sciurid (American red squirrel, yellow-bellied marmot); Carnivora: felid (cat); Primates: hominid (human); Accipitriformes: accipitrid (marsh hawk); Anseriformes: anatid (wood duck); Caprimulgiformes: caprimulgid (common nighthawk); Charadriiformes: charadriid (killdeer, Wilson's plover); Galliformes: odontophorid (northern bobwhite), phasianid **(**turkey, quail, chicken, greater prairie chicken, pheasant, ruffed grouse, greater sage-grouse); Passeriformes: corvid (jackdaw), emberizid (bunting), icterid (southern meadowlark), mimid (unspecified), passerellid (seaside sparrow, Florida sparrow, savannah sparrow, eastern towhee, white-eyed towhee), sturnid (Eurasian meadowlark), troglodytid (Florida wren), turdid (red-winged blackbird)		North America
H. (*Aboimisalis*) *cinnabarina* (syn. *H. sanguinolenta*)	Artiodactyla: bovid (cattle, zebu, mouflon, sheep, mouflon, goat), cervid (European fallow deer), suid (pig); Perissodactyla: equid (horse, donkey); Eulipotyphla: erinaceid (European hedgehog); Lagomorpha: leporid (European rabbit, jackrabbit, mountain hare, European hare); Rodentia: dasyproctid (red acouchi), sciurid (red squirrel, little ground squirrel); Carnivora: canid (dog, wolf, fox), ursid (bear); Chiroptera: rhinolophid (greater horseshoe bat); Primates: hominid (human); Accipitriformes: accipitrid (golden eagle, marsh hawk, Griffon vulture); Caprimulgiformes: caprimulgid (common nighthawk); Charadriiformes: scolopacid	trauma, irritation (vector for anaplasmosis, babesiosis, Q fever)	Africa, Eurasia, Americas

	(ruff); Galliformes: odontophorid (northern bobwhite), phasianid (chicken, turkey, ring-necked pheasant, common partridge, rock partridge, red-legged partridge, blue grouse, spruce grouse, willow grouse, ruffed grouse, sharp-tailed grouse, greater sage-grouse, greater prairie chicken); Gruiformes: rallid (corn crake); Passeriformes: alaudid (Eurasian skylark), corvid (jackdaw), motacillid (white wagtail), muscicapid (common redstart), sturnid (Eurasian meadowlark), turdid (common blackbird, red-winged blackbird, song thrush, mistle thrush); Strigiformes: strigid (long-eared owl); Sauria: lacertid (common wall lizard, ocellated lizard, European green lizard); Serpentes: viperid (horned viper) (3-host cycle)		
H. colasbelcouri (syn. *H. vietnamensis*)	Artiodactyla: bovid (cattle, buffalo), cervid (unspecified deer); Primates: hominid (human)		Asia
H. (*Rhipistoma*) *colesbergensis*	Eulipotyphla: erinaceid (hedgehog); Carnivora: canid (dog), felid (cat, wildcat, caracal)		Africa
H. (*Haemaphysalis*) *concinna* (bush tick)	Artiodactyla: bovid (cattle, water buffalo, sheep, goat, mouflon, chamois), cervid (red deer, roe deer, Siberian roe deer, European fallow deer, white-tailed deer, sika deer, red deer, elk, reindeer), suid (pig); Perissodactyla: equid (horse, donkey); Eulipotyphla: erinaceid (European hedgehog, northern white-breasted hedgehog), soricid (common shrew, Eurasian pygmy shrew), talpid (European mole); Lagomorpha: leporid (mountain hare, tolai hare, European hare, Manchurian hare, European rabbit), ochotonid (alpine pika); Rodentia: cricetid (common vole, bank vole, tundra vole, reed vole, meadow vole, narrow-headed vole, northern red-backed vole, grey red-backed vole, Maximowicz's vole, European water vole, northern mole vole, giant red-headed hamster, European hamster), murid (Eurasian harvest mouse, striped field mouse, large Japanese field mouse, yellow-necked mouse, wood mouse, brown rat, black rat, great gerbil, Tamarisk jird), sciurid (red squirrel, long-tailed ground squirrel, European ground squirrel, Siberian chipmunk, Korean chipmunk, groundhog), sminthid (long-tailed birch mouse), spalacid (transbaikal zokor); Carnivora: canid (dog, raccoon dog, wolf, red fox, Arctic fox); felid (cat, caracal, leopard cat, leopard), mustelid (European badger, European pine marten, stoat, ferret, Siberian weasel); Primates: hominid (human); Accipitriformes: accipitrid (lesser spotted eagle, northern black kite, goshawk, Eurasian sparrowhawk, western marsh harrier, Montagu's harrier, common buzzard, European honey buzzard); Anseriformes: anatid (mallard); Bucerotifiormes: upudid (Eurasian hoopoe); Caprimulgiformes: caprimulgid (European nightjar); Charadriiformes: charadriid (northern lapwing), scolopacid (common snipe, Swinhoe's snipe, Eurasian woodcock); Cuculiformes: cuculid (common cuckoo); Galliformes: odontophorid (California quail), phasianid (ring-necked pheasant, common quail, rock partridge, chukar partridge, hazel grouse); Gruiformes: rallid (corn crake); Passeriformes: acrocephalid (great reed warbler, thick-billed warbler, Oriental reed warbler, moustached warbler), alaudid (Eurasian skylark), cettid (Cetti's warbler), corvid (carrion crow, hooded crow, Eurasian magpie, Eurasian jay), emberizid (yellowhammer, yellow-breasted bunting, red-headed bunting, corn bunting, meadow bunting, yellow-throated bunting, chestnut-eared bunting, common reed bunting, black-faced bunting, Tristram's bunting), fringillid (European goldfinch, hawfinch, common chaffinch), laniid (red-backed shrike, bull-headed shrike, tiger shrike), locustellid (river warbler, lanceolated warbler, Pallas's grasshopper warbler, Gray's grasshopper warbler), motacillid (white wagtail, western yellow wagtail, forest wagtail, tree pipit, olive-backed pipit, Richardson's pipit, Pechora pipit), muscicapid (European robin, common nightingale, thrush nightingale, Siberian rubythroat, Siberian blue	trauma, irritation (vector for viral encephalitis, rickettsioses, borreliosis, anaplasmosis, Q fever, tularemia and possibly Crimean-Congo haemorrhagic fever, Omsk haemorrhagic fever and Tamdy virus)	Eurasia

	robin, collared flycatcher, spotted flycatcher, common redstart, African stonechat), oriolid (Eurasian golden oriole), parid (great tit, marsh tit, cinereous tit, Eurasian blue tit), passerid (house sparrow, Spanish sparrow, Eurasian tree sparrow), phylloscopid (wood warbler, willow warbler), prunellid (dunnock), sittid (European nuthatch), sittid (Eurasian nuthatch), sturnid (common starling, white-cheeked starling, Daurian starling), sylviid (garden warbler, barred warbler, Eurasian blackcap, common whitethroat), troglodytid (Eurasian wren), turdid (common blackbird, Eurasian blackbird, mistle thrush, grey-backed thrush, song thrush); Piciformes: picid (great spotted woodpecker, middle spotted woodpecker, Eurasian wryneck); Strigiformes: strigid (short-eared owl, tawny owl); Serpentes: colubrid (grass snake); Sauria: lacertid (sand lizard, European green lizard) (3-host cycle)		
H. cooleyi	Hyracoidea: procaviid (rock hyrax); Rodentia: pedetid (South African springhare)		Africa
H. (*Kaiseriana*) *cornigera* (syn. *H. ias, proxima, taiwana*)	Artiodactyla: bovid (cattle, zebu, buffalo, water buffalo, guar), cervid (Indian muntjac, sambar deer, Indian sambar deer, Javan rusa), suid (pig, boar); Rodentia: dasyproctid (agouti), hystricid (porcupine), murid (striped field mouse, long-tailed giant rat), sciurid (Pallas's squirrel); Diprotodontia: phalangerid (cuscus); Scandentia: tupaiid (northern treeshrew); Lagomorpha: leporid (common tapeti, European rabbit); Eulipotyphla: soricid (shrew); Carnivora: canid (dog, wolf), felid (tiger), mustelid (weasel),viverrid (civet); Primates: hominid (human); Galliformes: phasianid (red junglefowl); Passeriformes: corvid (crow), timaliid (scimitar babbler), turdid (blackbird)		Asia
H. (*Aboimisalis*) *cornupunctata*	Artiodactyla: bovid (cattle, buffalo, yak, sheep, goat); Perissodactyla: equid (horse); Rodentia: murid (unspecified mouse); Lagomorpha: leporid (hare), ochotonid (pika)		India
H. (*Alloceraea*) *cretacea*	fossil (amber)		Myanmar
H. (*Kaiseriana*) *cuspidata*	Artiodactyla: bovid (cattle, buffalo, goat), cervid (deer), tragulid (spotted chevrotain); Eulipotyphla: soricid (Asian house shrew); Lagomorpha: leporid (Indian hare, black-naped hare); Rodentia: murid (mouse, black rat, Blanford's rat), hystricid (crested porcupine), sciurid (jungle palm squirrel); Carnivora: canid (dog, jackal), felid (leopard), herpestid (Indian brown mongoose, Indian grey mongoose), viverrid (lesser civet cat, Indian palm civet); Primates: cercopithecid (bonnet macaque, northern plains gray langur); Bucerotiformes: bucerotid (Malabar gray hornbill); Cuculiformes: cuculid (greater coucal); Galliformes: phasianid (gray junglefowl); Passeriformes: muscicapid (magpie robin), sylviid (warbler)	(possible vector for Kyasanur forest disease virus)	Sri Lanka
H. dangi	Artiodactyla (unspecified); Rodentia: hystricid (porcupine); Carnivora: mustelid (unspecified)		Asia
H. (*Allophysalis*) *danieli* (syn. *H. xinjiangensis*)	Artiodactyla: bovid (goat); Lagomorpha: ochotonid (Royle's pika); Rodentia: cricetid (grey dwarf hamster, Royle's mountain vole), murid (yellow-necked mouse), sciurid (long-tailed marmot)		Central Asia
H. (*Haemaphysalis*) *darjeeling*	Artiodactyla: bovid (goral, serow), cervid (Indian muntjac), suid (Indian boar); Carnivora: mustelid (hog-badger); Primates: hominid (human)		Asia
H. (*Kaiseriana*) *davisi*	Artiodactyla: bovid (cattle, Indian bison, guar, gyacha, sheep, goat), cervid (sambar deer, Indian muntjac); Perissodactyla: equid (horse, mule); Carnivora: felid (tiger), mustelid (hog-badger)		Asia
H. demidovae	Rodentia: cricetid (vole), sciurid (ground squirrel); Lagomorpha: ochotonid (pika)		Eurasia
H. dentipalpis	Carnivora: canid (golden jackal), felid (jungle cat, leopard, tiger), viverrid (Asian palm civet, Malayan civet, large Indian civet)		Malaysia
H. (*Ornithophysalis*) *doenitzi*	Chiroptera (unspecified bat); Rodentia: murid (mouse); Lagomorpha: leporid (Chinese hare); Afrosoricida: tenrecid		Australasia

	(lowland streaked tenrec, greater hedgehog tenrec, tailless tenrec); Primates: hominid (human); Accipitriformes: accipitrid (pied harrier); Bucerotiformes: upupid (hoopoe); Coraciiformes: coraciid (roller); Cuculiformes: cuculid (lesser coucal, greater coucal, pheasant coucal); Galliformes: phasianid (red junglefowl, green pheasant, ring-necked pheasant, quail, Chinese bamboo partridge); Gruiformes: rallid (water hen); Passeriformes: alaudid (lark), hirundinid (swallow), muscicapid (flycatcher), paradoxornithid (vinous-throated parrotbill), pittid (pitta), pycnonotid (bulbul), sylviid (whitethroat), timaliid (Taiwan scimitar babbler), sturnid (common mynah), turdid (dusky thrush, pale thrush, scaly thrush); Piciformes: megalaimid (Taiwan barbet); Strigiformes: strigid (owl); Testudines: geoemydid (turtle)		
H. elliptica	Macroscelidea: macroscelidid (elephant shrew); Rodentia: murid (unspecified); Carnivora: canid (dog), felid (cat, cheetah, lion, leopard); Passeriformes: cisticolid (rattling cisticola, Levaillant's cisticola), ploceid (long-tailed widowbird) (3-host cycle)	(vector for canine babesiosis)	Africa
H. elongata	Chiroptera (unspecified bat); Afrosoricida: tenrecid (lowland streaked tenrec, greater hedgehog tenrec, lesser hedgehog tenrec, tailless tenrec, Talazac's shrew tenrec); Eulipotyphla: erinaceid (hedgehog); Rodentia: murid (unspecified mouse); Carnivora: euplerid (Malagasy mongoose); Primates: hominid (human)		Madagascar
H. (*Rhipistoma*) *erinacei* (syn. *H. yalvaci*) (incl. subspp. *erinacei, taurica, turanica*)	Artiodactyla: bovid (unspecified); Lagomorpha: leporid (hare), ochotonid (pika); Eulipotyphla: erinaceid (North African hedgehog, European hedgehog, southern white-breasted hedgehog, northern white-breasted hedgehog, long-eared hedgehog, desert hedgehog); Rodentia: calomyscid (mouse-like hamster), cricetid (jird), dipodid (William's jerboa), glirid (garden dormouse), murid (black rat, Cairo spiny mouse, eastern broad-toothed field mouse, Shaw's jird, Tristram's jird, North African gerbil, great gerbil), sciurid (Daurian ground squirrel, Siberian chipmunk); Carnivora: canid (dog, red fox, Anatolian red fox), felid (cat), hyaenid (striped hyena), mustelid (European badger, beech marten, least weasel, marbled polecat, steppe polecat), ursid (bear); Chiroptera: vespertilionid (unspecified); Primates: hominid (human); Apodiformes: apodid (swift); Coraciiformes: meropodid (bee-eater); Falconiformes: falconid (lesser kestrel); Passeriformes: emberizid (bunting), motacillid (pipit), muscicapid (wheatear); Strigiformes: strigid (Eurasian eagle-owl); Testudines: testudinid (tortoise) (3-host cycle)	(possible vector for rickettsiosis)	Africa, Eurasia
H. (*Rhipistoma*) *eupleres*	Carnivora: euplerid (falanouc)		Madagascar
H. expositus	Artiodactyla: bovid (cattle); Lagomorpha: leporid (rabbit)		North America
H. filippovae	host unknown, collected from vegetation		Russia
H. flava	Artiodactyla: bovid (cattle, zebu, sheep, goat, Japanese serow), cervid (sambar deer, Formosan sambar deer, sika deer), suid (pig, Indian boar, Japanese boar, Formosan boar); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit, mountain hare, Indian hare, Japanese hare); Rodentia: cricetid (grey red-backed vole), murid (large Japanese field mouse), sciurid (red squirrel); Carnivora: canid (dog, raccoon dog, jackal, red fox), felid (cat), mustelid (Japanese badger, Siberian weasel), ursid (Asian black bear); Primates: hominid (human); Accipitriformes: accipitrid (besra); Columbiformes: columbid (Oriental turtle dove); Galliformes: phasianid (green pheasant, copper pheasant); Passeriformes: aegithalid (long-tailed tit), corvid (Eurasian jay), emberizid (meadow bunting, yellow-throated bunting, rustic bunting, black-faced bunting, yellow-browed bunting, little bunting), motacillid (grey wagtail, olive-backed pipit), parid (coal tit, great tit), turdid (pale thrush, brown-headed thrush, grey-backed thrush, scaly thrush, White's thrush, Izu thrush, Japanese thrush)	trauma, irritation (vector for hepatozoonosis)	Japan, India

	(3-host cycle)		
H. (*Aborphysalis*) *formosensis*	Artiodactyla: cervid (sambar deer, Indian sambar deer), moschid (musk deer), suid (Formosan boar); Lagomorpha: leporid (hare); Scandentia: tupaiid (common treeshrew); Rodentia: hystricid (Malayan porcupine), murid (unspecified); Carnivora: canid (dog), herpestid (mongoose), mustelid (badger), ursid (Asian black bear); Chiroptera: vespertilionid (unspecified); Charadriiformes: scolopacid (Amami woodcock); Galliformes: phasianid (red junglefowl); Passeriformes: corvid (large-billed crow), turdid (eyebrowed thrush, pale thrush, Siberian thrush, White's thrush, gray-backed thrush, scaly thrush)		Asia
H. fossae	Carnivora: euplerid (falanouc, Malagasy civet, fossa)		Madagascar
H. fujisana	Artiodactyla: bovid (cattle)		Japan
H. (*Rhipistoma*) *galidia*	Carnivora: euplerid (ring-tailed vontsira)		Madagascar
H. (*Allophysalis*) *garhwalensis*	Artiodactyla: bovid (cattle, yak, sheep, goat); Perissodactyla: equid (horse); Rodentia: cricetid (mountain vole), murid (field mouse, rat)		India
H. genevrayi	Artiodactyla: cervid (sambar deer)		Indo-China
H. gestroi	Carnivora: felid (clouded leopard), viverrid (large Indian civet)		Central Asia
H. (*Haemaphysalis*) *goral*	Artiodactyla: bovid (goral)		China
H. (*Kaiseriana*) *grochovskajae*	Artiodactyla: bovid (cattle)		Asia
H. heinrichi	Artiodactyla: bovid (buffalo); Eulipotyphla: soricid (shrew); Rodentia: murid (unspecified), sciurid (ground squirrel); Carnivora: canid (dog), herpestid (mongoose), mustelid (Burmese ferret-badger, Chinese ferret-badger), viverrid (civet); Primates: hominid (human)		Asia
H. (*Herpetobia*) *himalaya*	Artiodactyla: bovid (cattle, buffalo, zhum, goral, sheep, goat, Himalayan tahr, blackbuck), cervid (sambar deer, chital deer, Indian muntjac)		India
H. (*Kaiseriana*) *hirsuta*	Artiodactyla: bovid (unspecified), cervid (deer), suid (pig); Rodentia: hystricid (porcupine); Carnivora: canid (dog), mustelid (badger), viverrid (civet)		Indonesia
H. hispanica	Lagomorpha: leporid (European rabbit); Accipitriformes: accipitrid (hawk); Strigiformes: strigid (little owl) (3-host cycle)		Europe
H. (*Ornithophysalis*) *hoodi*	Artiodactyla: bovid (harnessed bushbuck); Lagomorpha: leporid (hare); Hyracoidea: procaviid (yellow-spotted rock hyrax); Rodentia: hystricid (African brush-tailed porcupine), murid (gerbil), sciurid (striped ground squirrel); Carnivora: canid (dog), viverrid (genet); Primates: indriid (Verreaux's sifaka); Accipitriformes: accipitrid (Egyptian vulture); Bucerotiformes: bucerotid (African grey hornbill, Abyssinian ground hornbill, red-billed hornbill): Ciconiiformes: ciconiid (Abdim's stork); Coliiformes: coliid (black-naped mouse bird); Columbiformes: columbid (African green pigeon, emerald-spotted wood dove); Coraciiformes: coraciid (blue-bellied roller); Cuculiformes: cuculid (white-browed coucal, western blue-headed coucal, black coucal, Burchell's coucal, Senegal coucal, Malagasy coucal, Madagascar coucal), musophagid (plaintain-eater); Falconiformes: falconid (lanner falcon); Galliformes: numidid (white-breasted guineafowl, helmeted guineafowl), phasianid (chicken, partridge, scaly spurfowl, double-spurred spurfowl, yellow-necked spurfowl, Clapperton's spurfowl, Heuglin's spurfowl, Natal spurfowl, Swainson's spurfowl, Ahanta spurfowl, white-throated francolin, yellow-beaked francolin, double-spurred francolin, Grant's crested francolin, common quail, blue quail); Gruiformes: rallid (African crake); Passeriformes: alaudid (clapper lark, flappet lark), cisticola (rattling cisticola, croaking cisticola, short-winged cisticola, Levaillannt's cisticola), corvid (piapiac), leiothrichid (arrow-marked babbler), malaconotid (black-crowned tchagra, tchagra shrike, black-headed gonolek, Abyssinian gonolek, southern		Africa

	boubou), motacillid (striped pipit, buffy pipit, yellow-throated longclaw), muscicapid (white-browed scrub robin, white-throated rock thrush, Arnott's chat, capped wheatear), musophagid (bare-faced go-away bird), ploceid (Holub's golden weaver, white-billed buffalo-weaver), sturnid (lesser blue-eared glossy starling, Meve's starling, red-winged starling, blue-eared starling, long-tailed glossy starling), turdid (olive thrush)		
H. hoogstraali	Carnivora: mephitid (Palawan stink badger)		Philippines
H. (*Rhipistoma*) *horaki*	Rodentia: bathyergid (Cape dune mole-rat)		Africa
H. houyi (syn. *H. calcarata*)	Eulipotyphla: erinaceid (hedgehog), soricid (shrew); Hyracoidea: procaviid (tree hyrax); Lagomorpha: leporid (scrub hare); Rodentia: murid (mouse), sciurid (striped ground squirrel, unstriped ground squirrel); Carnivora: felid (cat), herpestid (mongoose), mustelid (weasel), viverrid (civet)		Africa
H. (*Ornithophysalis*) *howletti*	Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Rodentia: murid (black rat, greater bandicoot rat, little Indian field mouse), sciurid (northern palm squirrel); Carnivora: felid (cat), herpestid (mongoose); Cuculiformes: cuculid (greater coucal); Galliformes: phasianid (pheasant)		Central Asia
H. (*Ornithophysalis*) *humerosa* (bandicoot tick)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Dasyuromorphia: dasyurid (yellow-footed antechinus, Atherton antechinus, northern quoll); Diprotodontia: macropodid (red-legged pademelon), phalangerid (common brushtail possum, coppery brushtail possum), potoroid (rufous rat kangaroo); Peramelemorphia: peramelid (southern brown bandicoot, northern brown bandicoot, Cape York brown bandicoot, long-nosed bandicoot, western barred bandicoot, common spiny bandicoot); Monotremata: tachyglossid (short-beaked echidna); Rodentia: murid (black rat, bush rat, common rock rat, dusky field rat, pale field rat, giant white-tailed rat, large New Guinea spiny field rat, rakali, fawn-footed mosaic-tailed rat, black-footed tree rat, brush-tailed rabbit rat, Gould's mouse); Primates: hominid (human); Coraciiformes: coraciid (Oriental dollarbird); Cuculiformes: cuculid (pheasant coucal)		Australia
H. hylobatis	Artiodactyla: tragulid (Java mouse deer); Primates: hylobatid (siamang); Rodentia: murid (Rajah spiny rat); Cuculiformes: cuculid (coucal)		Indonesia
H. (*Rhipistoma*) *hyracophila*	Hyracoidea: procaviid (rock hyrax); Macroscelidea: macroscelidid (elephant shrew)		Africa
H. (*Kaiseriana*) *hystricis*	Artiodactyla: bovid (cattle, buffalo, water buffalo), cervid (sambar deer, Reeve's muntjac), suid (pig, Indian boar, Celebes warty pig); Perissodactyla: equid (horse); Eulipotyphla: erinaceid (hedgehog); Scandentia: tupaiid (common treeshrew); Rodentia: hystricid (Malayan porcupine), murid (black rat, chestnut white-bellied rat, Southeast Asian house rat, Whitehead's spiny rat, northeastern peninsula bunomys, Hellwald's Sulawesi maxomys, Musschenbroek's Sulawesi maxomys), sciurid (Asian red-cheeked squirrel); Carnivora: canid (dog), felid (leopard, clouded leopard, tiger), mephitid (stink badger), mustelid (yellow-throated marten, European badger, Burmese ferret-badger, greater hog-badger, Sumatran hog-badger), ursid (sun bear, Asian black bear), viverrid (Asian palm civet); Primates: hominid (human); Cuculiformes: cuculid (coucal); Passeriformes: sturnid (common mynah), timaliid (large scimitar babbler), turdid (grey-backed thrush, scaly thrush); Testudines: geoemydid (spiny turtle)		Asia
H. (*Rhipistoma*) *indica*	Artiodactyla: cervid (chital deer), suid (boar); Eulipotyphla: erinaceid (hedgehog), soricid (house shrew); Lagomorpha: leporid (Indian hare); Rodentia: murid (mouse); Chiroptera (unspecified bat); Carnivora: canid (dog, Asiatic jackal, Bengal fox), felid (jungle-cat, leopard), herpestid (Indian gray mongoose, Indian small mongoose), hyaenid (hyena), mustelid (honey badger), viverrid (African palm civet, large Indian civet); Cuculiformes:		Eurasia, Africa

	cuculid (coucal); Galliformes: phasianid (fowl); Passeriformes: laniid (shrike), motacillid (forest wagtail), muscicapid (flycatcher), timaliid (babbler), turdid (thrush); Pelecaniformes: threskiornithid (black ibis)		
H. (Haemaphysalis) indoflava	Artiodactyla: bovid (cattle, sheep), suid (wild boar); Carnivora: canid (dog, jackal, fox); Primates: hominid (human)		India
H. (*Alloceraea*) *inermis* (syn. *H. ibrikliensis*) (winter tick)	Artiodactyla: bovid (cattle, zebu, Himalayan zebu, water buffalo, sheep, mouflon, goat, Japanese serow), cervid (red deer, fallow deer, roe deer, sambar deer, sika deer), suid (pig); Perissodactyla: equid (horse, donkey); Eulipotyphla: erinaceid (northern white-breasted hedgehog), soricid (common shrew), talpid (European mole); Lagomorpha: leporid (European hare); Rodentia: cricetid (bank vole, common vole, European pine vole, European water vole), glirid (European edible dormouse, hazel dormouse), murid (house mouse, yellow-necked mouse, wood mouse, Black Sea field mouse); Carnivora: canid (dog, red fox), felid (wildcat); Primates: hominid (human); Charadriiformes: scolopacid (Eurasian woodcock); Galliformes: phasianid (grey partridge, common quail); Passeriformes: corvid (Eurasian jay), muscicapid (spotted flycatcher), phylloscopid (willow warbler), sylviid (unspecified babbler); Sauria: lacertid (sand lizard, common wall lizard, Caucasus emerald lizard, European green lizard); Serpentes: viperid (meadow viper); Testudines: testudinid (Greek tortoise) (3-host cycle)	(vector for tick-borne encephalitis virus, babesiosis and possibly rickettsioses)	Eurasia
H. (*Kaiseriana*) *intermedia*	Artiodactyla: bovid (cattle, buffalo, water buffalo, sheep, goat), cervid (sambar deer, Indian muntjac, Sri Lankan axis deer), suid (wild boar), tragulid (Sri Lankan spotted chevrotain); Perissodactyla: equid (horse); Lagomorpha: leporid (Indian hare, black-naped hare); Rodentia: sciurid (jungle palm squirrel); Carnivora: canid (dog, golden jackal), felid (cat, jungle cat, leopard cat, leopard); Primates: cercopithecid (bonnet macaque); Columbiformes: columbid (dove); Cuculiformes: cuculid (plaintive cuckoo, coucal); Galliformes: phasianid (chicken, gray francolin, painted spurfowl, Sri Lankan junglefowl); Passeriformes: acrocephalid (Blyth's reed warbler), alaudid (Bengal bush lark), cisticolid (common tailorbird), dicrurid (ashy drongo, gray drongo), laniid (brown shrike), leiothrichid (white-headed babbler), motacillid (forest wagtail), muscicapid (Indian robin, Oriental magpie-robin), pittid (Indian pitta), pycnotid (red-vented bulbul), sturnid (common mynah, Brahminy starling), turdid (yellow-billed babbler), vangid (common woodshrike); Piciformes: picid (unspecified)		Asia
H. japonica (syn. *H. jezoensis*)	Artiodactyla: bovid (cattle, goat, Japanese serow), cervid (chital deer, sika deer, Chinese roe deer, Siberian roe deer, red deer, elk), suid (pig); Perissodactyla: equid (horse); Eulipotyphla: erinaceid (hedgehog); Lagomorpha: leporid (Manchurian hare); Rodentia: cricetid (grey red-backed vole), murid (striped field mouse, large Japanese field mouse, wood mouse), sciurid (red squirrel, Siberian chipmunk); Carnivora: canid (dog), felid (Eurasian lynx), mustelid (yellow-throated marten, European badger), ursid (bear); Primates: hominid (human); Charadriiformes: scolopacid (common snipe): Galliformes: phasianid (hazel grouse); Passeriformes: corvid (Eurasian jay, Eurasian magpie), emberizid (meadow bunting, yellow-throated bunting, black-faced bunting), fringillid (hawfinch), laniid (red-backed shrike), motacillid (olive-backed pipit, forest wagtail, western yellow wagtail), muscicapid (Siberian blue robin, Siberian rubythroat), passerid (Eurasian tree sparrow), sittid (Eurasian nuthatch), sturnid (Daurina starling), turdid (green-backed thrush); Strigiformes: strigid (owl)		Asia
H. juxtakochi (syn. *H. kochi*)	Artiodactyla: bovid (cattle, sheep, goat), camelid (alpaca, vicugna), cervid (white-tailed deer, Panama white-tailed deer, chital, pampas deer, red brocket, small red brocket, Central American red brocket, brown brocket, Amazonian brown brocket, grey brocket, pygmy		Americas

	brocket, guazuncho, cuagu pita), suid (pig), tayassuid (white-lipped peccary, collared peccary); Perissodactyla : equid (horse, mule), tapirid (Baird's tapir, South American tapir); Cingulata: chlamyphorid (southern three-banded armadillo); Didelphimorphia: didelphid (common opossum, big-eared opossum, brown four-eyed opossum, unspecified mouse opossum); Pilosa: myrmecophagid (northern tamandua); Lagomorpha: leporid (common tapeti, eastern cottontail); Rodentia: cricetid (Azara's grass mouse, red hocicudo), dasyproctid (black agouti, red-rumped agouti, Central American agouti, Azara's agouti), echimyid (armoured rat, Tome's spiny rat), erethizontid (Andean porcupine), sciurid (Brazilian squirrel, North Amazon red squirrel); Carnivora: canid (dog, maned wolf, coyote, crab-eating fox), felid (cougar), procyonid (white-nosed coati, South American coati); Primates: cebid (wedge-capped capuchin, Kaapori capuchin), hominid (human); Accipitriformes: accipitrid (harpy eagle, roadside hawk); Galliformes: cracid (dusky-legged guan); Passeriformes: corvid (plush-crested jay), passerellid (saffron-billed sparrow), thamnophilid (spot-backed antbird, common scale-backed antbird), thraupid (chestnut-headed tanager), turdid (white-necked thrush, pale-breasted thrush, rufous-bellied thrush), tyrannid (brownish twistwing)		
H. (*Ornithophysalis*) *kadarsani*	Rodentia: murid (Sulawesi giant rat, central Sulawesi echiothrix)		Indonesia
H. (*Herpetobia*) *kashmirensis*	Artiodactyla: bovid (sheep, goat); Rodentia: murid (house mouse), sciurid (white-bellied giant flying squirrel); Sauria: agamid (tuberculated agama)		India
H. (*Kaiseriana*) *kinneari*	Artiodactyla: bovid (cattle, buffalo), suid (boar), tragulid (chevrotain); Lagomorpha: leporid (hare); Eulipotyphla: soricid (shrew); Rodentia: hystricid (crested porcupine), murid (rat, Asiatic long-tailed mouse), sciurid (squirrel); Carnivora: canid (dog, Asiatic jackal); felid (tiger, leopard), herpestid (Indian gray mongoose), ursid (black bear); Primates: cercopithecid (bonnet macaque, langur monkey); Bucerotiformes: bucerotid (hornbill); Cuculiformes: cuculid (coucal); Galliformes: phasianid (fowl); Passeriformes: sylviid (warbler), timaliid (babbler); Piciformes: capitonid (barbet)		Asia
H. (*Alloceraea*) *kitaokai*	Artiodactyla: bovid (cattle, sika deer, Japanese serow), cervid (sika deer); Perissodactyla: equid (horse); Galliformes: phasianid (fowl)		Asia
H. knobigera	Artiodactyla: bovid (cattle, goat)		India
H. (*Alloceraea*) *kolonini*	host unknown, collected from vegetation		China
H. konigsbergeri	Rodentia: murid (black rat), sciurid (red giant flying squirrel, Hose's pygmy flying squirrel); Scandentia: ptilocercid (pen-tailed treeshrew); Carnivora: felid (cat, marbled cat, leopard cat, leopard, clouded leopard, tiger), mephitid (Sunda stink badger), mustelid (yellow-throated marten, Malayan weasel, Malayan glutton), viverrid (binturong, masked palm civet, banded palm civet, small-toothed palm civet, Asian palm civet, Malayan civet); Primates: hominid (human)		Asia
H. kopetdaghica	Artiodactyla: bovid (goat); Perissodactyla: equid (horse); Carnivora: felid (leopard)		Eurasia
H. krijgsmani	Artiodactyla: suid (wild boar)		New Guinea
H. (*Herpetobia*) *kumaonensis*	hosts unknown		India
H. kutchensis	Artiodactyla: bovid (cattle, sheep); Lagomorpha: leporid (black-naped hare); Rodentia: murid (rat); Carnivora: canid (dog, Indian wolf, golden jackal), felid (cat, jungle cat, caracal, lynx), herpestid (mongoose), hyaenid (striped hyena); Cuculiformes: cuculid (greater coucal); Galliformes: phasianid (grey francolin, painted francolin, Indian peafowl, ring-necked pheasant); Passeriformes: alaudid (Indian bush lark, red-winged lark), leiothrichid (common babbler), muscicapid (Indian robin), passerid (house sparrow), sturnid (rosy starling), sylviid (common whitethroat); Strigiformes:		Central Asia

	strigid (owl)		
H. (*Aborphysalis*) *kyasanurensis*	Artiodactyla: bovid (cattle, buffalo), suid (boar), tragulid (chevrotain); Eulipotyphla: soricid (Asian house shrew); Lagomorpha: leporid (rabbit, Indian hare); Rodentia: hystricid (Indian crested porcupine), murid (black rat, Blanford's rat, Asiatic long-tailed climbing mouse), sciurid (jungle palm squirrel, red giant flying squirrel); Carnivora: canid (dog, dhole), felid (leopard cat); Primates: cercopithecid (bonnet macaque, northern plains gray langur); Galliformes: phasianid (chicken)		Central Asia
H. (*Ornithophysalis*) *lagostrophi*	Diprotodontia: macropodid (banded hare-wallaby, rufous hare-wallaby, black-flanked rock-wallaby); Peramelemorphia: peramelid (western barred bandicoot)		Australia
H. (*Kaiseriana*) *lagrangei*	Artiodactyla: bovid (cattle, gaur), cervid (Indian muntjac, Indian sambar deer), suid (Indian boar), tragulid (Java mouse-deer); Scandentia: tupaiid (lesser treeshrew); Rodentia: murid (unspecified rat), sciurid (black giant squirrel, ground squirrel, Asian red-cheeked squirrel); Carnivora: canid (red dog), herpestid (small Indian mongoose, small Asian mongoose, Javan mongoose), mustelid (Burmese ferret-badger), Ursid (Asian black bear), viverrid (Asian palm civet, small Indian civet, small-toothed palm civet); Primates: hominid (human); Falconiformes: falconid (common kestrel); Galliformes: phasianid (red junglefowl); Passeriformes: laniid (shrike), muscicapid (flycatcher); Sauria: varanid (monitor)		Asia
H. laocayensis	Artiodactyla: cervid (deer); Carnivora: mustelid (weasel)		Asia
H. (*Rhipistoma*) *latitudinis*	Artiodactyla: bovid (cattle); Rodentia: murid (multimammate mouse, gerbil); Carnivora: canid (wolf), felid (cat), herpestid (marsh mongoose, white-tailed mongoose, banded mongoose, Gambian mongoose, common kusimanse), mustelid (African striped weasel), viverrid (African civet, rusty-spotted genet, Cape genet, Hausa genet); Chiroptera: molossid (Sierra Leone free-tailed bat)		Africa
H. leachii (syn. *Ixodes, H. elliptica, muhsami*) (yellow dog tick)	Artiodactyla: bovid (cattle, zebu, sheep, goat, steenbok, southern reedbuck, harnessed bushbuck, Coke's hartebeest, Lelwel hartebeest, Gunther's dikdik, Kirk's dikdik, common duiker, bay duiker, black duiker, Maxwell's duiker, tiang, oribi), suid (pig, red river hog, desert warthog); Perissodactyla: equid (horse), rhinocerotid (rhinoceros); Proboscidea: elephantid (African elephant); Eulipotyphla: erinaceid (four-toed hedgehog, European hedgehog, South African hedgehog, Sudanese hedgehog, African pygmy hedgehog), soricid (greater red musk shrew, African musk shrew, African giant shrew, Etruscan shrew, Asian house shrew); Pholidota: manid (pangolin); Lagomorpha: leporid (bush hare, scrub hare, Cape hare, Somalian hare, Natal red rock hare); Hyracoidea: procaviid (rock hyrax, yellow-spotted rock hyrax); Macroscelidea: macroscelid (western rock elephant shrew); Tubulidentata: orycteropid (aardvark); Rodentia: bathyergid (Cape dune mole-rat), dipodid (jerboa), heterocephalid (mole-rat), hystricid (crested porcupine, Cape porcupine), murid (house mouse, fat mouse, flat-haired mouse, little Indian field mouse, typical striped grass mouse, four-striped grass mouse, Griselda's striped grass mouse, Peter's striped mouse, Guinean grass mouse, eastern spiny mouse, southern multimammate mouse, Natal multimammate mouse, Guinea multimammate mouse, Hubert's multimammate mouse, Tullberg's soft-furred mouse, sub-Saharan pygmy mouse, black rat, acacia rat, red veld rat, Namaqua rock rat, Tanezumi rat, South African vlei rat, African grass rat, Abyssinian grass rat, gray brush-furred rat, rusty-bellied brush-furred rat, gracile tateril, savannah gerbil, bushveld gerbil, Cape gerbil, Guinea gerbil, Cape short-eared gerbil, Kemp's gerbil, common dasymys), nesomyid (Gambian pouched rat, South African pouched mouse), pedetid (South African springhare, West African springhare), sciurid (striped ground squirrel, unstriped ground squirrel, red bush	trauma, irritation (vector for babesiosis, rickettsiosis, Q fever)	Africa, Asia, Australia

	squirrel, Smith's bush squirrel, Cape ground squirrel, Thomas's rope squirrel, Lord Derby's scaly-tailed squirrel, Indian giant flying squirrel), spalacid (Aberdare Mountains African mole-rat), thryonomyid (greater cane rat); Carnivora: canid (dog, hunting dog, African wild dog, wolf, African wolf, golden jackal, silver jackal, black-backed jackal, side-striped jackal, Indian jackal, Senegalese jackal, red fox, pale fox, Cape fox, bat-eared fox), felid (cat, black-footed cat, bushcat, wildcat, junglecat, serval, caracal, lion, leopard cat, leopard, clouded leopard, cheetah, panther, tiger), herpestid (common kusimanse, meerkat, common dwarf mongoose, Somalian dwarf mongoose, common slender mongoose, Somalian slender mongoose, marsh mongoose, water mongoose, yellow mongoose, white-tailed mongoose, short-tailed mongoose, black-legged mongoose, banded mongoose, Indian gray mongoose, Cape gray mongoose, Egyptian mongoose, Gambian mongoose), hyaenid (spotted hyena, striped hyena, brown hyena, aardwolf), mustelid (ferret, honey badger, African clawless otter, spotted-necked otter, Malayan glutton, stoat, striped polecat, Cape polecat, yellow-throated marten, African striped weasel), ursid (sun bear), viverrid (African civet, large Indian civet, small Indian civet, African palm civet, Asian palm civet, common genet, small spotted genet, rusty spotted genet, pardine genet, servaline genet, king genet, Cape genet, Angolan genet, Haussa genet); Primates: cercopithecid (grivet), hominid (human), lorisid (Sunda slow loris); Anseriformes: anatid (knob-billed duck); Cuculiformes: cuculid (white-browed coucal, Senegal coucal, African emerald cuckoo); Galliformes: phasianid (red junglefowl, double-spurred spurfowl); Passeriformes: callaeid (huia), malaconotid (bush shrike, brown-crowned tchagra, black-crowned tchagra), motacillid (forest wagtail), muscicapid (bearded scrub robin, Miombo scrub robin, thrush nightingale, northern anteater chat), ploceid (red-collared widowbird), turdid (arrow-marked babbler); Strigiformes: strigid (Verreaux's eagle-owl); Testudines: geoemydid (Indian black turtle), testudines (elongated tortoise, leopard tortoise) (3-host cycle)		
H. lemuris	Primates: cheirogaleid (mouse lemur), indriid (Verreaux's sifaka), lemurid (ring-tailed lemur, black-and-white ruffed lemur), lepilemurid (red-tailed sportive lemur)		Madagascar
H. leporispalustris (syn. *Ixodes leporis, leporisproxima, proxima*) (rabbit tick)	Artiodactyla: bovid (cattle, goat, blackbuck), cervid (white-tailed deer), tayassuid (collared peccary); Perissodactyla: equid (horse); Lagomorpha: leporid (European hare, marsh hare, snowshoe hare, rabbit, swamp rabbit, black-tailed jackrabbit, white-tailed jackrabbit, brush rabbit, marsh rabbit, pygmy rabbit, common tapeti, eastern cottontail, desert cottontail, mountain cottontail, Mearn's cottontail, South America cottontail, New England cottontail, common tapeti, Central American tapeti); Didelphimorphia: didelphid (brown four-eyed opossum, Virginia opossum); Rodentia: cricetid (deer mouse, pinyon mouse, cotton mouse, northern grasshopper mouse, pack rat, hispid cotton rat, bushy-tailed woodrat, eastern woodrat, desert woodrat, Southern Plains woodrat), dasyproctid (Azara's agouti, Central American agouti), dipodid (Merriam's rat kangaroo, chisel-toothed rat kangaroo, Ord's rat kangaroo), echimyid (Guyenne spiny rat), geomyid (southern pocket gopher), heteromyid (Great Basin pocket mouse), murid (house mouse, northern golden mouse, white-footed mouse, black rat, brown rat, Florida wood rat), sciurid (least chipmunk, woodchuck, groundhog, pine squirrel, rock squirrel, fox squirrel, gray squirrel, striped ground squirrel, California ground squirrel, Mexican ground squirrel, Richardson's ground squirrel, thirteen-lined ground squirrel, yellow-bellied marmot); Carnivora: canid (dog, red fox, gray fox), felid (cat, bobcat), mephitid (striped skunk), procyonid (raccoon), viverrid (palm civet); Primates: hominid (human); Accipitriformes: accipitrid (eagle, red-tailed	trauma, irritation (vector for tularemia, Lyme disease, Rocky Mountain spotted fever)	Americas

	hawk); Apodiformes: trochilid (broad-tailed hummingbird); Caprimulgiformes: caprimulgid (common nighthawk); Charadriiformes: larid (gull), scolopacid (sandpiper), sternid (tern); Columbiformes: columbid (mourning dove); Cuculiformes: cuculid (greater roadrunner, black-billed cuckoo, groove-billed ani); Galliformes: cracid (dusky-legged guan), odontophorid (northern bobwhite quail, California desert quail), phasianid (chicken, prairie chicken, sage hen, turkey, greater sage-grouse, ruffed grouse, spruce grouse, sharp-tailed grouse, Gambel's quail, Mexican scaled quail, ring-necked pheasant); Gruiformes: rallid (American coot, sora rail); Passeriformes: alaudid (horned lark, prairie horned lark), cardinalid (rose-breasted grosbeak, painted bunting, indigo bunting, western tanager, northern cardinal, dickcissel), corvid (jackdaw, Eurasian magpie, blue jay, plush-crested jay, California scrub jay, American crow, raven), emberizid (saffron-billed sparrow, half-collared sparrow, black-striped sparrow), fringillid (American goldfinch), icterid (brown-headed cowbird, red-winged blackbird, bronze grackle, purple grackle, eastern meadowlark, western meadowlark, yellow-breasted chat), laniid (loggerhead shrike), mimid (brown thrasher, sage thrasher, crissal thrasher, curve-billed thrasher, grey catbird, mockingbird, northern mockingbird), muscicapid (common redstart), parid (tufted titmouse, black-capped chickadee), parulid (ovenbird, Louisiana water thrush, hooded warbler, two-banded warbler, black-throated blue warbler, black-throated grey warbler, prairie warbler, palm warbler, Audubon's warbler, common yellowthroat), passerid (house sparrow, English sparrow), passerellid (chipping sparrow, field sparrow, song sparrow, vesper sparrow, swamp sparrow, savannah sparrow, fox sparrow, grasshopper sparrow, golden-crowned sparrow, white-crowned sparrow, white-throated sparrow, black-throated sparrow, black-striped sparrow, half-collared sparrow, American tree sparrow, Bachman's sparrow, Bell's sparrow, Brewer's sparrow, Gambel's sparrow, Lincoln's sparrow, eastern towhee, canyon towhee, green-tailed towhee, red-eyed towhee, white-eyed towhee, Alabama towhee, Arctic towhee, dark-eyed junco), polioptilid (blue-grey gnatcatcher), regulid (ruby-crowned kinglet), sturnid (common starling), thamnophilid (chestnut-backed antbird, variable antshrike), thraupid (black-goggled tanager, blue-black grassquit, green-winged saltator), troglodytid (house wren, moustached wren, bay wren, rock wren, tropical wren, canyon wren, Carolina wren, Bewisk's wren), turdid (yellow-throated nightingale-thrush, hermit thrush, gray-cheeked thrush, olive-backed thrush, wood thrush, Swainson's thrush, rufous-bellied thrush, mountain bluebird, eastern bluebird, red-winged blackbird, Brewer's blackbird, Townsend's solitaire, American robin), tyrannid (eastern kingbird, southern antpipit, masked water tyrant, olive-sided flycatcher, brown-crested flycatcher, ash-throated flycatcher, American grey flycatcher), vireonid (blue-headed vireo); Tinamiformes: tinamid (Tataupa tinamou); Piciformes: picid (golden-fronted woodpecker, ladder-backed woodpecker, hairy woodpecker, northern flicker, red-shafted flicker); Strigiformes: strigid (buffy prairie owl, screech owl, barred owl) (3-host cycle)		
H. lobachovi	Rodentia: hystricid (crested porcupine)		Africa
H. (*Kaiseriana*) *longicornis* (bush tick, Asian longhorned tick)	Artiodactyla: bovid (cattle, sheep, goat), cervid (elk, white-tailed deer, sambar deer, fallow deer, Javan rusa), suid (pig); Perissodactyla: equid (horse, donkey); Diprotodontia: macropodid (eastern grey kangaroo, common wallaroo, pademelon, black-striped wallaby), phalangerid (common brushtail possum), pseudocheirid (common ringtail possum); Peramelemorphia: peramelid (northern brown bandicoot); Didelphimorphia: didelphid (Virginia opossum); Eulipotyphla: erinaceid (European hedgehog); Lagomorpha: leporid (European rabbit, European hare); Rodentia:	trauma, irritation, reduced production, damaged hides (vector for babesiosis, theileriosis, rickettsioses, hepatozoonosis)	Eurasia, Americas, Australasia

	murid (house mouse, black rat, brown rat); Carnivora: canid (dog), felid (cat), mustelid (stoat, ferret, least weasel, Japanese badger), procyonid (raccoon); Primates: hominid (human); Accipitriformes: accipitrid (swamp harrier); Anseriformes. anatid (mallard); Apterygiformes: apterygid (North Island brown kiwi); Charadriiformes: larid (gull); Galliformes: phasianid (chicken, turkey, ring-necked pheasant); Gruiformes: rallid (buff-banded rail, weka); Passeriformes: alaudid (Eurasian skylark), artamid (Australian magpie), emberizid (yellowhammer), passerid (house sparrow), sturnid (common myna), turdid (song thrush, dusky thrush, pale thrush); Psittaciformes: psittaculid (budgerigar) (3-host cycle)		
H. longipalpis	Artiodactyla: tragulid (Indian spotted chevrotain)		Sri Lanka
H. (*Kaiseriana*) *luzonensis*	Artiodactyla: cervid (Philippine deer), suid (Philippine warty pig)		Philippines
H. (*Ornithophysalis*) *madagascariensis*	Cuculiformes: cuculid (Malagasy coucal); Passeriformes: vangid (vanga)		Madagascar
H. (*Kaiseriana*) *mageshimaensis*	Artiodactyla: bovid (cattle, buffalo, goat), cervid (muntjac, Reeve's muntjac, sika deer), suid (pig); Rodentia: murid (rat); Carnivora: canid (dog), felid (leopard cat, tiger), viverrid (masked palm civet); Primates: hominid (human); Passeriformes: pycnonotid (brown-eared bulbul), zosteropid (warbling white-eye)		Eurasia
H. megalaimae	Piciformes: megalaimid (small green barbet, white-cheeked barbet)		Asia
H. megaspinosa	Artiodactyla: bovid (cattle, buffalo), cervid (deer), suid (pig); Perissodactyla: equid (horse); Carnivora: canid (dog), felid (cat), ursid (giant panda); Primates: hominid (human)		Eurasia
H. megaventralis	Passeriformes: hirundinid (cave swallow)		North America
H. (*Kaiseriana*) *menglaensis*	Artiodactyla: cervid (deer)		China
H. menui	Artiodactyla: cervid (Indian sambar deer)		Indo-China
H. mesnardi	Carnivora: ursid (Asian black bear)		Vietnam
H. (*Ornithophysalis*) *minuta*	Artiodactyla: bovid (buffalo, sheep, goat); Rodentia: hystricid (crested porcupine); Rodentia: murid (rat); Carnivora: herpestid (mongoose), viverrid (small Indian civet); Primates: cercopithecid (northern plains gray langur); Cuculiformes: cuculid (coucal); Galliformes: phasianid (chicken, Sri Lankan junglefowl); Passeriformes: timaliid (babbler)		Asia
H. mjoebergi	Artiodactyla: bovid (cattle), cervid (sambar deer)		Malaysia
H. monospinosa	Artiodactyla: tragulid (lesser mouse-deer)		Indonesia
H. montgomeryi	Artiodactyla: bovid (cattle, zebu, buffalo, sheep, goat, Sumatran serow), camelid (camel), cervid (deer); Perissodactyla: equid (horse, mule); Eulipotyphla: erinaceid (hedgehog), soricid (shrew); Rodentia: cricetid (mountain vole), murid (rat, mouse), sciurid (long-tailed marmot, squirrel); Carnivora: canid (dog), felid (leopard), herpestid (mongoose); Primates: hominid (human); Galliformes: phasianid (partridge); Passeriformes: corvid (spotted nutcracker)		China, Nepal
H. (*Rhipistoma*) *moreli*	Rodentia: murid (grass rat, Defua rat, Tullberg's soft-furred mouse); Eulipotyphla: erinaceid (four-toed hedgehog, African hedgehog); Lagomorpha: leporid (Cape hare, African savanna hare); Carnivora: canid (dog, side-striped jackal, pale fox), felid (cat, African wildcat, leopard, lion, serval), herpestid (marsh mongoose), hyaenid (striped hyena), nandiniid (African palm civet), viverrid (African civet, common genet, forest genet, large-spotted genet, Villier's genet, Cape genet, Pardine genet, Senegal genet, false genet); Primates: galagid (Senegal bushbaby)		Africa
H. (*Haemaphysalis*) *moschisuga*	Artiodactyla: bovid (yak), moschid (dwarf musk deer); Lagomorpha: leporid (hare); Galliformes: phasianid (fowl)		China
H. muhsami	Eulipotyphla: erinaceid (four-toed hedgehog); Tubulidentata: orycteropodid (aardvark); Rodentia: murid (typical striped grass mouse, fat mouse), nesomyid (Gambian pouched rat); Carnivora: herpestid (common dwarf mongoose, marsh mongoose, banded		Africa

	mongoose, water mongoose, Egyptian mongoose), hyaenid (spotted hyena), viverrid (common genet, Cape genet, African civet); Passeriformes: muscicapid (Miombo scrub-robin); Strigiformes: strigid (Verreaux's eagle-owl)		
H. murinus	Eulipotyphla: soricid (Asian house shrew); Rodentia: murid (Indian black rat, Blanford's rat, bandicoot rat), sciurid (jungle palm squirrel)		India
H. nadchatrami	Artiodactyla: bovid (cattle, buffalo), cervid (unspecified), suid (pig, bearded pig), tragulid (chevrotain); Perissodactyla: equid (horse), tapirid (tapir); Rodentia: murid (unspecified), sciurid (ground squirrel); Carnivora: canid (dog), felid (tiger), mustelid (weasel); viverrid (civet); Primates: hominid (human)		Asia
H. (*Herpetobia*) *nepalensis*	Artiodactyla: bovid (cattle, yak, buffalo, sheep, goat, Sumatran serow); Rodentia: murid (white-bellied rat); Carnivora: felid (wildcat), ursid (Asian black bear); Primates: hominid (human)		China, Nepal
H. (*Dermaphysalis*) *nesomys*	Rodentia: nesomyid (Island mouse, red forest rat)		Madagascar
H. neumanni	Artiodactyla: bovid (cattle, guar, sheep, goat), cervid (sika deer, chital deer, red deer); Perissodactyla: equid (horse, mule); Rodentia: murid (striped field mouse); Carnivora: canid (dog, golden jackal), mustelid (European badger)		Japan
H. nishiyamai	Artiodactyla: cervid (sambar deer, Reeve's muntjac), suid (Taiwan pig); Carnivora: canid (dog); Primates: hominid (human)		Taiwan
H. norvali	Eulipotyphla: erinaceid (South African hedgehog)		Africa
H. (*Haemaphysalis*) *numidiana*	Artiodactyla: bovid (cattle, sheep); Eulipotyphla: erinaceid (long-eared hedgehog, northern white-breasted hedgehog, European hedgehog, Brandt's hedgehog), soricid (lesser white-toothed shrew); Lagomorpha: leporid (tolai hare, desert hare, European hare), ochotonid (Pallas's pika); Rodentia: cricetid (flat-headed vole, European snow vole, grey dwarf hamster), dipodid (thick-tailed three-toed jerboa, dwarf fat-tailed jerboa, small five-toed jerboa, northern three-toed jerboa, great jerboa), murid (house mouse, yellow-necked mouse, eastern broad-toothed field mouse, wood mouse, short-tailed bandicoot rat, Turkestan rat, midday jird, Libyan jird, Tamarisk jird), pedetid (springhare), sciurid (yellow ground squirrel, little ground squirrel, long-clawed ground squirrel, European ground squirrel); Carnivora: canid (red fox, corsac fox), felid (sand cat, African wildcat), mustelid (beech marten, stoat, steppe polecat, marbled polecat, European polecat, least weasel, ferret), ursid (brown bear); Primates: hominid (human); Falconiformes: falconid (Eurasian hobby); Passeriformes: emberizid (red-headed bunting), muscicapid (isabelline wheatear); Testudines: testudinid (Russian tortoise)		Central Asia
H. obesa	Artiodactyla: bovid (cattle), cervid (Tibetan black deer, muntjac), suid (Indian boar); Perissodactyla: tapirid (Malayan tapir); Carnivora: canid (dog), mustelid (badger), ursid (bear); Primates: cercopithecid (capped langur), hominid (human)		Vietnam, India
H. obtusa	Afrosoricida: tenrecid (tenrec); Rodentia: murid (mouse), nesomyid (pouched rat); Carnivora: canid (dog), euplerid (fossa, ring-tailed vontsira), viverrid (small Indian civet)		Madagascar
H. (*Rhipistoma*) *oliveri*	Artiodactyla: bovid (unspecified antelope); Rodentia: murid (African grass rat, Cairo spiny mouse); Carnivora: canid (side-striped jackal), felid (wild cat, serval), herpestid (white-tailed mongoose), viverrid (small spotted genet)		Africa
H. orientalis	Artiodactyla: bovid (klipspringer); Hyracoidea: procaviid (yellow-spotted rock hyrax)		Africa
H. (*Ornithophysalis*) *ornithophila*	Artiodactyla: bovid (klipspringer, bharal); Lagomorpha: leporid (hare); Carnivora: mustelid (Siberian weasel); Galliformes: phasianid (red junglefowl, Swinhoe's pheasant, Taiwan partridge); Passeriformes: chloropseid (leafbird), pittid (rusty-naped pitta), turdid (pale thrush, scaly thrush, Amami ground thrush)		Eurasia
H. palawanensis	Artiodactyla: cervid (Javan rusa), suid (Philippine warty pig); Rodentia: hystricid (Philippine porcupine), murid (Palawan pencil-		Philippines

	tailed tree mouse), sciurid (Palawan flying squirrel); Carnivora: felid (small cave cat), herpestid (short-tailed mongoose), mephitid (Palawan stink badger), viverrid (Malayan civet); Primates: hominid (human)		
H. (*Kaiseriana*) *papuana*	Artiodactyla: bovid (cattle, banteng, buffalo, water buffalo), cervid (Indian sambar deer), tragulid (Javan mouse-deer), suid (pig, babirusa, banded pig, Philippine warty pig, Indian boar, Bornean bearded pig); Perissodactyla: equid (horse), tapirid (Malayan tapir); Eulipotyphla: soricid (Asian house shrew); Rodentia: hystricid (porcupine), murid (mouse, Asiatic long-tailed climbing mouse, black rat, Indian black rat, rice field rat, Blanford's rat, Bower's white-toothed rat, Malayan field rat, long-tailed giant rat, Muller's giant Sunda rat, red spiny rat, Musschenbroek's spiny rat, Rajah spiny rat), sciurid (jungle palm squirrel, shrew-faced squirrel); Carnivora: canid (dog, pariah dog, dhole), felid (cat, leopard, tiger), mustelid (greater hog-badger), ursid (sun bear), viverrid (masked palm civet); Primates: cercopithecid (bonnet macaque, northern plains gray langur), hominid (human); Galliformes: phasianid (unspecified); Passeriformes: muscicapid (unspecified)	(vector for Kyasanur forest disease virus)	Asia, New Guinea
H. (*Rhipistoma*) *paraleachi*	Artiodactyla: bovid (cattle, buffalo, water buffalo, bushbuck), moschid (musk deer); Rodentia: cricetid (gerbil), hystricid (porcupine), murid (unspecified); Carnivora: canid (dog, African hunting dog, side-striped jackal, black-backed jackal, golden jackal, red fox), felid (cat, African wild cat, serval, lion, leopard), herpestid (grey mongoose, white-tailed mongoose), hyaenid (hyena), viverrid (African civet, genet, bush genet); Primates: cercopithecid (black-and-white colobus), hominid (human); Galliformes: phasianid (junglefowl)		Africa
H. paraturturis	Artiodactyla: bovid (cattle, goat), suid (Indian boar); Eulipotyphla: soricid (shrew); Rodentia: murid (rat), sciurid (squirrel); Carnivora: canid (Indian wolf, Ussuri dhole), felid (jungle cat), herpestid (mongoose), ursid (bear); Cuculiformes: cuculid (greater coucal); Passeriformes: timaliid (babbler)		India
H. (*Kaiseriana*) *parmata*	Artiodactyla: bovid (cattle, zebu, buffalo, forest buffalo, sheep, goat, hartebeest, Lichtenstein's hartebeest, harnessed bushbuck, Cape bushbuck, harnessed antelope, royal antelope, common duiker, black duiker, bay duiker, zebra duiker, blue duiker, red forest duiker, black-fronted duiker, red-flanked duiker, Maxwell's duiker, Harvey's duiker, Peter's duiker, Bate's pygmy antelope, impala, kob, puku, bongo, oribi), giraffid (okapi), suid (pig, bushpig, red river hog, warthog), tragulid (water chevrotain); Macroscelidea: macroscelidid (black-and-rufous elephant shrew); Lagomorpha: leporid (hare); Pholidotes: manid (pangolin); Rodentia: hystricid (African brush-tailed porcupine), murid (black rat, gerbil), nesomyid (Gambian pouched rat), sciurid (forest giant squirrel), thryonomyid (greater cane rat); Carnivora: canid (dog), felid (cat, leopard), herpestid (marsh mongoose, white-tailed mongoose), viverrid (African civet, African palm civet, common genet, rusty-spotted genet, king genet, servaline genet); Primates: cercopithecid (moustached guenon), hominid (human); Bucerotiformes: bucerotid (eastern piping hornbill); Galliformes: numidid (helmeted guineafowl, forest guineafowl, plumed guineafowl, black guineafowl, southern crested guineafowl), phasianid (double-spurred spurfowl, Ahanta spurfowl, Latham's francolin, grey-necked rock fowl); Passeriformes: estrildid (unspecified finch), viduid (pin-tailed whydah); Serpentes: atractaspidid (mole viper), lamprophiid (burrowing asp)		Africa
H. (*Haemaphysalis*) *parva* (syn. *H. otophila*)	Artiodactyla: bovid (cattle, zebu, water buffalo, sheep, goat, wild goat), camelid (camel), cervid (roe deer, red deer), suid (pig); Perissodactyla: equid (horse, donkey); Eulipotyphla: erinaceid (long-eared hedgehog, northern white-breasted hedgehog, European hedgehog); Lagomorpha: leporid (mountain hare, European hare), ochotonid (African pika); Rodentia: calomyscid	(vector for babesiosis and possibly Q fever, tularemia and rickettsioses)	Europe

	(Hotson's mouse-like hamster); cricetid (social vole, Gunther's vole, grey dwarf hamster, Ciscaucasian hamster), dipodid (William's jerboa), glirid (forest dormouse), murid (house mouse, wood mouse, gerbil, Tristram's jird, Persian jird, Libyan jird), sciurid (speckled ground squirrel), spalacid (lesser blind mole-rat); Carnivora: canid (dog, wolf, golden jackal, red fox), felid (cat, fishing cat, panther), mustelid (European badger, least weasel, ferret), viverrid (small Indian civet); Primates: hominid (human); Accipitriformes: accipitrid (tawny eagle, Bonnelli's eagle, Montagu's harrier); Charadriiformes: burhinid (Eurasian stone curlew), charadriid (sociable lapwing), scolopacid (common snipe, Eurasian woodcock); Columbiformes: columbid (dove, European turtle dove); Coraciiformes: coraciid (European roller), meropid (European bee-eater); Falconiformes: falconid (lesser kestrel); Galliformes: phasianid (common quail, common partridge, grey partridge, ring-necked pheasant); Otidiformes: otidid (little bustard); Passeriformes: alaudid (crested lark, Calandra lark, Eurasian skylark), corvid (raven, rook, carrion crow, Eurasian magpie), emberizid (yellowhammer, corn bunting, rock bunting, black-headed bunting, Ortolan bunting), motacillid (tree pipit), muscicapid (common redstart, common rock thrush, blue rock thrush, western black-eared wheatear, isabelline wheatear, northern wheatear), passerid (house sparrow), passerellid (Eurasian tree sparrow), sturnid (common starling), sylviid (garden warbler), turdid (song thrush, common blackbird); Piciformes: picid (woodpecker); Strigiformes: strigid (short-eared owl, little owl); Sauria: agamid (Caucasian agama), anguid (sheltopusik), lacertid (snake-eyed lizard, sand lizard, common wall lizard, felseneidechse, Caspian green lizard, European green lizard, Crimean wall lizard, rapid racerunner); Serpentes: colubrid (grass snake, Balkan whip snake), psammophiid (eastern Montpellier snake); Serpentes: viperid (meadow viper); Testudines: testudinid (Greek tortoise) (3-host cycle)		
H. pavlovskyi	Eulipotyphla: erinaceid (long-eared hedgehog); Lagomorpha: leporid (desert hare, tolai hare); Galliformes: phasianid (common quail, white-winged pheasant); Passeriformes: phylloscopid (willow warbler), sylviid (unspecified warbler)		Eurasia
H. (*Rhipistoma*) *pedetes*	Rodentia: pedetid (South African springhare); Carnivora: felid (unspecified cat), herpestid (unspecified mongoose), mustelid (unspecified polecat)		Africa
H. pentalagi	Lagomorpha: leporid (Amami rabbit)		Japan
H. peregrinus	Pterocliformes: pteroclid (Pallas's sandgrouse)		Europe
H. (*Ornithophysalis*) *petrogalis*	Diprotodontia: macropodid (unadorned rock-wallaby)		Australia
H. (*Ornithophysalis*) *phasiana*	Artiodactyla: cervid (sika deer, Chinese muntjac); Lagomorpha: leporid (rabbit); Charadriiformes: turnicid (barred buttonquail); Galliformes: phasianid (green pheasant, ring-necked pheasant, hazel grouse); Passeriformes: emberizid (chestnut bunting, Siberian grey-headed bunting), locustellid (Middendorf's grasshopper warbler), muscicapid (blue rock thrush)		Asia
H. (*Allophysalis*) *pospelovashtromae* (syn. *H. aksarensis*)	Artiodactyla: bovid (cattle, yak, sheep, goat), suid (pig); Lagomorpha: leporid (hare), ochotonid (pika), Rodentia: sciurid (ground squirrel); Passeriformes: sittid (nuthatch)		Central Asia
H. (*Alloceraea*) *primitiva*	host unknown, collected from vegetation		China
H. (*Rhipistoma*) *princeps*	Artiodactyla: bovid (unspecified antelope); Lagomorpha: leporid (Cape hare); Eulipotyphla: erinaceid (four-toed hedgehog), soricid (African giant shrew); Rodentia: murid (Cairo spiny mouse, Natal multimammate mouse, African grass rat, unspecified gerbil, Kemp's gerbil) Carnivora: canid (wolf, side-striped jackal, golden jackal, pale fox), felid (cat, wildcat, serval, lion), herpestid (marsh mongoose, banded mongoose, white-tailed mongoose, Egyptian		Africa

	mongoose, Gambian mongoose, Pousargues's mongoose), mustelid (striped polecat), viverrid (African civet, common genet, rusty-spotted genet, Hausa genet)		
H. (Kaiseriana) psalistos	Artiodactyla: bovid (cattle, anoa), cervid (Javan rusa, Philippine deer), suid (pig, Philippine warty pig, Celebes warty pig); Rodentia: murid (common bunomys, Pacific rat, Hoffmann's Sulawesi rat, marmoset xanthurus rat)		Philippines
H. (*Rhipistoma*) *punctaleachi*	Artiodactyla: bovid (royal antelope); Rodentia: hystricid (porcupine); Carnivora: canid (dog), felid (leopard), nandiniid (African palm civet), viverrid (African civet, Cape genet, Senegal genet, Johnston's genet)		Africa
H. (*Aboimisalis*) *punctata*	Artiodactyla: bovid (cattle, water buffalo, sheep, mouflon, goat, wild goat), camelid (camel, dromedary), cervid (European fallow deer, red deer, roe deer), suid (pig); Perissodactyla: equid (horse, donkey); Eulipotyphla: erinaceid (northern white-breasted hedgehog, long-eared hedgehog, eastern hedgehog, European hedgehog), soricid (common shrew, garden shrew), talpid (European mole); Lagomorpha: leporid (desert hare, mountain hare, tolai hare, European hare, European rabbit); Rodentia: cricetid (bank vole, common vole, European water vole, northern mole vole, grey dwarf hamster), glirid (garden dormouse, forest dormouse), murid (house mouse, yellow-necked mouse, wood mouse, striped field mouse, Turkestan rat, Tamarisk jird), sciurid (red squirrel, little ground squirrel, relict ground squirrel, European ground squirrel); Carnivora: canid (dog, wolf, red fox), felid (cat), mustelid (European polecat, steppe polecat, least weasel, European badger), ursid (bear); Chiroptera (unspecified bat); Primates: hominid (human); Accipitriformes: accipitrid (common buzzard, hen harrier, Montagu's harrier, marsh hawk); Bucerotiformes: bucerotid (Eurasian hoopoe); Caprimulgiformes: caprimulgid (European nightjar); Charadriiformes: burhinid (Eurasian stone curlew), charadriid (northern lapwing, sociable lapwing), haematopodid (Eurasian oystercatcher), larid (herring gull, black-headed gull, common tern), scolopacid (Eurasian curlew, Eurasian woodcock, common sandpiper); Columbiformes: columbid (pigeon, hill pigeon, Oriental turtle dove, European turtle dove); Coraciiformes: coraciid (European roller), meropid (European bee-eater); Cuculiformes: cuculid (common cuckoo); Falconiformes: falconid (common kestrel, lesser kestrel, Eurasian hobby); Galliformes: phasianid (chicken, red junglefowl, snow cock, turkey, common partridge, Daurian partridge, grey partridge, rock partridge, chukar partridge, see-see partridge, red-legged partridge, common pheasant, ring-necked pheasant, ruffed grouse, black grouse, Pallas's sandgrouse, common quail, black francolin); Gruiformes: rallid (corncrake, common moorhen); Otidiformes: otidid (great bustard, little bustard); Passeriformes: acrocephalid (great reed warbler, Blyth's reed warbler, sedge warbler, melodius warbler), alaudid (woodlark, crested lark, horned lark, red-capped lark, bimaculated lark, Calandra lark, Eurasian skylark), corvid (raven, rook, hooded crow, carrion crow, chough, western jackdaw, Eurasian magpie, Eurasian jay), emberizid (yellowhammer, reed bunting, rock bunting, corn bunting, pine bunting, red-headed bunting, Ortolan bunting), fringillid (hawfinch, common chaffinch, common linnet, white-winged grosbeak), hirundinid (barn swallow), laniid (red-backed shrike, red-tailed shrike, brown shrike, lesser grey shrike), motacillid (meadow pipit, tawny pipit, water pipit, tree pipit, white wagtail, grey wagtail, western yellow wagtail, pied wagtail), muscicapid (African stonechat, whinchat, wheatear, robin, spotted flycatcher, thrush nightingale, common nightingale, bluethroat, common redstart, Guldenstadt's redstart, common rock thrush, blue rock thrush, European robin, isabelline wheatear, northern wheatear, variable wheatear, pied wheatear), parid (great tit, azure tit, cinereous tit), passerid (house sparrow,	trauma, irritation, toxicosis, paralysis (vector for babesiosis, theileriosis, anaplasmosis, rickettsioses, viral encephalitis, Congo-Crimean haemorrhagic fever, Bhanja, Palma, Tribec and louping-ill viruses)	Eurasia, Africa

	Spanish sparrow, Eurasian tree sparrow), passerellid (rock sparrow), phylloscopid (willow warbler, Siberian chiffchaff), prunellid (dunnock), sittid (western rock nuthatch), sturnid (common starling, rosy starling), sylviid (common whitethroat, lesser whitethroat, barred warbler), turdid (common blackbird, song thrush, fieldfare, mistle thrush, red-throated thrush); Pelecaniformes: ardeid (squacco heron); Piciformes: picid (great spotted woodpecker, white-winged woodpecker, Nuttall's woodpecker); Pterocliformes: pteroclid (black-bellied sandgrouse); Strigiformes: strigid (Eurasian eagle-owl, long-eared owl); Struthioniformes: struthionid (ostrich); Sauria: agama (Caucasian agama), anguid (European glass lizard), lacertid (snake-eyed lizard, sand lizard, common wall lizard, ocellated lizard, Maderian wall lizard, felseneidechse, European green lizard, Caspian green lizard, spiny-footed lizard, steppe runner, rapid racerunner); Serpentes: viperid (aspic viper); Testudines: testudinid (Russian tortoise) (3-host cycle)		
H. quadriaculeata	Rodentia: spalacid (mole-rat); Carnivora: canid (dog, gray wolf), mustelid (unspecified)		Vietnam
H. (Haemaphysalis) qinghaiensis	Artiodactyla: bovid (cattle, yak, sheep, goat); Perissodactyla: equid (horse, donkey, mule); Lagomorpha: leporid (rabbit); Primates: hominid (human) (3-host cycle)		Asia
H. (*Kaiseriana*) *ramachandrai*	Artiodactyla: bovid (cattle, buffalo, goat), cervid (sambar deer, chital deer, Indian muntjac); Carnivora: felid (leopard, tiger); Primates: hominid (human)		India
H. (*Ornithophysalis*) *ratti*	Dasyuromorphia: dasyurid (fawn antechinus, kowari); Peramelemorphia: peramelid (western barred bandicoot); Diprotodontia: phalangerid (common brushtail possum); Rodentia: murid (bush rat, long-haired rat, eastern rat, dusky field rat, fawn-footed mosaic-tailed rat, brush-tailed rabbit-rat, canefield rat)		Australia, New Guinea
H. (*Kaiseriana*) *renschi*	Artiodactyla: bovid (cattle, banteng, buffalo, water buffalo, goat), cervid (Javan rusa deer), suid (Celebes warty pig); Perissodactyla: equid (horse); Rodentia: murid (Pacific rat, mouse); Carnivora: canid (dog); Charadriiformes: larid (greater crested tern); Anura: ranid (unspecified frog)		Australasia
H. rhinilophi	Chiroptera: rhinolophid (greater horseshoe bat, Geoffroy's horseshoe bat)		Europe
H. roubaudi	Artiodactyla: cervid (Indian sambar deer); Primates: hominid (human)		Vietnam
H. (*Kaiseriana*) *rugosa*	Artiodactyla: bovid (cattle, waterbuck, tsessebe, Bohor reedbuck, harnessed bushbuck, tiang, oribi); Lagomorpha: leporid (Crawshay's hare); Rodentia: murid (pygmy gerbil); Carnivora: felid (serval), herpestid (Egyptian mongoose, white-tailed mongoose), viverrid (African civet, forest genet, Villier's genet)		Africa
H. rusae	Artiodactyla: cervid (rusa deer, Philippine deer), suid (Philippine warty pig), Diprotodontia: macropodid (unspecified wallaby)		Philippines, New Guinea
H. (*Haemaphysalis*) *sambar*	Artiodactyla: cervid (sambar deer)		India
H. (*Ornithophysalis*) *sciuri*	Rodentia: sciurid (Mindanao squirrel)		Philippines
H. (*Kaiseriana*) *semermis*	Artiodactyla: cervid (muntjac, sambar deer), suid (bushpig, Indian boar, Bornean bearded pig); Artiodactyla: tragulid (Javan mouse-deer); Perissodactyla: tapirid (Malayan tapir); Scandentia: tupaiid (common treeshrew); Rodentia: murid (long-tailed giant rat, Bower's white-toothed rat, Muller's giant Sunda rat, Malaysian house rat, Rajah spiny rat, red spiny rat), sciurid (plaintain squirrel, slender squirrel); Carnivora: canid (dog, dhole); felid (leopard, clouded leopard, tiger), ursid (sun bear), viverrid (Malayan civet); Primates: hominid (human)		Asia
H. (*Rhipistoma*) *setosa*	Hyracoidea: procaviid (hyrax); Lagomorpha: leporid (Cape hare), Rodentia: murid (Angoni vlei rat, Southern African vlei rat, maned rat); Carnivora: felid (cat), herpestid (white-tailed mongoose,		Africa

	Egyptian mongoose), viverrid (African civet, common genet, Cape genet); Primates: hominid (human)		
H. sewelli	Artiodactyla: bovid (goat)		India
H. (Kaiseriana) shimoga	Artiodactyla: bovid (cattle, bison, sheep, goat, gaur), cervid (sambar deer), suid (boar); Rodentia: murid (rat), sciurid (squirrel); Primates: hominid (human)		Asia
H. silacea	Artiodactyla: bovid (cattle, gaur, sheep, goat, eland, kudu, Cape bushbuck, Nyala bushbuck, common duiker, blue duiker); Perissodactyla: rhinocerotid (rhinoceros); Lagomorpha: leporid (hare); Macroscelidea: macroscelidid (elephant shrew); Rodentia: murid (Namaqua rock mouse); Carnivora: canid (dog, black-backed jackal), felid (caracal, lynx), herpestid (white-tailed mongoose, yellow mongoose), hyaenid (hyena); Primates: hominid (human); Galliformes: numidid (helmeted guineafowl); Passeriformes: alaudid (rufous-naped lark), corvid (Cape raven), pycnonotid (black-eyed bulbul), sturnid (Cape glossy starling); Pelecaniformes: threskiornithid (Hadada ibis)		Africa
H. silvafelis	Lagomorpha: leporid (hare); Rodentia: sciurid (squirrel); Carnivora: felid (jungle cat); Cuculiformes: cuculid (coucal)		India
H. (*Ornithophysalis*) *simplex*	Afrosoricida: tenrecid (greater hedgehog tenrec, lesser hedgehog tenrec, tailless tenrec, lowland streaked tenrec, Talazac's shrew tenrec); Eulipotyphla: erinaceid (hedgehog); Rodentia: murid (rat); Primates: cheirogaleid (mouse lemur), indriid (sifaka); Pelecaniformes: threskiornithid (Madagascar ibis)		Madagascar
H. simplicima	Afrosoricida: tenrecid (tenrec)		Madagascar
H. sinensis	Artiodactyla: bovid (cattle, goat)		Asia
H. (*Kaiseriana*) *spinigera*	Artiodactyla: bovid (cattle, zebu, buffalo, Indian bison, water buffalo, sheep), cervid (sambar deer, Indian sambar deer), tragulid (chevrotain); Peramelemorphia: peramelid (northern brown bandicoot, southern brown bandicoot); Diprotodontia: macropodid (unspecified); Eulipotyphla: soricid (Asian house shrew); Lagomorpha: leporid (black-naped hare); Rodentia: hystricid (Indian crested porcupine), murid (black rat, Indian black rat, brown rat, rakali, bandicoot rat, dusky field rat, Blanford's rat), sciurid (jungle palm squirrel, Malabar giant squirrel); Carnivora: canid (dog, Asiatic jackal), felid (leopard, tiger, panther), herpestid (gray mongoose), ursid (sloth bear, Indian bear), viverrid (small Indian civet); Primates: cercopithecid (bonnet macaque, northern plains gray langur), hominid (human); Cuculiformes: cuculid (greater coucal); Galliformes: phasianid (grey junglefowl, peacock); Passeriformes: leiothrichid (jungle babbler), motacillid (forest wagtail), muscicapid (Indian robin, white-throated ground thrush), pycnonotid (red-vented bulbul), sturnid (jungle myna), turdid (orange-headed thrush) (3-host cycle)	trauma, irritation (vector for Kyasanur forest disease)	India, Sri Lanka, Australia
H. spinulosa (syn. *H. ethiopica*)	Artiodactyla: bovid (common eland); Lagomorpha: leporid (scrub hare); Carnivora: canid (dog, bat-eared fox), felid (cat, caracal, leopard), herpestid (marsh mongoose, common dwarf mongoose, white-tailed mongoose, banded mongoose), mustelid (African striped weasel), nesomyid (Gambian pouched rat), viverrid (common genet, Cape genet); Primates: galagid (brown greater galago, Senegal bushbaby)		Africa
H. subelongata	Afrosoricida: tenrecid (tailless tenrec, lowland streaked tenrec); Rodentia: murid (unspecified rodents)		Madagascar
H. (*Kaiseriana*) *subphilippensis*	Artiodactyla: cervid (Philippine deer), suid (Philippine warty pig)		Philippines
H. subterra	Rodentia: murid (red veld rat, Natal multimammate mouse), spalacid (East African mole-rat); Carnivora: herpestid (common slender mongoose, marsh mongoose, white-tailed mongoose, banded mongoose, Egyptian mongoose), viverrid (rusty-spotted genet)		Africa
H. (*Herpetobia*) *sulcata*	Artiodactyla: bovid (cattle, water buffalo, sheep, mouflon, Asiatic mouflon, argali, goat, wild goat, goitered gazelle), camelid (camel),	(vector for brucellosis,	Europe

(syn. *H. angorense, cretica, cholodkovskyi*)	cervid (red deer, European fallow deer), suid (pig); Perissodactyla: equid (horse, donkey); Eulipotyphla: erinaceid (long-eared hedgehog, European hedgehog); Lagomorpha: leporid (tolai hare, European hare), ochotonid (pika); Rodentia: calomyscid (Hotson's mouse-like hamster), cricetid (narrow-headed vole, grey dwarf hamster), dipodid (William's jerboa), murid (wood mouse, Turkestan rat), sciurid (red squirrel, little ground squirrel, yellow ground squirrel, European ground squirrel); Carnivora: canid (dog, red fox), felid (cat), mustelid (badger); Chiroptera: vespertilionid (pipistrelle); Primates: hominid (human), lemurid (common brown lemur); Accipitriformes: accipitrid (golden eagle, Griffon vulture); Bucerotiformes: bucerotid (Eurasian hoopoe); Charadriiformes: burhinid (Eurasian stone curlew), scolopacid (European woodcock); Columbiformes: columbid (pigeon); Coraciiformes: coraciid (European roller), meropid (European bee-eater); Falconiformes: falconid (lesser kestrel); Galliformes: phasianid (chicken, rock partridge, Daurian partridge, common quail, ring-necked pheasant); Gruiformes: rallid (corncrake); Otidiformes: otid (little bustard); Passeriformes: alaudid (crested lark, desert lark, lesser short-toed lark, Calandra lark, Eurasian skylark), corvid (Eurasian magpie), emberizid (red-headed bunting, corn bunting, rock bunting, black-headed bunting, white-capped bunting), fringillid (common linnet), laniid (brown shrike), motacillid (tawny pipit, tree pipit, Richardson's pipit, western yellow wagtail), muscicapid (thrush nightingale, common rock thrush, blue rock thrush, European robin, isabelline wheatear, northern wheatear, variable wheatear, pied wheatear), passerid (house sparrow, Eurasian tree sparrow), sittid (western rock nuthatch), sturnid (common starling, rosy starling), sylviid (common whitethroat), turdid (common blackbird, song thrush); Strigiformes: strigid (little owl); Sauria: agamid (sunwatcher toadhead agama, steppe agama, starred agama, Caucasian agama, small-scaled rock agama, Anderson's rock agama, Turkestan rock agama, Olivier's horny-scaled agama), anguid (slow worm, slender glass lizard, Pallas's glass lizard, European glass lizard), gekkonid (comb-toed gecko, Turkestan thin-toed gecko), lacertid (snake-eyed lizard, sand lizard, common wall lizard, Caspian green lizard, European green lizard, Crimean wall lizard, Fraa's lizard, felseneidechse, greenish eidechse, Anatolian lizard, European green lizard, Bosc's fringe-toed lizard, small-toed lizard, steppe runner, Pleske's racerunner, rapid racerunner, regel racerunner, multi-ocellated racerunner, Kirghiz racerunner, Strauch's racerunner), scincid (desert lidless skink, gold skink), varanid (desert monitor); Serpentes: colubrid (grass snake, steppe rat snake, slender whip snake, spotted whip snake, dotted dwarf racer, smooth snake, Balkan whip snake, green whip snake), psammophiid (eastern Montpellier snake), viperid (horned viper, meadow viper, saw-scaled viper, Halys pit viper); Testudines: testudinid (Russian tortoise) (3-host cycle)	anaplasmosis, Q fever and rickettsiosis)	
H. sumatraensis	Artiodactyla: cervid (sambar deer), suid (banded pig); Carnivora: canid (dog), felid (Sumatran tiger), viverrid (civet)		Indonesia
H. (*Herpetobia*) *sundrai*	Artiodactyla: bovid (sheep, goat), cervid (muntjac)		India
H. (*Aborphysalis*) *suntzovi*	Artiodactyla: suid (pig); Rodentia: hystricid (Malayan porcupine)		Vietnam
H. (*Kaiseriana*) *susphilippensis*	Artiodactyla: cervid (Philippine deer), suid (Celebes warty pig)		Philippines
H. tauffliebi	Rodentia: hystricid (African brush-tailed porcupine, tufted-tailed porcupine), murid (typical striped grass mouse, Indian gerbil); Carnivora: felid (caracal); Passeriformes: motacillid (plain-backed pipit)		Africa
H. taurica	Eulipotyphla: erinaceid (northern white-breasted hedgehog)		Israel
H. theilerae	Afrosoricida: tenrecid (tailless tenrec, greater hedgehog tenrec)		Madagascar

H. (*Allophysalis*) *tibetensis*	Artiodactyla: bovid (cattle, buffalo, sheep); Carnivora: canid (dog)		China
H. tiptoni	Afrosoricida: tenrecid (tailless tenrec, highland streaked tenrec, lowland streaked tenrec)		Madagascar
H. toxopei	Carnivora: canid (dog); Chiroptera: pteropodid (Sulawesi rousette, lesser short-nosed fruit bat)		Indonesia
H. traguli	Artiodactyla: tragulid (Java mouse-deer, lesser mouse-deer), suid (boar); Scandentia: tupaiid (common treeshrew); Rodentia: murid (Rajah spiny rat)		Malaysia
H. (*Haemaphysalis*) *traubi*	Artiodactyla: cervid (Indian muntjac, sambar deer), suid (boar)		Malaysia
H. (*Kaiseriana*) *turturis*	Artiodactyla: bovid (cattle, buffalo, goat, Nilgiri tahr), cervid (muntjac, sambar deer, Indian sambar deer, chital deer, spotted deer), suid (pig, boar), tragulid (chevrotain); Eulipotyphla: soricid (Asian house shrew); Lagomorpha: leporid (hare, black-naped hare); Rodentia: hystricid (Indian crested porcupine), murid (black rat, bandicoot rat, Blanford's rat), sciurid (jungle palm squirrel, white-bellied giant flying squirrel); Carnivora: canid (dog, Asiatic jackal), felid (jungle cat, leopard), viverrid (small Indian civet); Primates: cercopithecid (bonnet macaque, northern plains gray langur), hominid (human); Columbiformes: columbid (spotted dove); Cuculiformes: cuculid (coucal); Galliformes: phasianid (fowl); Passeriformes: corvid (large-billed crow), turdid (thrush); Piciformes: picid (unspecified); Psittaciformes: psittacid (unspecified); Sauria: varanid (monitor); Serpentes: pythonid (python); Testudines: testudinid (tortoise)		Central Asia
H. verticalis	Artiodactyla: bovid (cattle, Przewalski's gazelle); Rodentia: murid (long-clawed jird), sciurid (Daurian ground squirrel); Carnivora: canid (dog); Passeriformes: passerid (sparrow)		China
H. vidua	Carnivora: viverrid (palm civet, Malayan civet)		Malaysia
H. (*Rhipistoma*) *walkerae*	Carnivora: canid (bat-eared fox), hyaenid (aardwolf), mustelid (striped polecat); Rodentia: pedetid (East African springhare)		Africa
H. (*Allophysalis*) *warburtoni*	Artiodactyla: bovid (cattle, buffalo, yak, zhum, sheep, argali, goat, wild goat, Himalayan tahr, goral, Siberian ibex, mainland serow, Japanese serow, Sumatran serow), camelid (camel), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit, tolai hare), ochotonid (large-eared pika, Pallas's pika, steppe pika); Rodentia: cricteid (flat-headed vole, narrow-headed vole, silver mountain vole, Gobi Altai mountain vole, Tien Shan red-backed vole, European snow vole, grey dwarf hamster, golden hamster), murid (wood mouse), sciurid (long-tailed ground squirrel, gray marmot, long-tailed marmot), sminthid (birch mouse); Carnivora: canid (dog, red fox), felid (cat); Primates: hominid (human); Galliformes: phasianid (chicken, monal pheasant); Passeriformes: sittid (western rock nuthatch)		China
H. (*Kaiseriana*) *wellingtoni*	Artiodactyla; bovid (cattle, zebu, buffalo, water buffalo), cervid (barking deer), tragulid (chevrotain); Eulipotyphla: soricid (Asian house shrew); Rodentia: hystricid (crested porcupine), murid (black rat, rajah spiny rat, dark-tailed tree rat, Hellwald's Sulawesi maxomys); Carnivora: canid (dog), viverrid (Asian palm civet); Primates: cercopithecid (bonnet macaque, northern plains gray langur), hominid (human); Accipitriformes: accipitrid (hawk); Anseriformes: anatid (ducks, goose); Charadriiformes: charadriid (plover); Bucerotiformes: bucerotid (hornbill); Cuculiformes: cuculid (greater coucal); Galliformes: phasianid (chicken, turkey, red junglefowl, red spurfowl); Gruiformes: rallid (rail); Passeriformes: turdid (Japanese thrush)		Australasia
H. yeni	Artiodactyla: bovid (sheep, goat), cervid (sambar deer); Lagomorpha: leporid (hare); Carnivora: canid (dog, dhole), felid (jungle cat), viverrid (civet); Cuculiformes: cuculid (lesser coucal)		Vietnam
H. zambeziae	Artiodactyla: bovid (klipspringer); Hyracoidea: procaviid (southern tree hyrax)		Africa
H. (*Rhipistoma)*	Carnivora: felid (cat, black-footed cat, caracal, Southern African		Africa

zumpti	wildcat), herpestid (yellow mongoose, common slender mongoose, meerkat), hyaenid (aardwolf), mustelid (striped polecat), viverrid (common genet, Cape genet); Rodentia: sciurid (Cape ground squirrel, Smith's bush squirrel)		

Parasite morphology: *Haemaphysalis* spp. form 4 different types of morphological stages during their developmental cycles: namely, eggs, larvae, nymphs and adults. The eggs are shiny brown spherical stages measuring around 0.5 mm in diameter. Larvae (sometimes known as seed ticks) are somewhat dorsoventrally flattened and oval-pyriform in dorsal profile measuring 0.5-0.6 mm long. They are usually yellow to brown, but become darker in colour after feeding. They have a conspicuous capitulum (head) with anterior mouthparts, and a larger posterior idiosoma (body) with 3 pairs of long pale legs arising ventrally. Larvae lack respiratory openings (stigmata) and tracheae (respiration and fluid regulation occurs through the cuticle). Nymphs have discoid-ovoid bodies that are flattened ventrally and slightly convex dorsally. They are larger and darker than larvae, and may swell up to 1-2 mm in length after feeding. Nymphs have 4 pairs of long pale legs attached to the ventral idiosoma and possess a pair of lateral respiratory stigmata surrounded by round plates. Adult ticks are small in size compared to other ixodid genera, ranging in length from 2.5-3.5 mm (although engorged females may grow up to 8-9 mm long). Unfed adults are usually yellow-brown to red-brown in colour, but engorged individuals often develop blue-black bodies with dark brown legs. Adults have 2 major tagma: a small anterior capitulum (head) and a larger robust idiosoma (body). The capitulum projects forwards and is visible from above (whereas that of argasids is ventral and not visible from above). It comprises the basis capitulum (integumental ring encircling mouthparts) and the gnathosoma bearing palps and the feeding mouthparts (chelicerae and hypostome) but lacks antennae (as do all ticks). The basis capitulum is rectangular with straight lateral margins, and not triangular (like *Ixodes*), nor hexagonal (like *Rhipicephalus*/*Boophilus*) nor pentagonal (like *Bothriocroton*). The gnathosoma is retractable and has 2 short lateral palps with pronounced lateral spur-like projections at the bases of their second segments . The palps are sensory and do not enter the skin when feeding but move laterally out of the way. The mouthparts are short (around same length as basis capitulum) and are well adapted for piercing skin and sucking blood. The 2 chelicerae have tubular shafts with dentate tips and are used to cut host skin creating pools of blood in the dermis. The barbed hypostome is inserted into the pooled blood to facilitate feeding as well as to aid attachment to the host. A buccal feeding canal is formed dorsally by the chelicerae and ventrally by the hypostome and used to suck blood and inject saliva from long paired salivary glands. Blood is taken up by a muscular pharynx (with pharyngeal valve) and delivered via a short oesophagus to the large saccular midgut (ventriculus) with several pairs of blind-ending lateral diverticula (caeca). Waste from the gut and excretory Malpighian tubules is collected in a rectal sac that opens to the subterminal ventral anus. The anus is partially encircled by a posterior (metastriate) anal groove (unlike *Ixodes* which has an anterior (prostriate) anal groove). The dorsal idiosoma possesses a hard sclerotized dorsal plate (scutum) which almost completely covers males (= conscutum) but is limited to a smaller anterior shield in females. The rest of the cuticle has tiny surface patterns, sometimes with larger indentations, and a number of sensory setae and pores (openings of dermal glands and sensillae). In *Haemaphysalis* spp., the scutum (and conscutum) are plain and inornate, whereas those of *Amblyomma*/*Aponomma*, *Bothriocroton,* and some *Rhipicephalus* and *Dermacentor* spp. are ornate (with coloured patterns). The posterior body margin has a series of invaginated grooves (called festoons) which may be unclear in engorged females, but dorsal 'eyes' are not present. The ventral idiosoma gives rise to 4 pairs of well-developed pale-brown legs (without pale rings) which remain tightly folded against the body when the tick is stationary. Each leg contains 6 segments (coxae, trochanter, femur, patella (genu), tibia, and tarsus) and all end in pair of claws with pad-like pulvilli (adult argasids lack pulvilli). Haemaphysalids have a large tapering internal spur on coxae I, and short blunt internal spurs on coxae II-IV. A unique sensory structure (Haller's organ) is located on tarsus I and used to detect odours, heat and vibrations. Adults have a pair of lateral respiratory stigmata surrounded by round-comma-shaped plates located ventrally behind coxae IV (while argasids have smaller stigmata between coxae III). Adult ticks exhibit considerable sexual dimorphism in that males are smaller than females, their dorsal scutum is much larger, and females have porose areas (clusters of pores) on the dorsal aspects of their basis capituli. Males also lack ventral shields which are present in *Ixodes*, *Rhipicephalus*/*Boophilus* and *Hyalomma* spp. The male reproductive tract comprises 2 tubular testes with vas efferentia fusing to form a common vas deferens (with a large multilobed accessory gland) leading to the ejaculatory duct and genital opening (gonopore) located ventrally between coxae IV. Males lack external copulatory structures and they produce packets of spermatids (spermatophores) that they transfer to females. The female reproductive system comprises a single saccular ovary with paired tubular oviducts that join to form a common uterus leading to a bipartite vagina (with a cervical region acting as a receptaculum seminis to store spermatophores, and a vestibular region that prolapses during oviposition). The gonopore is U- or V-shaped with marginal folds and situated near the ventral midbody. During oviposition, eggs are coated with waxy waterproof secretions by the porose areas and by a special tubular accessory gland (Gene's organ) located near the female gonopore.

Site of infection: Larvae, nymphs and adults are obligate ectoparasites that attach to the skin of vertebrate hosts to feed on host blood. Infestations have been found on mammals belonging to 82 families in 22 orders (including ungulates, insectivores, shrews, lagomorphs, carnivores, rodents, marsupials, bats, primates), birds belonging to 49 passerine families and 40 non-passerine families in 24 orders (including shorebirds, waterfowl, landfowl, nightjars, doves, woodpeckers and birds of prey), reptiles belonging to 6 lizard families, 6 snake families and 2 tortoise families, as well as one amphibian family. Most *Haemaphysalis* spp. have broad host ranges, although many seem to exhibit preferences for particular hosts. Larvae and nymphs are found mostly on small mammals, birds and reptiles, whereas adult ticks infest larger mammals, including livestock. Ticks may be found anywhere on the host body, but are commonly found on the head, ears, muzzle, lower legs, axilla, escutcheon and udders.

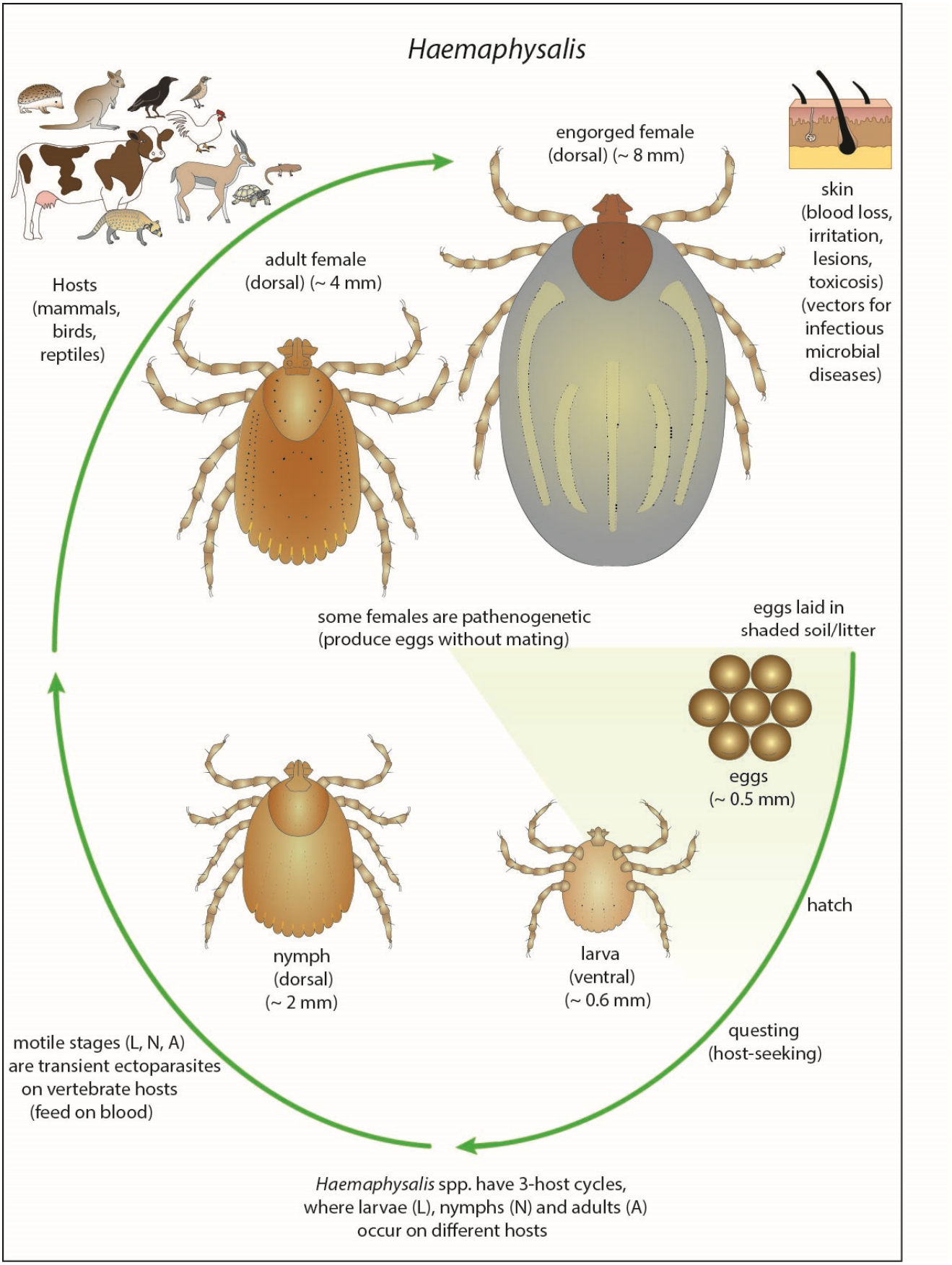
Pathogenesis: All motile developmental stages are haematophagous ectoparasites that feed only once but for extended periods over days (in contrast, argasid ticks feed transiently for short periods over minutes). Light infestations by a few larvae, nymphs or adults may go unnoticed by the host, but heavier infestations cause irritation and discomfort with skin lesions, blood loss and poor health. Feeding stages use their chelicerae to cut skin creating dermal blood pools, and then insert their hypostomes into the pools to suck blood (feeding process known as telmophagy). During feeding, ticks inject saliva (with various vaso-active compounds, including cytolytic, analgesic, anticoagulant, vasodilatory and vascular permeability activities) as well as produce proteinaceous cement (for attachment). Tick bites cause traumatic damage to skin with irritation, inflammation, erythema, oedema, pruritus, focal necrosis, haemorrhage and granuloma formation. Infestations by as few as 30 ticks may cause enough blood loss to manifest as anaemia, which may persist for several weeks. Infested animals suffer considerable tick worry, becoming listless, restless, anorexic and sometimes feverish. Heavy infestations in livestock may affect productivity due to poor growth, reduced weight gains, decreased milk yields, damaged hides due to tick punctures and host reactions, and occasional mortalities. Some animals may develop hypersensitivity reactions to bites and attempt to lick, bite, scratch or rub affected areas, sometimes causing open wounds which are prone to secondary bacterial infections. Some tick species (e.g. *H. punctata, H. inermis*) may also cause tick paralysis as their saliva contains neurotoxins which produce progressive ascending motor paralysis with hindlimb incoordination, weakness, respiratory abnormalities and death. *Haemaphysalis* spp. may also act as vectors (biological or mechanical) for the transmission of various infectious diseases. Microbes may amplify in tick tissues; most survive tick metamorphic changes (trans-stadial transmission) and some even undergo vertical transfer to tick eggs (trans-ovarian transmission). They may be transmitted during feeding (via saliva), during fluid regulation (via regurgitation) or during waste elimination (via defaecation). Various tick species have been found to transmit haemoprotozoan parasites causing babesiosis (tick fever) and theileriosis; rickettsial bacteria causing Mediterranean and Japanese spotted fevers, Boutonneuse fever, and anaplasmosis; spirochaetes causing borreliosis (relapsing fever, Lyme disease); coccobacilli causing brucellosis and tularaemia; gammaproteobacteria causing coxiellosis (Q fever); and viruses causing Russian spring-summer encephalitis, Kyasanur Forest disease, Powassan encephalitis, Crimean-Congo haemorrhagic fever, and human haemorrhagic fever (thrombocytopenia syndrome).

Developmental cycle and mode of transmission: *Haemaphysalis* spp. exhibit incomplete (hemimetabolous) metamorphosis where eggs hatch larvae which moult to nymphs and then adults. Each stage feeds on blood once and then drops off the host, so they have 3-host life-cycles as larvae, nymphs and adults parasitize 3 separate hosts (often different host species). Gravid females lay eggs in clusters in the external environment (shaded cryptic sites in vegetation or soil) where they hatch in 60-90 days depending on the temperature and humidity (longer in colder drier conditions). The emergent larvae climb vegetation where they wait for hosts (ambush strategy). When triggered by sensory cues associated with passing hosts (odours, heat, vibrations), they actively quest by waving their forelegs in the air. They may wait for hosts for several days to weeks, depending on environmental conditions (longer in colder conditions). Upon contact with a host, they crawl onto the skin and migrate to preferred attachment sites. Most species have preferred hosts and they may reject a host as unsuitable and drop off after taking a small sample meal. On suitable hosts, the larvae attach and feed to repletion on host blood for 4-6 days. They then drop to the ground and shelter in dark moist places to digest their bloodmeals over 14-30 days depending on environmental conditions (longer in cold conditions). The larvae then moult to nymphs which climb vegetation and quest for hosts over several days to months depending on prevailing climatic conditions. Like other ixodids, haemaphysalids only form one nymphal instar (whereas argasids form 2-7 nymphal instars). While all unfed stages may overwinter, nymphs commonly do so as they appear to be better able to survive cold conditions and frosts. When nymphs find a suitable host, they attach and feed on blood for around a week. When replete, they drop off the host and shelter in vegetation for up to 40 days before moulting to adult ticks. Adults climb vegetation and may quest for hosts for several day to months. Having found a suitable host, they attach and feed on blood for a week or longer, growing new cuticle to accommodate larger bloodmeals. Reproductive cycles in adult ticks are complicated as some species (or races/strains/populations) are obligate parthenogenetic triploid (females may produce fertile eggs without mating), others are bisexual diploid (females produce fertile eggs after mating), and some may be aneuploid (capable of both bisexual and parthenogenetic reproduction). Male ticks are rarely seen, as they take small meals and remain unattached while moving about searching for mates. Female ticks remain attached and engorge with host blood swelling to many times their original size before dropping off after 1-2 weeks. Gravid females lay large batches of several thousand eggs over several days, although oviposition may be delayed for several weeks in adverse cold conditions. Adult ticks do not have long life-spans and males die soon after mating while females die soon after oviposition. The duration of the whole life-cycle depends largely on prevailing environmental conditions influencing the survival and longevity of off-host stages (longer in colder climates, sometimes with diapause). Most species have annual cycles (one generation per year) in temperate regions with alternating seasons. Larvae usually develop over late summer, nymphs may develop in autumn but generally overwinter and engorge in spring, while adults develop and engorge in late spring and early summer. In more tropical warm moist regions with mild summers, some tick species may complete 2 generations each year with larvae being found in early spring as well as in summer and autumn. In temperate or polar regions with cold winters, some tick species only have one generation every 2-3 years as the successive developmental stages must overwinter each year.

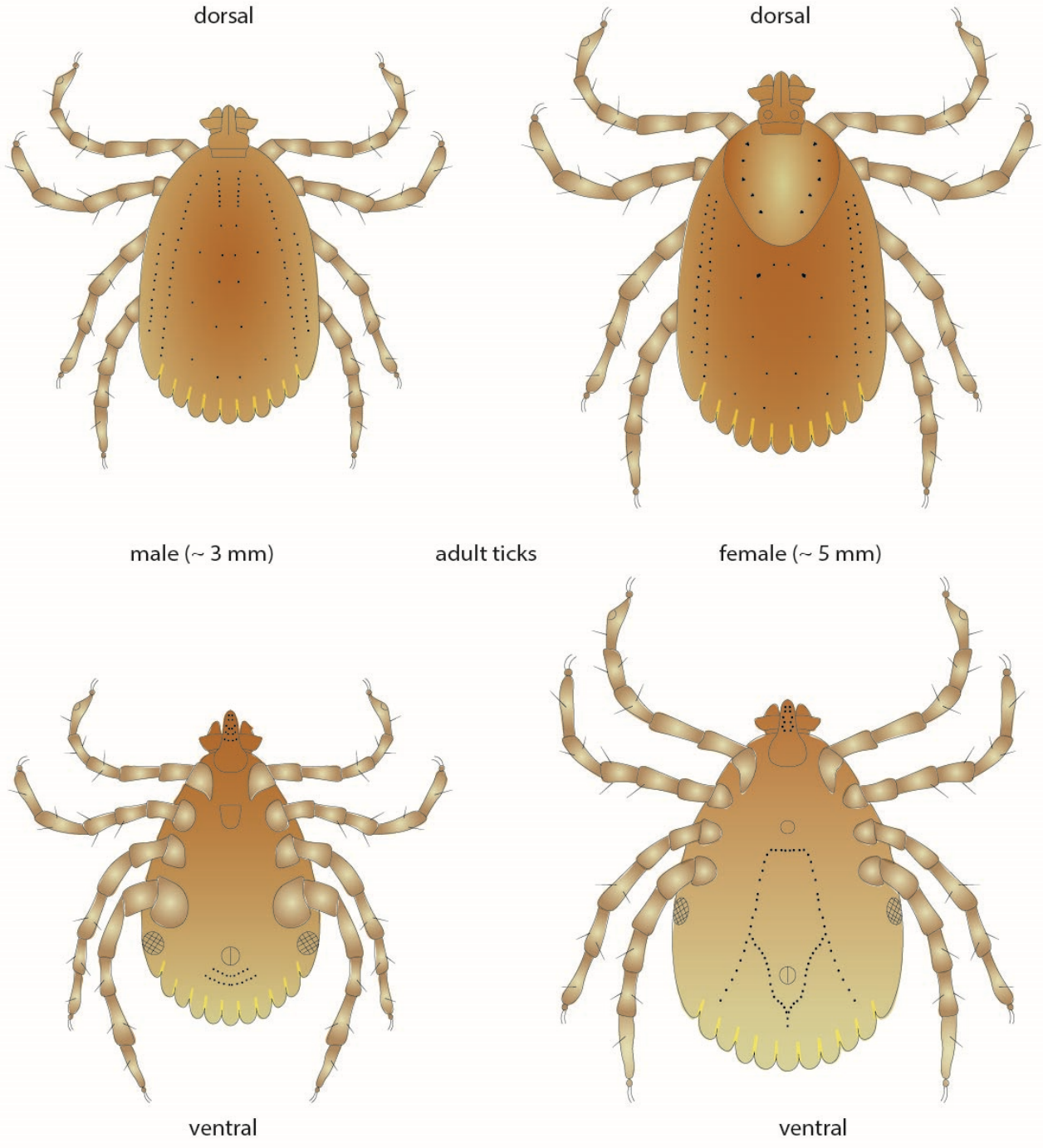
Differential diagnosis: Infestations are difficult to diagnose on clinical grounds as any symptoms and signs (skin lesions, granulomas, anaemia, anorexia) may be caused by a range of other infectious or non-infectious disease conditions. Diagnosis is generally afforded by the direct detection of attached ticks feeding on hosts. Specimens may be carefully removed and examined

microscopically for unique morphological characteristics (especially rectangular basis capituli, coxal and palpal spurs). Samples may be frozen of fixed for subsequent molecular analyses (proteins or DNA). Ticks can also be collected from the environment (pastures and bushland) by dragging blankets or using dry ice (carbon dioxide) traps. Molecular biological techniques have been used to help identify stages, strains (races) and species following polymerase chain reaction (PCR) amplification of nuclear (18S and 28S ribosomal RNA, internal transcribed spacers 1 and 2) and mitochondrial (12S and 16S ribosomal RNA, cytochrome c oxidase subunit I, nicotinamide adenine dinucleotide dehydrogenase subunit 5) gene sequences.

Treatment and control: Infestations on humans usually only involve a few ticks which may be carefully removed and the bite sites treated with disinfectants, analgesics, antipuritics and antihistamines to provide symptomatic relief and even antibiotics to prevent secondary bacterial infections. Tick removal may be accomplished using fine forceps or tweezers or special tick removal devices (ticks keys, loops, lassos, twists or V-shaped tools) but taking care not to squeeze them or break off their mouthparts (tick fluids and fragments are pro-inflammatory). Some success has been reported in removing attached ticks by applying freezing sprays or pyrethroid acaricides directly onto their backs. People at risk may discourage tick bites by using insect repellents on their skin or clothing, including diethyl-meta-toluamide (DEET), picaridin, oil of lemon eucalyptus, para-methane-diol, undecanone and permethrin. Infestations on companion animals and livestock are treated using topical or systemic acaricidal chemicals which are available in a wide range of sprays/showers, baths/dips, emulsions, dusts, pour-ons, spot-ons, injections, drenches, tablets, chewables, and impregnated collars, eartags and tailtags. Animals have been successfully treated using arsenical preparations, organochlorines (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (dioxathion, fenchlorphos), organophosphonates (chlorfenvinphos, dichlorvos, tetrachlorvinphos, trichlorfon), monothiophosphates (chlorpyrifos, coumaphos, cythioate, diazinon, fenthion, propetamphos), dithiophosphates (malathion, phosmet), carbamates (carbaryl), pyrethroids (permethrin, flumethrin, deltamethrin, decamethrin, cypermethrin, cyprothrin, alphametrin), formamidines (amitraz), macrocyclic lactones (ivermectin, selamectin), phenylpyrazoles (fipronil), chloronicotinyls (imidacloprid), isoxazolines (afoxolaner, fluralaner), some natural products (rotenone) and some insect growth regulators (methoprene, pyriproxyfen). Multiple treatments are often required as animals rapidly become re-infested, although slow-release formulations and compounds with long-lasting residual activity may help reduce treatment frequency. Unfortunately, the incorrect or over-usage of many chemicals has led to the development of acaricide resistance in many tick populations, particularly against arsenical compounds and organochlorines, as well as some organophosphates, pyrethroids and formamidines. Recommendations to combat resistance include cyclic rotation between major classes of acaricides, using co-formulations (cocktails), avoiding under-dosing and regularly screening for resistance (using *in situ* or *in vitro* egg hatch or larval/adult survival tests). Due to the time-consuming nature of these tests, studies are currently underway to develop more rapid molecular tests (such as immunoassays or DNA analyses). Pastoralists are encouraged to adopt integrated tick control programmes as haemophysalids are difficult to eradicate because they may survive on pastures for many months and may infest a wide range of reservoir hosts. Programmes should include animal health interventions (surveillance, strategic treatment, culling, cohort separation, quarantine, sensible stocking), grazing management (pasture rotation, pasture spelling/cultivation, stabling, clearing vegetation (cut, slash, burn, plough)), environmental decontamination (cleaning animal holding facilities (water, steam, disinfectants), sealing crevices in housing, applying residual acaricides (pyrethroids) to confined spaces) and wildlife control (excluding reservoir hosts (fencing, hunting, trapping), diverting migration routes, giving access to medicated supplementary feed or self-treatment devices (rubbing posts, rollers) and encouraging grooming birds such as oxpeckers). Several mathematical prediction models have also become available for producers to schedule interventions based on climatic factors (temperature, rainfall, humidity, photoperiod), location (latitude, longitude, elevation), land-use, vegetation structure, and animal husbandry. Other preventive strategies include selective breeding programmes for tick-resistant livestock, particularly involving indigenous *Bos indicus* breeds which have an innate resistance to tick infestations. A range of experimental immunological studies have also been conducted on *H. longicornis* infestations in rabbits, with variable protection being afforded following vaccination with many tick extracts, including subolesin, paramyosin, lipocalin, hexokinase, serpin, metalloprotease, cystatin and a salivary-gland associated protein (p29). Preliminary studies on biological control have investigated several predators, pests and pathogens of ticks, with indications that tick populations may be moderated by entomopathogenic fungi (*Beauveria* and *Metarhizum*), predatory antlions (*Euroleon*), and possibly by endosymbiotic bacteria (*Wolbachia*).


Haemaphysalis
Hosts
(mammals,
birds,
reptiles)
adult female
(dorsal) (~ 4 mm)
engorged female
(dorsal) (~ 8 mm)
skin
(blood loss,
irritation,
lesions,
toxicosis)
(vectors for
infectious
microbial
diseases)
some females are pathenogenetic
(produce eggs without mating)
eggs laid in
shaded soil/litter
eggs
(~ 0.5 mm)
hatch
larva
(ventral)
(~ 0.6 mm)
questing
(host-seeking)
nymph
(dorsal)
(~ 2 mm)
motile stages (L, N, A)
are transient ectoparasites
on vertebrate hosts
(feed on blood)
Haemaphysalis spp. have 3-host cycles,
where larvae (L), nymphs (N) and adults (A)
occur on different hosts

Haemaphysalis





Haemaphysalis adult



Haemaphysalis adult



Haemaphysalis larva

***Amblyomma* (includes most *Aponomma*)**
(arachnid: tick)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ticks have respiratory stigmata posterior to their legs. They are obligate blood-feeding ectoparasites on vertebrate hosts and their hypostomes are toothed and exposed. Two families are recognized: Argasidae and Ixodidae, known as soft and hard ticks, respectively. Ixodids have hard bodies with a dorsal scutum (shield-shaped plate) and the capitulum is not covered by the body. Larvae, nymphs and adults attach and feed on host blood, their life-cycles involving one, two or three hosts depending on whether moulting occurs on or off the host. Some 650 species of hard ticks infest mammals, birds and reptiles. Infestations by *Amblyomma* (incl. *Aponomma*) spp. occur as three-host ticks on mammals and reptiles, sometimes causing skin lesions and transmitting a range of microbial diseases.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on capitulum)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Ixodida (Metastigmata) (ticks, macroscopic, stigmata posterior to legs, hypostome toothed, ectoparasites)
Family: Ixodidae (hard ticks, with dorsal scutum, capitulum projects anteriorly, attach and feed on 1, 2 or 3 hosts)
Genus: *Amblyomma* (includes most *Aponomma*) (parasitic on skin of mammals/reptiles)
Species: various species cause skin lesions in mammals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial

Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on capitulum) [34 superfamilies]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs (behind coxae III or IV); and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Ticks are further characterized by macroscopic bodies with an exposed ventral hypostome (toothed with backwardly-directed barbs), chelicerae with only 2 joints, long legs with free articulated coxae (not fused to the body wall) and a complex sensory pit (Haller's organ) on tarsus I. They are obligate blood-sucking parasites which feed on terrestrial vertebrates (mammals, birds, reptiles and some amphibians) as larvae, nymphs and adults with 1-, 2- or 3-host life-cycles. Almost 1,000 species have been classified within some 20 genera from numerous wild and domesticated animals around the world. Two main families are recognized: the Argasidae containing ~200 species of 'soft' ticks with flexible leathery cuticles, ventral capitula, short feeding times (< 1 hour) and long life-spans (up to 20 years); and the Ixodidae containing ~800 species of 'hard' ticks with rigid dorsal scutal plates, anterior capitula, long feeding times (hours to days) and shorter life-span (2-6 years). Basic characteristics of representative genera considered in this resource are tabulated below.

Genus	**Capitulum**				**Idiosoma**				**Usual no. of hosts**
	location	**basis capitulum**	**mouth-parts**	**palps**	**integument**	**festoons**	**eyes**	**male ventral plates**	

Argasidae (soft ticks with leathery cuticle, stigmata between coxae III)									
Argas	ventral	triangular	short	leg-like	stippled with lateral suture	absent	absent	absent	>3
Ornithodorus	ventral	rectangular	short	leg-like	mamillated	absent	usually absent	absent	>3
Otobius	ventral	rectangular	short	leg-like	spinose (nymphs), granulated (adult)	absent	absent	absent	1
Ixodidae (hard ticks with sclerotized dorsal plate (scutum), stigmata behind coxae IV)									
Prostriata (anal groove anterior)									
Ixodes	anterior	triangular	long	long	inornate	absent	absent	present	3
Metastriata (anal groove posterior)									
Amblyomma	anterior	rectangular	long	long	ornate	present	present	indistinct	3
(*Aponomma*)	anterior	rectangular	long	long	often ornate	present	absent	absent	3
Rhipicephalus	anterior	hexagonal	short	medium	some ornate	present	present	present	3
(*Boophilus*)	anterior	hexagonal	short	short	inornate	absent	present	present	1
Dermacentor	anterior	rectangular	short	medium	often ornate	present	present	absent	3
Haemaphysalis	anterior	rectangular	short	short	inornate	present	absent	absent	3
Hyalomma	anterior	rectangular	long	long	inornate	present	present	present	2
Bothriocroton	anterior	pentagonal	long	long	ornate	present	absent	absent	3

The family Ixodidae contains 6 subfamilies (Amblyomminae, Bothriocrotoninae, Haemaphysalinae, Hyalomminae, Ixodinae and Rhipicephalinae) which vary in their morphology, biology, host ranges and specificity. [Note that some taxonomic authorities have merged the subfamilies Rhipicephalinae and Hyalomminae, while others have subsequently assigned the subfamilies Amblyomminae and Rhipicephalinae into the new family Amblyommidae, predominantly on the basis of molecular phylogenetic studies]. Hard ticks had previously been divided into 2 groups: the Prostriata (with the anal groove anterior to the anus) and the Metastriata (anal groove absent or posterior to anus). The Prostriata essentially comprises the subfamily Ixodinae with over 230 species assigned to the single extant genus *Ixodes* [plus one fossil genus (*Cornupalpatum*)], while the Metastriata contains members of the remaining subfamilies with over 600 species classified into 18 genera. The subfamily Amblyomminae comprises metastriate ornate ticks with eyes and festoons and males possess indistinct ventral plaques but lack adanal plates. It is a monotypic taxon and contains the single genus *Amblyomma,* which also includes several members (~30) of the defunct genus *Aponomma* (whereas other Australian *Aponomma* spp. have been split off into the new genus *Bothriocroton*). The genus is represented by large ticks with long mouthparts that inflict a painful bite, highly ornate bodies with iridescent patterns and long banded legs. Most are presumed to have 3-host life-cycles and over 130 species have been described in 13 subgenera: namely, *A.* (*Adenopleura*), *A.* (*Amblyomma*), *A.* (*Amerindia*), *A.* (*Anastosiella*), *A.* (*Aponomma*), *A.* (*Brasiliana*), *A.* (*Cernyomma*), *A.* (*Fifippovania*), *A.* (*Keiransiella*), *A.* (*Koloninum*), *A.* (*Macintosheilla*), *A.* (*Theileriana*), and *A.* (*Walkeriana*). Most are parasites of reptiles, but several species feed on domestic and wild mammals and marsupials and are important parasites of livestock causing dermal lesions, anaemia, toxicoses, paralysis and transmitting infectious viral, bacterial and protozoal diseases.

***Amblyomma* species**	**Hosts**	**Clinical signs**	**Distribution**
A. acutangulatum	Artiodactyla: bovid (cattle), suid (pig); Sauria: varanid (monitor)		Fiji
A. agamum	Sauria: lacertid (ocellated lizard, European green lizard); Serpentes: boid (boa constrictor), colubrid (grass snake, Aesculapian snake, Wagler's snake), viperid (jararacussu); Anura: alytid (painted frog), bufonid (Argentine toad, European green toad), ranid (edible frog); Testudines: emydid (European pond turtle), testudinid (Greek tortoise)		South America
A. (*Cernyomma*) *albolimbatum*	Sauria: scincid (sleepy lizard, Centralian blue-tongued skink, western blue-tongued lizard, bull skink, Stoke's skink,), varanid (bob-tailed goanna, lace monitor); Serpentes: elapid (eastern brown snake, dugite, gwardar, tiger snake), pythonid (northwestern carpet python); Testudines: chelid (western swamp turtle)		Australia
A. albopictum (syn. *A. haitianum*)	Sauria: iguanid (Cuban rock iguana, Andros Island iguana, Cayman Island brown iguana, blue iguana, rhinoceros iguana, Turks and Caicos rock iguana), leiocephalid (northern curly-tailed lizard); Serpentes: boid (Cuban boa); Rodentia: hystricid (tricoloured tree porcupine)		Americas
A. americanum (syn. *A. foreli, Ixodes nigua,*	Artiodactyla: bovid (cattle, sheep, goat, blackbuck), cervid (white-tailed deer, sambar deer), suid (pig), tayassuid (collared peccary); Perissodactyla: equid (horse, mule); Didelphimorphia: didelphid	trauma, irritation, toxicosis, paralysis, 'red-	North America

unipunctata) (lone star tick)	(Florida opossum, Virginia opossum); Lagomorpha: leporid (eastern cottontail, rabbit, marsh rabbit, swamp rabbit, black-tailed jackrabbit, hare); Rodentia: cricetid (hispid cotton rat, marsh rice rat), geomyid (southern pocket gopher), murid (black rat, brown rat, house mouse, white-footed mouse, Florida mouse, fulvous harvest mouse, eastern woodrat), sciurid (red squirrel, pine squirrel, eastern gray squirrel, rock squirrel, fox squirrel, Mexican ground squirrel, yellow-bellied marmot, groundhog, southeastern pocket gopher, Baird's pocket gopher); Cingulata: dasypodid (nine-banded armadillo); Carnivora: canid (dog, wolf, red wolf, coyote, red fox, gray fox), felid (cat, bobcat, Florida bobcat, ocelot, mountain lion, Florida panther), mephetid (striped skunk, Florida striped skunk, eastern spotted skunk, western hog-nosed skunk), mustelid (North American river otter, American badger, Florida mink), procyonid (raccoon, ringtail), ursid (American black bear); Primates: hominid (human); Accipitriformes: accipitrid (sparrow hawk, Swainson's hawk), cathartid (turkey vulture); Caprimulgiformes: caprimulgid (common poorwill, Chuck-Will's-widow); Ciconiiformes: ardeid (little green heron); Columbiformes: columbid (common ground dove, mourning dove); Cuculiformes: cuculid (yellow-bellied cuckoo, greater roadrunner); Falconiformes: falconid (American kestrel); Galliformes: odontophorid (northern bobwhite quail), phasianid (chicken, turkey); Gruiformes: rallid (sora), Passeriformes: cardinalid (northern cardinal, summer tanager, blue grosbeak, painted bunting), corvid (American crow), fringillid (house finch, lesser goldfinch), icterid (eastern meadowlark), laniid (loggerhead shrike), mimid (brown thrasher, northern mockingbird), parid (black-crested titmouse), parulid (ovenbird, black-throated blue warbler, Florida yellowthroat), passerellid (field sparrow, lark sparrow, rufous-crowned sparrow, eastern towhee), troglodytid (canyon wren, Bewick's wren, Carolina wren), turdid (woodthrush), tyrannid (least flycatcher, scissor-tailed flycatcher, great crested flycatcher, western wood-pewee); Strigiformes: strigid (owl) (3-host cycle)	meat' allergy (vector for rickettsial spotted fever, tularemia, Lyme disease, Q fever, ehrlichiosis, cytauxzoonosis)	
A. anicornuta	Artiodactyla: cervid (Philippine deer), suid (Philippine warty pig)		Philippines
A. annandalei	Testudines: geomydid (spiny turtle)		India
A. antillorum	Sauria: iguanid (lesser Antillean iguana, Anegada rock iguana), teiid (Dominican ground lizard); Serpentes: boid (Dominican boa), colubrid (Dominican racer)		Central America
A. argentinae (syn. *A. diemeniae*)	Anura: bufonid (cane toad); Sauria: teiid (four-toed tegu), tropidurid (spiny larva lizard, Etheridge's lava lizard); Serpentes: boid (boa, rainbow boa, yellow anaconda), viperid (jararaca pintada, Cascabel rattlesnake); Testudines: chelid (Hilaire's toadhead turtle), testudinid (Chaco tortoise); Passeriformes: turdid (Austral thrush)		South America
A. arianae	Serpentes: colubrid (Puerto Rican racer)		Central America
A. astrion	Artiodactyla: bovid (cattle, buffalo, sheep, goat), suid (pig, warthog); Proboscidea: elephantid (elephant); Afrosoricida: tenrecid (tenrec); Carnivora: canid (dog); Galliformes: phasianid (fowl)	(vector for ehrlichiosis (heartwater / cowdriosis))	Africa
A. atrogenatum	Testudines: testudinid (Indian star tortoise)		India
A. aureolatum (syn. *A. oblongum, striatum*)	Artiodactyla: bovid (cattle, goat), cervid (brown brocket, marsh deer), suid (pig); Perissodactyla: equid (horse); Didelphimorphia: didelphid (white-eared opossum, big-eared opossum, big lutrine opossum); Pilosa: bradypodid (three-toed sloth, brown-throated sloth), myrmecophagid (southern tamandua); Rodentia: caviid (capybara), ctenomyid (tuco-tuco), echimyid (Fischer's guiara), erethizontid (Bahia porcupine), sciurid (Brazilian squirrel); Carnivora: canid (dog, maned wolf, gray fox, crab-eating fox, Azara fox, Pampas fox), felid (cat, Geoffroy's cat, margay, ocelot, jaguarundi, oncilla, cougar, southern tiger cat), mustelid (lesser grison, greater grison), procyonid (South American coati, crab-eating raccoon); Primates: atelid (brown howler), hominid (human);	trauma, irritation (vector for rickettsiosis)	South America

	Accipitriformes: accipitrid (roadside hawk), Passeriformes: conopophagid (rufous gnateater), emberizid (uniform finch, buff-throated warbling finch, green-winged saltator, rufous-collared sparrow), furnariid (white-eyed foliage-gleaner, olive spinetail, pallid spinetail, grey-bellied spinetail, rufous-capped spinetail, rufous hornero), parulid (white-rimmed warbler), passerellid (half-collared sparrow, rufous-collared sparrow), thamnophilid (plain antvireo, squamate antbird, white-shouldered fire-eye, variable antshrike, rufous-capped antshrike), thraupid (uniform finch, buff-throated warbling-finch, black-and-rufous warbling-finch, ruby-crowned tanager, black-goggled tanager, green-winged saltator, double-collared seedeater), troglodytid (house wren), turdid (white-necked thrush, creamy-bellied thrush, rufous-bellied thrush, pale-breasted thrush), tyrannid (white-throated spadebill); Strigiformes: strigid (barn owl) (3-host cycle)		
A. aureum	Perissodactyla: rhinocerotid (black rhinoceros)		Africa
A. auricularium (syn. *A. beaurepairei*, *curruca*)	Artiodactyla: suid (pig), tayassuid (collared peccary); Perissodactyla: equid (horse); Cingulata: chlamyphorid (pichi, greater naked-tailed armadillo, northern naked-tailed armadillo, screaming hairy-tailed armadillo, big hairy armadillo, six-banded armadillo, southern three-banded armadillo, Brazilian three-banded armadillo), dasypodid (nine-banded armadillo, seven-banded armadillo, southern six-banded armadillo, greater long-nosed armadillo, southern long-nosed armadillo, Llanos long-nosed armadillo, dwarf armadillo); Didelphimorphia: didelphid (common opossum, white-eared opossum, gray short-tailed opossum, gray four-eyed opossum, agile gracile opossum); Pilosa: myrmecophagid (giant anteater, northern tamandua, southern tamandua); Rodentia: caviid (capybara, Spix's yellow-toothed cavy, Chacoan mara), chinchillid (plains viscacha), cricetid (hispid cotton rat, spy hocicudo), dasyproctid (Azara's agouti), echimyid (common punare, highlands punare, Sao Lourenco punare, broad-headed spiny rat, Tome's spiny rat, armored rat), erethizontid (Mexican hairy dwarf porcupine); Carnivora***: c***anid (dog, maned wolf, gray fox, crab-eating fox, hoary fox), felid (cat), mephitid (striped hog-nosed skunk), mustelid (greater grison, lesser grison), procyonid (raccoon, white-nosed coati, South American coati); Passeriformes: cardinalid (green-winged saltator, ultramarine grosbeak), furnariid (pale-legged hornero, great xenops), passerellid (rufous-collared sparrow), piprid (pale-bellied tyrant-manakin), thamnophilid (bicolored antbird, stripe-backed antbird, silvery-cheeked antshrike, Caatinga antshrike), thraupid (grey pileated finch, green-winged saltator), troglodytid (tropical wren, long-billed wren), turdid (creamy-bellied thrush, clay-coloured thrush, rufous-bellied thrush), tyrannid (fuscous flycatcher, lesser wagtail-tyrant), vireonid (rufous-browed peppershrike); Strigiformes: strigid (burrowing owl); Sauria: iguanid (unspecified iguana)		Americas
A. (*Adenopleura*) *australiense*	Monotremata: tachyglossid (long-beaked echidna, short-beaked echidna); Sauria: varanid (unspecified monitor); Serpentes (unspecified snake)		Australia
A. avecolens	Passeriformes: furnariid (wedge-billed woodcreeper), vireonid (white-eyed vireo)		South America
A. babirussae	Artiodactyla: bovid (cattle, dwarf buffalo, water buffalo), cervid (Javan rusa), suid (pig, babirusa); Perissodactyla: equid (horse); Rodentia: murid (Pacific rat, Hoffmann's Sulawesi rat); Carnivora: viverrid (Malayan civet); Primates: hominid (human)		Indonesia
A. badium	Pholidota: manid (Sunda pangolin)		Indonesia
A. barbaricum	Artiodactyla: bovid (buffalo)		Africa
A. barbouri (syn. *Aponomma*)	Serpentes: pythonid (reticulated python)		Indonesia
A. bengalense	Serpentes: pythonid (python)		India
A. bibroni	Sauria: iguanid (rhinoceros iguana); Serpentes: boid (boa), colubrid		South America

(syn. *A. adspersum, deminutivum, irroratum*)	(yellow rat snake, banded cat-eyed snake, Wagler's snake), viperid (jararacussu, Wagler's pit viper); Anura (unspecified frog)		
A. birmitum	fossil (amber)		Myanmar
A. boeroi	Artiodactyla: tayassuid (Chacoan peccary)		South America
A. boneti	Sauria: iguanid (iguana)		North America
A. boulengeri	Sauria: iguanid (marine iguana, Galapagos land iguana), tropidurid (Galapagos lava lizard, Hood lava lizard)		Galapagos Islands
A. bouthieri	Carnivora: canid (dog)		Africa
A. brasiliense (syn. *A. superbrasiliense*)	Artiodactyla: cervid (pampas deer, red brocket, grey brocket), suid (pig), tayassuid (collared peccary, white-lipped peccary); Perissodactyla: tapirid (South American tapir); Rodentia: caviid (capybara), cuniculid (lowland paca), dasyproctid (Azara's agouti); Pilosa: myrmecophagid (giant anteater, southern tamandua); Didelphimorphia: didelphid (big-eared opossum); Carnivora: canid (dog, maned wolf, gray fox, crab-eating fox), felid (cougar, jaguar), procyonid (South American coati); Primates: hominid (human); Accipitriformes: accipitrid (black-and-white hawk-eagle); Coraciiformes: momotid (rufous-capped motmot), Galliformes: cracid (dusky-legged guan, rusty-margined guan); Gruiformes: rallid (slaty-breasted woodrail); Passeriformes: passerellid (rufous-collared sparrow), piprid (blue manakin), thamnophilid (white-shouldered fire-eye), thraupid (ruby-crowned tanager, black-goggled tanager)		South America
A. (*Cernyomma*) *breviscutatum* (syn. *A. cyprium*)	Artiodactyla: bovid (cattle, banteng, buffalo, water buffalo), cervid (Javan rusa), suid (pig, New Guinea pig, Celebes warty pig); Perissodactyla: equid (horse); Diprotodontia: phalangerid (northern common cuscus); Scandentia: tupaiid (Mindanoi treeshrew); Rodentia: murid (black rat, Polynesian rat); Carnivora: canid (dog); Primates: hominid (human); Columbiformes: columbid (common emerald dove); Coraciiformes: alcedinid (collared kingfisher); Galliformes: phasianid (red junglefowl); Trogoniformes: trogonid (Philippine trogon); Testudines: cheloniid (unspecified tortoise), geoemydid (black-breasted leaf turtle, keeled box turtle)		Australia, New Guinea
A. brimonto	Testudines: testudinid (yellow-footed tortoise)		Africa
A. caelaturum	Testudines: geomydid (spiny turtle)		Indonesia
A. cajennense (syn. *I. cayennense, crenatus, herrerae*) (Cayenne tick)	Artiodactyla: bovid (cattle, buffalo, water buffalo, sheep, goat), cervid (white-tailed deer, rainforest white-tailed deer, Apara brocket deer, red brocket, brown brocket), suid (pig), tayassuid (collared peccary, white-lipped peccary); Perissodactyla: equid (horse, donkey, mule), tapirid (Baird's tapir, South American tapir); Pilosa: bradypodid (pale-throated sloth), myrmecophagid (giant anteater, southern tamandua); Cingulata: chlamyphorid (six-banded armadillo), dasypodid (nine-banded armadillo); Didelphimorphia: didelphid (common opossum, white-eared opossum, Guianan white-eared opossum, bare-tailed woolly opossum, brown four-eyed opossum); Lagomorpha: leporid (rabbit, eastern cottontail); Rodentia: caviid (guinea pig, capybara), cricetid (long-whiskered rice rat), cuniculid (lowland paca), dasyproctid (agouti, orange agouti, Azara's agouti), echimyid (armored rat, Tome's spiny rat), murid (unspecified rat), sciurid (Mexican gray squirrel); Carnivora: canid (dog, coyote, gray fox, Azara fox, crab-eating fox), felid (cat, ocelot, puma, jaguar, Mexican lion), mustelid (giant otter), procyonid (raccoon, crab-eating raccoon, South American coati); Chiroptera: phyllostomid (Jamacian fruit bat, Heller's broad-nosed bat); Primates: atelid (red-faced spider monkey, Columbian red howler), hominid (human); Accipitriformes: accipitrid (roadside hawk, harpy eagle); Apodiformes: trochilid (Planalto hermit, white-vented violetear, glittering-bellied emerald, sapphire-spangled emerald, fork-tailed woodnymph); Cariamiformes: cariamid (red-legged seriema); Ciconiiformes: ardeid (heron); Columbiformes: columbid (grey-fronted dove); Cuculiformes: cuculid (great lizard cuckoo); Falconiformes: falconid (falcon); Galliformes: cracid	trauma, irritation, fever (vector for rickettsial spotted fever, leptospirosis)	Americas

	(great curassow, bare-faced curassow, crested guan, rufous-vented chachalaca), odontophorid (northern bobwhite quail), phasianid (chicken, turkey); Passeriformes: dendrocolatid (olivaceous woodcreeper, lesser woodcreeper), emberizid (masked yellowthroat), formicariid (variable antshrike, rufous-winged antshrike, plain antvireo, black-capped antwren, white-shouldered fire-eye, rufous gnat-eater), furnariid (rufous-capped spinetail, sooty-fronted spinetail, buff-browed foliage-gleaner, white-eyed foliage-gleaner, sharp-tailed streamcreeper), muscicapid (sooty thrush, rufous-bellied thrush, creamy-bellied thrush, pale-breasted thrush, white-collared blackbird), parulid (flavescent warbler, white-bellied warbler), passerellid (rufous-collared sparrow, saffron-billed sparrow), piprid (blue manakin, blue-backed manakin, pin-tailed manakin, greenish manakin), thraupid (bananaquit, green-winged saltator, cinnamon tanager, white-banded tanager, ruby-crowned tanager, black-goggled tanager, red-necked tanager, burnished buff-tanager, blue dacnis, uniform finch, stripe-tailed yellow-finch, serra finch, blue-black grassquit, double-collared seedeater), troglodytid (house wren), turdid (pale-breasted thrush), tyrannid (olivaceous elaenia, plain-crested elaenia, lesser elaenia, highland elaenia, grey-hooded flycatcher, sepia-capped flycatcher, mottle-cheeked tyrannulet, pearly-vented tody-tyrant, yellow-olive flatbill, white-throated spadebill, bran-coloured flycatcher, Euler's flycatcher, fuscous flycatcher, short-crested flycatcher), vireonid (rufous-browed peppershrike, rufous-crowned greenlet, red-eyed vireo); Pelecaniformes: ardeid (unspecified heron); Piciformes: picid (white-barred piculet), ramphastid (toco toucan); Strigiformes: strigid (striped owl); Struthioniformes: struthionid (ostrich); Tinamiformes: tinamid (red-winged tinamou); Sauria: iguanid (green iguana, black spiny-tailed iguana), teiid (whiptail); Serpentes: colubrid (indigo snake), viperid (rattlesnake); Testudines: emydid (common box turtle, pond slider), geoemydid (furrowed wood turtle), pelomedusid (side-necked turtle), podocnemid (yellow-spotted river turtle), testudinid (yellow-footed tortoise); Crocodilia: crocodylid (American crocodile); Anura: bufonid (cane toad) (3-host cycle)		
A. (*Cernyomma*) *calabyi*	Sauria: varanid (perentie, sand goanna)		Australia
A. calcaratum (syn. *A. leucozomum*)	Artiodactyla: cervid (red brocket); Perissodactyla: tapirid (South American tapir); Pilosa: choloepodid (Hoffman's two-toed sloth), cyclopedid (silky anteater), myrmecophagid (giant anteater, lesser anteater, two-toed anteater, southern tamandua, northern tamandua, long-tailed tamandua); Carnivora: canid (dog), procyonid (crab-eating raccoon); Chiroptera: phyllostomid (shadowy broad-nosed bat, long-legged bat); Primates: hominid (human); Accipitriformes: accipitrid (roadside hawk); Caprimulgiformes: trochilid (scale-throated hermit, long-tailed hermit); Coraciiformes: momotid (rufous motmot, rufous-capped motmot); Passeriformes: cardinalid (green-winged saltator, blue black grosbeak), conopophagid (rufous gnateater, black-cheeked gnateater), emberizid (pectoral sparrow, saffron-billed sparrow, red-pileated finch, thick-billed seed finch), furnariid (ochre-crested foliage-gleaner, white-collared foliage-gleaner, white-eyed foliage-gleaner, buff-browed foliage-gleaner, white-throated woodcreeper, wedge-billed woodcreeper, red-billed woodcreeper, ocellated woodcreeper, Brigida's woodcreeper, Planalto woodcreeper, rufous hornero), mimid (chalk-browed mockingbird), parulid (masked yellowthroat, golden-crowned warbler), passerellid (saffron-billed sparrow, pectoral sparrow), piprid (red-capped manakin, band-tailed manakin, blue manakin, blue-crowned manakin, blue-tailed manakin, white-crowned manakin, white-bearded manakin), thamnophilid (common scale-backed antbird, spot-backed antbird, dusky-tailed antbird, white-		South America

	cheeked antbird, spot-backed antbird, bicolored antbird, white-shouldered fire-eye, black-crowned antshrike, white-shouldered antshrike, fasciated antshrike, tufted antshrike, variable antshrike, Planalto slaty antshrike, streak-capped antwren, plain antvireo), thraupid (chestnut-headed tanager, ruby-crowned tanager, silver-beaked tanager, black-goggled tanager, burnished-buff tanager, palm tanager, Sayaca tanager, red pileated finch, black-and-rufous warbling finch, thick-billed seed-finch, green-winged saltator, buffy-fronted seedeater, sooty grassquit), tityrid (greenish schiffornis), troglodytid (house wren, Cabani's wren, southern nightingale-wren), turdid (white-necked thrush, rufous-bellied thrush, creamy-bellied thrush, pale-breasted thrush, clay-coloured thrush, eastern slaty thrush, wood thrush, Swainson's thrush), tyrannid (fuscous flycatcher, brown-crested flycatcher, short-crested flycatcher, rusty-fronted tody-flycatcher, Euler's flycatcher, ochre-bellied flycatcher, gray-hooded flycatcher, sepia-capped flycatcher, ochre-faced tody-flycatcher, pearly-vented tody-tyrant, white-throated spadebill, large-headed flatbill, gray-hooded attila), vireonid (rufous-browed peppershrike, rufous-crowned greenlet); Piciformes: bucconid (white-whiskered puffbird); Strigiformes: strigid (spectacled owl)		
A. calcaris	Primates: hominid (human)		China
A. castanedai	Sauria: iguanid (iguana)		Mexico
A. chabaudi	Testudines: testudinid (spider tortoise, radiated tortoise, serrated hinge-back tortoise); Lagomorpha: leporid (rabbit)		Madagascar
A. clypeolatum	Serpentes: boid (boa); Testudines: testudinid (Indian star tortoise, serrated hinge-back tortoise)		Asia
A. coelebs (syn. *A. bispinosum*)	Artiodactyla: bovid (cattle), cervid (red brocket), suid (pig), tayassuid (white-lipped peccary, collared peccary); Perissodactyla: equid (horse), tapirid (South American tapir, Baird's tapir); Cingulata: dasypodid (nine-banded armadillo); Didelphimorphia: didelphid (common opossum, white-eared opossum, big-eared opossum, big lutrine opossum, brown four-eyed opossum); Lagomorpha: leporid (common tapeti); Pilosa: megalonychid (sloth), myrmecophagid (anteater); Rodentia: caviid (capybara), cricetid (common bristly mouse, Cerrado climbing mouse), cuniculid (lowland paca), dasyproctid (Azara's agouti), echimyid (common punare); Carnivora: canid (crab-eating fox), felid (cougar, jaguar, jaguarundi), mustelid (tayra), procyonid (white-nosed coati, South American coati); Primates: cebid (large-headed capuchin), hominid (human); Accipitriformes: accipitrid (gray-lined hawk, white-necked hawk); Columbiformes: columbid (white-tipped dove); Coraciiformes: momotid (rufous-capped motmot, Amazonian motmot); Passeriformes: conopophagid (rufous gnateater), mitrospingid (dusky-faced tanager), piprid (red-capped manakin, long-tailed manakin), thamnophilid (black-spotted bare-eye, East Amazon fire-eye, Planalto slaty antshrike), turdid (creamy-bellied thrush, rufous-bellied thrush, white-necked thrush, pale-breasted thrush); Piciformes: bucconid (white-whiskered puffbird, crescent-chested puffbird)		South America
A. cohaerens	Artiodactyla: bovid (cattle, buffalo, forest buffalo, sheep, goat, waterbuck, harnessed bushbuck, eland), hippopotamid (hippopotamus), suid (warthog); Perissodactyla: rhinocerotid (black rhinoceros); Proboscidea: elephantid (elephant); Rodentia: murid (house mouse, tree rat, Macmillan's thicket rat), thryonomyid (greater cane rat); Carnivora: hyaenid (hyena), viverrid (Cape genet); Primates: cercopithecid (olive baboon), hominid (human); Galliformes: numidid (helmeted guineafowl), phasianid (Clapperton's francolin); Passeriformes: turdid (Kurrichane thrush); Testudines (unspecified tortoise)		Africa
A. compressum (syn. *A. javanense cuneatum*)	Artiodactyla: bovid (harnessed bushbuck, black duiker), suid (giant forest hog); Hyracoidea: procaviid (western tree hyrax); Pholidota: manid (giant pangolin, long-tailed pangolin, tree pangolin);		Africa

	Rodentia: hystricid (African brush-tailed porcupine); Bucerotiformes: bucerotid (hornbill); Ciconiiformes: bucorvid (hornbill); Galliformes: numidid (black guineafowl, plumed guineafowl); Musophagiformes: musophagid (Guinea turaco); Sauria: varanid (Nile monitor)		
A. concolor (syn. *I. auricularis*)	Cingulata: dasypodid (big hairy armadillo, southern three-banded armadillo, Brazilian three-banded armadillo, nine-banded armadillo); Carnivora: mephitid (hog-nosed skunk), mustelid (badger)		South America
A. cordiferum	Artiodactyla: bovid (water buffalo), suid (pig); Pholidota: manid (pangolin); Rodentia: caviid (guinea pig), murid (black rat, Malaysian wood rat, Malayan field rat, Muller's giant Sunda rat); Primates: hominid (human); Crocodilia: alligatorid (Cuvier's dwarf caiman), crocodylid (saltwater crocodile); Sauria: varanid (monitor); Serpentes: colubrid (beauty rat snake, Sulawesi black racer, king rat snake Oriental rat snake), elapid (king cobra), pythonid (reticulated python, ball python, Sumatran short-tailed python); Testudines: geoemydid (snake-eating turtle)		Asia
A. (*Aponomma*) *crassipes*	Artiodactyla: bovid (cattle); Pholidota: manid (pangolin); Rodentia: hystricid (porcupine), sciurid (ground squirrel); Scandentia: tupaiid (treeshrew); Carnivora: canid (dog), mustelid (weasel), viverrid (civet); Sauria: varanid (desert monitor, Asian water monitor); Serpentes: boid (green anaconda), elapid (banded krait), pythonid (reticulated python, black-tailed python)		Asia
A. crassum	Testudines: geoemydid (brown wood turtle), kinosternid (white-lipped mud turtle), testudinid (red-footed tortoise, yellow-footed tortoise); Cingulata: dasypodid (nine-banded armadillo)		South America
A. crenatum (syn. *A. subluteum*)	Perissodactyla: rhinocerotid (black rhinoceros, Javan rhinoceros)		Asia
A. cruciferum	Sauria: iguanid (rhinoceros iguana, mona ground iguana)		Central America
A. curruca (syn. *A. beaurepairei*)	Cingulata: dasypodid (nine-banded armadillo)		South America
A. darlingi	Artiodactyla: cervid (white-tailed deer); Carnivora: canid (dog); Accipitriformes: cathartid (black vulture); Galliformes: cracid (great curassow)		South America
A. darwini (incl. subspp. *darwini, wollebaeki*)	Sauria: iguanid (marine iguana), tropidurid (Galapagos lava lizard); Charadriiformes: scolopacid (least sandpiper)		Galapagos Islands
A. diemeniae	Serpentes: elapid (eastern brown snake)		Europe (zoo)
A. dissimile (syn. *A. bibronii*, *cubanum, flavidus, infumatum*, *Aponomma thumbi, Ixodes boarum, humanus, pulchellus, testudinis*)	Artiodactyla: bovid (cattle, sheep), cervid (marsh deer), tayassuid (peccary); Perissodactyla: equid (horse); Didelphimorphia: didelphid (common opossum, white-eared opossum, gray four-eyed opossum, gray short-tailed opossum, woolly mouse opossum, Linnaeus's mouse opossum); Rodentia: capromyid (hutia), caviid (capybara, Brazilian guinea pig), cricetid (terraced rice rat, cotton mouse), dasyproctid (red-rumped agouti, Central American agouti), echimyid (common punare, Tome's spiny rat), erethizontid (prehensile-tailed porcupine); Carnivora: canid (dog, crab-eating fox, South American fox), procyonid (white-nosed coati); Pilosa: bradypodid (pale-throated sloth), choleopodid (Linnaeus's two-toed sloth); Primates: hominid (human); Anura: bufonid (South American common toad, western giant toad, eastern giant toad, granular toad, lesser granulated toad, Chaco granulated toad, cane toad, cururu toad, rococo toad, tropical toad, Cuban toad, Jimi's toad); Crocodilia: alligatorid (spectacled caiman, Yacare caiman), crocodylid (American crocodile, Morelet's crocodile); Sauria: corytophanid (common basilisk), dactylid (grass anole), gekkonid (tropical house gecko), iguanid (green iguana, black iguana, Andros iguana, northeastern spiny-tail iguana, black spiny-tailed iguana, Utila spiny-tail iguana, Mexican spiny-tail iguana, rhinoceros		Americas, Africa

	iguana, Turks and Caicos rock iguana, northern Bahamian rock iguana), phrynosomatid (green spiny lizard, eastern fence lizard, horned lizard), teiid (green amieva, khaki amieva, giant amieva, Gaige's rainbow lizard, gold tegu), tropidurid (neotropical lava lizard, northern curly-tailed lizard), varanid (Bengal monitor); Serpentes: boid (boa, rainbow boa, brown rainbow boa, garden tree boa, mangrove tree boa, northern boa, Argentine boa, Bahamian boa, Hispaniolan boa, Mexican boa, green anaconda, yellow anaconda), colubrid (corn snake, black rat snake, tiger rat snake, indigo snake, falcon indigo snake, cobra-cipo, false water cobra, Shaw's dark ground snake, common king snake, banded cat-eyed snake, rhombic cat-eyed snake, Boddaert's tropical racer, Rio tropical racer, Baron's green racer, two-coloured massurana, green vine snake, brown vine snake, Daudin's vine snake, pine snake, ratonel, Brazilian sipo, Wagler's sipo, Wagler's snake, Shropshire's puffing snake, chicken snake, Amazon whip snake, Amazon false fer-de-lance, Japanese striped snake, South American hog-nosed snake, crowned false boa, black false boa, neotropical snail-eater, neotropical blunt-headed treesnake, royal ground snake, Shaw's dark ground snake, Norman's keelback, Mato Grosso burrowing snake, Argentine pampas snake, Troschel's pampas snake), elapid (short-tailed coral snake, Caatinga coral snake), viperid (fer-de-lance, jararaca, Martinique lancehead, eastern diamondback rattlesnake, pygmy rattlesnake, Cascabel rattlesnake, South American bushmaster, crossed pit viper, Wagler's pit viper); Testudines: chelid (big-headed pantanal swamp turtle, Geoffroy's side-necked turtle), emydid (northern map turtle, Spanish pond turtle, furrowed wood turtle, painted wood turtle, Mexican spotted wood turtle, common box turtle, Mexican box turtle, pond slider, Mediterranean pond turtle, red-eared slider), geoemydid (black-breasted leaf turtle, Indian black turtle, furrowed wood turtle, painted wood turtle, Colombian wood turtle, Mexican spotted wood turtle), kinosternid (white-lipped mud turtle, scorpion mud turtle, Tabasco mud turtle), pelomedusid (marsh terrapin), podocnemid (river tortoise), testudinid (elongated tortoise, red-footed tortoise, yellow-footed tortoise, African spurred tortoise, Chaco tortoise); Ciconiiformes: ardeid (boat-billed heron); Passeriformes: parulid (Connecticut warbler), thamnophilid (white-flanked antwren, black-crowned antshrike); Pelecaniformes: ardeid (boat-billed heron); Psittaciformes: psittacid (blue-winged macaw)		
A. (*Aponomma*) *draconis*	Sauria: varanid (Komodo dragon)		Indonesia
A. dubitatum (syn. *A. cooperi, lutzi, ypsilophorum*)	Artiodactyla: bovid (cattle, buffalo), cervid (chital, brown brocket), suid (pig), tayassuid (white-lipped peccary); Perissodactyla: equid (horse), tapirid (South American tapir); Pilosa: myrmecophagid (giant anteater, southern tamandua); Didelphimorphia: didelphid (common opossum, white-eared opossum, big-eared opossum, big lutrine opossum, yellow-sided opossum); Lagomorpha: leporid (European hare); Rodentia: caviid (capybara, Brazilian guinea pig), chinchillid (plains viscacha), cricetid (Azara's grass mouse, large-headed rice rat, Maracaju oryzomys, greater marsh rat, hairy-tailed bolo mouse, climbing mouse, small-footed bristly mouse, dark hocicudo, yellow pygmy rice rat, Argentine swamp rat, Waterhouse's swamp rat), echimyid (highlands punare, Paraguayan punare), erethizontid (Paraguayan hairy dwarf porcupine), myocastorid (coypu); Carnivora: canid (dog, maned wolf, crab-eating fox), felid (cougar), procyonid (South American coati, crab-eating raccoon); Chiroptera: phyllostomid (Pallas's long-tongued bat); Primates: atelid (black howler, brown howler), hominid (human); Passeriformes: fringillid (European goldfinch), furnariid (rufous hornero), passerellid (rufous-collared sparrow), turdid (rufous-bellied thrush); Rheiformes: rheid (greater rhea); Strigiformes: strigid (tropical screech owl)	(possible vector of rickettsioses)	Europe, South America

A. eburneum	Artiodactyla: bovid (cattle, buffalo, eland, antelope), giraffid (giraffe), suid (pig); Perissodactyla: rhinocerotid (rhinoceros); Carnivora: felid (lion); Sauria: varanid (tree monitor, water monitor, Nile monitor)		Africa
A. (*Cernyomma*) *echidnae*	Monotremata: tachyglossid (short-beaked echidna); Squamata (unspecified reptile)		Australia
A. (*Aponomma*) *elaphense*	Rodentia: murid (rat); Serpentes: colubrid (Trans-Pecos rat snake, black rat snake, pine snake, Texas lyre snake), viperid (black-tailed rattlesnake)		North America
A. elephantinum	Proboscidea: elephantid (Indian elephant)		India
A. (*Aponomma*) *exornatum* (syn. *A. arcanum, flavomaculatum, halli, Ixodes varani*)	Artiodactyla: bovid (cattle, goat, suni), suid (desert warthog); Pholidota: manid (tree pangolin); Rodentia: sciurid (striped ground squirrel, spiny-tailed squirrel, Lord Derby's scaly-tailed squirrel); Carnivora: canid (dog), herpestid (yellow mongoose); Chiroptera: pteropodid (straw-coloured fruit bat); Accipitriformes: accipitrid (black-chested snake eagle); Sauria: iguanid (iguana), scincid (giant legless skink), varanid (perentie, savannah monitor, rock monitor, Nile monitor, yellow-spotted monitor); Serpentes: boid (boa), elapid (Egyptian cobra, black-necked spitting cobra, rinkhals), pythonid (ball python, reticulated python, Central African rock python), viperid (snouted night adder, puff adder); Crocodilia: crocodylid (Nile crocodile); Testudines: testudinid (leopard tortoise, Bell's hinge-back tortoise)		Africa, Australia
*A. extraoculatum (*syn. *A. romitii, tasquei*)	Rodentia: caviid (capybara); Didelphimorphia: didelphid (opossum)		South America, Africa, Asia
A. (*Aponomma*) *fimbriatum* (syn. *Aponomma ecinctum, simplex, trabeatum, pulchrum, undatum fimbriatum*)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Monotremata: tachyglossid (short-beaked echidna); Galliformes: phasianid (chicken, Bulwer's pheasant); Sauria: agamid (frill-necked lizard), varanid (perentie, sand goanna, Rosenberg's goanna, lace monitor, black-headed monitor, yellow-spotted monitor, roughneck monitor, Asian water monitor, mangrove monitor); Serpentes: colubrid (green tree snake), elapid (eastern brown snake, gwardar, dugite, red-bellied black snake, mainland tiger snake, coastal taipan, rough-scaled snake), hydrophiid (sea snake), pythonid (amethystine python, black-headed python, carpet python, olive python, reticulated python, water python, woma python), typhlopid (proximus blind snake)	(possible vector for rickettsioses, tularaemia)	Australasia
A. foai	Perissodactyla: rhinocerotid (rhinoceros)		Africa
A. fulvum	Serpentes: boid (green anaconda)		South America
A. furcosum (syn. *A. decoratum*)	Sauria: varanid (Asian water monitor); Serpentes: colubrid (mangrove snake, oriental rat snake), pythonid (reticulated python, Burmese python); Testudines: geoemydid (giant Asian pond turtle)		Indonesia, Philippines
A. (*Aponomma*) *fuscolineatum*	Serpentes: pythonid (reticulated python, black-tailed python)		Asia
A. fuscum	Didelphimorphia: didelphid (big-eared opossum, white-eared opossum, woolly mouse-opossum, brown four-eyed opossum, gray short-tailed opossum); Cingulata: dasypodid (nine-banded armadillo, seven-banded armadillo); Rodentia: cricetid (montane grass mouse, small-footed bristly mouse, terraced rice rat, russet rice rat, hucicudo), echimyid (Sao Lourenco punare), sciurid (Brazilian squirrel); Carnivora: canid (dog, crab-eating fox), felid (southern tiger cat); Primates: hominid (human); Sauria: teiid (golden tegu, Argentine black-and-white tegu); Serpentes: boid (boa), colubrid (indigo snake, black mussurana); Crocodilia: alligatorid (broad-snouted caiman); Anura: bufonid (Argentine toad)		Central America
A. geayi	Didelphimorphia: didelphid (common opossum, gray four-eyed opossum, Eaton's opossum, Derby's woolly opossum, brown-eared woolly opossum, Robinson's mouse opossum); Pilosa: bradypodid (brown-throated sloth, pale-throated sloth), choloepodid (two-toed sloth, Hoffman's two-toed sloth), cyclopedid (silky anteater), myrmecophagid (northern tamandua, southern tamandua);		South America

	Rodentia: echimyid (Tome's spiny rat), erethizontid (Brazilian porcupine); Chiroptera: phyllostomid (great fruit-eating bat); Primates: atelid (Amazon black howler, mantled howler monkey), callitrichid (pied tamarin); Columbiformes: columbid (grey-chested dove); Coraciiformes: momotid (rufous motmot); Passeriformes: cardinalid (blue-black grosbeak), fringillid (thick-billed euphonia), furnariid (Hoffmanns's woodcreeper, wedge-billed woodcreeper, red-billed woodcreeper, chestnut-rumped woodcreeper), passerellid (black-striped sparrow), piprid (red-capped manakin, blue-backed manakin, white-crowned manakin, white-bearded manakin, golden-collared manakin, crimson-hooded manakin, wire-tailed mankin), thamnophilid (bicolored antbird, black-headed antbird, common scale-backed antbird, cinereous antshrike, black-crowned antshrike, barred antshrike), thraupid (grey-headed tanager), turdid (white-necked thrush, black-billed thrush, pale-breasted thrush), tyrannid (bright-rumped attila, sepia-capped flycatcher, ochre-bellied flycatcher, olivaceous flatbill); Piciformes: ramphastid (channel-billed toucan); Strigiformes: strigid (tropical screech owl); Sauria: iguanid (green iguana); Serpentes: colubrid (tiger rat snake); Crocodilia: alligatorid (spectacled caiman); Testudines: testudinid (yellow-footed tortoise)		
A. gemma	Artiodactyla: bovid (cattle, buffalo, sheep, goat, bushbuck, waterbuck, impala, eland, greater kudu, lesser kudu, gnu, fringe-eared oryx, East African oryx), camelid (camel), giraffid (giraffe), suid (desert warthog); Perissodactyla: equid (horse, donkey, mule, plains zebra), rhinocerotid (black rhinoceros); Rodentia: sciurid (ground squirrel); Lagomorpha: leporid (hare); Carnivora: felid (lion), herpestid (white-tailed mongoose); Primates: hominid (human); Accipitriformes: accipitrid (hawk); Galliformes: numidid (helmeted guineafowl), phasianid (fowl); Otidiformes: otid (bustard); Passeriformes: ploceid (weaver); Struthioniformes: struthionid (ostrich); Serpentes: viperid (puff adder); Testudines: testudinid (leopard tortoise) (3-host cycle)	trauma, irritation (vector for ehrlichiosis)	Africa
A. geochelone	Testudines: testudinid (ploughshare tortoise)		Madagascar
A. geoemydae (syn. *Ixodes, A. caelaturum, formosanum, malayanum*)	Artiodactyla: bovid (unspecified), cervid (unspecified), suid (pig); Pholidota: manid (Indian pangolin); Scandentia: tupaiid (common treeshrew, large treeshrew); Rodentia: hystricid (porcupine), sciurid (unspecified); Carnivora: canid (unspecified), felid (marbled cat), mustelid (unspecified), viverrid (small-toothed palm civet, banded palm civet); Primates: hominid (human); Bucerotiformes: bucerotid (black hornbill); Coraciiformes: alcedinid (Oriental dwarf kingfisher, banded kingfisher), ardeid (black bittern); Cuculiformes: cuculid (greater coucal); Galliformes: phasianid (long-billed partridge); Passeriformes: corvid (crested jay), megalaimid (red-throated barbet), pellorneid (large wren-babbler), pittid (giant pitta, Indian pitta, blue-winged pitta, hooded pitta), timaliid (gray-headed babbler), turdid (dark-sided thrush); Sauria: varanid (desert monitor, Asian water monitor, Dumeril's monitor); Serpentes: colubrid (Ryukyu odd-toothed snake, Pryer's keelback, Ryukyu green snake), elapid (unspecified), pythonid (reticulated python); Testudines: geoemydid (snake-eating turtle, yellow-marginated box turtle, Amboina box turtle, Chinese box turtle, Indochinese box turtle, keeled box turtle, Asian leaf turtle, Ryukyu black-breasted leaf turtle, black-breasted leaf turtle, yellow-headed temple turtle, Arakan forest turtle, spiny turtle, Japanese pond turtle, yellow pond turtle, Chinese pond turtle, Indian black turtle), testudinid (Asian forest tortoise, elongated tortoise, Forsten's tortoise, Asian forest tortoise, impressed tortoise)		Asia
A. gertschi	Pilosa: bradypodid (pale-throated sloth, Hoffmann's three-toed sloth)		South America
A. (*Aponomma*) *gervaisi*	Artiodactyla: bovid (gayal, bharal), suid (Indian boar); Pholidota: manid (pangolin); Rodentia: anomalurid (scaly-tailed squirrel);		Eurasia, Africa

(syn. *Ixodes ophiophilus, varanensis*)	murid (rat), sciurid (ground squirrel); Carnivora: canid (wolf, jackal), mustelid (smooth-coated otter); Chiroptera: pteropodid (straw-coloured fruit bat); Anseriformes: anatid (pygmy goose); Sauria: agamid (oriental garden lizard), varanid (savannah monitor, desert monitor, mangrove monitor, clouded monitor, Nile monitor, Bengal monitor, Asian water monitor); Serpentes: boid (boa, rough-scaled sand boa), colubrid (chicken snake, Oriental rat snake, Indian rat snake, snail-eater snake, checkered keelback), elapid (Indian cobra, rinkhals, banded krait), pythonid (black-headed python, reticulated python, Asian rock python), viperid (Indian krait, Russell's viper)		
A. (*Cernyomma*) *glauerti*	Sauria: varanid (twilight monitor, Kimberley rock monitor)		Australia
A. goldii	Pilosa: bradypodid (three-toed sloth), myrmecophagid (giant anteater, southern tamandua); Carnivora: canid (dog); Serpentes: boid (boa), elapid (coral snake), viperid (South American bushmaster); Anura: bufonid (cane toad, tropical toad, yellow cururu toad)		South America
A. hadanii	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse), tapirid (tapir); Carnivora: canid (dog, crab-eating fox); Primates: hominid (human)		South America
A. hainanense	Serpentes (unspecified snake)		China
A. hassalli	Artiodactyla: bovid (buffalo); Proboscidea: elephantid (elephant)		Africa
A. hebraeum (syn. *A. theileri. Ixodes poortmani*) (South African bont tick)	Artiodactyla: bovid (cattle, sheep, goat, buffalo, forest buffalo, eland, impala, roan antelope, blackbuck, duiker, blue wildebeest, suni, nyala, steenbok, greater kudu, nyala, harnessed bushbuck, Cape bushbuck), giraffid (giraffe, Cape giraffe), suid (pig, warthog); Perissodactyla: equid (horse, donkey, mule), rhinocerotid (black rhinoceros, white rhinoceros); Proboscidea: elephantid (African elephant); Lagomorpha: leporid (scrub hare, savannah hare); Pholidota: manid (ground pangolin); Rodentia: thrynomyid (greater cane rat); Carnivora: canid (dog, African wild dog, Cape fox), felid (cat, black-footed cat, leopard, cheetah, lion, tiger), herpestid (banded mongoose, common dwarf mongoose), hyaenid (painted hyena, aardwolf), viverrid (African civet); Primates: cercopithecid (grivet, chacma baboon), galagid (brown greater galago), hominid (human); Accipitriformes: accipitrid (black sparrowhawk); Bucerotiformes: bucerotid (southern yellow-billed hornbill, northern red-billed hornbill); Caprimulgiformes: caprimulgid (fiery-necked nightjar, rufous-cheeked nightjar); Coraciiformes: coraciid (European roller, racket-tailed roller); Cuculiformes: cuculid (white-breasted coucal, Senegal coucal); Galliformes: numidid (helmeted guineafowl, southern crested guineafowl), phasianid (chicken, turkey, crested francolin, Natal spurfowl, Swainson's spurfowl); Otidiformes: otidid (Kori bustard); Passeriformes: leiothrichid (white-rumped babbler), malaconotid (orange-breasted bushshrike), muscicapid (Kalahari scrub robin), ploceid (white-browed sparrow-weaver), sturnid (greater blue-eared starling); Pelecaniformes: scopid (hamerkop); Piciformes: picid (bearded woodpecker); Pterocliformes: pteroclid (double-banded sandgrouse, Burchell's sandgrouse); Struthioniformes: struthionid (ostrich); Sauria: gerrhosaurid (plated lizard), varanid (rock monitor, black-throated monitor, lace monitor, Nile monitor); Serpentes: viperid (unspecified viper); Testudines: testudinid (leopard tortoise) (3-host cycle)	trauma, irritation, foot abscesses (vector for ehrlichiosis, rickettsial Boutonneuse fever, African tick-bite fever, theileriosis, fowl aegyptianellosis)	South Africa
A. helvolum (syn. *feuerborni*)	Artiodactyla: bovid (water buffalo), suid (pig); Rodentia: murid (unspecified rat); Primates: hominid (human); Sauria: agamid (Philippine sailfin lizard), iguanid (iguana), scincid (many-lined sun skink), varanid (clouded monitor, roughneck monitor, Asian water monitor, Dumeril's monitor, Komodo dragon); Serpentes: boid (boa), colubrid (brown rat snake, oriental rat snake, radiated rat snake, black copper rat snake, Chinese rat snake, red-tailed racer,		Asia

	mangrove snake, triangle keelback, orange-neck keelback, Sulawesi black racer), elapid (Indian cobra, Indian krait), pythonid (reticulated python); Testudines: geoemydid (giant Asian pond turtle)		
A. hirtum	host unknown, collected from environment		Galapagos Islands
A. humerale (syn. *A. brimonti, gypsatum*)	Perissodactyla: tapirid (Baird's tapir); Didelphimorphia: didelphid (common opossum, slender opossum, brown four-eyed opossum, gray four-eyed opossum, white-bellied woolly mouse opossum); Cingulata: dasypodid (nine-banded armadillo); Pilosa: bradypodid (pale-throated sloth), cyclopedid (silky anteater), myrmecophagid (southern tamandua); Rodentia: caviid (capybara), cricetid (common bristly mouse, unspecified rice rat), dasyproctid (red acouchi), echimyid (Roberto's spiny rat); Carnivora: procyonid (South American coati); Chiroptera: phyllostomid (big-eared woolly bat); Coraciiformes: momotid (Amazonian motmot); Passeriformes: furnariid (Hoffmann's woodcreeper, black-tailed leaftosser, olivaceous woodcreeper, buff-throated woodcreeper), thamnophilid (spot-backed antbird, spot-winged antbird, white-flanked antwren, East Amazonian fire-eye, cinereous antshrike, bluish-slate antshrike, common scale-backed antbird), thraupid (fulvous-crested tanager), tyrannid (olivaceous flatbill); Sauria: teiid (forest whiptail, striped forest whiptail), tropidurid (collared tree lizard, blue-lipped tree lizard, diving lizard, neotropical ground lizard); Serpentes: colubrid (velvet swamp snake, Amazon whipsnake, Guianan green snake); Testudines: geoemydid (brown wood turtle), podocnemid (South American river turtle), testudinid (yellow-footed tortoise, red-footed tortoise, ornate box turtle); Crocodilia: alligatorid (broad-snouted caiman, smooth-fronted caiman, spectacled caiman)		South America
A. incisum (syn. *A. brasiliense superbrasiliense*)	Artiodactyla: cervid (red deer, brown brocket, small red brocket); Perissodactyla: equid (horse), tapirid (South American tapir); Didelphimorphia: didelphid (big-eared opossum); Pilosa: myrmecophagid (giant anteater, southern tamandua); Lagomorpha: leporid (rabbit); Rodentia: caviid (capybara), dasyproctid (agouti); Carnivora: canid (crab-eating fox, Azara fox), felid (jaguar, cougar), procyonid (South American coati); Primates: hominid (human)		South America
A. ininii	Pilosa: myrmecophagid (giant anteater); Serpentes: viperid (pit viper)		Africa
A. interandinum	Artiodactyla: cervid (unspecified deer)		South America
A. (*Aponomma*) *inopinatus*	Artiodactyla: bovid (sheep); Carnivora: canid (red fox); Sauria: varanid (savannah monitor)		Mediterranean
A. (*Aponomma*) *inornatum*	Artiodactyla: bovid (cattle, goat), cervid (white-tailed deer), tayassuid (collared peccary); Perissodactyla: equid (horse); Cingulata: dasypodid (nine-banded armadillo); Didelphimorphia: didelphid (Virginia opossum); Lagomorpha: leporid (European rabbit, eastern cottontail, desert cottontail, black-tailed jackrabbit, hare); Rodentia: caviid (guinea pig), cricetid (hispid cotton rat, southern plains woodrat), sciurid (ground squirrel); Carnivora: canid (dog, red wolf, coyote), felid (cat, bobcat), mephitid (striped skunk), mustelid (badger), procyonid (raccoon); Primates: hominid (human); Cuculiformes: cuculid (greater roadrunner); Galliformes: phasianid (quail); Passeriformes: icterid (unspecified blackbird), mimid (unspecified), turdid (veery)		Americas
A. integrum	Artiodactyla: bovid (cattle, zebu, buffalo, water buffalo), cervid (sambar deer), suid (pig); tragulid (Sri Lankan spotted chevrotain); Proboscidea: elephantid (Asian elephant); Lagomorpha: leporid (Indian hare); Rodentia: hystricid (porcupine); Carnivora: canid (dog), felid (fishing cat), ursid (bear), viverrid (small Indian civet); Primates: hominid (human); Galliformes: phasianid (chicken)		India, Sri Lanka
A. interandinum	Artiodactyla: cervid (unspecified deer)		South America
A. (*Aponomma*)	Artiodactyla: cervid (sambar deer), suid (pig); Pholidota: manid		Indonesia, Sri

javanense (syn. *A. compressum javanense)*	(Indian pangolin, Sunda pangolin, Philippine pangolin); Rodentia: hystricid (porcupine), murid (rat); Carnivora: hyaenid (striped hyena), ursid (bear); Chiroptera: vespertilionid (Javan pipistrelle); Primates: hominid (human); Sauria: scincid (unspecified long-tailed skink), varanid (Asian water monitor); Serpentes: pythonid (black-tailed python); Testudines: geoemydid (tricarinate hill turtle)		Lanka
A. (*Aponomma*) *komodoense*	Sauria: varanid (Komodo dragon, Asian water monitor)		Indonesia
A. (Aponomma) *kraneveldi*	Serpentes: pythonid (black-tailed python, reticulated python, Timor python)		Indonesia
A. (Aponomma) *laevatum*	Serpentes: boid (boa constrictor)		South America
A. (*Aponomma*) *laeve*	Serpentes: colubrid (Central African egg-eating snake), elapid (Egyptian cobra)		Africa
A. latiscutatum	Serpentes: pythonid (python)		India
A. (*Aponomma*) *latum* (syn. *Aponomma falsolaeve, laeve*)	Artiodactyla: bovid (goat); Perissodactyla: rhinocerotid (black rhinoceros); Rodentia: hystricid (porcupine), murid (red veld rat); Eulipotyphla: soricid (musk shrew); Pholidota: manid (pangolin); Primates: hominid (human); Sauria: scincid (striped skink, variable skink, giant legless skink, Cape legless skink, Guinean forest skink), varanid (rock monitor, Nile monitor); Serpentes: atractaspidid (western forest centipede-eater, slender burrowing asp), boid (sand boa), colubrid (boomslang, northern green bush snake, egg-eating snake, modest keelback, Blanding's tree snake, Blanding's cat snake, Fischer's tree snake, black-lined green snake, Angolan green snake, trinket snake, white-lipped herald snake, egg-eating snake, Smith's African water snake, olive marsh snake, forest vine snake, oriental rat snake), elapid (rinkhals, forest cobra, black-headed spitting cobra, shield-nose snake, Cape cobra, Egyptian cobra, Indian cobra, Goldie's tree cobra, snouted cobra, mamba, black mamba, eastern green mamba, western green mamba, Jameson's mamba, zebra snake, Sundevall's garter snake, golden snake), lamprophiid (rufous beaked snake, striped house snake, olive house snake, dark-bellied house snake, African house snake, Aurora house snake, brown house snake, wolf snake, Cape wolf snake, western forest file snake, black file snake, Cape file snake, Crosse's file snake, Gasca's Ethiopian snake), psammophid (olive grass snake, hissing sand snake, western yellow-bellied sand snake, Schokari sand racer), pseudaspidid (mole snake), pythonid (ball python, black-headed python, Central African rock python, Calabar python), viperid (aspic viper, Gaboon viper, pit viper, night adder, green bush viper, mole viper, puff adder, horned puff adder, Somali puff adder, snouted night adder, rhombic night adder); Testudines: testudinid (land tortoise, leopard tortoise); Anura: bufonid (toad)		Africa
A. lepidum (East African bont tick)	Artiodactyla: bovid (cattle, buffalo, forest buffalo, sheep, goat, Grant's gazelle, Thomson's gazelle, antelope, roan antelope, eland, tiang, hartebeest, Roosevelt's hartebeest, blue wildebeest, korrigum), camelid (camel**,** dromedary), giraffid (giraffe), suid (bushpig); Perissodactyla: equid (horse, mule, donkey, Burchell's zebra), rhinocerotid (rhinoceros); Lagomorpha: leporid (rabbit); Tubulidentata: orycteropodid (aardvark); Carnivora: canid (dog), felid (African wildcat, cheetah), hyaenid (spotted hyena), herpestid (meerkat); Primates: hominid (human); Accipitriformes: accipitrid (hawk); Charadriiformes: burhinid (Eurasian stone curlew); Ciconiiformes: ciconiid (cuckoo); Columbiformes: columbid (pigeon); Musophagiformes: musophagid (turaco); Otidiformes: otidid (great bustard, Denham's bustard); Strigiformes: strigid (short-eared owl); Struthioniformes: struthionid (ostrich) (3-host cycle)	(vector for ehrlichiosis (heartwater / cowdriosis))	Africa
A. (*Cernyomma*) *limbatum*	Sauria: agamid (frill-necked lizard), scincid (sleepy lizard, common blue-tongued skink, Centralian blue-tongued skink), varanid (sand goanna, spiny-tailed monitor, yellow-spotted monitor, black-headed monitor, black-palmed rock monitor, spotted tree monitor, Argus		Australia

	monitor, Mitchell's water monitor); Serpentes: colubrid (green tree snake, brown tree snake), elapid (red-bellied black snake, mulga snake, northern death adder), pythonid (woma python, northwestern carpet python, olive python, water python, black-headed python, Children's python); Primates: hominid (human)		
A. (*Adenopleura*) *loculosum* (syn. *A. sternae*)	Artiodactyla: bovid (cattle); Primates: hominid (human); Charadriiformes: larid (sooty tern, brown noddy, black noddy); Procellariiformes: procellariid (wedge-tailed shearwater); Suliformes: fregatid (lesser frigatebird, great frigatebird), sulid (red-footed booby); Squamata: scincid (Seychelles mabuya)		Africa, Asia, Australia
A. longirostre (syn. *A. avecolens*)	Artiodactyla: cervid (marsh deer); Perissodactyla: equid (horse); Didelphimorphia: didelphid (common opossum); Rodentia: cricetid (large-headed rice rat), echimyid (soft-spined Atlantic spiny rat, Guyenne spiny rat), erethizontid (bristle-spined rat, bicoloured-spined porcupine, tri-coloured tree porcupine, brown hairy dwarf porcupine, pallid hairy dwarf porcupine, Bahai hairy dwarf porcupine, Andean porcupine, Mexican hairy dwarf porcupine, Paraguayan hairy dwarf porcupine, Brazilian porcupine, Rothschild's porcupine), sciurid (red-tailed squirrel); Pilosa: bradypodid (maned sloth, pale-throated sloth), myrmecophagid (giant anteater); Carnivora: canid (dog, crab-eating fox), felid (oncilla, Geoffroy's cat), mustelid (tayra); Chiroptera: phyllostomid (great fruit-eating bat, shadowy broad-nosed bat); Primates: cebid (capuchin), hominid (human); Accipitriformes: accipitrid (broad-winged hawk, bicolored hawk, white-necked hawk, roadside hawk, black-and-white hawk-eagle); Caprimulgiformes: caprimulgid (pauraque), trochilid (rufous-tailed hummingbird, swallow-tailed hummingbird, white-throated hummingbird, sombre hummingbird, glittering-bellied emerald, green hermit, long-tailed hermit, violet-capped woodnymph, grey-breasted sabre wing, Brazilian ruby, black jacobin); Columbiformes: columbid (grey-fronted dove, white-tipped dove, ruddy ground dove, ruddy quail-dove); Coraciiformes: alcedinid (American pygmy kingfisher), momotid (Amazonian motmot, rufous motmot, rufous-capped motmot); Cuculiformes: cuculid (smooth-billed ani, greater ani, squirrel cuckoo); Falconiformes: falconid (laughing falcon, barred forest falcon); Galliformes: cracid (dusky-legged guan); Gruiformes: rallid (white-throated crake); Passeriformes: cardinalid (ultramarine grosbeak, blue black grosbeak, hepatic tanager, black-headed saltator, buff-throated saltator, green-winged saltator, red-throated ant tanager, red-crowned ant tanager, sooty ant tanager), conopophagid (rufous gnateater, black-cheeked gnateater), corvid (curl-crested jay), cotingid (purple-throated fruit crow, brown-winged schiffornis, greenish schiffornis), fringillid (yellow-throated euphonia, thick-billed euphonia, chestnut-bellied euphonia, violaceous euphonia, orange-bellied euphonia), furnariid (white-browed foliage-gleaner, white-collared foliage-gleaner, white-eyed foliage-gleaner, buff-throated foliage-gleaner, buff-fronted foliage-gleaner, buff-browed foliage-gleaner, black-capped foliage-gleaner, plain-winged woodcreeper, yellow-chinned spinetail, white-chinned woodcreeper, rufous-capped spinetail, Spix's spinetail, plain xenops, plain brown woodcreeper, streak-headed woodcreeper, long-tailed woodcreeper, white-throated woodcreeper, spot-throated woodcreeper, buff-throated woodcreeper, tawny-winged woodcreeper, straight-billed woodcreeper, wedge-billed woodcreeper, narrow-billed woodcreeper, red-billed woodcreeper, chesnut-rumped woodcreeper, scaled woodcreeper, olivaceous woodcreeper, elegant woodcreeper, lesser woodcreeper, black-striped woodcreeper, black-banded woodcreeper, cocoa woodcreeper, Amazonian barred woodcreeper, Brigida's woodcreeper, Hoffmann's woodcreeper, point-tailed palm creeper, black-billed scythe bill, red-billed scythe bill), icterid (yellow-backed oriole, yellow-rumped cacique, red-rumped cacique, scarlet-		Americas

	rumped cacique, Venezuelan troupial), parulid (chesnut-capped warbler, golden-crowned warbler, flavescent warbler, white-bellied warbler, white-rimmed warbler, rufous-capped warbler, masked yellowthroat), passerellid (black-striped sparrow), piprid (blue manakin, golden-headed manakin, red-capped manakin, helmeted manakin, long-tailed manakin, blue-backed manakin, blue-crowned manakin, white-crowned manakin, pin-tailed manakin, white-collared manakin, white-bearded manakin, band-tailed manakin, pin-tailed manakin, fiery-capped manakin, crimson-hooded manakin, kinglet manakin, pale-bellied tyrant-manakin), thamnophilid (dusky antbird, bicolored antbird, spotted antbird, black-headed antbird, spot-backed antbird, band-tailed antbird, common scale-backed antbird, ferruginous antbird, ferruginous-backed antbird, ocellated antbird, plain antvireo, spot-breasted antvireo, tufted antshrike, great antshrike, black antshrike, barred antshrike, bar-crested antshrike, cinereous antshrike, white-shouldered antshrike, white-bearded antshrike, black-hooded antshrike, black-crowned antshrike, variable antshrike, fasciated antshrike, northern slaty antshrike, Planalto slaty antshrike, white-eyed stipplethroat, black-bellied antwren, long-winged antwren, white-flanked antwren, black-spotted bare-eye, white-shouldered fire-eye, East Amazonian fire-eye, white-eyed stipplethroat), thraupid (bananaquit, yellow-faced grassquit, blue dacnis, palm tanager, grey-headed tanager, hooded tanager, fawn-breasted tanager, silver-beaked tanager, crimson-collared tanager, ruby-crowned tanager, flame-crested tanager, black-backed tanager, white-shouldered tanager, white-lined tanager, fulvous-crested tanager, burnished-buff tanager, green-headed tanager, chesnut-headed tanager, orange-headed tanager, golden-chevroned tanager, swallow tanager, black-goggled tanager, Brazilian tanager, Sayaca tanager, red-crowned ant tanager, sepia-capped flycatcher, black-headed saltator, lesser Antillean saltator, buff-throated saltator, green-winged saltator, uniform finch, saffron finch, chesnut-bellied seed finch, lined seedeater, double-collared seedeater, variable seedeater, white-bellied seedeater, yellow-bellied seedeater, lined seedeater), tityrid (chesnut-crowned becard, white-winged becard, brown-winged shiffornis, greenish schiffornis), troglodytid (house wren, song wren, white-breasted wood wren, black-throated wren, long-billed wren, bay wren, rufous-and-white wren, tropical wren, Cabani's wren, southern nightingale-wren), turdid (white-necked thrush, creamy-bellied thrush, rufous-bellied thrush, yellow-legged thrush, cocoa thrush, clay-coloured thrush, pale-breasted thrush, spectacled thrush, black-billed thrush, pale-breasted thrush, pale-vented thrush, sooty thrush, eastern slaty thrush, Andean slaty thrush, Hauxwell's thrush, Swainson's thrush, Varzea thrush), tyrannid (grey-hooded attila, bright-rumped attila, rufous casiornis, fuscous flycatcher, willow flycatcher, social flycatcher, bearded flycatcher, grey-hooded flycatcher, sepia-capped flycatcher, slaty-capped flycatcher, ochre-bellied flycatcher, streaked flycatcher, boat-billed flycatcher, short-crested flycatcher, royal flycatcher, yellow olive flycatcher, olive-striped flycatcher, bran-coloured flycatcher, fork-tailed flycatcher, dusky-capped flycatcher, Acadian flycatcher, Alder flycatcher, Euler's flycatcher, McConnell's flycatcher, common tody-flycatcher, rusty-fronted tody-flycatcher, slaty-headed tody-flycatcher, cattle tyrant, pearly-vented tody-tyrant, hangnest tody-tyrant, Snethlage's tody-tyrant, whiskered myiobius, southern beardless tyrannulet, mottle-cheeked tyrannulet, Restinga tyrannulet, rufous-browed peppershrike, great kiskadee, plain-crested elaenia, yellow-bellied elaenia, olivaceous elaenia, small-billed elaenia, greenish elaenia, stub-tailed spadebill, russet-winged spadebill, white-throated spadebill, golden-crowned spadebill, eye-ringed flatbill, grey-crowned flatbill, olivaceous flatbill, yellow-olive flatbill, southern bentbill, tropical kingbird,		

	grey monjita, white-rumped monjita), vireonid (white-eyed vireo, red-eyed vireo, Chivi vireo); Piciformes: bucconid (crescent-chested puffbird, white-whiskered puffbird), capitonid (gilded barbet), galbulid (rufous-tailed jacamar), picid (blond-crested woodpecker, yellow-eared woodpecker, white-barred piculet, golden-spangled piculet, ochre-collared piculet), ramphastid (red-necked aracari, chesnut-eared aracari, green-billed toucan, channel-billed toucan); Strigiformes: strigid (tawny-browed owl, tropical screech owl, striped owl, Stygian owl); Trogoniformes: trogonid (green-backed trogon)		
A. macfarlandi	Testudines: testudinid (Galapagos tortoise (subspp. Cerro Azul giant tortoise, western Santa Cruz tortoise)); Primates: hominid (human)		Galapagos Islands
A. (*Cernyomma*) *macropi*	Diprotodontia: macropodid (unspecified kangaroo)		Australia
A. maculatum (syn. *A. rubripes*) (Gulf coast tick)	Artiodactyla: bovid (cattle, zebu, sheep, goat), cervid (Cove's white-tailed deer, Florida coastal white-tailed deer, pampas deer, sambar deer, grey brocket, guazuncho), suid (pig), tayassuid (collared peccary); Perissodactyla: equid (horse, donkey, mule); Lagomorpha: leporid (rabbit, cottontail, black-tailed jackrabbit, hare); Didelphimorphia: didelphid (common opossum); Pilosa: myrmecophagid (southern tamandua); Rodentia: caviid (guinea pig, Brazilian guinea pig, capybara), cricetid (woodland vole, hispid cotton rat, marsh rice rat, deer mouse, white-footed mouse, Florida mouse), murid (black rat, brown rat), sciurid (eastern gray squirrel, fox squirrel); Carnivora: canid (dog, maned wolf, culpeo, coyote, red fox, gray fox, South American gray fox, pampas fox, crab-eating fox, Azara fox), felid (cat, African wildcat, bobcat, Florida panther), mephitid (skunk), procyonid (raccoon), ursid (bear); Primates: hominid (human); Sauria: teiid (common golden tegu); Charadriiformes: charadriid (killdeer); Columbiformes: columbid (pigeon); Galliformes: phasianid (quail), odontophorid (northern bobwhite quail); Passeriformes: cardinalid (northern cardinal), corvid (blue jay), icterid (grackle, cowbird, eastern meadowlark, red-winged blackbird, Bower's blackbird), laniid (loggerhead shrike), mimid (northern mockingbird, brown thrasher), parulid (palm warbler), passerid (house sparrow), passerellid (eastern towhee, red-eyed towhee, white-eyed towhee, field sparrow, white-throated sparrow, swamp sparrow, grasshopper sparrow, Bachman's sparrow, dark-eyed junco), piprid (white-collared manakin), sturnid (meadowlark), troglodytid (house wren, short-billed marsh wren, Carolina wren), turdid (wood thrush, American robin, bluebird); Piciformes: picid (red-bellied woodpecker); Tinamiformes: tinamid (red-winged tinamou, spotted nothura) (3-host cycle)	trauma, irritation, gotch ear, paralysis (vector for hepatozoonosis, rickettsiosis, ehrlichiosis)	Americas
A. margaritae	Serpentes: colubrid (dark-headed red false boa)		South America
A. marmoreum (syn. *A. falsomarmoreum*)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, eland, blackbuck, impala, black wildebeest, bontebok, springbok, greater kudu, red forest duiker, gemsbok, grey rhebok, reedbuck, mountain reedbuck), camelid (camel), giraffid (giraffe), suid (bushpig, warthog); Perissodactyla: equid (horse, Cape mountain zebra), rhinocerotid (black rhinoceros, white rhinoceros); Eulipotyphla: erinaceid (African hedgehog); Lagomorpha: leporid (Smith's red rock rabbit, scrub hare, Cape hare); Macroscelidea: macroscelidid (rock elephant shrew); Hyracoidea: procaviid (rock hyrax); Rodentia: caviid (guinea pig), murid (bush Karoo rat); Carnivora: canid (hunting dog, black-backed jackal, bat-eared fox), felid (cat, African wildcat, leopard, cheetah, caracal, lion), herpestid (yellow mongoose, white-tailed mongoose, banded mongoose), hyaenid (spotted hyena, aardwolf), viverrid (pardine genet, large spotted genet, civet cat); Primates: hominid (human); Bucerotiformes: upupid (African hoopoe); Galliformes: numidid (helmeted guineafowl), phasianid (chicken, common quail, graywing	(vector for ehrlichiosis (heartwater))	Africa

	francolin, Cape francolin, crested francolin, Swainson's francolin); Passeriformes: emberizid (cinnamon-breasted bunting), malaconotid (brown-crowned tchagra), ploceid (red-headed weaver, red-billed quelea); Pelecaniformes: ardeid (cattle egret); Pterocliformes: pteroclid (double-banded sandgrouse); Sauria: gerrhosaurid (giant plated lizard), varanid (rock monitor, ocellated monitor, Nile monitor, white-throated monitor, warrener); Serpentes: boid (boa), colubrid (tiger rat snake, common egg eater, boomslang), elapid (unspecified), pythonid (reticulated python, Central African rock python), viperid (Gaboon viper, puff adder); Testudines: cheloniid (loggerhead sea turtle), testudinid (leopard tortoise, pancake tortoise, geometric tortoise, serrated tortoise, tent tortoise, angulate tortoise, Karoo tortoise, common padloper, Karoo padloper, areolate padloper, greater padloper, southern speckled padloper, African spurred tortoise, Bell's hinge-back tortoise, Speke's hinge-back tortoise, Greek tortoise) (3-host cycle)		
A. mixtum	Artiodactyla: bovid (cattle, buffalo, water buffalo, sheep, goat), cervid (red deer, white-tailed deer, red brocket), suid (pig), tayassuid (collared peccary, white-lipped peccary); Perissodactyla: equid (horse, donkey, mule), tapirid (Baird's tapir); Didelphimorphia: didelphid (common opossum, Virginia opossum, brown four-eyed opossum); Cingulata: dasypodid (nine-banded armadillo); Pilosa: myrmecophagid (northern tamandua); Lagomorpha: leporid (rabbit); Rodentia: caviid (lesser capybara), cricetid (long-whiskered rice rat), cuniculid (lowland paca), echimyid (armored rat, Tome's spiny rat), murid (unspecified rat), sciurid (Mexican gray squirrel); Carnivora: canid (dog, coyote, gray fox), felid (cat, jaguar), procyonid (raccoon, white-nosed coati); Chiroptera: phyllostomid (Jamacian fruit bat); Primates: hominid (human): Accipitriformes: accipitrid (roadside hawk); Cuculiformes: cuculid (great lizard cuckoo); Galliformes: cracid (rufous-vented chachalaca), phasianid (chicken, turkey); Pelecaniformes: ardeid (unspecified heron); Crocodilia: crocodylid (American crocodile); Sauria: iguanid (green iguana, black spiny-tailed iguana); Testudines: emydid (common box turtle, red-eared slider), geoemydid (furrowed wood turtle)	(vector for anaplasmosis)	Americas
A. (*Cernyomma*) *moreliae* (syn. *Ixodes*)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Diprotodontia: macropodid (unspecified macropod); Primates: hominid (human); Sauria: agamid (water dragon, eastern bearded dragon, frill-necked lizard), scincid (tree-crevice skink, sleepy lizard, common blue-tongued skink, blotched blue-tongued skink), varanid (goanna, lace monitor, black-headed monitor, yellow-spotted monitor); Serpentes: colubrid (green tree snake), elapid (eastern brown snake, mainland tiger snake, coastal taipan, red-bellied black snake, mulga snake), pythonid (carpet python, northwestern carpet python, black-headed python, diamond python, water python)		Australia
A. (*Cernyomma*) *moyi*	Monotremata: tachyglossid (short-beaked echidna)		Australia
A mudaliari	Artiodactyla: bovid (cattle, buffalo); Primates: hominid (human)		India
A. multipunctum	Artiodactyla: antilocaprid (cattle, pronghorn); Perissodactyla: tapirid (mountain tapir); Serpentes: elapid (unspecified black snake); Testudines (unspecified tortoise)		North America, Australia
A. naponense (syn. *A. mantiquirense*)	Artiodactyla: cervid (white-tailed deer, brown brocket), suid (wild boar), tayassuid (collared peccary, white-lipped peccary); Perissodactyla: tapirid (South American tapir); Didelphimorphia: didelphid (common opossum, Robinson's mouse opossum); Pilosa: myrmecophagid (giant anteater, northern tamandua, southern tamandua); Rodentia: caviid (guinea pig, capybara), cricetid (unspecified rice rat), cuniculid (lowland paca), dasyproctid (black agouti, red-rumped agouti, Central American agouti, Azara's agouti, red acouchi), echimyid (armored rat, Tome's spiny rat);		South America

	Carnivora: canid (dog, crab-eating fox, gray fox), mustelid (grison), procyonid (white-nosed coati, South American coati, raccoon, crab-eating raccoon); Primates: hominid (human); Coraciiformes: momotid (rufous motmot); Galliformes: cracid (razor-billed curassow); Passeriformes: furnariid (plain-brown woodcreeper, scaly-throated leaftosser), piprid (red-capped manakin, blue-crowned manakin), thamnophilid (white-shouldered fire-eye, Planalto slaty antshrike), thraupid (ruby-crowned tanager), troglodytid (song wren), tyrannid (grey-hooded attila)		
A. (*Aponomma*) *neglectum*	Sauria: varanid (rock monitor)		Africa
A. neumanni (syn. *A. furcula*)	Artiodactyla: bovid (cattle, sheep, goat), cervid (red brocket, brown brocket), suid (pig), tayassuid (collard peccary, Chacoan peccary); Perissodactyla: equid (horse, donkey, mule), tapirid (tapir); Pilosa: myrmecophagid (giant anteater); Carnivora: canid (dog, Pampas fox, crab-eating fox); Primates: hominid (human)		South America
A. nitidum (syn. *A. laticaudae*)	Serpentes: elapid (yellow-lipped sea krait, blue-lipped sea krait)		Asia
A. nodosum	Perissodactyla: tapirid (South American tapir); Rodentia: cuniculid (lowland paca), dasyproctid (agouti), erethizontid (Brazilian porcupine); Cingulata: chlamyphorid (six-banded armadillo); Pilosa: bradypodid (three-toed sloth, brown-throated sloth), myrmecophagid (giant anteater, lesser anteater, northern tamandua, southern tamandua); Carnivora: canid (dog); Accipitriformes: accipitrid (white-necked hawk); Caprimulgiformes: trochilid (swallow-tailed hummingbird); Columbiformes: columbid (ruddy ground dove, ruddy quail-dove, white-tipped dove); Coraciiformes: momotid (rufous-capped motmot); Cuculiformes: cuculid (greater ani, squirrel cuckoo), Passeriformes: cardinalid (red-throated ant tanager, red-crowned ant tanager, blue-black grosbeak, buff-throated saltator, green-winged saltator), conopophagid (rufous gnateater, black-cheeked gnateater), fringillid (blue-naped chlorophonia), furnariid (white-collared foliage-gleaner, white-eyed foliage-gleaner, rusty-backed spinetail, plain xenops, straight-billed woodcreeper, wedge-billed woodcreeper, narrow-billed woodcreeper, buff-throated woodcreeper, cocoa woodcreeper, scaled woodcreeper, Planalto woodcreeper), icterid (red-rumped cacique, yellow-backed oriole, shiny cowbird), parulid (golden-crowned warbler, flavescent warbler), passerellid (saffron-billed sparrow, black-striped sparrow), piprid (blue manakin, red-capped manakin, white-crowned manakin, blue-crowned manakin, white-bearded manakin, band-tailed manakin, golden-collared manakin), polioptilid (tawny-faced gnatwren), thamnophilid (scaled antbird, spotted antbird, plumbeous antbird, ocellated antbird, band-tailed antbird, white-cheeked antbird, chesnut-backed antbird, southern chesnut-tailed antbird, plain antvireo, spot-breasted antvireo, slaty antwren, southern white-fringed antwren, rusty-backed antwren, black-capped antwren, great antshrike, barred antshrike, variable antshrike, fasciated antshrike, plain-winged antshrike, rufous-winged antshrike, barred antshrike, bluish-slate antshrike, black-crowned antshrike, Planalto slaty antshrike, black-spotted bare-eye), thraupid (palm tanager, silver-beaked tanager, flame-crested tanager, white-shouldered tanager, red-shouldered tanager, white-lined tanager, gray-headed tanager, ruby-crowned tanager, black-goggled tanager, flame-crested tanager, burnished-buff tanager, golden-chevroned tanager, Brazilian tanager, Sayaca tanager, greyish saltator, buff-throated saltator, green-winged saltator, streaked saltator, chesnut-bellied seed finch, double-collared seedeater, grey seedeater, lined seedeater, red pileated finch, red-legged honeycreeper), tityrid (white-winged becard), troglodytid (bay wren, moustached wren, house wren), turdid (creamy-bellied thrush, rufous-bellied thrush, pale-breasted thrush, clay-coloured thrush, white-necked thrush, black-billed thrush, Swainson's		South America

	thrush), tyrannid (rufous casiornis, fuscous flycatcher, sepia-capped flycatcher, brown-crested flycatcher, lesser elaenia, yellow-bellied elaenia, plain-crested elaenia, highland elaenia, olivaceous elaenia, sepia-capped flycatcher, brown-crested flycatcher, alder flycatcher, social flycatcher, Euler's flycatcher, white-throated spadebill, yellow olive flatbill, pearly-vented tody-tyrant, spotted tody-flycatcher, rusty-fronted tody-flycatcher, large-headed flatbill, olivaceous flatbill, yellow-olive flatbill); Piciformes: capitonid (gilded barbet); Strigiformes: strigid (spectacled owl); Trogoniformes: trogonid (green-backed trogon); Serpentes: boid (boa)		
A. nuttalli (syn. *A. faiai, silvai, werneri*)	Artiodactyla: bovid (buffalo, common duiker, black duiker, royal antelope, oribi), cervid (sika deer), suid (desert warthog), tragulid (water chevrotain); Eulipotyphla: erinaceid (hedgehog); Lagomorpha: leporid (hare), ochotonid (pika); Rodentia: caviid (guinea pig), cricetid (short-tailed field vole, narrow-headed vole, tundra vole, European water vole, grey red-backed vole, northern red-backed vole, Chinese striped hamster, muskrat), hystricid (tufted-tailed porcupine), murid (house mouse, striped field mouse, Large Japanese field mouse, Eurasian harvest mouse, brown rat), sciurid (marmot, long-tailed ground squirrel, Siberian chipmunk), thryonomyid (greater cane rat); Carnivora: felid (cat, leopard, panther), herpestid (Egyptian mongoose), viverrid (civet); Chiroptera: nycterid (hairy slit-faced bat); Primates: cercopithecid (western red colobus), hominid (human); Coraciiformes: coraciid (roller); Cuculiformes: cuculid (Senegal coucal); Galliformes: numidid (black guineafowl, southern crested guineafowl, plumed guineafowl), phasianid (turkey, Clapperton's francolin, double-spurred spurfowl); Passeriformes: corvid (rook, western jackdaw), emberizid (yellow-breasted bunting, pine bunting), macrosphenid (moustached grass warbler), passerellid (Eurasian tree sparrow), turdid (olive thrush); Strigiformes: strigid (Sjostedt's barred owlet); Sauria: agamid (Elmenteita rock agama), varanid (rock monitor, savannah monitor, Nile monitor); Serpentes: pythonid (ball python, Central African rock python), viperid (gaboon viper, puff adder); Testudines: pelomedusid (serrated hinged terrapin, African helmeted turtle), testudinid (leopard tortoise, mountain tortoise, Bell's hinge-back tortoise)		Africa, Eurasia
A. oblongoguttatum (syn. *A. exophthalmum, vittatum*)	Artiodactyla: bovid (cattle, buffalo, water buffalo, goat), cervid (red brocket, Central American red brocket, white-tailed deer, Sinoloa white-tailed deer), suid (pig), tayassuid (collared peccary, white-lipped peccary); Perissodactyla: equid (horse), tapirid (South American tapir, Baird's tapir); Cingulata: dasypodid (nine-banded armadillo); Pilosa: myrmecophagid (giant anteater, southern tamandua); Didelphimorphia: didelphid (common opossum, water opossum, gray four-eyed opossum); Pilosa: choloepodid (Hoffmann's two-toed sloth), myrmecophagid (giant anteater, northern tamandua); Rodentia: caviid (capybara, lesser capybara), cricetid (unspecified rice rat), cuniculid (lowland paca), dasyproctid (black agouti, Azara's agouti, Central American agouti), echimyid (Tome's spiny rat; Carnivora: canid (dog, coyote, gray fox, crab-eating fox), felid (cat, jaguarundi, jaguar, cougar), mustelid (tayra), procyonid (raccoon, crab-eating raccoon, white-nosed coati, South American coati); Chiroptera: phyllostomid (Seba's short-tailed bat); Primates: cebid (white-faced capuchin), hominid (human); Accipitriformes: cathartid (black vulture); Galliformes: cracid (great curassow), phasianid (chicken); Passeriformes: cotingid (Guianan cock-of-the-rock), thamnophilid (black-crowned antshrike)		Americas
A. (*Aponomma*) *ochraceum*	Sauria: gerrhosaurid (Sudan plated lizard), scincid (African striped skink); Serpentes: elapid (cobra), viperid (snouted night adder)		Africa
A. (*Aponomma*) *omissus*	Serpentes: colubrid (western indigo snake)		South America

A. (*Aponomma) orlovi*	Serpentes: pythonid (Burmese python)		Africa
A. ovale (syn. *A. auronitens*, *beccarii, confine, fossum*)	Artiodactyla: bovid (cattle), cervid (marsh deer, brown brocket, red brocket, white-tailed deer), suid (pig), tayassuid (collared peccary, white-lipped peccary); Perissodactyla: equid (horse, donkey, mule), tapirid (South American tapir, Central American tapir, Baird's tapir); Didelphimorphia: didelphid (common opossum, big-eared opossum, white-eared opossum, gray four-eyed opossum, Robinson's mouse opossum); Pilosa: bradypodid (sloth), myrmecophagid (giant anteater, southern tamandua); Cingulata: dasypodid (nine-banded armadillo); Rodentia: caviid (capybara), cricetid (montane grass mouse, russet rice rat, marsh rice rat, Amazonian marsh rat, large-headed rice rat, web-footed marsh rat, scaly-footed water rat, yellow pygmy rice rat, black-footed pygmy rice rat, hispid cotton rat, rat-headed rice rat, long-whiskered rice rat, Talamancan rice rat, short-tailed cane mouse, hamster), cuniculid (lowland paca), dasyproctid (Central American agouti, Azara's agouti), echimyid (armored rat, Colombian spiny rat, Guyenne spiny rat, Napo spiny rat, Tome's spiny rat, common punare, highlands punare, Paraguayan punare), erethizontid (Paraguayan hairy dwarf porcupine), heteromyid (Trinidad spiny pocket mouse), murid (black rat); Carnivora: canid (dog, bush dog, maned wolf, coyote, gray fox, crab-eating fox, pampas fox, Azara's fox), felid (cat, Geoffroy's cat, cougar, jaguar, jaguarundi, ocelot, oncilla, margay, panther), mephitid (striped hog-nosed skunk), mustelid (tayra, greater grison, lesser grison, neotropical river otter), procyonid (white-nosed coati, South American coati, raccoon, crab-eating raccoon); Primates: atelid (brown howler), cebid (tufted capuchin, Central American squirrel monkey), hominid (human); Accipitriformes: cathartid (black vulture); Coraciiformes: momotid (rufous motmot); Galliformes: cracid (razor-billed curassow, rusty-margined guan); Gruiformes: rallid (saracura); Passeriformes: cardinalid (ultramarine grosbeak), conopophagid (rufous gnateater), formicariid (black-faced ant-thrush), furnariid (olivaceous woodcreeper), icterid (shiny cowbird), parulid (northern waterthrush), passerellid (saffron-billed sparrow, black-striped sparrow), thamnophilid (tufted antshrike, variable antshrike, southern white-fringed antwren, chesnut-backed antbird, Bertoni's antbird, Planalto slaty antshrike), thraupid (yellow-bellied seedeater, ruby-crowned tanager, black-goggled tanager), tityrid (brown-winged schiffornis), troglodytid (house wren, song wren, tropical wren), turdid (white-necked thrush, creamy-bellied thrush, pale-breasted thrush, rufous-bellied thrush), tyrannid (short-crested flycatcher, tropical kingbird); Anura: bufonid (unspecified toad); Testudines (unspecified turtle) (3-host cycle)	trauma, irritation (vector for hepatozoonosis)	South America
A. pacae (syn. *A. fiebrigi, nigrum*)	Artiodactyla: suid (pig), tayassuid (white-lipped peccary); Perissodactyla: tapirid (Baird's tapir); Pilosa: myrmecophagid (southern tamandua); Rodentia: caviid (capybara), cricetid (Cerrado climbing mouse), cuniculid (lowland paca), dasyproctid (black agouti, Central American agouti), echimyid (armored rat, Tome's spiny rat); Didelphimorphia: didelphid (common opossum, brown four-eyed opossum, gray four-eyed opossum); Carnivora: canid (dog); Primates: hominid (human); Gruiformes: cariamid (seriema)		South America
A. (*Cernyomma*) *papuanum*	Artiodactyla: cervid (deer); Monotremata: tachyglossid (short-beaked echidna); Casuariformes: casuariid (cassowary); Columbiformes: columbid (dove); Galliformes: megapodiid (megapode)		Australia
A. parkeri	Didelphimorphia: didelphid (common opossum, white-eared opossum); Rodentia: erethizontid (Paraguayan hairy dwarf porcupine, Brazilian porcupine); Carnivora: procyonid (South American coati); Primates: atelid (brown howler, unspecified howler monkey), pithecid (black-fronted titi); Accipitriformes:		South America

	accipitrid (gray-headed kite, roadside hawk, black hawk-eagle); Caprimulgiformes: trochilid (violet-capped woodnymph); Galliformes: cracid (dusky-legged guan); Passeriformes: conopophagid (rufous gnateater, black-cheeked gnateater), furnariid (white-collared foliage-gleaner, black-capped foliage-gleaner, scaled woodcreeper, olivaceous woodcreeper, plain-winged woodcreeper), piprid (blue manakin, white-bearded manakin), thamnophilid (tufted antshrike, variable antshrike), thraupid (buff-throated saltator, ruby-crowned tanager, black-goggled tanager, sooty grassquit), troglodytid (house wren), turdid (white-necked thrush), tyrannid (sepia-capped flycatcher, grey-crowned flycatcher, short-crested flycatcher, white-throated spadebill); Strigiformes: strigid (tropical screech owl)		
A. parviscutatum	Pilosa: myrmecophagid (anteater)		South America
A. parvitarsum (syn. *A. altiplanum*)	Artiodactyla: bovid (cattle, sheep, goat), camelid (alpaca, llama, guanaco, vicuna); Perissodactyla: equid (horse); Rheiformes: rheid (greater rhea, Darwin's rhea)); Sphenisciformes: spheniscid (Magellanic penguin); Sauria: liolaemid (brilliant tree iguana, black tree iguana, many-spotted tree iguana, Andes tree iguana, James's tree iguana, Muller's tree iguana, Eleonor's tree iguana, Puritama's lizard, Patricia Iturra's lizard, Caylloma smooth-throated lizard, Parinacota smooth-throated lizard)		South America
A. parvum	Artiodactyla: bovid (cattle, buffalo, sheep, goat), camelid (guanaco), cervid (white-tailed deer, brown brocket), suid (pig), tayassuid (collared peccary, Chacoan peccary); Perissodactyla: equid (horse, donkey), tapirid (South American tapir); Pilosa: bradypodid (sloth), myrmecophagid (giant anteater, southern tamandua, northern tamandua); Cingulata: chlamyphorid (giant armadillo, screaming hairy armadillo, six-banded armadillo, southern three-banded armadillo), dasypodid (nine-banded armadillo, greater long-nosed armadillo); Didelphimorphia: didelphid (white-eared opossum, Virginia opossum, agile gracile opossum, gray short-tailed opossum, Karimi's fat-tailed mouse opossum, Paraguayan fat-tailed mouse opossum); Lagomorpha: leporid (eastern cottontail); Rodentia: caviid (rock cavy, common yellow-toothed cavy, Spix's yellow-toothed cavy, Chacoan mara, capybara), chinchillid (plains viscacha), cricetid (central leaf-eared mouse, Marinho's rice rat, Mamore arboreal rice rat, hispid cotton rat), dasyproctid (Azara's agouti), echimyid (broad-headed spiny rat, common punare, highlands punare), murid (house mouse, wood rat); Carnivora: canid (dog, maned wolf, coyote, gray fox, crab-eating fox, pampas fox, gray fox), felid (cat, pampas cat, Geoffroy's cat, ocelot, cougar, jaguar, jaguarundi), mustelid (lesser grison), procyonid (raccoon, crab-eating raccoon, white-nosed coati, South American coati); Chiroptera: phyllostomid (gray short-tailed bat); Primates: cebid (tufted capuchin), hominid (human); Accipitriformes: cathartid (black vulture); Columbiformes: columbid (white-tipped dove); Passeriformes: cardinalid (ultramarine grosbeak), parulid (flavescent warbler), passerellid (rufous-collared sparrow), thamnophilid (stripe-backed antbird, great antshrike, silvery-cheeked antshrike, Caatinga antshrike, Planalto slaty antshrike), thraupid (grey pileated finch, blue dacnis, silver-beaked tanager, rufous-backed thrush, golden-billed saltator, green-winged saltator, many-coloured Chaco finch, saffron finch, double-collared seedeater, yellow-bellied seedeater), troglodytid (long-billed wren, tropical wren), turdid (creamy-bellied thrush, rufous-bellied thrush), tyrannid (rufous casiornis, fuscous flycatcher, brown-crested flycatcher, fork-tailed flycatcher, white-rumped monjita, lesser wagtail-tyrant, great kiskadee); Serpentes: boid (boa); Testudines: testudinid (Chaco tortoise)		Americas
A. patinoi	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse)		South America
A. pattoni (syn. *Aponomma*	Artiodactyla: bovid (cattle); Carnivora: herpestid (small Indian mongoose); Sauria: varanid (monitor); Serpentes: colubrid (oriental		Indo-China

pseudolaeve)	rat snake, king rat snake, yellow-necked snake, unspecified black snake), elapid (cobra), pythonid (black-tailed python); Passeriformes: chloropseid (leafbird)		
A. paulopunctatum (syn. *A. ovatum, Aponomma trimaculatum*)	Artiodactyla: bovid (cattle, zebu), cervid (Javan rusa), hippopotamid (hippopotamus), suid (pig, bushpig, giant forest hog); Perissodactyla: equid (horse); Proboscidea: elephantid (elephant); Rodentia: thryonomyid (cane rat); Carnivora: hyaenid (striped hyena); Primates: hominid (human); Galliformes: phasianid (fowl); Sauria: scincid (prehensile-tailed skink), varanid (mangrove monitor, black-headed monitor, emerald tree monitor, yellow-spotted monitor, Bengal monitor, Asian water monitor); Serpentes: colubrid (Indian rat snake), pythonid (amethystine python)		New Guinea, Australia
A. pecarium	Artiodactyla: cervid (brown brocket, red brocket), tayassuid (white-lipped peccary, collared peccary); Perissodactyla: tapirid (South American tapir); Carnivora: canid (unspecified), procyonid (white-nosed coati)		Central America
A. personatum	Artiodactyla: bovid (unspecified); Perissodactyla: rhinocerotid (black rhinoceros, white rhinoceros); Primates: hominid (human)		Africa
A. philipi	Lagomorpha: leporid (cottontail, rabbit); Carnivora: canid (coyote)		North America
A. pictum (syn. *A. conspicuum*)	Pilosa: myrmecophagid (giant anteater, southern tamandua); Carnivora: canid (dog)		South America
A. pilosum	Testudines: testudinid (Galapagos tortoise (subspp. Pinzon Island giant tortoise, Santiago Island giant tortoise))		South America
A. (Aponomma) politum	Serpentes: pythonid (Indian python)		Asia
A. pomposum (Angolan bont tick)	Artiodactyla: bovid (cattle, buffalo, forest buffalo, sheep, goat, striped antelope, sable antelope, roan antelope, duiker, suni, nyala, lechwe, oribi, eland, red hartebeest, Lichtenstein's hartebeest, greater kudu, korrigum, Uganda topi, waterbuck, steenbok, southern reedbuck, harnessed bushbuck), suid (pig, bushpig, desert warthog); Perissodactyla: equid (horse, donkey, mule, Burchell's zebra), rhinocerotid (black rhinoceros); Proboscidea: elephantid (African elephant); Rodentia: thryonomyid (greater cane rat); Carnivora: canid (dog), felid (leopard), herpestid (Angolan mongoose); Primates: cercopithecid (grivet), hominid (human); Ciconiiformes: ciconiid (stork); Sauria: agamid (unspecified) (3 host cycle)	(vector for ehrlichiosis (heartwater/cowdriosis))	Africa
A. (*Cernyomma*) *postoculatum*	Diprotodontia: macropodid (banded hare-wallaby): Primates: hominid (human)		Australia
A. pseudoconcolor	Artiodactyla: bovid (cattle, buffalo, water buffalo), cervid (brown brocket); Perissodactyla: tapirid (South American tapir); Cingulata: chlamyphorid (six-banded armadillo, southern three-banded armadillo, greater naked-tailed armadillo, southern naked-backed armadillo, greater fairy armadillo, screaming hairy armadillo, big hairy armadillo, giant armadillo, pichi), dasypodid (nine-banded armadillo, southern long-nosed armadillo); Didelphimorphia: didelphid (white-eared opossum, gray four-eyed opossum); Pilosa: myrmecophagid (giant anteater, southern tamandua); Carnivora: canid (dog), mustelid (lesser grison); Primates: hominid (human); Tinamiformes: tinamid (white-bellied nothura, spotted nothura, red-winged tinamou)		South America
A. pseudoparvum	Artiodactyla: bovid (cattle, goat), cervid (brown brocket); Cingulata: chlamyphorid (big hairy armadillo, southern three-banded armadillo); Lagomorpha: leporid (rabbit); Rodentia: caviid (Chacoan mara), chinchillid (plains viscacha); Carnivora: canid (dog); Primates: hominid (human)		South America
A. (*Aponomma*) *quadricavum*	Sauria: iguanid (iguana); Serpentes: boid (Hispaniolan boa, Cuban boa, Jamacian boa), colubrid (Puerto Rican racer, Cuban racer)		Central America
A. quadrimaculatum	Sauria: varanid (Asian water monitor); Serpentes: pythonid (reticulated python)		Indonesia
A. quantini	Artiodactyla: bovid (buffalo)		Africa
A. quasicyprium	Artiodactyla: bovid (cattle); Primates: atelid (Geoffroy's spider		Mexico, Fiji

	monkey)		
A. robinsoni	Sauria: varanid (Komodo dragon)		Indonesia
A. romarioi	Primates: pithecid (black-fronted titi); Passeriformes: cardinalid (ultramarine grosbeak, red-crowned ant tanager), conophagid (rufous gnateater), furnariid (plain xenops, rufous-breasted leaftosser, plain-winged woodcreeper, scalloped woodcreeper, olivaceous woodcreeper, lesser woodcreeper, white-eyed foliage-gleaner), parulid (golden-crowned warbler), piprid (blue manakin), thamnophilid (white-shouldered fire-eye), thraupid (black-goggled tanager, ruby-crowned tanager, Brazilian tanager), tityrid (greenish schiffornis), turdid (white-necked thrush, creamy-bellied thrush, yellow-legged thrush, pale-breasted thrush, rufous-bellied thrush), tyrannid (grey-hooded attila, sepia-capped flycatcher, white-throated spadebill)		South America
A. rotundatum	Artiodactyla: suid (pig); Rodentia: caviid (capybara, cavy); Cingulata: dasypodid (nine-banded armadillo); Pilosa: bradypodid (brown-throated sloth), myrmecophagid (southern tamandua); Carnivora: procyonid (South American coati); Chiroptera: phyllostomid (lesser long-tongued bat); Primates: hominid (human); Sauria: iguanid (green iguana), lacertid (ocellated lizard, European green lizard), phrynosomatid (horned lizard), scincid (greater Martinique skink, Noronha skink), teiid (green ameiva, Argentine black-and-white tegu), tropidurid (diving lizard, collared tree lizard, Amazon lava lizard, Peter's lava lizard); Serpentes: boid (boa, rainbow boa, Argentine boa, green anaconda), colubrid (black false boa, indigo snake, tiger rat snake, common green racer, Lichtenstein's green racer, Paraguay green racer, Boddaert's tropical racer, Rio tropical racer, Wagler's snake, grass snake, banded cat-eyed snake, green whip snake, hognose snake, giant parrot snake, Gunther's ground snake, Lema's ground snake, Wucherer's ground snake, Neuweid's tree snake, Boettger's sipo, South American sipo, Wagler's sipo, Weid's keelback, cobra-lesma, false water cobra, false coral snake, Brazilian false coral snake, Tschudi's false coral snake), elapid (painted coral snake, South American small-eyed coral snake, short-tailed coral snake, Caatinga coral snake), pythonid (Stimson's python), viperid (urutu, fer-de-lance, whitetail lancehead, golden lancehead, Brazilian lancehead, Caatinga lancehead, Martinique lancehead, jararaca, jararacussu, jararaca pintada, Cascabel rattlesnake, South American bushmaster, South American rattlesnake); Crocodilia: alligatorid (yacare caiman, smooth-fronted caiman, broad-snouted caiman, Cuvier's dwarf caiman); Urodela: salamandrid (palmate newt); Anura: alytid (painted frog), bufonid (South American common toad, cane toad, southern toad, granular toad, lesser granulated toad, Chaco granulated toad, crucifer toad, cururu toad, yellow cururu toad, jimi toad, ornate forest toad, rococo toad, common midwife toad, yellow-bellied toad, striped toad, smooth-sided toad, natterjack toad, Gild's toad, Rio Parahyba toad, European green toad, beaked toad), leptodactylid (smoky jungle frog, Cuyaba dwarf frog), pipid (Suriname toad), ranid (common frog, edible frog), scaphiopodid (plains spadefoot toad); Testudines: chelid (Argentine snake-necked turtle, Vanderhaege's toad-headed turtle, twist-necked turtle, tuberculate toadhead turtle), emydid (European pond turtle, D'Orbigny's slider), geoemydid (yellow-headed temple turtle, furrowed wood turtle), kinosternid (scorpion mud turtle), podocnemid (yellow-spotted river turtle, Arrau turtle), testudinid (red-footed tortoise, yellow-footed tortoise, Chaco tortoise, Greek tortoise)		Americas
A. rugosum	Serpentes: viperid (puff adder); Testudines: testudinid (leopard tortoise)		Africa
A. sabanerae	Didelphimorphia: didelphid (common opossum, brown four-eyed opossum, gray four-eyed opossum, Robinson's mouse opossum); Rodentia: cricetid (Talamacan rice rat), echimyid (armored rat,		South America

	Tome's spiny rat); Carnivora: canid (dog), procyonid (crab-eating raccoon); Primates: hominid (human); Columbiformes: columbid (ruddy quail-dove); Passeriformes: piprid (white-collared manakin), thamnophilid (white-cheeked antbird, black-crowned antshrike); Sauria: iguanid (green iguana); Serpentes: boid (boa), colubrid (Cope's parrot snake); Testudines: emydid (pond slider, common box turtle, Mexican box turtle, Yucatan box turtle), geoemydid (large-nosed wood turtle, brown wood turtle, black wood turtle, painted wood turtle, furrowed wood turtle, spot-legged wood turtle, Colombian wood turtle, black terrapin), kinosternid (scorpion mud turtle); Anura: bufonid (forest toad)		
A. scalpturatum (syn. *A. latepunctatum, myrmecophagae*)	Artiodactyla: suid (pig), tayassuid (white-lipped peccary); Perissodactyla: tapirid (South American tapir); Didelphimorphia: didelphid (common opossum); Pilosa: myrmecophagid (giant anteater); Rodentia: caviid (capybara), cuniculid (lowland paca), dasyproctid (black agouti, Azara's agouti); Carnivora: canid (dog), felid (jaguar); Primates: hominid (human)		South America
A. sculptum	Artiodactyla: bovid (cattle, buffalo, sheep), cervid (marsh deer, red brocket, brown brocket), suid (pig), tayassuid (collared peccary, white-lipped peccary); Perissodactyla: equid (horse, donkey, mule), tapirid (South American tapir); Didelphimorphia: didelphid (white-eared opossum, big-eared opossum, agile gracile opossum, southeastern four-eyed opossum); Pilosa: bradypodid (maned sloth, brown-throated sloth), myrmecophagid (giant anteater, southern tamandua); Cingulata: chlamyphorid (southern naked-tailed armadillo, six-banded armadillo, Brazilian three-banded armadillo, giant armadillo), dasypodid (nine-banded armadillo); Lagomorpha: leporid (common tapeti); Rodentia: caviid (capybara), chinchillid (plains viscacha), cricetid (large vesper mouse, Cerrado climbing mouse, Paraguayan rice rat, highlands punare), dasyproctid (Azara's agouti), erethizontid (Brazilian porcupine, Paraguayan hairy dwarf porcupine); Carnivora: canid (dog, bush dog, maned wolf, hoary fox, crab-eating fox), felid (cat, jaguar, cougar, ocelot), mephitid (striped hog-nosed skunk), procyonid (crab-eating raccoon, South American coati); Primates: atelid (brown howler), hominid (human); Accipitriformes: accipitrid (black-collared hawk, short-tailed hawk, savannah hawk, roadside hawk, Harris's hawk, Chaco eagle, black hawk-eagle, small kite), cathartid (black vulture); Caprimulgiformes: caprimulgid (little nightjar); Caraiamiformes: cariamid (red-legged seriema); Falconiformes: falconid (crested caracara, yellow-headed caracara, American kestrel); Galliformes: cracid (red-billed curassow, bare-faced curassow, dusky-legged guan); Gruiformes: aramid (limpkin); Passeriformes: furnariid (plain-winged woodcreeper), thraupid (ruby-crowned tanager), turdid (pale-breasted thrush); Pelecaniformes: threskiornithid (buff-necked ibis); Psittaciformes: psittacid (turquoise-fronted amazon); Rheiformes: rheid (greater rhea); Strigiformes strigid (striped owl, tropical screech owl), tytonid (barn owl); Sauria: iguanid (green iguana), teiid (Argentine black-and-white tegu)	(vector for rickettsiosis)	South America
A. scutatum	Artiodactyla: cervid (white-tailed deer); Pilosa: myrmecophagid (giant anteater); Didelphimorphia: didelphid (large American opossum, diminutive opossum); Rodentia: dasyproctid (orange agouti); Chiroptera: noctilionid (lesser bulldog bat); Accipitriformes: cathartid (turkey vulture, black vulture); Sauria: iguanid (green iguana, northeastern spiny-tailed iguana, black spiny-tailed iguana, Mexican spiny-tailed iguana), teiid (South American ground lizard); Serpentes: boid (boa), colubrid (western indigo snake), viperid (Martinique lancehead); Anura: bufonid (Cuban toad)		South America
A. serpentinum	Serpentes: pythonid (Burmese python)		
A. (*Aponomma*) *soembawense*	Sauria: varanid (Asian water monitor); Serpentes: pythonid (reticulated python)		Indonesia

A. sparsum (syn. *A. schlottkei, werneri poematium*)	Artiodactyla: bovid (cattle, buffalo, eland), camelid (dromedary), giraffid (giraffe), suid (warthog); Perissodactyla: rhinocerotid (black rhinoceros); Proboscidea: elephantid (elephant); Macroscelidea: macroscelidid (elephant shrew); Lagomorpha: leporid (scrub hare, Natal red rock hare); Tubulidentata: orycteropid (aardvark); Rodentia: hystricid (crested porcupine, African brush-tailed porcupine); Carnivora: felid (lion); Primates: hominid (human); Coraciiformes: upupid (Eurasian hoopoe); Galliformes: numidid (guineafowl); Passeriformes: viduid (indigobird); Sauria: agamid (unspecified), iguanid (iguana), varanid (Nile monitor, savannah monitor); Serpentes: colubrid (yellow rat snake, chicken snake), pythonid (Central African rock python), viperid (puff adder); Testudines: testudinid (Greek tortoise, Mediterranean spur-thighed tortoise, leopard tortoise)	(vector for ehrlichiosis (heartwater))	Africa
A. sphenodonti (syn. *Aponomma ludovici*)	Rhynchocephalia: sphenodontid (tuatara); Sauria: gekkonid (Duvaucel's gecko)		New Zealand
A. splendidum	Artiodactyla: bovid (cattle, zebu, buffalo, forest buffalo, sheep, goat, bay duiker, Maxwell's duiker, roan antelope, royal antelope, Bate's dwarf antelope, eland, waterbuck), suid (pig, red river hog); Proboscidea: elephantid (elephant); Rodentia: thryonomyid (greater cane rat); Carnivora: canid (dog); Galliformes: numidid (helmeted guineafowl), phasianid (turkey, double-spurred spurfowl)		Africa
A. squamosum	Sauria: varanid (mangrove monitor)		Guam
A. strobelii	Perissodactyla: tapirid (South American tapir)		Central America
A. sublaeve	Pholidota: manid (Chinese pangolin, Sunda pangolin); Carnivora: hyaenid (striped hyena); Chiroptera: vespertilionid (pipistrelle); Sauria: scincid (unspecified), varanid (Asian water monitor); Serpentes: pythonid (black-tailed python); Testudines: geoemydid (tricarinate hill turtle)		Asia
A. superbum	Artiodactyla: bovid (cattle)		Africa
A. supinoi	Carnivora: herpestid (small Asian mongoose); Rodentia: hystricid (porcupine); Sauria: varanid (Bengal monitor); Testudines: geoemydid (spiny turtle, Indian black turtle), testudinid (elongated tortoise)		Asia
A. sylvaticum (syn. *Ixodes*)	Artiodactyla: cervid (white-tailed deer); Rodentia: murid (mouse); Sauria: agamid (southern spiny agama), lacertid (Knox's desert lizard); Serpentes: pseudaspidid (mole snake); Testudines: testudinid (angulate tortoise, tent tortoise, common padloper, southern speckled padloper, geometric tortoise)		Africa
A. tapirellum	Artiodactyla: bovid (cattle), cervid (white-tailed deer), suid (pig), tayassuid (collared peccary, white-lipped peccary); Perissodactyla: equid (horse), tapirid (Baird's tapir); Didelphimorphia: didelphid (common opossum); Pilosa: myrmecophagid (giant anteater); Rodentia: caviid (capybara), dasyproctid (Central American agouti); Carnivora: canid (dog), felid (cat), procyonid (white-nosed coati, raccoon); Chiroptera: phyllostomid (Seba's short-tailed bat); Primates: hominid (human)		Central America
A. tenellum (syn. *A. imitator*)	Artiodactyla: bovid (cattle, sheep, goat), cervid (white-tailed deer), tayassuid (collared peccary); Perissodactyla: equid (horse, donkey, mule); Didelphimorphia: didelphid (opossum); Rodentia: sciurid (Mexican gray squirrel); Carnivora: canid (dog); Primates: hominid (human); Cuculiformes: cuculid (greater roadrunner); Galliformes: phasianid (turkey); Passeriformes: emberizid (bunting), turdid (thrush)		Americas
A. (*Aponomma*) *tenimberense*	Sauria: varanid (mangrove monitor)		Indonesia
A. testudinarium (syn. *A. distinctum, fallax, infestum, I. auriscutellatus*)	Artiodactyla: bovid (cattle, banteng, nelore, zebu, buffalo, water buffalo, sheep, guar, goat, Japanese serow, Taiwan serow), cervid (Indian muntjac, sambar deer), suid (pig, bushpig, banded pig, wild boar, Celebes warty pig, Javan warty pig, Philippine warty pig, Bornean bearded pig), tragulid (mouse-deer); Perissodactyla: equid		Indo-China, Asia

	(horse), rhinocerotid (Javan rhinoceros, Sumatran rhinoceros), tapirid (Malayan tapir); Proboscidea: elephantid (elephant); Pholidota: manid (long-tailed pangolin, Chinese pangolin); Scandentia: tupaiid (common treeshrew); Rodentia: hystricid (Indian crested porcupine, Philippine porcupine), murid (Bower's white-toothed rat), sciurid (Culion tree squirrel, parti-coloured flying squirrel, white-bellied giant flying squirrel); Carnivora: canid (dog, golden jackal), felid (tiger), herpestid (Javan mongoose), hyaenid (striped hyena), mephitid (Palawan stink-badger), mustelid (Burmese ferret-badger), viverrid (Asian palm civet); Primates: hominid (human), hylobatid (Hoolock gibbon); Charadriiformes: scolopacid (sandpiper); Galliformes: phasianid (chicken); Passeriformes: corvid (raven); Sauria: varanid (monitor); Serpentes: colubrid (tiger keelback, steppes ratsnake), pythonid (python), viperid (ussuri pit viper); Testudines: emydid (pond turtle); Anura: microhylid (ornate chorus frog)		
A. tholloni	Artiodactyla: bovid (cattle, buffalo, sheep, goat, antelope, dorcas gazelle), hippopotamid (hippopotamus), suid (pig, bushpig, red river hog); Perissodactyla: equid (horse), rhinocerotid (black rhinoceros, white rhinoceros); Proboscidea: elephantid (African elephant); Carnivora: canid (dog), felid (leopard), herpestid (banded mongoose); Primates: hominid (human); Accipitriformes: accipitrid (hawk); Musophagiformes: musophagid (turaco); Passeriformes: pittid (green-breasted pitta); Sauria: chamaeleonid (graceful chameleon); Testudines: testudinid (Bell's hinge-back tortoise, Speke's hinge-back tortoise, leopard tortoise)		Africa
A. tigrinum (syn. *A. complanatum*)	Artiodactyla: bovid (cattle, sheep, goat), cervid (marsh deer, brown brocket), suid (pig), tayassuid (peccary); Perissodactyla: equid (horse); Rodentia: caviid (common yellow-toothed cavy, Spix's yellow-toothed cavy, capybara), cricetid (dolorous grass mouse, Molina's grass mouse, Spegazzini's grass mouse, small vesper mouse, drylands vesper mouse, Cordoba vesper mouse, central leaf-eared mouse, yellow-rumped leaf-eared mouse, fulvous pygmy rice rat, long-tailed pygmy rice rat, Argentine bolo mouse), murid (black rat); Cingulata: dasypodid (armadillo); Carnivora: canid (dog, maned wolf, crab-eating fox, culpeo, pampas fox, South American gray fox, hoary fox), felid (cat, ocelot, cougar, jaguar), procyonid (South American coati); Primates: hominid (human); Columbiformes: columbid (Picui ground dove, eared dove); Cuculiformes: cuculid (guira cuckoo); Galliformes: odontophorid (California quail); Passeriformes: furnariid (short-billed canastero, lark-like brushrunner, crested hornero, rufous hornero, brown cacholote, pale-breasted spinetail, Chaco earthcreeper, scimitar-billed woodcreeper), icterid (grayish baywing, shiny cowbird), passerellid (Chaco sparrow, rufous-collared sparrow), polioptilid (masked gnatcatcher), rhinocryptid (crested gallito), thraupid (red pileated finch, black-crested finch, ringed warbling finch, red-crested cardinal, saffron finch, many-coloured Chaco finch, grassland yellow finch, golden-billed saltator, Brazilian tanager, blue-black grassquit), troglodytid (house wren), turdid (creamy-bellied thrush), tyrannid (great kiskadee); Strigiformes: strigid (striped owl); Tinamiformes: tinamid (elegant crested tinamou, red-winged tinamou, Chilean tinamou, spotted nothura)	(vector for rickettsiosis and possibly Q fever)	South America
A. tonelliae	Artiodactyla: bovid (cattle), cervid (brocket deer), tayassuid (collared peccary, white-lipped peccary, Chacoan peccary); Perissodactyla: equid (horse); Pilosa: myrmecophagid (giant anteater, southern tamandua); Rodentia: caviid (capybara); Carnivora: canid (dog), felid (cougar); Primates: hominid (human)	(possible vector for rickettsiosis)	South America
A. torrei	Sauria: iguanid (Cuban rock iguana, northern Bahamian rock iguana, Mona ground iguana, Cayman Island brown iguana), tropidurid (Cuban side-blotched curlytail); Anura: bufonid (toad)		Americas
A. (*Aponomma*) *transversale*	Artiodactyla: bovid (sable antelope); Serpentes: boid (boa), pythonid (Central African rock python, ball python, Asian python)		Africa

(syn. *I. globulus, transversalis*)			
A. (*Cernyomma*) *triguttatum* (incl. subspp. *ornatissimum, queenslandicus, rosei, triguttatum*) (ornate kangaroo tick)	Artiodactyla: bovid (cattle, zebu, sheep, goat), suid (pig); Perissodactyla: equid (horse); Monotremata: ornithorhynchid (platypus), tachyglossid (short-beaked echidna); Dasyuromorphia: myrmecobiid (numbat); Diprotodontia: macropodid (eastern grey kangaroo, western grey kangaroo, common wallaroo, red kangaroo, black-striped wallaby, agile wallaby, tammar wallaby, swamp wallaby, bridled nailtail wallaby), phascolarctid (koala), potoroid (northern bettong); Lagomorpha: leporid (rabbit); Rodentia: murid (black rat); Carnivora: canid (dog, dingo), felid (cat); Primates: hominid (human); Sauria: scincid (sleepy lizard) (3-host cycle)	trauma, irritation	Australia
A. triste	Artiodactyla: bovid (cattle, goat), cervid (marsh deer, brocket deer, pampas deer), suid (pig); Perissodactyla: equid (horse), tapirid (South American tapir); Didelphimorphia: didelphid (common opossum, yellow-sided opossum, gray short-tailed opossum, agile gracile opossum); Pilosa: myrmecophagid (giant anteater); Rodentia: caviid (Brazilian guinea pig, capybara), cricetid (Azara's grass mouse, large vesper mouse, delicate vesper mouse, unspecified climbing mouse, web-footed marsh rat, Amazonian marsh rat, hairy-tailed bolo mouse, dark bolo mouse, yellow pygmy rice rat, black-footed pygmy rice rat, Marinho's rice rat, long-nosed hocicudo, spy hocicudo, red hocicudo, Argentine swamp rat, Waterhouse's swamp rat), echimyid (common punare); Carnivora: canid (dog, maned wolf, crab-eating fox, hoary fox), felid (cat, pampas cat, jaguar, jaguarundi, cougar); Chiroptera: vespertilionid (silver-tipped myotis); Primates: hominid (human); Gruiformes: rallid (russet-crowned crake); Passeriformes: furnariid (pale-legged hornero, rufous hornero, greater thornbird), passerellid (rufous-collared sparrow), thraupid (black-and-rufous warbling finch, double-collared seedeater), turdid (rufous-bellied thrush)		Americas
A. tuberculatum	Artiodactyla: bovid (cattle), cervid (white-tailed deer); Lagomorpha: leporid (cottontail); Rodentia: sciurid (gray squirrel, Sherman's fox squirrel, southeastern pocket gopher); Carnivora: canid (dog, red fox, gray fox); Primates: hominid (human); Accipitriformes: accipitrid (unspecified hawk); Falconiformes: falconid (American kestrel); Galliformes: phasianid (chicken); Passeriformes: sturnid (southern meadowlark), turdid (hermit thrush); Strigiformes: strigid (unspecified owl); Sauria: phrynosomatid (eastern fence lizard); Testudines: emydid (diamondback terrapin), testudinid (gopher tortoise)		South America
A. uncatum	Pilosa: myrmecophagid (southern tamandua)		South America
A. usingeri	Sauria: iguanid (Galapagos land iguana); Testudines: testudinid (Galapagos tortoise (3 subspp. Volcan Wolf giant tortoise, Darwin volcano giant tortoise, Alcedo volcano giant tortoise); Primates: hominid (human)		Galapagos Islands
A. (*Aponomma*) *varanense* (syn. *Aponomma fraudigerum, lucasi*)	Artiodactyla: bovid (gayal, bharal), suid (Indian boar); Pholidota: manid (Sunda pangolin); Carnivora: canid (dog, jackal), herpestid (short-tailed mongoose), mustelid (smooth-coated otter), viverrid (small-toothed palm civet); Sauria: agamid (sailfin lizard), varanid (desert monitor, mangrove monitor, clouded monitor, roughneck monitor, Asian water monitor, Bengal monitor, Dumeril's monitor); Serpentes: boa (Russell's boa), colubrid (mangrove snake, Oriental rat snake), elapid (king cobra, Indian cobra, banded krait, Indian krait), pythonid (reticulated python, Indian python), viperid (Russell's viper); Testudines: geoemydid (Amboina box turtle)		Africa
A. variegatum (syn. *A. elegans, venustum*) (variegated/tropical bont tick)	Artiodactyla: bovid (cattle, zebu, gaur, buffalo, water buffalo, sheep, goat, eland, giant eland, klipspringer, southern reedbuck, Bohor reedbuck, bushbuck, harnessed bushbuck, steenbok, waterbuck, blackbuck, roan antelope, sable antelope, blue wildebeest, hartebeest, Lelwel hartebeest, Lichtenstein's hartebeest, tiang, impala, nyala, common duiker, blue duiker, red-flanked	trauma, irritation (vector for ehrlichosis, Q fever, rickettsial African tick bite fever, theileriosis,	Africa, Caribbean

	duiker, red-fronted gazelle, Arabian gazelle, Bright's gazelle, Grant's gazelle, Thomson's gazelle, forest antelope, long-snouted dikdik, Gunther's dikdik, Kirk's dikdik, Roosevelt's duikerbok, oribi, nyala, lechwe, kob**,** topi, tiang, korrigum, suni, tsessebe, sitatunga, greater kudu, kongoni), camelid (dromedary), cervid (sambar deer), giraffid (giraffe), suid (pig, bushpig, red river hog, warthog); Perissodactyla: equid (horse, donkey, mule, plains zebra, Burchell's zebra), rhinocerotid (white rhinoceros, black rhinoceros); Proboscidea: elephantid (African bush elephant); Tubulidentata: orycteropodid (aardvark); Eulipotyphla: erinaceid (four-toed hedgehog, North African hedgehog, Sudanese hedgehog); Pholidota: manid (ground pangolin); Lagomorpha: leporid (savannah hare, Cape hare); Afrosoricida: tenrecid (tailless tenrec, Madagascar tenrec); Rodentia: hystricid (Indian crested porcupine), murid (house mouse, black rat, yellow-spotted brush-furred rat, gracile tateril), sciurid (striped ground squirrel), thryonomyid (greater cane rat); Carnivora: canid (dog, African wolf, Arabian wolf, golden jackal, silver jackal, long-eared fox, bat-eared fox, Arabian red fox), felid (cat, leopard, cheetah, lion, serval), herpestid (common slender mongoose, white-tailed mongoose, Egyptian mongoose, small Indian mongoose), hyaenid (spotted hyena), viverrid (civet, Cape genet); Primates: cercopithecid (patas monkey, mona monkey, grivet), galagid (brown greater galago, Senegal bushbaby), hominid (human); Accipitriformes: accipitrid (long-legged buzzard, hooded vulture, white-backed vulture); Anseriformes: anatid (muscovy duck, white-faced whistling duck, spur-winged goose); Bucerotiformes: bucerotid (African grey hornbill, Abyssinian ground hornbill); Columbiformes: columbid (common ground dove); Cuculiformes: cuculid (Malagasy coucal, Senegal coucal); Galliformes: numidid (helmeted guineafowl), phasianid (chicken, double-spurred spurfowl, Clapperton's francolin, yellow-necked spurfowl, turkey); Otidiformes: otidid (black-bellied bustard, long-legged bustard); Passeriformes: acanthizid (grey thornbill, ground thornbill), icterid (Carib grackle), laniid (black-crowned tchagra), malaconotid (black-crowned tchagra), muscicapid (sooty chat), thraupid (black-faced grassquit); Pelecaniformes: ardeid (cattle egret), ciconiid (Abdim's stork), pelecanid (brown pelican); Strigiformes: strigid (Verreaux's eagle-owl); Struthioniformes: struthionid (ostrich); Sauria: chamaeleonid (panther chameleon, African chameleon), varanid (Nile monitor); Serpentes: viperid (puff adder, Somali puff adder) (3-host cycle)	Nairobi sheep disease virus, tularaemia, Crimean-Congo haemorrhagic fever, dermatophilosis)	
A. varium	Artiodactyla: bovid (steenbok), tayassuid (peccary); Pilosa: bradypodid (pale-throated sloth, brown-throated sloth, maned sloth), choloepodid (Linnaeus's two-toed sloth, Hoffman's two-toed sloth), myrmecophagid (southern tamandua); Didelphimorphia: didelphid (common opossum, Eaton's opossum); Rodentia: caviid (cavy), dasyproctid (red-rumped agouti), echimyid (Tome's spiny rat); Carnivora: canid (dog), procyonid (white-nosed coati); Columbiformes: columbid (grey-fronted dove); Passeriformes: cardinalid (red-throated ant tanager), furnariid (buff-throated foliage-gleaner, plain-brown woodcreeper, wedge-billed woodcreeper, buff-throated woodcreeper), icterid (shiny cowbird), piprid (red-capped manakin, golden-collared manakin, pale-bellied tyrant-manakin), thamnophilid (white-cheeked antbird), troglodytid (song wren), turdid (orange-billed nightingale-thrush), tyrannid (golden-faced tyrannulet); Piciformes: bucconid (white-whiskered puffbird); Sauria: iguanid (northeastern spinytail iguana); Serpentes: boid (boa, green anaconda); Anura: bufonid (cane toad)		South America
A. venezuelense	Pilosa: myrmecophagid (southern tamandua)		South America
A. versicolor	Perissodactyla: equid (horse)		Mexico
A. (*Cernyomma*) *vikirri*	Sauria: scincid (Gidgee skink, Stokes's skink, sleepy lizard)		Australia

A. williamsi	Sauria: iguanid (Galapagos land iguana, unspecified sea iguana)		Galapagos Islands
A. yajimai	Artiodactyla: bovid (cattle, buffalo, water buffalo)		Taiwan
A. yucumense	Didelphimorphia: didelphid (big-eared opossum); Rodentia: cricetid (montane grass mouse, russet rice rat, rat-headed rice rat, hocicudo)		South America

Parasite morphology: *Amblyomma* spp. form 4 distinct types of morphological stages during their development: eggs; larvae; nymphs; and adults. Eggs are glossy brown oval stages measuring 0.4-0.5 mm long and they occur in large clusters. Larvae (also known as seed ticks) are discoidal (round flattened) stages measuring 0.5-1.0 mm long and they are usually pale yellow-brown in colour. They have an anterior capitulum (head) with long forwardly-projecting palps and mouthparts. The posterior idiosoma (body) has a sclerotized dorsal shield (scutum), lateral eyes, posterior festoons and 6 long ventral legs. Larvae lack respiratory stigmata and tracheae, and the anus does not yet have a posterior groove. Nymphs are also discoidal stages measuring 1.5-2.5 mm long and they are usually darker brown in colour with irregular coloured patterns on their dorsal surfaces. The capitulum has a subrectangular basis capitulum and long palps, and the idiosoma has a dorsal scutum, lateral eyes, posterior festoons and the ventral anus now has a posterior anal groove. Nymphs have 8 long ventral legs and a pair of lateral respiratory stigmata surrounded by rounded plates. Adults are large robust ticks with oval dorsal profiles but are somewhat dorsoventrally flattened when unfed (different species range in length from 3-10 mm long when unfed). However, female ticks may swell enormously in size when engorging with blood, forming large globular sacs up to 20 mm long. *Amblyommma* ticks are usually quite distinctive due to their highly ornate bodies and long banded legs. Females are often brown in colour when unfed, but may change to blue-grey to black when engorged, while males usually remain pale orange to brown. Both sexes have a hardened sclerotized shield or plate (scutum) on the anterior dorsal surface of the idiosoma (almost completely covering males (= conscutum) but restricted to an anterior shield in females). The scutum contains elaborate patterns of coloured iridescent enamel ranging from white-cream to orange to pink-red depending on species. Adults have an anterior capitulum that is visible from above (whereas argasids have a ventral capitulum not visible from above). The capitulum comprises the basis capitulum (integumental ring encircling mouthparts) and the gnathosoma bearing the mouthparts (palps, chelicerae and hypostome), but lacks antennae (like all ticks). The basis capitulum is rectangular (sometimes subtriangular) with straight lateral margins (not triangular like *Ixodes*, nor hexagonal like *Rhipicephalus*/*Boophilus*, nor pentagonal like *Bothriocroton*). On females, the dorsal surface of the basis capitulum bears 2 porose areas (clusters of pores) which are used to help waterproof eggs. The mouthparts are long and well-adapted for piercing skin and sucking blood. The lateral palps are segmented and have long second segments and short third segments. The palps are sensory structures that move laterally and do not enter the skin when feeding. The chelicerae are specialized cutting structures with long curved shafts terminating in cutting digits with recurved teeth. They are used horizontally to cut a channel in skin ripping and tearing flesh to form small pools of blood. The central barbed hypostome is then inserted in the pools to facilitate feeding as well as to help anchor the tick to the host. A feeding tube (buccal canal) is formed dorsally by the chelicerae and ventrally by the hypostome and used to ingest blood as well as to inject saliva from long paired salivary glands. Blood is sucked up by a muscular pharynx (with pharyngeal valve) and delivered via a short tubular oesophagus to the large saccular midgut (ventriculus) with several pairs of blind-ending lateral diverticula (caeca) often looped or branched. Waste material from the midgut and from excretory Malpighian tubules is collected into a rectal sac that opens to the ventral subterminal anus. The anus has a posterior (metastriate) anal groove (whereas *Ixodes* has anterior (prostriate) anal groove). The posterior body margin has a series of grooves (festoons) which impart a toothed appearance (unclear in engorged females). In some species (e.g. *A. hebraeum*) the festoons have pale enamel colourings, whereas other species (e.g. *A. variegatum*) have no festoon enamelling. *Amblyomma* spp. also have a pair of simple (convex or flat) eyes located laterally on the scutum. However, members of the subgenus *A.* (*Aponomma*) (comprising former *Aponomma* spp.) lack eyes, and are sometimes referred to as eyeless *Amblyomma* spp. All adult ticks have 8 long well-developed legs arising from the ventral idiosoma. The legs are jointed and have 6 segments (coxae, trochanter, femur, patella (genu), tibia and tarsus), all terminating in a pair of claws and a pad-like pulvillus (the latter absent in argasids). The legs of most species are banded, with pale rings around the distal ends of central segments. Both sexes have a long external spur and a short internal spur on coxae I (argasid coxae without spurs), and they have a sensory structure (Haller's organ) located on dorsal tarsi I which is used to detect odours, body heat and vibrations. Adults also have respiratory stigmata with large rounded plates located behind coxae IV (cf. argasids have small stigmata between coxae III). Adults display marked sexual dimorphism in body size (females are larger, especially when engorged), scutal plates (small in females, large in males), and secretory structures (females with porose areas). Males also have ventral plaques which are more or less indistinct sclerotized plates just anterior to the ventral scutes, but they do not have distinct adanal shields (like *Rhipicephalus*/*Boophilus* and *Hyalomma*) and the ventral plaques are lacking in the eyeless Amblyomma spp. Males have paired tubular testes connected by vas efferentia to a common vas deferens (with a large multilobed accessory gland) leading to the ejaculatory duct. The genital opening (gonopore) is situated on the ventral midbody and has a sclerotized flap (genital apron) but no external genitalia. Males produce packets of spermatids (spermatophores) which are transferred to females. Adult female ticks have a single saccular ovary with paired oviducts connecting to the common uterus which has tubular accessory glands (including Gene's organ) which secrete coatings to waterproof eggs. The vagina has a cervical region that acts as receptaculum seminis (to store spermatophores) and a vestibular region (that prolapses during oviposition). The gonopore is V- or U-shaped and is located on the ventral midbody and partly covered by an anterior genital apron.

Site of infection: All motile developmental stages (larvae, nymphs and adults) are ectoparasitic on a range of vertebrate hosts. Infestations have been reported on reptiles (16 lizard families, 12 snake families, 10 tortoise families, 2 crocodile families),

amphibians (7 frog families, one newt family), birds (35 passerine families, 54 non-passerine families belonging to 28 orders, including waterfowl, seabirds, shore birds, terrestrial birds, forest birds and birds of prey) and mammals (69 families belonging to 20 orders, including ungulates, insectivores, marsupials, monotremes, lagomorphs, rodents, carnivores, bats and primates). Most species have broad host ranges, although different developmental stages seem to have host preferences, with larvae and nymphs generally infesting small ground-dwelling animals, while adults are also able to infest larger animals. Ticks usually infest skin with plentiful folds and sparse coverings of hair, feathers or scales, notably the ears, axillae and udders, but they may be found on other body regions during heavy infestations.

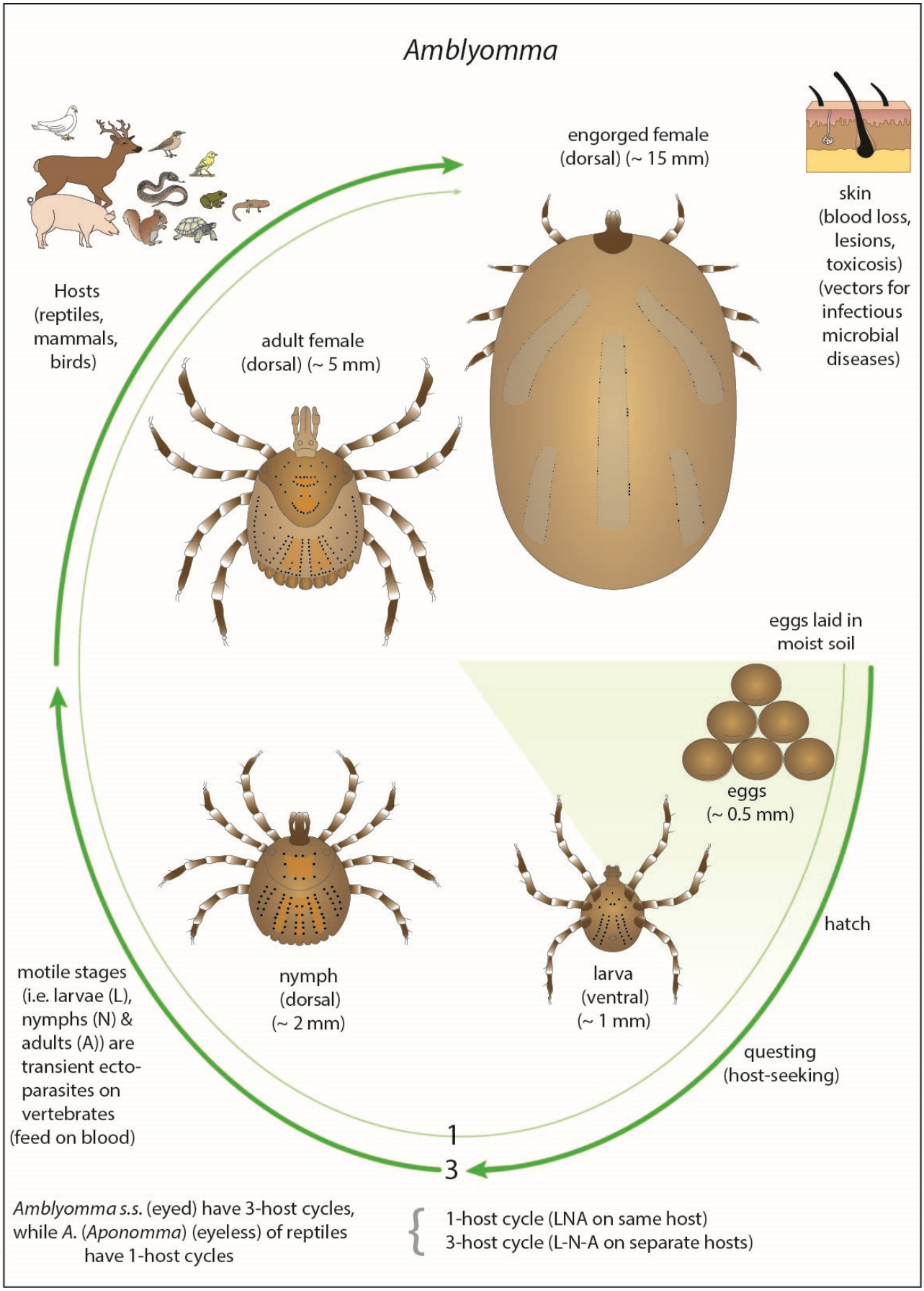
Pathogenesis: *Amblyomma* spp. are haematophagous parasites that require bloodmeals in order to develop further and complete their life-cycles. Larvae, nymphs and adults feed on blood before dropping off to digest their meals, moult to the next stage or to lay eggs. All developmental stages feed once to repletion over several days. They have long mouthparts that inflict painful bites as their chelicerae rip and tear tissues creating blood pools into which they insert their hypostomes (feeding process known as telmophagy). They attach firmly during feeding using a salivary cement that helps create a feeding lesion in the dermis. Tick saliva also contains many vaso-active compounds with analgesic, anticoagulatory, vasodilatory and vascular permeability properties. Heavy infestations may cause significant blood loss resulting in anaemia and sometimes jaundice. Tick bites cause local tissue trauma with irritation, inflammation, erythema, oedema, pruritus, focal necrosis and granuloma formation. Some hosts may exhibit allergic or hypersensitivity reactions to tick saliva which heightens inflammation and granuloma formation (sometimes causing a deformity in the ears of cattle known as gotch ear). Animals exhibit biting-stress (tick worry) and attempt to groom by licking, biting, scratching, rubbing affected areas, often worsening wounds and making them susceptible to secondary infections by bacteria, or screwworms and other myiasis flies. Livestock are distracted from feeding efficiently and may exhibit production losses due to anorexia, poor growth, reduced weight gain, reduced milk production and the decreased value of hides due to bites and granulomas. Some species (e.g. *A americanum*) have also been associated with tick paralysis in people and dogs, where neurotoxins in the saliva cause motor paralysis with muscular paresis, incoordination, and sometimes respiratory abnormalities. The species *A. variegatum* has also been found to cause transient immuno-suppression in sheep and cattle, allowing bacteria skin infections to flourish resulting in dermatophilosis (lumpy wool, foot rot). Feeding ticks may act as efficient biological or mechanical vectors for the transmission of various infectious microbial diseases, with transmission occurring during feeding (via saliva), during fluid regulation (via regurgitation) or during waste elimination (via defaecation). Some microbes may multiply in tick tissues (amplification vectors), most survive tick metamorphic changes (trans-stadial transmission), and some are even transferred vertically to tick eggs (trans-ovarian transmission). Various tick species have been shown to transmit haemoprotozoan parasites causing babesiosis (tick fever) and theileriosis; rickettsial bacteria causing heartwater (cowdriosis), monocytic and granulocytic ehrlichioses, spotted fevers, African tick bite fever, and anaplasmosis; spirochaetes causing borreliosis, Lyme disease, and southern tick-associated rash illness; proteobacteria causing coxiellosis (Q fever); coccobacilli causing tularemia; viruses causing yellow fever and Crimean-Congo haemorrhagic fever, as well as a range of arthropod-borne (arbo-) viruses (e.g. Dugbe, Thogoto, Bhanja, Jos and Heartland viruses). Ticks bites by *A. americanum* have also been associated with predisposing humans to red meat allergies (called alpha-gal syndrome) by transferring carbohydrate allergens (galactose-alpha-1,3-galactose) resulting in delayed urticarial or anaphylactic reactions when the body becomes overloaded with IgE antibodies.

Developmental cycle and mode of transmission: Like all ticks, *Amblyomma* spp. undergo incomplete (hemimetabolous) metamorphosis, where eggs hatch larvae which moult to nymphs and then adults. Each motile stage feeds on a separate host, so members of the genus *Amblyomma sensu stricto* (i.e. the eyed *Amblyomma* spp.) have 3-host life-cycles. In contrast, the 30 former *Aponomma* spp. transferred to the subgenus *Amblyomma* (*Aponomma*) (that is, the eyeless *Amblyomma* spp.) have one-host life-cycles, where all developmental stages occur on the same host, usually reptiles. The following description pertains to ticks with 3-host cycles. Gravid female ticks lay eggs in large clusters on shaded moist soil where they hatch after 4-15 weeks depending on environmental conditions (longer in cold conditions). The emergent 6-legged larvae then spend time seeking hosts, usually small ground-dwelling reptiles, birds or mammals (particularly rodents). The larvae of many species ascend vegetation and wait for passing hosts (ambush strategy). They respond to host odours, body heat and vibrations by actively waving their forelegs in the air (questing behaviour). The larvae of some species have also been shown to scuttle along the ground towards hosts (hunter strategy) when stimulated by host odours (and also pheromones released by resident ticks). Larvae may survive in the external environment for several weeks to months searching for hosts depending on environmental conditions. Having located a host, the larvae attach and feed on blood for 4-6 days and then drop off onto the ground. They seek shelter and enter a pre-moult phase for 2-3 weeks to digest their bloodmeals. They moult to 8-legged nymphs which then spend time seeking hosts (usually small ground-dwelling animals but also larger animals), mostly by questing, sometimes by hunting. Ixodids only form one nymphal instar, whereas argasids may form 2-7 instars. Nymphs can also survive in the external environment for several months depending on prevailing conditions (longer in colder climates). Once a host is located, they attach to the skin and feed on blood for 4-7 days before dropping off. They seek shelter to digest their bloodmeals over several weeks before moulting to adult ticks. Adults seek hosts (larger animals including livestock) by questing or hunting and they may survive for several months before locating a host. Both male and female ticks require a bloodmeal to become sexually mature, but males feed sporadically while moving about the host for mates, while females attach to feed and wait for a roving mate. Following mating, the females engorge on blood swelling to many times their original body size. When replete, the females detach and drop off the host onto the ground. Fertilized females rest for several days and then begin laying eggs in large batches over a few weeks. Females may lay up to 5,000 eggs before becoming spent and dying shortly thereafter. Some species may complete their entire life-cycle in as little as 80-100 days under ideal conditions, but they generally

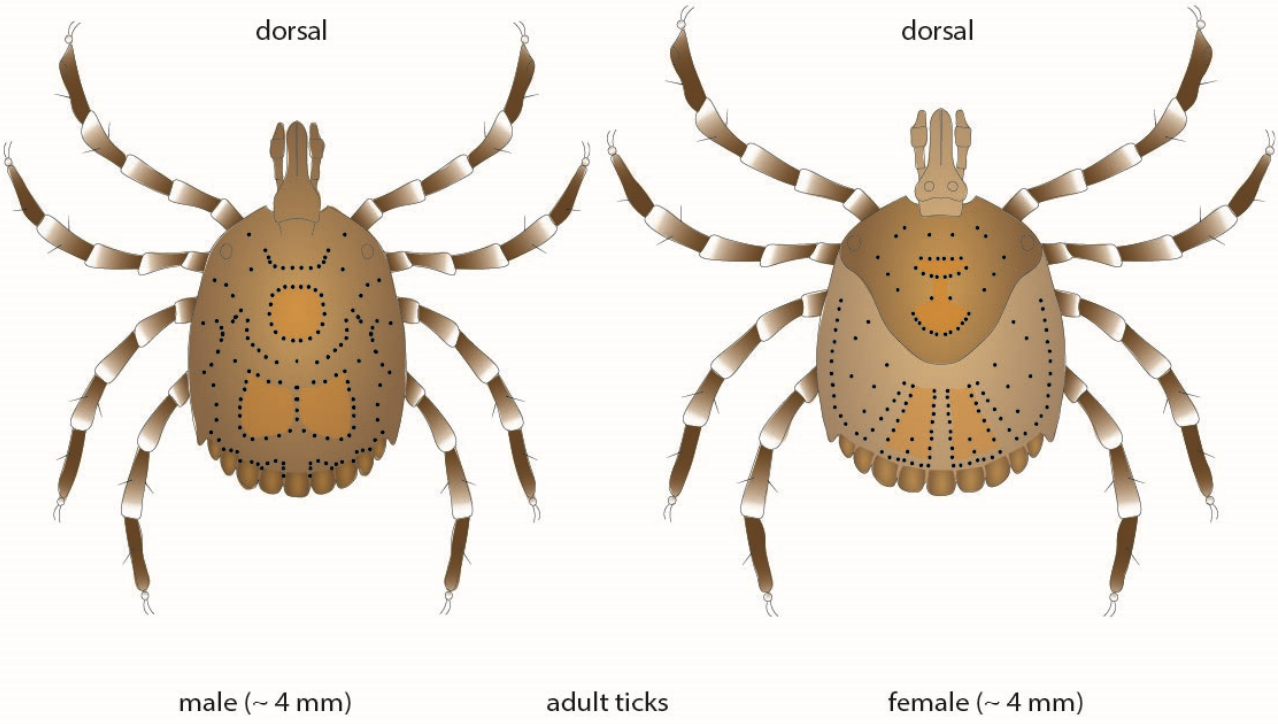
take longer as each stage rests in the environment before moulting and then may take some time to locate a host. The duration of the life-cycle is influenced mainly by seasonal variations in climatic factors (particularly temperature and humidity) as well as the availability of hosts. Tick stages are most active during mild conditions in spring and autumn, and may overwinter in the environment and over-summer on hosts. The life-cycle may be completed twice a year in tropical and subtropical regions, once a year in temperate regions with mild winters, and sometimes once every 2-3 years in temperate regions with cold winters.

Differential diagnosis: While infestations may be suspected on clinical grounds (skin lesions, anaemia), other disease entities may cause similar non-specific symptoms/signs, including other ectoparasites and a range of dermatological conditions. Infestations are conventionally diagnosed by the direct detection of tick stages feeding on the skin, with confirmation provided by their careful removal and subsequent microscopic examination. *Amblyomma* ticks are readily identified by their unique morphological characteristics, notably their ornate bodies with festoons, long banded legs and long mouthparts. Specimens may be snap frozen or fixed in alcohol for molecular characterization studies. Free-living stages may be collected by dragging or flagging blankets over pastures and bushes (for questing stages) or by using static dry ice (carbon dioxide) traps (for hunting stages). Molecular biological techniques have also been used to characterize species by polymerase chain reaction (PCR) amplification of nuclear (18S and 28S ribosomal RNA, internal transcribed spacer regions 1 and 2) and mitochondrial (12S and 16S ribosomal RNA, cytochrome c oxidase subunit I, nicotinamide adenine dinucleotide dehydrogenase subunit 5) gene sequences.

Treatment and control: Infestations are usually treated using topical or systemic acaricides, as ticks are difficult to remove intact due to their long mouthparts. Successful treatments have been reported using arsenical preparations, organochlorines (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (coumaphos, malathion, chlorpyrifos, fenthion, dichlorvos, cythoate, diazinon, propetamphos, phosmet, ronnel, chlorfenvinphos, dioxathion, fenchlorvos, stirofos, trichlorfon), carbamates (carbaryl), pyrethroids (permethrin, flumethrin, deltamethrin, decamethrin, cypermethrin, cyprothrin, alphametrin), formamidines (amitraz), macrocyclic lactones (ivermectin, selamectin), phenylpyrazoles (fipronil), chloronicotinyls (imidacloprid), isoxazolines (afoxolaner, fluralaner), some natural products (rotenone) and some insect growth regulators (methoprene, pyriproxyfen). These chemicals are available in a range of sprays, dips, dusts, emulsions, impregnated collars or tags, drenches, tablets, spot-ons, pour-ons, or injections. Treatment often needs to be repeated as animals rapidly become re-infested, although slow-release formulations or compounds with long-lasting residual activity help reduce treatment frequency. Livestock that are corralled every night have been shown to benefit from evening footbaths as larvae attaching to the feet tend to migrate upwards overnight. Regrettably, the incorrect or over-usage of many acaricides has led to the development of drug resistance in many tick populations, particularly against arsenic compounds, organochlorines (especially DDT), and some organophosphates, pyrethroids and formamidines. It is recommended that acaricides be used in cyclic rotation and that tick populations be regularly tested drug resistance (by *in situ* or *in vitro* egg hatch tests, and larval or adult development tests). Integrated tick management strategies should be adopted by producers, particularly those based around strategic treatments, spelling pastures and wildlife control. Livestock health management should include regular screening for ticks, placing new livestock into temporary quarantine, treating animals therapeutically and prophylactically during peak seasons, and even culling heavily infested livestock or those refractory to treatment. Grazing management strategies include rotating animals between pastures, de-stocking or cultivating pastures for a season, clearing excess vegetation (cut, slash, burn, or plough), avoiding over-stocking, treating small areas and holding facilities with long-lasting environmental acaricides (e.g. pyrethroids), and stabling or housing animals indoors overnight. Wildlife management should aim to reduce the availability of suitable reservoir hosts by fencing, hunting, trapping, diverting migration routes, providing medicated supplementary feeds or installing self-treatment devices (rubbing posts, rollers). A number of mathematical prediction models have recently been developed to help producers manage interventions based on many bionomic factors, including location (latitude, longitude, elevation), climate (temperature, moisture, rainfall, photoperiod), vegetation type and structure, land-use and animal husbandry. Several studies on biocontrol have shown that spraying hosts or pastures with entomopathogenic fungi (*Beauveria* and *Metarhizum*) have reduced populations of *A. variegatum* in experimental and field situations, but no products have yet been commercialized.


Amblyomma
engorged female
(dorsal) (~ 15 mm)
skin
(blood loss,
lesions,
toxicosis)
(vectors for
infectious
microbial
diseases)
Hosts
(reptiles,
mammals,
birds)
adult female
(dorsal) (~ 5 mm)
eggs laid in
moist soil
eggs
(~ 0.5 mm)
hatch
nymph
(dorsal)
(~ 2 mm)
larva
(ventral)
(~ 1 mm)
motile stages
(i.e. larvae (L),
nymphs (N) &
adults (A)) are
transient ecto-
parasites on
vertebrates
(feed on blood)
questing
(host-seeking)
1
3
Amblyomma s.s. (eyed) have 3-host cycles,
while A. (Aponomma) (eyeless) of reptiles
have 1-host cycles
1-host cycle (LNA on same host)
3-host cycle (L-N-A on separate hosts)

Amblyomma

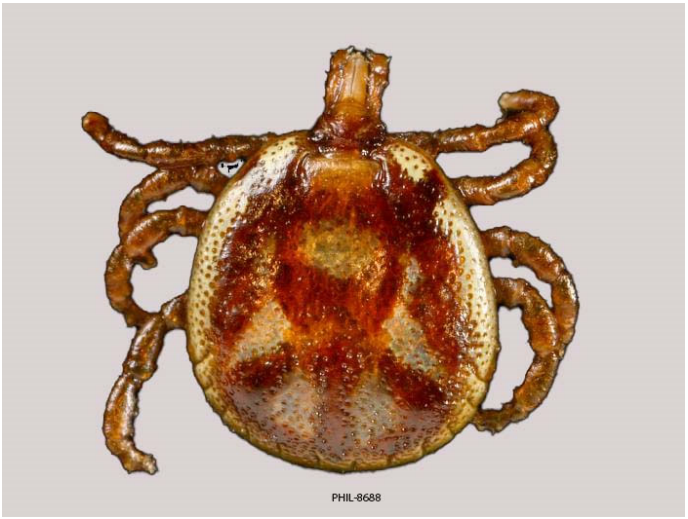

dorsal
dorsal
male (~ 4 mm)
adult ticks
female (~ 4 mm)
ventral
ventral



Amblyomma adults



Amblyomma adult, engorged female and eggs



Amblyomma (*Aponomma*) adult



Amblyomma larva

***Bothriocroton* (includes some *Aponomma*)**
(arachnid: tick)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ticks have respiratory stigmata posterior to their legs. They are obligate blood-feeding ectoparasites on vertebrate hosts and their hypostomes are toothed and exposed. Two families are recognized: Argasidae and Ixodidae, known as soft and hard ticks, respectively. Ixodids have hard bodies with a dorsal scutum (shield-shaped plate) and the capitulum is not covered by the body. Larvae, nymphs and adults attach and feed on host blood, their life-cycles involving one, two or three hosts depending on whether moulting occurs on or off the host. Some 650 species of hard ticks infest mammals, birds and reptiles. Infestations by *Bothriocroton* (established for various *Aponomma* spp.) occur as three-host ticks mainly on reptiles, but including some Australian marsupials.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on capitulum)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Ixodida (Metastigmata) (ticks, macroscopic, stigmata posterior to legs, hypostome toothed, ectoparasites)
Family: Ixodidae (hard ticks, with dorsal scutum, capitulum projects anteriorly, attach and feed on 1, 2 or 3 hosts)
Genus: *Bothriocroton* (syn. *Aponomma p.p.*) (parasitic on skin of reptiles/mammals)
Species: various species may cause skin lesions

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on capitulum) [34 superfamilies]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs (behind coxae III or IV); and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Ticks are further characterized by macroscopic bodies with an exposed ventral hypostome (toothed with backwardly-directed barbs), chelicerae with only 2 joints, long legs with free articulated coxae (not fused to the body wall) and a complex sensory pit (Haller's organ) on tarsus I. They are obligate blood-sucking parasites which feed on terrestrial vertebrates (mammals, birds, reptiles and some amphibians) as larvae, nymphs and adults with 1-, 2- or 3-host life-cycles. Almost 1,000 species have been classified within some 20 genera from numerous wild and domesticated animals around the world. Two main families are recognized: the Argasidae containing ~200 species of 'soft' ticks with flexible leathery cuticles, ventral capitula, short feeding times (< 1 hour) and long life-spans (up to 20 years); and the Ixodidae containing ~800 species of 'hard' ticks with rigid dorsal scutal plates, anterior capitula, long feeding times (hours to days) and shorter life-span (2-6 years). Basic characteristics of representative genera considered in this resource are tabulated below.

Genus	**Capitulum**				**Idiosoma**				**Usual no. of hosts**
	location	**basis capitulum**	**mouth-parts**	**palps**	**integument**	**festoons**	**eyes**	**male ventral**	

								plates	
Argasidae (soft ticks with leathery cuticle, stigmata between coxae III)									
Argas	ventral	triangular	short	leg-like	stippled with lateral suture	absent	absent	absent	>3
Ornithodorus	ventral	rectangular	short	leg-like	mamillated	absent	usually absent	absent	>3
Otobius	ventral	rectangular	short	leg-like	spinose (nymphs), granulated (adult)	absent	absent	absent	1
Ixodidae (hard ticks with sclerotized dorsal plate (scutum), stigmata behind coxae IV)									
Prostriata (anal groove anterior)									
Ixodes	anterior	triangular	long	long	inornate	absent	absent	present	3
Metastriata (anal groove posterior)									
Amblyomma	anterior	rectangular	long	long	ornate	present	present	indistinct	3
(*Aponomma*)	anterior	rectangular	long	long	often ornate	present	absent	absent	3
Rhipicephalus	anterior	hexagonal	short	medium	some ornate	present	present	present	3
(*Boophilus*)	anterior	hexagonal	short	short	inornate	absent	present	present	1
Dermacentor	anterior	rectangular	short	medium	often ornate	present	present	absent	3
Haemaphysalis	anterior	rectangular	short	short	inornate	present	absent	absent	3
Hyalomma	anterior	rectangular	long	long	inornate	present	present	present	2
Bothriocroton	anterior	pentagonal	long	long	ornate	present	absent	absent	3

The family Ixodidae contains 6 subfamilies (Amblyomminae, Bothriocrotoninae, Haemaphysalinae, Hyalomminae, Ixodinae and Rhipicephalinae) which vary in their morphology, biology, host ranges and specificity. [Note that some taxonomic authorities have merged the subfamilies Rhipicephalinae and Hyalomminae, while others have subsequently assigned the subfamilies Amblyomminae and Rhipicephalinae into the new family Amblyommidae, predominantly on the basis of molecular phylogenetic studies]. Hard ticks had previously been divided into 2 groups: the Prostriata (with the anal groove anterior to the anus) and the Metastriata (anal groove absent or posterior to anus). The Prostriata essentially comprises the subfamily Ixodinae with over 230 species assigned to the single extant genus *Ixodes* [plus one fossil genus (*Cornupalpatum*)], while the Metastriata contains members of the remaining subfamilies with over 600 species classified into 18 genera. The subfamily Bothriocrotoninae comprises metastriate ornate ticks with festoons but lacking eyes and ventral shields. The subfamily is monotypic and only contains one genus, namely *Bothriocroton* [this genus is essentially a partial synonym of the defunct genus *Aponomma* as it was erected on the basis of molecular studies to accommodate several Australian *Aponomma* spp., while the remaining *Aponomma* spp. were transferred to the genus *Amblyomma*]. A small number of *Bothriocroton* spp. are recognized as ectoparasites feeding not only on varanid lizards but also on some Australian marsupials (wombat and echidna). They are relatively large ticks with long palps and an ornate scutum with posterior festoons but lacking eyes. Recent molecular screening studies have detected rickettsial bacteria in several species, possibly involved in the transmission of Flinders Island spotted fever.

***Bothriocroton* species**	**Hosts**	**Clinical signs**	**Distribution**
B. auruginans (syn. *Aponomma*)	Diprotodontia: vombatid (common wombat, hairy-nosed wombat); Carnivora: canid (dog), felid (cat); Primates: hominid (human) (3-host cycle)	trauma, irritation	Australia
B. concolor (syn. *Aponomma concolor, tropicum*)	Monotremata: tachyglossid (short-beaked echidna); plus doubtful records on Peramelemorphia: peramelid (bandicoot), Artiodactyla: bovid (cattle); Perissodactyla: equid (horse) (3-host cycle)	trauma, irritation	Australia
B. glebopalma (syn. *Aponomma*)	Squamata: varanid (twilight monitor, Kimberley rock monitor)		Australia
B. hydrosauri (syn. *Amblyomma*, *Ixodes, Aponomma trachysauri*) (southern reptile tick)	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Peramelemorphia: peramelid (long-nosed bandicoot); Monotremata: tachyglossid (short-beaked echidna); Rodentia: murid (mouse); Primates: hominid (human); Sauria: agamid (eastern bearded dragon, central bearded dragon, mountain heath dragon, superb two-line dragon), scincid (metallic skink, White's skink, southern blue-tongued lizard, western blue-tongued lizard, common blue-tongued skink, pygmy blue-tongued lizard, blotched blue-tongue lizard, sleepy lizard), varanid (sand goanna, lace monitor); Serpentes: elapid (common death adder, lowland		Australia

	copperhead, Australian copperhead, eastern brown snake, white-lipped snake, mainland tiger snake, peninsula black tiger snake); Testudines: chelid (eastern long-necked tortoise)		
B. oudemansi (syn. *Aponomma*)	Monotremata: tachyglossid (long-beaked echidna, short-beaked echidna)		New Guinea
B. tachyglossi (syn. *Aponomma*)	Monotremata: tachyglossid (short-beaked echidna); Artiodactyla: bovid (cattle)		Australia
B. undatum (syn. *Aponomma, B. decorosum, I. decorosus*) (goanna tick)	Monotremata: tachyglossid (short-beaked echidna); Sauria: scincid (common blue-tongued skink), varanid (sand goanna, lace monitor, perentie, Dampier Peninsula monitor, Asian water monitor); Serpentes: pythonid (carpet python, Darwin carpet python)		Australia

Parasite morphology: Like other ticks, *Bothriocroton* spp. form 4 different types of morphological developmental stages: namely, eggs, larvae, nymphs and adults. The eggs are small brown ovoid stages measuring 0.4-0.5 mm in diameter and generally occur in small clusters. Larvae are dorsoventrally flattened stages that are oval-pyriform in dorsal profile measuring 0.5-1.0 mm long. The idiosoma (body) has a dorsal plate (scutum) and is often brown in colour with pale margins and posterior festoons. The ventral surface gives rise to 3 pairs of long pale legs. The anterior capitulum (head) projects forwards and has long palps and mouthparts. Larvae lack respiratory stigmata and do not have a groove around the anus. Nymphs are similar in shape but larger in size, measuring 1.0-2.5 mm and having slightly darker bodies. The idiosoma has a dorsal scutum, posterior festoons, lateral respiratory stigmata, a ventral anus with a posterior anal groove and 4 pairs of long ventral legs. The anterior capitulum has a subrectangular basis capitulum supporting long palps and mouthparts. Adult ticks vary considerably in size and shape depending on their gender and feeding status. Unfed males and females have a flat ventrum, slightly convex dorsum and are oval-pyriform in outline (males measuring 2-5 mm long, females 3-7 mm). They become more convex when feeding, with engorging females swelling markedly to become large ovoid-ellipsoid globular stages measuring up to 15-20 mm in length. Adults range in colour from pale cream to yellow-brown to red-brown, with males appearing darker and engorged females appearing lighter, sometimes even grey-blue. The anterior capitulum is visible from above (while that of argasids is ventral and not visible from above) and consists of a basis capitulum (integumental ring encircling mouthparts) and gnathosoma containing the mouthparts (palps, chelicerae and hypostome), but lacks antennae. The basis capitulum is pentagonal (not triangular, rectangular or hexagonal like other ixodids) and the dorsal surface bears a pair of porose areas (clusters of pores) that are involved in waterproofing eggs. The 2 sensory palps are long and have unequal segments (long segment 2, short segment 3), all of which move laterally during feeding and do not enter the skin. The mouthparts are also long and have a central barbed hypostome flanked by 2 chelicerae with tubular shafts and terminal digits with recurved denticles. The chelicerae cut the skin allowing the hypostome to be inserted into pooling blood. A feeding tube (buccal canal) is formed dorsally by the chelicerae and ventrally by the hypostome allowing blood to be ingested and saliva to be injected from long saccular salivary glands. Blood is sucked up by a muscular pharynx into a short tubular oesophagus and delivered to the digestive midgut (ventriculus) with several pairs of lateral diverticula (caeca). Waste material from the midgut and excretory Malpighian tubules is collected into a rectal sac and voided through a ventral subterminal anus. Externally, the anus has a posterior (metastriate) anal groove (while Ixodes has an anterior (prostriate) anal groove). The idiosoma bears a sclerotized dorsal scutum which occupies most of dorsal surface in males (= conscutum) but appears as smaller shield in females). It is often ornate and has irregular pale enamel markings, white in some species and pitted in others. The posterior body margin bears a series of regular festoons, often with pale edges imparting a dentate appearance. *Bothriocroton* spp. do not possess lateral eyes on the scutum, nor do all other former *Aponomma* spp. transferred to the genus *Amblyomma.* The anteroventral body is the point of attachment for 4 pairs of long jointed legs, usually lighter in colour and ornamented with conspicuous pale rings or bands. Each leg has 6 segments (coxa, trochanter, femur, patella (genu), tibia, and tarsus) and terminates in a pair of claws with a pad-like pulvillus. The coxae have 2 spurs, the trochanters have single subterminal spurs and the tarsi on the forelegs have a unique sensory structure (Haller's organ) used to detect odours and vibrations. Adults have a pair of lateral respiratory stigmata surrounded by oval plates located behind coxae IV (while argasids have small stigmata between coxae III). Adult male ticks do not have ventral adanal or accessory plates or plaques (which are present in *Ixodes*, *Rhipicephalus*/*Boophilus*, *Hyalomma* and eyed *Amblyomma*). Mature males have paired tubular testes with vas efferentia fusing to form a common vas deferens (with a lobular accessory gland) leading to the ejaculatory duct and genital aperture (gonopore) opening mid-ventrally with an anterior sclerotized flap (genital apron). Copulation involves the transfer of packets of spermatids (spermatophores) to the genital operculum of females. Mature females have a single saccular ovary with paired tubular oviducts joined to a common uterus (with accessory glands) and bipartite vagina (with a cervical region that acts as a receptaculum seminis to store spermatophores, and a vestibular region that prolapses during oviposition). The genital aperture is U-shaped and located on the ventral midbody behind an anterior genital apron. Eggs are coated with waxy waterproofing secretions from a special gland (Gene's organ) located near the capitulum-idiosoma as well as from porose areas on the basis capitulum.

Site of infection: All motile developmental stages (larvae, nymphs and adults) are ectoparasitic on native Australian animals, particularly reptiles but also including mammals. Infestations have been recorded on reptiles belonging to 3 lizard families, 2 snake families and one tortoise family, as well as on mammals belonging to 9 families in 8 orders (notably marsupials (esp. wombats), monotremes (esp. echidnas), some carnivores, ungulates, rodents, and occasionally humans). Seven species with variable host

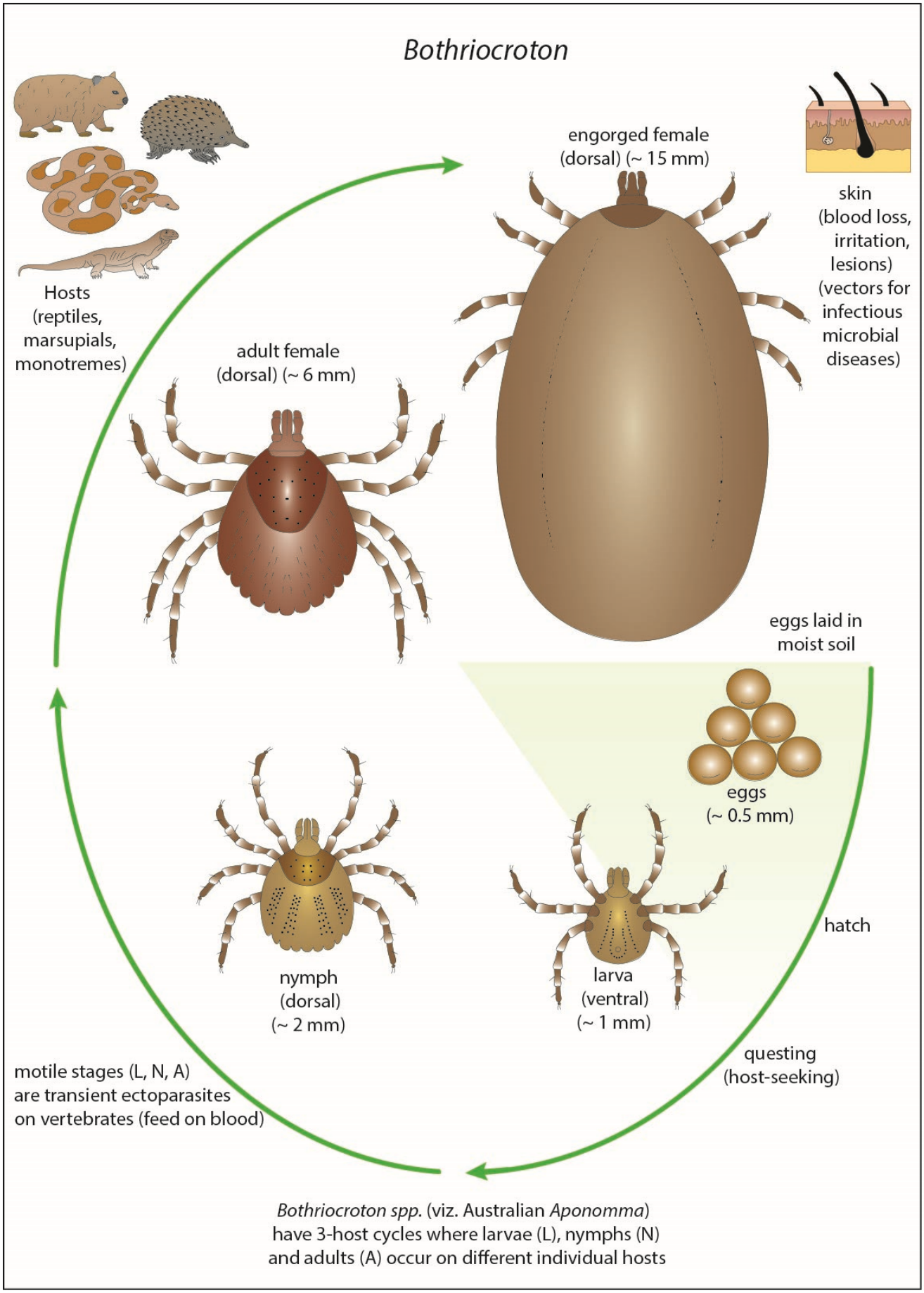
ranges are recognized, several being confined to small host groups but others having broad host specificities (or host preferences) for both reptilian and mammalian hosts. Ticks also exhibit some site specificity and attach to hosts in regions that are difficult to groom, such as around the head (including the ears and nostrils), the back of the neck and the axillae of the forelegs. They are generally found in skin folds or under scales depending on the host species.

Pathogenesis: Larvae, nymphs and adult ticks are obligate haematophagous parasites that must feed on host blood for several days in order to develop further. They use their cutting/sucking mouthparts to lacerate the skin creating pools of blood into which they insert their hypostomes to ingest blood (feeding process known as telmophagy). During feeding, they inject saliva containing numerous vaso-active compounds (with analgesic, anticoagulatory and vasodilatory properties) as well as a proteinaceous cement to secure their attachment and form a closed feeding lesion. Tick bites cause local tissue trauma with irritation, inflammation, erythema, oedema, pruritus, focal necrosis and granuloma formation. Reptiles may harbour a few or many feeding stages, often clustered together and sometimes without apparent ill effect. Heavy infestations may develop on burrowing animals (wombats and echidnas) producing granulomatous lesions with ill-health and haematological perturbations associated with numerous engorging females. Infestations on pets (cats and dogs) generally involve larvae and nymphs particularly around the faces of animals visiting wombat burrows. Infestations on livestock and humans appear incidental and may cause localized lesions with inflammation and variable pruritus. Epidemiological and experimental studies have shown that these ticks may act as transmission vectors for several infectious microbial diseases. *B. hydrosauri* appears to be vector for rickettsial bacteria causing Flinders Island spotted fever in humans and proteobacteria causing coxiellosis (Q fever) in ungulates. Molecular screening studies have recently detected several spirochaete bacteria (*Borrelia* spp.) in echidna ticks (*B. concolor*), but their involvement in any disease transmission is unknown.

Developmental cycle and mode of transmission: *Bothriocroton* spp. have life-cycles involving incomplete (hemimetabolous) metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Studies on several species have shown that they have 3-host life-cycles, with each developmental stage feeding once to repletion on a separate host. However, each stage infests the same range of hosts, so all stages may sometimes be present on the same individual host. Gravid females lay eggs on the ground where they hatch after 25-70 days depending on prevailing conditions (faster in warmer conditions). The emergent larvae aggregate at the soil-litter interface, a behaviour thought to be aided by the release of aggregation pheromones. Larvae are susceptible to desiccation so they seek locations with stable microclimates (without temperature extremes or low humidity), often aggregating in burrows, refuges or hides used by animals. Here they quest for hosts (ambush strategy) using sensory structures to detect odours and vibrations associated with passing hosts. They have been shown to quest for up to 200 days in cold conditions but with high humidity. Having located a host, they crawl onto the skin and attach at preferred sites to feed on blood. They feed to repletion over several days (occasionally up to 30 days) before dropping off into the external environment, usually the next time the host enters its shelter. They then enter a pre-moult period lasting 15-24 days to digest their bloodmeals before moulting to nymphs (only one nymphal instar is formed, whereas argasids may form 2-7 instars). Nymphs also aggregate low in leaf litter and appear to be more susceptible to desiccation than larvae. They quest for hosts over several weeks and only disperse from aggregation sites when hosts are detected nearby (within 20-50 cm). Nymphs crawl onto the skin of hosts brushing past and move to preferred sites to attach and feed on blood for several days (some feeding for up to 23 days). When replete they detach and drop from the host onto the ground, again in the vicinity of animal refuges. Nymphs enter a shorter pre-moult period lasting around one week before moulting to adult ticks (both males and females). Adults shelter in litter and vegetation while questing for passing hosts and have been shown to survive unfed for up to 100 days. Having located a host, the adults crawl onto the skin to attach and feed (both sexes requiring a bloodmeal to become sexually mature). Mating occurs on hosts when feeding females emit an air-borne excitant pheromone which induces feeding males to detach and search for sexually receptive females. If males are not activated, they may remain attached for months, feeding sparingly and waiting for mating opportunities. Once mated, females are not subsequently approached by males but continue feeding to massive engorgement over 1-2 weeks. They then detach and drop off the host, again in the vicinity of animal shelters. They enter a pre-oviposition period lasting up to one month (longer in colder conditions) and then begin laying large batches of several thousand eggs (1,500-2,000) over several weeks (up to 40 days) before becoming spent and dying. The whole life-cycle is usually completed in 18 months but may vary according to climatic conditions (longer in colder conditions) and the host abundance (longer when hosts are scarce).

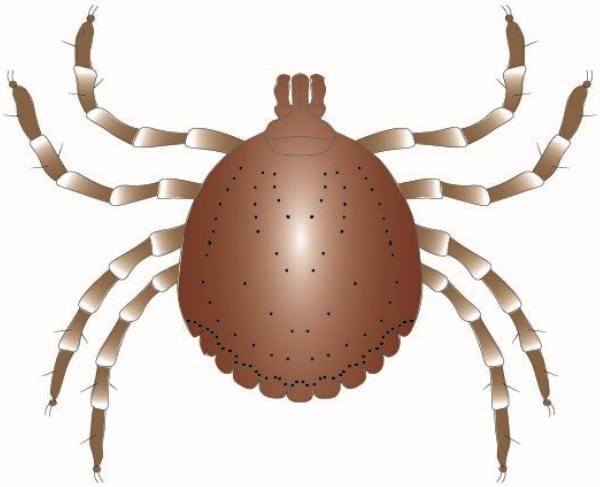
Differential diagnosis: The incidental detection of bite sites and skin lesions on animals is not pathognomonic as many aetiological agents may be involved, including other ectoparasites. Infestations are typically diagnosed by the direct observation of feeding or engorged ticks attached to hosts. Specimens may be carefully removed for microscopic examination and identification by their morphological characteristics (namely, ornate eyeless bodies with festoons, long palps and mouthparts, pentagonal basis capituli, and males lacking ventral plates). Molecular biological techniques have been used to characterize species and reconstruct phylogenies following the polymerase chain reaction (PCR) amplification of nuclear (18S and 28S ribosomal RNA, internal transcribed spacer regions 1 and 2) and mitochondrial (12S and 16S ribosomal RNA, cytochrome c oxidase subunit I, nicotinamide adenine dinucleotide dehydrogenase subunit 5) gene sequences. Comparative molecular characterization studies were instrumental in the creation of the genus *Bothriocroton* to accommodate several former *Aponomma* spp. from Australian animals, while the remaining *Aponomma* spp. were transferred to the genus *Amblyomma* (often referred to as eyeless *Amblyomma*).

Treatment and control: Infestations vary significantly in their intensity with many hosts (reptiles and mammals) having few ticks but some individuals developing heavy infestations (particularly wombats and some larger lizards). Although infestations may be regarded as transient and not requiring treatment (because feeding stages eventually drop off of their own accord when replete), medical or veterinary interventions may be required in cases involving large numbers of ticks (especially different stages at different periods of development), in hosts developing severe clinical signs (including small animals infested by several large engorged females) and even for cosmetic purposes in animals kept for display in vivaria (such as zoological collections and wildlife parks). Individual ticks may be removed by carefully pulling them off with tweezers, forceps or special tick removal tools. Physical removal may cause some temporary minor bleeding, but caution is advised as squeezing or tearing ticks may increase the risk of systemic reactions and anaphylaxis due to the release of allergenic compounds. Similarly, care should be exercised using folklore remedies that involve freezing ticks or applying oils, solvents or volatile fluids to their backs as they may release pro-inflammatory compounds before detaching or dying. Infestations are best treated using acaricidal chemicals which may be applied as sprays, emulsions, dusts, pour-ons, drenches, tablets or injections, but attention should be paid to any contra-indications as some formulations have toxic or adverse side-effects in certain host species. Treatments have organochlorines (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (dichlorvos, coumaphos, malathion, diazinon, trichlorfon), carbamates (carbaryl), pyrethroids (permethrin, deltamethrin, cypermethrin) and more recently, formamidines (amitraz), macrocyclic lactones (ivermectin, selamectin), phenylpyrazoles (fipronil), chloronicotinyls (imidacloprid) and isoxazolines (afoxolaner, fluralaner). There are growing concerns over the development of drug resistance in other tick genera, particularly to organochlorines, organophosphates, pyrethroids and formamidines, so it is recommended that acaricides belonging to different chemical classes be used in cyclic rotation or as combination cocktails. People at rick may also use personal protection by applying repellents (such as diethyltoluamide (DEET) or picaridin) to their skin or clothing. Few studies have been conducted specifically on the prevention of *Bothriocroton* infestations, but sensible measures should include regular health surveillance, quarantine, strategic prophylactic treatments, environmental management (clearing excess vegetation, livestock pasture rotation, treating local environments with residual acaricides) and wildlife control (through fencing, trapping or hunting). In the case of captive wildlife collections, every effort should be made to keep vivaria clean and to not introduce infested animals into enclosures. Researchers have occasionally suggested the possibility for biological control as they have observed that off-host stages are particularly prone to predation, notably by ants.


Bothriocroton
Hosts
(reptiles,
marsupials,
monotremes)
engorged female
(dorsal) (~ 15 mm)
skin
(blood loss,
irritation,
lesions)
(vectors for
infectious
microbial
diseases)
adult female
(dorsal) (~ 6 mm)
eggs laid in
moist soil
eggs
(~ 0.5 mm)
hatch
nymph
(dorsal)
(~ 2 mm)
larva
(ventral)
(~ 1 mm)
questing
(host-seeking)
motile stages (L, N, A)
are transient ectoparasites
on vertebrates (feed on blood)
Bothriocroton spp. (viz. Australian Aponomma)
have 3-host cycles where larvae (L), nymphs (N)
and adults (A) occur on different individual hosts

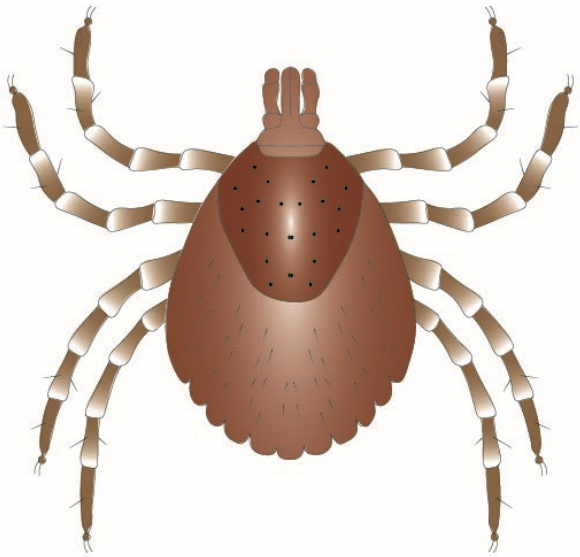
Bothriocroton

dorsal



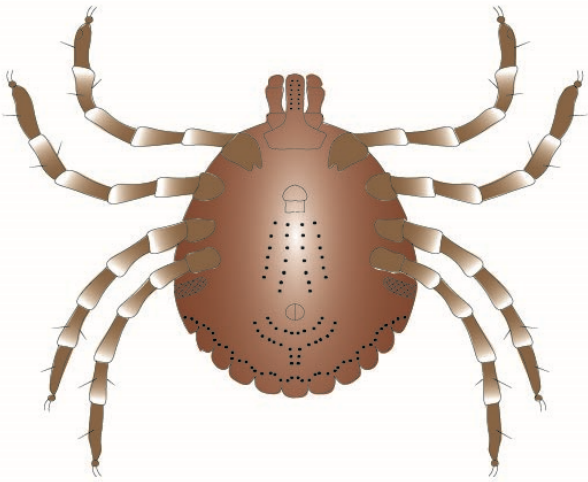
male (~ 4 mm)

dorsal

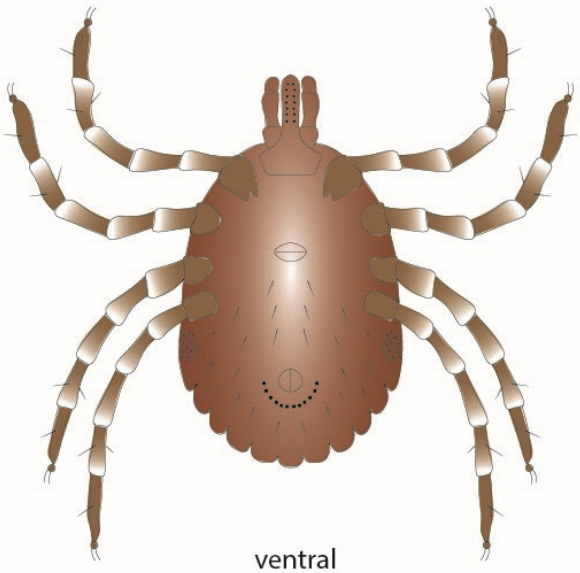


female (~ 6 mm)

adult ticks



ventral



ventral



Bothriocroton adult



Bothriocroton adult, engorged female

Dermacentor
(arachnid: tick)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ticks have respiratory stigmata posterior to their legs. They are obligate blood-feeding ectoparasites on vertebrate hosts and their hypostomes are toothed and exposed. Two families are recognized: Argasidae and Ixodidae, known as soft and hard ticks, respectively. Ixodids have hard bodies with a dorsal scutum (shield-shaped plate) and the capitulum is not covered by the body. Larvae, nymphs and adults attach and feed on host blood, their life-cycles involving one, two or three hosts depending on whether moulting occurs on or off the host. Some 650 species of hard ticks infest mammals, birds and reptiles. Infestations by *Dermacentor* spp. are found as one- or three-host ticks on various mammals, sometimes causing paralysis and transmitting a range of microbial diseases.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on capitulum)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Ixodida (Metastigmata) (ticks, macroscopic, stigmata posterior to legs, hypostome toothed, ectoparasites)
Family: Ixodidae (hard ticks, with dorsal scutum, capitulum projects anteriorly, attach and feed on 1, 2 or 3 hosts)
Genus: *Dermacentor* (parasitic on skin of mammals)
Species: various species cause lesions and paralysis in mammals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on capitulum) [34 superfamilies]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs (behind coxae III or IV); and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Ticks are further characterized by macroscopic bodies with an exposed ventral hypostome (toothed with backwardly-directed barbs), chelicerae with only 2 joints, long legs with free articulated coxae (not fused to the body wall) and a complex sensory pit (Haller's organ) on tarsus I. They are obligate blood-sucking parasites which feed on terrestrial vertebrates (mammals, birds, reptiles and some amphibians) as larvae, nymphs and adults with 1-, 2- or 3-host life-cycles. Almost 1,000 species have been classified within some 20 genera from numerous wild and domesticated animals around the world. Two main families are recognized: the Argasidae containing ~200 species of 'soft' ticks with flexible leathery cuticles, ventral capitula, short feeding times (< 1 hour) and long life-spans (up to 20 years); and the Ixodidae containing ~800 species of 'hard' ticks with rigid dorsal scutal plates, anterior capitula, long feeding times (hours to days) and shorter life-span (2-6 years). Basic characteristics of representative genera considered in this resource are tabulated below.

Genus	**Capitulum**				**Idiosoma**				**Usual no. of hosts**
	location	**basis capitulum**	**mouth-parts**	**palps**	**integument**	**festoons**	**eyes**	**male ventral**	

								plates	
Argasidae (soft ticks with leathery cuticle, stigmata between coxae III)									
Argas	ventral	triangular	short	leg-like	stippled with lateral suture	absent	absent	absent	>3
Ornithodorus	ventral	rectangular	short	leg-like	mamillated	absent	usually absent	absent	>3
Otobius	ventral	rectangular	short	leg-like	spinose (nymphs), granulated (adult)	absent	absent	absent	1
Ixodidae (hard ticks with sclerotized dorsal plate (scutum), stigmata behind coxae IV)									
Prostriata (anal groove anterior)									
Ixodes	anterior	triangular	long	long	inornate	absent	absent	present	3
Metastriata (anal groove posterior)									
Amblyomma	anterior	rectangular	long	long	ornate	present	present	indistinct	3
(*Aponomma*)	anterior	rectangular	long	long	often ornate	present	absent	absent	3
Rhipicephalus	anterior	hexagonal	short	medium	some ornate	present	present	present	3
(*Boophilus*)	anterior	hexagonal	short	short	inornate	absent	present	present	1
Dermacentor	anterior	rectangular	short	medium	often ornate	present	present	absent	3
Haemaphysalis	anterior	rectangular	short	short	inornate	present	absent	absent	3
Hyalomma	anterior	rectangular	long	long	inornate	present	present	present	2
Bothriocroton	anterior	pentagonal	long	long	ornate	present	absent	absent	3

The family Ixodidae contains 6 subfamilies (Amblyomminae, Bothriocrotoninae, Haemaphysalinae, Hyalomminae, Ixodinae and Rhipicephalinae) which vary in their morphology, biology, host ranges and specificity. [Note that some taxonomic authorities have merged the subfamilies Rhipicephalinae and Hyalomminae, while others have subsequently assigned the subfamilies Amblyomminae and Rhipicephalinae into the new family Amblyommidae, predominantly on the basis of molecular phylogenetic studies]. Hard ticks had previously been divided into 2 groups: the Prostriata (with the anal groove anterior to the anus) and the Metastriata (anal groove absent or posterior to anus). The Prostriata essentially comprises the subfamily Ixodinae with over 230 species assigned to the single extant genus *Ixodes* [plus one fossil genus (*Cornupalpatum*)], while the Metastriata contains members of the remaining subfamilies with over 600 species classified into 18 genera. The subfamily Rhipicephalinae contains 7 genera (*Anomalohimalaya*, *Cosmiomma*, *Dermacentor*, *Margaropus*, *Nosomma*, *Rhipicentor* and *Rhipicephalus* (syn. *Boophilus p.p.*)) comprising metastriate ticks (often ornate) with eyes and festoons and adult males have ventral plates. The genus *Dermacentor* contains 34 species described from a range of mammals; with larval and nymphal stages found mainly on small ground-dwelling species while adult ticks prefer larger hosts such as carnivores and ungulates. They are medium-sized ticks with short mouthparts and an ornate scutum with posterior festoons and lateral eyes. Most species are thought to have 3-host life-cycles but some have 1-host cycles. Several species cause problems in animal health and production, with infestations causing local irritation, anaemia, reduced production and sometimes paralysis and mortality. Epidemiological and clinical studies have implicated several species in the transmission of various infectious disease (viral, bacterial and protozoal) to livestock.

***Dermacentor* species**	**Hosts**	**Clinical signs**	**Distribution**
D. abaensis (syn. *D. birulai, everestianus*, *Cynorhaestes*)	Artiodactyla: bovid (cattle, yak, dzo, sheep, bharal, Himalayan goral), camelid (camel), moschid (musk deer); Perissodactyla: equid (horse, onager); Lagomorpha: ochotonid (plateau pika, Chinese red pika, hare, rabbit); Rodentia: murid (wood mouse); Carnivora: ursid (Asian black bear) (3-host cycle)	(vector for anaplasmosis, rickettsioses)	China, Tibet
D. albipictus (syn. *D. salmoni, variegatus, varius, Cynorhaestes, C. nigrolineatus*) (winter tick, moose tick, elk tick, horse tick)	Artiodactyla: antilocaprid (pronghorn), bovid (cattle, American bison, sheep, bighorn sheep, mountain sheep, Barbary sheep, mountain goat), cervid (American moose, European fallow deer, mule deer, elk, wapiti, woodland caribou, white-tailed deer, Columbian black-tailed deer, red brocket); tayassuid (collared peccary); Perissodactyla: equid (horse, donkey, mule); Lagomorpha: leporid (rabbit, jackrabbit); Rodentia: castorid (beaver), caviid (guinea pig), cricetid (deer mouse, brush mouse), erethizontid (North American porcupine), heteromyid (Mexican spiny pocket mouse), murid (mouse); Carnivora: canid (wolf, coyote), felid (cat), ursid (American black bear); Primates: hominid (human); Accipitriformes: accipitrid (hawk); Charadriiformes: scolopacid (American woodcock) (1-host cycle)	trauma, irritation, anaemia, paralysis (vector for anaplasmosis, borreliosis, rickettsial spotted fever)	North America

D. andersoni (syn. *D. venustus*) (Rocky Mountain wood tick)	Artiodactyla: antilocaprid (pronghorn), bovid (cattle, American bison, sheep, bighorn sheep, goat, mountain goat), cervid (mule deer, white-tailed deer, elk), suid (pig); Perissodactyla: equid (horse, donkey, mule); Lagomorpha: leporid (rabbit, pygmy rabbit, black-tailed jackrabbit, white-tailed jackrabbit, mountain cottontail, desert cottontail, snowshoe rabbit, hare, snowshoe hare), ochotonid (American pika); Eulipotyphla: soricid (American water shrew); Rodentia: caviid (guinea pig), cricetid (muskrat, bushy-tailed woodrat, desert woodrat, Mexican woodrat, deer mouse, pinyon mouse, northern grasshopper mouse, bank vole, meadow vole, southern red-backed vole, long-tailed vole, eastern meadow vole, montane vole, cantankerous vole, prairie vole, sagebrush vole, hamster), erethizontid (North American porcupine, yellow-haired porcupine), geomyid (pocket gopher), heteromyid (kangaroo rat, Ord's kangaroo rat, Great Basin pocket mouse), murid (house mouse, meadow mouse, western harvest mouse, white-footed mouse), sciurid (buff-bellied chipmunk, yellow pine chipmunk, cliff chipmunk, least chipmunk, pallid chipmunk, red-tailed chipmunk, painted chipmunk, yellow-bellied chipmunk, Uinta chipmunk, Colorado chipmunk, Siberian chipmunk, black-tailed prairie dog, groundhog, American red squirrel, Douglas squirrel, Abert's squirrel, rock squirrel, chickaree, golden-mantled ground squirrel, Montana mantled ground squirrel, thirteen-lined ground squirrel, little gray ground squirrel, California ground squirrel, Uinta ground squirrel, Belding's ground squirrel, Richardson's ground squirrel, Townsend's ground squirrel, Oregon ground squirrel, Columbian ground squirrel, Franklin's ground squirrel, northern flying squirrel, pallid yellow-bellied woodchuck, northern pocket gopher, yellow-bellied marmot, hoary marmot), zapodid (western jumping mouse); Carnivora: canid (dog, wolf, coyote), felid (cat, bobcat, lynx), mustelid (American badger, marten, long-tailed weasel, short-tailed weasel, stoat), mephitid (skunk), ursid (brown bear, grizzly bear, American black bear); Chiroptera: vespertilionid (Yuma myotis); Primates: hominid (human); Accipitriformes: accipitrid (unspecified); Galliformes: phasianid (ruffed grouse, turkey): Passeriformes: passerellid (vesper sparrow) (3-host cycle)	trauma, irritation, anaemia, paralysis (vector for babesiosis, theileriosis, anaplasmosis, rickettsial spotted fever, tularaemia, Colorado tick fever)	North America
D. antrorum	Rodentia: cricetid (common vole, European snow vole)		Central Asia
D. asper	Eulipotyphla: erinaceid (hedgehog)		China
D. atrosignatus	Artiodactyla: bovid (buffalo, water buffalo), suid (pig, banded pig, Bornean bearded pig, Palawan bearded pig, Celebes warty pig); Eulipotyphla: soricid (house shrew); Pholidota: manid (Sunda pangolin); Rodentia: murid (black rat, yellow-haired hill rat, Hellwald's Sulawesi maxomys, Hoffmann's Sulawesi rat, giant Sulawesi rat, Pacific rat, marmoset xanthurus rat); Carnivora: canid (dog), ursid (Malayan sun bear); Chiroptera: pteropodid (lesser tube-nosed fruit bat, Sulawesi rousette); Primates: hominid (human); Sauria: varanid (Asian water monitor); Serpentes: elapid (Indian cobra)		Malaysia
D. auratus (syn. *Indocentor, D. astrosignatus*)	Artiodactyla: cervid (chital, sambar deer, Indian sambar deer), suid (pig, banded pig, Indian boar, bushpig), tragulid (chevrotain); Perissodactyla: rhinocerotid (Sumatran rhinoceros); Eulipotyphla: erinaceid (moonrat); Scandentia: tupaiid (common treeshrew, pygmy treeshrew); Rodentia: caviid (guinea pig), hystricid (Indian crested porcupine), murid (house mouse, black rat, greater bandicoot rat, Annadale's rat, ricefield rat, Bower's white-toothed rat, southeast Asian house rat, long-tailed giant rat, Edward's long-tailed giant rat, Malayan field rat, Muller's giant Sunda rat, red spiny rat, Rajah spiny rat, Whitehead's spiny rat), sciurid (plaintain squirrel, variable squirrel, slender squirrel, Anderson's squirrel, Pallas's squirrel, Asian red-cheeked squirrel,		Indo-China

	three-striped ground squirrel, black giant squirrel, Indian giant squirrel); Carnivora: canid (dhole), felid (leopard cat, leopard, tiger), herpestid (small Asian mongoose), mustelid (hog badger, Burmese ferret-badger), ursid (sloth bear, Asian black bear), viverrid (small Indian civet, Asian palm civet); Primates: cercopithecid (bonnet macaque, northern plains brown langur); hominid (human); Galliformes: phasianid (chicken); Serpentes: pythonid (unspecified python)		
D. bellulus (syn. *Indocentor*)	Artiodactyla: bovid (water buffalo), suid (boar); Lagomorpha: leporid (Chinese hare); Scandentia: tupaiid (common treeshrew); Rodentia: murid (large Japanese field mouse, Ryukyu mouse, brown rat, black rat, oriental house rat, greater bandicoot rat, lesser bandicoot rat, Chinese white-bellied rat, Coxing's white-bellied rat, Losea rat,); Carnivora: canid (dog), mustelid (Chinese ferret-badger); Primates: hominid (human); Galliformes: phasianid (Chinese bamboo partridge)		Asia
D. circumguttatus (syn. *Amblyocentor*)	Artiodactyla: bovid (common duiker), suid (boar); Proboscidea: elephantid (African elephant, African forest elephant); Primates: hominid (human)		Africa
D. compactus (syn. *Indocentor*)	Artiodactyla: suid (banded pig, bushpig); Rodentia: murid (ricefield rat, Malaysian field rat, Muller's saundamys, Indomalayan leopoldamys), sciurid (gray-bellied squirrel, black-striped squirrel, plaintain squirrel, Prevost's squirrel, pale giant squirrel, black giant squirrel, shrew-faced squirrel, horse-tailed squirrel, Low's squirrel, slender squirrel, Javanese flying squirrel, Vordermann's flying squirrel, Himalayan striped squirrel); Carnivora: canid (dog), ursid (unspecified bear); Serpentes; colubrid (spotted keelback)		Indonesia
D. confragus (syn. *Indocentor*)	host unknown, collected from vegetation		Indonesia
D. cruentus	Artiodactyla: bovid (cattle, sheep, goat)		Europe
D. dispar	Artiodactyla: cervid (unspecified deer), tayassuid (white-lipped peccary); Cingulata: dasypodid (nine-banded armadillo)		Central America
D. dissimilis	Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Carnivora: canid (dog) (1-host cycle)		Americas
D. falsosteini	Artiodactyla: suid (pig, Bornean bearded pig); Perissodactyla: tapirid (tapir); Primates: hominid (human)		Asia
D. feae (syn. *D. foai*)	Testudines: geoemydid (Indian black turtle), testudinid (elongated tortoise)		
D. filippovae	Artiodactyla: suid (pig)		Asia
D. halli	Artiodactyla: bovid (cattle), tayassuid (collared peccary); Perissodactyla: equid (horse), tapirid (Baird's tapir); Rodentia: erethizontid (Mexican hairy dwarf porcupine), murid (mouse); Pilosa: bradypodid (sloth); Carnivora: canid (dog), mephitid (skunk); Chiroptera: vespertilionid (black myotis); Primates: hominid (human)		Americas
D. hunteri	Artiodactyla: bovid (bighorn sheep, desert bighorn sheep), cervid (mule deer); Lagomorpha: leporid (mountain cottontail); Rodentia: caviid (guinea pig), cricetid (desert woodrat, cactus mouse, deer mouse); Primates: hominid (human)		North America
D. imitans	Artiodactyla: cervid (red brocket, Central American red brocket), tayassuid (collared peccary, white-lipped peccary); Primates: hominid (human)		Central America
D. kamtshadalus (syn. *D. varius kamschadalus*)	Artiodactyla: bovid (sheep)		Asia
D. laothaiensis	Artiodactyla: suid (pig)		Asia
D. latus	Perissodactyla: tapirid (Baird's tapir); Carnivora: canid (dog); Primates: hominid (human)		Central America
D. limbooliati	Artiodactyla: suid (pig); Primates: hominid (human)		Asia
D. marginatus (incl. subspp.	Artiodactyla: bovid (cattle, water buffalo, sheep, goat, Siberian ibex, argali, mouflon), camelid (camel), cervid (red deer, fallow	trauma, irritation (vector for	Europe

lacteolus, *marginatus*) (syn. *Cynorhaestes*) (sheep tick)	deer, roe deer, Siberian roe deer), suid (pig, boar); Perissodactyla: equid (horse, donkey); Eulipotyphla: erinaceid (long-eared hedgehog, northern white-breasted hedgehog, European hedgehog), soricid (common shrew, bicolored shrew, lesser white-toothed shrew, Eurasian water shrew), talpid (European mole); Lagomorpha: leporid (European rabbit, desert hare, mountain hare, tolai hare, European hare, Cape hare), ochotonid (steppe pika, Turkestan red pika, Pallas's pika); Rodentia: caviid (guinea pig), cricetid (common vole, bank vole, juniper vole, tundra vole, social vole, silver mountain vole, flat-headed vole, grey red-backed vole, northern red-backed vole, northern mole vole, European water vole, European snow vole, European pine vole, Tien Shan forest vole, narrow-headed vole, Carruther's vole, winter white dwarf hamster, golden hamster, European hamster, Turkish hamster, Chinese striped hamster, Eversmann's hamster, grey dwarf hamster, steppe lemming), dipodid (northern three-toed jerboa, dwarf fat-tailed jerboa, small five-toed jerboa, great jerboa, thick-tailed pygmy jerboa, thick-tailed three-toed jerboa, William's jerboa, Zhitkov's jerboa), glirid (garden dormouse, forest dormouse, hazel dormouse, European edible dormouse), murid (house mouse, striped field mouse, Ural field mouse, yellow-necked mouse, wood mouse, eastern broad-toothed field mouse, Eurasian harvest mouse, Black Sea mouse, brown rat, Turkestan rat, Libyan jird, Tamarisk jird), sciurid (red squirrel, red-cheeked ground squirrel, yellow ground squirrel, russet ground squirrel, little ground squirrel, relict ground squirrel, spectacled ground squirrel, European ground squirrel, Brandt's ground squirrel, grey marmot, long-tailed marmot), sminthid (southern birch mouse, Nordmann's birch mouse), spalacid (greater blind mole-rat); Carnivora: canid (dog, wolf, red fox), felid (cat, wildcat), mustelid (stoat, steppe polecat, European polecat, least weasel, European badger, European pine marten), procyonid (raccoon), ursid (brown bear); Chiroptera (unspecified bat); Primates: hominid (human); Accipitriformes: accipitrid (cinereous vulture, black kite); Bucerotiformes: upupid (Eurasian hoopoe); Charadriiformes: burhinid (Eurasian stone curlew); Columbiformes: columbid (rock dove, European turtle dove); Coraciiformes: coraciid (European roller), meropid (European bee-eater); Galliformes: phasianid (common quail); Passeriformes: alaudid (crested lark, horned lark, Mediterranean short-toed lark), corvid (carrion crow, western jackdaw), emberizid (corn bunting), hirundinid (swallow), laniid (brown shrike), motacillid (citrine wagtail), muscicapid (bluethroat, common rockthrush), passerid (sparrow); sturnid (common starling), turdid (thrush); Strigiformes: strigid (owl); Sauria: lacertid (sand lizard, European green lizard); Anura: ranid (unspecified frog) (3-host cycle)	babesiosis, theileriosis, anaplasmosis, Q fever, Rocky Mountain spotted fever, tularaemia, brucellosis, rickettsial Boutonneuse fever, Omsk haemorrhagic fever, Russian spring-summer viral encephalitis)	
D. modestus	Perissodactyla: equid (horse)		North America
D. montanus	Artiodactyla: bovid (cattle); Lagomorpha: ochotonid (Turkestan red pika); Rodentia: cricetid (vole), murid (unspecified), sciurid (long-tailed marmot)		Central Asia
D. nitens (syn. *Anocentor colombianus*) (tropical horse tick)	Artiodactyla: bovid (cattle, buffalo, sheep, goat), cervid (marsh deer, white-tailed deer, brown brocket), suid (pig); Perissodactyla: equid (horse, mule, donkey), tapirid (South American tapir, Baird's tapir); Rodentia: caviid (capybara), cuniculid (lowland paca); Carnivora: canid (dog, hoary fox, crab-eating fox), felid (cat, oncilla, ocelot, jaguar, cougar, Florida panther), herpestid (small Asian mongoose); Primates: hominid (human); Serpentes: boa (Cuban tree boa); Anura: bufonid (eastern giant toad) (1-host cycle)	trauma, irritation (vector for babesiosis and possibly rickettsiosis)	Americas

D. niveus (syn. *Cynorhaestes, D. daghestanicus*) (possible synonym of *D. marginatus*)	Artiodactyla: bovid (cattle, zebu, sheep, goat, wild goat), camelid (camel), cervid (red deer, maral deer, roe deer, Siberian roe deer, sika deer, Bactrian deer, reindeer), suid (pig, boar); Perissodactyla: equid (horse, donkey); Eulipotyphla: erinaceid (long-eared hedgehog, European hedgehog, Brandt's hedgehog); Lagomorpha: leporid (desert hare, tolai hare, European hare), ochotonid (steppe pika, Afghan pika); Rodentia: cricetid (common vole, narrow-headed vole, European water vole, European snow vole, grey dwarf hamster, European hamster, Eversmann's hamster, steppe lemming), dipodid (dwarf fat-tailed jerboa, small five-toed jerboa, great jerboa), glirid (forest dormouse), murid (house mouse, striped field mouse, wood mouse, short-tailed bandicoot rat, Turkestan rat, Libyan jird, Tamarisk jird, Persian jird, great gerbil), sciurid (yellow suslik, little ground squirrel, Brandt's ground squirrel, bobak marmot); Carnivora: canid (dog, wolf, golden jackal, red fox), felid (cat); Chiroptera (unspecified bat); Primates: hominid (human); Accipitriformes: accipitrid (tawny eagle); Coraciiformes: coraciid (European roller); Passeriformes: corvid (carrion crow), emberizid (red-headed bunting), laniid (great grey shrike), muscicapid (common nightingale, thrush nightingale), passerid (house sparrow); Testudines: testudinid (Greek tortoise)		Africa, Eurasia
D. nuttalli	Artiodactyla: bovid (cattle, sheep, goat), camelid (camel), suid (pig); Perissodactyla: equid (horse, onager); Eulipotyphla: erinaceid (hedgehog); Lagomorpha: leporid (tolai hare), ochotonid (Daurian pika, Pallas's pika); Rodentia: cricetid (common vole, reed vole, narrow-headed vole, tundra vole, silver mountain vole, grey-red-backed vole, northern red-backed vole, Blyth's vole, long-tailed dwarf hamster, European hamster, Chinese striped hamster, Mongolian hamster, Roborovski's dwarf hamster, winter white dwarf hamster), dipodid (northern three-toed jerboa, Mongolian five-toed jerboa, Siberian jerboa), murid (striped field mouse, yellow-necked mouse, Eurasian harvest mouse, midday jird, Mongolian gerbil), sciurid (long-tailed ground squirrel, Daurian ground squirrel, Tarbagan marmot); Carnivora: canid (dog, wolf, corsac fox), felid (cat), mustelid (ferret, weasel, European badger); Primates: hominid (human); birds (3-host cycle)	trauma, irritation (vector for rickettsiosis)	Russia, China
D. occidentalis (Pacific coast tick)	Artiodactyla: bovid (cattle, sheep, goat, mountain goat), cervid (mule deer, black-tailed deer, elk); Perissodactyla: equid (horse, donkey, mule); Lagomorpha: leporid (desert cottontail, brush rabbit, rock rabbit, black-tailed jackrabbit, hare); Rodentia: caviid (guinea pig), cricetid (brush mouse, deer mouse, California deer mouse, pinyon mouse, white-footed mouse, large-eared woodrat, bushy-tailed woodrat, dusky-footed woodrat, desert woodrat, California vole), dipodid (kangaroo rat), heteromyid (pocket mouse), heteromyid (California pocket mouse), murid (house mouse, white-footed mouse, western harvest mouse, mountain rat), sciurid (rock squirrel, pine squirrel, Douglas squirrel, western grey squirrel, golden-mantled ground squirrel, California ground squirrel, Douglas ground squirrel, Merriam chipmunk, Townsend's chipmunk, Siskiyou chipmunk, gopher, woodchuck); Carnivora: canid (dog, coyote, gray fox), mephitid (striped skunk, western spotted skunk), procyonid (raccoon); Primates: hominid (human) (3-host cycle)	trauma, irritation, paralysis (vector for anaplasmosis, Q fever, Colorado tick fever, tularaemia)	North America
D. panamensis	Rodentia: cricetid (Aztec mouse, Mexican deer mouse, Chiriqui harvest mouse, Mexican harvest mouse, Alston's brown mouse, Peter's climbing rat, yellow pygmy rice rat, large-headed rice rat, yellow isthmus rat, Sumichrast's vesper rat, Boquete rice rat), erethizontid (Mexican hairy dwarf porcupine), heteromyid (Desmarest's spiny pocket mouse, Panamanian spiny pocket		Central America

	mouse), sciurid (red-tailed squirrel); Pilosa: bradypodid (sloth); Chiroptera: vespertilionid (black myotis, Chilean myotis)		
D. parumapertus (syn. *Cynorhaestes*)	Artiodactyla: bovid (cattle), cervid (Columbian black-tailed deer); Lagomorpha: leporid (desert cottontail, mountain cottontail, antelope jackrabbit, black-tailed jackrabbit, white-tailed jackrabbit, California jackrabbit, Colorado desert jackrabbit, Great Plains jackrabbit, pygmy rabbit, hare); Rodentia: cricetid (northern grasshopper mouse, southern grasshopper mouse, deer mouse, canyon mouse, pinyon mouse, cactus mouse, bushy-tailed woodrat, desert woodrat, southern plains woodrat, packrat), dipodid (desert kangaroo rat, Merriam's kangaroo rat, Mohave kangaroo rat, chisel-toothed kangaroo rat, Ord's kangaroo rat, Richardson's kangaroo rat, banner-tailed kangaroo rat), geomyid (Botta's pocket gopher), heteromyid (little pocket mouse, long-tailed pocket mouse, Great Basin pocket mouse, Tejon pocket mouse, dark kangaroo mouse), murid (brown rat, western harvest mouse), sciurid (spotted ground squirrel, thirteen-lined ground squirrel, rock squirrel, white-tailed antelope squirrel, cliff chipmunk, least chipmunk, white-tailed prairie dog, black-tailed prairie dog, marmot); Carnivora: canid (coyote, kit fox), felid (cat, bobcat), procyonid (ringtail); Primates: hominid (human); Accipitriformes: accipitrid (golden eagle); Galliformes: phasianid (chicken)		Nearctic
D. pasteuri (syn. *Indocentor*)	Artiodactyla: suid (boar)		Asia
D. pavlovskyi	Artiodactyla: bovid (cattle, sheep, argali, goat, Siberian ibex), camelid (camel); Perissodactyla: equid (horse); Lagomorpha: leporid (tolai hare), ochotonid (large-eared pika); Rodentia: cricetid (silver mountain vole, juniper vole, narrow-headed vole, Carruther's vole, northern mole vole, grey dwarf hamster), murid (wood mouse), sciurid (gray marmot, long-tailed marmot), sminthid (birch mouse); Carnivora: canid (red fox); Passeriformes: corvid (red-billed chough)	(vector for brucellosis)	Central Asia
D. pomerantzevi	Eulipotyphla: erinaceid (European hedgehog)		Russia
D. pseudocompactus	Artiodactyla: suid (pig)		Nepal
D. raskemensis	Artiodactyla: bovid (yak, zo, sheep, goat); Lagomorpha: leporid (hare), ochotonid (pika); Rodentia: calomyscid (mouse-like hamster); Carnivora: canid (dog); Primates: hominid (human)		Eurasia
D. reticulatus (syn. *D. albicollis, ferrugineus, pictus, pardalinus, punctulatus, Ixodes holsatus*, *Haemaphysalis marmorata*) (marsh tick, meadow tick, ornate cow tick)	Artiodactyla: bovid (cattle, water buffalo, sheep, argali, goat), camelid (dromedary), cervid (moose, red deer, wapiti, roe deer, Siberian roe deer, European fallow deer), hippopotamid (hippopotamus), suid (pig, Sardinian wild boar); Perissodactyla: equid (horse, donkey), rhinocerotid (black rhinoceros); Eulipotyphla: erinaceid (northern white-breasted hedgehog, European hedgehog), soricid (common shrew, Eurasian pygmy shrew, Eurasian water shrew), talpid (European mole); Lagomorpha: leporid (European hare, mountain hare, European rabbit), ochotonid (steppe pika); Rodentia: cricetid (muskrat, common vole, bank vole, tundra vole, social vole, narrow-headed vole, short-tailed field vole, grey red-backed vole, northern red-backed vole, European pine vole, European water vole, European snow vole, European hamster), dipodid (great jerboa), glirid (forest dormouse), murid (house mouse, striped field mouse, yellow-necked mouse, wood mouse, Eurasian harvest mouse, brown rat), sciurid (red squirrel, red-cheeked ground squirrel, Siberian chipmunk, bobak marmot), sminthid (northern birch mouse); Carnivora: canid (dog, wolf, red fox), felid (cat), mustelid (European badger, stoat, least weasel, steppe polecat, European polecat, ferret, European pine marten); Chiroptera: miniopterid (common bentwing bat), rhinolophid (Geoffroy's horseshoe bat), vespertilionid (brown long-eared bat); Primates: hominid (human); Charadriiformes: charadriid (plover), scolopacid (green sandpiper); Columbiformes: columbid	trauma, irritation (vector for babesiosis, theileriosis, Q fever, tularaemia, brucellosis, rickettsial Boutonneuse fever, anaplasmosis, Omsk haemorrhagic fever, infectious encephalomyelitis)	Europe, Africa

	(European turtle dove); Gruiformes: otid (bustard); Passeriformes: corvid (Eurasian jay), motacillid (meadow pipit), parid (great tit), sittid (Eurasian nuthatch), turdid (true thrush, fieldfare); Sauria: lacertid (sand lizard, ocellated lizard, European green lizard); Serpentes: boid (boa); Anura: ranid (unspecified frog) (3-host cycle)		
D. rhinocerotis (syn. *Amblyocentor, Amblyomma petersi, rhinocerinus, Ixodes*)	Artiodactyla: bovid (cattle, buffalo, forest buffalo, sheep, common eland, blackbuck, roan antelope), hippopotamid (hippopotamus), suid (warthog); Perissodactyla: equid (donkey), rhinocerotid (black rhinoceros, white rhinoceros, northern white rhinoceros); Proboscidea: elephantid (elephant); Rodentia: murid (mouse); Carnivora: canid (jackal), felid (lion); Primates: hominid (human); Sauria: varanid (monitor); Serpentes: pythonid (unspecified python); Testudines (unspecified tortoise)		Africa
D. rosmari *nomen nudum*	Carnivora: odobenid (walrus)		Russia
D. silvarum (incl. subspp. *ablutus, silvarum*) (syn. *D. asiaticus*)	Artiodactyla: bovid (cattle, sheep, goat), camelid (camel), cervid (red deer, Chinese roe deer, Siberian roe deer, sika deer, elk, reindeer), suid (pig); Perissodactyla: equid (horse, donkey); Eulipotyphla: erinaceid (long-eared hedgehog, northern white-breasted hedgehog, European hedgehog), soricid (common shrew, Eurasian pygmy shrew, Eurasian water shrew); Lagomorpha: leporid (mountain hare, European hare, Manchurian hare), ochotonid (alpine pika); Rodentia: cricetid (common vole, reed vole, narrow-headed vole, tundra vole, Bucharian vole, transcaspian vole, Maximoxicz's vole, European water vole, grey red-backed vole, northern red-backed vole, giant rat-headed hamster, Chinese hamster, European hamster, steppe lemming), dipodid (great jerboa, dwarf fat-tailed jerboa), murid (house mouse, striped field mouse, Large Japanese field mouse, wood mouse, Eurasian harvest mouse, black rat, brown rat), sciurid (red squirrel, long-tailed ground squirrel, little ground squirrel, russet ground squirrel, speckled ground squirrel, Asian chipmunk, Siberian chipmunk), sminthid (northern birch mouse, southern birch mouse), spalacid (greater blind mole-rat); Carnivora: canid (dog, raccoon dog, wolf, red fox), felid (cat, leopard cat, Siberian tiger), mustelid (yellow-throated marten, sable, steppe polecat, least weasel, Siberian weasel); Primates: hominid (human); Charadriiformes: scolopacid (Swinhoe's snipe); Columbiformes: columbid (Oriental turtle dove); Galliformes: phasianid (hazel grouse); Passeriformes: acrocephalid (thick-billed warbler), emberizid (yellow-breasted bunting, meadow bunting, black-faced bunting, chesnut bunting, chesnut-eared bunting), motacillid (olive-backed pipit), passerid (sparrow), phylloscopid (dusky warbler), sittid (Eurasian nuthatch), sylviid (babbler); Piciformes: picid (lesser spotted woodpecker, hairy woodpecker); Sauria: lacertid (European green lizard) (3-host cycle)	trauma, irritation, paralysis (vector for piroplasmosis, anaplasmosis, rickettsial typhus)	Asia
D. similis	host unknown, collected from vegetation		North America
D. sinicus (incl. subspp. *pallidor, sinicus)*	Eulipotyphla: erinaceid (hedgehog); Rodentia: caviid (guinea pig), cricetid (hamster)		Eurasia
D. steini (syn. *Indocentor ater, steini*)	Artiodactyla: bovid (water buffalo, goat), suid (pig, wild boar, banded pig, Bornean bearded pig, Palawan bearded pig, Celebes warty pig, Philippine warty pig), tragulid (Java mouse-deer); Perissodactyla: tapirid (Malayan tapir); Pholidota: manid (Sunda pangolin); Rodentia: hystricid (Asiatic brush-tailed porcupine), murid (long-tailed giant rat, Muller's giant Sunda rat); Carnivora: canid (dog), felid (leopard, tiger), ursid (Malayan sun bear), viverrid (small-toothed palm civet); Primates: hominid (human);		Asia

	Sauria: varanid (Asian water monitor); Serpentes: elapid (king cobra), pythonid (reticulated python)		
D. taiwanensis	Artiodactyla: suid (boar); Lagomorpha: leporid (Chinese hare); Rodentia: murid (greater bandicoot rat), sciurid (Pallas's squirrel, Himalayan striped squirrel); Carnivora: canid (dog), mustelid (Chinese ferret-badger, Siberian weasel), ursid (giant panda, Asian black bear); Galliformes: phasianid (Chinese bamboo partridge)		Asia
D. tamokensis	Artiodactyla: suid (pig)		Indo-China
D. (*Serdjukovia*) *ushakovae* (possible synonym of *D. marginatus*)	Artiodactyla: bovid (cattle); Lagomorpha: leporid (hare); Rodentia: cricetid (vole), dipodid (jerboa), murid (mouse)		Central Asia
D. variabilis (syn. *D. americanus, electus, Ixodes quinquestriatus*) (American dog tick, wood tick)	Artiodactyla: bovid (cattle, sheep, goat), cervid (moose, white-tailed deer, sambar deer), suid (pig), tayassuid (collared peccary); Perissodactyla: equid (horse, donkey, mule); Lagomorpha: leporid (rabbit, eastern cottontail, desert cottontail, black-tailed jackrabbit, white-sided jackrabbit, marsh rabbit, swamp rabbit, snowshoe hare); Didelphimorphia: didelphid (common opossum, Virginia opossum); Eulipotyphla: soricid (common shrew, Say's least shrew, northern short-tailed shrew, long-tailed shrew), talpid (eastern mole); Rodentia: caviid (guinea pig), cricetid (meadow vole, prairie vole, eastern meadow vole, pine vole, woodland vole, western harvest mouse, eastern harvest mouse, deer mouse, golden mouse, cotton mouse, white-footed mouse, Oldfield mouse, hispid cotton rat, marsh rice rat, muskrat, eastern woodrat, southern plains woodrat, packrat), erethizontid (North American porcupine), geomyid (pocket gopher), heteromyid (Baird's pocket mouse), murid (house mouse, field mouse, golden harvest mouse, Cooper's mouse, black rat, brown rat, gray rat), sciurid (groundhog, woodchuck, red squirrel, fox squirrel, eastern gray squirrel, thirteen-lined ground squirrel, Franklin's ground squirrel, Richardson's ground squirrel, southern flying squirrel, eastern chipmunk), zapodid (meadow jumping mouse); Carnivora: canid (dog, red wolf, coyote, red fox, kit fox, gray fox), felid (cat, wildcat, Florida bobcat, Florida panther, mountain lion, jaguar, Mexican cougar), mephetid (striped skunk, spotted skunk), mustelid (wolverine, North American river otter, American badger, stoat, weasel, fisher, ferret), phocid (unspecified seal), procyonid (raccoon), ursid (American black bear), viverrid (civet); Chiroptera (unspecified pygmy bat); Primates: hominid (human); Apodiformes: apodid (chimney swift); Galliformes: odontophorid (northern bobwhite); Passeriformes: cardinalid (cardinal), corvid (crow), emberizid (painted bunting), icterid (red-winged blackbird, cowbird), mimid (mockingbird), parulid (palm warbler), passerellid (white-crowned sparrow, junco, eastern towhee), sturnid (starling), troglodytid (Carolina wren), turdid (American robin); Sauria: agamid (unspecified) (3-host cycle)	trauma, irritation, paralysis (vector for anaplasmosis, ehrlichiosis, rickettsial spotted fever, tularaemia, cytauxzoonosis, Lyme disease, encephalitis virus)	North America

Parasite morphology: *Dermacentor* spp. form 4 different morphological types of developmental stages: eggs, larvae, nymphs and adults. Eggs are small brown ovoid stages measuring 0.4-0.5 mm in diameter and they are often clustered together in small masses. Larvae are roughly discoidal (dorsoventrally flattened, oval-pyriform in dorsal profile) measuring up to 0.6 mm in length. They are usually yellow-brown in colour but may become slaty grey-black when engorged. The head (capitulum) projects forward anteriorly and contains conspicuous palps and mouthparts. The body (idiosoma) has a hardened anterodorsal plate (scutum) that occasionally has irregular patches of white enamel ornamentation. The scutum has posterior festoons, 2 lateral flat eyes (sometimes with adjacent red markings) and 3 pairs of long jointed legs arising ventrally. Larvae lack respiratory openings (stigmata) and the ventral subterminal anus is not encompassed by an anal groove. Nymphs also have discoidal ovate bodies but they are larger ranging from 1-4 mm in length. They have similar features and colouration to larvae, but have 4 pairs of long ventral legs, one pair of respiratory stigmata surrounded by round plates, and the anus has a posterior anal groove, but they lack genital openings (gonopores). Adult ticks have pyriform bodies that are ventrally flattened but dorsally convex. They range in length from 3-5 mm when unfed, while

engorging females may distend up to 10-16 mm long. They are typically ornate ticks with reddish-brown bodies adorned with gray-silver markings. The anterior capitulum is visible from above (while that of argasids is ventral and not visible from above) and consists of a basis capitulum (integumental ring supporting mouthparts) and gnathosoma (bearing mouthparts). The basis capitulum is rectangular (not triangular, hexagonal or pentagonal) and the dorsal surface has 2 porose areas (clusters of pores used for waterproofing eggs during oviposition). The piercing/sucking mouthparts are short (same length as basis capitulum but as wide or wider) and comprise 2 sensory lateral palps and a central hypostome flanked by 2 chelicerae. The palps are short and broad (often wider than long) and do not enter the skin when feeding. The chelicerae have tubular shafts tipped with digits with recurved teeth used to cut and tear skin forming pools of blood. The barbed hypostome is inserted into the blood pools to facilitate feeding as well as to anchor the tick to the host. A feeding tube is formed between the chelicerae and hypostome to suck blood and inject saliva from long paired salivary glands. The alimentary tract consists of a muscular pharynx, a short tubular oesophagus, a large saccular midgut (ventriculus) with lateral diverticula (caeca), a short intestine (with excretory Malpighian tubules), a rectal sac and a subterminal ventral anus with a posterior (metastriate) anal groove. The idiosoma bears a conspicuous shield-like scutum which occupies most of the dorsum in males (= conscutum) but is restricted to an anterodorsal shield in females. The scutum is ornate (with pale enamel markings) and has 2 simple eyes located on the anterior margins. The idiosoma has a series of indentations (festoons) along the posterior margin, which are indistinct in engorged females. The ventral idiosoma bears 4 pairs of long jointed legs which often appear paler than the body or sometimes have light-coloured ends to some segments (but not evident as distinct rings). Each leg consists of 6 segments (coxae, trochanter, femur, patella (genu), tibia, and tarsus) and terminates in a pair of claws with a pad-like pulvillus. The coxae increase in size posteriad with coxae IV greatly enlarged in males, coxae 1 bearing 2 large spurs (in both sexes), and tarsi I having a unique sensory structure (Haller's organ) used to detect host odours, heat and vibrations. Respiratory stigmata are located behind coxae IV and the spiracular plates are paler and containing numerous shallow depressions (termed goblets). Adult ticks display marked sexual dimorphism, particularly in body size (males 3-5 mm, females 4-16 mm), colouration (females usually more colourful), scutum size (large covering plate in males, small anterior shield in females), and the occurrence of porose areas on the basis capitulum (present only on females). Adult male ticks do not have sclerotized ventral plates, which are present in the genera *Ixodes*, *Amblyomma*, *Rhipicephalus*/*Boophilus*, and *Hyalomma*. They have paired tubular testes, vas efferentia fusing to form a common vas deferens (with a multilobular accessory gland) and an ejaculatory duct leading to the genital aperture (gonopore) situated on the ventral midbody. Adult females have a saccular ovary with paired oviducts leading to a common uterus (with accessory glands) and a bipartite vagina (cervical region acting as a receptaculum seminis to store spermatophores, and vestibular region prolapsing during oviposition). The anteroventral gonopore is U-shaped with an anterior flap (genital apron) and located near a special glandular structure (Gene's organ) used to produce waxy coatings for eggs during oviposition.

Site of infection: The larvae, nymphs and adults of *Dermacentor* spp. are ectoparasitic on the skin of a wide range of vertebrate hosts: including mammals belonging to 55 families in 14 orders (ungulates, insectivores, marsupials, shrews, lagomorphs, rodents, carnivores, bats and primates), birds belonging to 20 passerine families and 14 non-passerine families in 10 orders (shore birds, landfowl, kingfishers, doves, birds of prey), reptiles belonging to 4 snake families, 3 lizard families and 2 tortoise families, and amphibians belonging to 2 frog families. Most species have diverse host ranges, as the larval and nymphal stages tend to occur on smaller ground-dwelling animals than adult stages. Feeding stages exhibit some site preferences, generally infesting the head, neck, groin and back, although they may occur in other regions in heavy infestations. Those species infesting humans usually migrate to the head behind the ears, or attach underneath waistbands or hems of tight-fitting clothing.

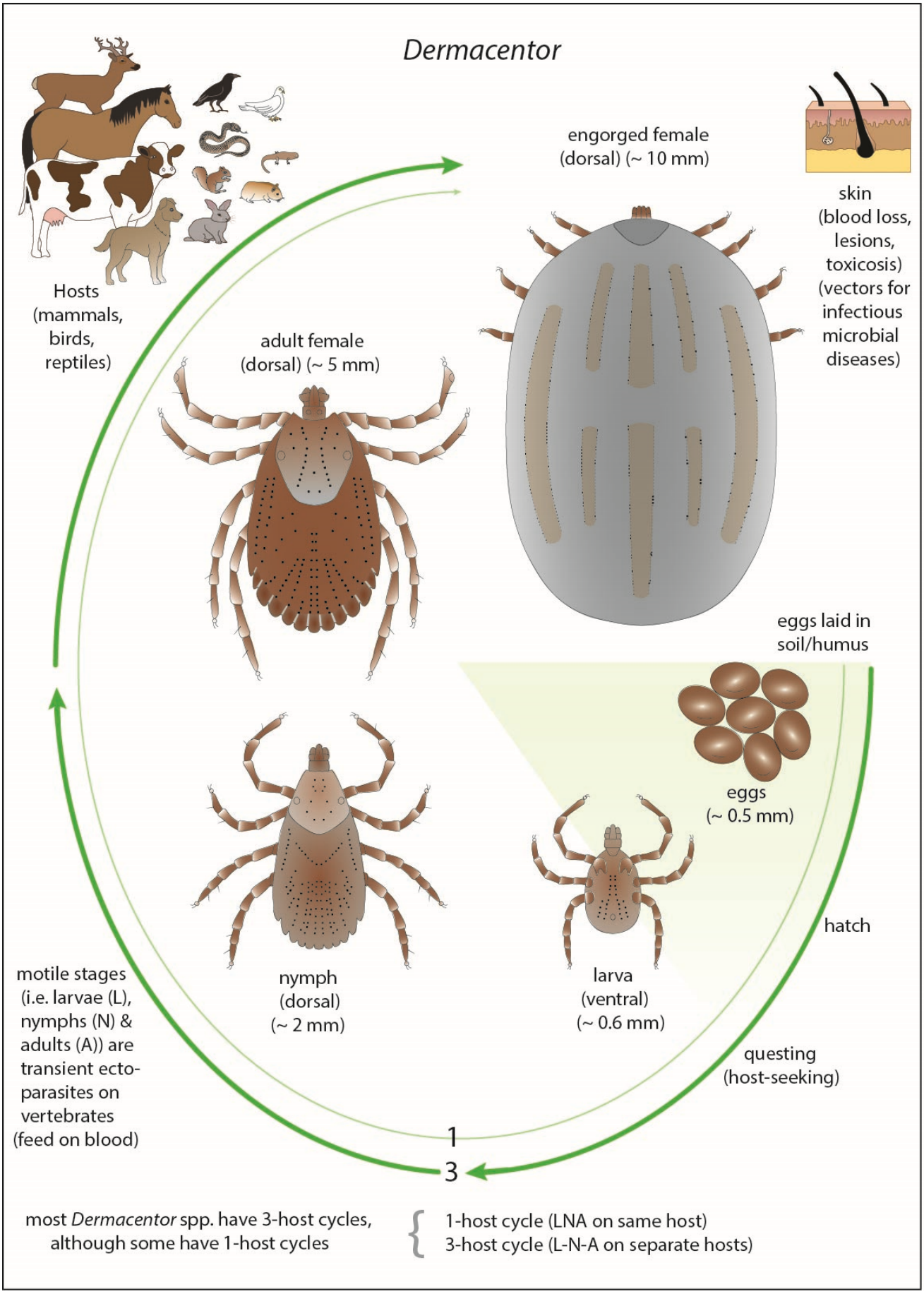
Pathogenesis: All motile stages are transient haematophagous parasites that feed once on host blood for several days before dropping off to develop further in the external environment. They use their cutting chelicerae to lacerate the skin creating pools of blood in the dermis from which they imbibe blood (feeding process known as telmophagy). They embed their mouthparts in feeding lesions using proteinaceous salivary cement and inject other salivary compounds with cytolytic, analgesic, anticoagulant, vasodilatory and vascular permeability activities. Their bites not only result in local tissue trauma but cause considerable dermal irritation with inflammation (erythema, oedema), pruritus, granuloma formation, rough coat and even alopecia. Heavy infestations may cause significant blood loss resulting in anaemia, iron deficiencies and even exsanguination in extremes cases. Infestations of the ears cause otoacariasis with inflammation and waxy discharges. Ticks may cause severe biting stress (tick worry) to their hosts, which may elicit aggressive grooming behaviours (licking, biting, scratching, rubbing) resulting in self-trauma and opening wounds to secondary bacterial infections. Livestock may be distracted from feeding efficiently and show loss of condition, poor growth and reduced meat and/or milk production. Some individual animals may also develop hypersensitivity reactions to tick saliva resulting in enhanced inflammation and granuloma formation. The saliva of several tick species (notably *D. variabilis* and *D. andersoni*) may also cause flaccid ascending paralysis in canines, ungulates and sometimes humans (particularly children) due to the presence of neurotoxins affecting motor function, reflexes, coordination and respiration, sometimes proving fatal. Feeding ticks may also act as biological and mechanical vectors for the transmission of various microbial infectious diseases. They are efficient vectors because they move frequently between hosts (most have 3-host life-cycles), microbes may multiply in tick tissues (amplification vectors) and survive metamorphic changes (trans-stadial transmission), with some even undergoing vertical transfer by infecting tick eggs (trans-ovarian transmission). Ticks may transmit microbes either during feeding (via saliva), during fluid regulation (via regurgitation) or during waste elimination (via defaecation). *Dermacentor* spp. have been shown to transmit haemoprotozoa causing babesiosis, rickettsial bacteria causing Rocky Mountain spotted fever and anaplasmosis, coccobacilli causing tularemia, Gram-negative bacteria causing chlamydiosis, and viruses causing Powassan encephalitis virus, tick-borne encephalitis, Colorado tick fever and Omsk haemorrhagic fever.

Developmental cycle and mode of transmission: Like all ticks, *Dermacentor* spp. undergo incomplete (hemimetabolous) metamorphosis where eggs hatch larvae which moult to nymphs and then adults. Most species have 3-host life-cycles where each stage feeds on a separate host, but some species (e.g. *D. albipictus, D. nitens*) have one-host cycles where all stages occur on the same host. Gravid females lay eggs in soil or humus where they hatch in 26-40 days (longer in colder conditions). The emergent 6-legged larvae climb vegetation and wait for passing hosts (ambush strategy). They actively quest (wave their forelegs in the air) when stimulated by sensory cues (odours, heat, vibrations) associated with the close proximity of a host. They may survive for several weeks to months (up to 11 months) depending on prevailing environmental conditions (they are prone to desiccation in warm dry conditions). Most species have preferred hosts (generally small ground-dwelling animals, especially rodents) and are reluctant to feed on unusual hosts (as evidenced by prolonged probing, taking small meal samples and then dropping off to seek and alternative host). Having located a suitable host, they attach and feed for several days (2-14 days depending on species) before detaching and dropping off when replete. On the ground, they shelter in the litter to digest their bloodmeals over a week (longer in colder conditions) before moulting to 8-legged nymphs (only one nymphal instar is formed, whereas argasids form 2-7 nymphal instars). Nymphs ascend vegetation and quest for hosts, surviving for several weeks to months depending on prevailing conditions. They attach to suitable hosts and feed for 3-10 days before dropping off to digest their meals over 3 weeks to several months. Nymphs then moult into adult ticks (both male and female) which climb vegetation (often along trails and tracks) and quest for hosts (most species seek larger animals). Adults have been shown to survive without feeding for up to 2 years, even in adverse environmental conditions. Once a suitable host is located, the adult ticks attach and begin feeding (both sexes requiring a bloodmeal to mature). Mating occurs on hosts when males detach and search the host for receptive attached females. Females mate once and then continue feeding for 6-14 days until they become massively engorged with host blood. Females then detach and seek shelter in ground litter for 4-10 days before laying large batches of eggs (totaling up to 4,000-6,500) over several days to weeks. The whole life-cycle may be completed in as little as 54 days, but it usually takes 1-3 years depending on host availability and climatic factors. Many species exhibit some seasonality, being most active on hosts over autumn and winter. Most species inhabit temperate and cold regions, being found mainly in open landscapes (steppes, forest-steppes, savannas, sparsely forested areas with wooded, shrubby and long-grass areas).

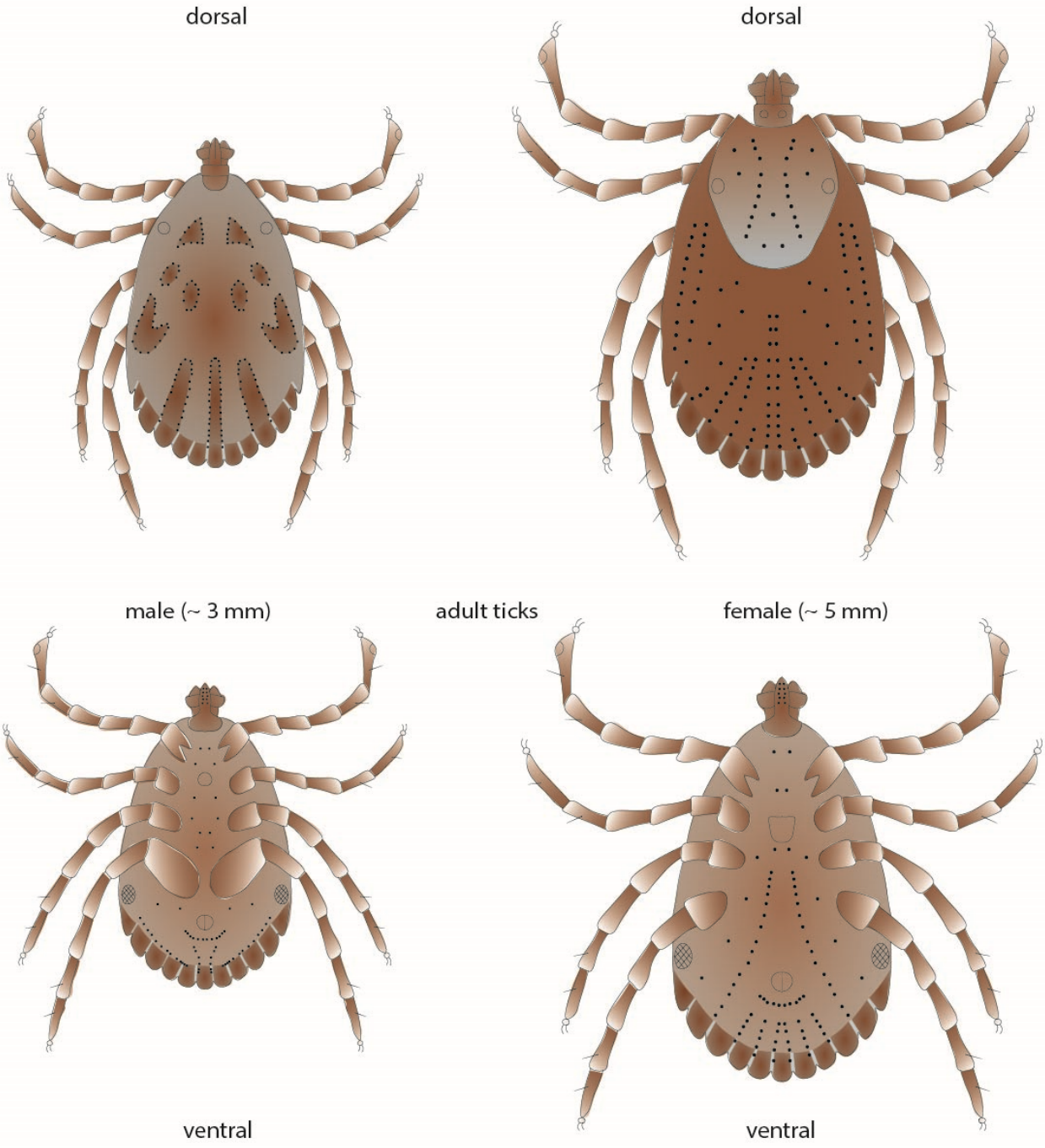
Differential diagnosis: Infestations may be suspected on clinical grounds (skin lesions, anaemia, illthrift, even paralysis) but all symptoms/signs are variable, nonspecific and hence not pathognomonic. Diagnoses are made by the direct detection of feeding stages on hosts, followed by their collection for microscopic examination and identification (medium-sized ornate ticks with festoons and eyes, rectangular basis capituli, medium palps, short mouthparts, male ventral plates absent). Ticks may be preserved by freezing of fixation for subsequent molecular studies, and free-living stages may also be collected from the environment by blanket drags or dry-ice traps. Various molecular biological techniques have been used to characterize species and infer phylogenies following the polymerase chain reaction (PCR) amplification of nuclear (18S and 28S ribosomal RNA, internal transcribed spacer regions 1 and 2) and mitochondrial (12S and 16S ribosomal RNA, cytochrome c oxidase subunit I, nicotinamide adenine dinucleotide dehydrogenase subunit 5) gene sequences.

Treatment and control: Individual ticks may be physically removed from humans and compliant animals using fine tweezers or special removal devices (tick keys, lassos, twists or V-shaped tools), but taking care not to crush and tear them as tick secretions and fragments may cause further inflammation and even systemic reactions. Symptomatic relief may be afforded by the application of topical disinfectants, analgesics, antipuritics, antihistamines or even antibiotics to prevent secondary infections. Although the literature is riddled with many suggestions to apply freezing agents, solvents or volatile fluids to the backs of ticks, such treatments should be used cautiously as they may also increase the risk of systemic reactions as stricken ticks may release potentially toxic compounds. More conventionally, infestations on livestock and companion animals are treated using chemical acaricides, including arsenical preparations, organochlorines (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (dioxathion, fenchlorphos), organophosphonates (chlorfenvinphos, dichlorvos, tetrachlorvinphos, trichlorfon), monothiophosphates (chlorpyrifos, coumaphos, cythioate, diazinon, fenthion, propetamphos), dithiophosphates (malathion, phosmet), carbamates (carbaryl), pyrethroids (permethrin, flumethrin, deltamethrin, decamethrin, cypermethrin, cyprothrin, alphametrin), formamidines (amitraz), macrocyclic lactones (ivermectin, selamectin), phenylpyrazoles (fipronil), chloronicotinyls (imidacloprid), isoxazolines (afoxolaner, fluralaner), some natural products (rotenone) and some insect growth regulators (methoprene, pyriproxyfen). These chemicals are available as a range of dips, footbaths, sprays, showers, dusts, emulsions, pour-ons, spot-ons, collars, eartags, tailtags, tablets, chewables, drenches, or injections. Repeated treatments are often required as animals may become rapidly re-infested, but the use of slow-release formulations or those with long-lasting residual activity helps reduce treatment frequency. Regrettably, the incorrect and over-usage of some acaricides has resulted in the development of drug resistance in many tick populations, particularly against arsenic compounds, organochlorines, and some organophosphates, pyrethroids and formamidines. It is therefore recommended that different classes of acaricides be used in cyclic rotation or as cocktail co-formulations, if possible after resident ticks have been tested for resistance using *in situ* or *in vitro* egg hatch, larval development, or adult survival tests. Because resistance tests take a long time to perform, several studies are attempting to develop faster tests using immunoassays or molecular screening tests. A number of preventive strategies have also been recommended to break transmission cycles through integrated animal and environmental management. Livestock should undergo regular health surveillance that informs strategic treatment, stocking density (including cohort separation), quarantine (especially during translocations) and even culling (removing heavily-infested animals).

Because ticks spend more time in the environment than on hosts, efforts should be directed at reducing pasture contamination and making the surrounding landscape inhospitable (pasture rotation, spelling or cultivation; clearing encroaching vegetation, especially along fence lines; applying residual acaricides; cleaning animal holding facilities). Wildlife may act as reservoir hosts, so attempts should be made to exclude them from farms (using barriers, diverting migration routes), reduce their numbers (hunting, trapping, vermin control) or treat them (via medicated supplementary feeds or self-treatment devices such as rubbing posts or rollers). Several mathematical prediction models have been developed to help producers schedule interventions based on analyses of multiple bionomic factors, including climate (temperature, moisture, rainfall, photoperiod), location (longitude, latitude, elevation), vegetation (type, structure), land-use and animal husbandry (stocking rates, grazing histories). People most at risk of infestation may adopt personal protective measures by wearing better clothing (boots, socks, light-coloured trousers gathered or taped at cuffs, long-sleeved shirts), applying repellents to their skin or clothing (such as diethyltoluamide (DEET), permethrin, picaridin, oil of eucalyptus), or simply avoiding tick-infested bushy habitats. Many countries have adopted public health education campaigns to inform the general public about the risks of tick infestations as well as the microbial diseases they may carry.

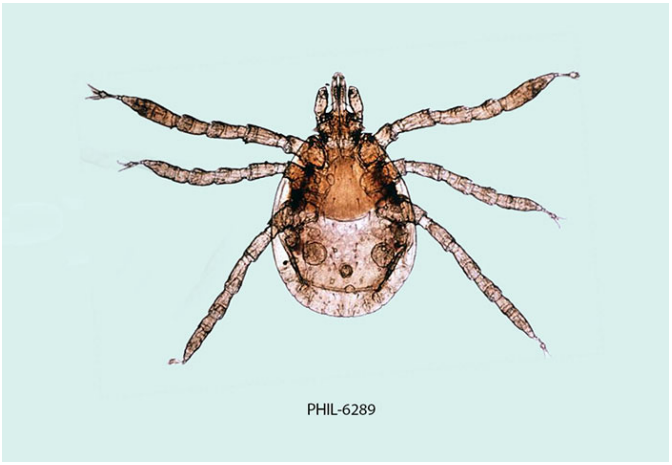

Dermacentor
Hosts (mammals, birds, reptiles)
engorged female (dorsal) (~ 10 mm)
skin (blood loss, lesions, toxicosis) (vectors for infectious microbial diseases)
adult female (dorsal) (~ 5 mm)
eggs laid in soil/humus
eggs (~ 0.5 mm)
hatch
nymph (dorsal) (~ 2 mm)
larva (ventral) (~ 0.6 mm)
motile stages (i.e. larvae (L), nymphs (N) & adults (A)) are transient ecto-parasites on vertebrates (feed on blood)
questing (host-seeking)
1
3
most Dermacentor spp. have 3-host cycles, although some have 1-host cycles
1-host cycle (LNA on same host)
3-host cycle (L-N-A on separate hosts)

Dermacentor

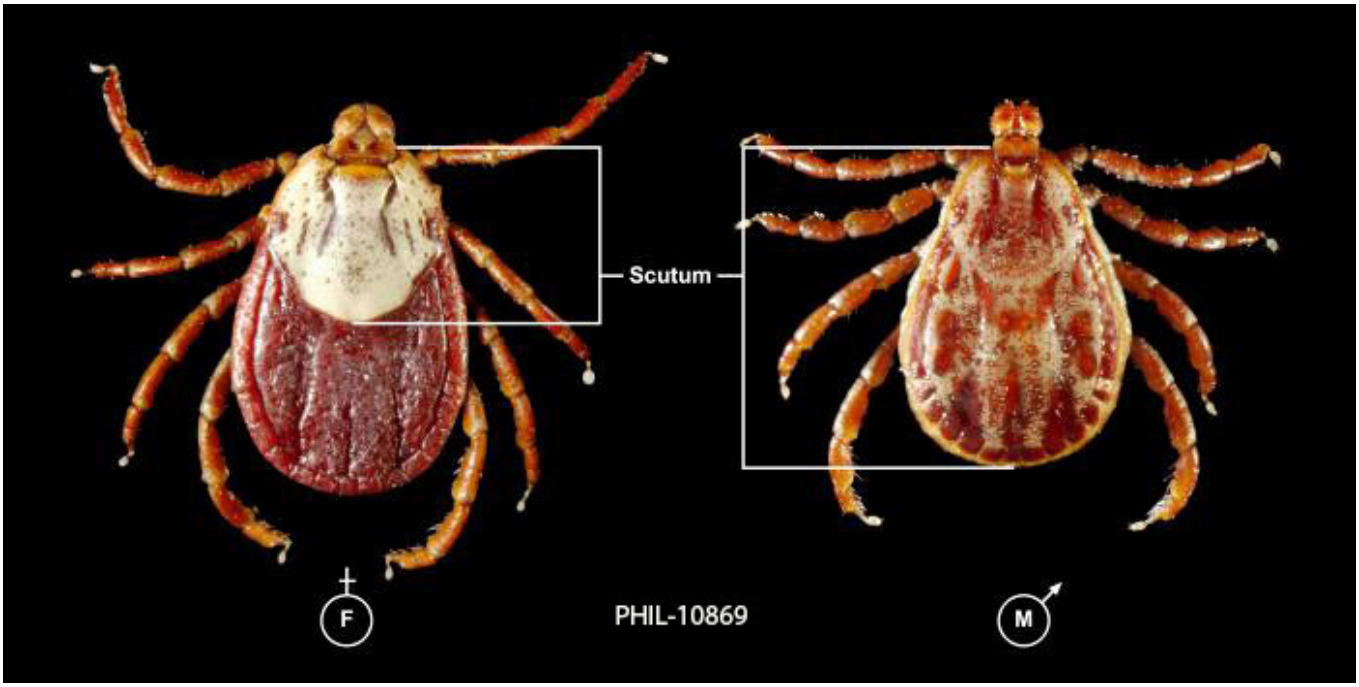




Dermacentor adult



Dermacentor larva



Dermacentor adults

Hyalomma
(arachnid: tick)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ticks have respiratory stigmata posterior to their legs. They are obligate blood-feeding ectoparasites on vertebrate hosts and their hypostomes are toothed and exposed. Two families are recognized: Argasidae and Ixodidae, known as soft and hard ticks, respectively. Ixodids have hard bodies with a dorsal scutum (shield-shaped plate) and the capitulum is not covered by the body. Larvae, nymphs and adults attach and feed on host blood, their life-cycles involving one, two or three hosts depending on whether moulting occurs on or off the host. Some 650 species of hard ticks infest mammals, birds and reptiles. Infestations by *Hyalomma* spp. occur as 2- or 3-host ticks on a range of mammals and birds, sometimes causing skin lesions, toxicoses and paralysis as well as transmitting several microbial diseases.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on capitulum)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Ixodida (Metastigmata) (ticks, macroscopic, stigmata posterior to legs, hypostome toothed, ectoparasites)
Family: Ixodidae (hard ticks, with dorsal scutum, capitulum projects anteriorly, attach and feed on 1, 2 or 3 hosts)
Genus: *Hyalomma* (parasitic on skin of mammals)
Species: various species cause lesions, toxicosis and paralysis in mammals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior capitulum. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on capitulum) [34 superfamilies]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs (behind coxae III or IV); and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Ticks are further characterized by macroscopic bodies with an exposed ventral hypostome (toothed with backwardly-directed barbs), chelicerae with only 2 joints, long legs with free articulated coxae (not fused to the body wall) and a complex sensory pit (Haller's organ) on tarsus I. They are obligate blood-sucking parasites which feed on terrestrial vertebrates (mammals, birds, reptiles and some amphibians) as larvae, nymphs and adults with 1-, 2- or 3-host life-cycles. Almost 1,000 species have been classified within some 20 genera from numerous wild and domesticated animals around the world. Two main families are recognized: the Argasidae containing ~200 species of 'soft' ticks with flexible leathery cuticles, ventral capitula, short feeding times (< 1 hour) and long life-spans (up to 20 years); and the Ixodidae containing ~800 species of 'hard' ticks with rigid dorsal scutal plates, anterior capitula, long feeding times (hours to days) and shorter life-span (2-6 years). Basic characteristics of representative genera considered in this resource are tabulated below.

Genus	**Capitulum**				**Idiosoma**				**Usual no. of hosts**
	location	**basis capitulum**	**mouth-parts**	**palps**	**integument**	**festoons**	**eyes**	**male ventral**	

								plates	
Argasidae (soft ticks with leathery cuticle, stigmata between coxae III)									
Argas	ventral	triangular	short	leg-like	stippled with lateral suture	absent	absent	absent	>3
Ornithodorus	ventral	rectangular	short	leg-like	mamillated	absent	usually absent	absent	>3
Otobius	ventral	rectangular	short	leg-like	spinose (nymphs), granulated (adult)	absent	absent	absent	1
Ixodidae (hard ticks with sclerotized dorsal plate (scutum), stigmata behind coxae IV)									
Prostriata (anal groove anterior)									
Ixodes	anterior	triangular	long	long	inornate	absent	absent	present	3
Metastriata (anal groove posterior)									
Amblyomma	anterior	rectangular	long	long	ornate	present	present	indistinct	3
(*Aponomma*)	anterior	rectangular	long	long	often ornate	present	absent	absent	3
Rhipicephalus	anterior	hexagonal	short	medium	some ornate	present	present	present	3
(*Boophilus*)	anterior	hexagonal	short	short	inornate	absent	present	present	1
Dermacentor	anterior	rectangular	short	medium	often ornate	present	present	absent	3
Haemaphysalis	anterior	rectangular	short	short	inornate	present	absent	absent	3
Hyalomma	anterior	rectangular	long	long	inornate	present	present	present	2
Bothriocroton	anterior	pentagonal	long	long	ornate	present	absent	absent	3

The family Ixodidae contains 6 subfamilies (Amblyomminae, Bothriocrotoninae, Haemaphysalinae, Hyalomminae, Ixodinae and Rhipicephalinae) which vary in their morphology, biology, host ranges and specificity. [Note that some taxonomic authorities have merged the subfamilies Rhipicephalinae and Hyalomminae, while others have subsequently assigned the subfamilies Amblyomminae and Rhipicephalinae into the new family Amblyommidae, predominantly on the basis of molecular phylogenetic studies]. Hard ticks had previously been divided into 2 groups: the Prostriata (with the anal groove anterior to the anus) and the Metastriata (anal groove absent or posterior to anus). The Prostriata essentially comprises the subfamily Ixodinae with over 230 species assigned to the single extant genus *Ixodes* [plus one fossil genus (*Cornupalpatum*)], while the Metastriata contains members of the remaining subfamilies with over 600 species classified into 18 genera. The subfamily Hyalomminae comprises metastriate inornate ticks with eyes and festoons and adult males have ventral plates. It only contains 2 genera (*Hyalomma* and *Nosomma*) which are medium-sized ticks with elongate palps, an inornate scutum (ornate in the single *Nosomma* sp.) with simple eyes and indistinct festoons, banded legs and males with adanal shields. Around 33 *Hyalomma* species described from a range of mammals, birds and reptiles, most having 2-host life-cycles but some having 3-hosts. Three subgenera have been recognized: namely, *H.* (*Hyalomma*)*, H.* (*Hyalommasta*) and *H.* (*Hyalommina*)*;* but many species remain to be allocated to subgenera. Infestations in domestic animals may cause lesions, anaemia, toxicoses, and sometimes paralysis. The ticks may also transmit infectious viral, bacterial and protozoal diseases to livestock.

***Hyalomma* species**	**Hosts**	**Clinical signs**	**Distribution**
H. (*Hyalommasta*) *aegyptium* (syn. *H. affine, algeriense, cornuger, I. fabricii, forskaelii, gracilentis, hispanus, syriacum, utriculus*) (tortoise tick)	Artiodactyla: bovid (cattle, zebu, buffalo, water buffalo, sheep, urial, goat, west Caucasian tur, Nilgiri tahr, blue wildebeest, Lichtenstein's hartebeest, blackbuck, greater kudu, common eland, oribi, Sudan oribi, Nile lechwe, sitatunga, grysbok, impala, duiker, fringe-eared oryx, sable antelope, roan antelope, Grant's gazelle), camelid (Bactrian camel, dromedary), cervid (red deer, Tibetan red deer), giraffid (giraffe, Cape giraffe), suid (pig, boar, bushpig, warthog, desert warthog); Perissodactyla: equid (horse, donkey, mule, plains zebra, Crawshay's zebra), rhinocerotid (black rhinoceros); Eulipotyphla: erinaceid (four-toed hedgehog, collared hedgehog, northern white-breasted hedgehog, European hedgehog, South African hedgehog, Brandt's hedgehog); Lagomorpha: leporid (rabbit, scrub hare, European hare, Cape hare), ochotonid (pika); Rodentia: caviid (guinea pig), cricetid (grey dwarf hamster), dipodid (jerboa), murid (wood mouse, black rat, fat sand rat); Carnivora: canid (dog, black-backed jackal, Karaganka fox), felid (cat, wildcat, lion), ursid (sloth bear); Primates: hominid (human); Accipitriformes: accipitrid (black kite, Swainson's hawk); Bucerotiformes: upupid (European hoopoe); Charadriiformes: burhinid (spotted thick-knee), charadriid (plover); Columbiformes: columbid (pigeon, European turtle dove); Coraciiformes: coraciid (European roller);	trauma, irritation (vector for reptile haemogregarines, rickettsiosis, Q fever, borreliosis and possibly anaplasmosis and ehrlichiosis)	Europe, Asia

	Galliformes: phasianid (rock partridge, grey partridge, common quail, chicken, turkey); Passeriformes: alaudid (large-billed lark), dicrurid (black drongo), callaeid (huia), emberizid (Cretzschmar's bunting), hirundinid (swallow), laniid (woodchat shrike), motacillid (tree pipit), muscicapid (whinchat, spotted flycatcher, thrush nightingale, Cape robin-chat, common wheatear, northern wheatear, isabelline wheatear, common redstart), passerid (Spanish sparrow), parulid (warbler), phylloscopid (willow warbler), sturnid (common starling), sylviid (common whitethroat, lesser whitethroat), turdid (chat), vangid (rufous vanga); Pelecaniformes: ardeid (cattle egret); Strigiformes: strigid (little owl, barn owl, spotted eagle-owl); Struthioniformes: struthionid (ostrich); Sauria: agamid (starred agama), anguid (glass lizard), chamaeleonid (common chameleon), gekkonid (comb-toed gecko, Mediterranean house gecko), lacertid (snake-eyed lizard, western green lizard, Lebanon lizard); Serpentes: pythonid (African rock python), viperid (puff adder); Testudines: emydid (eastern box turtle, European pond turtle), testudinid (radiated tortoise, yellow-footed tortoise, spur-thighed tortoise, marginated tortoise, geometric tortoise, Greek tortoise, Russian tortoise, Hermann's tortoise, Horsfield's tortoise, Kleinmann's tortoise) (2-host cycle)		
H. aequipunctatum	Artiodactyla: camelid (camel), cervid (sika deer)		Middle-East
H. (*Euhyalomma*) *albiparmatum*	Artiodactyla: bovid (cattle, buffalo, sheep, goat, gemsbok, eland, hartebeest, blue wildebeest, greater kudu, impala, Grant's gazelle), giraffid (Masai giraffe), suid (desert warthog); Perissodactyla: equid (Burchell's zebra, Grant's zebra), rhinocerotid (black rhinoceros); Lagomorpha: leporid (Cape hare); Carnivora: canid (dog), felid (lion, leopard); Primates: hominid (human); Struthioniformes: struthionid (ostrich) (3-host cycle)	(vector for rickettsiosis)	Africa
H. (*Hyalomma*) *anatolicum* (syn. *H. depressum, grossum*, *pusillum*) (bont-legged tick)	Artiodactyla: bovid (cattle, zebu, buffalo, water buffalo, sheep, karakul sheep, argali, goat, alpine ibex, antelope), camelid (camel, dromedary), cervid (red deer), suid (pig); Perissodactyla: equid (horse, donkey, mule, onager); Eulipotyphla: erinaceid (long-eared hedgehog, Egyptian hedgehog); Lagomorpha: leporid (European rabbit, desert hare, tolai hare, European hare, Cape hare), ochotonid (pika); Rodentia: cricetid (northern mole vole), dipodid (small five-toed jerboa, lesser Egyptian jerboa), hystricid (Indian crested porcupine), murid (short-tailed bandicoot rat, fat sand rat, Turkestan rat, house mouse, wood mouse, golden spiny mouse, great gerbil, Mongolian gerbil, lesser Egyptian gerbil, midday jird, Libyan jird, Sundevall's jird, Tamarisk jird), sciurid (yellow ground squirrel, long-clawed ground squirrel); Carnivora: canid (dog, golden jackal, fox), felid (cat), mustelid (marbled polecat, least weasel); Primates: hominid (human); Charadriiformes: burhinid (European stone curlew); Galliformes: phasianid (chicken, common quail, turkey); Passeriformes: acrocephalid (Eurasian reed warbler), corvid (hooded crow), hirundinid (barn swallow), motacillid (tree pipit), muscicapid (flycatcher), passerid (Spanish sparrow), turdid (Eurasian blackbird); Sauria: lacertid (wall lizard); Crocodilia: crocodylid (crocodile); Testudines: testudinid (Russian tortoise) (2- or 3-host cycle)	trauma, irritation, toxicosis, sweating sickness (vector for theileriosis, anaplasmosis, Crimean-Congo haemorrhagic fever, arboviruses)	Asia, Middle East, Africa
H. (*Hyalommina*) *arabica*	Artiodactyla: bovid (sheep, goat); Rodentia: murid (spiny mouse) (3-host cycle)		Arabia
H. asiaticum (syn. *H. amurense*) (incl. subspp. *asiaticum, caucasicum, kozlovi*)	Artiodactyla: bovid (cattle, buffalo, water buffalo, sheep, karakul sheep, goat, wild goat, argali, urial, saiga, goitered gazelle), camelid (Bactrian camel, dromedary), cervid (red deer, Bactrian deer), suid (pig, wild boar); Perissodactyla: equid (horse, donkey, mule, onager), Eulipotyphla: erinaceid (long-eared hedgehog, European hedgehog, Brandt's hedgehog), soricid (tundra shrew,	(vector for theileriosis, Q fever, rickettsiosis (Siberian tick typhus) and possibly Crimean-	Indo-China

	lesser white-toothed shrew, piebald shrew); Lagomorpha: leporid (rabbit, tolai hare, European hare), ochotonid (Afghan pika); Rodentia: cricetid (desert hamster, golden hamster, grey dwarf hamster, northern mole vole, steppe lemming), dipodid (Gobi jerboa, small five-toed jerboa, northern three-toed jerboa, hairy-footed gerboa, long-eared gerboa, dwarf fat-tailed jerboa, thick-tailed three-toed jerboa, lesser Egyptian jerboa, William's jerboa), hystricid (Indian crested porcupine), murid (house mouse, wood mouse, short-tailed bandicoot rat, brown rat, great gerbil, midday jird, Libyan jird, Persian jird, Tamarisk jird, Tristram's jird, Vinogradov's jird), sciurid (long-tailed ground squirrel, long-clawed ground squirrel, yellow ground squirrel, yellow suslik, little ground squirrel, European ground squirrel); Carnivora: canid (dog, wolf, jackal, red fox, Karaganka fox), felid (sand cat), mustelid (steppe polecat, marbled polecat, least weasel); Chiroptera (unspecified bat); Primates: hominid (human); Accipitriformes: accipitrid (long-legged buzzard); Bucerotiformes: upupid (European hoopoe); Columbiformes: columbid (rock pigeon); Coraciiformes: coraciid (European roller); Galliformes: phasianid (chicken); Passeriformes: corvid (European magpie), emberizid (red-headed bunting), laniid (red-tailed shrike), motacillid (pied wagtail, white wagtail, western yellow wagtail), muscicapid (pied wheatear), sturnid (common starling), sylviid (common whitethroat, lesser whitethroat); Strigiformes: strigid (Eurasian eagle-owl); Sauria: gekkonid (Przewalski's wonder gecko), lacertid (Strauch's racerunner), scincid (Berber skink); Serpentes: colubrid (dotted dwarf racer, smooth snake), viperid (Halys pit viper); Testudines: testudinid (Greek tortoise, Russian tortoise) (3-host cycle)	Congo haemorrhagic fever, Tamdy and Wad Medani viruses)	
H. (*Hyalommina*) *brevipunctatum*	Artiodactyla: bovid (cattle, buffalo, sheep, goat, nilgai), camelid (camel), cervid (spotted deer, sambar); Perissodactyla: equid (horse); Eulipotyphla: soricid (Asian house shrew); Rodentia: murid (mouse, little Indian field mouse, flat-haired mouse, Asiatic long-tailed climbing mouse, black rat, soft-furred rat, Blanford's rat), sciurid (jungle palm squirrel); Carnivora: canid (dog), felid (cat, cheetah); Primates: hominid (human); Cuculiformes: cuculid (cuckoo) (3-host cycle)	(vector for Kyasanur forest disease)	India, Pakistan
H. bubi (nymphs) *nomen nudum*	Strigiformes: strigid (Eurasian eagle-owl)		India
H. dromedarii (syn. *H. delpyi, yakimovi*) (camel tick)	Artiodactyla: bovid (cattle, zebu, buffalo, sheep, goat, oryx, Arabian antelope), camelid (dromedary), suid (pig, warthog); Perissodactyla: equid (horse, donkey); Eulipotyphla: erinaceid (long-eared hedgehog, desert hedgehog); Lagomorpha: leporid (tolai hare, Egyptian hare, Cape hare); Rodentia: dipodid (lesser Egyptian jerboa), geomyid (gopher), murid (black rat, fat sand rat, short-tailed bandicoot rat, Libyan jird, Shaw's jird, Sundevall's jird, four-spotted gerbil, Cheesman's gerbil, lesser Egyptian gerbil, great gerbil, greater Egyptian gerbil, North African gerbil), sciurid (long-clawed ground squirrel); Carnivora: canid (dog, red fox, Ruppell's fox), felid (cat), hyaenid (hyena); Primates: hominid (human); Charadriiformes: charadriid (Egyptian plover); Falconiformes: falconid (common kestrel); Galliformes: phasianid (common quail); Struthioniformes: struthionid (ostrich); Sauria: lacertid (Bosc's fringe-toed lizard), scincid (long-tailed skink) (1-, 2- or 3-host cycle)	trauma, irritation, toxicosis, sweating sickness (vector for theileriosis, hepatozoonosis, Q fever, rickettsiosis, Crimean-Congo haemorrhagic fever, Kadam, Dera Ghazi Khan, Sindbis and Dhori viruses)	Eurasia, Africa
H. excavatum (syn. *I. algeriensis, savignyi*) (brown ear tick)	Artiodactyla: bovid (cattle, buffalo, water buffalo, sheep, Asiatic mouflon, goat, eland, unspecified gazelle), camelid (dromedary), cervid (deer), suid (pig, desert warthog); Perissodactyla: equid (horse, donkey); Eulipotyphla: erinaceid (European hedgehog); Lagomorpha: leporid (rabbit, mountain hare, European hare,	trauma, irritation, toxicosis (vector for theileriosis and possibly	Africa, Eurasia

	Cape hare), ochotonid (pika); Rodentia: dipodid (lesser Egyptian jerboa), murid (eastern broad-toothed field mouse, Cairo spiny mouse, fat sand rat, bushy-tailed gerbil, lesser Egyptian gerbil, greater Egyptian gerbil, Wagner's gerbil, Sundevall's jird, Shaw's jird, Tristram's jird), sciurid (ground squirrel); Carnivora: canid (dog), mustelid (tayra); Primates: hominid (human); Galliformes: phasianid (partridge); Passeriformes: motacillid (grey wagtail), muscicapid (common redstart, black redstart), oriolid (Eurasian golden oriole); Sauria: lacertid (Bosc's fringe-toed lizard) (2- or 3-host cycle)	rickettsiosis and borreliosis)	
H. franchinii	Artiodactyla: bovid (cattle, sheep), camelid (camel); Perissodactyla: equid (donkey); Rodentia: murid (golden spiny mouse); Primates: hominid (human); Sauria: agamid (desert agama), lacertid (Bosc's fringe-toed lizard, Nidua fringe-toed lizard, Schreiber's fringe-toed lizard); Testudines: testudinid (Greek tortoise) (3-host cycle)		Europe
H. glabrum (syn. *H. marginatum turanicum*) (enameled bont-legged tick, pale-legged bont-legged tick)	Artiodactyla: bovid (cattle, sheep, goat, gemsbok, eland); Perissodactyla: equid (horse, Cape mountain zebra), rhinocerotid (black rhinoceros); Lagomorpha: leporid (scrub hare); Hyracoidea: procaviid (hyrax); Rodentia: pedetid (springhare); Carnivora: canid (dog); Primates: hominid (human); Galliformes: numidid (guineafowl); Passeriformes: emberizid (cinnamon-breasted bunting), ploceid (red-billed quelea); Strigiformes: strigid (Eurasian eagle-owl) (3-host cycle)	(vector for Crimean-Congo fever)	Africa
H. (*Hyalommina*) *hussaini*	Artiodactyla: bovid (cattle, zebu, buffalo, sheep, goat, nilgai), camelid (dromedary), cervid (chital, sambar deer), suid (pig); Perissodactyla: equid (horse); Eulipotyphla: soricid (shrew); Rodentia: murid (black rat); Carnivora: canid (dog), felid (tiger), ursid (sloth bear); Primates: hominid (human) (3-host cycle)		India, Pakistan, Burma
H. (*Hyalommina*) *hystricis*	Artiodactyla: bovid (cattle, buffalo), cervid (reeve's muntjac), suid (pig, wild boar); Perissodactyla: equid (horse); Scandentia: tupaiid (tree shrew); Rodentia: hystricid (Indian crested porcupine, Bengal porcupine), murid (Southeast Asian house rat, chesnut-bellied white rat); Carnivora: canid (dog), felid (tiger), mephitid (stink badger), mustelid (hog badger), ursid (Himalayan black bear); Primates: hominid (human); Passeriformes: timaliid (large scimitar babbler); Testudines: geoemydid (spiny tortoise)		India
H. impeltatum (syn. *H. brumpti, erythraeum, sinaii, somalicum*)	Artiodactyla: bovid (cattle, zebu, sheep, goat, gazelle, blue wildebeest, gemsbok, eland, Arabian oryx, unspecified gazelle), camelid (dromedary, camel), suid (pig); Perissodactyla: equid (horse, donkey, zebra), rhinocerotid (black rhinoceros); Eulipotyphla: erinaceid (European hedgehog); Lagomorpha: leporid (Cape hare); Rodentia: caviid (guinea pig), dipodid (lesser Egyptian jerboa), murid (fat sand rat, eastern spiny mouse, bushy-tailed gerbil, greater Egyptian gerbil, lesser Egyptian gerbil); Carnivora: canid (dog), felid (caracal); Primates: hominid (human); Passeriformes: muscicapid (northern wheatear, isabelline wheatear, common redstart, black redstart); Struthioniformes: struthionid (ostrich); Sauria: lacertid (Bosc's fringe-toed lizard) (2 or 3-host cycle)	(vector for theileriosis, rickettsiosis, Crimean-Congo haemorrhagic fever)	Africa, South Central Asia
H. impressum (syn. *H. transiens*) (bont-legged tick)	Artiodactyla: bovid (cattle, zebu, buffalo, forest buffalo, sheep, goat, gemsbok, eland, nyala, waterbuck, greater kudu, blue wildebeest, Lichtenstein's hartebeest, sable antelope, roan antelope), camelid (dromedary, camel), giraffid (giraffe), suid (boar, bushpig, red river hog, common warthog, desert warthog); Perissodactyla: equid (horse, donkey, plains zebra), rhinocerotid (black rhinoceros); Lagomorpha: leporid (savannah hare); Eulipotyphla: erinaceid (four-toed hedgehog, South African	trauma, irritation (vector for Crimean-Congo haemorrhagic fever)	Africa

	hedgehog); Tubulidentata: orycteropodid (aardvark); Rodentia: murid (mouse); Carnivora: canid (dog), felid (cat, lion, Indian leopard); Primates: hominid (human); Bucerotiformes: bucerotid (eastern yellow-billed hornbill); Struthioniformes: struthionid (ostrich) (3-host cycle)		
H. isaaci	Artiodactyla: bovid (cattle, buffalo, sheep, goat), camelid (camel), cervid (Central Asian red deer); Perissodactyla: equid (horse, donkey); Lagomorpha: leporid (Indian hare, rabbit); Rodentia: caviid (guinea pig); Carnivora: canid (dog), herpestid (mongoose); Primates: hominid (human); Cuculiformes: cuculid (coucal); Passeriformes: muscicapid (blue rock thrush), passerid (house sparrow) (2-host cycle)	trauma, irritation (vector for Crimean-Congo haemorrhagic fever, rickettsioses, piroplasmosis, anaplasmosis, trypanosomiasis)	Eurasia
H. (*Hyalommina*) *kumari*	Artiodactyla: bovid (cattle, zebu, buffalo, sheep, goat, Nilgiri tahr), camelid (camel), cervid (unspecified deer); Perissodactyla: equid (horse); Eulipotyphla: soricid (shrew); Rodentia: murid (black rat); Carnivora: canid (dog), felid (tiger); Passeriformes: estrildid (munia) (3-host cycle)		India, Pakistan, South Central Asia
H. (*Hyalomma*) *lusitanicum*	Artiodactyla: bovid (cattle, sheep, goat), camelid (camel), cervid (red deer, roe deer, European fallow deer), suid (pig, boar); Perissodactyla: equid (horse); Eulipotyphla: erinaceid (hedgehog); Lagomorpha: leporid (European rabbit, hare); Rodentia: glirid (garden dormouse), murid (mouse, black rat); Carnivora: canid (dog, red fox), herpestid (mongoose), mustelid (European polecat, least weasel); Otidiformes: otidid (bustard); Primates: hominid (human); Galliformes: phasianid (red partridge); Passeriformes: fringillid (finch), turdid (blackbird); Strigiformes: strigid (eagle-owl); Struthioniformes: struthionid (ostrich) (3-host cycle)	(vector for theileriosis, babesiosis and possibly anaplasmosis, ehrlichiosis, tularemia, borreliosis, Q fever and Crimean-Congo haemorrhagic fever)	Europe
H. (*Hyalomma*) *marginatum* (syn. *H. cypriacum, dentatum, plumbeum*) (bont-legged tick, Mediterranean hyalomma)	Artiodactyla: bovid (cattle, zebu, buffalo, water buffalo, sheep, argali, goat, eland, saiga antelope, goitered gazelle, springbok, black wildebeest), camelid (camel), cervid (red deer, roe deer), giraffid (giraffe), suid (pig, wild boar); Perissodactyla: equid (horse, donkey, mule, plains zebra, mountain zebra, onager); Eulipotyphla: erinaceid (long-eared hedgehog, desert hedgehog, European hedgehog); Lagomorpha: leporid (rabbit, scrub hare, tolai hare, Smith's red rock hare, Cape hare, Indian hare, European hare); Rodentia: caviid (guinea pig), cricetid (common vole, social vole, Major's pine vole), didpodid (small five-toed jerboa), erethizontid (porcupine), murid (house mouse, striped field mouse, wood mouse, fat sand rat, Libyan jird, Shaw's jird, Sundevall's jird, Tamarisk jird, Tristram's jird, great gerbil, lesser Egyptian gerbil), pedetid (springhare), sciurid (red squirrel, little ground squirrel, European ground squirrel); Carnivora: canid (dog, red fox), felid (cat, leopard), herpestid (Indian brown mongoose), mustelid (steppe polecat, marbled polecat, least weasel); Primates: hominid (human); Accipitriformes: accipitrid (great spotted eagle, booted eagle, tawny eagle, western marsh harrier, hen harrier, pallid harrier, common buzzard, Himalayan buzzard, dark chanting goshawk, Egyptian vulture); Anseriformes: anatid (mallard, goose); Bucerotiformes: upupid (Eurasian hoopoe); Caprimulgiformes: caprimulgid (European nightjar); Charadriiformes: burhinid (Eurasian stone curlew), charadriid (northern lapwing, European golden plover, little ringed plover), scolopacid (common snipe); Columbiformes: columbid (common wood pigeon, yellow-eyed pigeon, rock dove, laughing dove, European turtle dove); Coraciiformes: coraciid (European roller), meropid (European bee-eater, blue-cheeked bee-eater); Cuculiformes: cuculid (common cuckoo); Falconiformes: falconid (common kestrel, lesser kestrel, saker	trauma, irritation, paralysis (vector for theileriosis, babesiosis, anaplasmosis, rickettsiosis, Q fever, Crimean-Congo haemorrhagic fever and possibly West Nile virus)	Africa, Asia, Europe

	falcon); Galliformes: phasianid (chicken, common partridge, Daurian partridge, grey partridge, rock partridge, chukar partridge, see-see partridge, mountain partridge, common quail, black francolin, ring-necked pheasant, turkey); Gruiformes: gruid (common crane, Demoiselle crane), rallid (spotted crake); Otidiformes: otidid (great bustard, little bustard); Passeriformes: acrocephalid (marsh warbler, sedge warbler, melodius warbler, Eurasian reed warbler), alaudid (woodlark, crested lark, red-capped lark, bimaculated lark, Calandra lark, lesser short-toed lark, Hume's short-toed lark, Eurasian skylark, Oriental skylark), corvid (common raven, carrion crow, rook, western jackdaw, Eurasian magpie, Eurasian jay, Turkestan ground jay), emberizid (red-headed bunting, grey-necked bunting, corn bunting, eastern meadow bunting, white-capped bunting, Cretzschmar's bunting, Ortolan bunting, yellowhammer), fringillid (hawfinch, common chaffinch, desert finch, grey-crowned goldfinch, European goldfinch, European greenfinch, common linnet, white-winged snowfinch), laniid (red-backed shrike, brown shrike, lesser grey shrike, masked shrike, long-tailed shrike, woodchat shrike), leiothrichid (yellow-billed babbler), locustellid (Savi's warbler), motacillid (tawny pipit, tree pipit, white wagtail, grey wagtail, citrine wagtail, western yellow wagtail), muscicapid (common rock thrush, blue rock thrush, blue whistling thrush, common nightingale, thrush nightingale, common redstart, black redstart, Guldenstadt's redstart, rufous-tailed scrub robin, European robin, European pied flycatcher, whinchat, pied bush chat, African stonechat, northern wheatear, isabelline wheatear, variable wheatear, western black-eared wheatear, pied wheatear, common nightingale, thrush nightingale, collared flycatcher, spotted flycatcher, European pied flycatcher), oriolid (Eurasian golden oriole), parid (great tit), passerid (house sparrow, tree sparrow, rock sparrow, Spanish sparrow), phylloscopid (greenish warbler, willow warbler, sulphur-bellied warbler), scotocercid (streaked scrub warbler), sittid (western rock nuthatch, eastern rock nuthatch), sturnid (common starling, rosy starling, Brahminy starling, Tristram's starling, common mynah), sylviid (common whitethroat, lesser whitethroat, Hume's whitethroat, garden warbler, western subalpine warbler, Eurasian blackcap), turdid (common blackbird, song thrush, red-throated thrush, mistle thrush); Pterocliformes: pteroclid (black-bellied sandgrouse); Strigiformes: strigid (little owl, boreal owl, short-eared owl, Eurasian scops owl, Eurasian eagle-owl); Sauria: agamid (Caucasian agama), lacertid (sand lizard, Caucasus emerald lizard, European green lizard, Bosc's fringe-toed lizard); Testudines: testudinid (Greek tortoise) (2-host cycle)		
H. marinatum	Struthioniformes: struthionid (ostrich)		
H. monstrosum	Artiodactyla: suid (Indian boar); Perissodactyla: equid (horse)		India
H. (*Euhyalomma*) *nitidum*	Artiodactyla: bovid (cattle, buffalo, goat, gemsbok, eland, roan antelope, waterbuck, kob), camelid (camel), suid (red river hog, warthog); Perissodactyla: equid (horse, zebra); Lagomorpha: leporid (African savannah hare); Rodentia: murid (striped grass mouse); Carnivora: canid (golden jackal); Primates: hominid (human) (3-host cycle)	(possible vector for Crimean-Congo haemorrhagic fever)	Africa
H. (*Hyalommina*) *punt*	Artiodactyla: bovid (cattle, sheep, goat, antelope, gazelle), camelid (camel) (3-host cycle)		Somalia, Ethiopia
H. puta	Charadriiformes: chionid (black-faced sheathbill); Procellariiformes: diomodeid (sooty albatross); Sphenisciformes: spheniscid (Gentoo penguin)		Kerguelen Islands
H. (Hyalommina) *rhipicephaloides*	Artiodactyla: bovid (sheep, goat, alpine ibex, Nubian ibex, Arabian gazelle); Lagomorpha: leporid (Cape hare); Rodentia:		Middle-East

	murid (eastern spiny mouse, golden spiny mouse, Cairo spiny mouse); Carnivora: canid (Ruppell's fox) (3-host cycle)		
H. rufipes (coarse bont-legged tick)	Artiodactyla: bovid (cattle, buffalo, sheep, goat, eland, common duiker, hartebeest, blue wildebeest, gemsbok, springbok, blesbok, bushbuck, greater kudu, roan antelope, sable antelope), camelid (camel), giraffid (giraffe, Masai giraffe); Perissodactyla: equid (horse, Burchell's zebra, Grant's zebra, Hartmann's mountain zebra), rhinocerotid (black rhinoceros), suid (desert warthog); Eulipotyphla: erinaceid (four-toed hedgehog, South African hedgehog); Macroscelidea: macroscelidid (elephant shrew, bushveld elephant shrew); Lagomorpha: leporid (Jameson's red rock hare, scrub hare, Egyptian hare, Cape hare); Rodentia: caviid (guinea pig), murid (striped grass mouse, four-striped grass mouse, eastern spiny mouse, African grass rat, Namaqua rock rat, Woosnam's brush-furred rat, Cape short-eared gerbil); Carnivora: canid (dog, black-backed jackal), felid (cat, leopard), herpestid (yellow mongoose); Primates: hominid (human); Accipitriformes: accipitrid (black kite, yellow-billed kite, martial eagle, common buzzard); Bucerotiformes: bucerotid (African grey hornbill), phoeniculid (green wood hoopoe, common scimitarbill); Charadriiformes: burhinid (spotted thick-knee); Coliiformes: coliid (red-faced mousebird); Columbiformes: columbid (laughing dove, Namaqua dove); Coraciiformes: alcedinid (striped kingfisher), meropid (little bee-eater); Cuculiformes: cuculid (common cuckoo, Senegal coucal); Falconiformes: falconid (common kestrel); Galliformes: numidid (helmeted guineafowl, tiara'd guineafowl), phasianid (chicken, red-billed spurfowl, yellow-necked spurfowl, crested francolin); Gruiformes: gruid (black-crowned crane); Otidiformes: otidid (southern black korhaan, black bustard, white-bellied bustard); Passeriformes: alaudid (greater short-toed lark, large-billed lark, spike-heeled lark, monotonous lark, Sabota lark), cisticolid (black-chested prinia), dicrurid (fork-tailed drongo), estrildid (blue waxbill), fringillid (white-throated canary, black-throated canary, streaky-headed seedeater), hirundinid (barn swallow), laniid (magpie shrike, southern fiscal shrike, masked shrike, woodchat shrike), malaconotid (southern boubou, brown-crowned tchagra, crimson-breasted shrike, black-headed puffback), motacillid (tawny pipit, Cape longclaw), muscicapid (fiscal flycatcher, southern black flycatcher, Marico flycatcher, mocking cliff chat, Cape robin chat, anteater chat, northern wheatear, black-eared wheatear, isabelline wheatear, rufous-tailed scrub-robin, common rock thrush, spotted flycatcher, common redstart), oriolid (black-headed oriole), parid (coal tit, grey tit, cinereous tit, southern black tit, ashy tit), passerid (northern grey-headed sparrow), ploceid (lesser masked weaver, southern masked weaver, white-browed sparrow-weaver, village weaver, red-billed quelea), pycnonotid (common bulbul, white-spectacled bulbul, dark-capped bulbul), scotocercid (streaked scrub warbler), sturnid (wattled starling, black-bellied starling, Meve's starling), sturnid (red-winged starling), turdid (olive thrush, Cape thrush, Karoo thrush, Kurrichane thrush, Namaqua thrush), vangid (white-crested helmetshrike), viduid (pin-tailed whydah); Strigiformes: strigid (Cape barn owl, Verreaux's eagle-owl); Struthioniformes: struthionid (ostrich); Suliformes: phalacrocoracid (bank cormorant) (2-host cycle)	irritation, abscesses (vector for babesiosis, theileriosis, anaplasmosis, rickettsioses, Crimean-Congo haemorrhagic fever, fowl aegyptianellosis, trypanosomiasis)	Africa
H. schulzei	Artiodactyla: bovid (cattle, sheep, goat), camelid (camel); Perissodactyla: equid (horse, donkey, mule); Eulipotyphla: erinaceid (hedgehog); Lagomorpha: leporid (Cape hare); Rodentia: murid (fat sand rat, bushy-tailed jird, Sundevall's jird), sciurid (red-cheeked ground squirrel); Carnivora: canid (dog);		Arabia

	Primates: hominid (human); Sauria: agamid (unspecified agama) (2-host cycle)		
H. scupense (syn. *H. detritum, mauritanicum, sharifi, steineri, uralense, volgense*) (bont-legged tick, shiny hyalomma)	Artiodactyla: bovid (cattle, zebu, buffalo, water buffalo, sheep, argali, arkhar, goat, argali, antelope, goitered gazelle), camelid (camel), cervid (red deer, Bactrian deer, roe deer), suid (pig, wild boar); Perissodactyla: equid (horse, donkey, mule, onager); Eulipotyphla: erinaceid (hedgehog); Lagomorpha: leporid (rabbit, desert hare, tolai hare, European hare); Rodentia: hystricid (Indian crested porcupine), murid (great gerbil, Libyan jird, Tamarisk jird); Carnivora: canid (dog, golden jackal, true fox), hyaenid (striped hyena), mustelid (marbled polecat); Primates: hominid (human); Accipitriformes: accipitrid (golden eagle); Bucerotiformes: upupid (Eurasian hoopoe); Galliformes: phasianid (chicken, common quail); Gruiformes: gruid (Demoiselle crane), rallid (corn crake); Passeriformes: corvid (black-billed magpie, European jay), passerid (tree sparrow), turdid (common blackbird, true thrush, song thrush); Sauria: lacertid (common wall lizard, European green lizard) (1 or 2-host cycle)	trauma, irritation, toxicosis, sweating sickness (vector for theileriosis, babesiosis, rickettsiosis, Q fever, Bhanja virus and possibly Crimean-Congo haemorrhagic fever, tularemia and brucellosis)	Eurasia, Africa
H. (Euhyalomma) truncatum (syn. *H. lewisi, planum, rhinocerotis, zambesianum, Hyalommina lewisi*) (small smooth bont-legged tick)	Artiodactyla: bovid (cattle, zebu, buffalo, forest buffalo, sheep, goat, roan antelope, sable antelope, black wildebeest, blue wildebeest, hartebeest, red hartebeest, Lichtenstein's hartebeest, brindled gnu, sassaby, tiang, eland, greater kudu, harnessed bushbuck, waterbuck, gemsbok, kob, impala, springbok, blesbok, korrigum, oryx, duiker, nyala), camelid (camel), giraffid (giraffe), suid (pig, Egyptian wild boar, bush pig, red river hog, desert warthog); Perissodactyla: equid (horse, donkey, mule, plains zebra, Hartmann's mountain zebra, Cape mountain zebra, Burchell's zebra), rhinocerotid (black rhinoceros, white rhinoceros); Lagomorpha: leporid (scrub hare, savannah hare, Cape hare, Smith's red rock hare); Macroscelidea: macroscelidid (elephant shrew); Eulipotyphla: erinaceid (four-toed hedgehog); Tubulidentata: orycteropodid (aardvark); Rodentia: hystricid (African porcupine, Cape porcupine), murid (four-striped grass mouse, African grass rat, bush vlei rat, Namaqua rock rat, Brown's whistling rat, bushveld gerbil, Cape gerbil); Carnivora: canid (dog, jackal), felid (cat, African wildcat, cheetah, lion, leopard), herpestid (white-tailed mongoose); Primates: cercopithecid (Chacma baboon), hominid (human); Accipitriformes: sagittarid (secretary bird); Bucerotiformes: bucerotid (yellow-billed hornbill, eastern yellow-billed hornbill, African gray hornbill); Charadriiformes: burhinid (spotted thick-knee); Columbiformes: columbid (laughing dove); Coraciiformes: coraciid (lilac-breasted roller); Galliformes: phasianid (Natal spurfowl, Swainson's spurfowl); Otidiformes: otidid (Denham's bustard, Kori bustard); Passeriformes: alaudid (crested lark), corvid (pied crow), sturnid (wattled starling); Strigiformes: strigid (barn owl); Struthioniformes: struthionid (ostrich); Sauria: agamid (black-necked agama), chamaeleonid (flap-necked chameleon); Testudines: testudinid (leopard tortoise, geometric tortoise, Bell's hinge-back tortoise) (2-host cycle)	trauma, irritation, toxicosis, sweating sickness, paralysis (vector for piroplasmosis, rickettsioses, Q fever, Crimean-Congo haemorrhagic fever)	Africa
H. tunesiacum	Artiodactyla: bovid (cattle, sheep, goat), camelid (camel); Perissodactyla: equid (horse, donkey, mule); Eulipotyphla: erinaceid (hedgehog); Carnivora: canid (dog); Primates: hominid (human); Sauria: agamid (unspecified agama)		Africa
H. turanicum	Artiodactyla: bovid (cattle, sheep), camelid (camel), suid (pig); Perissodactyla: equid (horse); Lagomorpha: leporid (hare); Eulipotyphla: erinaceid (hedgehog); Primates: hominid (human); Accipitriformes: accipitrid (Egyptian vulture); Bucerotiformes: upupid (Eurasian hoopoe); Columbiformes: columbid (rock dove, eastern stock pigeon, yellow-eyed pigeon, European turtle dove); Coraciiformes: coraciid (European roller), meropid (blue-cheeked	trauma, irritation (vector for Crimean-Congo haemorrhagic fever, rickettsioses, piroplasmosis, anaplasmosis,	South Central Asia, Africa

	bee-eater); Galliformes: phasianid (chukar partridge, common pheasant, ringneck pheasant); Passeriformes: alaudid (Calandra lark, Oriental skylark, Oriental short-toed lark, Hume's lark), emberizid (corn bunting, white-capped bunting, grey-necked bunting, red-headed bunting), fringillid (European goldfinch), laniid (lesser grey shrike, red-backed shrike), motacillid (tawny pipit), muscicapid (variable wheatear, African stonechat, white-headed chat, Strickland's chat, black redstart), passerid (house sparrow, tree sparrow), phylloscopid (green warbler), sittid (eastern rock nuthatch), sturnid (common starling, rosy starling), sylviid (lesser whitethroat, Hume's whitethroat) (2-host cycle)	trypanosomiasis)	
H. verae	Artiodactyla: bovid (goitered gazelle)		China

Parasite morphology: *Hyalomma* spp. form 4 different types of morphological stages; namely, eggs, larvae, nymphs, and adults. Eggs are small brown oval stages measuring 0.4-0.5 x 0.3-0.4 mm and usually clustered together in large batches. Larvae have dorso-ventrally flattened oval-pyriform bodies measuring from 0.5-1.0 mm in length. They range in colour from pale yellow to reddish-brown and have a small anterodorsal dorsal shield (scutum) without coloured enamel ornamentation but with lateral eyes. The small anterior capitulum (head) bears long mouthparts while the large posterior idiosoma (body) has poorly developed indentations (festoons) along the posterior margin. Larvae have 3 pairs of long pale legs arising ventrally, but they lack respiratory openings (stigmata). Nymphs are similar in shape and colouration but are larger measuring from 1-4 mm in length. They have 4 pairs of long ventral legs, a pair of lateral stigmata with round plates, and the anus has a posterior anal groove. Adult ticks have ovate-ellipsoidal bodies that are ventrally flattened but dorsally convex (slightly when unfed but strongly when engorged). Unfed ticks are light-yellow to red-brown in colour and range in length from 4-7 mm, while engorged females are often blue-grey in colour and are grossly distended up to 10-20 mm in length. The anterior capitulum is small and visible from above (whereas that of argasids is ventral and not visible from above) and consists of a basis capitulum (basal ring encircling mouthparts) and projecting gnathosoma (bearing mouthparts). The basis capitulum is rectangular (not triangular, hexagonal or pentagonal) with angular lateral margins, and the dorsal surface of females has 2 porose areas (clusters of pores) involved in waterproofing eggs during oviposition. The mouthparts are longer than, but as wide as, the basis capitulum, and bears 2 lateral sensory palps and a central hypostome flanked by 2 cutting chelicerae. The palps are elongate (especially the second segment) and they do not enter the skin when feeding but move laterally. The chelicerae have long curved tubular shafts terminating in cutting digits with recurved teeth. They are used cut skin with a horizontal action tearing flesh to form small pools of blood. The barbed hypostome is inserted into the pools to facilitate feeding and help anchor the tick to the host. A feeding tube (buccal canal) is formed between the chelicerae and hypostome to suck blood and inject saliva from long paired salivary glands. The alimentary tract consists of a muscular pharynx (with pharyngeal valve), a short oesophagus, a large saccular midgut (ventriculus) with lateral diverticula (caeca), a short intestine (with excretory Malpighian tubules), a rectal sac, and a subterminal ventral anus. The anus has a posterior (metastriate) anal groove, unlike Ixodes which has an anterior (prostriate) groove. The posterior idiosoma is large and bears a sclerotized dorsal plate (scutum) which nearly covers the dorsal surface of males (= conscutum), but is restricted to a small anterior shield in females. The scutum is inornate (without coloured enamel ornamentation) but may have longitudinal striations, several ridges and depressions and a few shallow scattered punctuations. The lateral margins of the scutum contain 2 simple orbited convex eyes. The posterior margin of the idiosoma has a series of indented grooves (festoons) which are irregular and partly coalesced (indistinct on engorged females). The ventral idiosoma gives rise to 4 pairs of long legs, which are very distinctive in most species as they have conspicuous pale rings around the distal portions of most segments. While *Hyalomma* spp. are often known as bont-legged (banded legged) ticks, some species actually do not have bands (e.g. *H. anatolicum, H. scupense*). Each leg contains 6 segments (coxae, trochanter, femur, patella (genu), tibia, and tarsus) and ends in a pair of claws with a pad-like pulvillus (argasids do not have pulvilli). Coxae I possess a pair of large and equal spurs in both sexes, tarsi I have a unique sensory structure (Haller's organ) used to detect host odours, heat and vibrations, and a pair of lateral respiratory stigmata with large spiracular plates are located behind coxae IV (the stigmata on argasids are located between coxae III). Adult ticks display marked sexual dimorphism, with external differences mainly involving body size (females are larger), scutal plates (larger in males), and glands (females with porose areas). Male *Hyalomma* also have sclerotized ventral plates (adanal, subanal and accessory plates) like *Ixodes* and *Rhipicephalus* (incl. *Boophilus*). Mature males have 2 tubular testes with vas efferentia joining to form a common vas deferens (with accessory gland) leading to the ejaculatory duct and genital aperture (gonopore) situated anteroventrally behind a sclerotized flap (genital apron). Mature females have a single saccular ovary with paired tubular oviducts joining to a common uterus (with lateral accessory glands). The vagina has 2 regions with the cervical region acting as a receptaculum seminis to store spermatophores and the vestibular vagina prolapsing during oviposition. The gonopore may be V- or U-shaped and is located anteroventrally behind a genital apron and adjacent to a special secretory structure (Gene's organ) which produces waxy coating for eggs.

Site of infection: All motile developmental stages are transient ectoparasites on the skin of vertebrate hosts. Infestations have been recorded on mammals belonging to 36 families in 12 orders (including ungulates, insectivores, lagomorphs, rodents, carnivores and primates), birds belonging to 31 passerine families and 29 non-passerine families in 20 orders (including shore birds, sea birds, terrestrial birds, fowl, doves and birds of prey), reptiles belonging to 6 lizard families, 3 snake families, 3 tortoise families and one

crocodile family. Most species exhibit variable host specificities (or host preferences), as smaller stages (larvae and nymphs) tend to occur on smaller animals (mammals (especially rodents), ground-dwelling birds and reptiles) while adult ticks occur on larger animals (mainly ungulates but also including carnivores, lagomorphs, passeriform and galliform birds, and some nocturnal birds of prey). Their favoured feeding sites also vary greatly but are often regions with sparse hair/feathers that are difficult for the host to groom. Feeding stages on birds and reptiles are often found around the head (face, eyes, ears), neck and foreleg axillae. On mammals, they are usually found around the ears, eyes, belly, inner thighs, scrotum, udders, perineum and between the toes (depending on host species). In heavy infestations, however, ticks may occur over the whole body.

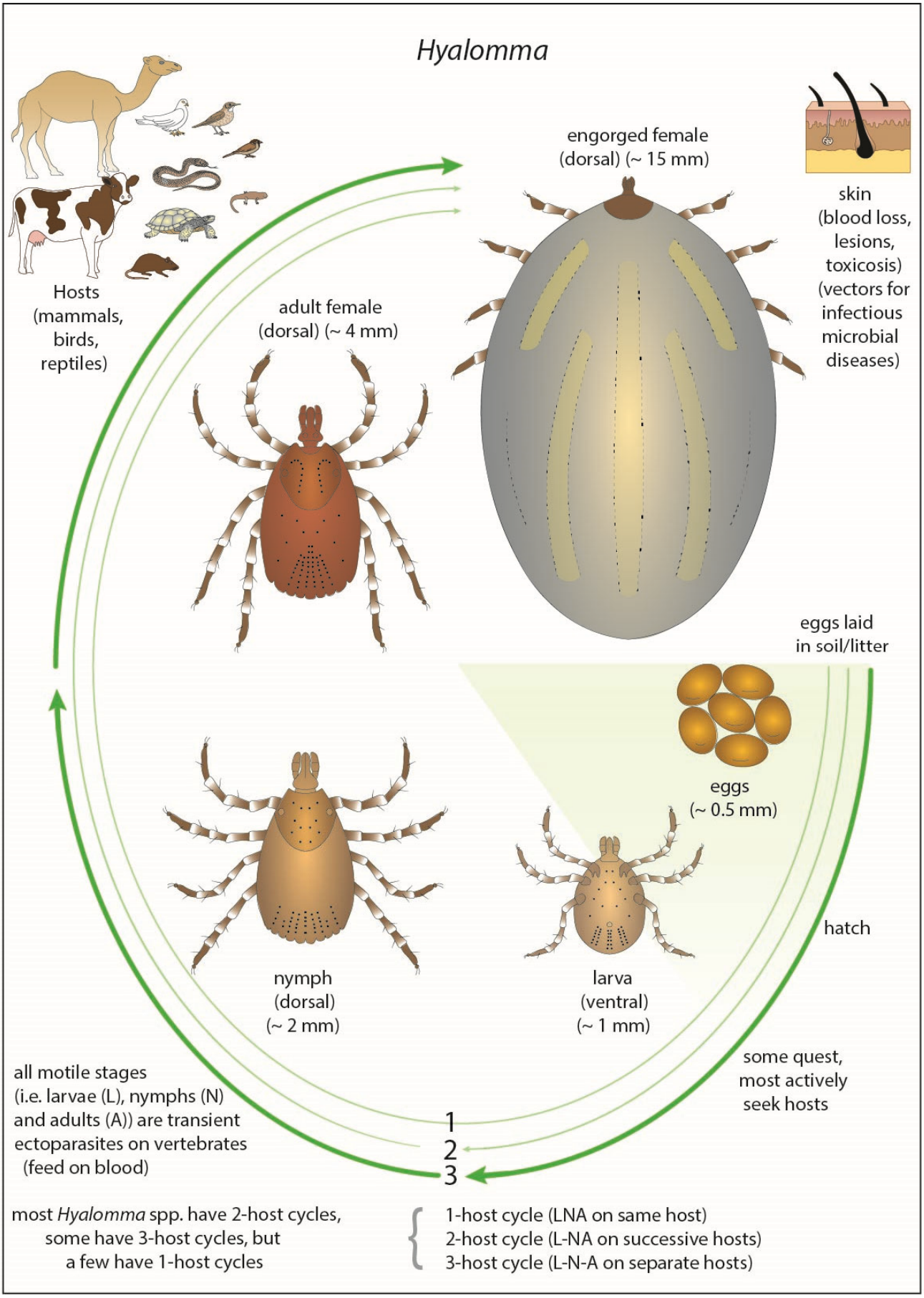
Pathogenesis: Larvae, nymphs and adult ticks are haematophagous parasites that attach to vertebrate hosts to feed using their cutting mouthparts to form pools of blood from which they suck up blood (feeding process known as telmophagy). Their attachment to the host is aided by the secretion of a salivary cement which helps create a feeding lesion in the dermis. During feeding, they inject saliva containing many haemodynamic compounds, including those with cytolytic, analgesic, anticoagulatory and vasodilatory properties. When replete with blood, they detach to digest their bloodmeals before undergoing further development. Despite their transient feeding, heavy infestations may cause blood loss severe enough to manifest as anaemia (females shown to engorge with blood volumes up to 8 ml). Tick bites cause local tissue trauma with irritation, pruritus, inflammation (erythema, oedema), focal necrosis and granuloma formation. Animals may aggressively groom infested regions (biting, scratching, rubbing) resulting in self-trauma and predisposing conditions for secondary infections, abscess formation, pyaemia and even myiasis. Infestations of the ear may cause otoacariasis, with ear pain, inflammation, exudates and frequent head-shaking. Livestock may exhibit considerable biting stress (tick worry) with interrupted feeding, weakness, poor growth and reduced meat and/or milk production. These effects may be exacerbated in animals where ticks have infested interdigital clefts resulting in reduced mobility and lameness. Saliva from engorging females of several species has also been associated with toxicosis in certain hosts, producing a sweating sickness with profuse moist eczema and hyperaemia of mucous membranes in pigs and ruminants, ascending flaccid paralysis with unsteady gait, lameness and recumbency in camels and lambs, and even facial nerve paralysis in humans. Feeding stages may also act as vectors for the transmission of several infectious microbial diseases. Some microbes may undergo massive amplification in tick tissues, most survive tick moults (trans-stadial transmission) and some are even transferred vertically to tick eggs (trans-ovarian transmission). Hosts may become infected when ticks feed (via saliva), regulate fluids (via regurgitation) or eliminate wastes (via defaecation). Various *Hyalomma* spp. have been shown to transmit haemoprotozoa causing babesiosis, theileriosis and trypanosomiasis, rickettsial bacteria causing spotted fevers, anaplasmosis, Siberian tick typhus, Boutonneuse fever and canine ehrlichiosis, proteobacteria causing coxiellosis (Q fever) and brucellosis, and viruses causing African horse sickness and Crimean-Congo haemorrhagic fever. Screening studies have also detected a range of arthropod-borne (arbo-) viruses in ticks, including Bhanja, Chick Ross, Dhori, Kadam, Sindbis, Thogoto and West Nile viruses, but their involvement in the transmission of disease remains to be established.

Developmental cycle and mode of transmission: *Hyalomma* spp. undergo incomplete (hemimetabolous) metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Most species have 3-host life-cycles (all stages on separate hosts) although some have 2-host cycles (larvae and nymphs on one host, adults on another) and a few have one-host cycles (all stages on the same host). Some 3-host species can adopt one- or 2-host cycles, a facultative ability unique to this genus. Each developmental stage feeds once to repletion, with larvae and nymphs feeding for several days and adults for a few weeks. Gravid female ticks lay eggs in ground litter where they hatch after 21-43 days, sometimes up to 60 days depending on prevailing conditions. The emergent 6-legged larvae then seek hosts on which to feed, preferring small mammals, ground-dwelling birds or reptiles. Many species actively hunt for hosts by scuttling along the ground after sensing nearby vibrations, body heat or chemical odours (especially exhaled carbon dioxide, but also including pheromones produced by ticks already resident on hosts). Some ticks may also adopt an ambush strategy by climbing onto vegetation and questing for passing hosts. Larvae may survive without feeding for several weeks to months as they appear to be quite resistant to cold and dry conditions. Having located a host, the larvae crawl onto the skin and attach to feed for 2-5 days (rarely up to 21 days). When replete, the larvae detach and those species with 3-host cycles drop to the ground while those with 1- or 2-host cycles stay on the host. After 4-18 days to digest their bloodmeals, the larvae moult to form 8-legged nymphs (only one nymphal instar is formed, while argasids form 2-7 nymphal instars). Free nymphs then seek small animal hosts either by hunting or questing and they may survive unfed for several weeks. Nymphs attach to their hosts and feed for 6-8 days, sometimes up to 23 days. Those attached to migratory birds have been shown to undergo widespread dispersal. When replete, nymphs detach and those species with 2- or 3-host cycles drop to the ground while those with 1-host cycles stay on the host. Fed nymphs take several days to digest their bloodmeals before moulting to adult ticks. Both male and female ticks seek hosts by hunting or questing, preferentially infesting larger animals, particularly ungulates. Adult ticks may survive unfed for several weeks depending on environmental conditions (longer in moist conditions). Having located a suitable host, both males and females begin feeding as they require bloodmeals to become sexually mature. Males take small meals and move about the host seeking attached females presumably following pheromone cues. Mating takes place on hosts when males transfer spermatophores to receptive females. Once fertilized, attached females continue feeding for 5-14 days until engorgement, sometimes up to 52 days in a few species. When replete, they drop off the host onto the ground and after 3-12 days begin to lay large batches of eggs (totaling 4,000-15,500) over 8-12 days (sometimes up to 40 days) before becoming spent and dying. The duration of the entire life-cycle depends on the tick species, whether 1, 2 or 3 hosts are required and their availability, and the geographic location and climate. Experimental and epidemiological studies have shown that the life cycle may be completed in as little as 70-180 days, but it often takes longer when hosts are sparsely distributed or only seasonally available. Species with 1-host cycles complete one generation each year,

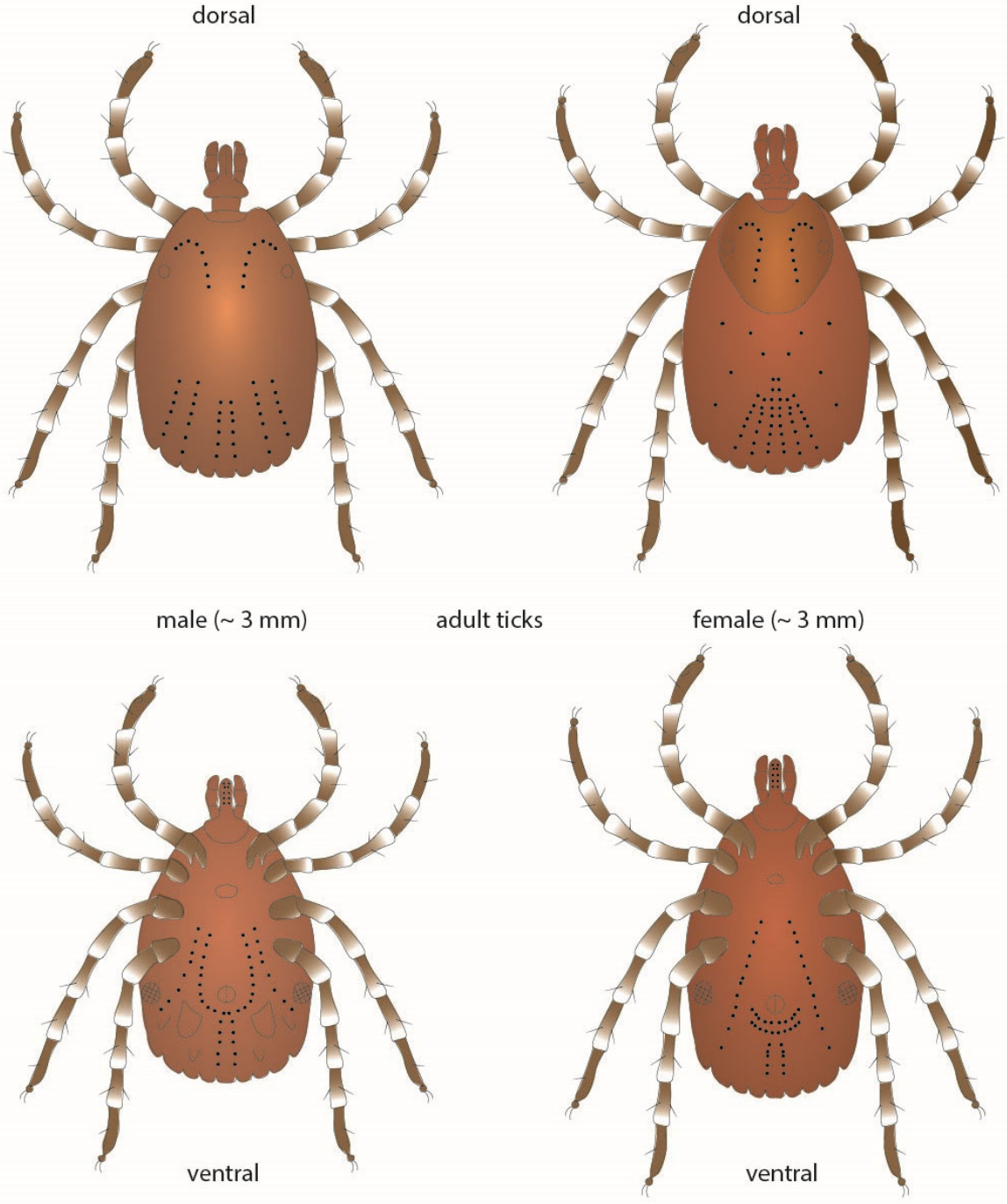
those with 2-host cycles generally take 1-2 years while those with 3-host cycles take 2-3 years. *Hyalomma* ticks are most abundant in warm arid and semiarid regions with long dry seasons. Nymphs and unfed adults survive the dry winter seasons in cracks and crevices in rocks, stone walls and stables, or amongst the litter in weedy or fallow fields.

Differential diagnosis: Infestations are rarely diagnosed on clinical grounds as symptoms and signs (skin lesions, anaemia, illthrift) are nonspecific and could be attributed to a number of causes (including other ectoparasites). Diagnoses are made by direct detection of feeding stages attached to hosts which are subsequently collected for microscopic examination and identification on the basis of their morphological characteristics (e.g. inornate ticks with festoons and eyes, banded legs, rectangular basis capituli, long mouthparts, long palps, males with ventral plates). Specimens may be preserved by freezing or fixation for molecular characterization, with phylogenetic analyses usually conducted following polymerase chain reaction (PCR) amplification of nuclear (18S and 28S ribosomal RNA, internal transcribed spacer regions 1 and 2) and mitochondrial (12S and 16S ribosomal RNA, cytochrome c oxidase subunit I, nicotinamide adenine dinucleotide dehydrogenase subunit 5) gene sequences.

Treatment and control: Individual ticks may be removed from compliant hosts using fine forceps, special tick removal devices (keys, lassos, twists) and even spearing with sharp thorns. Care should be taken not to squeeze or break ticks as fluids and fragments may cause further inflammation or systemic reactions. Caution should also be exercised if using folklore remedies that include applying freezing agents, solvents or volatile fluids to the backs of ticks as they may release potentially toxic compounds when dying. Bite sites should be treated with disinfectants and symptomatic relief may be provided using analgesics, antipuritics, antihistamines or even antibiotics to forestall secondary bacterial infections. Infestations on livestock and companion animals are more usually treated using chemical acaricides applied as topical or systemic sprays/showers, dips/baths, dusts, emulsions, pour-ons, spot-ons, collars, eartags, tailtags, drenches, tablets or injections. Successful treatments have been reported using arsenical preparations, organochlorines (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (coumaphos, malathion, chlorpyrifos, fenthion, dichlorvos, diazinon, phosmet, chlorfenvinphos, dioxathion, fenchlorvos, trichlorfon), carbamates (carbaryl), pyrethroids (permethrin, flumethrin, deltamethrin, decamethrin, cypermethrin, cyprothrin), formamidines (amitraz), macrocyclic lactones (ivermectin, selamectin), phenylpyrazoles (fipronil), chloronicotinyls (imidacloprid), isoxazolines (afoxolaner, fluralaner), some natural products (rotenone) and insect growth regulators (methoprene, pyriproxyfen). Animals may require periodic treatments as they may become re-infested, although the use of slow-release formulations or those with long residual activities reduces treatment frequency. Unfortunately, tick populations have developed resistance to many acaricides, including organochlorines, organophosphates and some pyrethroids and formamidines. Recommendations to combat the development of resistance include avoiding under-dosing, periodic cycling between major acaricide classes, and testing for resistance (by *in situ* or *in vitro* egg hatch, larval development or adult survival assays). A range of preventive measures may be used to minimize transmission cycles through strategic health management (screening, quarantine, treatment, culling), grazing management (pasture rotation, spelling, cultivation, avoiding overstocking), environmental management (clearing vegetation, cleaning holding facilities, treating with residual acaricides) and wildlife control (vermin control through hunting or trapping, excluding wildlife using barriers, diverting migration routes, treating using medicated supplementary feeds or installing self-medicating devices such as rollers and rubbing posts). People at risk should improve their personal protection by wearing better clothing (boots, socks, trousers with gathered cuffs, long-sleeved shirts), applying repellents to skin or clothing (such as diethyltoluamide (DEET), permethrin, picaridin, oil of eucalyptus), or by avoiding tick-infested grassy habitats. Preliminary vaccination studies using *H. anatolicum* gut antigens have demonstrated some success in protecting cattle against subsequent tick challenge.


Hyalomma
Hosts
(mammals,
birds,
reptiles)
engorged female
(dorsal) (~ 15 mm)
skin
(blood loss,
lesions,
toxicosis)
(vectors for
infectious
microbial
diseases)
adult female
(dorsal) (~ 4 mm)
eggs laid
in soil/litter
eggs
(~ 0.5 mm)
hatch
nymph
(dorsal)
(~ 2 mm)
larva
(ventral)
(~ 1 mm)
some quest,
most actively
seek hosts
all motile stages
(i.e. larvae (L), nymphs (N)
and adults (A)) are transient
ectoparasites on vertebrates
(feed on blood)
1
2
3
most Hyalomma spp. have 2-host cycles,
some have 3-host cycles, but
a few have 1-host cycles
1-host cycle (LNA on same host)
2-host cycle (L-NA on successive hosts)
3-host cycle (L-N-A on separate hosts)

Hyalomma


dorsal
dorsal
male (~ 3 mm)
adult ticks
female (~ 3 mm)
ventral
ventral



Hyalomma adult

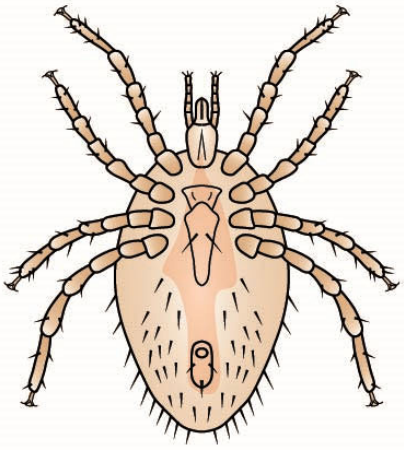


Hyalomma larva

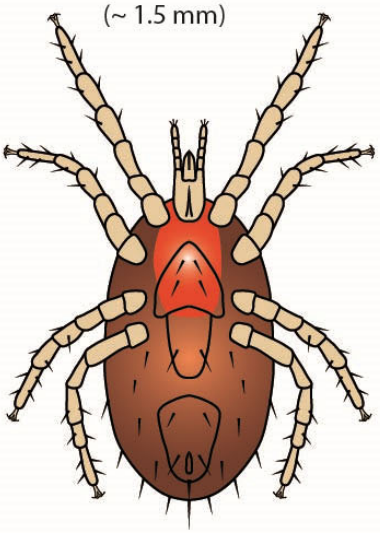
Mesostigmata
(mites)

Acari: Mesostigmata

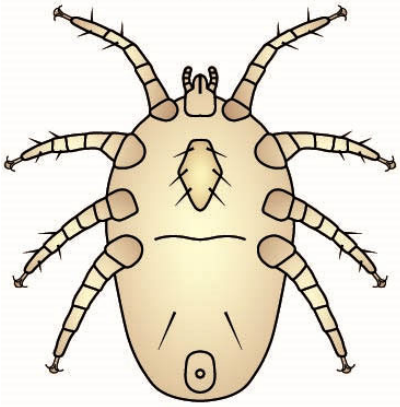
Ornithonyssus
adult female (ventral)
(~ 1 mm)



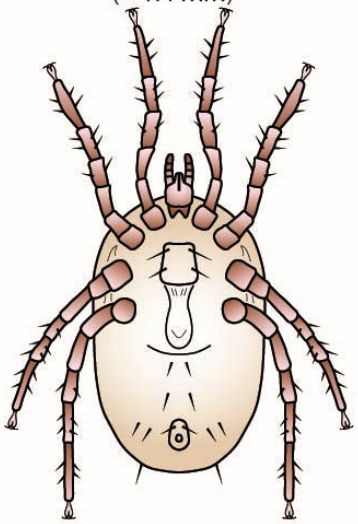
Dermanyssus
adult female (ventral)
(~ 1.5 mm)



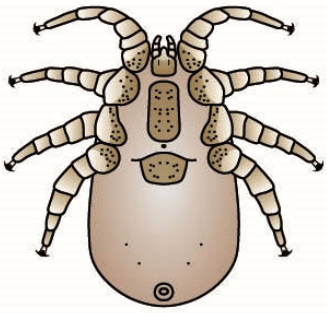
Pneumonyssus
adult female (ventral)
(~ 1.3 mm)



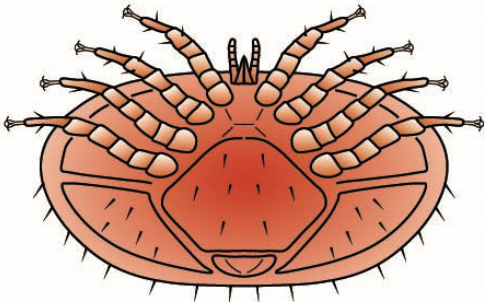
Raillietia
adult female (ventral)
(~ 1.4 mm)



Sternostoma
adult female (ventral)
(~ 0.7 mm)



Varroa
adult female (ventral)
(~ 1.5 mm)



Ornithonyssus
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Gamesid mites have anterior legs with respiratory stigmata located between the second and fourth legs. Most species are predatory, but some are ectoparasitic on mammals, birds and insects. They usually have a large sclerotized dorsal shield and a series of smaller ventral shields. Macronyssid mites are large blood-sucking ectoparasites with long legs, but only the protonymphs and adults feed. Infestations by *Ornithonyssus* spp. may cause scabbing and anaemia in domestic poultry and dermatitis in rodents.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Mesostigmata (gamesid mites, legs grouped anteriorly, stigmata between second and fourth legs)
Suborder: Dermanyssina (sclerotized shields, reduced setae, legs with claws)
Superfamily: Dermanyssoidea (elongate edentate chelicerae, diverse life-styles)
Family: Macronyssidae (blood-sucking ectoparasites, only protonymph and adults feed, relatively long legs)
Genus: *Ornithonyssus* (parasitic on skin/feathers of birds)
Species: various species cause dermatitis and anaemia in poultry and rodents

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma (capitulum). Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					

Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs; and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Mesostigmatid mites are further characterized by possessing unbarbed hypostomes, and long legs with free coxae (not fused to the body wall). The order Mesostigmata contains thousands of mites, with over 5,000 species recognized in 660 genera and 100 families. Nine suborders are recognized (Antennophoria, Arctacarina, Cercomegistina, Dermanyssina, Epicriina, Microgyniina, Parasitina, Sejina, and Uropodina). The suborder Dermanyssina contains robust mites with distinct sclerotized dorsal and ventral shields, reduced setae, palps with 2-tined apoteles, and legs with tarsal claws. Five superfamilies are recognized (Ascoidea, Dermanyssoidea, Eviphidoidea, Rhodacaroidea, and Veigaioidea). The superfamily Dermanyssoidea contains a diverse array of mites including free-living predators, nidicoles in the nests of vertebrates and insects, obligate and facultative ectoparasites of vertebrates and arthropods, and even respiratory and auditory endoparasites of mammals, birds, and some reptiles. The mites have elongated chelicerae (long first or second segment) with small edentate digits and concave interior margins (functioning as a tube when in opposition). A total of 11 families are recognized (Dermanyssidae, Haemogamasidae, Halarachnidae, Hirstionyssidae, Ixodorhynchidae, Laelapidae, Macronyssidae, Raillietiidae, Rhinonyssidae, Spinturnicidae, and Varroidae), many of them exclusively parasitic.

The family Macronyssidae contains blood-sucking mites that are parasitic as later-stage nymphs and adults on vertebrates, mostly bats and rodents, and a few genera infesting birds or reptiles. They are often nidicolous and leave their hosts to lay eggs around dens, burrows and nests. The mites are comparatively large and long-legged, with a pronounced ridge or spur on the palpal trochanter. Some 34 genera are recognized, with 8 placed in the subfamily Liponyssinae (*Bdellonyssus, Chiroptonyssus, Hirstesia, Kolenationyssus, Liponyssus, Neoichoronyssus, Neoliponyssus, Radfordiella*), 4 in the subfamily Ornithonyssinae (*Ophionyssus*, *Ornithonyssus*, *Pellonyssus*, *Steatonyssus*), 2 in the subfamily Macronyssinae (*Macronyssus, Macronyssoides*) and 20 genera unplaced (*Acanthonyssus, Arachnyssus, Argitis, Chiroecetes, Coprolactistus, Cryptonyssus, Draconyssus, Endophionyssuus, Glauconyssus, Lagidonyssus*, *Lepidodorsum, Lepronyssoides, Mitonyssoides, Mitonyssus, Nycteronyssus, Oudemansiella, Parichoronyssus, Synasponyssus, Thigmonyssus, Trichonyssus*). The genus *Ornithonyssus* is characterized by adult mites with large dorsal plates with pointed posterior margins but not nearly covering the body, well-defined narrowing genital plates (like *Dermanyssus*), oval anal plates (more elongate in *Dermanyssus*), long legs grouped anteriorly and ending in paired claws with a pulvillus, and short stout chelicerae (not long whip-like in *Dermanyssus*) with toothless blade-like chelae at their tips. The genus contains over 30 species that infest the plumage of birds or the pelage of small mammals (especially rodents and bats). Several species, esp. *O. sylviarum* (northern fowl mite) and *O. bursa* (tropical fowl mite), feed on chickens and other caged and wild birds (opportunistically feeding on mammals, including humans) and some, notably *O. bacoti* (tropical rat mite) infests a wide range of rodents and other mammals throughout temperate regions of the world, sometimes associated with anaemia, pruritus and alopecia.

***Ornithonyssus* species**	**Hosts**	**Clinical signs**	**Distribution**
O. acrobates	Diprotodontia: acrobatid (feathertail glider)		Australia
O. africanus	Chiroptera: rhinolophid (Geoffroy's horseshoe bat)		Africa
O. aridus	Rodentia: sciurid (white-tailed antelope squirrel)		North America
O. bacoti (syn. *Leiognathus, Liponyssus, Macronyssus, Haemogamasus sanguineus*) (tropical rat mite)	Rodentia: murid (black rat, brown rat, African grass rat, house mouse, typical striped grass mouse, four-striped grass mouse, Dalton's mouse, Natal multimammate mouse, Indian gerbil, great gerbil, Persian jird), cricetid (cotton mouse, golden mouse, northern pygmy mouse, northern grasshopper mouse, brush mouse, canyon mouse, cactus mouse, white-footed mouse, white-ankled mouse, Pinyon mouse, Florida mouse, Oldfield mouse, deer mouse, eastern meadow vole, eastern wood rat, southern plains wood rat, hispid cotton rat, marsh rice rat), nesomyid (African tree mouse, gerbil mouse, Mexican spiny pocket mouse), heteromyid (Ord's kangaroo rat, hispid pocket mouse, Great Basin pocket mouse), sciurid (least chipmunk, eastern grey squirrel, Mexican ground squirrel, Townsend's ground squirrel), zapodid (Preble's meadow jumping mouse); Eulipotyphla: soricid (greater red musk shrew, swamp musk shrew, African giant shrew); Didelphimorphia: didelphid (Virginia opossum); Lagomorpha: leporid (eastern cottontail, marsh rabbit); Carnivora: canid (gray fox), herpestid (Cape gray mongoose), mephitid (striped skunk, eastern spotted skunk), procyonid (raccoon); Primates: hominid (human)	irritation, dermatitis, anaemia	worldwide
O. benoiti	Rodentia: anomalurid (pygmy scaly-tailed flying squirrel)		Africa
O. brasiliensis (syn. *Liponyssus, Bdellonyssus*)	Rodentia: caviid (Brazilian guinea pig), cricetid (marsh rat, Amazonian marsh rat, scaly-footed water rat, hispid hocicudo, blackish grass mouse), echimyid (Fischer's guiara); Didelphimorphia: didelphid (big-eared opossum, Brazilian gracile opossum); Lagomorpha: leporid (common tapeti); Carnivora: mustelid (greater grison); Primates: hominid (human)		South America
O. bursa (syn. *Liponyssus, Leiognathus*) (tropical fowl mite, bird mite, starling mite)	Galliformes: phasianid (chicken, turkey), Anseriformes: anatid (duck); Columbiformes: columbid (pigeon); Coliiformes: coliid (white-backed mousebird); Passeriformes: malaconitid (crimson-breasted shrike, bokmakierie), passerid (sparrow), sturnid (common starling, red-winged starling, mynah); Accipitriformes: accipitrid (Eurasian sparrowhawk, besra, swallow-tailed kite, Australian black-shouldered kite, small kite), cathartid (turkey vulture); Falconiformes: falconid (Australian kestrel); Strigiformes: strigid (Indian scops-owl, barn owl); Rodentia: cricetid (white-footed mouse, eastern meadow vole)	irritation, matting, scabbing, anaemia (plus vectors for fowlpox, Newcastle disease, chlamydiosis)	India, China, Africa, Australia, Americas
O. campester	Chiroptera: emballanurid (common sheath-tail bat),		Australia

	vespertilionid (hoary wattled bat, yellow-lipped bat)		
O. capensis	Macroscelidia: macroscelidid (eastern rock elephant shrew)		Africa
O. coendou	Rodentia: erethizonitid (Andean porcupine)		South America
O. conciliatus	Chiroptera: phyllostomid (flat-faced fruit-eating bat)		Central America
O. cornutus	Chiroptera: molossid (Egyptian free-tailed bat)		Egypt
O. costai	Rodentia: spalacid (Middle-East blind mole-rat)		Israel
O. dasyuri	Dasyuromorphia: dasyurid (eastern quoll)		Australia
O. desultorius (syn. *Cryptonyssus*)	Chiroptera: vespertilionid (big brown bat, cave myotis, California myotis, canyon bat)		North America
O. flexus	Chiroptera: vespertilionid (little brown bat)		North America
O. galagus	Rodentia: glirid (woodland dormouse); Primates: galagid (Senegal bush baby)		Africa
O. garridoi	Rodentia: echimyid (prehensile-tailed hutia)		Cuba
O. hoogstraali	Chiroptera: molossid (European free-tailed bat)		Egypt
O. hypertrichus	Rodentia: cricetid (cactus mouse, white-ankled mouse, Pinyon mouse)		North America
O. iheringi	Accipitriformes: accipitrid (sharp-shinned hawk); Cingulata: chlamyphorid (dwarf armadillo), dasypodid (armadillo)		Europe, South America
O. latro	Chiroptera: vespertilionid (eastern forest bat)		Australia
O. longisetosus	Didelphimorphia: didelphid (Linnaeus's mouse opossum)		South America
O. lukoschusi	Rodentia: glirid (woodland dormouse)		Africa
O. matogrosso (syn. *Neoichoronyssus, Hirstionyssus, Lepronyssoides*)	Rodentia: echimyid (punare)		South America
O. monteiroi (syn. *Liponyssus, Bdellonyssus, O. lutzi*)	Rodentia: cricetid (cursor grass mouse, hairy-tailed bolo mouse, terraced rice rat, yellowish rice rat, scaly-footed water rat, Robert's hocicudo), caviid (guinea pig, Brazilian guinea pig), echimyid (Fischer's guiara, Pacific spiny rat), murid (black rat, brown rat)		South America
O. nitedulae	Rodentia: glirid (forest dormouse)		Israel
O. noeli	Rodentia: echimyid (hutia)		Cuba
O. nyctinomi	Chiroptera: molossid (free-tailed bat)		Africa
O. parvus	Rodentia: hystricid (Philippine porcupine)		Philippines
O. pavlovskii	Rodentia: glirid (hazel dormouse)		Romania
O. petauri	Diprotodontia: petuarid (sugar glider)		Australia
O. pereirai (syn. *Liponyssus, Lepronyssoises*)	Rodentia: caviid (rock cavy, Spix's yellow-toothed cavy), cricetid (hairy-tailed bolo mouse, Atlantic forest climbing mouse, terraced rice rat, angular hocicudo), echimyid (highlands punare), murid (black rat); Didelphimorphia: didelphid (gray short-tailed opossum)		South America
O. pipistrelli (now *Cryptonyssus*)	Chiroptera: vespertilionid (pond bat)		Russia
O. praedo	Rodentia: murid (fawn-footed mosaic-tailed rat)		Australia
O. roseinnesi	Rodentia: murid (Namaqua rock rat, four-striped grass mouse)		Africa
O. simulatus	Afrosoricida: tenerecid (least shrew tenrec)		Madagascar
O. spinosa	Chiroptera: vespertilionid (New Zealand long-tailed bat)		New Zealand
O. steidii	Rodentia: spalacid (lesser mole-rat)		Bulgaria
O. stigmaticus	Chiroptera: emballonurid (yellow-bellied sheath-tailed bat)		Australia
O. sylviarum (syn. *Liponyssus americanus, pacificus, 0. banksi*) (northern fowl mite)	Galliformes: phasianid (chicken, turkey); Passeriformes: cisticolid (Karoo prinia), fringillid (canary), motacillid (white wagtail), muscicapid (ant-eating chat), pycnonotid (common bulbul); Accipitriformes: accipitrid (northern goshawk); Falconiformes: falconid (Australian kestrel); Strigiformes: strigid (barn owl); Rodentia: heteromyid (Mexican spiny pocket mouse), murid (house mouse, black rat), sciurid (yellow-bellied marmot, alpine chipmunk); Lagomorpha: leporid (mountain cottontail); Chiroptera: vespertilionid (big brown bat, cave myotis); Primates: hominid (human)	irritation, matting, scabbing, anaemia (plus vectors for fowlpox, Newcastle disease, chlamydiosis, St Louis encephalitis, western equine	temperate zones

		encephalomyelitis)	
O. taphozous	Chiroptera: emballonurid (common sheath-tailed bat)		Australia
O. vitzthumi (syn. *Liponyssus, Bdellonyssus*)	Rodentia: cricetid (montane grass mouse, gray leaf-eared mouse, vesper mouse, hairy-tailed bolo mouse, black-footed pygmy rice rat, hispid hocicudo, long-nosed hocicudo), caviid (common yellow-toothed cavy), echimyid (Fischer's guiara), sciurid (Bolivian squirrel)		South America
O. wernecki (syn. *Liponyssus, Neoichoronyssus*)	Rodentia: murid (brown rat), cricetid (hispid cotton rat); Didelphimorphia: didelphid (white-eared opossum, big-eared opossum, Virginia opossum)		South America

Parasite morphology: *Ornithonyssus* spp. form 4 different types of morphological developmental stages; namely, eggs, larvae (one instar), nymphs (2 instars), and adults (both males and females). Eggs are sticky white ovoid-ellipsoidal stages measuring 0.2-0.3 mm in length. Larvae have ovate flattened bodies measuring 0.2-0.3 mm long, each with 3 pairs of anteroventral legs and a small anterior gnathosoma (head or capitulum). They are grey-white in colour and have little to no sclerotization and no external genitalia. Nymphs have larger longer bodies that are more ellipsoidal in shape measuring up to 0.3-0.4 mm in length. They have 4 pairs of long tapering legs which appear to be arranged in 2 sets, the first 2 pairs directed anteriorly and the hind 2 pairs directed posteriorly. There are 2 nymphal instars (the first known as protonymphs, the second as deutonymphs) which exhibit progressive differentiation of sclerotized shields with each moult. Nymphs do not have genital openings but they possess small epigynal shields. The anterior gnathosoma bears conspicuous mouthparts flanked by long sensory palps. Adult mites have ellipsoidal bodies which are flattened ventrally and slightly convex dorsally. They usually range in length from 0.5-1.0 mm, although mature specimens of some species may be as large as 2 mm long. They are opaque grey-white but become reddish-brown to black when engorged on host blood. They have 2 distinct tagma, a small anterior gnathosoma and the larger posterior idiosoma (body). The gnathosoma in these sucking mites bears long stylet-like mouthparts (not claw-like mouthparts like burrowing mites) that project forwards when fully extended but are retracted when not in use. The mouthparts (chelicerae and hypostome) are flanked by a pair of sensory palps, each composed of 5-6 segments and terminating in a 2-tined claw (apotele). Like other mesostigmatid mites, the basal segments of the palps are fused to form a basis capitulum which encloses the chelicera and give rise to the hypostome. The chelicerae are elongate and have 3 segments, the first segment being the longest in macronyssids (while the second segment is the longest in dermanyssids). The third segment terminates in stylet-like chelae (pincers) with distinct fixed and movable digits without excrescences (cf. dermanyssid chelicerae are whip-like with highly reduced chelae). The oral opening (mouth) comprises a dorsal rostrum, ventral buccal cone and an unbarbed hypostome (barbed in ticks). The alimentary tract consists of a tubular foregut (pharynx and oesophagus connected to salivary glands), a saccular midgut (branched ventriculus with gastric caeca) and a short tubular hindgut (intestines with excretory Malpighian tubules connected to rectum and subterminal anus). The idiosoma narrows posteriorly (slightly in *O. bursa*, considerably in *O. sylviarum*) and is setate (more than *Dermanyssus*) with many long setae. Species are often differentiated by their distinctive chaetotaxy (number, position and size of setae). During feeding, the idiosoma does not usually expand (whereas it does in ticks). Adult mites possess a sclerotized dorsal shield and 3 ventral shields (sternal, genitoventral and anal). The dorsal shield is oval-pyriform and occupies less than a third of the dorsal surface and is distinctly pointed posteriorly (whereas that of *Dermanyssus* is larger, smoothly tapered and posteriorly truncated). The shield surface is reticulated (not striated) and bears several long setae. The sternal shield may be entire or eroded, with 1-3 pairs setae (females typically with 2 pairs). The genitoventral shield may be tongue- or knife-shaped with 0-1 pairs of setae (while that of *Dermanyssus* is posteriorly rounded and bears one pair of setae). The anus is located in the anterior half of the anal shield which may be oval to elongate (longer than *Dermanyssus*) and bears 3 circum-anal setae. The ventral idiosoma gives rise to 4 pairs of long powerful legs arranged in 2 anteroventral sets (like nymphs) but with different pairs arising from the sternal plate (first 2 pairs for *O. sylviarum,* first 3 pairs for *O. bursa*). The first pair of legs (forelegs) are generally longer and slenderer than the others. Each leg is jointed with 6 main segments (coxa, trochanter, femur, genu, tibia and tarsus), although the tarsus has a stalked pretarsus with an expanded pretarsal apparatus (ambulacrum) bearing paired claws and an empodium (pad-like pulvillus). Like all Mesostigmata, the coxae are not fused to the ventral body and the respiratory openings (stigmata) are located posteriorly between the second and fourth legs, often with elongated processes (peritremes). Adult mites exhibit moderate sexual dimorphism, with males being slightly smaller in body size and having a holoventral shield (fusion of sternal and genitoventral shields). They have 2 testes with tubular vas deferens connected to the ejaculatory duct and long sheathed chitinous aedeagus (penis). The genital opening (gonopore) is located on the ventral midbody between the last 2 pairs of legs, and mating involves direct transfer of sperm to the female via copulation. Females have 2 ovaries (with ovarioles) connected by tubular oviducts to the uterus (with a muscular shell-gland) and vagina (with accessory organs for sperm storage (known as the bursa copulatrix, or spermathecae)). The gonopore is located on the ventral midbody and has an epigynal shield with a narrowly rounded posterior.

Site of infection: *Ornithonyssus* spp. are non-burrowing ectoparasites of vertebrate hosts (mammals and birds). While all developmental stages occur amongst the pelage/plumage of their hosts, only the protonymph and adult stages feed by sucking host blood. Many *Ornithonyssus* spp. are uncommon and have only been reported on a few host species, whereas a few species are much more common and have broader host ranges being found on a variety of mammals and birds. In total, 41 *Ornithonyssus* spp. have been recorded on mammals belonging to 35 families in 12 orders (mostly rodents, but also bats, insectivores, carnivores,

lagomorphs and primates, incl. humans). Three species (*O. bursa, O. sylviarum* and *O. iheringi*) have been recorded a few mammals, but mostly on birds belonging to 8 passerine families and 8 non-passerine families in 7 orders (waterfowl, landfowl, pigeons, mousebirds and birds of prey). While infestations may occur over the whole body of their hosts, feeding stages are regularly found on the head, neck, chest, abdomen and extremities of mammals, and near the bases of feathers of birds, particularly around the vent and along the back.

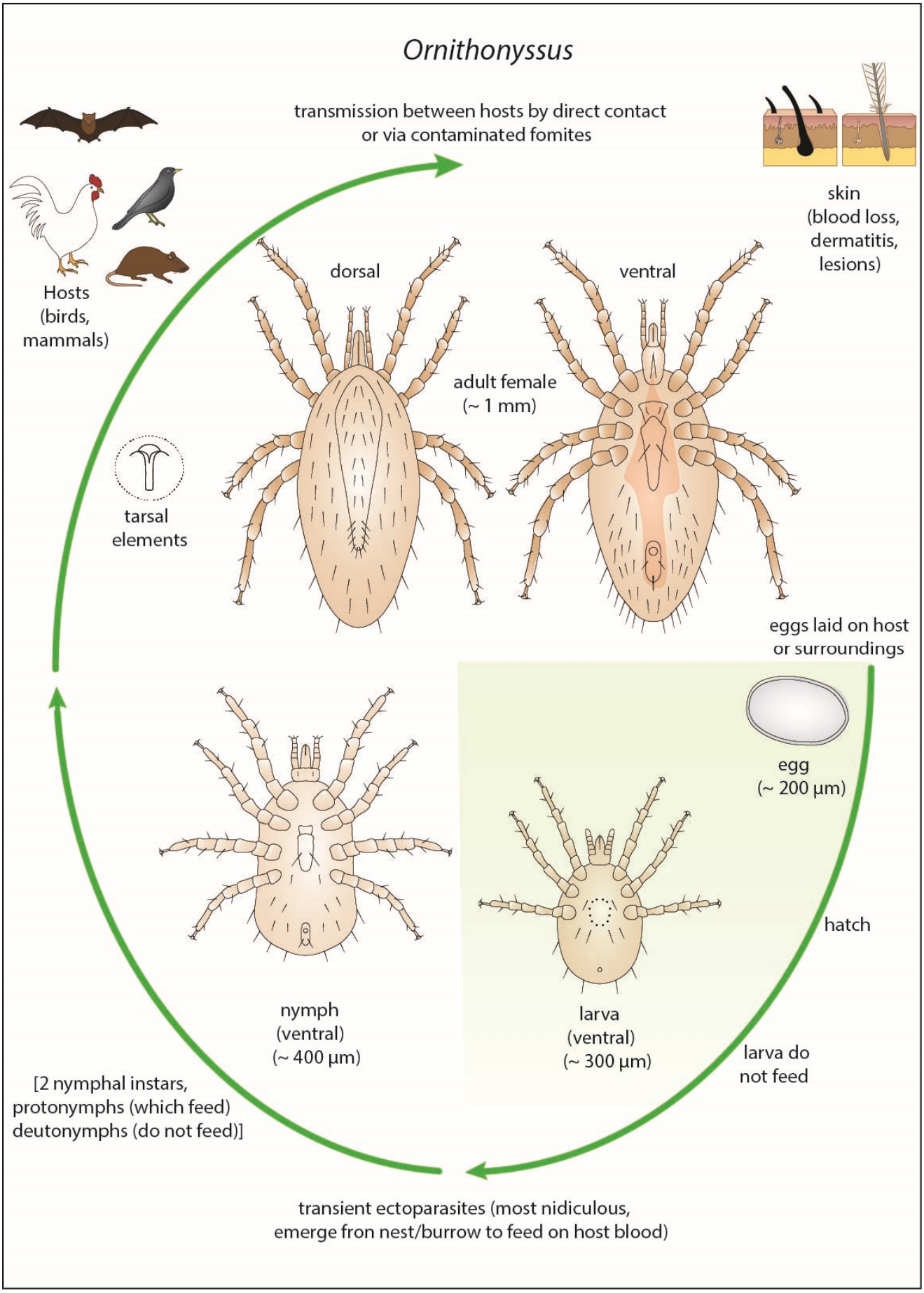
Pathogenesis: Mite infestations may cause a disease condition known as acariasis, with non-burrowing surface mites typically causing skin lesions at feeding sites, blood loss and poor condition (whereas burrowing mites may cause severe dermatitis or mange). Protonymphs and adults of *Ornithonyssus* spp. use their long piercing-sucking mouthparts to penetrate the skin and take rapid meals from underlying blood vessels. Several species cause inflammation and anaemia in poultry and rodents, some even biting humans causing small irritating skin lesions and sometimes allergic reactions with intense skin inflammation. Heavy infestations may cause significant blood loss resulting in anaemia and even death due to exsanguination, particularly in poultry (in extreme infestations, mites have been reported to take up to 6% of the blood volume daily in chickens). Mite bites cause traumatic damage to the skin with irritation, inflammation (erythema, oedema), pruritus, papule formation, rough scaly skin with hair/feather loss, crusting and scabbing, particularly around the vent of birds. Surrounding feathers often develop a dirty matted grey-black appearance due to accumulations of debris consisting of mites, mite faeces, mite eggs, mite exuvia (cast skins), dried blood and scabs. Infested animals exhibit biting stress with restlessness, depressed appetites, weakness, debility and exaggerated grooming behaviours (preening, biting, scratching and rubbing). The species *O. bursa* (tropical fowl mite) and *O. sylvarium* (northern fowl mite) are notorious pests of poultry with significant production losses due to reduced meat and egg production. Infestations are worse in egg layer and breeder operations where birds are maintained for longer periods. Mite populations are also higher on birds that have had their beaks trimmed as they are less able to self-groom. The species *O. bacoti* (tropical rat mite) is recognized as a serious pest in laboratory rodent colonies with heavy infestations causing morbidity (anaemia, pruritic papular dermatitis, soiled fur, alopecia) and occasional deaths. Infestations of humans are usually incidental to handling infested animals or having starving mites from recently-vacated nests or burrows invade households seeking hosts. There is growing evidence that animals may develop an age-related acquired immunity as mite populations decline in adulthood although low numbers may persist for life. Studies have indicated that chronic infestations result in thickened hardened skin due to host immune responses making it more difficult for mites to feed with their small mouthparts. Mites have also been shown to act as vectors for the transmission of various infectious diseases, including bacteria causing chlamydiosis, and viruses causing fowl-pox, Newcastle disease, St Louis encephalitis, western equine encephalomyelitis and Korean (epidemic) haemorrhagic fever. Experimental studies have also confirmed that mites may carry rickettsial bacteria associated with murine typhus and rickettsial pox, coccobacilli associated with plague and tularaemia, and viruses associated with Coxsackie diseases, but their roles in disease transmission are unclear.

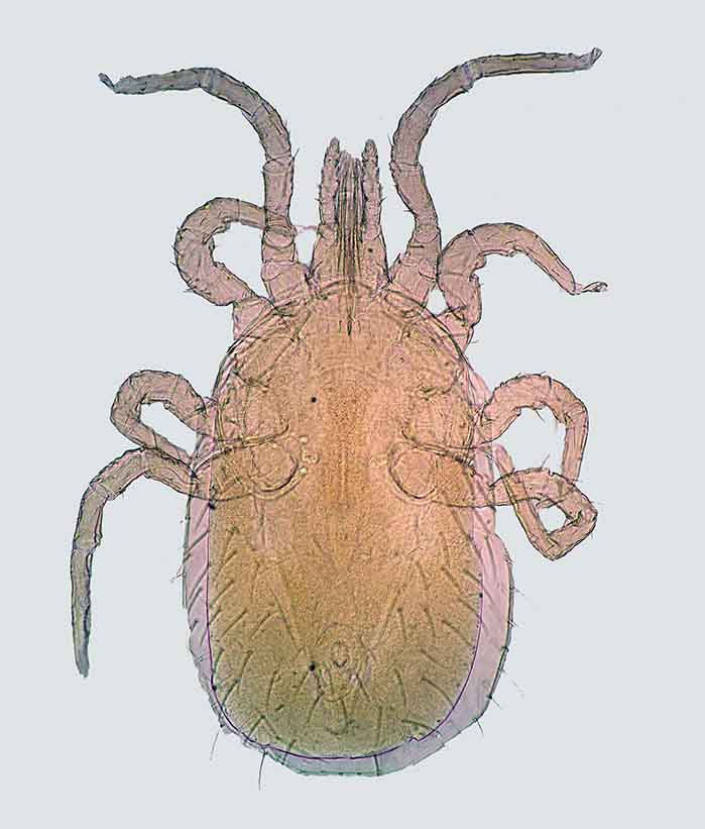
Developmental cycle and mode of transmission: Like all mites, *Ornithonyssus* spp. undergo hemimetabolous (incomplete) metamorphosis where eggs hatch larvae which moult to nymphs and then adults. Transmission between hosts is by direct contact or via fomites as mites spend most of the time on hosts or in their homes (nests/burrows). Gravid females lay eggs either on their hosts around the bases of feathers (e.g. *O. sylvarium*) or off hosts in litter in nests/burrows (e.g. *O. bursa, O. bacoti*). The eggs do not survive for longer than 10 days and usually hatch within 1-3 days releasing 6-legged larvae. The larvae do not feed and rapidly moult to the first nymphal instar (protonymph) in about 8 hours. The protonymphs move to feeding sites on suitable hosts and feed intermittently on host blood for 4-7 days before moulting to the second nymphal instar (deutonymphs, some texts erroneously calling them tritonymphs). The deutonymphs do not feed on host blood (whereas those of dermanyssids do) and they moult in about 5 days to become adult mites. Adults feed rapidly and intermittently on host blood and usually leave the leave the host after each bloodmeal to rest and reproduce in the surrounding environment, particularly nests/burrows (nidicolous behaviour). They are active mites with powerful legs and can crawl several hundred metres to locate hosts. Adults usually survive for 1-4 weeks off hosts, sometimes up to 120 days under favourable conditions. Female mites may live for up to 70 days, feeding every 2-3 days either diurnally (e.g. *O. bursa*) or nocturnally (e.g. *O. sylvarium*). They lay small numbers of eggs (1-5) after each bloodmeal, totalling up to 100 eggs over their life-spans. The whole life-cycle may be completed in as little as 5-16 days, so mite populations can quickly escalate (up to 20,000 mites per host in 9-10 weeks). Infestations are more common when food sources are regularly available (e.g. gregarious hosts, crowded farmed animals, nestling birds) and when warm moist environmental conditions prevail (e.g. in subtropical regions, or during spring in temperate regions).

Differential diagnosis: Infestations may be suspected on clinical grounds (skin lesions, anaemia, poor condition, dirty plumage/coat) but other aetiological agents must be considered. Diagnoses are generally made by direct detection of mites on the hosts, often visible due to their contrasting colour following feeding. Mites are usually present on birds during the daylight (unlike *Dermanyssus*), particularly around the bases of feathers and the cloaca, sometimes adhering to recently laid eggs. Skin scrapings may be collected for microscopic examination after caustic digestion (usually 10% potassium hydroxide), but test sensitivity is low especially in light or transient infestations of those involving cryptic species. Alternatively, mites may be collected by plucking, combing or brushing hairs/feathers, by applying adhesive tape to the skin, by massaging live animals over blank paper, or by washing dead animals in plastic bags. Any specimens collected should be examined microscopically and identified on the basis of their morphological characteristics. Molecular biological techniques have been used to characterize species following the

polymerase chain reaction (PCR) amplification of nuclear (18S and 28S ribosomal RNA) and mitochondrial (16S ribosomal RNA)gene sequences.

Treatment and control: Clinical infestations are treated by the application of chemical acaricides, including sulphur dusts, organochlorines (dichloro-diphenyl-trichloroethane (DDT), lindane), organophosphates (tetrachlorvinphos, dichlorvos, malathion), pyrethrin and synthetic pyrethroids (permethrin), carbamates (carbaryl), macrocyclic lactones (ivermectin, selamectin), arylpyrazole (fipronil), isoxazolines (fluralaner), spinosyns (spinosad), some natural products (rotenone) and even some essential oils (thyme, hemp, ajowan, garlic). Treatments may be applied topically as sprays, baths, dusts, or emulsions, or systemically as spot-ons, pour-ons, oral drenches or in-water medications. The strategic and regular treatment of closed animal populations can reduce or eliminate infestations, but there is growing concern about the development of acaricide resistance in some mite populations, particularly to organochlorines and some organophosphates and macrocyclic lactones. Some success has been reported in reducing mite populations in poultry by providing dust-baths (diatomaceous earth, kaolin clay) which acts to desiccate mites on contact. Incidental infestations in humans also benefit greatly by the provision of symptomatic relief in the form of antipuritics and anti-inflammatories (corticosteroids and antihistamines). Various preventive strategies may be adopted to help break transmission cycles through improved health management (regular screening, treatment, quarantine, culling), sensible animal husbandry (avoid over-crowding, separate cohorts, cease beak trimming to allow self-grooming), environmental decontamination (proper sanitation of fomites, frequent removal or litter and/or treatment with residual acaricides (e.g. pyrethroids), cleaning and disinfection of equipment and roosts, leaving bird houses empty for at least 4 weeks in hot weather or 8 weeks in cooler weather, removing bird nests in roofs and eaves) and wildlife management (exclude wild animals using barriers, trapping or hunting, routine vermin control). Preliminary studies on biological control have shown that the topical application of entomopathogenic fungi (*Beauveria*) reduced mite numbers on infested birds. Vaccination options should also be explored as animals have been shown to develop an immune-mediated resistance with age following persistent natural exposure. Studies on poultry have also indicated that mite resistance may be a heritable trait that could be incorporated into selective breeding programs.


Ornithonyssus
transmission between hosts by direct contact
or via contaminated fomites
skin
(blood loss,
dermatitis,
lesions)
Hosts
(birds,
mammals)
dorsal
ventral
adult female
(~ 1 mm)
tarsal
elements
eggs laid on host
or surroundings
egg
(~ 200 µm)
hatch
nymph
(ventral)
(~ 400 µm)
larva
(ventral)
(~ 300 µm)
larva do
not feed
[2 nymphal instars,
protonymphs (which feed)
deutonymphs (do not feed)]
transient ectoparasites (most nidiculous,
emerge fron nest/burrow to feed on host blood)



Ornithonyssus adult



Ornithonyssus eggs

Dermanyssus
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma (capitulum). Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Gamesid mites have anterior legs with respiratory stigmata located between the second and fourth legs. Most species are predatory, but some are ectoparasitic on mammals, birds and insects. They usually have a large sclerotized dorsal shield and a series of smaller ventral shields. Dermanyssid mites are large blood-feeding ectoparasites with greyish-white bodies becoming red when engorged. Infestations by *Dermanyssus* spp. may cause irritation and anaemia in domestic poultry, and mites may also bite mammals (including humans) in proximity to infested sheds.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Mesostigmata (gamesid mites, legs grouped anteriorly, stigmata between second and fourth legs)
Suborder: Dermanyssina (sclerotized shields, reduced setae, legs with claws)
Superfamily: Dermanyssoidea (elongate edentate chelicerae, diverse life-styles)
Family: Dermanyssidae (blood-feeding ectoparasites, greyish-white bodies becoming red when engorged)
Genus: *Dermanyssus* (parasitic on skin/feathers of mammals/birds)
Species: various species cause irritation and anaemia in poultry

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					

Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs; and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Mesostigmatid mites are further characterized by possessing unbarbed hypostomes, and long legs with free coxae (not fused to the body wall). The order Mesostigmata contains thousands of mites, with over 5,000 species recognized in 660 genera and 100 families. Nine suborders are recognized (Antennophoria, Arctacarina, Cercomegistina, Dermanyssina, Epicriina, Microgyniina, Parasitina, Sejina, and Uropodina). The suborder Dermanyssina contains robust mites with distinct sclerotized dorsal and ventral shields, reduced setae, palps with 2-tined apoteles, and legs with tarsal claws. Five superfamilies are recognized (Ascoidea, Dermanyssoidea, Eviphidoidea, Rhodacaroidea, and Veigaioidea). The superfamily Dermanyssoidea contains a diverse array of mites including free-living predators, nidicoles in the nests of vertebrates and insects, obligate and facultative ectoparasites of vertebrates and arthropods, and even respiratory and auditory endoparasites of mammals, birds, and some reptiles. The mites have elongated chelicerae (long first or second segment) with small edentate digits and concave interior margins (functioning as a tube when in opposition). A total of 11 families are recognized (Dermanyssidae, Haemogamasidae, Halarachnidae, Hirstionyssidae, Ixodorhynchidae, Laelapidae, Macronyssidae, Raillietiidae, Rhinonyssidae, Spinturnicidae, and Varroidae), many of them exclusively parasitic.

The family Dermanyssidae contains haematophagous mites that are ectoparasitic primarily on birds, although several species infest mammals. Mites are often nidicolous living in nesting materials and intermittently infesting hosts for blood meals. Dermanyssids have ovoid bodies (idiosoma) that are rounded posteriorly and they have elongated extrusible chelicerae with long second segments. Many species also exhibit neopodospermy (sperm transfer through accessory insemination pores located closer to legs) where the male chelicerae are broader and modified as gonopodes possessing enlarged chelae with long spermatodactyls (movable digits used for sperm transfer). Four genera are recognized on birds and rodents (*Dermanyssus, Draconyssus, Laelaspisella, Liponyssoides*). The genus *Dermanyssus* is characterized by adult mites with long dorsal shields, narrow sternal shields bearing 1-2 pairs of setae, well-defined genital shields (like *Ornithonyssus*), elongate anal shields (more oval in *Ornithonyssus*), and long whip-like chelicerae (not short and stout like *Ornithonyssus*) with tiny terminal chelae. Some 26 species are recognized mostly on avian hosts although many may opportunistically feed on mammals. Several species (especially *D. gallinae*) have been associated with significant economic losses on poultry farms due to lowered meat and egg production, as well as acting as vectors for the transmission of several viral and bacterial diseases.

***Dermanyssus* species**	**Hosts**	**Clinical signs**	**Distribution**
D. alaudae (syn. *D. truncatus*)	Passeriformes: alaudid (Eurasian skylark, woodlark)		Eurasia
D. americanus (syn. *D. oti*) (American bird mite)	Passeriformes: emberizid (meadow bunting), fringillid (canary, house finch), passerid (house sparrow, Eurasian tree sparrow), sittid (nuthatch); Accipitriformes: accipitrid (sharp-shinned hawk); Strigiformes: strigid (eastern screech owl, northern saw-whet owl, long-eared owl); Chiroptera: vespertilionid (canyon bat); Primates: hominid (human)	trauma, irritation	Americas
D. antillarum	Passeriformes: mimid (northern mockingbird), passerid (house sparrow); Accipitriformes: accipitrid (sharp-shinned hawk); Apodiformes: apodid (Antillean palm swift)		North America
D. apodis	Apodiformes: apodid (common swift, pallid swift)		Europe
D. brevirivulus	Passeriformes: alaudid (crested lark)		Eurasia
D. brevis	Passeriformes: alaudid (Eurasian skylark, horned lark)		Eurasia
D. carpathicus	Passeriformes: muscicapid (common redstart), parid (great tit)		Eurasia
D. chelidonis	Passeriformes: fringillid (European goldfinch), hirundinid (sand martin, common house martin, barn swallow, Eurasian crag martin), parid (Eurasian blue tit)		Eurasia, Africa, Americas
D. faralloni	Procellariiformes: hydrobatid (ashy storm petrel); Charadriiformes: alcid (pigeon guillemot, Cassin's auklet)		North America
D. gallinae (syn. *D avium, evotomydis, hominis*) (chicken mite, poultry mite, red mite, roost mite)	Galliformes: phasianid (chicken); Passeriformes: acrocephalid (great reed warbler), emberizid (yellowhammer), fringillid (canary, European goldfinch, Eurasian siskin), hirundinid (common house martin, sand martin, barn swallow), muscicapid (European robin, collared flycatcher, European pied flycatcher, common redstart), parid (great tit, coal tit), passerid (house sparrow, Eurasian tree sparrow), remizid (Eurasian penduline tit), sittid (Eurasian nuthatch), sturnid (common starling); Piciformes: picid (Eurasian wryneck); Columbiformes: columbid (pigeon, rock dove); Coraciiformes: meropid (European bee-eater); Psittaciformes: psittaculid (lovebird); Accipitriformes: accipitrid (white-backed vulture); Falconiformes: falconid (saker); Strigiformes: strigid (boreal owl); Rodentia: cricetid (northern grasshopper mouse, canyon mouse, southern red-backed vole, desert wood rat), murid (black rat); Lagomorpha: leporid (marsh rabbit); Carnivora: canid (dog), felid (cat); Perissodactyla: equid (horse); Chiroptera: vespertilionid (cave myotis, tricolored bat); Primates: hominid (human)	trauma, irritation, erythema, pruritus, anaemia (plus vectors for avian spirochaetosis)	worldwide
D. gallinoides	Piciformes: picid (pileated woodpecker, Lewis's woodpecker, downy woodpecker, red-shafted flicker, yellow-bellied sapsucker)		North America
D. grochovskae	Passeriformes: corvid (spotted nutcracker); Piciformes: picid (white-backed woodpecker, great spotted woodpecker, Japanese green woodpecker)		Palearctic
D. hirsutus (syn. *D. scutatus*)	Piciformes: picid (northern flicker)		North America
D. hirundinis	Accipitriformes: accipitrid (lesser spotted eagle); Anseriformes: anatid (tufted duck, common pochard, greylag goose);	trauma, irritation	North America

	Apodiformes: apodid (little swift, chimney swift); Columbiformes: columbid (rock dove); Coraciiformes: meropid (European bee-eater); Passeriformes: acrocephalid (great reed warbler, marsh warbler, Eurasian reed warbler), estrilidid (zebra finch), hirundinid (common house martin, sand martin, barn swallow, tree swallow, cliff swallow), laniid (lesser grey shrike, red-backed shrike), motacillid (tree pipit), muscicapid (collared flycatcher, common nightingale, black redstart), parid (Eurasian blue tit, great tit, marsh tit), passerid (house sparrow, Eurasian tree sparrow), remizid (Eurasian penduline tit), sittid (Eurasian nuthatch), sturnid (common starling), troglodytid (house wren, Eurasian wren), turdid (ring ouzel), vireonid (red-eyed vireo); Piciformes: picid (downy woodpecker); Strigiformes: strigid (tawny owl, long-eared owl); Primates: hominid (human)		
D. longipes	Passeriformes: passerid (house sparrow)		Europe
D. nipponensis	Piciformes: picid (Japanese green woodpecker)		Japan
D. passerinus	Passeriformes: emberizid (yellowhammer), muscicapid (collared flycatcher), parid (great tit), passerid (Italian sparrow), sturnid (common starling); Piciformes: picid (Eurasian wryneck)		Eurasia
D. prognephilus	Passeriformes: hirundinid (purple martin), icterid (brown-headed cowbird), muscicapid (eastern bluebird); Piciformes: picid (red-shafted flicker, downy woodpecker, red-headed woodpecker)		North America
D. quintus	Piciformes: picid (great spotted woodpecker, downy woodpecker, white-backed woodpecker, Eurasian three-toed woodpecker, European green woodpecker)		Eurasia
D. richiardii	Hymenoptera: apid (carpenter bee); Lepidoptera: cossid (goat moth)		Europe
D. rwandae	Apodiformes: apodid (little swift)		Europe
D. transvaalensis	Passeriformes: hirundinid (South African cliff swallow)		Africa
D. triscutatus	Passeriformes: hirundinid (cliff swallow)		Americas
D. trochilinis	Apodiformes: trochilid (hummingbird)		Americas
D. wutaiensis	Passeriformes: passerid (Eurasian tree sparrow)		Eurasia

A small range of other *Dermanyssus* spp. originally described from other vertebrate hosts have subsequently been re-assigned to other genera; including: *D. musculi, murinus = Steatonyssus; D. arcuatus, albatus, carnifex, coriaceus, lanius, noctulae, pipistrellae = Echinonyssus; D. natricis = Ophionyssus; D. flavus, glutinosus, granulosus = Macronyssus; D. ambulans = Haemogamasus; D. aegypticus, brasiliensis, intermedius, muris, sanguineus = Liponyssoides;* and *D. lacertarum = Neoliponyssus.*

Parasite morphology: Like all mites, *Dermanyssus* spp. form 4 different types of morphological stages during their development: namely, eggs, larvae (one instar), nymphs (2 instars) and adults (males and females). Eggs are small pearly-white ovoid stages measuring around 0.4 mm in length. Larvae are small white-tan stages measuring 0.4-0.6 mm in length. The have a small anterior gnathosoma (head or capitulum) earing small mouthparts and a larger ovate-discoidal idiosoma (body) with 3 pairs of long jointed legs arising from the anteroventral surface. Nymphs are larger in size and have 4 pairs of long legs and their mouthparts have long thin chelicerae with elongate second segments. Two nymphal instars are formed, the first (protonymphs) having tan ovate bodies measuring 0.5-0.8 mm long, and the second (deutonymphs) having reddish-brown ellipsoidal bodies measuring 0.7-1.0 mm long. Adult mites have robust ovoid bodies measuring 0.7-1.5 mm in length. They range from cream to grey in colour but become reddish-brown when engorged on host blood. Morphometric studies have indicated that most *Dermanyssus* spp. may be allocated to 2 species groups: the *gallinae*-group containing species with soft expandable bodies and thin legs (*D. antillarum, D. carpathicus, D. chelidonis, D. faralloni, D. gallinae, D. gallinoides, D. hirundinis, D. longipes, D. nipponensis, D. prognephilus, D. transvaalensis, D. triscutatus, D. trochilinis,* and *D. wutaiensis*); and the *hirsutus*-group comprising species with compact bodies and thicker legs (*D. alaudae, D. americanus, D. brevirivulus, D. brevis, D. grochovskae, D. hirsutus, D. passerines, D. quintus* and *D. rwandae*). The anterior gnathosoma bears long mouthparts (chelicerae, hypostome) flanked by long sensory palps. Like other mesostigmatid mites, the palps have 5 segments (whereas those of prostigmatid and astigmatid mites have 1-2 segments) and they terminate in 2-tined claws (apoteles). The basal segments of the palps are also fused to form a basis capitulum supporting the chelicerae and hypostome. The stylet-like chelicerae are extrusible and form a long piercing structure when fully extended for feeding, but are kept retracted when not in use. They have 3 long thin segments, with the second segment being the longest (whereas the first segment is longest in macronyssids). The chelicerae terminate in small chelae (pincers) with edentate digits (one fixed, one movable) and medially concave faces that form a tube when in opposition. The mouth has a dorsal rostrum, ventral buccal cone and an unbarbed hypostome (barbed in ticks). The alimentary tract comprises the mouth (with paired salivary glands), foregut (with tubular oesophagus and pharynx), midgut (saccular ventriculus with gastric caeca, and short tubular intestine), hindgut (with excretory Malpighian tubules, tubular rectum, and subterminal anus). The idiosoma bears numerous long setae and has distinct sclerotized

dorsal and ventral (sternal, genitoventral, and anal) shields. The dorsal shield is trapezoidal with tapering sides and a truncated posterior margin (while that of *Ornithonyssus* has a rounded posterior margin). The shield usually occupies more than half of the dorsal surface and its surface is reticulated (not striated) with a network of up to 5 fine lines. The sternal shield is short and crescent-shaped with 1-2 pairs of setae (while that of *Liponyssoides* is hexagonal with 3 pairs of setae). The genitoventral shield is rounded posteriorly and has one pair of setae. The anus is located in the posterior half of the anal plate which is broadly triangular with 3 setae. The anteroventral idiosoma gives rise to 4 pairs of long powerful legs, each with 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) with the last segment having a stalked pretarsus with an expanded pretarsal apparatus (ambulacrum) bearing paired claws and an empodium (pad-like pulvillus). The coxae lack spurs and most segments have long setae arranged in characteristic patterns (chaetotaxy often species-specific). Adults have 2 lateral respiratory openings (stigmata) located between the second and fourth pairs of legs (Mesostigmata), often with elongated processes (peritremes). Adult mites exhibit sexual dimorphism, with males being smaller and exhibiting more extensive sclerotization with fusion of sternal and genitoventral elements forming an intercoxal sternogenital (holoventral) shield in many cases. The mouthparts of adult males have broader chelicerae, enlarged chelae and long spermadactyla on the movable digits so they may function as gonopods to transfer sperm to females during mating (process known as neopodospermy). Mature males have paired testes with tubular vas deferens leading to the ejaculatory duct and long sheathed aedeagus (penis). The genital orifice (gonopore) is conspicuous and located presternally. Mature females have 2 ovaries (with ovarioles) which are connected by tubular oviducts to the uterus (with a muscular accessory shell-gland) and vagina (with a bursa copulatrix to receive sperm during mating, and a spermathecae to store sperm after mating). The female gonopore is located anteroventrally and has an epigynal shield.

Site of infection: These non-burrowing mites are found as ectoparasites on a wide range of birds and occasionally on mammals. Infestations have been reported on 25 species of birds belonging to 20 passerine families and 13 non-passerine families in 12 orders (including seabirds, shorebirds, woodpeckers, doves, fowl and birds of prey). Several species may also infest mammals, with mites recorded on miscellaneous mammals belonging to 8 families in 6 orders (including rodents, lagomorphs, carnivores, horses, bats and humans). All mite species show a strong preference for avian hosts, and several reports indicate that they are often unable to reproduce when feeding on mammalian blood. Nymphs (both instars) and adults (both sexes) feed on hosts and may be found anywhere on the skin, but they tend to target the breast, legs and vent of birds (preferring fluffy downy feathered areas), and the belly, back, limbs and muzzle of mammals (including the arms and chests of humans).

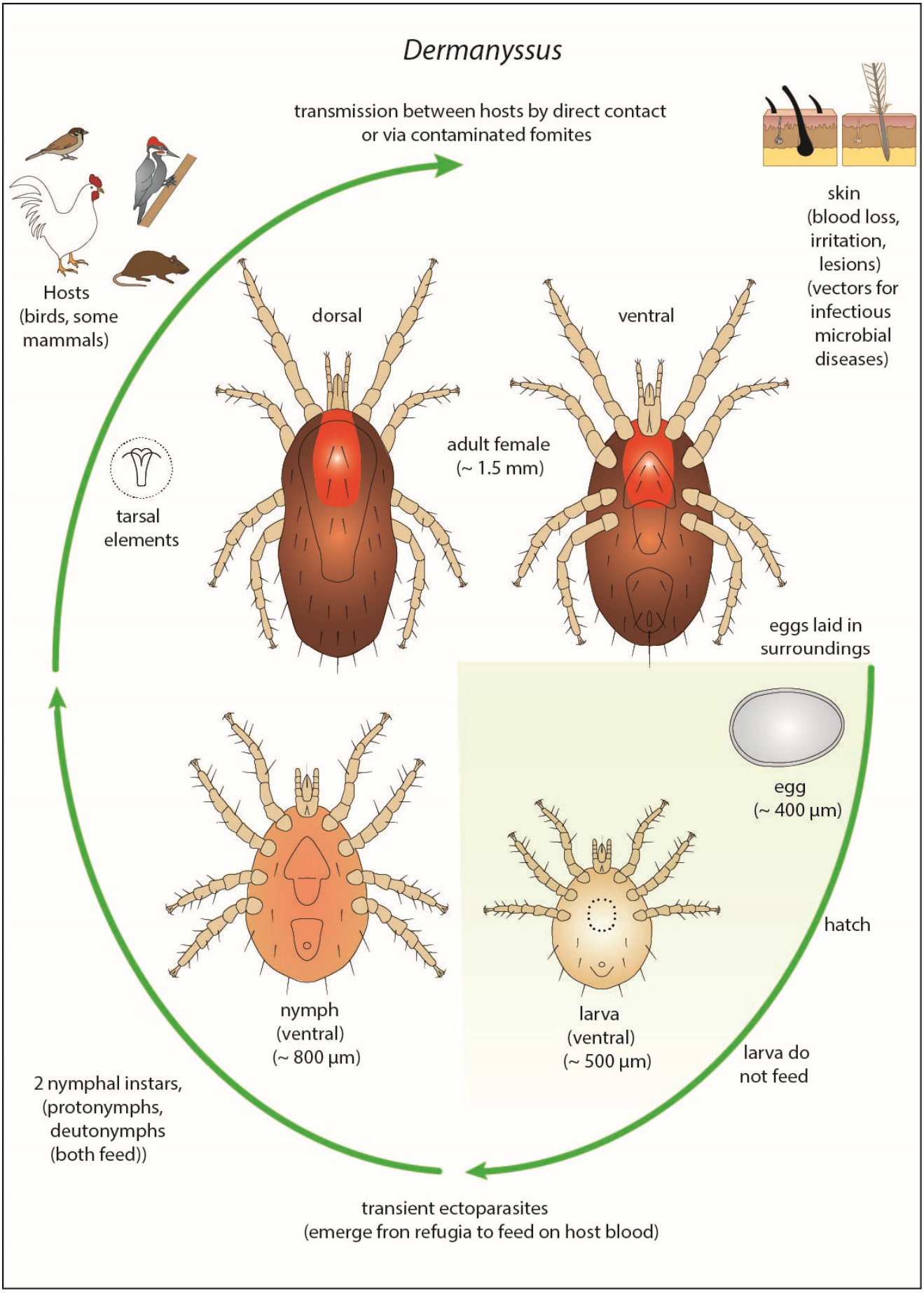
Pathogenesis: Dermanyssid mites are haematophagous parasites that use their long piercing mouthparts to suck blood from their vertebrate hosts. Light infestations may remain subclinical but heavier infestations often cause clinical disease (acariasis) characterized by anaemia and inflamed skin lesions. Nymphs and adults locate hosts and feed rapidly every few days, with adults taking up to 0.2 µl of blood each meal. Heavy infestations may involve thousands of mites resulting in significant blood loss leading to anaemia (evident in poultry as pale combs and wattles). Mites cause local tissue trauma at bite sites producing irritation, pain, pruritus, dermatitis (inflammation) with erythema (redness) and oedema (swelling), pustule formation, scaly skin with hyperpigmentation, scab formation, and plumage damage (dirty discolouration, feather loss). Infestations cause hosts considerable biting stress with restlessness, weakness, poor condition, excessive grooming (preening, biting, scratching, rubbing) and dishevelled appearance. The red mite, *D. gallinae,* is a significant pest in the poultry industry with infestations leading to serious production losses through reduced egg production, smaller egg size, poor egg quality, reduced weight gains despite increased feed and water intake, decreased reproductive potential in males and diminished disease resistance contributing to mortalities in young and ill birds. Mite numbers on poultry increase for 4-6 months and then tend to plateau or drop. Infestations in layer sheds can increase up to 25,000-50,000 mites per bird, and in extreme cases treble that number, resulting in significant morbidity and mortality. Mites may also opportunistically infest humans, mainly poultry workers or residents of houses with bird nests in the roof or under the eaves (starving mites migrate indoors seeking food sources). Such infestations cause dermatological problems varying in severity, with inflammation, pruritus, rashes, papule formation and skin crusting. Domestic and companion animals (such as horses, dogs and cats) may also develop papular skin lesions, particularly in the vicinity of poultry sheds or yards. *Dermanyssus* spp. may also serve as vectors for the transmission of various infectious microbial diseases, including proteobacteria causing pasteurellosis (fowl cholera), coxiellosis (Q fever), enterobacteria causing salmonellosis and escherichiosis, rickettsial bacteria causing avian spirochaetosis, and viruses causing fowl pox, avian influenza and possibly equine encephalitis. Many microbes multiply in mite tissues, most survive mite metamorphosis (trans-stadial transmission) and some may be transferred to mite eggs (trans-ovarian transmission).

Developmental cycle and mode of transmission: *Dermanyssus* spp. undergo hemimetabolous (incomplete) metamorphosis where eggs hatch larvae which moult to nymphs and then adults. Transmission between hosts is often via fomites as mites spend most of the time in the surrounding environment although transmission by direct host-to-host contact may also occur. It has been suggested that 2 ecological species-groups occur: the *gallinae*-group comprising species that are nest-dwelling (nidicolous) and have broad host specificities; and the *hirsutus*-group containing species that spend more time on their hosts and have narrow host specificities. Gravid females lay eggs in the external environment, predominantly in nests, litter and cracks/crevices in dwellings. The eggs hatch in 1-3 days releasing hexapod (6-legged) larvae which do not feed but moult in 17-24 hours to form octopod (8-legged) first-stage nymphs (protonymphs). The protonymphs crawl onto hosts to feed on blood before detaching and moulting in 1-2 days to form second-stage nymphs (deutonymphs). The deutonymphs locate hosts and feed on blood (whereas macronyssid deutonymphs do not feed). When replete, they detach and moult in 1-2 days to form adults which then seek hosts on which to feed. Mites spend most of

the time off hosts in the surrounding environment and generally only make contact to feed rapidly over 30-60 minutes every 2-3 days. During the daytime, mites lie concealed in refugia (cracks and crevices) to rest and reproduce. They are often found in clusters formed by thigmokinesis: with larvae in the centre, females on the outside, and males on top. Adult mites are quite hardy and may survive in the environment for up to 34 weeks without feeding. Most species are nocturnal and feed on birds during the night, although starving mites will feed during the day and will attack any both birds and mammals. Mating takes place off hosts and involves the transfer of spermatophores (packets of around 200 sperm) from males to females. Fertilized females lay 4-8 eggs 12-24 hours after each blood meal, producing up to 8 clutches totalling 30-50 eggs in their lifetime. The whole life-cycle may be completed in as little as 5-17 days, so mite populations can increase very rapidly. Mites prefer mild humid conditions and are susceptible to heat but can survive cold conditions but not freezing. Mite populations tend to increase during the winter months, and decrease over summer. Infestations in wild birds are generally attuned to host breeding seasons, and the presence of nestlings facilitates rapid reproduction with peak mite numbers coinciding with fledging. Higher mite populations develop in layer chickens than in broilers (as layers are kept longer) and in birds kept in less intensive systems (such as barns, free-range and organic farms) where more hiding/resting places are available for mites. Poultry sheds may remain infested for 4-5 months after birds are removed, and mites may be dispersed between farms by the transport of contaminated equipment (crates, egg trays, etc) or the translocation of infested animals (and humans).

Differential diagnosis: Infestations may be suspected on the basis of clinical grounds (skin lesions, inflammation, anaemia, poor condition) but other aetiological agents may cause similar signs/symptoms, including other ectoparasites (such as *Ornithonyssus*). Diagnosis is confirmed by the detection of mites on hosts, with examination techniques involving manual manipulation of coats, plucking plumage/pelage, collecting skin scrapings for caustic digestion, applying adhesive tape to the skin, massaging hosts over blank paper or washing bodies in plastic bags. Any specimens collected may be identified by microscopic examination of their morphological characteristics. Some infestations may be overlooked, however, as the mites are small and feed only intermittently on hosts often at night. Mites are often found at the edges of lesions, particularly those involving flaking or crusted skin. Molecular biological techniques have been used to characterize species (and ratify species-groups) by polymerase chain reaction (PCR) amplification of nuclear (18S, 5.8S and 28S ribosomal RNA, internal transcribed spacers 1 and 2) and mitochondrial (cytochrome c oxidase subunit 1) gene sequences.

Treatment and control: Incidental infestations on humans are usually treated symptomatically using antihistamines and topically administered steroids to provide relief. Infestations on domestic animals and aviary birds are usually treated using chemical acaricides, but careful attention must be given to any drug contra-indications and with-holding periods applicable to animals destined for human consumption. A range of products are available for topical or systemic use as sprays, baths/dips, dusts/powders, pour-ons, spot-ons, impregnated tags, oral drenches or injectable formulations. Infestations have been successfully treated with organochlorines (lindane), organophosphates (malathion, coumaphos, tetrachlorvinphos, methoxychlor, diazinon), pyrethrin and synthetic pyrethroids (permethrin), carbamates (carbaryl), macrocyclic lactones (ivermectin, moxidectin, selamectin) and some natural products (rotenone). Repeated or prolonged treatment may be required, particularly for generalized infestations, but the use of formulations with long-lasting residual activity helps reduce treatment frequency. There are growing reports of mite populations developing resistance to acaricides (organochlorines, organophosphates, pyrethroids and macrocyclic lactones), so it is recommended that different acaricides be used in cyclic rotation. Residual acaricides may also be applied to bird houses, nests, runs and litter to suppress off-host mite populations, with various agencies recommending organophosphate (dimethoate and fenthion, when birds are not present) or pyrethroid sprays, or carbaryl or lime sulphur powders. Alternatively, birds may be given access to dust baths (silica, diatomaceous earth) which have been shown to adhere to mites resulting in their desiccation. Various preventive strategies may be adopted to break transmission cycles, preferably integrated into holistic pest management programs involving health management (screening, treatment, quarantine, culling), animal husbandry (lower stocking rates, cohort separation, not trimming beaks to preserve self-grooming, manipulating photoperiods to shorten night cycles), environmental management (improved hygiene and sanitation, removal of litter, disinfecting cages, repairing or replacing housing to eliminate crevices, treating with residual acaricides) and wildlife management (excluding wild birds and rodents). Preliminary studies on vaccine development and biological control have suggested that birds may develop some protective immunity with age and that entomopathogenic fungi may suppress mite populations.


Dermanyssus
transmission between hosts by direct contact
or via contaminated fomites
skin
(blood loss,
irritation,
lesions)
(vectors for
infectious
microbial
diseases)
Hosts
(birds, some
mammals)
dorsal
ventral
adult female
(~ 1.5 mm)
tarsal
elements
eggs laid in
surroundings
egg
(~ 400 µm)
hatch
nymph
(ventral)
(~ 800 µm)
larva
(ventral)
(~ 500 µm)
larva do
not feed
2 nymphal instars,
(protonymphs,
deutonymphs
(both feed))
transient ectoparasites
(emerge fron refugia to feed on host blood)



Dermanyssus adult



Dermanyssus adult, female with egg



Dermanyssus eggs

***Pneumonyssus* (incl. *Pneumonyssoides*)**
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Gamesid mites have anterior legs with respiratory stigmata located between the second and fourth legs. Most species are predatory, but some are ectoparasitic on mammals, birds and insects. They usually have a large sclerotized dorsal shield and a series of smaller ventral shields. Halarachnid mites are obligate parasites in the respiratory tracts or ears of mammals. Infestations by *Pneumonyssus* (syn. *Pneumonyssoides*) spp. occur in the nasal passages of dogs and the lungs of primates, sometimes causing congestive inflammation.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Mesostigmata (gamesid mites, legs grouped anteriorly, stigmata between second and fourth legs)
Suborder: Dermanyssina (sclerotized shields, reduced setae, legs with claws)
Superfamily: Dermanyssoidea (elongate edentate chelicerae, diverse life-styles)
Family: Halarachnidae (obligate parasites in respiratory tracts or ears of mammals)
Genus: *Pneumonyssus* (syn. *Pneumonyssoides*) (parasitic in lungs of monkeys and nasal passages of dogs)
Species: various species cause rhinitis, sinusitis and pulmonary conditions

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					

Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs; and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Mesostigmatid mites are further characterized by possessing unbarbed hypostomes, and long legs with free coxae (not fused to the body wall). The order Mesostigmata contains thousands of mites, with over 5,000 species recognized in 660 genera and 100 families. Nine suborders are recognized (Antennophoria, Arctacarina, Cercomegistina, Dermanyssina, Epicriina, Microgyniina, Parasitina, Sejina, and Uropodina). The suborder Dermanyssina contains robust mites with distinct sclerotized dorsal and ventral shields, reduced setae, palps with 2-tined apoteles, and legs with tarsal claws. Five superfamilies are recognized (Ascoidea, Dermanyssoidea, Eviphidoidea, Rhodacaroidea, and Veigaioidea). The superfamily Dermanyssoidea contains a diverse array of mites including free-living predators, nidicoles in the nests of vertebrates and insects, obligate and facultative ectoparasites of vertebrates and arthropods, and even respiratory and auditory endoparasites of mammals, birds, and some reptiles. The mites have elongated chelicerae (long first or second segment) with small edentate digits and concave interior margins (functioning as a tube when in opposition). A total of 11 families are recognized (Dermanyssidae, Haemogamasidae, Halarachnidae, Hirstionyssidae, Ixodorhynchidae, Laelapidae, Macronyssidae, Raillietiidae, Rhinonyssidae, Spinturnicidae, and Varroidae), many of them exclusively parasitic.

The family Halarachnidae contains mites that are obligate parasites in the respiratory tracts of mammalian hosts. Adult mites have bodies have small sclerotized plates (shields), stigmata with small peritremes located between their legs, chelicerae with movable digits, palps with 4-5 segments and terminal bifurcate or simple tines, and legs with protarsi, caruncles and claws. A total of 7 genera are recognized (*Halarachne*, *Orthohalarachne*, *Pneumonyssoides*, *Pneumonyssus*, *Rhinophaga*, *Sciurinyssus*, *Zumptiella*) in marine mammals, porcupines, squirrels, canids, and nonhuman primates. The genus *Pneumonyssus* is characterized by robust mites lacking genital plates that occur in the airways of monkeys (Old World monkeys and great apes). Similar mites found in the nasal passages of dogs were originally described as *Pneumonyssus caninum* but were later transferred to the genus *Pneumonyssoides* to distinguish them from *Pneumonyssus* lung mites of monkeys (this reclassification has often been questioned but remains to be resolved - many texts simply report the 2 genera as synonyms).

***Pneumonyssus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
P. africanus	Primates: cercopithecid (blue monkey)	lungs		Europe (zoo)
P. bakeri	Rodentia: sciurid (Douglas squirrel)	respiratory tract		North America
P. caninum (syn. *Pneumonyssoides*) (dog nasal mite)	Carnivora: canid (dog, silver fox)	nasal passages, frontal sinus	head shaking, sneezing, rhinitis, sinusitis, tonsillitis	North America, Europe, Africa, Australia
P. capricorni	Diprotodontia: phalangerid (common spotted cuscus)			Papua New Guinea
P. congoensis	Primates: cercopithecid (baboon)	trachea, lungs		Africa
P. dentatus (now *Domrownyssus*)	Dasyuromorphia: dasyurid (yellow-footed antechinus); Rodentia: murid (fawn-footed mosaic-tailed rat)			Australia
P. dinolti	Primates: cercopithecid (rhesus macaque)	maxillary sinus		zoo (Europe, ex: Indonesia)
P. duttoni	Primates: cercopithecid (greater spot-nosed monkey)	trachea, bronchi		Congo
P. foxi	Primates: cercopithecid (rhesus macaque)			North America (zoo)
P. longus	Primates: cercopithecid (red-tailed monkey), hominid (chimpanzee)	bronchi, trachea		Africa
P. mossambicenis	Primates: cercopithecid (chacma baboon)	lungs		Mozambique
P. oudemansi	Primates: hominid (chimpanzee, gorilla), cercopithecid (guenon)	bronchi, bronchioles		Africa
P. pangorillae	Primates: hominid (western gorilla, bonobo)			Africa
P. procavians	Hyracoidea: procaviid (rock hyrax)	lungs		South Africa
P. rodhaini	Primates: cercopithecid (western red colobus)	lungs, nasal fossae		Africa
P. santos-diasi	Primates: cercopithecid (vervet monkey, chacma baboon)	lungs		Mozambique
P. schoutedeni	Hyracoidea: procaviid (southern tree hyrax)	trachea, bronchus		Africa
P. simicola (syn. *P. foxi, griffithi, Pneumotuber macaci*) (monkey lung mite)	Primates: cercopithecid (rhesus macaque, crab-eating macaque, southern pig-tailed macaque, yellow baboon, silvered leaf monkey, red-shanked douc, gelada, proboscis monkey); Dermoptera: cyanocephalid (flying lemur)	lungs	nodular lesions	tropical and subtropical zones
P. stammeri	Primates: atelid (woolly monkey)	larynx		zoo (Europe, ex: South America)
P. vitzthumi	Primates: hominid (Bornean orangutan)	bronchi, sinuses, nasal fossae		Europe (zoo)
P. vocalis	Primates: cercopithecid (chacma baboon)	larynx		South Africa
Pneumonyssoides				
Pn. phacochoeri	Artiodactyla: suid (desert warthog)	nasal passages		Africa
Pn. potamochoeri	Artiodactyla: suid (red river hog)			Africa

Parasite morphology: Recent studies have shown that *Pneumonyssus* spp. form 4 different types of morphological stages; namely, eggs (but only seen in gravid females); larvae (birthed by females); nymphs (previously thought not to occur, but 2 instars have now been detected); and adults (both males and females). Eggs observed *in utero* were ovoid in shape and measured around 0.5 mm in length. Larvae have ovate bodies measuring up to 0.7 mm in length and they characteristically possessed 3 pairs of anteroventral legs. The 2 nymphal stages detected (protonymphs and deutonymphs) were apparently reduced to ephemeral non-feeding forms. They have ovate bodies measuring 0.7-1.0 mm in length, and 4 pairs of legs with rudimentary tarsal claws. Following moulting, the protonymph exuvia was often retained by the deutonymph, and the exuvia of both nymphal stages was cast simultaneously by teneral adults. The bodies of both male and female adult mites were ovoid measuring 1.0-1.5 x 0.5-0.9 mm with smooth white-yellow cuticles without striations and with few setae. The gnathosoma (head or capitulum) was small and located anteriorly with short mouthparts comprising 2 chelicerae and a hypostome flanked by 2 sensory palps. The palps were short and consisted of 4-5 segments, terminating in bifurcate or simple tines (whereas the palps of other mesostigmatid mites have 5-6 segments, and those of prostigmatids and astigmatids have 1-2 segments). The bases of the palps were fused to form a basis capitulum supporting the mouthparts, and the ventral basis capitulum possessed a longitudinal median (deutosternal) groove with a single column of denticles (while that of other halarachnids had broad denticular rows). The chelicerae were composed of 3 segments ending in claw-like chelae (pincers) with small fixed digits and larger movable digits (in males, the movable digits varied from tubular and sinuate to hook-like and enlarged). The mouth had a dorsal rostrum, ventral buccal cone and unbarbed hypostome (barbed in ticks). The alimentary tract comprised the mouth (with paired salivary glands), tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with gastric caeca, short intestine), tubular hindgut (with excretory Malpighian tubules, rectum) and subterminal anus. The large idiosoma (body) possessed some dorsal and ventral body armour in the form of small sclerotized plates (shields). The single dorsal shield was irregular and elongate in shape, and densely punctate due to muscle insertions on the inner surface. The ventral idiosoma had 2 shields, a small anterior sternal shield that was variable in shape, and a small posterior anal shield that was circular and encircled the anus. Adults have 4 pairs of stout legs which are attached anteroventrally and project well beyond the body margin. Each leg is jointed with 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus), with the latter having a short pretarsus and pretarsal apparatus (ambulacrum) bearing slender claws (larger on forelegs) with a median empodium (pad-like pulvillus). Many leg segments bear multiple setae (hypertrichy) while the legs of other halarachnids are sparsely setose (hypotrichy). The mites have 2 respiratory openings (stigmata) located between coxae II and IV (like all mesostigmatids) with small processes (peritremes). Adult mites exhibit little external sexual dimorphism, other than males being smaller and having larger movable digits on their chelicerae. Females have paired ovaries (with ovarioles) connected by tubular oviducts to the uterus (with muscular shell-gland) and vagina (with accessory organs (bursa copulatrix and spermathecae) for sperm reception and storage). The genital opening (gonopore) is a transverse slit between coxae IV and lacks a genital (epigynal) plate. Males have 2 testes with tubular vas deferens leading to the ejaculatory duct and sheathed aedeagus (penis). The male gonopore is located at the anterior margin of the sternal shield and lacks an epigynal plate.

Site of infection: *Pneumonyssus* (syn. *Pneumonyssoides* p.p.) are considered to be endoparasitic lung and nasal mites as the larvae, nymphs and adults occur in tissues of the lower and upper respiratory tracts of mammals, particularly cercopithecid and hominid primates, but also a few rodents, hyraxes, marsupials, canids and suids. Many infestations occur in the nasal passages (especially in dogs) while others involve the sinuses, trachea, bronchi and lung tissue (especially in Old World monkeys and great apes).

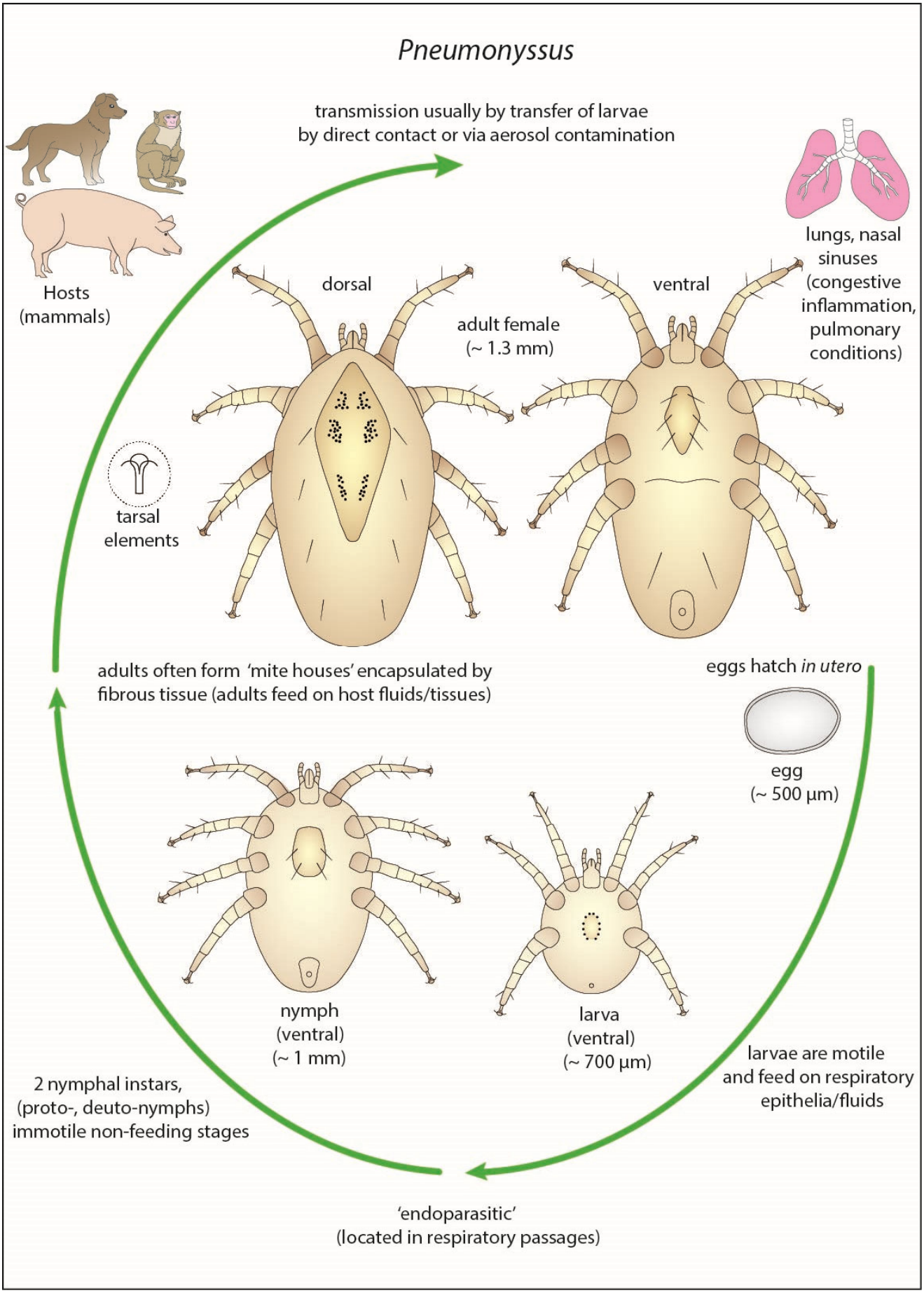
Pathogenesis: Most infestations by nasal and lung mites remain asymptomatic and are detected incidental to other studies. Heavy infestations by a few species, however, may cause disease (acariasis) notably in domestic dogs and captive primates. The active stages are larvae and adult mites which use their chelicerae to pierce the respiratory epithelium to feed on host fluids (lymph and blood) and epithelial cells (nymphs are thought to be non-feeding immotile stages). Feeding stages cause tissue trauma with inflammation, nodule formation, congestion and sometimes respiratory distress. In dogs, nasal mites (*P. caninum*) infesting the upper respiratory tract may cause rhinitis, sinusitis, excessive nasal discharges, mucosal hyperaemia, sneezing, reverse sneezing, epistaxis (nosebleed), impaired sense of smell (notably in working (tracking/hunting) dogs), pruritus, head shaking, stridor (noisy breathing), and sometimes coughing, restlessness, loss of appetite and collapse. Epidemiological investigations do not support any breed, age or sex predilection, although one report suggested that dogs older than 3 years and large breed dogs were affected more often. In non-human primates, lung mites (e.g. *P. simicola*) infesting the lower respiratory tract may cause pulmonary acariasis with inflammation of the respiratory passages, pulmonary nodules, lung congestion, and host death. Mites attach to the walls of airways and pierce the parenchyma to feed on blood, lymph, and pulmonary epithelial cells. They cause severe inflammation with cellular infiltrates and granulomatous host reactions that encapsulate mites with fibrous connective tissues producing yellowish-grey cystic nodules a few millimetres in diameter. Adjacent nodules may coalesce to form blister-like bullae measuring up to 10 mm in diameter and containing up to 20 mites. These so-called ‘mite-houses’ have a central lumen mostly containing females, although larvae, nymphs and males may also be present. The lesions and surrounding parenchyma often contain birefringent golden brown to black mite pigment. Hosts may develop chronic bronchitis with bronchiolectasis and peribronchiolitis, and focal lobular pneumonitis with alveolar collapse or consolidation, resulting in severe coughing and dyspnoea. In massive infestations, deaths occur due to congestion of the lungs and alveolar collapse. Other complications reported in some monkeys include pneumothorax and pulmonary arteritis, as well as extensive pleuritis and pericarditis associated with ruptured nodules.

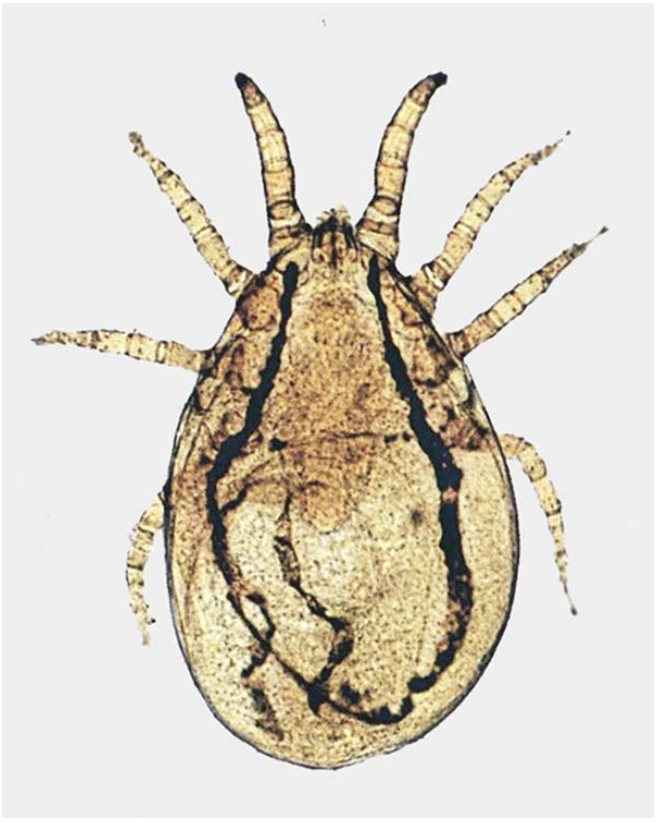
Infestations may also predispose monkeys to other pulmonary diseases due to bronchiolar epithelial changes and impaired mucociliary clearance

Developmental cycle and mode of transmission: Although details about the life-cycles of these mites are largely unknown, they do undergo hemimetabolous (incomplete) metamorphosis whereby larvae moult to nymphs and then adults. All stages occur within the respiratory tract of the host but not all stages actively feed. Gravid females are ovo-viviparous as they produce eggs which hatch *in utero* so they give birth to larvae (free eggs are rarely seen in host tissues). The larvae feed on host fluids and cells and then moult through 2 nymphal instars (protonymphs and deutonymphs) which appear to be ephemeral non-feeding non-motile forms (early studies erroneously thought that larvae transformed directly to adults). The final nymphal stages moult to form male and female adult mites which feed on host fluids and tissues, and often become encapsulated by host fibrous tissue (sometimes forming 'mite houses'). Mating occurs within the respiratory tract and females eventually produce the next generation of larvae. The kinetics and dynamics of metamorphic changes occurring throughout the life-cycle are not known. Transmission is presumed to occur by the transfer of mites from host-to-host by direct contact or via aerosol contamination through sneezing and coughing. Larvae are thought to be the main infective stages as they are small and motile, whereas nymphs are thought to be immotile and adult females in the lungs are generally considered to be too large to climb narrow bronchioles in the respiratory tree, although they may be dislodged from nasal passages.

Differential diagnosis: Infestations are difficult to diagnose due to their cryptic location (respiratory passages) and nonspecific clinical signs (sinusitis, pneumonitis). Other aetiologies include rhinitis (idiopathic, bacterial, fungal, parasitic), oronasal neoplasia, oronasal fistula, and nasopharyngeal disease (foreign body or mass lesions). Medical imaging technologies may help visualize the extent of affected areas with radiographic and computed tomographic (CT) findings including increased interstitial pulmonary and peribronchial density, thickened bronchial walls, pleural thickening, pleural adhesions, and cavitary pulmonary lesions (bullae and subpleural blebs). Diagnosis is generally afforded by antemortem recovery of mites by endoscopic biopsy or washings/lavages of respiratory organs (upper airways) or the post-mortem detection of mites and lesions by histological examination of pulmonary tissues. Endoscopy is suitable for examination of the upper airways and includes rhinoscopy or retroflex nasopharyngoscopy which facilitates nasal biopsies or flushing. Flooding the nasal chambers with anaesthetic gas or oxygen seems to encourage mites to migrate toward the nasopharynx, and nasal flushing is usually performed under general anaesthesia with a cuffed endotracheal tube. Infestations of the lower respiratory tract have been detected by tracheobronchiolar lavage, although false-negative results may occur. Any mites should be identified by microscopic examination. Histological examination of post-mortem samples may be used to reveal mites in tissue lesions containing characteristic dark mite pigments and crystals. There have also been several reports of detecting mites in the faeces on infested nonhuman primates.

Treatment and control: Clinical infestations by lung and nasal mites have been successfully treated with a small range of chemical acaricides, notably systemic applications of macrocyclic lactones (ivermectin, milbemycin, and selamectin). Many treatments had to be repeated or prolonged to eliminate mites, particularly in generalized infestations, and there have been some reports of ivermectin resistance developing in some mite populations. Even when mites are eliminated, the lesions of chronic bronchiolitis, bronchiectasis, and pigmentation persist for some time. Other systemic acaricides have been used without success and some animals also developed toxic reactions to several chemicals. While topical formulations are generally unsuitable for respiratory application, one study used vapours from organophosphate (dichlorvos) strips as inhalants to treat nasal infections in a dog. Various preventive strategies used to curb infestations, primarily in primate colonies, have involved regular health screening (with isolation and treatment of infested individuals), cohort separation (rearing newborns in isolation from infested mothers), and thorough cleaning and disinfection of holding facilities (cages, pens, runs, nests). While hard data are lacking, it is reasoned that the application of residual environmental acaricides (organophosphates and pyrethroids) and the exclusion of vermin from animal colonies should assist in the prevention and spread of infestations.


Pneumonyssus
transmission usually by transfer of larvae
by direct contact or via aerosol contamination
Hosts
(mammals)
lungs, nasal
sinuses
(congestive
inflammation,
pulmonary
conditions)
dorsal
ventral
adult female
(~ 1.3 mm)
tarsal
elements
adults often form 'mite houses' encapsulated by
fibrous tissue (adults feed on host fluids/tissues)
eggs hatch in utero
egg
(~ 500 µm)
nymph
(ventral)
(~ 1 mm)
larva
(ventral)
(~ 700 µm)
larvae are motile
and feed on respiratory
epithelia/fluids
2 nymphal instars,
(proto-, deuto-nymphs)
immotile non-feeding stages
'endoparasitic'
(located in respiratory passages)



Pneumonyssus adult

Raillietia
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Gamesid mites have anterior legs with respiratory stigmata located between the second and fourth legs. Most species are predatory, but some are ectoparasitic on mammals, birds and insects. They usually have a large sclerotized dorsal shield and a series of smaller ventral shields. Halarachnid mites are found in the respiratory tracts or ears of mammals. Infestations by *Raillietia* spp. occur in the ears of cattle and goats, but do not appear to cause clinical disease.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Mesostigmata (gamesid mites, legs grouped anteriorly, stigmata between second and fourth legs)
Suborder: Dermanyssina (sclerotized shields, reduced setae, legs with claws)
Superfamily: Dermanyssoidea (elongate edentate chelicerae, diverse life-styles)
Family: Raillietiidae (obligate parasites in ears of mammals)
Genus: *Raillietia* (parasitic in ears of mammals)
Species: various species cause asymptomatic infestation in cattle, goats

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					

Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs; and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Mesostigmatid mites are further characterized by possessing unbarbed hypostomes, and long legs with free coxae (not fused to the body wall). The order Mesostigmata contains thousands of mites, with over 5,000 species recognized in 660 genera and 100 families. Nine suborders are recognized (Antennophoria, Arctacarina, Cercomegistina, Dermanyssina, Epicriina, Microgyniina, Parasitina, Sejina, and Uropodina). The suborder Dermanyssina contains robust mites with distinct sclerotized dorsal and ventral shields, reduced setae, palps with 2-tined apoteles, and legs with tarsal claws. Five superfamilies are recognized (Ascoidea, Dermanyssoidea, Eviphidoidea, Rhodacaroidea, and Veigaioidea). The superfamily Dermanyssoidea contains a diverse array of mites including free-living predators, nidicoles in the nests of vertebrates and insects, obligate and facultative ectoparasites of vertebrates and arthropods, and even respiratory and auditory endoparasites of mammals, birds, and some reptiles. The mites have elongated chelicerae (long first or second segment) with small edentate digits and concave interior margins (functioning as a tube when in opposition). A total of 11 families are recognized (Dermanyssidae, Haemogamasidae, Halarachnidae, Hirstionyssidae, Ixodorhynchidae, Laelapidae, Macronyssidae, Raillietiidae, Rhinonyssidae, Spinturnicidae, and Varroidae), many of them exclusively parasitic.

The family Raillietiidae contains unique mesostigmatid mites with robust bodies and long legs that inhabit the auditory (ear) canals of mammalian hosts. They have respiratory stigma with peritremata that extend to the level of the first coxae similar to that of other ectoparasitic Mesostigmata (whereas other parasitic mites in the respiratory tracts of birds and mammals have reduced or absent peritremata). The family Raillietiidae is monotypic and only contains one genus (*Raillietia*) with 8 described species from domestic and wild ruminants (bovids) and one marsupial host (wombat). The ear mites are not haematophagous and feed on epithelial cells and ear wax, but heavy infestations may cause blockages manifesting in vestibular disease.

***Raillietia* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
R. acevedoi	Artiodactyla: bovid (alpine ibex)	ears		North America
R. auris (cattle ear mite)	Artiodactyla: bovid (cattle)	ears	blockage, ulceration	Americas, Eurasia, Australia
R. australis	Diprotodontia: vombatid (common wombat)	ears	subclinical	Australia
R. caprae (goat ear mite)	Artiodactyla: bovid (goat)	ears	subclinical	Americas, Europe, Australia
R. flechtmanni	Artiodactyla: bovid (buffalo, cattle)	ears		South America
R. hopkinsi	Artiodactyla: bovid (waterbuck)	ears		Africa
R. manfredi	Artiodactyla: bovid (goat)	ears		Australia
R. whartoni	Artiodactyla: bovid (kob)	ears		Africa

Parasite morphology: The ear mites *Raillietia* spp. form 4 different morphological stages during their development: eggs; larvae; nymphs (2 instars); and adult mites (immature (teneral) and mature males and females). Mite eggs are small white ovoid stages measuring around 0.5 mm in length. Larvae have white-cream ovoid bodies (idiosoma) measuring 0.5-0.7 mm long with a small anterior gnathosoma (head or capitulum) and 3 pairs of long anteroventral legs. Nymphs also have white-cream ovoid bodies with a small anterior gnathosoma. However, they are larger than larvae and measure from 0.6-1.0 mm in length and they have 4 pairs of long jointed legs. Two nymphal instars are formed: protonymphs with 3 pairs of sternal setae and a single hair on each palpal trochanter; and deutonymphs with 4 pairs of sternal setae and 2 hairs on each palpal trochanter. Protonymphs have also been observed to sometimes retain the larval exuvia after moulting. Adult mites are spherical-ovoid stages measuring from 1.0-1.5 mm in length with the idiosoma being white-cream coloured while the gnathosoma and legs are tan to reddish-brown. The small anterior gnathosoma bears the mouthparts (chelicerae and hypostome) flanked by long sensory palps. The palps have 5-6 segments (like other mesostigmatid mites) with a terminal claw (apotele), and the basal segments are fused to form a basis capitulum supporting the mouthparts. The chelicerae are long slender cutting structures with 3 segments terminating in claw-like chelae (pincers), each with a dorsal fixed digit and a ventral scythe-shaped movable digit with 3 fang-like projections. The oral opening (mouth) has a dorsal rostrum, ventral buccal cone and central unbarbed hypostome (barbed in ticks). The alimentary tract comprises the mouth (with paired salivary glands), tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus branched with gastric caeca), and tubular hindgut (with excretory Malpighian tubules, and rectum) opening through the subterminal anus. The idiosoma is ovoid to sacciform in shape and usually domed in females and humped in males. It possesses small sclerotized plates (shields) located both dorsally and ventrally. The single dorsal shield covers around a third of the dorsal surface and is rhomboid to diamond-shaped with 12-34 pairs of setae ((species on ungulates have 10 podonotal pairs and 2-7 opisthonotal pairs, while the species on wombats have 19 podonotal and 15 opisthonotal pairs). There are 3 small ventral shields: a small rectangular sternal shield with a straight or slightly arched posterior margin; a narrow but well-developed genitoventral shield (most other halarachnids lack this shield) with a fringed anterior margin and a rounded posterior margin; and a small oval anal shield located around the anus. The anteroventral margin of the idiosoma has a longitudinal bifid tritosternum (lacking on other halarachnids). Adult mites have 4 pairs of long hairy legs, each composed of 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) and ending in a short pretarsus bearing a well-developed ambulacrum with paired claws and an empodium (pad-like pulvillus). Femora II have ventral processes and a pair of respiratory openings (stigmata) are located between coxae II and IV with elongate peritreme processes (whereas other halarachnids have reduced to vestigial peritremes). Adult males have 2 testes with tubular vas deferens leading to the ejaculatory duct. They have a long sheathed aedeagus (penis) which extends through the ventral genital opening (gonopore) during copulation. Female mites have paired ovaries (with ovarioles) which are connected by tubular oviducts to a common uterus (with muscular accessory shell-gland). The terminal vagina has accessory organs for sperm reception (bursa copulatrix) and storage (spermathecae) and the gonopore is a transverse slit.

Site of infection: *Raillietia* spp. are commonly known as ear mites, with *R. auris* known as the cattle ear mite, and *R. caprae* known as the goat ear mite. Larvae and adult mites are ectoparasitic in the external ear canals (including the surface of the tympanic membrane) of both domestic and wild ruminants. Infestations have been recorded predominantly from bovid artiodactylans (cattle, buffalo, goat, ibex, waterbuck, kob) and occasionally from vombatid marsupials (wombats).

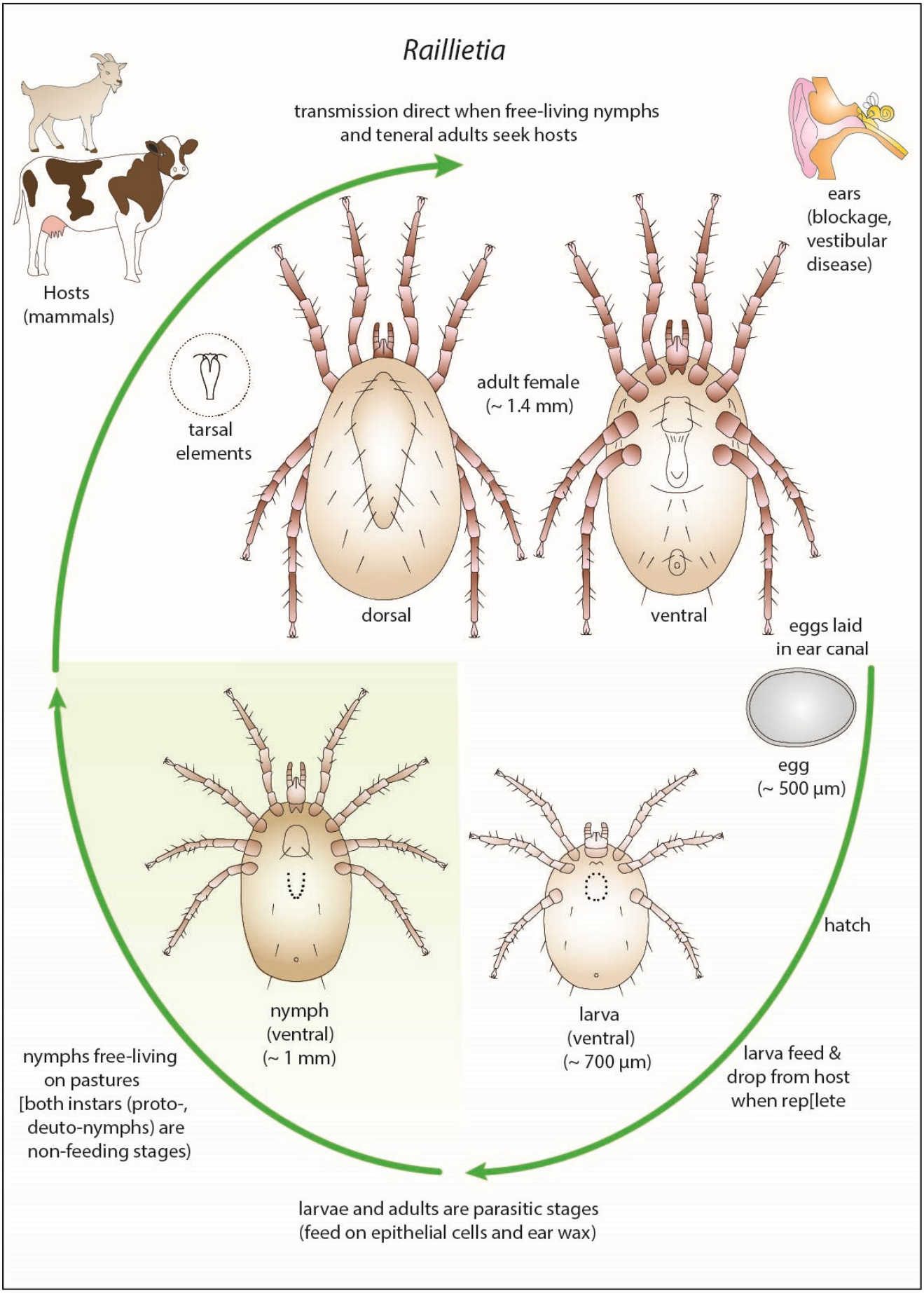
Pathogenesis: These ear mites are generally considered to be relatively harmless as larvae and adults live in the external ear canals. Although their chelicerae are adapted to lacerate epithelia, these mites do not suck blood but feed on cerumen (earwax) and cellular debris (their guts contain amber cheesy masses). Nonetheless, their claws and chelicerae damage the surface of the ear canal not

only promoting cerumen production that may cause plug-like blockages but also creating sites for the invasion and multiplication of bacteria causing ear infections. The resultant cumulative effects may result in otitis media (sometimes called parasitic otitis), vestibular disease and occasionally neurological signs when the eardrum is perforated. External ear lesions may include suppurative otitis media, parakeratotic hyperkeratosis, acanthosis and inflammation of the intact tympanic membrane. Severe cases can result in ulcerated lesions as well as vestibular disease due to blockage by plugs of paste-like wax, resulting in hearing loss, head shaking and ear rubbing. Infrequently, the tympanic membranes may become perforated and mites may infest the tympanic cavity. Animals may exhibit suppurative otitis media and bulla osteitis with purulent debris, necrosis and stenosis. These changes often contribute to the development of neurological signs including ataxia, head tilting, head pressing, unilateral facial paralysis, circling, lack of coordination, and lateral recumbency with loss of righting reflex. Infestations in livestock have been associated with significant production losses through anorexia, restlessness, decreased libido, dysphagia, debilitation and emaciation. The prevalence of infestations in cattle and goats increases with age (suggesting the absence of acquired immunity) and *Bos indicus* breeds (especially Zebu) appear to be more susceptible than *Bos taurus* breeds. Ear mites may also act as biological or mechanical vectors for the transmission of various microbes to cattle, buffalo and goats, notably bacteria causing mycoplasmosis. Screening studies have detected over 28 different types of bacteria in association with mites from infested cattle, with the most common being *Proteus, Pseudomonas* and *Corynebacterium* spp. Ear infections were more prevalent in calves than in adult cows; due mainly to secondary infections with the bacteria *Pseudomonas*, *Corynebacterium*, *Escherichia*, *Haemophilus*, *Pasteurella*, *Mannheimia*, *Streptococcus*, *Mycoplasma* and *Listeria*, and the fungi *Malassezia* and *Actinomyces*. The cattle ear mite has also been associated with the transmission of a rhabditiform nematode to bovids.

Developmental cycle and mode of transmission: These mites undergo incomplete (hemimetabolous) metamorphosis whereby eggs hatch larvae which moult to nymphs and then to adults. However, not all stages occur on hosts, only larvae and adults are ectoparasitic, while nymphs (and teneral adults) are free-living on pastures. All immature stages are short-lived (survive < 2 days) whereas adults have been found to live for up to 30 days, so transmission usually occurs when teneral adults crawl into the ears of grazing hosts. Once inside the ear canal, they feed, mature and mate. Fertilized females oviposit eggs in the ear canal where they hatch releasing hexapod larvae. Studies have shown the time interval from infestation by teneral adults to the hatching of larvae to be as little as 2-4 days. Fed larvae then leave the host and drop onto pasture where they moult nymphs. Both nymphal instars (protonymphs and deutonymphs) are short-lived non-feeding stages that soon moult to form immature adults. These teneral adults wait on pastures for grazing hosts and then crawl over the pelage to enter the ears to feed and mature. Experimental studies have been able to complete the whole life-cycle in 4-8 days under favourable conditions of temperature (30°C) and relative humidity (85-90%).

Differential diagnosis: Infestations are frequently asymptomatic and therefore go undetected. Even when clinical signs become apparent (otitis, blockages), they are non-specific and may be attributable to a range of conditions (particularly bacterial infections as mites predispose hosts to secondary infections). Mites are usually detected in the ear canal by direct otoscopic examination, especially near the external opening of auditory canal. Larvae and adults are evident as small (0.5-1.5 mm) motile white spheres with legs. However, they are difficult to detect when earwax and/or pus are present as they are usually located beneath obstructive plugs. Mites may sometimes be collected by flushing the ear canal with warm water or saline or by swabbing with cotton-tipped applicators. Any specimens collected should be subject to microscopic examination for definitive identification.

Treatment and control: The occurrence of mites deep in the ear canal makes chemotherapeutic treatment difficult, particularly since concomitant or secondary infections with bacterial and/or fungal agents may be present. Clinicians often resort to triple therapy, using antibiotics to target bacteria, acaricides to target mites and supportive glucocorticoids to relieve inflammation. Mites were eliminated by direct application of pyrethroids (flumethrin or permethrin) in mineral oil into the ear canal. Treatment efficacy was aided by prior application of saline lavages to the ear canal to loosen plugs of wax/pus. Contradictory reports have been made on the use of systemic macrocyclic lactones to control infestations, with some reporting selamectin and ivermectin to be effective, while others found them to be ineffective. There are growing suspicions that some mite populations have developed resistance particular acaricides, including ivermectin. A range of precautionary measures may be adopted in order to prevent mite transmission, involving regular health surveillance (facilitating quarantine, treatment, culling), grazing management (pasture rotation, cohort separation), environmental management (pasture spelling or cultivation, applying environmental residual acaricides, cleaning stalls and pens) and wildlife control (excluding potential reservoir hosts).


Raillietia
transmission direct when free-living nymphs and teneral adults seek hosts
Hosts (mammals)
ears (blockage, vestibular disease)
tarsal elements
adult female (~ 1.4 mm)
dorsal
ventral
eggs laid in ear canal
egg (~ 500 µm)
hatch
nymph (ventral) (~ 1 mm)
larva (ventral) (~ 700 µm)
nymphs free-living on pastures [both instars (proto-, deuto-nymphs) are non-feeding stages)
larva feed & drop from host when rep[lete
larvae and adults are parasitic stages (feed on epithelial cells and ear wax)



Raillietia adults

Sternostoma
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Gamesid mites have anterior legs with respiratory stigmata located between the second and fourth legs. Most species are predatory, but some are ectoparasitic on mammals, birds and insects. They usually have a large sclerotized dorsal shield and a series of smaller ventral shields. Rhinonyssid mites are found in the nasopharynx of wild and domestic birds. Infestations by *Sternostoma* spp. may cause respiratory problems in aviary birds.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
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Order: Mesostigmata (gamesid mites, legs grouped anteriorly, stigmata between second and fourth legs)
Suborder: Dermanyssina (sclerotized shields, reduced setae, legs with claws)
Superfamily: Dermanyssoidea (elongate edentate chelicerae, diverse life-styles)
Family: Rhinonyssidae (parasites of nasopharynx of birds)
Genus: *Sternostoma* (parasitic in nasal passages of birds)
Species: various species cause respiratory problems in caged birds

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					

Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs; and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Mesostigmatid mites are further characterized by possessing unbarbed hypostomes, and long legs with free coxae (not fused to the body wall). The order Mesostigmata contains thousands of mites, with over 5,000 species recognized in 660 genera and 100 families. Nine suborders are recognized (Antennophoria, Arctacarina, Cercomegistina, Dermanyssina, Epicriina, Microgyniina, Parasitina, Sejina, and Uropodina). The suborder Dermanyssina contains robust mites with distinct sclerotized dorsal and ventral shields, reduced setae, palps with 2-tined apoteles, and legs with tarsal claws. Five superfamilies are recognized (Ascoidea, Dermanyssoidea, Eviphidoidea, Rhodacaroidea, and Veigaioidea). The superfamily Dermanyssoidea contains a diverse array of mites including free-living predators, nidicoles in the nests of vertebrates and insects, obligate and facultative ectoparasites of vertebrates and arthropods, and even respiratory and auditory endoparasites of mammals, birds, and some reptiles. The mites have elongated chelicerae (long first or second segment) with small edentate digits and concave interior margins (functioning as a tube when in opposition). A total of 11 families are recognized (Dermanyssidae, Haemogamasidae, Halarachnidae, Hirstionyssidae, Ixodorhynchidae, Laelapidae, Macronyssidae, Raillietiidae, Rhinonyssidae, Spinturnicidae, and Varroidae), many of them exclusively parasitic.

The family Rhinonyssidae contains obligate endoparasites living their entire lives within the respiratory systems of birds. Some 30 genera have been described (*Agapornyssus*, *Astridiella*, *Charadrinyssus*, *Falconyssus*, *Hapalognatha*, *Larinyssus*, *Locustellonyssus*, *Mesonyssoides*, *Mesonyssus*, *Neonyssus*, *Neotyranninyssus*, *Passeronyssus*, *Pipronyssus*, *Psittonyssus*, *Ptilonyssoides*, *Ptilonyssus*, *Rallinyssus*, *Rhinoecius*, *Rhinonyssus*, *Rhinosterna*, *Ruandanyssus*, *Sternoecius*, *Sternonyssus*, *Sternostoma*, *Sternostomoides*, *Sternostomum*, *Tinaminyssus*, *Trochilonyssus*, *Tyranninyssus*, *Zumptnyssus*) and differentiated primarily by the morphology of stigmata (presence or absence of peritremes), gnathosoma (shape of mouthparts, presence of 1 or 2 fingers of chelicerae,) sclerotization of idiosoma (shape and size of shields) and chaetotaxy (patterns of setae). Rhinonyssid protonymphs and deutonymphs are similar in appearance; they do not have well-developed dorsal shields, the tritosternum is absent in all developmental stages, and the anus is located ventrally or terminally. The genus *Sternostoma* comprises mites with dorsolateral stigmata (lacking peritremes), ventral gnathosoma (only the most distal part extending beyond the idiosoma), 2 dorsal shields, and 3 ventral shields (the genital shield being rudimentary). The genus is specious and contains over 70 species parasitizing the nasal cavities, trachea and air sacs of a wide range of birds (belonging to over 10 avian orders).

***Sternostoma* species**	**Hosts**	**Clinical signs**	**Distribution**
S. alexfaini	Passeriformes: laniid (great grey shrike, red-backed shrike)		Europe
S. alexmironi	Passeriformes: muscicapid (northern wheatear)		Russia
S. artami	Passeriformes: artamid (white-breasted wood swallow)		Papua New Guinea
S. augei	Strigiformes: strigid (burrowing owl)		South America
S. batis	Passeriformes: furnariid (Spix's woodcreeper)		South America
S. boydi	Charadriiformes: scolopacid (sanderling, greater yellowlegs), larid (herring gull, ring-billed gull, common tern)		North America
S. bruxellarum (syn. *Ptilonyssus elbeli*)	Passeriformes: sturnid (common starling, black-collared starling, rosy starling, common mynah)		Eurasia, North America
S. castroae	Passeriformes: motacillid (yellow-throated longclaw)		Africa
S. chakarovae	Passeriformes: muscicapid (northern wheatear)		Russia
S. christinae	Passeriformes: phylloscopid (common chiffchaff)		Europe
S. cisticolae	Passeriformes: cisticolid (rattling cisticola)		Africa
S. clementei	Passeriformes: tyrannid (blue-billed black tyrannt)		South America
S. colii	Passeriformes: coliid (speckled mousebird)		Africa
S. constricta	Passeriformes: paradisaeid (Raggiana bird-of-paradise)		Papua New Guinea
S. cooremani	Coraciiformes: meropid (European bee-eater), alcedinid (collared kingfisher)		Africa, Malaysia
S. cordiscutata	Cuculiformes: cuculid (white-eared bronze cuckoo)		Papua New Guinea
S. crotophagae	Cuculiformes: cuculid (groove-billed ani)		North America
S. cryptorhynchum	Passeriformes: passerid (house sparrow)		Europe
S. cuculorum (syn. *S. zosteropus*)	Cuculiformes: cuculid (red-chested cuckoo, Diederik cuckoo, Levaillant's cuckoo); Passeriformes: laniid (magpie shrike), zosteropid (silvereye)		Africa, Australia
S. darlingi	Passeriformes: tyrannid (northern tufted flycatcher)		Central America
S. delianovae	Passeriformes: turdid (fieldfare)		Russia
S. dumetellae	Passeriformes: mimid (gray catbird)		North America
S. dureni	Passeriformes: turdid (common blackbird, olive thrush, mountain thrush), leiothrichid (arrow-marked babbler, black-faced babbler)		Africa, Australia, Russia
S. epistomata (syn. *S. chlidoniadis*)	Charadriiformes: larid (black tern, whiskered tern)		Russia
S. eurocephali	Passeriformes: laniid (southern white-crowned shrike)		Africa
S. ficedulae	Passeriformes: muscicapid (collared flycatcher)		Europe
S. francolini	Galliformes: phasianid (Coqui francolin)		Africa
S. fulicae	Gruiformes: rallid (Eurasian coot)		Europe
S. furmani	Galliformes: phasianid (bar-backed partridge)		Malaysia
S. gallowayi	Passeriformes: alaudid (horned lark)		North America
S. giganteum	Passeriformes: platysteirid (chinspot batis)		Africa
S. gliciphilae	Passeriformes: meliphagid (brown honeyeater)		Australia
S. guevarai	Galliformes: phasianid (red-legged partridge)		Europe
S. hedonophilum	Passeriformes: tyrannid (cinnamon-crested spadebill)		South America
S. hirundinis	Passeriformes: hirundinid (white-headed saw-wing, pearl-breasted swallow, barn swallow, purple martin), cisticolid (lazy cisticola)		Africa, North America

S. hirundo	Passeriformes: hirundinid (barn swallow, pearl-breasted swallow, Ethiopian swallow)		Africa
S. hutsoni	Passeriformes: turdid (Swainson's thrush)		North America
S. hylandi	Piciformes: picid (downy woodpecker)		North America
S. inflatum	Passeriformes: leiothrichid (arrow-marked babbler, black-faced babbler)		Africa
S. isabelae	Passeriformes: alaudid (red-capped lark)		Europe
S. kelloggi	Passeriformes: mimid (gray catbird, brown thrasher)		North America
S. lagonostictae	Passeriformes: estrildid (African firefinch)		Africa
S. laniorum	Passeriformes: laniid (red-backed shrike, great grey shrike, southern fiscal), platysteirid (chinspot batis)		Africa
S. longosetosa	Passeriformes: tyrannid (eastern kingbird)		North America
S. loxiae	Passeriformes: fringillid (red crossbill)		Europe
S. marchae	Passeriformes: fringillid (canary)		Russia
S. mortelmansi	Apodiformes: trochilid (hummingbird)		South America
S. motacilli	Passeriformes: motacillid (water pipit)		North America
S. nectarinia	Passeriformes: nectariniid (copper sunbird, scarlet-crested sunbird, purple-breasted sunbird)		Africa
S. neosittae	Passeriformes: neosittid (varied sitella)		Australia
S. opistaspis	Passeriformes: artamid (hooded butcherbird)		Papua New Guinea
S. paddae	Passeriformes: estrildid (Java sparrow)		Asia
S. pastor	Passeriformes: sturnid (rosy starling)		Europe (zoo)
S. pencei	Passeriformes: tyrannid (yellowish flycatcher)		Central America
S. pirangae	Passeriformes: cardinalid (summer tanager)		North America
S, porteri	Piciformes: picid (northern flicker, downy woodpecker)		North America
S. quiscali	Passeriformes: icterid (Carib grackle)		Central America
S. sayornis	Passeriformes: tyrannid (black phoebe)		North America
S. schiffornis	Passeriformes: tityrid (brown-winged schiffornis)		South America
S. setifer	Passeriformes: tyrannid (least flycatcher)		North America
S. sialiphilus	Passeriformes: turdid (eastern bluebird)		North America
S. sinense	Passeriformes: leiothrichid (red-billed leiothrix)		Europe (zoo)
S. spatulatum	Passeriformes: turdid (olive-backed thrush, hermit thrush)		North America
S. sternahirundo	Charadriiformes: larid (common tern)		Russia
S. straeleni	Passeriformes: sturnid (violet-backed starling)		Africa
S. strandtmanni	Passeriformes: icterid (tricolored blackbird, red-winged blackbird, brown-headed cowbird, common grackle, boat-tailed grackle)		North America, Europe
S. strigitis	Strigiformes: strigid (long-eared owl)		Russia
S. sturnicola	Passeriformes: sturnid (Ruppell's starling), buphagid (yellow-billed oxpecker)		Africa
S. tangarae	Passeriformes: thraupid (turqoise tanager, summer tanager)		Americas
S. technaui (syn. *S. borceanum, turdi*)	Passeriformes: turdid (American robin, true thrush, olive thrush, song thrush, Abyssinian thrush, cocoa thrush, red-throated thrush, spectacled thrush, common blackbird, fieldfare, ring ouzel), cinclid (white-throated dipper)		Africa, Eurasia, North America
S. thienponti	Passeriformes: dicrurid (fork-tailed drongo)		Africa
S. tracheacolum (syn. *S. meddai*) (air-sac mite, canary mite)	Passeriformes: fringillid (canary, finch, goldfinch), emberizid (bunting), hirundinid (swallow, tree swallow), icterid (brown-headed cowbird, oriole), motacillid (wagtail), parulid (water thrush), passerid (sparrow), sturnid (starling, meadowlark), sylviid (warbler), thraupid (tanager), turdid (blackbird), tyrannid (great crested flycatcher); Psittaciformes: psittacid (parrot), psittaculid (parakeet)	illness, death	Africa, North America
S. tyrannus	Passeriformes: tyrannid (olive-sided flycatcher)		North America
S. ubedai	Passeriformes: sylviid (Sardinian warbler)		Europe
S. ziegleri	Cuculiformes: cuculid (brush cuckoo)		Papua New Guinea
S. zini	Cuculiformes: cuculid (common cuckoo)		Russia

Parasite morphology: *Sternostoma* spp. form 4 different types of morphological stages during their development: eggs; larvae; nymphs; and adults. Eggs observed *in utero* were oval-round measuring from 0.10-0.35 mm long and surrounded by a thin smooth shell. They embryonated *in utero* to contain fully-formed larvae. Depending on the mite species, the eggs either hatched rapidly after oviposition (ovoviviparity) or they hatched *in utero* so females birthed live larvae (viviparity). Free larvae were ovate measuring 0.2-0.4 mm long and were lightly sclerotized and colorless (almost transparent). They possessed a small but well-developed gnathosoma (head or capitulum) with rudimentary mouthparts and short palps. The larger idiosoma (body) lacked sclerotized plates (shields) in most species, although a few displayed vague anal and podosomal shields (e.g. *S. technaui*). All larvae characteristically had 3 pairs of jointed legs (albeit weakly-developed with reduced claws) and lacked respiratory openings (stigmata). Nymphs were ovate to ellipsoidal measuring 0.3-0.5 mm long and were light brown to white (almost transparent), but became reddish-brown when gorged. They characteristically had 4 pairs of jointed legs and a pair of lateral stigmata with short peritremes. All nymphs had a ventral or terminal anus but lacked a tritosternum. They possessed a growing number of setae, but not quite as many as adults. There were 2 nymphal instars (protonymphs and deutonymphs) which were similar in appearance, except that protonymphs were slightly smaller and had well-developed mouthparts with sclerotized chelicerae and sharp movable digits (while deutonymphs had poorly sclerotized chelicerae that ended bluntly). The idiosoma of protonymphs usually lacked sclerotized shields, although a few species had a vague opisthosomal dorsal shield. The idiosoma of deutonymphs had a small anal shield and while most species lacked other shields, several had precursors of shields present in adults. In these cases deutonymphs could be differentiated from adults by the absence of genital apparatus. Adult mites had thick oval-ellipsoidal bodies that were cream-yellow in colour and ranged in dimensions from 0.25-0.80 x 0.15-0.40 mm. Females were larger in size than males (0.4-0.8 x 0.2-0.4 mm v. 0.25-0.35 x0.15-0.23 mm) and their genital openings (gonopores) were located posterior to the sternal plate (rather than anterior like males). Adults had a small gnathosoma, the bulk of which was ventral and only the most distal portions extended beyond the idiosoma. The gnathosoma contained the mouthparts (paired chelicerae and central hypostome) flanked by sensory palps. The palps were segmented with distal segments curved inwards and bearing a small terminal claw (apotele) while the basal segments were fused to form a basis capitulum. The chelicerae had 3 segments with the basal segments having swollen bases and the terminal segments bearing claw-like chelae (pincers) with a small fixed digit and a larger movable digit (modified in males for sperm transfer). The mouth consisted of a dorsal rostrum, a ventral buccal cone and a central unbarbed hypostome. The alimentary tract comprised the mouth (with long paired salivary glands), foregut (with tubular oesophagus and pharynx), midgut (with saccular ventriculus with gastric caeca) and the hindgut (short intestines with excretory Malpighian tubules) leading to the rectum and ventral or terminal anus. The idiosoma possessed numerous short setae and had distinctive sclerotized shields, 2 dorsal (podosomal and opisthosomal) and 3 ventral (sternal, genitoventral, and anal), most of them patterned by fine lines. The podosomal shield was pentagonal-triangular in shape with rounded edges, while the opisthosomal shield was smaller and elongate. The sternal shield was rectangular while the genitoventral shield was similar in size but oval. The anal shield was small and rounded, and females had a rudimentary genital (epigynal) plate. The anteroventral idiosoma lacked a tritosternum but was the point of attachment for 4 pairs of stout legs. Each leg had 6 segments (coxa, trochanter, femur, genu, tibia and tarsus) and ended in a short stalked pretarsus bearing an expanded pretarsal apparatus (ambulacrum) with large paired curved claws and an empodium (pad-like pulvillus). The forelegs had poorly-developed elongate claws, while the remaining legs had well-developed larger claws. Adults had a pair of lateral stigmata located between coxae II and IV (like other mesostigmatid mites) but most species lacked peritremes. Males had paired testes with tubular vas deferens leading to the ejaculatory duct and sheathed aedeagus (penis). Females had 2 ovaries with ovarioles) joined by tubular oviducts to the uterus (with accessory shell-glands) and a bipartite vagina (with a bursa copulatrix for sperm reception, and saccular spermathecae for sperm storage).

Site of infection: Rhinonyssid nasal mites are permanent endoparasites that inhabit the respiratory tracts of birds. Most species live in the upper respiratory tract in the nasal cavity and buccal cavity (primarily in the region between the larynx and the palatal folds). However, some species may occupy the trachea, syrinx, primary bronchi, air passages of the lungs and all major air sacs (including the cervical, interclavicular, anterior and posterior thoracic, and abdominal air sacs). On rare occasions, mites have been found in the oesophagus, the proximal pneumatized humerus, and in the body cavity on the mesentery near the liver, kidneys, intestines and ovaries/testes. Around 75 mite species have been described from birds belonging to 35 passerine families and 13 nonpasserine families in 9 orders (including shorebirds, kingfishers, cuckoos, woodpeckers, hummingbirds, fowl, parrots, owls). While all stages occur within the same host, gravid females are more often found lower in the respiratory tree than non-gravid non-gorged females which occur mainly in the upper respiratory passages.

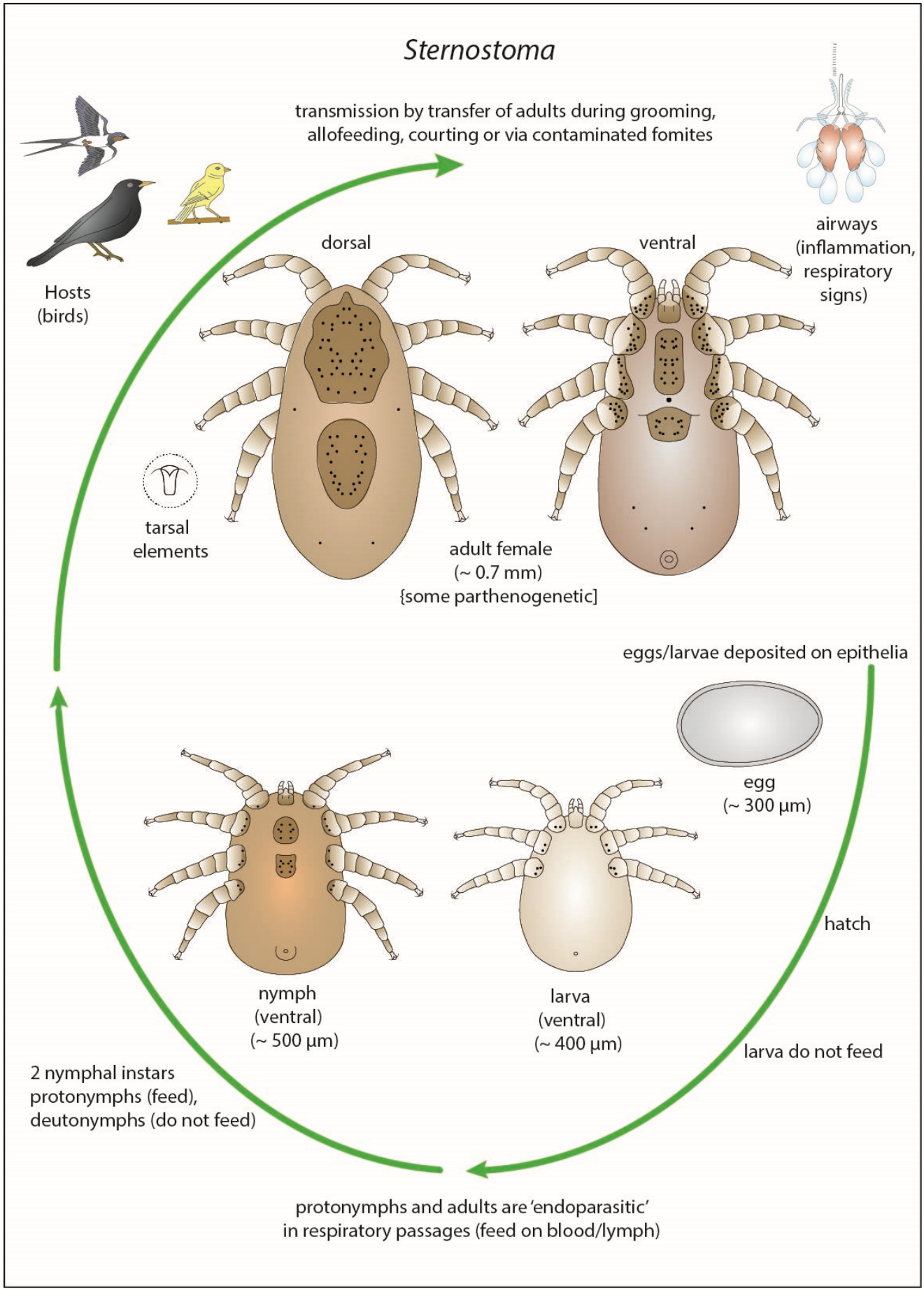
Pathogenesis: Many infestations by nasal mites are light and remain asymptomatic, but heavier infestations may cause respiratory distress which can prove fatal (disease called rhinonyssidosis). Protonymphs and adult mites use their mouthparts to lacerate respiratory epithelia to feed on host blood and lymph, in so doing causing traumatic lesions, irritation, catarrhal inflammation, petechial haemorrhages and excessive mucus production leading to congestion and even pneumonia. Infested birds exhibit a range of clinical signs, including throat clearing, sneezing, coughing, audible dyspnoea (wheezing with squeaking, gurgling or clicking), open-mouthed breathing, excessive salivation (ptyalism), wet nostrils, bill wiping, head shaking, tail bobbing, and aphonia. Inflammation of the respiratory tree may range from the trachea (tracheitis) to the air-sacs (aerocystitis). Birds become less active and weak, exhibit exercise intolerance and fly less often for shorter periods, lose weight to the point of emaciation, and appear fluffy with deteriorating feather quality. Affected birds may also develop secondary pyogenic infections. Mite infestations may persist for months and mortality rates can be high with deaths due to occlusion of the respiratory passages and suffocation. Disease is more

severe in captive birds than wild birds, and in young birds than in adults. Clinical signs are exacerbated by handling, exercise, and other stresses. Mite populations in surviving individual birds decline over 1-2 years but may persist at low numbers for extended periods. The prevalence and intensity of infestations was not correlated to host biological events such as breeding, nesting, fledgling or seasonal migration. There has been much speculation as to whether *Sternostoma* mites act a vectors or reservoirs for infectious microbial diseases (such as bacterial Q fever and Lyme disease or viral West Nile fever and avian influenza), but their role in the maintenance or transmission of these pathogens remains to be determined.

Developmental cycle and mode of transmission: Nasal mites undergo incomplete (hemimetabolous) metamorphosis whereby eggs hatch larvae which moult to nymphs and then to adults. The whole life cycle may be completed in the respiratory system of the host, but only protonymphs and adults are blood-feeding stages (whereas larvae and deutonymphs have rudimentary mouthparts and are considered to be non-feeding stages). Depending on the species, gravid female mites are either larviparous or ovoviviparous and give birth to live larvae or larvated eggs that rapidly hatch. Studies on *S. tracheacolum* found that eggs hatched within 20 hours of oviposition on respiratory epithelia, while eggs of other species are rarely encountered. All species demonstrated rapid development to adults within 4-5 days. Larvae did not feed on blood and moulted to the first nymphal instar (protonymphs) in 1-2 days. The protonymphs did feed on blood and they moulted rapidly after bloodmeals to form the second nymphal instar (deutonymphs). Deutonymphs were not observed to feed and any blood found in their guts was attributed to the carry-over of undigested blood from the previous protonymph stages. Deutonymphs moulted rapidly to adult mites which then commenced to feed by apparently taking multiple small meals. The reproductive cycles of the few mite species that have been studied indicate that female mites may produce progeny with or without mating. Eggs that have been fertilized by sperm develop into diploid females, whereas unfertilized eggs undergo a form of parthenogenesis (called arrhenotoky) whereby they develop into haploid males (this is distinct from most other cases of parthenogenesis where females are exclusively produced). Under experimental conditions, the whole life-cycle was completed in as little as 6 days, and female mites were found to live for 9-10 days. Gravid females were found more frequently in the air sacs, syrinx and trachea of the host, while non-gravid non-gorged females were commonly found in the upper respiratory system, particularly the buccal and nasal cavities. It is therefore thought that transmission occurs by the direct transfer of non-gravid non-gorged females to birds in close proximity (via billing behaviour, or parents feeding young). Indeed, these stages are often encountered on the head plumage, bill and nares of infested birds. It is also possible that some indirect transmission may occur via water, perches or other surfaces contaminated by birds coughing or sneezing. The transmission stages have been observed to survive off-hosts for at least 8 hours, but rarely more than 20 hours, and they have been observed to migrate towards heat sources. The transfer of non-gravid females also explains the unusual dynamics observed in the establishment of new infestations. The non-gravid females produced unfertilized eggs giving rise to parthenogenetic haploid males (thus accounting for the large male bias observed in initial infections) whereas subsequent progeny from mated females producing fertilized eggs were diploid females (thus accounting for the large female bias observed in established infections).

Differential diagnosis: Infestations are rarely diagnosed on the basis of symptomatology, as many other aetiological agents may cause similar signs of respiratory disease (dyspnoea and congestion). Ante-mortem diagnosis is generally afforded by the direct demonstration of mites in the upper respiratory tract, usually by otoscopic examination of the nasal mucosa or endoscopy of the trachea. Transillumination of the trachea of infested birds (using a bright light in a darkened room after moistening the neck) has also been used occasionally to reveal dark specks moving in the lumen. Medical imaging technologies may assist in localizing infestations, with radiography revealing radio-opacities in the pulmonary and air-sac fields. Specimens of mites may sometimes be detected in oral or nasal swabs or lavages, and occasionally in faecal samples. Molecular biological techniques have been used to characterize species and infer phylogenetic relationships following polymerase chain reaction (PCR) amplification of nuclear (5.8S ribosomal RNA, internal transcribed spacers 1 and 2) and mitochondrial (16S ribosomal RNA) gene sequences.

Treatment and control: Clinical infestations should be treated promptly as they may worsen rapidly leading to airway blockages with significant morbidity and mortality. Chemotherapy with acaricides is generally the only option, but care should be exercised as an aggressive course may kill too many mites at once leading to further obstructions and too little medication may not resolve the condition. Treatments should be administered quickly with minimal handling in warm comfortable surroundings, and recovering birds should be rested with easy access to water and food. Supportive care may be required during treatment in the form of anti-inflammatories, decongestants and possibly antibiotics in the case of secondary infections. Good success has been reported in the control and elimination of infestations using macrocyclic lactones (ivermectin or moxidectin) repeated after 2 weeks. It is recommended that all birds in contact be treated at the same time and that attention be paid to any contra-indications to avoid toxicity or residual issues. Preventive measures designed to break transmission cycles should involve animal management (regular health surveillance to inform treatment, quarantine and culling), environmental management (cleaning cages, roosts and nests, spraying residual environmental acaracides (pyrethroids), water disinfection), and wildlife control (excluding wild birds from poultry facilities and aviaries).


Sternostoma
transmission by transfer of adults during grooming, allofeeding, courting or via contaminated fomites
airways (inflammation, respiratory signs)
Hosts (birds)
dorsal
ventral
tarsal elements
adult female (~ 0.7 mm) {some parthenogenetic]
eggs/larvae deposited on epithelia
egg (~ 300 µm)
hatch
nymph (ventral) (~ 500 µm)
larva (ventral) (~ 400 µm)
larva do not feed
2 nymphal instars protonymphs (feed), deutonymphs (do not feed)
protonymphs and adults are 'endoparasitic' in respiratory passages (feed on blood/lymph)



Sternostoma adult

Varroa
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Gamesid mites have anterior legs with respiratory stigmata located between the second and fourth legs. Most species are predatory, but some are ectoparasitic on mammals, birds and insects. They usually have a large sclerotized dorsal shield and a series of smaller ventral shields. Varroid mites have flat discoid bodies and feed on haemolymph from bees. Infestations by *Varroa* spp. have been associated with mortalities in honeybees.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)
Order: Mesostigmata (gamesid mites, legs grouped anteriorly, stigmata between second and fourth legs)
Suborder: Dermanyssina (sclerotized shields, reduced setae, legs with claws)
Superfamily: Dermanyssoidea (elongate edentate chelicerae, diverse life-styles)
Family: Varroidae (bee mites, flat button shape, red-brown colouration, suck haemolymph)
Genus: *Varroa* (parasitic on cuticle of bees)
Species: various species cause mortalities in honeybees

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					

Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Parasitiformes comprises acarines with posterior respiratory stigmata and includes two major orders: the ixodid ticks (order Metastigmata) with stigmata located posterior to the legs; and the gamesid mites (order Mesostigmata) where they are located between the legs, sometimes associated with sinuous processes (peritremes). Mesostigmatid mites are further characterized by possessing unbarbed hypostomes, and long legs with free coxae (not fused to the body wall). The order Mesostigmata contains thousands of mites, with over 5,000 species recognized in 660 genera and 100 families. Nine suborders are recognized (Antennophoria, Arctacarina, Cercomegistina, Dermanyssina, Epicriina, Microgyniina, Parasitina, Sejina, and Uropodina). The suborder Dermanyssina contains robust mites with distinct sclerotized dorsal and ventral shields, reduced setae, palps with 2-tined apoteles, and legs with tarsal claws. Five superfamilies are recognized (Ascoidea, Dermanyssoidea, Eviphidoidea, Rhodacaroidea, and Veigaioidea). The superfamily Dermanyssoidea contains a diverse array of mites including free-living predators, nidicoles in the nests of vertebrates and insects, obligate and facultative ectoparasites of vertebrates and arthropods, and even respiratory and auditory endoparasites of mammals, birds, and some reptiles. The mites have elongated chelicerae (long first or second segment) with small edentate digits and concave interior margins (functioning as a tube when in opposition). A total of 11 families are recognized (Dermanyssidae, Haemogamasidae, Halarachnidae, Hirstionyssidae, Ixodorhynchidae, Laelapidae, Macronyssidae, Raillietiidae, Rhinonyssidae, Spinturnicidae, and Varroidae), many of them exclusively parasitic.

The family Varroidae contains relatively large hairy mites that are ectoparasitic on wild and domestic honeybees. The mites possess modified chelicerae (lacking fixed digits), stigmata without peritremal plates, and discoidal bodies with sclerotized dorsal and ventral shields sporting unique patterns of striations and chaetotaxy (setae). Two genera have been differentiated primarily by differences in the dentition of the deutosternal groove (denticles absent in *Varroa,* present in *Euvarroa*) and the occurrence of sternal pores (present in *Varroa,* absent in *Euvarroa*). Mites feed on the fat bodies and haemolymph of bees (pupae and adults) and infestations have been associated with significant bee mortalities and reduced honey production in many countries around the world.

Parasite species	Hosts	Clinical signs	Distribution
Varroa			
V. destructor (parasitic bee mite)	Hymenoptera: apid (*Apis mellifera*, western honeybee; *Apis cerana*, Asian honeybee)	mortalities (plus vector for deformed wing virus, Israeli acute paralysis virus)	worldwide (except Australia)
V. jacobsoni (syn. *V. ricinus, Myrmozercon reidi*)	Hymenoptera: apid (*Apis indica*, Indian honeybee)	mortalities	Asia
V. rindereri	Hymenoptera: apid (*Apis koschevnikovi*, Koschevnikov's honeybee)		Malaysia
V. underwoodi	Hymenoptera: apid (*Apis cerana*, Asian honeybee)		Nepal
Euvarroa			
E. sinhai	Hymenoptera: apid (*Apis florea*, dwarf honeybee)		India, South-East Asia
E. wongsirii	Hymenoptera: apid (*Apis andreniformis*, black dwarf honeybee)		Thailand

Parasite morphology: *Varroa* mites form 3 different types of morphological developmental stages: namely, eggs; nymphs (2 instars); and adults. The eggs are small oval-rounded stages measuring from 0.3-0.5 mm in length and surrounded by a thin milky-white shell. They hatch to release the first nymphal instar (protonymphs) which have circular discoidal bodies measuring 0.4-0.6 mm long. Protonymphs are transparent white in colour and have 4 pairs of short stumpy legs located anteroventrally and a small anterior gnathosoma (head or capitulum) bearing mouthparts with pointed chelicerae. Both male and female stages occur but they are indistinguishable without dissection. Protonymphs moult to form the second nymphal instar (deutonymphs) which are larger (0.5-0.8 mm long) and have oval discoidal bodies. They are cream-tan in colour and have 4 pairs of longer stouter legs and longer mouthparts with pointed chelicerae. In most respects, deutonymphs resemble adult mites but are slightly smaller and have fewer setae. Adult *Varroa* mites have distinctive oval bodies (wider than long) that are flattened ventrally but convex dorsally (while *Euvarroa* mites have broadly triangular bodies that are wider posteriorly). Adults range in dimensions from 1.0-1.8 mm long and 1.5-2.0 mm wide and they exhibit conspicuous sexual dimorphism, with females being larger than males (1.0-1.8 x 1.5-2.0 mm cf. 0.7-1.0 x 0.7-0.9 mm) and females having reddish-brown to dark-brown ovate bodies, while males have yellowish-white spherical bodies with lightly tanned legs. The small anterior gnathosoma lack eyes and bears piercing mouthparts (paired chelicerae and central hypostome) flanked by sensory palps. The palps consisted of 5-6 segments (like other mesostigmatid mites) with the terminal segment bearing an apotele with setae having 2 unequal tines. The basal palpal segments were fused to form a basis capitulum supporting the mouthparts, and the ventral basis capitulum possessed a smooth longitudinal median (deutosternal) groove lacking denticles (whereas the groove in the genus *Euvarroa* had 13-14 small triangular denticles). The chelicerae had 3 segments ending in claw-like chelae with slender movable dentate digits but lacking fixed digits. Male chelicerae become modified at the final moult and change to hollow tubes used to transfer packets of sperm to female mites. The mouth was located ventrally and had a dorsal rostrum, ventral buccal cone, central unbarbed hypostome and a pair of slender horn-like lateral projections (corniculi). The digestive tract included a tubular foregut (oesophagus and pharynx), saccular midgut (ventriculus with gastric caeca), tubular hindgut (with excretory Malpighian tubules) and rectum opening through a terminal anus. The idiosoma possessed heavily sclerotized plates (shields), one dorsal and 3 ventral (sternal, genitoventral, and anal). The single dorsal shield was entire (covering the entire dorsum) and had narrow thickened margins. It was ornamented with an extensive polygonal network of striations and was covered by a dense pattern of setae which were simple or barbed, and stouter around the margins (cf. *Euvarroa* had fewer (47-54) long lanceolate setae). The ventral idiosoma had a weakly-developed bifurcate tritosternum just anterior to the well-developed sternal shield which was strongly curved (inverted-U-shaped) and had 5-6 pairs of setae (3 pairs in *Euvarroa*) and 4-6 pores (absent in *Euvarroa*). The middle genitoventral shield was large and pentagonal-shaped with a rounded anterior margin and more than 10 setae. The posterior anal shield was small and triangular to semicircular with 3 setae (while that of *Euvarroa* was broader). The anteroventral surface of the idiosoma was the point of attachment for 4 pairs of stout legs which usually exhibited a distinctive configuration, the forelegs being thinner and projecting forwards, while the remaining pairs were stouter and curved laterally. Each leg consisted of 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) and ended in a short stalked pretarsus with an expanded apparatus (ambulacrum) bearing paired claws and a central empodium (pad-like pulvillus). Adult mites had a pair of respiratory stigmata located laterally between coxae III and IV with strongly looped peritremes directed posteriorly or laterally near coxae IV. Mature males had paired testes with tubular vas deferens leading to the ejaculatory duct and sheathed aedeagus. The male genital opening (gonopore) was located anteriorly near the sternal shield and males used modified mouthparts used to transfer packets of

sperm to females. Mature female mites had 2 ovaries (with ovarioles) joined by tubular oviducts to a globular uterus (with accessory shell-glands) and vagina (with accessory bursa copulatrix and spermathecae for sperm reception and storage). The female gonopore was located on the genitoventral shield approximately level to the bases of the third pair of legs.

Site of infection: Bee mites are obligate ectoparasites of honeybees *Apis* spp., with adult mites attaching to the abdomen between ventral sclerites, particularly the underside of the metasoma. Their flat domed bodies fit well into abdominal folds of the adult bee and they are held fast by their abundant setae. Nymphal stages of the mites are mainly found in brood cells on bee larvae, pupae or developing adults, particularly on drones. Four *Varroa* spp. have been described from 4 honeybee species, with infestations usually being quite host specific. Another 2 species infesting dwarf honeybees have been allocated to the sister genus *Euvarroa* on the basis of differences in parasite morphology (sclerotization, chaetotaxy) and biology (host specificity and biogeography).

Pathogenesis: The species *V. destructor* originally infested *Apis cerana* (eastern or Asian honeybee) which over time evolved natural defenses to infestations (via more efficient grooming, brood hygiene (removal of infested pupae) or physiological resistance mechanisms). In the mid-1900s, however, this mite species expanded its host range to *A. mellifera* (western honeybee) which did not have a co-evolutionary history and had not developed natural defenses. These bees are more commonly used throughout the world for crop pollination, and infestations have now become almost cosmopolitan in distribution. Many countries impose strict quarantine procedures to lessen the chances of mite importation as *V. destructor* is considered to be a devastating pest for apiaries in particular and horticulture in general. Infestations have pronounced economic impacts on the beekeeping industry through mortalities, lost production and increased maintenance costs. Mites tend to invade colonies in summer leading to high mite populations in autumn which can cause a crisis when drone rearing ceases and mites are forced to switch to worker larvae, precipitating rapid population crashes and even hive death. *Varroa* mites have piercing mouthparts that are used to feed on fat body tissues, and possibly extracellular fluid (haemolymph), in immature and adult honeybees. Bees have large fat body reserves just beneath the cuticle of the ventral metasoma which is a major predilection site for feeding mites. Fat bodies are nutrient-rich stores essential for many physiological functions, including energy regulation, hormone production, immune responses and even pesticide detoxification. Adult honeybees only become infested by female mites, whereas bee larvae, pupae and young adults still in brood cells may be infested by nymphal and adult mites of both sexes. Adult bees are rarely killed but they do lose weight and become weakened with impaired flying and navigational abilities, and generally have shorter lifespans (infested bees are absent from the hive more frequently). Most infestations in brood cells do not compromise bee pupation and eclosion, but the presence of numerous mites in a brood cell can result in larval or pupal death (disease condition called varroosis, or varroatosis). Pathogenicity is correlated to the intensity of brood cell infestation - the more mother mites (or foundresses) in a cell, the less likely the immature bee will develop successfully and emerge as an adult. Infestations are also thought to suppress innate immune responses in bees, thus predisposing them to a range of concomitant infections. Adult mites are highly motile and move between bees leaving open wounds, thus making them efficient vectors for the transmission of debilitating viral pathogens, including deformed-wing virus, acute bee-paralysis virus, Kashmir bee virus, black queen cell virus and possibly many more.

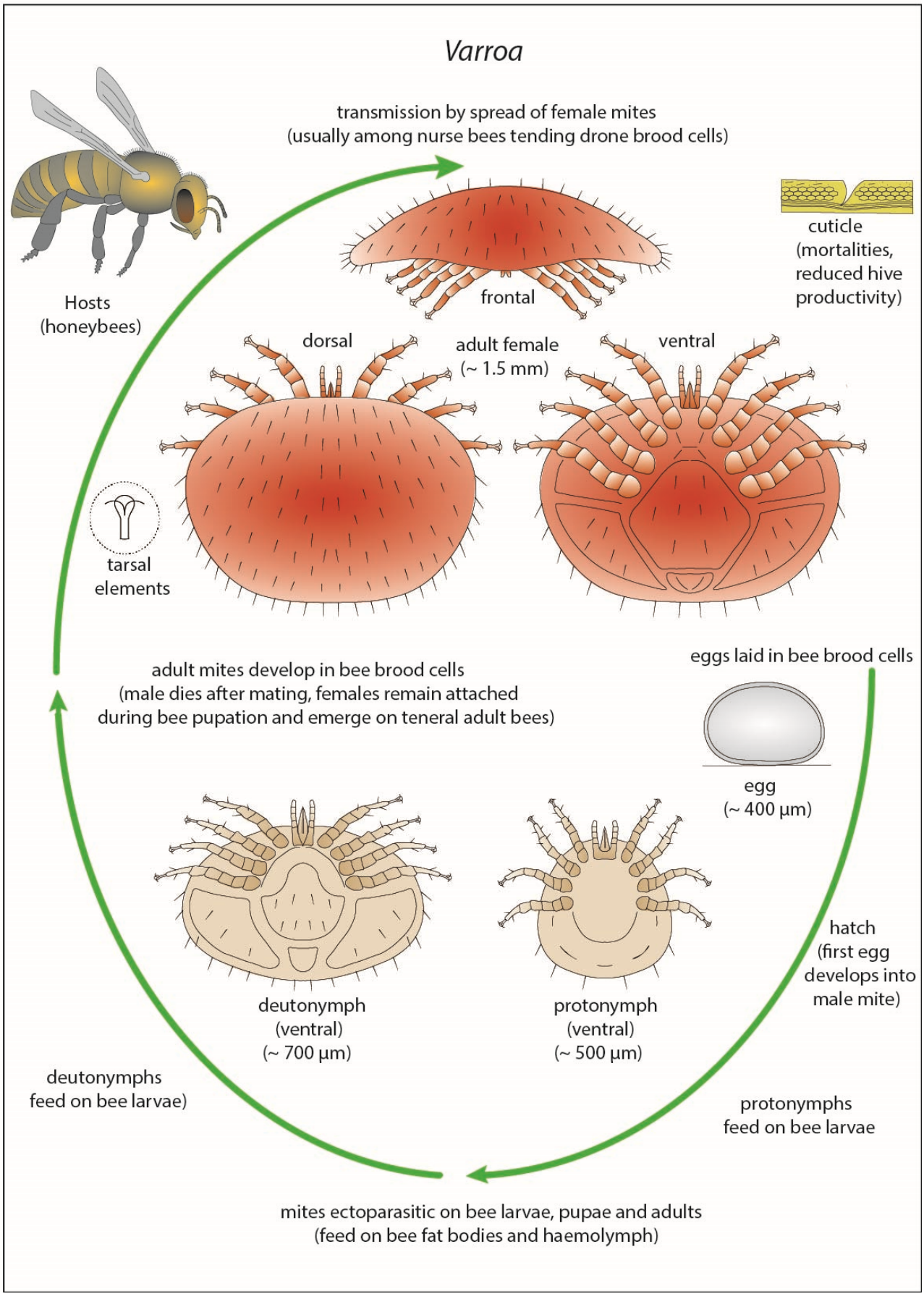
Developmental cycle and mode of transmission: *Varroa* spp. undergo incomplete (hemimetabolous) metamorphosis in which eggs hatch protonymphs that moult to deutonymphs and then to adults. The mites only reproduce when honeybee brood is present in hives. Honeybees reproduce using hexagonal brood cells constructed of waxy matrix in which the queen bee deposits eggs that hatch in 3 days. The emergent bee larvae feeds on brood food placed in the cell and worker bees close the cell with a waxy cap once the larvae reach a certain age. The encased larvae develop into prepupae and then pupae in which complete metamorphosis occurs forming adult bees which eclose after several weeks (16, 21 or 24 days for queen bees, worker bees and drone bees). The bee mites use these brood cells for their own reproductive purposes. Mated female mites (called mother mites or foundresses) enter brood cells containing mature bee larvae just before they are capped. The mites move to the bases of the cells and submerge themselves in the brood food. When the cells are capped, the bee larvae consume the rest of the brood food thus freeing the mother mites. The mites climb onto the bee larvae and begin feeding intermittently on haemolymph and fat body tissues. The mother mites then begin laying up to 5-6 mite eggs in the brood cell, the first egg being unfertilized and deposited after 60-70 hours, whereas the remaining eggs are fertilized and deposited every 25-30 hours thereafter. The first egg always develops into a male mite, while all subsequent eggs develop into daughter female mites. The long interval between the deposition of individual eggs means that mites at different stages of development will occur in the one cell. The mite eggs hatch within 12 hours releasing protonymphs that feed on the bee larvae, often at the same site as the mother mite. The protonymphs moult to form larger deutonymphs which also feed and then moult to form adult mites. It takes about 5–6 days for male mites to develop and 7–8 days for female mites to develop. Mating occurs in the brood cell, with the single male mite mating with his sisters (usually producing 1-2 mated daughter mites in worker bee brood cells, and 2-3 mated daughter mites in drone bee brood cells which take longer to mature). Male mites then die inside the brood cell shortly after mating, and mated female mites undergo reproductive modifications that prevent further mating. When the newly-formed adult bee emerges from the brood cell, the mother mite and her young daughter mites also leave, often on the emerging bee, and spread to other bees. Female mites are highly mobile and readily transfer between adult bees to attach and feed on fat bodies and haemolymph (often called ‘phoretic’ mites). They usually attach to young worker bees tending brood cells (i.e. nurse bees) for several weeks until brood cells of a suitable age become available for them to detach and enter in order to reproduce. Because nurse bees spend more time tending drone brood cells that take longer to mature than worker bee brood cells, many more drone cells become infested with mites (10-12 times more frequently). When the bee colony is not breeding and brood cells are absent, female

mites may survive attached to adult bees for 2-3 months (sometimes over-wintering for up to 5 months). However, female mites do not survive long away from host lasting only up to 5 days without food. Because mites are mobile and regularly seek hosts by crawling over combs, infestations may spread between bee colonies during normal apiary management practices when infested hives, equipment and bees (brood, queens and adults) are interchanged. Infestations are not spread in honey, but they may be spread during other normal bee behaviours, including brood nursing, comb construction and repair, foraging, swarming, robbing (taking nectar from other hives) and drifting (entering another hive by mistake). In the case of foraging, mites have been known to move onto flowers and then attach to other bees or insects visiting the same flower. Mites have been found incidentally on some bumble bees, flower flies, wasp larvae and scarab beetles, but their role in any phoretic transfer remains speculative. Mite population dynamics exhibit exponential growth when bee broods are available, and exponential decline when broods are absent. Various factors have been found to affecting mite population growth, including geographic location and climate (temperature, photoperiod), bee colony strength (species, vitality, innate resistance), and the incidence of other pests/pathogens (especially viruses). Mite populations grow faster in warmer regions where broods are available year-round, and slower in cooler areas where brood are not present over-winter. Mites weaken and kills colonies typically by out-reproducing their hosts. Bee populations usually peak in spring-summer with a steady decline thereafter, while mite populations follow suit but offset by a number of weeks. This means mite populations are peaking when bee populations are declining, thus precipitating colony collapse.

Differential diagnosis: Infestations are diagnosed by the direct detection of mites on bees or in hives using a range of examination techniques. Visual examination of adult bees may readily reveal reddish-brown mites attached to the abdomen or crawling over the body, although some think that the stress of bee capture and sedation may encourage mites to detach and drop off. Close inspection of bee brood, especially drones, may reveal dark mites on white developing bee stages. Authorities recommend regular screening of colonies (at least quarterly) to facilitate prompt action, and there have been several suggestions to adopt quantitative diagnostic methods, the most popular being sticky screens, ether rolls, or sugar shakes. Sticky screens involve coating pieces of cardboard in vaseline or petroleum jelly, covering them with fine-wire mesh (3 mm) and placing them under combs for 1-3 days to collect any dislodged mites (technique therefore samples from whole colony rather than from a small subset of bees). Ether rolls involve placing around 300 bees in a glass jar, spraying with ether and rolling the jar so dislodged mites adhere to the inside walls of the jar. Sugar shakes involve placing about 300 bees in a jar with a tablespoon of powdered sugar (icing sugar), gently shaking for several minutes and then tipping out the sugar onto white paper or dissolving it in water to reveal dislodged mites. Other variations involve submerging dead bees in alcohol (70% or higher) and then examining the washings for mites. A range of molecular biological techniques have been used to detect and characterize mite species and populations by polymerase chain reaction (PCR) amplification of random amplified polymorphic DNA (RAPD) or nuclear (18S ribosomal RNA) and mitochondrial (12S and 16S ribosomal RNA, cytochrome oxidase) gene sequences. Next generation sequencing has also been used to determine the while nuclear and mitochondrial genome, thus facilitating proteogenomic studies on proteins differentially expressed across developmental stages and following various acaricidal treatments.

Treatment and control: Traditionally, infestations in bee hives have been controlled by the application of chemical acaricides (miticides) as fumigants (vapours released from strips, pads, gels), sprays (water or oil based), powders or in medicated food sources (sugars). Variable successes have been reported following treatments with organophosphates (coumaphos), pyrethroids (fluvalinate), amidines (amitraz), organic acids (oxalic acid, formic acid, beta acid) and mineral oil or essential oils (lemon, mint, thyme). Careful attention should be paid to any treatment contra-indications to minimize the contamination of honey and prevent any side-effects that may include reduced longevity and fecundity of queen bees and/or drones. Regrettably, there are growing numbers of reports of mite populations developing resistance to pyrethroid and organophosphate acaricides, particularly those used as general insecticides in horticulture to which bees may be exposed (e.g. sprays used in orchards, gardens, etc). An alternative treatment strategy that yielded variable results was the application of powdered sugar or talcum powder (grain size 5-15 μm) to bees which apparently interfered with mite respiration. There have also been numerous suggestions for non-chemical (physical) methods to control mite populations, mostly by changing beehive architecture and comb maintenance. The installation of perforated bottom boards or open screen floors (3 mm holes or mesh) in hives so that dislodged mites fall through has been credited with 10-20% reductions in mite populations, particularly if glue traps or sticky boards are also included so that mites do not crawl back into the hive. Experimental studies have shown that heating hive frames to at least 40 C for several hours causes mites to drop from bees, and several ventures are currently exploring engineering options. Mite populations have also been reduced by manipulating bee broods by the regular removal of capped broods every 9 days for several cycles, by selectively excising drone broods (identified at the ‘purple-eye’ stage of development along the bottom and outer margins of frames) or by removing and freezing capped broods for 48 hours (which kills both drones and mites). While these methods change both bee population dynamics (numbers) and kinetics (time course), nurse bees clean out dead brood, drones are usually in excess and queen bees replace lost brood. Government agencies in many countries have declared *Varroa* mite infestations as notifiable diseases with specific courses of action to be undertaken in the event of outbreaks, including strict quarantine, compulsory treatment and even hive destruction. Sentinel bee populations have also been established for biosecurity purposes near possible points of ingress, notably airports and wharves. Beekeepers are urged to practise good sanitation and hygiene by obtaining brood stock from reputed pest-free sources, regularly disinfecting hives and equipment using hot washing soda or hypochlorite bleaches, and regularly inspecting and replacing brood combs. There have been several interesting developments in bee breeding programmes, with encouraging results obtained breeding from bees with enhanced grooming behaviours (self- and allo-grooming), heightened brood hygiene (better able to detect problems with brood even if capped, and abort the affected brood), and bee strains that have developed a general resistance or tolerance to mites (e.g. bees from endemic Russian

regions have greater resistance/tolerance). Recent molecular biological studies have also begun to examine the possibility of using RNA interference techniques to knock out genes in *Varroa* mites.

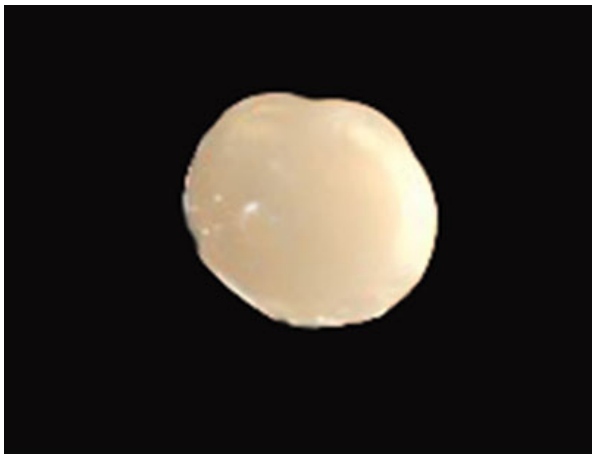

Varroa
transmission by spread of female mites
(usually among nurse bees tending drone brood cells)
Hosts
(honeybees)
frontal
cuticle
(mortalities,
reduced hive
productivity)
dorsal
adult female
(~ 1.5 mm)
ventral
tarsal
elements
eggs laid in bee brood cells
adult mites develop in bee brood cells
(male dies after mating, females remain attached
during bee pupation and emerge on teneral adult bees)
egg
(~ 400 µm)
deutonymph
(ventral)
(~ 700 µm)
protonymph
(ventral)
(~ 500 µm)
hatch
(first egg
develops into
male mite)
deutonymphs
feed on bee larvae)
protonymphs
feed on bee larvae
mites ectoparasitic on bee larvae, pupae and adults
(feed on bee fat bodies and haemolymph)



Varroa adult on bee pupa



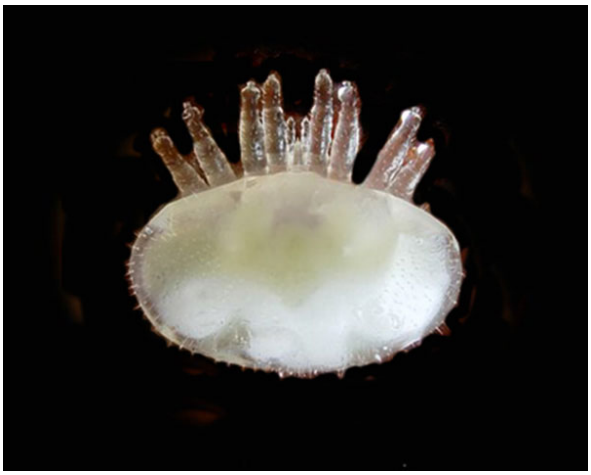
Varroa adult



Varroa egg



Varroa protonymph



Varroa deutonymph

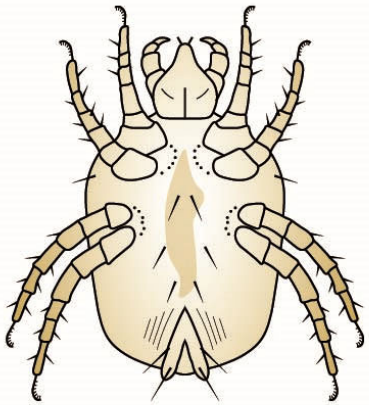
Prostigmata
(mites)

Acari: Prostigmata

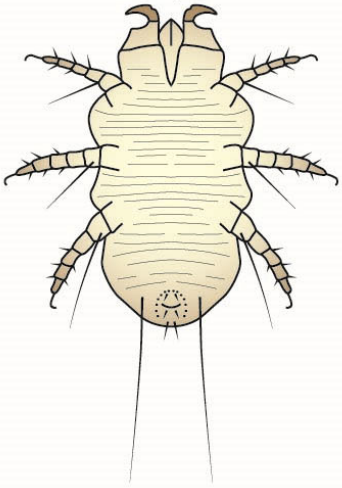
Demodex
adult (ventral)
(~ 400 µm)



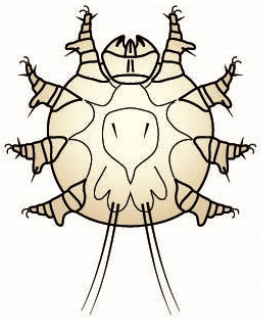
Cheyletiella
adult female (ventral)
(~ 500 µm)



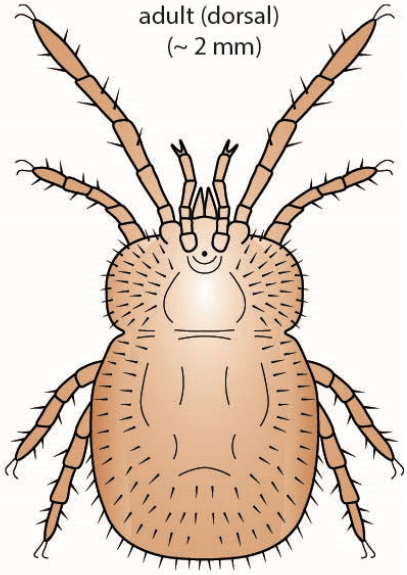
Myobia
adult female (ventral)
(~ 500 µm)



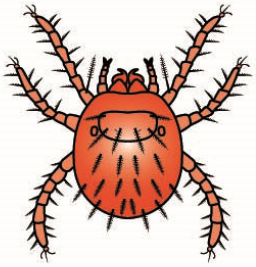
Psorobia
adult female (ventral)
(~ 200 µm)



Trombicula
adult (dorsal)
(~ 2 mm)



Trombicula
larva (dorsal)
(~ 500 µm)



Demodex
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Trombidiform mites have stigmata on the gnathosoma and distinct setae on their bodies and legs. Many species are free-living, some have been associated with allergy (including asthma), and several are obligate ectoparasites on mammals or birds. Demodecids are small follicle mites with elongate cigar-shaped bodies and stumpy anterior legs. Infestations by *Demodex* spp. occur on many mammalian hosts, sometimes associated with follicular, squamous or pustular dermatitis (demodectic mange).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Prostigmata [Trombidiformes] (sucking mites, stigmata on gnathosoma)
Suborder: Eleutherengona (thumb-claw process, tube-like midgut, females with adjacent anal-genital openings)
Superfamily: Cheyletoidea (chelicerae with basal stylophore and stylet-shaped movable segments)
Family: Demodecidae (small follicle mites, elongate cigar-shaped body, 4 pairs stumpy legs at front of body)
Genus: *Demodex* (parasitic on skin/hairs of mammals)
Species: various species cause demodectic mange in animals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					

Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of prostigmate mites have been described: many species being free-living (including most trombiculids although some have parasitic larvae); and others being obligate ectoparasites on mammals or birds. Parasitic species spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Prostigmatid mites are characterized by having oval-ellipsoidal bodies (sometimes vermiform) with distinctive setation, piercing chelicerae (sometimes pincer-like), unbarbed hypostomes, well-developed palps, and short legs with coxae fused to the body wall and terminal tarsi with 1-2 claws (but lacking complex pulvilli). A total of 34 superfamilies have been recognized in 4 suborders: Anystina (with 17 superfamilies); Eleutherengona (10); Endeostigmata (3); and Eupodina (4). Many members of the suborders Anystina and Eleutherengona have legs with distinctive arrangements of the terminal tibiotarsal segments referred to as the 'thumb-claw' process. Eleutherengone mites have simple tube-like postventricular midguts, small salivary glands (if present), females with anal and genital openings located close together posteriorly, and males with few glandular components of their testicular epithelia and accessory glands. Ten superfamilies are recognized (Cheyletoidea, Eriophyoidea, Pomerantzioidea, Pterygosomatoidea, Pyemotoidea, Pygmephoroidea, Raphignathoidea, Tarsocheyloidea, Tarsonemoidea, Tetranychoidea)

The superfamily Cheyletoidea comprises free-living predators, nidicolous forms and highly specialized ecto- or endo-parasites. Adult mites have chelicerae with basal segments fused into a single unit (stylophore), movable segments that are stylet-shaped, and the female anal and genital openings are located ventrally. A total of 8 families are recognized (Cheyletidae, Cloacaridae, Demodicidae, Harpyrhynchidae, Myobiidae, Ophioptidae, Psorergatidae, Syringophilidae). The family Demodecidae contains the follicle mites infesting the hair follicles and skin pores of mammals. They have unique elongate bodies, often referred to as cigar-, crocodile-, or worm-like (vermiform), with transverse annulations on the long posterior idiosoma. They have 4 pairs of short stumpy legs located at the front of the idiosoma, and highly reduced chaetotaxy (setae usually absent on body and legs). Eight genera have been recognized (*Apodemodex*, *Demodex*, *Epimyodex*, *Ophthalmodex*, *Pterodex*, *Rhinodex*, *Soricidex*, and *Stomatodex*) differing primarily in their host specificity, tissue tropism and geographic distribution. Over 100 species have been described in the genus *Demodex*, most species being specific for individual mammalian hosts, including bats, rodents, lagomorphs, insectivores, carnivores, ungulates and primates (including humans). Many species are considered to be commensals living within the hair follicles of their hosts, but an increasing number have been associated with clinical disease (demodeciosis) characterized by inflammation (folliculitis) and sometimes skin lesions.

***Demodex* species**	**Hosts**	**Clinical signs**	**Distribution**
D. acutipes	Artiodactyla: cervid (red deer)		Europe
D. aelleni	Chiroptera: vespertilionid (Daubenton's bat)		Europe
D. agrarii	Rodentia murid (striped field mouse)		Europe
D. ailuropodae	Carnivora: ursid (giant panda)		Asia
D. antechini	Dasyuromorphia: dasyurid (agile antechinus)		Australia
D. apodemi	Rodentia murid (wood mouse)		Europe
D. aries	Artiodactyla: bovid (sheep)		New Zealand
D. artibei	Chiroptera: phyllostomid (Aztec fruit-eating bat)		North America
D. arvicolae	Rodentia: cricetid (short-tailed field vole)		Europe
D. aurati	Rodentia: cricetid (golden hamster)		North America (lab.) ex: Europe
D. bandicotae	Rodentia: murid (bandicoot rat)		Asia
D. bicaudatus	Chiroptera: pteropodid (long-tongued nectar bat)		Australia
D. bisonianus	Artiodactyla: bovid (European bison)		Europe
D. bovis	Artiodactyla: bovid (cattle, European bison)	mange, caseous nodules, pyoderma, furunculosis, ulceration, crusting	worldwide
D. brevis	Primates: hominid (human)	subclinical, occasionally itching, inflammation, blepharitis	worldwide
D. buccalis	Rodentia: cricetid (bank vole)		Europe
D. caballi	Perissodactyla: equid (horse)	mange	worldwide (except Australia)
D. cafferi	Artiodactyla: bovid (African buffalo)		Africa
D. canis	Carnivora: canid (dog, wolf)	mange (squamous, pustular or follicular), alopecia, thickened skin, pustules (red mange ooze serum)	worldwide
D. caprae	Artiodactyla: bovid (goat)	mange, caseous nodules, pyoderma, furunculosis, ulceration, crusting	worldwide
D. carollia	Chiroptera: pteropodid (Seba's short-tailed bat)		South America
D. cati	Carnivora: felid (cat)	mange, alopecia, thickened skin, papules, scaling	worldwide
D. caviae	Rodentia: caviid (guinea pig)		South America
D. cervi	Artiodactyla: cervid (red deer)		Europe
D. chiropteralis	Chiroptera: vespertilionid (brown long-eared bat)		Europe
D. conicus	Rodentia: murid (house mouse)		Europe
D. cornei	Carnivora: canid (dog)		North America
D. corniculatus	Rodentia: murid (yellow-necked mouse)		Europe
D. criceti	Rodentia: cricetid (golden hamster)		North America (lab.) ex: Europe
D. cricetuli	Rodentia: cricetid (grey dwarf hamster)		North America (lab.) ex: Eurasia
D. cuniculi	Lagomorpha: leporid (European rabbit)		cosmopolitan
D. cyonis	Carnivora: canid (dog)		Japan

D. dasypodi	Cingulata: dasypodid (nine-banded armadillo)		North America
D. desmodi	Chiroptera: phyllostomid (common vampire bat)		South America
D. equi	Perissodactyla: equid (horse)	mange (squamous or pustular), papules, pustules, alopecia, scaling	worldwide (except Australia)
D. erinacei	Eulipotyphla: erinaceid (European hedgehog)		Europe
D. erminae	Carnivora: mustelid (stoat)		Europe
D. flagellurus	Rodentia murid (house mouse)		Europe
D. folliculorum	Primates: hominid (human)	subclinical, occasionally itching, inflammation, blepharitis	worldwide
D. foveolator	Eulipotyphla: soricid (lesser white-toothed shrew)		Europe
D. fusiformis	Rodentia: murid (house mouse)		Europe
D. gapperi	Rodentia: cricetid (southern red-backed vole)		North America
D. gatoi	Carnivora: felid (cat)	mange, alopecia	worldwide
D. ghanensis	Artiodactyla: bovid (cattle)	mange	worldwide
D. glareoli	Rodentia: cricetid (bank vole)		Europe
D. gliricolens	Rodentia: cricetid (European water vole)		Europe
D. gracilentus	Rodentia: murid (striped field mouse)		Europe
D. huttereri	Rodentia murid (striped field mouse)		Europe
D. injai	Carnivora: canid (dog, wolf)	mange, pruritus, alopecia	worldwide
D. intermedius	Scandentia: tupaiid (common treeshrew)		Asia
D. kutzeri	Artiodactyla: cervid (sika deer, red deer)		Europe
D. lacrimalis	Rodentia murid (wood mouse)		Europe
D. leucogasteri	Rodentia: cricetid (grasshopper mouse)		North America
D. longior	Rodentia murid (wood mouse)		Europe
D. longissimus	Chiroptera: pteropodid (Seba's short-tailed bat)		South America
D. lutrae	Carnivora: mustelid (European otter)		Europe
D. macaci	Primates: cercopithecid (rhesus macaque)		North America (lab: ex Asia)
D. macroglossi	Chiroptera: pteropodid (long-tongued nectar bat)		Australia
D. marculus	Rodentia: murid (mouse)		Europe
D. marsupiali	Didelphimorphia: didelphid (common opossum)		North America
D. melanopteri	Chiroptera: vespertilionid (Brazilian brown bat)		South America
D. melesinus	Carnivora: mustelid (European badger)		Europe
D. mexicanus	Chiroptera: vespertilionid (Mexican big-eared bat)		North America
D. microti	Rodentia: cricteid (common vole)		Europe
D. molossi	Chiroptera: molossid (velvety free-tailed bat)		South America
D. muscardini	Rodentia: glirid (hazel dormouse)		Europe
D. musculi	Rodentia: murid (mouse)	mange (follicular)	cosmopolitan
D. mystacina	Chiroptera: mystacinid (New Zealand lesser short-tailed bat)		New Zealand
D. nanus	Rodentia murid (black rat, brown rat)		cosmopolitan
D. neomydis	Eulipotyphla: soricid (Mediterranean water shrew)		Europe
D. neoopisthosomae	Chiroptera: pteropodid (cave nectar bat)		Asia
D. norvegicus	Rodentia murid (brown rat)		Europe
D. novazelandica	Chiroptera: mystacinid (New Zealand lesser short-tailed bat)		New Zealand
D. nycticeii	Chiroptera: vespertilionid (evening bat)		North America
D. odocoilei	Artiodactyla: cervid (white-tailed deer)		North America
D. ovis	Artiodactyla: bovid (sheep)	mange, papular/nodular lesions, alopecia, scaling	worldwide
D. peromysci	Rodentia: cricetid (white-footed mouse)		North America
D. phocidi	Carnivora: phocid (harbor seal)		North America
D. phodopi	Rodentia: cricetid (winter white dwarf hamster)		North America (lab.) ex: Asia
D. phylloides	Artiodactyla: suid (pig)	mange, erythema, papules, thickened skin	worldwide
D. phyllostomatis	Chiroptera: phyllostomatid (greater spear-nosed bat)		South America
D. plecoti	Chiroptera: vespertilionid (brown long-eared bat)		Eurasia

D. ponderosus	Rodentia: murid (brown rat)		Europe
D. pseudaxisi	Artiodactyla: cervid (sika deer)		Asia
D. ratti	Rodentia murid (brown rat)		Europe
D. ratticola	Rodentia murid (brown rat)	mange (follicular)	Europe
D. rosus	Rodentia: murid (yellow-necked mouse)		Europe)
D. sabani	Rodentia murid (long-tailed giant rat)		Asia
D. saimiri	Primates: cebid (Guianan squirrel monkey)		South America
D. sciurinus	Rodentia: sciurid (red squirrel)		Europe
D. sinocricetuli	Rodentia: cricetid (Chinese striped hamster)		North America (lab.) ex: Asia
D. soricinus	Eulipotyphla: soricid (common shrew)		Europe
D. spelaea	Chiroptera: pteropodid (cave nectar bat)		Asia
D. sungori	Rodentia: cricetid (winter white dwarf hamster)		North America (lab.) ex: Asia
D. talpae	Eulipotyphla: talpid (European mole)		Europe
D. tauri	Artiodactyla: bovid (cattle)	mange	worldwide
D. tigris	Carnivora: felid (tiger)		Asia
D. tortellinioides	Dasyuromorphia: dasyurid (agile antechinus)		Australia
D. uncii	Carnivora: felid (snow leopard)		North America (zoo)
D. ursi	Carnivora: ursid (American black bear)		North America
D. vibrissae	Rodentia: murid (house mouse)		Europe
D. zalophi	Carnivora: otariid (California sea lion)		North America

Parasite morphology: *Demodex* spp. form 4 different types of morphological stages during their developmental cycles: eggs; larvae; nymphs (2 instars); and adults. Eggs are quite variable in size and shape depending on species, ranging from elliptical to fusiform to arrowhead-shaped and measuring from 25-88 µm in length (e.g. *D. folliculorum* arrowhead 80-100 x 40 µm, *D. brevis* fusiform 60 x 34 µm, *D. musculi* elliptical 25-45 x 10-21 *µm*). Larvae are elongate fusiform (spindle- or carrot-shaped) stages ranging in length from 45-200 µm (e.g. *D. folliculorum* ~150 µm, *D. brevis* ~100 µm, *D. musculi* ~60 µm). They have a small anterior gnathosoma (head or capitulum) bearing lateral supracoxal spines (minute sclerotized pegs) and short stout palps (terminating in 1-3 anterior spines). The posterior idiosoma (body) is semitransparent, colourless to beige-coloured and divided into the anterior podosoma (bearing legs) and the posterior opisthosoma (tapering to a blunt tail). Larvae are hexapods with 3 pairs of unsegmented legs, each ending in a single claw with 2-3 prongs (tines). They have 2-3 pairs of small shelf-like epimeral scutes located between each pair of legs and the opisthosoma usually lacks annulations. Several reports in the literature suggest that a second hexapod larval stage occurs, although others consider it to be the first nymphal instar (protonymph) that often only displays 3 pairs of legs (a rudimentary fourth pair can sometimes be observed). The protonymphs have small rectangular heads and elongate tapering bodies measuring from 60-200 µm in length depending on species (e.g. *D. folliculorum* 150-250 µm, *D. brevis* ~150 µm, *D. musculi* 60-140 µm). The first 3 pairs of legs are beginning to show segmentation and they terminate in one pair of claws with 3 denticles, while the fourth pair of legs (when present) appear as rudimentary stubs. Ventral epimeral scutes are present between each pair of legs and the opisthosoma shows lateral indentations consistent with developing annulations. Deutonymphs are larger in size ranging from 140-400 µm in length (e.g. *D. folliculorum* 250-400 µm, *D. brevis* 150-200 µm, *D. musculi* 140-200 µm). The gnathosoma has spatulate supracoxal spines, and short stout palps with 2 movable segments ending in a curved dorsal spine and 2 anteroventral spines. Deutonymphs have 4 pairs of short anteroventral legs projecting from the lateral body margins, each leg ending in 2 claws and each claw having 4 apices. There are 4 pairs of ventral epimeral scutes located between the legs and the annulations on the opisthosoma have become more evident. Adult *Demodex* mites have distinctive body profiles, being described variously as crocodile-like, carrot-like, cigar-like, oblanceolate, obovate to spathulate. Their bodies are slender, elongate, truncated anteriorly, gradually tapering posteriorly, flattened ventrally and convex dorsally. Different mite species vary in size from long- to short-bodied, most of it attributable to the length of the opisthosoma. Adult mites range in size from 80-400 µm in length (e.g. *D. bovis* up to 400 µm, *D. folliculorum* 300-400 µm, *D. injai* 330-370 µm, *D. canis* 180-300 µm, *D. cati* 180-220 µm, *D. brevis* 150-200 µm, *D. musculi* 118-193 µm, *D. gatoi* 80–115 µm). They are all bound by chitinous cuticles which are partially transparent and appear colourless to creamy white with slightly darker mouthparts and feet. Their bodies lack setae, antennae and wings. The anterior gnathosoma is rectangular to horseshoe-shaped, usually with large supracoxal spines, and bears short blunt mouthparts (paired chelicerae and central hypostome) flanked by sensory palps. The palps are stout and consist of 3 segments, the second segment often with lateral horn-like projections, and the terminal segment ending in a hyaline denticulus with a lateral horn and 2-3 claw-like ventral spines (apotele absent). The paired chelicerae are adapted for piercing and consist of 3-segmented needle-like stylets whose basal segments were fused into a single stylophore. The oral opening (mouth) was pincer-like with a dorsal rostrum, ventral buccal cone and small unbarbed hypostome. The digestive tract was rudimentary and comprised a tubular foregut (oesophagus, pharyngeal bulb), saccular midgut (ventriculus and diverticulae), and a tubular hindgut (with excretory Malpighian tubules). Many early studies considered these mites to lack an anus (suggesting that faecal waste accumulated in the body during their brief lifespans and was only released when they died), but recent studies found they do have a minute subterminal anus located ventrally. Similarly, few descriptions recorded the occurrence of respiratory openings (stigmata), but like all prostigmatid mites, they are presumably located

laterally near the ventral bases of the chelicerae. The idiosoma lacked sclerotized shields and was divided into an anterior trapezoidal podosoma and a posterior elongate opisthosoma (the latter usually comprising >50% of the total body length). The opisthosoma contained the reproductive organs and its exterior surface was distinctly annulated with many transverse striations. The ventral podosoma was the point of attachment for 4 pairs of short stout legs that projected laterally outwards, many having dorsal sensory setae (solenidia). The legs were segmented, with basal epimeral plates (coxal fields) fused to the body wall giving rise to 3 movable segments (some with spurs) and all ending in a tegumental fold with a pair of bifid claws and a recurved spur (complex pulvilli or suckers absent). Adult mites exhibited sexual dimorphism, with males being smaller than females and having genital openings located dorsally rather than ventrally like females. Mature female mites have ovaries joined by oviducts to a uterus that opens to a longitudinal slit-like vulva located on the ventral midbody just behind the last pair of legs. Mature male mites have testes connected by vas deferens to an ejaculatory duct leading to an elongate aedeagus (penis with bulbous base and long sheath) situated longitudinally along the dorsal idiosoma with the genital opening appearing as a longitudinal slit around the level of the first and second pair of legs.

Site of infection: *Demodex* mites are obligate ectoparasites in the skin of mammals, but they live sheltered within hair follicles, sebaceous glands, Meibomian glands and epidermal pits (whilst within the bulk of the skin, they are technically external to the epidermis and are considered ectoparasitic). Over 100 mite species have been described in mammals belonging to 31 families in 12 orders (particularly rodents, but also ungulates, carnivores, insectivores, lagomorphs, bats, and primates). Most mite species were oioxenous, (specific for individual host species) although a few were able to live on other closely-related hosts but not as successfully. A few hosts also had multiple mite species found on them, but they occurred in different sites (exhibited tissue tropism). For example, humans were found to host 2 species: *D. folliculorum* which occurs primarily in the follicular infundibulum of hairs (often in groups of up to 15 mites); and *D. brevis* which is found deeper within the follicle in the sebaceous gland where more oil is produced (usually as solitary mites). Infestations on humans have been found mainly in facial skin (forehead, scalp, cheeks, nose, eyebrows and eyelashes) but occasionally in the external ear canals, chest, nipples, mons veneris, buttocks, and even sebaceous glands in the buccal mucosa. Infestations on livestock and pets generally involve the face (muzzle, eyelids) and neck but may extend to the shoulders, flanks and legs.

Pathogenesis: Mites live embedded head-down in skin follicles and glands using their pincer-like chelicerate mouthparts to puncture epithelial and sebaceous cells to feed on sebum (oil) and cellular debris. In normal healthy hosts, *Demodex* mites occur in low numbers and most infestations are asymptomatic (often to the point that the mites are considered to be commensals rather than parasites). However, under certain conditions (when hosts are stressed or immuno-compromised), heavier infestations may develop causing clinical disease (known as demodicosis or demodectic mange). Feeding mites cause direct damage to the epidermis of hair follicles and glands resulting in inflammation, skin lesions, alopecia and predisposing to secondary bacterial infections. Hosts recognize mite antigens locally or in regional lymph nodes leading to humoral and/or cellular immune responses resulting in either protection or hypersensitivity. Two main types of skin lesions may develop: squamous and pustular lesions. The most common are squamous lesions that appear as dry scaly patches of skin with enlarged and inflamed hair follicles (folliculitis) exhibiting follicular hyperplasia and hyperkeratosis, mononuclear inflammatory cellular infiltrates, irregular thickening of the skin, variable pruritus (often developing secondary to bacterial infections), alopecia (due to follicular apoptosis) and skin pigmentation (increased sun exposure due to alopecia). Papular nodules may also occur when hair follicles or gland ducts become obstructed resulting in cyst-like swellings. The second type of lesions are pustular lesions that occur less commonly but are more severe. They appear as red pustules on thickened wrinkled skin and are the result of ruptured follicles and glands leading to more extensive inflammation with pruritus and secondary bacterial infections (commonly *Staphylococcus* spp.) leading to purulent exudates. In domestic animals, demodicosis is more common in dogs, pigs and goats, but rarer in horses, cats, cattle and sheep. Infestations may cause severe mange in dogs, especially immuno-compromised individuals which often develop concurrent staphylococcal pyoderma and fungal (*Malassezia*) dermatitis due to reduced T-cell function. This renders dogs susceptible to massive mite proliferation leading to generalized skin thickening with corrugations and alopecia. Infestations manifest differently depending on whether they are juvenile-onset (3-18 months of age, exacerbated by puberty and oestrus) leading to localized disease, or adult-onset (> 2 years old, often associated with underlying disease (diabetes, cancer) or immunosuppression (chemotherapy, excessive cortisone) leading to generalized disease. Localized demodicosis usually involves 1-2 areas on the head/limbs with circumscribed scaly lesions and erythematous alopecic areas. The occurrence of pruritus is variable and most localized infestations heal spontaneously. Generalized demodicosis is a more severe condition complicated by secondary bacterial infection (pyoderma) and involves multiple alopecic lesions over the body which frequently coalesce, leading to extensive folliculitis, erythema, comedones, scaling. crusting, plaques, and pruritus. There is often an underlying lymphadenopathy and mites around the ears may cause otitis externa. Mites have occasionally been found in internal tissues (lymph nodes, kidneys, intestinal walls, thyroid gland) after their dissemination by lymph or blood, but they have usually been killed by host responses. Infestations in pigs are frequently associated with papular skin nodules, and those in cats with underlying immuno-suppressive conditions are usually associated with mild localized self-limiting disease on the head (including the eyelids and external ear canals) and neck. Infested ruminants may develop inflammatory and hypersensitive reactions leading to widespread thickening of the skin, including sebaceous glands which fill with mites and secretions (sometimes becoming caseous). Dermal papules and flat nodules may form on the neck, shoulders, brisket and forelegs, with occasional ulceration, abscess formation, crusting and alopecia occurring in conjunction with follicular rupture and/or secondary bacterial infections. Most infestations on rodents appear to be well tolerated, but those occurring in immunocompromised mouse breeds kept in laboratory animal colonies may progress to cause severe dermatitis with pruritus, alopecia, ulcer and/or

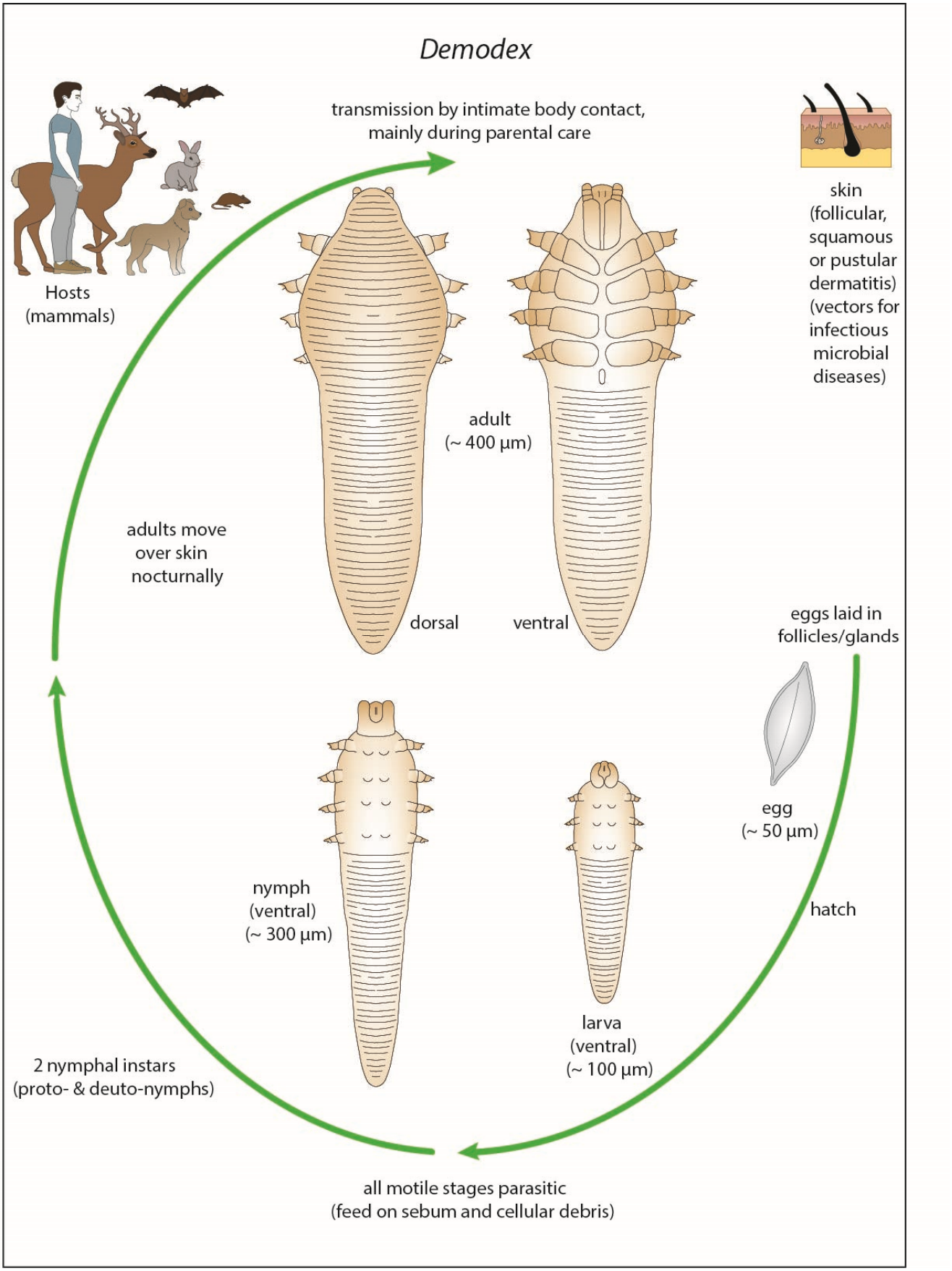
abscess formation. The 2 mite species (*D. folliculorum* and *D. brevis*) found in humans are apparently very prevalent with reports suggesting that up to 50-95% of the population may be infested. The vast majority of infestations are asymptomatic, but those occurring in individuals with immuno-deficiencies (genetic or acquired due to chemotherapy, concomitant infections or disease) may contribute to dermatological and ocular conditions. Individuals may develop mild-severe inflammation, with squamous and/or pustular lesions, alopecia, pruritus, blepharitis, and sometimes granuloma formation. Infestations have tentatively been linked to rosacea, acne and perioral dermatitis in some humans. Studies have shown that *Demodex* mites may act as mechanical or biological vectors for the carriage and transmission of microbes causing disease, including the Gram-negative bacterium *Bacillus oleronius* associated with rosacea, and the Gram-positive bacteria *Mycobacterium leprae* causing Hansen's disease (leprosy) and *Staphylococcus* spp. causing opportunistic dermal or systemic infections.

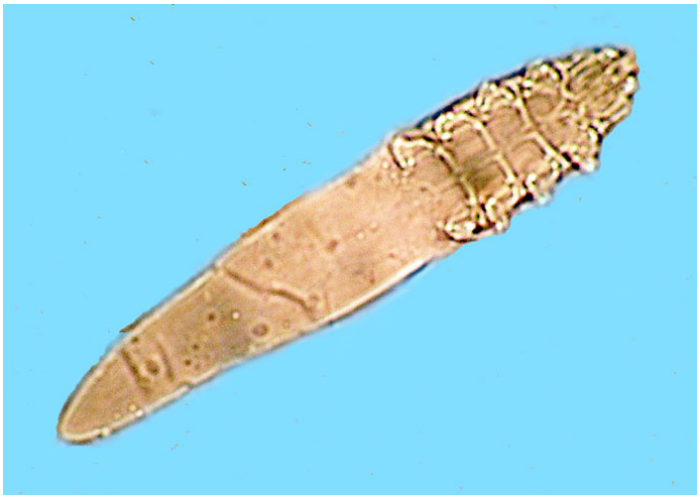
Developmental cycle and mode of transmission: Like all mites, *Demodex* spp. undergo incomplete (hemimetabolous) metamorphosis whereby eggs hatch larva that moult to nymphs and then to adult mites. The entire life cycle takes place within hair follicles and skin glands on the same host, and mites are transmitted between hosts by intimate body contact, predominantly during parental care. Mite eggs are laid in follicles/glands where they hatch after 5 days releasing hexapod (6-legged) larvae. The larvae feed and moult in 2 days to the first nymphal instar (protonymphs) which are usually hexapod (some reports have described a rudimentary fourth pair of legs, while a few have reported them to be octopod (8-legged)). The protonymphs feed in the follicle/gland and then move to the opening around 3 days later to moult to the second nymphal instar (deutonymphs), all described as octopod. The deutonymphs migrate to the surface of the skin and then re-enter follicles/glands to moult after 5 days to form adult mites. The adults are not sedentary but leave follicles/glands onto contiguous skin during the evening in search of mates or other food sources. They have been found to move at 8-16 mm/h during their nocturnal wanderings and they are negatively phototactic retreating back into follicles/glands in the presence of bright light. Mating occurs on the surface of the skin and in openings of follicles/glands. Gravid females then lay 20-40 eggs in follicles/glands, thus completing the whole life cycle in 18-35 days. Adults do not have long lifespans and die soon after mating/oviposition within 5 days. All mite stages are very sensitive to desiccation and are unable to survive off hosts. Transmission between hosts therefore only occurs through direct physical contact (skin-to-skin), particularly from parent to progeny during parental care (nursing, pacifying, cuddling, grooming, sleeping, etc.). Infestations are commonly found in adults as they produce more sebum than infants and some reports indicate that infestations are more common in developing countries due to lax hygienic practices.

Differential diagnosis: Infestations may be suspected on clinical grounds (squamous or pustular lesions, alopecia), although other aetiological agents may be the culprits and secondary bacterial infections are common in clinical demodicosis. Differential diagnoses are conventionally made by the direct detection of mites in skin samples, particularly deep skin scrapings, and sometimes trichograms (hair plucks). Mites are resistant to caustic agents so skin samples are usually digested in warm 10% potassium hydroxide so sediments can be easily screened for mites using high contrast light microscopy. It is advised that multiple skin scrapings be examined from early primary lesions (follicular papules/pustules) or the periphery of active lesions, that the skin be squeezed before and during scraping, and that the area be scraped until capillary bleeding occurs. Superficial skin scrapings are inadequate, as are sticky-tape impressions or smears of expressed pustule contents. Skin biopsies have occasionally been used in cases where lesions are inaccessible for scraping or plucking (e.g. feet, eyes, ears). More recently, a range of molecular biological techniques have been applied to the diagnosis and characterization of mite species, strains and isolates by polymerase chain reaction (PCR) amplification of nuclear (18S ribosomal RNA, chitin synthase) and mitochondrial (16S ribosomal RNA, cytochrome c oxidase I) gene sequences.

Treatment and control: Most clinical cases of localised demodicosis resolve spontaneously within 6-8 weeks, but more severe or generalized infestations often require treatment with chemical acaricides (miticides). Successful treatments have been reported using sulphur-based preparations (e.g. lime sulphur), natural products (rotenone, tea tree oil), organo-chlorines (lindane (gamma-benzene hexachloride)), organo-phosphates (trichlorfon, malathion, fenchlorphos, phosmet), pyrethroids (permethrin), anilides (crotamiton), carbamates (carbaryl), formamidines (amitraz) and macrocyclic lactones (ivermectin, moxidectin, doramectin or milbemycin). Topical treatments may be improved by clipping the hair beforehand, or using shampoos (e.g. benzoyl peroxide) to clean the skin by removing oil and cellular debris. It is recommended that all animals in contact be treated at the same time and that attention be paid to any drug contra-indications regarding side-effects, toxicity issues and even with-holding periods in the case of meat/milk animals. Treatment often needs to be repeated as recurrences are common, although the use of acaricides with long-lasting residual activity helps to reduce treatment frequency. Generalized infestations may require lengthy and aggressive treatment, usually in conjunction with oral antibiotics and topical antiseptics to eliminate any concurrent pyoderma. Treatment efficacy should be assessed through regular (monthly) skin scrapings, and hosts should be screened for any underlying disorders that may compromise their immune function. The use of glucocorticoids to alleviate inflammation should be avoided as the resultant immuno-suppression may foster generalized infestations and pyoderma. Animals should be placed on nutritious diets and kept as stress-free as possible to avoid reduced immune functions. Veterinarians may consider neutering severely affected animals as oestrus can precipitate disease. It has also been observed that the development of disease may have a genetic predisposition so breeding from affected animals should be discouraged. While transmission involves intimate body contact between hosts, some simple preventive precautions may help reduce risks, such as regularly washing with soap and water (helps considerably in cases involving blepharitis), maintaining strict

hygiene when nursing/suckling, not sharing bedding or towelling, cleaning animal holding facilities (especially those used for breeding) and avoiding situations where skin pores may become blocked (body/facial lotions, cosmetics, cooking oil vapours, etc.).


Demodex
transmission by intimate body contact, mainly during parental care
Hosts (mammals)
skin (follicular, squamous or pustular dermatitis) (vectors for infectious microbial diseases)
adult (~ 400 µm)
dorsal
ventral
adults move over skin nocturnally
eggs laid in follicles/glands
egg (~ 50 µm)
hatch
larva (ventral) (~ 100 µm)
nymph (ventral) (~ 300 µm)
2 nymphal instars (proto- & deuto-nymphs)
all motile stages parasitic (feed on sebum and cellular debris)



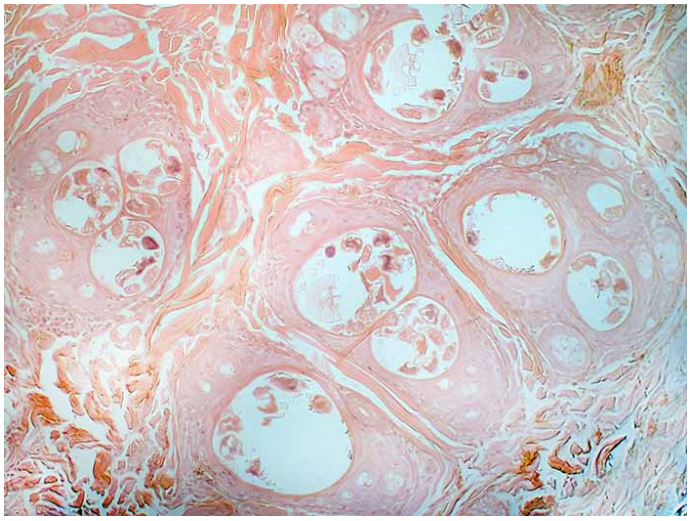
Demodex adult, ventral



Demodex adult, lateral



Demodex nymph



Demodex sections in dog skin

Cheyletiella
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Trombidiform mites have stigmata on the gnathosoma and distinct setae on their bodies and legs. Many species are free-living, some have been associated with allergy (including asthma), and several are obligate ectoparasites on mammals or birds. Cheyletiellids include predatory and parasitic mites whose bodies have a waist, enlarged palps and legs terminating in combs. Infestations by *Cheyletiella* spp. may cause scaly dermatitis on dogs, cats and rabbits.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Prostigmata [Trombidiformes] (sucking mites, stigmata on gnathosoma)
Suborder: Eleutherengona (thumb-claw process, tube-like midgut, females with adjacent anal-genital openings)
Superfamily: Cheyletoidea (chelicerae with basal stylophore and stylet-shaped movable segments)
Family: Cheyletiellidae (predatory and parasitic mites, body with waist, palps enlarged, legs terminate in combs)
Genus: *Cheyletiella* (parasitic on skin of dogs/cats/rabbits)
Species: various species cause scaly dermatitis on dogs, cats, rabbits

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					

Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of prostigmate mites have been described: many species being free-living (including most trombiculids although some have parasitic larvae); and others being obligate ectoparasites on mammals or birds. Parasitic species spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Prostigmatid mites are characterized by having oval-ellipsoidal bodies (sometimes vermiform) with distinctive setation, piercing chelicerae (sometimes pincer-like), unbarbed hypostomes, well-developed palps, and short legs with coxae fused to the body wall and terminal tarsi with 1-2 claws (but lacking complex pulvilli). A total of 34 superfamilies have been recognized in 4 suborders: Anystina (with 17 superfamilies); Eleutherengona (10); Endeostigmata (3); and Eupodina (4). Many members of the suborders Anystina and Eleutherengona have legs with distinctive arrangements of the terminal tibiotarsal segments referred to as the 'thumb-claw' process. Eleutherengone mites have simple tube-like postventricular midguts, small salivary glands (if present), females with anal and genital openings located close together posteriorly, and males with few glandular components of their testicular epithelia and accessory glands. Ten superfamilies are recognized (Cheyletoidea, Eriophyoidea, Pomerantzioidea, Pterygosomatoidea, Pyemotoidea, Pygmephoroidea, Raphignathoidea, Tarsocheyloidea, Tarsonemoidea, Tetranychoidea)

The superfamily Cheyletoidea comprises free-living predators, nidicolous forms and highly specialized ecto- or endo-parasites. Adult mites have chelicerae with basal segments fused into a single unit (stylophore), movable segments that are stylet-shaped, and the female anal and genital openings are located ventrally. A total of 8 families are recognized (Cheyletidae, Cloacaridae, Demodicidae, Harpyrhynchidae, Myobiidae, Ophioptidae, Psorergatidae, Syringophilidae). The family Cheyletidae contains many free-living predatory mites (sometimes feeding on other mites) but also some ectoparasitic mites living in the fur of mammals. Adult mites have oval bodies with a middle waist-like constriction, one or more dorsal shields, enlarged palps with large terminal claws (often toothed), a strong peritreme which frames the gnathostoma, and legs terminating in narrow pad-like empodia with comb-like pulvilli. Three subfamilies have been recognized (Cheyletinae, Metacheyletiinae, Niheliinae) and 10 tribes have been described for the subfamily Cheyletinae (Acaropsellini, Bakini, Cheletogenini, Cheletomorphini, Cheletosomatini, Chelonotini, Cheyletiellini, Cheyletiini, Cheyletini, and Criokerontini). The tribe Cheyletiellini contains 2 genera (*Cheyletiella*, *Eucheyletiella*) comprising mites with anterior stigmata opening at the cheliceral bases with a conspicuous M-shaped peritreme framing the gnathosoma, chelicerae fused with the rostrum to form a cone, opposable palps with a thumb-claw complex, most legs with claws, and short oval bodies with some elongate and some feathery setae. Some 18 species have been described in the genus *Cheyletiella,* most as ectoparasites on lagomorphs and carnivores, but sometimes on primates (including humans) and birds. Several species have been associated with inflammatory skin conditions in domestic pets and laboratory animals, including exfoliative dermatitis evident as dry scaly skin producing white flakes (infestations known as 'walking dandruff').

***Cheyletiella* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
C. blakei (cat fur mite)	Carnivora: felid (cat); Primates: hominid (human)	skin (face, occasionally over body)	irritation, pruritus, dermatitis, scaling	worldwide
C. canadensis	Piciformes: picid (European green woodpecker)			North America
C. chanayi	Passeriformes: motacillid (white wagtail)			Europe
C. curvidens	Carnivora: herpestid (slender mongoose)			Africa
C. dengi	Lagomorpha: leporid (European rabbit)			China
C. furmani	Lagomorpha: leporid (marsh rabbit)			North America
C. johnstoni	Lagomorpha: ochotonid (American pika)			North America
C. katangae	Lagomorpha: leporid (African savannah hare)			Africa
C. lemuricola	Primates: galagid (brown greater galago)			Africa
C. mexicana	Lagomorpha: leporid (volcano rabbit)			North America
C. microrhyncha	Passeriformes: hirundinid (barn swallow)			Europe
C. ochotonae	Lagomorpha: ochotonid (large-eared pika)			Asia
C. parasitivorax (rabbit fur mite)	Lagomorpha: leporid (European rabbit, marsh rabbit, volcano rabbit, eastern cottontail, Jameson's red rock hare, snowshoe hare); Carnivora: felid (cat); Primates: hominid (human)	skin (back, occasionally over body)	irritation, dermatitis, scaling (plus vector for myxomatosis virus)	worldwide
C. pinguis	Passeriformes: turdid (common blackbird)			Europe
C. romerolagi	Lagomorpha: leporid (volcano rabbit)			North America
C. strandtmanni	Lagomorpha: leporid (rabbit)			Asia
C. takahashii	Lagomorpha: ochotonid (northern pika)			Japan
C. yasguri	Carnivora: canid (dog); Primates: hominid (human)	skin (back, head, occasionally over body)	irritation, dermatitis, scaling	worldwide

Parasite morphology: *Cheyletiella* spp. form 4 different types of morphological developmental stages: namely, eggs, larvae (within eggs), nymphs (2 instars), and adults. The eggs are elongate ellipsoidal stages ranging in size from 190-260 x 115-135 µm. They are non-operculate and cream-tan in colour. They are glued along their long axes to hair shafts 2-3 mm above the skin and are held in place by a tangled web of threads. Within the eggs, prelarvae appear as legless sacs which then develop into hexapod (6-legged) larvae. Many studies have reported that the hexapod larvae hatch from eggs and then rapidly moult to octopod nymphs, but a few studies have reported that fully-developed octopod nymphs emerge from eggs. Observations on free hexapod larva show semitransparent ovate stages 200-300 µm long with a small midbody waist-like constriction, 2 prominent caudal setae and conspicuous anterior palps with recurved claws. Nymphs are more robust and larger with a triangular anterior gnathosoma (head or capitulum) and a posterior ovate-rounded idiosoma (body) measuring 250-400 µm in length. Two nymphal instars occur

(protonymphs and deutonymphs), both having 4 pairs of anteroventral legs, with the first 2 pairs often projecting anteriorly and the last 2 pairs extending backwards. Adult mites have slightly elongated ovoid bodies measuring from 400-500 μm long with a middle waist-like constriction. The integument is white-yellow and has light striations around the margins and near the waist. They have a distinct anterior gnathosoma bearing stout mouthparts (chelicerae) flanked by robust palps. The palps have 4 segments whereas other mites have 2-3 (prostigmatids and astigmatids) or 5-6 (mesostigmatids). The palps are unique in that they have large terminal recurved claws (often toothed) used to grasp fur or feathers when feeding. The palpal femur also bears long serrated dorsal setae. The paired chelicerae are adapted for piercing and have distal stylet-shaped segments that are movable, while the basal segments are fused with the rostrum to form a cone over the mouth. The alimentary tract comprises a tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with diverticulae), tubular hindgut (with excretory Malpighian tubules) and a subterminal ventral anus. The idiosoma has a sclerotized dorsal shield located anteriorly in front of the waist-like constriction. The body surface bears several large setae, sometimes plumose (with a finely-feathered appearance) and with a pair of long plain setae projecting posteriorly. Four pairs of well-developed legs arise ventrally, each leg comprising 6 segments (coxa, trochanter, femur, genu, tibia and tarsus) and terminating in narrow pad-like empodia with comb-like pulvilli (not claws or suckers). The coxae are fused to the body wall and are extended in at least the first 2 pairs of legs into sclerotized epimerites. The legs bear short branched setae, and the genu of the forelegs have special sensory projections (called solenidia) that vary in shape depending on species (globose in *C. parasitovorax*, conical in *C. blakei*, heart-shaped in *C. yasguri*). Adults have lateral respiratory openings (stigmata) located anteriorly near the cheliceral bases and they have strong M-shaped peritremes framing the gnathosoma. Male and female mites exhibit moderate external sexual dimorphism, with females being slightly larger in body size and having larger genital openings. Males have paired testes linked by tubular vas deferens to an ejaculatory duct and long sheathed aedeagus (straight or curved penis) that extends from between the hindlegs to the posterior of the body. Female mites have paired ovaries (with ovarioles) joined by tubular oviducts to a globular uterus (with accessory glands) and vagina (with accessory organs for sperm reception and storage). The genital opening (gonopore) appears as a short longitudinal cleft supported by lateral plates on the ventrum of the posterior body.

Site of infection: *Cheyletiella* spp. are non-burrowing mites that attach to the hair or feathers of their hosts. Infestations by 14 mite species have been recorded on mammals belonging to 7 families in 3 orders (including small carnivores, lagomorphs and primates). Mites are found most often on the back, shoulders and neck, but may extend over the whole body in heavy infestations. They vary in their host specificity, with many being specific for individual hosts (particularly lagomorphs) while a few have broader specificities and may infest several mammalian hosts, including humans. Another 4 species have been found exclusively on birds belonging to 3 passerine families and one non-passerine family (woodpeckers).

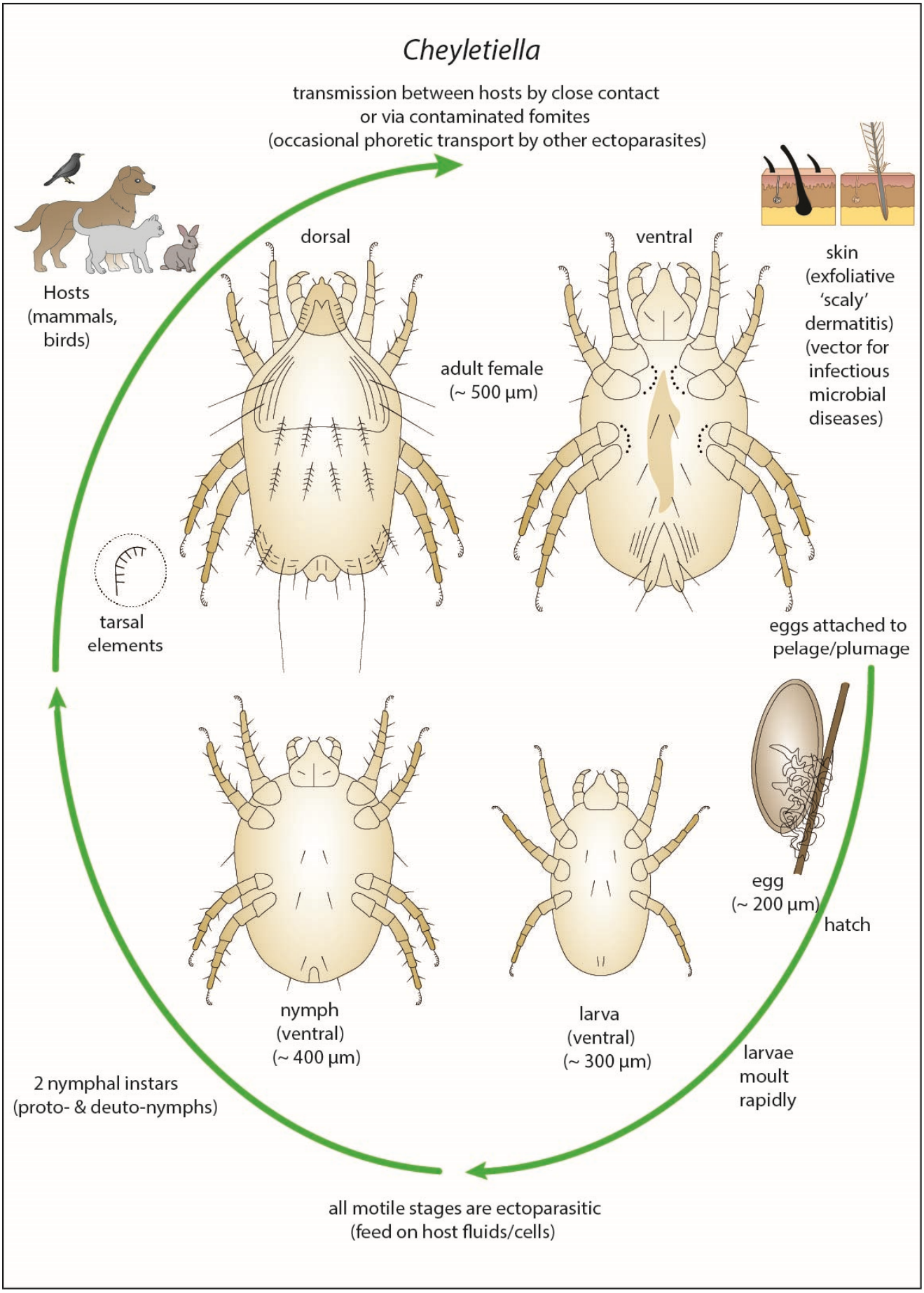
Pathogenesis: Light infestations may remain asymptomatic, but heavier infestations can cause mild-severe disease (cheyletiellosis) manifest as exfoliative (scaling) dermatitis with variable pruritus, sometimes exacerbated by host hypersensitivity responses. Mites live on the surface of the skin in close association with the keratin layer where they use their palpal claws to grasp hairs/feathers and their stylet-like mouthparts to secrete digestive enzymes and feed on liquefied skin cells, extracellular fluid and lymph. The most common clinical signs observed in non-hypersensitive animals are irritation, hyperkeratosis, and exfoliative (dry scaly) dermatitis producing white flakes (dandruff) resulting in eczema-like skin lesions (more common in dogs and rabbits than cats). Mites may be observed as 'walking dandruff' moving among the scurf, particularly along the dorsal midline. Animals may develop oily coats, erythema, excoriated lesions and alopecia, but pruritus is usually minimal. In animals that develop hypersensitivity, there may be extreme irritation and discomfort with severe pruritus and self-inflicted lesions due to scratching resulting in alopecia (loose hair can sometimes be pulled out in clumps) and scab formation (sometimes evident as miliary dermatitis with small crusted lesions). Heavy infestations may cause papules (which become pustules), but macules, plaques, vesicles or crusts may also occur. Several *Cheyletiella* spp. have zoonotic potential as mites can bite humans but do not complete their development. Infestations often cause pruritic red papules, particularly on the arms and trunk of people handling animals, and often before any clinical signs are observed in the animals. The papules may become vesicular, then pustular, and burst to produce yellow crusts, sometimes accompanied by peripheral eosinophilia, and immune complex formation with joint pain. Cheyletiellosis occurs more frequently in young individuals (puppies, kittens and kits) kept in poor husbandry conditions or crowded situations (such as breeding facilities or pet shops). The species *C. parasitovorax* has also been shown to act as a vector for the transmission of the myxoma virus causing myxomatosis in rabbits.

Developmental cycle and mode of transmission: Like all mites, *Cheyletiella* spp. exhibit incomplete (hemimetabolous) metamorphosis in that eggs produce larvae that moult to nymphs and then adult mites. All developmental stages in the life-cycle may occur on the same host, but mites can survive off hosts for longer periods than most other mange mites. Gravid females attach eggs to host hairs using glue-like secretions and webs of threads. The eggs embryonate over 2-7 days and then hatch releasing hexapod (6-legged) larvae which rapidly moult to the first octopod (8-legged) nymphal instar (protonymphs), although there have been a few reports that the eggs of some mite species hatch to release octopod nymphs. All reports indicate that 2 nymphal stages occur, wherein the protonymph feed for several days before moulting to the second nymphal instar (deutonymphs). The deutonymphs feed for several days before moulting to adult mites. Adults are highly motile and able to move rapidly through the pelage where they feed, mature and mate. Fertilized females oviposit eggs attaching them to host hairs/feathers, sometimes several close together. Little is known about mite fecundity and longevity, but the entire life-cycle may be completed in 2-5 weeks. Transmission is often by direct physical contact when mites crawl from host-to-host, especially when they are crowded together

when nursing, huddling, sleeping, etc. Female mites have been shown to survive for up to 10 days off hosts, while other stages do not survive for longer than 2 days. Some transmission may therefore occur by contamination of fomites when mites are spread on objects such as bedding, pens, leashes, collars, and grooming equipment. People regularly handling or sleeping with animals may be bitten by mites as accidental hosts, but there is no evidence that mites can be transmitted from person-to-person. Curiously, there are a growing number of reports of *Cheyletiella* mites being found attached to fleas, flies and lice, and it has been posited that these larger arthropods may assist in transmission by phoretic transfer (phoresis).

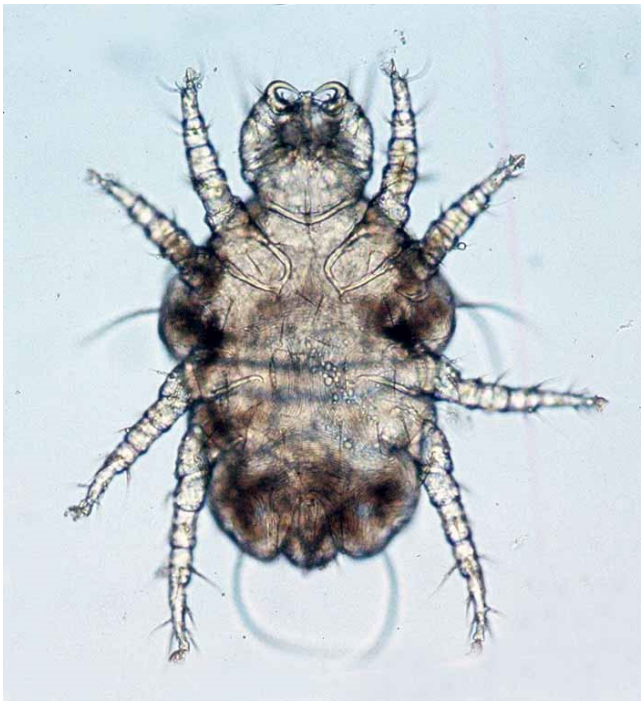
Differential diagnosis: While clinical signs may be suggestive of cheyletiellosis, other conditions may cause similar exfoliative dermatitis, such as other mites, fleas, diabetes mellitus, liver disease, seborrhoea, poor nutrition and even ineffective grooming due to dental disease, obesity or spinal disorders. Hypersensitivity responses may also be caused by food allergies, atopic dermatitis, flea bites and other mites. In the presence of excess scaling, the skin should be examined for mites and various samples collected for microscopic examination. Mites may be detected by visual examination of affected patches of skin as motile stages (walking dandruff) in the scurf, especially if a magnifying glass is used. Specimens may be collected by combing, brushing or even vacuuming the pelage, plucking hairs (trichograms) or taking sticky tape impressions from the skin. Animals may also be massaged or handled over paper or plastic drop sheets and collecting any debris. Mites are quite motile so any samples collected should be wetted (in water, saline, alcohol, or mineral oil) to prevent them from escaping. Alternatively, samples may be subject to caustic (potassium hydroxide) digestion as one would process skin scrapings (but actual skin scrapings are not highly effective in this instance as the mites are non-burrowing surface dwellers). Coprological examination of faecal samples by floatation techniques may also reveal mites or eggs swallowed during grooming.

Treatment and control: Clinical infestations may be difficult to treat due to the large numbers of mites present and the high probability of re-infestation from the environment. Animals are usually treated with topical or systemic acaricides, including lime-sulphur, organophosphates (dichlorvos, phosmet, chlorpyriphos, malathion, diazinon), carbamates (carbaryl), pyrethrin and synthetic pyrethroids (permethrin), amidines (amitraz), arylpyrazoles (fipronil) and macrocyclic lactones (ivermectin, selamectin). In severe cases involving crusted lesions, shampoos and/or conditioners may be used to remove crusts and debris before topical treatment. All in-contact animals should be treated at the same time, and repeated or prolonged treatments may be required (even after the resolution of clinical signs). Lesions on humans generally disappear after the elimination of infestations on pets. Various preventive measures may be adopted to break transmission cycles, including regular health surveillance (predicating treatment, isolation/quarantine or culling), improved sanitation and hygiene (cleaning animal holding facilities and bedding, especially in breeding quarters) and possibly using residual acaricides (e.g. pyrethroids) to help decontaminate porous and nonporous fomites (e.g. runs or hides with timber or paved areas, pebbles, mulch and other organic litter).


Cheyletiella
transmission between hosts by close contact
or via contaminated fomites
(occasional phoretic transport by other ectoparasites)
Hosts
(mammals,
birds)
dorsal
ventral
adult female
(~ 500 µm)
skin
(exfoliative
'scaly'
dermatitis)
(vector for
infectious
microbial
diseases)
tarsal
elements
eggs attached to
pelage/plumage
egg
(~ 200 µm)
hatch
nymph
(ventral)
(~ 400 µm)
larva
(ventral)
(~ 300 µm)
larvae
moult
rapidly
2 nymphal instars
(proto- & deuto-nymphs)
all motile stages are ectoparasitic
(feed on host fluids/cells)



Cheyletiella adult



Cheyletiella adult



Cheyletiella egg

Myobia
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Myobiid mites have lateral bulges of the body between their legs which are modified for grasping hairs of fur-bearing mammals. Infestations by *Myobia musculi* may cause dermatitis (myobiic mange) in mice.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Prostigmata [Trombidiformes] (sucking mites, stigmata on gnathosoma)
Suborder: Eleutherengona (thumb-claw process, tube-like midgut, females with adjacent anal-genital openings)
Superfamily: Myobioidea (anal-genital openings dorsal, first pair legs modified for attachment)
Family: Myobiidae (parasitic on fur-bearing mammals, esp. bats, body with lateral bulges)
Genus: *Myobia* (parasitic on skin/hair of mice)
Species: *M. musculi* causes myobiic mange in mice

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					

Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
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Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
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Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
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Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of prostigmate mites have been described: many species being free-living (including most trombiculids although some have parasitic larvae); and others being obligate ectoparasites on mammals or birds. Parasitic species spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Prostigmatid mites are characterized by having oval-ellipsoidal bodies (sometimes vermiform) with distinctive setation, piercing chelicerae (sometimes pincer-like), unbarbed hypostomes, well-developed palps, and short legs with coxae fused to the body wall and terminal tarsi with 1-2 claws (but lacking complex pulvilli). A total of 34 superfamilies have been recognized in 4 suborders: Anystina (with 17 superfamilies); Eleutherengona (10); Endeostigmata (3); and Eupodina (4). Many members of the suborders Anystina and Eleutherengona have legs with distinctive arrangements of the terminal tibiotarsal segments referred to as the 'thumb-claw' process. Eleutherengone mites have simple tube-like postventricular midguts, small salivary glands (if present), females with anal and genital openings located close together posteriorly, and males with few glandular components of their testicular epithelia and accessory glands. Ten superfamilies are recognized (Cheyletoidea, Eriophyoidea, Pomerantzioidea, Pterygosomatoidea, Pyemotoidea, Pygmephoroidea, Raphignathoidea, Tarsocheyloidea, Tarsonemoidea, Tetranychoidea)

The superfamily Cheyletoidea comprises free-living predators, nidicolous forms and highly specialized ecto- or endo-parasites. Adult mites have chelicerae with basal segments fused into a single unit (stylophore), movable segments that are stylet-shaped, and the female anal and genital openings are located ventrally. A total of 8 families are recognized (Cheyletidae, Cloacaridae, Demodicidae, Harpyrhynchidae, Myobiidae, Ophioptidae, Psorergatidae, Syringophilidae), but some recent studies have transferred the Myobiidae to a new superfamily Myobioidea on the basis of molecular studies and observations that the female anal and genital openings are dorsal, and the first pair of legs are highly modified for attachment. The family Myobiidae is further characterized by mites with oval-elongate bodies with sparse non-feathery setae and some legs modified for grasping host hairs using claws. Some 46 genera have been recognized (*Acanthophthirius*, *Acrobatobia*, *Amorphacarus*, *Anuncomyobia*, *Australomyobia*, *Binunculoides*, *Binuncus*, *Blarinobia*, *Calcarmyobia*, *Chimarrogalobia*, *Crocidurobia*, *Cryptomyobia*, *Eadiea*, *Eudusbabekia*, *Eutalpacarus*, *Ewingana*, *Foliomyobia*, *Furipterobia*, *Gundimyobia*, *Gymnomyobia*, *Hipposiderobia*, *Idiurobia*, *Ioannela*, *Limnogalobia*, *Madamyobia*, *Metabinuncus*, *Microgalobia*, *Myobia*, *Mystacobia*, *Myzopodobia*, *Natalimyobia*, *Nectogalobia*, *Neomyobia*, *Nycterimyobia*, *Oryzorictobia*, *Phyllostomyobia*, *Placomyobia*, *Proradfordia*, *Protomyobia*, *Pteracarus*, *Pteropimyobia*, *Radfordia*, *Schizomyobia*, *Thyromyobia*, *Ugandobia*, and *Xenomyobia*), most occurring as ectoparasites on the fur of mammals, especially bats and rodents. Some 16 species have been described in the genus *Myobia*, with most allocated to 3 subgenera, *M.* (*Myobia*), *M.* (*Angomyobia*) and *M.* (*Otomyobia*). They occur as ectoparasites living in the fur of rodents, although the species *M. murismusculi* (often incorrectly referred to as *M. musculi*) has also been found on dogs, cats and humans.

***Myobia* species**	**Hosts**	**Clinical signs**	**Distribution**
M. afromuris	Rodentia: murid (Jackson's soft-furred mouse)		Africa
M. (*Myobia*) *agraria*	Rodentia: murid (striped field mouse)		Eurasia
M. (*Myobia*) *annae*	Rodentia: murid (eastern broad-toothed field mouse)		Eurasia
M. apodemi	Rodentia: murid (small Japanese field mouse)		Asia
M. apomys	Rodentia: murid (Mindanao lowland forest mouse)		Asia
M. (*Myobia*) *hyatti*	Rodentia: murid (Asiatic long-tailed climbing mouse)		Asia
M. kobayashii	Rodentia: murid (Korean field mouse)		Asia
M. (*Angomyobia*) *machadoi*	Rodentia: murid (typical striped grass mouse)		Africa
M. (*Myobia*) *malaysiensis*	Rodentia: murid (Indomalayan pencil-tailed tree mouse)		Asia
M. micromydis	Rodentia: murid (Eurasian harvest mouse)		Eurasia
M. multivaga	Rodentia: murid (house mouse, wood mouse, Ural field mouse, Black Sea field mouse, Steppe field mouse, yellow-necked mouse)		Europe
M. murismusculi (syn. *M. musculi, muris?, coarctata?*)	Rodentia: murid (house mouse, wood mouse, Ural field mouse, Black Sea field mouse, Steppe field mouse, yellow-necked mouse, brown rat), cricetid (western harvest mouse, Pinyon mouse); Carnivora: canid (dog), felid (cat); Primates: hominid (human)	myobiic mange, pruritus, inflammation, alopecia	worldwide
M. nodae	Rodentia: murid (large Japanese field mouse)		Asia
M. (*Otomyobia*) *otomyia*	Rodentia: murid (southern African vlei rat)		Africa
M. (*Angomyobia*) *pelomys*	Rodentia: murid (Creek groove-toothed swamp rat)		Africa
M. stewardi	Rodentia: murid (black rat)		Asia

Many other species previously thought to belong to the genus *Myobia* have been re-assigned to other genera, including: *M. affinis =Radfordia; M. blairi = Crocidurobia; M. brevihamata = Eadiea; M. canadensis = Acanthophthirus caudata; M. capensis = Acanthophthirius; M. caudata = Neomyobia; M. chalinolobus = Pteracarus; M. chiropteralis = Foliomyobia; M. claperedi = Protomyobia; M. clara = Acanthophthirius; M. davisi = Radfordia; M. elongata = Amorphacarus; M. ensifera = Radfordia; M. ewingi = Radfordia; M. heteronycha = Hipposiderobia; M. ingens = Crocidurobia; M. jacksoni = Neomyobia; M. lancearia = Radfordia; M. longa = Ewingana; M. longirostris = Fischeria bicolor; M. magna = Binuncus; M. michaeli = Crocidurobia; M. minima = Acanthophthirius; M. miniopteris = Acanthophthirius minimus; M. minuta = Pteracarus; M. mystacinalis = Acanthophthirius; M. noctulia = Radfordia; M. oudemansi = Radfordia; M. pantopus = Acanthophthirius; M. phillipsi = Radfordia; M. pipistrellia = Pteracarus; M. plecotius = Acanthophthirius; M. poppei = Acanthophthirius; M. ratti = Radfordia ensifera; M. rhinolophia = Binuncus; M. rollinati = Neomyobia; M. rotundata = Cryptomyobia; M. simplex = Blarinobia*; *M. trouessarti = Afromyobia;* and *M. zibethicalis = Radfordia*.

Parasite morphology: *Myobia* spp. form 4 different types of morphological developmental stages: namely, eggs, larvae (1-2 instars), nymphs (2-3 instars), and adults (males and females). Eggs are pale oval stages around 200 µm long and attached to the

bases of host hairs. Larvae are small ovate stages ranging in length from 200-300 μm. They are hexapodal with 3 pairs of legs comprising an anterior pair of short pincer-like forelegs and then 2 lateral pairs of longer jointed legs (tarsi II with claws, tarsi III without). The larvae have distinctive chaetotaxy (patterns of setation) with the gnathosoma (head) bearing a pair of dorsal setae, and the idiosoma (body) having 12 pairs of dorsal setae and a single pair of ventral setae. Some early descriptions of parasite development reported that a second larval instar occurred in some species, but few details are available. Nymphs are larger ellipsoidal stages that are octopodal with 4 pairs of legs (short anterior forelegs and longer lateral hindlegs). Most descriptions indicate that 2 nymphal instars are formed (protonymphs and deutonymphs) although a few studies have reported a third instar (tritonymphs) for some species. Nymphs increased progressively in size from 250 μm up to a maximum of 500 μm in length. Protonymphs and deutonymphs had setate legs (including small microchaetae), a single scale-like seta on coxae I, ventral setae on the gnathosoma, and claws on tarsi II-III. Tritonymphs had more leg setae, 2 scale-like setae on coxae I, claws on tarsi II-IV and lacked anal setae. Adult mites had irregular oval bodies, often elongate with distinct lateral bulges between their legs. They were translucent in appearance and the integument had small elaborate transverse striations. Adults varied in size depending on species and gender, with females ranging in length from 400–500 μm compared to males which measured from 285–320 μm. The anterior gnathosoma was small and simple, bearing small mouthparts comprising paired stylet-like chelicerae flanked by sensory palps. The palps were minute and lacked terminal claws (apoteles). The chelicerae had 3 segments with the basal segments fused into a single unit (stylophore) and the other movable segments being stylet-shaped. The oral opening (mouth) was bounded by a dorsal rostrum, ventral buccal cone and central unbarbed hypostome. The alimentary tract consisted of a tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with caeca), tubular hindgut (with excretory Malpighian tubules) and a cuticle-lined rectum leading to a dorsal anus flanked by a long pair of setae (up to 40 μm long). The idiosoma had characteristic bulges between legs II-IV and the dorsal surface had sparse but stout bristle-like setae of various shapes, sometimes expanded, spine-like, striated, or barbed (but not feathery). he ventral idiosoma was the point of attachment for 4 pairs of legs, but the first pair was short and pincer-like being highly modified for grasping hairs (often giving the impression that the mites only had 3 pairs of legs). The first pair of legs projected forwards and only had 3 movable segments, with the tibia and tarsus completely fused, and the genu partly fused with the tibiotarsus. The forelegs lacked claws, but terminated in strongly laterally-curved hooks. The remaining walking legs had 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus), and all ended in a single tarsal empodial claw (whereas tarsi II in the genus *Radfordia* terminated in paired claws). The coxae were fused to the body wall, and all legs were setate, with the first pair of legs bearing specialized sensory solenidia. Like other prostigmatid mites, adults possessed lateral respiratory openings (stigmata) near the bases of the chelicerae. Male mites had paired testes with tubular vas deferens leading to the ejaculatory duct and the long straight sheathed aedeagus (penis). The genital opening (gonopore) was dorsal and subterminal with a chitinized cone-like genital plate bearing 3 pairs of apical setae. Female mites had a single ovary with a long complex oviduct leading to the uterus and cuticular vagina with a receptaculum seminis (for sperm receipt). Vitellogenic oocytes develop in ovarian pouches (like other trombidiform mites) and the oviduct was tripartite (2 proximal portions producing egg-shell components, and a distal portion never containing oocytes but thought to produce special glue-like secretions). The female anal and genital openings are both located dorsally (unusual for mites), and the vulva had well-developed lobes.

Site of infection: These fur mites are found worldwide clasping to the hairs of mice, and rarely other rodents. They are usually host-specific and some 16 species have been described, mostly from murids and some cricetids, although one species (*M. murismusculi*) has also been found on dogs, cats and humans. Mites are generally found on the head, neck and shoulders of their hosts.

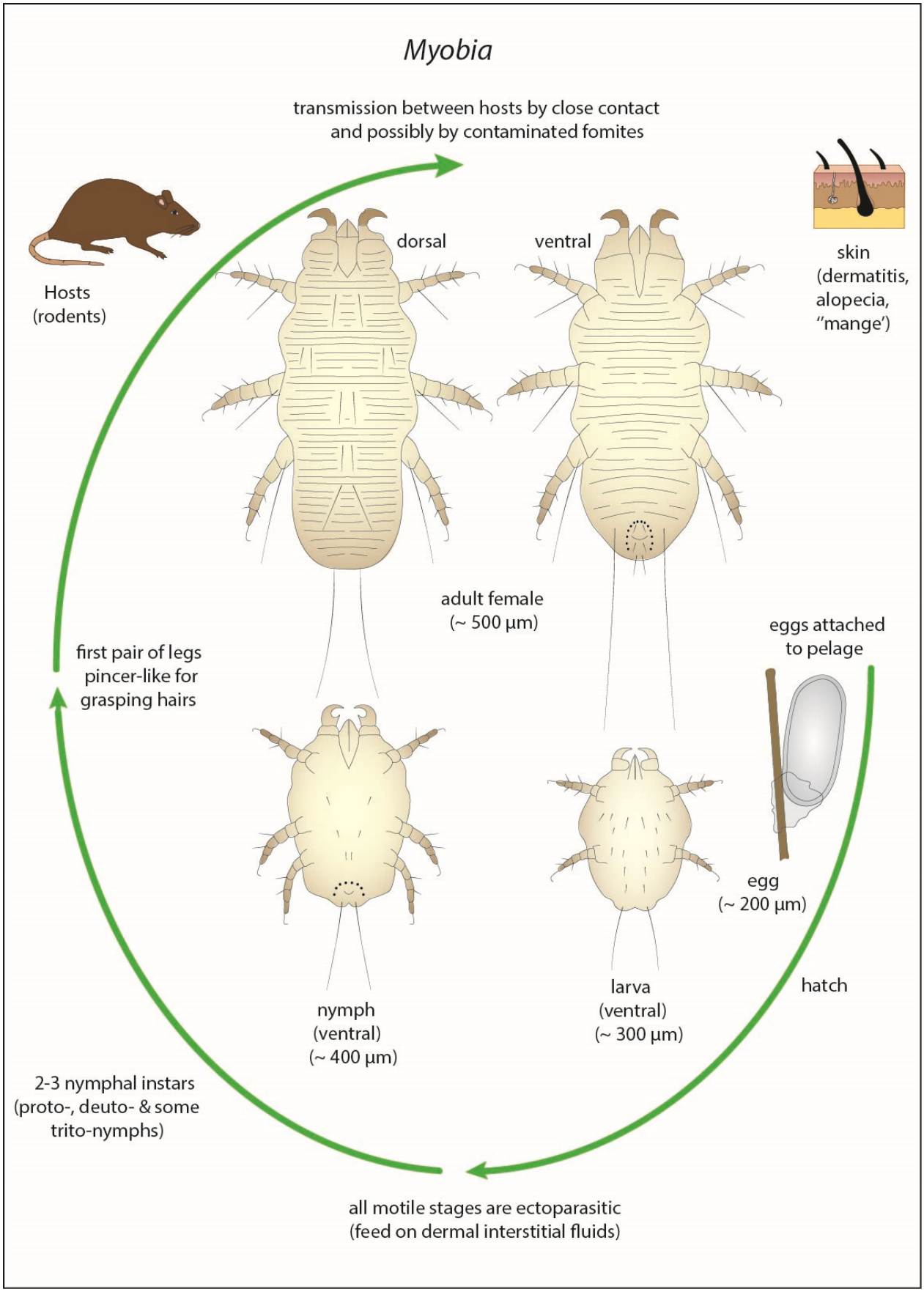
Pathogenesis: Many infestations are light and remain asymptomatic or subclinical, but heavier infestations can lead to dermatitis and alopecia, exacerbated in hypersensitive individuals. Developing and mature mites feed on dermal tissue fluids (cellular interstitial fluids), and sometimes blood from superficial capillaries, but they do not invade or burrow into the skin. Host responses vary greatly depending on the age, sex, strain and immunological status of the mice. Most animals do not develop clinical signs unless they are stressed, immunocompromised or have become sensitized to mite antigens. Infestations can then lead to dermatitis, pruritus, harsh fur or alopecia, with epidermal excoriations worsened by allergic reactions. Sensitized hosts often engage in vigorous scratching to relieve biting-stress which can result in self-trauma with ulcerative dermatitis secondary to bacterial infections. Severely affected mice may show self-mutilation damage to the ears and eyes, and in some cases death. Infestations can be problematic in laboratory animal colonies where most mice become infested and disease become rampant in genetically-modified mice strains. Persistent infestations may also affect the general health of the colony by contributing to physiological alterations, immune perturbations, chronic inflammation, fibrosis, hyperkeratosis, reduced body weights, decreased fertility and shorter life-spans.

Developmental cycle and mode of transmission: *Myobia* mites undergo incomplete (hemimetabolous) metamorphosis wherein eggs hatch larvae that moult to nymphs and then adults. The whole life-cycle may be completed on the same host and transmission between hosts occurs by close contact and/or contamination of fomites. Gravid females lay eggs singly, gluing them to the bases of hair shafts (whereas *Myocoptes* spp. attach them distally). The eggs hatch in 7–8 days releasing hexapod larvae which feed over 4-10 days before moulting to the first octopod nymphal instar (protonymphs). The nymphs feed and develop through further nymphal instars over 5 days, all species forming second nymphal instars (deutonymphs) and some species forming a third nymphal instar (tritonymphs). The final nymphal instar moults to form adult male and female mites which feed and mate on their hosts. Female mites may produce fertile eggs within 24 hours of mating but little is known about the fecundity or longevity of the mites. Under

experimental conditions, the whole life-cycle has been completed in 12-23 days. Transmission occurs through direct physical contact when mites crawl from one host to another, particularly when they are in close quarters when nursing, huddling or sleeping. Mouse pups may become infested 4-5 days after birth shortly after they begin to grow hair. Adult mites have also been found to leave dead mice as the carcase cools, and it is possible that some animals may become infested when in contact with contaminated fomites, such as bedding and nesting materials. However, little is known about the environmental survival capabilities of the different mite developmental stages when dislodged from hosts. Adult *M. murismusculi* appear to be readily transferred to other hosts in close contact (such as cats, dogs and humans).

Differential diagnosis: Infestations are difficult to diagnose on the basis of symptomatology as most clinical signs (dermatitis, alopecia) only develop in immunocompromised hosts and may be attributable to other aetiological agents or disease conditions. Diagnosis is afforded by the microscopic detection of mites in skin scrapings, hair plucks (trichograms) or adhesive tape impression. Mites are often found in skin scrapings from the edges of lesions or in flakes or crusts that have been subject to caustic digestion (usually 10% potassium hydroxide) to break down skin (the mite's cuticle is impervious to digestion). Mites and mite eggs may be detected amongst hairs plucked from the edges of lesions or on sticky tape applied against the grain of fur. Mites may also be detected at postmortem by placing carcases/pelts to cool on dark paper so that mites vacating the host may be visible as white specks. Several molecular biological techniques have recently been developed to diagnose infestations and characterize mite species by polymerase chain reaction (PCR) amplification of nuclear gene sequences (18S, 5.8S and 28S ribosomal RNA, internal transcribed spacers 1 and 2).

Treatment and control: Clinical infestations may be treated using chemical acaricides as topical or systemic formulations, including organophosphates (dichlorvos) and macrocyclic lactones (ivermectin, selamectin), although some drug resistance has been noted to ivermectin. Acaricides work well against all feeding stages (larvae, nymphs, adults) but less so against mite eggs encased in tough eggshells. Treatments are therefore often repeated at intervals to prevent re-infestations by newly-hatched stages. Various preventive measures may be adopted to break transmission cycles through regular health monitoring (as a prelude to treatment, isolation/quarantine, or culling), improved sanitation and hygiene (clean cages/fomites, replace bedding, apply residual acaricides (pyrethroids) to porous fixtures and litter) and animal management (cohort separation, especially nursing rodent pups, exclude wild rodents using barriers (screens) or other vermin control strategies).


Myobia
transmission between hosts by close contact
and possibly by contaminated fomites
Hosts
(rodents)
dorsal
ventral
skin
(dermatitis,
alopecia,
"mange')
adult female
(~ 500 µm)
eggs attached
to pelage
first pair of legs
pincer-like for
grasping hairs
egg
(~ 200 µm)
hatch
larva
(ventral)
(~ 300 µm)
nymph
(ventral)
(~ 400 µm)
2-3 nymphal instars
(proto-, deuto- & some
trito-nymphs)
all motile stages are ectoparasitic
(feed on dermal interstitial fluids)



Myobia adult

Psorobia, Psorergates
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Trombidiform mites have stigmata on the gnathosoma and distinct setae on their bodies and legs. Many species are free-living, some have been associated with allergy (including asthma), and several are obligate ectoparasites on mammals or birds. Psorergatid mites have circular bodies with regularly spaced legs with inward-curved spines. Infestations by the itch mites *Psorobia* and *Psorergates* spp. may cause irritation and hair loss in sheep, cattle and rodents.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Prostigmata [Trombidiformes] (sucking mites, stigmata on gnathosoma)
Suborder: Eleutherengona (thumb-claw process, tube-like midgut, females with adjacent anal-genital openings)
Superfamily: Cheyletoidea (chelicerae with basal stylophore and stylet-shaped movable segments)
Family: Psorergatidae (body circular, legs regularly spaced, long posterior setae, legs with inward-curved spines)
Genus: *Psorobia* (parasitic on skin of ruminants)
Genus: *Psorergates* (parasitic on skin of rodents)
Species: various species cause irritation and hair loss in sheep and cattle

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					

Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of prostigmate mites have been described: many species being free-living (including most trombiculids although some have parasitic larvae); and others being obligate ectoparasites on mammals or birds. Parasitic species spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Prostigmatid mites are characterized by having oval-ellipsoidal bodies (sometimes vermiform) with distinctive setation, piercing chelicerae (sometimes pincer-like), unbarbed hypostomes, well-developed palps, and short legs with coxae fused to the body wall and terminal tarsi with 1-2 claws (but lacking complex pulvilli). A total of 34 superfamilies have been recognized in 4 suborders: Anystina (with 17 superfamilies); Eleutherengona (10); Endeostigmata (3); and Eupodina (4). Many members of the suborders Anystina and Eleutherengona have legs with distinctive arrangements of the terminal tibiotarsal segments referred to as the 'thumb-claw' process. Eleutherengone mites have simple tube-like postventricular midguts, small salivary glands (if present), females with anal and genital openings located close together posteriorly, and males with few glandular components of their testicular epithelia and accessory glands. Ten superfamilies are recognized (Cheyletoidea, Eriophyoidea, Pomerantzioidea, Pterygosomatoidea, Pyemotoidea, Pygmephoroidea, Raphignathoidea, Tarsocheyloidea, Tarsonemoidea, Tetranychoidea)

The superfamily Cheyletoidea comprises free-living predators, nidicolous forms and highly specialized ecto- or endo-parasites. Adult mites have chelicerae with basal segments fused into a single unit (stylophore), movable segments that are stylet-shaped, and the female anal and genital openings are located ventrally. A total of 8 families are recognized (Cheyletidae, Cloacaridae, Demodicidae, Harpyrhynchidae, Myobiidae, Ophioptidae, Psorergatidae, Syringophilidae). The family Psorergatidae comprises the 'itch' mites with small disc-shaped bodies with long trailing setae, dorsal shields with striated margins, and 4 pairs of legs regularly spaced around the ventral idiosoma (the legs possessing inwardly-curved spines). Three genera have been recognized: namely, *Psorergates*, *Psorergatoides*, and *Psorobia* (although some texts list them as subgenera of the genus *Psorergates,* thus causing considerable confusion with respect to species assignations). These itch mites have a conspicuous gnathosoma, palps without thumb-claw complexes, short stubby legs with pronounced hooks, and sparsely setate bodies (females with 2 pairs of long posterior setae while males only have a single pair). Some 45 *Psorergates* spp. (with smooth palp-tibial setae, and 3 pairs of setae on their dorsal shields) have been described from rodents and insectivores, 18 *Psorergatoides* spp. (with serrate palp-tibial setae, and 4 pairs of dorsal shield setae) from bats, and 10 *Psorobia* spp. (with serrate palp-tibial setae, and 5 pairs of dorsal shield setae) from a range of mammals (rodents, insectivores, lagomorphs, carnivores, primates and ungulates). The latter includes 2 notorious species, namely *P. ovis* (sheep itch mite) and *P. bos* (cattle itch mite) which impact on the livestock industries by causing psorergatic mange (dermatitis with alopecia) contributing to lost productivity.

Parasite species	Hosts	Clinical signs	Distribution
Psorobia (ectoparasitic on various mammals)			
P. bos (*bovis*) (cattle itch mite)	Artiodactyla: bovid (cattle)	occasionally alopecia, desquamation	Australia, Americas, Africa
P. castoris	Rodentia: castorid (American beaver)		North America
P. cercopitheci	Primates: cercopithecid (grivet, white eyelid mangabey)		Africa
P. elephantuli	Macroscelidea: macroscelidid (North African elephant shrew)		Africa
P. foinae	Carnivora: mustelid (beech marten)		Europe
P. hystrici	Rodentia: hystricid (Cape porcupine)		Africa
P. lagomorphae	Lagomorpha: leporid (eastern cottontail)		North America
P. mustelae	Carnivora: mustelid (stoat, least weasel)		Europe
P. ovis (syn. *Psorergates*) (sheep itch mite)	Artiodactyla: bovid (sheep)	irritation, pruritus, scabs, wool break	Australia, Americas, Africa
P. zumpti	Rodentia: bathyergid (common mole-rat)		Africa
Psorergates (ectoparasitic on rodents and insectivores)			
P. agrestis	Rodentia: cricetid (short-tailed field vole)		Europe
P. apodemi	Rodentia: murid (wood mouse, yellow-necked mouse, Ural field mouse)		Europe
P. arvalis	Rodentia: cricetid (common vole)		Europe
P. auricola	Rodentia: cricetid (Mediterranean pine vole)		Europe
P. baueri	Eulipotyphla: soricid (Eurasian water shrew)		Europe
P. callipides	Rodentia: murid (wood mouse)		Europe
P. canadensis	Rodentia: cricetid (eastern meadow vole)		North America
P. cinereus	Eulipotyphla: soricid (cinereus shrew)		North America
P. crocidurae	Eulipotyphla: soricid (greater white-toothed shrew)		Europe
P. cryptotis	Eulipotyphla: soricid (blackish small-eared shrew)		North America
P. deomydis	Rodentia: murid (link rat)		Africa
P. desmanae	Eulipotyphla: talpid (Pyrenean desman)		Europe
P. dissimilis	Rodentia: cricetid (bank vole)		Europe
P. doriae	Eulipotyphla: soricid (Bornean shrew)		Asia
P. dremomydis	Rodentia: sciurid (Asian red-cheeked squirrel)		Asia
P. eliomydis	Rodentia: glirid (garden dormouse)		Europe
P. etruscus	Eulipotyphla: soricid (Etruscan shrew)		Europe
P. fritzi	Scandentia: tupaiid (common treeshrew)		Asia
P. glaucomys	Rodentia: sciurid (southern flying squirrel)		North America
P. hispanicus	Rodentia: murid (Algerian mouse, house mouse)		Eurasia
P. mexicanus	Eulipotyphla: soricid (Crawford's gray shrew)		North America
P. micromydis	Rodentia: murid (Eurasian harvest mouse)		Europe
P. muricola	Rodentia: murid (Peter's striped mouse, house mouse, wood mouse, gray brush-furred rat, tropical vlei rat)		Africa, Europe
P. muscardinus	Rodentia: glirid (hazel dormouse)		Europe

P. musculinus	Rodentia: cricetid (bank vole, short-tailed field vole), murid (wood mouse)		Europe
P. neerlandicus	Rodentia: cricetid (tundra vole)		Europe
P. oeconomi	Rodentia: cricetid (tundra vole)		Europe
P. oettlei	Rodentia: murid (Natal multimammate mouse)		Africa
P. olawaensis	Eulipotyphla: soricid (lesser white-toothed shrew)		Europe
P. paraxeri	Rodentia: sciurid (Smith's bush squirrel)		Africa
P. peromysci	Rodentia: cricetid (deer mouse, white-footed mouse)		North America
P. pinetorum	Rodentia: cricetid (woodland vole)		North America
P. pitymidis	Rodentia: cricetid (Mediterranean pine vole)		Europe
P. polonicus	Rodentia: cricetid (European pine vole)		Europe
P. quercinus	Rodentia: glirid (garden dormouse)		Europe
P. rattus	Rodentia: murid (brown rat)		Pacific
P. simplex	Rodentia: murid (house mouse), cricetid (short-tailed field vole, common vole)	irritation, nodules	Europe
P. sorici	Eulipotyphla: soricid (common shrew)		Europe
P. squamipes	Eulipotyphla: soricid (Chinese mole shrew)		Asia
P. talpae	Eulipotyphla: talpid (European mole)		Europe
P. townsendi	Rodentia: cricetid (Townsend's vole)		North America
P. tupaiae	Scandentia: tupaiid (striped treeshrew)		Asia
P. urotrichi	Eulipotyphla: talpid (Japanese shrew mole)		Asia
P. watsoni	Rodentia: cricetid (deer mouse)		North America
P. zibethicalis	Rodentia: cricetid (muskrat)		Europe
Psorergatoides (ectoparasitic on bats)			
P. artibei	Chiroptera: phyllostomid (great fruit-eating bat)		South America
P. australiensis	Chiroptera: vespertilionid (eastern forest bat, yellow-lipped cave bat, Arnhem long-eared bat, pygmy long-eared bat)		Australia
P. desmodus	Chiroptera: desmodontid (common vampire bat)		South America
P. emballanurae	Chiroptera: emballonurid (dark sheath-tailed bat)		Asia
P. glossophage	Chiroptera: phyllostomid (Pallas's long-tongued bat)		South America
P. guyanensis	Chiroptera: phyllostomid (dwarf little fruit bat)		South America
P. hipposideros	Chiroptera: hipposiderid (Sundevall's roundleaf bat, dusky leaf-nosed bat)		Africa
P. indicicola	Chiroptera: emballonurid (frosted sac-winged bat, greater sac-winged bat)		South America
P. kerivoulae	Chiroptera: vespertilionid (copper woolly bat, lesser woolly bat, wall-roosting mouse-eared bat, rufous mouse-eared bat, whiskered bat, brown long-eared bat)		Africa
P. laviae	Chiroptera: megadermatid (yellow-winged bat)		Africa
P. lonchorhina	Chiroptera: phyllostomid (Tome's sword-nosed bat), emballonurid (frosted sac-winged bat)		South America
P. molossi	Chiroptera: molossid (black mastiff bat, velvety free-tailed bat)		South America
P. nyctali	Chiroptera: vespertilionid (common noctule)		Europe
P. nycteris	Chiroptera: nycterid (large-eared slit-faced bat)		Africa
P. peropteryx	Chiroptera: emballonurid (lesser dog-like bat, chesnut sac-winged bat)		South America
P. rhinolophi	Chiroptera: rhinolophid (lesser horseshoe bat, intermediate horseshoe bat, greater horseshoe bat, Hildebrandt's horseshoe bat, Ruppell's horseshoe bat, Geoffroy's horseshoe bat, Mehely's horseshoe bat, Mediterranean horseshoe bat)		Africa, Europe, Asia
P. surinamensis	Chiroptera: phyllostomid (pygmy round-eared bat, Carriker's round-eared bat)		South America
P. tadaridae	Chiroptera: molossid (Malayan free-tailed bat)		Asia

Parasite morphology: Psorergatid mites form 4 different types of morphological developmental stages: eggs, larvae (one instar), nymphs (2-3 instars), and adults (males and females). Eggs are circular-oval tan stages measuring from 70-117 μm in diameter. The eggs embryonate to contain prelarval stages containing 2 small sclerotized sickle-shaped structures and a distinct gnathosoma (head) and idiosoma (body). Larvae are rounded to disc-shaped measuring 70-108 μm in diameter. They have a prominent gnathosoma

protruding anteriorly and adorned with short setae. They are hexapods with 3 pairs of short stumpy legs, each composed of 2 segments with 2 terminal (3 pointed) claws. The proximal leg segments bear a basal spur, and the first 2 pairs of legs have small sensory solenidia on the apical segments. All nymph stages are octopod with 4 pairs of legs that become progressively larger and more setate with each instar. Many early reports described 2 nymphal instars (protonymphs and deutonymphs), but experimental studies revealed the occurrence of a third instar (tritonymphs) for some species. Protonymphs were rounded stages measuring 80-130 μm in diameter with 4 pairs of short stubby legs regularly spaced along each side. Deutonymphs were rounded stages measuring 120-170 μm in diameter 4 pairs of slightly longer legs located laterally, with the fourth pair shifted slightly posteriorly. Tritonymphs were pyriform stages measuring 150-200 μm long with 4 pairs of legs similar to those of adult mites. Adults were round to oval in dorsal profile but had dorsoventrally-flattened disc-shaped bodies ranging in size from 150-200 μm in length (females 170-200 μm, males 150-170 μm). The cuticle was thin, finely striate and only possessed sparse setation. However, these itch mites were characterized by the possession of long trailing whip-like setae (2 pairs in females, one pair in males), as well as short stout legs with pronounced elbow-like protuberances on middle segments. The anterior gnathosoma was small but conspicuous, containing well-developed mouthparts (chelicerae and hypostome) flanked by sensory palps. The palps contained 2 stout segments terminating not in a thumb-claw complex (apotele) but in claw-like setae (smooth in *Psorergates,* but serrate in *Psorobia* and *Psorergatoides*). The stylet-like segmented chelicerae were well adapted for piercing and cutting, being pincer-like with toothed condyles and movable digits. The mouth was formed by confluence of a dorsal rostrum, ventral buccal cone and central hypostome. The hypostome was not barbed and the antero-dorsal region formed part of the stylophore capsule. Adult mites possessed anterior respiratory openings (stigmata) located near the bases of the chelicerae (like some other prostigmatid mites), but the stigmata lacked cuticular peritremes. The alimentary tract consisted of a tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with caeca/diverticulae), tubular hindgut (with excretory Malpighian tubules) and a short rectum opening to a subterminal ventral anus. The large discoidal idiosoma bears a lightly-sclerotized dorsal shield covering most of the dorsum. The shield is punctate with striated margins and possesses 3-5 pairs of spine-like setae (3 pairs for *Psorergates*, 4 pairs for *Psorergatoides*, and 5 pairs for *Psorobia* (4 long lateral pairs, 1 short antero-median pair)). The 4 pairs of short stubby legs are regularly spaced around the ventral idiosoma, each leg consisting of 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) and terminating in 2 apical claws (with 1, 2 or 3 points) and a bilobed pad-like empodium. The coxae are fused to the body wall and often have a thickened extension (apodeme) joining them. The trochanter has a small anterior proximal spur directed downwards and the femur has a distinctive hooked appearance due to the possession of an elbow-like posteriad protuberance. Female mites have 2 ovaries (with ovarioles) joined by tubular oviducts to a globular uterus (with muscular shell-gland) and vagina with accessory organs for sperm receipt and storage (bursa copulatrix, spermathecae). The genital opening (gonopore) is located posteroventral between 2 adanal lobes. Male mites have 2 testes connected by tubular vas deferens to the ejaculatory duct and an elongate sheathed aedeagus (penis) which is unusual in that it is located dorsally and extends from the mid-body to the gonopore near the front body margin.

Site of infection: These mites are commonly known as itch mites that live on the surface and superficial layers of the epidermis. Although they are non-burrowing mites, they feed, reproduce and lay eggs in hair follicles and small pits in epidermis, with adults frequently found on the surface of the skin but larval and nymphal stages usually found within the stratum corneum. *Psorergates* spp. have been described from 4 families of rodents (mainly cricetids and murids, but also some sciurids and glirids) and 2 families of insectivores (soricid and talpid shrews). *Psorergatoides* spp. have been described exclusively from bats belonging to 9 different families. *Psorobia* spp. have been described from a range of mammals, including artiodactylans, carnivores, primates, lagomorphs, shrews, and some specialized rodents (mole rats, porcupines, beavers). Infestations have been reported on many body locations, but mites prefer less-keratinized areas of skin, particularly around the head, neck and dorsal midline. In sheep, they are commonly found in heavily wooled areas along the flanks between the shoulders and hips.

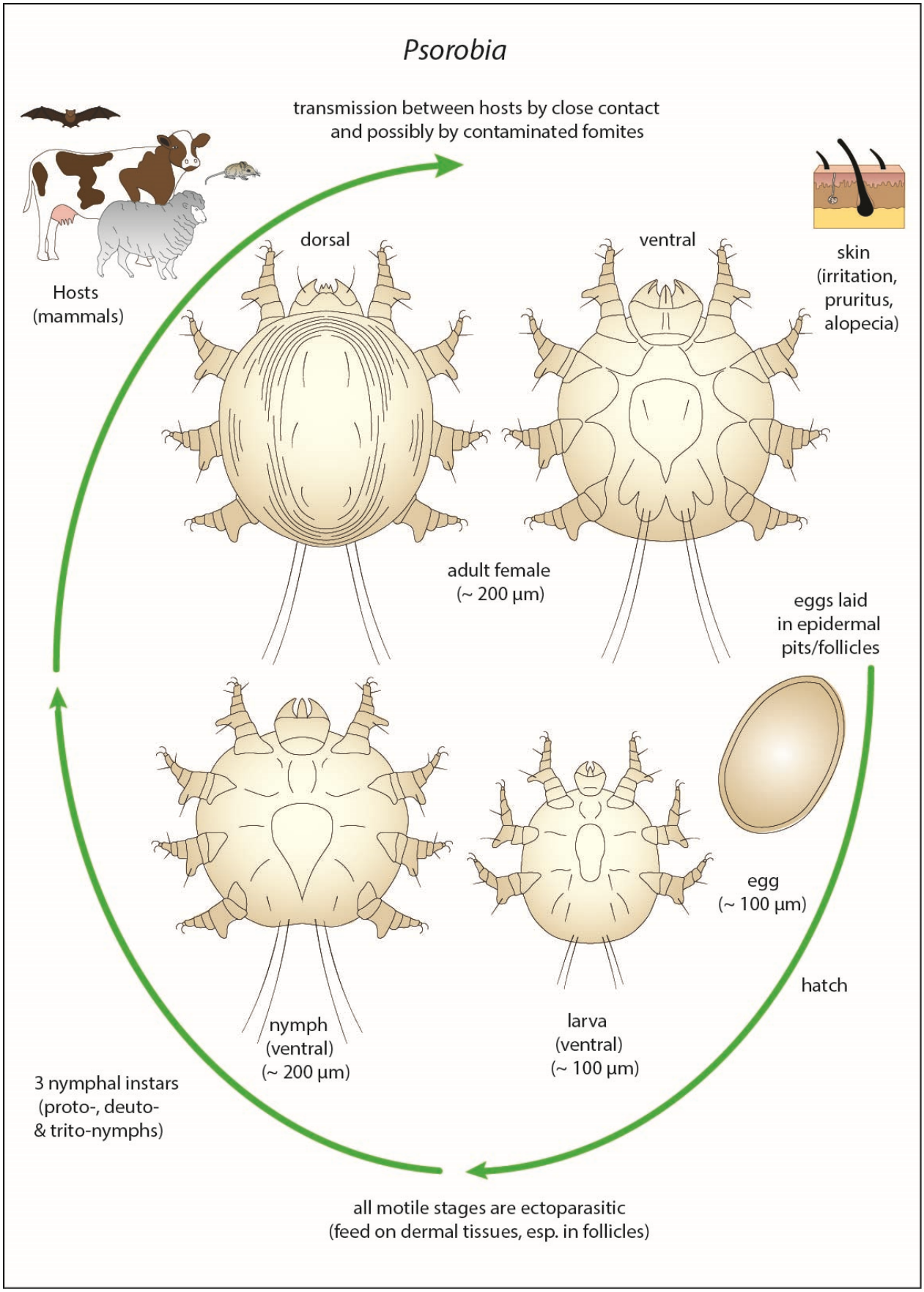
Pathogenesis: Infestations often remain asymptomatic or subclinical and rarely cause disease in wild animals. Heavier infestations, however, may cause skin disease (known as psorergatic mange), particularly on domestic sheep, laboratory rodents and some laboratory primates. While these mites do not burrow into the skin, they may invade hair follicles and even excavate small body-sized epidermal pits. They use their piercing/cutting chelicerae to feed within the stratum corneum of skin by puncturing cell walls. They often feed on cells in the root sheath of hair follicles causing cellular hypertrophy and hyperkeratosis, sometimes disrupting neighbouring hair follicles to form nodular cysts. Female mites may also excavate small pits in the epidermis creating egg nests. Immature mites developing in these pits may enlarge them forming fluid- or keratin-filled papular lesions that often rupture causing inflammation and other host immune responses. Infestations may cause significant irritation and pruritus, especially in animals that develop hypersensitivity reactions to mite antigens, resulting in chronic dermatitis with alopecia and scaling (scurf is often seen varying from sparse white-powdery skin particles to thick white-yellow flakes). Animals attempt to relieve the irritation and pruritus by intense self-grooming with rubbing, scratching and biting causing further damage to the skin and pelt/fleece. In sheep, infestations may cause decreased wool quantity and quality, due to fleece derangement (pulled and matted wool) and wool discoloration (slightly yellowish colour), especially common along the lateral thorax, hindquarters and thighs. Infestations by sheep itch mites are particularly problematic in Merino sheep which develop hypersensitivity reactions leading to fleece derangement and downgrading of the clip. Infestations on cattle are usually asymptomatic, but may sometimes involve mild pruritus and patchy alopecia with increased frequency of self-grooming (licking and rubbing). Several *Psorergates* spp. have been associated with clinical disease in rodents (mice and rats) involving nodule formation on the head and neck, alopecia and self-mutilation due to intense scratching. Several *Psorobia* spp. have also been found to cause mange in colonies of laboratory primates, as well as pruritus, scaly skin and multifocal alopecia in a siamang in a zoo. The clinical significance of *Psorergatoides* spp. infestations on

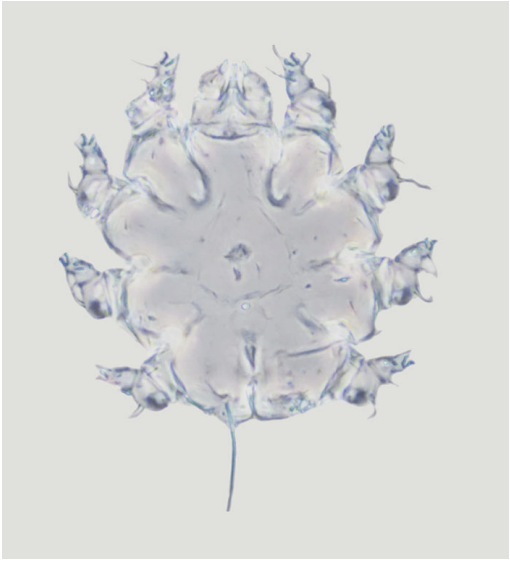
bats is not known, but mites have been associated with dermatitis, alopecia and thickened skin on wing membranes which may affect their ability to fly and forage effectively.

Developmental cycle and mode of transmission: Like all mites, psorergatid mites undergo incomplete (hemimetabolous) metamorphosis where eggs hatch larvae which moult to nymphs and then adult mites. Gravid females lay eggs in hair follicles and epidermal pits where they hatch after 8 days. All immature developmental stages have rudimentary legs and are not highly mobile remaining confined to the stratum corneum. Newly emergent hexapod larvae feed for several days (up to one week) before moulting to the first nymphal instar (protonymphs). These stages feed and rapidly moult to deutonymphs within a few days, and then to tritonymphs within 7 days. Tritonymphs feed and moult within a week to form adult mites which have stubby legs and are more mobile (only adults and some tritonymphs are found on the surface of skin). Adult mites feed and mate on hosts, with fertilized females producing up to 40-50 eggs over their short life-spans of around 16 days. The entire life-cycle may be completed in 35-42 days. Transmission occurs when adult mites transfer between hosts that are in close physical contact, particularly when mothers suckle their young or when animals are crowded together for extended periods. Adult mites are very sensitive to desiccation and they only survive for short periods (up to 1-2 days) when dislodged from hosts. They also do not tolerate exposure to sunlight so when sheep are shorn, adult mites often seek alternate hosts or refuges away from sunlight, thus increasing transmission rates between animals at shearing time. Nonetheless, infestations spread slowly over individuals and through flocks, taking 3-4 years to become established, and often restricted to hypersensitive individuals. Mite populations have been observed to peak during winter and decline over summer.

Differential diagnosis: Infestations in sheep may be suspected on clinical grounds, particularly when fleece derangement is involved with chewed wool on the flanks and rump. Physical examination may reveal papular lesions and scurf (dandruff) is often present as white powdery particles or yellowish flakes. Diagnoses are made by the microscopic detection of mites in skin scrapings or scurf, usually following treatment with 10% potassium hydroxide to digest skin material (mites have cuticles impervious to digestion). Biopsies may also be conducted by excising skin nodules and processing them for routine histological examination.

Treatment and control: It is difficult to treat psorergatic mange using conventional topical acaricides due to the location of the mites (within hair follicles and epidermal pits) and application problems (such as inadequate wetting, poor penetration, risks involved in dipping full-wooled, pregnant or young sheep, especially in cold weather). Nevertheless, some successes have been reported using sulphur preparations (lime sulphur, arsenic-sulphur), organophosphates (coumaphos, diazinon, malathion, methoxychlor), and formamidines (amitraz). Treatment efficacy was greatly improved through the use of systemic acaricides, particularly macrocyclic lactones (ivermectin, abamectin, moxidectin). The widespread use of such drenches for other endo- and ecto-parasite control has greatly reduced the incidence of itch mite infestations and disease is now considered rare. Various preventive measures may be adopted to break transmission cycles, including regular health surveillance (as a prelude to treatment, isolation or culling), routine prophylactic treatment of high-risk cohorts (laboratory animals, sheep around shearing) and maintaining hygiene around animal holding facilities (cleaning pens/stalls/yards, and replacing bedding/nesting materials).


Psorobia
transmission between hosts by close contact
and possibly by contaminated fomites
Hosts
(mammals)
dorsal
ventral
skin
(irritation,
pruritus,
alopecia)
adult female
(~ 200 µm)
eggs laid
in epidermal
pits/follicles
egg
(~ 100 µm)
hatch
larva
(ventral)
(~ 100 µm)
nymph
(ventral)
(~ 200 µm)
3 nymphal instars
(proto-, deuto-
& trito-nymphs)
all motile stages are ectoparasitic
(feed on dermal tissues, esp. in follicles)



Psorergates adult from rodent



Psorobia adult from sheep

Trombicula, Eutrombicula, Neotrombicula, Leptotrombicula
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Trombidiform mites have stigmata on the gnathosoma and distinct setae on their bodies and legs. Many species are free-living, some have been associated with allergy (including asthma), and several are obligate ectoparasites on mammals or birds. Trombiculid mites are free-living pasture mites whose larval stages are facultative parasites on mammalian and avian hosts. Infestations by a small range of species belonging to different genera may cause dermatitis and allergic hypersensitivity in domestic animals and humans in close contact with pastures.

Classification:

Domain:	Eukaryota (membrane-bound nucleus)
Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class:	Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass:	Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder:	Acariformes (diverse group of mites, without posterior stigmata)
Order:	Prostigmata [Trombidiformes] (sucking mites, stigmata on gnathosoma)
Suborder:	Anystina (legs with thumb-claw process, free-living predatory mites, but some with parasitic larvae)
Superfamily:	Trombidioidea (larval stages parasitic, nymphs calyptostatic or free-living, adults free-living predators)
Family:	Trombiculidae (hexapod larvae with oval bodies, feathery setae, most legs with claws)
Genus:	*Trombicula* (parasitic on skin of mammals/birds)
Genus:	*Eutrombicula* (parasitic on skin of mammals/birds)
Genus:	*Neotrombicula* (parasitic on skin of mammals/birds)
Genus:	*Leptotrombicula* (parasitic on skin of mammals/birds)
Species:	various species cause dermatitis in mammals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of prostigmate mites have been described: many species being free-living (including most trombiculids although some have parasitic larvae); and others being obligate ectoparasites on mammals or birds. Parasitic species spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Prostigmatid mites are characterized by having oval-ellipsoidal bodies (sometimes vermiform) with distinctive setation, piercing chelicerae (sometimes pincer-like), unbarbed hypostomes, well-developed palps, and short legs with coxae fused to the body wall and terminal tarsi with 1-2 claws (but lacking complex pulvilli). A total of 34 superfamilies have been recognized in 4 suborders: Anystina (with 17 superfamilies); Eleutherengona (10); Endeostigmata (3); and Eupodina (4). Many members of the suborders Anystina and Eleutherengona have legs with distinctive arrangements of the terminal tibiotarsal segments referred to as the 'thumb-claw' process. Anystina mites are mostly free-living predators that occur in soil litter, vegetation and the seashore, but include some representatives that have parasitic larvae that are often large, hairy, and bright red in

coloration. Some 17 anystine superfamilies are recognized (Adamystoidea, Anystoidea, Arrenuroidea, Caeculoidea, Calyptostomatoidea, Chyzeroidea, Erythraeoidea, Eylaoidea, Hydrachnoidea, Hydrovolzioidea, Hydryphantoidea, Hygrobatoidea, Labidostommatoidea, Lebertioidea, Paratydeoidea, Stygothrombioidea, Trombidioidea).

The superfamily Trombidioidea contains mites that have evolved relatively complex life-cycles involving eggs, pre-larvae, larvae, protonymphs, deutonymphs, tritonymphs and adult male and female mites. Unlike other prostigmatid mites, the pre-larvae, protonymphs and tritonymphs are calyptostatic (instars with regressive traits, such as non-functional mouthparts and/or legs), whereas the larvae are ectoparasitic on invertebrates or vertebrates, and the deutonymphs and adults are free-living predators in soils and litters. Some 11 families have been recognized (Eutrombidiidae, Johnstonianidae, Leeuwenhoekiidae, Microtrombidiidae, Neothrombiidae, Neotrombidiidae, Podothrombiidae, Tanaupodidae, Trombellidae, Trombiculidae, Trombidiidae). The family Trombiculidae contains numerous species whose larval forms are important parasites of terrestrial vertebrates and man. The parasitic larval stages are commonly known as chiggers, or alternatively as harvest mites, black soil itch mites, scrub-itch mites, duck-shooters itch mites, bush mites, berry bugs, red bugs, heel-bugs, herbstmilben, akamushi, tsutsugamushi, kedani, qhapas, aoutat, lepte autumnalis, bichos colorados, coloraditos, coloradilla, niguas or tlazahuatl. They have oval bodies with feathery setae, conspicuous palps with more than 2 segments, and 3 pairs of legs often bearing claws. The larvae are transient ectoparasites that feed on invertebrate or vertebrate hosts for several days (1-2 weeks) by embedding their mouthparts in the skin causing irritation, wheals, dermatitis and intense pruritus. More than 1,500 species have been recognized and allocated to 3 subfamilies (Hemitrombiculinae, Schoengastiinae, Trombiculinae). The subfamily Trombiculinae contains 43 genera (*Acariscus*, *Aniatrus*, *Aplodontophila*, *Babiangia*, *Blankaartia*, *Chiroptella*, *Crotiscus*, *Elianella*, *Endotrombicula*, *Euschoengastoides*, *Eutrombicula*, *Fonsecia*, *Heaslipia*, *Heaslipioides*, *Hoffmanniella*, *Hyponeocula*, *Kaaia*, *Leptotrombidium*, *Megatrombicula*, *Microtrombicula*, *Miyatrombicula*, *Multgniella*, *Myotrombicula*, *Neacariscus*, *Neotrombicula*, *Nothotrombicula*, *Novotrombiucla*, *Oaxacarus*, *Oenschongastia*, *Pentagonella*, *Phrynacarus*, *Polylopadium*, *Riedlinia*, *Speotrombicula*, *Tecomatlana*, *Trombicula*, *Trombiculoides*, *Trombigastia*, *Vanidicus*, *Vercammenia*, *Whartonacarus*, *Willmannium*, *Womersleyia*). Over 50 trombiculid species are known to attack humans and livestock causing severe pruritus, including *Eutrombicula, Leptotrombicula, Neotrombicula* and *Trombicula* spp. The larvae are opportunistic polyphagic ectoparasites that exhibit limited host specificity. While some apparently have preferred hosts, most are able to feed on many species of mammals and birds that happen to be available in particular habitats, sometimes occurring on sympatric reptiles, amphibians and insects. Several trombiculid species have also been implicated in the transmission of bacterial infections causing scrub typhus.

Parasite species	Hosts (for larval stages)	Location	Clinical signs	Distribution
Eutrombicula (scutum transverse rectangular to quadrate, stippled)				
E. alfreddugesi (chigger mite)	Carnivora: canid (dog), felid (cat); Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Primates: hominid (human); Accipitriformes: accipitrid (red-tailed hawk, zone-tailed hawk), cathartid (black vulture); Strigiformes: strigid (ferruginous pygmy-owl, mottled owl); Serpentes: colubrid (South American sipo, Wagler's sipo, Brazilian woodland racer, Paraguay green racer, caninana); Saura: anolid (calango-bandeira), gymnophthalmid (yellowbelly arthrosaura, Eigenmann's prionodactylus), leiosaurid (Ihering's fathead anole), phyllodactylid (turnip-tailed gecko), scincid (Paraguay mabuya, black-spotted skink, noronha skink), teiid (striped forest whiptail), tropidurid (calango); Anura: hylid (southern walking leaf frog)	skin (body parts close to grass)	irritation, pruritus, hypersensitivity	Americas, Europe
E. batatas	Accipitriformes: accipitrid (great black hawk); Falconiformes: falconid (crested caracara); Primates: hominid (human)	skin		Americas
E. hirsti	Peramelemorphia: peramelid (northern brown bandicoot, long-nosed bandicoot); Diprotodontia: macropodid (agile wallaby), phalangerid (common brushtail possum); Rodentia: murid (bush rat, fawn-footed mosaic-tailed rat, Papua grassland mosaic-tailed rat); Primates: hominid (human); Sauria: agamid (Australian water dragon)	skin		Australia
E. lipovsky	Primates: hominid (human)	skin		Americas

E. macropus	Diprotodontia: macropodid (agile wallaby, red-necked wallaby, western grey kangaroo, eastern grey kangaroo); Primates: hominid (human)	skin		Australia
E. ophidica	Sauria: teiid (striped forest whiptail), tropidurid (mountain calango)	skin		South America
E. rara	Sauria: scincid (bar-sided forest skink)	skin		Australia
E. samboni	Artiodactyla: bovid (cattle, sheep); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Primates: hominid (human); Passeriformes: turdid (common blackbird)	skin		Australia
E. sarcina (scrub itch mite, black soil itch mite)	Diprotodontia: macropodid (eastern grey kangaroo, wallaroo, wallaby); Artiodactyla: bovid (sheep); Perissodactyla: equid (horse); Carnivora: canid (dog); Primates: hominid (human): Passeriformes: corcoracid (apostlebird)	skin	intense irritation (plus larvae act as vectors for scrub typhus)	Australasia
E. splendens (chigger mite)	Carnivora: canid (dog), felid (cat); Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Primates: hominid (human)	skin (body parts close to grass)	irritation, pruritus, hypersensitivity	North America
E. southcotti	Sauria: scincid (blue-throated rainbow skink, Challenger's shade skink)	skin		Australia
E. thori	Sauria: scincid (tree-base litter-skink)	skin		Australia
E. tinami	Primates: hominid (human)	skin		Europe
E. tovelli	Sauria: scincid (brown four-fingered skink, Challenger's shade skink, lined rainbow skink, desert rainbow skink, copper-tailed skink, bar-shouldered ctenotus), varanid (lace monitor)	skin		Australia
E. tropica	Sauria: scincid (Hoge's mabuya)	skin		South America
E. vandiemeni	Sauria: scincid (White's skink, southern grass skink, metallic cool skink, spotted skink)	skin		Australia
E. wichmanni	Primates: hominid (human)	skin		Asia
Leptotrombicula (scutum rectangular with weak shoulders, stippled)				
L. akamushi	Strigiformes: strigid (short-eared owl); Primates: hominid (human)	skin, nest	irritation (plus larvae act as vectors for scrub typhus)	Holarctic
L. arenicola	Primates: hominid (human)	skin		Asia
L. deliense	Rodentia: murid (black rat, bush rat, rakali, dusky field rat, giant white-tailed rat, Cape York rat, fawn-footed mosaic-tailed rat, Papua grassland mosaic-tailed rat); Dasyuromorphia: dasyurid (red-cheeked dunnart); Diprotodontia: hypsiprymnodontid (musky rat-kangaroo); Peramelemorphia: peramelid (northern brown bandicoot, long-nosed bandicoot); Primates: hominid (human); Strigiformes: strigid (Indian scops-owl, reddish scops-owl, Eurasian scops-owl)	skin	irritation (plus larvae act as vectors for scrub typhus)	Asia
L. fletcheri	Primates: hominid (human)	skin		Asia
L. fugi	Primates: hominid (human)	skin		Asia
L. intermedium	Primates: hominid (human)	skin		Asia
L. kitasatoi	Primates: hominid (human)	skin		Asia
L. nissani	Passeriformes: artamid (black butcherbird, grey butcherbird, Australian magpie), campephagid (black-faced cuckooshrike, white-bellied cuckooshrike), corcoracid (apostlebird), corvid (Torresian crow), melephagid (moisy miner, little friarbird, silver-crowned friarbird, dusky myzomela, yellow honeyeater, yellow-spotted honeyeater, white-throated honeyeater, tawny-breasted honeyeater, blue-faced honeyeater), monarchid (leaden flycatcher, frill-necked	skin, nest		Australia

	monarch, spectacled monarch), oriolid (green oriole); pachycephalid (rufous whistler, grey shrikethrush, Arafura shrikethrush), paradisaeid (trumpet manucode, magnificent riflebird), petroicid (pale-yellow robin, eastern yellow robin), pomatostomid (grey-crowned babbler); Columbiformes: columbid (crested pigeon, Pacific emerald dove, bar-shouldered dove); Coraciiformes: alcedinid (sacred kingfisher), coraciid (Oriental dollarbird); Cuculiformes: cuculid (pallid cuckoo); Galliformes: phasianid (Indian peafowl); Podargiformes: podargid (tawny frogmouth, Papuan frogmouth); Psittaciformes: psittaculid (pale-headed rosella); Falconiformes: falconid (Australian kestrel, Nankeen kestrel, brown falcon); Strigiformes: strigid (barking owl, morepork, barn owl)			
L. pallidum	Primates: hominid (human)	skin		Asia
L. palpale	Primates: hominid (human)	skin		Asia
L. pavlovskyi	Primates: hominid (human)	skin		Asia
L. robustum	Passeriformes: meliphagid (yellow honeyeater, yellow-spotted honeyeater, dusky honeyeater, tawny-breasted honeyeater), oriolid (green oriole), pachycephalid (grey shrikethrush, Arafura shrikethrush), petroicid (eastern yellow robin); Podargiformes: podargid (tawny frogmouth)	skin		Asia
L. scutellare	Strigiformes: strigid (mountain scops-owl); Primates: hominid (human)	skin, nest		Asia
L. subquadratum	Primates: hominid (human)	skin		Africa
Neotrombicula (scutum pentagonal with a shallow convex posterior margin, stippled)				
N. antechinus	Dasyuromorphia: dasyurid (brown antechinus); Rodentia: murid (bush rat, fawn-footed mosaic-tailed rat)	skin		Australia
N. autumnalis (harvest mite)	Carnivora: canid (dog), felid (cat); Artiodactyla: bovid (cattle); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Primates: hominid (human); Strigiformes: strigid (little owl)	skin (body parts close to grass)	irritation, allergy	Europe
N. comata	Dasyuromorphia: dasyurid (brown antechinus, swamp antechinus, dusky antechinus, tiger quoll): Peramelemorphia: peramelid (long-nosed bandicoot); Diprotodontia: macropodid (parma wallaby); Rodentia: murid (bush rat); Passeriformes: acanthizid (white-browed scrubwren), climacterid (white-throated treecreeper)	skin		Australia
N. gemini	Dasyuromorphia: dasyurid (dusky antechinus): Rodentia: murid (bush rat)	skin		Australia
N. greenlyi	Sauria: gekkonid (marbled gecko, Bynoe's gecko)	skin		Australia
N. mackayensis	Dasyuromorphia: dasyurid (brown antechinus); Peramelemorphia: peramelid (long-nosed bandicoot); Diprotodontia: macropodid (swamp wallaby); Rodentia: murid (bush rat); Primates: hominid (human)	skin		Australia
N. nagayoi	Primates: hominid (human)	skin		Asia
N. novaehollandiae	Dasyuromorphia: dasyurid (brown antechinus, swamp antechinus, dusky antechinus, tiger quoll, eastern quoll); Diprotodontia: macropodid (parma wallaby, red-necked wallaby, swamp wallaby, Tasmanian pademelon), phalangerid (common brushtail possum), potoroid (long-nosed potoroo); Peramelemorphia: peramelid (southern brown bandicoot); Monotremata: tachyglossid (short-beaked echidna); Rodentia: murid (bush rat,			Australia

	Australian swamp rat); Carnivora: canid (dog); Passeriformes: acanthizid (white-browed scrubwren)			
N. pentagona	Lepidoptera: papilionid (Cairns birdwing butterfly) - accidental			Australia
N. thylogale	Peramelemorphia: peramelid (long-nosed bandicoot); Diprotodontia: macropodid (red-legged pademelon)	skin		Australia
Trombicula (scutum transverse rectangular with a deeply convex posterior margin, punctate-aerolate)				
T. chiroptera	Chiroptera: vespertilionid (Gould's wattled bat)	skin		Australia
T. dasyphloea	Chiroptera: hipposiderid (Semon's leaf-nosed bat)	skin		Australia
T. dewae	Chiroptera: emballonurid (common sheath-tail bat)	skin		Australia
T. geckobia	Sauria: gekkonid (unidentified gecko)	skin		Australia
T. lukoschusi	Chiroptera: emballonurid (common sheath-tail bat)	skin		Australia
T. mitchellensis	Chiroptera: emballonurid (common sheath-tail bat), megadermatid (ghost bat)	skin		Australia
T. quadriensis	Dasyuromorphia: dasyurid (brown antechinus, swamp antechinus, yellow-footed antechinus); Diprotodontia: phalangerid (short-eared possum, common brushtail possum); Rodentia: murid (rakali, bush rat, giant white-tailed rat)	skin		Australia
T. rugosa	Rodentia: murid (common rock rat)	skin		Australia
T. southcotti	Diprotodontia: macropodid (short-eared rock-wallaby)	skin		Australia
T. thomsoni	Chiroptera: emballonurid (common sheath-tail bat), vespertilionid (Gould's wattled bat, eastern forest bat)	skin		Australia

Parasite morphology: Trombiculid mites form 4 different types of morphological stages during their developmental cycles; namely, eggs, larvae, nymphs, and adults. The eggs are dark spherical-ovoid stages measuring around 150-200 µm in diameter which often become larger and more elongated during embryonic development. The outer eggshell eventually ruptures releasing an inactive incompletely-developed larva (known as a deutovum). The deutovum grows and develops to an active hexapod larva measuring up to 300 µm which is initially deep red in colour. These larvae are the only stages in the life-cycle that are parasitic on vertebrate hosts (all other stages are free-living). Parasitic larvae (often known as chiggers) feed on host fluids and may grow up to 400-600 µm in size, usually changing colour to orange-yellow. Trombiculid genera are differentiated mainly on the basis of differences in scutum shape, leg structure (especially genu and tarsi segments), sensillae thickness (uniform or thinning distally), and chaetotaxy (patterns of setation). The body is ovoidal to ellipsoidal in shape (slightly flattened laterally) and has a small anterior gnathosoma (head) bearing prominent mouthparts flanked by a pair of palps. The palps each have 5 segments (coxa, femur, genu, tibia and tarsus) and terminate in a thumb-claw pincer (formed by a tibial claw opposing a tarsal thumb-like process). The claw may have 3 prongs (trifurcate, e.g. *N. autumnalis*) or 2 prongs (bifurcate, e.g. *E. alfreddugesi*). The palpal femur and genu each have a single seta, the tibia has 3 setae, and the tarsus bears 4-7 setae depending on the species. The biting-sucking mouthparts are well-developed and nonretractile, with a central unbarbed hypostome flanked by short segmented blade-like chelicerae. During feeding, an elongate feeding tube (stylostome or histosiphon) develops from hardened mite saliva and host tissues. Larvae do not possess respiratory organs but breath through the cuticle. In trombiculid genera of medical and veterinary significance, the larval idiosoma (body) has a single anterodorsal shield (scutum) with 4-6 plumose (feathery) setae. The scutum varies in shape from transverse rectangular to quadrate in the genus *Eutrombicula,* pentagonal with a shallow convex posterior margin in *Neotrombicula*, rectangular with weak shoulders in *Leptotrombicula*, and transverse rectangular with a deeply convex posterior margin in the genus *Trombicula.* The scutum texture varies from stippled (*Neotrombicula, Leptotrombicula, Eutrombicula*) to punctate-aerolate (*Trombicula*, not rugose as sometimes stated) and often bears small transverse annulations. A pair of simple eyes are located laterally on either side of the scutum. The ventral idiosoma bears 3 pairs of long setate legs, each composed of 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) and ending in a pair of large claws flanking a long fine empodium. Coxae I and II are contiguous with the body wall and encompass an ovate chemosensory (Claprede) organ. Genu I have one (*Neotrombicula*), 2 (*Trombicula*, *Leptotrombicula*) or 3 (*Eutrombicula*) genuala. The uropore (anus) is located subterminally and ventrally. Trombiculid larvae appear to be highly setose, with the body and legs being covered with 20-50 fine long velvet-like setae (most plumose but some smooth). Nymphs are nonparasitic free-living stages and 3 instars have been described: an inactive nymphochrysalis (protonymph); an active and predaceous octopod (8-legged) nymph (deutonymph); and an inactive imagochrysalis (tritonymph). Nymphs are oval-shaped with an anterior constriction (imparting a stout figure-of-eight shape) and they range in size from 0.8-1.2 mm in length. They have respiratory openings (stigmata) near the bases of their chelicerae and their bodies are covered in setae. Adult mites have a stout figure-of-eight shape with the 'waist-like' constriction located between the last 2 pairs of legs. They are typically reddish in colour and range in size from 1-2 mm in length. They are covered with tiny dense hairs giving them a velvet-like

appearance. They have an anterior gnathosoma bearing conspicuous mouthparts and palps. Adults are predaceous and have piercing-cutting mouthparts with long stylet-like (sometimes pincer-like) chelicerae flanking the central unbarbed hypostome. They have respiratory stigmata located near the bases of the chelicerae (like other prostigmatid mites). The lateral palps are well-developed segmented structures but lack terminal claws (apoteles). The alimentary tract comprises a tubular foregut, saccular midgut (with caecae) and tubular hindgut (with excretory Malpighian tubules) leading to a subterminal anus. The idiosoma lacks dorsal shields and the ventral surface gives rise to 4 pairs of long setose legs, each consisting of 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) and all ending in 1-2 claws without complex pulvulli. Female mites have 2 ovaries connected by tubular oviducts to a common uterus (with accessory shell-glands) and vagina (with accessory organs for sperm receipt and storage). Male mites have 2 testes joined by tubular vas deferens to an elongate ejaculatory duct. Males produce stalked spermatophores which are taken up by females during mating.

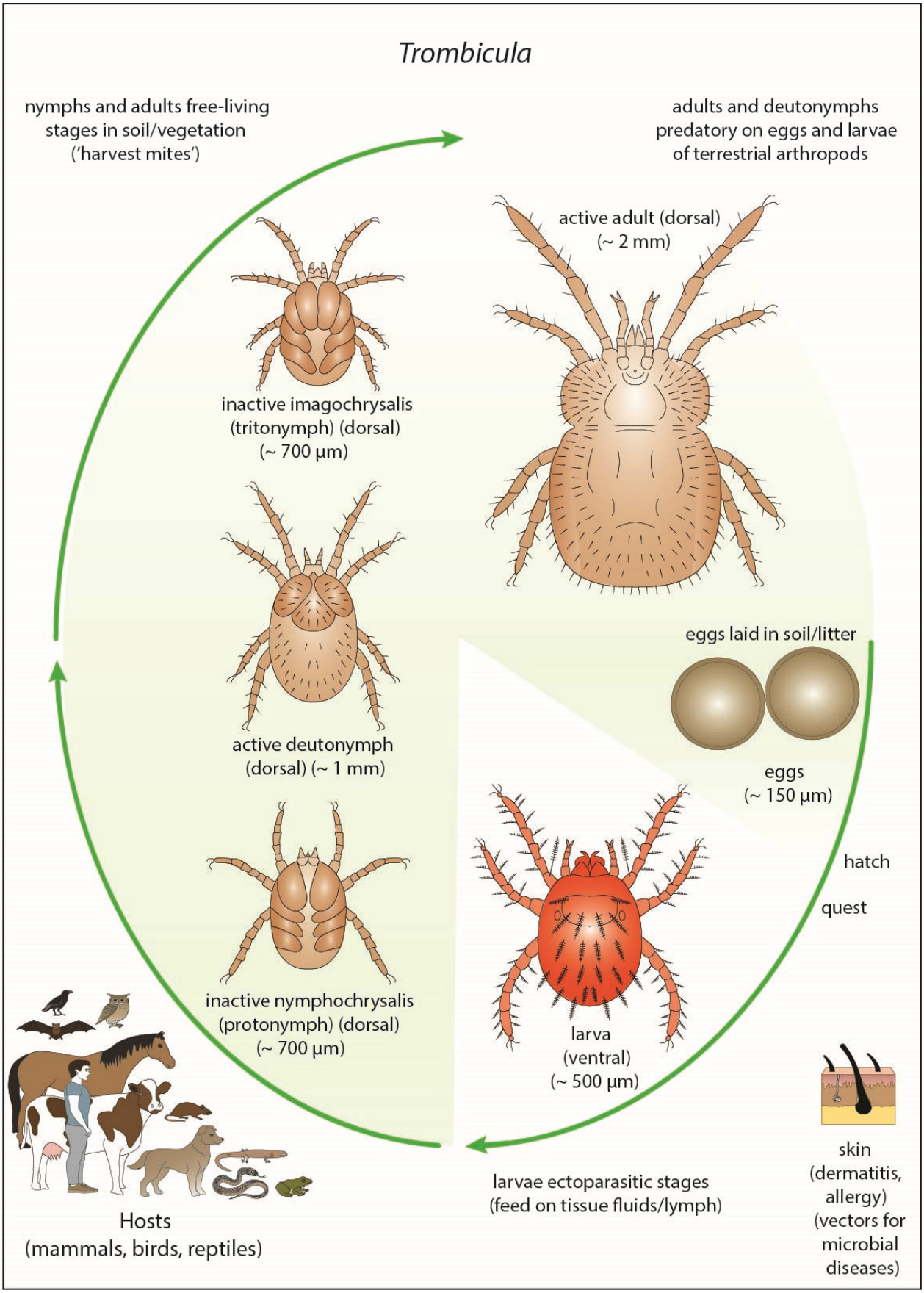
Site of infection: Adult and nymphal trombiculid mites are free-living terrestrial predators on the eggs and larvae of other arthropods. However, their larval stages are obligate ectoparasites on a range of vertebrate hosts, including mammals (especially rodents, but also including humans), birds, reptiles and some amphibians. *Trombicula* spp. have been recorded on bats, rodents, marsupials, and humans; *Neotrombicula* spp. on carnivores, marsupials, rodents, ungulates, lagomorphs, lizards, birds, and humans; *Eutrombicula* spp. on carnivores, ungulates, lagomorphs, marsupials, rodents, birds, snakes, lizards, frogs, and humans; and *Leptotrombicula* on birds, rodents, marsupials, and humans. Larvae crawl onto vegetation and wait for hosts to brush past so they can crawl onto available skin. Once on hosts, larvae migrate over the host (sometimes for hours) exhibiting strong site preferences for attachment and feeding, often clustering together in groups. Infestations on humans usually involve soft thin skin around the ankles, behind the knees, in the armpits, over the groin, stomach (often under belts or straps) and also the hands and face. In animals, infestations often involve areas that come in contact with the ground, e.g., the head (muzzle, face, ears), limbs, interdigital areas and ventrum, although other body sites may also be infested. On dogs and cats, larvae may cluster on the ear pinnae, sometimes in the ear canals, and eyelid margins. On birds, larvae are usually found under the wings, around the vent, or on the head (on combs and wattles and around the eyes). Some species have also been shown to exhibit differences in site preferences according to the host species infested; e.g. *L. deliense* clusters on the ear fossae of rats, but on the ventral midline of tree-shrews.

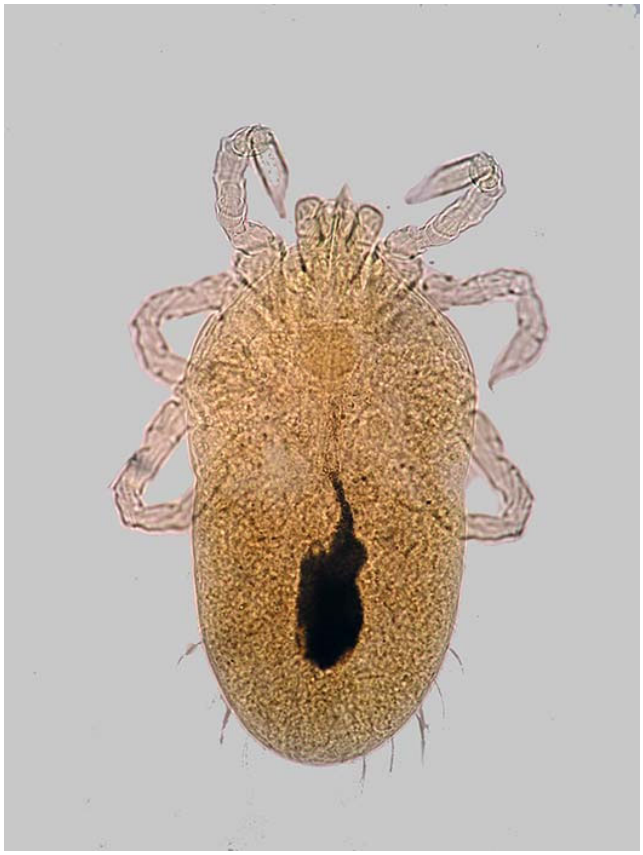
Pathogenesis: While trombiculid larvae are obligate ectoparasites on vertebrate hosts, infestations on natural hosts are generally thought to be well tolerated remaining asymptomatic or subclinical, but infestations on accidental hosts often trigger allergic immune responses leading to clinical disease (termed trombiculidiasis or trombiculosis). Chigger larvae do not burrow into the skin, but pierce the epidermis using their mouthparts. They do not suck blood, but feed on tissue fluids and lymph, although a few red blood cells may be ingested during feeding. The larvae inject saliva containing digestive enzymes that cause autolysis of epidermal cells. They suck up the resultant liquefied food (lysed semi-digested cells, intracellular fluids, extracellular fluids, incl. lymph) via a tube-like structure (stylostome or histosiphon) formed by solidified saliva and hardened tissues. Larvae remain on hosts for variable periods ranging from a few hours to several days, engorging to become bright red spheres before detaching and falling to the ground. Hosts may not react to the first few bites, but mite saliva and stylosomes are irritants and lead to allergic reactions minutes to hours after the mite has fed. Bites are evident as tiny red papules, spots or welts, typically in clusters, accompanied by intense and painful pruritus, local erythema, inflammation (dermatitis) and rash formation. Large scabs may appear around bite sites and stylostomes as the salivary enzymes degrade epithelial tissues. Hypersensitivity reactions may develop in some individuals with vesicles and bullae formation. Because larvae tend to cluster together, skin lesions and host reactions can become quite extensive. Hosts attempt to relieve the discomfort by intense self-grooming (biting, licking scratching, rubbing) which can lead to self-trauma and excoriation with lesions becoming susceptible to secondary bacterial infections. Dogs and cats may experience severe biting stress with intensely pruritic papules on the limbs, ventrum, genitalia and around the head, sometimes accompanied by mild wheal and flare reactions. Infestations may lead to alopecia, scales, crusts and scabs with moist serous or dried yellow exudates. Cattle and horses often develop irritating lesions around the face which cause them to bite, stamp and rub against objects leading to self-mutilation in heavy infestations. Birds also develop lesions around body parts coming into contact with vegetation (mainly the head and ventral surfaces) and heavy infestations in poultry may cause significant morbidity (depression, anorexia) and mortality (from starvation and exhaustion) contributing to production losses. Humans often experience transient inflammatory pustular lesions and dermatitis particularly on the hands, face and around the waistline (under belts or straps), usually seen from spring to late summer. Some trombiculid species have gained notoriety as causative agents of scrub itch, an extremely irritating and maddening affliction due to delayed host reactions to mite salivary secretions. Epidemiological investigations have linked infestations to activities associated with handling cut vegetation (e.g. during harvest), hiking and trekking through grasslands or bushlands, and contact with animals. In several countries, infestations have been associated with a summer penile syndrome involving inflammation, pruritus and erythema of the penis and scrotal skin often in boys younger than 12 years old resulting in dysuria. Microbiological studies have also implicated several *Leptotrombicula* species as vectors for rickettsial bacterial infections to humans, notably tsutsugamushi fever caused by *Orientia tsutsugamushi* (formerly *Rickettsia tsutsugamushi*) in Asia and scrub typhus caused by *Orientia australis* in Australia. These acute infectious diseases are characterized by fever, chills, headaches, myalgia, and sometimes hearing loss. The bacteria exhibit trans-stadial transmission (persisting through nymphal and adult stages) and then trans-ovarian transmission (passing from gravid females to eggs and then larvae). *Ehrlichia* and *Borrelia* spp. have also been detected in larvae collected from birds, but their role in the transmission of disease remains speculative.

Developmental cycle and mode of transmission: Trombiculid mites undergo gradual (hemimetabolous) metamorphosis whereby eggs hatch larvae which moult through several nymphal stages to form adults. Only the larval stages attach to vertebrate hosts as ectoparasites, while nymphal and adult stages are free-living predators on other arthropods. Gravid female mites lay small clutches of 1-15 eggs on leaf litter, shaded vegetation or damp well-drained soils, including pastures, grasslands, scrublands and along riverbanks. The eggshell splits after 1-2 weeks exposing the pre-larva (deutovum) which remains in the eggshell to mature for another week before emerging as a hexapod larva (or chigger). The larvae crawl onto low vegetation in their grassland or woodland habitats and remain quiescent until stimulated by air currents containing expired carbon dioxide from approaching animals. Larvae are often referred to as 'harvest mites' as they are found in significant numbers in hay and other harvested products. Depending on prevailing environmental conditions, larvae may survive for up to 30 days waiting for hosts. Upon contact, they latch onto passing hosts and crawl to their preferred attachment sites. Larvae often congregate together on vegetation so hosts often become infested by multiple larvae which then cluster at preferred attachment sites. They are ectoparasitic on a wide variety of vertebrates, including mammals (commonly small rodents, but also humans), birds, reptiles and amphibians. Trombiculid species exhibit variable host specificity, with some species infesting a narrow range of hosts while others infest a wide range of hosts (including natural, opportunistic and accidental hosts). Larvae attach to the surface of the skin and begin feeding on host fluids by secreting saliva which helps form the stylostome feeding tube. They generally feed for 3-5 days, but the feeding time may be extended up to 10 days in hosts developing severe dermal reactions. When replete, the engorged larvae detach and drop to the ground burying themselves under leaves or just below the soil. Within 3 days they enter a quiescent phase as an inactive nymphochrysalis (protonymph) before moulting to become an active octopod nymph (deutonymph). Deutonymphs are free-living predators that feed on the eggs and larvae of other arthropods for 1-2 weeks. They then enter another quiescent phase as an inactive imagochrysalis (tritonymph) for several days. The tritonymphs finally moult to form adult mites which actively crawl around in soil feeding on a variety of soft-bodied arthropod developmental stages (notably insect eggs and larvae), plant juices and decaying plant material. Adult males produce spermatophores which are used to inseminate receptive adult female mites which then begin laying 1-15 eggs each day for up to 3-5 months. Mites are most active in warm conditions and egg laying may occur year round. However, in cooler conditions, mites suspend egg production and enter partial hibernation burrowed beneath the soil. Adult females usually live for one year, generally dying in autumn. The whole life-cycle may be completed in as little as 2 months under ideal environmental conditions. Many mite species in tropical regions undergo multiple generations each year, those in subtropical regions often undergo 2-3 generations each year, while those in cooler temperate regions only undergo a single generation each year. Mites often exhibit fragmented patchy distributions (sometimes called mite islands) due to their complex ecological requirements (e.g. free-living stages requiring moist soils with plentiful food sources, and parasitic larval stages requiring a regular supply of small vertebrates).

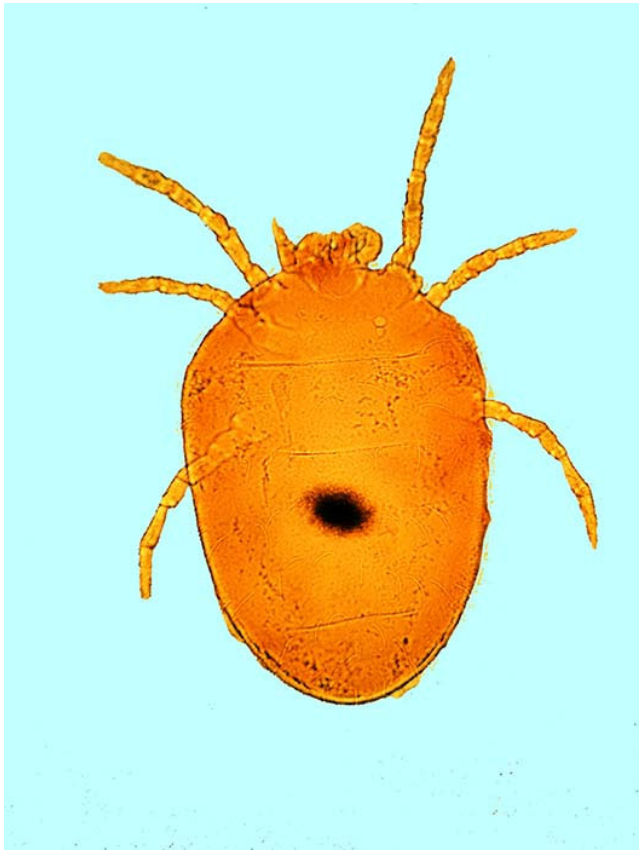
Differential diagnosis: Chigger mite infestations are difficult to detect on the basis of symptomatology as they are transient surface dwellers, easily brushed off and have often left the host when clinical signs first arise (pruritus, rash, crusting dermatosis). Nonetheless, when larvae are present, they may be observed as orange-red roundish specks (0.15-0.3 mm), usually grouped together in small clusters up to 1 mm in diameter. Specimens may be removed using probes, tweezers or swabs, examined microscopically and identified by their unique morphological characteristics. Dermatoscopy has recently been used to diagnose infestations by detecting mites on the skin with strong orange-reddish fluorescence. Modern molecular biological techniques have been used to characterize trombiculid species and infer phylogenetic relationships, following the polymerase chain reaction (PCR) amplification of nuclear (internal transcribed spacers (ITS) of ribosomal RNA, citrate synthase (gltA) gene sequences. Similar techniques may also be used to screen mites for the presence of the aetiological agent of scrub typhus, namely *Orientia* (formerly *Rickettsia*) major outer membrane protein (56 kDa), chaperonin 60 (GroE1) and ribosomal RNA (16S rRNA) by conventional or nested PCR.

Treatment and control: While chigger mite infestations are transient and clinical signs usually resolve spontaneously, treatment is often warranted in cases where severe clinical disease develops, particularly in sensitized individuals, even though mites may have already detached. Symptomatic relief may be provided by the application of cold compresses, antipruritic lotions (e.g. calamine) or baths (e.g. Epsom salts), topical corticosteroids, and oral antihistamines. Topical antiseptics may be used to help prevent secondary bacterial infections in excoriated wounds, or patients may be given a course of antibiotics (note that hospitalization and extended antibiotic treatment may be required for cases involving scrub typhus). In situations where mites are detected still attached to the skin, they should be removed mechanically using probes or tweezers, and the affected areas washed thoroughly with soap and water. A range of chemical acaricides have been used to treat chigger mites, including sulphur compounds (lime sulphur, potassium sulphur), natural products (rotenone), carbamates (carbaryl), organophosphates (coumaphos, chlorpyriphos, malathion, diazinon), pyrethrins (permethrin) and arylpyrazoles (fipronil). Hosts resident in endemic regions are exposed to constant re-infestation during peak seasons, especially farm workers handling supplementary feeds (harvested hay, etc.). Preventing infestations may be accomplished by avoiding endemic regions, not handling cut vegetation, wearing protective clothing (boots and long-sleeved tight-fitting clothes) and applying repellents (permethrin, diethyltoluamide (DEET), dimethyl phthalate, dibutyl phthalate, dimethyl carbamate, ethyl hexanediol) to exposed skin or clothing. Studies on environmental control of chigger populations have shown that clearing vegetation (mowing, slashing, or weeding) was relatively ineffectual, but the application of residual acaricides (e.g. permethrin) as sprays or dusts to vegetation around residential premises helped lower mite populations and infestation rates. Other preventive measures involve denying larvae access to hosts by moving livestock off infested pastures, restricting pet roaming and undertaking vermin (rodent) control.

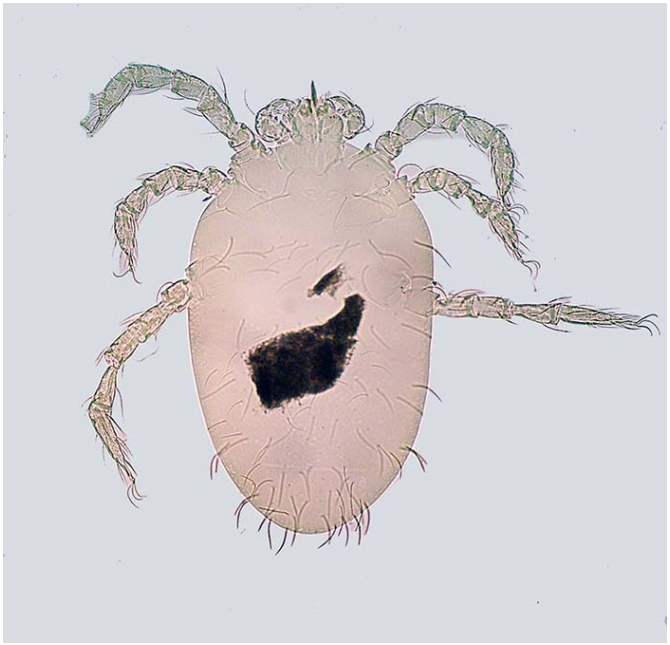

Trombicula
nymphs and adults free-living stages in soil/vegetation ('harvest mites')
adults and deutonymphs predatory on eggs and larvae of terrestrial arthropods
active adult (dorsal) (~ 2 mm)
inactive imagochrysalis (tritonymph) (dorsal) (~ 700 µm)
active deutonymph (dorsal) (~ 1 mm)
eggs laid in soil/litter
eggs (~ 150 µm)
hatch
quest
inactive nymphochrysalis (protonymph) (dorsal) (~ 700 µm)
larva (ventral) (~ 500 µm)
Hosts (mammals, birds, reptiles)
larvae ectoparasitic stages (feed on tissue fluids/lymph)
skin (dermatitis, allergy) (vectors for microbial diseases)



Trombicula larva



Trombicula larva



Trombicula larva

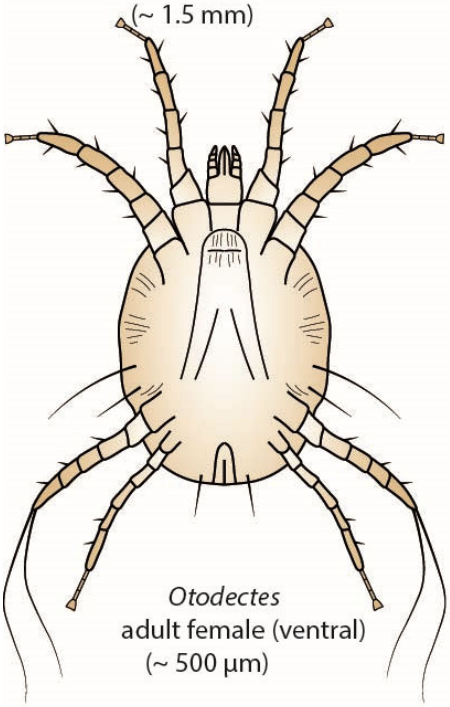


Trombicula larva

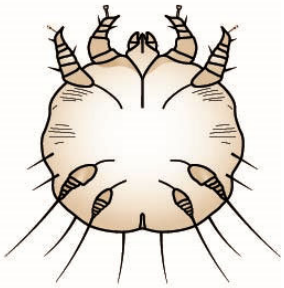
Astigmata
(mites)

Acari: Astigmata 1

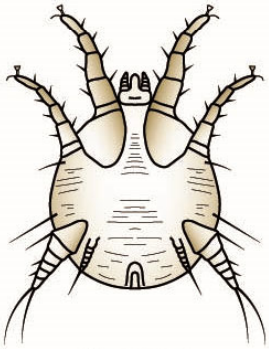
Psoroptes
adult female (ventral)
(~ 1.5 mm)



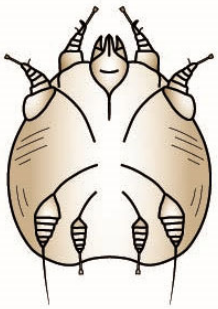
Sarcoptes
adult female (ventral)
(~ 400 µm)



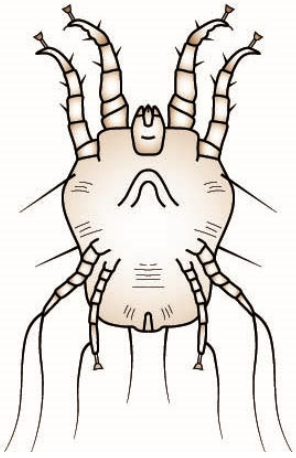
Otodectes
adult female (ventral)
(~ 500 µm)



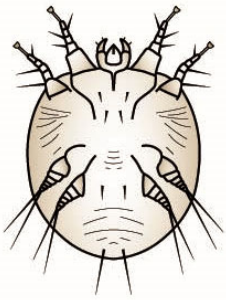
Notoedres
adult male (ventral)
(~ 300 µm)



Chorioptes
adult female (ventral)
(~ 500 µm)

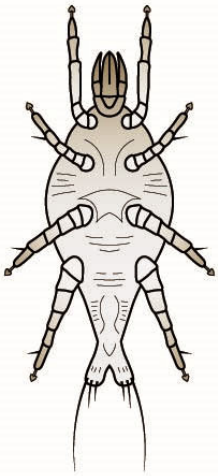


Trixacarus
adult female (ventral)
(~ 240 µm)

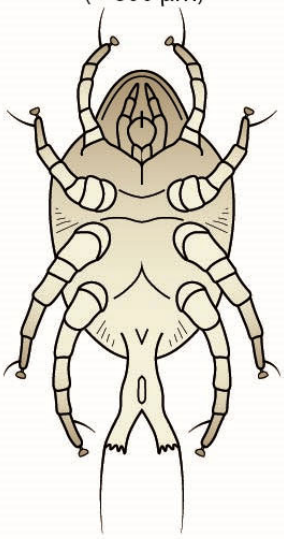


Acari: Astigmata 2

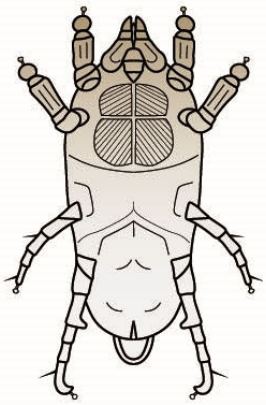
Lynxacarus
adult male (ventral)
(~ 500 µm)



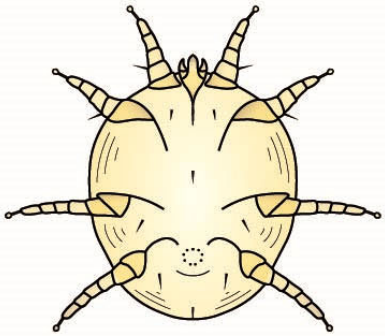
Leporacarus
adult male (ventral)
(~ 600 µm)



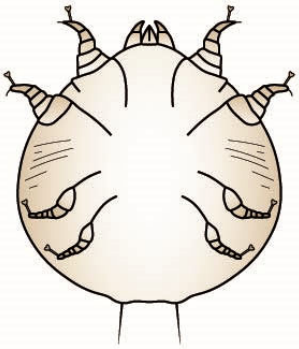
Chirodiscoides
adult male (ventral)
(~ 500 µm)



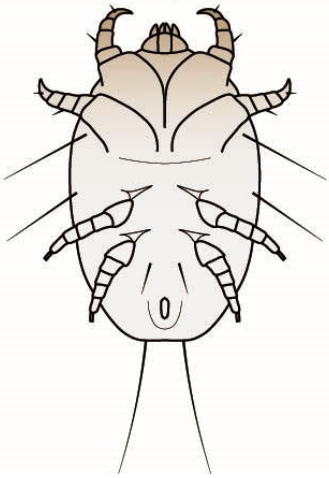
Cytodites
adult male (ventral)
(~ 500 µm)



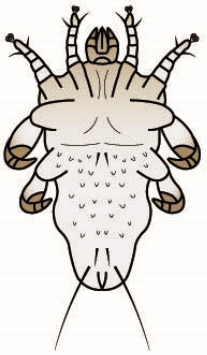
Knemidocoptes
adult male (ventral)
(~ 500 µm)



Laminosioptes
adult male (ventral)
(~ 700 µm)



Myocoptes
adult male (ventral)
(~ 380 µm)



Psoroptes
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Psoroptids are non-burrowing mites with oval bodies and the last two pairs of legs project beyond the body margin. Infestations by *Psoroptes* spp. may cause psoroptic mange in ruminants and ear canker in rabbits.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Sarcoptoidea (mites associated with mammals, ecto- or endo-parasitic)
Family: Psoroptidae (non-burrowing mites, oval bodies, third and fourth pairs of legs project beyond body margin)
Genus: *Psoroptes* (parasitic on skin of ruminants/horses/rabbits)
Species: various species cause psoroptic mange in ruminants and ear canker in rabbits

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

Early classification schemes identified different assemblages principally on the basis of host and site specificity; including bird-associated feather mites (e.g. Analgoidea); bird-associated skin mites (e.g. Knemidokoptidae), mammal-associated fur mites (e.g. Listrophoridae), mammal-associated skin mites (e.g. Psoroptidae); and mammal-associated skin-burrowing mites (e.g. Sarcoptoidea). However, phylogenetic studies (both cladistic and molecular) have revealed that many groups are not monophyletic but para- or poly-phyletic, so further studies are required to resolve the fidelity of most groups. Recently, molecular studies suggested that 16 sarcoptoidean families may belong to 2 main lineages: 13 families identified in a 'sarcoptid' complex (Atopomelidae, Audycoptidae, Chirodiscidae, Chirorhynchobiidae, Galagalgidae, Gastronyssidae, Lemurnyssidae, Listrophoridae, Listropsoralgidae, Myocoptidae, Pneumocoptidae, Rhyncoptidae, Sarcoptidae), and 3 families in a 'psoroptid' complex (Lobalgidae, Paracoroptidae, Psoroptidae). Nevertheless, most families can still be categorized into 4 broad 'morphoecotypes': namely; fur mites (Atopomelidae, Chirodiscidae, Listrophoridae, Lobalgidae), skin mites (Chirorhynchobiidae, Myocoptidae, Psoroptidae), skin-burrowing and follicle mites (Rhyncoptidae, Sarcoptidae), and respiratory mites (Gastronyssidae, Lemurnyssidae, Pneumocoptidae). The family Psoroptidae contains non-burrowing skin mites with oval bodies and 4 pairs of legs projecting well beyond the body margin. They are obligate mammalian ectoparasites commonly known as scab mites as their feeding activity causes dermatitis resulting in scab formation at the bite site. A total of 17 genera have been identified (*Acaroptes*, *Caparinia*, *Cheiroalalges*, *Choriopsoroptes*, *Chorioptes*, *Choriotodectes*, *Echimyalges*, *Hyracoptes*, *Listropsoralges*, *Listropsoralgoides*, *Myoproctalges*, *Nasalialges*, *Otodectes*, *Paracoroptes*, *Petauralges*, *Psorochorioptes*, and *Psoroptes*). The genus *Psoroptes* is characterized by oval mites with U-shaped genital openings and long legs lacking claws, but with long 3-jointed pretarsal stalks on most legs, and long setae on the others. While 6 species have been described from domestic animals and rabbits, recent genotypic studies revealed little inter-specific variation between *P. ovis, P. equi, P. cuniculi* and *P. cervinae*, suggesting that they may be strains of the same species (synonymized under the name *P. ovis* by precedent), but *P. natalensis* and *P. pienaari* exhibited greater variation. [Note that all 6 species are listed separately in the following table to highlight differences in other characters, such as tissue tropism, pathogenicity and distribution.]

***Psoroptes* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
body mites				
P. equi	Perissodactyla: equid (horse, donkey, mule)	skin	psoroptic mange, otoacariasis	Australia, Europe, North and South Africa
P. natalensis	Artiodactyla: bovid (cattle, zebu, water buffalo); Perissodactyla: equid (horse)	skin (esp. legs)	mange, irritation, pruritus, papules, crusts, excoriation, lichenification	South Africa, South America, France, New Zealand
P ovis (sheep scab mite)	Artiodactyla: bovid (sheep, bighorn sheep, goat, cattle), camelid (llama, alpaca), giraffid (giraffe); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit); Primates: hominid (human)	skin (esp. legs)	mange, irritation, pruritus, papules, crusts, excoriation, lichenification	worldwide (except Australia, North America)
P. pienaari	Artiodactyla: bovid (African buffalo)	skin	mange	Africa
ear mites				
P. cervinae	Artiodactyla: cervid (deer, elk), bovid (sheep, bighorn sheep)	ears	otoacariasis, scabs	North America
P. cuniculi (ear canker mite, rabbit ear mite)	Lagomorpha: leporid (European rabbit, European hare); Artiodactyla: bovid (sheep, goat, cattle); Perissodactyla: equid (horse, donkey)	ears	mange, scabs, alopecia, excoriation, otoacariasis	worldwide

Parasite morphology: *Psoroptes* spp. form 4 different types of morphological stages during their development: namely, eggs, larvae, nymphs and adults. The eggs are ovoid translucent stages that vary considerably in size depending on the species/strain and their maturity, ranging from 70 x 50 µm for *P. cuniculi* up to 250 x 115 µm for *P. ovis*. They have been described as having an anisotropic shell surrounding central granular-flocculent material. Mature eggs hatch to release larvae with tan bodies measuring around 330 µm long. They have 6 legs arranged in 3 pairs; comprising 2 stout antero-ventral pairs (each terminating in a funnel sucker-like pulvillus) and one small postero-ventral pair (each ending in 2 long distinct setae). Larvae do not exhibit sexual dimorphism and they all have 4 pairs of dorsal setae and 9 pairs of ventral setae. The larvae moult to form nymphs which have 8 legs, having developed a fourth pair of small postero-ventral legs (each terminating in a sucker-like pulvillus and small indistinct setae). Two nymphal stages are formed: firstly, protonymphs around 400-500 µm long with 10 pairs of dorsal setae and 5 pairs of ventral setae with developing subterminal cuticular pits; and secondly, deutonymphs (sometimes called tritonymphs in early literature) around 500-700 µm long with 11 pairs of dorsal setae and 5 pairs of ventral setae with 2 well-developed cuticular pits. Female deutonymphs are readily distinguished by the occurrence of a pair of dorsal copulatory protuberances (tubercles) at the posterior end of the body. Deutonymphs moult to form adult mites which have small pearly-white to pale-brown oval bodies that are dorsoventrally flattened measuring from 0.75-2.0 mm in length. They have 2 conspicuous tagma, a small anterior head (gnathosoma

or capitulum) and a larger posterior body (idiosoma). The cuticular covering appears striated with scattered setae but no spines. The gnathosoma bears prominent pointed mouthparts consisting of a pair of segmented chelicerae terminating in claw-like chelae (pincers) flanked by a pair of small sensory segmented palps (without apotele). The oral opening (mouth) is framed by a dorsal rostrum, a ventral buccal cone and a central unbarbed hypostome. The alimentary tract comprises a tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with caeca), tubular hindgut (with excretory Malpighian tubules) and rectum leading to the postero-ventral anus. The idiosoma is divided into 2 regions: an anterior podosoma bearing the legs; and the posterior opisthosoma bearing the genitalia. The idiosoma does not possess a shield-like scutum, but females mites have an anterodorsal cuticular plate behind the mouthparts and male mites have an additional larger posterodorsal cuticular plate. Like all members of the order Astigmata, respiratory stigmata are absent. The idiosoma is adorned with 10 pairs of dorsal setae (2 long pairs, 8 short pairs) and 5 pairs of ventral setae (of variable length) but most setae are long enough to protrude beyond the body margins. The ventral idiosoma bears 4 pairs of long legs which also protrude beyond the body margin and are thus visible from above. The first and second pair of legs are directed anteriorly and are well separated from the third and fourth pair which are directed posteriorly. Each leg is composed of 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus), with the coxae attached to the body with distinct thickened cuticular extensions (known as epimeres or coxal apodemes). The legs lack tarsal claws and terminate in distinctive 3-jointed pretarsi comprising a long stalked pedicel ending in a complex funnel-shaped sucker (caruncle or pulvillus) on most legs (pairs I, II and III in males, I, II and IV in females) and long setae on others (cf. *Chorioptes* have smaller non-jointed pretarsi ending in cup-shaped suckers). Adult mites exhibit sexual dimorphism, with males being smaller in size than females (0.5-0.65 v. 0.6-0.8 mm) and having a pair of terminal posterior lobes bearing 4-5 setae (of varying lengths) and a pair of ventral adanal suckers (copulatory structures which engage with the copulatory tubercles of female deutonymphs). In males, the first pair of epimeres are not fused medially and the genital opening (gonopore) is U-shaped and located ventrally around the midbody. Adult males have 2 testes with tubular vas deferens leading to the ejaculatory duct and copulatory organ (sheathed aedeagus). Adult females have 2 genital suckers (replacing the copulatory tubercles seen in deutonymphs) next to the ventral vulva located between the second pair of legs. They have 2 nutrimental ovaries connected by tubular oviducts to a globular uterus where large ellipsoidal eggs can be seen developing in gravid females. The uterus is connected to a seminal receptacle and bursa copulatrix (for the receipt and storage of sperm) and an ovipositor leads to the U-shaped gonopore located mid-ventrally.

Site of infection: *Psoroptes* mites are obligative non-burrowing ectoparasites that live on the surface layers of the skin of their hosts. Some 6 species were initially recognized on the basis of variations in parasite morphology (principally chaetotaxy and male genital structures) and host occurrence (apparent host and site specificity). Four species were found on the bodies of ungulates (equids, bovids, camelids, giraffids), lagomorphs (leporids) and primates (humans), particularly along the backline but also on the neck, shoulders and flanks. Another 2 species were found in the ears of ungulates (bovids, cervids, equids) and lagomorphs (leporids). However, recent genotypic studies have suggested that most species may be strains of a single species (named after the type species *P. ovis*), which vary in morphology, host specificity, tissue tropism and pathogenicity.

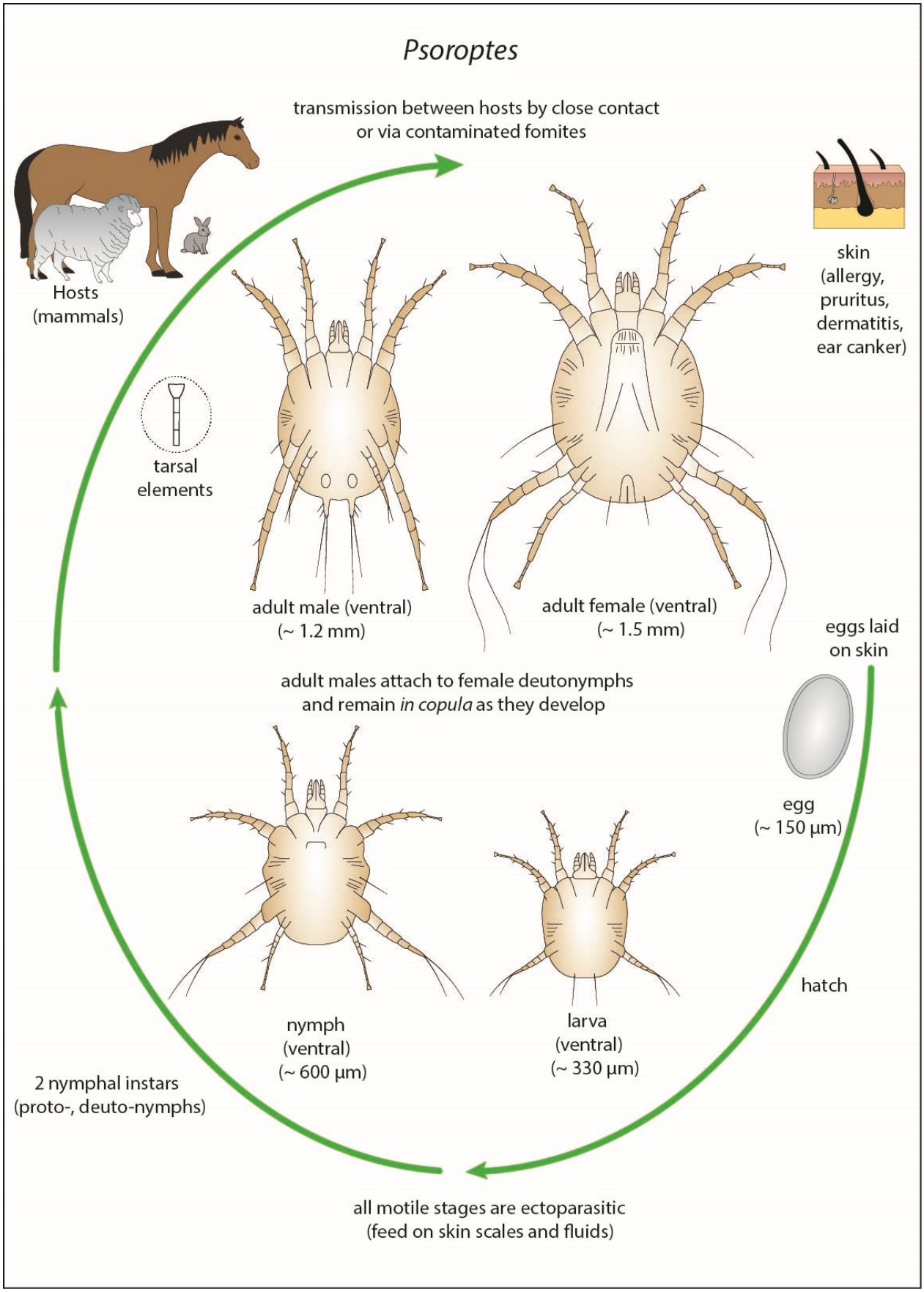
Pathogenesis: Light infestations often remain asymptomatic or subclinical, but heavier infestations may cause mild to severe pruritic dermatitis in wild and domestic animals. Genotypic studies have indicated that variations in the site, intensity and severity of infestations reported on domestic animals may be due to differences in the virulence (pathogenicity) of *P. ovis* strains (with the most severe form known as sheep scab). These mites do not burrow into the epidermis but live on the surface of the skin where they feed on skin scales from the stratum corneum, superficial tissue fluids (e.g. lipid emulsions of skin cells and skin secretions), lymph and bacteria. Their mouthparts do not pierce the epidermis and they do not suck blood, but haemoglobin and other blood components may occasionally be ingested when small haemorrhages occur at abraded sites. Infestations may produce clinical disease (known as psoroptic mange) with irritation, pruritus, localized perivascular dermatitis, oedema, erythematous macules progressing to papules, crusts, scabs, yellow-orange staining of the pelage, lichenification, excoriation, alopecia and sometimes otoacariasis. Much of the skin pathology associated with infestation is thought to arise from host allergic responses (esp. type I hypersensitivity reactions) to mite antigens, particularly mite faeces. The resultant inflammation leads to surface exudation with excoriation due to host scratching/rubbing which may exacerbate small haemorrhages caused by feeding mites. This leads to skin breakage and serous exudates which dry to form yellowish crusts, scales or scabs on the skin. Mites tend to live in the moist borders around dry crusts and they migrate outwards sometimes leading to expansive lesions. Infestations of sheep often start along the back and spread downwards leaving behind depilated, raw and scabby skin. Sheep become distressed and restless with severe pruritus, compulsive self-grooming (biting, rubbing, scratching), sometimes abnormal behaviours (nibbling, lip smacking, tongue protrusion, occasionally fits lasting 5-10 minutes), depilation/alopecia (wool loss), anaemia, reduced weight gain or weight loss, sometimes emaciation and death. Infestations may also cause exudative dermatitis in beef and dairy cattle, with lesions usually appearing on the shoulders and around base of the tail and then spreading over the body. Animals may experience intense pruritus with papular lesions leading to sticky yellowish crusts with alopecia, thickened skin, lichenification, all exacerbated by self-trauma. Persistent infestations may result in reduced meat and milk production, and predispose animals to secondary bacterial infections. Papular lesions generally develop on horses on body parts covered by thick hair (mane, forelocks, tail base) with pruritus, alopecia and thick haemorrhagic crusts and scabs. Infestations may also occur in the ear canals of sheep, goats, cattle and horses, with haematomas, scabby plugs and waxy plaques developing near the tympanic membrane causing chronic irritation, head shaking, scratching and hearing impairment (contributing to an increased risk of predation in wild animals). In rabbits, infestations generally cause ear mange (psoroptic otocariasis) with inflammatory otitis leading to ear canker typified by the accumulation of serum and brown crusts in the ear. Animals may exhibit torticollis (twisted neck) with frequent head shaking and scratching, and poor condition with weight

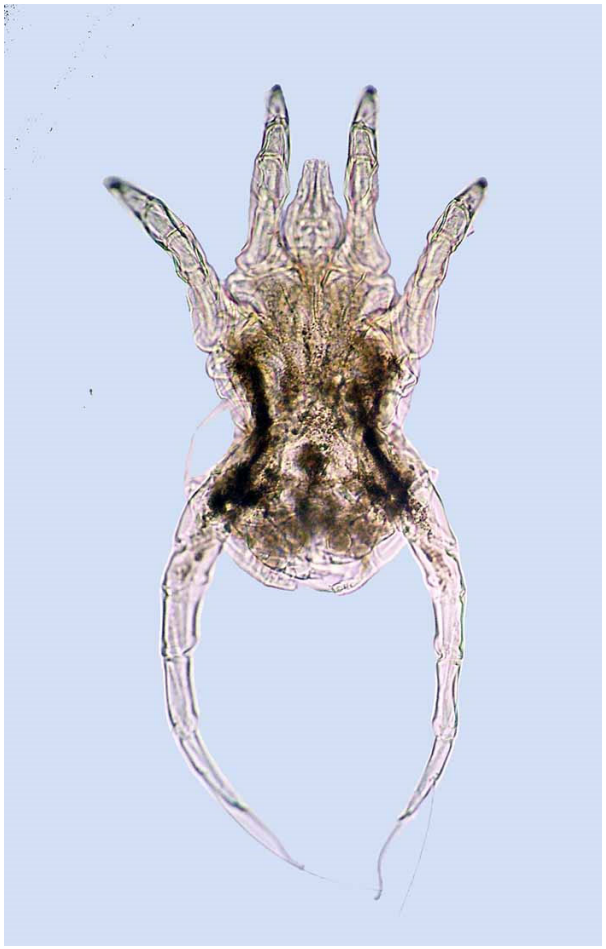
loss and secondary bacterial infections. Epidemiological studies have shown that mite populations wax and wane seasonally, with mites being more prevalent and active over winter, but becoming fewer in number over summer and taking refuge in protected sites (axilla, groin, eyes (infra-orbital fossa), ears (inner pinnae and auditory canal), and even folds in the skin. In temperate regions, infestations often become progressively worse over time as host immune responses are compromised by sustained allergic (hypersensitivity) reactions (large numbers of regulatory T cells are recruited to the skin). Infested animals become highly prone to secondary infections causing pneumonia and septicaemia due to their altered immune status. Infestations may occur on animals of all ages but are more severe in young animals and those in poor condition. While mites do not actively infest humans, studies have suggested that exposure may produce hypersensitivity reactions is some individuals (similar to Derp1 allergen responses to house dust mites associated with some forms of asthma).

Developmental cycle and mode of transmission: *Psoroptes* mites undergo hemimetabolous (incomplete) metamorphosis where eggs hatch larvae which moult through 2 nymphal stages before forming adults. All life-cycle stages may occur on the same individual host and all motile stages feed on host tissues. Transmission occurs horizontally when mites are transferred between hosts via direct contact or via contaminated fomites as mites may survive off hosts for several days-weeks. Gravid female mites lay 1-3 eggs each day under dried crusts or scabs forming at bite sites. The eggs develop and hatch after 4 days releasing hexapod larvae which move about under the scab feeding for several days. Larvae then moult to form octopod nymphs, the first nymphal stages known as protonymphs. These stages feed for a short time and then moult to form second stage nymphs known as deutonymphs (sometimes referred to as tritonymphs in early literature). The deutonymphs also feed for a short time before moulting to form adult mites which commence feeding. Reproduction is unusual in that adult male mites attach to female deutonymphs and remain *in copula* until the females moult for the final time at which point insemination occurs. Female mites may survive for 40-60 days on the host laying up to 40-100 eggs during their lifespans. Egg production is influenced by ambient temperature with more eggs produced at lower temperatures when mites are more active over winter. The entire life-cycle may be completed in as little as 11-20 days. Transmission between animals is by contagion through direct physical contact or by fomite contamination. Mites are quite robust and may survive off hosts in cool humid conditions for 10-21 days in pieces of fleece or detached crusts/scabs attached to trees, posts, fences, chutes, trucks, etc. All life-cycle stages may be transmitted between hosts, but new infestations are only established following the transfer of gravid female mites, especially young ones. Infestations are more prevalent in areas where farm stocking densities are high, when animals are grazed intensively together and when husbandry practices muster animals frequently into close quarters. Outbreaks have been traced to lateral spread between animals in adjacent paddocks, and the co-mingling of livestock at market as well as the contamination of holding pens, shearing sheds and livestock transports.

Differential diagnosis: Psoroptic mite infestations may be indicated on clinical grounds (exudative dermatitis, pruritus, crusty-scabby lesions, alopecia), but need to be differentiated from other causes (including dermatophilosis, ring worm, pediculosis, and sarcoptic mange). Infestations are confirmed by the detection of mites in skin scrapings taken from the edges of lesions or from wax removed from the ear canals. Samples are best examined microscopically after hot potassium hydroxide digestion of skin and exudates followed by centrifugation to pellet the undigested mites. Otoscopes may also be used to detect pale adult mites moving over darker ear wax. Immunoserological tests (enzyme immunoassays) have also been developed to detect specific host antibodies in infested animals. Molecular biological techniques have also been used to characterize species and strains following the polymerase chain reaction (PCR) amplification of nuclear (ribosomal RNA, internal transcribed spacers) and mitochondrial (ribosomal RNA, transfer RNA and protein coding) genes.

Treatment and control: Clinical infestations are usually treated using chemical acaricides, either as topical (sprays, dips) or as systemic (oral, injectable, spot-on) formulations. Successful treatments have been reported using traditional lime sulphur compounds, organochlorides (lindane), organophosphates (coumaphos, phosmet, toxaphene, crotoxyphos, trichlorfon, chlorpyrifos, diazinon, propetamphos), pyrethroids (flumethrin, cypermethrin), amidines (amitraz), and more recently macrocyclic lactones (ivermectin, selamectin, doramectin, eprinomectin, milbemycin, moxidectin). Given the long survival time of mites off hosts, there is a great propensity for re-infestation so repeated or prolonged treatments are often required. There are growing reports of acaricide resistance against some organochlorines, organophosphates, synthetic pyrethroids, and macrocyclic lactones, so it is recommended that different classes of acaricides be used in cyclic rotation to forestall the further development of drug resistance. The treatment of animals with severe crusted lesions is best expedited after they have been bathed with anti-seborrheic shampoos to loosen and remove debris. The treatment of animals with otoacariasis is also aided by cleaning the ears with ceruminolytic agents to remove waxy plugs. A range of prophylactic measures should also be adopted to prevent rapid re-infestations from other animals or from contaminated fomites. Infested animals should be isolated during treatment and animal holding facilities should be thoroughly cleaned. Acaricides with long-lasting residual activity (usually pyrethroids) may be used to spray the immediate environment to reduce off-host mite populations. Many countries have introduced legislative control programs involving compulsory stock inspections, quarantine measures and restricting stock movements, often with great success in eradication campaigns. Experimental vaccination studies conducted on rabbits, sheep and cattle have produced some measure of protection (as evidenced by reduced mite numbers and clinical signs) when animals were vaccinated with mite antigens (soluble proteins apparently more protective than membrane-bound proteins), but no commercial products have yet been produced.


Psoroptes
transmission between hosts by close contact
or via contaminated fomites
Hosts
(mammals)
skin
(allergy,
pruritus,
dermatitis,
ear canker)
tarsal
elements
adult male (ventral)
(~ 1.2 mm)
adult female (ventral)
(~ 1.5 mm)
eggs laid
on skin
adult males attach to female deutonymphs
and remain in copula as they develop
egg
(~ 150 µm)
hatch
nymph
(ventral)
(~ 600 µm)
larva
(ventral)
(~ 330 µm)
2 nymphal instars
(proto-, deuto-nymphs)
all motile stages are ectoparasitic
(feed on skin scales and fluids)



Psoroptes adult



Psoroptes eggs

Otodectes
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Psoroptids are non-burrowing mites with oval bodies and the last two pairs of legs project beyond the body margin. Infestations by *Otodectes* spp. in the ear canals of carnivores (cats, dogs, foxes, ferrets) may cause intense irritation and otitis.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Sarcoptoidea (mites associated with mammals, ecto- or endo-parasitic)
Family: Psoroptidae (non-burrowing mites, oval bodies, third and fourth pairs of legs project beyond body margin)
Genus: *Otodectes* (parasitic in ears of cats/dogs/foxes/ferrets)
Species: various species cause otitis in carnivores

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

Early classification schemes identified different assemblages principally on the basis of host and site specificity; including bird-associated feather mites (e.g. Analgoidea); bird-associated skin mites (e.g. Knemidokoptidae), mammal-associated fur mites (e.g. Listrophoridae), mammal-associated skin mites (e.g. Psoroptidae); and mammal-associated skin-burrowing mites (e.g. Sarcoptoidea). However, phylogenetic studies (both cladistic and molecular) have revealed that many groups are not monophyletic but para- or poly-phyletic, so further studies are required to resolve the fidelity of most groups. Recently, molecular studies suggested that 16 sarcoptoidean families may belong to 2 main lineages: 13 families identified in a 'sarcoptid' complex (Atopomelidae, Audycoptidae, Chirodiscidae, Chirorhynchobiidae, Galagalgidae, Gastronyssidae, Lemurnyssidae, Listrophoridae, Listropsoralgidae, Myocoptidae, Pneumocoptidae, Rhyncoptidae, Sarcoptidae), and 3 families in a 'psoroptid' complex (Lobalgidae, Paracoroptidae, Psoroptidae). Nevertheless, most families can still be categorized into 4 broad 'morphoecotypes': namely; fur mites (Atopomelidae, Chirodiscidae, Listrophoridae, Lobalgidae), skin mites (Chirorhynchobiidae, Myocoptidae, Psoroptidae), skin-burrowing and follicle mites (Rhyncoptidae, Sarcoptidae), and respiratory mites (Gastronyssidae, Lemurnyssidae, Pneumocoptidae). The family Psoroptidae contains non-burrowing skin mites with oval bodies and 4 pairs of legs projecting well beyond the body margin. They are obligate mammalian ectoparasites commonly known as scab mites as their feeding activity causes dermatitis resulting in scab formation at the bite site. A total of 17 genera have been identified (*Acaroptes*, *Caparinia*, *Cheiroalalges*, *Choriopsoroptes*, *Chorioptes*, *Choriotodectes*, *Echimyalges*, *Hyracoptes*, *Listropsoralges*, *Listropsoralgoides*, *Myoproctalges*, *Nasalialges*, *Otodectes*, *Paracoroptes*, *Petauralges*, *Psorochorioptes*, and *Psoroptes*). The genus *Otodectes* was previously thought to contain numerous species that colonized separate mammalian hosts, but molecular characterization studies have indicated that mites from different hosts may be the same species (or at most, strains of the same species). The genus is now considered to be monotypic with the single species (*O. cynotis*) being recognized as a common ear mite of carnivores (both companion animals and wildlife). The mites have oval bodies with distinctive chaetotaxy (setation) and leg anatomy (2 anterior pairs with short stalked pretarsi, 2 posterior pairs with terminal whip-like setae). Infestations have been associated with otoacariasis (ear mange or otodectic mange) usually manifest as otitis externa (inflammation of the outer ear and ear canal) but sometimes causing lesions on the face and body of companion animals.

***Otodectes* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
O. cynotis (syn. *O. furonis*) (ear mite, ear canker mite)	Carnivora: canid (dog, timber wolf, coyote, golden jackal, red fox, Arctic fox, pampas fox, crab-eating fox), felid (cat, ocelot, Eurasian lynx), mustelid (European polecat, American mink, American marten, North American river otter, short-tailed weasel, wolverine), procyonid (common raccoon, South American coati), ursid (American black bear); Lagomorpha: leporid (rabbit); Artiodactyla: cervid (white-tailed deer); Primates: hominid (human)	skin (external ear canal, head)	irritation, pruritus, otitis, dark waxy exudates, emaciation	worldwide

Parasite morphology: *Otodectes* form 4 different types of morphological stages during their development: namely, eggs; larvae; nymphs (2 instars); and adults. The eggs are elliptical to oblong stages measuring from 160-210 µm in length and they are slightly flattened along one side. They are pearly-white in colour and attached to the skin surface by a sticky cement. They hatch by splitting longitudinally releasing hexapod larvae with pale-grey oval bodies measuring 135-225 µm in length. Their legs are located ventrally and arranged in 3 pairs: 2 anterior pairs of long legs each ending in a cup-shaped sucker, and a posterior pair of shorter legs each ending in 2 long setae. They are covered by a finely-striated integument except for a sclerotized triangular propodosomal plate. Larvae moult to form octopod nymphs which have developed a fourth pair of very short inconspicuous legs located posteriorly and not extending beyond the body margin. Two nymphal stages are formed: firstly, protonymphs measuring 180-300 µm long and with more setae than larvae; and then deutonymphs measuring 225-355 µm long and possessing a pair of postero-dorsal attachment suckers. Deutonymphs then moult to form adult mites which have oval-rounded white bodies that are dorsally compressed measuring 0.3-0.5 mm long. Adults have weakly sclerotized cuticles divided into 2 main tagma: a small anterior gnathosoma and a large posterior idiosoma. The gnathosoma does not possess antennae but has well developed mouthparts consisting of segmented chelicerae (blunt in males, sharp in females) flanked by small sensory 2-segmented palps without terminal claws. The oral opening has a dorsal rostrum, a ventral buccal cone and a central unbarbed hypostome. The alimentary tract consists of a tubular foregut (oesophagus, pharynx), a saccular midgut (ventriculus with caeca) and a tubular hindgut (with excretory Malpighian tubules) leading to the subterminal anus. The idiosoma lacks dorsal shields and spines but has several long setae usually protruding beyond the body margin. Ear mites respire directly through the tegument and lack stigmata and tracheae (like all members of the order Astigmata). The ventral idiosoma gives rise to 4 pairs of legs that are well developed and protrude beyond the body margin (except for the fourth pair in females). Each leg consists of 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) with the coxae fused to the body wall and the first 2 pairs of legs having thickened epimeres (apodemes) that are joined. The first 2 pairs of legs are located anteriorly projecting forwards and are long and stout, while the hind 2 pairs are located posteriorly and project backwards and are somewhat smaller (the last pair being tiny especially on females). All legs on males and the first 2 pairs of legs on females have short stalked pretarsi with an unsegmented ambulacrum (not jointed like *Psoroptes*) consisting of a short pedicel ending in

cup-shaped empodial suckers (not trumpet-shaped like *Psoroptes*). The last 2 pairs of legs on females each end in 2 whip-like setae, and the third pair of legs on males also bears 2 long setae in addition to its ambulacrum. The first 3 pairs of legs on males and the first 2 pairs on females also have small hooked tarsal claws. The sexual dimorphism between adult mites also extends to body size (males smaller than females, 0.27-0.36 v. 0.35-0.5 mm long) and their genitalia. Adult males have 2 postero-ventral copulatory adanal suckers (each with 5 hair-like setae) used for attachment during copulation (suckers engage with copulatory tubercles of female deutonymph). Males have 2 testes with tubular vas deferens leading to an ejaculatory duct, long sheathed aedeagus (penis) and subterminal genital pore. The posterior end of *Otodectes* males is only slightly excavated medially with simple setae (whereas that of *Chorioptes* males is deeply incised medially forming 2 distinct lobes bearing foliate setae). Adult females are ovigerous (egg bearing) and have 2 ovaries with tubular oviducts leading to a common uterus (with muscular shell-glands), vagina (with bursa copulatrix and spermathecae accessory organs for sperm receipt and storage) and a ventral vulva opening as a transverse slit with trailing genital apodemes (but no suckers).

Site of infection: These mites are obligate ectoparasites mostly in the ear canals of carnivorous mammals, including domestic pets, farmed fur-bearing animals and wildlife (canids, felids, mustelids, procyonids, ursids) and occasionally lagomorphs, cervids and humans. Several species were originally described from different animals, but molecular characterization studies have shown them all to belong to the single species *O. cynotis*. The mites are non-burrowing and parasitize the external surface of the skin in the external ear canal (auditory meatus), but they may sometimes spread to other body parts in heavy infestations, moving to the head, neck, rump and tail on animals and the arms and torso on humans.

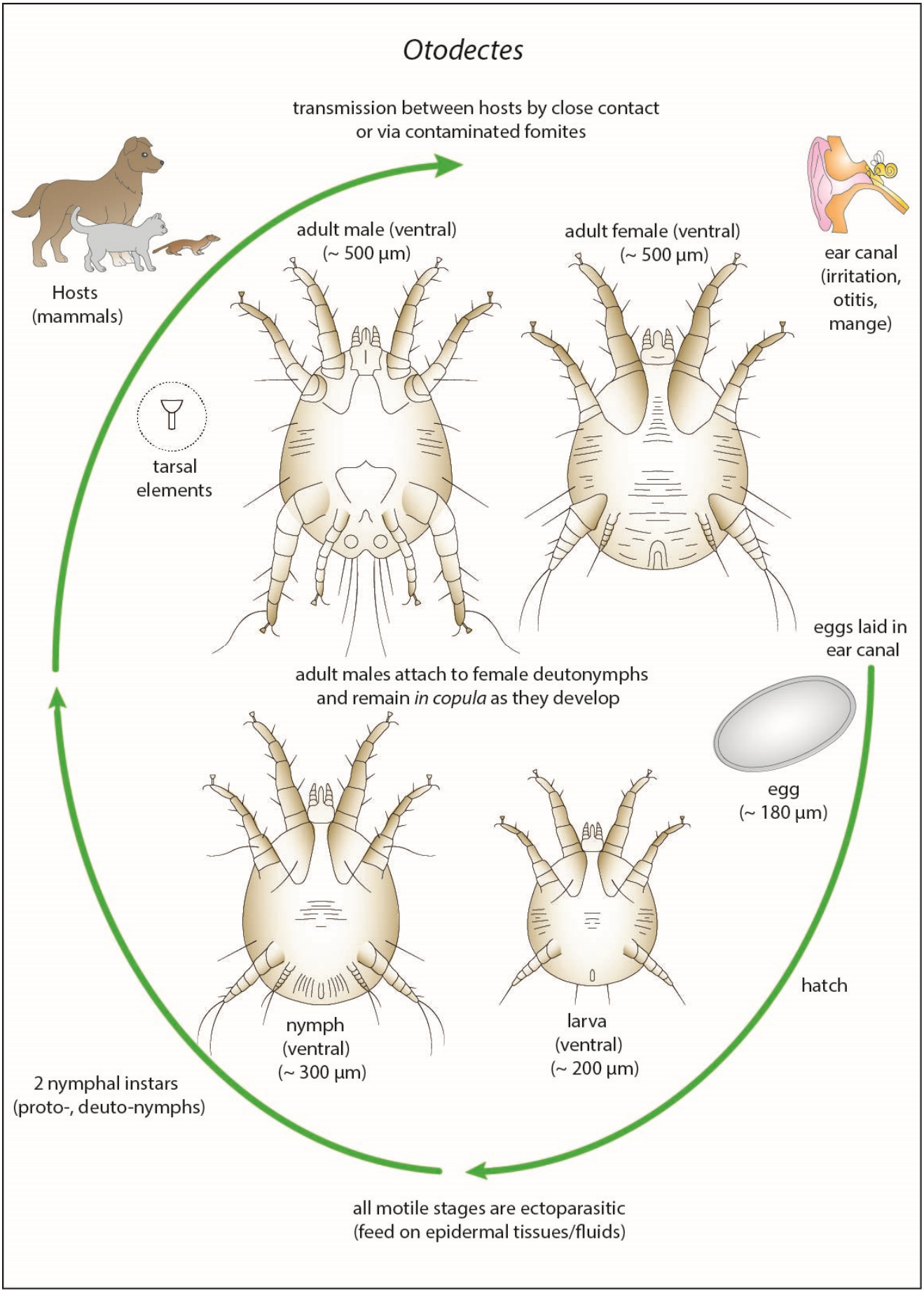
Pathogenesis: Infestations by these ear mites are often only mildly pathogenic, but they can lead to a severe inflammatory disease of the outer ear and ear canal (otitis externa), known variously as otoacariasis, ear canker, ear mange or otodectic mange. All motile mite stages are parasitic and feed on the skin surface on epidermal debris and probably host tissue fluids. There is considerable variation in the host responses to the presence of mites but the release of mite antigens (saliva and faeces) can provoke severe inflammation and probably hypersensitivity reactions in some animals. Hosts experience aural irritation with intense pruritus (itching) and inflammation (otitis) with the 4 cardinal signs of calor (warmth), rubor (redness), tumor (swelling) and dolor (pain) causing otitis externa. Irritation causes the epithelium to become hyperkeratotic and sheets of dry scaly material may slough off filling the ear canal with wax, blood and mite debris evident as thick brown-grey waxy exudates. Heavy infestations may result in the formation of reddish-brown crusts and/or scabs on inner surface of the ear covering feeding mites next to skin. Animals attempt to relieve the irritation and clear the ears with frequent and vigorous head shaking, scratching and rubbing, often resulting in self-mutilation with excoriation of the pinnae, aural haematoma formation, scabbing and alopecia (hair loss). Inflamed waxy ears are prone to secondary bacterial or fungal infection causing purulent otitis externa, or vestibular signs including torticollis which may cause otitis media. In heavy infestations, lesions may not be restricted to the external ear canal but may be found more widely over the body as mites roam. Extra-aural infestations may sometimes cause pruritic dermatitis with scabby lesions and hair loss over parts of the head, neck, base of the tail and paws, often exacerbated by self-trauma. Young animals (especially puppies and kittens) are more susceptible to infestation than older animals, which suggests that hosts may acquire some immunity against mite proteins. Cats vary in their responses to mites, many seemingly able to tolerate moderate numbers without clinical signs, but some individuals develop marked inflammation with copious aural exudative discharges. Dogs may also tolerate moderate mite burdens and generally display mild otitis externa with minimal discharges. Humans exposed to infestations may develop uncomfortable pruritic vesicular rashes, papules or wheals on exposed body regions. Immunological studies have shown some antigenic cross-reactivity between ear mites (*O. cynotis*) and house dust mites (*Dermatophagoides*) associated with allergies, atopic dermatitis, asthma and anaphylaxis, suggesting some cross-sensitization may occur.

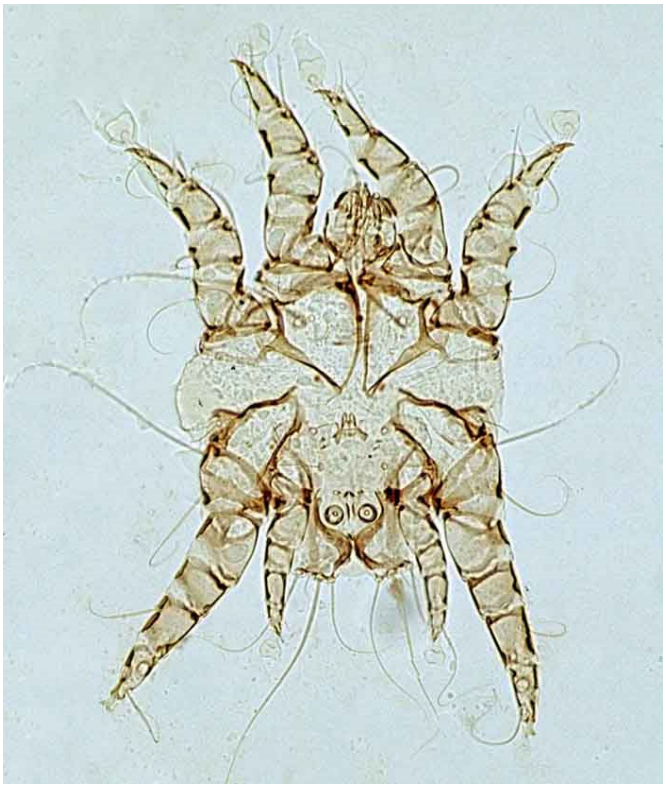
Developmental cycle and mode of transmission: Ear mites exhibit hemimetabolous (incomplete) metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. The whole life-cycle may occur on the same host, and transmission between hosts occurs via direct contact. Gravid female mites lay eggs one at a time attaching them to the ear canal lining using a sticky cement. The eggs hatch after 2-6 days (longer at cooler temperatures) releasing hexapod larvae which feed actively for 3-10 days followed by a short quiescent resting period (10-30 hours) before they moult to octopod nymphs. The first nymphal instars (protonymphs) feed for 3-5 days followed by a short quiescent period before they moult to the second instars (deutonymphs) which exhibit similar active and resting cycles. During this time, adult male mites may approach deutonymphs and attach themselves end-to-end to the nymphal postero-dorsal suckers using the cup-shaped empodial suckers on their hindlegs. Both coupled and uncoupled deutonymphs subsequently moult to form adult mites. This pre-moult coupling strategy appears to be required for the production of fertile females mites. Coupled deutonymphs that moult to form adult females copulate with the attached male and then begin to produce eggs, whereas uncoupled deutonymphs moulting to adult females remain infertile and do not lay eggs. Coupled deutonymphs that moult to form adult males simply uncouple both seek mates, while uncoupled deutonymphs moulting to adult males become reproductively active and seek mates (deutonymphs). Adult mites live for 50-60 days and continually reproduce during their life-spans. The entire life-cycle may be completed in 18-28 days, but may take longer in cooler climates when mites move deeper into the ear canal. Infestations are highly contagious and mites are usually transmitted between hosts by direct contact, especially from mothers to suckling young. Occasionally, transmission may occur through the contamination of fomites as mites are able to survive off hosts for several days in humid conditions. Infestations become established on new hosts following the transfer of

mated adult female mites, and sometimes by deutonymphs coupled with males that subsequently moult to form female mites. Humans are usually bitten by mites when they handle infested animals.

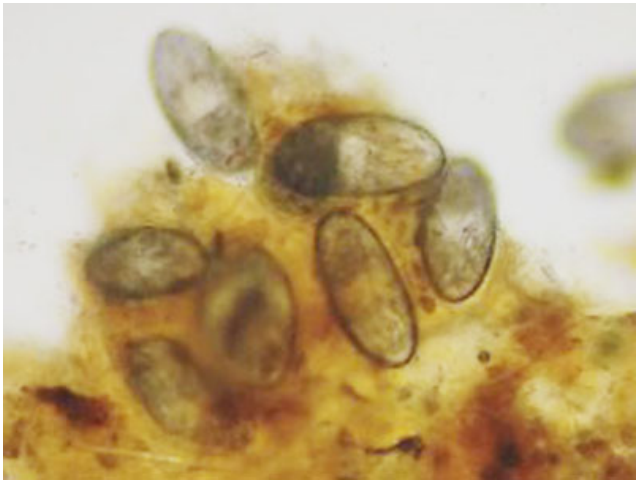
Differential diagnosis: Ear mite infestations may be strongly suspected on clinical grounds when animals have reddish-brown waxy aural exudates and exhibit frequent head-shaking and ear scratching. Infestations may be confirmed by the direct detection of ear mites by otoscopic observation or microscopy of ear swab samples (the mites are said to have the appearance of 'moving sand'). Care should be taken in otoscopic procedures as irritation of the attendant inflammation can cause pain and distress. Ear swab samples may also be examined against a dark background using an incandescent lamp to heat the ear wax and expel mites. More recently, molecular biological techniques have been used to detect and characterize mite isolates following the polymerase chain reaction (PCR) amplification of random amplified polymorphic DNA (RAPD), by real-time PCR as well as by sequencing specific nuclear (ribosomal DNA, internal transcribed spacer 2) and mitochondrial (16S ribosomal DNA) genes.

Treatment and control: Clinical infestations are conventionally treated using topical or systemic acaricidal chemicals, including pyrethroids (permethrin), benzimidazole-thiazolyls (thiabendazole), amidines (amitraz), dithiocarbamates (monosulfram), phenylpyrazole (fipronil), insect growth regulators (pyriproxyfen) and macrocyclic lactones (ivermectin, selamectin, moxidectin). Repeated treatments are often required 10-14 days later as infestations are quite persistent and re-infestations can rapidly occur. Careful attention should be paid to any drug contra-indications as some formulations such as ivermectin can cross the blood-brain barrier in collies, sheepdogs and similar breeds and cause neurological signs (ataxia, tremors, mydriasis, salivation, depression, coma and death). Otic treatment efficacy can also be improved by using ceruminolytic preparations to remove crusts and cerumen from infested ear canals. Animals should also be tested for secondary bacterial or fungal infections and treated accordingly. Due to the highly contagious nature of ear canker, all dogs and cats in contact or in the immediate vicinity of infested animals should also be treated. Pets and farmed animals should be regularly monitored for infestations and preventive measures should be adopted to forestall the spread of infestations. Such measures should include thoroughly cleaning animal holding facilities, bedding, grooming equipment and other potentially-contaminated fomites, possibly even spraying the immediate environment with acaricides with long-lasting residual activity (such as pyrethroids). Animals should be placed in isolation during treatment, new animals should be quarantined before their introduction to farms and households, and wild animals should be excluded from domestic animals by barriers, traps or baits. Disease developing in humans in contact with infested animals usually does not require treatment (although cortico-steroids can be used to ameliorate inflammation) and often resolves spontaneously once animal contact is curtailed or infestations in animals are successfully treated.


Otodectes
transmission between hosts by close contact
or via contaminated fomites
Hosts
(mammals)
adult male (ventral)
(~ 500 µm)
adult female (ventral)
(~ 500 µm)
ear canal
(irritation,
otitis,
mange)
tarsal
elements
eggs laid in
ear canal
adult males attach to female deutonymphs
and remain in copula as they develop
egg
(~ 180 µm)
hatch
nymph
(ventral)
(~ 300 µm)
larva
(ventral)
(~ 200 µm)
2 nymphal instars
(proto-, deuto-nymphs)
all motile stages are ectoparasitic
(feed on epidermal tissues/fluids)



Otodectes adult, male



Otodectes eggs

Chorioptes
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Psoroptids are non-burrowing mites with oval bodies and the last two pairs of legs project beyond the body margin. Infestations by *Chorioptes bovis* may cause allergic exudative dermatitis (chorioptic mange) in domestic animals.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Sarcoptoidea (mites associated with mammals, ecto- or endo-parasitic)
Family: Psoroptidae (non-burrowing mites, oval bodies, third and fourth pairs of legs project beyond body margin)
Genus: *Chorioptes* (parasitic on skin of horses/sheep/cattle)
Species: *C. bovis* causes mange in domestic animals

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
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Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

Early classification schemes identified different assemblages principally on the basis of host and site specificity; including bird-associated feather mites (e.g. Analgoidea); bird-associated skin mites (e.g. Knemidokoptidae), mammal-associated fur mites (e.g. Listrophoridae), mammal-associated skin mites (e.g. Psoroptidae); and mammal-associated skin-burrowing mites (e.g. Sarcoptoidea). However, phylogenetic studies (both cladistic and molecular) have revealed that many groups are not monophyletic but para- or poly-phyletic, so further studies are required to resolve the fidelity of most groups. Recently, molecular studies suggested that 16 sarcoptoidean families may belong to 2 main lineages: 13 families identified in a 'sarcoptid' complex (Atopomelidae, Audycoptidae, Chirodiscidae, Chirorhynchobiidae, Galagalgidae, Gastronyssidae, Lemurnyssidae, Listrophoridae, Listropsoralgidae, Myocoptidae, Pneumocoptidae, Rhyncoptidae, Sarcoptidae), and 3 families in a 'psoroptid' complex (Lobalgidae, Paracoroptidae, Psoroptidae). Nevertheless, most families can still be categorized into 4 broad 'morphoecotypes': namely; fur mites (Atopomelidae, Chirodiscidae, Listrophoridae, Lobalgidae), skin mites (Chirorhynchobiidae, Myocoptidae, Psoroptidae), skin-burrowing and follicle mites (Rhyncoptidae, Sarcoptidae), and respiratory mites (Gastronyssidae, Lemurnyssidae, Pneumocoptidae). The family Psoroptidae contains non-burrowing skin mites with oval bodies and 4 pairs of legs projecting well beyond the body margin. They are obligate mammalian ectoparasites commonly known as scab mites as their feeding activity causes dermatitis resulting in scab formation at the bite site. A total of 17 genera have been identified (*Acaroptes*, *Caparinia*, *Cheiroalalges*, *Choriopsoroptes*, *Chorioptes*, *Choriotodectes*, *Echimyalges*, *Hyracoptes*, *Listropsoralges*, *Listropsoralgoides*, *Myoproctalges*, *Nasalialges*, *Otodectes*, *Paracoroptes*, *Petauralges*, *Psorochorioptes*, and *Psoroptes*). The genus *Chorioptes* is characterized by oval non-burrowing mites with rounded styliform mouthparts and distinctive leg structures (with all 4 pairs of legs bearing short-stalked pretarsi bearing cup-shaped sucker-like pulvilli, except for the third pair of legs in females which lack ambulacra but bear 2 long setae). A range of *Chorioptes* spp. were originally described from different mammals on the basis of their presumed host specificity, but subsequent biological studies found that many *Chorioptes* spp. were able to interbreed (and thus may be the same species). Recent molecular characterization studies have also shown many isolates belong to 2 clades, most referable to *C. bovis* and some to *C. texanus*. Further studies are required to resolve species differentiation for isolates from both domesticated and wild animals. At present, 7 species are considered valid in ungulates and carnivores around the world. Several species have gained notoriety as the aetiological agents of an allergic exudative dermatitis (known as chorioptic mange or barn itch) particularly in cattle, horses and sometimes sheep, goats and camelids.

***Chorioptes* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
C. bovis (syn. *C. caprae, cuniculi, equi, ovis*)	Artiodactyla: bovid (cattle, sheep, goat), camelid (llama); Perissodactyla: equid (horse); Lagomorpha: leporid (rabbit)	skin (esp. legs)	mange, irritation, pruritus, scabs, scales, crusts	worldwide
C. crewei	Artiodactyla: bovid (red-flanked duiker)		mange	Africa
C. japonensis	Artiodactyla: bovid (Japanese serow)			Japan
C. mydaus	Carnivora: mephitid (Sunda stink-badger)			South-East Asia
C. panda	Carnivora: ursid (giant panda, Asian black bear)			Asia
C. sweatmani	Artiodactyla: cervid (moose)			Europe
C. texanus	Artiodactyla: bovid (goat, cattle, Taiwan serow), cervid (moose, European elk, reindeer, fallow deer)	skin	mange, irritation, pruritus	worldwide

Parasite morphology: *Chorioptes* spp. form 4 different types of morphological stages during their development: eggs; larvae; nymphs; and adults. The eggs are ovoid white-grey transparent stages measuring around 160 x 80-90 µm. They are embryonated when laid and attached to the host skin with a sticky substance. Larvae have ovoid somewhat flattened bodies measuring around 150-200 µm long with well-developed anterior mouthparts and 3 pairs of ventral legs. The first 2 pairs of legs are well-developed, segmented, anteriorly directed and terminate in cup-shaped suckers. The third pair of legs are smaller, posteriorly directed and terminate in long setae. Nymphs are larger in size than larvae and have developed a fourth pair of legs (albeit short and slender) located posteriorly. Two nymphal instars are formed, both showing increasing sexual dimorphism with respect to body size, leg structure and developing genitalia. First nymphal instars are known as protonymphs. Females measure around 200 µm long, their first 2 pairs of legs are well-developed, the third pair have long setae, the fourth pair are small with short setae, and the hind end of the body has a developing gonopore (birthing tract). Males measure around 150 µm long and are similar in morphology to larvae but are larger and have a fourth pair of short legs. The second nymphal instars are known as deutonymphs. Females measure around 250 µm long and are similar to protonymphs but the hindlegs have longer setae and the gonopore is clearly visible as a transverse subterminal slit. Males measure around 200 µm long and have smaller hindlegs as well as 2 developing posterior protuberances. Adult mites have oval dorsoventrally-flattened bodies that measure from 300-600 µm in length and are covered with a finely striated cuticle. The have 2 distinct tagma: a small anterior gnathosoma (head) and larger posterior idiosoma (body). The gnathosoma is short, rounded and bears styliform chewing mouthparts comprising a pair of 3-segmented chelicerae with terminal stylet-like chelae flanked by a pair of small sensory 2-segmented palps (without a terminal claw or apotele). The oral opening (mouth) has a dorsal rostrum, ventral buccal cone and unbarbed hypostome. The alimentary tract consists of a tubular foregut (oesophagus, pharynx),

saccular midgut (ventriculus with caeca), tubular hindgut (with excretory Malpighian tubules) leading to subterminal anus. The idiosoma has inconspicuous anterior and posterior dorsal shields with several setae but no spines. Respiratory stigmata and tracheae are absent as the mites respire through their cuticles. The ventral surface gives rise to 4 pairs of legs divided into 2 anterior pairs projecting forwards well beyond the body margin and 2 posterior pairs projecting backwards (the fourth pair being small and often not projecting beyond the body margin). The legs consist of 6 segments (coxa, trochanter, femur, genu, tibia, tarsus) with the coxae fused to the body wall and coxae 1 and 2 well separated from coxae 3 and 4. All legs (except the third pair on females) terminate in short pretarsi with unsegmented stalks or pedicels (not jointed like *Psoroptes*) ending in cup-shaped suckers (rather than trumpet-shaped pulvilli like *Psoroptes*). The third pair of legs on both females and males each have 2 long whip-like setae, and short curved tarsal claws are also present on the first 3 pairs of legs in males, and the first 2 pairs in females. In addition to differences in leg structures, adult mites exhibit considerable sexual dimorphism with males being smaller than females and having a bi-lobed posterior end rather than a rounded end like females. Male mites range in length from 300-450 μm and possess a pair of adanal copulatory suckers each having 5 distinctive setae (2 broad and 3 hair-like). The posterior end of the body is deeply incised medially with foliate setae (whereas the posterior end of *Otodectes* males is only slightly excavated medially with simple setae). Males have 2 testes with tubular vas deferens leading to the ejaculatory duct and a long sheathed aedeagus (penis) opening through the genital pore. Female mites range in length from 400-600 μm and have a subterminal genital opening (gonopore or ovipore) which appears as a transverse slit with a pair of trailing apodemes. Females have 2 ovaries with tubular oviducts connecting to a common uterus (with muscular shell-glands) and a saccular vagina (with accessory organs (bursa copulatrix, spermathecae) for sperm receipt and storage).

Site of infection: *Chorioptes* are non-burrowing mites living on the surface of the skin, mainly on herbivores. Many species were originally described on the basis of host occurrence, but genetic and molecular characterization studies have reconciled most into some 7 species found on domestic and semi-domestic ungulates (bovids, camelids, cervids equids), lagomorphs (rabbits) and some carnivores (mephitids, ursids). Infestations exhibit considerable site specificity with most found on lower portions of the host, especially the feet and legs, but sometimes also extending to the udders/scrotum, base of the tail, perineum, and occasionally the ears.

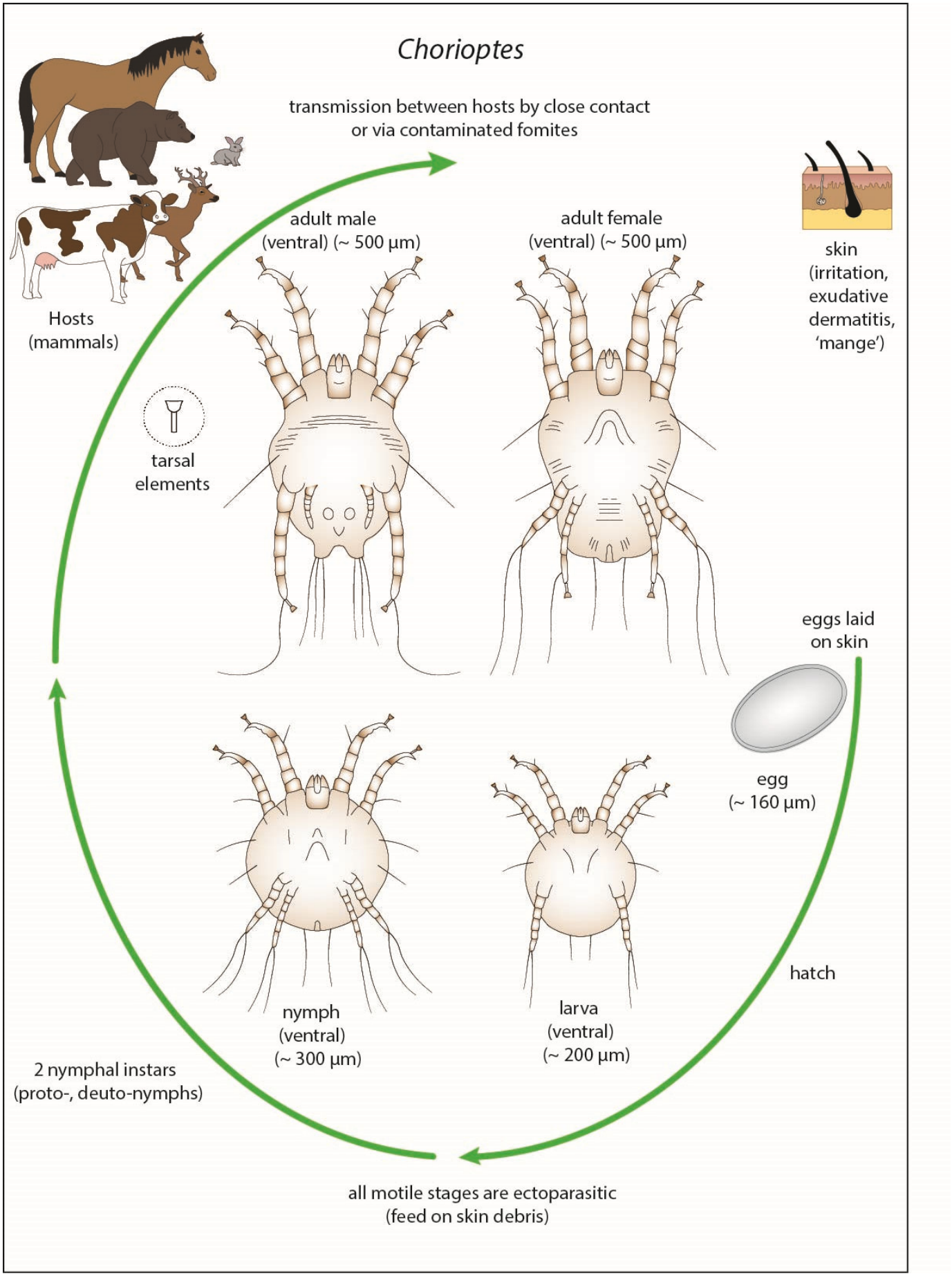
Pathogenesis: Many infestations remain asymptomatic, even to the extent that some texts refer to these surface-dwelling mites as ecto-commensals as they feed on skin debris rather than on the living skin itself. However, infestations on certain hosts can cause a clinical disease (known variously as chorioptic mange, barn itch, leg mange, foot mange, tail mange, scrotal mange and symbiotic scab) mostly on cattle and horses and sometimes on sheep, goats and camelids. The disease is relatively mild, less pruritic and more localized than psoroptic or sarcoptic mange, and is characterized by an allergic exudative dermatitis which dries to form crusts. Heavily infested animals may experience alopecia (hair loss) and moderate loss of production. All motile developmental stages use their chewing mouthparts to feed on epidermal debris on the skin surface, but they may cause local irritation exacerbated by the release of mite antigens (saliva and faeces) causing the host to scratch and abrade the skin surface. This may produce small skin lesions, typically tiny blisters with serum or tissue fluid seeping from the wound. As mites multiply, these blisters may fuse locally and rupture with the contents desiccating to form crusts or scabs (roughly 3 mm in diameter). In cattle, infestations usually involve the legs or base of the tail, but may spread to other regions. Clinical signs include skin irritation, inflammation, erythema, pruritus, papules, restlessness, self-trauma, ulceration, exudates, crusts, scabs, scaling and alopecia. Infestations may worsen when animals are crowded or confined leading to production losses (reduced weight gains and decreased milk production). In horses, mites are usually confined to the legs below the knees, but may extend to the belly, axilla and groin. Clinical signs include inflammation, oedema, erythema, pruritus, skin lesions with serous exudates which dry to form crusts, and sometimes ulceration with scab formation. Animals may stamp, paw or kick their feet and rub the hind pastern on hard objects. Draft horses with feathered fetlocks may develop chronic pastern dermatitis progressing to lichenification and excessive skin folds forming verruciform lesions. In severe cases, exudative dermatitis in the pastern region can spread to carpal and tarsal joints. Infestations in sheep usually involve the lower hind legs and ventral abdomen but they are generally light and frequently overlooked even when papules and crusts occur. However, heavy infestations in the scrotum of rams may cause exudative dermatitis with yellowish crusty lesions (scrotal mange) which may lead to a rise in scrotal temperature and temporary infertility (reversible following elimination of mites). Chorioptic mange is primarily a winter disease as mite numbers increase during the cooler winter months. However, mites often persist at low numbers over warmer summer months in the absence of clinical disease.

Developmental cycle and mode of transmission: *Chorioptes* spp. undergo gradual (hemimetabolous) metamorphosis in that eggs hatch hexapod larvae that moult to octopod nymphs and then adult mites. The whole life-cycle may be completed on the same host, and transmission between host occurs via direct contact or contaminated fomites. Gravid female mites oviposit eggs onto the skin of the host, cementing 14-20 eggs/female on the skin surface or on flakes of the scurf. The eggs hatch in around 4 days to release 6-legged larvae which feed for 3-5 days before resting for a day prior to moulting to nymphs. The first nymphal instar (protonymphs) also feed for 3-5 days before resting for a day before moulting into the second nymphal instars (deutonymphs). This developmental stage feeds for 7-8 days before resting for a day prior to moulting into adult mites. Adults commence feeding and seek mates with males inseminating females. Adult mites live for 2-7 weeks, and fertilized females lay 1-2 eggs per day. The whole life-cycle may be completed in 10-21 days but often takes longer in cooler conditions. The primary mode of transmission between animals is through direct physical contact allowing the mites to transfer between hosts, particularly on farms where animals are kept in close

proximity for extended periods. However, mites can live off hosts for several weeks so some transmission occurs via the contamination of fomites (pens, stalls, bedding, grooming equipment, etc).

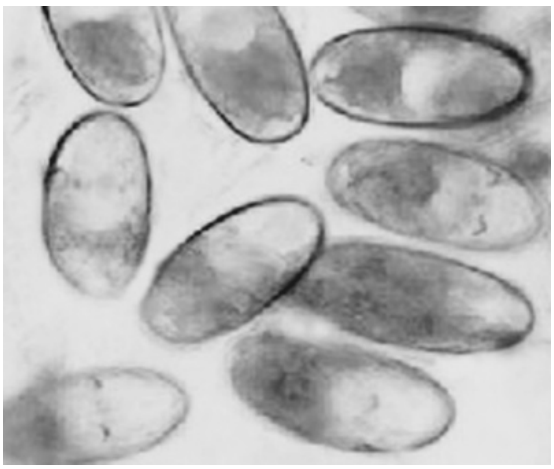
Differential diagnosis: While infestations may be indicated on clinical grounds (exudative dermatitis), they should be confirmed and differentiated from other possible causative agents, including other mites (such as *Psoroptes* and *Sarcoptes*) as well as bacteria, fungi and some allergic reactions. Confirmation of diagnosis is best achieved by direct detection of mites, mite eggs or mite faeces (scybala) in skin scrapings taken at the edges of lesions or in crusts/scabs. Samples are usually subject to caustic digestion in potassium hydroxide solutions to break down host material (mite cuticles are resistant to digestion) and mites can then be identified microscopically by their unique morphological features. Skin biopsies have also been used to diagnose infections but they have shown low sensitivity. Molecular biological techniques have been used to detect and characterize infestations following the polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA, internal transcribed spacer regions) gene sequences. Molecular studies have also been used to examine the allergenic properties of mite proteins by transcriptome analyses of isolated RNA followed by bioinformatic comparisons with sequences lodged in the mite allergen database. Preliminary results suggest that some cross-reactivity may occur with allergens from house dust mites (*Dermatophagoides*).

Treatment and control: Most infestations are self-limiting and do not progress to clinical disease. However, when chorioptic mange becomes evident, infestations respond well to treatment with topical or systemic chemical acaricides, including traditional chemicals (such as lime sulphur), organophosphates (coumaphos, phosmet, crotoxyphos, malathion, methoxychlor, trichlorfon), pyrethroids (permethrin), amidines (amitraz) and macrocyclic lactones (ivermectin, doramectin, moxidectin, eprinomectin). Repeated treatments are often required after 7-10 days as relapses or re-infestations are common. Attention should be paid to any drug contra-indications and with-holding periods as some drugs have toxic side-effects or persist within host tissues for some time. Various preventive measures should also be adopted to break transmission cycles by regularly monitoring livestock, isolating infested animals, placing new livestock into temporary quarantine, cleaning animal holding facilities and grooming equipment, treating the immediate environment with acaricides with long-lasting residual activity, and reducing animal contact with wildlife using barriers or traps.


Chorioptes
transmission between hosts by close contact
or via contaminated fomites
Hosts
(mammals)
adult male
(ventral) (~ 500 µm)
adult female
(ventral) (~ 500 µm)
skin
(irritation,
exudative
dermatitis,
'mange')
tarsal
elements
eggs laid
on skin
egg
(~ 160 µm)
hatch
nymph
(ventral)
(~ 300 µm)
larva
(ventral)
(~ 200 µm)
2 nymphal instars
(proto-, deuto-nymphs)
all motile stages are ectoparasitic
(feed on skin debris)



Chorioptes adult



Chorioptes eggs

Sarcoptes
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Sarcoptids are burrowing mites with circular bodies and the last two pairs of legs do not project beyond the body margin. Infestations by *Sarcoptes scabiei* are commonly found in the skin of many domestic animals, and humans, causing mild to severe dermatitis (sarcoptic mange, scabies in humans).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Sarcoptoidea (mites associated with mammals, ecto- or endo-parasitic)
Family: Sarcoptidae (burrowing mites, circular bodies, third and fourth legs do not project beyond body margin)
Genus: *Sarcoptes* (parasitic on skin of humans/dogs)
Species: *S. scabiei* (causes scabies in humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					

Argasidae (soft ticks)	5 genera, 193 species	birds, mammals	larvae, nymphs, adults	blood-sucking	viral, bacterial
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea,

Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

Early classification schemes identified different assemblages principally on the basis of host and site specificity; including bird-associated feather mites (e.g. Analgoidea); bird-associated skin mites (e.g. Knemidokoptidae), mammal-associated fur mites (e.g. Listrophoridae), mammal-associated skin mites (e.g. Psoroptidae); and mammal-associated skin-burrowing mites (e.g. Sarcoptoidea). However, phylogenetic studies (both cladistic and molecular) have revealed that many groups are not monophyletic but para- or poly-phyletic, so further studies are required to resolve the fidelity of most groups. Recently, molecular studies suggested that 16 sarcoptoidean families may belong to 2 main lineages: 13 families identified in a 'sarcoptid' complex (Atopomelidae, Audycoptidae, Chirodiscidae, Chirorhynchobiidae, Galagalgidae, Gastronyssidae, Lemurnyssidae, Listrophoridae, Listropsoralgidae, Myocoptidae, Pneumocoptidae, Rhyncoptidae, Sarcoptidae), and 3 families in a 'psoroptid' complex (Lobalgidae, Paracoroptidae, Psoroptidae). Nevertheless, most families can still be categorized into 4 broad 'morpho-ecotypes': namely; fur mites (Atopomelidae, Chirodiscidae, Listrophoridae, Lobalgidae), skin mites (Chirorhynchobiidae, Myocoptidae, Psoroptidae), skin-burrowing and follicle mites (Rhyncoptidae, Sarcoptidae), and respiratory mites (Gastronyssidae, Lemurnyssidae, Pneumocoptidae). The family Sarcoptidae comprises the burrowing mites that invade the skin of mammalian hosts causing intense pruritus. These 'itch mites' have soft circular bodies and 4 pairs of legs, the posterior 2 pairs not projecting beyond the body margin. Numerous genera have been recognized and allocated to 3 subfamilies (Caenolestocoptinae, Diabolicoptinae, Sarcoptinae). although another 5 genera remain unplaced (*Chirophagoides*, *Grammolichus*, *Lophuromyopus*, *Rodentopus*, *Sclerolichus*). The subfamily Sarcoptinae contains 15 genera (*Chirnyssoides*, *Chirobia*, *Cynopterocoptes*, *Kutzerocoptes*, *Mysarcoptes*, *Notoedres*, *Nycteridocoptes*, *Prosarcoptes*, *Prosopodectes*, *Rousettocoptes*, *Sarcoptes*, *Satanicoptes*, *Teinocoptes*, *Trixacarus*, *Tychosarcoptes*). The genus *Sarcoptes* is characterized by small round mites with dorsal striations broken by strong pointed scales, strong spine-like dorsal setae, palps with 2 segments, short stubby legs without claws, a terminal posterior anus, and females with genital openings appearing as transverse slits paralleling the body striations.

Infestations by *Sarcoptes* mites cause the disease scabies in humans and sarcoptic mange in animals. Scabies has been known for a long time throughout human history having been described by ancient Greeks and Romans, but the aetiological agent was not discovered until the mid-19th century. It has been estimated that over 300 million people are affected worldwide. Scabies is endemic in Africa, South and Central America, India, Southeast Asia and Australia, but can be found in many other areas as sporadic cases or institutional outbreaks. Infestations have been recorded worldwide in more than 100 species of animals belonging to 10 mammalian orders; including primates (chimpanzee, gorilla, macaque, orangutan, gibbon), carnivores (dog, dingo, wolves, coyote, jackal, raccoon dog, fox, cat, cheetah, cougar, serval, lynx, lion, jaguar, leopard, tiger, martens, fisher, badger, stoat, polecat, red panda, coati, bears), artiodactyls (cattle, buffalo, sheep, goat, ibex, chamois, impala, hartebeest, springbok, oryx, gazelle, antelope, waterbuck, kudu, camel, lama, alpaca, guanaco, vicuna, moose, deer, giraffe, boar, pig, peccary), pinnipeds (seal), perissodactyls (horse, donkey, tapir), hyracoids (hyrax), rodents (rats, mice, guinea pig, capybara, porcupine, squirrels), lagomorphs (rabbits, hare), insectivores (hedgehogs) and marsupials (wombats, koala, wallabies, possums). Sarcoptic mange is epizootic in wild canids in North America, Europe and Australia, in wild cats in Europe and Africa, in great apes and wild bovids in Africa, in wild ungulates and boar in Europe, and in wombats and koalas in Australia. Early studies tentatively identified different *Sarcoptes* spp. principally on the basis of their host occurrence, but subsequent studies revealed them to be very similar morphologically (with some minor variations in their patches of dorsal and ventral spines). The genus *Sarcoptes* was therefore considered to be monotypic, with only one recognized species, *S. scabiei,* known variously as the scab, itch or scabies mite. Experimental cross-transmission studies indicated that many isolates may be specific for particular hosts, or at least adapted to particular hosts, so a range of varieties ('strains') were recognized; including *S. scabiei* var. *hominis* on humans, *S. scabiei* var. *canis* on dogs and *S. scabiei* var. *suis* on pigs. However, the fidelity of this apparent host specificity has been challenged by several observations: namely, the cross-infectivity of some varieties in epizootics involving sympatric wild animal populations (e.g. foxes to martens); the occurrence of transient infestations in heterologous hosts (e.g. dogs to humans); and the experimental cross-transmission of some varieties to closely-related hosts (e.g. goats to sheep) or to laboratory animals (e.g. dogs to rabbits). Immunological studies found both host-specific and cross-reactive molecules within and between different varieties, and recent molecular phylogenetic studies have indicated that the extent of genetic variation may be greater than anticipated (e.g. multiple clades of genotypes detected in humans).

Varieties of *Sarcoptes scabiei*	**Hosts (natural and experimental)**	**Clinical signs**	**Distribution**
S. scabiei variety not determined	over 100 hosts from 10 mammalian orders (27 families)	scabies in humans, sarcoptic mange in animals	varied
S. scabiei var. *aucheniae*	Artiodactyla: camelid (llama, alpaca, vicuna, guanaco)	sarcoptic mange	South America
S. scabiei var. *bovis*	Artiodactyla: bovid (cattle)	sarcoptic mange, head mange	worldwide
S. scabiei var. *cameli*	Artiodactyla: camelid (camel)	sarcoptic mange	Middle-East
S. scabiei var. *canis* (syn. *S. canis*)	Carnivora: canid (dog, fox, wolf, coyote, jackal, dingo), felid (cat); Lagomorpha: leporid (rabbit); Rodentia: caviid	sarcoptic mange	worldwide

	(guinea pig); Artiodactyla: bovid (sheep, goat, cattle); Diprotodontia: vombatid (wombat), phascolarctid (koala); Primates: hominid (human)		
S. scabiei var. *caprae*	Artiodactyla: bovid (goat, chamois, sheep); Perissodactyla (donkey)	sarcoptic mange	worldwide
S. scabiei var. *cuniculi*	Lagomorpha: leporid (rabbit); Rodentia: murid (mouse)	sarcoptic mange	worldwide
S. scabiei var. *equi* (syn. *S. equi*)	Perissodactyla: equid (horse, donkey)	sarcoptic mange	patchy
S. scabiei var. *hominis*	Primates: hominid (human, gorilla, chimpanzee)	scabies	worldwide
S. scabiei var. *ovis* (syn. *S. ovis*)	Artiodactyla: bovid (sheep, goat); camelid (camel)	sarcoptic mange	worldwide
S. scabiei var. *rupicaprae*	Artiodactyla: bovid (northern chamois); Accipitriformes: accipitrid (golden eagle)	sarcoptic mange	Europe, North America
S. scabiei var. *suis*	Artiodactyla: suid (pig, wild boar)	sarcoptic mange	worldwide
S. scabiei var. *vulpes*	Carnivora: canid (fox, wolf, raccoon dog); mustelid (marten); felid (lynx)	sarcoptic mange	worldwide
S. scabiei var. *wombati*	Diprotodontia: vombatid (common wombat, southern hairy-nosed wombat), macropodid (wallabies)	sarcoptic mange	Australia
S. tapiri	Perissodactyla: tapirid (South American tapir)	sarcoptic mange	South America

Various *Sarcoptes* spp. have also been transferred to other genera on the basis of morphotypic and/or genotypic studies: *S. bovis p.p.* and *S. caprae* being transferred to the genus *Chorioptes*; *S. mutans* to *Knemidokoptes*; *S. musculinus* to *Dromiciocoptes; S. cynotis* to *Otodectes; S. laevis* to *Picicnemidocoptes; S. pitheci* to *Prosarcoptes; S. chiropteralis* to *Prosopodectes; S. scabiei* var. *cati, S. cati* and *S. minor cati* to *Notoedres cati*; *S. lasionycteris* and *S. myotis* to *Notoedres lasionycteris;* and *S. anacanthos* to *Trixacarus diversus.*

Parasite morphology: Mites form four developmental stages: eggs, larvae, nymphs and adults. The eggs are oval, measuring 175-250 µm in length by 150-200 µm in width, which is large compared to the size of the adult mites (about one third their length). Emergent larvae have three pairs of legs but undergo metamorphosis to form nymphs (protonymphs for males and females, then tritonymphs for females). Nymphs have four pairs of legs but pairs 3 and 4 do not project beyond the body margin. These developmental stages are variable in size but successively become larger. Adult mites have ovoid bodies that are ventrally flattened and dorsally convex (tortoise-like). They are creamy white in colour but may have darkened appendages and organs. Female mites range in size from 0.3-0.5 mm in length by 0.2-0.4 mm in width, while adult males are smaller measuring from 0.2-0.3 mm long by 0.16-0.21 mm wide. Both sexes have thin sclerotized integuments which are covered with coarse transversely-ridged cuticular striations. Mites respire through tegumental surfaces so distinct stigmata, tracheae and peritremes are absent. The dorsal surface has a precapsular shield, 6-7 pairs of cuticular spines, stout lateral and dorsal setae (spine-like hairs), a central patch of triangular scales, 2 pairs of genital setae and the anus is terminal (only slightly dorsal). Variations in body structure and chaetotaxy (patterns of setation) are used to differentiate the genera *Sarcoptes, Notoedres* (precapsular shield absent) and *Trixacarus* (idiosomal setae setose rather than spine-like), the latter 2 genera causing mange in cats and guinea-pigs respectively. In adult female *Sarcoptes*, the copulatory bursa is situated anterior to the anal opening, while the genital opening is on the mid-ventral surface and consists of a transverse slit through which the eggs are laid. Adult mites have two body parts, the anterior gnathosoma (capitulum) bearing small specialized mouthparts (short lateral 2-segmented palps, paired chelicerae, unbarbed hypostome), and the posterior idiosoma bearing four pairs of stumpy legs and elongate sensory setae. The idiosoma is divided into two parts by an integumentary fold, two pairs of legs arising ventrally from each region. The first two pairs of legs project forwards beyond the body margin and they possess cutting plates which are used (with the chelicerae) to assist in burrowing. The last two pairs of legs are well separated from the anterior pairs and they project backwards but not beyond the body margin and they are therefore not visible in dorsal view. The legs consist of 5 free segments (trochanter, femur, genu, tibia and tarsus) arising from the basal coxae. The legs do not bear claws but terminate in stalked claw-like empodia (spines) with bell-shaped pulvilli (suckers) borne on stalk-like pretarsi on the first two pairs of legs in adult males and females (also on the fourth pair of legs in males), while the remaining legs terminate in long setae. The first segments of the first two pairs of legs have apodemes (cuticular flanges) joined in a Y-shape, while those of the last two pairs of legs have small unjoined apodemes. Mature females have 2 ovaries ('nutritive'-type) with tubular oviducts converging on a muscular shell-gland that opens into the cuticle-lined vagina. Females remain fertile after mating once and they have accessory organs for sperm receipt, storage and transport (bursa copulatrix and spermathecae). Mature males have testes connected by tubular vas deferens to an ejaculatory duct equipped with a long sheathed aedeagus (penis) opening to a postcoxal genital pore.

Site of infection: Sarcoptid mites are obligate parasites in the skin of their hosts. They are burrowing mites and live as endoparasites within the epidermis. Female mites burrow within the stratum corneum, sometimes down to the boundaries of the stratum granulosum, to lay their eggs. Infestations can occur anywhere on the body, but are more common in areas where the skin is thin and wrinkled, such as between the fingers, toes and genitals of humans, and the ears, muzzle and face of animals. Larvae, nymphs and adult male mites form moulting pouches usually in the hair follicles of their hosts.

Pathogenesis: *S. scabiei* causes ordinary (classical) or crusted scabies in humans as well as acute or chronic sarcoptic mange in animals. The mites cause direct damage to the skin and their secretions and excreta (scybala) cause inflammation and allergic hypersensitivity reactions involving both humoral and cell-mediated components and circulating immune complexes. In otherwise healthy hosts, cell-mediated immune responses are mounted against mite antigens and the resultant acquired immunity limits the spread of mites and prevents overwhelming infestations. Mites have also been shown to produce anti-inflammatory, anti-complement and anti-immune substances allowing them to circumvent host protective responses. Infestations in immunocompromised or undernourished hosts may become intense, extensive and severe. Mites excavate long winding burrows in the skin, in so doing, feeding on the horny layer of the epidermis and on intercellular fluids (lymph and serum) that seep into the burrow. Their burrowing/feeding activity causes intense agonizing itching (pruritus) with erythema and maculopapular rashes with occasional vesicles. The pruritus is characteristically nocturnal and aggravated by warmth. It leads to consequent scratching, excoriation and inflammation (dermatitis) accompanied by hair loss (alopecia), thickening (hyperkeratosis), scaling and crusting of the skin with dried serum exudates. Pruritic areas may be reddened, pink, brown or tan, and when evident, burrows appear as thin slightly-elevated straight or serpentine (S-shaped) lines up to 15 mm long, sometimes with an adult mite seen as a small dot towards one end. The severity of disease does not correlate well with the intensity of infestation. Most infested hosts only have 5-15 mites, but hypersensitivity reactions to just a few mites may induce intense pruritus and dermatitis. In patients with severe crusted lesions, mite populations may build up to thousands (even millions) but paradoxically they may cause little or no pruritus.

Infestations have been associated with people living in poor overcrowded communities practicing inadequate hygiene. Outbreaks have been documented in residential aged-care facilities, hospitals, prisons, disaster relief and refugee camps. Epidemics of scabies have been found to occur in human populations in 20-30 year cycles, putatively associated with fluctuations in 'herd immunity' over the same time-frame. Classic scabies (sometimes called papular scabies) is more prevalent in the young and the elderly, with the onset of symptoms 3-6 weeks after first infestation or 1-3 days after re-infestation. The most commonly infested sites are the interdigital (webbed) spaces on the hands, the ulnar margins of the wrists and the elbows, followed by the anterior axillae (armpits), breasts in females, waistline, buttocks, penis and scrotum in males, backs of knees, ankles and toes. Lesions are generally absent on the head, face, neck, palms and soles, although atypical scabies may develop in infants, characterized by acropustulosis with blisters and pustules extending to these areas. Many patients may also develop complications including impetigo, eczema, urticaria, folliculitis, cellulitis or abscesses, and extensive thickening and crusting of the skin may occur in immunocompromised patients. Open or cracked skin lesions are highly susceptible to secondary bacterial infections resulting in sepsis, pyoderma and even septicaemia. In some individuals, burrowing mites may cause vesicles in the epidermis to become enlarged to form bullae (macro-vesicles), a condition known as bullous scabies. Mites may sometimes penetrate to the dermis eliciting cellular infiltrates (primarily lymphocytes) and the formation of dark firm pruritic masses, a condition known as nodular scabies. A more severe form of disease known as crusted (or Norwegian) scabies may develop in immunocompromised people, particularly the elderly with physical or mental conditions that reduce pruritus or scratching (e.g. paralysis, sensory defects, mental impairment). This form of disease is characterized by massive orthokeratosis and parakeratosis affecting the great cutaneous surfaces showing multiple scales and crusts with large numbers of mites but paradoxically less intense itching. Crusts may be loose, scaly, flaky or thick and adherent, being localized (palms, elbows, scalp, ears, soles and toes) or more extensive (neck, face, eyelids, under nails). They appear as horny plaques 3-15 mm thick and being cream, grey, yellow-brown to yellow-green in colour. Complications may include pyoderma, impetigo, cellulitis, lymphangitis, lymphadenopathy and septicaemia. Mild transient infestations (pseudo-scabies) have also been attributed to the transmission of mites from infested animals to humans in close contact (e.g. herders, hunters, trappers, wildlife biologists, animal care personnel, pet owners). Most zoonotic infestations have been confined to areas of skin exposed to animals (or their carcases or hides) and they have been short-lived and self-limiting with clinical signs disappearing within days to weeks (mites often unable to complete their development and rarely forming burrows).

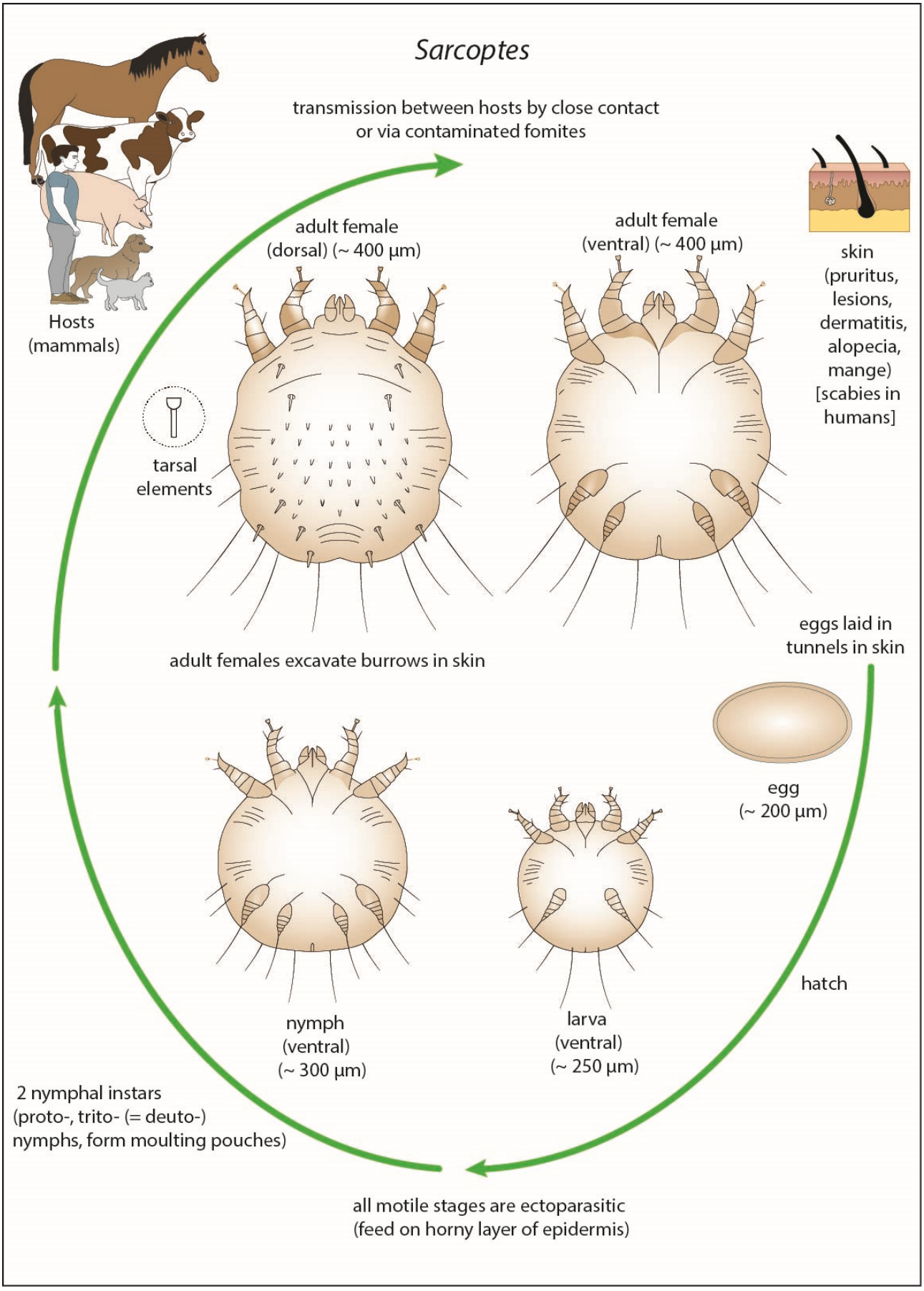
In animals, infestations may cause skin damage, fluid loss, allergic reactions (immediate (type I) and delayed (type IV) hypersensitivity) and secondary bacterial infections. Acute clinical signs include intense pruritus, erythematous eruptions, papule formation, seborrhea and alopecia, while chronic mange is characterized by skin thickening, crusting, hyperkeratosis, lichenification and foul aromatic odours with lymphadenopathy and subcutaneous oedema in severe cases. Lesions usually first appear on the head (esp. ears), neck and shoulders of most animals, then spread to the chest, abdomen, back, flanks and tail. The severity of infestation ranges from asymptomatic carriage to vexing irritation and unthriftiness potentially leading to stress, anorexia, weight loss, emaciation, exhaustion, debilitation and death. Infested animals may exhibit frequent and aggressive grooming behaviours resulting in traumatic lesions and self-mutilation. Young growing pigs may develop acute disease with significant production losses while sows may develop chronic disease with thick crusted lesions. Hyperkeratosis is most notable in canids, with animals inflicting considerable self-trauma through scratching and rubbing leading to excoriations, ulcers, bleeding, scabs, hair-matting, alopecia and secondary infections. Infestations are rare in cats, often invoking crusted parakeratotic lesions with little or no pruritus. Infested livestock (sheep, cattle, horses) may exhibit severe pruritus with scales, lichenification, thickened and wrinkled skin and scratching leading to hide damage. Most infestations in wombats have been severe with extensive thickening and cracking of skin around the face and skin cracks or folds becoming secondarily infected. Many outbreaks of sarcoptic mange in domestic and zoo animals have been associated with intensive husbandry practices and crowded unsanitary conditions, while epizootics in wildlife have been linked to animal migrations, translocations, malnutrition and poor seasonal conditions.

Developmental cycle and mode of transmission: Mites spend most of their lives in intimate contact with their hosts, indeed the entire life cycle can be completed on an individual host, so transmission between hosts is mainly by direct physical contact or via contamination of fomites (bedding, clothing). The females lay eggs in tunnels ranging from 5-15 mm in length in the stratum corneum of the skin. The eggs mature and hatch within 3-4 days. Emergent six-legged larvae may remain in their tunnel, form pockets or extensions of the tunnel or migrate to the skin surface where they form temporary shallow pits or invade hair follicles. These residences are used as moulting pouches as well as for food and shelter. The larvae moult within 3-4 days to form eight-legged protonymphs which then moult 3-4 days later to form larger tritonymphs (sometimes called deutonymphs) or adult males. Tritonymphs moult 3-4 days later to form adult females, thus males reach adulthood faster than females as they undergo one less moult. Mating usually occurs after the active male mites penetrate the moulting pouches of the adult females. All motile life stages have been observed to leave their burrows and wander around on the skin. Even with low numbers of mites present on a host, males and females find each other presumably via pheromones. The males often die after mating (although they can live for 9-11 days) and the fertilized females leave their pouches and search for suitable sites for permanent burrows. The females excavate characteristic serpentine (S-shaped) burrows at a rate of 2-5 mm per day, laying eggs in the process. Females live for about 30 days (sometimes up to 60 days) and they lay around 40-50 eggs at a rate of 1-3 eggs per day. Only about 10% of the eggs eventually give rise to adult mites, even under the most favourable conditions. The entire life cycle is usually completed within 2 weeks but can range from 1-3 weeks days depending on conditions. Adults dislodged from hosts use odour and thermal stimuli to seek new hosts but they are very susceptible to desiccation and can only survive for 24-36 hours at room (20°C) temperature with normal (40-80%) humidity, or longer (2-9 days) at lower temperatures with high humidity. Transmission only occurs when fecund female mites move between hosts, so host behaviours and activities that involve prolonged contact between individuals sharing common environments are most conducive to the spread of infestations.

Differential diagnosis: The presumptive diagnosis of scabies is clinical and confirmed by visualization of mites, eggs and faeces (scybala). Symptoms and signs typically include pruritus, rash and skin lesions (papules, pustules, burrows, nodules and occasionally plaques), with burrows being pathognomonic. While mite burrows may sometimes be observed by direct visual examination, they are better visualized after staining the skin with ink or by applying topical tetracycline and examining under ultraviolet illumination (Woods lamp) for fluorescence. More recently, high resolution videodermatoscopy has been used to reveal burrows by their characteristic 'jet-with-contrail' appearance and mites by their denser triangular 'delta-wing' mouthparts. Burrows, however, are not always easy to find and may be obscured by secondary lesions. Recourse is often made to the microscopic examination of skin scrapings for intact mites, mite fragments, eggs, eggshell fragments or mite faecal pellets. Deep skin scrapings may be mixed with glycerol or mineral oil and examined directly or they may be heated in potassium hydroxide solutions which digests skin but not mite cuticles. Finding and scraping infested lesions can be difficult so multiple sites should be examined from individual hosts. Nonetheless, negative results should not exclude diagnoses because scrapings may have missed low mite numbers, even in crusted lesions. A range of immunoserological tests (enzyme immunoassays) have been developed to detect host antibody isotypes against a range of crude and defined mite antigens with variable success depending on the kinetics and dynamics of infestation and the target antigen used. Phylogenetic studies have recently been used to characterize many mite isolates by polymerase chain reaction (PCR) amplification of specific gene sequences (internal transcribed spacer regions of nuclear ribosomal RNA, hypervariable microsatellite markers, mitochondrial cytochrome c oxidase subunit 1 and mitochondrial 16S ribosomal RNA).

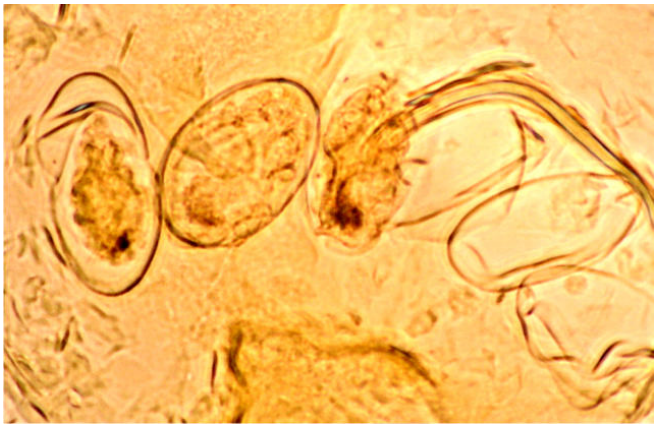
Treatment and control: A wide variety of insecticides and acaricides have been used to treat scabies mite infestations in humans; including topical applications of macrocyclic lactones (ivermectin), pyrethroids (permethrin), benzoic esters (benzyl benzoate), anilides (crotamiton), organophosphates (malathion) and even sulphur ointment in petroleum jelly, and orally administered macrocyclic lactones (ivermectin, moxidectin). Topical lindane (gamma-benzene hexachloride) was used previously but has been replaced due to concerns over neurotoxicity. Current chemotherapy usually consists of combination treatment with topical permethrin and oral ivermectin, although the latter is not recommended during pregnancy or lactation nor in patients with liver disease. There are mounting concerns about the emergence of drug resistance in mite populations and there have been reports of some resistance to permethrin and ivermectin. A range of alternative therapies have been investigated with variable success when using neem oil, tea tree oil, lippia oil, tumeric, camphor oil, coconut and jojoba oil as topical treatments or repellents. Given the allergic and hypersensitivity responses involved in many infestations, topical steroids should not be used on humans. Symptomatic treatments include antihistamines for pruritus, emollients for dry skin, keratolytic agents (salicylic acid, urea, warm baths) for crusted lesions and broad-spectrum antibiotics for secondary bacterial infections and septicaemia. Treatments should also be extended to other people in close contact, including family members and at-risk healthcare personnel. Infestations in animals can be treated with topical (lotions, spray-ons or spot-ons) or systemic (oral, in-feed or injectable) acaricides, including traditional compounds (lime sulphur), organochlorines (bromocyclen, lindane), organophosphates (chlorfenvinphos, coumaphos, crotoxyphos, diazinon, fenchlorvos, malathion, methoxychlor, phosmet, trichlorfon), pyrethroids (permethrin), amidines (amitraz), arylpyrazoles (fipronil) and the macrocyclic lactones (moxidectin, ivermectin, selamectin, doramectin). Careful attention should be paid to pharmacological guidelines to avoid adverse side-effects (e.g. macrocyclic lactones in Murray grey cattle and collie dog breeds), accidental poisoning (e.g. oral ingestion of lindane), residues in food items, and environmental toxicity. Many formulations contain surfactants which serve to soften crusts and remove skin scales. Hair can also be clipped from affected areas; mechanical debridement of crusts may be attempted and the skin cleaned with anti-seborrhoeic shampoos prior to acaricide treatment. Lime-sulphur dips have also been used at 10 day intervals for treating dogs and cats. Treatments should be repeated weekly for several weeks to ensure newly emergent mites are killed. Infested animals should be isolated or treatments extended to animals in close

proximity. Corticosteroids can also be used in severely distressed animals to reduce pruritus and prevent further excoriation. Some measure of environmental control should be attempted to prevent the spread of infestations via the contamination of fomites. Washing clothing and bedding in hot water followed by prolonged drying has been shown to be effective against dislodged developmental stages of *S. scabiei*, as has dry-cleaning, steam-cleaning, vacuuming and even sealing contaminated items in plastic bags for at least 3 days. Livestock and zoo animals can be quarantined and treated before being introduced into new facilities, and strategic treatments of pregnant females in breeding facilities should be used to prevent vertical transmission. Immunological studies have demonstrated a range of cellular and humoral immune responses in humans and animals against *Sarcoptes* antigens, but experimental vaccination studies with a range of candidate immunogens have not yet succeeded in generating any strong protective immunity against infection or disease, further highlighting the complex interactions between host immunocompetency and disease expression.


Sarcoptes
transmission between hosts by close contact
or via contaminated fomites
Hosts
(mammals)
adult female
(dorsal) (~ 400 µm)
adult female
(ventral) (~ 400 µm)
skin
(pruritus,
lesions,
dermatitis,
alopecia,
mange)
[scabies in
humans]
tarsal
elements
adult females excavate burrows in skin
eggs laid in
tunnels in skin
egg
(~ 200 µm)
hatch
nymph
(ventral)
(~ 300 µm)
larva
(ventral)
(~ 250 µm)
2 nymphal instars
(proto-, trito- (= deuto-)
nymphs, form moulting pouches)
all motile stages are ectoparasitic
(feed on horny layer of epidermis)



Sarcoptes adult



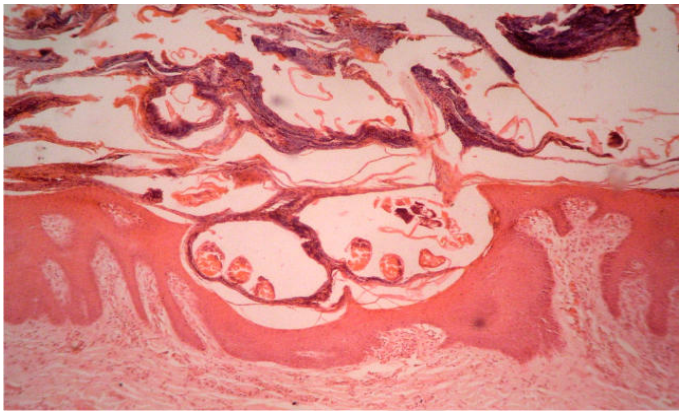
Sarcoptes eggs



Sarcoptes larva



Sarcoptes nymph



Sarcoptes skin lesion



Sarcoptes mange in dog

Notoedres
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Sarcoptids are burrowing mites with circular bodies and the last two pairs of legs do not project beyond the body margin. Infestations by *Notoedres* spp. are found mainly in the ears of cats and may cause mild dermatitis (notoedric mange).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Sarcoptoidea (mites associated with mammals, ecto- or endo-parasitic)
Family: Sarcoptidae (burrowing mites, circular bodies, third and fourth legs do not project beyond body margin)
Genus: *Notoedres* (parasitic on skin of cats/rabbits/rats)
Species: various species cause mange in cats

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

Early classification schemes identified different assemblages principally on the basis of host and site specificity; including bird-associated feather mites (e.g. Analgoidea); bird-associated skin mites (e.g. Knemidokoptidae), mammal-associated fur mites (e.g. Listrophoridae), mammal-associated skin mites (e.g. Psoroptidae); and mammal-associated skin-burrowing mites (e.g. Sarcoptoidea). However, phylogenetic studies (both cladistic and molecular) have revealed that many groups are not monophyletic but para- or poly-phyletic, so further studies are required to resolve the fidelity of most groups. Recently, molecular studies suggested that 16 sarcoptoidean families may belong to 2 main lineages: 13 families identified in a 'sarcoptid' complex (Atopomelidae, Audycoptidae, Chirodiscidae, Chirorhynchobiidae, Galagalgidae, Gastronyssidae, Lemurnyssidae, Listrophoridae, Listropsoralgidae, Myocoptidae, Pneumocoptidae, Rhyncoptidae, Sarcoptidae), and 3 families in a 'psoroptid' complex (Lobalgidae, Paracoroptidae, Psoroptidae). Nevertheless, most families can still be categorized into 4 broad 'morphoecotypes': namely; fur mites (Atopomelidae, Chirodiscidae, Listrophoridae, Lobalgidae), skin mites (Chirorhynchobiidae, Myocoptidae, Psoroptidae), skin-burrowing and follicle mites (Rhyncoptidae, Sarcoptidae), and respiratory mites (Gastronyssidae, Lemurnyssidae, Pneumocoptidae). The family Sarcoptidae comprises the burrowing mites that invade the skin of mammalian hosts causing intense pruritus. These 'itch mites' have soft circular bodies and 4 pairs of legs, the posterior 2 pairs not projecting beyond the body margin. Numerous genera have been recognized and allocated to 3 subfamilies (Caenolestocoptinae, Diabolicoptinae, Sarcoptinae). although another 5 genera remain unplaced (*Chirophagoides*, *Grammolichus*, *Lophuromyopus*, *Rodentopus*, *Sclerolichus*). The subfamily Sarcoptinae contains 15 genera (*Chirnyssoides*, *Chirobia*, *Cynopterocoptes*, *Kutzerocoptes*, *Mysarcoptes*, *Notoedres*, *Nycteridocoptes*, *Prosarcoptes*, *Prosopodectes*, *Rousettocoptes*, *Sarcoptes*, *Satanicoptes*, *Teinocoptes*, *Trixacarus*, *Tychosarcoptes*). The genus *Notoedres* (syn. *Chironyssus, Bakeracarus, Mysarcoptes p.p., Suncicoptes*) is characterized by small round mites with dorsal striations not broken by strong pointed scales, dorsal setae that are not spine-like, palps with 2 segments, short stubby legs without claws, long pretarsi on the 2 front pairs of legs, a dorsal anus, and females with genital openings appearing as transverse slits paralleling the body striations. Over 45 species have been described and assigned to 4 subgenera: namely, *N.* (*Bakeracarus*), *N.* (*Mesonotoedres*), *N.* (*Neonotodres*) and *N.* (*Notoedres*). The mites burrow into the living layers of skin on small mammals (cats, rabbits, rats, bats) and may cause pruritic lesions and dermatitis (condition known as mange).

***Notoedres* species**	**Hosts**	**Clinical signs**	**Distribution**
Subgenus *N.* (*Notoedres*)			
N. N. africanus	Chiroptera: emballonurid (African sheath-tailed bat)		Africa
N. N. alexfaini	Chiroptera: molossid (hairless bat, lesser naked bat)		Singapore
N. N. benoiti	Chiroptera: emballonurid (African sheath-tailed bat)		Africa
N. N. cati (syn. *N. minor cuniculi, Sarcoptes*) (notoedric cat mite)	Carnivora: felid (cat, European wildcat, serval, cheetah, snow leopard, tiger, Siberian tiger, ocelot, lynx, mountain lion, Florida panther, bobcat), viverrid (Formosan masked civet, palm civet, Asian palm civet), canid (dog, wolf, fox), procyonid (white-nosed coati, raccoon), herpestid (small Indian mongoose, Javan mongoose); Lagomorpha: leporid (European rabbit); Eulipotyphla: erinaceid (African pygmy hedgehog); Diprotodontia: phascolarctid (koala); Rodentia: caviid (guinea pig), cricetid (golden hamster); Primates: hominid (human)	notoedric mange (face mange, feline scabies), irritation, erythema, intense pruritus, scales, crusts, excoriation, thickened skin, systemic sequelae	worldwide
N. N. centrifera (syn. *N. douglasi*)	Rodentia: sciurid (black giant squirrel, western gray squirrel, eastern gray squirrel, fox squirrel, southern flying squirrel, eastern chipmunk), erethizontid (porcupine)	squirrel mange, dermatitis, pustules	Indonesia, North America
N. N. cheiromeles	Chiroptera: molossid (hairless bat)		Indonesia
N. N. chiropteralis (synonymized with *N. vanschaiki,* both recently transferred to *Prosopodectes)*	Chiroptera: vespertilionid (serotine bat, common noctule, common pipistrelle, Java pipistrelle, lesser Asiatic yellow bat, lesser bamboo bat)		Eurasia
N. N. dewitti	Chiroptera: molossid (wrinkle-lipped free-tailed bat, Malayan free-tailed bat, Angolan free-tailed bat, northern freetail bat, hairless bat)		Asia, Africa, Australia
N. N. dohanyi	Chiroptera: molossid (wrinkle-lipped free-tailed bat, Malayan free-tailed bat, hairless bat)		Asia
N. N. galagoensis	Primates: galagid (Demidoff's dwarf galago)	ear cysts	Africa
N. N. indicus (syn. *Suncicoptes*)	Eulipotyphla: soricid (Asian house shrew)		Asia
N. N. ismaili	Chiroptera: molossid (wrinkle-lipped free-tailed bat, Malayan free-tailed bat)		Asia
N. N. jamesoni	Rodentia: murid (lesser bandicoot rat, ricefield rat, Malayan field rat, Annandale's rat)		Asia

N. N. longisetosus	Chiroptera: molossid (hairless bat)		Asia
N. N. mimetilli	Chiroptera: vespertilionid (Moloney's mimic bat, Thomas's flat-headed bat)		Africa
N. N. miniopteri	Chiroptera: vespertilionid (common bent-wing bat, greater long-fingered bat, banana serotine)		Africa
N. N. muris (syn. *Sarcoptes*)	Rodentia: murid (brown rat, black rat, pale field rat, fawn-footed mosaic-tailed rat), cricetid (European hamster, European water vole, California vole, web-footed marsh rat), caviid (guinea pig); Peramelemorphia: peramelid (northern brown bandicoot); Diprotodontia: phalangerid (common brushtail possum); Eulipotyphla: erinaceid (European hedgehog)	irritation, erythema, crusts	worldwide
N. N. musculi	Rodentia: murid (house mouse, striped field mouse, yellow-necked mouse, white-footed mouse)	irritation, erythema, crusts	worldwide
N. N. myoticola	Chiroptera: vespertilionid (greater mouse-eared bat, lesser mouse-eared bat, long-fingered bat, Daubenton's bat)		Europe
N. N. myotis	Chiroptera: vespertilionid (cave myotis)		North America
N. N. namibiensis	Chiroptera: molossid (Egyptian free-tailed bat)		Africa
N. N. nigricans	Chiroptera: vespertilionid (black myotis)		South America
N. N. oudemansi	Rodentia: murid (black rat); Eulipotyphla: erinaceid (African hedgehog)	dermatitis	Africa
N. N. ovatus	Chiroptera: molossid (Angolan free-tailed bat)		Africa
N. N. pahangi	Rodentia: murid (ricefield rat, chesnut white-bellied rat, inland hill rat, African grass rat, Polynesian rat, Malayan wood rat, Hoffman's rat, Amami spinous rat, Bower's white-toothed rat, Namaqua rock rat)		Asia, Africa
N. N. paucipilis	Rodentia: murid (Creek groove-toothed swamp rat)		Asia
N. N. philippinensis	Chiroptera: vespertilionid (common bent-wing bat, greater bent-wing bat, little bent-wing bat)		Asia
N. N. pseudomuris	Rodentia: murid (house mouse, wood mouse, ricefield mouse), cricetid (transcaspian vole)	irritation, erythema, crusts	worldwide
N. N. rajamanickami	Chiroptera: molossid (hairless bat)		Malaysia
N. N. roesleri	Chiroptera: vespertilionid (black myotis)		South America
N. N. schoutedeni	Chiroptera: vespertilionid (white-winged serotine bat)		Africa
N. N. tadaridae	Chiroptera: molossid (gland-tailed freetail bat, northern freetail bat, Angolan free-tailed bat, Midas free-tailed bat, Malayan free-tailed bat), emballonurid (gray sac-winged bat)		Africa, Asia
N. N. tristis	Chiroptera: molossid (northern freetail bat)		Australia
N. N. vanschaiki (synonymized with *N. chiropteralis,* both recently transferred to *Prosopodectes*)	Chiroptera: vespertilionid (serotine bat, common noctule)		Europe
N. N. verheyeni	Chiroptera: emballonurid (African sheath-tailed bat)		Africa
N. N. yunkeri	Chiroptera: molossid (Coiban mastiff bat)		South America
Subgenus *N.* (*Bakeracarus*)			
N. B. americanus	Chiroptera: vespertilionid (little brown bat, black myotis, cave myotis, Yuma myotis, long-legged myotis)		South America
N. B. anisothrix	Chiroptera: molossid (velvety free-tailed bat)		South America
N. B. coreanus	Chiroptera: vespertilionid (Savi's pipistrelle)		Asia
N. B. corynorhini	Chiroptera: vespertilionid (Rafinesque's big-eared bat, Townsend's big-eared bat)		North America
N. B. eptesicus	Chiroptera: vespertilionid (Brazilian brown bat)		South America
N. B. helicothrix	Chiroptera: molossid (southern dog-faced bat)		South America
N. B. lasionycteris (syn. *Sarcoptes lasionycteris, myotis*) (incl. subspp. *lasionycteris*, *minimus*, *intermedius*)	Chiroptera: molossid (velvety free-tailed bat, black mastiff bat, Pallas's mastiff bat, free-tailed bat, Mexican free-tailed bat, broad-eared bat, little goblin bat), mormoopid (Macleay's mustached bat), vespertilionid (big brown bat, neotropical bat, silvery bat, cave myotis)		Americas
N. B. noctilionis	Chiroptera: noctilionid (greater bulldog bat)		Cuba

N. B. paraguayensis	Chiroptera: vespertilionid (black myotis)		South America
N. B. plecoti	Chiroptera: vespertilionid (brown long-eared bat)		Europe
Subgenus *N.* (*Mesonotoedres*)			
N. M. notoedres	Rodentia: cricetid (hamster)		Europe
Subgenus *N.* (*Neonotoedres*)			
N. N. elongatus	Chiroptera: molossid (hairless bat, lesser naked bat)		Indonesia

Parasite morphology: *Notoedres* spp. form 4 different types of morphological stages during their developmental cycles: namely, eggs, larvae, nymphs and adults. The eggs are ovoid transparent stages measuring around 100 μm in length. They hatch to release larvae which have oval flattened (discoid) bodies around 100 μm long and containing 3 pairs of ventral legs (2 short anterior pairs and one small posterior pair). Larvae moult to form nymphs which are larger in size measuring 150-200 μm long and possessing 4 pairs of ventral legs (having developed another small posterior pair). Two successive nymphal instars are formed (protonymphs and deutonymphs), both being similar in morphology to adult mites but lacking genital openings. Adult mites have small round dorsally-compressed bodies measuring 150-300 μm in length and covered by a finely-striated cuticle with dorsal concentric (thumb-print) patterns not interrupted by pointed spines/scales (like *Sarcoptes*). They have 2 main tagma: a small anterior gnathosoma (head) and larger posterior idiosoma (body). The gnathosoma bears short cutting-sucking mouthparts comprising a pair of 3-segmented chelicerae terminating in stylet-like chelae flanked by small sensory 2-segmented palps without terminal claws (apoteles). The oral opening (mouth) has a short square dorsal rostrum, a ventral buccal cone and an unbarbed hypostome. The alimentary tract comprises a tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with caeca), and tubular hindgut (with excretory Malpighian tubules) ending in a subterminal anus located on the dorsal surface (unlike *Sarcoptes* which has a terminal anus). The idiosoma lacks a precapsular dorsal shield (present in *Trixacarus* and *Sarcoptes*). The dorsal surface has group of rod-like setae and a few rounded backward-pointing scales (while *Trixacarus* has setose setae and *Sarcoptes* has spine-like setae). Adult *Notoedres* only have one pair of genital setae (while *Sarcoptes* and *Trixacarus* have 2 pairs). Like all members of the order Astigmata, respiratory stigmata and tracheae are absent as the mites breathe through their cuticles. The ventral idiosoma is the point of attachment for 4 pairs of legs, arranged in 2 anterior pairs projecting forwards just beyond the body margin and 2 small posterior pairs projecting backwards but not extending beyond the body. Each leg has 6 short segments (coxa, trochanter, femur, genu, tibia, and tarsus) with the coxae fused to body wall and sunk into body contributing to their short-legged appearance. The first 2 pairs of legs have thickened coxal apodemes (thickened ridges) joined in a Y-shape, while those on the hindlegs are not joined. Most legs have typical sarcoptiform pretarsi with long unsegmented pedicels bearing claw-like pulvilli. Male mites have small cup-shaped suckers (caruncles) on the ends of the first, second, and fourth pairs of legs, while females only have suckers on the first and second pairs of legs, the remaining legs terminating in long setae. Adult mites exhibit sexual dimorphism in body size (females larger than males, 200-300 v. 150-200 μm long), cuticular plates (mid-dorsal shield lacking in females) and genital structures. Males have genital apodemes (absent in *Sarcoptes*) and 2 testes with tubular vas deferens connected to an ejaculatory duct and long sheathed aedeagus (penis) which is located ventrally. Females have 2 ovaries with tubular oviducts joined to a globular uterus (with muscular shell-glands) and vagina (with accessory organs (bursa copulatrix, spermathecae) for sperm receipt and storage). The female gonopore (genital opening) appears as a transverse subterminal slit paralleling body striations and the cuticle behind the vulva is often pale and weakly striate.

Site of infection: These mites live in groups in deep burrows within the dermis of mammalian hosts. Almost 50 species have been described: mainly from bats (emballonurids, molossids, mormoopids, noctilionids, vespertilionids) as well as from various carnivores (canids, felids, herpestids, procyonids, viverrids) and some lagomorphs (leporids), shrews (erinaceids, soricids), diprotodontids (phascolarctids, phalangerids), peramelemorphs (peramelids), rodents (caviids, cricetids, erethizontids, murids, sciurids) and primates (galagids and hominids). The are found commonly on hairless or sparsely-haired regions of the body, such as the ear pinnae, nose, face, eyelids, head, neck, elbows, tail, and sometimes the perineum, external genitalia and legs.

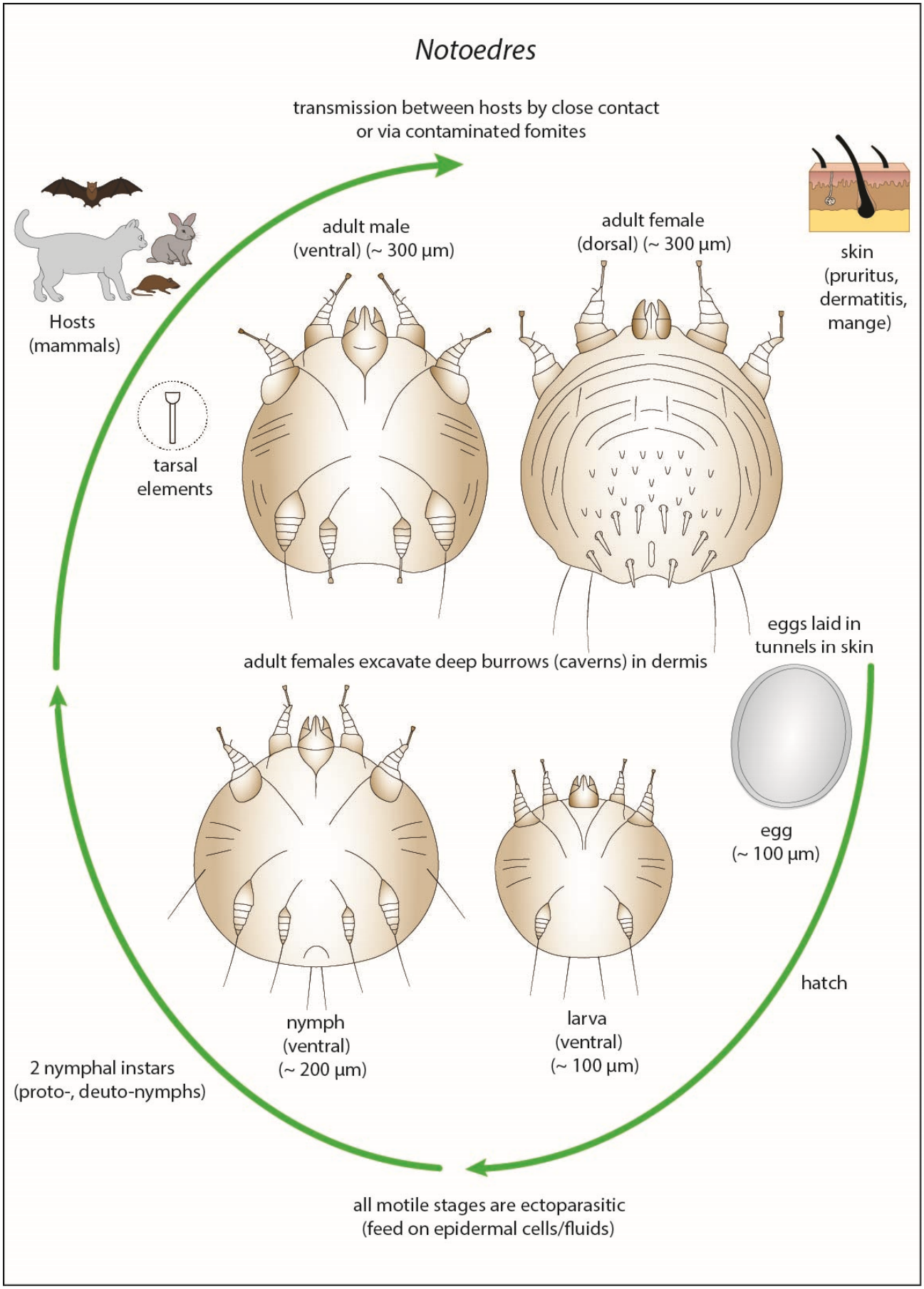
Pathogenesis: While some infestations remain subclinical, many produce mild to severe clinical disease (known as notoedric mange, sometimes called ‘feline scabies’ in cats) with skin inflammation (dermatitis) and intense pruritus exacerbated by hypersensitivity reactions leading to self-mutilation, yellow crusted lesions, patchy alopecia, secondary bacterial infections, and sometimes death. The mites burrow into the skin, usually being restricted to the stratum corneum, but occasionally penetrating this layer giving rise to more severe skin reactions and serum exudation. The mites feed on epidermal cells and tissue fluids as they burrow through the skin. Their tunnels contain mites, mite eggs, mite secretions (saliva) and excretions (faeces) which provoke allergic hypersensitive responses involving the release of cytokines (especially interleukin-1) from damaged keratinocytes. The skin becomes inflamed locally with an influx of neutrophils, eosinophils, mast cells and sometimes lymphocytes. Lesions first appear as red papules and progress to erythematous vesicles, both typically accompanied by intense pruritus. Exudates dry to form thick adherent yellow-gray crusts and sometimes scabs overlying ulcers. Hyperkeratosis occurs as epidermal cells proliferate and gradually cornify resulting in thickened wrinkled skin (lichenification). Lesions first appear on the ear pinnae, and rapidly spread to the rest of the ear, face, eyelids, neck, and paws. In severe cases, the outer ear may be completely eroded. Perineal lesions are also common, particularly in animals that sleep in a curled position. Animals attempt to relieve the pain and irritation by vigorous self-grooming, leading to skin damage (excoriation), hair loss (alopecia), gross self-mutilation and behavioural changes in hunting and foraging activities. Lesions become susceptible to secondary bacterial infections and peripheral lymphadenopathy may occur.

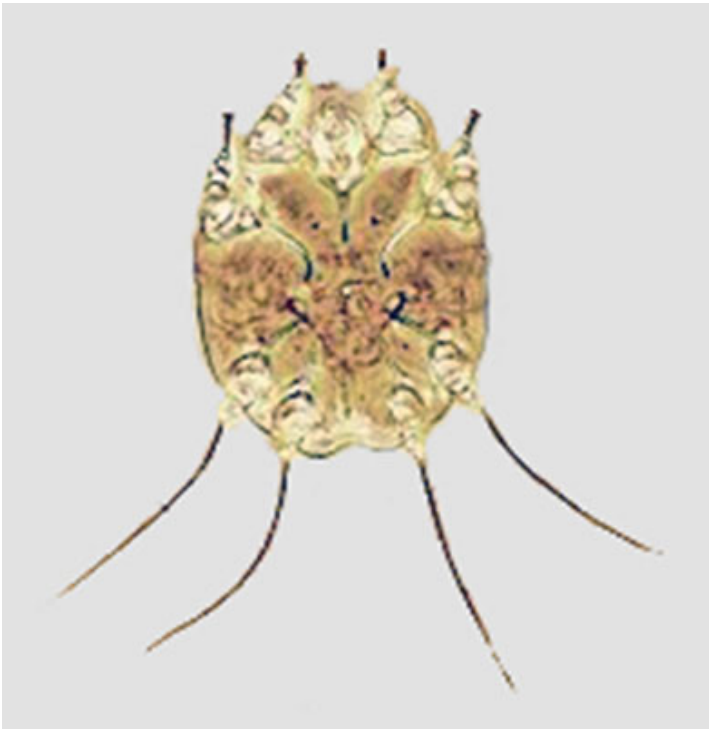
Changes in haematological and biochemical clinical parameters include mild anaemia, elevated ions (phosphates, sodium, chlorides), hypoglycaemia and low levels of serum creatinine, cholesterol, albumin and globulin (consistent with protein loss through the damaged skin). Chronically infested animals may become severely debilitated, depressed, dehydrated, anorexic, emaciated, and often die over 4-6 months. They do not appear to develop any protective immunity, although some individuals have been observed to undergo spontaneous recovery. Generally, notoedric mange in progressive and re-infestations are common after treatment. Infestations are more common in young, malnourished or immunosuppressed animals, or those with cognitive deficiencies or neuropathies that interfere with self-grooming.

Developmental cycle and mode of transmission: *Notoedres* spp. undergo incomplete (hemimetabolous) metamorphosis whereby eggs hatch larvae that moult through nymphal stages to form adult mites. The entire life-cycle may be completed on the same host and transmission to other hosts mainly involves direct contact. Female mites excavate deep burrows in the epidermis laying eggs at regular intervals, sometimes in a semicircle in a larger cavern. The eggs hatch after 4-5 days releasing hexapod (6-legged) larvae which emerge onto the surface of the skin before digging their own shallow burrows (larvae rarely remain in the maternal burrow). The larvae feed for several days before moulting to the first octopod (8-legged) nymphal stages (protonymphs) which leave the larval burrows before digging their own shallow burrows. The protonymphs feed for several days before moulting to the second nymphal stages (deutonymphs) which similarly leave their nymphal burrows before digging a third burrow. The deutonymphs feed for several days and then moult to form adult mites, usually within 12-18 days of oviposition. Adult females tend to stay in the third nymphal burrow, whereas adult males emerge seeking mates on neighbouring burrows. Following copulation, fertilized females dig deeper into the skin and lay 3-4 eggs each day for several weeks. The whole life-cycle may be completed in 19-21 days, but may take longer. Infestations are highly contagious and transmission occurs by direct contact between hosts with the transfer or wandering larvae and nymphs. Motile stages have also been found to survive for several days off hosts in humid conditions, so some transmission may occur via the contamination of fomites (particularly animal sleeping and resting places and bedding).

Differential diagnosis: *Notoedres* infestations may be strongly indicated on clinical grounds (intensely pruritic dermatitis with crusted lesions) but they need to be differentiated from dermatitis caused by other ectoparasites (other mites, lice, fleas, mosquitoes), bacterial pyoderma, fungal infections, endocrinopathies, atopic dermatitis, auto-immune diseases (pemphigus, systemic lupus erythematosus) and even adverse food reactions. Diagnosis is afforded by the direct detection of mites in deep skin scrapings, usually following caustic digestion (10% potassium hydroxide) to break down skin and other organic debris (mite cuticles are impervious to digestion). Mites are often found at the edges of lesions, and may also occur in large numbers in crusts. Histopathology of skin biopsies may reveal mite fragments in the thickened stratum corneum with focal hyperkeratosis and superficial perivascular dermatitis. Coprological studies may also reveal mites or fragments in host faeces after centrifugal floatation, as mites ingested during grooming are subsequently passed in faeces. Molecular biological techniques have also been used to detect and characterize mite isolates from faeces and skin scrapings following the polymerase chain reaction (PCR) amplification of nuclear gene sequences (notably internal transcribed spacer 2 from ribosomal DNA).

Treatment and control: Clinical infestations have responded well to chemotherapy using chemical acaricides, including topical or systemic applications of lime sulphur, organophosphates (malathion), organochlorines (lindane), pyrethroids (flumethrin), phenylpyrazoles (fipronil), neonicotinoids (imidacloprid) and macrocyclic lactones (ivermectin, selamectin, doramectin, moxidectin). Treatment efficacy is greatly improved if animals are sprayed/bathed with antiseborrheic shampoos to soften or remove crusts before the application of the acaricides. However, repeated or prolonged acaricidal treatment may be required to eliminate mite stages subsequently emerging from burrows, particularly in persistent and generalized infestations. There have been a number of reports of mite populations developing resistance to some acaricides, including organochlorines and macrocyclic lactones. Treatment is best augmented by vitamin supplementation (especially vitamin K to prevent incidental anticoagulant toxicosis), steroid formulations (to manage self-trauma and hypersensitivity) and broad-spectrum antibiotic regimes (to combat secondary bacterial infections). All in-contact animals should be treated at the same time, particularly in infested households, kennels/catteries and laboratory animal facilities. Effective prevention and control relies on a combination of regular monitoring as a prelude to timely treatment with animal isolation and quarantine, environmental decontamination through stringent sanitation of fomites (animal housing and bedding), and the exclusion of wildlife from households and holding facilities using barriers or traps.


Notoedres
transmission between hosts by close contact
or via contaminated fomites
Hosts
(mammals)
adult male
(ventral) (~ 300 µm)
adult female
(dorsal) (~ 300 µm)
skin
(pruritus,
dermatitis,
mange)
tarsal
elements
adult females excavate deep burrows (caverns) in dermis
eggs laid in
tunnels in skin
egg
(~ 100 µm)
hatch
nymph
(ventral)
(~ 200 µm)
larva
(ventral)
(~ 100 µm)
2 nymphal instars
(proto-, deuto-nymphs)
all motile stages are ectoparasitic
(feed on epidermal cells/fluids)



Notoedres adult

Trixacarus
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Sarcoptids are burrowing mites with circular bodies and the last two pairs of legs do not project beyond the body margin. Infestations by *Trixacarus caviae* occur in the skin of guinea pigs and may cause dermatitis (mange).

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Sarcoptoidea (mites associated with mammals, ecto- or endo-parasitic)
Family: Sarcoptidae (burrowing mites, circular bodies, third and fourth legs do not project beyond body margin)
Genus: *Trixacarus* (parasitic on skin of guinea pigs)
Species: *T. caviae* causes mange in guinea pigs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

Early classification schemes identified different assemblages principally on the basis of host and site specificity; including bird-associated feather mites (e.g. Analgoidea); bird-associated skin mites (e.g. Knemidokoptidae), mammal-associated fur mites (e.g. Listrophoridae), mammal-associated skin mites (e.g. Psoroptidae); and mammal-associated skin-burrowing mites (e.g. Sarcoptoidea). However, phylogenetic studies (both cladistic and molecular) have revealed that many groups are not monophyletic but para- or poly-phyletic, so further studies are required to resolve the fidelity of most groups. Recently, molecular studies suggested that 16 sarcoptoidean families may belong to 2 main lineages: 13 families identified in a 'sarcoptid' complex (Atopomelidae, Audycoptidae, Chirodiscidae, Chirorhynchobiidae, Galagalgidae, Gastronyssidae, Lemurnyssidae, Listrophoridae, Listropsoralgidae, Myocoptidae, Pneumocoptidae, Rhyncoptidae, Sarcoptidae), and 3 families in a 'psoroptid' complex (Lobalgidae, Paracoroptidae, Psoroptidae). Nevertheless, most families can still be categorized into 4 broad 'morphoecotypes': namely; fur mites (Atopomelidae, Chirodiscidae, Listrophoridae, Lobalgidae), skin mites (Chirorhynchobiidae, Myocoptidae, Psoroptidae), skin-burrowing and follicle mites (Rhyncoptidae, Sarcoptidae), and respiratory mites (Gastronyssidae, Lemurnyssidae, Pneumocoptidae). The family Sarcoptidae comprises the burrowing mites that invade the skin of mammalian hosts causing intense pruritus. These 'itch mites' have soft circular bodies and 4 pairs of legs, the posterior 2 pairs not projecting beyond the body margin. Numerous genera have been recognized and allocated to 3 subfamilies (Caenolestocoptinae, Diabolicoptinae, Sarcoptinae). although another 5 genera remain unplaced (*Chirophagoides*, *Grammolichus*, *Lophuromyopus*, *Rodentopus*, *Sclerolichus*). The subfamily Sarcoptinae contains 15 genera (*Chirnyssoides*, *Chirobia*, *Cynopterocoptes*, *Kutzerocoptes*, *Mysarcoptes*, *Notoedres*, *Nycteridocoptes*, *Prosarcoptes*, *Prosopodectes*, *Rousettocoptes*, *Sarcoptes*, *Satanicoptes*, *Teinocoptes*, *Trixacarus*, *Tychosarcoptes*). The genus *Trixacarus* (syn. *Caviacoptes*) is characterized by small oval mites with short stubby legs lacking claws, dorsal striations interrupted by many pointed scales, and a dorsal anus. Three species have been described as ectoparasites on rodents, with the species *T. caviae* recognized as a common cause of mange (dermatitis and alopecia) in guinea pigs around the world.

***Trixacarus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
T. caviae (guinea pig mite, Sellnick mite)	Rodentia: caviid (guinea pig)	skin (body)	irritation, inflammation, pruritus, alopecia	worldwide
T. diversus	Rodentia: murid (brown rat, black rat, house mouse), cricetid (hamster, Drylands vesper mouse)			Europe
T. eliurus	Rodentia: nesomyid (dormouse tufted-tailed rat)			Madagascar

Parasite morphology: *Trixacarus* spp. form 4 different types of morphological stages during their developmental cycles: namely, eggs, larvae, nymphs and adults. Eggs are ovoid transparent stages ranging in size from 115-165 x 70-110 μm. They hatch to release larvae which have oval slightly-flattened bodies measuring 110-160 x 70-120 μm. They have striated cuticles adorned with small spines. They possess 3 pairs of short legs, the 2 anterior pairs ending in stalked suckers and the posterior pair terminating in long setae. Larvae moult to form nymphs, which have 4 pairs of legs (having developed another posterior pair). Two nymphal instars are formed: protonymphs measuring 120-175 x 85-135 μm; and deutonymphs (sometimes called tritonymphs) measuring 150-200 x 110-160 μm. The final nymphal stages moult to form oval-circular adult mites with discoidal (ventrally-flattened) bodies measuring 120-240 x 85-180 μm. Adults have 2 tagma: a small anterior gnathosoma (head) and a large posterior idiosoma (body). The gnathosoma bears cutting-sucking mouthparts comprising a pair of segmented chelicerae terminating in claw-like chelae flanked by a pair of small 2-segmented sensory palps without terminal apoteles. The oral opening (mouth) has a dorsal rostrum, ventral buccal cone and unbarbed hypostome. The alimentary tract comprises a tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with caeca) and a tubular hindgut (with excretory Malpighian tubules) opening to a dorsal anus (located more posteriorly in males than females). The idiosoma bears a small precapsular shield (like *Sarcoptes*) and the cuticle bears fine striations which are interrupted dorsally by numerous scales which are more sharply-pointed than those of *Sarcoptes* (unlike *Notoedres* which only has a few rounded scales). The idiosomal setae are setose, while those of *Sarcoptes* are spine-like and those of *Notoedres* are rod-like. *Trixacarus* adults also have at least 2 pairs of genital setae (like *Sarcoptes*, but unlike *Notoedres* which has only one pair at most). Like all members of the Astigmata, *Trixacarus* mites lack respiratory stigmata and tracheae (they respire through their cuticles). The ventral idiosoma bears 4 pairs of short stubby legs, with 2 pairs projecting anteriorly beyond the body margin, and 2 pairs projecting posteriorly but not extending beyond the body. The legs have 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) with the coxae fused and sunk into body wall contributing to their short-legged appearance. The tarsi have small terminal hooks (not claws) and the 2 pairs of anterior legs terminate in long pretarsal stalks bearing cup-shaped suckers, while the 2 pairs of posterior legs end in long setae. Adult mites display sexual dimorphism with females being larger than males (160-240 x 120-180 μm cf. 120-150 x 85-100 μm). Male mites have 2 testes with tubular vas deferens leading to the ejaculatory duct and long sheathed aedeagus (penis) opening to the subterminal ventral genital pore. Female mites have 2 ovaries with tubular oviducts leading to the globular uterus (with shell-glands) and vagina (with accessory organs (bursa copulatrix and spermathecae) for sperm receipt and storage). The female genital opening appears as a subterminal ventral transverse slit paralleling the cuticular body striations.

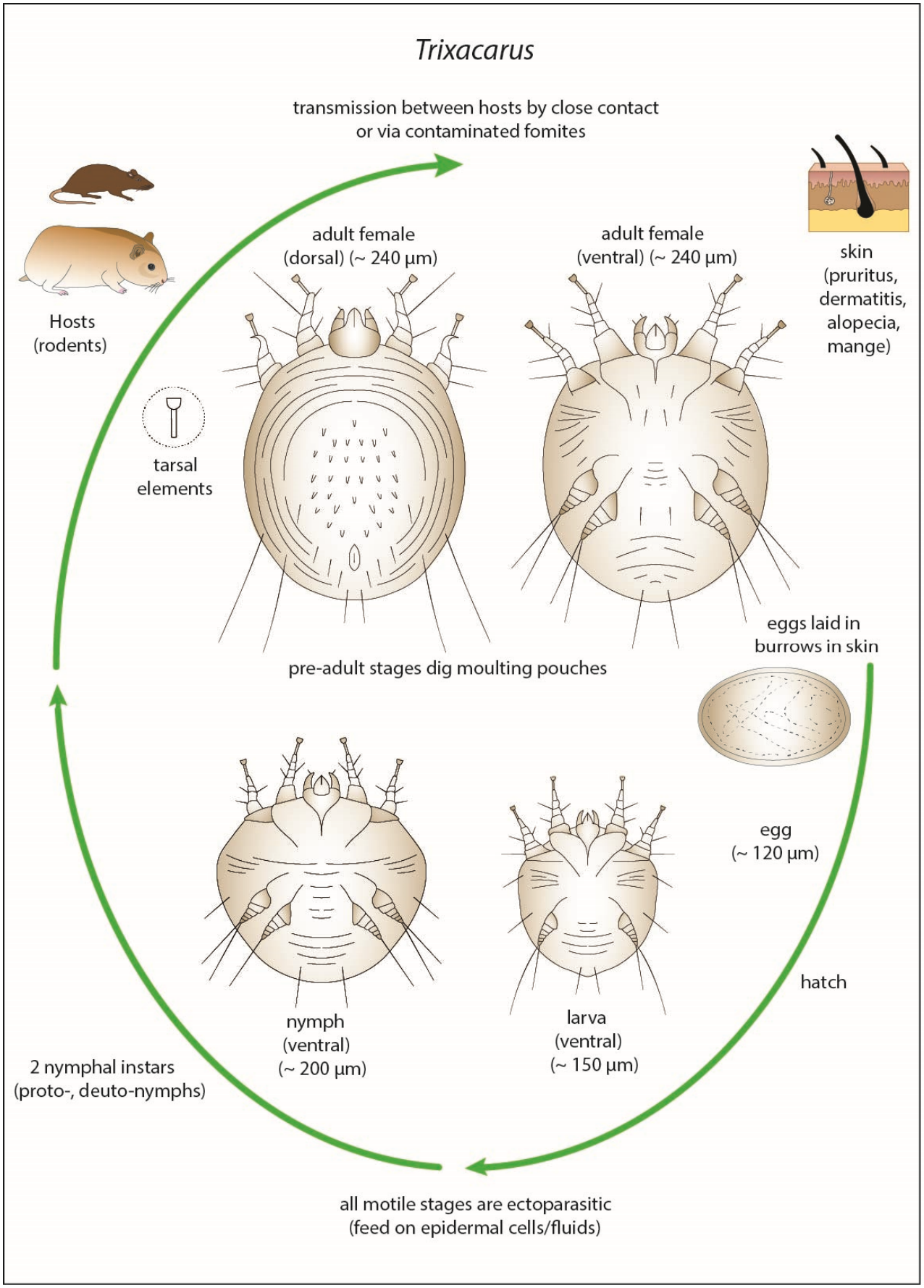
Site of infection: These burrowing mites are obligate ectoparasites in the skin of various rodents, usually infesting the back and flanks but sometimes extending over the shoulders and neck. Three species have been reported from caviid, cricetid, murid and nesomyid rodents around the world, with the species *T. caviae* recognized as a common cause of mange in guinea pigs.

Pathogenesis: Infestations are often progressive, initially causing mild dermatitis (mange) that worsens over time leading to excoriations, lichenification, alopecia, sometimes seizures and death. The mites burrow under the skin provoking inflammatory changes involving the 4 cardinal signs of rubor (redness), calor (heat), tumor (swelling) and dolor (pain), probably exacerbated by allergic/hypersensitive reactions to mite antigens (surface proteins, saliva and faeces). Hosts experience considerable irritation with intense pruritus and skin lesions progressing from erythematous papules to exudative vesicles that dry to form yellow scales and crusts. The skin exhibits orthokeratotic hyperkeratosis, marked acanthosis, lichenification and alopecia, occasionally forming eosinophilic microabscesses and necrotic areas. Animals undertake vigorous self-grooming, often inflicting severe self-trauma and excoriations through their frantic biting, scratching and rubbing. Open skin lesions are highly prone to secondary bacterial infections which may become pustular. Persistent infestations may kill the host after 3-4 months, with death being attributed to severe dehydration (from expanding sores) and starvation (from failure to eat due to extreme pain and discomfort). In severe infestations, animals may also experience seizures (often induced during handling) which resolve following successful mite treatment (not requiring anti-convulsant medication). Chronic infestations may also affect reproduction performance, with abortion and foetal resorption seen in pregnant animals. Infestations are most severe in young and aged animals, those subject to stress and poor environmental conditions, and those with concomitant disease (including hypovitaminosis C). Infestations may remain subclinical for several months (even years), but become problematic when guinea pigs reproduce or are subject to illness or stress. In several instances, a nonclinical carrier state has been mooted when clinical outbreaks have occurred in animals or colonies long isolated from other animals. These mange mites are not zoonotic, but on rare occasions they may cause temporary pruritic papulovesicular skin lesions in some people even though mites cannot live or reproduce on humans

Developmental cycle and mode of transmission: *Trixacarus* spp. undergo hemimetabolous (gradual or incomplete) metamorphosis where eggs hatch larvae which moult to nymphs and then adult mites. All stages in the life-cycle may occur on the same host, and transmission to other hosts occurs by direct contact or via contaminated fomites. Adult female mites oviposit eggs in their burrows which hatch in 4-5 days to release hexapod larvae. The larvae move onto the skin surface and dig their own shallow burrows (called moulting pouches). They feed for several days before moulting into the first nymphal instar (called protonymphs). The protonymphs move onto the skin surface and excavate their own shallow moulting pouches. They feed for several days before moulting to form the second nymphal instar (known as deutonymphs, but sometimes called tritonymphs in early literature). These nymphs migrate onto the skin surface and dig shallow moulting pouches before forming adult mites. Male mites leave their pouches to seek mates, while female mites remain in place. Mating occurs when an adult male penetrates the moulting pouch of an adult female. Impregnated females then expand their moulting pouches into deeper burrows, laying eggs as they go. The whole life-cycle may be completed in 14-21 days. Transmission occurs primarily through direct contact with infested animals, particularly through close contact between mother and offspring. Mites seldom leave their hosts unless dislodged onto bedding or as a result of overpopulation or the death of the host. All developmental stages can survive for several weeks off hosts, so some transmission must occur via contaminated fomites, such as animal holding facilities and bedding.

Differential diagnosis: Infestations may be suspected on the basis of symptomatology (dermatitis, crusting and alopecia) but other aetiological agents may cause similar clinical signs. Differential diagnosis is made by the microscopic examination of deep skin scrapings. Mites are often found at the edges of lesions as well as in skin flakes and crusts. Samples are usually subject to caustic digestion in potassium hydroxide to break down skin cells and debris, while mites remain unscathed as their cuticles are impervious to digestion. Occasionally, infestations have been detected by the histopathological examination of skin biopsies which reveal mites, mite fragments or eggs in the stratum corneum. Changes in clinical haematological and biochemical parameters are relatively nonspecific and include leukocytosis, monocytosis, eosinophilia and basophilia (consistent with cellular inflammation) as well as hypoglycaemia and low levels of serum albumin and globulin (consistent with protein loss).

Treatment and control: Clinical infestations respond well to treatment with chemical acaricides, with early topical treatments with sulphur compounds, organochlorines (lindane), organophosphates (malathion, coumaphos) and pyrethroids (permethrin) now largely superseded by systemic treatments with arylpyrazoles (fipronil) and macrocyclic lactones (ivermectin, selamectin, doramectin). Nonetheless, most drugs are not ovicidal and do not kill eggs, so repeated or protracted treatments are required to eliminate newly-emergent stages. Drug efficacy is also improved if animals are bathed beforehand with antiseborrheic shampoos to remove crusts and debris. Careful attention should be paid to any drug contra-indications, as some macrocyclic lactones are not well absorbed by guinea pigs and several commonly used diluents (such as propylene glycol) may cause dermal inflammation or necrosis. Control programs designed to prevent the spread of infestations are based around animal management (regular monitoring and treatment of cohorts, isolation and quarantine, hygienic husbandry), environmental sanitation (cleaning animal housing and bedding, fomite decontamination), and wildlife exclusion (vermin control using barriers, traps or baits).


Trixacarus
transmission between hosts by close contact
or via contaminated fomites
Hosts
(rodents)
tarsal
elements
adult female
(dorsal) (~ 240 µm)
adult female
(ventral) (~ 240 µm)
skin
(pruritus,
dermatitis,
alopecia,
mange)
pre-adult stages dig moulting pouches
eggs laid in
burrows in skin
egg
(~ 120 µm)
hatch
nymph
(ventral)
(~ 200 µm)
larva
(ventral)
(~ 150 µm)
2 nymphal instars
(proto-, deuto-nymphs)
all motile stages are ectoparasitic
(feed on epidermal cells/fluids)



Trixacarus adult



Trixacarus egg

Cytodites
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Ctyoditid mites lack chelicerae and the palps are fused to form a sucking organ. They are parasites of the respiratory tracts of birds, rodents and bats. Infestations by *Cytodites nudus* in the air passages of poultry and canaries have been associated with respiratory disorders and emaciation.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Family: Ctyoditidae (respiratory parasites of birds, chelicerae absent, palps fused to form sucking organ)
Genus: *Cytodites* (parasitic in air sacs of birds)
Species: *C. nudis* causes airsacculitis in poultry and canaries

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

Early classification schemes identified different assemblages principally on the basis of host and site specificity; including bird-associated feather mites (e.g. Analgoidea); bird-associated skin mites (e.g. Knemidokoptidae), mammal-associated fur mites (e.g. Listrophoridae), mammal-associated skin mites (e.g. Psoroptidae); and mammal-associated skin-burrowing mites (e.g. Sarcoptoidea). Phylogenetic studies (both cladistic and molecular) have revealed that many groups are not monophyletic but para- or poly-phyletic, so further studies are required to resolve the fidelity of most groups. Most families can still be categorized into 4 broad 'morphoecotypes': namely; fur mites (Atopomelidae, Chirodiscidae, Listrophoridae, Lobalgidae), skin mites (Chirorhynchobiidae, Myocoptidae, Psoroptidae), skin-burrowing and follicle mites (Rhyncoptidae, Sarcoptidae), and respiratory mites (Gastronyssidae, Lemurnyssidae, Pneumocoptidae, Cytoditidae). The family Cytoditidae constitutes a unique group of small oval nude mites with reduced mouthparts (lacking chelicerae but with fused palps forming a sucking organ) that infect the respiratory passages of birds (hence their common names of nasal or airsac mites). The family is monotypic containing a single genus (*Cytodites*) with 10 species described from a range of bird species belonging to passerine and non-passerine families. In particular, one species (*C. nudus*) is problematic in poultry production by causing respiratory disease in chickens.

***Cytodites* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
C. amandavae	Passeriformes: estrilidid (red avadavat), ploceid (speckle-fronted weaver)			India, Africa
C. arae	Psittaciformes: psittacid (red-and-green macaw)			South America
C. faini	Passeriformes: laniid (red-backed shrike)			Europe
C. geopeliae	Columbiformes: columbid (bar-shouldered dove)			Australia
C. hendrickxi	Psittaciformes: psittacid (green-thighed parrot)			South America
C. nudus (syn. *Cytoleichus sarcoptoides, Cytodites glaber, Sarcoptes gerlachi*) (airsac mite)	Galliformes: phasianid (chicken, turkey, golden pheasant); Anseriformes: anatid (mallard); Columbiformes: columbid (pigeon); Coraciiformes: meropid (European bee-eater); Passeriformes: corvid (blue jay), fringillid (canary), leiothrichid (black-faced babbler)	air passages, lungs	excess mucus, coughing, respiratory difficulties, airsacculitis, loss of balance, emaciation	worldwide
C. psittaci	Psittaciformes: psittacid (Meyer's parrot)			Africa
C. psittaculae	Psittaciformes: psittaculid (rose-ringed parakeet)			Africa
C. therae	Cuculiformes: cuculid (black-billed cuckoo)			North America
C. tympanistriae	Columbiformes: columbid (tambourine dove)			Africa

Parasite morphology: Like all mites, *Cytodites* spp. are thought to form 4 different types of morphological stages during their developmental cycles: namely, eggs, larvae, nymphs and adults. However, due to their inaccessibility in the respiratory tract, it has not been definitively established whether eggs hatch *in utero* or after oviposition, that is, whether these mites are viviparous or oviparous. Only motile developmental stages have been detected crawling over respiratory surfaces, with most reports indicating the occurrence of one larval and 2 nymphal instars. Larvae are small ovoid stages measuring around 150-200 μm long with 3 pairs of short stout legs (2 anterior pairs and one posterior pair). Nymphs are also ovoid but larger measuring 200-400 μm and having 4 pairs of stout legs (2 anterior pairs and 2 posterior pairs). The first nymphal instars (known as protonymphs) are around 230 μm in length and have irregularly striated cuticles and their legs terminate in short simple pretarsal ambulacra. The second nymphal instars (known as deutonymphs, although some earlier texts call them tritonymphs) are around 370 μm long and have fine but irregular cuticular striations, poorly developed setae (chaetotaxy) and legs ending in slightly longer ambulacra. Adult mites have oval slightly flattened bodies that are broader anteriorly and narrow posteriorly. They range considerably in size from 345-650 μm long by 230-500 μm wide. They have white chitinous cuticles often without striations, and very few fine setae which are often absent (adults are often referred to as 'nude' mites). They have 2 main tagma: a small anterior gnathosoma (head) and a large posterior idiosoma (body). The gnathosoma bears weakly-developed mouthparts where chelicerae are absent (or barely recognizable as minute highly-reduced pincer-like appendages) flanked by small smooth palps that are fused to form a soft sucking tube used to imbibe fluids. The alimentary tract comprises a tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with caeca), short tubular hindgut (with excretory Malpighian tubules) and subterminal ventral anus. The idiosoma lacks sclerotized shields and respiratory stigmata and tracheae are absent (the mites breathe through their cuticles, like other Astigmata). The ventral idiosoma gives rise to 4 pairs of stout jointed legs, 2 pairs projecting forwards, 2 pairs projecting backwards and all extending well beyond the body margin. Each leg has 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) with the basal coxae fused to the body wall near thickened ridges (called epimeres or apodemes). The apodemes linked to the first pair of legs are characteristically fused distally to form a Y-shape. All legs end in short pretarsi with small rounded pulvilli (usually stalked in females, but not in males). Adult mites display sexual dimorphism with females being larger than males (450-650 cf. 450-550 μm). Male mites have 2 testes with vas deferens

leading to the ejaculatory duct and long sheathed aedeagus (penis) opening to a ventral subterminal genital pore located near a V-shaped lobe. Female mites have 2 ovaries with oviducts leading to the uterus and vagina (with accessory organs (bursa copulatrix and spermathecae) for sperm reception and storage). Females have a longitudinal slit-like genital opening (gonopore) located around the ventral midbody.

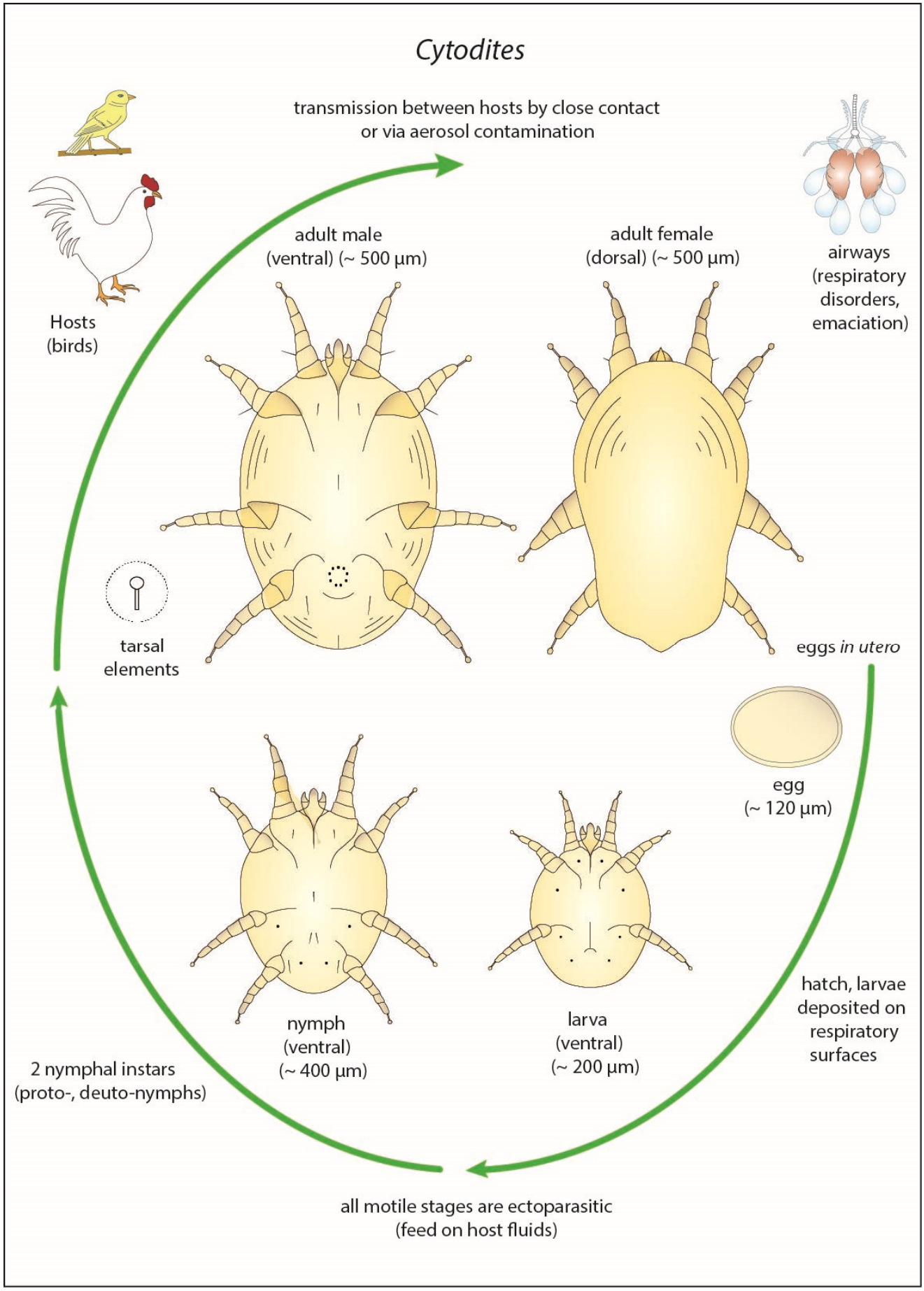
Site of infection: *Cytodites* spp. occur in the respiratory systems of birds, with 10 species described in 13 families of birds belonging to 7 orders, including poultry, ducks, doves, cuckoos, parrots, bee-eaters and various passeriforms. While mites are conventionally considered to be ecto-parasites, these mites behave as endo-parasites as they commonly infest the air sacs, lungs and bronchial passages, although they are occasionally found in pneumatic bone cavities, the alimentary tract, peritoneum and body cavity.

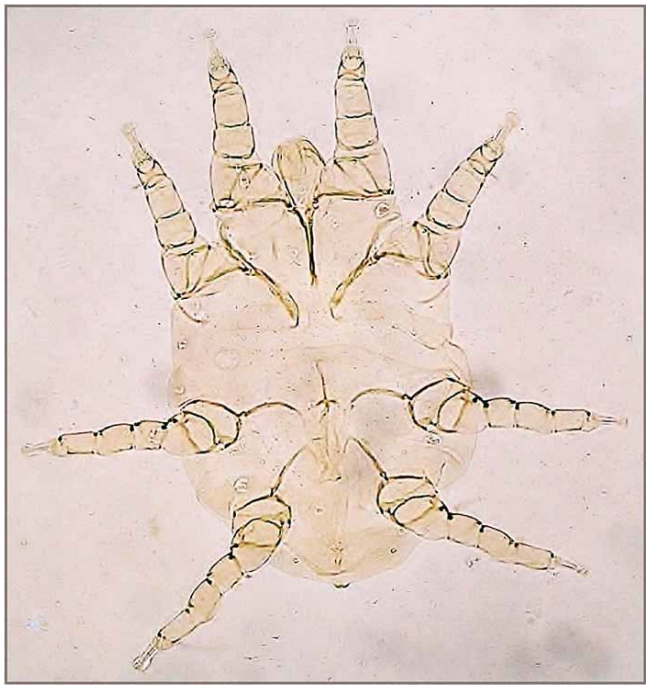
Pathogenesis: Light infestations in birds may go unnoticed but heavier infestations may cause mild to severe respiratory disease. Birds have a pair of lungs and numerous thin-walled air sacs that extend into some bones thus reducing weight. They do not have diaphragms but rely on muscular contractions to respire. The presence of mites in the respiratory system feeding on host fluids may cause sufficient inflammation to compromise respiratory function, with granulomatous pneumonia and airsacculitis leading to excessive mucus, pulmonary oedema, creamy deposits, airway obstruction, dyspnoea, coughing, sneezing, gasping, clicking sounds, change in vocalization, wheezing and frequent swallowing. Infested birds become fluffed-up as they try to conserve body heat since the compromised respiratory system cannot maintain body temperature. Birds may exhibit frequent tail bobbing (due to the exertion of abdominal breathing), head shaking, beak rubbing, weakness, lethargy, weight loss, emaciation, incoordination, and death. Infiltrates of macrophages, eosinophils and plasma cells are often associated with histiocytic, lymphoplasmacytic, or granulomatous inflammation resulting in cloudy and thickened air sacs and firm red consolidations in the lungs with thick yellow pus in the bronchi. infested birds are thought to be prone to secondary infections, including avian tuberculosis. In several cases, mites have been found outside the respiratory system, but their location in cavities or tubular organs may be the consequence of airsac rupture or penetration. These ectopic infestations have sometimes been tentatively associated with peritonitis, enteritis, and occasionally deaths in chickens.

Developmental cycle and mode of transmission: *Cytodites* spp. undergo gradual (hemimetabolous) metamorphosis involving eggs hatching larvae which moult through nymphs to form adults. All stages occur in the respiratory spaces of birds and the mode of transmission between birds remains speculative. It is not known whether gravid female mites lay eggs or retain them with the uterus until they hatch (some reports suggest they are oviparous, others viviparous). In either case, larval stages move about on respiratory surfaces feeding on host fluids using their small sucking mouthparts. The larvae moult through 2 nymphal instars before forming adult mites. All feeding stages appear as small white motile specks on the transparent host membranes. The life cycle appears to be completed in 14-21-days but little is known about the longevity or fecundity of the adults. It has been suggested that mites may undergo aerosol transmission between birds via respiratory secretions broadcast by coughing or sneezing, or by direct contact of bird nasal cavities during social behaviours (such as courtship, grooming or parents feeding their young). It is thought that the ‘endo-parasitic’ mites do not survive long outside of their hosts and they do not voluntarily leave hosts, even following host death. These speculations contra-indicate transmission via contaminated fomites, water or feed, but this remains to be demonstrated.

Differential diagnosis: Clinical infestations may be suspected on the basis of symptomatology, but other aetiological agents may cause similar respiratory signs, particularly bacterial or fungal pathogens but also including other mites (e.g. *Sternostoma*). Few ante-mortem diagnostic tests have proven effective, although the examination of oral/nasal swabs, tracheal trans-illumination and tracheal endoscopy may sometimes reveal the presence of mites. Radiography may reveal generalized nonspecific opacities in pulmonary and airsac fields. Most often, differential diagnosis can only be afforded by the post-mortem detection of mites in air sacs and bronchial passages and confirmed by their microscopic identification.

Treatment and control: Early studies reported some successes treating infestations using aerosol formulations of insecticidal dusts incorporating organophosphates (such as malathion), but now the most effective treatments involve the systemic application of macrocyclic lactones (ivermectin, moxidectin, selamectin). Repeated or prolonged treatment may be required, due to the partly privileged and protected site of infestation in the airways. In heavy infestations, the initial massive mortality of mites may cause respiratory symptoms to worsen temporarily prior to improving. Supportive therapy should also be provided using heat lamps to help birds maintain their body temperatures and antibiotics to combat bacterial infections. While intricacies of the transmission cycle have yet to be determined, common-sense preventive measures should be used to help contain infestations, including isolation and quarantine procedures (sometimes culling infested birds), excluding wild birds from aviaries and poultry sheds, implementing strict hygiene and sanitation (cleaning cages/coops, replacing bedding/nesting materials), and even undertaking some environmental decontamination (spraying litter, cracks and crevices with long-lasting insecticides/acaricides).


Cytodites
transmission between hosts by close contact
or via aerosol contamination
Hosts
(birds)
adult male
(ventral) (~ 500 µm)
adult female
(dorsal) (~ 500 µm)
airways
(respiratory
disorders,
emaciation)
tarsal
elements
eggs in utero
egg
(~ 120 µm)
nymph
(ventral)
(~ 400 µm)
larva
(ventral)
(~ 200 µm)
hatch, larvae
deposited on
respiratory
surfaces
2 nymphal instars
(proto-, deuto-nymphs)
all motile stages are ectoparasitic
(feed on host fluids)



Cytodites adult

Lynxacarus
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Listrophorid mites have a distinct dorsal shield and their legs are modified for grasping hairs of fur-bearing mammals. Infestations by *Lynxacarus* spp. may cause unkempt coats and pruritus in cats.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Sarcoptoidea (mites associated with mammals, ecto- or endo-parasitic)
Family: Listrophoridae (parasitic on fur-bearing mammals, distinct dorsal shield, legs modified for grasping hairs)
Genus: *Lynxacarus* (parasitic on skin of cats)
Species: various species cause unkempt coats and pruritus in cats

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

Early classification schemes identified different assemblages principally on the basis of host and site specificity; including bird-associated feather mites (e.g. Analgoidea); bird-associated skin mites (e.g. Knemidokoptidae), mammal-associated fur mites (e.g. Listrophoridae), mammal-associated skin mites (e.g. Psoroptidae); and mammal-associated skin-burrowing mites (e.g. Sarcoptoidea). However, phylogenetic studies (both cladistic and molecular) have revealed that many groups are not monophyletic but para- or poly-phyletic, so further studies are required to resolve the fidelity of most groups. Recently, molecular studies suggested that 16 sarcoptoidean families may belong to 2 main lineages: 13 families identified in a 'sarcoptid' complex (Atopomelidae, Audycoptidae, Chirodiscidae, Chirorhynchobiidae, Galagalgidae, Gastronyssidae, Lemurnyssidae, Listrophoridae, Listropsoralgidae, Myocoptidae, Pneumocoptidae, Rhyncoptidae, Sarcoptidae), and 3 families in a 'psoroptid' complex (Lobalgidae, Paracoroptidae, Psoroptidae). Nevertheless, most families can still be categorized into 4 broad 'morphoecotypes': namely; fur mites (Atopomelidae, Chirodiscidae, Listrophoridae, Lobalgidae), skin mites (Chirorhynchobiidae, Myocoptidae, Psoroptidae), skin-burrowing and follicle mites (Rhyncoptidae, Sarcoptidae), and respiratory mites (Gastronyssidae, Lemurnyssidae, Pneumocoptidae). The family Listrophoridae comprises small elongate mites with palps and legs modified for grasping hairs in a wide variety of fur-bearing mammalian hosts. Some 26 genera have been recognized: namely, *Aeromychirus*, *Afrolistrophorus*, *Asiochirus*, *Carnilistrophorus*, *Centetesia*, *Chirodiscoides, Cryptocoptes*, *Echinosorella*, *Eurychiroides*, *Geomylichus*, *Hemigalichus*, *Indochirus*, *Lemuroecius*, *Lemuroptes*, *Leporacarus*, *Listrophorus*, *Lynxacarus*, *Metalistrophorus*, *Olistrophorus*, *Prolistrophorus*, *Pteromychirus*, *Quasilistrophorus*, *Schizocarpus*, *Sclerolistrophorus*, *Spalacarus*, and *Tenrecobia*. The genus *Lynxacarus* (syn. *Felistrophorus*) comprises robust mites with striated bodies that are flattened ventrally so that their sternal plates accommodate host hairs. A total of 16 species have been described predominantly from carnivores, rodents and some insectivores. Several authorities have recognized 3 subgenera: namely, *L.* (*Lynxacarus*) with 3 species, *L.* (*Dubininetta*) with 4 species, and *L.* (*Lutracarus*) with 2 species (the remaining species being unplaced). The species *L. radovskyi* is considered to be mildly pathogenic in cats (particularly ferals/strays) in tropical and subtropical regions, with infestations producing unkempt coats and inciting excessive grooming with regurgitative sequalae (vomiting, hairballs).

***Lynxacarus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
Subgenus *L.* (*Lynxacarus*)				
L. (*L.*) *morlani*	Carnivora: felid (bobcat)			North America
L. (*L.*) *mustelae*	Carnivora: mustelid (river otter, least weasel, long-tailed weasel, European polecat, stoat, European pine marten, beech marten, European badger)			Europe, North America
L. (*L.*) *nearcticus*	Carnivora: mustelid (American mink, European mink, long-tailed weasel); Rodentia: sciurid (chipmunk)			North America
L. (*L.*(*radovskyi* (cat fur mite)	Carnivora: felid (cat)	hair	dull unkempt coat, pruritus, excessive grooming, vomiting, hairballs, anorexia	North America, Australia, Pacific Islands
L. (*L.*) *serrafreirei*	Carnivora: mustelid (lesser grison)			South America
Subgenus *L.* (*Lutracarus*)				
L. (*Lu.*) *canadensis*	Carnivora: mustelid (river otter)			North America
L. (*Lu.*) *visoni*	Carnivora: mustelid (American mink)			North America
Subgenus *L.* (*Dubininetta*)				
L. (D.) *dubinini* (syn. *Dubininetta*)	Eulipotyphla: talpid (Russian desman, Pyrenean desman, Japanese mole)			Eurasia
L. (*D.*) *echinosorex* (now *Echinosorella*)	Eulipotyphla: erinaceid (moonrat)			Asia
L. (*D.*) *taiwanensis* (syn. *Dubininetta*)	Eulipotyphla: talpid (insular mole)			Asia
L. (*D.*) *talpae* (syn. *Dubininetta*)	Eulipotyphla: talpid (long-nosed mole)			Asia
Unplaced				
L. grandior	Rodentia: murid (mountain giant Sunda rat)			Asia
L. lyncodon	Carnivora: mustelid (Patagonian weasel)			South America
L. palawanensis	Scandentia: tupaiid (Palawan treeshrew)			Asia
L. semnopitheci	Carnivora: viverrid (Asian palm civet); Scandentia: tupaiid (Horsfield's treeshrew); Primates: cercopithecid (Hose's langur, Paitan langur)			South-East Asia

L. tupaiae	Scandentia: tupaiid (common treeshrew, northern treeshrew, mountain treeshrew)			Asia

Parasite morphology: *Lynxacarus* spp. form 4 different types of morphological developmental stages: eggs, larvae, nymphs and adults. The eggs are elongate ellipsoidal stages ranging in dimensions from 200-250 x 80-100 μm and they have rounded tapering poles and are slightly flattened along one side (the side they are attached to host hair shafts). Larvae have elongated oval bodies measuring from 200-300 μm in length with a flattened ventral surface giving rise to 3 pairs of legs (the first 2 pairs projecting forwards, the third pair projecting backwards). Larvae, like all subsequent nymphal and adult stages, are equipped with sternal plates that partly encircle host hairs, and together with the first two pairs of legs allow the mites to move like monorails along the hair shafts. It is thought that 2 nymphal instars occur, protonymphs and deutonymphs, ranging from 300-515 μm long, both stages with elongate flattened bodies with 4 pairs of ventral legs. They are generally similar in morphology to adult female mites but are smaller, lack propodosomal plates, and have shorter legs and fewer setae. Adult mites have characteristic elongate narrow bodies that are somewhat cylindrical but laterally compressed, flattened ventrally and arched dorsally. They range in size from 350-530 μm long by 95-125 μm wide, with females being larger than males (420-530 x 120-125 cf. 350-450 x 95-110 μm). They have 2 main tagma: a small anterior gnathosoma (head) with a well-developed head plate that is often light-dark brown in colour and ventrally directed, and a long posterior idiosoma (body) that is transparent white-tan with a strongly-patterned cuticle (numerous transverse striations). The gnathosoma has short mouthparts comprising a pair of segmented chelicerae terminating in claw-like chelae arising from a basis capitulum flanked by a pair of sensory palps (the chelae are adapted for grasping hair shafts between the basis capitulum and palps). The oral opening (mouth) has a dorsal rostrum, ventral buccal cone and unbarbed hypostome. The alimentary tract consists of a short tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with caeca), and short tubular hindgut (with excretory Malpighian tubules) opening to a terminal anal pore (flanked by caudal lobes and anal suckers only in males only). Like all Astigmata, respiratory stigmata and tracheae are absent as the mites breathe through their cuticles. The striated idiosoma is sparsely setate but has long caudal setae (longer in males) and distinct dorsal and ventral plates. The dorsal propodosomal plates are well developed (with some species having an anterior bridge-like projection to the head plate), and the propodonotal plates have pre- and post-scapular portions separated by small strip of striated cuticle. Adult male mites also have lateral opisthosomal plates (lacking in females). Ventrally, adult mites have sternal plates with curved flap-like extensions used with the legs to help encircle hair shafts. All adults have 4 pairs of short hooked legs clustered on the anterior two-thirds of the body, 2 pairs projecting forwards and 2 pairs backwards. Each leg comprises 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) with the coxae fused to the body wall (coxae I may be fused to the head plate) and the anterior coxal fields expanded and flattened (longer than wide) with thickened grooved surfaces (apodemes) for attachment. The femurs often have dorsal preapical prominences, the tarsi have short setae, and all legs terminate in sucker-like feet (short pretarsal stalk with spearhead-like pulvilli). Male mites have enlarged hindlegs and a tapering posterior end, cleft medially with two lobular processes bearing long slender lateral setae. Males have 2 testes with tubular vas deferens leading to the ejaculatory duct and a long rod-like aedeagus (penis) with the genital apparatus opening ventrally between coxae 4. Female mites have rounded posterior ends (without lobes or suckers) but with several setae around the terminal anus. They have 2 ovaries with tubular oviducts leading to a globular uterus (with shell glands) and vagina (with large accessory organs (bursa copulatrix, spermathecae) for sperm reception and storage) opening to a ventral midbody gonopore.

Site of infection: These non-burrowing fur mites are found attached to hairs of small mammalian hosts. Some 16 species have been described mainly from carnivores (felids, mustelids, viverrids), but also from some rodents (sciurids, murids) and several other small mammals (treeshrews, moles, moonrats and langurs). Infestations are commonly found on the perineum, around the anus, on the tail and the lateral hindlimbs, but may sometimes extend over the dorsum and rarely the whole body.

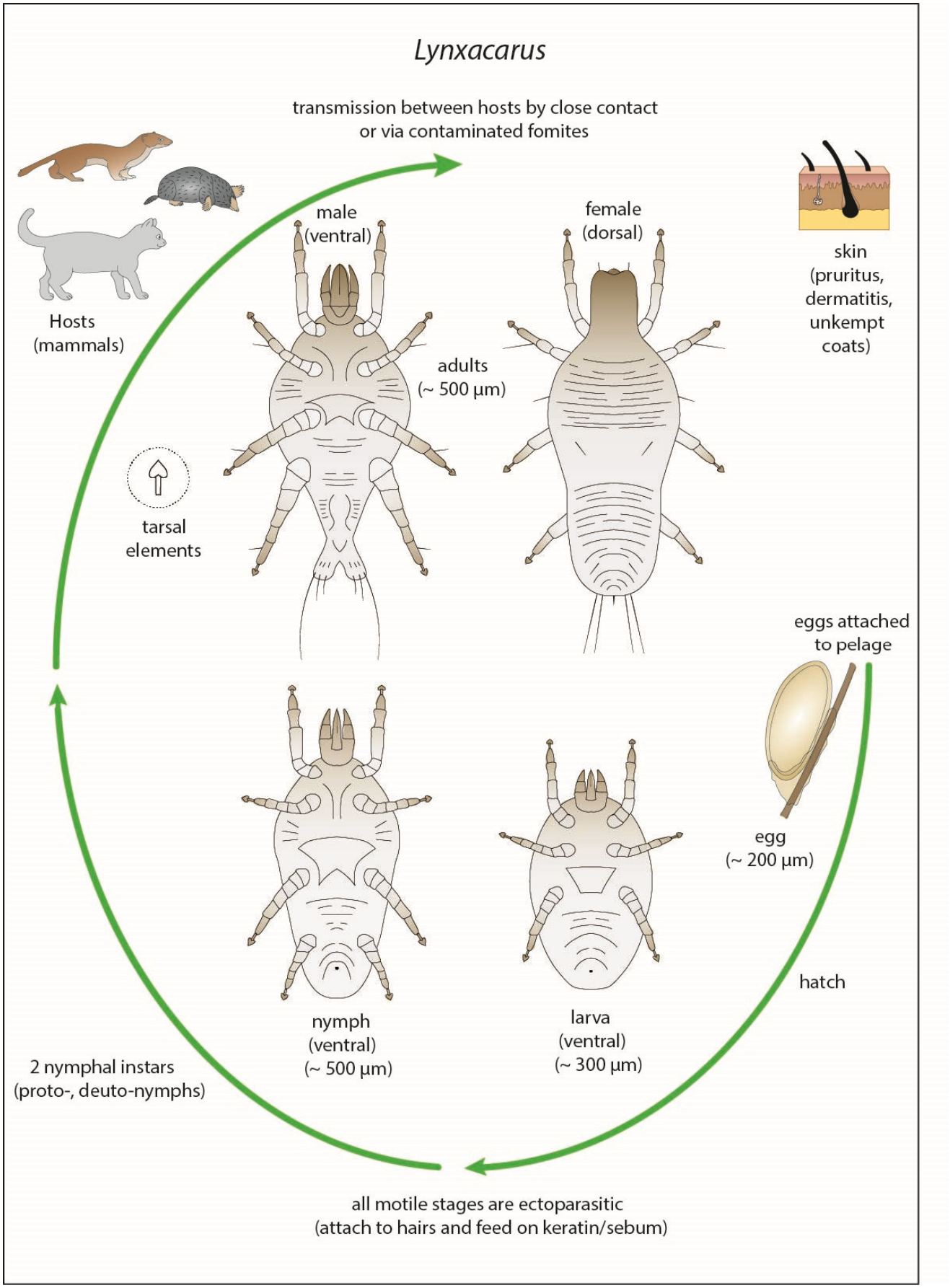
Pathogenesis: Infestations vary greatly in the number of parasites and their clinical impact, ranging from light inapparent infestations to mild infestations causing some pruritus to heavy infestations causing marked discomfort and generalised maculopapular exfoliative dermatitis (scurfy mange). Mites feed on the keratin of the hair and sebaceous skin secretions and often cause little harm. However, the presence of mites can lead to dermatitis probably exacerbated by allergic/hypersensitivity reactions to mite secretions/excretions that result in papulocrustous rashes with variable pruritus, scaling and dandruff (scurf) leading to dry dull unkempt dirty coats with a rusty granular appearance (colloquially called salt-and-pepper coats). Animal attempts at self-grooming often result in self-mutilation contributing to the development of papules, macules, crusts, excoriations, and alopecia (hairs easily epilated), particularly on the dorsal and lateral aspects of the hind limbs. Chronically infested animals may exhibit restlessness, fever, anorexia, and weight loss. Infested animals (especially cats) may also develop gingivitis, rectal irritation, and gastrointestinal disturbances with emesis (vomiting) of trichobezoars (hairballs) due to chronic over-grooming.

Developmental cycle and mode of transmission: Despite their occurrence as non-burrowing ectoparasites on the pelage of their hosts, the life-cycles of these fur mites remains poorly described. They undergo hemimetabolous (gradual or incomplete) metamorphosis where eggs hatch larvae that moult through nymphs to form adults. All stages may occur on the same individual host and transmission between hosts likely occurs by direct contact and possibly by contamination of fomites. Observations conducted on infested animals have revealed the presence of single eggs glued to host hair shafts as well as hexapod larvae, small octopod protonymphs, larger octopod deutonymphs and adult male and female mites attached firmly to hair shafts. Experimental studies

have been conducted on mite developmental stages removed from hosts and cultured in humid chambers under laboratory conditions. They demonstrated that eggs hatched within 1-4 days, and that all motile stages (larvae, nymphs and adults) survived for 1-5 days. However, little is known about the duration of the developmental stages under natural conditions, nor the longevity and fecundity of adult mites. Epidemiological studies have suggested that infestations are not highly contagious and it has been proposed that most transmission may occur between hosts through direct contact, particularly when hosts come together socially for comfort, resting, sleeping, mating or nursing. Nonetheless, considering that motile stages may survive off hosts for short periods, some transmission may occur via contaminated fomites, probably through bedding in dens, burrows, nests and other resting places.

Differential diagnosis: While clinical infestations may be indicated on clinical grounds (scurfy pruritic mange), most signs are nonspecific and may be attributed to other causative agents, including other mites (trombiculids, *Notoedres*, *Otodectes, Cheyletiella*, *Sarcoptes*), lice (*Felicola*), fleas (*Pulex, Ctenocephalides*, *Echidnophaga*), miliary dermatitis (which includes food allergy dermatitis), eosinophilic granuloma complex, and some fungal infections. Diagnosis is conventionally made by the direct detection of mites in the pelage using magnifying glasses (or even an otoscope) or by the microscopic examination of hair plucks (trichograms), material collected by brushing fur or combing hair, or material adherent to transparent adhesive tape (skin scrapings are inappropriate). The fur mites can be readily identified by their distinct elongate shapes and their firm attachment to hairs. Mites and mite eggs ingested during grooming may also be occasionally detected in faecal samples following centrifugal floatation. Preliminary molecular biological studies have also been used to partially characterize mite samples by polymerase chain reaction (PCR) amplification of nuclear (18S ribosomal RNA) and mitochondrial (cytochrome oxidase I) gene sequences.

Treatment and control: Animals have been successfully treated using conventional topical acaricides (as shampoos, baths, sprays or powders) and more contemporary systemic acaricides (as spot-on, oral or injectable formulations); including lime sulphur, organochlorines (lindane), organophosphates (malathion), pyrethrin and synthetic pyrethroids (flumethrin), phenylpyrazoles (fipronil), neonicotinoids (imidacloprid), isoxazolines (afloxolaner) and macrocyclic lactones (selamectin, ivermectin, moxidectin, milbemycin). Many formulations are not strongly ovicidal, so repeated or protracted treatment is often required to combat newly-emergent stages and prevent re-infestation. Animals also seem to benefit from corticosteroid therapy to subdue allergic/hypersensitivity reactions. Even though infestations are not regarded as highly contagious, common-sense preventive measures should include animal isolation during treatment, the quarantine of new animals introduced to farms/households, good sanitation by the regular cleaning of cages, pens and bedding, and the exclusion of wildlife from animal holding areas. Early recommendations to use insecticides or acaricides with good residual activity as environmental sprays, mists or fogs to decontaminate animal facilities have largely gone out of favour since the introduction of long-lasting systemic formulations for resident animals.


Lynxacarus
transmission between hosts by close contact
or via contaminated fomites
Hosts
(mammals)
male
(ventral)
female
(dorsal)
adults
(~ 500 µm)
skin
(pruritus,
dermatitis,
unkempt
coats)
tarsal
elements
eggs attached
to pelage
egg
(~ 200 µm)
hatch
nymph
(ventral)
(~ 500 µm)
larva
(ventral)
(~ 300 µm)
2 nymphal instars
(proto-, deuto-nymphs)
all motile stages are ectoparasitic
(attach to hairs and feed on keratin/sebum)



Lynxacarus adult



Lynxacarus egg

Leporacarus
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Listrophorid mites have a distinct dorsal shield and their legs are modified for grasping hairs of fur-bearing mammals. Infestations by *Leporacarus* spp. are found on the skin of rabbits and hares where they may cause dermatitis and pruritus.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Sarcoptoidea (mites associated with mammals, ecto- or endo-parasitic)
Family: Listrophoridae (parasitic on fur-bearing mammals, distinct dorsal shield, legs modified for grasping hairs)
Genus: *Leporacarus* (parasitic on skin of rabbits/hares)
Species: several species cause dermatitis and pruritus in rabbits

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
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Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
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Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph- feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
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Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

Early classification schemes identified different assemblages principally on the basis of host and site specificity; including bird-associated feather mites (e.g. Analgoidea); bird-associated skin mites (e.g. Knemidokoptidae), mammal-associated fur mites (e.g. Listrophoridae), mammal-associated skin mites (e.g. Psoroptidae); and mammal-associated skin-burrowing mites (e.g. Sarcoptoidea). However, phylogenetic studies (both cladistic and molecular) have revealed that many groups are not monophyletic but para- or poly-phyletic, so further studies are required to resolve the fidelity of most groups. Recently, molecular studies suggested that 16 sarcoptoidean families may belong to 2 main lineages: 13 families identified in a 'sarcoptid' complex (Atopomelidae, Audycoptidae, Chirodiscidae, Chirorhynchobiidae, Galagalgidae, Gastronyssidae, Lemurnyssidae, Listrophoridae, Listropsoralgidae, Myocoptidae, Pneumocoptidae, Rhyncoptidae, Sarcoptidae), and 3 families in a 'psoroptid' complex (Lobalgidae, Paracoroptidae, Psoroptidae). Nevertheless, most families can still be categorized into 4 broad 'morphoecotypes': namely; fur mites (Atopomelidae, Chirodiscidae, Listrophoridae, Lobalgidae), skin mites (Chirorhynchobiidae, Myocoptidae, Psoroptidae), skin-burrowing and follicle mites (Rhyncoptidae, Sarcoptidae), and respiratory mites (Gastronyssidae, Lemurnyssidae, Pneumocoptidae). The family Listrophoridae comprises small elongate mites with palps and legs modified for grasping hairs in a wide variety of fur-bearing mammalian hosts. Some 26 genera have been recognized: namely, *Aeromychirus*, *Afrolistrophorus*, *Asiochirus*, *Carnilistrophorus*, *Centetesia*, *Chirodiscoides, Cryptocoptes*, *Echinosorella*, *Eurychiroides*, *Geomylichus*, *Hemigalichus*, *Indochirus*, *Lemuroecius*, *Lemuroptes*, *Leporacarus*, *Listrophorus*, *Lynxacarus*, *Metalistrophorus*, *Olistrophorus*, *Prolistrophorus*, *Pteromychirus*, *Quasilistrophorus*, *Schizocarpus*, *Sclerolistrophorus*, *Spalacarus*, and *Tenrecobia*. The genus *Leporacarus* (syn. *Listracarus*) contains stout mites with flat ventral surfaces possessing expanded coxal fields with grooved surfaces to aid in host attachment. Male mites possess large adanal clasping organs, seen as parallel rectangular protrusions extending well beyond the posterior margin of the body. Four species have been described from rabbits (domestic and wild) and hares, occasionally causing moist dermatitis and alopecia.

***Leporacarus* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
Subgenus *L.* (*Leporacarus*)				
L. (*L.*) *gibbus* (syn. *Listrophorus gibbus*)	Lagomorpha: leporid (European hare, Cape hare, European rabbit, black-tailed jackrabbit); Rodentia: murid (black rat); Carnivora: felid (cat); Primates: hominid (human)	hair	mange	Africa, Europe, North America
Subgenus *L.* (*Leporacaroides*)				
L. (*L.*) *brevicaudatus*	Lagomorpha: leporid (European hare, mountain hare)			Europe
L. (*L.*) *leporicolus*	Lagomorpha: leporid (scrub hare); Carnivora: viverrid (common slender mongoose)			Africa
L. (*L.*) *sylvilagi*	Lagomorpha: leporid (brush rabbit, cottontail rabbit)			North America

Parasite morphology: *Leporacarus* spp. have been shown to form 4 different types of morphological stages during their development; namely, eggs, larvae, nymphs (2 instars) and adult mites (males and females). The eggs are elongate ellipsoid measuring around 210 x 80 μm and are flattened along one side. They are attached to host hairs at one pole by proteinaceous secretions such that the egg lies tangential to the hair shaft. Mature eggs hatch by splitting down the dorsal midline, leaving empty egg cases with a 2-winged appearance. Larvae are oval in dorsal view, but flattened ventrally and curved (hunched) dorsally. They range in size from 200-300 μm in length and have 3 pairs of ventral legs, 2 anterior pairs projecting forwards and a midbody pair projecting backwards. The first pair of legs have clasping membranous flaps used to attach to host hairs (these characteristic flaps persist throughout subsequent mite development). Nymphs are similar in shape and configuration to larvae, but are larger (measuring 300-500 μm) and now have 4 pairs of legs (having developed another pair of posterior legs). Two nymphal stages are thought to occur: protonymphs and deutonymphs (the latter sometimes called teleonymphs as they have most characteristics of adult female mites but have immature genital structures). Adult mites (both males and females) have oval-subcylindrical bodies that are flattened laterally, flattened ventrally and curved dorsally. They are tan-brown in colour and range in size from 400-610 x 200-350 μm. Adults have 2 main tagma: a small anterior sclerotized gnathosoma (head) with a rounded dorsal protrusion that extends slightly beyond the mouthparts imparting a dark hooded appearance, and a large posterior idiosoma (body) with a transparent cuticle bearing distinct transverse striations (in thumbprint patterns). The gnathosoma had a basis capitulum with ventral hood-like claspers, mouthparts comprising a pair of 3-segmented chelicerae terminating in claw-like chelae, and a pair of small flanking sensory palps (without terminal apoteles) pressed against the central unbarbed hypostome. The capitular claspers and cheliceral chelae are adapted for grasping hairs and have been described by some as chitinous lips. The alimentary tract comprises a tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with caeca) and tubular hindgut (with excretory Malpighian tubules) opening to a subterminal anus. The idiosoma possesses a distinct dorsal propodonotal shield whose pre- and post-scapular portions are separated by a small suture in males but fused in females. Like all Astigmata, respiratory stigma and tracheae are absent as the mites breathe through their cuticles. The ventral idiosoma gives rise to 4 pairs of legs arranged in 2 fields: 2 anterior pairs and 2 posterior pairs,

but all legs extending well beyond the body margin. Each leg has 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) with the coxae fused to the body wall and having expanded flat anterior fields (wider than long) with thickened grooved apodemes (or epimeres) that join to form a Y-shape for the first pair of legs and a V-shape for the second pair of legs. Most distinctively, the coxae of the first pair of legs each have 2 striated clasping membranous flaps used to attach to hairs. All legs have tarsal setae and all legs terminate in sucker-like caruncles (short pretarsal stalks with cup-like pulvilli). Adults display considerable sexual dimorphism with males being smaller than females (400-510 x 200-330 v. 450-610 x 250-350 μm) and bearing 2 round adanal suckers and 2 rectangular posterior processes with long caudal setae (clasping organs imparting a unique 'double-tail' appearance). Adult males have 2 testes with tubular vas deferens leading to an ejaculatory duct and long sheathed aedeagus (penis) which is surrounded by fused prescapular (pregenital) sclerites. Female mites have a more hunched appearance with rounded posterior ends. They have 2 ovaries with tubular oviducts leading to a globular uterus (with shell glands) and vagina (with accessory organs for sperm reception (bursa copulatrix) and storage (spermathecae)) opening to a rounded terminal gonopore.

Site of infection: These non-burrowing fur mites are found on the hairs of the dorsum and abdomen mostly on lagomorphs (wild and domestic leporids) and occasionally on a few rodents (murids), carnivores (viverrids) and rarely on primates (humans).

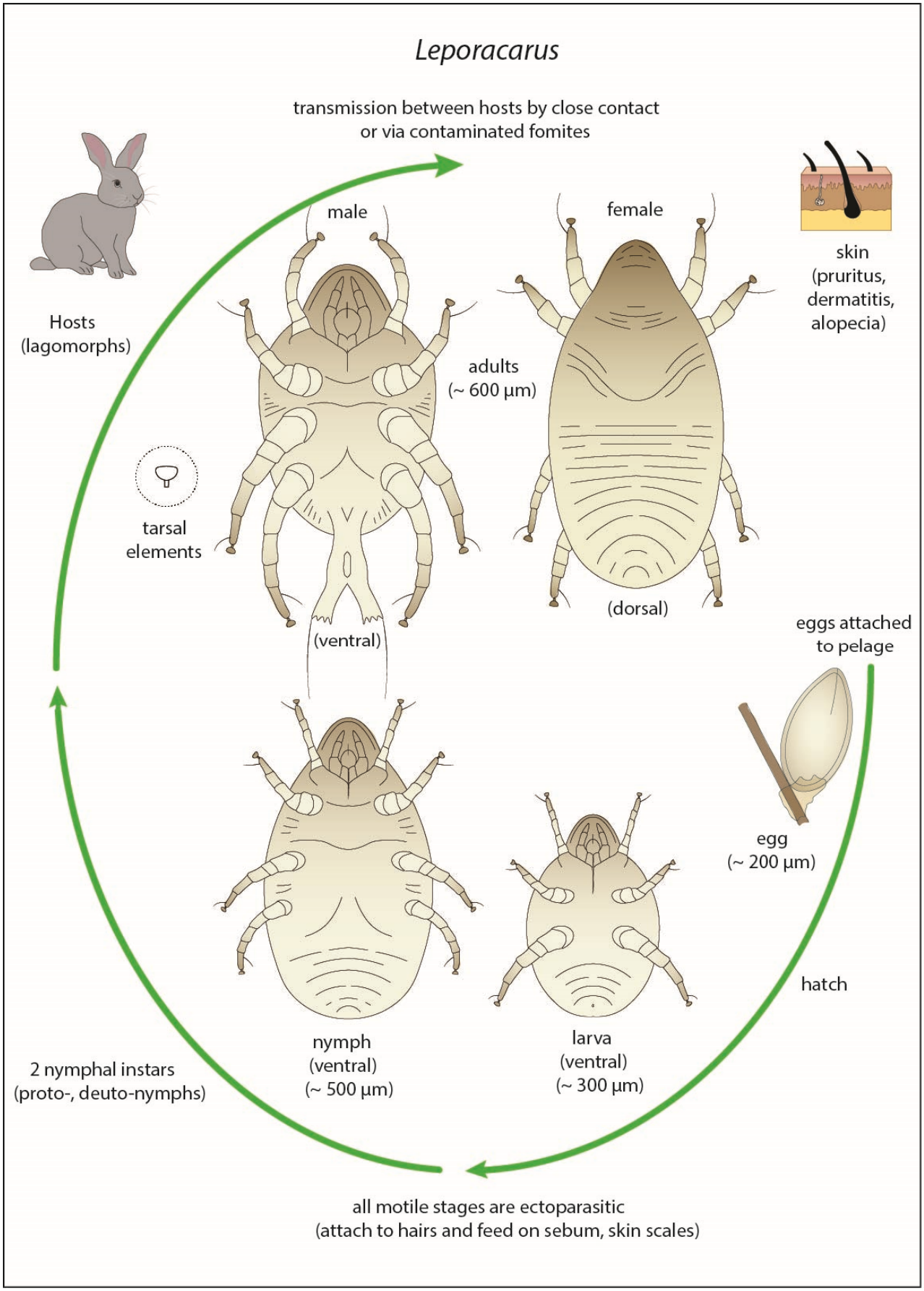
Pathogenesis: Most infestations are well tolerated by their hosts and often remain asymptomatic (to the extent that the mites were initially considered to be commensals), but heavier infestations have been associated with a mild clinical disease characterized by dermatitis with alopecia. It has been suggested that disease expression is the result of allergic/hypersensitivity reactions to the presence of feeding mites and their secretions (saliva) and excretions (faeces). Mites are surface dwellers which attach to host hairs and feed on sebaceous secretions (sebum), epithelial cells, skin and hair scales and other debris. Infestations have been associated with pruritus, moist dermatitis, erythema, seborrhoea, mild scurfing and scaling (not pronounced like cheyletiellosis), poorly demarcate alopecia, abnormal moulting and self-trauma due to biting, scratching or rubbing, normally around the rump area. Heavy infestations may give the coat a salt-and-pepper appearance, especially when wet. The exuviae (cast 'skins') of immature stages (eggs, larvae and nymphs) remain attached to host hairs contributing to the speckled appearance of infested (or previously infested) areas. Clinical infestations are more common on long-haired rabbits, young animals and those with underlying problems that interfere with grooming (including obesity, spinal disorders, dental conditions and other debilitating diseases). *Leporacarus* mites have also been associated with transient dermatitis and papular urticaria in humans, usually those regularly handling infested animals.

Developmental cycle and mode of transmission: These fur mites undergo hemimetabolous (gradual or incomplete) metamorphosis in that eggs hatch larvae that moult to nymphs and then adults. All life-cycle stages may occur on the same individual host, and transmission between hosts appears to occur by direct contact or possibly via contaminated fomites. Few details are known about the dynamics and kinetics of the life-cycle, but field observations and laboratory studies have shown that gravid females attach eggs singly to hair shafts where they hatch in several days to release hexapod (6-legged) larvae. The larvae moult through 2 octopod (8-legged) nymphal instars several days apart before finally moulting to adult male and female mites. All immature developmental stages moult while attached to hairs using clasping parts of their mouthparts as well as the clasping membranous flaps associated with the coxae of the first pair of legs. Movement along and between hairs is achieved using their remaining pairs of legs. Larval and nymphal exuviae (cast exoskeletons) usually remain attached to hairs after moulting. Adult mites mate on their hosts and gravid females begin ovipositing eggs on hair shafts. The whole life-cycle may be completed in 14-20 days but may take longer in unsuitable conditions due to apparent delayed development or diapause. Field studies conducted on hares suggested that infestations exhibited seasonal changes, with summer populations being 'generative' (with slower development, nymphal diapause, and prolonged life-spans) and winter populations being 'vegetative' (with accelerated development and shorter life-spans).

Differential diagnosis: Any clinical signs exhibited by animals are usually mild, generally involving moist dermatitis with patchy alopecia. They are nonspecific and may be attributed to a range of conditions, including microbial infections and other ectoparasites as well as diseases caused by stress, allergies, nutritional deficiencies and other skin conditions. Definitive diagnosis is made by the direct demonstration of mites on hosts. Visual examination may real the presence of mites in the pelage, often evident as small dark specks moving away from light, particularly noticeable on hosts with light-colored coats. Antemortem samples may be collected for microscopy by vacuum aspiration, hair plucks (trichograms), brushing or combing the fur, or by sticky-tape impressions (skin scrapings are inappropriate for these surface-dwelling mites). Postmortem samples may also be collected by placing bodies or pelage samples in bags or dishes and collecting any stages that migrate to the tips of hairs as the samples cool down. Mites can be readily identified microscopically by their characteristic morphological features, especially adult male with their unique posterior clasping organs. Molecular biological techniques have recently been used to characterize species by polymerase chain reaction (PCR) amplification of mitochondrial gene sequences (cytochrome oxidase I).

Treatment and control: Infestations by fur mites have been successfully treated using conventional topical acaricides (dusts, sprays, baths) as well as more contemporary systemic preparations (oral, injectable or spot-on formulations). Early treatments

involved sulphur-based compounds, paraffin oil, organophosphates (diazinon), carbamates (carbaryl), benzoic esters (benzyl benzoate) and synthetic pyrethroids (deltamethrin, permethrin), which have now largely been superseded by neonicotinoids (imidacloprid), amidines (amitraz) and macrocyclic lactones (ivermectin, eprinomectin, doramectin, selamectin, moxidectin, abamectin). Attention should be paid to any drug contra-indications as some formulations may have serious adverse side-effects (e.g. fipronil may cause depression, anorexia, seizures and death in rabbits). If bathing the animal is required, care should be taken to reduce the risks of hypothermia (warm bath, towel dry, provide supplemental warmth using heat lamps). Some clinicians have also found that animals may benefit from the use of non-acaricidal chemicals (cleansing agents, antifungals or anti-inflammatories) commonly used to treat seborrhea (the reduction in skin keratin and sebum content provides unsuitable conditions for feeding mites). Various preventive measures have also been adopted to help break putative transmission cycles, involving regular health surveillance (monitoring to facilitate treatment, isolation and quarantine), animal husbandry (avoid over-crowding in holding and nursing facilities), improved sanitation (cleaning cages/pens/hutches, applying residual acaricides such as methoprene/permethrin sprays to cracks/crevices and porous fomites such as carpets), and wildlife management (excluding wild animals from farms, stores, breeding centres and households).


Leporacarus
transmission between hosts by close contact
or via contaminated fomites
Hosts
(lagomorphs)
male
female
adults
(~ 600 µm)
skin
(pruritus,
dermatitis,
alopecia)
tarsal
elements
(ventral)
(dorsal)
eggs attached
to pelage
egg
(~ 200 µm)
hatch
nymph
(ventral)
(~ 500 µm)
larva
(ventral)
(~ 300 µm)
2 nymphal instars
(proto-, deuto-nymphs)
all motile stages are ectoparasitic
(attach to hairs and feed on sebum, skin scales)



Leporacarus adult male

Chirodiscoides
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Listrophorids are fur mites found on small mammals and birds. Infestations by *Chirodiscoides caviae* may cause dermatitis in guinea pigs.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Sarcoptoidea (mites associated with mammals, ecto- or endo-parasitic)
Family: Listrophoridae (parasitic on fur-bearing mammals, distinct dorsal shield, legs modified for grasping hairs)
Genus: *Chirodiscoides* (parasitic on skin of guinea pigs)
Species: *C. caviae* causes dermatitis in guinea pigs

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

Early classification schemes identified different assemblages principally on the basis of host and site specificity; including bird-associated feather mites (e.g. Analgoidea); bird-associated skin mites (e.g. Knemidokoptidae), mammal-associated fur mites (e.g. Listrophoridae), mammal-associated skin mites (e.g. Psoroptidae); and mammal-associated skin-burrowing mites (e.g. Sarcoptoidea). However, phylogenetic studies (both cladistic and molecular) have revealed that many groups are not monophyletic but para- or poly-phyletic, so further studies are required to resolve the fidelity of most groups. Recently, molecular studies suggested that 16 sarcoptoidean families may belong to 2 main lineages: 13 families identified in a 'sarcoptid' complex (Atopomelidae, Audycoptidae, Chirodiscidae, Chirorhynchobiidae, Galagalgidae, Gastronyssidae, Lemurnyssidae, Listrophoridae, Listropsoralgidae, Myocoptidae, Pneumocoptidae, Rhyncoptidae, Sarcoptidae), and 3 families in a 'psoroptid' complex (Lobalgidae, Paracoroptidae, Psoroptidae). Nevertheless, most families can still be categorized into 4 broad 'morphoecotypes': namely; fur mites (Atopomelidae, Chirodiscidae, Listrophoridae, Lobalgidae), skin mites (Chirorhynchobiidae, Myocoptidae, Psoroptidae), skin-burrowing and follicle mites (Rhyncoptidae, Sarcoptidae), and respiratory mites (Gastronyssidae, Lemurnyssidae, Pneumocoptidae). The family Listrophoridae comprises small elongate mites with palps and legs modified for grasping hairs in a wide variety of fur-bearing mammalian hosts. Some 26 genera have been recognized: namely, *Aeromychirus*, *Afrolistrophorus*, *Asiochirus*, *Carnilistrophorus*, *Centetesia*, *Chirodiscoides, Cryptocoptes*, *Echinosorella*, *Eurychiroides*, *Geomylichus*, *Hemigalichus*, *Indochirus*, *Lemuroecius*, *Lemuroptes*, *Leporacarus*, *Listrophorus*, *Lynxacarus*, *Metalistrophorus*, *Olistrophorus*, *Prolistrophorus*, *Pteromychirus*, *Quasilistrophorus*, *Schizocarpus*, *Sclerolistrophorus*, *Spalacarus*, and *Tenrecobia*. The genus *Chirodiscoides* (syn. *Campylochirus*) contains long narrow mites with triangular 'heads' (gnathosoma) and dorsoventrally flattened 'bodies' (idiosoma). They have 4 pairs of legs (2 pairs directed anteriorly, 2 pairs posteriorly), all legs bearing bell-like pulvilli on very short stalks. A total of 12 species have been described from a small range of rodents and marsupials from South America, although the species *C. caviae* is common on guinea pigs around the world, sometimes causing pruritic dermatitis and alopecia.

***Chirodiscoides* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
C. ascuamatus (= *asquamatus*?)	Didelphimorphia: didelphid (Linnaeus's mouse opossum)			South America
C. bolivianus	Rodentia: echimyid (Tome's spiny rat)			South America
C. caviae (syn. *Campylochirus caviae, Indochirus utkalensis*) (guinea pig fur mite)	Rodentia: caviid (guinea pig, Brazilian guinea pig, southern mountain cavy, common yellow-toothed cavy)	skin	irritation, dermatitis, pruritus, scales, crusts, alopecia	worldwide, esp. Asia, Europe
C. cercomys	Rodentia: echimyid (common punare)			South America
C. didelphicola	Didelphimorphia: didelphid (white-eared opossum); Rodentia: echimyid (Atlantic bamboo rat)			South America
C. echimys	Rodentia: echimyid (giant Atlantic tree rat)			South America
C. euryzygomatomys	Rodentia: echimyid (Fischer's guiara)			South America
C. galeae	Rodentia: caviid (Spix's yellow-toothed cavy)			South America
C. inglesae	Carnivora: canid (pampas fox); Rodentia: echimyid (Guyenne spiny rat)			South America
C. interruptus	Rodentia: echimyid (Guyenne spiny rat); Didelphimorphia: didelphid (bare-tailed woolly opossum)			South America
C. longipilis	Rodentia: echimyid (Atlantic bamboo rat)			South America
C. proechimys	Rodentia: echimyid (Guyenne spiny rat, short-tailed spiny rat, Cuvier's spiny rat, Napo spiny rat)			South America

Parasite morphology: *Chirodiscoides* spp. form 4 different morphological types of developmental stages: eggs; larvae; nymphs (2 instars); and adult mites (males and females). The eggs are thin-shelled prolate-ellipsoidal stages measuring 250-262 x 60-81 µm that are glued at one pole to host hair shafts by mucilaginous material such that egg is directed towards the hair tip. Larvae are oval stages that are ventrally flattened but dorsally arched, ranging in size from 214-343 x 81-114 µm. They have small triangular heads and rounded posterior ends with distinct tail processes. The body has a small lightly-reticulated pro-dorsal plate, a ventral sternal plate with unique strong tangential striations arranged in 4 quartile fields, and the rest of the integument bears small denticles. Larvae have 3 pairs of ventral legs, 2 anterior pairs of small legs projecting forwards and a third pair of longer legs arising from the midbody and projecting backwards. Two nymphal stages have been described: protonymphs measuring 288-455 x 119-171 µm; and deutonymphs (sometimes called tritonymphs) measuring 371-498 x 136-176 µm. All nymphs have rounded pro-dorsal plates

while the rest of the dorsum is ornamented with large denticles anteriorly grading into smaller ones posteriorly, but with the midline having a ridge of paired intersecting denticles. They all have ventral sternal plates with the characteristic tangential striations, but none have genital openings. Nymphs have 4 pairs of legs, having developed another pair of long well-developed hindlimbs. Female nymphs have pocket-like structures in the posterior coxal epimera of the second pair of legs, and male nymphs have wrinkled tail-like processes. Adult mites have long narrow dorso-ventrally flattened bodies ranging in length from 340-530 μm. They have 2 main tagma: a small anterior gnathosoma (head) and a large posterior idiosoma (body). The gnathosoma is well developed and distinctly triangular, with a dorsal gnathosomal plate. The anterior mouthparts are modified for grasping hairs and consist of a pair of 3-segmented chelicerae terminating in claw-like chelae, and a flanking pair of 2-segmented palps without terminal claws (apoteles) but with short anterior solenidia (sensory hairs) and cup-like membranous flaps. The alimentary tract consists of a ventral mouth (with an unbarbed hypostome), a short tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with caeca), and short tubular hindgut (with excretory Malpighian tubules) opening to a posterior anus. The cuticular covering of the idiosoma has numerous striations running transversely or tangentially across the body. Adult mites have 3 dorsal plates (quadrate pro-dorsal, trapezoidal mid-dorsal and elongate post-dorsal) which are sclerotized and ornamented with polygonal reticulum. The post-dorsal plate covers the entire hysterosoma in males but only the anterior half in females. Ventrally, adults have retained the unique propodosomal sternal shield which has strong tangential striations located in 4 quartile fields. Like other Astigmata, respiratory stigmata are absent, but tracheal tubes have sometimes been observed under the cuticle. The ventral idiosoma is the point of attachment for 4 pairs of long slender legs modified for grasping hairs; 2 small stout pairs directed anteriorly, and 2 longer slender pairs directed posteriorly. The legs consist of 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus) except for the third pair of legs in males and the fourth pair in females which have 5 segments (fused tibio-tarsi). The coxae are fused to the body wall with the first 2 pairs of legs having anterior coxal ridges used for grasping hairs. The tibia and tarsi have modified club-like structures also used for grasping hairs. All tarsi have setae and an apical ambulacrum (sucker-like caruncle) with a short pretarsal stalk supporting a bell-like pulvillus. Adult mites display considerable sexual dimorphism, with males being smaller than females (340-400 x 130-148 μm cf. 480-529 x 140-174 μm). The posterior margin of male mites has pairs of small and large adanal suckers with caudal setae, as well as a distinctive semicircular flap supported by bifid sclerites (inferior ventral and superior sub-dorsal rods). Males have 2 testes with tubular vas deferens leading to the ejaculatory duct and long sheathed aedeagus (penis) opening through a genital pore located between the coxae of the hindlegs. Males also have a conspicuous transverse arch joining the coxae of the last pair of legs, which are notably longer and hook-shaped. Most adult males are found attached to the backs of female nymphs, with their posterior legs hooked into the pocket-like structures on the second epimera on the sternum of the females. These joined pairs are not in copula, but the males are simply carried around and are readily available for mating with newly emergent females. Adult female mites have rounded posterior ends with a terminal anus surrounded by para-anal plates. Females have 2 ovaries with tubular oviducts leading to a globular uterus (with shell gland) and vagina (with accessory organs (bursa copulatrix, spermathecae) for sperm reception and storage). The genital opening is slit-like or V-shaped and located on the ventral midbody between the coxae of the third pair of legs.

Site of infection: These mites are non-burrowing surface dwellers that live on hairs rather than the skin of a variety of fur-bearing mammals. A total of 12 species have been described from several rodents (caviids, echimyids), marsupials (didelphids) and one carnivore (pampas fox) from South America, while the species *C. caviae* is common on guinea pigs around the world.

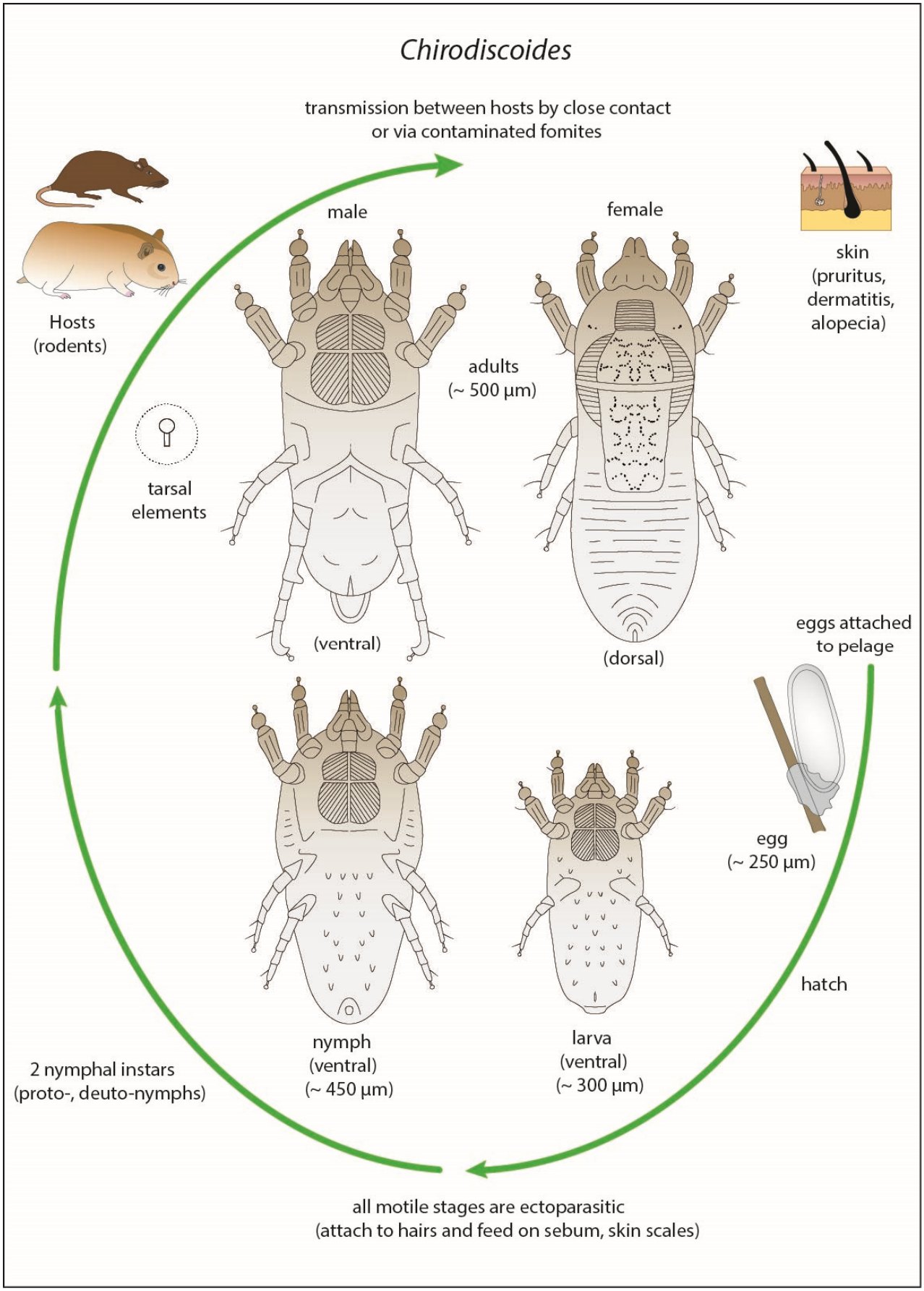
Pathogenesis: Most infestations remain asymptomatic or subclinical, even when mites are present in large numbers. However, heavy infestations have occasionally been associated with mild disease (pruritic dermatitis and patchy alopecia) in some individuals, possibly aggravated by allergic/hypersensitivity reactions to mite antigens (saliva/faeces). All motile mite stages are thought to feed on hair scales, cellular debris and possibly tissue fluid at the bases of hair shafts. Infestations may cause pruritus, rough coat and alopecia, while the underlying skin may be unaffected or show mild inflammation with erythema and some scaling, but rarely overt lesions with crusting and scabbing. Animals may experience some irritation and resort to grooming behaviours (biting, scratching, rubbing) exacerbating hair loss (fragmented alopecia), particularly along the posterior trunk, flanks and around the perineum. Infestations appear to be heavier on sick and debilitated animals unable to groom properly. Small scale outbreaks have been reported in guinea pigs and rats raised in laboratory animal colonies, pet stores and private households.

Developmental cycle and mode of transmission: *Chirodiscoides* spp. exhibit gradual/incomplete (hemimetabolous) metamorphosis whereby eggs hatch larvae that moult through nymphs to form adults. The entire development cycle may take place on the same individual host, and transmission generally occurs through direct host-to-host contact or via contaminated fomites. Few details are known about the duration of the different developmental stages, nor the fecundity and longevity of adult mites. Gravid females glue eggs individually to hair shafts where they hatch in several days releasing hexapod larvae. The larvae attach to hairs using their modified mouthparts and forelimbs and move along and between hairs using their remaining pairs of legs. They moult after several days to form octopod nymphs, the first-stage nymphs (protonymphs) subsequently moulting to second-stage nymphs (deutonymphs, sometimes called tritonymphs) after several days. In turn, the nymphs moult to form adult male and female mites. Adult male mites are most frequently found paired with female nymphs, riding on their backs using their hooked hindlimbs. The paired mites are not copulating as the nymphs lack genital orifices. It seems that the males are being carried about while waiting for the female nymphs to moult to adults so that copulation may occur. Following mating, fertilized females then begin producing eggs one at a time and ovipositing them on hair shafts. The whole life cycle may be completed in as little as 14 days. Studies on

laboratory animal colonies have shown that transmission may occur by direct physical contact between animals (especially in crowded cages, in animals huddling together for security and/or warmth, from mothers nursing their young, and even by contact with infested carcases) as well as by contact with cage materials (especially litter and bedding) contaminated with mites displaced from hosts (off-host survival times are not known).

Differential diagnosis: Most infestations are subclinical and go unnoticed until mites are observed moving in the fur. Careful visual examination may reveal the presence of paired mites (adult males carried on female nymphs) and some animal handlers report that they can feel bumpy coats when stroking the fur due to the presence of mites and eggs attached to hairs. Many infestations are first detected post-mortem when mites are observed leaving the cooling carcase. When clinical signs are apparent (pruritus, inflammation, alopecia), other aetiological agents need to be discounted, including other ectoparasites (mites, lice and fleas) and other dermatological conditions (infections and allergies). Definitive diagnosis is made by the direct detection and microscopic identification of mites in samples collected by vacuum aspiration, hair plucks (trichograms), sticky tape impressions, brushing or combing fur, and sometimes simply by massage animals over paper and examining what drops off. The examination of skin scrapings is not appropriate for these surface-dwelling fur mites which do not borrow or live on the skin.

Treatment and control: Infestations in laboratory animals have been successfully managed by treatment with chemical acaricides, either as topical (dusts, sprays, baths) or systemic (oral, injectable, spot-on) applications, including carbamates (carbaryl), organophosphates (malathion), pyrethroids (pyrethrin), neonicotinoids (imidacloprid) and macrocyclic lactones (ivermectin, selamectin, moxidectin). Many chemicals are not strongly ovicidal so repeated or protracted treatments are required to combat newly emergent stages. Animals may also benefit by pre-treatment bathing in medicated shampoos to remove cutaneous debris, or by trimming or shaving infested areas. A variety of preventive measures have been adopted to curtail transmission cycles, including health surveillance (regular monitoring and treatment with isolation or quarantine), improved sanitation (cleaning cages and other animal holding facilities, periodically replacing litter and bedding), environmental decontamination (using insecticidal/acaricidal dusts or sprays with long-lasting residual activity) and maintaining biosecurity (not breeching physical or procedural barriers in animal colonies, avoiding cross-cohort contamination, and excluding wildlife and vermin).


Chirodiscoides
transmission between hosts by close contact
or via contaminated fomites
Hosts
(rodents)
male
female
skin
(pruritus,
dermatitis,
alopecia)
adults
(~ 500 µm)
tarsal
elements
(ventral)
(dorsal)
eggs attached
to pelage
egg
(~ 250 µm)
hatch
nymph
(ventral)
(~ 450 µm)
larva
(ventral)
(~ 300 µm)
2 nymphal instars
(proto-, deuto-nymphs)
all motile stages are ectoparasitic
(attach to hairs and feed on sebum, skin scales)



Chirodiscoides adult



Chirodiscoides eggs

Myocoptes
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Listrophorid mites have a distinct dorsal shield and their legs are modified for grasping hairs of fur-bearing mammals. Infestations by *Myocoptes musculinus* may cause dermatitis (myocoptic mange) in wild and laboratory mice.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Sarcoptoidea (mites associated with mammals, ecto- or endo-parasitic)
Family: Myocoptidae (parasitic on rodents, some legs adapted as pincers)
Genus: *Myocoptes* (parasitic on skin/hair of mice)
Species: *M. musculinus* causes myocoptic mange in mice

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

Early classification schemes identified different assemblages principally on the basis of host and site specificity; including bird-associated feather mites (e.g. Analgoidea); bird-associated skin mites (e.g. Knemidokoptidae), mammal-associated fur mites (e.g. Listrophoridae), mammal-associated skin mites (e.g. Psoroptidae); and mammal-associated skin-burrowing mites (e.g. Sarcoptoidea). However, phylogenetic studies (both cladistic and molecular) have revealed that many groups are not monophyletic but para- or poly-phyletic, so further studies are required to resolve the fidelity of most groups. Recently, molecular studies suggested that 16 sarcoptoidean families may belong to 2 main lineages: 13 families identified in a 'sarcoptid' complex (Atopomelidae, Audycoptidae, Chirodiscidae, Chirorhynchobiidae, Galagalgidae, Gastronyssidae, Lemurnyssidae, Listrophoridae, Listropsoralgidae, Myocoptidae, Pneumocoptidae, Rhyncoptidae, Sarcoptidae), and 3 families in a 'psoroptid' complex (Lobalgidae, Paracoroptidae, Psoroptidae). Nevertheless, most families can still be categorized into 4 broad 'morphoecotypes': namely; fur mites (Atopomelidae, Chirodiscidae, Listrophoridae, Lobalgidae), skin mites (Chirorhynchobiidae, Myocoptidae, Psoroptidae), skin-burrowing and follicle mites (Rhyncoptidae, Sarcoptidae), and respiratory mites (Gastronyssidae, Lemurnyssidae, Pneumocoptidae). The family Myocoptidae comprises small elongate mites whose palps and legs are modified to grasp hairs in the fur of their hosts. Ten 10 genera have been recognized as ectoparasites on small mammals; namely, *Apocalypsis, Criniscansor*, *Dromicioptes, Dromiciocoptes*, *Gliricoptes*, *Histiophorus, Myocoptes*, *Sciurocoptes*, *Trichobius,* and *Trichoecius*. Members of the genus *Myocoptes* have oval bodies with 2 anterior pairs of legs bearing short-stalked pretarsi with flap-like heart-shaped pulvilli, and 2 posterior pairs of legs equipped with large hook-like pincers for clasping hairs. Some 34 species have been described from rodents (murids, cricetids, nesomyids), 11 species have been assigned to the subgenus *M.* (*Myocoptes*), 3 species to the subgenus *M.* (*Comyoptes*), while the remaining species are unplaced. The species *M. musculinus* causes myocoptic mange in mice, characterized by pruritic dermatitis and alopecia.

***Myocoptes* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
Subgenus *M.* (*Myocoptes*)				
M. M. dendromus	Rodentia: nesomyid (gray climbing mouse, Brants' climbing mouse, chesnut climbing mouse)			Africa
M. M. gerbillicola	Rodentia: murid (Kemp's gerbil, Congo gerbil)			Africa
M. M. grammomys	Rodentia: murid (woodland thicket rat, common rufous-nosed rat)			Africa
M. M. hybomys	Rodentia: murid (Peter's striped mouse)			Africa
M. M. ictonyx	Carnivora: mustelid (striped polecat)			Africa
M. M. kivuensis	Rodentia: murid (African marsh rat), geomyid (Botta's pocket gopher)			Africa
M. M. malacomys	Rodentia: murid (Edward's swamp rat, big-eared swamp rat)			Africa
M. M. nudus	Rodentia: murid (yellow-spotted brush-furred rat, Nyika rock rat)			Africa
M. M. spinulatus	Rodentia: nesomyid (gray climbing mouse, Brants's climbing mouse)			Africa
M. M. hoogstraali	Rodentia: murid (lesser Egyptian gerbil)			Egypt
M. M. neotomae	Rodentia: cricetid (eastern woodrat)			North America
Subgenus *M.* (*Comyoptes*)				
M. C. nesokia	Rodentia: murid (short-tailed bandicoot rat)			Asia
M. C. striatus	Rodentia: nesomyid (South African pouched mouse, Pousargues's African fat mouse)			Africa
M. C. verrucosus	Rodentia: murid (gerbil)			Africa
Unplaced				
M. brevipes	Rodentia: cricetid (Gunther's vole)			Europe
M. canadensis	Rodentia: cricetid (lemming)			North America
M. glareoli	Rodentia: cricetid (bank vole)			Europe
M. glirinus	Rodentia: glirid (European edible dormouse)			Europe
M. hintoni	Rodentia: sciurid (red squirrel)			Europe
M. jamesoni	Rodentia: cricetid (eastern meadow vole)			North America
M. japonensis (incl. subspp. *japonensis*, *canadensis*)	Rodentia: cricetid (grey red-backed vole, southern red-backed vole, Smith's vole, bank vole, common vole, short-tailed field vole, European water vole, European snow vole, European pine vole, tatra pine vole, eastern meadow vole, tundra vole, singing vole, northern collared lemming), sciurid (groundhog)			Eurasia, North America

M. kalrai	Rodentia: muris (lesser Egyptian gerbil)			Egypt
M. lepidotus	Rodentia: murid (red rock rat)			Africa
M. lophuromys	Rodentia: murid (Woosnam's brush-furred rat)			Africa
M. meriones	Rodentia: murid (Tamarisk jird, Libyan jird)			Asia
M. musculinus	Rodentia: murid (house mouse, wood mouse, yellow-necked mouse, spinifex hopping mouse), cricetid (white-footed mouse), caviid (guinea pig); Dasyuromorphia: dasyurid (tiger quoll)	fur	myocoptic mange, pruritus, inflammation, scales, crusts, alopecia	worldwide
M. ondatrae	Rodentia: cricetid (muskrat)			Europe
M. persicus	Rodentia: cricetid (grey dwarf hamster)			Middle-East
M. pitymys	Rodentia: cricetid (woodland vole)			North America
M. queenslandicus	Rodentia: murid (black-footed tree rat)			Australia
M. rattus	Rodentia: murid (brown rat)			Africa
M. romboutsi	Rodentia: murid (house mouse)			Europe
M. squamosus	Rodentia: cricetid (tundra vole, eastern meadow vole)			Europe, North America
M. tenax	Rodentia: cricetid (short-tailed field vole)			Europe

Parasite morphology: *Myocoptes* spp. produce 4 different types of morphological stages during their developmental cycles: eggs; larvae; nymphs (2 instars); and adult mites. The eggs are pale opaque prolate ellipsoidal stages measuring around 200 x 80 μm and are glued onto hairs by one pole such that they lay along the hair shaft. Larvae are squat oval stages measuring from 180-280 μm in length. They are hexapod, bearing 3 pairs of ventral legs, the first 2 anterior pairs ending in flap-like pulvilli and the third midbody pair terminating in pincer-like hooks for grasping hairs. Nymphs are slightly larger measuring from 250-350 μm in length and 2 sequential instars are thought to occur (protonymphs followed by deutonymphs, sometimes called tritonymphs). All nymphs are octopod, bearing 4 pairs of legs, having developed another pair posterior to the ventral midbody which end in conspicuous pincer-like hooks. Adult mites have irregular oval bodies that are elongated ventrally and dorsoventrally flattened. They range in size from 160-380 x 93-135 μm and have chitinized cuticles that are lightly tanned. Adults have 2 main tagma: a small anterior gnathosoma (head); and a large posterior idiosoma (body). The gnathosoma is triangulate with a truncated tip bearing well-developed mouthparts modified for grasping hairs. The mouthparts consist of a pair of long stylet-like chelicerae with terminal chelae flanked by small sensory palps without claws (apoteles). The mouth has a dorsal rostrum and a ventral unbarbed hypostome. The alimentary tract consists of a tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with caeca) and a short tubular hindgut (with excretory Malpighian tubules) terminating in a postero-ventral anus. The idiosoma has a distinct dorsal plate with numerous scale-like striations while the ventral surface is ornamented with many small spine-like denticles. The body has 4 distinct pairs of dorsal setae and a pair of long caudal setae, but lacks respiratory stigmata. The ventral idiosoma gives rise to 4 pairs of stout legs which are heavily chitinized and often darker brown in colour. Most legs have 6 segments (coxa, trochanter, femur, genu, tibia, and tarsus), except for the fourth pair in males which have 5 segments (fused tibia-tarsi). All legs have coxae fused to anteroventral body wall and the 2 anterior pairs of legs end in short-stalked pretarsi with large flap-like (heart-shaped) pulvilli, while the 2 posterior pairs are equipped with large hook-like pincers for clasping hairs (the tibia and tarsi fold against the inner striated surface of the genu and femur). Adult mites display considerable sexual dimorphism, with males being smaller than females (160-210 x 93-135 cf. 265-380 x 110-130 μm), their bodies having less pronounced striations, their posterior margins being bilobed, and their fourth pair of legs enlarged to grasp females during copulation. Adult males have 2 testes with tubular vas deferens leading to an ejaculatory duct and long sheathed aedeagus (penis) opening to a deltoid ventral genital opening. Adult females have 2 ovaries with tubular oviducts leading to a globular uterus (with shell glands) and vagina (with accessory organs for sperm reception (bursa copulatrix) and storage (spermathecae)) opening to a ventral slit-like genital opening.

Site of infection: These mites are surface-dwellers and live in the pelage (fur) mostly of rodents. Some 34 species have been described from 6 rodent families, including caviids (guinea pigs), cricetids (voles, woodrats, hamsters, lemmings, muskrats, mice), geomyids (pocket gophers), glirids (dormice), murids (rats, gerbils, mice, jirds), nesomyids (climbing mice, pouched mice) and sciurids (squirrels, groundhogs), as well as from dasyurid marsupials (tiger quolls) and mustelid carnivores (striped polecats). Mites are frequently found on hair shafts, and sometimes on the skin surface, particularly over the flanks and rumps of their hosts, but sometimes extending over the entire dorsum in heavy infestations.

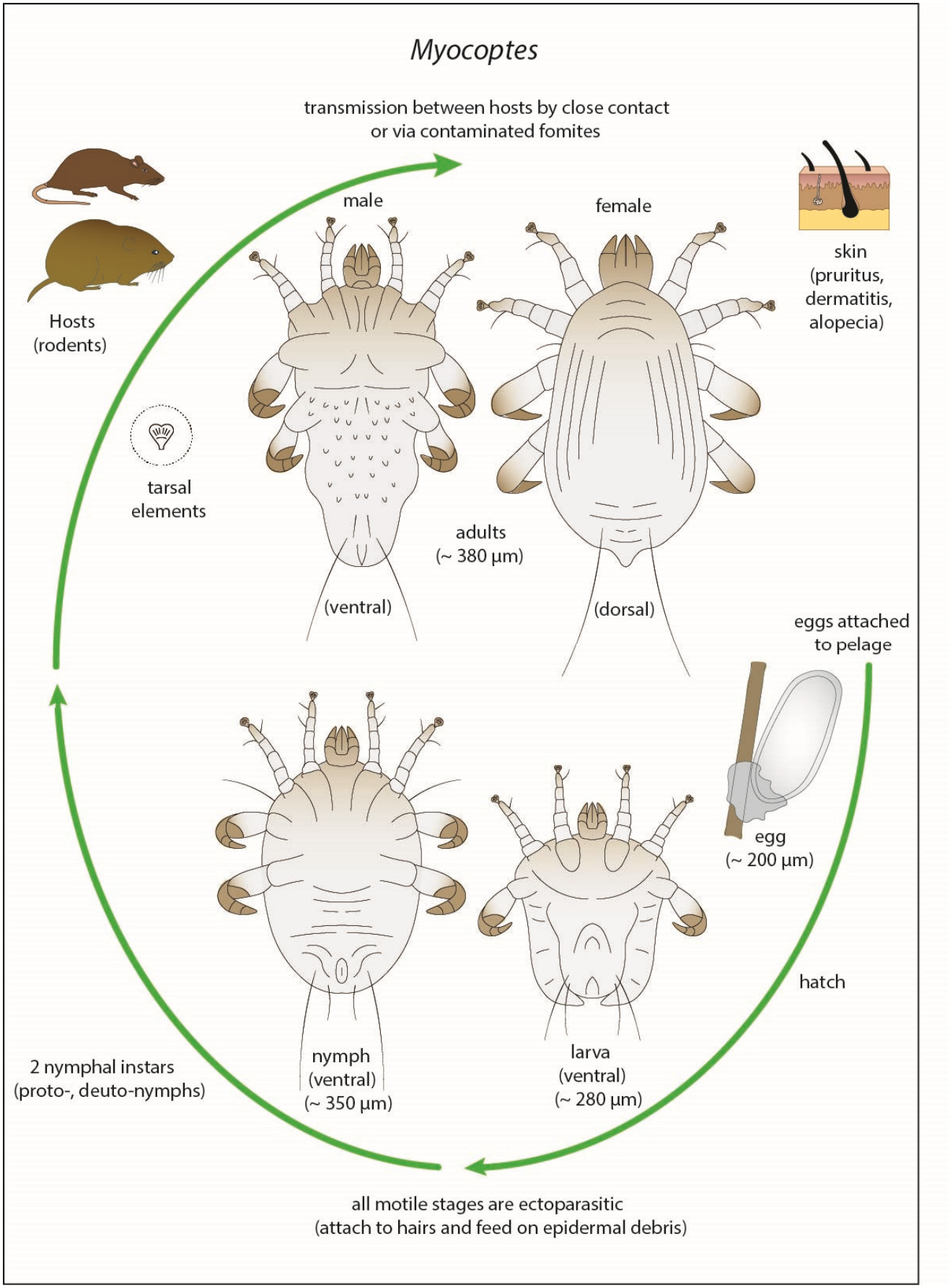
Pathogenesis: Infestations can be quite widespread and abundant in rodent hosts, but are often benign and of little clinical significance. Heavy infestations, however, can cause pruritic dermatitis (myocoptic mange), particularly in stressed, ill or immuno-compromised animals living in confined crowded situations (including laboratory colonies). These fur mites clasp to hairs and do not burrow into the skin. They feed on superficial epidermal material (hair/skin scales, cellular debris) at base of hairs, and their presence has been found to be less immunologically sensitizing than other mite infestations (such as *Myobia* spp.). Infestations may cause inflammation, erythema and pruritus leading to biting-stress, scratching and alopecia. Signs may remain mild, including ruffled fur and patchy hair loss, or become more severe, with generalized alopecia, ulcerations and self-mutilation. In some mouse

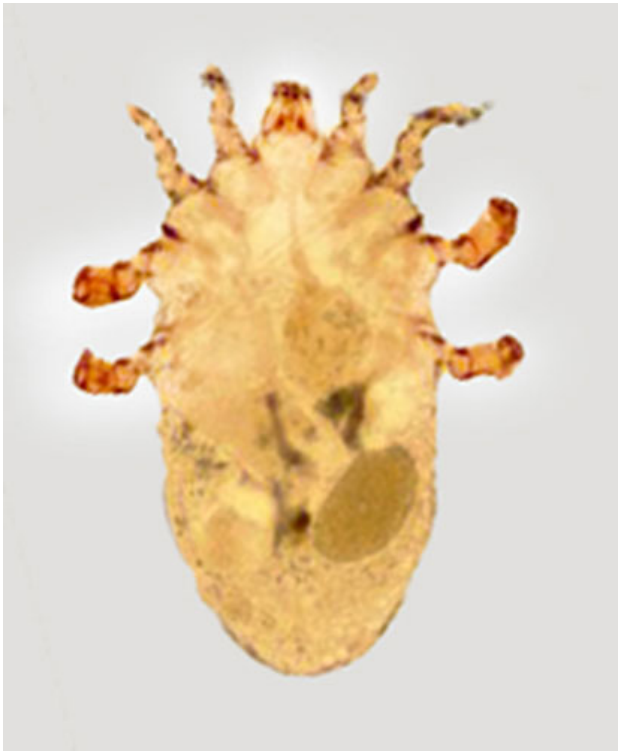
strains (especially those genetically manipulated to be immunodeficient), infestations may progress to cause epidermal excoriation, ulcerative dermatitis, hypersensitivity dermatitis and pyoderma. Infestations may occur in rodents of all ages, and neonates as young as 5 days old may be infested as soon as they grow fur.

Developmental cycle and mode of transmission: *Myocoptes* spp. undergo gradual/incomplete (hemimetabolous) metamorphosis whereby eggs hatch larvae that moult through nymphal stages to form adult mites. All developmental stages may occur on the same individual host and transmission occurs through direct contact with infested hosts or infested fomites. Gravid female mites glue their eggs one at a time onto hair shafts (more distally on the hair than those deposited by Myobia spp.). The eggs hatch within 5 days releasing hexapod larvae which attach to hairs and feed on epidermal debris for several days before moulting to first-stage nymphs (protonymphs). These stages attach to hairs and feed for a short period before moulting to second-stage nymphs (deutonymphs, sometimes called tritonymphs). These final nymphal stages attach to hairs and feed for several days before undergoing their final moult to form adult mites (either males or females). Adult stages mate on their hosts and fertilized female mites begin oviposition. The whole life-cycle may be completed in as little as 14 days, but little is known about the longevity or fecundity of mites. Adult stages have been shown to abandon dead rodents as the carcase cools, but their survival characteristics off-host are unknown. Transmission is through direct animal to animal contact (especially in crowded cages/nests, when animals huddle together for security or warmth, during maternal suckling of young, or even contact with infested carcases) or via contact with infested fomites (such as cages, litter, bedding containing viable mites displaced from hosts).

Differential diagnosis: The diagnosis of infestations on rodents is difficult due to the asymptomatic nature of most infestations, the small size of the mites and their cryptic locations within pelts. Even when clinical signs of mange become apparent, they are nonspecific (dermatitis, alopecia) and may be attributed to many potential causes (such as other ectoparasites, bacterial and fungal infections, and even allergies and hypersensitivities). Infestations are diagnosed by the direct microscopic detection of mites and mite eggs on hosts or in samples collected by vacuum aspiration, hair plucks (trichograms), or by sticky tape impressions (applied against the grain of fur). Mites can be readily identified microscopically by their unique morphological characteristics. Skin scrapings have sometimes been used but they are not ideal for detecting non-burrowing mites living on hairs on the skin surface. Infestations can be detected at post-mortem by placing carcases or pelts in bags or dishes to collect mites as they leave cooling samples. More recently, molecular biological techniques have been used to detect infestations in faecal samples, skin swabs or cage swabs by the polymerase chain reaction (PCR) amplification of specific nuclear (18S and 28S ribosomal RNA) or mitochondrial (cytochrome b, cytochrome c oxidase subunit 2, ATP synthase F0 subunit 6) gene sequences.

Treatment and control: Infestations in laboratory animal colonies and pet stores have been successfully treated with topical acaricides (dusts, sprays, baths) or systemic acaricides (oral, injectable, pour-ons), including arsenic and sulphur mixtures, carbamates (carbaryl), organochlorines (dieldrin, chlorfenethol, benzene hexachloride), organophosphates (chlorpyrifos, dichlorvos) and macrocyclic lactones (ivermectin, selamectin, eprinomectin). Repeated treatments are often required as most chemicals are not strongly ovicidal and will not kill eggs. Various preventive measures have been used in animal production and holding facilities to contain the spread of mites, including regular health surveillance (monitoring to presage treatment, isolation and quarantine), enhanced sanitation (cleaning cages/pens, regularly changing litter/bedding, treating animal houses with acaricidal sprays/dusts with long residual activity) and promoting biosecurity (maintaining barrier containment in specific-pathogen-free colonies, excluding wildlife/vermin).


Myocoptes
transmission between hosts by close contact
or via contaminated fomites
Hosts
(rodents)
male
female
skin
(pruritus,
dermatitis,
alopecia)
tarsal
elements
adults
(~ 380 µm)
(ventral)
(dorsal)
eggs attached
to pelage
egg
(~ 200 µm)
hatch
2 nymphal instars
(proto-, deuto-nymphs)
nymph
(ventral)
(~ 350 µm)
larva
(ventral)
(~ 280 µm)
all motile stages are ectoparasitic
(attach to hairs and feed on epidermal debris)



Myocoptes adult



Myocoptes egg

Knemidocoptes
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Knemidocoptids are burrowing scaly leg and face mites of birds with round bodies, no dorsal spines and short stubby legs. Infestations by *Knemidocoptes* spp. cause dermatitis characterized by feather depluming or scaly leg lesions in domestic poultry.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Acaroidea (stout body with transverse groove, small gnathosoma, chelicerae chelate)
Family: Knemidocoptidae (burrowing scaly leg and face mites, round body, no dorsal spines, short stubby legs)
Genus: *Knemidocoptes* (parasitic on skin of birds)
Species: various species cause depluming itch or scaly leg in domestic poultry

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph- feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidocoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

The superfamily Acaroidea contains a large number of free-living mites that feed on mould and decomposing organic waste (some being notorious pests of stored foods such as grains, cheese, fruits, straw) as well as some nidicolous species inhabiting the nests of vertebrates (mammals and birds) and invertebrates (termites, beetles, bees, wasps, ants). They have small stout white-fawn bodies distinctly divided by transverse grooves into a proterosoma and hysterosoma, small heads (gnathosoma), chelate chelicerae, 4 pairs of legs conspicuously divided into 2 forward-facing pairs and 2 rear-facing pairs, and distinctive chaetotaxy (patterns of setae). Some 23 families have been recognized (Acaridae, Alloptidae, Analgidae, Apionacaridae, Avenzoariidae, Dermationidae, Dermoglyphidae, Epidermoptidae, Gaudoglyphidae, Knemidocoptidae, Kytoditidae, Laminosioptidae, Lardoglyphidae, Proctophyllodidae, Psoroptoididae, Pyroglyphidae, Sapracaridae, Saproglyphidae, Suidasiidae, Thysanocercidae, Trouessartiidae, Turbinoptidae, and Xolalgidae). The family Knemidocoptidae comprises burrowing mites with round bodies (lacking dorsal spines) and short stubby legs that invade the skin and/or feather shafts of birds. Six genera have been described (*Apocnemidocoptes*, *Evansacarus*, *Knemidocoptes*, *Micnemidocoptes*, *Neoknemidocoptes*, *Picicnemidocoptes*, *Procnemidocoptes*). Adult mites belonging to the genus *Knemidocoptes* (= *Knemidokoptes* = *Cnemidocoptes*) have rounded bodies with dorsal striations (broken or unbroken) forming simple or scale-like patterns, dorsal setae that are not spine-like, palps with 2 segments, legs without claws but with claw-like tarsi with terminal setae, posterior anus, and the female genital opening appears as a transverse slit paralleling body striations. Several species occur on domestic poultry and aviary birds in association with clinical disease. Leg and face mites cause local dermatitis (conditions known as scaly leg and scaly face), while feather mites may cause significant feather loss (depluming itch).

Parasite species	Hosts	Location	Clinical signs	Distribution
Knemidocoptes				
K. derooi	Apodiformes: apodid (African palm swift)	legs		Africa
K. fossor	Passeriformes: estrilidid (white-headed munia), fringillid (common chaffinch)			Asia
K. glaberrimus	Piciformes: picid (middle spotted woodpecker)			Europe
K. intermedius	Passeriformes: prunellid (rufous-breasted accentor), corvid (common raven, forest raven), artamid (pied currawong), menurid (superb lyrebird)	legs	scaly leg	Eurasia
K. jamaicensis	Passeriformes: alaudid (Eurasian skylark), corvid (common crow, American crow, rook), drepanid (Hawaii amakihi), emberizid (greater Antillean bullfinch, eastern towhee), estrilid (Gouldian finch), fringillid (canary, common chaffinch, European goldfinch, common linnet, common redpoll, twite, Eurasian siskin, brambling, red crossbill, Eurasian bullfinch, evening grosbeak), icterid (red-winged blackbird, Brewer's blackbird, brown-headed cowbird, common grackle), motacillid (pipit, Cape wagtail), mimid (gray catbird, northern mockingbird), parulid (prairie warbler, palm warbler, Cape May warbler, green-tailed warbler), parid (great tit, Eurasian blue tit, black-capped chickadee), passerellid (rufous-sided towhee), phaenicophilid (black-crowned palm tanager), sittid (white-breasted nuthatch), sturnid (common mynah), sylviid (sedge warbler), turdid (white-chinned thrush, golden thrush, spectacled thrush, American robin), tyrannid (Hispaniolan pewee, great crested flycatcher); Piciformes: picid (woodpecker),	legs	scaly leg	cosmopolitan
K. laevis (depluming mite)	Passeriformes: fringillid (common chaffinch), passerid (house sparrow); Columbiformes: columbid (pigeon)	skin (feather shafts)		Europe
K. mutans (scaly leg mite)	Galliformes: phasianid (chicken, turkey, pheasant, partridge); Anseriformes: anatid (Cape Barren goose); Strigiformes: strigid (great horned owl)	skin (esp. feet, legs)	raised leg scales, lameness, malformation, emaciation	worldwide
K. philomelae	Passeriformes: muscicapid (thrush nightingale)			Europe
K. pilae	Psittaciformes: psittaculid (budgerigar, yellow-	skin (esp.	scaly face,	cosmopolitan

	crowned parakeet, Alexandrine parakeet, ring-necked parakeets, scarlet-chested parrot, Princess parrot, yellow-fronted kakariki), psittacid (Amazon parrot, red-and-green macaw), cacatuid (sulphur-crested cockatoo, palm cockatoo, cockatiel); Passeriformes: fringillid (canary, European goldfinch)	beak, mouth, cere)	white proliferative encrustations, warty lesions, ribbon-like skin proliferations (tassel foot), overgrowth of toenails, affect ability to perch	
Neoknemidocoptes				
N. australiensis	Passeriformes: estrilidid (zebra finch)			Australia
N. columbicola	Columbiformes: columbid (pigeons)	skin (feathered areas)	pruritus, dermatitis	Eurasia
N. columbigallinae	Columbiformes: columbid (pigeon, croaking ground dove)	skin (feathered areas)	pruritus, dermatitis	South America
N. gallinae (syn. *Knemidokoptes*) (depluming itch mite)	Galliformes: phasianid (chicken, turkey, pheasant, partridge); Anseriformes: anatid (goose); Columbiformes: columbid (pigeon)	skin (feather shafts)	depluming itch, scales, papules, thickened skin	worldwide
N. philetairus	Passeriformes: ploceid (sociable weaver)			Africa

Parasite morphology: These bird mites produce 3 different types of morphological developmental stages: larvae, nymphs (2 instars) and adult mites (male and female). Females are ovoviviparous and give birth to larvae rather than laying eggs. The larvae have oval-round bodies measuring 200-300 μm in length and they have 3 pairs of short stubby legs, all terminating in stalked pulvilli. Two nymphal stages have been described: protonymphs followed by deutonymphs (sometimes called tritonymphs). They have rounded bodies measuring from 250-400 μm in length and they have 4 pairs of legs without pulvilli. Nymphs generally appear as smaller versions of adults but they lack genitalia. Adult mites have round-globose bodies ranging in size from 200-500 μm depending on species. They have 2 main tagma: a small anterior gnathosoma (head) and large posterior idiosoma (body). The gnathosoma is short (wider than long) and bears small mouthparts consisting of a pair of short 3-segmented chelicerae flanked by small 2-segmented palps. The mouth is directed ventrally and has a dorsal rostrum and an unbarbed hypostome. The alimentary tract appears to consist of a short tubular foregut (oesophagus, pharynx), saccular midgut (ventriculus with caeca), and a short hindgut (with excretory Malpighian tubules) opening through a terminal dorsal anus. The dorsal surface of the idiosoma is covered with fine cuticular striations that are broken mid-dorsally in a plate- or scale-like pattern (in *Knemidocoptes* spp.) or simple and unbroken, sometimes distally denticulate (in *Neoknemidocoptes* spp.). Adult mites have a distinctive anterior dorsal shield marked by a pair of longitudinal medial apodemes running to the base of mouthparts, and male mites also have a median posterior dorsal shield. The idiosoma also contains several dorsal setae that are not spine-like or triangular, and a pair of long caudal setae. Like other Astigmata, mites do not have respiratory stigmata but they breathe through their cuticles. The ventral idiosoma possesses 4 pairs of short stubby legs (longer in males than females), with 2 larger anterior pairs projecting forwards beyond the body margin, and 2 small posterior pairs projecting backwards but not beyond the body margin. The legs have 6 small segments (coxa, trochanter, femur, genu, tibia, and tarsus) with all coxae fused to the body wall. The first 2 pairs of legs have cuticular thickenings (apodemes or epimeres) that are widely separated, but join on males to form a midventral Y shape. The apodemes on the 2 posterior pairs of legs are long but not joined. All the legs on female mites end in short setae (suckers are absent), while all the legs on male mites have long setae and small cup-shaped suckers (pulvilli) on long stalks. Adult mites display additional sexual dimorphism, with males being smaller than females (200-250 x 145-160 cf. 340-500 x 280-380 μm). Males have 2 testes with tubular vas deferens leading to an ejaculatory duct and long sheathed aedeagus (penis) opening to a subterminal ventral genital pore. Female mites have 2 ovaries with tubular oviducts leading to a globular uterus and vulva which opens to a transverse slit-like genital pore.

Site of infection: These astigmatid mites are obligate ectoparasites that burrow into the superficial layers of the skin of birds. Most mite species exhibit high host specificity and tissue tropism, infesting particular bird species at different anatomical sites. Some 9 *Knemidocoptes* spp. have been described from 23 passerine families (alaudids, artamids, corvids, drepanids, emberizids, estrilids, fringillids, icterids, menurids, motacillids, mimids, muscicapids, parulids, parids, passerids, passerellids, phaenicophilids, prunellids, sittids, sturnids, sylviids, turdids, and tyrannids); and another 9 non-passerine families (anatids, apodids, columbids, phasianids, picids, psittaculids, psittacids, cacatuids, and strigids). Many species infest bare or lightly-feathered areas, especially around the beak, while others infest the lower legs, feet, and occasionally the combs and wattle. Another 5 *Neoknemidocoptes* spp. have been described from 2 passerine families (estrilidids, ploceids) and another 3 non-passerine families (anatids, columbids and phasianids, including domestic poultry). Mites generally infest the bases of feather shafts on the back, head, neck, wing and around the vent.

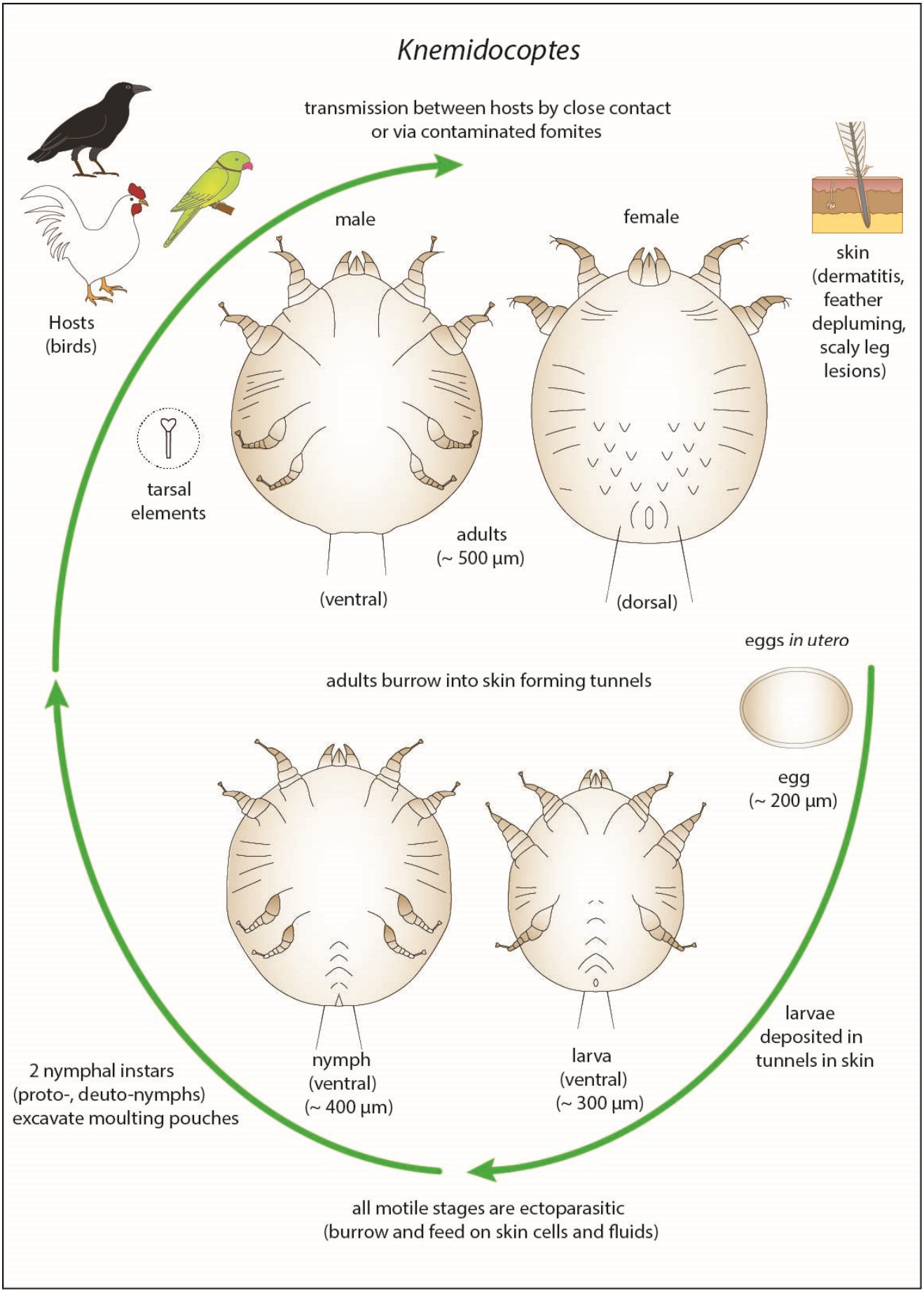
Pathogenesis: Many infestations remain subclinical, but some may cause severe deforming diseases, particularly when birds are stressed, immuno-compromised or otherwise genetically susceptible. Different mite species cause different diseases in birds which can be life-threatening by affecting their ability to perch, preen or feed. Mites burrow into the stratum corneum of the skin forming tunnels in which they live, feeding on skin cells and fluids. Infestations may cause 3 different types of knemidocoptic mange depending on which mite species are involved and which part of the body is attacked. Some species infest non-feathered areas on the legs and feet causing a scaly mange condition known as scaly leg, some species infest lightly-feathered areas around the beak causing scaly face, and some infest feathered areas over the body causing feather loss known as depluming itch. These conditions are not completely independent of each other, as several species may infest multiple sites causing 2 or more conditions (e.g. *K. mutans* and *K. pilae* may infest both the legs and faces of psittacine and galliform birds). Mites on the legs are found under skin scales where they cause local inflammation (dermatitis) with hyperplasia and hyperkeratosis resulting in white scaly encrustations (known as scaly leg). Sometimes, ribbon-like skin proliferations are observed (condition known as tassel foot in canaries and finches, often accompanied by overgrowth of the toenails affecting the ability of birds to perch). Persistent infestations lead to nodular thickening of the skin, elevation of the leg scales, lameness and deformity of feet, legs and claws, sometimes loss of digits. Birds become highly stressed, indulge in intensive self-grooming, stop feeding and waste away. Infestations in poultry sheds can lead to significant losses in production. Mites on the face also cause local dermatitis with hyperkeratosis leading to white proliferative encrustations (known as scaly face), particularly on the beak, cere (fleshy tissue above the beak), around the corners of the mouth and sometimes around the eyes. Infestations cause significant irritation and stress to birds and may affect their ability to feed and preen leading to emaciation and death. Mites infesting feathered areas of the body burrow into the bases of feather shafts, particularly on the back, head, neck, wings and around the vent. They cause inflammation with intense pruritus and the skin may become thickened, papular, scaly and wrinkled. The feathers break easily and are often pulled out by the bird when preening resulting in significant feather loss (depluming) with bare patches on the back which may spread to the wings, neck and head. Infestations by knemidocoptic mange mites are more common in birds with ground access and more prevalent in barn-yard and deep-litter farming systems than in caged production facilities.

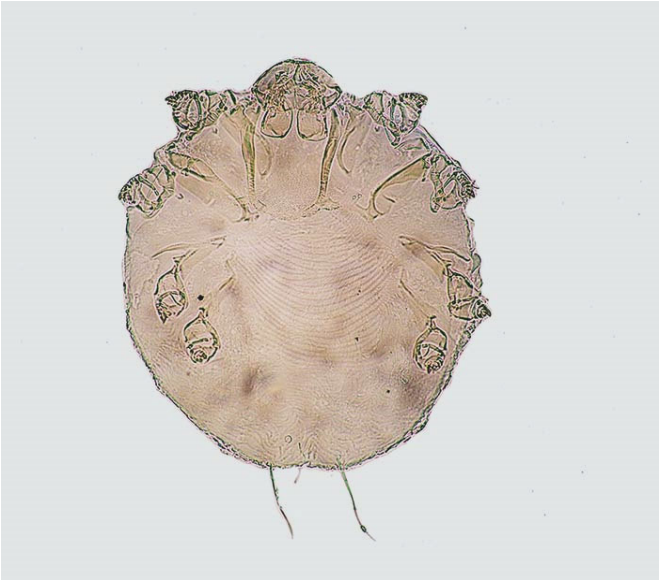
Developmental cycle and mode of transmission: Knemidocoptic mites undergo incomplete (hemimetabolous) metamorphosis involving a gradual transition in body plan via successive moults from larvae to nymphs to adults. These mites are unusual, however, in that females are ovoviviparous rather than oviparous and give birth to larvae rather than laying eggs. All life-cycle stages may occur on the same individual host, and transmission between hosts occurs by contact with infested birds or infested fomites. Adult mites live in burrows or tunnels in the superficial layers of the skin. Gravid females produce larvae in these tunnels which subsequently crawl to the skin surface, and then excavate their own shallow burrows (or moulting pockets) in the skin. After several days, the larvae moult to form first-stage nymphs (protonymphs), most of which emerge and form their own moulting pouches where they moult to second-stage nymphs (deutonymphs, sometimes called tritonymphs) after several days. The deutonymphs may remain in these burrows or emerge to dig their own moulting pouches. After several days, they undergo their final moult to adult mites. Male mites emerge and seek females either on the skin surface or in moulting burrows. After fertilization, females expand their moulting pouches or create new tunnels and begin producing larvae one at a time. Little is known about the longevity or fecundity of the mites, but their whole life-cycle may be completed in 17-21 days. Infestations are regarded to be highly contagious and most transmission is thought to occur by close and prolonged contact between birds (sometimes involving only one species in a mixed aviary). There have been some reports of mites being transmitted to unfeathered offspring in nests, and studies have shown that mites may survive for up to 4-9 days off hosts. This means that some transmission probably occurs via fomites (cages, nests, boxes, perches, litter, soil) contaminated with mites dislodged from hosts.

Differential diagnosis: Clinical infestations cause relatively specific clinical signs (scaly face, scaly leg, depluming itch) which can be used to facilitate provisional diagnosis. Diagnoses are confirmed by the direct detection and microscopic identification of mites in clinical samples, notably skin scrapings taken from affected areas, including the bases of feathers. Mites are generally found in burrows at the edges of skin lesions and amongst skin scales and crusts. Skin samples are best subjected to caustic digestion in potassium hydroxide solutions to break down host material leaving the mites untouched (their cuticles are impervious to digestion). Mites may also be detected in histological sections prepared from antemortem skin biopsies or post-mortem skin samples. More recently, molecular biological techniques have been used to detect and characterize mite species by polymerase chain reaction (PCR) amplification of nuclear (18S ribosomal DNA) and mitochondrial (cytochrome c oxidase subunit I) gene sequences.

Treatment and control: Birds have been successfully treated for scaly mange using a variety of conventional topical acaricides (dusts, sprays, showers, baths) and more contemporary systemic formulations (oral, injectable, spot-ons), including sulphur baths, mineral oil, carbamates (carbaryl), anilides (crotamiton), organochlorines (lindane), organophosphates (coumaphos, malathion) and macrocyclic lactones (ivermectin, selamectin, moxidectin). Repeated or prolonged treatments are often required, as the mites are somewhat protected by their cryptic locations in skin burrows. Careful attention should also be paid to any drug contra-indications as some chemicals are toxic to birds and may cause adverse reactions. Animals should also be given supportive therapies during treatment, particularly with antiseptics and antibiotics to combat secondary bacterial infections, especially when open lesions are present. A range of preventive measures have been used to control infestations, including regular health surveillance (careful monitoring to facilitate timely treatment, isolation and quarantine), good sanitary practices (cleaning and disinfection of aviaries,

cages, food and water dispensers, regularly changing litter and nesting materials, treating porous fomites with residual acaricides) and securing animal holding facilities (excluding wildlife and vermin using barriers, traps or baits).


Knemidocoptes
transmission between hosts by close contact
or via contaminated fomites
Hosts
(birds)
male
female
skin
(dermatitis,
feather
depluming,
scaly leg
lesions)
tarsal
elements
adults
(~ 500 µm)
(ventral)
(dorsal)
eggs in utero
adults burrow into skin forming tunnels
egg
(~ 200 µm)
larvae
deposited in
tunnels in skin
2 nymphal instars
(proto-, deuto-nymphs)
excavate moulting pouches
nymph
(ventral)
(~ 400 µm)
larva
(ventral)
(~ 300 µm)
all motile stages are ectoparasitic
(burrow and feed on skin cells and fluids)



Knemidocoptes adult



Knemidocoptes adult

Laminosioptes
(arachnid: mite)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Arachnids have chelicerate mouthparts, two tagmata (cephalothorax and abdomen), four pairs of legs and slit sensilla, but no antennae or wings. All species exhibit incomplete metamorphosis whereby eggs hatch larvae which moult to nymphs and then adults. Acarines comprise the ticks and mites which have sac-like bodies with inconspicuous segmentation and their mouthparts are confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata: ixodid ticks (Metastigmata), gamesid mites (Mesostigmata), trombidiform mites (Prostigmata) and sarcoptiform mites (Astigmata). Ectoparasitic mites inhabit the skin of mammals and birds, feeding on fluids and/or tissues. Most spend their entire lives on individual hosts, so horizontal transmission between hosts is primarily by physical contact. Sarcoptiform mites lack stigmata but respire directly through the cuticle. They have unique legs which lack claws but have terminal sucker-like modifications. They are ectoparasitic on a range of birds and mammals and may cause severe dermatitis (known as mange). Laminosioptids are small mites with smooth elongated bodies bearing few setae. Infestations by *Laminosioptes* spp. cause subcutaneous nodules in birds, sometimes resulting in condemnation of poultry carcases.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Chelicerata (chelicerate mouthparts, two tagmata, no antennae)
Class: Arachnida (spiders & allies, four pairs of legs, slit sensilla, incomplete metamorphosis)
Subclass: Acari (Acarina) (ticks and mites, segmentation inconspicuous, sac-like body, mouthparts on gnathosoma)
Superorder: Acariformes (diverse group of mites, without posterior stigmata)
Order: Astigmata [Sarcoptiformes] (mange mites, without stigmata, legs separated, with suckers)
Superfamily: Acaroidea (stout body with transverse groove, small gnathosoma, chelicerae chelate)
Family: Laminosioptidae (small mites, smooth elongated body, few setae, affect muscles of birds)
Genus: *Laminosioptes* (parasitic in subcutaneous tissues of birds)
Species: *L. cysticola* causes carcase condemnations in poultry

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. The chelicerates typically have appendages (chelicerae) in the form of pincers or fangs anterior to the mouthparts, 2 body parts (cephalothorax and abdomen), but no antennae or wings. Three classes are recognized: Arachnida (spiders and allies), Merostomata (horseshoe crabs) and Pycnogonida (sea spiders). Arachnids have 8 legs, slit sensilla and life-cycles involving incomplete metamorphosis whereby larvae and nymphs resemble adults. They are classified in 4 orders: Acari (acarines), Araneae (spiders), Opiliones (harvestmen) and Scorpiones (scorpions). The Acari comprises the ticks and mites which have saccular bodies and mouthparts confined to an anterior gnathosoma. Four major groups are recognized primarily on the location of their respiratory stigmata (called spiracles in insects): ixodid ticks (posterior Metastigmata), gamesid mites (middle Mesostigmata), trombidiform mites (anterior Prostigmata) and sarcoptiform mites (without stigmata = Astigmata).

Major parasitic families	Biodiversity	Hosts	Parasitic stages	Pathogenesis	Disease transmission
Superorder: Parasitiformes (ticks and some mites, with posterior stigmata)					
Order: Ixodida [Metastigmata] (ticks, macroscopic, stigmata posterior to legs) [3 families]					
Argasidae	5 genera,	birds, mammals	larvae, nymphs,	blood-sucking	viral, bacterial

(soft ticks)	193 species		adults		
Ixodidae (hard ticks)	14 genera, 705 species	birds, mammals	larvae, nymphs, adults	blood-sucking, paralysis	viral, bacterial, protozoal
Order: Mesostigmata [Gamasida] (gamesid mites, stigmata between 2nd & 4th legs) [100 families, 662 genera, 5,360 species]					
Macronyssidae (sucking mites)	26 genera, 127 species	birds, reptiles, mammals	nymphs, adults	blood-sucking	bacterial
Dermanyssidae (sucking mites)	5 genera, 37 species	birds, mammals	nymphs, adults	blood-sucking	viral, bacterial
Halarachnidae (lung/ear mites)	7 genera, 10 species	mammals	nymphs, adults	mucosal erosion	-
Raillietiidae (ear mites)	1 genus, 7 species	mammals	nymphs, adults	ear wax	-
Rhinonyssidae (nasal mites)	30 genera, 160 species	birds	nymphs, adults	inflammation	-
Varroidae (bee mites)	1 genus, 5 species	bees	nymphs, adults	haemolymph-feeding	viral
Superorder: Acariformes (diverse group of mites, without posterior stigmata) [351 families, 32,000 species]					
Order: Prostigmata [Trombidiformes, Actinedida] (sucking mites, stigmata on gnathosoma) [121 families, 17,000 species]					
Demodecidae (follicle mites)	7 genera, 65 species	mammals	larvae, nymphs, adults	inflammation	-
Cheyletidae (fur mites)	80 genera, 500 species	mammals (dogs, cats, rabbits), birds	larvae, nymphs, adults	pruritus	-
Myobiidae (fur mites)	46 genera, 185 species	mammals (rodents, bats, marsupials)	larvae, nymphs, adults	mange	-
Psorergatidae (itch mites)	3 genera, 77 species	mammals (rodents, artiodactyls)	larvae, nymphs, adults	mange	-
Trombiculidae (chigger mites)	71 genera, 3,000 species	mammals, birds	larvae	skin-feeding	bacterial
Order: Astigmata [Sarcoptiformes, Acaridida] (fur/feather/itch/dust mites, lacking stigmata) [230 families, 15,000 species]					
Sarcoptidae (itch mites)	3 genera, 42 spp./ssp.	mammals	larvae, nymphs, adults	scabies, mange	-
Psoroptidae (scab mites)	20 genera, species	mammals (carnivores, ungulates)	larvae, nymphs, adults	mange	-
Listrophoridae (fur mites)	20 genera, 170 species	mammals (esp. rodents)	larvae, nymphs, adults	mange	-
Myocoptidae (fur mites)	10 genera, 70 species	mammals (esp. rodents)	larvae, nymphs, adults	myocoptic mange	-
Cytoditidae (airsac/nasal mites)	2 genera, 12 species	birds	larvae, nymphs, adults	respiratory signs	-
Knemidokoptidae (burrowing mites)	7 genera, 16 species	birds	larvae, nymphs, adults	scaly face, scaly leg	-
Laminosioptidae (quill/skin mites)	8 genera, 25 species	birds	larvae, nymphs, adults	flesh/skin lesions	-

The superorder Acariformes comprises acarines without posterior respiratory stigmata and includes two major orders of parasites: trombidiform mites (order Prostigmata) with stigmata on the gnathosoma (capitulum) or propodosoma; and sarcoptiform mites (order Astigmata) which lack stigmata and peritremes and respire through their cuticles. Over 16,000 species of astigmate mites have been described in 230 families: with around 12,000 species in 154 families being free-living or predatory in terrestrial or aquatic environments (including a large assemblage of soil-dwelling oribatid mites); and some 4,000 species in 76 families occurring as commensals or parasites of arthropods and vertebrates (notably birds and mammals). Parasitic species may be ectoparasitic (on external surfaces of the host) or endoparasitic (within host epidermal or respiratory tissues) and their development often only includes 2 nymphal stages (in contrast to 3 nymphal stages in free-living species, sometimes including a specialized heteromorphic deutonymph (hypopus) adapted for phoretic dispersal or tolerance of adverse conditions). Common names for many of the parasitic groups include mange, itch, or scab mites as they may cause serious inflammatory skin conditions in their hosts. Adult mites tend to be small, slow moving, whitish stages with soft cuticles and round-oval bodies (never vermiform) often with long setae. They possess chelate or dentate chelicerae, unbarbed hypostomes, small inconspicuous palps, legs with coxae fused to the body wall and tarsal segments bearing complex pulvilli (pad-like or trumpet-like) and empodia (claw-like or sucker-like, but never bearing tenet hairs). Most parasitic species may complete their entire life-cycles on individual hosts, so horizontal transmission between hosts is primarily by physical contact. A total of 10 astigmate superfamilies have been recognized (Acaroidea, Analgoidea, Canestrinioidea, Freyanoidea, Glycyphagoidea, Hemisarcoptoidea, Histiostomatoidea, Hypoderatoidea, Pterolichoidea, Sarcoptoidea) and an additional 2 families are currently unplaced (Cytoditidae, Heteropsoridae).

The superfamily Acaroidea contains a large number of free-living mites that feed on mould and decomposing organic waste (some being notorious pests of stored foods such as grains, cheese, fruits, straw) as well as some nidicolous species inhabiting the nests of vertebrates (mammals and birds) and invertebrates (termites, beetles, bees, wasps, ants). They have small stout white-fawn bodies distinctly divided by transverse grooves into a proterosoma and hysterosoma, small heads (gnathosoma), chelate chelicerae, 4 pairs of legs conspicuously divided into 2 forward-facing pairs and 2 rear-facing pairs, and distinctive chaetotaxy (patterns of setae). Some 23 families have been recognized (Acaridae, Alloptidae, Analgidae, Apionacaridae, Avenzoariidae, Dermationidae, Dermoglyphidae, Epidermoptidae, Gaudoglyphidae, Knemidokoptidae, Kytoditidae, Laminosioptidae, Lardoglyphidae, Proctophyllodidae, Psoroptoididae, Pyroglyphidae, Sapracaridae, Saproglyphidae, Suidasiidae, Thysanocercidae, Trouessartiidae, Turbinoptidae, and Xolalgidae). The family Laminosioptidae comprises small quill/skin mites with smooth elongated bodies and few setae that infest birds, often affecting their muscles. The family is monotypic with a single genus *Laminosioptes* but with 5 species assigned to 4 subgenera: *L.* (*Laminosioptes*) (cheliceral movable digit with 3 tines, dorsum with 3 median and 2 paramedian plates); *L.* (*Psittaciella*) (cheliceral movable digit with 2 tines, dorsum with 4 median plates); *L.* (*Columbietta*) (cheliceral movable digit with single tine, dorsum with 5 median plates); and *L.* (*Passeriella*) (cheliceral movable digit with single tine, dorsum with 3 large median plates). These mites have elongated bodies with long setae, well-developed mouthparts, and four pairs of legs with claw-like tarsi on the first 2 pairs and long spatulate pretarsi on the posterior 2 pairs. One species (*L. L. cysticola*) invades the subcutaneous tissues of birds (mainly galliforms) and causes small flat oval nodules (hence their common name of fowl cyst mites).

***Laminosioptes* species**	**Hosts**	**Location**	**Clinical signs**	**Distribution**
Subgenus *L.* (*Laminosioptes*)				
L. (*L.*) *cysticola* (fowl cyst mite, subcutaneous mite)	Galliformes: phasianid (chicken, red-necked spurfowl, turkey); Columbiformes: columbid (pigeon)	subcutaneous tissues, lungs, peritoneum	carcase lesions, occasionally neurological lesions	worldwide
L. (*L.*) *hymenopterus*	Passeriformes: corvid (American crow)			North America
Subgenus *L.* (*Columbietta*)				
L. (*C.*) *collaris*	Columbiformes: columbid (plain-breasted ground dove)			Europe (zoo)
Subgenus *L.* (*Passeriella*)				
L. (*P.*) *reticulata*	Passeriformes: fringillid (Chinese grosbeak)			Europe (zoo)
Subgenus *L.* (*Psittaciella*)				
L. (*P.*) *myiopsittae*	Psittaciformes: psittacid (monk parakeet)			Europe (zoo)

Parasite morphology: Few details are available on the morphological characteristics of the various developmental stages of *Laminosioptes* spp. due to their cryptic and often encysted location within host tissues. Some information has been forthcoming from histological studies performed on tissue sections or by the microscopic study of stages recovered from skin scrapings. These mites are thought to produce 4 different types of stages during their development: eggs, larvae, nymphs and adults. Developing eggs have been observed *in utero* in female mites, and some species are thought to lay embryonated eggs while other species (e.g. *L. cysticola, L. collaris*) appear to be larviparous and give birth to fully-formed larvae. The larvae are oval-elliptical in shape measuring up to 140 µm long and they have 3 pairs of ventral legs without tarsal suckers. Nymphs are similar in shape but larger measuring up to 250 µm long and they have 4 pairs of ventral legs, the first pair having coxal epimeres joining to form a Y-shape. It is unclear how many nymphal stages are formed, although some reports suggest 2 instars occur (protonymphs and then deutonymphs). Adult mites have elongated oval-cylindrical bodies that are dorsoventrally flattened. They range considerably in size according to species, measuring from 240-860 µm in length. They have 2 main tagma: a small anterior gnathosoma (head) and a large posterior idiosoma (body). The gnathosoma is small (wider than long) and not visible in dorsal view. It bears small but well-developed mouthparts comprising a pair of 3-segmented chelicerae terminating in claw-like chelae (pincers) formed by fixed and movable digits (the latter with 1, 2 or 3 apical tines differentiating the subgenera *L.* (*Columbietta*) plus *L.* (*Passeriella*) from *L.* (*Psittaciella*) and *L.* (*Laminosioptes*) respectively. The chelicerae are flanked by short sensory palps (without apoteles) and the mouth is directed ventrally with an unbarbed hypostome. It is thought the gut comprises a short foregut, an expanded midgut and a short hindgut terminating in a ventral anus. The idiosoma has 3-5 punctate dorsal plates depending on subgenus: *L.* (*Passeriella*) with 3 large median plates, *L.* (*Laminosioptes*) with 3 median and 2 paramedian plates, *L.* (*Psittaciella*) with 4 median plates, and *L.* (*Columbietta*) *w*ith 5 median plates. The rest of the cuticle is generally smooth although some species have transverse striations located between the dorsal plates. The body also bears a few long setae, including 2 caudal setate, but respiratory stigmata are absent. Adults have 4 pairs of well-developed ventral legs, 2 anterior pairs and 2 longer posterior pairs, all legs protruding beyond the body margin. The legs appear to have 5 short segments, with the basal coxae solidly fused to the body wall with pronounced thickened ridges (apodemes or epimeres). The apodemes of the first pair of legs join into a Y shape, and those on the posterior 2 pairs of legs appear to have lateral spurs. The first 2 pairs of legs terminate in claw-like tarsi with 1-2 pointed apical processes (not

spines), while the posterior 2 pairs of legs end in long spatulate pretarsal stalks (pedicels without suckers). Adult mites display sexual dimorphism in size and structure, with males being smaller than females (240-400 cf. 250-860 μm) Male mites have 2 testes with tubular vas deferens leading to the long sheathed aedeagus (penis) opening to a ventral genital pore. Female mites have 2 ovaries with tubular oviducts leading to a globular uterus and an inverted Y-shaped vulva located ventrally between the coxae of the third pair of legs. Female mites may be oviparous (laying embryonated eggs) or larviparous (birthing live larvae).

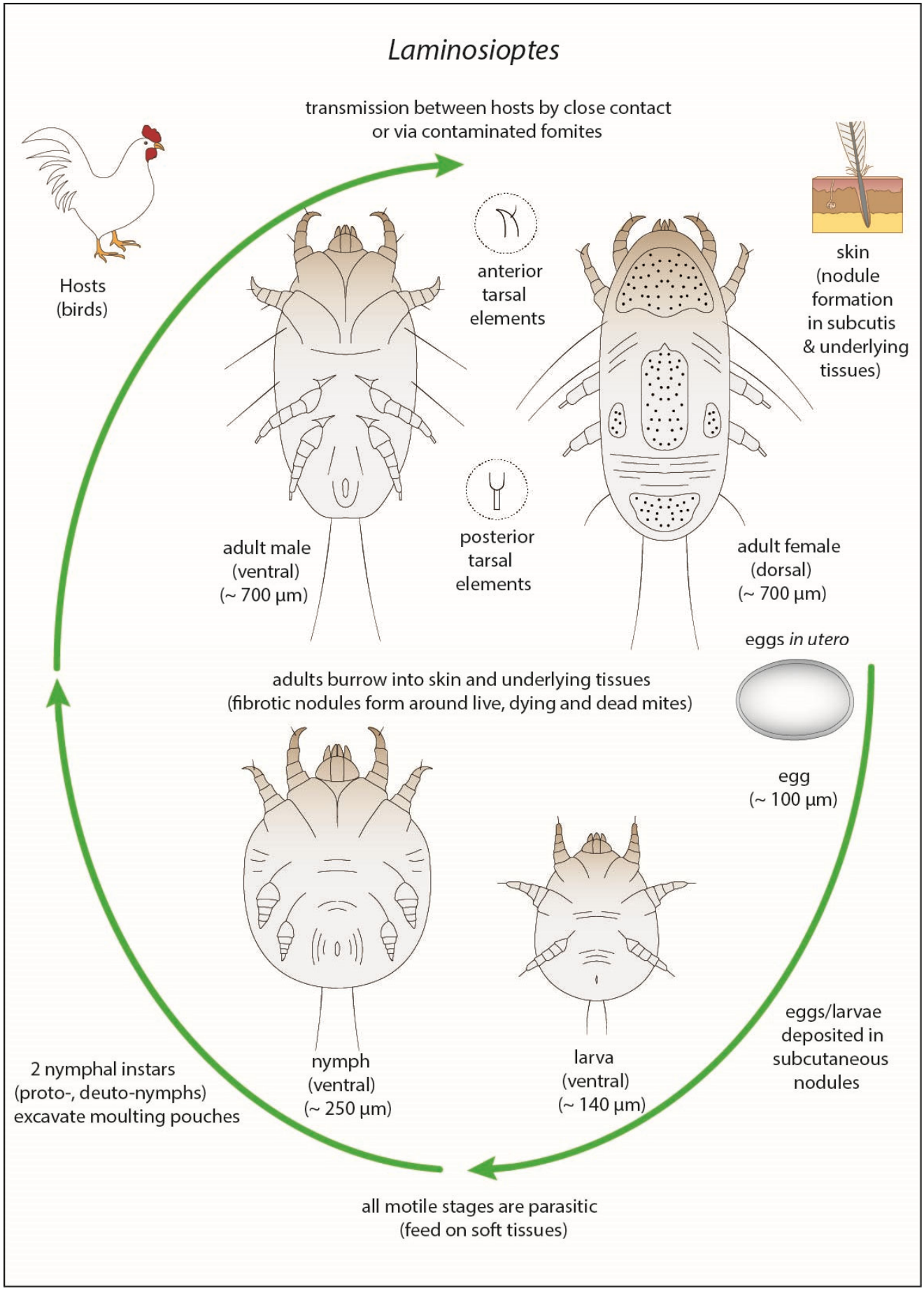
Site of infection: These mites are obligate parasites of birds, although they behave more like endoparasites than ectoparasites. The mites invade subcutaneous tissues and reside in the fascia surrounding muscles, but may occur deeper in the lungs, peritoneum, and abdominal viscera. They often occur in clumps in the subcutis around the neck, breast, flanks and vent. A total of 5 species have been described from 2 passerine families (corvids, fringillids) and 3 non-passerine families (columbids, phasianids, psittacids).

Pathogenesis: Infestations do not appear to cause acute clinical disease, but heavy and protracted infestations may result in nodule and cyst formation within internal tissues, leading to unsightly lesions and chronic disease manifestations. Mites penetrates into subcutaneous tissues where they feed on soft tissues (not blood). There is little or no inflammation associated with intact mites, and the only clinical signs at this stage seem to involve mild pruritus. Eventually the mites die in the tissues and become encysted in collagen forming white-cream flat oval nodules (hence the common name of cyst mite). Cysts are most frequently found in loose subcutaneous connective tissue, muscle fascia, abdominal viscera (kidneys, liver), peritoneum, lungs and air sacs. Degenerating mites and their fragments elicit mild to moderate granulomatous reactions and mineralization resulting in yellowish caseous and calcareous nodules up to several millimeters in diameter. Heavily infested birds may show lethargy, damaged plumage, feather loss, wasting, growth retardation, reduced egg production, and even death. Neurological signs have also been described in turkeys where mites infesting peripheral nerves caused incoordination, torticollis and drooping wings. Birds also appear to be highly susceptible to secondary bacterial infections. Nodular lesions in poultry reduce carcase quality and value and may result in condemnation upon meat inspection. Clinical manifestations in poultry occur more frequently in older, emaciated birds kept in unsanitary conditions, particularly in backyard and free-range conditions rather than intensive indoor poultry houses.

Developmental cycle and mode of transmission: The complete life-cycles of *Laminosioptes* spp. are not yet known, but like other acarines, they typically involve incomplete (hemimetabolous) metamorphosis where immature stages gradually transition through successive moults from larvae to nymphs to adults. All developmental stages have been observed on individual birds but their mode of transmission between birds is unclear due to their location and encystation beneath the skin. Adult mites live in nodules under the skin close to the surface of muscles where females produce live larvae or lay embryonated eggs. The larval stages are thought to feed on soft tissues before moulting to nymphs (possibly through 2 instars), which likewise feed before moulting to adult mites. It is not known whether any or all stages migrate to the skin surface or through the skin before forming their own nodules (like other astigmatid mites which create their own moulting burrows or pouches). It is therefore unclear as to which stages may be involved in the transmission of infestations between birds. Whilst all developmental stages have been found below the skin, mites have been collected from bird carcases washed and placed into bags, suggesting they may have transient surface-dwelling stages or mites may simply be leaving carcases as they cool. This has implications for their transmission, as most infestations have been associated with backyard or free-range operations where environmental contamination with off-host stages would be greatest. Further studies are required to determine the developmental cycle, longevity, fecundity and survival characteristics of these cryptic skin mites.

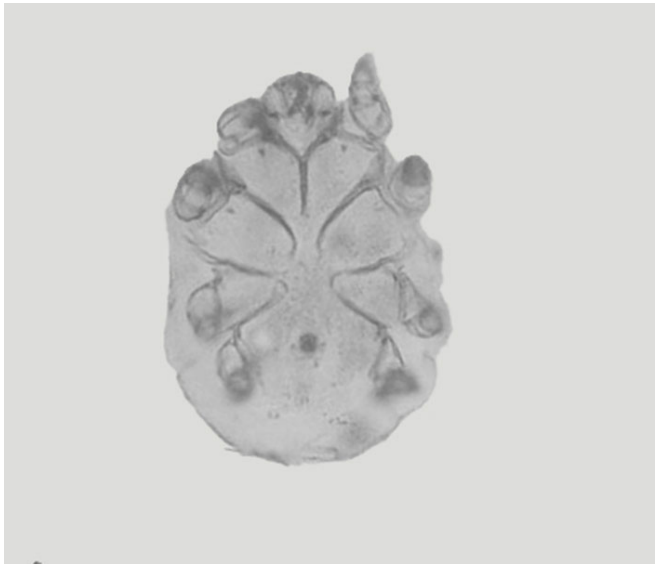
Differential diagnosis: Infestations are usually diagnosed at post-mortem by the detection of flat oval nodules containing mites in the subcutis or on muscles and visceral organs. Nodules may be observed visually when inspecting or dressing carcases and their contents examined more closely using a dissecting microscope. Infestations in poultry need to be differentiated from other causes of nodule formation, including subcutaneous nodules formed by acid-fast bacilli causing tuberculosis, and respiratory and visceral nodules caused by poultry air sac mites (*Cytodites*). Necropsy tissue samples may be collected for histological examination to reveal encysted mites or mite fragments. Mites have also been recovered from carcases washed in detergent and placed in bags. Alternatively, some infestations have been detected antemortem by the detection of mites in skin scrapings.

Treatment and control: Until recently, the most effective form of control has been to cull and destroy infested birds, and sometimes those in the immediate vicinity. While nodule/cyst formation is generally a chronic manifestation, chemotherapy with contemporary acaricides has been found to relatively effective, notably using systemic macrocyclic lactones (ivermectin). Protracted treatment may be required to reach invasive and encysted stages, and supportive therapy with antibiotics may be required to combat secondary bacterial infections. Several common-sense measures may also be adopted to reduce the risk of transmission, including the rapid removal and disposal of carcases, regularly cleaning cages, pens and runs, replacing litter and nesting materials, and routine health surveillance to monitor bird health and inform acaricidal treatments.

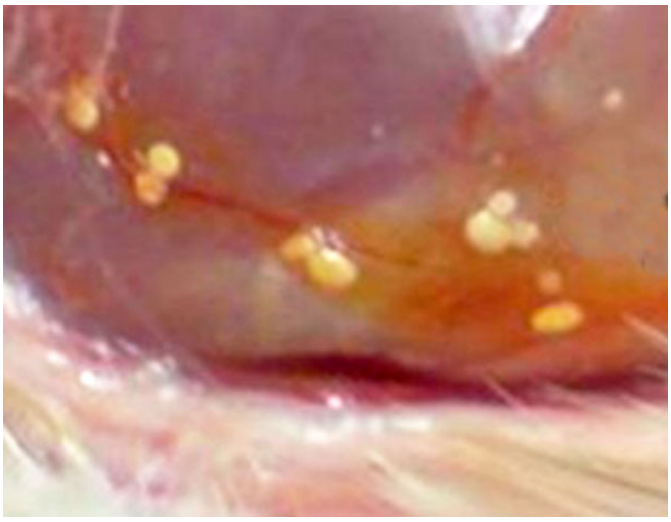

Laminosioptes
transmission between hosts by close contact
or via contaminated fomites
Hosts
(birds)
anterior
tarsal
elements
skin
(nodule
formation
in subcutis
& underlying
tissues)
adult male
(ventral)
(~ 700 µm)
posterior
tarsal
elements
adult female
(dorsal)
(~ 700 µm)
eggs in utero
adults burrow into skin and underlying tissues
(fibrotic nodules form around live, dying and dead mites)
egg
(~ 100 µm)
nymph
(ventral)
(~ 250 µm)
larva
(ventral)
(~ 140 µm)
eggs/larvae
deposited in
subcutaneous
nodules
2 nymphal instars
(proto-, deuto-nymphs)
excavate moulting pouches
all motile stages are parasitic
(feed on soft tissues)



Laminosioptes adult



Laminosioptes adult

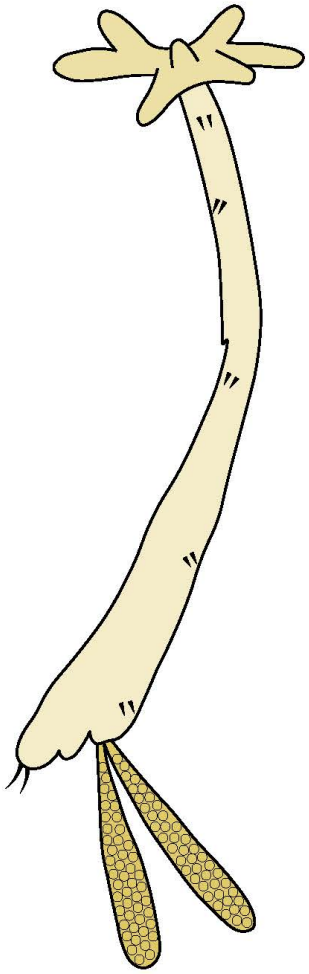


Laminosioptes cystic lesions

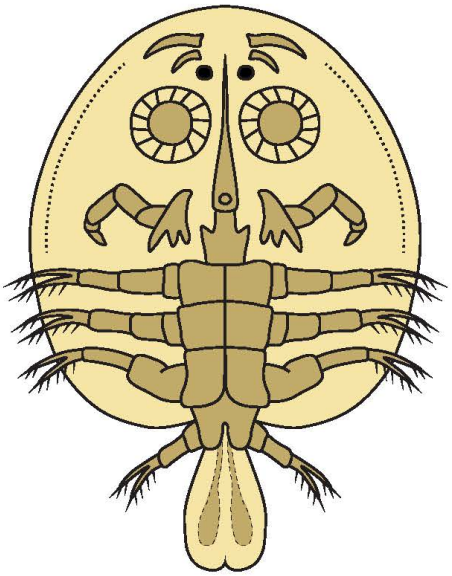
Crustacea
(copepods, brachiurans)

Crustacea

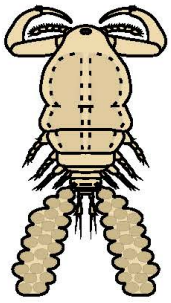
Lernaea
adult female
(~ 15 mm)



Argulus
adult (ventral)
(~ 10 mm)



Ergasilus
adult female (dorsal)
(~ 1.5 mm)



Lernaea
(crustacean: copepod)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and most grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Crustaceans have a very strong cuticle strengthened by calcium salts; thus their growth must proceed through repeated moults. Most species are aquatic with internal or external gills, two pairs of antennae, mouthparts comprising one pair of mandibles and two pairs of maxillae, and each heteronomous body segment usually bears a pair of ventral biramous extremities (podia). Maxillopods lack appendages on abdominal segments and the nauplius larval stage has a unique maxillopodan eye. Copepods have an elongate segmented body (first few thoracic segments fused with head to form cephalothorax) and they undergo gradual metamorphosis with a series of copepodid instars succeeding naupliar instars. Many species are free-living, although some are ectoparasitic on fish. Cyclopoid copepods have short antennules with 10-16 articles and an open buccal cavity. Lernaeids have a free-swimming naupliar stage, five copepodid stages and the adults attach to aquatic hosts. Females insert anterior attachment organs into host tissues and develop paired egg sacs. Infestations by *Lernaea cyprinacaea* may cause lesions and mortalities in a wide range of freshwater fishes, especially in aquaculture facilities.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Crustacea (mandibular mouthparts, gills, two pairs antennae, biramous podia, larval nauplius/zoea)
Class: Maxillipoda (nauplius with maxillipodan eye)
Subclass: Copepoda (elongate body, series of copepodid instars succeeding naupliar instars, several ectoparasites)
Order: Cyclopoida (antennules short with 10-16 articles, buccal cavity open)
Family: Lernaeidae (attachment organ inserted into host, paired egg sacs)
Genus: *Lernaea* (parasitic on gills/skin of fish)
Species: *L. cyprinacaea* causes lesions and mortalities in freshwater fishes

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Crustaceans have very strong cuticles strengthened by calcium salts, so they moult periodically as they grow and metamorphose through different types of larval stages before forming adults. Most species are aquatic and have internal or external gills, while terrestrial species have internal gills which are kept moist. Crustaceans have mouthparts with two pairs of maxillae (to handle food) and paired mandibles (with opposing biting and grinding surfaces). They have two sets of antennae and each body segment usually gives rise to a pair of ventral biramous appendages (podia). Six crustacean classes are recognized: Brachiopoda, Cephalocarida, Malacostraca, Maxillipoda, Ostracoda and Remipedia. Maxillopods usually have a body plan comprising 5 cephalic, 6 thoracic and 4 abdominal segments followed by a telson. The thoracic segments bear biramous (sometimes uniramous) limbs, but the abdominal segments lack appendages. The carapace is present or reduced, most feed using maxillae, and the nauplius larval stages have unique eyes with three cups, each with tapetal cells (= maxillopodan eye). Six maxillopodan subclasses are recognized: Branchiura, Cirripedia, Copepoda, Mystacocarida, Pentastomatida and Tantulocarida.

Major parasitic crustacean families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Class: Maxillipoda					
Subclass: Copepoda (copepods)					
Order: Cyclopoida (open buccal cavity)					
Family: Lernaeidae	19 genera,	freshwater fishes	copepodids	skin	direct (water)

(anchor worms)	114 spp.		and adults	lesions	
Former order: Poecilostomatoida (slit-like buccal cavity)[now a "poecilostome" lineage within the Cyclopoida]					
Family: Ergasilidae (gill lice)	27 genera 61 spp.	freshwater and marine fish	adult ♀	gill/skin lesions	direct (water)
Subclass: Branchiura (head with flattened bilobed cephalic fold, carapace expands laterally)					
Order: Argulidea (discoid bodies, attach using hooks, suckers and barbs)					
Family: Argulidae (fish lice)	4 genera 150 spp.	marine and freshwater fish	juveniles, adults	skin lesions	direct (water)
Subclass: Pentastomatida (tongue worms, elongate annulated bodies, 2 pairs tiny anterior claws near mouth)					
Order: Porocephalida (mouth between/below anterior hooks)					
Family: Porocephalidae	5 genera, 10 spp.	snakes (rodent IH)	adults	lung lesions	indirect (via IH*)
Family: Linguatulidae	1 genus, 4 spp.	carnivorous mammals (mammal IH)	adults	naso-pharyngeal lesions	indirect (via IH*)

*IH = intermediate host

Copepods are small aquatic crustaceans that are one of the most speciose metazoan groups in aquatic communities (over 13,000 morpho-species known). They inhabit a wide range of water sources, ranging from oceans and marine sediments, freshwater streams, rivers, lakes, subterranean cave pools, and even damp leaf litter and puddles in bromeliad leaves. Most species are free-living (important as both predators and prey in planktonic food chains) and some are symbiotic or internal/external parasites of other metazoa, including commercial fish species. Copepods lack a carapace and have elongate segmented bodies (first few thoracic segments fused with head to form cephalothorax) with a single pair of uniramous maxillipods and four pairs of biramous thoracic swimming appendages. They undergo gradual metamorphosis with a series of copepodid instars succeeding naupliar instars. Copepods have been classified within 2 superorders: Gymnoplea (prosome-urosome division posterior to fifth leg-bearing somite) with 2 orders (Calanoida and Platycopioida) and Podoplea (prosome-urosome division anterior to fifth leg-bearing somite) with 9 orders (Canuelloida, Cyclopoida (incl. Poecilostomatoida which is no longer recognised as a valid order as all its cognate families form a well-defined "poecilostome" lineage within the Cyclopoida), Gelyelloida, Harpacticoida, Misophrioida, Monstrilloida, Mormonilloida, Platycopioida and Siphonostomatoida). Members of the order Cyclopoida s.s. form adults with an open buccal cavity and have short antennules with 10-16 articles. Some 27 families are recognized: including the family Lernaeidae which contains 17 genera (*Afrolernaea*, *Amazolernaea*, *Areotrachelus*, *Bedsylernaea*, *Catlaphila*, *Dysphorus*, *Indolernaea*, *Indopeniculus*, *Lamproglena*, *Lamproglenoides*, *Lernaea*, *Lernaeogiraffa*, *Minilernaea*, *Opistholernaea*, *Pillainus*, *Pseudolamproglena* and *Taurocheros*) assigned to 2 subfamilies, Lamprogleninae (prevalent in Palaearctic, Oriental and Afrotropical regions) and Lernaeinae (found in all zoogeographic regions except Antarctica). Lernaeids have free-swimming naupliar stages but all subsequent copepodid and adult stages are ectoparasitic on the skin and gills of freshwater fishes (in contrast, only the female adults of poecilostome ergasilids are parasitic). Adult females insert an anterior holdfast (attachment organ) into host tissues and develop paired egg sacs posteriorly. Those belonging to the genus *Lernaea* form a unique holdfast resembling an anchor with antler-like processes. All *Lernaea* spp. occur in freshwater systems, or those with low salinity levels. Early studies described over 100 nominal species, but the small number of morphological traits and their pleomorphy has confounded species discrimination, so over half the nominal species are considered synonymous with other species. At present, some 55 species are considered valid, with many recorded in cultured fish species (both ornamental and farmed), sometimes in association with morbidity and mortality.

***Lernaea* species**	**Hosts**	**Distribution**
L. arcuata	Cypriniformes: cyprinid (Java barb); Perciformes: osphronemid (Vaillant's chocolate gourami)	Asia
L. argentinensis	Siluriformes: pimelodid (spotted sorubim, barred catfish)	South America
L. bagri	Siluriformes: bagrid (kampango)	Africa
L. barbicola	Cypriniformes: cyprinid (smallmouth yellowfish); Siluriformes: malapterurid (electric catfish)	Africa
L. barilii	Cypriniformes: cyprinid (goldfish, lake salmon), danionid (bariline fish)	Africa, Asia
L. barnimii (syn. *Lernaeocera barnimiana, temnocephala)*	Cypriniformes: cyprinid (largescale yellowfish, smallmouth yellowfish, ningu, moggel, rednose labeo, massas, redeye labeo, purple labeo, Orange River mudfish, Ethiopia barb, Zanzibar barb, Niger barb, chikasu, Ripon barbel); Cichliformes: cichlid (Mweru hump-backed bream, Victoria tilapia, Nile tilapia, Mozambique tilapia, longfin tilapia, blue-spotted tilapia, Singida tilapia, redbelly tilapia, blue Victoria mouthbrooder); Perciformes: latid (Nile perch)	Africa
L. bengalensis	Anabantiformes: channid (spotted snakehead)	India
L. bhadraensis	Cypriniformes: cyprinid (rohu, Indian carp)	India
L. bistricornis	Cichliformes: cichlid (featherfin cichlid, giant cichlid, sinievahiekkahautoja, glanzmaulbruter)	Africa

L. brachycera	Ababantiformes: channid (northern snakehead)	China
L. catostomi (syn. *Lernaeocera catostomi*, *pectoralis*, *tortua*)	Siluriformes: ictalurid (brown bullhead, white bullhead); Cypriniformes: cyprinid (common shiner), catostomid (shorthead redhorse, northern hogsucker, lake chubsucker), leuciscid (weed shiner); Perciformes: centrarchid (bluegill)	North America
L. chackoensis	Cypriniformes: cyprinid (Indian carp); Anabantiformes: osphronemid (giant gourami)	India
L. composita (syn. *Lernaeocera werneri*)	Siluriformes: malapterurid (electric catfish), clariid (African sharptooth catfish); Characiformes: distichodontid (Nile distichodus)	Africa
L. cruciata (syn. *Lernaeocera*) (maybe conspecific with *L. cyprinacea* according to recent molecular studies)	Cypriniformes: cyprinid (goldfish), catostomid (shorthead redhorse); Cyprinodontiformes: poecilid (eastern mosquitofish); Perciformes: percid (sauger), moronid (white bass, white perch), centrarchid (largemouth bass, smallmouth bass, spotted bass, pale river bass, redspotted sunfish, warmouth, pumpkinseed, rock bass); Siluriformes: ictalurid (channel catfish)	Asia, Americas
L. ctenopharyngodontis	Cypriniformes: cyprinid (grass carp)	Asia
L. cyprinacea (syn. *L. carassii*, *elegans, ranae, tentaculis*, *Lernaeocera cyprinacea*, *gastrostei*) (incl. subspp. *brachycera, chakoensis, cyprinacea, elegans, macropodi, mastacembeli*) (anchor worm)	Acanthuriformes: sciaenid (freshwater drum); Amiiformes: amiid (bowfin); Anabantiformes: anabantid (climbing perch), channid (northern snakehead, forest snakehead, giant snakehead, striped snakehead, spotted snakehead), helostomatid (kissing gouramy), osphronemid (snakeskin gourami, threespot gourami, giant gourami, Siamese fighting fish, paradise fish, long-tailed paradise fish); Anguilliformes: anguillid (European eel, American eel, Japanese eel); Atheriniformes: atherinopsid (pejerrey); Beloniformes: adrianichthyid (Japanese rice fish); Blenniiformes: blenniid (woundfin); Characiformes: anostomid (piava), characid (pike characin, twospot astyanax), prochilodontid (streaked prochilod); Cichliformes: cichlid (Mozambique tilapia, Victoria tilapia, redbelly tilapia, Singida tilapia, black tilapia, blue tilapia, Mozambique tilapia, Nile tilapia, redbreast tilapia, southern mouthbrooder); Clupeiformes: clupeid (Allis shad); Cypriniformes: catostomid (razorback sucker, golden redhorse, bluehead sucker, Sonora sucker, largescale sucker, Sacramento sucker, white sucker, desert sucker, lake chubsucker, creek chubsucker, northern hogsucker, quillback, smallmouth buffalo, bigmouth buffalo, black buffalo), cobitid (pond loach, spined loach), cyprinid (goldfish, silver crucian carp, crucian carp, Japanese crucian carp, grass carp, common carp, koi carp, Mossul bleak, Kinneret bleak, Sellal bleak, bit, silver carp, black carp, Eurasian carp, Indian carp, bighead carp, bigeye carp, predatory terling, gudgeon, field gudgeon, Suwa gudgeon, barbell steed, topmouth gudgeon, Japanese dace, dark chub, pale chub, Yunnani silemokk, Java barb, common shiner, silver labeo, rednose labeo, Orange River mudfish, purple labeo, redeye labeo, largescale yellowfish, largemouth yellowfish, shabout, asp, dali poorpuntius, barbell, yellow barbell, common barbel, yellowfin barbel, Italian barbel, Jordan barbel, Jordan himri, Mesopotamian himri, mangar, binni, ogaramul, Levantine scraper, sharpray, common nase, brond-snout, kangal fish, ida-napploug, hiina napploug, red garra, sharpbelly, hitch, ide, common roach, Tigris asp, peppered chub, Wuchang bream, black Amur bream, Moapa dace, black sharkminnow, hardhead, golden shiner, threelips, Sacramento blackfish, hardlipped barb, Moltrecht's minnow, suckermouth minnow, common minnow, southern redbelly dace, bluntnose minnow, fathead minnow, bullhead minnow, stone moroko, pehmeium-soorhuul, Siambarbe, tinfoil barb, gold barb, European bitterling, rosy bitterling, common roach, common rudd, tench), leuciscid (big-scaled redfin, Mesopotamian pike chub, eastern blacknose dace, longnose dace, speckled dace, northern pikeminnow, Colorado squawfish, satinfin shiner, rosefin shiner, redffin shiner, emerald shiner, river shiner, minnilus, Arkansas River shiner, spottail shiner, red shiner, spotfin shiner, sand shiner, mimic shiner, steelcolor shiner, Allegheny pearl dace, Mississippi silvery minnow, chiselmouth, Tigris bream, asp, central stoneroller, creek chub, Utah chub, roundtail chub), xenocyprid (barbel chub, kulter niulansky, sale niglask, predatory carp); Cyprinodontiformes: cyprinodontid (Arabian toothcarp, Zagros pupfish), goodeid (White River springfish), fundulid (northern studfish, mummichog, plains killifish, northern plains killifish, blackstripe topminnow), poeciliid	worldwide

	(southern platyfish, dusky millions fish, molly, short-finned molly, Yucatan molly, guppy, rainbow fish, livebearer, eastern mosquitofish, western mosquitofish); Esociformes: esocid (chain pickerel, northern pike, redfin pickerel), umbrid (central mudminnow, eastern mudminnow); Gadiformes: lotid (burbot); Galaxiiformes: galaxiid (western galaxias, mountain galaxias); Gasterosteiformes: gasterosteid (three-spined stickleback, ninespine stickleback); Gobiiformes: gobiid (monkey goby, round goby), odontobutid (sleeper), oxudercid (mudskipper); Mugiliformes: mugilid (greenback mullet, liza, flathead grey mullet, thinlip mullet, Abu mullet); Osmeriformes: retropinnid (Australian grayling); Osteoglossiformes: osteoglossid (Asian arowana, pirarucu); Perciformes: centrarchid (white crappie, black crappie, longear sunfish, orange-spotted sunfish, warmouth, green sunfish, rock bass, bluegill, largemouth bass, pumpkinseed, smallmouth bass, spotted bass, largemouth bass, Sacramento perch), channid (snakehead), cichlid (freshwater angelfish), gobiid (edohaze, jyuzukakehaze, dusky tripletooth goby), moronid (white bass), percichthyid (Creole perch, southern pygmy perch, Macquarie perch, Murray cod, trout cod, nightfish, western pygmy perch, river blackfish), percid (walleye, blackside darter, redfin perch, mud darter, johnny darter, orangethroat darter, banded darter, Eurasian ruffe), sinipercid (mandarin fish), terapontid (silver perch); Salmoniformes: plecoglossid (ayu), salmonid (trout, rainbow trout, brown trout, brook trout, chinook salmon); Scombriformes: stromateid (silver pomfret); Scorpaeniformes: cottid (banded sculpin, European bullhead); Siluriformes: bagrid (Tigris mystus, cut-tailed bullhead, semutundu), heptapterid (South American catfish), heteropneustid (Asian singing catfish), plotosid (freshwater cobbler, eel-tailed catfish), silurid (Amur catfish, wels catfish, Tigris catfish), ictalurid (brown bullhead, black bullhead, channel catfish); Synbranchiformes: mastacembelid (lesser spiny eel); Tetraodontiformes: tetraodontid (pufferfish); Caudata: salamandrid (Japanese fire belly newt); Anura: ranid (tadpoles)(American bullfrog, northern leopard frog, marsh frog, green frog, foothill yellow-legged frog)	
L. devastatrix	Characiformes: characid (tetra), erythrinid (wolf fish); Cypriniformes: cyprinid (Eurasian carp); Siluriformes: heptapterid (South American catfish)	South America
L. diceracephala (syn. *Lernaeocera*)	Siluriformes: clariid (African sharptooth catfish, vundu)	Africa
L. dolabrodes	Perciformes: centrarchid (bluegill)	America
L. gambusiae	Cyprinodontiformes: poecilid (western mosquitofish)	India
L. gamitanae	Characiformes: serrasalmid (tambaqui)	South America
L. gobioptera	Gobiiformes: godiid (macrolepis mosquitofish)	Eurasia
L. gonionoti	Cypriniformes: cyprinid (Java barb)	Asia
L. haplocephala (syn. *Lernaeocera bichiri*)	Cypriniformes: cyprinid (smallmouth yellowfish); Polypteriformes: polypterid (saddled bichir, barred bichir, Congo bichir, ornate bichir, gray bichir)	Africa
L. hardingi	Cichliformes: cichlid (Nile tilapia, redbelly tilapia, mango tilapia, happy, tigerfish, snaileater); Characiformes: alestid (nurse tetra); Siluriformes: claroteid (monde), mochokid (spotted squeaker)	Africa
L. hesaragattensis	Cyprinodontiformes: poecilid (guppy)	India
L. incisor	Perciformes: centrarchid (bluegill)	North America
L. inflata	Cypriniformes: cyprinid (rosefin barb)	Africa
L. lagenula (syn. *Lernaeocera*)	host unknown	South America
L. lavareti (maybe *Ergasilus sieboldi*)	Salmoniformes: salmonid (whitefish)	Europe
L. longa	Perciformes: latid (Nile perch)	Africa
L. lophiara	Cichliformes: cichlid (redbelly tilapia, redcheek, golden mola hap, happy, tigerfish, saguga, ndunduma, chisawasawa, utaka, Lake Malawi cichlid); Cypriniformes: cyprinid (redeye labeo, ngumbo); Siluriformes: clariid (mudfish), malapterurid (electric catfish)	Africa
L. minima	Salmoniformes: salmonid (salmon)	Europe
L. multiobosa	Cypriniformes: cyprinid (large razorbelly minnow)	Pakistan
L. octocornua	Abantiformes: channid (spotted snakehead)	China
L. oryzophila	Cypriniformes: cyprinid (Eurasian carp, Java barb); Gobiiformes: gobiid	Asia

	(goby)	
L. osphronemi	Anabantiformes: osphronemid (giant gourami)	Asia
L. palati	Cichliformes: cichlid (happy (white blaze))	Asia
L. papuensis	Osteoglossiformes: osteoglossid (northern saratoga)	Papua New Guinea
L. parasiluri	Siluriformes: silurid (Amur catfish)	Asia
L. phoxinacea (syn. *Lernaeocera*)	Cypriniformes: leuciscid (common minnow)	Eurasia
L. pirapitingae	Characiformes: serrasalmid (pirapitinga)	South America
L. piscinae	Cypriniformes: cyprinid (bighead carp)	Asia
L. polymorpha	Cypriniformes: cyprinid (Eurasian carp)	Europe
L. pomotidis (syn. *Lernaeocera*)	Perciformes: centrarchid (bluegill, flier)	North America
L. quadrinucifera	Cypriniformes: cyprinid (grass carp)	Asia
L. rhodei	Cypriniformes: cyprinid (rosy bitterling)	China
L. senegali (syn. *Lernaeocera*)	Polypteriformes: polypterid (gray bichir)	Africa
L. taipila	Cichliformes: cichlid (Mozambique tilapia, chambo, lingara)	Africa
L. tenuis (syn. *Lernaeocera*)	Acanthuriformes: sciaenid (freshwater drum)	North America
L. tilapiae	Cichliformes: cichlid (lingara, chambo, lidole)	Africa
L. tuberosa	Cypriniformes: cyprinid (Lake Malawi sardine)	Africa
L. variabilis (syn. *Lernaeocera*)	Perciformes: centrarchid (bluegill)	Americas

Numerous species have also been reclassified to other genera: including *L. abyssicola = Lernaeocera abyssicola*; *L. adunca, L. pinnarum, L. uncinata* and *L. unicinata = Clavella adunca*; *L. anomala* and *L. insolens = Clavella anomala*; *L. asellina = Lernentoma asellina*; *L. brachialis* and *L. lumpi = Lernaeocera branchialis*; *L. cirrhosa = Pennella filosa*; *L. clavata = Hatschekia clavata*; *L. cornuta = Acanthochondria cornuta*; *L. cyclopterina = Haemobaphes cyclopterina*; *L. dalmanni = Charopinus dalmanni*; *L. diodontis = Pennella sagitta*; *L. elongata = Ommatokoita elongata*; *L. encrasicholi = Lernaeenicus encrasicholi*; *L. esocina = Lernaeocera esocina*; *L. exocoeti = Pennella exocoeti*; *L. gobina = Diocus gobinus*; *L. godfroyi = Trifur godfroyi*; *L. hemirhamphi = Lernaeolophus sultanus*; *L. huchonis = Basanistes huchonis*; *L. laterobrachialis = Opistholernaea laterobrachialis*; *L. longa = Opistholernaea longa*; *L. lotellae* and *L. rigida = Trifur tortuosus*; *L. lusci = Lernaeocera lusci*; *L. merluccii* and *L. merlangi = Chondracanthus merluccii*; *L. minuta = Lernaeocera minuta*; *L. nodosa = Chondracanthus nodosus*; *L. pectoralis = Lepeophtheirus pectoralis*; *L. radiata = Chondracanthodes radiatus*; *L. salmonea = Salmincola salmonea*; *L. sieboldi = Lernaeolophus sultanus*; *L. cyclophora, L. ocularis, L. surrirai* and *L. spratta = Lernaeenicus sprattae*. another 3 species are considered *species inquirenda* (*L. basteri*, *L. lotae* and *L. squamicola*), and 2 as *nomen nudum* (*L. luciopercae* and *L. ninnii).*

Parasite morphology: *Lernaea* spp. form 5 different types of morphological stages during their developmental cycles: namely, eggs; nauplii (3 free-living instars); copepodids (5 parasitic instars); cyclopoids (free-living pre-metamorphic males and females); and adults (parasitic females only). Females carry eggs in 2 posterior elongate egg sacs that may measure up to 2 mm long. The eggs are small (0.07-0.08 mm), multiseriate, often dark in colour and variable in shape (elongate-conical-ovoid) depending on their age. They hatch to release the first larval stages known as nauplii (singular nauplius) which are free-living stages that are transparent or light-green in colour. *Lernaea* spp. form 3 naupliar instars (N1-3) whereas free-living copepods may form up to 6 naupliar stages. The nauplii are small measuring 0.7-1.0 mm wide, oval-elliptical is shape and have a unique maxillopodan eye located anteriorly. They typically have unsegmented bodies possessing only 3 pairs of functional appendages (antennules, antennae and mandibles) with reduced setation (the antennae also lack the feeding processes on the coxae found in free-living taxa). This anatomy is typical for parasitic copepods which have lecithotrophic nauplii that rely on yolk stores for nutrients (rather than planktotrophic copepods (like ergasilids) which feed on other planktonic organisms). Copepodid stages are then formed with elongate segmented bodies that are parasitic on fish, mostly on the gills. They develop through 5 copepodid instars (Co1-5) with one body somite added at each moult. Their body segments are divided between 2 major body tagmata, an anterior prosome and a posterior urosome. All stages have a full complement of cephalic appendages but a variable number of thoracic limbs (as early stages have fewer pedigerous somites) and no abdominal limbs (all maxillopods lack appendages on abdominal segments). Their body segmentation conforms to the basic maxillopodan plan, with 5 cephalic, 6 thoracic and 4 abdominal somites, but the first 5 thoracic segments are fused with the head to form the prosome. Parasitic copepods usually have this 'podoplean' body plan with 4 pairs of legs and the division of the prosome and urosome located posterior to the fourth leg-bearing somite (whereas free-living copepods have a 'gymnoplean' body plan with 5 pairs of legs and the division located posterior to the fifth leg-bearing somite). The anterior prosome thus comprises the cephalosome made up of 5 cephalic somites (bearing antennules, antennae, mandibles, maxillules and maxillae, respectively - typical for all crustaceans) plus 5 thoracic somites (first thoracic somite bearing maxillipeds, then another 4 thoracic somites bearing legs 1-4), while the posterior urosome comprises the sixth thoracic somite plus the genital somite and 4 free abdominal somites. The mouthparts are gnathostome (open mouths with short broad hooked mandibles) rather than poecilostome (slit-like mouths with

sickle-shaped mandibles) or siphonostome (tubular mouth with stylet-like mandibles). Larvae attached to hosts are unable to swim because their swimming legs are reduced to short stumps and their setae are lost, but when they moult between stages, they reform their appendages and are able to swim. The last copepodid stage moults to form free-swimming pre-metamorphic males and females (cyclopoid-like). The cephalothorax has a transverse chitinous bar dividing it into anterior and posterior sections, and the furcal rami have dorsal, lateral (plumose) and 3 apical setae. They have short antennules with 10-16 articles and open buccal cavities. Both males and females have 4 pairs of swimming legs, but the first legs of males have larger claws and small inner spines. Females have 5-segmented antennules while males have 6-segmented antennules and shorter antennae with larger claws. Mating occurs during this free-swimming cyclopoid stage of development. Males then die while females become parasitic by burrowing their heads into the flesh of fishes with their elongate bodies dangling as threads from the skin. Females grow from 5-23 mm in length and have distinctive bulbous heads joined by a slender neck to a cylindrical trunk (bearing eggs sacs when mature). The female cephalothorax has an anterior knob-like head with broad lateral margins containing 1-2 pairs of simple or forked cephalic horns (anchors) acting as attachment or holdfast organs (hence the common name of anchor-worm). The holdfast usually comprises 2 pairs (one pair in *L. cruciata*) of antler-shaped processes arranged perpendicular to the long axis of the body. The processes may extend laterally for 1.5-4.0 mm and can exhibit a high degree of inter- and intra-specific variation, usually comprising 2 larger bifurcate dorsal processes (branching at the tips to become T- or Y-shaped) plus 2 smaller (unbranched) ventral processes. Smaller specimens often have undivided dorsal processes (or sporting incipient bumps) and ventral processes being no more than conical pegs. Some mid-sized specimens appear X-shaped with 4 simple short processes approximately equal in size. The structure of the anterior mouthparts is unclear as they are clustered together and deeply embedded in host flesh. A small projection acts as an upper lip covering part of the mouth and the mandibles, while a larger separate projection acts as a lower lip and closes the oral space behind the maxillae. The neck and trunk sometimes exhibit body torsion (either sinistral or dextral) as they dangle from the host. The trunk carries 4 pairs of swimming legs which are conspicuous on juveniles, but highly reduced on mature females. The legs are small and biramous, with each branch having 3 segments. Legs 1 are located just behind the holdfast while legs 2-4 are widely spaced along the body. Some authorities report the presence of a fifth pair of legs located near the pregenital prominences but they are apparently highly reduced to rudimentary stumps. The abdomen is short and rounded with 3 inconspicuous segments terminating in a pair of small segmented caudal rami. As the females mature, the trunk develops a bilobed or double pregenital prominence in front of the vulva, from which projects a pair of elongate egg sacs (similar to other podoplean copepods). Egg sacs may contain from 100-500 eggs which are released into the water column to hatch.

Site of infection: Anchor-worm parasites live in freshwater systems, or those with low salinity levels (0.07-1.7%) consistent with the designation ‘sweet water’ (in contrast, the salinity of seawater is 3.5%). The parasites are therefore found not only on freshwater fishes but also on some estuarine or anadromous species. The naupliar stages are free-living, while the copepodid stages are parasitic mostly on the gills, and the adult females are parasitic mainly on the skin. Different *Lernaea* spp. were thought to exhibit some tissue tropism (site specificity), but heavy infections have been found over most body surfaces, including the inside of the buccal cavity and gill chambers, and occasionally on gill filaments or even the eyes. Most parasite species have exhibited a broad host specificity involving a large range of host species. Infections have been detected on many small Cypriniformes, but also on fish from another 27 orders, as well as on some salamandrids (newts) and ranids (frogs, and their tadpoles). Infections have been found throughout the world in wild and cultured fishes, including aquarium fishes. The parasites develop best in warm conditions, with temperatures between 23-30°C reported as the most favourable.

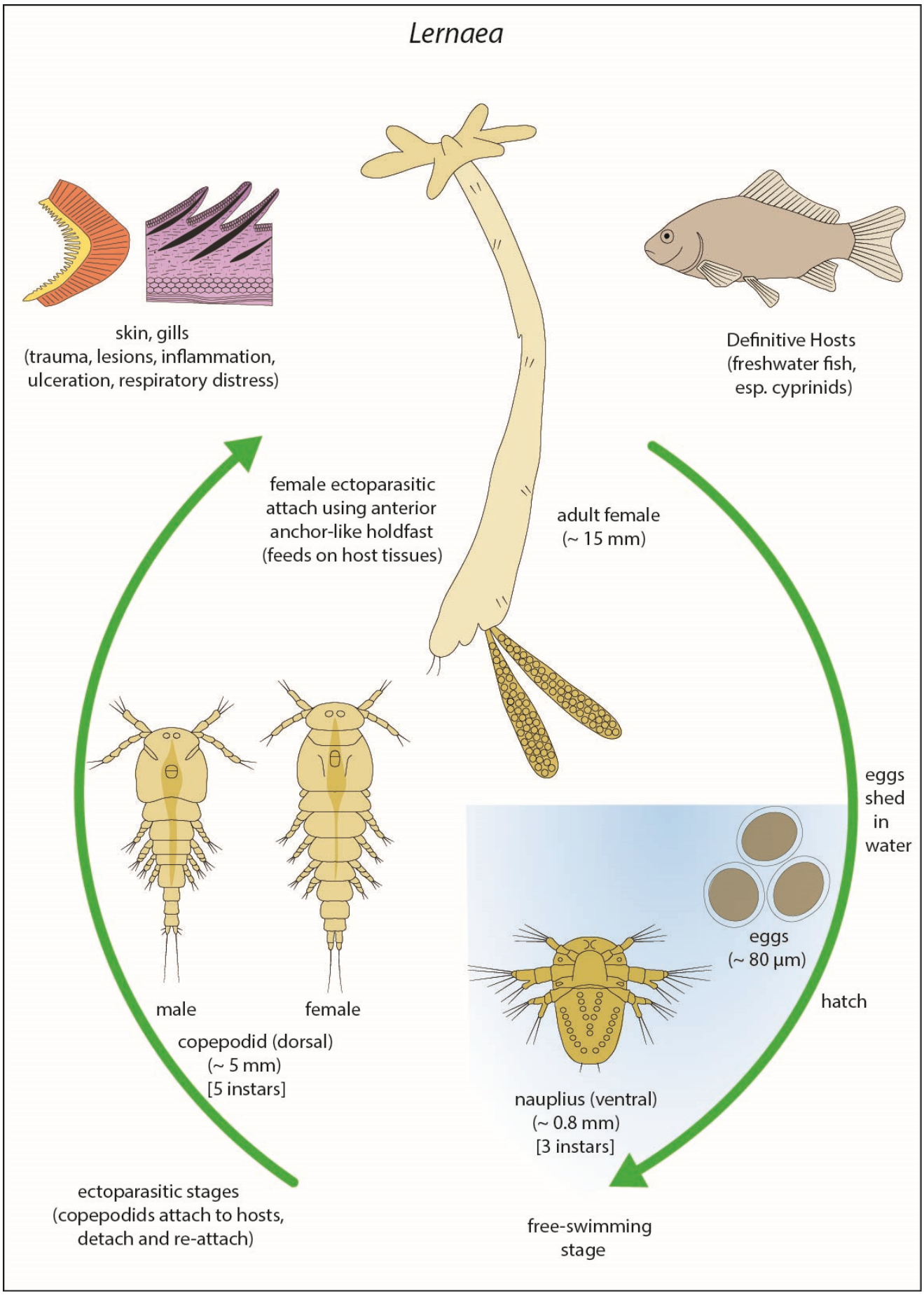
Pathogenesis: Disease (lernaeosis) may be produced by copepodid stages and adult females, both causing tissue trauma with inflammation and ulceration. Copepodid stages are often found on the gills where they attach to gill filaments and feed on host tissue. Light infestations may go unnoticed but large numbers can kill small fish by damaging their gills causing respiratory distress and hypoxia. After mating, immature females penetrate fish hosts by attaching their heads and mouthparts to body surfaces and burrowing deep into the underlying tissues to embed their anterior anchors. Hosts react by trying to isolate the invading parasite by forming ingrowths (tongues) of epidermal cells and sheaths of fibres and cellular infiltrates (fibroblasts and leucocytes) around areas of penetration. The tissues show extensive epidermal hyperplasia and metaplasia, degradation of subepidermal connective tissues, fibrous nodules, muscular breakdown and de-differentiation, all accompanied by progressive inflammation and erythema, with occasional haemorrhages, ulceration and necrosis. Fish may exhibit frequent rubbing or flashing, breathing difficulties and general lethargy with traumatic damage to the skin, scales, fins and underlying muscles (fin damage may also lead to sterility in fish species whose males lose use of their sexual fins). Invasion sites are also prone to secondary bacterial infections (e.g. *Aeromonas hydrophila*) and fungal infections, which worsen and contribute to loss of condition, reduced appetite, poor growth and reproductive performance, and sometimes death. Infections can build to high levels in cultured fish populations leading to severe disease and production losses due to disfigurement and death, particularly in small fishes.

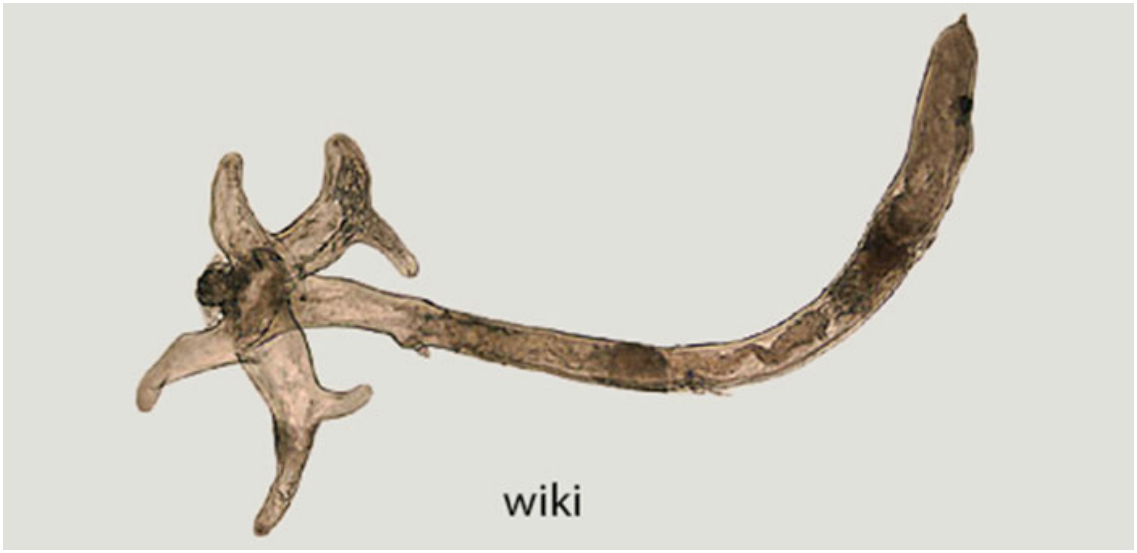
Developmental cycle and mode of transmission: Like all copepods, *Lernaea* spp. undergo gradual metamorphosis where they slowly change from larval naupliar stages (several instars) to subadult copepodid stages (several instars) and then to adults which mate with females producing egg strings. Unlike many copepods, not all stages are free-living in aquatic environments, as some developmental stages have become parasitic on fish hosts: in this case, all copepodid instars and adult females. Eggs released by gravid females hatch in water in 1-3 days releasing free-swimming nauplii larvae, which develop through 3 instars (N1-3) over 3-16 days depending on species and temperature (most species faster in warmer waters). The nauplii do not feed on plankton but are

lecithotrophic and are nourished by yolk stores. N3 then moult to copepodid stages which are parasitic and actively seek fish hosts, attaching to the gills or body with attrition of their swimming legs to short stumps. They are obligate parasites as no further development will occur if they do not find a host. The parasite develops through 5 copepodid instars (Co1-5) over 7-12 days. With each moult, the copepodids reform their appendages regaining the ability to swim. They move about but quickly re-attach, usually to the same host but sometimes to other hosts. The final copepodid moult produces pre-metamorphic males and females which are free-swimming cyclopoid-like stages. Mating occurs at this time, with males subsequently dying (within 24 hours) but fertilized females actively seeking fish hosts (the same or new hosts). Females use their heads and mouthparts to penetrate the host skin and permanently attach by developing the characteristic large anterior holdfast (anchor). Their bodies also elongate and transform into cylindrical worm-like threads hanging from the fish's body. The swimming legs remain but quickly atrophy and any body segmentation becomes inconspicuous. They develop long paired posterior egg sacs as early as 24 hours after attachment. The first egg sacs produced are small with approximately 100 eggs, while new eggs sacs are produced every 3-7 days while the female is reproductively active (usually for around 4 weeks). Subsequent egg sacs may contain up to 500 eggs for 3-4 cycles before slowly diminishing to exhaustion. The entire life-cycle may be completed in as little as 18-25 days under optimal conditions (temperatures from 25-30ºC), but juveniles cannot complete development at temperatures below 20ºC and female will not produce egg sacs at temperatures under 14ºC. However, females can overwinter on fish hosts and resume egg production when temperatures rise in the spring. Parasites are usually multivoltine in tropical and subtropical regions producing several generations each year, but univoltine in colder temperate regions with only one generation per year. Infections are more common on fishes in stagnant and slowly-moving water bodies. Because the parasitic stages (copepodids and adult female) do not necessarily occur on the same individual fish, some early authorities suggested that copepodid infections should be recorded as occurring on intermediate hosts while adult females parasitize definitive hosts. This has not gained great acceptance as piscine intermediate and definitive hosts tend not to differ, particularly in small closed systems, and infections by both stages have been recorded on many fish. Transmission between fish is direct via free-swimming stages in water, and is readily achieved in confined spaces or in crowded populations.

Differential diagnosis: Infections may be diagnosed by the direct detection of adult female parasites dangling from host surfaces as small thin threads or hairs around 20 mm long. They often appear as tiny white-green or red worms embedded in small patches of inflamed tissues. Under magnification, adult female worms are readily identified by their embedded anchors, tubular bodies and paired posterior egg sacs. At necropsy, infections by copepodid stages may detected by microscopy of wet mounts of gill filaments, skin or fins. Molecular biological studies have been conducted to characterize species by polymerase chain reaction (PCR) amplification of nuclear (ribosomal DNA) and mitochondrial (cytochrome oxidase 1) gene sequences.

Treatment and control: Infections by a few anchor worms in a few fish can be treated by manual extraction using tweezers or forceps, although the worms may tear leaving the embedded anchors to fester. Fish should be regularly monitored for wounds by careful observation, and optimal water quality should be maintained to minimize the risk of secondary infections. *Lernaea* spp. develop best at warmer temperatures (especially above 25ºC) and parasite populations can escalate quickly under those conditions. While water temperatures in small aquaria may be lowered to limit parasite numbers, thermal regulation in larger culture systems and outdoor ponds and streams is nigh on impossible. Chemical treatments, however, can be used to suppress parasite populations, but they must be repeated at regular intervals (several weeks) as the embedded adult females are quite resistant to many treatments. The most commonly applied treatment, which is approved for use on food fish species, is the application of salt in the form of salinity baths. Good results have been recorded using 0.5% salinity (1/7 that of seawater) for up to 30 days in those fish species that can tolerate such exposure. Many studies have experimented with concentration-time variations (ranging from low salinity for long periods to high salinity for short periods) depending on host tolerances. Alternatively, traditional treatments with quicklime, potassium permanganate and formalin baths have yielded variable results, but none of these are suitable for food fish species. Ornamental fishes have been successfully treated with several pesticides incorporated into baths; including organophosphates (trichlorfon), pyrethroids (fenvalerate) and insect growth regulators (diflubenzeron). There is some anecdotal evidence to suggest that fish that have been successfully treated may be more resistant to subsequent infections. Indeed, fish that have recovered from infection without treatment appear to be somewhat resistant to subsequent infection. Health checks should be instigated before and after fish translocations, with quarantine measures being adopted when new stocks are introduced into culture facilities.

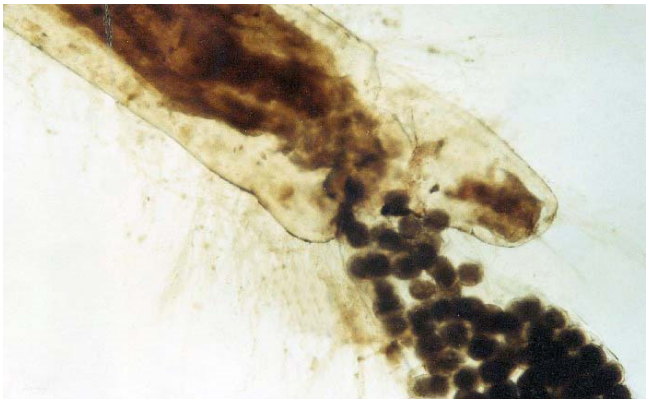

Lernaea
skin, gills
(trauma, lesions, inflammation,
ulceration, respiratory distress)
Definitive Hosts
(freshwater fish,
esp. cyprinids)
female ectoparasitic
attach using anterior
anchor-like holdfast
(feeds on host tissues)
adult female
(~ 15 mm)
eggs
shed
in
water
eggs
(~ 80 µm)
hatch
male
female
copepodid (dorsal)
(~ 5 mm)
[5 instars]
nauplius (ventral)
(~ 0.8 mm)
[3 instars]
ectoparasitic stages
(copepodids attach to hosts,
detach and re-attach)
free-swimming
stage



Lernaea adult



Lernaea adult, egg sacs



Lernaea adult, egg sac junction

Ergasilus
(crustacean: copepod)

Introduction

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and most grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Crustaceans have a very strong cuticle strengthened by calcium salts; thus their growth must proceed through repeated moults. Most species are aquatic with internal or external gills, two pairs of antennae, mouthparts comprising one pair of mandibles and two pairs of maxillae, and each heteronomous body segment usually bears a pair of ventral biramous extremities (podia). Maxillopods lack appendages on abdominal segments and the nauplius larval stage has a unique maxillopodan eye. Copepods have an elongate segmented body (first few thoracic segments fused with head to form cephalothorax) and they undergo gradual metamorphosis with a series of copepodid instars succeeding naupliar instars. Many species are free-living, although some are ectoparasitic on fish. Poecilostomatoid copepods range from simple parasitic forms of fishes to bizarre symbiotic forms of invertebrates. Adult segmentation is often lost, the antennules are small in size and the buccal cavity is slit-like. Ergasilids have antennae highly modified to attach to freshwater and marine fishes. Infestations by *Ergasilus* spp. on the gills cause respiratory problems and mortalities, particularly in aquaculture facilities.

Classification:

Supergroup:	Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom:	Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group:	Protostomia (triploblastic, spiral cleavage)
Subgroup:	Ecdysozoa (cuticle moulted = ecdysis)
Phylum:	Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum:	Crustacea (mandibular mouthparts, gills, two pairs antennae, biramous podia, larval nauplius/zoea)
Class:	Maxillipoda (nauplius with maxillipodan eye)
Subclass:	Copepoda (elongate body, series of copepodid instars succeeding naupliar instars, several ectoparasites)
Order:	Cyclopoida (formerly Poecilostomatoida, now 'poecilostome' lineage comprising simple parasitic forms of fishes to bizarre symbiotic forms of invertebrates)
Family:	Ergasilidae (antennae modified into powerful attachment organs, parasitic in freshwater and marine fishes)
Genus:	*Ergasilus* (parasitic on gills of fish)
Species:	various species cause respiratory problems in fishes

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Crustaceans have very strong cuticles strengthened by calcium salts, so they moult periodically as they grow and metamorphose through different types of larval stages before forming adults. Most species are aquatic and have internal or external gills, while terrestrial species have internal gills which are kept moist. Crustaceans have mouthparts with two pairs of maxillae (to handle food) and paired mandibles (with opposing biting and grinding surfaces). They have two sets of antennae and each body segment usually gives rise to a pair of ventral biramous appendages (podia). Six crustacean classes are recognized: Brachiopoda, Cephalocarida, Malacostraca, Maxillipoda, Ostracoda and Remipedia. Maxillopods usually have a body plan comprising 5 cephalic, 6 thoracic and 4 abdominal segments followed by a telson. The thoracic segments bear biramous (sometimes uniramous) limbs, but the abdominal segments lack appendages. The carapace is present or reduced, most feed using maxillae, and the nauplius larval stages have unique eyes with three cups, each with tapetal cells (= maxillopodan eye). Six maxillopodan subclasses are recognized: Branchiura, Cirripedia, Copepoda, Mystacocarida, Pentastomatida and Tantulocarida.

Major parasitic crustacean families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Class: Maxillipoda					
Subclass: Copepoda (copepods)					
Order: Cyclopoida (open buccal cavity)					
Family: Lernaeidae	19 genera,	freshwater fishes	copepodids	skin	direct (water)

(anchor worms)	114 spp.		and adults	lesions	
Former order: Poecilostomatoida (slit-like buccal cavity)[now a "poecilostome" lineage within the Cyclopoida]					
Family: Ergasilidae (gill lice)	27 genera 61 spp.	freshwater and marine fish	adult ♀	gill/skin lesions	direct (water)
Subclass: Branchiura (head with flattened bilobed cephalic fold, carapace expands laterally)					
Order: Argulidea (discoid bodies, attach using hooks, suckers and barbs)					
Family: Argulidae (fish lice)	4 genera 150 spp.	marine and freshwater fish	juveniles, adults	skin lesions	direct (water)
Subclass: Pentastomatida (tongue worms, elongate annulated bodies, 2 pairs tiny anterior claws near mouth)					
Order: Porocephalida (mouth between/below anterior hooks)					
Family: Porocephalidae	5 genera, 10 spp.	snakes (rodent IH)	adults	lung lesions	indirect (via IH*)
Family: Linguatulidae	1 genus, 4 spp.	carnivorous mammals (mammal IH)	adults	naso-pharyngeal lesions	indirect (via IH*)

*IH = intermediate host

Copepods are small aquatic crustaceans that are one of the most speciose metazoan groups in aquatic communities (over 13,000 morpho-species known). They inhabit a wide range of water sources, ranging from oceans and marine sediments, freshwater streams, rivers, lakes, subterranean cave pools, and even damp leaf litter and puddles in bromeliad leaves. Most species are free-living (important as both predators and prey in planktonic food chains) and some are symbiotic or internal/external parasites of other metazoa, including commercial fish species. Copepods lack a carapace and have elongate segmented bodies (first few thoracic segments fused with head to form cephalothorax) with a single pair of uniramous maxillipods and four pairs of biramous thoracic swimming appendages. They undergo gradual metamorphosis with a series of copepodid instars succeeding naupliar instars. Copepods have been classified within 2 superorders: Gymnoplea (prosome-urosome division posterior to fifth leg-bearing somite) with 2 orders (Calanoida and Platycopioida) and Podoplea (prosome-urosome division anterior to fifth leg-bearing somite) with 9 orders (Canuelloida, Cyclopoida (incl. Poecilostomatoida which is no longer recognised as a valid order as all its cognate families form a well-defined "poecilostome" lineage within the Cyclopoida), Gelyelloida, Harpacticoida, Misophrioida, Monstrilloida, Mormonilloida, Platycopioida and Siphonostomatoida). Members of the former order Poecilostomatida (now the 'poecilostome' lineage in the order Cyclopoida s.s.) form adults with slit-like buccal cavities as simple parasitic forms on fish or as bizarre symbiotic forms on invertebrates. A total of 64 'poecilostome' families are recognized, including the family Ergasilidae. This family is unusual in that only adult females are parasitic (typically on fishes) while all developmental stages and males are free-living. Females have modified claw-like antennae which act as powerful organs of prehension used to attach to the gills (and sometimes skin) mostly of freshwater and some marine fishes, although some occur on bivalve molluscs. A total of 30 genera have been described (*Abergasilus*, *Acusicola*, *Amplexibranchius*, *Anklobrachius*, *Brasergasilus*, *Dermoergasilus*, *Duoergasilus*, *Ergasilus*, *Gamidactylus*, *Gamispatulus*, *Gamispinus*, *Gauchergasilus*, *Majalincola*, *Miracetyma*, *Mugilicola*, *Neoergasilus*, *Nipergasilus*, *Paeonodes*, *Paraergasilus*, *Pindapixara*, *Prehendorastrus*, *Pseudovaigamus*, *Rhinergasilus*, *Sinergasilus*, *Teredophilus*, *Therodamas*, *Thersitina*, *Tiddergasilus*, *Urogasilus* and *Vaigamus*) from hosts found near the coasts of all continents except Antarctica. The genus *Ergasilus* contains 158 species of gill lice recorded from a wide range of fish species, sometimes in association with lesions and respiratory diseases, particularly in aquaculture facilities, aquaria or overstocked fisheries.

***Ergasilus* species**	**Hosts**	**Distribution**
E. acusicestraeus	Mugiliformes: mugilid (Goldie River mullet)	Papua New Guinea
E. anchoratus	Siluriformes: silurid (Amur catfish); Tetraodontiformes: balistid (yellowmargin triggerfish)	Asia
E. argulus	Beloniformes: belonid (freshwater needlefish, shoulderspot needlefish)	Americas
E. arthrosis	Acanthuriformes: sciaenid (freshwater drum); Atheriniformes: atherinopsid (brook silverside); Beloniformes: belonid (Atlantic needlefish); Carangiformes: carangid (crevalle jack); Clupeiformes: clupeid (skipjack shad); Perciformes: centrarchid (warmouth, bluegill, dollar sunfish, longear sunfish, redear sunfish, spotted sunfish, spotted bass, largemouth bass, white crappie, black crappie), moronid (striped bass, white perch, yellow bass), percid (common logperch, yellow perch); Percopsiformes: aphredoderid (pirate perch); Pleuronectiformes: achirid (lined sole); Siluriformes: ictalurid (flathead catfish, blue catfish, black bullhead, yellow bullhead, brown bullhead, channel catfish)	North America
E. atafonensis	Mugiliformes: mugilid (fantail mullet, redeye mullet, white mullet, Lebranche mullet)	North America
E. auritus	Gasterosteiformes: gasterosteid (ninespine stickleback, three-spined stickleback); Gobiiformes: oxudercid (longjaw mudsucker); Osmeriformes: osmerid (rainbow smelt); Salmoniformes: salmonid (lake trout, brook trout, sockeye salmon, coho salmon, lake whitefish, cisco); Scorpaeniformes: cottid (Amur sculpin)	North America

E. australiensis	Mugiliformes: mugilid (yellow-eye mullet); Perciformes: sparid (goldsilk seabream, black bream, yellowfin bream), toxotid (largescale archerfish)	Australia
E. bagarii	Siluriformes: sisorid (devil catfish)	China
E. bahiensis	Mugiliformes: mugilid (white mullet)	Americas
E. bani	free-swimming	Japan
E. barbi	Cypriniformes: cyprinid (shabout)	Asia
E. batai	Cypriniformes: cyprinid (bata)	India
E. bengalensis	Siluriformes: silurid (wallago catfish)	Asia
E. boettgeri	Cyprinodontiformes: poecilid short-finned molly)	North America
E. boleophthalmi	Gobiiformes: gobiid (brown frillfin), oxudercid (mudskipper)	Middle-East, Africa
E. borneoensis	Perciformes: serranid (Malabar grouper); Labriformes: labrid (rainbow wrasse)	Indonesia
E. brari	Siluriformes: silurid (wallago catfish)	Asia
E. brevimanus	free-swimming	Africa
E. briani (syn. *E. minor*)	Cypriniformes: cyprinid (bitterling, redfin, yellowfin, Amur ide, white Amur bream, stone moroko, sunbleak, silver carp, spotted steed, yellowcheek, goldfish, common bleak, Chinese bleak, common bream, zope, Khanka gudgeon, threelips, Mossul bleak, Eurasian carp, gudgeon, sharpbelly, tench, common roach), cobitid (pond loach), gobionid (Soldatov's gudgeon), xenocypridid (grass carp); Gobiiformes: odontobutid (sleeper); Osmeriformes: osmerid (European smelt); Perciformes: sparid (blackhead seabream), percid (redfin perch); Salmoniformes: salmonid (pink salmon, rainbow trout); Siluriformes: bagrid (yellowhead catfish)	Eurasia, Africa
E. bryconis	Characiformes: characid (red-tailed brycon); Siluriformes: doradid (granulated catfish)	Americas
E. caeruleus	Acanthuriformes: sciaenid (freshwater drum); Anguilliformes: anguillid (American eel); Cypriniformes: catostomid (silver redhorse, lake chubsucker, white sucker, longnose sucker, quillback, golden redhorse, shorthead redhorse), cyprinid (fallfish, creek chub, redfin shiner, common shiner, Eurasian carp), leuciscid (chiselmouth, longnose dace); Cyprinodontiformes: fundulid (golden topminnow); Esociformes: esocid (muskellunge); Gadiformes: lotid (burbot); Lepisosteiformes: lepisosteid (alligator gar, shortnose gar, longnose gar); Perciformes: centrarchid (black crappie, redbreast sunfish, dollar sunfish, red-ear sunfish, spotted sunfish, bluespotted sunfish, flier, rock bass, green sunfish, pumpkinseed, warmouth, orange-spotted sunfish, bluegill, longear sunfish, smallmouth bass, spotted bass, largemouth bass, white crappie, black crappie), moronid (white bass), percid (blue walleye, black-banded darter, yellow perch, sauger, walleye, cisco, lake whitefish, brook trout, lake trout); Percopsiformes: aphredoderid (pitate perch), percopsid (trout-perch); Petromyzontiformes: petromyzontid (sea lamprey); Salmoniformes: salmonid (sockeye salmon, round whitefish); Siluriformes: ictalurid (stonecat, tadpole madtom)	cosmopolitan
E. callophysus	Siluriformes: pimelodid (vulture catfish)	South America
E. caraguatatubensis	Mugiliformes: mugilid (white mullet, redeye mullet, liza)	Atlantic
E. celestis (syn. *E. osburni*)	Anguilliformes: anguillid (American eel); Gadiformes: lotid (burbot); Perciformes: percid (walleye)	North America
E. centrarchidarum (syn. *E. nigritus*)	Cypriniformes: catostomid (longnose sucker, lake chubsucker), cyprinid (creek chub); Gadiformes: gadid (frostfish); Osmeriformes: osmerid (European smelt, rainbow smelt); Perciformes: centrarchid (smallmouth bass, bluegill, pumpkinseed, rock bass, mud sunfish, redbreast sunfish, redear sunfish, flier, green sunfish, white crappie, black crappie, warmouth, bluegill, spotted bass, largemouth bass), moronid (white bass), percid (yellow perch, redfin perch, sauger, walleye)	North America
E. cerastes	Siluriformes: ictalurid (channel catfish, brown bullhead, yellow bullhead, white bullhead, blue catfish)	North America
E. ceylonensis	Cichliformes: cichlid (green chromide); Cypriniformes: cyprinid (olive barb)	India
E. chautauquaensis	free-swimming	North America
E. chelangulatus	Siluriformes: pimelodid (catfish)	South America
E. clupeidarum	Clupeiformes: clupeid (American gizzard shad, threadfin shad, blueback herring, skipjack shad)	North America
E. coatiarus	Perciformes: sparid (Australasian snapper)	Australasia
E. cochlearius	Siluriformes: sisorid (sucker catfish)	Asia
E. colomesus	Tetraodontiformes: tetraodontid (Amazon puffer)	South America
E. coniformis	Cypriniformes: cyprinid (pale bleak)	Asia
E. cotti	Perciformes: percid (rainbow darter); Scorpaeniformes: cottid (mottled sculpin)	North America

E. cunningtoni	Characiformes: alestid (African tigerfish, elongate tigerfish, nurse tetra, kawara), distichodontid (grass-eater, African pike-characin, harmaahertta tetra); Cichliformes: cichlid (microdon, lohe, Congo cichlid); Clupeiformes: clupeid (pellonula, small-toothed pellonula); Cypriniformes: cyprinid (Senegal trout-barb, blackstripe barb); Osteoglossiformes: mormyrid (Cornish jack, elephant fish, elephant-nosed fish, rypoun obrooky, lundembe, mbamzogh, Niger mormyrid, Greshoff's mormyrid); Siluriformes: mochokid (blotched upside-down catfish), schilbeid (schilbid catfish)	Africa
E. curticrus	Characiformes: characid (black fin)	South America
E. cyanopictus	Mugiliformes: mugilid (flathead grey mullet	Asia
E. cyprinaceus	Cypriniformes: cyprinid (creek chub, silver chub, bluehead chub, golden shiner, bandfin shiner, bluntnose minnow), leuciscid (weed shiner, blacktail shiner, rough shiner, greenhead shiner, highscale shiner, longnose shiner, cherryfin shiner, central stoneroller, clear chub); Cyprinodontiformes: fundulid (black-spotted top minnow); Gasterosteiformes: gasterosteid (brook stickleback); Perciformes: centrarchid (black crappie); Siluriformes: ictalurid (freckled madtom, yellow bullhead, brown bullhead)	North America
E. danjiangensis	Cypriniformes: cyprinid (pale bleak(, xenocypridid (ahmattibarbi)	China
E. davidi	Perciformes: centropomid (common snook), lutjanid (yellow snapper)	Americas
E. divergens	free-swimming	Europe
E. ecuadorensis	Mugiliformes: mugilid (white mullet, hospe mullet)	Atlantic
E. egyptiacus	Cichliformes: cichlid (redbelly tilapia)	Africa
E. enshiensis	Cypriniformes: cyprinid (sichuani sirgsuu)	China
E. extensus	Mugiliformes: mugilid (pinkeye mullet)	Australia
E. felichthys (syn. *E. elongatus, thomseni*)	Acipenseriformes: polyodontid (American paddlefish); Siluriformes: ariid (hardhead catfish, gafftopsail catfish)	North America
E. fidiformis	Cypriniformes: leuciscid (big-scaled redfin)	Asia
E. flaccidus	Cichliformes: cichlid (Tanganyika tilapia)	Africa
E. foresti	free-swimming	South America
E. fryeri	Cichliformes: cichlid (redbelly tilapia); Mugiliformes: mugilid (golden grey mullet, thinlip mullet, flathead grey mullet)	Africa
E. funduli	Atheriniformes: atherinopsid (inland silverside); Cyprinodontiformes: cyprinodontid (American flagfish, sheepshead minnow), fundulid (mummichog, longnose killifish, Gulf killifish, diamond killifish, Bayou killifish, marsh killifish, rainwater killifish), poecilid (western mosquitofish, sailfin molly); Gasterosteiformes: gasterosteid (three-spined stickleback, black-spotted stickleback); Osmeriformes: osmerid (rainbow smelt)	North America
E. genuinus (syn. *Limnoncaea*)	free-swimming	Japan
E. gibbus	Anguilliformes: anguillid (European eel); Gobiiformes: gobiid (round goby)	Europe
E. glyptothoracis	Siluriformes: sisorid (kani tengra)	Asia
E. gobiorum	Gobiiformes: gobiid (racer goby, monkey goby, bighead goby)	Eurasia
E. hamiltoni	Anabantiformes: anabantid (climbing perch)	Asia
E. hemibagri	Siluriformes: bagrid (largefin longbarbel catfish)	China
E. holobryconis	Characiformes: bryconid (mourning tetra)	South America
E. hydrolycus	Characiformes: cynodontid (payara)	South America
E. hypomesi	Cypriniformes: cyprinid (bronze gudgeon); Osmeriformes: osmerid (pond smelt)	Eurasia
E. hypophthalmi	Siluriformes: pimelodid (highwaterman catfish)	South America
E. ilani	Mugiliformes: mugilid (flathead grey mullet, South African mullet)	Africa
E. inflatipes	Beloniformes: belonid (Senegal needlefish)	Africa
E. intermedius	Clupeiformes: cluperid (bony bream); Perciformes: percichthyid (golden perch, trout cod); Siluriformes: plotosid (eel-tailed catfish)	Australia
E. iraquensis	Mugiliformes: mugilid (greenback mullet)	Indo-Pacific
E. jaraquensis	Characiformes: prochilodontid (kissing prochilodus)	South America
E. jiangxiensis	Cypriniformes: cyprinid (sharpbelly)	North America
E. kabatai	free-swimming	India
E. kandti	Characiformes: citharinid (moonfish); Cichliformes: cichlid (latticed cichlid, Tanganyika tilapia, Congo cichlid, hump-back bream, Mweru hump-backed bream, tanga, petokotiloahven, juovasuomunsyoja, juhmurisuomunsyoja); Perciformes: latid (Nile perch); Siluriformes: bagrid (bayad); mochokid (moustache catfish), schilbeid (silver butter catfish)	Africa

E. kimi	Myliobatiformes: dasyatid (marbled whipray)	Indonesia
E. labracis	Atheriniformes: atherinopsid (golden silverside); Gadiformes: gadid (Atlantic tomcod); Gasterosteiformes: gasterosteid (three-spined stickleback); Osmeriformes: osmerid (rainbow smelt); Perciformes: moronid (white perch, striped bass); Salmoniformes: salmonid (Atlantic salmon, brook trout)	North America
E. lacusauratus	Characiformes: characid (golden dorado)	South America
E. lagunaris	free-swimming	Europe
E. lamellifer	Cichliformes: cichlid (Alluaud's haplo, bicolor haplo, degen haplo, guiarti haplo, longirostris haplo, obesus haplo, nuchisquamulatus, obliquidens); Siluriformes: schilbeid (glass schilbid)	Africa
E. lanceolatus	Clupeiformes: clupeid (American gizzard shad); Hiodontiformes: hiodontid (mooneye)	North America
E. latus	Cichliformes: cichlid (redbelly tilapia, Nile tilapia, Guinean tilapia, mango tilapia, blackchin tilapia, ekouni); Siluriformes: claroteid (giraffe catfish, bagrid catfish), schilbeid (African butter catfish)	Africa
E. leiocassi	free-swimming	China
E. leporinidis	Characiformes: anostomid (black-banded leporinus)	South America
E. lizae (syn. *E. nanus*)	Acanthuriformes: sciaenid (Atlantic croaker, spot croaker); Anguilliformes: anguillid (European eel); Carangiformes: carangid (Florida pompano); Cichliformes: cichlid (blue tilapia, redbelly tilapia, mango tilapia); Clupeiformes: clupeid (twait shad); Cypriniformes: cyprinid (common barbel, white bream, gudgeon, common chub, common minnow); Cyprinodontiformes: cyprinodontid (sheepshead minnow, gold-spotted killifish), fundulid (Gulf killifish, banded killifish, longnose killifish); Gobiiformes: gobiid (round goby); Mugiliformes: mugilid (thinlip mullet, thicklip grey mullet, flathead grey mullet, leaping mullet, longarm mullet, fantail mullet, pinkeye mullet, golden grey mullet, goldspot mullet, white mullet, so-iuy mullet); Ovalentaria: embiotocid (shiner perch); Perciformes: centrarchid (largemouth bass, redear sunfish, bluegill), ephippid (Atlantic spadefish), moronid (striped bass), sparid (pinfish, yellowfin bream, goldsilk seabream, black bream); Pleuronectiformes: soleid (common sole); Siluriformes: clariid (mudfish)	Americas, Eurasia, Australia
E. lobus	Perciformes: serranid (Malabar grouper)	Asia
E. longicaudatus	free-swimming	Europe
E. longimanus	Mugiliformes: mugilid (flathead grey mullet	Asia
E. longipalpus	Tetraodontiformes: diodontid (bridled burrfish)	Americas
E. luciopercarum (syn. *E. confusus, skrjabini*)	Anguilliformes: anguillid (American eel); Clupeiformes: clupeid (alewife); Cypriniformes: catostomid (white sucker), cyprinid (fathead minnow); Esociformes: esocid (northern pike); Gadiformes: lotid (burbot); Perciformes: centrarchid (rock bass, smallmouth bass, largemouth bass), moronid (white perch, white bass), percid (yellow perch, redfin perch, sauger, walleye), percopsid (trout-perch); Salmoniformes: salmonid (Atlantic salmon, rainbow trout, cisco, lake whitefish, round whitefish, chinook salmon, brown trout, brook trout, lake trout)	North America
E. ludhianata	Cypriniformes: cyprinid (Eurasian carp)	Eurasia
E. macrodactylus	Characiformes: alestid (imberi); Cichliformes: cichlid (haplo, tilapia, sandeater, mbuna)	Africa
E. magnicornis	Cypriniformes: cyprinid (goldfish, crucian carp); Mugiliformes: mugilid (greenback mullet)	Australasia
E. malnadensis	Siluriformes: silurid (wallago catfish)	Asia
E. manicatus	Atheriniformes: atherinopsid (inland silverside, tidewater silverside, Atlantic silverside); Cypriniformes: catostomid (lake chubsucker); Cyprinodontiformes: fundulid (mummichog, striped killifish, rainwater killifish, sheepshead minnow); Gasterosteiformes: gasterosteid (three-spined stickleback, blackspotted stickleback); Osmeriformes: osmerid (rainbow smelt)	North America
E. megaceros (syn. *E. fragilis*)	Clupeiformes: clupeid (American gizzard shad); Cypriniformes: catostomid (lake chubsucker, creek chubsucker, blacktail redhorse, white sucker), cyprinid (fallfish, golden shiner, silver chub, blacktail shiner, pretty shiner, cherryfin shiner, pugnose minnow, fathead minnow, bullhead minnow), leuciscid (Mississippi silvery minnow, silver chub, weed shiner, fluvial shiner, silverband shiner); Esociformes: esocid (chain pickerel, redfin pickerel); Perciformes: centrarchid (rock bass, largemouth bass); Petromyzontiformes: petromyzontid (sea lamprey); Siluriformes: ictalurid (channel catfish, black bullhead, yellow	North America

	bullhead)	
E. megacheir	Cichliformes: cichlid (Congo cichlid, humphead cichlid, scale-eater, raitapetoahven, pikkupetoahven, petosuuhautoja, kalterilevahautoja, keltavatsahautoja, juhmurisusomunsyoja); Siluriformes: mochokid (upside-down catfish, cuckoo catfish)	Africa
E. mendisi	Siluriformes: silurid (butter catfish)	Asia
E. mirabilis	Characiformes: alestid (African tigerfish, spot-tail), hepsetid (African pike characin); Cichliformes: cichlid (banded jewel cichlid); Cypriniformes: cyprinid (rednose labeo, Hamilton's barb); Gobiiformes: gobiid (tank goby); Osteoglossiformes: mormyrid (Zambesi parrotfish, bulldog, churchill); Siluriformes: clariid (African sharptooth catfish, blunt-toothed African catfish), mochokid (leopard squeaker, largespot squeaker, blackspotted squeaker, brown squeaker), schilbeid (silver catfish, African butter catfish)	Africa
E. monodi	Perciformes: lobotid (Atlantic tripletail); Siluriformes: ariid (hardhead catfish)	Americas
E. mosulensis	Cyprinformes: cyprinid (Mesopotamian himri, kangal fish); Mugiliformes: mugilid (Abu mullet, largescale mullet, rock mullet, bluespot mullet)	Africa
E. mugilis	Acanthuriformes: sciaenid (spot croaker, Atlantic croaker); Elopiformes: elopid (ladyfish); Mugiliformes: mugilid (thinlip mullet, flathead grey mullet, white mullet)	North America
E. myctarothes	Carcharhiniformes: sphyrnid (smooth hammerhead shark)	Jamacia
E. nerkae	Cypriniformes: catostomid (longnose sucker, white sucker, largescale sucker, Utah sucker, shorthead redhorse), cyprinid (peamouth), leuciscid (lake chub, Utah chub, spottail shiner, redside shiner, northern squawfish); Gasterosteiformes: gasterosteid (three-spined stickleback, ninespine stickleback); Hiodontiformes: hiodontid (goldeneye); Perciformes: centrarchid (largemouth bass), percopsid (trout-perch); Salmoniformes: salmonid (sockeye salmon, coho salmon, lake trout, rainbow trout, lake whitefish, round whitefish, mountain whitefish, cisco, Arctic grayling); Scorpaeniformes: cottid (slimy sculpin)	North America
E. nodosus	Characiformes: alestid (nurse tetra, kawara), distichodontid (harmaahertta tetra, African pike-characin); Cichliformes: cichlid (Congo cichlid, lohe, microdon); Clupeiformes: clupeid (small-toothed pellonula); Osteoglossiformes: mormyrid (elephant-nosed fish, stonebasher, rypoun-obrooky); Siluriformes: bagrid (bayad), mochokid (blotched upside-down catfish)	Africa
E. ogawai	Carangiformes: latid (barramundi); Rhinopristiformes: pristid (largetooth sawfish)	Australia
E. orientalis	Beloniformes: belonid (reef needlefish, nanaifichi); Gobiiformes: oxudercid (yellowfin goby); Mugiliformes: mugilid (squaretail mullet, kanda)	Asia
E. osmeri	Osmeriformes: osmerid (smelt)	Eurasia
E. ovatus	Cypriniformes: cyprinid (goldfish)	Europe
E. pakistanicus	Synbranchiformes: mastacembelid (zig-zag eel)	Asia
E. parabahiensis	Mugiliformes: mugilid (mountain mullet)	South America
E. pararostralis	Mugiliformes: mugilid (greenback mullet)	Middle-East
E. parasiluri	Siluriformes: silurid (Amur catfish)	Asia
E. parvitergum	Acanthuriformes: leiognathid (splendid ponyfish), siganid (golden-lined spinefoot); Anabantiformes: anabantid (climbing perch); Beloniformes: hemiramphid (halfbeak); Carangiformes: carangid (Malabar trevally); Centrarchiformes: terapontid (Jarbua terapon); Cichliformes: cichlid (green chromide, orange chromide, Mozambique tilapia); Clupeiformes: clupeid (Bloch's gizzard shad); Gonorynchiformes: chanid (milkfish); Mugiliformes: mugilid (flathead gray mullet); Ovalentaria: ambassid (bald glassy); Perciformes: lutjanid (snapper); Siluriformes: bagrid (catfish); Tetraodontiformes: triacanthid (short-nosed tripodfish)	Sri Lanka
E. peregrinus	Ababantiformes: channid (northern snakehead); Anguilliformes: anguillid (Japanese eel); Cypriniformes: cyprinid (grass carp, Eurasian carp, yellowcheek, chub, Amur ide), cobitid (pond loach); Gobiiformes: odontobutid (dark sleeper); Perciformes: sinipercid (mandarin fish, golden mandarin fish)	Eurasia
E. philippinensis	Gobiiformes: gobiid (tank goby)	Asia
E. piriformis	Mugiliformes: mugilid (yellowtail mullet)	India
E. pitalicus	Cichliformes: cichlid (cichlid)	Americas
E. plecoglossi	Osmeriformes: plecoglossid (ayu)	Asia
E. polynemi	Perciformes: polynemid (fourfingered threadfin)	Indo-Pacific
E. ponticus	Syngnathiformes: syngnathid (black-stiped pipefish)	Europe

E. rhinos	Perciformes: centrarchid (flier, redbreast sunfish, pumpkinseed)	North America
E. rostralis	Mugiliformes: mugilid (Abu mullet, largescale mullet, goldspot mullet, bluespot mullet, greenback mullet, Tade gray mullet, longarm mullet)	India
E. rotundicorpus	Perciformes: siganid (orange-spotted spinefoot)	Asia
E. salmini	Characiformes: characid (golden dorado)	South America
E. sarsi	Characiformes: alestid (spot-tail); Cichliformes: cichlid (microdon, hump-back bream, Mweru hump-backed bream, paratilapia, mbuna cichlid); Cyprinodontiformes: poecilid (Tanganyika killifish); Osteoglossiformes: mormyrid (bulldog); Siluriformes: clariid (mudfish, blunt-toothed African catfish, African sharptooth catfish, eel-like fattyfin catfish), mormyrid (elephantnose fish), mochokid (blackspotted squeaker)	Africa
E. scalaris	Cypriniformes: cyprinid (yellowcheek); Siluriformes: silurid (Soldatov's catfish)	Eurasia
E. scotti	Siluriformes: silurid (wallago catfish)	Asia
E. sergipensis	free-swimming	South America
E. shehyangensis	Mugiliformes: mugilid (mullet)	Asia
E. sieboldi (syn. *E. baicalensis*, *depressus, esocis, hoferi*, *surbecki, trisetaceus*)	Acanthuriformes: leiognathid (splendid ponyfish); Anabantiformes: anabantid (climbing gourami); Anguilliformes: anguillid (European eel); Beloniformes: hemiramphid (halfbeak), Cichliformes: cichlid (green chromide, orange chromide, Mozambique tilapia); Clupeiformes: clupeid (Bloch's gizzard shad, Pontic shad, Atlantic herring); Cypriniformes: cyprinid (ziege, chub, gudgeon, longspine scraper, seven khramulya, Orontes bleak, Mossul bleak, sunbleak, zope, common bream, white bream, shabout, Mesopotamian himri, binni, crucian carp, broad-snout, asp, Tigris asp, silver carp, ide, Amur ide, common roach, tench, common bleak, grass carp, Eurasian carp, common rudd), gobionid (Soldatov's gudgeon), leuciscid (asp); Esociformes: esocid (northern pike); Gadiformes: lotid (burbot); Gasterosteiformes: gasterosteid (three-spined stickleback); Gobiiformes: gobiid (round goby); Gonorynchiformes: chanid (milkfish); Mugiliformes: mugilid (flathead gray mullet, thinlip mullet, Abu mullet, golden grey mullet, leaping mullet); Osmeriformes: osmerid (European smelt); Ovalentaria: ambassid (bald glassy); Perciformes: centrarchid (warmouth, pumpkinseed), lutjanid (snapper), percid (zander, Volga pikeperch, Eurasian ruffe, redfin perch), siganid (golden-lined spinefoot), terapontid (jarbua terapon); Pleuronectiformes: pleuronectid (European flounder, European plaice), scophthalmid (turbot); Salmoniformes: salmonid (rainbow trout, brown trout, cisco, common whitefish, peled, blaufelchen, grayling); Siluriformes: bagrid (catfish), ictalurid (brown bullhead), silurid (wels catfish)	cosmopolitan
E. sinefalcatus	Characiformes: bryconid (golden dorado)	South America
E. sittangenesis	Mugiliformes: mugilid (Burmese mullet)	Asia
E. spatulus	Beloniformes: belonid (Atlantic needlefish, timucu needlefish)	Americas
E. spinilaminatus	Perciformes: percichthyid (golden perch), terapontid (leathery grunter)	Australia
E. spinipes	Perciformes: sparid (goldsilk seabream)	Africa
E. suboculatus	Mugiliformes: mugilid (thinlip mullet)	Asia
E. synanceiensis	Perciformes: synanceiid (blackfin stonefish)	India
E. thailandensis	free-swimming	Asia
E. thatcheri	Siluriformes: heptapterid (South American catfish)	South America
E. tipurus	Characiformes: cynodontid (biara); Siluriformes: pimelodid (vulture catfish, duckbill catfish)	South America
E. tissensis	Cypriniformes: cyprinid (common barbel)	Europe
E. triangularis	Characiformes: anostomid (striped headstander)	Asia
E. trygonophilus	Myliobatiformes: pomatotrygonid (freshwater stingray, long-tailed river stingray)	South America
E. tumidus	Cypriniformes: cyprinid (bitterling, common minnow, lake minnow); Perciformes: sparid (blackhead seabream)	North America
E. turgidus	Gasterosteiformes: gasterosteid (three-spined stickleback); Ovalentaria: embiotocid (shiner perch); Salmoniformes: salmonid (sockeye salmon); Scorpaeniformes: cottid (roughback sculpin)	North America
E. turkayi	Characiformes: serrasalmid (redhook piranha)	South America
E. turucuyus	Characiformes: acestrorhynchid (pirapuco), characid (pikili)	Africa
E. uniseriatus	Gobiiformes: gobiid (tank goby)	Australasia
E. urupaensis	Characiformes: prochilodontid (black prochilodus)	South America
E. vembanadensis	Siluriformes: silurid (wallago catfish)	Asia
E. ventriosus	Cypriniformes: acheilognathid (uyeki bitterling), cyprinid (pale bleak, giant	Asia

	Chinese bitterling)	
E. versicolor (syn. *E. elegans*)	Anguilliformes: anguillid (American eel); Clupeiformes: clupeid (skipjack shad); Cypriniformes: catostomid (shorthead redhorse, blacktail redhorse, white sucker, spotted sucker, smallmouth buffalo, bigmouth buffalo, lake chubsucker, creek chubsucker, sharpfin chubsucker); Eupercaria: sciaenid (black drum); Gasterosteiformes: gasterosteid (brook stickleback); Lepisosteiformes: lepisosteid (longnose gar, short-nosed gar, alligator gar, Cuban gar); Mugiliformes: mugilid (flathead grey mullet, striped mullet, white mullet); Perciformes: centrarchid (green sunfish, warmouth, bluegill, longear sunfish, largemouth bass, rock bass, spotted bass), moronid (white bass, yellow bass); Siluriformes: ictalurid (black bullhead, brown bullhead, blue catfish, black bullhead, yellow bullhead, brown bullhead, mud cat, Fulton cat, channel catfish, stonecat, flathead catfish, tadpole madtom)	North America
E. wareaglei	Cypriniformes: catostomid (white sucker, northern hog sucker, Alabama hog sucker)	North America
E. wilsoni	Cypriniformes: cyprinid (Zeravshan dace); Gasterosteiformes: gasterosteid (three-spined stickleback); Gobiiformes: gobiid (dusky tripletooth goby, biringo, ukigori); Osmeriformes: osmerid (pond smelt); Salmoniformes: salmonid (pink salmon)	Eurasia
E. xenomelanirisi	Atheriniformes: atherinopsid (Brazilian silverside)	South America
E. xinguensis	Cichliformes: cichlid (Xingu blue streak eartheater, freshwater eartheater)	South America, Asia
E. xinjiangensis	Cypriniformes: cyprinid (balkhash marinka)	China
E. yaluzangbus	Cypriniformes: cyprinid (naked schizothoracin)	Asia
E. yandemontei	Atheriniformes: atherinopsid (pejerrey); Perciformes: percichthyid (perch)	South America
E. youngi	Siluriformes: ariid (cangata)	South America
E. yumaricus	Characiformes: serrasalmid (red-bellied piranha, Eigenmann's piranha, redeye piranha)	South America
E. zacconis	Cypriniformes: cyprinid (pale bleak); Osmeriformes: plecoglossid (ayu)	Asia

Several species have also been reclassified to other genera: including *E. amplectens* = *Dermoergasilus*; *E. biuncinatus* = *Thersitina gasterostei*; *E. coleus* = *Dermoergasilus*; *E. efficatus* = *Bomolochus*; *E. euripedesi* = *Gauchergasilus*; *E. gasterostei* = *Thersitina*; *E. iheringi* = *Tiddergasilus; E. intermedius* = *Dermoergasilus*; *E. japonicus* = *Neoergasilus*; *E. semicoleus* = *Dermoergasilus*; and *E. tenax* = *Acusicola*.

Parasite morphology: *Ergasilus* spp. form 4 different morphological stages during their developmental cycles: eggs; nauplii (3-6 free-swimming instars), copepodids (5 free-swimming instars); and adults (free-swimming males and females, but fertilized females become parasitic on fish gills). The eggs are small (around 0.05 mm), ovoid, white to light brown and located in eggs sacs in multiseriate arrangements until dispersed into the water column. They hatch to release small free-swimming naupliar stages, with different studies reporting 3 or 6 instars (most parasitic taxa have 3 instars, while most free-living taxa have 6). The nauplii grow in size from 0.08-0.25 mm with their small unsegmented bodies possessing only 3 pairs of functional appendages (antennules, antennae, mandibles) and a single unique maxillopodan eye. The antennae do possess feeding processes on the coxae (common to free-living taxa) which supports the view that ergasilid copepodids are planktotrophic and feed on other planktonic organisms (esp. unicellular algae), whereas parasitic copepods have lecithotrophic nauplii relying on yolk stores for nutrients. The final naupliar stage moults to form a copepodid stage which is also free-swimming. Copepodids develop through 5 instars (common to most free-living taxa) and their segmented bodies grow from 0.3-0.8 mm long, adding a body somite at each moult (thus growing from 6-10 segments). They have a cyclopoid body plan similar to adult stages, with a full set of cephalic appendages but the antennae are not modified into claspers and they only have 2 pairs of swimming legs. The final copepodid stages moult into male and female copepods which are free-swimming as they become sexually mature. After mating, the males die while the fertilized females become parasitic on the gills of fish. The most conspicuous change exhibited by parasitic females is the modification of the antennae into large prehensile claws used to clasp gill filaments. The antennae consist of 4 slender segments, the first short, the second long, the third directed inwards, and the fourth ending in a sharp hooked claw. The third and fourth segments are opposable with the second (subchelate) and may pierce gill filaments or completely encircle them. The body lies parallel to the gill filament with the head facing towards the base. Adults have cyclopoid bodies which are pyriform (tapering posteriorly) and range in size from 0.5-2.0 mm in length. The carapace may be transparent to opaque white, sometimes lightly pigmented brown with traces of purple. The elongate body contains 11 segments in males and 10 in females. Segmentation conforms to a podoplean body plan with 4 pairs of legs and the division of the anterior prosome and the posterior urosome occurring after the fourth leg-bearing somite (in contrast to the gymnoplean plan exhibited by many free-living copepods with 5 pairs of legs and the division occurring after the fifth leg-bearing somite). The body is divided into 4 regions: the cephalothorax (with antennules, antennae, mandibles, maxillules, maxillae, and maxillipeds (present only on males)), free thorax (with swimming legs), genital segment (with egg sacs), and abdomen (with caudal structures). The cephalothorax consists of the head fused with the first few thoracic segments. It is dorsoventrally flattened, longer than wide, and rounded anteriorly with a single eye with pigmented inner margins located close to the anterior midline. The

small antennules have 5-6-segments and are sensory with setae on their anterior borders. The mouthparts are small and located ventrally near the centre of the cephalothorax. They are used for scraping or rasping delicate gill tissues (not for biting and chewing) and have been described as poecilostome (slit-like mouths with sickle-shaped mandibles) rather than gnathostome (open mouths with short broad mandibles) or siphonostome (tubular mouth with stylet-like mandibles). A plate-like labrum fused to the ventral surface of the carapace acts like an upper lip, and the mouth contains saw-like mandibles with 3 serrated blades that oppose the elongate maxillae. The maxillules are reduced and appear as lobate papillae bearing setae. The maxillae also have spiny tips that are thought to help grasp gill filaments. The maxillipeds are absent in parasitic females and only develop on males midway through their copepodid developmental stages. Parasitic females are able to move between gill filaments using 4 pairs of swimming legs (their setae are lost soon after attachment). The first legs are attached to the cephalothorax and are often rigid with blade-like spines thought to be used to assist feeding. All legs are biramose with broad coxae and bases, the first endopod contains 2 or 3 segments, the fourth exopod contains 3 segments (except for the fourth pair of legs which have 2 segments), and all other rami have 3 segments. There are conflicting reports about the presence of a fifth pair of legs, but in those instances where they are considered to be present, they are highly reduced to stumpy papillae, sometimes with 1-2 setae. Patterns of leg segmentation and setation have been used to differentiate many ergasilid species. The mouth feeds into the digestive tract consisting of lobulate stomach (with median, diagonal and lateral lobes), tubular intestines (with excretory tubules) and posterior rectum. The free thorax has 4 segments, the fourth one often being reduced and adjoining a robust genital segment (wider than long) bearing oviductal openings. The abdomen narrows posteriorly and lacks appendages (like all maxillopods). The female urosome has 4 well-defined segments (5 in males) and the terminal telson consisting of simple furcal (forked) rami (arms) with long setae (the inner setae being the longest). Fertile females bear paired egg sacs that hang posteriorly from either side of the genital segment (similar to other podoplean copepods). The sacs are initially white ovoid structures but become long cylindrical trailing ‘tails’ that often darken with age to brown. Mature females produce clutches of up to 200-220 multiseriate eggs which are ultimately dispersed to hatch. Males are entirely free-living and do not become parasitic. They are smaller and slenderer than females, their antennae are smaller (but still prehensile), their mouthparts are similar, they possess maxillipeds with long curved terminal segments, their swimming legs have rami with 3 segments, and their abdomens have one more segment than females.

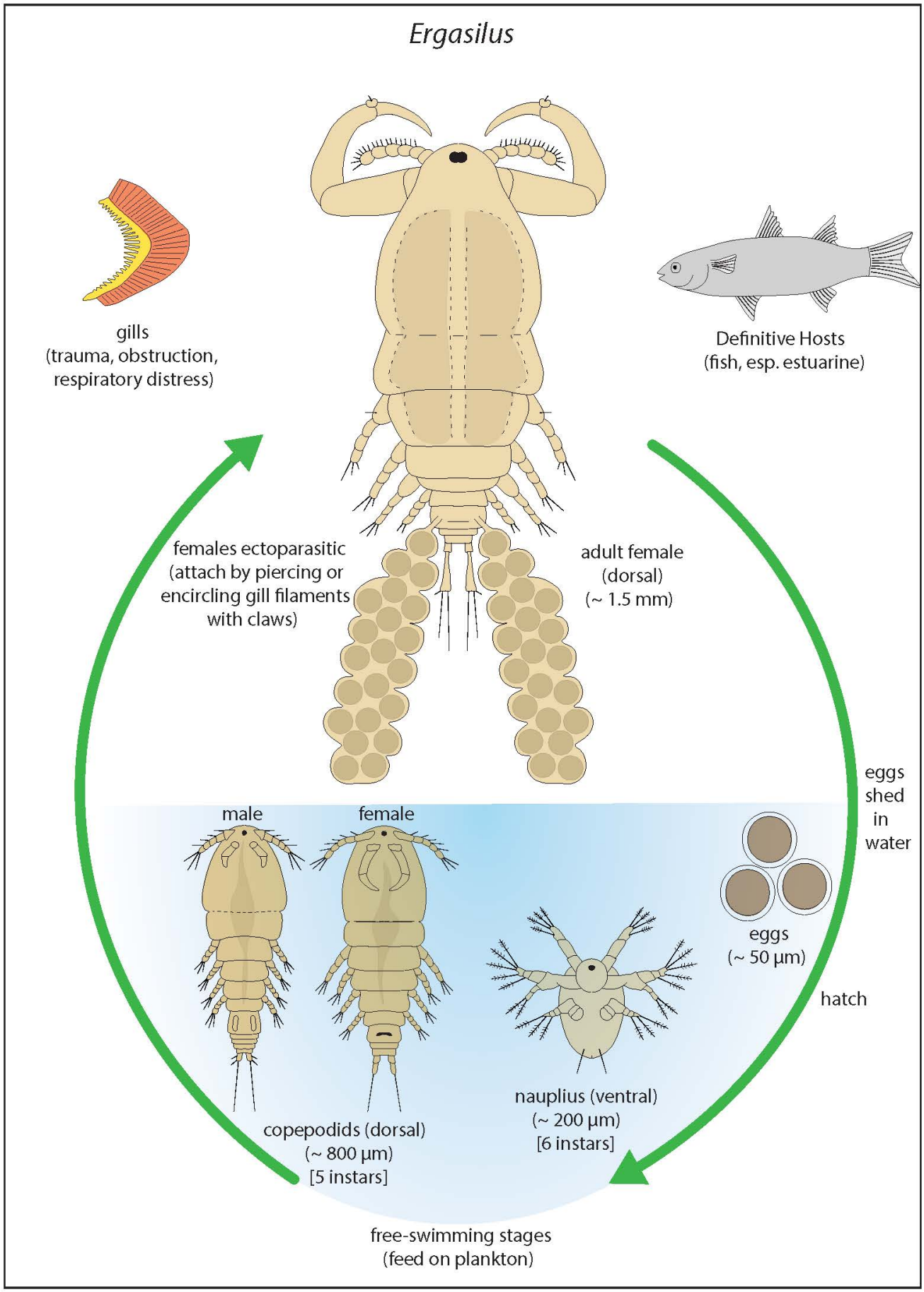
Site of infection: The larval stages (nauplii and copepodids) and young adults are all free-swimming stages living in aquatic environments. However, females become parasitic after mating and seek out fish hosts on which to attach. They typically invade the gill chambers and cling onto gill filaments, but some have been found in the nasal fossae and a few occasionally on the skin and fins. They are typically found on fish around coastal regions, mostly in freshwater but also euryhaline (estuarine and marine) environments. They have a broad host specificity and have been recorded on fish from 33 different orders, as well as on a few sharks and rays. They are most abundant on Cypriniformes, Perciformes, Siluriformes and Mugiliformes.

Pathogenesis: Ergasalid copepods are notorious in aquaculture for causing morbidity (respiratory distress and hypoxia) and mortality. They are often called gill lice, and sometimes gill maggots (due to the appearance of their mature egg sacs). Fertilized females attach to the gills by piercing or encircling gill filaments with their large claws. They use their rasping mouthparts, and possibly enzyme secretions, to feed on epithelial tissues, mucus and blood. Both attachment and feeding cause a range of pathological alterations to the gills, with loss of normal structure and disruption of blood flow leading to respiratory problems. The parasites cause traumatic lesions on the gill filaments with erosion of the surface epithelium, cell necrosis, tissue loss and sometimes small haemorrhages. The host reacts by mounting inflammatory responses with hyperplasia (proliferation) of epithelial cells, rodlet cells, and mucous cells. This leads to compression of the tissues which constricts and occludes blood vessels, further exacerbated by parasites constricting gill filaments with their claw-like antennae. Heavily-infested fish exhibit respiratory distress with hypoxia due to disrupted gas exchange and lamellar fusion, as well as reduced osmoregulatory function, loss of condition, retarded growth and sluggish behaviour sometimes culminating in death. Infested fish are less tolerant of environmental changes associated with local weather patterns (fluctuating temperatures and oxygen levels) and are less able to survive seasonal variations (particularly over-winter). Lesions caused by the parasites are also highly susceptible to secondary infections with bacteria, fungi and viruses. There are anecdotal reports that ergasilids may be able to act as mechanical or even biological vectors for other fish diseases, but further studies (particularly molecular screening) need to confirm these suspicions.

Developmental cycle and mode of transmission: These copepods undergo gradual metamorphosis whereby a succession of free-living planktonic larval stages slowly transform into adults. Only fertilized females then go on to parasitize fish hosts culminating in the production of numerous eggs which embryonate in attached egg sacs. The eggs hatch after 3-6 days releasing small unsegmented nauplii (singular, nauplius) into the water column. Current studies indicate that there are 6 naupliar instars that feed on other planktonic organisms (especially algae) over several weeks. The parasites then form more complex segmented copepodid stages that also swim about feeding on planktonic organisms. There are 5 copepodid instars which become progressively more like adults by the additional of an extra body somite at each moult. Both male and female adult copepods are formed after several weeks and they mate as free-swimming stages. The males do not parasitize fish but die after mating, whereas the fertilized females seek out freshwater, estuarine or marine fishes and become parasitic on their gills by developing specialized claw-like antennae for attachment. Parasitic females may live for up to 1 year and they usually produce 2-5 clutches of 200-200 eggs in that time. The whole life-cycle may be completed in 30-70 days depending on environmental conditions (longer at lower temperatures) and females can over-winter on their fish hosts.

Differential diagnosis: Infestations may be suspected when fish exhibit respiratory distress despite good oxygen levels in the water. Diagnoses are made ante-mortem or post-mortem by direct observation of ergasilids (gill lice or gill maggots) on gill filaments. Gravid female copepods are readily seen as their white-tan egg sacs dangle freely from the tips of gill filaments. The parasites cannot be easily removed intact so biopsy samples of the gill filaments are collected should microscopy be required. Molecular biological techniques have been used to identify and characterize species by polymerase chain reaction (PCR) amplification of nuclear genes sequences (28S ribosomal RNA and internal transcribed spacers 1 and 2).

Treatment and control: The treatment of infestations is difficult for a range of reasons, including the lack of suitable and effective chemotherapeutic agents, the resistance of all developmental stages to a wide range of environmental conditions (salinity, temperature), the persistence of free-living planktonic stages in the water column, the long life-spans and high fecundity of parasitic females, the cryptic nature of many infestations (remaining subclinical for long periods) and the sporadic appearance of outbreaks (often triggered by unknown factors). Nevertheless, because the parasites affect the gills, infested fish are generally more sensitive to changes in water quality and low dissolved oxygen levels. Maintaining good water quality and high oxygen levels will help fish respire and lessen the impact of infestations. Various attempts have been made to treat infections with chemical baths (potassium permanganate, formalin, quicklime, copper solutions, and even organophosphate and pyrethroid insecticides), but none were proven to be very effective. The only way to eradicate parasites and their free-living stages would be to de-stock, drain and lime the entire fishery, which is simply impractical in most situations. Implementing some sensible management procedures may help in controlling infestations in culture facilities; such as carefully managing fish stocks (regular health surveillance, quarantine new stock, avoid over-crowding, culling sick individuals, increasing water flow) and maintaining hygiene (periodically disinfect holding tanks and equipment).


Ergasilus
gills
(trauma, obstruction,
respiratory distress)
Definitive Hosts
(fish, esp. estuarine)
females ectoparasitic
(attach by piercing or
encircling gill filaments
with claws)
adult female
(dorsal)
(~ 1.5 mm)
eggs
shed
in
water
male
female
eggs
(~ 50 µm)
hatch
nauplius (ventral)
(~ 200 µm)
[6 instars]
copepodids (dorsal)
(~ 800 µm)
[5 instars]
free-swimming stages
(feed on plankton)



Ergasilus adults on fish gills



Ergasilus nauplius

Argulus
(crustacean: branchiuran)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and most grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Crustaceans have a very strong cuticle strengthened by calcium salts; thus their growth must proceed through repeated moults. Most species are aquatic with internal or external gills, two pairs of antennae, mouthparts comprising one pair of mandibles and two pairs of maxillae, and each heteronomous body segment usually bears a pair of ventral biramous extremities (podia). Maxillopods lack appendages on abdominal segments and the nauplius larval stage has a unique maxillopodan eye. Branchiurans have dorsoventrally flattened bodies with a head, thorax and abdomen. The head has a flattened bilobed cephalic fold incompletely fused to the first thoracic somite, and the carapace expands laterally to form respiratory alae. They undergo direct (rather than metamorphic) development with eggs releasing juveniles. They are blood-sucking ectoparasites on marine and freshwater fishes, and occasionally amphibians. Argulids (fish lice) have discoid bodies and attach to hosts using hooks, suckers and barbs. Infestations by *Argulus* spp. on the skin and gills may cause lesions, haemorrhage, lethargy and erratic aversion behaviours in afflicted fishes.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Crustacea (mandibular mouthparts, gills, two pairs antennae, biramous podia, larval nauplius/zoea)
Class: Maxillipoda (nauplius with maxillipodan eye)
Subclass: Branchiura (head with bilobed cephalic fold, carapace expands laterally, respiratory alae, blood suckers)
Order: Argulida (single order)
Family: Argulidae (fish lice, discoid body, attaches using hooks/suckers/barbs, stylus inserted to feed on blood)
Genus: *Argulus* (parasitic on skin/gills of fish)
Species: various species cause skin and/or gill lesions in fishes

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Crustaceans have very strong cuticles strengthened by calcium salts, so they moult periodically as they grow and metamorphose through different types of larval stages before forming adults. Most species are aquatic and have internal or external gills, while terrestrial species have internal gills which are kept moist. Crustaceans have mouthparts with two pairs of maxillae (to handle food) and paired mandibles (with opposing biting and grinding surfaces). They have two sets of antennae and each body segment usually gives rise to a pair of ventral biramous appendages (podia). Six crustacean classes are recognized: Brachiopoda, Cephalocarida, Malacostraca, Maxillipoda, Ostracoda and Remipedia. Maxillopods usually have a body plan comprising 5 cephalic, 6 thoracic and 4 abdominal segments followed by a telson. The thoracic segments bear biramous (sometimes uniramous) limbs, but the abdominal segments lack appendages. The carapace is present or reduced, most feed using maxillae, and the nauplius larval stages have unique eyes with three cups, each with tapetal cells (= maxillopodan eye). Six maxillopodan subclasses are recognized: Branchiura, Cirripedia, Copepoda, Mystacocarida, Pentastomatida and Tantulocarida.

Major parasitic crustacean families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Class: Maxillipoda					
Subclass: Copepoda (copepods)					
Order: Cyclopoida (open buccal cavity)					
Family: Lernaeidae	19 genera,	freshwater fishes	copepodids	skin	direct (water)

(anchor worms)	114 spp.		and adults	lesions	
Former order: Poecilostomatoida (slit-like buccal cavity)[now a "poecilostome" lineage within the Cyclopoida]					
Family: Ergasilidae (gill lice)	27 genera 61 spp.	freshwater and marine fish	adult ♀	gill/skin lesions	direct (water)
Subclass: Branchiura (head with flattened bilobed cephalic fold, carapace expands laterally)					
Order: Argulidea (discoid bodies, attach using hooks, suckers and barbs)					
Family: Argulidae (fish lice)	4 genera, 150 species	marine and freshwater fish	juveniles, adults	skin lesions	direct (water)
Subclass: Pentastomatida (tongue worms, elongate annulated bodies, 2 pairs tiny anterior claws near mouth)					
Order: Porocephalida (mouth between/below anterior hooks)					
Family: Porocephalidae	5 genera, 10 spp.	snakes (rodent IH)	adults	lung lesions	indirect (via IH*)
Family: Linguatulidae	1 genus, 4 spp.	carnivorous mammals (mammal IH)	adults	naso-pharyngeal lesions	indirect (via IH*)

*IH = intermediate host

Branchiura (commonly referred to as fish lice) are blood-sucking ectoparasites of freshwater and marine fishes, sometimes amphibians and aquatic invertebrates. One family is recognized, the Argulidae whose adults have dorsoventrally-flattened discoid bodies with a head, thorax and abdomen. The head has a flattened bilobed cephalic fold incompletely fused to the first thoracic somite, and the carapace expands laterally to form respiratory alae. They attach to external surfaces of their fish hosts using modified maxillae bearing hooks or suction discs, and insert a stylus to feed on blood, mucus and/or extracellular material. They undergo direct (rather than metamorphic) development with eggs releasing juveniles. Over 150 spp. have been described in 4 genera: 129 *Argulus* spp. with a worldwide distribution (except Antarctica); 13 *Dolops* spp. and one *Dipteropeltis* sp. from South America; and 14 *Chonopeltis* spp. from Africa. Argulids are transient ectoparasites (semipermanent, intermittent feeders) or micropredators characterized by their ubiquity in natural ecosystems, their low host specificity and their pathogenic potential, especially to overcrowded cultured or aquarium fishes. Several *Argulus* spp. are considered to be serious pests in aquaculture (both freshwater and marine) with heavy infections on cyprinids and salmonids causing traumatic lesions with significant morbidity and mortality. A growing number of species have also proven problematic to the aquarium trade with infections causing mortalities particularly in small ornamental fishes.

***Argulus* species**	**Hosts**	**Distribution**
A. africanus	Anguilliformes: anguillid (African mottled eel); Characiformes: alestid (African tigerfish); Cichliformes: cichlid (Singida tilapia, longfin tilapia, Nile tilapia, Victoria tilapia, thickskin haplo, guiarti haplo, obesus haplo, retrodens haplo); Cypriniformes: cyprinid (labeo); Dipnoi: lepidosirenid (marbled lungfish); Osteoglossiformes: mormyrid (Cornish jack, eastern bottle-nosed mormyrid); Perciformes: latid (forktail lates); Polyperiformes: polypterid (bichir); Siluriformes: bagrid (semutundu, kampango, degeni), clariid (African sharptooth catfish, eel-like fattyfin catfish, mudfish, vundu), claroteid (kibonde), schilbeid (golden barbel)	Africa, Asia
A. alexandrensis	Zeiformes: zeid (dory)	Africa
A. alosae	Batrachoidiformes: batrachoidid (toadfish); Clupeiformes: clupeid (alewife); Gadiformes: gadid (Atlantic tomcod); Gasterosteiformes: gasterosteid (three-spined stickleback); Osmeriformes: osmerid (rainbow smelt); Salmoniformes: salmonid (brook trout)	North America
A. amazonicus	Cichliformes: cichlid (speckled peacock bass), Amazon peacock bass)	South America
A. ambloplites	Anabantiformes: channid (obscure snakehead), Characiformes: alestid (African tigerfish); Siluriformes: clariid (African sharptooth catfish)	Africa
A. ambystoma	Urodela: ambystomatid (Lake Patzcuaro salamander)	Mexico
A. americanus	Amiiformes: amiid (bowfin); Esociformes: umbrid (central mudminnow); Siluriformes: ictalurid (yellow bullhead); Anura: ranid (river frog); Urodela: sirenid (southern dwarf siren)	North America
A. angelae	Characiformes: anostomid (three-spot leporinus, karp-jonn, lisa), curimatid (branquinha, boquiche, beiru, mocinha), cynodontid (biara), hemiodontid (halftooth), prochilodontid (flag-tailed prochilodus), triportheid (pechon)	South America
A. angusticeps	no host recorded	Africa
A. appendiculosus (syn. *A. biramosus*)	Acanthuriformes: sciaenid (freshwater drum); Amiiformes: amiid (bowfin); Clupeiformes: clupeid (American gizzard shad); Cypriniformes: catostomid (quillback, smallmouth buffalo, bigmouth buffalo, white sucker), cyprinid (Eurasian carp), leuciscid (emerald shiner); Esociformes: esocid (northern pike);	North America

	Hiodontiformes: hiodontid (goldeneye); Lepisosteiformes: lepisosteid (longnose gar); Perciformes: centrarchid (largemouth bass, smallmouth bass, white crappie), moronid (white bass), percid (yellow perch, walleye, sauger); Salmoniformes: salmonid (cisco); Siluriformes: ictalurid (brown bullhead, black bullhead, flat bullhead, channel catfish, brindled madtom)	
A. araucanus	Atheriniformes: atherinopsid (neotropical silverside)	South America
A. arcassonensis (syn. *A. otolithi, zei*)	Eupercaria: sciaenid (longneck croaker); Zeiformes: zeid (John dory)	Africa
A. australiensis	Perciformes: sparid (bream)	Australia
A. belones	Beloniformes: belonid (flat needlefish); Istiophoriformes: sphyraenid (great barracuda)	Africa
A. bengalensis	Cypriniformes: cyprinid (carp)	India
A. bicolor	Beloniformes: belonid (redfin needlefish); Carangiformes: carangid (Florida pompano); Perciformes: moronid (striped bass), sparid (western Atlantic seabream)	Americas
A. borealis	Pleuronectiformes: pleuronectid (flathead sole, rock sole), Ovalentaria: embiotocid (shiner perch)	Americas
A. brachypeltis	Characiformes: alestid (African tigerfish); Siluriformes: clariid (African sharptooth catfish)	Africa
A. caecus	Cephalopoda: ommastrephid (Japanese flying squid); Tetraodontiformes: tetraodontid (coastal puffer)	Japan
A. capensis	Anabantiformes: anabantid (Cape kurper)	Africa
A. carteri	Characiformes: erythrinid (wolf fish)	South America
A. catostomi	Cypriniformes: catostomid (white sucker, quillback, longnose sucker, lake chubsucker, northern hogsucker, shorthead redhorse), cyprinid (golden shiner, creek chub), leuciscid (finescale dace); Perciformes: centrarchid (pumpkinseed), percid (Iowa darter, johnny darter); Siluriformes: ictalurid (black bullhead)	North America
A. cauveriensis	free-swimming	India
A. celioi	Siluriformes: loricariid (cascudo preto velho)	South America
A. cheni	Cypriniformes: cyprinid (grass carp)	China
A. chesapeakensis	Pleuronectiformes: paralichthyid (summer flounder)	North America
A. chicomendesi	Characiformes: prochilodontid (black prochilodus)	South America
A. chilensis	Atheriniformes: atherinopsid (neotropical silverside)	South America
A. chinensis	Ababantiformes: channid (northern snakehead); Cypriniformes: cyprinid (black carp); Siluriformes: bagrid (catfish), ictalurid (yellow-barbeled catfish)	China
A. chiropteroideus	Siluriformes: pimelodid (barred sorubim, spotted soru bim)	South America
A. chromidis	Ovalenteria: pomacentrid (chromis?)(maybe a cichlid)	North America
A. confusus sp. inq.	(probably a male of *Argulus ambloplites*)	Africa
A. coregoni (syn. *A. phoxini*)	Cichliformes: cichlid (red tilapia); Cypriniformes: acheilognathid (tanago), cyprinid (black carp); Osmeriformes: plecoglossid (ayu); Salmoniformes: salmonid (rainbow trout, brook trout, cherry trout, white-spotted char)	Asia
A. cubensis	Cichliformes: cichlid (Cuban cichlid)	Americas
A. cunningtoni	Characiformes: distichodontid (Nile distichodus); Cichliformes: cichlid (yellow-belly bream); Perciformes: latid (Nile perch); Siluriformes: bagrid (bayad), clariid (African sharptooth catfish), claroteid (giraffe catfish), mochokid (wahrindi)	Africa
A. dactylopteri	Dactyloperiformes: dactylopterid (flying gurnard)	Africa
A. dageti	Siluriformes: clariid (mudfish, eel-like fattyfin catfish); Tetraodontiformes: tetraodontid (Fahaka puffer)	Africa
A. dartevellei	Perciformes: polynemid (giant African threadfin), serranid (grouper)	Africa
A. diversicolor	Perciformes: sparid (bream)	Australia
A. diversus	Siluriformes: ictalurid (yellow bullhead); Anura: ranid (river frog)	North America
A. ellipticaudatus	Cypriniformes: cyprinid (Eurasian carp)	China
A. elongatus	Characiformes: serrasalmid (red-bellied piranha, catirina, speckled piranha); Cichliformes: cichlid (tucanare peacock bass)	South America
A. ernsti	Cypriniformes: cyprinid (goldfish)	Eurasia
A. exiguus	Cichliformes: cichlid (kalterilevahautoja); Cyprinodontiformes: poecilid (Tanganyika killifish)	Africa
A. flavescens	Acanthuriformes: sciaenid (freshwater drum); Amiiformes: amiid (bowfin); Siluriformes: ictalurid (flathead catfish)	North America
A. floridensis	host unknown (erroneous record in mullet)	North America
A. fluviatilis	free-swimming	India
A. foliaceus (syn. *A. argulus,*	Anguilliformes: anguillid (European eel); Carangiformes: carangid (Atlantic horse mackerel); Cypriniformes: cyprinid (Eurasian carp, zope, common bleak, tench, silver	cosmopolitan

armiger, charon, delphinus, rothschildi, viridis)	carp, ide**,** common roach, goldfish, crucian carp, white bream, seven khramulya, longspine scraper, chub, rudd), leuciscid (Danube bleak); Esociformes: esocid (northern pike); Gasterosteiformes: gasterosteid (three-spined stickleback); Gobiiformes: odontobutid (Chinese sleeper); Mugiliformes: mugilid (Abu mullet); Perciformes: centrarchid (pumpkinseed), percid (redfin perch, zander); Salmoniformes: salmonid (rainbow trout, brown trout); Siluriformes: silurid (wels catfish); Synbranchiformes: mastacembelid (Euphrates spiny eel); Urodela: salamandrid (smooth newt)	
A. fryeri	Cichliformes: cichlid (redbelly tilapia)	Africa
A. funduli (syn. *A. latus*)	Cyprinodontiformes: fundulid (mummichog, striped killifish)	North America
A. fuscus	Carangiformes: carangid (Florida pompano); Perciformes: haemulid (pigfish); Eupercaria: sciaenid (silver perch)	North America
A. giordanii	free-swimming	Europe
A. gracilis	Siluriformes: claroteid (giraffe catfish)	Africa
A. hylae nomen nudum	Anura: hylid (map tree frog)	South America
A. ichesi	Clupeiformes: clupeid (alewife)	South America
A. incisus	Siluriformes: claroteid (giraffe catfish)	Africa
A. indicus	Anabantiformes: channid (giant snakehead, spotted snakehead), osphronemid (snakeskin gourami, Siamese fighting fish); Cypriniformes: cyprinid (Eurasian carp)	Asia
A. ingens	Lepisosteiformes: lepisosteid (Cuban gar)	Americas
A. intectus	Perciformes: sparid (scup)	North America
A. izintwala	Clupeiformes: clupeid (Kelee shad)	Africa
A. japonicus (syn. *A. matritensis, pelucidus*) (Japanese fish louse)	Cichliformes: cichlid (Mozambique tilapia, banded tilapia); Clupeiformes: clupeid (American gizzard shad); Cypriniformes: cyprinid (goldfish, crucian carp, Eurasian carp, common carp, koi carp, Korean carp, grass carp, mrigal carp, Orange River mudfish, Indian carp, Hoven's carp, largescale yellowfish, moggel, smallmouth yellowfish, largemouth yellowfish, papermouth, rohu, fathead minnow, rosy bitterling); Perciformes: percid (yellow perch); Salmoniformes: salmonid (rainbow trout); Siluriformes: clariid (African sharptooth catfish); Siluriformes: ictalurid (channel catfish)	Africa
A. jollymani	Cichliformes: cichlid (fenestratus, haplo)	Africa
A. juparanensis	Characiformes: characid (twospot astyanax); serrasalmid (red-bellied piranha, spotted piranha, speckled piranha); Eupercaria: sciaenid (La Plata croaker, pescada); Siluriformes: pimelodid (barred catfish): Myliobatiformes: potamotrygonid (Thorny river stingray, Ocellate river stingray, Raspy river stingray, smooth back river stingray)	South America
A. kosus (syn. *A. smalei*)	Cichliformes: cichlid (Mozambique tilapia); Elopiformes: elopid (tenpounder); Mugiliformes: mugilid (flathead grey mullet, St Lucia mullet); Perciformes: haemulid (smallspotted grunter, cock grunter), sciaenid (tigertooth croaker), sparid (Cape stumpnose, salema porgy); Tetraodontiformes: monacanthid (unicorn leatherjacket)	Africa
A. kunmingensis	free-swimming	China
A. kusafugu	Tetraodontiformes: tetraodontid (grass puffer)	Japan
A. laticauda	Anguilliformes: anguillid (common eel); Batrachoidiformes: batrachoidid (oyster toadfish); Blenniformes: blennid (blenny); Gadiformes: gadid (Atlantic tomcod); Perciformes: serranid (Atlantic goliath grouper); Pleuronectiformes: paralichthyid (southern flounder, summer flounder), pleuronectid (winter flounder); Scorpaeniformes: cottid (sculpin); Siluriformes: ariid (hardhead catfish); Myliobatiformes: dasyatid (Atlantic stingray); Rajiformes: rajid (little skate)	Americas
A. lepidostei	Lepisosteiformes: lepisosteid (longnose gar, shortnose gar)	North America
A. longicaudatus	Cypriniformes: leuciscid (emerald shiner); Perciformes: centrarchid (bluegill, white crappie)	North America
A. lunatus	Cypriniformes: cyprinid (goldfish)	North America
A. macropterus	Mugiliformes: mugilid (mullet)	Australia
A. maculosus	Esociformes: esocid (muskellunge); Perciformes: centrarchid (rock bass); Siluriformes: ictalurid (brown bullhead, yellow bullhead)	North America
A. maharashtrians	free-swimming	India
A. major	Cypriniformes: cyprinid (Eurasian carp)	China
A. mangalorensis	free-swimming	India
A. matuii	Eupercaria: haemulid (three-lined grunt)	China
A. meehani	Lepisosteiformes: lepisosteid (gar)	North America

A. megalops	Batrachoidiformes: batrachoidid (oyster toadfish); Cyprinodontiformes: fundulid (killifish); Gadiformes: gadid (Atlantic tomcod), Lophiiformes: lophiid (European angler); Pleuronectiformes: paralichthyid (summer flounder, spotted sand flounder), pleuronectid (winter flounder, American smooth flounder, American plaice): Rajiformes: rajid (common skate); Scorpaeniformes: cottid (longhorn sculpin), triglid (northern sea robin)	Europe, Americas
A. melanostictus	plankton sample	Asia
A. melita	unidentified shark species	Africa
A. mexicanus	Cichliformes: cichlid (Mayan cichlid)	Americas
A. mississippiensis	Lepisosteiformes*:* lepisosteid (shortnose gar)	North America
A. mongolianus	not known	Manchuria
A. monodi	Characiformes: alestid (African tigerfish); Cichliformes: cichlid (redbelly tilapia)	Africa
A. moratoi	Osteoglossiformes: osteoglossid (pirarucu)	South America
A. mugili	Mugiliformes: mugilid (mullet)	?
A. multicolor	Characiformes: anostomid (black-banded leporinus, threespot leporinus, piau coco), cynodontid (payara, biara), erythrinid (wolf fish), prochilodontid (black prochilodus), serrasalmid (red-bellied piranha, spotted piranha, speckled piranha, tambaqui), triportheid (asandiki); Cichliformes: cichlid (Nile tilapia, oscar, demon eartheater, speckled peacock bass, butterfly peacock bass, Rio Jari peacock bass); Eupercaria: sciaenid (corvina); Siluriformes: auchenipterid (manduba), pimelodid (redtail catfish, spotted tiger shovelnose catfish, tiger sorubim)	South America
A. multipocula	Mugiliformes: mugilid (South African mullet)	Africa
A. nativus	Perciformes: serranid (giant grouper)	Sri Lanka
A. nattereri (syn. *A. silvestrii*)	Characiformes: characid (golden dorado), serrasalmid (big-belly spine); Siluriformes: pimelodid (spotted sorubim, tiger sorubim, sailfin pim, redtail catfish, barred catfish, moncholo)	South America
A. nobilis	Lepisosteiformes: lepisosteid (Cuban gar)	Americas
A. onodai	Tetraodontiformes: tetraodontid (Hong Kong pufferfish)	Japan
A. papuensis	Gobiiformes: eleotrid (snakehead gudgeon)	Papua New Guinea
A. paranensis	Characiformes: characid (golden dorado)	South America
A. patagonicus	Perciformes: percichthyid (Creole perch)	South America
A. personatus	Cichliformes: cichlid (raitapetoahven, pikkupetoahven)	Africa
A. peruvianus	Gadiformes: merlucciid (Peruvian hake)	South America
A. pestifer	Characiformes: characid (golden dorado), erythrinid (gold wolf fish); Siluriformes: pimelodid (barred catfish, spotted sorubim, tiger sorubim, zebra shovelnose)	South America
A. piperatus	free-living	North America
A. plecoglossi	Osmeriformes: plecoglossid (ayu)	Japan
A. pugettensis (syn. *A. niger*)	Ovalentaria: embiotocid (shiner perch, walleye surfperch, striped surfperch); Salmoniformes: salmonid (rainbow trout)	Pacific
A. puthenveliensis	Anabantiformes: osphronemid (spiketail paradisefish); Cypriniformes: cyprinid (Indian flying barb, greenstripe barb); Cyprinodontiformes: aplocheilid (green panchax)	India
A. quadristriatus	Carangiformes: latid (Waigieu seaperch), rachycentrid (cobia)	India
A. reticulatus	Characiformes: alestid (goliath tigerfish)	Africa
A. rhamdiae	Siluriformes: heptapterid (pale catfish)	Americas
A. rhipidiophorus	Characiformes: alestid (elongate tigerfish, African tigerfish, pebbly fish); Cichliformes: cichlid (blue-spotted tilapia, Nile tilapia, entonga); Cypriniformes: cypriniod (barbel, labeo); Perciformes: latid (Nile perch); Siluriformes: bagrid (bayad), clariid (African sharptooth catfish), mochokid (wahrindi)	Africa
A. rijckmansii	host not recorded	Africa
A. rothschildi	Cypriniformes: cyprinid (common bream)	Europe
A. rotundus	host unknown	
A. rubescens	Siluriformes: claroteid (kibonde)	Africa
A. rubropunctatus	Perciformes: latid (Tanganyika lates, forktail lates)	Africa
A. salminei (syn. *A. paulensis*)	Characiformes: characid (dorado)	South America
A. schoutedeni	Characiformes: citharinid (imbaza), distichodontid (sharktail distichodus)	Africa
A. scutiformis	Abantiformes: channid (striped snakehead, spotted snakehead); Cypriniformes: cyprinid (rohu); Tetraodontiformes: molid (ocean sunfish), tetraodontid (pufferfish)	Asia, India
A. siamensis	Anabantiformes: osphronemid (gourami); Cypriniformes: cyprinid (carp, mrigal carp); Perciformes: ambassid (Indian glassy fish)	India
A. sindhensis	Cypriniformes: cyprinid (rohu)	India

A. spinulosus	Characiformes: cynodontid (payara), erythrinid (wolf fish); Cichliformes: cichlid (Nile tilapia)	Americas
A. stizostethii (syn. *A. canadensis)*	Acipenseriformes: acipenserid (lake sturgeon); Clupeiformes: clupeid (American shad, American gizzard shad); Cypriniformes: catostomid (white sucker), leuciscid (spottail shiner); Esociformes: esocid (northern pike, muskellunge); Gasterosteiformes: gasterosteid (three-spined stickleback, ninespine stickleback, blackspotted stickleback); Perciformes: percid (yellow perch, walleye, sauger), moronid (white bass); Salmoniformes: salmonid (A*tlantic salmon,* cisco, lake whitefish, brook trout)	North America
A. striatus	Cichliformes: cichlid (Tanganyika tilapia); Siluriformes: clariid (African sharptooth catfish, dinopterus, African catfish), claroteid (giraffe catfish, kibonde)	Africa
A. taliensis	free-swimming	China
A. tientsinensis	Siluriformes: bagrid (yellowhead catfish)	China
A. trachynoti	Carangiformes: carangid (snubnose dart)	Africa
A. trilineatus	Cypriniformes: cyprinid (goldfish)	North America
A. tristramellae	Cichliformes: cichlid (shortjaw tristramella)	Middle-East
A. varians	Carangiformes: echeneid (live sharksucker); Lophiiformes: ogcocephalid (shortnose batfish); Perciformes: sparid (pinfish); Tetraodontiformes: diodontid (striped burrfish, baiacu)	Americas
A. ventanensis	Anura: hylid (Montevideo tree frog, tadpoles)	South America
A. versicolor	Esociformes: esocid (chain pickerel); Perciformes: centrarchid (rock bass), percid (yellow perch, walleye), percopsid (trout perch)	North America
A. vierai	Cyprinodontiformes: poecilid (ten-spotted livebearer)	South America
A. violaceus	Atheriniformes: atherinopsid (pejerrey); Characiformes: erythrinid (wolf fish); Siluriformes: heptaptetrid (South American catfish), loricariid (cascudo), pimelodid (mandi-branco)	South America
A. vittatus (syn. *A. giganteus, purpureus*)	Perciformes: sparid (bogue, common pandora, red porgy, gilt-head bream); Tetraodontiformes: tetraodontid (lunartail puffer, oblong blowfish)	Africa, India
A. wilsoni	Characiformes: alestid (goliath tigerfish)	Africa
A. ybatecobe	Characiformes: curimatid (mocinha)	South America
A. yucatanus	Cichliformes: cichlid (Mayan cichlid)	North America
A. yuii	Cypriniformes: cyprinid (Eurasian carp, black carp)	China
A. yunnanensis	free-swimming	China

Parasite morphology: *Argulus* spp. are commonly known as fish lice but they are brachiuran parasites that form 4 different types of developmental stages: namely, eggs; metanaupliar larvae; juveniles (5-11 instars); and adults (males and females). The eggs are brown ovoid-ellipsoid stages measuring 0.2-0.3 mm long (a few species produce larger eggs up to 0.7 mm long). They are bound by thick waxy shells and contain numerous yolk globules. They hatch to release the first larval stage commonly called a metanauplius (or postnauplius) which is discoidal in shape measuring 0.7-1.0 mm in diameter. Metanauplii possess up to 9 pairs of ventral appendages; namely (in order posteriad), antennules, setose antennae, mandibular palps, rudimentary maxillules and maxillae, and swimming legs (first pair well developed, next 3 pairs rudimentary). They attach to fish hosts using their anterior appendages and feed using mouthparts containing the mandibles. They then moult and transform into juvenile stages which subsequently undergo another 5-11 moults, depending on the species. Juveniles grow from 1-10 mm in length (some species up to 30 mm) and they exhibit various morphological changes: with strong claws replacing setae on the antennae, the loss of setose palps on the mandibles, the development of 4 pairs of thoracic swimming legs, the appearance of reproductive organs, and the most pronounced change occurs in the last juvenile stage when the maxillules transform from long claws into powerful circular sucker. These suckers are retained when the juveniles moult to form adult males and females. Adults range in size from 5-20 mm in length, although some species grow up to 34 mm long. They are covered by a semitransparent carapace, usually milky white with pale yellow, green or brown cryptic colourations. The body is disc-shaped being broadly ovoid, dorso-ventrally flattened and dorsally convex. The body plan comprises a large discoid head and a slender tapering trunk (thorax plus abdomen). The head has well-developed carapace lobes formed as posterior extensions of the dorsal head shield, and they typically cover the thorax, and sometimes the abdomen. The carapace also has 2 special ventrolateral areas initially described as respiratory alae (but now thought to be involved in osmoregulation). Ventrally, the head bears 5 pairs of appendages (antennules, antennae, mandibles, maxillules and maxillae), and a pair of prominent compound eyes. The thorax bears 4 pairs of swimming legs and the abdomen has a pair of caudal rami. [This body plan differs from that of copepods as argasilids have a carapace, compound eyes, conspicuous ventral sucking discs, no thoracic segments are completely fused with the head, and the abdomen is unsegmented behind the genital apertures.] In brachiurans, the antennules are short, clawed and setate, while the antennae have characteristic hooks with 2 small distal segments. The tubular sucking mouthparts form a suctorial proboscis (mouth tube) with rasping dentate hooked mandibles at the tip. They also possess a preoral piercing stylet (sting) located just anterior to the mouth. The maxillules (some texts refer to them as first maxillae) are modified into large powerful muscular suckers (cup-shaped discs) used for attachment. Females generally have more support rods (with more sclerites) in their suckers than males. The maxillae are large, stout and dentate and are apparently used to both maintain

position and to clean other appendages. The thorax has 4 segments, each with a lateral pair of biramous swimming legs. The first 2 pairs of legs bear recurved processes known as flabella (singular, flabellum) while the last 3 pairs of legs on males have sclerotized segments as sexual modifications that are absent on females. The short unsegmented abdomen contains most of the sexual reproductive organs. Males have a pair of elongate testes with vas deferens leading to a seminal vesicle and a tubular ejaculatory duct. Females have a pair of ovaries (lacking ovisacs) connected by oviducts to a large uterus with lateral spermathecae (for sperm storage), The uterus becomes so distended by developing eggs that they may be seen not only in the abdomen but also in the thorax and sometimes in the lobes of the carapace. Eggs are deposited by female in clutches on hard substrates in the water.

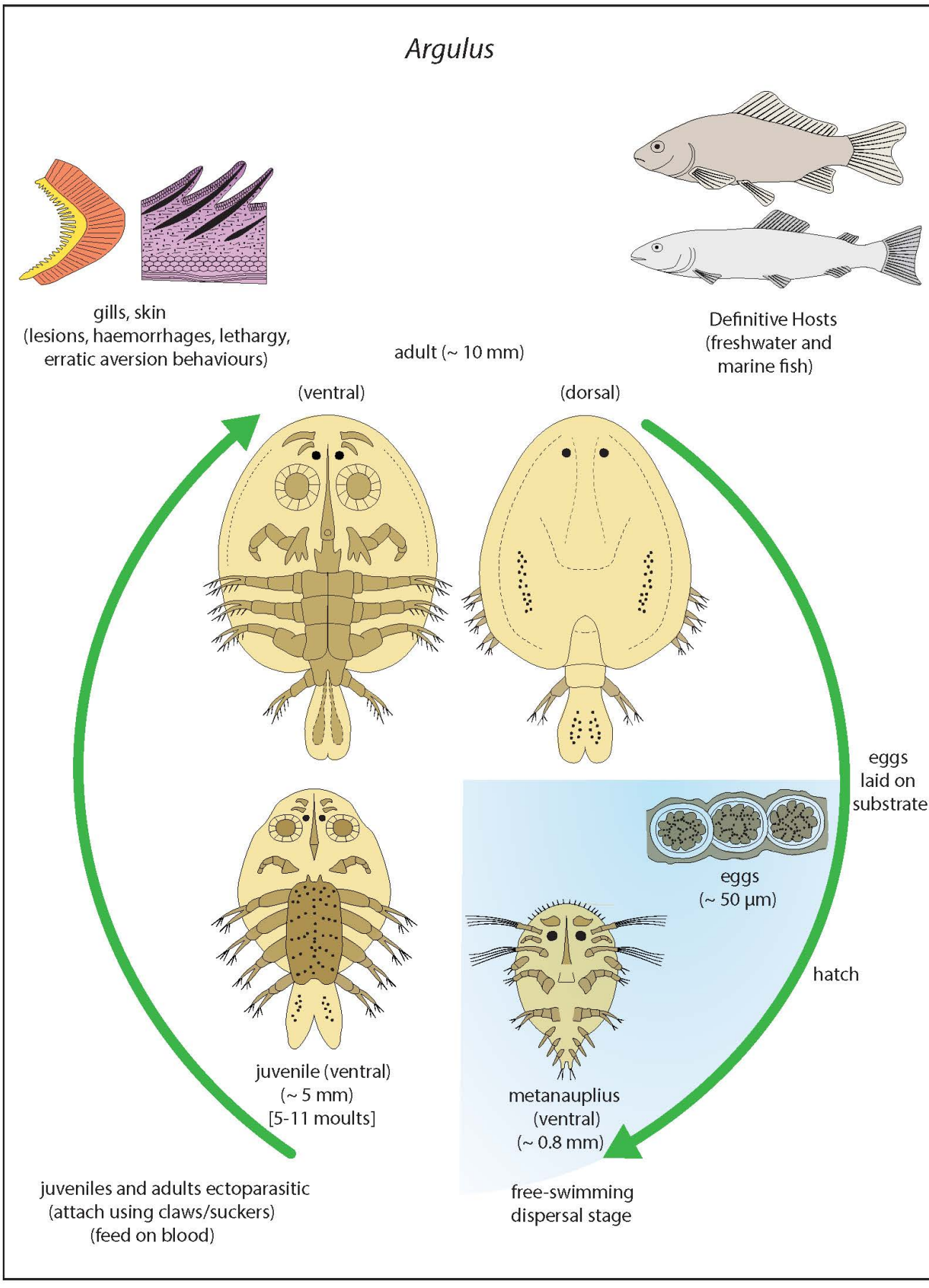
Site of infection: These fish lice are ectoparasitic crustaceans which attach to the skin of the body, gill chambers and mouths of fishes. All motile stages are parasitic and may move about on their hosts; if disturbed, they may detach and swim freely in the water column. The genus *Argulus* has a worldwide distribution (except Antarctica) and most species infest freshwater fish (in running or static waters), although some are found on fishes from estuarine and coastal waters (but not open oceanic waters). They are particularly common on pond-raised freshwater fish and some ornamental species, and are occasionally found on tadpoles of frogs and toads.

Pathogenesis: The larval and adult stages of fish lice attach to the skin and gills of fishes using a variety of claws, hooks, spines and suckers (the latter only in the last stage larvae and adults). All species feed on mucus, epidermal tissues and extracellular material (including sloughed-off scales), and adults may also feed on internal fluids including plasma and blood. Adults also insert their preoral stylets (stings) into host tissues and inject substances (enzymes and anticoagulants) to better facilitate feeding. After engorging themselves, the parasites may wait 2-3 weeks before feeding again. All stages are able to move about on their hosts detaching then reattaching to new sites. Light infestations may not produce any clinical signs, but heavier infestations may cause skin lesions and loss of condition. Hosts often show localized inflammation at attachment and feeding sites due to the mechanical damage caused by holdfast structures as well as reactions to injected enzymes. Fish develop focal skin lesions with petechial (pinpoint or spot) haemorrhages, fin and scale loss, increased mucus production, anaemia with low erythrocyte and haemoglobin levels, decreased osmoregulatory function (unable to balance internal fluids and salt levels), reduced feeding and general loss of body condition. Infested fish may develop a variety of behavioural changes ranging from lethargy, avoiding swimming or erratic swimming, congregating at the water surface or near flowing water inlets, and flashing or rubbing against substrates to relieve irritation and remove parasites. Clinical outbreaks may cause serious problems for aquaculture, with high densities developing particularly in closed culture systems, aquaria, ornamental fishponds and even reservoirs. The open wounds left by parasites are also susceptible to secondary infection by fungi (e.g. *Saprolegnia*) and bacteria (e.g. *Pseudomonas, Aeromonas*). Recent studies indicate that argulids may also transmit the viral agent of spring viremia of carp as well as carp pox, and that they may act as intermediate hosts for various nematodes, including skrjabillanid worms infesting marine fishes, and dracunculid worms parasitizing cichlid and poecilid fishes.

Developmental cycle and mode of transmission: Argulids undergo gradual (incomplete) metamorphosis whereby larval stages gradually transform into adult stages. Gravid females leave their fish hosts and swim to submerged objects with hard surfaces (rocks, sticks, plants) to lay rows of up to 200-400 eggs attached with adhesive secretions. Egg production generally only occurs when water temperatures are above 16°C. The eggs hatch asynchronously after 10-80 days, the duration depending on the species and water temperature (faster in warmer water). In some species, eggs laid in autumn have been found to survive over the winter period to hatch in spring. Hatching releases the first larval stages which are dispersal stages often called metanauplius (their swimming apparatus is too well developed for them to be considered a nauplius). These free-swimming larvae opportunistically find fish and attach with their hooked antennae within 2-4 days.
After 5-7 days, they moult to second stage larvae (called juveniles) which feed, grow and develop through a series of moults at regular intervals over 28-40 days. The number of juvenile moults varies according to the parasite species, ranging from 5-11 moults (representing 6-12 stages). The juveniles all have clawed maxillules for attachment, except for the last juvenile stages which develop prominent suckers which are retained over the next moult to adults. Juveniles, and sometimes adults, may overwinter on hosts surrounded by mucus. Adults that are disturbed or dislodged from hosts can survive free-swimming in the water column for several days (in some instances, up to 3 weeks). Mating occurs on fish hosts when males clasp females using their modified legs. The spermathecal spine of the female is inserted into the genital atrium of the male and pierces the wall of the ejaculatory duct. Sperm are then pumped from the ejaculatory duct into the female spermathecae for storage. The sperm are filiform and motile and have been found to have a fine structure similar to that of pentastomes. There have been several reports of females developing eggs parthenogenetically in the absence of males for mating. Developing eggs are held in the uterus until ready for oviposition. Females detach and leave their fish hosts to lay eggs on hard submerged substrates. The whole life-cycle may be completed in 30-60 days, but longer in colder regions where eggs over-winter in water or juveniles over-winter on hosts. Most infestations peak in summer and autumn. Transmission between fish hosts is direct, via the contamination of water with eggs releasing free-swimming metanauplii which actively seek hosts. Juveniles and adults on hosts may also transfer to other hosts if they become dislodged or when females return from spawning.

Differential diagnosis: Infestations may be suspected on clinical grounds when fish exhibit aberrant behaviours, skin lesions, and loss of condition. Diagnoses are conventionally made by the direct observation of fish lice attached to host skin or moving around in protected areas such as behind the fins or near the eyes or gills. Juvenile and adult stages are usually evident as small round green discs which are also able to swim free in the water, particularly if disturbed. These stages are best identified under magnification in wet mounts taken from fish, but samples should be collected quickly from captured fish as the parasites rapidly leave hosts removed from water. Free-swimming stages may also be captured using fine mesh plankton nets for examination. All stages are readily identified on the basis of their unique carapace and body plan, with species differentiated by variations in morphometrics and appendage anatomy. Molecular biological techniques have been used to characterize *Argulus* species and indicate phylogenetic relationships following polymerase chain reaction (PCR) amplification of random amplified polymorphic DNA (RAPD), nuclear (18S ribosomal RNA) or mitochondrial (cytochrome c oxidase subunit 1, NADH dehydrogenase subunits 1 and 4) gene sequences.

Treatment and control: While individual fish lice can be removed from fish using tweezers and the wounds cleansed with antiseptics (such as hydrogen peroxide), such intervention is impractical in systems larger than small aquaria. Removing lice has also been shown to be relatively ineffective due to rapid re-infestation of fish by free-swimming stages. Recourse is therefore made to chemical treatments which ideally target all life stages on hosts or in the water. In culture systems, fish are usually bathed in separate treatment tanks while their usual holding facilities are cleansed of eggs by disinfection or drying. Some facilities also introduce wooden slats or boards into tanks and ponds on which females may preferentially deposit their eggs, the hard substrates are then regularly removed and disinfected. Fish lice infestations in freshwater fish are conventionally treated by bathing fish in potassium permanganate or salt solutions (formalin baths are not very effective). Good success has also been reported using baths containing insecticidal organophosphates (trichlorfon) to kill parasites by neuro-interference, and some insect growth regulators which inhibit moulting (diflubenzuron, lufenuron). More recently, the use of macrocyclic lactones (emamectin) given as feed additives has shown promise for managing infestation in both freshwater and marine fishes. Several studies have also indicated that ponds treated with tobacco leaf dust (containing nicotine) seemed to reduce infestations in freshwater fishes. A range of management procedures may be adopted in aquaculture enterprises not only to help fish survive infestations but also to suppress parasite populations. Depending on facilities, such procedures usually involve imposing strict biosecurity (health surveillance, quarantine, cull sick fish), sensible stock management (ovoid overcrowding, esp. juvenile fish as they are more susceptible than adults) and maintaining good water quality (check source water, implement water filtration and/or disinfection practices, maintain good oxygen levels, and where possible, reduce water temperatures).


Argulus
gills, skin
(lesions, haemorrhages, lethargy,
erratic aversion behaviours)
Definitive Hosts
(freshwater and
marine fish)
adult (~ 10 mm)
(ventral)
(dorsal)
eggs
laid on
substrates
eggs
(~ 50 µm)
hatch
juvenile (ventral)
(~ 5 mm)
[5-11 moults]
metanauplius
(ventral)
(~ 0.8 mm)
juveniles and adults ectoparasitic
(attach using claws/suckers)
(feed on blood)
free-swimming
dispersal stage



Argulus adult



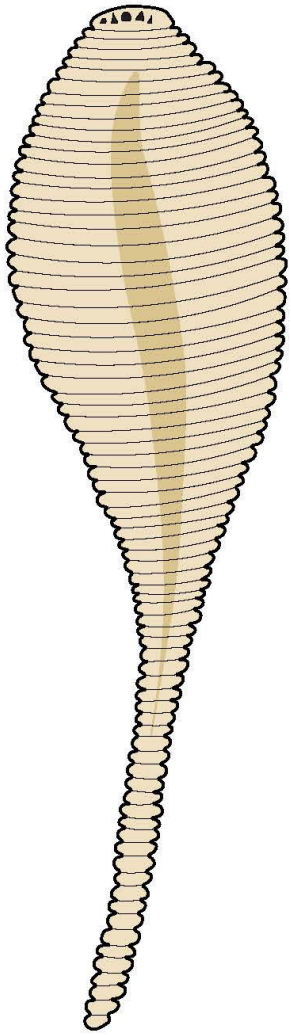
Argulus adult

Crustacea
(pentastomes)

Pentastomes

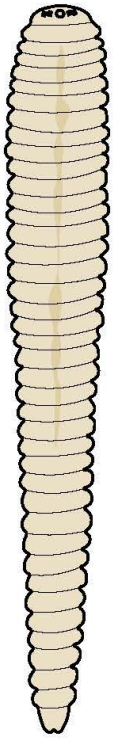
Linguatula

adult (ventral)
(~ 100 mm)



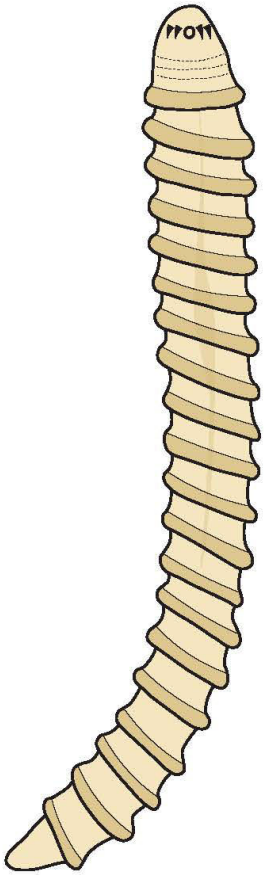
Porocephalus

adult (ventral)
female ~60 mm
male ~ 30 mm



Armillifer

adult (ventral)
(female ~ 90 mm)
(male ~ 30 mm)



Porocephalus, Armillifer
(arthropod: pentastome)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Crustaceans have a very strong cuticle strengthened by calcium salts; thus their growth must proceed through repeated moults. Most species are aquatic with internal or external gills, two pairs of antennae, mouthparts comprising one pair of mandibles and two pairs of maxillae, and each heteronomous body segment usually bears a pair of ventral biramous extremities (podia). Maxillipods lack appendages on abdominal segments and the nauplius larval stage has a unique maxillipodan eye. Pentastomatids (tongue worms) are unusual endoparasites with elongate worm-like bodies that have lost virtually all their appendages, apart from two pairs of tiny anterior claws near the mouth (collectively accounting for their penta-stome appearance). Most live in the respiratory systems of reptiles, although a few live in the air sacs of seabirds and the nasopharynx of dogs and cats. Eggs passed into the environment release oval larvae with four stumpy legs and an anterior penetration organ used to invade the tissues of an intermediate host (insect, fish, amphibian, reptile or mammal) where it forms a quiescent nymph which is infective to the definitive host. Porocephalids have their mouths between or below the anterior hooks, the hooks have a fulcrum, and the vulva is posterior. Infections by *Porocephalus* and *Armillifer* spp. are found in the respiratory passages of snakes and they have rodents as intermediate hosts, but may sometimes accidentally infect humans.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Crustacea (mandibular mouthparts, gills, two pairs antennae, biramous podia, larval nauplius/zoea)
Class: Maxillipoda (nauplius with maxillipodan eye)
Subclass: Pentastomatida (tongue worms, anterior end with mouth and two pairs of tiny claws)
Order: Porocephalida (horizontally-aligned hooks, posterior genital openings)
Family: Porocephalidae (cylindrical adults, parasites of snakes)
Genus: *Porocephalus* (parasitic in respiratory passages of snakes)
Genus: *Armillifer* (parasitic in respiratory passages of snakes)
Species: various species may cause respiratory disease in reptiles and visceral lesions in humans

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Crustaceans have very strong cuticles strengthened by calcium salts, so they moult periodically as they grow and metamorphose through different types of larval stages before forming adults. Most species are aquatic and have internal or external gills, while terrestrial species have internal gills which are kept moist. Crustaceans have mouthparts with two pairs of maxillae (to handle food) and paired mandibles (with opposing biting and grinding surfaces). They have two sets of antennae and each body segment usually gives rise to a pair of ventral biramous appendages (podia). Six crustacean classes are recognized: Brachiopoda, Cephalocarida, Malacostraca, Maxillipoda, Ostracoda and Remipedia. Maxillipods usually have a body plan comprising 5 cephalic, 6 thoracic and 4 abdominal segments followed by a telson. The thoracic segments bear biramous (sometimes uniramous) limbs, but the abdominal segments lack appendages. The carapace is present or reduced, most feed using maxillae, and the nauplius larval stages have unique eyes with three cups, each with tapetal cells (= maxillipodan eye). Six maxillipodan subclasses are recognized: Branchiura, Cirripedia, Copepoda, Mystacocarida, Pentastomatida and Tantulocarida.

Major parasitic crustacean families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Class: Maxillipoda					

Subclass: Copepoda (copepods)					
Order: Cyclopoida (open buccal cavity)					
Family: Lernaeidae (anchor worms)	19 genera, 114 spp.	freshwater fishes	copepodids and adults	skin lesions	direct (water)
Former order: Poecilostomatoida (slit-like buccal cavity)[now a "poecilostome" lineage within the Cyclopoida]					
Family: Ergasilidae (gill lice)	27 genera 61 spp.	freshwater and marine fish	adult ♀	gill/skin lesions	direct (water)
Subclass: Branchiura (head with flattened bilobed cephalic fold, carapace expands laterally)					
Order: Argulidea (discoid bodies, attach using hooks, suckers and barbs)					
Family: Argulidae (fish lice)	4 genera 150 spp.	marine and freshwater fish	juveniles, adults	skin lesions	direct (water)
Subclass: Pentastomatida (tongue worms, elongate annulated bodies, 2 pairs tiny anterior claws near mouth)					
Order: Porocephalida (horizontally-aligned hooks)					
Family: Porocephalidae	8 genera, 40 spp.	snakes, lizards (mammal, reptile IH)	adults	lung lesions	indirect (via IH*)
Family: Sebekidae	8 genera, 34 spp.	crocodiles, turtles (fish IH)	adults	lung lesions	indirect (via IH)
Family: Subtriquetridae	1 genus, 4 spp.	crocodiles (fish IH)	adults	lung lesions	indirect (via IH)
Order: Cephalobaenida (obliquely-paired hooks)					
Family: Linguatulidae	1 genus, 4 spp.	carnivorous mammals (mammal IH)	adults	naso-pharyngeal lesions	indirect (via IH)
Family: Cephalobaenidae	1 genus, 1 sp.	snakes (unknown IH)	adults		indirect?
Family: Raillietiellidae	2 genera, 43 spp.	amphibians, snakes, lizards, sugar glider (arthropod IH)	adults	lung lesions	indirect (via IH)
Family: Reighardidae	2 genera, 3 spp.	birds	adults	nasal lesions	direct?

*IH = intermediate host

Morphological and ultrastructural studies on immature and adult stages suggested that pentastomatids (tongue worms) were related to branchiurans, esp. argulids (fish lice). Analyses of mitochondrial DNA gene sequences indicated unambiguously that pentastomatids are a group of modified branchiurans [the name Ichthyostraca has recently been proposed for a 'Branchiura+Pentastomatida' clade]. Pentastomatids are unusual endoparasites with elongate non-chitinous annulated vermiform bodies that have lost virtually all their appendages, apart from two pairs of tiny anterior claws near the mouth (collectively accounting for their penta-stome appearance). Most live in the respiratory systems of reptiles and amphibians, although a few live in the air sacs of seabirds and the nasopharynx of dogs, big cats and deer. Eggs passed into the environment release oval larvae with four stumpy legs and an anterior penetration organ used to invade the tissues of an intermediate host (coprophagous insects, fish, amphibian, reptile or mammal) where it forms a quiescent nymph which is infective to the definitive host. Some species have a direct life-cycle, but this appears limited to the genus *Reighardia* in birds, and possibly the species *Linguatula arctica* in ungulates. Two orders have been recognized: Cephalobaenida (adults with medial genital openings, and a single oviduct); and Porocephalida (adults with posterior genital openings, and 2 oviducts). Members of the order Porocephalida have the mouth positioned between or below the anterior hooks, the hooks have a fulcrum, and the female vulva is located near the posterior end. Several families are recognized: including the Porocephalidae; Subtriquetridae; Sebekidae (now containing the former families Diesingidae and Sambonidae); and Linguatulidae (although recent molecular studies suggest that the linguatulids should be placed in the order Cephalobaenida). Porocephalids are cylindrical pentastomes with horizontally-aligned hooks and reptilian final hosts. Five porocephalid genera (*Armillifer*, *Cubirea*, *Gigliolella*, *Kiricephalus*, and *Porocephalus*) have been recognized as heteroxenous (2-host) parasites with adult pentastomes infecting the respiratory passages of snakes and larval/nymphal stages infecting the viscera of various prey animals (rodents, insectivores, lizards, frogs and some birds). Nine *Porocephalus* spp. have been described from viperid snakes in Africa and the Americas, and 8 *Armillifer* spp. in boid snakes in Africa and elapid snakes in Asia. Four of these species (*A. armillatus, A. grandis, A. moniliformis* and *P. crotali*) have been reported to opportunistically infect humans in Africa and Asia, with larval/nymphal stages encysting in visceral tissues (this is primarily through the ingestion of pentastome eggs via the consumption of contaminated snake meat).

Pentastome species	**Definitive hosts** (adults in respiratory passages)	**Intermediate hosts** (larvae/nymphs in viscera)	**Distribution**
Porocephalus (accessory spines on hooks)			
P. basiliscus	Serpentes: viperid (basilisk		Americas

	rattlesnake)		
P. benoiti	Serpentes: elapid (cobra)		Africa
P. clavatus (syn. *Pentastoma didelphis, imperatoris, proboscideum, subcylindricum p.p.)*	Serpentes: viperid (terciopelo, common European viper, common lancehead, rhombic night adder, bushmaster), boid (rainbow boa, common northern boa, red-tailed boa, Paraguay regenbogenboa, green anaconda, Cuban tree boa), colubrid (grass snake, black-striped snake)	Rodentia: murid (house mouse); Didelphimorphia: didelphid (Virginia opossum, Linnaeus's mouse opossum, bare-tailed woolly opossum); Primates: cebid (common squirrel monkey); Sauria: agamid (Oriental garden lizard), teiid (northern caiman lizard), varanid (Nile monitor)	Americas
P. crotali (syn. *P. humboldtii, quadriuncinata, subcylindricum p.p.*)	Serpentes: viperid (Cascavel rattlesnake, Yucatan neotropical rattlesnake, northwestern neotropical rattlesnake, Santa Catalina rattlesnake, basilisk rattlesnake, western diamondback rattlesnake, timber rattlesnake, South American rattlesnake, cottonmouth, water moccasin, fer-de-lance, jararaca), boid (black-tailed python, common boa, northern boa, green anaconda), colubrid (tiger rat snake, Chinese rat snake, spotted desert racer, Rio tropical racer, Wagler's snake, false water cobra)	Rodentia: cricteid (red-nosed mouse, cotton mouse, blackish grass mouse, Florida mouse, muskrat, marsh rice rat, hispid cotton rat), murid (house mouse, black rat); Didelphimorphia: didelphid (Virginia opossum, gray four-eyed opossum, water opossum, bare-tailed woolly opossum, long-furred woolly mouse opossum, Linnaeus's mouse opossum); Cingulata: chlamyphorid (screaming hairy armadillo, southern three-banded armadillo), dasypodid (nine-banded armadillo); Carnivora: canid (dog), mephitid (striped skunk), mustelid (giant otter), procyonid (common raccoon, crab-eating raccoon, white-nosed coati); Chiroptera: phyllostomid (pale spear-nosed bat); Primates: callitrichid (black lion tamarin); Sauria: teiid (gold tegu)	Americas
P. dominicana	Serpentes: boid (Dominican boa)		Americas
P. stilesi	Serpentes: viperid (jararaca, jararacassu, South American bushmaster, Martinique lancehead, fer-de-lance, crossed pit viper), colubrid (brown-banded water snake, tiger rat snake)	Rodentia: caviid (guinea pig); Sauria: teiid (gold tegu); Primates: cebid (common squirrel monkey)	Americas
P. subuliferum (syn. *P. bouvieri, cercopitheci*)	Serpentes: elapid (Indian cobra), lamprophiid (western forest file snake, Congo file snake, Cape file snake), viperid (Gaboon viper, rhinoceros viper, rhombic night viper)	Primates: cercopithecid (green monkey), galagid (Senegal bushbaby), hominid (human); Serpentes: lamprophiid (Cape file snake), psammophiid (hissing sand snake)	Africa
P. taiwana		Primates: hominid (human)	Taiwan
P. tortugensis	Serpentes: viperid (Tortuga Island rattlesnake)		Mexico
Armillifer (annuli raised by muscle bands)			
A. aborealis	Serpentes: boid (green tree python), colubrid (brown tree snake)	Dasyuromorphia: dasyurid (northern quoll); Peramelemorphia: peramelid (northern brown bandicoot)	Australia
A. agkistrodontis	Serpentes: viperid (Chinese moccasin), pythonid (black-tailed python)	Rodentia: murid (house mouse); Primates: cercopithecid (crab-eating macaque)	China
A. armillatus (syn. *Porocephalus, P. moniliformis, Linguatula, L. constricta, diesingii*)	Serpentes: boid (reticulated python, ball python, African rock python, Burmese python), elapid (Indian cobra, rinkhals), lamprophiid (striped house snake, red-black striped snake), viperid (puff adder, Gaboon viper, horned desert viper, rhinoceros viper, rhombic night viper)	Rodentia: murid (black rat), nesomyid (Gambian pouched rat), caviid (guinea pig), hystricid (African brush-tailed porcupine), anomalurid (Lord Derby's scaly-tailed squirrel), sciurid (striped ground squirrel); Carnivora: canid (dog, striped hyena, brown hyena), euplerid (broad-striped Malagasy mongoose), felid (cat, lion, tiger, leopard, cheetah, serval), herpestid (marsh mongoose, long-nosed mongoose, banded mongoose, white-tailed mongoose, bushy-tailed mongoose, Pousargue's mongoose, Java mongoose,	Africa, Arabian Peninsula

		Egyptian mongoose, common kusimanse), mustelid (Eurasian otter, spotted-necked otter, honey badger), nandiniid (African palm civet), viverrid (Asian palm civet, Malabar large-spotted civet, genet, pardine genet); Eulipotyphla: erinaceid (long-eared hedgehog, four-toed hedgehog, desert hedgehog, southern African hedgehog); Tubulidentata: orycteropodid (aardvark); Macroscelidea: macroscelidid (elephant shrew); Artiodactyla: bovid (cattle, southern reedbuck, harnessed bushbuck, white-bellied duiker, Weyns's duiker, roan antelope, royal antelope), giraffid (giraffe), tragulid (water chevrotain), suid (pig, common warthog, desert warthog, red river hog); Chiroptera: hipposiderid (cyclops roundleaf bat); Primates: galagid (southern needle-clawed bushbaby, brown greater galago, Senegal bushbaby), cercopithecid (mandrill, yellow baboon, Chacma baboon, Guinea baboon, sooty mangabey, crab-eating macaque, rhesus macaque, grivet, malbrouck, tantulus monkey, mona monkey, patas monkey, greater spot-nosed monkey), lorisid (potto), hominid (chimpanzee, human); Accipitriformes: accipitrid (European honey buzzard); Strigiformes: strigid (spotted eagle-owl)	
A. australis	Serpentes: pythonid (amethystine python, carpet python)	Peramelemorphia: peramelid (long-nosed bandicoot); Rodentia: murid (Cape York rat)	Australia, Indonesia
A. grandis (syn. *Porocephalus*) (visceral tongue worm)	Serpentes: viperid (Gaboon viper, rhinoceros viper, horned desert viper)	Primates: hominid (human)	Africa
A. mazzai	Serpentes: homalopsid (Macleay's water snake), pythonid (amethystine python)	Dasyuromorphia: dasyurid (quoll)	Australia, New Guinea
A. moniliformis (syn. *Pentastoma, P. aonycis, constrictum, tornatum, wedlii*)	Serpentes: pythonid (reticulated python, black-tailed python, carpet python, royal python, amethystine python, African rock python), boid (Madagascar boa), colubrid (painted keelback)	Rodentia: murid (Cape York rat); Carnivora: hyaenid (aardwolf), herpestid (Javan mongoose), felid (cat, fishing cat, flat-headed cat, tiger, leopard), mustelid (Eurasian otter, Asian small-clawed otter, smooth otter), ursid (sloth bear), viverrid (Asian palm civet, small Indian civet, large Indian civet, binturong); Scandentia: tupaiid (common treeshrew); Artiodactyla: suid (boar), tragulid (Java mouse-deer); Perissodactyla: tapirid (Malayan tapir); Primates: lorisid (red slender loris, Sunda slow loris), cercopithecid (rhesus macaque, crab-eating macaque, southern pig-tailed macaque), hominid (human)	South-East Asia, Australia
A. yoshidai	Serpentes: pythonid (black-tailed python)		Japan

Several other species have also been reclassified to other genera: including *A. brumpti = Gigliolella*; *P. bifurcatus = Raillietiella furcocercum*; *P. boulengeri = Raillietiella*; *P. crocodili = Leiperia gracilis*; *P. nematoides = Leiperia cincinnalis*; *P. globicephalus, P. herpetodryados* and *P. seurati = Kiricephalus coarctatus*; *P. pattoni = Kiricephalus*; *P. tortus = Kiricephalus*; *P. indicus = Alofia*; *P. joubini = Sebekia*; *P. kachugensis = Diesingia*; *P. pomeroyi = Cubirea*; and *P. wardi = Sambonia*; while *P. crocidurae* and *P. siamensis* are considered *species inquirenda.*

Parasite morphology: Porocephalid pentastomes form 4 different types of morphological stages during their developmental cycles: namely, eggs, larvae, nymphs, and adults. The eggs are ovoid ranging in size from 100-150 x 70-100 μm (cf. Linguatula eggs average 130 x 80 μm). They are bound by a bladder-like envelope with thin outer shell membrane and thick inner membrane with a unique funnel-shaped facette (thought to deliver sticky secretions from the contained embryo to the outer membrane). Eggs are fully embryonated when mature and contain an ovoid ('mite-like') primary larva with 2 pairs of anterior hooks and budding or short stumpy limbs. When hatched, the primary larvae measure 130-200 x 60-100 μm and have an ovoid non-segmented body with 4 stumpy legs (each with 1-2 retractable claws), a pair of small curved hamuli either side of the mouth, an anterior penetration apparatus on the rostral cephalothorax and a short bifurcate tail. The penetration apparatus comprises a media spear and 2 lateral pointed forks, and dorsal accessory hooks are present. Various studies have reported that larval stages may undergo several moults (ranging from 3-10 depending on species) before metamorphosing into segmented nymph stages that lack larval characteristics (lost legs, penetration apparatus, and tail). Studies have also reported that nymphs may undergo a series of moults (up to 5 depending on species) gradually increasing in size (sometimes up to 15-23 mm long) and segments. Nymphs stages are often described as surrounded by the exuvia of previous stages, and they are reported to form their circumoral hooks and primordial genital organs after 4-5 moults. Generally, they have cylindrical bodies with distinct annulations, the number and orientation of annuli differing between genera. *Porocephalus* nymphs possess 38-40 annuli evident as circular rings, whereas *Armillifer* nymphs have around 20 annuli that are slightly transverse and therefore impart a spiral screw-like appearance. The annuli often have small spines, and the cuticle has many pit-like openings to various glandular elements. The nymphs have small ventral mouths surrounded by a U-shaped sclerotized cadre opening to a simple digestive system with an oesophagus expanding into a blind sac, and sometimes a small hindgut. Mature nymphs are heavily encapsulated in host tissues and they already bear 4 sets of circumoral hooks. Adult porocephalids have elongate vermiform cylindrical bodies (in contrast to *Lingulatula* spp. which have flattened spatulate bodies). They usually grow up to 20-70 mm long, although some species may grow as big as 160 mm long. Like the nymphs, adults are conspicuously annulated with 7-40 ring-like segments, depending on taxa. In additions, the circular and parietal muscles of *Armillifer* spp. are arranged in thick bands, so that the annuli are prominently raised into spiral ridges. Adults have a thin chitinous exoskeleton that is soft enough to allow for peristaltic motion, and they have sclerotized parts around the mouth and accessory genitalia. The body is roughly into a head (or forebody), trunk (or hindbody), and tail (sometimes bifurcated at the tip). The head has virtually lost all appendages, except for the 2 pairs of tiny anterior hooks near the oval mouth (collectively accounting for their penta-stome appearance). The hooks are sclerotized and arc-shaped with a boat- or U-shaped fulcrum. The hooks are horizontally aligned in a straight line with the mouth (not obliquely like *Linguatula*), and those of *Porocephalus* spp. have accessory spines. The mouth is quite muscular and functions as a pump as adults feed on blood. The digestive system is simple and tubular, and now includes a posterior anus. The nervous system comprises a ventral nerve cord with ganglia in each segment (similar to other arthropods). Although adults have a haemocoel, they do not have circulatory, respiratory or excretory organs. The body lacks limbs but may sometimes have vestigial papilla-like outgrowths as well as numerous cuticular pores. Males are commonly smaller than females (*Porocephalus* males 27-36 mm long, females 44-78 mm; *Armillifer* males 12-50 mm, females 70-140 mm). Males have a single tubular testis (2 testes in *Linguatula*) that is connected to a seminal vesicle and a pair of ejaculatory bulbs opening into a long penis (cirrus) located in a dilator organ (cirrus sac). They have distinctive copulatory spicules (not club-shaped) and the genital pore is located near the mouth. Females have a single ovary with bifurcating oviducts that unite into a tubular extensively-coiled uterus with diverticula (including spermatheca). The vagina opens through a ventral posterior gonopore separated from anus by a few annuli (heterogyne condition).

Site of infection: Pentastomes are obligate internal parasites whose larval and nymphal stages are found in small animals (intermediate hosts) infected through consumption of eggs, while the adult stages are found in carnivorous vertebrates (definitive hosts). The intermediate hosts of *Porocephalus* and *Armillifer* spp. include a range of rodents, insectivores, lizards, frogs and some birds, with larval/nymphal stages infecting the viscera. Adult stages are more host specific and only occur in the respiratory tracts (lungs, trachea, nasal passages) of reptiles (namely, viperid, boid, pythonid, lamprophiid, colubrid and elapid snakes). In contrast, adult *Linguatula* spp. are found in the nasopharyngeal passages of mammals. Nonetheless, infections by 4 species (*A. armillatus, A. grandis, A. moniliformis* and *P. crotali*) have been found opportunistically in humans, where larval/nymphal stages have been detected encysting in visceral tissues, usually in the serosa around abdominal organs, abdominal lymph nodes, in the liver parenchyma, the mesenterium and intestinal wall, sometimes the pleura or lung parenchyma, and rarely the heart or eye.

Pathogenesis: Most infections by developing pentastomes in intermediate hosts or by adults in definitive hosts are asymptomatic or remain subclinical, although some may produce morbidity associated with parasites feeding on host blood, larval/nymphal migration and moulting within visceral tissues, traumatic damage to the pulmonary lining by adult hooks, and secondary bacterial and fungal infections. The mouth hooks of both larvae and adults are used to tear tissues during migration as well as to attach to the mucosa when feeding. Both larvae and adults are haematophagous and feed on blood from capillary beds via sucking mouthparts. Morbidity and mortality due to adult pentastome infections in reptiles are usually associated with infected lesions causing septicaemia, enterocolitis and pneumonia. Hosts appear to tolerate these large parasites in their tissues by inflammatory and immunological responses being modified by encapsulation processes (particularly around nymphs which become quiescent for extended periods) and by voluminous parasite excretory/secretory (ES) products that coat the parasites in protective substances. Both nymphal and adult pentastomes are very glandular and produce many different types of coatings that appear to protect them from host cellular and

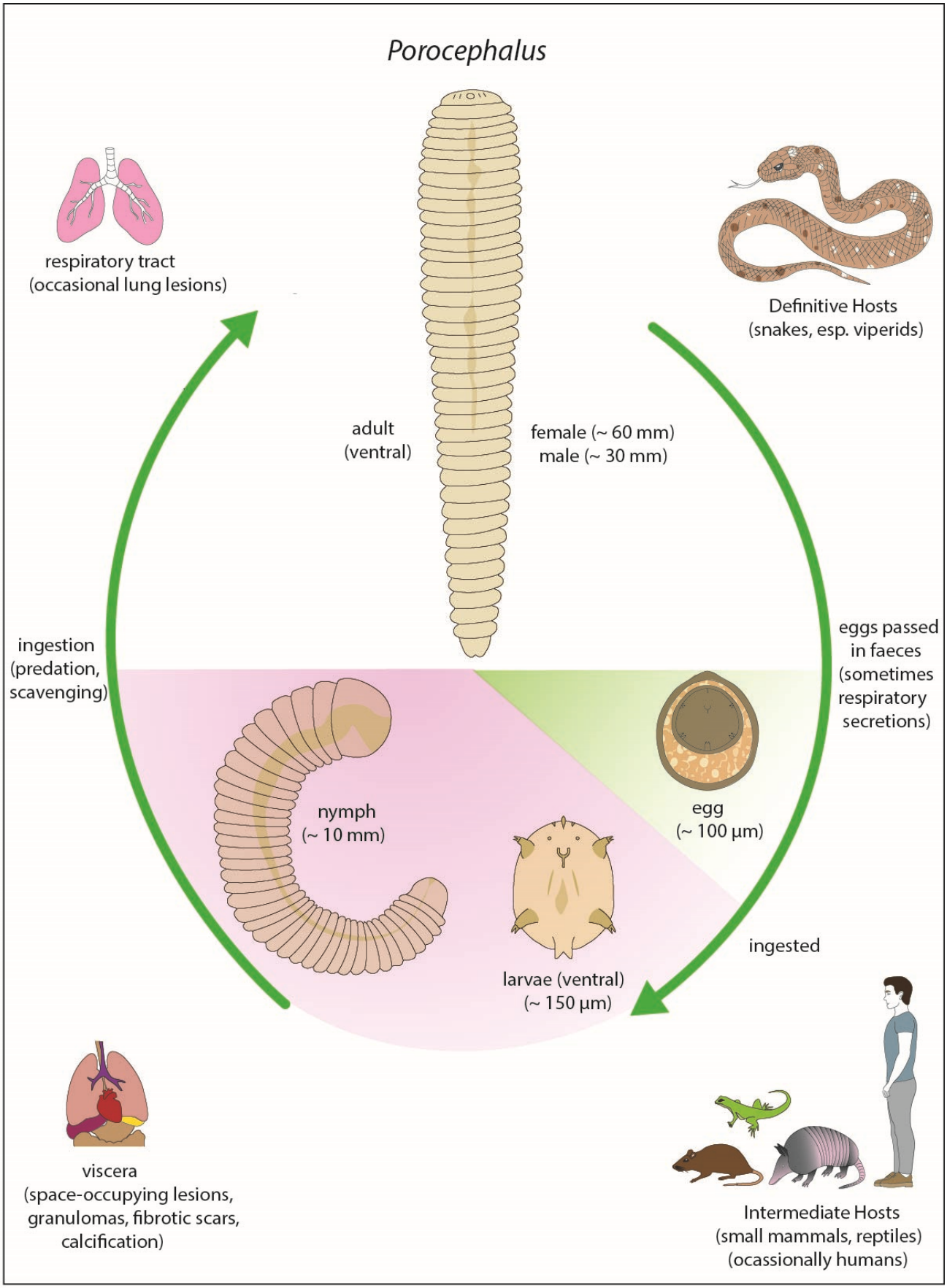
humoral responses. The migration of larvae and the encystment of nymphs can cause distinctive lesions in intermediate hosts, sometimes in accidental definitive hosts. Three types of lesions have been described: progressing from viable nymphs encysted within a thin layer of refractile eosinophilic material with little or no adjacent cellular infiltration; to necrotic granulomas surrounded by fibrotic and hyalinized connective tissues with cellular infiltrates (giant cells, macrophages, lymphocytes, plasma cells, eosinophils) in concentric rings; and finally granulomatous scars (cuticle granulomas) with acellular hyalinized fibrous tissue surrounding a central mass of amorphous calcified material. Humans may act as accidental intermediate hosts for several species of *Armillifer* and *Porocephalus*, with larvae invading visceral organs only to eventually die and calcify as they are unable to complete further development. Most visceral infections remain asymptomatic and are incidental findings during surgery or necropsy. However, they may sometimes cause a range of clinical symptoms and signs, depending on the intensity of infection and the tissues/organs involved. Visceral lesions may be confused with malignancies and infections are more abundant in men (particularly snake handlers or snake-eaters). The initial phase of infection is transient as larvae penetrate intestinal tissues causing pyrexia and colic. Larvae and nymphs are then subsequently found in the serosa around abdominal organs, sometimes within the organs themselves (mainly liver and lungs). Living, intact and encysted nymphs produce few signs, whereas dying and dead parasites may release considerable foreign material contributing to clinical illness, with eosinophilia, abdominal pain, oedema, chronic cough, night sweats, fever, sepsis with acute abdomen, and hepatic or neurological symptoms. In severe infections, death may occur due to disseminated disease, hypersensitivity reactions, intestinal obstruction, enterocolitis and septicaemia. Infections in the eye may cause substantial visual damage with loss of vision, often permanent.

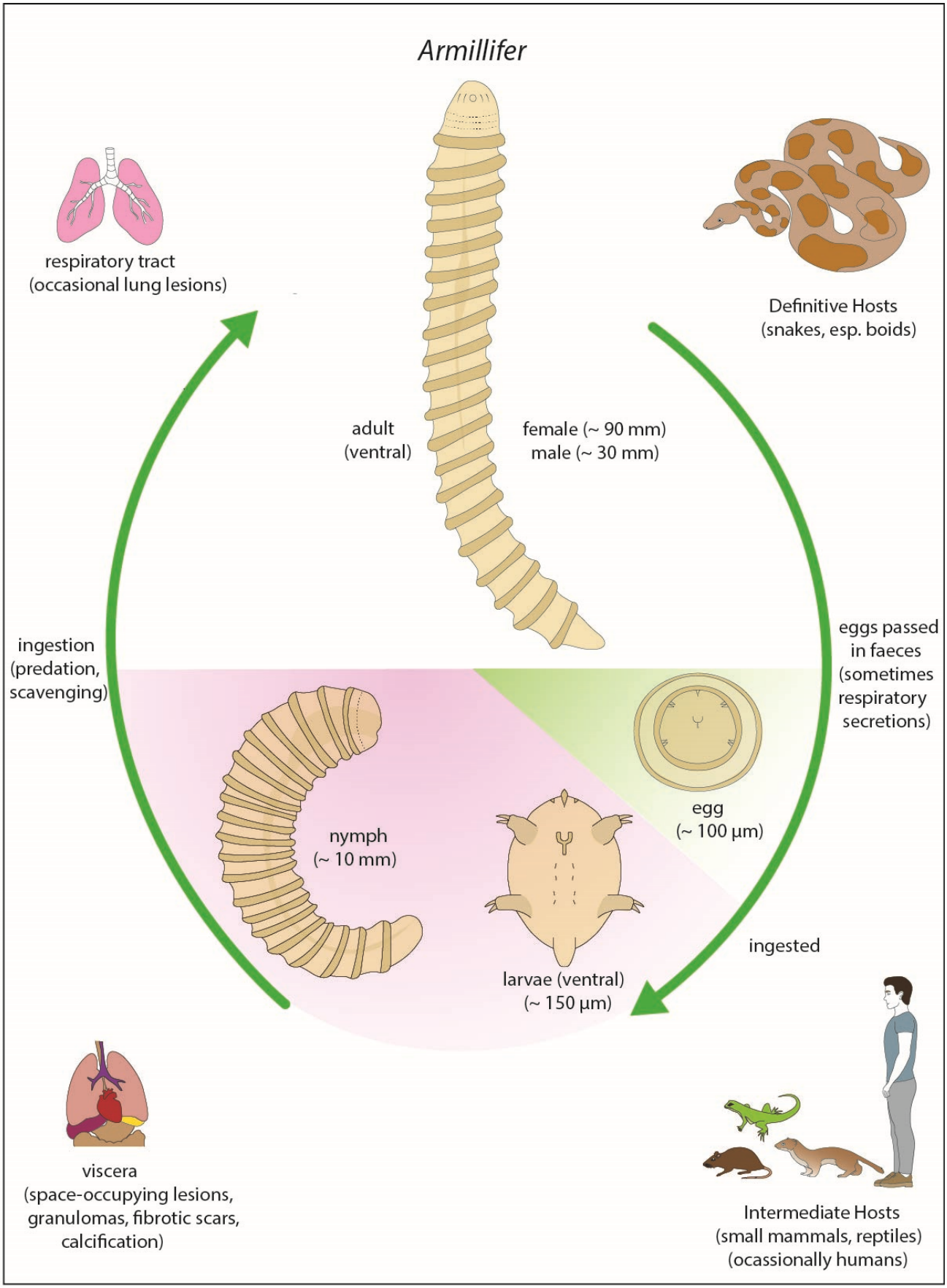
Developmental cycle and mode of transmission: Pentastomes are heteroxenous (2-host) parasites with predator-prey transmission occurring between larval/nymphal stages infecting the viscera of various prey animals (intermediate hosts) and adult stages infecting the respiratory passages of snakes (definitive hosts). Female pentastomes lay fully-embryonated eggs in the respiratory passages which then pass to the trachea and may be coughed/sneezed up but are more likely to be swallowed and subsequently passed in host faeces. The eggs are viscid and often cling together. They may withstand dry conditions for 2 weeks and have been found to remain viable in cool water for up to 6 months. When ingested by a suitable intermediate host (coprophagous or scavenging mammals, lizards or birds), the eggs hatch releasing primary larvae which have 4 stumpy legs and an anterior penetration apparatus used to invade host tissues. They may penetrate the intestines within one hour of ingestion and then migrate randomly in the body cavity for 7-8 days before encapsulating in serosal or soft tissues (they rarely invade striated muscles). Studies on developmental cycles report variable numbers of larval moults before they metamorphose into nymphs (lacking larval features) which grow and also undergo several moults before becoming heavily encapsulated as quiescent (dormant) stages that may persist for months in host tissues. Mature nymphs are recognizable by the presence of genital primordia and the development of 4 sets of circumoral hooks (characteristic for adults). When mature nymphs encysted within prey flesh are eaten by predation or scavenging by suitable definitive hosts (in this case, snakes), the nymphs excyst, penetrate the intestines and migrate by moving up the oesophagus to the nasal passages and then the lungs. Note that if definitive hosts accidentally ingest eggs, they may act as transient intermediate hosts when larvae hatch and penetrate tissues but they are unable to complete their development to adults. Male and female pentastomes mate once within their definitive hosts, but then anatomical changes in gravid females preclude further matings. Both sexes feed on host blood, but males do not live long, so most long-term infections consist of maturing females (which may live for up to 2 years or longer). Patent females lay massive numbers of eggs (up to several million) throughout their reproductive lives. Infections in humans occur when eggs are inadvertently ingested following the handling of snakes or snake products (including meat and bile) or by the consumption of undercooked snake meat or water contaminated with eggs. The eggs hatch releasing larvae which invade host tissues and may cause a range of clinical conditions. Those most at risk are snake owners (including groups that use snakes as totems), workers at snake farms, snake keepers at zoos and pet shops, veterinarians, as well as those that process and eat snake meat. Infections by at least 4 species (*A. armillatus, A. grandis, A. moniliformis* and *P. crotali*) have been found opportunistically in humans mainly in Africa and Asia.

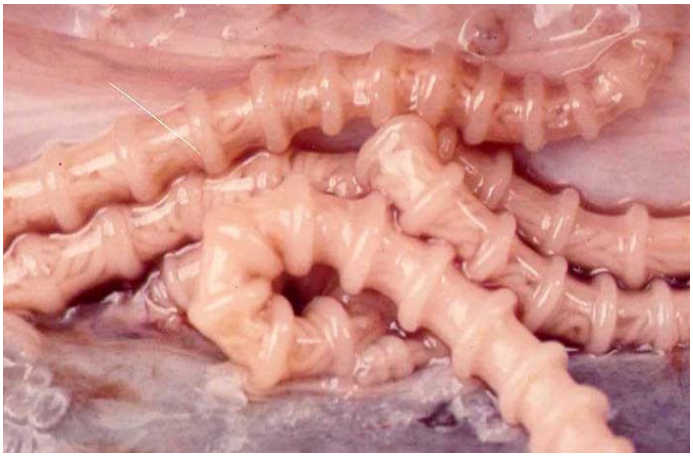
Differential diagnosis: Infections in reptiles may be detected ante-mortem by finding pentastome eggs upon microscopic examination of faecal floatations (sometimes lung washes) or by finding adult stages incidentally in lungs upon surgery or necropsy. On occasion, endoscopic techniques have been used to detect adult pentastomes in the lungs of large snakes (mostly pythons). Visceral infections in intermediate hosts may be indicated by radiographic findings of nodular lesions containing calcified C-shaped nymphs in host abdominal tissues, rarely in striated musculature (unlike the calcified cysticerci of tapeworms). More often, visceral infections are detected incidentally at surgery or necropsy, and confirmed by gross or histopathological observations (cuticular structures are readily observed, even in calcified specimens). Several studies have developed immunoserological tests (enzyme-linked immunosorbent assays, Western blots) to detect specific host antibodies against antigenic extracts from larval and adult pentastomes, but they are not widely available. More recently, molecular biological techniques have been used to identify and characterize pentastome species following the polymerase chain reaction (PCR) amplification of nuclear (ribosomal RNA) and mitochondrial (cytochrome c oxidase) gene sequences.

Treatment and control: Clinical infections in snakes may be treated after stabilizing hosts with thermal, fluid and nutritional support, and providing antibiotics in the case of secondary bacterial infections. Adult pentastomes may be removed from large snakes by endoscopic manipulation, taking care not to tear the parasite cuticle. Killing adult stages with antiparasitic drugs has been attempted using diethylenediamines (diethylcarbamazine), isoquinolines (praziquantel), imidazothiazoles (levamisole),

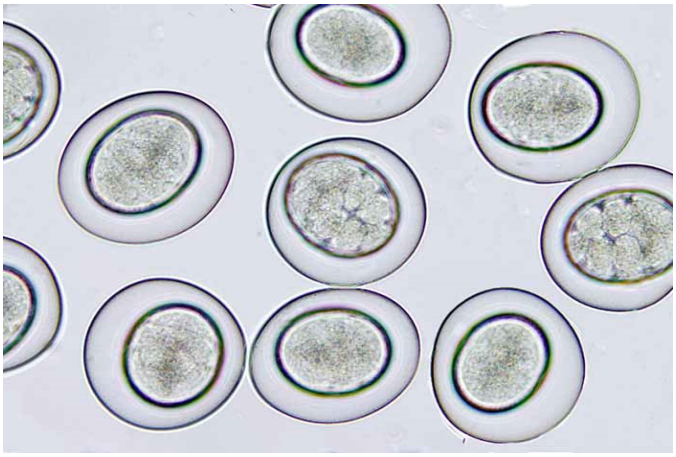
benzimadazoles (thiabendazole, fenbendazole, mebendazole) and macrocyclic lactones (ivermectin), but complications have sometimes arisen with the release of large amounts of antigenic material from dying parasites leading to allergic reactions, including anaphylaxis. Asymptomatic infections in humans with larval/nymphal stages are usually not treated as the parasites begin to degenerate and break down after several months. In symptomatic patients with visceral pentastomiasis, surgical approaches may have to be considered as there are no recommended antiparasitic chemotherapies available because the parasites are usually encapsulated in host tissues and coated with ES secretions. Nonetheless, clinicians have sometimes resorted to using diethylcarbamazine, praziquantel, levamisole, thiabendazole, fenbendazole, mebendazole, ivermectin and even fluoroquinolone antibiotics (ciprofloxacin), hematinics (haematopoetic nutrients) and some Chinese herbal medicines. The use of glucocorticoids to moderate allergic or inflammatory responses in contra-indicated. The prevention of infections revolves around personal hygiene (washing after handling snakes), meat hygiene (cleaning and cooking snake meat), good sanitation (disposing of snake faeces) and water treatment (filtration and disinfection).


Porocephalus
respiratory tract
(occasional lung lesions)
adult
(ventral)
female (~ 60 mm)
male (~ 30 mm)
Definitive Hosts
(snakes, esp. viperids)
ingestion
(predation,
scavenging)
eggs passed
in faeces
(sometimes
respiratory
secretions)
nymph
(~ 10 mm)
egg
(~ 100 µm)
larvae (ventral)
(~ 150 µm)
ingested
viscera
(space-occupying lesions,
granulomas, fibrotic scars,
calcification)
Intermediate Hosts
(small mammals, reptiles)
(ocassionally humans)


Armillifer
respiratory tract
(occasional lung lesions)
Definitive Hosts
(snakes, esp. boids)
adult
(ventral)
female (~ 90 mm)
male (~ 30 mm)
ingestion
(predation,
scavenging)
eggs passed
in faeces
(sometimes
respiratory
secretions)
nymph
(~ 10 mm)
egg
(~ 100 µm)
larvae (ventral)
(~ 150 µm)
ingested
viscera
(space-occupying lesions,
granulomas, fibrotic scars,
calcification)
Intermediate Hosts
(small mammals, reptiles)
(ocassionally humans)



Armillifer adults



Armillifer eggs



Porocephalus adult head



Porocephalus egg

Linguatula
(arthropod: pentastome)

Overview

Arthropods are coelomate metameric invertebrate animals with a chitinous exoskeleton and jointed limbs. They undergo protostomial embryonic development and grow by cuticular moulting (ecdysis). Three main subphyla are recognized: Chelicerata, Crustacea and Hexapoda. Crustaceans have a very strong cuticle strengthened by calcium salts; thus their growth must proceed through repeated moults. Most species are aquatic with internal or external gills, two pairs of antennae, mouthparts comprising one pair of mandibles and two pairs of maxillae, and each heteronomous body segment usually bears a pair of ventral biramous extremities (podia). Maxillipods lack appendages on abdominal segments and the nauplius larval stage has a unique maxillipodan eye. Pentastomatids (tongue worms) are unusual endoparasites with elongate worm-like bodies that have lost virtually all their appendages, apart from two pairs of tiny anterior claws near the mouth (collectively accounting for their penta-stome appearance). Most live in the respiratory systems of reptiles, although a few live in the air sacs of seabirds and the nasopharynx of dogs and cats. Eggs passed into the environment release oval larvae with four stumpy legs and an anterior penetration organ used to invade the tissues of an intermediate host (insect, fish, amphibian, reptile or mammal) where it forms a quiescent nymph which is infective to the definitive host. Porocephalids have their mouths between or below the anterior hooks, the hooks have a fulcrum, and the vulva is posterior. Infections by adult *Linguatula* spp. are found in the respiratory passages of carnivores (occasionally humans), and nymphal stages occur in small mammals (occasionally humans) as intermediate hosts.

Classification:
Domain: Eukaryota (membrane-bound nucleus)
Supergroup: Amorphea (unikonts with single flagellum, or nonflagellated amoebae)
Kingdom: Metazoa (multicellular eukaryotes, heterotrophs, notably animals)
Group: Protostomia (triploblastic, spiral cleavage)
Subgroup: Ecdysozoa (cuticle moulted = ecdysis)
Phylum: Arthropoda (chitinous exoskeleton, segmented body, jointed limbs, haemocoel)
Subphylum: Crustacea (mandibular mouthparts, gills, two pairs antennae, biramous podia, larval nauplius/zoea)
Class: Maxillipoda (nauplius with maxillipodan eye)
Subclass: Pentastomatida (tongue worms, anterior end with mouth and two pairs of tiny claws)
Order: Cephalobaenida (obliquely-paired hooks, medial genital openings)
Family: Linguatulidae (spatulate adults, parasites of mammals)
Genus: *Linguatula* (parasitic in respiratory passages of mammals)
Species: various species cause respiratory problems in carnivores (sometimes humans)

Parasite biodiversity and host range: Most Metazoa are multicellular triploblastic animals with differentiated tissues, many being bilaterally symmetrical with a body cavity. Most invertebrate animals are protostomes as their embryonic development involves spiral determinate cleavage. Those that moult their external cuticles during their life-cycles (process known as ecdysis) are grouped together in the unique clade Ecdysozoa, including the nematodes (roundworms), onychophorans (velvet worms), tardigrades (water bears) and arthropods (myriapods, chelicerates, crustaceans and hexapods). Arthropods have small segmented bodies encased in chitinous exoskeletons with articulated limbs. Most species are free-living in terrestrial and aquatic habitats, although a small range are ectoparasitic on other animals, some feeding on the blood or skin of vertebrates. Five subphyla are recognized: Chelicerata, Crustacea, Hexapoda, Myriapoda and Trilobita. Crustaceans have very strong cuticles strengthened by calcium salts, so they moult periodically as they grow and metamorphose through different types of larval stages before forming adults. Most species are aquatic and have internal or external gills, while terrestrial species have internal gills which are kept moist. Crustaceans have mouthparts with two pairs of maxillae (to handle food) and paired mandibles (with opposing biting and grinding surfaces). They have two sets of antennae and each body segment usually gives rise to a pair of ventral biramous appendages (podia). Six crustacean classes are recognized: Brachiopoda, Cephalocarida, Malacostraca, Maxillipoda, Ostracoda and Remipedia. Maxillipods usually have a body plan comprising 5 cephalic, 6 thoracic and 4 abdominal segments followed by a telson. The thoracic segments bear biramous (sometimes uniramous) limbs, but the abdominal segments lack appendages. The carapace is present or reduced, most feed using maxillae, and the nauplius larval stages have unique eyes with three cups, each with tapetal cells (= maxillipodan eye). Six maxillipodan subclasses are recognized: Branchiura, Cirripedia, Copepoda, Mystacocarida, Pentastomatida and Tantulocarida.

Major parasitic crustacean families	Biodiversity	Hosts	Parasitic stages	Patho-genesis	Disease transmission
Class: Maxillipoda					
Subclass: Copepoda (copepods)					

Order: Cyclopoida (open buccal cavity)					
Family: Lernaeidae (anchor worms)	19 genera, 114 spp.	freshwater fishes	copepodids and adults	skin lesions	direct (water)
Former order: Poecilostomatoida (slit-like buccal cavity)[now a "poecilostome" lineage within the Cyclopoida]					
Family: Ergasilidae (gill lice)	27 genera 61 spp.	freshwater and marine fish	adult ♀	gill/skin lesions	direct (water)
Subclass: Branchiura (head with flattened bilobed cephalic fold, carapace expands laterally)					
Order: Argulidea (discoid bodies, attach using hooks, suckers and barbs)					
Family: Argulidae (fish lice)	4 genera 150 spp.	marine and freshwater fish	juveniles, adults	skin lesions	direct (water)
Subclass: Pentastomatida (tongue worms, elongate annulated bodies, 2 pairs tiny anterior claws near mouth)					
Order: Porocephalida (horizontally-aligned hooks)					
Family: Porocephalidae	8 genera, 40 spp.	snakes, lizards (mammal, reptile IH)	adults	lung lesions	indirect (via IH*)
Family: Sebekidae	8 genera, 34 spp.	crocodiles, turtles (fish IH)	adults	lung lesions	indirect (via IH)
Family: Subtriquetridae	1 genus, 4 spp.	crocodiles (fish IH)	adults	lung lesions	indirect (via IH)
Order: Cephalobaenida (obliquely-paired hooks)					
Family: Linguatulidae	1 genus, 4 spp.	carnivorous mammals (mammal IH)	adults	naso-pharyngeal lesions	indirect (via IH)
Family: Cephalobaenidae	1 genus, 1 sp.	snakes (unknown IH)	adults		indirect?
Family: Raillietiellidae	2 genera, 43 spp.	amphibians, snakes, lizards, sugar glider (arthropod IH)	adults	lung lesions	indirect (via IH)
Family: Reighardidae	2 genera, 3 spp.	birds	adults	nasal lesions	direct?

*IH = intermediate host

Morphological and ultrastructural studies on immature and adult stages suggested that pentastomatids (tongue worms) were related to branchiurans, esp. argulids (fish lice). Analyses of mitochondrial DNA gene sequences indicated unambiguously that pentastomatids are a group of modified branchiurans [the name Ichthyostraca has recently been proposed for a 'Branchiura+Pentastomatida' clade]. Pentastomatids are unusual endoparasites with elongate non-chitinous annulated vermiform bodies that have lost virtually all their appendages, apart from two pairs of tiny anterior claws near the mouth (collectively accounting for their penta-stome appearance). Most live in the respiratory systems of reptiles and amphibians, although a few live in the air sacs of seabirds and the nasopharynx of dogs and cats. Eggs passed into the environment release oval larvae with four stumpy legs and an anterior penetration organ used to invade the tissues of an intermediate host (coprophagous insects, fish, amphibian, reptile or mammal) where it forms a quiescent nymph which is infective to the definitive host. Two orders have been recognized: Cephalobaenida (adults with medial genital openings, and a single oviduct); and Porocephalida (adults with posterior genital openings, and 2 oviducts). The family Linguatulidae has traditionally been placed in the order Porocephalida on the basis of several shared morphotypic characters (especially adult hook structure, reproductive anatomy), but recent molecular studies have suggested that the family be better placed in the order Cephalobaenida. Indeed, linguatulids are flattened spatulate pentastomes with pairs of obliquely-arranged hooks and mammalian final hosts, whereas typical porocephalids are cylindrical with horizontally-aligned hooks and reptilian final hosts. Most linguatulids have heteroxenous (2-host) life-cycles involving cyclic transmission between mammals where adult stages infect the respiratory passages of carnivores (acting as definitive hosts) and larval/nymphal stages infect the viscera of herbivores and omnivores (acting as intermediate hosts). However, one unusual species (*L. arctica*) has been found to have a monoxenous (1-host) life-cycle involving direct transmission between ungulates (reindeer) as the sole hosts. Another genus (*Neolinguatula*) was erected for linguatulid pentastomes with a caudal cleft (namely, *L. nuttali* from lions from Africa and *L. recurvata* from jaguars from South America), but the validity of the genus has been repeatedly questioned.

***Linguatula* species**	**Definitive hosts** (adults in respiratory passages)	**Intermediate hosts** (larvae/nymphs in viscera)	**Distribution**
L. arctica	Artiodactyla: cervid (reindeer/caribou)	none (unusual direct cycle)	Europe
L. multiannulata	Carnivora: canid (spotted hyena)	Artiodactyla: bovid (African buffalo, korrigum, topi, blue wildebeest, hartebeest)	Africa
L. nuttalli (syn. *Neolinguatula*)	Carnivora: felid (lion, leopard)	Artiodactyla: bovid (water buffalo, blue wildebeest, blue duiker, greater kudu), suid	Africa

		(desert warthog); Primates: cebid (‘*Cebus defassa*’?)	
L. recurvata (syn. *Neolinguatula*)	Carnivora: felid (jaguar)	Perissodactyla: tapirid (Baird’s tapir); Artiodactyla: tayassuid (collared peccary), bovid (harnessed bushbuck); Rodentia: hystricid (crested porcupine); Primates: pitheciid (titi)	Americas
L. serrata (syn. *L. caviae, caprina, denticulata, dingoensis, dingophila, ferox, integerrima, lanceolata, rhinaria, taenioides*) (European tongue worm)	Carnivora: canid (dog, dingo, African wild dog, side-striped jackal, black-backed jackal, wolf, maned wolf, culpeo, red fox), felid (cat, lion), procyonid (crab-eating raccoon); Perissodactyla: equid (horse, ass); Artiodactyla: bovid (sheep, goat); Primates: hominid (human)	Rodentia: murid (black rat, brown rat, greater bandicoot rat, Arabian spiny mouse, house mouse, Mongolian gerbil), abrocomid (Bennett’s chinchilla rat), caviid (guinea pig, cavy), hystricid (crested porcupine), octodontid (common degu); Didelphimorphia: didelphid (common opossum); Diprotodontia: macropodid (red-necked wallaby); Lagomorpha: leporid (European rabbit, eastern cottontail, European hare, Cape hare, Granada hare); Eulipotyphla: erinaceid (long-eared hedgehog, western European hedgehog); Artiodactyla: bovid (cattle, zebu, African buffalo, water buffalo, sheep, goat, hartebeest, blue wildebeest, impala, nilgai, korrigum, blue duiker, East African oryx, Mongolian gazelle, goitered gazelle), antilocaprid (pronghorn antelope), cervid (roe deer, fallow deer, reindeer/caribou), camelid (dromedary, Bactrian camel, vicuna), suid (pig), tayassuid (collared peccary); Perissodactyla: equid (horse); Carnivora: felid (cat); Primates: hominid (human); Serpentes: viperid (Gaboon viper)?; Charadriiformes: larid (sea gull)?	worldwide

A few other species were also reclassified to other pentastome genera: including *L. armillata* = *Armillifer*; *L. diesingii* = *Armillifer armillatus*; and *L. clavata* = *Porocephalus*.

Parasite morphology: *Linguatula* spp. form 4 different types of morphological stages during their development: eggs, larvae (several stages), nymphs (several stages), and adults. The eggs are oval, measuring 90-133 x 70-120 µm and surrounded by a thick eggshell with a yellow inner layer and a transparent membrane-like outer layer (which wrinkles when dry). They are embryonated and contain an ovoid primary larva with 2 pairs of hooks and developing legs. Hatched larvae have elongated club-like transparent bodies up to 200-250 µm in length with 4 distinct legs (each with 2 claws), an anterior penetration apparatus (consisting of a median spine and bifid lateral spines) and a short spiny tail. Different studies have reported that larvae undergo several moults growing in size to 4-6 mm long before metamorphosing into nymphs that lack larval characteristics (lost legs, penetration apparatus, and tail). It has also been reported that nymphs may undergo several moults increasing in size up to 16 mm long. The body has become broadly cylindrical with a somewhat flattened anterior portion tapering posteriorly, eventually becoming recurved and forming a prominent C-shape. Nymphs are segmented with up to 90 circular annulations, each with a row of small spines, and the chitinous cuticle is penetrated by numerous ring-like structures which are the sclerotized openings of subcuticular glands. Mature nymphs become heavily encapsulated in host tissues and are often surrounded by the exuvia of previous stages. They have ventrally located mouths with circumoral jointed chitinous hooks, large acidophilic anterior glands, simple tubular digestive tracts and primordial genitalia. Adult stages have dorsoventrally-flattened bodies that are distinctly spatulate being broadened anteriorly and tapering posteriorly (in contrast to porocephalid adults which are cylindrical). They are often called tongue worms because their shape resembles that of the mammalian tongue, but they are sometimes called sinus worms after their location in the host. They grow up to 130 mm long and have a translucent white-yellow cuticle with numerous small spines 16-32 µm long. The body is roughly divided into a small rounded head, broad trunk, and elongate blunt tail. The papillar-like head bears an oval mouth that is flanked by 2 pairs of chitinous hooks with double points. The hooks are jointed and have U-shaped campanulate fulcra. The close positioning of the 4 hooks to the mouth is why they were (erroneously) named penta-stomes (meaning 5-mouthed). In *Linguatula* spp., the hooks are arranged obliquely to the mouth (and not horizontally like porocephalids). The digestive system remains simple and tubular with the oesophagus expanding into a saccular stomach, and tubular hindgut and posterior anus. The nervous system consists of a ventral nerve cord with segmental ganglia. While adult pentastomes have a haemocoel, they do not have circulatory, respiratory or excretory organs. The trunk is distinctly annulated (segmented) with 65-92 circular rings, depending on species. The annuli also

bear small cup-shaped sensory organs on their lateral margins, and their posterior edges are roughened by numerous tiny spines projecting backwards. The cuticle contains numerous small circular depressions (pores) that are the apical portions of cuticular chloride cells. The trunk lacks limbs but sometimes the caudal trunk has a pair of small outgrowths (vestigial papillae). The tail is usually short and blunt, although 2 species have a bifid posterior extremity with a terminal cleft (characters used by some to erect the new genus *Neolinguatula,* which remains to be validated). Males are smaller than females; e.g. *L. serrata* males are 18-45 mm long while the females are 42-130 mm long. The genital opening in both sexes is flanked bilaterally by papillar (in males) or leaf-like (in females) structures. Males have 2 testes (unlike porocephalids which have one) with tubules leading to ejaculatory bulbs and a long cirrus (penis) in a cirrus sac. The male genital opening is located medioventrally and has copulatory spicules which are not club-shaped. Females have a single ovary but with bifid oviducts opening into a tubular uterus (greatly elongated and irregularly coiled) with diverticula (spermathecae). The female gonopore is located postero-ventrally and separated from the anus by several annulations (heterogyne condition).

Site of infection: Larval and nymphal stages occur in the visceral tissues of a wide range of herbivorous hosts (ungulates, rodents, lagomorphs) while adult stages occur in the nasopharyngeal cavities of a small number of carnivores (particularly canids, sometimes humans). Encysted nymphal stages have been detected in the peritoneal lining and mesenteries of the abdomen, the pleural lining of the thorax and on the surfaces of organs, as well as in lymph nodes, spleen, liver, lymph nodes, and sometimes the parenchyma of the lungs. Nymphs have also been detected in the viscera of humans, particularly in lymph nodes. Adult pentastomes have been found in the nasal airways, frontal sinuses, and tympanic cavity of canines and felines, and sometimes in the nasal passages of humans. One species, *L. arctica*, only occurs in the respiratory passages of reindeer and caribou.

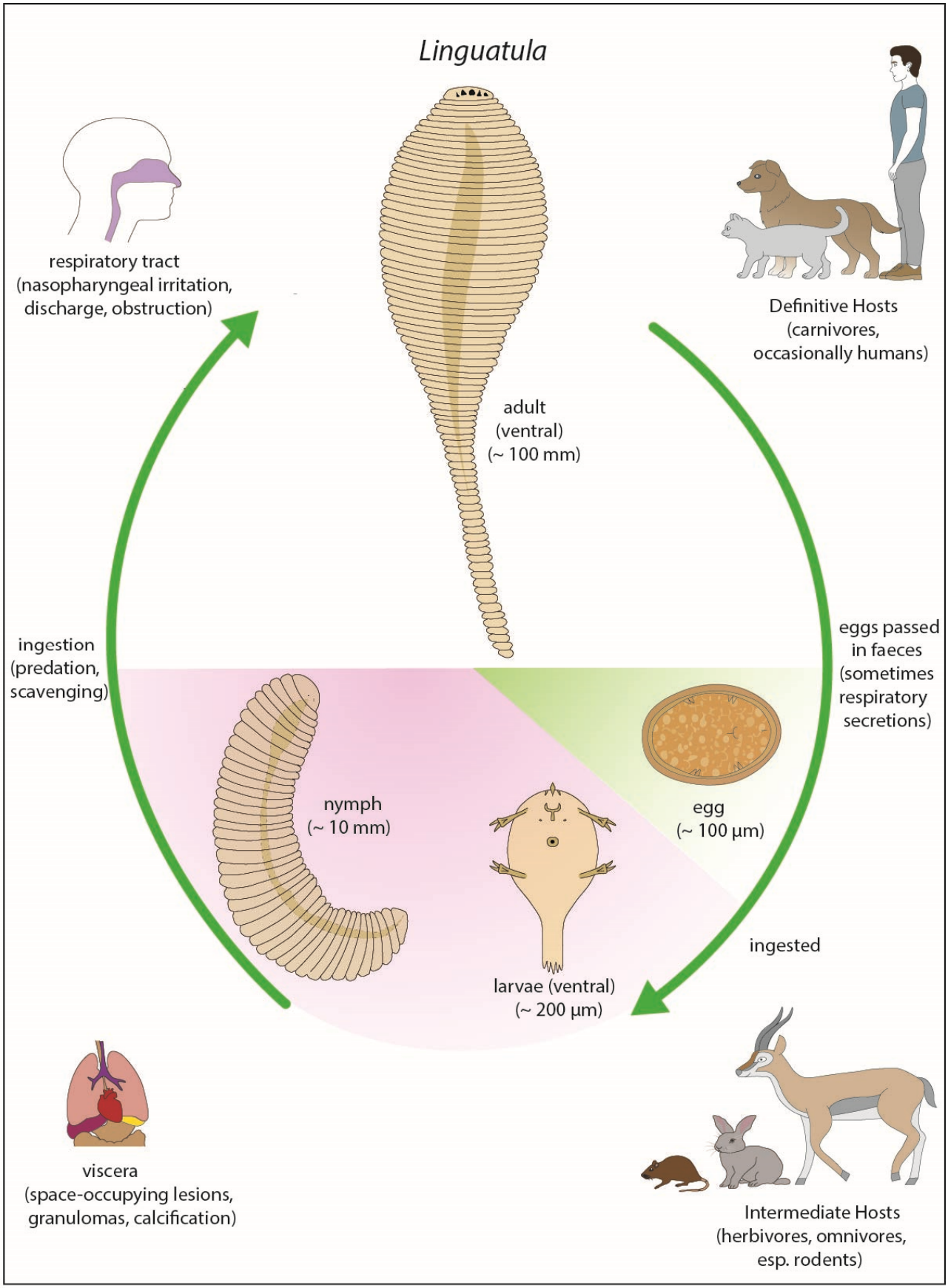
Pathogenesis: All larval, nymphal and adult pentastomes are endoparasitic and may migrate and feed on host tissues using their claws, spines, hooks and mouths. All stages feed on host cells, fluids and secretions, with variable reports of blood-feeding (unlike many other pentastomes which actively feed on blood). Infections may cause 2 types of disease depending on the host and stage of infection: visceral disease in intermediate hosts caused by developing larvae and nymphs; or nasopharyngeal disease in definitive hosts caused by developing adults. Most infections by nymphs in intermediate hosts (herbivores and omnivores) are inapparent as the nymphs encapsulate in visceral serosa, but the preceding larval stages may damage host tissues as they migrate through the gut wall into the viscera. Heavy infections may cause transient abdominal signs, enterocolitis, septicaemia, cough, pneumonia, and sometimes death. Encapsulated nymphs may also die and become calcified releasing large amounts of antigenic material which may provoke inflammatory and allergic responses. Adult pentastomes residing in the nasopharynx may grow quite large and cause irritation, respiratory sounds, nose rubbing, sniffing, nasal discharge and obstruction of the upper airways in their definitive hosts (carnivores). Humans may inadvertently act as either intermediate or definitive hosts for *L. serrata*, becoming infected with larvae after consuming eggs contaminating food or water, or becoming infected with adults after consuming encysted nymphs in offal. The occurrence and severity of disease often depends on the precise site of infection, the physiological condition of the host and the intensity of the infection. Visceral linguatulosis may develop when larvae invade tissues (mesenteries, liver, spleen, lungs, eyes) and form nymphs encapsulated in connective tissues. Migration may cause inflammatory tracts and organ perforation, while encapsulation may cause nodular space-occupying lesions with pressure atrophy on surrounding tissues. Viable nymphs are initially encysted in a thin layer of homogenous eosinophilic material with little or no adjacent cellular infiltration. However, they subsequently deteriorate forming necrotic granulomas with thick fibrotic and hyalinized walls and numerous cellular infiltrates (giant cells, macrophages, lymphocytes, plasma cells, and eosinophils), eventually forming granulomatous scars with acellular hyalinized fibrous tissue surrounding amorphous calcified material. Common clinical signs and complications include abdominal pain, enterocolitis, septicaemia, vomiting, bile duct blockage, pneumonitis, bronchitis, lung collapse, night sweats, cough, hepatitis, fibrosis, abdominal pain, headache and uveitis. Nasopharyngeal linguatulosis (regional variations called halzoun or marrara syndrome) occurs when humans eat raw or undercooked offal containing encysted nymphs which subsequently migrate from the stomach up the oesophagus to the pharynx and nasal passages and develop into adults. Migrating stages may cause discomfort and prickling in the throat a few hours after ingestion, whereas developing adults in the nasopharynx cause oedema (larynx, tonsils, fauces, Eustachian tubes, nasal passages, lips, conjunctiva), nasal and lachrymal discharges, episodic sneezing and coughing, dyspnoea, dysphagia, nausea, headache and sometimes abscesses, facial swelling and paralysis, asphyxiation and death. Infections in humans are commonly observed in Africa and Asia, but there are growing numbers being reported in Europe and the Americas, often in travellers.

Developmental cycle and mode of transmission: Pentastomes have indirect heteroxenous (2-host) life-cycles and undergo predator-prey transmission involving larval stages in intermediate hosts and adult stages in definitive hosts. *Linguatula* spp. utilize mammalian definitive hosts and the adults reside in the nasopharyngeal cavities (in contrast, porocephalids have reptilian definitive hosts and adults reside in the lungs). Gravid females lay numerous eggs which exit the host in nasal secretions but more usually are swallowed and excreted in host faeces. Eggs may remain viable on the ground on pastures or in water sources for several months. They are fully embryonated and contain an ovoid primary larva (resembling a small mite). Eggs are ingested by mammalian intermediate host when they consume contaminated food or water. A small range of animals serve as intermediate hosts, mostly herbivorous ungulates (especially bovids, some equids) but also smaller omnivores or scavengers (rodents and lagomorphs). Humans and small monkeys may also become accidentally infected. The eggs hatch in the intestines and the primary larvae penetrate the gut wall and migrate for a short time in visceral tissues. They have been reported to undergo several moults before

transforming into nymphs which lose their larval characteristics (legs and tail) and encapsulate in host tissues, particularly the mesenteries, lymph nodes and serosa of organs (liver, lungs). There are also a few reports suggesting that the nymphs undergo a few moults before they finally mature to the quiescent but infective final stage. Encysted nymphs persist with host tissues for many months, but ultimately seem to degenerate and calcify. The encysted nymphs are then eaten by carnivorous definitive hosts by predation or scavenging, mostly canids and felids. Humans may also become infected with *L. serrata* by eating raw or undercooked offal (livers, lymph nodes) from sheep and goats. Once ingested, the nymphs excyst in the stomach or intestines and migrate up the oesophagus to the nasopharynx where they attach, feed and grow into adults. Pentastomes mate in their hosts with males traversing tissues to locate females. It is thought that females only mate once as subsequent structural changes in gravid females precludes further mating. Males only live for several months whereas females may live for up to 2 years, producing millions of eggs after 6 months. The infective ova are discharged into the environment along with host respiratory secretions and faeces to complete the cycle.

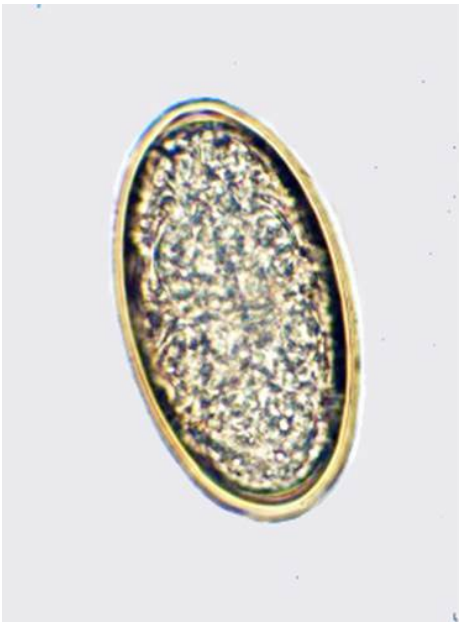
Differential diagnosis: Infections by pentastomes are difficult to diagnose on clinical grounds, as many patients are asymptomatic, infections may persist for many years without ill-effect, and even when clinical signs become apparent they are non-specific. Most infections are found fortuitously during medical or veterinary consultation, on surgery or at necropsy. Patent infections may be detected by the detection of pentastome eggs in faecal samples or nasal/sinus washes (gravid females produce millions of distinctive eggs containing small ovoid mite-like embryos). Various medical imaging technologies (radiology, computed tomography, ultrasonography) may be used to assist diagnosis through the detection of internal foreign bodies. Calcified nymphs are conspicuous in mesenteries and soft tissues, but are rarely found in striated muscles (unlike the calcified cysticerci of tapeworms). Adult pentastomes may be detected as soft spatulate tissue masses in nasal passages. Endoscopy may also be used on larger hosts to examine major passages for the presence of segmented adults. Infections are usually confirmed by gross and histopathological studies on specimens collected on biopsy or necropsy (their cuticular annulations remain recognizable). Several studies have developed an enzyme-linked immunosorbent assay (ELISA) to detect specific host antibodies against parasite excretory/secretory (ES) and somatic (S) antigens. Molecular biological studies have also been used to identify and characterize pentastome species by polymerase chain reaction (PCR) amplification of nuclear (18S ribosomal RNA) and mitochondrial (cytochrome c oxidase subunit 1) gene sequences.

Treatment and control: There is no particular treatment advocated for pentastome infections. Long-term monitoring of asymptomatic cases have observed that both nymphs in the viscera and adults in the nasopharynx tend to degenerate over 2 years, slowly being absorbed by host cellular reactions or becoming calcified. However, clinicians often intervene in clinical infections to alleviate symptoms and remove or kill parasites. Recourse may be made to the surgical removal of adults from the sinuses, often aided by endoscopy. Care should be taken not to damage the parasites as the sudden release of copious antigenic material may provoke inflammation and allergic reactions. Several studies have also used anti-parasitic drugs in attempts to kill parasites in humans and animals, including diethylenediamines (diethylcarbamazine), isoquinolines (praziquantel), imidazothiazoles (levamisole), and benzimadazoles (mebendazole), but they were not always effective as the parasites were partly protected (nymphal stages are highly encapsulated and adult stages are bathed in copious excretory/secretory material). The use of glucocorticoids is not recommended to moderate inflammatory responses. Recent studies have shown that treatment with macrocyclic lactones (ivermectin) were effective against some animal infections, including the enigmatic *L. arctica* in reindeer (which has an atypical direct cycle not involving intermediate hosts). A range of preventive procedures may be employed to help break the parasite life-cycle, usually involving water treatment (filtration and disinfection to remove and kill eggs), improved sanitation (disposal of faeces and avoiding nasal secretions from pets, burning or burying carcases), maintaining personal hygiene (wash hands after handling pets and preparing meat), and adopting suitable food hygiene protocols (cook meat and do not feed raw meat or offal). Education campaigns have been developed in several countries in attempts to break culturally-embedded eating habits (e.g. the consumption of raw liver and lymph nodes in certain parts of Africa).


Linguatula
respiratory tract
(nasopharyngeal irritation,
discharge, obstruction)
adult
(ventral)
(~ 100 mm)
Definitive Hosts
(carnivores,
occasionally humans)
ingestion
(predation,
scavenging)
eggs passed
in faeces
(sometimes
respiratory
secretions)
nymph
(~ 10 mm)
egg
(~ 100 µm)
larvae (ventral)
(~ 200 µm)
ingested
viscera
(space-occupying lesions,
granulomas, calcification)
Intermediate Hosts
(herbivores, omnivores,
esp. rodents)



Linguatula adult



Linguatula egg

DIAGNOSIS

DIAGNOSTIC PARASITOLOGY

The diagnosis of parasitic infections is a holistic integrated science involving inductive and deductive inference using multiple clinical/paraclinical parameters covering host-parasite biology, morphology, physiology, biochemistry and immunology. Diagnostic parasitology seeks to identify the aetiological (causative) agent of disease thus enabling appropriate management (treatment/control) options. Diagnosis is based on a sound working knowledge of the taxonomy of living organisms, but the identification/characterization/classification of individual parasite taxa (species/strains/genotypes) is not the primary aim. Often, the identity of the actual parasite species is not required by the clinician, e.g. knowledge that gastro-intestinal nematodes have been implicated as the cause of neonatal scours may be sufficient to commence treatment with an anthelmintic.

Diagnostic parasitology is not a dry esoteric exercise conducted by technicians/scientists in remote laboratories, but rather a detailed reasoning exercise conducted by the clinician who interacts with the patient and is ideally cognizant of most relevant facts and uses a variety of technologies and support services to gain further knowledge to make a differential diagnosis. While the mental processes involved in clinical reasoning and differential diagnosis are difficult to categorize (involving many cognitive and metacognitive processes), there are certain things that are obviously known to the clinician which can be used to make some common-sense predictions.

- The clinician should always know the host species involved - medical practitioners should recognize their patients as humans, and veterinary practitioners should be able to identify the animal species they are working on. This simple information already allows clinicians to consciously/subconsciously access information on host specificity, host range, host distribution, host susceptibility/resistance, etc.

- The clinician should be able to determine why the patient has presented – symptoms can be described, signs can be observed. This allows an assessment of how serious and urgent the situation may be, as well as helps to pin-point the tissue/organ systems involved. Most parasites have predilection sites of infection and exhibit tissue tropism and this information helps to facilitate diagnosis, to assess disease development and progression, and to predict possible outcomes (prognosis).

- Samples can then be collected for further examination, and it is a poor clinician who does not know that they are up to their armpits in faeces, urine, vomitus, sputum, blood, tissue aspirates, tissue biopsies, etc. In selecting specific samples, the clinician is seeking further information to help rule in or rule out certain aetiological agents. It is also up to the clinician to request the most appropriate tests to be conducted (e.g. full blood count, differential, haematocrit, liver enzymes, worm egg count, etc.).

However self-evident, all of this host-parasite information helps in the clinical reasoning process so that the clinician can make a working diagnosis to begin disease management. In addition to providing detailed information about the specific case in hand, it also allows the clinician to predict the mode of transmission of the parasite so that preventive measures can be implemented to avoid further cases. For example, many parasites in the digestive tract causing enteritis and diarrhoea are transmitted by the faecal-oral route; many parasites in the circulation causing fever and anaemia are vector-borne; and many parasites in visceral organs causing lesions and organ malfunction are transmitted by carnivorism. Other horizontal transmission strategies used by parasites include venereal (sexual), transdermal (percutaneous) and air-borne (respiratory) transmission. Water-borne and food-borne transmission usually involves faecal-oral or predator-prey transmission. Some parasites also exhibit vertical transmission between generations, including transplacental and transmammary transmission. Knowledge of the mode of transmission allows affirmative action to be taken to minimize the spread of infections within host populations. Clinicians not only have a responsibility for their individual patients, but also a broader responsibility for the general community to identify disease clusters and prevent outbreaks by recommending appropriate control strategies.

TYPES OF DIAGNOSTIC TESTS

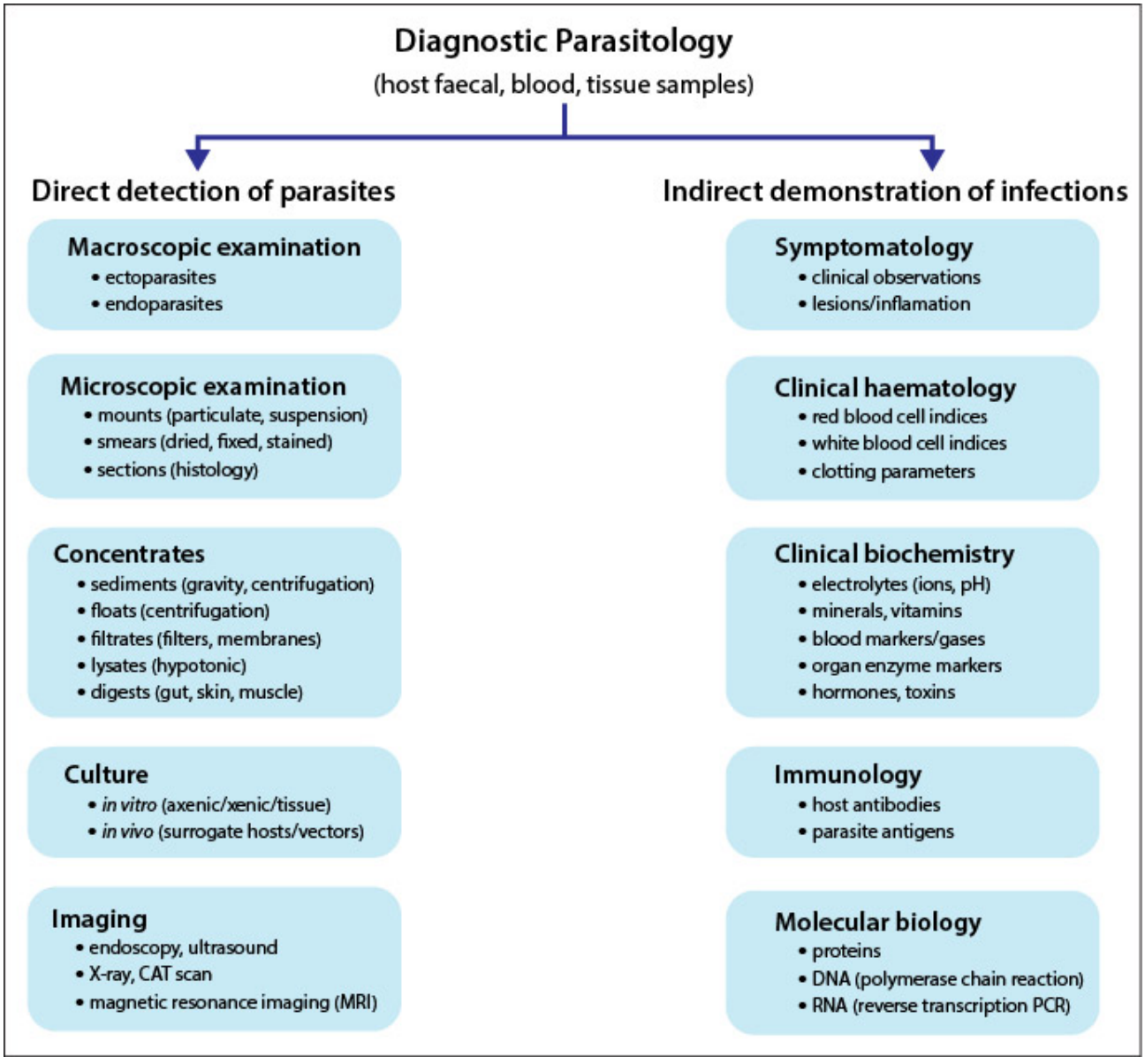
A variety of medical and veterinary tests are used to diagnose parasitic infections and diseases. Different techniques are employed to either directly detect parasites in host tissues/fomites or provide presumptive evidence of infection by the demonstration of specific clinical, biochemical, immunological or molecular parameters.

Direct detection techniques include:

- macroscopic examination of host surfaces, orifices or fomites (for visible parasites);
- microscopic examination of host faeces, blood or tissues (for microscopic parasites);
- physical concentration of parasites from samples (qualitative or quantitative);
- *in vitro* culture of parasites from samples (axenic, monoxenic or tissue culture);
- *in vivo* culture of parasites from samples (by laboratory animal inoculation); and
- medical imaging of parasites in tissues (by endoscopy, ultrasound, X-rays, CT scans or MRI)

Indirect demonstration techniques include:

- detecting specific disease symptoms or signs (by clinical observations);
- detecting specific host blood parameters (by clinical haematological tests);
- detecting specific host plasma proteins/enzymes (by clinical biochemical tests);
- detecting specific host antibodies or parasite antigens (by immunological tests); and
- detecting specific parasite proteins or nucleic acids (by molecular biological tests).

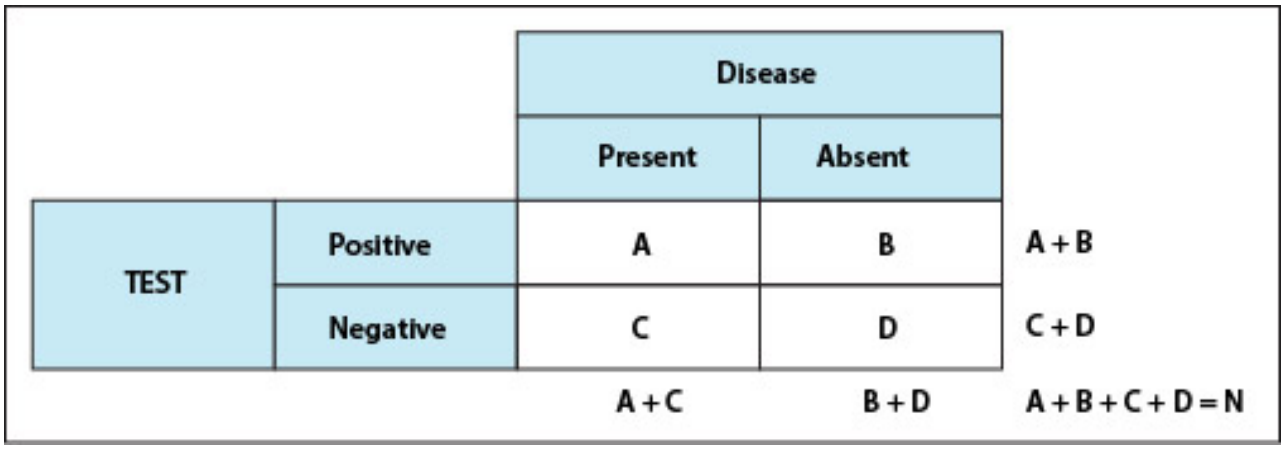


Parasitic diseases vary greatly in their presentation and exhibit marked fluctuations in their dynamics (quantitative measures) and kinetics (time courses). Thus there is no single type of test appropriate for the diagnosis of specific infections. A plethora of tests have been developed over many years to differentially detect different life-cycle stages of different parasites or different host responses to different parasites. Clinicians often request a small battery of relevant tests to be conducted to either exclude or include parasites as the aetiological agent of disease. Ideally, diagnostic tests should exhibit the following desirable characteristics:

- safety (pose little risk to patient and test operator);
- cost efficiency (be cheap and affordable);
- time efficiency (provide a rapid result);
- simplicity (by easy to perform);
- durability (be robust with stable long-lived reagents);
- reproducibility (give the same results within test conditions);
- accuracy (discriminate between infected and non-infected individuals);
- specificity (detect the correct parasite, and give few false positive reactions); and
- sensitivity (detect low level infections, and give few false negative reactions).

INTERPRETATION OF DIAGNOSTIC TESTS

Few diagnostic tests are absolutely perfect; they may give erroneous results for a variety of reasons, both technological and biological. Inappropriate samples may be tested, samples may be stored or transported improperly, reagents may be too old, test conditions may be violated, and many human errors may have been made by the test operator (pipetting errors, steps accidentally omitted, time delays, etc.). Many tests cannot identify recently acquired infections (e.g. during the incubation or pre-patent period), many cannot differentiate between chronic infections and previous exposure (e.g. antibodies persist long after infection has resolved), many cannot detect low level infections (e.g. parameter below detectable threshold), and many tests cannot identify specific infections (e.g. cross-reactivity between parasites). It is therefore important that users of any particular test know how good it is, as determined by objective quantitative assessment. Test efficacy is quantified by comparing results with disease status in a reference population (disease status being the 'gold' standard). Regrettably, gold standards are not always available so test efficacy may be poorer than reported. Bayes' theorem is used to quantify test accuracy, sensitivity, specificity, and predictive values. Four outcomes are possible when testing the host population: as shown in the following 2x2 matrix:



Outcomes (and consequences):

A = true positive:	test correctly diagnoses disease, facilitating treatment.
B = false positive:	test falsely diagnoses disease, resulting in unnecessary treatment.
C = false negative:	test falsely rules out disease, allowing disease progression, death
D = true negative:	test correctly rules out disease, suggesting other cause.

Prevalence (proportion positive or diseased at a particular point in time)

Disease prevalence	= (A+C)/N	[total diseased over total population]
Test prevalence	= (A+B)/N	[total test-positive over total population]

Accuracy (probability of correct test result)

Test accuracy	= (A+D)/N	[total true results over total population]

Sensitivity (probability of positive test in diseased person)

Test sensitivity = A/(A+C) [true positives over total diseased]

Ideally, test will have low rate of false negatives, thus a negative test often rules out disease

[SNNOUT = SeNsitive test, Negative test rules OUT diagnosis]

When a disease is very serious and missing it will have dire consequences, select a sensitive test.

Specificity (probability of negative test in non-diseased person)

Test specificity = D/(B+D) [true negatives over total non-diseased]

Ideally, test will have low rate of false positives, thus a positive test often rules in disease

[SPPIN = SPecific test, Positive test rules IN diagnosis]

When a disease is suggested by other data, select a specific test to rule in a diagnosis.

Predictive values (probability of disease in test-positives, probability of non-disease in test-negatives)

Positive Predictive Value (PPV) = A/(A+B) [true positives over total positives]

Negative Predictive Value (NPV) = D/(C+D) [true negatives over total negatives]

Most governments have regulations where numeric scores for these parameters (expressed as proportions or percentages) must be included in the product information accompanying commercial test kits, so users (laboratory scientists or clinicians) know the limitations of the test selected. Most pathology laboratories also conform to best practice standards advocated by impartial agencies which recommend the adoption of standard operating procedures and ongoing compliance with quality assurance/control programs (through routinely testing positive reference samples and negative controls) to ensure test performance is within acceptable standards. International test standardization is particularly important when considering import/export certification and quarantine requirements in our global society.

THRESHOLD OF DETECTION

The term sensitivity often has an ambiguous meaning. Bayes theorem uses a mathematical expression to measure the diagnostic or clinical sensitivity to be the probability of a obtaining a positive test result in an infected individual. Alternatively, the analytical sensitivity of a test can mean the smallest detectable number of parasites (or antibodies, or DNA); also known as the threshold limit of detection (LOD), below which the test gives a negative result although some parasites may be present (but not in detectable numbers). The LOD can be quantified both in terms of how much sample should be examined and how few parasites could be detected. It becomes a numbers game!

How much of a sample can be examined?

Depending on the host species, you could collect faecal samples weighing up to several hundred grams (g) or millilitres (mL) or more. How much of the sample can you, or should you, physically process and examine? A single faecal smear contains around 0.001 g of faeces and it takes at least 10 minutes to examine thoroughly under a light microscope. To detect just one parasite (say, one worm egg) in 1 g of faeces, theoretically you would need to look at 1,000 smears which would take 10,000 minutes (= 167 hours = 7 days). Clearly, this is impractical. The minimum LOD achieved by looking at just one faecal smear is therefore $1/1{,}000^{th}$ of 1 egg/g; the equivalent of 1,000 eggs/g. In reality, worm egg counting techniques aim to detect as few as 60 eggs/g of faeces. They achieve this not by examining more sample or by increasing examination time, but by concentrating and/or harvesting parasites from samples. Similarly, a blood sample collected into a haematological tube may be as much as 5 mL, but many haematological tests rely on the examination of one thin blood smear (approximately 2 µL) for 10 minutes. To process the whole 5 mL sample, you would need to prepare 2,500 smears and examine them for 25,000 minutes (= 416 hours = 17.4 days). Even when one blood smear is examined, it is unusual to examine every single blood cell, more often 100 high-power microscope fields are examined, each containing around 10^2 cells. If you detected just one parasite in those 100 fields, the threshold LOD would be 1 parasite in 100 x 10^2 (= 10^4) cells, that is, 0.01% parasitaemia. This may be improved by examining more fields per smear, or by concentrating parasites from samples.

The LODs of tests may be enhanced by several orders of magnitude by concentrating parasites through centrifugation, filtration, culture, cell sorting or DNA amplification (improvements of 10^2-10^3 times for coprological tests, 10^3-10^4 for haematological tests, and 10^4-10^6 for biochemical and molecular biological tests). To compare conventional and contemporary techniques, it is necessary (but difficult) to convert the units of one type of test to those of another. Early PCR tests reported LODs enigmatically as 50 ng to 10 fg (spanning 6 orders of magnitude), but these quantities simply referred to the amount of DNA template provided in the sample without any way of reconciling how many parasites they might represent. Theoretically, a positive PCR test could indicate the presence of DNA from a single parasite. However, molecular tests do not detect whole parasite genomes but use small primers to amplify partial gene sequences (often 500 bases). Given that one nucleotide base weighs on average 650 Daltons (Da) and that 1 g = 6.022 x 10^{23} Da, then a gene fragment of 500 bases can be calculated to weigh ~5 x10^{-19} g (= 0.5 ag). By comparison, the average parasite genome size

is ~ 500 megabases (Mb) [protozoa range from 10 Mb to 100 Gb; helminths from 100 Mb to 1 Gb] which can be calculated to weigh 5 x 10^{-13} g (= 0.5 pg). [Interestingly, primers looking for 500 bases in a 500 Mb genome means you are effectively only looking for 0.0001% of the parasite]. The lowest reported LOD of 10 fg DNA could therefore theoretically represent anywhere from 0.001 of a parasite (0.1% of a whole 500 Mb parasite genome) to 20,000 parasites (maximum number of copies of 500 b gene fragment). Clearly, these values are meaningless and cannot be used to express LOD in terms of parasite load (concentration) without knowing what sample sizes were used for DNA extractions, what aliquot sizes were used for PCRs, how DNA amounts were measured, how much host DNA may have been included, etc.

More recently, experimental studies have used serial dilutions of DNA extracted from samples spiked with known numbers of parasites and found LODs to range from 1-6 oocysts/g faeces (for *Cryptosporidium*), 1 parasite/µL blood (for *Plasmodium*), 1 parasite/mL (for *Leishmania*), etc. In some instances, unit conversions are required to compare old and new tests: e.g. what percentage parasitaemia does 1 parasite/µl correspond to? The mean cell volume of a human erythrocyte is ~90 fL (= 90 x 10^{-12} mL), so there may be up to ~10^{10} erythrocytes in 1 mL of blood (realistically, there will be fewer as the whole blood volume is not composed of cells – actual blood counts show there are up to 5 x 10^9 red blood cells/mL of blood, plus 8 x 10^6 white blood cells /mL). If you can detect 1 parasite/µL (= 10^3 parasites/mL), then the threshold LOD would correspond to 10^3 parasites in 10^{10} erythrocytes, the equivalent of 0.00001% parasitaemia. Clearly, the analytical sensitivities of modern molecular tests are better than those of conventional tests that rely on the detection of whole organisms. While the detection of whole organisms does allow additional morphotypic features to be examined, molecular tests are becoming more sophisticated in detecting specific genotypes and facilitating phylogenetic analyses.

How much space does a parasite occupy in a sample?

Let us assume that a sample of 1 g = 1 mL = 1 cc = 10^{12} µm^3. One intact stereotypical spherical protozoan cyst measuring 10 µm in diameter occupies a volume = 4/3 πr^3 = 524 µm^3. The cyst therefore occupies 0.00000005% of the 1 g sample. For comparison, one stereotypical spherical helminth egg measuring 100 µm in diameter occupies a volume = 4/3 πr^3 = 524,000 µm^3. The egg therefore occupies 0.00005% of the 1 g sample. One stereotypical spherical arthropod measuring 1,000 µm (1 mm) in diameter occupies a volume = 4/3 πr^3 = 524,000,000 µm^3. The arthropod therefore occupies 0.05% of the 1 g sample. Obviously, looking for one parasite developmental stage can be like looking for a needle in a haystack. Various techniques are employed to improve the chances of detection: such as concentrating parasites from samples, separating them from confounding material, and making them more readily observable by using histochemical or immunological stains. By comparison, the amount of host sample occupied by specific parasite molecules (proteins or DNA) may be extremely miniscule, but their detection relies on a huge range of factors in addition to their concentration, notably their reactivity under test conditions.

How many parasites does it take to cause disease?

This is the quintessential question, one for which we have few answers. By definition, parasites cause harm to their hosts, but the harm may not be sufficient to even be noticed by the host. Parasites cause disease by:

- stealing nutrients (ingestion, absorption..)
- destroying cells (ingestion, lysis…)
- migrating through tissues (tunneling, tracking..)
- lodging in tissues (obstruction, space-occupying lesions..)
- provoking host reactions (toxicoses, inflammation, hypersensitivity..)

At what stage does the resultant perturbation in structure/function of host tissues (= pathology) become manifest as disease, with recognizable symptoms and signs? Parasitic infections are dynamic processes, with parasites numbers changing markedly over time (increasing during multiplicative phases, and decreasing during senescent phases or due to host immunity). The relationship between parasite numbers and disease expression is further complicated by how susceptible the host is to infection and disease, and how virulent the parasite is in terms of invasiveness, appetite, growth and multiplication. Protozoan parasites usually undergo massive multiplication in host tissues often giving rise to acute disease syndromes (rapid onset, short duration). Helminth parasites do not multiply but accumulate in host tissues often giving rise to chronic disease syndromes (slow onset, long duration). Arthropod parasites vary in their abundance, some multiplying in host tissues and others accumulating on host surfaces. All types of parasites can cause severe disease if the cumulative damage to the host overwhelms homeostasis and repair processes. Attempts to quantify pathogenic doses for some parasites have been made in experimental animal models, but the results often cannot be extrapolated to natural field infections. Theoretically, disease may ultimately result from infection by one parasite, but in reality it takes more to establish clinical infections.

The minimum level of detection of a diagnostic test should therefore be better than the number of parasites required to cause disease, otherwise the test would give unacceptable numbers of false negative results, with potentially disastrous consequences. Most tests, especially modern molecular tests, have a very low threshold level of detection and they can detect small amounts of parasitic material in host samples. However, this can also bring about problems in interpretation, because detection does

not unequivocally imply causation. Subclinical parasitic infections occur in many hosts, so although parasites may be detected, it does not mean that they caused the disease. They were simply fortuitous or opportunistic findings in hosts succumbing to disease due to other causes. Concomitant infections by more than one parasite species are also common in clinically-affected hosts, as many parasites utilize the same modes of transmission that have resulted in infection. Which parasite was responsible for disease, the most abundant, the most virulent, or various combinations of those present?

The interpretation of diagnostic test results is therefore not straightforward, with many potential problems in sensitivity, specificity, diagnostic threshold and clinical threshold confounding differential diagnosis. It must be remembered that the clinician makes the diagnosis based on a wealth of evidence gleaned from observation, history, physical examination and laboratory investigation.

SYMPTOMATOLOGY (SYMPTOMOLOGY)

The diagnosis of parasitic disease on the basis of clinical symptoms (described by patient) or clinical signs (observed by clinician) is difficult because most are nonspecific. Diarrhoea may be caused by viral, bacterial, protozoal and helminth infections; likewise fever, anaemia, etc. It is important that clinicians carefully record presentation signs (abnormal structure/function, pain, etc.), obtain an appropriate history (nature, intensity, location, duration, onset, concomitant, aggravating, relieving), monitor vital signs (respiration, circulation, temperature), and request appropriate laboratory investigations (diagnostic tests). Few parasitoses can be diagnosed on the basis of clinical presentation, other than those where the aetiological agent is conspicuous in host tissues (such as visible ectoparasites). Nonetheless, clinical presentation helps the diagnostic process by allowing the clinician to consider the usual suspects in each case, collect the most appropriate samples and request the most appropriate diagnostic tests from their service laboratories.

Characteristics of common parasitic infections

Site	Symptoms	Transmission	PROTOZOA	HELMINTHS	ARTHROPODS
Gut	diarrhoea, blockage, anaemia	faecal-oral, vector-borne, direct	amoebae diplomonads coccidia ciliates	round-, pin-, whip-, thread-, hookworms tapeworms enteric flukes	bot flies
Blood	anaemia, fever, ischaemia	vector-borne	trypanosomes haemosporidia piroplasms	filarial worms blood flukes	(most ecto- parasites feed on blood)
Organs	lesions dysfunction inflammation	predator-prey, direct	cyst-forming coccidia microspora	hydatids cysticerci liver flukes *Trichinella*	bot flies
Skin	lesions inflammation	direct, vector-borne	leishmanias	larval migrans, filarial worms	flies fleas lice mites ticks

By definition, parasites cause harm to their hosts, but that harm may be overlooked in asymptomatic or subclinical infections involving few parasites of low virulence. However, heavier infections involving more parasites, or more virulent parasites, can cause sufficient harm for disease expression to become apparent to the host and clinician. Clinical symptoms are felt and described by human patients to their doctors, while clinical signs are observed in human or animal patients by medical or veterinary practitioners. Although certain clinical manifestations may ‘typically’ be associated with certain parasites, in many instances their occurrence is not pathognomonic (e.g. eosinophilia and helminthiases) as other aetiological agents or disease processes may be involved. Nonetheless, diagnosticians should be cognizant of the ‘usual suspects” in their deliberations.

Symptomatology regularly associated with parasitic infections

Tissue/organ system	Clinical symptoms/signs*	Usual suspects (human parasitoses)*
alimentary	anorexia, fever, pain, diarrhoea, vomiting, dehydration, oedema, unthriftiness, anaemia, eosinophilia, hypoalbuminaemia	amoebiasis, giardiasis, leishmaniasis, coccidiosis, cryptosporidiosis, balantidiasis, enterobiasis, trichuriasis, ascariasis, hookworm diseases, strongyloidiasis, capillariasis, anisakiasis, taeniasis, fascioliasis, schistosomiasis, clonorchiasis, opisthorchiasis,
urogenital	haematuria, eosinophilia, abortion, sterility	trichomoniasis, toxoplasmosis, sarcocystosis, schistosomiasis
respiratory	anorexia, sneezing, coughing, nasal discharge, tachypnoea, dyspnoea, eosinophilia	leishmaniasis, lungworm diseases, hookworm diseases, paragonimiasis, echinococcosis
nervous	anorexia, depression, stupor coma, ataxia, paresis, paralysis, seizures, tremors, dysmetria, eosinophilia	toxoplasmosis, African trypanosomiasis, malaria, onchocercosis, angiostrongyliasis, paragonimiasis, cysticercosis, echinococcosis, coenurosis, schistosomiasis
circulatory	anorexia, cardiac dysfunction, vasculitis, fever, lethargy, oedema, anaemia, leucopenia, eosinophilia	American trypanosomiasis, malaria, babesiosis, filariasis, onchocercosis, schistosomiasis
musculature	anorexia, weakness, myalgia, haemorrhages, bruising	toxoplasmosis, sarcocystosis, microsporidiosis, trichinosis, gnathostomiasis, cysticercosis, echinococcosis, coenurosis, pentastomiasis
skin	pruritus, erythema, scales, crusts, excoriations, alopecia, nodules, papules, vesicles, lichenification, pigmentation abnormalities, anaemia	leishmaniasis, hookworm diseases, dracunculiasis, onchocercosis, scabies, tungiasis, pediculosis, myiasis, demodecosis, tick bites, insect bites

**cf. Mehlhorn H (Ed) 2001 Encyclopedic Reference of Parasitology, 2nd ed, Springer*

SAMPLES/SPECIMENS

A wide range of clinical samples may be collected from diseased hosts for testing in the laboratory, including fluids, solids and suspended material (blood, urine, cerebrospinal fluid, faeces, vomitus, sputum, aspirates, swabs, scrapings, tissue biopsies, etc.). It is important that the integrity of the sample be preserved so that no contamination occurs and the samples do not rapidly degrade. There are numerous guidelines available from diagnostic agencies as to what samples are considered appropriate for individual tests, how to collect them, how to store them and how to transport them. These guidelines generally comply with occupational health and safety, biohazard, transportation and even quarantine regulations in order to protect people and industries. Remember that parasites cause infectious diseases so all diagnostic samples should be considered as potentially infectious. The vast majority of samples submitted to diagnostic laboratories consist of faeces, blood or tissue biopsies from live patients, or post-mortem tissue samples from deceased patients. A range of coprological, haematological, biochemical, immunological, molecular biological and histopathological techniques has been developed to process samples for evidence of parasitic infections.

DIRECT DETECTION OF PARASITES

Indisputable evidence of infection is obtained when the parasites themselves are recovered from clinical samples. A variety of techniques have been developed to find, recover and identify parasites from host material, some involving little more than visual examination of hosts or host material, but most involving microscopic examination of host tissues or concentrates and comparative morphometry.

Parasite size

Parasites range greatly in size - covering seven orders of magnitude. Some adult tapeworms are several metres in length (10^1 m) while some protozoa are only several micrometres (= microns) in size (10^{-6} m = 1 μm). As a rough guide to the sizes of parasites, protozoan (oo)cysts are measured in μm, helminth eggs (nematodes, cestodes, trematodes) in tens of μm, and arthropod eggs in hundreds of μm. The adult stages of metazoan parasites grow to larger sizes, adult arthropods ranging from millimetres to centimetres, and adult helminths from millimetres to metres. In comparison, bacteria are an order of magnitude smaller than protists (measuring only microns) while viruses are another two orders of magnitude smaller still (measuring only nanometres = 10^{-9} m).

Comparative sizes of parasites

Parasite assemblage	Approximate size range	
	(oo)cysts/eggs	trophozoites/adults
protozoa	4-50 μm	5-100 μm
cestodes	40-80 μm	1 cm – 10 m
nematodes	50-100 μm	1 mm – 1 m
trematodes	20-150 μm	1 mm – 5 cm
mites	150-250 μm	0.3-0.6 mm
lice	300-600 μm	2-4 mm
fleas	400-600 μm	1-2 mm
ticks	400-600 μm	0.2-2 cm
flies	800-1,200 μm	0.5-2 cm

Systems of magnification

Despite considerable size variation between parasites, most developmental stages used for diagnostic purposes are microscopic in size (comprising cellular and subcellular features), thus parasitologists need to develop good microscopy skills. Low power magnification of specimens can be made using hand-held magnifying lenses giving up to 10 times magnification, medium power magnification is achieved using dissecting microscopes whereby eyepiece and objective lenses give from 8-40 times magnification, and high-power magnification is provided by compound (dual-lens imaging) light microscopes where eyepiece and objective lenses give from 40-1,000 times magnification. Most eyepiece lenses provide 10 times magnification and the most commonly used objective lenses provide a further 4, 10-, 20-, 40- or 100-times magnification. All magnifications can be achieved using dry objectives (air between specimen and objective lens), except 1,000 times which can only be achieved using oil immersion (high refractive index of viscous oil between specimen and objective lens prevents light scatter and facilitates image capture). However, the higher the magnification of the objective lens, the smaller the working distance (WD) between the lens and the specimen (e.g. 10 times lens WD ~ 6.8 mm; 40 times lens WD ~ 0.73 mm; 100 times lens WD ~ 0.12 mm). This means that focussed images at high power magnifications can only be achieved with small flat specimens that can be positioned close to the objective lens (usually under thin coverslips). Optical resolution is defined as the smallest distance between two points on a specimen that can still be distinguished by the observer as separate entities. The human eye has a resolution limit of around 10^{-4} m (= 0.1 mm). In light microscopy, the resolving power of each objective lens (i.e. the size of the smallest object that can be seen clearly) can be calculated using the formula RP = λ/(2NA): where λ = light wavelength (usually set at 550 nm (halfway point between limits of visible light)); and NA = the numerical aperture of each lens (given by the manufacturer on the lens barrel). For the 10 times lens, the NA is usually 0.25 so the RP = 550/(2x0.25) = 1,100 nm = 1.1 μm. For the 40 times lens, the NA is usually 0.65 so the RP = 550/(2x0.65) = 423 nm = 0.42 μm. For the 100 times lens, the NA is usually 1.25 so the RP = 550/(2x1.25) = 220 nm = 0.22 μm. In comparison, electron microscopes have a resolution limit of around 10^{-10} m (= 0.1 nm = 0.0001 μm).

Parasite appearance

Most endoparasite developmental stages have little in the way of natural colour, most appearing opaque or translucent. Some appear coloured, however, by virtue of ingested host material (e.g. blood-sucking parasites often have a red gut) or because they contain pigmented internal elements. While the adult stages of many ectoparasites can be pigmented (sometimes elaborately), their immature developmental stages can often be quite inconspicuous. Parasites are therefore difficult to see in host material because they blend in with their surroundings. The visibility of parasites can be improved considerably either by staining the parasites or by introducing optical contrast into the specimen. Many histochemical staining techniques have been used to differentially stain parasite developmental stages in smears or sections, usually by darkly staining parasite cell nuclei and lightly staining their cytoplasmic contents (e.g. Giemsa, haematoxylin, Feulgens, fuchsin, Ziehl-Neelsen, acid-fast, methyl-green, Gentian/methyl-violet, iodine, Indian ink, nigrosin, carmine, Masson's trichrome, silver impregnation, etc.). When examined under a light microscope, optimal bright-field white-light illumination systems are used to provide visual acuity. More recently, a range of fluorochrome stains have been employed to detect parasites by their fluorescence when viewed under ultra-violet illumination (e.g. fluorescein isothiocyanate, Texas red, diamidino-phenylindole, acridine orange, SYBR green, ethidium bromide, SYTO blue/red fluorescent dyes, etc.). If unstained specimens are examined under the light microscope, suboptimal illumination (condenser down, diaphragm partially closed) or special illumination (dark-field, phase-contrast or differential interference-contrast) may be used to provide contrast by light diffraction or refraction. The developmental stages of many parasites often have refractile properties, especially in their external coverings (membranes, cuticle, tegument, etc.) and in any internal globular contents.

Parasite identification

When parasite developmental stages are found, they are usually identified by comparing their morphological characteristics to documented records. This is the conventional taxonomic approach to specific or generic identification. The level of identification required to implement an appropriate course of treatment for parasitic disease varies greatly, sometimes requiring the causative species (or even strain) to be identified, but often only requiring the genus or family to be identified (e.g. the diagnosis of gastro-intestinal nematodes is often sufficient to commence a course of anthelmintic treatment). Many morphotypic characters have been described for parasites, some being qualitative (presence/absence), some quantitative (size) but most being combinations of features (shape, appearance). Many generic characters relate to whole organismal features, such as body plan (tissues/organs/cells), motility, feeding, attachment, appendages, encystment, etc. Most species-specific characters involve progressively smaller features (internal structures, organs/organelles, adornments, etc.). After several centuries of conventional morphometric taxonomy, numerous taxonomic keys have been developed for the identification of parasite species. Most have been published as dichotomous taxonomic keys requiring the user to make a series of binary choices about different character states. Unfortunately, many keys require comprehensive knowledge of specialist terminology and they are often based on well-preserved and well-prepared specimens (both of which may be lacking). More recently, moves have been made to produce computerized taxonomic keys which are random-access (no fixed starting point), polychotomous (multiple choice), annotated (glossaries and illustrations provided) and multi-media (combining text, tables, figures, photos, videos, etc.). Irrespective of the resources used, diagnosticians still rely heavily on their learning and experiences with many different parasite groups. Conventional parasitological courses must therefore be preserved in undergraduate and postgraduate university programs to provide the necessary theoretical and practical expertise required by practitioners.

Diagnostic laboratories are quick to adopt new tests based on contemporary technologies. Over the last decade, numerous immunological and molecular biological techniques have been applied to the detection of specific host proteins (notably enzymes and immunoglobulins) as well as parasite antigens and nucleic acids. In particular, enzyme immunoassays and polymerase chain reactions have revolutionized diagnostic technologies, but many tests are still only available with research institutions and have yet to be adapted for use in diagnostic laboratories, medical or veterinary clinics or under field conditions. Naturally, the diagnostic accuracy, sensitivity and specificity of many of these tests remain to be determined before their commercial application. Modern biotechnology, nanotechnology and translational research endeavours are constantly inventing some very clever technologies which hopefully will make these new tests more available in the future (dot/spot technologies, new generation immuno-diffusion, immuno-magnetic separation, immuno-electrophoresis, novel substrates, etc.). Nonetheless, despite the rhetoric and promise of new technological advances, diagnostic parasitology should remain an integrated multidisciplinary exercise, where clinicians make decisions based on holistic evidence (including presentation, history, physical examination and laboratory findings).

MACROSCOPIC EXAMINATION

Visual examination of the patient is a key part of the physical examination process and should be conducted on all patients irrespective of presentation. While it may only reveal parasites that are large enough to be seen by the naked eye, it also serves to provide information about the possible site, extent and severity of infection through observation of clinical signs, such as body condition, coat condition, suspect lesions, etc. Indeed, signs of inflammation have long been known to assist in disease diagnosis (the four cardinal signs being *rubor* = redness, *calor* = heat, *tumor* = swollen, *dolor* = pain). The detection of visible parasites depends to a large extent on the sites of infection that can be examined. Ecto-parasitic arthropods (fleas, lice, flies, ticks, but not mites) may be found on external body surfaces hidden in hair, plumage or orifices, and sometimes in clothing or bedding. Looking for attached or embedded stages can be time-consuming, but cursory examination can have severe consequences (e.g. missing paralysis ticks on dogs can prove fatal). Often, finding ecto-parasites can be fortuitous, but it should not preclude a more detailed and systematic examination, particularly of predilection sites if specific parasites are suspected. Attention should also be paid to host products, such as excreta. Tapeworm segments or whole nematodes may occasionally be detected in or on fresh faecal samples, and whole worms may rarely be found in vomitus or sputum samples. Most endo-parasitic helminths detected by visual examination are adult life-cycle stages, as their eggs and larval stages are usually microscopic. Protistan parasites are unicellular and therefore microscopic in size, but occasionally feeding trophozoites or encysted stages may be macroscopic in size (e.g. white spot disease of fish caused by the ciliate *Ichthyophthirus*). The majority of parasites detected by visual examination may appear to be robust, but they degrade quite quickly when removed from the host and they can assume unnatural appearances unless properly preserved and processed.

Specimen preparation

In order to avoid preparative artefacts, macroscopic parasites should be recovered and processed according to standard protocols which have been developed for different parasitic groups. Larger rotund parasites (flies, bugs, ticks) may be prepared using entomological techniques designed to preserve and present whole organisms for macroscopic examination (often aided by magnifying glasses) of specimens pinned on boards, while smaller and/or flatter parasites (small arthropods, tapeworms, flukes, some nematodes) may be processed using histological/histochemical techniques designed to show internal features by microscopic examination (dissecting or compound microscopy) of specimens mounted on slides.

Removal/recovery: Individual ticks can be carefully removed with fine forceps (using slow lever action to avoid ripping out mouthparts), fleas can be pursued and picked out of the coat, lice can be picked out or combed out, adult flies can be trapped, fly larvae can be teased or excised from lesions, suspect skin lesions can be scraped with a scalpel blade, and whole or worm fragments worms can be picked out of excreta.

Fixation: Large insects or arachnids can be prepared as whole mount entomological specimens after they have been killed (usually using ethyl acetate fumes (nail polish remover) or injected with acetone), relaxed in a steam chamber (restoring some pliability for manipulation) and set by pinning on mounting boards and air-dried (in presence of antifungal compounds such as Lysol or camphor). Smaller macroscopic parasites may be preserved by hot or cold fixation for subsequent transport, storage, processing and mounting. Arthropods are best fixed in 70% alcohol, usually containing 5% glycerine to provide viscous support for delicate stages and appendages (they remain pliable for years). Larval insects can be relaxed during fixation by immersing in 30% alcohol, heating to almost boiling point, cooling to ambient temperature and transferring to 70% alcohol. Cestodes can be relaxed in tap water, wound onto a flat card to hold their shape and then fixed in hot 70% alcohol. Trematodes can be purged of gut content by transferring them several times between warm saline and warm water before sandwiching them between two slides and fixing in hot 70% alcohol. Alternatively, if parasites are required for DNA extraction, they can be snap-frozen in dry-ice/ethanol or liquid nitrogen (although such freezing is impractical in many situations) or fixed in absolute ethanol.

Cleaning: Arthropods can be cleansed of organic debris and decolourized either by alkaline digestion (10% potassium hydroxide digests soft tissues but not chitinized elements) or clearing in lactophenol. Larger specimens can be punctured with a small pin to allow reagents to enter and act on soft internal tissues. Specimens can be partially dissected at this stage if required (e.g. the posterior ends of fly larvae can be excised for separate mounting).

Staining: Prior to mounting, cestodes and trematodes may be stained with Mayer's haemalum or Mayer's paracarmine or lactocarmine (acid-alcohol is used to differentiate colour development).

Dehydration/clearing: Specimens are dehydrated (water interferes with mounting and observation) by placing in absolute alcohol (several changes if required) and then cleared (replacing alcohol) in methyl salicylate, xylol, cedar wood, clove or wintergreen oil (miscible with mounting media).

Mounting: Temporary and permanent mounts are usually made on glass slides by placing/covering specimens in liquid mounting media (mostly Canada balsam although synthetic analogues are available), manipulating them with fine probes (if required) to lie in

an appropriate orientation (dorso-ventral or lateral), covering with a coverslip ensuring all air-bubbles are expressed and then curing (hardening) mounts either at room temperature or in an oven for several days.

MICROSCOPIC EXAMINATION

Most parasite developmental stages are too small to be seen unaided by the human eye, but they can be found and viewed in all their glory when magnified by microscopy. A range of techniques have been developed to prepare and process samples of host materials (predominantly faeces, blood and tissues) for microscopic examination: involving smears, suspensions, swabs, sediments, floats, concentrates, filtrates, cultures and sections. All vary in the amount of host material that can be conveniently examined so their thresholds of detection vary considerably. Those techniques which concentrate parasites from host materials have a higher level of detection than those which examine host materials raw or even diluted. In all cases, it is assumed that the intensity of infection (parasite abundance) is high enough for infections to be detected. However, it is best to remember that the lack of detection does not always mean absence of infection. Parasites are also not homogenously distributed throughout host materials and many exhibit intermittent excretion or release of developmental stages during the course of infection. It is therefore hoped that samples were collected from the host during the patent (infectious) period of infection (when parasite developmental stages are being produced and released) rather than the pre-patent (incubation) period beforehand or the latent period thereafter. Some diagnostic protocols request that multiple consecutive samples be collected, some require multiple samples from different sites and most involve thoroughly mixing bulk samples before aliquots are taken (to ensure the aliquots are representative of the whole). International/national standard procedures have been developed for many diagnostic tests to ensure their integrity (reproducibility and reliability), particularly when import/export or quarantine certification is required. Considerable practice is required to confidently identify parasite stages in host materials by light microscopy. Novices frequently have problems with improper size perspective, wrong magnification, loss of plane of focus, lack of contrast, and the presence of air bubbles, artefacts and organic contaminants.

Sample collection

Biological samples may be collected from hosts ante-mortem (whilst alive) or post-mortem (when deceased). Obviously, less invasive techniques are used to collect samples from live hosts (excreta, exudates, venepuncture, scrapings, tissue biopsy) and the objective is to keep the patient alive through timely diagnosis and treatment. Nonetheless, considerable information may be obtained from post-mortem examinations of deceased patients (particularly relevant in outbreak situations), as more invasive procedures may be used to sample internal tissues and organs.

Blood: Samples of peripheral blood may be collected from vertebrate hosts by skin prick or venepuncture. The fresh blood is usually collected into sterile tubes containing chemicals designed to inhibit or enhance blood coagulation and to preserve blood elements. When whole blood or plasma is required when still fluid, most blood samples are collected into tubes with added EDTA, citrate or heparin anticoagulant (commercial tubes with pink, blue or green tops). When serum samples are required, blood is collected into tubes without additives (white tops) or with added coagulants/clot-activators (gold or red tops). Haemolymph may also be collected from some larger invertebrate hosts by needle aspiration of vascular sinuses.

Faeces: Stool samples may be collected into range of containers, some with spoons fitted into the lids. Container size should be appropriate for the host, and the stool sample should be as fresh as possible and collected per rectum rather than off the ground. Veterinarians often use plastic gloves to collect samples direct from domestic animals (using digital stimulation to relax the anal sphincter). Human patients usually collect their own stool samples in their toilets, but often with great reluctance (thus compliance rates can be very low). Doctors should carefully explain to patients not only the importance of collecting samples, but also how to go about it (defaecate into a large bucket-like container and then transferring a subsample into the small container provided). If the patient is experiencing diarrhoea, collecting a stool sample can be quite a messy enterprise.

Vomitus: Stomach content is usually expelled spontaneously rather than on demand. Nonetheless, vomitus may be salvaged from various receptacles (sinks, trays, buckets, clean floors, etc.) and collected into appropriate airtight containers (often faecal containers).

Sputum: Mucus and phlegm can be collected from the respiratory tract by getting the patient to cough up sputum into containers. In cases involving heavy congestion, patients may require percussion drumming over the chest/back (with cupped hands) and postural drainage (head below level of lungs). Normal saline may sometimes be used for tracheal washes or bronchial lavages.

Swabs: Bacteriological swabs (sticks with cotton tips) may be used to collect fluids and/or cells from natural orifices (mouth, throat, nasal passages, ears, eyes, umbilicus, vagina, rectum) and surface lesions into sterile tubular containers.

Scrapings: Broad-bladed scalpels may be used to scrape suspect skin lesions for ecto-parasites. The epidermis is usually scraped until the subdermis is reached and begins to ooze serum. The scalpel blade and skin scrapings (plus any attached hair/feathers) are

placed into a sterile container for transport to the laboratory. An unusual skin-sampling technique used to diagnose pinworm infections is to use transparent adhesive (sticky) tape to harvest any eggs attached to peri-anal skin.

Biopsies: Small pieces of host tissues (mainly surface lesions but occasionally internal organs) may be collected from living hosts by needle aspiration, punch biopsy or scalpel excision (lumpectomy). The tissues are usually fixed or frozen for histological examination but they can also be examined as wet mounts or dried smears.

Necropsies: Blocks of any tissue can be taken from deceased hosts during post-mortem examination. Pathologists may sample a range of vital organs but they often only collect suspect tissues on the basis of their unusual appearance (inflammation, haemorrhage, lesions, etc.). The tissues are fixed or frozen for histological examination but they can be examined as wet or dry mounts or used in digestion, concentration or culture techniques. Tissues and any contained parasites may degrade quite quickly after death of the host so samples should be collected reasonably fresh to avoid post-mortem autolysis and artefactual appearances.

Wet suspensions/mounts

Host fluids can be examined under the light microscope simply by mounting drops on glass slides under coverslips. These wet mounts can be examined undiluted or diluted in warm saline (sometimes containing mucolysin to improve sample viscosity). The mounts may be examined for live motile organisms (protozoan trophozoites, worm larvae, small arthropods) or encysted stages (cysts, oocysts, eggs). Preservatives, stains or lytic agents can also be introduced under the coverslip to improve visibility. Drops of blood can be examined for motile trypomastigotes or microfilariae. Erythrocytes obscuring vision can be lysed by adding distilled water, dilute formalin, saponin or ammonium hydroxide. Faecal samples can be mixed with saline and examined for motile or encysted stages. Dilute iodine or methylene blue can be added to highlight protozoan nuclei (flagellates, ciliates, amoebae) and helminths (eggs, larvae). Tracheal washes can be examined for lungworm larvae. Skin, gill and fin scrapings can be diluted in appropriate media (saline for terrestrial hosts and source water for aquatic hosts) and examined for protozoan trophozoites, worm larvae or ecto-parasitic arthropods. Wet mounts can also be prepared of concentrates, filtrates or cultures to facilitate diagnosis.

Dried smears

Permanent mounts can be prepared by making smears on slides, air-drying them, fixing them by heat (flaming) or alcohol (transient immersion), and staining with a variety of histochemical stains. These procedures are routinely used in microbiology laboratories for Gram staining bacteria. In parasitology, they are used less often as many parasite developmental stages are destroyed by air-drying or have tough resistant walls and are relatively impervious to stains. Streak smears can be made of faecal material and mucosal swabs, impression smears can be made from the cut surfaces of solid organs, and thin or thick smears can be made of blood or other fluid samples. Dried smears can also be prepared of concentrates, filtrates or cultures to facilitate diagnosis. Faecal smears can be stained with iron haematoxylin, acid-fast, trichrome or nigrosin stains to highlight protozoan trophozoites and/or cysts. Blood smears are most often stained with Giemsa (Romanowsky) stains to highlight the nuclei and cytoplasm of blood cells (for differential counts) and parasitic cells (extracellular microfilariae and trypanosomes and intracellular haemogregarines, haemosporidia and piroplasms). The preparation of good thin blood smears requires considerable practice – trained haematologists just seem to know exactly how much blood to use, what angle to hold the spreader, how much pressure to exert during smearing, etc. The objective is to make a cell monolayer that tapers/feathers out along the slide. Most smears are examined by bright-field light microscopy using high-power oil-immersion lenses (1,000 times magnification).

Tissue sections

Pieces of host tissue collected by biopsy or autopsy can be processed immediately as squash/teased preparations or processed later after being preserved by chemical fixation or freezing. Small pieces of fresh tissue can be placed in saline on a glass slide and then squashed, macerated or teased apart to disrupt tissue structure and reveal (or release) any contained parasites (encysted worm larvae, protozoan cysts/spores, mites). Special tissue compression devices consisting of two glass plates (trichinoscopes) have even been developed for the examination of animal muscles for encysted *Trichinella* larvae (trichinoscopic examination). It is more usual, however, for blocks of tissue to be fixed in 10% phosphate-buffered formalin for subsequent histological processing. Formalin fixes proteins and prevents enzymatic degradation. It perfuses well into tissues so block sizes can be around 1 cm^3 (= 1 cc) and tissues can be held in fixative for long periods (2% glutaraldehyde is often used to fix tissues for electron microscopy - it better preserves membranous structures, but it does not perfuse far into tissues and long-term fixation causes tissues to become brittle). Once fixed, tissue blocks are dehydrated in a graded series of alcohol solutions, cleared in solvent (xylene, toluene or less volatile 'histo-clear'), and then infiltrated and embedded in paraffin wax. Tissue sections are cut at ~5 μm thickness on a microtome and enrobed onto glass slides. The sections are then stained (usually with haematoxylin and eosin, but many specialized stains may be employed), dehydrated in alcohol, cleared in solvent and mounted under coverslips in media (Canada balsam or synthetic media such as Deepex) prior to examination by bright-field light microscopy. Modern pathology laboratories have automated systems for bulk processing tissues into wax and staining sections. More recently, cryo-techniques have been developed to cut frozen sections on a cryomicrotome from pieces of tissues that have been snap-frozen (either in a mixture of

dry ice/ethanol or in liquid nitrogen). Freezing preserves the tissues without degrading proteins or antigenic epitopes so enzymatic-labelling or immuno-labelling techniques can be used to screen for parasitic material in the sections. DNA can also be better extracted from frozen tissues for molecular biological techniques.

Parasite concentration techniques

Various concentration techniques have been developed to recover parasites from larger sample volumes in order to improve the threshold of detection. Samples can be processed by sedimentation, floatation, filtration, centrifugation, digestion or culture. Concentrates can be examined qualitatively (presence/absence of parasites) or quantitatively (parasite count per volume/weight of sample, or percentage parasitaemia).

Concentration from faeces

Infectious micro-organisms voided with host faeces contaminate the environment and are transmitted to new hosts via the ingestion of contaminated food and/or water. Many of the stages passed into the external environment are well protected for their transient free-living sojourn by being encysted within membranous casings which are relatively impervious to external environmental influences. Most exogenous stages are non-feeding and live on their own food reserves but they can survive for long periods of time under the right conditions by being dormant with low metabolic requirements. Faecal samples may contain protozoan cysts (amoebae, flagellates, ciliates), protozoan oocysts (apicomplexans), worm eggs (nematodes, cestodes, trematodes) or worm larvae (some nematodes). As excrement, faecal samples also contain large amounts of waste material (including fibrous and particulate material) and huge numbers of bacteria - the presence of both masking the detection of parasites. Several techniques are used to remove confounding materials and to concentrate parasites on the basis of their differential buoyancy in various solutions.

Sedimentation: Most parasite developmental stages sediment in water so faecal samples placed in at least 10 volumes of water and thoroughly mixed will allow fibrous and fatty material to float to the top while parasites settle to the bottom. Sedimentation by gravity will take several hours so the process can be accelerated by mild centrifugation over several minutes. Long thin centrifuge tubes (usually 10 mL volume) are used to provide good separation between sedimented parasites and floating detritus. Faecal samples from herbivores frequently contain abundant fibrous plant material which can be removed after centrifugation by vacuum-trap aspiration. Faecal samples from some carnivores frequently contain abundant fatty material which can be removed by centrifuging the samples in 10% ether to dissolve the fat. Where significant biohazards are indicated, faecal samples can be fixed in dilute formalin (or formol-ether or merthiolate-iodine-formalin) prior to centrifugation. Stains can also be introduced during sedimentation - the most commonly used one being iodine-trichrome stain to stain protozoan nuclei or methylene blue to stain worm eggs. An aliquot of the sediment is recovered and examined for parasite ova/cysts by light microscopy. Sedimentation techniques are best used to detect trematode ova (especially fluke eggs) which sediment readily (presumably due to their high iron-content). The problem with simple sedimentation is that heavy particulate material and most bacteria also sediment thereby obscuring parasites.

Floatation: Various floatation techniques are therefore used to separate parasites from faecal samples and sediments. When placed in high specific-gravity (SG) solutions, most parasite ova/cysts float to the meniscus due to their high starch content in the form of food reserves. Solutions commonly used include saturated sugar (sucrose, Sheather's solution) or saturated heavy metal salt solutions (sodium chloride, sodium nitrate, sodium iodide, zinc sulphate, magnesium sulphate, potassium iodide) which have SG ranging from 1.2-1.3. Most coccidial oocysts and nematode eggs float in solutions with a SG ~1.2 (e.g. saturated sodium chloride), but larger oocysts and the eggs of most cestodes and trematodes are heavier and require solutions with a SG $\geq$ 1.3 (e.g. saturated sucrose or magnesium sulphate). Faecal samples or sediments are placed in at least 10 volumes of floatation medium and centrifuged for several minutes (~300 x*g* for 2-5 minutes) so that parasites float through the viscous media while particulate material (and most bacteria) continue to sediment. Platinum (bacteriological) loops are usually used to collect drops of the meniscus for mounting on glass slides. Alternatively, some techniques require the tubes to be slightly overfilled producing a convex meniscus projecting above the tube rim so that coverslips can be placed in direct contact for several minutes and then lifted off (not slid) and transferred to glass slides (the viscous meniscus sticks to the coverslip). Several test kits are commercially available to sediment and/or float faecal samples all in one tube. Mounts of faecal floats are examined by light microscopy using phase- or interference-contrast illumination if unstained or bright-field illumination if stained. Samples should be examined as soon as practicable because prolonged exposure of parasite ova/cysts to many of the floatation media results in artefactual appearances due to osmotic distortion. Most direct floatation or consecutive sedimentation-floatation techniques are used as qualitative screens for the presence/absence of parasites, or at best to semi-quantitate the numbers present according to arbitrary subjective ranks (e.g. +, ++, +++ and ++++ corresponding to <5, 5-20, 20-100 and >100).

Worm egg counts: A modification of a floatation technique is used with special glass slide chambers to quantitate the number of gastrointestinal nematode eggs present in faecal samples from domestic animals, especially ruminants. A set weight of faeces is diluted in a set volume of floatation medium and a thoroughly mixed aliquot is then added to graduated chambers of known volume (McMaster, Whitlock, Universal and paracytometer slides have chambers ranging from 0.3-0.6 mL). The top glass plates of these

chambers have been etched with grids so that a known area (and thus volume) can be examined. The number of nematode eggs present is counted by medium-power light microscopy and the number of eggs per gram of faeces (epg) is calculated as follows:

epg = (number of eggs counted in chamber / chamber volume in mL) x (faecal dilution factor)

where the faecal dilution factor = (total volume of diluted faeces in mL / weight of faeces added in g).

Most counts are conducted using 2 g of faeces mixed into a total of 60 mL of magnesium sulphate and then counting the number of eggs in one chamber, thus epg = (number/0.5) x (60/2) = number x 60. Variations of this basic protocol include using more faeces (4 g for horses, 5 g for cattle) and counting less than one whole chamber if eggs are numerous but then proportionally adjusting the formula. The relationship between faecal epg and the actual worm burden in the gut of the host varies considerably depending on the time course of infection and the worm species present. Infections may still be in the pre-patent period (before egg laying commences), host immune responses may suppress nematode reproduction, and worm fecundity has been shown to be reduced when the intensity of infection increases. Generally, there is a poor correlation between epg and worm burden for nematodes with low fecundity, such as many *Trichostrongylus* species; but a good correlation for nematodes which are prolific egg layers, such as *Haemonchus, Oesophagostomum* and *Chabertia* species. It is also important to remember that certain worms, such as *Haemonchus contortus*, *Trichostrongylus axei* and most *Teladorsagia*/*Ostertagia* species, can also undergo arrested larval development (hypobiosis) in the host when external environment conditions are unfavourable for parasite development and survival, thus animals are infected but not excreting worm eggs. Worm egg counts provide an indication, but not an exact measure, of what is going on inside the animal. Still, lots of eggs always means lots of worms. As a general rule, farmers are recommended to drench their animals if worm egg counts are greater than 1,000 epg.

Drench resistance testing: Nematode populations may be managed by a variety of anthelmintic drugs. At the turn of the century, various metal compounds (lead, tin, copper) were used to reduce worm burdens but they exhibited high toxicity to their hosts. They have now given way to synthetic compounds manufactured by the pharmaceutical industry. A very successful group of compounds called the benzimidazoles (or white drenches) were developed in the 1960's followed by another group called the levamisoles (or clear drenches). The first group acted upon microtubules causing worm paralysis and expulsion while the second group blocked cholinergic neurotransmission causing paralysis and expulsion. Regrettably, worm populations have now developed resistance against both groups of drugs. A third group of compounds called the avermectins (ivermectin in particular) was developed in the 1970's and they inhibited neurotransmission in worms. There are numerous reports of drench resistance against avermectins overseas and several in Australia. Producers are therefore faced with difficult choices – which drench to use and will it be effective? A subsidiary industry has now emerged which screens flocks for drench resistance and recommends the most appropriate drug to use to control worm populations. Basically, they involve drenching test groups of sheep with white, clear, combination and/or avermectin drenches (plus an untreated control group) and then testing 10-14 days later to see if faecal egg counts have been reduced by at least 95% for the drench to be declared effective.

Filtration: Several faecal filtration techniques have been developed to diagnose lungworm infections by facilitating the migration of lungworm larvae out of faecal samples. Adult lungworms lay eggs but they usually hatch while passing through the host intestines so that first stage larvae (L1) are found in faeces. The larvae will migrate out of faecal samples placed on filter paper or wrapped in gauze or muslin and placed in warm water in a funnel or Petri dish. Aliquots of the crude filtrate may be collected after several hours and examined for larvae by light microscopy.

Concentration from blood

Many parasites infect the blood of vertebrate hosts and rely on blood-sucking invertebrate vectors for their transmission between hosts. Vector-borne blood parasites include kinetoplastid flagellates (trypanosomes), eucoccidia (haemogregarines, haemococcidia), haematozoa (haemosporidia, piroplasms) and filarial nematodes (microfilarial stages). The blood stream of vertebrate hosts is a lovely place to live (rich in nutrients and oxygen) provided the parasite can survive living in pressurized vessels and avoiding host homeostatic mechanisms (e.g. clotting) and immune defences (e.g. innate phagocytic and inflammatory responses and adaptive humoral and cell-mediated responses). Blood contains many different cell types to infect: erythrocytes or red blood cells (anucleate in mammals, nucleate in birds, reptiles, fish); leucocytes or white blood cells (granulocytic neutrophils, basophils, eosinophils and agranulocytic lymphocytes and monocytes); as well as a viscous fluid medium (plasma) rich in sugar, proteins, etc. Many protozoan parasites specialize in infecting red blood cells in which they grow and divide, but with the consequence of lysing the cell when mature, thus contributing to host anaemia. Other parasites occur extracellularly in the plasma deriving nutrients at the expense of the host. Haemoparasites may be few in number and easily obscured by the masses of cells in blood samples so a range of filtration and centrifugation techniques have been developed to concentrate parasites from blood samples.

Knott's technique: Microfilariae can be concentrated from unclotted blood samples firstly by lysing red blood cells through the addition of a lytic agent (commercial 0.8% ammonium chloride buffers or distilled water or 2% formalin or 0.5% Triton or Saponin detergent) and then pelleting the worm larvae by mild centrifugation (~800 xg for 5 mins). Aliquots of the sediment may be mounted on slides, stained with methylene blue (0.1%) and examined by low-power light microscopy.

Membrane filtration: Microfilariae may be recovered from unclotted blood samples firstly by lysing red blood cells through the addition of a lytic agent (commercial 0.8% ammonium chloride buffers or distilled water or 2% formalin or 0.5% Triton or Saponin detergent) and then capturing worm larvae by syringe-chamber filtration through polycarbonate membranes (Nucleopore, 8 μm pore

size). The membrane may be washed and stained with methylene blue (0.1%) and then drained and mounted on a glass slide for low-power light microscopy.

Microhaematocrit (capillary tube) centrifugation: When unclotted blood samples are centrifuged, erythrocytes sediment (due to the heavy iron content in haemoglobin) while leucocytes settle on top of the red cell sediment as a white buffy coat. Extracellular haemo-parasites such as trypanosomes and microfilariae accumulate in the buffy coat layer and intra-erythrocytic parasites such as haemosporidia and piroplasms are often found in the upper portion of the red cell layer (infected cells are less heavy). Microhaematocrit centrifugation is often used to examine the buffy coat for parasites or to enrich parasitized cells in the red cell layer. Blood is taken up by capillary action into thin capillary glass tubes which are then sealed at one end with plasticine. The tubes are placed radially on a flat plate which is subject to mild centrifugation (~1,000 xg for 5 mins). A calibrated card can be used to read the haematocrit (percentage packed cell volume) and the tube can then be examined directly under a low-power light microscope (for parasites wriggling in the buffy coat) or the tube can be scored and snapped using a glass cutter or diamond pencil so the buffy coat can be expressed onto a slide for light microscopy.

Density gradient centrifugation: Unclotted blood samples can be centrifuged through solutions of increasing density so that sample components will band at different levels (technique known as density-gradient or isopycnic centrifugation or equilibrium sedimentation). The most commonly used media for blood cell separations are 20-70% sucrose solutions which can be prepared manually in 10% increments or obtained commercially as Ficoll-Paque/Hypaque solutions of high molecular weight sucrose polymers and sodium diatrizoate (note: caesium chloride solutions are inappropriate as they are used to harvest DNA by ultracentrifugation). The blood samples are loaded onto sucrose gradients and subject to low-speed centrifugation to avoid cell lysis (~60-100 xg for 10 mins). Such centrifugation is frequently used in cell biology and immunology laboratories to harvest lymphocytes for cell culture or hybridoma technologies. However, density-gradient techniques have been used to recover extracellular microfilariae and trypanosomes from whole blood samples, although the technique is more laborious and fastidious than filtration or microhaematocrit centrifugation.

Concentration from tissues

Many parasites are not content to dwell in the luminal spaces of tubular organs or the blood stream of their hosts – instead, some actively invade the deeper tissues and organs of their hosts either transiently (as migrating stages) or for prolonged intervals (as encysted stages). Many protozoa form multiplicative stages (trophozoites, tachyzoites, bradyzoites, cystozoites, amastigotes, meronts, schizonts, cysts, pseudocysts) in host tissues; many being temporary and linked to acute disease syndromes although some can persist and cause chronic lesions and/or disease. Many helminth parasites have juvenile (larval) or adult (immature and mature) developmental stages which actively penetrate tissues and lodge in internal organs, some even becoming dormant (hypobiotic). Some geohelminths infect their hosts by transdermal penetration of the skin resulting in larval migrans. Other nematodes exhibit an obligatory pulmonary migration through the lungs before maturing as adults in their final predilection sites. All cestodes form encysted larval stages (metacestodes) in the tissues of intermediate hosts, and most trematodes infect their hosts when cercariae penetrate host tissues. All ectoparasites (fleas, lice, flies, ticks, mites) feed on host fluids/tissues by penetrating the skin, and some even invade subdermal tissues for part or all of their life-cycles. A range of techniques have been developed to recover parasites from host tissues, including washes, perfusions, smears and digests.

Gut content (worm counts): At post-mortem, the entire gastro-intestinal tract may be removed from herbivorous animals (mainly domestic animals such as sheep, goats and cattle) and examined for parasitic nematodes (mostly in the abomasa and small intestines). The numbers of worms present can be quantitated by extrapolating counts made on aliquots of gut content. Different portions of the gut are ligated (tied off) and processed separately. Abomasa are opened by cutting along the greater curvature and expelling the content into a sizeable container (bucket). Intestines are stripped from mesentery and the contents expressed into a separate container. The organs are washed several times with small quantities of water and the washings collected into the appropriate containers. The final volume in each container is made up to 1 litre, the contents are thoroughly mixed and a 100 mL aliquot taken. The aliquot is passed through a 400 μm mesh sieve to remove fine particulate material and the filtrate containing worms is back-flushed from the sieve and made up to 300 mL in water. A 30 mL aliquot is taken, added to a petri-dish, stained with a few drops of iodine (decolourized with sodium thiosulphate after a few minutes) and examined under a dissecting microscope. The number of worms present is counted and the total number of worms calculated by accounting for the two dilution factors; i.e. total worms = count x 1000/100 x 300/30 = count x 10 x 10 = count x 100. In many instances, different worm genera (and sometimes species) can be identified on the basis of their size and appearance; e.g. abomasal contents may contain *Haemonchus* sp. (large barbers-pole worms up to 25 mm long, females with white ovaries wound spirally around red intestine), *Teladorsagia circumcincta* (slender brown worms up to 12 mm long, uniform in thickness) and *Trichostrongylus axei* (small worms up to 5 mm long, tapering markedly at anterior end).

Gut digests (developing worms): Hypobiotic larvae (L4) and immature adult worms that burrow into the gut of ruminants can be recovered by enzyme-acid digestion of host tissues. Whole abomasa or stripped intestinal mucosa are incubated in at least 2 volumes of 1% pepsin in 3% hydrochloric acid (pH ~1.0) at 42°C for at least 2-3 hours. The digest is washed through a 400 μm mesh sieve and the filtrate containing worms back-flushed and retained. Aliquots are then examined microscopically for nematode developmental stages.

Skin digests (burrowing mites): Ecto-parasitic mites that burrow in the skin of animals may be recovered by alkaline digestion of skin scrapings taken from suspect lesions. Hair/fleece/feathers from the site may be removed by clipping/shaving and paraffin or white oil may be used to coat the skin before a broad-bladed scalpel is used to scrape the skin to the required depth (at least to stratum granulosum). The skin scraping is added to at least 10 volumes of 5-10% potassium hydroxide (which digests skin, keratin and hair, but not mites or fungi) in a centrifuge tube and the tube placed in a hot water (slow rolling boil) for 10-20 minutes. It is then centrifuged at low speed (~400 xg) for 1-2 minutes. The supernatant is discarded and a drop of the slurry/sediment is mounted on a slide for microscopic examination for mites (medium-high power with contrast).

Muscle digests (encysted coccidia, worm larvae): Parasite developmental stages that encyst within host musculature may be recovered by enzyme-acid digestion of post-mortem meat samples to reveal cystozoites/bradyzoites of tissue cyst-forming coccidia (such as *Sarcocystis* and *Toxoplasma*) and encysted/hypobiotic nematode larvae (such as *Trichinella*). Muscle samples are blended in at least 2 volumes of 1% pepsin in 3% hydrochloric acid (pH ~1.0) and incubated at 42°C for at least 2-3 hours. The resultant slurry is centrifuged at medium speed (~1,000 xg) for 10 minutes to pellet particulate material, including freed parasites. Aliquots of the sediment are examined microscopically for protozoan zoites and nematode larvae.

Lung perfusions (lungworms): Larval and adult lungworms may be recovered from domestic animals by perfusing intact lungs or rinsing cut lungs (bronchi and bronchioles) with warm 10% sodium bicarbonate (to remove mucus). The resultant washings are then rinsed through nylon-/wire-mesh sieve (aperture 45 μm) with warm saline. The filtrate is examined by low power microscopy for lungworm developmental stages.

Tissue smears (piroplasms): Intraerythrocytic stages of piroplasms (*Babesia*/*Theileria*) concentrated/sequestered in capillary blood may be better observed in impression smears prepared from biopsy/necropsy material of brain, spleen, kidney or heart than in thin smears prepared from blood collected by peripheral venepuncture. Impression smears are air-dried, fixed by flooding with methanol, mordanted in May-Grünwald for 2 minutes and then stained with Giemsa prior to microscopic examination.

Parasite cultivation

The diagnosis of many infectious diseases involves the isolation of microbes from host samples and their cultivation in liquid media, on nutrient substrates or in tissue cell cultures for subsequent identification. Bacteria can be selectively cultivated in defined media and viruses amplified in susceptible cell lines. Conventional methods involving Petri dishes, test tubes and flask cultures are lengthy and laborious and have now been largely superseded by rapid mini-system assays (using strips of chambers containing defined reagents), immune-assays (for host antibodies or microbial antigens) or molecular biological assays (for microbial proteins or nucleic acids). By comparison, the cultivation of parasites for diagnostic purposes is uncommon and complicated by their complex life-cycles often involving multiple hosts, multiple developmental stages, slow development, long generation times and, for most species, unknown culture conditions. *In vitro* cultivation can therefore be tedious and time-consuming, often taking days before results become apparent. While specific parasite developmental stages may be cultivated *in vitro* under maintenance or growth conditions, to complete their life-cycles most parasites require cultivation *in vivo* in living hosts. Despite the inherent difficulties, suitable techniques have been developed to cultivate a small but growing number of parasite species for the:

- differential diagnosis of clinical infections;
- amplification of parasite numbers for phenotypic and/or genotypic characterization;
- assessment of parasite virulence/pathogenesis;
- isolation and maintenance of unique cultivars;
- comparison of clinical and/or environmental isolates for phylogenetic analyses;
- screening of potential therapeutic agents;
- testing for drug resistance/susceptibility;
- parasite attenuation and vaccine development; and
- producing defined reagents for immunological and/or biochemical assays.

***In vitro* culture**

A number of culture techniques have been developed for protozoan parasites but few are available for helminth parasites and even fewer for arthropod parasites (due to their more complex life-cycles and fastidious culture requirements). Parasites can be amplified in number from diagnostic samples (faeces, blood or tissues) by *in vitro* culture on semi-solid substrates (e.g. amoebae on agar plates/slopes), in liquid nutrient broths/media (e.g. haemoflagellates, helminth larvae) or in tissue cultures of host cells or surrogates (e.g. malaria in erythrocytes). Success depends on many factors, including the preparation of suitable inocula and recipient media/cells and their culture under appropriate conditions (time, temperature, atmosphere). In microbiology, there are three basic types of pre-culture isolation methods: enrichment (inoculation of sample into selective media); dilution (sequential dilution of sample in defined media); and physical methods (selection and transfer of individual cells by micropipetting, differential centrifugation, sieving, silicone oil plating, flow cytometry, agar plating or electromigration into defined media). Then, there are three basic types of culture systems: xenic (parasite grown in presence of undefined flora); monoxenic (parasite grown in presence of single additional species, usually provided as a feeder organism); and axenic (parasite grown alone in absence of any other metabolizing cells). The culture of parasites in tissue cell cultures involves their intra- or epi-cellular development in association with host cells (or surrogates) maintained as monolayers in chambers or as suspensions in flasks. Cultivars may be maintained by subculturing at suitable intervals, cryopreserved at ultra-low temperatures using cryoprotectants, and sometimes by desiccation of encysted resistant forms. There are a growing number of living or cryopreserved type cultures available from various governmental or institutional agencies (such as the ATCC = American Type Culture Collection, CDC = Centers for Disease Control), most being documented in registers maintained by parasitological societies or museums.

Parasitic protozoa have been isolated and grown in a variety of media and tissue cell cultures. Several free-living amoebae cause opportunistic tissue infections in humans known as PAM, SAM or GAM (= primary, secondary or granulomatous amoebic meningoencephalitis caused by *Naegleria, Entamoeba* and *Balamuthia* species respectively). Clinical isolates of these amoebae grow best in tissue cell cultures while environmental (water/soil) isolates grow best in diphasic xenic or monoxenic cultures. Enteric protozoa causing diarrhoeal diseases (including *Entamoeba, Giardia, Dientamoeba* and *Balantidium*) grow best in monophasic (liquid) or diphasic (liquid overlay on substrate) media and an increasing number of cultures have subsequently been axenized. The urogenital flagellate *Trichomonas* grows well in defined media and easy-to-use InPouch cultures have found widespread use in screening programmes. Enteric spore-forming protozoa, including the coccidian *Cryptosporidium* (known now to be a gregarine) and various microsporidian genera (known now to be fungi), grow well in tissue cell cultures, as does the tissue cyst-forming coccidian *Toxoplasma.* Two different methods are used to culture haemoprotozoa: monophasic or diphasic media culture for kinetoplastid haemoflagellates (blood or tissue stages of *Trypanosoma* and *Leishmania* species) and erythrocyte cell cultures for apicomplexan parasites (blood stages of haemosporidian *Plasmodium* and piroplasm *Babesia* species).

Cultivation of protozoan parasites

Protozoan parasite	Genus/species	Developmental stages	Cultivation*
tissue amoeba	opportunistic *Naegleria* spp.	trophozoites	xenic/monoxenic (non-nutrient agar); axenic (PYG, DGM 21A media); tissue culture (monkey kidney, rat glioma cells)
tissue amoeba	opportunistic *Acanthamoeba* spp.	trophozoites	xenic/monoxenic (non-nutrient agar); axenic (PYG, DGM 21A media); tissue culture (monkey kidney, rat glioma cells)
tissue amoeba	opportunistic *Balamuthia* spp.	trophozoites	xenic/monoxenic (non-nutrient agar); axenic (PYG, DGM 21A, BMS media); tissue culture (monkey kidney, rat glioma, human brain microvascular endothelial cells (HBMEC))
urogenital flagellate	*Trichomonas vaginalis*	trophozoites	xenic (InPouch TV, Trussell & Johnson's media); monoxenic (Cleveland's medium), axenic (Linstead's, Diamonds TYI-S-33, YI-S media)
enteric amoeba	*Entamoeba histolytica*	trophozoites	xenic (Locke-egg, Robinson's, Boeck & Drbohlav's, Balamuth's, Diamond's TYSGM-9 media); monoxenic (Diamond's TYI-S-33, YI-S, LYI-S-2, Cleveland's media); axenic (Diamond's TYI-S-33, YI-S, LYI-S-2 media)
enteric flagellate	*Giardia intestinalis*	trophozoites	axenic (modified Diamond's TYI-S, YI-S media; Keister's modified TYI-S-33 medium (= ATCC medium 2695))
enteric flagellate	*Dientamoeba fragilis*	trophozoites	xenic (Locke-egg, Robinson's, Loeffler's media)
enteric ciliate	*Balantidium coli*	trophozoites	xenic/monoxenic (Locke-egg, Robinson's, Barret & Yarbrough's, Glasser & Coria's, Boeck & Drbohlav's media)
enteric microsporan	various	meronts, sporonts, spores	tissue culture (Madin-Darby canine kidney (MDCK), monkey kidney (E6), human lung fibroblasts (HLF), foetal bovine lung fibroblasts (FBF), lung fibroblasts (MRC-5), rabbit kidney (RK-13) cells)
enteric coccidia	*Cryptosporidium* spp.	meronts (schizonts)	tissue culture (human rectal tumour (HRT), baby hamster kidney (BHK), chicken chorioallantoic membrane (CAM), HFL, primary chicken kidney (PCK), MDCK, human colonic adenocarcinoma (Caco-2) cells)
tissue coccidian	*Toxoplasma*	tachyzoites	tissue culture (African green monkey kidney cells (Vero), lung fibroblasts (MRC-5), Henrietta Lacks' "immortal" cells (HeLa) cells)
haemosporidian	*Plasmodium* spp.	erythrocytic stages	tissue culture (human 'O' erythrocytes in Rosewell Park Memorial Institute (RPMI) 1640 medium with human 'AB' serum in HEPES buffer)
haemosporidian	*Plasmodium falciparum*	exoerythrocytic stages	tissue culture (hepatoma, chimpanzee primary hepatocytes, human hepatocytes, rat hepatocytes in RPMI 1640/minimal essential medium (MEM)
haemosporidian	*Plasmodium falciparum*	gametocytogenesis	tissue culture (young erythrocytes in RPMI 1640 medium with hypoxanthine)
haemosporidian	*Plasmodium falciparum*	sporogonic stages	tissue culture (*Drosophila* cells on Matrigel substrate in RPMI 1640 medium)
blood piroplasm	*Babesia* spp.	merozoites	tissue culture (bovine erythrocytes in agitated suspension culture or microaerophilous stationary phase (MASP) culture; Ham's F10/12medium)
haemoflagellate	*Trypanosoma* spp.	trypomastigotes	axenic (Novy, McNeal & Nicolle (NNN) diphasic medium, salt-agar with rabbit blood)
tissue flagellate	*Leishmania* spp.	amastigotes	axenic (Schneider's, JH-31 with 25% foetal calf serum (FCS); tissue culture (mouse macrophage cells)
tissue flagellate	*Leishmania* spp.	promastigotes	axenic (Schneider's medium with inactivated 30% FCS; Trager's, Steiger's, Beren's media)

cf. Ahmed NH 2014 Cultivation of parasites. Trop Parasitol 4:80

Clark CG, Diamond LS 2002 Methods for cultivation of luminal parasitic protists of clinical importance. Clin Microbiol Rev 15:329

Parasitic helminths may be maintained in various crude and defined media, and a small number of culture techniques have been developed to support their continued development to the next life-cycle stage (thus allowing additional diagnostic characters to be examined). Xenic culture of faeces from humans and animals may facilitate the recovery of nematode larvae, notably threadworms (*Strongyloides*), hookworms (*Ancylostoma*, *Necator, Bunostomum*), lungworms (*Angiostrongylus, Metastrongylus*), strongyles (*Oesophagostomum*, *Chabertia*) and trichostrongyles (*Trichostrongylus*, *Ostertagia*, *Haemonchus, Nematodirus, Cooperia*); the latter two groups being most prevalent in ruminants. Faecal cultures involve incubating moist faeces at 29°C for several (7-10) days and then collecting any emergent nematode larvae (from condensate on container walls or by inverting the container into a Petri dish to allow larvae to migrate out). Several modifications include the following: Baermann technique (culture moist faeces in filter funnel and collect emergent larvae in filtrate); Harada-Mori technique (culture faeces in tube with filter paper insert onto which emergent larvae migrate); and agar plate technique (culture faecal sample on agar plate onto which emergent larvae migrate creating visible tracks). Emergent larvae are collected onto slides and then straightened by the application of gentle heat and fixed/stained with Lugol's iodine. Axenic or tissue cell cultures also support the maintenance or further larval development of microfilariae of the filarial nematodes (*Dirofilaria, Brugia, Wuchereria, Onchocerca, Stephanofilaria, Parafilaria, Setaria*) harvested from host blood or tissues. Axenic cultures have also allowed larvae of the tissue nematodes *Trichinella* and *Anisakis* to undergo further development.

The absence of a digestive tract in cestodes has provided challenges for their culture. Studies have been confined to hatching processes, metacestode (larval) development and maturation to adults (involving segmentation and organogenesis), mainly of aquatic (pseudophyllidean) species. However, various axenic media have been used to maintain specific developmental stages of cyclophyllidean *Taenia* and *Echinococcus* species to harvest oncosphere, cysticercus or adult worm excretory/secretory (ES) products for biotechnological purposes (esp. vaccine development). Similarly, trematodes with blind digestive tracts (sac-like) have proven difficult to culture, but a variety of axenic media have been found to support the partial development of digenean trematodes (*Schistosoma*, *Parvatrema, Metagonimus, Microphalloides* and *Paragonimus* species) from pre- or post-molluscan stages (ova to miracidia, or cercariae/metacercariae to adults).

Cultivation of helminth parasites

Helminth parasite	Genera	Developmental stages	Cultivation*
enteric nematode (rhabditid)	*Strongyloides* (threadworms)	ova to larvae	xenic (Harada-Mori, Baermann, agar plate cultures)
enteric nematode (ancylostomatoid)	*Ancylostoma, Necator, Bunostomum* (hookworms)	ova to larvae	xenic (Harada-Mori moisture culture); axenic (Waymouth's MB752/1 (WYM) medium)
enteric nematode (trichostrongyloid)	*Trichostrongylus*, *Ostertagia*, *Haemonchus, Nematodirus, Cooperia*	ova to larvae	xenic (Baermann, Harada-Mori, agar plate cultures)
enteric nematode (strongyloid)	*Oesophagostomum*, *Chabertia* (nodular worms)	ova to larvae	xenic (Baermann, Harada-Mori, agar plate cultures)
enteric/tissue nematodes (metastrongyloid)	*Angiostrongylus* spp. *Metastrongylus* sp. (lungworms)	ova to larvae to adults	axenic (Ham's F-12, modified White's (WMB), National Cancer Institute (NC) tissue culture (TC) 109, RPMI 1640, WYM media, Chernin's balanced saline solution (CBSS) with horse or calf serum)
enteric nematode (ascaridid)	*Anisakis* sp.	larvae to adults	axenic (TC 199 medium with bovine pepsin digestive fluid and bovine blood)
tissue nematode (enoplid)	*Trichinella* spp.	larvae to adults	axenic (NCTC 135 with bovine serum); tissue culture (human colonic adenocarcinoma (Caco-2) cells)
blood nematodes (filarial)	*Dirofilaria* sp. (heartworm)	microfilariae	tissue culture (mosquito cells in M41 or serum-free Ham's F-12 media)
blood/tissue nematodes (filarial)	*Onchocerca, Mansonella, Stephanofilaria, Parafilaria, Setaria*	microfilariae	axenic (various tissue culture media); tissue culture (monkey kidney feeder cells)
blood/tissue nematodes (filarial)	*Brugia* sp. *Wuchereria* sp.	microfilariae to adults	tissue culture (monkey kidney/mosquito cell lines)
tissue cestode (cyclophyllidean)	*Taenia* spp.	oncosphere to cysticercus	axenic (RPMI 1640 with 10% FCS, Dulbecco's MEM); tissue culture (calf kidney monolayer in Leibovitz's medium)
tissue cestode (cyclophyllidean)	*Echinococcus* sp.	protoscoleces	axenic (RPMI 1640, diphasic S.10E.H, Dulbecco's MEM media); tissue culture (murine Hepa 1-6 feeder cells)
blood trematode (digenean)	*Schistosoma* spp.	eggs to miracidia	axenic (RPMI/MEM with 10% FCS; Earle's buffered solution with glutamine)
blood trematode (digenean)	*Schistosoma* spp.	cercariae to schistosomula to adults	axenic (human serum; NCTC 109 medium with 50% human or rabbit serum)
enteric/liver trematodes (digenean)	*Parvatrema* sp. *Metagonimus* sp. *Microphalloides* sp. *Paragonimus* spp.	metacercariae to adults	axenic (NCTC 109 medium with 20% chicken, bovine or horse serum; or chicken embryo extract (CEE), Eagle's MEM with 20% bovine serum)

**cf. Ahmed NH 2014 Cultivation of parasites. Trop Parasitol 4:80*
Yasuraoka K, Hata H 2003 In vitro cultivation of parasitic helminths. Prog Med Parasitol in Japan 7:211.

***In vivo* culture**

Laboratory animals may be used as surrogate hosts to isolate and/or amplify parasites from diagnostic samples as their inoculation into natural hosts is often precluded by ethical and/or logistical considerations. However, most parasites are host-specific and their cross-transmission to surrogate (non-natural) hosts fails. Nonetheless, *in vivo* culture has been established as a successful diagnostic aid for several parasites, but unfortunately the process is time-consuming (taking up to weeks). Ideally, laboratory animals should be derived from specific-pathogen-free (SPF) colonies to rule out the possibility of natural infections. Mice have proven to be very susceptible to infections by the tissue cyst-forming coccidian *Toxoplasma gondii*, with tachyzoites becoming evident in peritoneal fluids 7-10 days after the intraperitoneal inoculation of test samples. Hamsters are susceptible to tissue-dwelling kinetoplastid *Leishmania* species, with amastigotes developing in their spleens 4-6 weeks after inoculation. Guinea pigs, rats and mice are susceptible to various blood-dwelling kinetoplastid *Trypanosoma* species, with trypomastigotes becoming evident in peripheral blood samples two weeks after inoculation. Triatomid bugs are susceptible to the kinetoplastid *Trypanosoma cruzi,* with epimastigotes developing in their intestines 10-30 days after being allowed to feed on patient's blood (procedure known as xeno-diagnosis).

A range of animal models of infection have been developed for various protozoan and helminth parasites, primarily to facilitate research on pharmacology (drug screening), immunology (vaccine development) and pathology (pathogenesis). Well-defined animal models* exist for amoebic dysentery (in mice, gerbils, hamsters), trichomoniasis (mice, rats, hamsters, guinea-pigs, squirrel monkeys), giardiasis (mice, rats, gerbils, rabbits, dogs, cats, sheep), sleeping sickness (mice, rats, monkeys), Chagas' disease (mice, hamsters, rabbits, dogs), leishmaniasis (hamsters, mice, rats), coccidia (mice, chickens), cryptosporidiosis (neonatal or immunocompromised mice, rats, ruminants), toxoplasmosis (mice, cats), malaria (mice), echinococcosis (mice, gerbils, voles, cotton rats), schistosomiasis (mice, snails), and various gastrointestinal nematodes, including hookworms (hamsters), ascarids (chickens) and trichostrongyles (jirds, rabbits). Other parasites, particularly those of veterinary significance, have been propagated in their natural hosts (domestic and wild captive animals) for a few (sometimes many) generations as part of applied research programmes conducted by public or private institutions around the world. Information on living parasite collections, and their availability to other workers, has been documented electronically by various agencies; such as ASPIC (Australian Society for Parasitology Information on Collections), ALA (Atlas of Living Australia) and GBIF (Global Biodiversity Information Facility).

**Zak O, Sande MA* (*eds*) *1999 Handbook of Animal Models of Infection. IV. Parasitic Infection Models. Chapters 92-106. Academic Press, Elsevier.*

Medical imaging

Medical imaging may be used to detect certain parasites, or their effects, in the internal tissues and organs of hosts, notably those parasites that reside or migrate within tissues often causing inflammatory or space-occupying lesions. Various specialized techniques have been developed whereby light, X-rays, sound waves, electromagnetic waves or charged particles are used to create images of internal tissues. Imaging techniques are generally described as non-invasive, but radiographic (X-ray) techniques often involve the introduction of radio-opaque contrast media (barium, iodine, air) to help visualize internal structures, and nuclear medicine functional imaging techniques involve the use of short-lived radio-isotopes or energetic particles to create images; e.g.

- endoscopy (EN): uses flexible fiber-optic endoscopes inserted into tubular organs to take images.
- ultrasound (US): uses high frequency sound waves that are reflected by tissues to produce images.
- radiography: uses X-rays (XR) to differentially penetrate soft and hard tissues to produce negative images.
- fluoroscopy: uses a constant flow of XR at low-doses to provide real-time images.
- computed (axial) tomography (CT scans): uses synchronized movements of XR sources and radiation detectors to create images of internal tissues.
- magnetic resonance imaging (MRI): uses powerful magnets and radio frequency pulses to excite and polarize hydrogen nuclei (protons) of water molecules in tissues producing detectable signals.
- positron emission tomography (PET, SPECT): uses short-lived isotopes that are metabolically active and/or preferentially absorbed by active tissues to identify abnormalities using gamma-cameras.

Imaging techniques may be used to detect specific macroscopic parasites, or collections of microparasites, within tissues, but they are often used to detect particular lesions (often inflammatory and/or space-occupying) previously shown to be associated with certain parasites. Definitive diagnosis using alternative techniques is often required. According to conventional radiological texts, there are four active parasitic infections where diagnosis can reliably be made using imaging alone: ascariasis, trichuriasis, cerebral cysticercosis and urinary schistosomiasis. Other parasites may be recognized by their images, but they are often dead (degenerating and/or calcified). Lesions typically associated with parasites have been found in the central nervous system (commonly brain, rarely spinal cord), thorax (often lungs, sometimes heart), abdomen (tubular and solid organs, hepatobiliary tree, spleen, urogenital system), muscles (striated musculature) and skin (subcutaneous tissues). Radiologic manifestations include calcifications, erosions, ulcerations, inflammation, oedema, organ distention (sometimes mega-organ syndrome), mucosal thickening, fibrosis, nodularities, strictures, filling defects, hypertension, ascites, varices and ischaemia.

Medical imaging of parasitic infections

Type of parasite	Disease	Site of infection	Imaging technique*
protist (archamoeba)	amoebiasis	brain, thorax, abdomen	XR, CT, MRI, EN
protist (diplomonad)	giardiasis	abdomen	XR, CT, MRI
protist (kinetoplastid)	leishmaniasis	abdomen	CT, MRI, PET
protist (kinetoplastid)	Afr. trypanosomiasis	brain	CT, MRI
protist (kinetoplastid)	Am. trypanosomiasis	brain, thorax, abdomen	XR, CT, MRI
protist (gregarine)	cryptosporidiosis	abdomen	US, CT
protist (coccidian)	toxoplasmosis	brain, thorax, abdomen	XR, CT, MRI, PET, SPECT
protist (piroplasm)	babesiosis	thorax	US, CT
protest (haemosporidian)	malaria	brain, abdomen	CT, MRI
nematode (metastrongyloid)	angiostrongyliasis	brain, abdomen	XR, CT
nematode (ascaridid)	ascariasis	thorax, abdomen	XR, CT, MRI, US, EN
nematode (rhabditid)	strongyloidiasis	thorax, abdomen	XR, CT
nematode (ascaridid)	toxocariasis	brain, thorax, abdomen	XR, CT, MRI
nematode (ascaridid)	baylisascariasis	brain	MRI
nematode (ancylostomatoid)	hookworm disease	abdomen, muscles	XR, EN
nematode (camallanid)	dracunculiasis	subcutaneous tissues	XR
nematode (filarioid)	filariasis	thorax, abdomen, subcutaneous	XR, US, CT, MRI, PET
nematode (spiruroid)	gnathostomiasis	subcutaneous tissues	CT
nematode (enoplid)	trichinosis	brain, muscle	CT
nematode (enoplid)	trichuriasis	abdomen	XR, CT, MRI
nematode (enoplid)	capillariasis	abdomen	XR, CT, MRI
cestode (cyclophyllidean)	cysticercosis	brain, muscle, thorax, abdomen	XR, CT, MRI, US
cestode (cyclophyllidean)	echinococcosis	brain, thorax, abdomen, bladder	XR, CT, MRI, US
cestode (cyclophyllidean)	coenurosis	brain	CT, MRI
cestode (pseudophyllidean)	sparganosis	brain, abdomen, muscles	XR, CT, MRI
trematode (digenean)	schistosomiasis	brain, thorax, abdomen, bladder	XR, CT, MRI, US, EN
trematode (digenean)	paragonimiasis	brain, thorax, abdomen, muscle	XR, CT, MRI
arthropod (pentastome)	pentastomiasis	muscle, thorax, abdomen	XR

**cf. Haddad MC, Abd El Bagi ME, Tamraz JC (Eds) 2008 Imaging of Parasitic Diseases. Springer.*
Palmer PE 1985 Diagnostic imaging in parasitic infections. Pediatr Clin Nth Amer 32:1019

INDIRECT DEMONSTRATION

The differential diagnosis of infectious diseases is frequently complicated by the nonspecific nature of any disease symptoms (such as diarrhoea or fever), difficulties in detecting organisms in test samples (few present and irregular occurrence) and their variable characteristics (pleomorphy, virulence, growth requirements, drug sensitivity, etc.). Recourse is therefore often taken to the indirect demonstration of parasitic infections by the detection of specific clinical parameters (haematology and blood biochemistry), specific host antibodies or parasite antigens (immunology), or specific parasite proteins or DNA (molecular biology). However, correlation does not always imply causation; therefore the association between the test parameter and the parasitic disease needs to have been rigorously established by longitudinal, cross-sectional or experimental studies involving test accuracy, sensitivity and specificity.

CLINICAL HAEMATOLOGY

As given previously, several haematological tests have been developed to directly detect intracellular or extracellular parasites in host blood samples, including protozoa (haemosporidia, piroplasms, trypanosomes) and helminths (microfilariae). Clinical haematology can also be used to provide indirect presumptive evidence of parasitic infection by the demonstration of specific abnormalities in cellular and acellular components of blood, some being attributable to parasites. In addition, variations in the size, shape and number of blood cells provides an insight into the general functioning of the blood and the health of the host. Techniques have been developed to measure erythrocyte (red blood cell) characteristics (especially haemoglobin and haematocrit associated with oxygenation and perfusion potentials), leucocyte (white blood cell) characteristics (especially differential counts associated with infection and immuno-competency), and platelet (thrombocyte) characteristics associated with coagulopathies. Whole blood samples are usually collected by peripheral venepuncture into anticoagulant and screened for:

- haemoglobin (HGB): oxygen carrier [low levels associated with anaemia; high levels with polycythaemia]
- red blood cell count (RBC): quantifies erythrocytes [low counts associated with anaemia, excess body fluid and blood loss; high counts with dehydration, polycythaemia]
- haematocrit (HCT) or packed cell volume: percentage of blood occupied by erythrocytes [low levels associated with blood loss, reduced production and various anaemic conditions]

- red cell indices, such as mean cell volume (MCV), mean cell haemoglobin (MCH), mean corpuscular haemoglobin concentration (MCHC) and red cell distribution width (RDW): provide details on volume and haemoglobin content of red blood cells [perturbations indicative of different types of anaemias; e.g. microcytic/hypochromic (often due to iron deficiency), normocytic/normochromic (due to chronic infections, inflammation, renal failure) or macrocytic (due to haemolysis, vitamin deficiency or liver disease); may also reveal haemozoin (HZ) pigment associated with malaria]

- white blood cell count (WBC): quantifies leucocytes [high levels associated with infection, stress; low levels with immuno-suppression, bone marrow failure]
- differential count: quantifies different types of white blood cells, including granulocytes (neutrophils (NEU), eosinophils (EOS), basophils (BAS)) and agranulocytes (lymphocytes (LYM), monocytes (MON)) [different levels provide information on host immuno-competency, many helminth infections associated with high EOS levels]

- platelet count (PLT): quantifies thrombocytes (coagulation agents) [high levels associated with inflammation and infection; low levels with spontaneous bleeding, disseminated intravascular coagulation (DIC), leukaemia]
- clotting indices, such as prothrombin time (PT), international normalized ratio (INR), activated thromboplastin time (APTT), thrombin clotting time (TCT), D-dimer, fibrinogen, anti-thrombin, bleeding time and viscosity [perturbations associated with various coagulopathies, including some caused by parasites]

Common haematological conditions include anaemias (nutritional, hypovolaemic, haemolytic, aplastic), cancers (lymphoma, leukemia, myeloma), haemorrhagic/clotting conditions (coagulopathies), immunodeficiencies (genetic/acquired, cellular/humoral) and microbial infections (viruses, bacteria, fungi, protozoa, helminths). Despite the excellent correlation between many haematological abnormalities and specific haemoparasites, similar abnormalities may be caused by other disease conditions therefore definitive diagnosis must be confirmed using alternative techniques. Nonetheless, a range of parasites may cause haematological conditions; either by feeding on blood, destroying blood cells, damaging vascular beds or eliciting hypersensitive responses.

Haematological changes associated with parasitic infections

Type of parasite	Disease	Site of infection	Changes to haematological parameters
protist (amoeba)	amoebiasis	gut	HGB ↓, RBC ↓, HCT ↓, WBC ↑
protist (kinetoplastid)	African trypanosomiasis	blood, brain	HGB ↓, RBC ↓, HCT ↓, MCV ↓, MCH ↓, WBC ↑, LYM ↑, MON ↑, PLT ↓, PT ↑, TCT ↑, APTT ↑, DIC
protist (kinetoplastid)	American trypanosomiasis	macrophages, tissues	RBC ↓, WBC ↑, LYM ↑, PLT ↓
protist (kinetoplastid)	leishmaniasis	skin, viscera	HGB ↓, RBC ↓, HCT ↓, WBC ↓, LYM ↓, EOS ↓, NEU ↑, MON ↑, PLT ↓, PT ↑, APTT ↑, DIC
protist (coccidian)	coccidiosis	gut	HGB ↓, RBC ↓, HCT ↓, MCV ↑, WBC ↑, LYM ↓, EOS ↑, NEU ↑
protist (coccidian)	toxoplasmosis	macrophages, brain, muscles	HGB ↓, RBC ↓, HCT ↓, WBC ↑, NEU ↑, LYM ↓, MON ↑, EOS ↑
protist (haemosporidian)	malaria	liver, erythrocytes	HGB ↓, RBC ↓, HCT ↓, MCV ↑, MCH ↑, MCHC ↑, HZ, WBC ↓, NEU ↓, MON ↓, LYM ↓, EOS ↓, PLT ↓, PT ↑, DIC
protist (piroplasm)	babesiosis	erythrocytes, spleen	HGB ↓, RBC ↓, HCT ↓, MCV ↓, MCHC ↓, WBC ↑, LYM ↑, MON ↑, NEU ↑, EOS ↑, PLT ↓, APTT ↓, DIC
protist (piroplasm)	theileriosis	blood cells	HGB ↓, RBC ↓, HCT ↓, WBC ↓
nematode (rhabditid)	strongyloidiasis	gut	HGB ↓, RBC ↓, HCT ↓, WBC ↑, EOS ↑
nematode (trichostrongyloid)	ostertagiasis	stomach	HGB ↓, RBC ↓, HCT ↓
nematode (trichostrongyloid)	haemonchosis	stomach	HGB ↓, RBC ↓, HCT ↓, WBC ↑, EOS ↑
nematode (trichostrongyloid)	trichostrongyliasis	stomach	HGB ↓, HCT ↓, WBC ↑, EOS ↑
nematode (ascaridid)	ascariasis	gut	HCT ↓, WBC ↑, EOS ↑, PLT ↑
nematode (ascaridid)	toxocariasis	gut, tissues	HGB ↓, RBC ↓, HCT ↓, MCV ↑, MCHC ↓, WBC ↑, EOS ↑, LYM ↓, BAS ↑
nematode (ancylostomatoid)	hookworm diseases	gut	HGB ↓, RBC ↓, HCT ↓, MCV ↓, WBC ↑, NEU ↑, LYM ↑, EOS ↑, PLT ↑
nematode (spiruroid)	gnathostomiasis	gut	WBC ↑, EOS ↑
nematode (enoplid)	trichinosis	gut, muscles	RBC ↓, HGB ↓, HCT ↓, WBC ↑, LYM ↑, EOS ↑
nematode (filarioid)	lymphatic filariasis	blood, lymphatics	RBC ↓, HGB ↓, HCT ↓, MCV ↑, MCH ↑, MCHC ↓, WBC ↑, EOS ↑, PLT ↑
nematode (filarioid)	onchocerciasis	skin, blood	WBC ↑, LYM ↑, EOS ↑, NEU ↓
cestode (cyclophyllidean)	cysticercosis	muscles, viscera	RBC ↓, HGB ↓, HCT ↓, WBC ↑, EOS ↑, LYM ↑, NEU ↓
cestode (cyclophyllidean)	echinococcosis	viscera	WBC ↑, EOS ↑, LYM ↑
trematode (digenean)	schistosomiasis	veins, viscera	HGB ↓, HCT ↓, WBC ↑, EOS ↑, MON ↑, NEU ↑, LYM ↓
trematode (digeneans)	liver flukes	liver	HGB ↓, RBC ↓, HCT ↓, MCV ↑, MCHC ↓, WBC ↑, MON ↑, LYM ↑, NEU ↑, EOS ↑
insects (flies, fleas, lice)	ectoparasites	skin	HGB ↓, RBC ↓, HCT ↓, MCHC ↓, WBC ↓, NEU ↓, PLT ↓
arachnids (ticks, mites)	ectoparasites	skin	HGB ↓, RBC ↓, HCT ↓, MCHC ↓, WBC ↓, NEU ↓, PLT ↓

CLINICAL BIOCHEMISTRY

A wide variety of chemical tests have been developed to detect small amounts of molecules present within blood samples; including electrolytes, blood gases, lipids, enzymes, hormones, toxins, tumour markers, acute phase proteins, antibodies and various medications. Blood is usually collected by peripheral venepuncture into colour-coded tubes containing different chemical preservatives and/or anticoagulants. Plasma or serum is harvested and micro-volume samples processed in automated systems for a predetermined panel of parameters. Blood samples are commonly analysed for:

- electrolytes: ions involved in membrane transport, water balance and acid-base regulation; including: sodium (Na), potassium (K), chloride (Cl), bicarbonate (HCO_3) [high levels associated with diarrhoea, kidney diseases; low levels with vomiting, excessive sweating, diabetes]; hydrogen ion concentration, pH [increased levels indicative of alkalosis; decreased levels with acidosis]; osmolality/osmolarity [increased levels of solutes associated with dehydration, uremia, kidney damage; decreased levels with hyponatremia].
- minerals: involved in numerous homeostatic mechanisms; including: calcium (Ca) [high levels associated with hyperparathyroidism, cancer; low levels with liver disease, malnutrition, pancreatitis, renal disorders]; magnesium [high levels associated with renal disorders, dehydration; low levels with malnutrition, diarrhoea, diabetes]; phosphorus/phosphate (P/PO_4) [high levels associated with kidney or liver disease, ketoacidosis; low levels with hyperparathyroidism, malnutrition, rickets]; copper [high levels associated with anaemia, jaundice, tremors; low levels with neutropenia, anaemia, osteoporosis]
- vitamins: essential for metabolic processes; including: vitamin A [deficiency associated with vision problems; excess with toxicities]; vitamins B9, B12 [low levels associated with malnutrition, anaemia, neuropathy, tapeworm infection, malabsorption, neural tube defects in developing foetus; high levels concomitant with cancer, diabetes, obesity, liver disease]; vitamin C [low levels associated with malnutrition, scurvy; high levels with erythrocyte fragility]; vitamin D [deficiency associated with bone malformation or weakness, some cancers, immune diseases]; homocysteine [increased levels associated with malnutrition, folate deficiency, homocystinuria, possibly heart attack, stroke]

- blood markers: involved in erythropoiesis; including: total serum iron (TSI) and ferritin [low levels associated with iron-deficiency anaemia, pica, chronic illness; high levels with haemolytic anaemia, haemochromatosis]; total iron-binding capacity (TIBC) and transferrin [low levels associated with haemolytic anaemia, haemochromatosis, chronic illness; high with iron deficiency anaemia]; zinc [increased levels indicate disruption to heme production, usually associated with iron deficiency or lead poisoning]
- blood gases: evaluate lung function; including: oxygen saturation, oxygen partial pressure (pO_2) [low levels indicate patient not getting enough oxygen]; carbon dioxide partial pressure (pCO_2) and bicarbonates [high levels associated with metabolic alkalosis (due to chronic vomiting, heart failure, cirrhosis) or respiratory acidosis (due to lung diseases); low levels with metabolic acidosis (due to kidney failure) or respiratory alkalosis (due to hyperventilation, anxiety, pain)]; lactate and pyruvate [increased levels associated with hypoxia (type A lactic acidosis due to respiratory insufficiency or ischaemia, type B due to excess demand due to disease)]
- cardiac markers; indicative of heart disorders; including: heart-type fatty acid binding protein (H-FABP), troponin (TRO) and brain natriuretic peptide (BNP) [high levels associated with myocardial ischaemia]

- lipid markers: fats involved in energy stores, cell membranes, metabolism; elevated levels of triglycerides (TRIG) and low-density lipoprotein (LDL) cholesterol (CHOL) associated with atherosclerosis and heart disease; elevated levels of high-density lipoprotein (HDL) CHOL considered cardio-protective.
- inflammation markers: parameters indicative of recent infection; including: C-reactive protein (CRP) and procalcitonin (PRO) [high levels associated with acute inflammation and/or infection]; alpha 1-antitrypsin (AAT) [low levels associated with acute systemic inflammation or emphysema]; erythrocyte sedimentation rate (ESR) [high levels associated with acute inflammation, infection, anaemia, pregnancy]

- liver markers: indicative of liver dysfunction; including: total protein (PROT), albumin (ALB), globulins (GLO), often expressed as ALB:GLO (A:G) ratio [low levels reflect overproduction of GLO (seen in multiple myeloma or autoimmune diseases), or underproduction of ALB (seen in cirrhosis) or loss of ALB from circulation (due to infection or nephrotic syndrome)]; glucose (GLU) [high levels associated with diabetes, kidney disease, pancreatitis; low levels with severe infections, liver disease, kidney failure]; ammonia [high levels associated with infant haemolytic disease, liver or kidney disease, encephalopathies, gastrointestinal bleeding]; bilirubin (BILI) [high levels of biliary pigment associated with poor liver function (haemolysis, cholestasis), jaundice]; aspartate transferase (AST) and alanine transferase (ALT) [high levels associated with hepatocellular damage]; gamma-glutamyl transferase (GGT) and alkaline phosphatase (ALP) [high levels associated with cholestasis]
- gastric markers: indicative of stomach disorders; including pepsinogen (PEP) [high levels associated with gastric mucosal infections, especially by nematodes]
- renal markers: used to assess kidney function; including: creatinine (CRE) [high levels associated with kidney disease, infection]; blood urea nitrogen (BUN) [hhigh levels associated with impaired kidney function, heart failure, dehydration];

uric acid (UA) [high levels seen in many disorders, gout, diabetes, kidney stones]; ketones (high levels associated with increased fat metabolism, ketoacidosis, diabetes]

- pancreas markers: indicate pancreatic problems; including: amylase (AMY) and lipase (LIP) [high levels associated with inflammation, disease]
- general markers: indicative of systemic/disseminated problems; including: lactate dehydrogenase (LDH) [high levels associated with tissue/cellular injury, anaemia, inflammation, infection: LDH-1 (heart, brain, erythrocytes); LDH-2 (reticulo-endothelial system); LDH-3 (lungs); LDH-4 (kidneys, pancreas, placenta); LDH-5 (liver, muscles); angiotensin-converting enzyme (ACE) [high levels associated with sarcoidosis, cirrhosis, infection; decreased levels with lung diseases, starvation]; eosinophilic cationic protein (ECP)(= ribonuclease 3) [high levels associated with inflammation, asthma, dermatitis, helminth infection]; creatine kinase (CK), myoglobin (MYO), aldolase (ALD) and carbonic anhydrase (CA-III) [high levels associated with muscle damage]

- endocrinology: levels determined for thyroid hormones (thyroxine, thyroid stimulating hormone, triiodothyroxine, thyroxine binding globulin, thyroglobulin), sex hormones (dihydrotestosterone, testosterone, hydroxyprogesterone, follicle-stimulating hormone, luteinizing hormone, estradoil, progesterone, dehydroepiandrosterone sulfate, beta human chorionic gonadotrophin) and others (adrenocorticotrophic hormone, cortisol, growth hormone, insulin-like growth factor, prolactin, parathyroid hormone, plasma renin activity, aldosterone)
- tumour markers: indicative of various cancers; e.g. alpha-fetoprotein (liver, testicular, ovarian cancer); carcinoembryonic antigen (colonic cancer); cancer antigen 19-9 (pancreatic cancer), CA-125 (ovarian cancer); calcitonin (thyroid cancer); acid phosphatase and prostate specific antigen (prostate cancer)

- immunoglobulin isotypes: antibody classes typed as IgA (secretory/mucosal), IgD (receptor), IgE (inflammatory/ allergenic), IgM (primary antibody responses, transient) or IgG (secondary antibody responses, persistent)
- auto-antibodies: a range of tests are available for auto-immune conditions (either systemic or organ-specific)
- toxins: blood tests are available for a range of toxic chemicals (e.g. lead, ethanol)

Parasites may damage tissues causing them to metabolize or release abnormal levels of particular chemicals, as evidenced by comparing levels with known reference ranges. Regrettably, few changes in chemical levels are specific for individual parasites, so biochemical screens are often used to supplement/complement clinical information by indicating which tissue systems have been compromised and to what extent. Some parasites may cause systemic or disseminated problems to the host, while others have more specific effects on particular organ/tissue systems involved in infection.

Blood biochemical changes associated with parasitic infections

Type of parasite	Disease	Site of infection	Changes to blood biochemical parameters
protist (amoeba)	amoebiasis	gut, liver, brain	ALP ↑, ESR ↑, CRP ↑, ALB ↓, AST ↑, ALT ↑
protist (diplomonad)	giardiasis	gut	CRE ↓, AMY ↓, GLU ↑, BUN ↑, PROT ↑, AST ↑, ALT ↑, Na ↑, K ↑
protist (kinetoplastid)	African trypanosomaisis	blood, brain	ESR ↑, PROT ↑, ALB ↓, IgM ↑, BUN ↑, GLO ↑
protist (kinetoplastid)	American trypanosomaisis	macrophages, tissues	CK ↑, PROT ↑, ALP ↑, ALD ↑, ALT ↑, GGT ↑, TRO ↑
protist (kinetoplastid)	leishmaniasis	skin, viscera	CHOL ↓, HDL ↓, LDL ↓, ALB ↓, TRI ↑, PROT ↑, GLO ↑, UA ↑, BUN ↑, CRE ↑, AST ↑, ALT ↑
protist (coccidian)	coccidiosis	gut	PROT ↓, ALB ↓, ALT ↓, AST ↓, ALP ↑
protist (coccidian)	toxoplasmosis	brain, muscles, viscera	PROT ↓, ALB ↓, ALT ↑, AST ↑, ALP ↑, CK ↑, BILI ↑, AMY ↑, LIP ↑, GLO ↑, ESR ↑, TRO ↑
protist (haemosporidian)	malaria	liver, erythrocytes	AST ↑, BILI ↑, GLU ↓, CRE ↑, BUN ↑, UA ↑, ESR ↑, ALB ↓, LDH ↓
protist (piroplasm)	babesiosis	erythrocytes, spleen	CK ↑, LDH ↑, AST ↑, ESR ↑, ALB ↓, BUN ↑, CRE ↑, CHOL (HDL, LDL) ↑, TRIG ↑, ALT ↑, BILI ↑, GLO ↓
protist (piroplasm)	theileriosis	blood cells	ALT ↑, AST ↑, ALP ↑, CK ↑, GGT ↑, UA ↑, BUN ↑, BILI ↑, P ↑, PROT ↓, ALB ↓, GLU ↓, CHOL ↓, Ca ↓
nematode (rhabditid)	strongyloidiasis	gut	ALB ↓, GLO ↑, CHOL ↓, GLU ↓, IgE ↑
nematode (trichostrongyloid)	ostertagiasis	stomach	PEP ↑, ALB ↓, PROT ↓, ALP ↑, AP ↑
nematode (trichostrongyloid)	haemonchosis	stomach, gut	PEP ↑, ALB ↓, PROT ↑
nematode (trichostrongyloid)	trichostrongyliasis	stomach, gut	PROT ↓, ALB ↓, GLO ↑, PEP ↑, Ca ↓, P ↓, vit. A ↓, ALP ↓
nematode (ascaridid)	toxocariasis	gut, tissues	ESR ↑, P ↓, Na ↓, K ↓, HCO_3 ↓, GLU ↓, PROT ↓, BUN ↓, CRE ↓, CHOL ↑, Ca ↑, Cl ↑, ALP ↑, AST ↑, ALT ↑
nematode (ancylostomatoid)	hookworm diseases	gut	CRP ↑, TSI ↓, IgE ↑, PROT ↓, ALB ↓, Na ↓, Cl ↓, ALP ↑, ALT ↑
nematode (enoplid)	trichinosis	gut, muscles	CK ↑, ALP ↑, AST ↑, ALT ↑, GLU ↑, K ↑, IgE ↑
nematode (filarioid)	lymphatic filariasis	blood, lymphatics	ESR ↑, ALT ↑, AST ↑, BILI ↑, PROT ↑, GLO ↑, GLU ↓, ALB ↓, BUN ↑, CRE ↑, P ↑, K ↑, Ca ↓, Na ↓
nematode (filarioid)	onchocerciasis	skin, blood	LDH ↑, ECP ↑, CRP ↑, CK ↑, ALD ↑
cestode (cyclophyllidean)	cysticercosis	viscera, muscles, brain	PROT ↓, AST ↑, ALT ↑, ALP ↑, CK ↑, LDH ↑, ALB ↓, GLO ↑
cestode (cyclophyllidean)	echinococcosis	viscera	GGT ↑, ALP ↑, BUN ↓, GLU ↓, AST ↑, CHOL ↓, BILI ↑, ALT ↑, AP ↑
trematode (digenean)	schistosomiasis	veins, viscera	GLO ↑, Ca ↑, K ↑, PROT ↑, ALB ↓, BUN ↑, UA ↓
trematode (digeneans)	liver flukes	liver	GGT ↑, BILI ↑, ALT ↑, AST ↑, LDH ↑, ESR ↑, PROT ↓, ALB ↓, ALP ↑
insects (flies, fleas, lice)	ectoparasites	skin	PROT ↑, GLO ↑, ALB ↓, GLU ↓, BILI ↓, AST ↓, Cu ↓, Zn ↓, Ca ↓, ALT ↑, TSI ↓, ALP ↓
arachnids (ticks, mites)	ectoparasites	skin	PROT ↑, GLO ↑, ALB ↓, GLU ↓, BILI ↓, AST ↓, Cu ↓, Zn ↓, Ca ↓, ALT ↑, TSI ↓, ALP ↓

IMMUNOLOGY

While most haematological and biochemical clinical parameters are non-specific for individual parasitoses, immunological techniques using highly specific antigen-antibody interactions can be used to diagnose infections by particular parasite species. Humans and animals respond to most infectious diseases by forming antibodies (Ab) against antigens (Ag) of the infecting pathogen as part of their immunological defenses. These antibodies (= gamma-globulins or immunoglobulins) are produced by plasma cells (transformed B lymphocytes) and are secreted into the blood stream to circulate through the body. When they come into contact with the relevant antigen, they bind to it and tag it for destruction.

Serum (or plasma) samples are usually tested for specific host antibodies, and sometimes for parasite antigens (antigenaemia usually associated with blood-borne parasites). More recently, techniques have been developed to test faecal samples for host secretory (mucosal) antibodies or parasite copro-antigens (usually associated with gastroenteric parasites). A range of immunological techniques are currently used to demonstrate host antibodies and/or parasite antigens; including complement fixation tests (CFT), dye tests (DT), direct or indirect haemagglutination test (HAT, IHAT), direct or indirect fluorescent-antibody tests (DFAT, IFAT), chemiluminescence analyses (automated PRISM system), enzyme-linked immunosorbent assays (ELISA) with various modifications (such as dot-ELISA, Falcon assay screening test ELISA (FAST-ELISA) and luciferase immunoprecipitation system (LIPS)], radioimmunoprecipitation assays (RIPA), rapid immunochromatographic antigen detection tests (RDT) and immunoblotting (IB).

In diagnostic tests, laboratory reagents (antigens or antibodies) are immobilized on substrates, incubated with test (and control) samples, an indicator system is added and the results best read objectively and quantitatively; i.e. without subjective interpretation by individual operators and with measurement of a related parameter, such as spectrophotometric absorbance (optical density), intensity of fluorescence, degree of haemolysis, etc. It is important to quantitate the amount of specific antibody present as this provides an indication of the severity of infection as well as the immunocompetence of the host. However, it is impossible to measure the absolute concentration (w/v) of specific antibodies by standard biochemical techniques, so the amount is estimated by serial dilution of test samples and reporting the 'end-titre' (last positive dilution); e.g. an end-point titre of 1/100 indicates there was enough specific antibody present to elicit a positive reaction when the blood was diluted 100 times.

Test results can be influenced by many factors which affect the integrity of the relationships between parameters (such as edge effects, detectable levels, accuracy, interference, competition, nonspecific background reactions, cross-reactivity with other microbes, reactions against vaccines previously given, poor test sensitivity and specificity). Positive and negative control samples can be used to indicate, and even mitigate, various problems, so the end-point titre of any particular sample can usually be given with a high degree of confidence. Interpreting the significance of the test results requires thorough knowledge of the kinetics (onset and duration) and dynamics (intensity) of the host response to infection. Longitudinal samples are often obtained to determine whether antibody titres in a particular individual remain stable or whether they are increasing or decreasing (plot titre over time).

Immunological tests available for parasitic infections in diagnostic pathology laboratories

Type of parasite	Disease	Test sample	Immunological tests*
protist (amoeba)	*Entamoeba histolytica*	serum (Ab)	ELISA
protist (amoeba)	*Entamoeba histolytica*	faeces (Ag)	ELISA, RDT
protist (amoebae)	*Naegleria, Acanthamoeba, Balamuthia* spp.	cerebrospinal fluid, tissues (Ag)	IFAT
protist (diplomonad)	*Giardia duodenalis*	faeces (Ag)	DFAT, ELISA, RDT
protist (trichomonad)	*Trichomonas vaginalis*	vaginal secretions (Ag)	DFAT, ELISA, IHAT
protist (kinetoplastid)	*Trypanosoma brucei*	serum (Ab)	HAT, IHAT, DFAT, IFAT, ELISA, dot-ELISA, IB
protist (kinetoplastid)	*Trypanosoma cruzi*	serum (Ab)	IFAT, ELISA, dot-ELISA, RIPA, PRISM, IB
protist (kinetoplastid)	*Trypanosoma cruzi*	serum (Ag)	RDT
protist (kinetoplastid)	*Leishmania* spp.	serum (Ab)	HAT, IHAT, ELISA, dot-ELISA
protist (coccidian)	*Cryptosporidium parvum, C. hominis*	faeces (Ag)	DFAT, IFAT, ELISA, RDT
protist (coccidian)	*Toxoplasma gondii*	serum (Ab)	DT, HAT, IHAT, DFAT, IFAT, ELISA, IB
protist (coccidian)	*Neospora caninum*	serum (Ab)	ELISA
protist (coccidian)	*Neospora caninum*	tissues, blood cells (Ag)	IFAT
protist (haemosporidian)	*Plasmodium falciparum, P. vivax, P. malariae*	serum (Ab)	IFAT, FAST-ELISA
protist (haemosporidian)	*Plasmodium falciparum, P. vivax, P. malariae, P. ovale*	serum, blood (Ag)	ELISA, RDT
protist (piroplasm)	*Babesia* spp.	serum (Ab)	IFAT, ELISA
protist (piroplasm)	*Babesia* spp.	tissues, blood cells (Ag)	IFAT
nematode (rhabditid)	*Strongyloides stercoralis*	serum (Ab)	HAT, IHAT, DFAT, IFAT, ELISA, IB, LIPS
nematode (trichostrongyloid)	carbohydrate larval antigens of *Haemonchus, Trichostrongylus, Telodorsagia, Cooperia, Nematodirus* spp.	saliva (Ab)	ELISA
nematode (ascarid)	*Toxocara canis*	serum (Ab)	ELISA
nematode (ascarid)	*Bayliascaris procyonis*	serum (Ab)	IB
nematode (metastrongyloid)	*Angiostrongylus cantonensis*	serum (Ab)	ELISA
nematode (filarial)	*Wuchereria bancrofti, Brugia malayi, B. timori, Loa loa*	serum (Ab)	HAT, IHAT, ELISA, dot-ELISA, LIPS
nematode (filarial)	*Wuchereria bancrofti*	serum, blood (Ag)	IHAT, ELISA, RDT
nematode (filarial)	*Dirofilaria immitis*	serum (Ab)	ELISA
nematode (filarial)	*Dirofilaria immitis*	serum (Ag)	ELISA, RDT
nematode (enoplid)	*Trichinella spiralis*	serum (Ab)	ELISA
cestode (cyclophyllidean)	*Taenia solium*	serum (Ab)	IB, ELISA
cestode (cyclophyllidean)	*Taenia solium*	faeces, serum (Ag)	ELISA
cestode (cyclophyllidean)	*Echinococcus granulosus, E. multilocularis*	serum (Ab)	HAT, IHAT, ELISA, dot-ELISA, IB
trematode (digenean)	*Fasciola hepatica, F. gigantica*	serum (Ab)	IB, ELISA, FAST-ELISA, dot-ELISA
trematode (digenean)	*Fasciola hepatica*	faeces (Ag)	ELISA
trematode (digenean)	*Paragonimus westermani*	serum (Ab)	IB
trematode (digenean)	*Schistosoma japonicum, S. mansoni, S. haematobium*	serum (Ab)	HAT, IHAT, ELISA, dot-ELISA, FAST-ELISA, IB
trematode (digenean)	*Schistosoma mansoni*	serum (Ag)	IB
insect (flea)	*Ctenocephalides* spp.	skin test (Ab)	intradermal inoculation
arachnid (mite)	*Sarcoptes scabiei*	serum (Ab)	ELISA

**cf. Ndao M 2009 Diagnosis of parasitic diseases: old and new approaches. Interdisciplinary Perspectives on Infectious Diseases doi:10.1155/2009/278246*

DPDx Laboratory Identification of Parasitic Diseases of Public Health Concern, Centers for Disease Control and Prevention (CDC) website www.cdc.gov

MOLECULAR BIOLOGY

Over the last several decades, molecular biology has undergone a dramatic revolution whereby techniques have become available to work directly with parasite proteins and nucleic acids (RNA and DNA). Research laboratories have utilized many different techniques to:

- characterize genetic variation within and between parasite species and different life-cycle stages;
- conduct disease screening and surveillance programs;
- explore parasite population genetics and molecular epidemiology;
- determine phylogenetic relationships between parasite taxa and assemblages;
- explore parasite biochemistry and protein expression (often related to drug resistance);
- produce defined immunoreagents (including vaccine development); and
- develop new diagnostic tests for field and laboratory use.

Early studies were conducted on parasite proteins and numerous electrophoretic systems were developed to detect species-specific polypeptides and isoenzymes by one- or two-dimensional electrophoresis in different gel matrices (polyacrylamide, cellulose nitrate, agarose) whereby molecules are separated on the basis of their size and charge. Specific molecules could be partly identified by their positions within the gels (with respect to molecular markers), by reacting them against specific substrates (for isoenzymes), or immunoblotting (IB) them against polyclonal or monoclonal antibodies. Rapid immunochromatographic techniques (RDT) have also been developed as dip-stick or spot-on tests to detect specific parasite proteins in test samples.

More recently, the advent of the polymerase chain reaction (PCR) allowed the rapid and specific amplification of specific parasite DNA or RNA sequences. Diagnostic PCRs work by using short synthetic (forward and reverse) primer pairs (around 20 bases) to amplify specific segments of known length and sequence of parasite DNA (usually 100-800 bases). Whole DNA is extracted from host samples (lysed blood/tissues) by precipitation and centrifugal filtration into elution buffer. [For RNA, reverse transcriptase is first used to synthesize cDNA which is then amplified by PCR (process known as reverse transcription PCR or RT-PCR)]. Eluted DNA (or cDNA) is then mixed with a solution containing the primers, *Taq* polymerase (from *Thermus aquaticus*), magnesium chloride and dinucleotide triphosphates (dNTPs). The solutions are then placed in a thermal cycler which starts with an initiation phase where high temperatures (~94°C) are used to denature double-stranded DNA into single strands. The temperature is then decreased to allow the primers to hybridize (anneal) to these single strands. The heat-stable polymerase then uses ambient nucleotides to copy (extend) the targeted sequence. These procedures are repeated through some 30 cycles thus facilitating the exponential amplification of parasite DNA (theoretically 2^{30} = 2 billion times). PCR products (amplicons) are then visualized, usually by agarose gel electrophoresis, where DNA bands are separated on the basis of their molecular size and charge. The agarose gel is treated with a fluorescent DNA stain that allows amplicons to be visualized under ultraviolet light. Smaller amplicons travel faster through the gel matrix than larger amplicons, and their final position can be used to determine band size by comparison with standard markers (DNA ladders). Positive results in a PCR test are indicated by the appearance of a specific band (the same size as the primer's targeted sequence) in the gel. Amplicons can also be examined by restriction fragment length polymorphism (RFLP) analysis (enzymes used to cleave DNA at specific sites) or by DNA sequencing if confirmation or further characterization is required.

Various PCR modifications have been examined in attempts to simplify the process, such as measuring amplification products in real-time, using single tubes, using constant temperatures, adopting multiplex formats, detecting amplicons by differential fluoroscopy, enzyme reactions or chromatography. Quantitative real-time PCR (qPCR) monitors DNA amplification in a single reaction vessel in real-time by measuring the fluorescence signal every cycle using a DNA-binding dye (e.g. SYBR-Green) or sequence-specific internal *Taq*Man probes (eliminating the need for subsequent gel electrophoresis). Loop-mediated isothermal amplification (LAMP) reactions are carried out at a constant temperature (eliminating the need for a thermal cycler) using six different primers recognizing eight distinct regions within a target gene. Luminex (LUM) technology is a bead-based flow-cytometric assay whereby probes (antigens, antibodies or oligonucleotides) are bound to microsphere beads and each emits a unique fluorescent signal when excited by laser. Quantitative nucleic acid sequence-based amplification (QT-NASBA) amplifies RNA sequences at a constant temperature using alternating treatments with reverse transcriptase to synthesize cDNA and then RNAse H to destroy RNA in RNA-DNA hybrids. Oligochromatography PCR (OC-PCR) visualizes amplicons on a dipstick through hybrization with a gold-conjugated probe. PCR-ELISA uses immunosorbent (or oligosorbent) assays to quantify amplicons after their immobilization on microtitre plates. Rather than being confined to research institutions, PCR technologies are now becoming more commonplace in diagnostic laboratories as they become easier and faster to use without elaborate specialized equipment.

The analytical sensitivities (limits of detection) of PCR for parasites have been variously reported to range from 50 ng to 10 fg of DNA, but it is impossible to convert these measurements into conventional parasite concentrations (such as numbers per weight or volume of sample, or percentage parasitaemia) without knowing many variables, including sample size, DNA extraction efficacy, PCR aliquot size, DNA purity and specificity, etc. Nowadays, experimental studies are conducted involving the serial titration of DNA extracted from samples spiked with known numbers of parasites, and analytical sensitivities (LODs) have been reported to be around one protozoan or helminth parasite per mL (or per gram) of sample; some even being as low as one cell (*T. cruzi*) per 20 mL of blood.

Molecular diagnostic tests for parasites

Type of parasite	Disease	Test sample	Type of test*
protist (amoebozoa)	*Entamoeba histolytica, E. dispar*	faeces	PCR, qPCR
protist (amoebozoa, heterolobosea)	*Naegleria, Acanthamoeba, Balamuthia* spp.	CSF, tissues	PCR
protist (kinetoplastid)	*Trypanosoma brucei*	blood	PCR, qPCR, OC-PCR, LAMP
protist (kinetoplastid)	*Trypanosoma cruzi*	blood	PCR, qPCR, LAMP
protist (kinetoplastid)	*Leishmania* spp.	blood	PCR, qPCR, OC-PCR, PCR-ELISA, QT-NASBA
protist (coccidian)	*Cryptosporidium parvum, C. hominis*	faeces, water	PCR, qPCR, LAMP, LUM
protist (coccidian)	*Cyclospora cayetanensis*	faeces	PCR, qPCR
protist (coccidian)	*Toxoplasma gondii*	blood	PCR, qPCR
protist (haemosporidian)	*Plasmodium falciparum, P. vivax, P. malariae, P. ovale*	blood	PCR, qPCR, PCR-ELISA, LAMP, LUM, QT-NASBA
protist (piroplasm)	*Babesia microti*	blood	PCR, qPCR
microsporidian (fungi)	various species	faeces	PCR
nematode (rhabditid)	*Strongyloides stercoralis*	faeces	PCR, qPCR
nematode (filarial)	*Wuchereria bancrofti, Brugia malayi, B. timori, Loa loa*	blood	PCR, PCR-ELISA
cestode (cyclophyllidean)	*Taenia solium*	faeces	PCR, LAMP
trematode (digenean)	*Schistosoma mansoni*	serum, faeces	PCR, qPCR, OC-PCR

**cf. DPDx 2017 Laboratory Identification of Parasitic Diseases of Public Health Concern, Centers for Disease Control and Prevention (CDC) website www.cdc.gov*
Ndao M 2009 Diagnosis of parasitic diseases: old and new approaches. Interdisciplinary Perspectives on Infectious Diseases dx.doi.org/10.1155/2009/278246

DNA sequencing of different gene fragments continues to fuel comprehensive genetic and phylogenetic analyses of both clinical and environmental isolates of many parasite species. Sequencing has facilitated the quantitation of genetic variation both between and within parasite species, leading to the recognition of particular 'genotypes' associated with clinical disease. Phylogenetic analyses use a range of computational algorithms (parsimony, maximum likelihood and Bayesian inference) to generate branching tree-like diagrams to represent estimated pedigrees of inherited characters. In many instances, molecular biology has validated conventional taxonomic classification systems (notably for families, genera and species), but in some cases they have led to the complete revision of classical classification systems, especially for higher taxa (kingdoms, phyla, classes and orders). While taxonomy underpins diagnosis, it must be remembered to be an ever-changing paradigm based on a constellation of characters (it is never absolute and cast in concrete).

CONTROL

PARASITE CONTROL

Parasitic infections have deleterious effects on many human and animal populations, being responsible for significant host morbidity and mortality. The impact of many parasitic infections has been quantified in economic terms by estimating the cost of the morbidity burden (YLD = years of life lost due to disability) and the mortality burden (YLL = years of life lost due to premature death), cumulatively contributing to the disease burden (DALY = disability adjusted life years = YLL + YLD). These estimates are used by health agencies to allocate finite resources on a priority basis (those diseases causing the greatest losses having more resources allocated). Animal industries also calculate the burden of subclinical production losses due to depressed growth and fertility, as well as the cost of control programmes. It is therefore advantageous on moral, ethical and economic grounds to try and control parasitic infections, especially those resulting in disease.

Three main strategies are utilized to control infectious diseases:

- drugs (to cure/curb/prevent infection);
- vaccines (to protect against infection/disease); and
- environmental management (to prevent transmission).

DRUGS

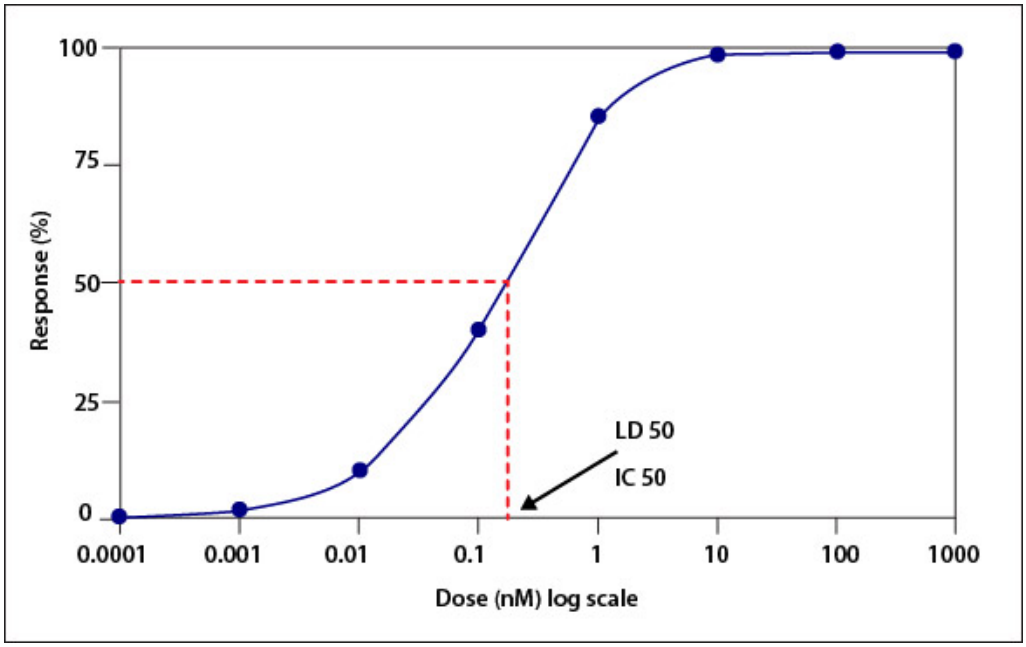
Throughout history, various substances have been endowed with medicinal qualities and folklore herbal remedies have long been used by humans (and even by some animal populations). Many drugs come from plants, particularly those species that have developed chemical defenses against pests, pathogens and disease. Scientists are continuing to identify the active ingredients in herbal remedies and they are constantly attempting to create synthetic analogues to overcome problems in supply and demand. Drugs may kill parasites ('-cidal' activity) or inhibit their growth or reproduction ('-static' activity). However, because parasites are eukaryotic organisms just like their hosts, the drugs may also act on the hosts. Anti-parasitic drugs must therefore exhibit a selective toxicity for the parasite many times greater than that for the host (selectivity index ≥ 30). Drugs may be used therapeutically to treat infections (chemotherapy), or prophylactically to prevent infection (chemoprophylaxis).

A huge range of prescription and nonprescription drugs are produced by multinational companies under a staggering number of names (one international non-proprietary name, but with several regional non-proprietary names and many proprietary brand names). Drugs come in a vast array of topical preparations (liniments, lotions, ointments, dips, shampoos, washes, pour-ons, spot-ons, collars, creams, sprays, powders, aerosols), oral formulations (tablets, pills, capsules, bolus, liquids, emulsions) or parenteral formulations (liquids in ampoules/vials, or solid implants, for subcutaneous, intramuscular, intravenous or intraperitoneal administration). Pharmacological modes of action may involve selective activity on parasite:

- DNA synthesis (alkylation, purine, cofactor);
- protein synthesis (inhibition, translation);
- energy metabolism (electron transport, reduction);
- neurotransmission (blockers, inhibition);
- membrane function (vacuoles, permeability);
- microtubule function (paralysis);
- haem(oglobin) interaction (disruption); or
- growth regulation (insect hormones).

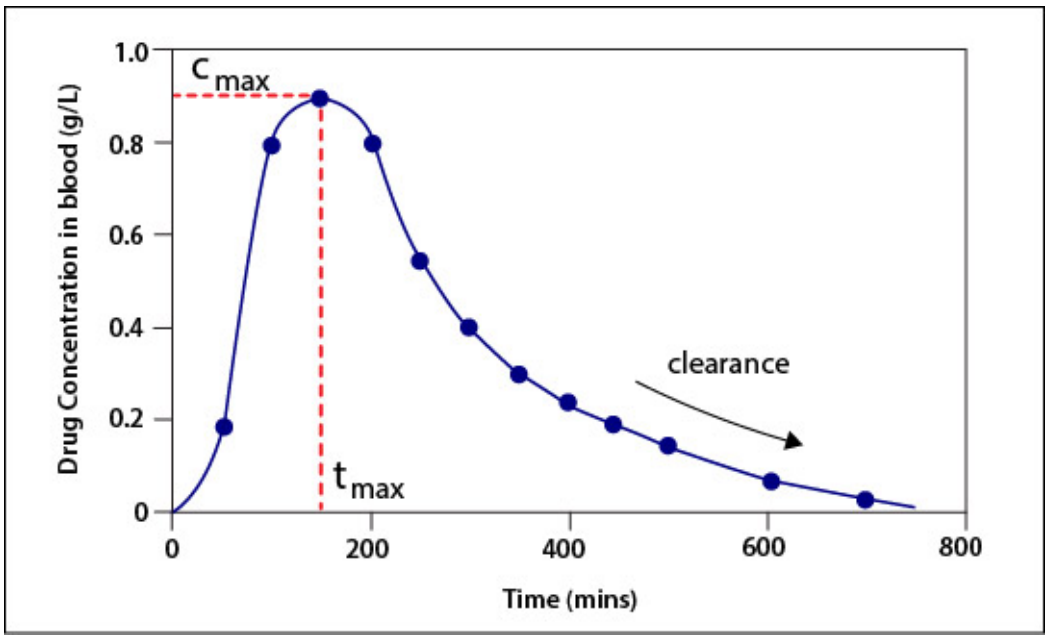
Pharmacodynamics (PD)

PD is the study of the biochemical and physiological effects of drugs on the body (or on infective microorganisms within the body) and the mechanisms of drug action and the relationship between drug concentration and effect. The majority of drugs either mimic or inhibit normal physiological/biochemical processes or inhibit pathological processes. Drugs may act as stimulants, depressants, toxins or substitutes in their chemical interactions with enzymes, structural proteins, carrier proteins, ion channels, hormones, neuromodulators or neurotransmitters. Many drugs act as ligands which bind to receptors influencing cellular processes, either resulting in enhanced action (agonist), blocked action (antagonist), or even opposite action (inverse agonist). For drugs to work, they must reach specific target concentrations. Many factors affect drug concentrations; such as patient size, age, genetic disposition, physiology, metabolism, etc. There may also be undesirable side-effects including: cell mutation (carcinogenic activity); metabolic disturbances, physiological damage and abnormalities. Plots of drug quantity (dose) against efficacy frequently yield sigmoidal (S-shaped) curves, conveniently modelled as logistic functions. The middle portion of the graph is close to linear and allows the accurate calculation of the LD_{50} (50% of lethal dose) or IC_{50} (50% of total inhibitory concentration).



Pharmacokinetics (PK)

PK is a branch of pharmacology dedicated to the determination of the fate of substances administered externally to a living organism (applies mainly to drugs, but in principle concerns other substances such as nutrients, metabolites, hormones, toxins, etc.). PK considers four main areas: the extent and rate of absorption, distribution, metabolism and excretion (ADME scheme). Pharmacokinetic analyses are performed by noncompartmental or compartmental methods. Noncompartmental methods estimate the exposure to a drug by estimating the area under the curve (AUC) of a concentration-time graph while compartmental methods use kinetic models to describe and predict the concentration-time curve. Such curves can often be modelled by surge functions (power function multiplied by exponential decay function) which yield maximum concentration (C_{max}), time of maximum concentration (t_{max}), clearance rate, clearance time, drug half-life as well as total exposure to drug (AUC); most parameters being compulsory prerequisites for drug registration.



Anti-parasitic drugs

Ideally, all drugs should have registered “terms of use”, including chemical composition, generic and trade names, intended application (spectrum of efficacy), target species (pathogen and host), dosages, course and route of administration, pharmacodynamics, mode of action (depressant, stimulant, toxin, substitute), pharmacokinetics (absorption, distribution, metabolism, excretion), toxicity, contra-indications, side effects, storage and disposal information (usually detailed on product inserts). These days, there are many web resources providing a structured approach to pharmacology (e.g. pharmacopoeia). Parasites belong to several disparate assemblages, so no single formulation exhibits broad-spectrum activity against all parasites. Indeed, anti-protozoal drugs generally do not work against helminths or arthropods, anthelmintics often do not work against protozoa or some arthropods, and acaricides and insecticides do not work against protozoa or most helminths.

Drugs used to treat parasitic protozoan infections

Drug class (generic exemplars)	Spectrum of efficacy	Mode of action
sulfonamides (sulfachloropyrazine, sulfadiazine, sulfadimethoxine, sulfadimidine, sulfadoxine, sulfaguanidine, sulfaisoxazole, sulfalene, sulfamerazine, sulfamethazine, sulfamethoxazole, sulfametoxypyridazine, sulfanilamide, sulfanitran, sulfathiazole, sulfaquinoxaline); sulfones (dapsone)	coccidia, haemosporidia	enzyme inhibition
diaminopyrimidines (diaveridine, epiroprim, ormetoprim, pirithrexim, pyrimethamine, trimethoprim)	coccidia, haemosporidia	enzyme inhibition
hydroxynaphthoquinones (atovaquone, buparvaquone, menoctone, parvaquone)	haematozoa	enzyme inhibition
aminobenzoic methyl esters (ethopabate)	coccidia	enzyme inhibition
quinazolinones (febrifugine, halofuginone)	coccidia, theileriids	enzyme inhibition
asymmertic triazines (clazuril, diclazuril)	coccidia	enzyme inhibition
symmetric triazines (toltrazuril)	coccidia	enzyme inhibition
nitrofurilidene derivative (nifurtimox)	trypanosomes	enzyme inhibition
biguanide derivatives (chlorproguanil, proguanil)	haemosporidia	enzyme inhibition
substitued amino acid (eflornithine, ornidyl)	trypanosomes	enzyme inhibition
azonaphthalene dyes (trypan blue)	babesiids	enzyme inhibition
aminoquinaldines (antrycide, quinapyramine, triguin, trypacide)	trypanosomes	protein inhibition
aminoglycoside antibiotics (paromomycin)	amoebae, leishmanias, diplomonads	protein inhibition
tetracyclines (doxycycline, chlortetracycline, minocycline, oxytetracycline, tetracycline)	haematozoa, diplomonads, ciliates	protein inhibition
cyclic undecapeptide (cyclosporin A)	kinetoplastids, coccidia	protein inhibition
alkaloids (emetine, dehydroemetine)	amoebae, leishmanias	protein inhibition
4-hydroxyquinolones (amquinate, buquinolate, decoquinate, methylbenzoquate)	coccidia	energy inhibition
arsenicals (arsanilic acid, carbasone, glycobiarsol, melarsoprol, roxarsone, tryparsamide)	kinetoplastids, trichomonads, coccidia	energy inhibition
polyether ionophorous antibiotics (laslocid, maduramicin, monensin, narasin, salinomycin, semduramicin)	coccidia	energy inhibition
guanidine derivatives (cycostat, robenidine, robenz, robenzidene)	coccidia	energy inhibition
pyridinoles (clopidol, clopindol, coyden, meticlorpindol)	coccidia	energy inhibition
naphthoquinones (atovaquone)	haemosporidia	energy inhibition
thiamine analogues (amprol, amprolium, amprovine, beclotiamine, corid)	coccidia	anti-metabolite
hydroxyquinoline derivatives (iodoquinol)	amoebae, ciliates	anti-metabolite
nitrobenzamides (aklomide, dinitolamide, nitromide, zoalene)	coccidia	anti-metabolite
nitrofurans (furaltadone, furazolidone, nifurtimox, nitrofurazone)	coccidia	anti-metabolite
purine analogues (aprinocid, glycarbylamide)	coccidia	anti-metabolite
naphthyridines (pyronaridine)	haemosporidia	anti-metabolite
bis-nitrophenols (nitrophenide)	coccidia	anti-metabolite
phenyl ureas (fluorophenylurea, nitrophenylurea)	coccidia	anti-metabolite
sulphated naphthylamines (antrypol, germanin, moranyl, naganol, naganin, naphuride, suramin)	trypanosomes	anti-metabolite
alkyl phospholipid compounds (miltefosine)	leishmanias, amoebae	lipid interference
antimonials: trivalent (antimony tartrate); pentavalent (meglumine antimoniate, sodium stibogluconate, stibophen)	kinetoplastids	DNA interference
diamidines (amicarbalide, carbesia, imidocarb, imixol, imizol, imizocarb)	piroplasms, trypanosomes	DNA interference
aromatic diamidines (azidin, berenil, diminazene, ganasag, isometamidium, pentamidine, phenamidine, samorin, trypamidium, trypan, veriben)	piroplasms, trypanosomes	DNA interference
nitroimidazoles (benznidazole, carnidizole, dimetronidazole, furazolidone, metronidazole, nimorazole, nitrofuratoin, ornidazole, radanil, rochagan, ronidazole, tinidazole)	flagellates, amoebae, ciliates	DNA interference
phenanthride derivatives (babidium, ethidium, dromilac, homidium, novidium, pyrithidium)	trypanosomes	DNA interference
dichloroacetamide derivatives (diloxanide, entamide, furamide)	luminal amoebae	DNA interference
urea derivatives (nicarbazin, quinuronium sulfate)	babesiids, coccidia	DNA interference

pyrazolopyrimidines (allopurinol, zyloric)	kinetoplastids	DNA interference
adenosine analogues (arprinocid, benzyl purine)	coccidia	DNA interference
pyrimidone analog (flucytosine)	amoebic keratitis	DNA interference
uridine analogs (tiazuril, azauracils)	coccidia	DNA interference
fluoromethanols (benflumetol, lumefantrine)	haemosporidia	DNA interference
peroxides (artemisinin (qinghaosu), artemether, arteether, artesunate, artelinic acid, dihydroartemisinin)	haemosporidia, coccidia	heme interference
aryl amino alcohols (halofantrine, mefloquine, quinidine, quinine)	haemosporidia	heme interference
4-aminoquinolines (amodiaquine, chloroquine)	haematozoa, amoebae	heme interference
8-aminoquinolines (pamaquine, primaquine)	haematozoa	heme interference
azacrine (pyronaridine)	haemosporidia	heme interference
iron chelating agents (desferrioxamine)	haemosporidia	heme interference
benzimidazole-methylcarbamates (albendazole, mebendazole)	diplomonads, microspora	microtubules
probenzimidazoles (febantel)	diplomonads	microtubules
polyene macrolide (amphotericin, azithromycin, clarithromycin, erythromycin, spiramycin) and lincosamide (clindamycin) antibiotics	amoebae, coccidia, flagellates, babesiids	membranes
aminoacridine (acriflavine, mepacrine, quinacrine)	haematozoa, diplomonads	membranes
azole antifungals (itraconazole, ketoconazole, miconazole)	amoebae, leishmanias	growth inhibition

Drugs used to treat parasitic helminth infections (anthelmintics)

Drug class (generic exemplars)	Spectrum of efficacy	Mode of action
aminoacetonitriles (monepantel)	nematodes	neuro-interference
aminophenylamidine (amidantel)	nematodes, cestodes	neuro-interference
symmetrical diamidine derivative of amidantel (tribendimidine)	nematodes, cestodes, trematodes	neuro-interference
organophosphates (bromophenophos, coumaphos, crufomate, dichlorvos, diuredosan, haloxon, fospirate, metrifonate, naphthalophos, pyraclofos, trichlorphon)	nematodes, cestodes, trematodes	neuro-interference
diethylenediamines (diethylcarbamazine, piperazine)	nematodes	neuro-interference
depsipeptides (emodepside)	nematodes	neuro-interference
tetrahydropyrimidines (morantel, oxantel, pyrantel)	nematodes, cestodes	neuro-interference
imidazothiazoles (butamisole, levamisole, tetramisole)	nematodes, cestodes	neuro-interference
ethanolamines (bephenium, methyridine, thenium)	nematodes	neuro-interference
alkaloids (nicotine), largely discontinued	nematodes	neuro-interference
macrocyclic lactones: avermectins (abamectin, doramectin, eprinomectin, ivermectin, selamectin), milbemycins (milbemycin, moxidectin)	nematodes	muscle interference
spiroindoles (derquantel)	nematodes	muscle interference
isoquinolines (praziquantel)	cestodes, trematodes	muscle interference
chenopodium oil	nematodes	paralytic
cyanoacetic acid hydrazides (cyacetacide)	nematodes	immobilization
phenothiazine, now discontinued	nematodes	microtubules
benzimidazole-thiazolyls (cambendazole, thiabendazole)	nematodes, trematodes	microtubules
benzimidazole-methylcarbamates (albendazole, cyclobendazole, fenbendazole, flubendazole, luxabendazole, mebendazole, oxfendazole, oxibendazole, parbendazole, ricobendazole)	nematodes, cestodes, trematodes	microtubules
halogenated benzimidazole-thiole (triclabendazole)	trematodes	microtubules
probenzimidazoles (febantel, netobimin, thiophanate)	nematodes, cestodes	microtubules
arsenicals (acetarsone, arsanilic acid, melarsamine, thiacetarsamide)	cestodes, nematodes	energy inhibition
salicylanilides (bromosalans, bromoxanide, brotianide, clioxanide, closantel, niclosamide, niclofolan, oxyclozanide, rafoxanide, resorantel)	cestodes, trematodes	energy inhibition
halogenated phenols: monophenols (disophenol, nitroxynil); bisphenols (bithionol, dichlorophene, hexachlorophene, meniclopholan)	cestodes, trematodes, nematodes	energy inhibition
substituted diphenylethers/isothiocyanates (bitoscanate, nitroscanate)	cestodes, nematodes	energy inhibition
substituted dihydroxybenzene (hexylresorcinol)	trematodes	energy inhibition
cyanine dyes (dithiazanine iodide, pyrvinium)	nematodes	energy inhibition
alkaloids (emetine)	trematodes	protein inhibition
glutarimide antibiotics (axenomycin)	cestodes	protein inhibition
glycopeptide antibiotics (streptothricin)	cestodes	protein inhibition
phenoxyalkane derivatives (coriban, diamfenetide)	trematodes	protein inhibition
cyclic undecapeptide (cyclosporin A)	trematodes, cestodes	protein inhibition
benzene sulphonamides (clorsulon, curatrem)	trematodes	enzyme inhibition
sulphated naphthylamines (suramin), mostly discontinued	nematodes	anti-metabolite
antimonies: trivalent (antimony tartrate); terahydroquinoline (oxamniquine)	trematodes	anti-metabolite
thiazolidinedione derivatives (nitrodan)	nematodes	anti-metabolite
nitrothiazoles (niridazole)	trematodes	growth inhibition
hexyloxynaphthamidines (bunamidine)	cestodes	tegument damage
hydropyrazinobenzazepine (epsiprantel)	cestodes	tegument damage
aminoglycoside antibiotics (paromomycin)	cestodes	tegument damage
tin compounds (tinostat), largely discontinued	nematodes, cestodes	cuticle damage
halogenated hydrocarbons (butyl chloride, butynorate, carbon tetrachloride, hexachloroethane, hexachloroparaxylene, tetrachloroethylene, toluene)	cestodes, nematodes, trematodes	purgative
alkaloids (arecoline)	cestodes	purgative
lead arsenate, largely discontinued	nematodes, cestodes	toxin, purgative
mineral salts (copper sulphate), largely discontinued	nematodes	toxin

Drugs used to treat parasitic arthropod infestations (insecticides, acaricides)

Drug class (generic exemplars)	Spectrum of efficacy	Mode of action
organochlorides (bromocyclen, bromopropylate, dichloro-diphenyl-trichloroethane (DDT), lindane, methoxychlor, toxaphene, cyclodiens (chlordane, dieldrin, endosulfan, heptachlor))	flies, lice, mites	neurotoxic
benzoic esters (benzyl benzoate)	mites, lice	neurotoxic
organophosphates (bendiocarb, dioxathion, fenchlorphos, haloxon, maldison, methomyl, metrifonate, naphthalofos, promacyl, propoxur), organophosphonates (chlorfenvinphos, dichlorvos, dicrotophos, heptenophos, naled, tetrachlorvinphos, trichlorfon), monothiophosphates (azamethiphos, chlorpyrifos, coumaphos, cythioate, diazinon, famphur, fenitrothion, fenthion, iodofenphos, pirimiphos, phoxim, propetamphos, temephos), dithiophosphates (dimethoate, ethion, malathion, phosmet)	flies, fleas, lice, ticks, mites	neuro-interference
carbamates (bendiocarb, carbaryl, methomyl, promacyl, propoxur)	flies, fleas, lice, ticks, mites	neuro-interference
chloronicotinyles (imidacloprid, nitenpyram)	fleas	neuro-interference
spinosyns (spinosad)	flies, fleas, lice	neuro-interference
arylpyrazoles (fipronil, pyriprole)	fleas, ticks, mites	neuro-interference
pyrethrins (cinerin, jasmolin, pyrethrin), type I pyrethroids (allethrin, bioallethrin, permethrin, phenothrin, resmethrin, tetramethrin), type II pyrethroids (alphamethrin, cypermethrin, cyfluthrin, cyhalothrin, deltamethrin, fenvalerate, flucythrinate, flumethrin, fluvalinate), non-ester pyrethroids (etofenprox)	flies, fleas, lice, ticks	neuro-interference
isoxazoline (afoxolaner)	fleas, ticks	neuro-interference
isoxazoline-substituted benzamide derivatives (fluralaner)	fleas, ticks	neuro-interference
alkaloids (nicotine), largely discontinued	ticks, mites, lice	neuro-interference
neonicotinoid (dinotefuran)	fleas, ticks	neuro-interference
semicarbazone (metaflumizone)	fleas, ticks	neuro-interference
oxadiazine (indoxacarb)	fleas	neuro-interference
macrocyclic lactones: avermectins (abamectin, doramectin, eprinomectin, ivermectin, selamectin); milbemycins (milbemycin, moxidectin)	flies, fleas, lice, ticks, mites	muscle interference
salicylanilides and substituted phenols (closantel)	flies (nasal bots)	energy depletion
amidines (amitraz, cymiazole)	mites, ticks, lice	anti-metabolite
natural product (deguelin, rotenone, tephrosine, toxicarol)	lice, flies, mites, ticks	anti-metabolite
anilides (crotamiton)	mites	unknown (antipruritic)
benzoylphenylureas (diflubenzuron, fluazuron, lufenuron, triflumuron)	fleas, lice, ticks	chitin inhibition
triazines (cyromazine, dicyclanil)	flies	growth inhibition
juvenile hormone mimetics (fenoxycarb, hydroprene, methoprene, pyriproxyfen)	flies, fleas	moult inhibition
sulphur (largely discontinued)	mites	toxic

The efficacies of many pharmacological interventions have been seriously compromised by the emergence of drug resistance in a wide range of parasites. Resistance is a consequence of evolution in response to environmental pressures. Individual parasites vary in their susceptibility to drugs and some with greater fitness survive drug treatment. Such traits are inherited by subsequent generations and can rapidly spread through parasite populations. Resistance problems are exacerbated when parasites are exposed to sub-lethal drug concentrations due to under-dosing and/or poor patient compliance (incomplete course of treatment). Widespread resistance has developed in parasites to many antimalarials, anticoccidials, anthelmintics and insecticides. Studies conducted on the possible mechanisms involved in the development of resistance have implicated a range of genetic mutations affecting drug accumulation (reduced influx, increased efflux, compartmentalization), drug activity (inactivation, modification, sequestration), drug metabolism (up/down regulation of antagonists/agonists) or target alteration (changes to binding sites). Drug residues may also accumulate in the food chain so most livestock industries mandate with-holding periods whereby drug application prior to slaughter is prohibited. Some drugs also persist in the environment and may exert deleterious effects on other organisms. The development of new drugs has assumed greater importance as drug resistance (especially multi-drug resistance) has severely challenged clinical care.

Successful chemotherapeutic treatment may cure the patient of current infection, but it does not impart any protection against re-infection. Patients go back to their homes and their old habits and often quickly become re-infected. To stop this from happening, patients require regular chemoprophylactic treatment, or vaccination, or re-education about parasite transmission.

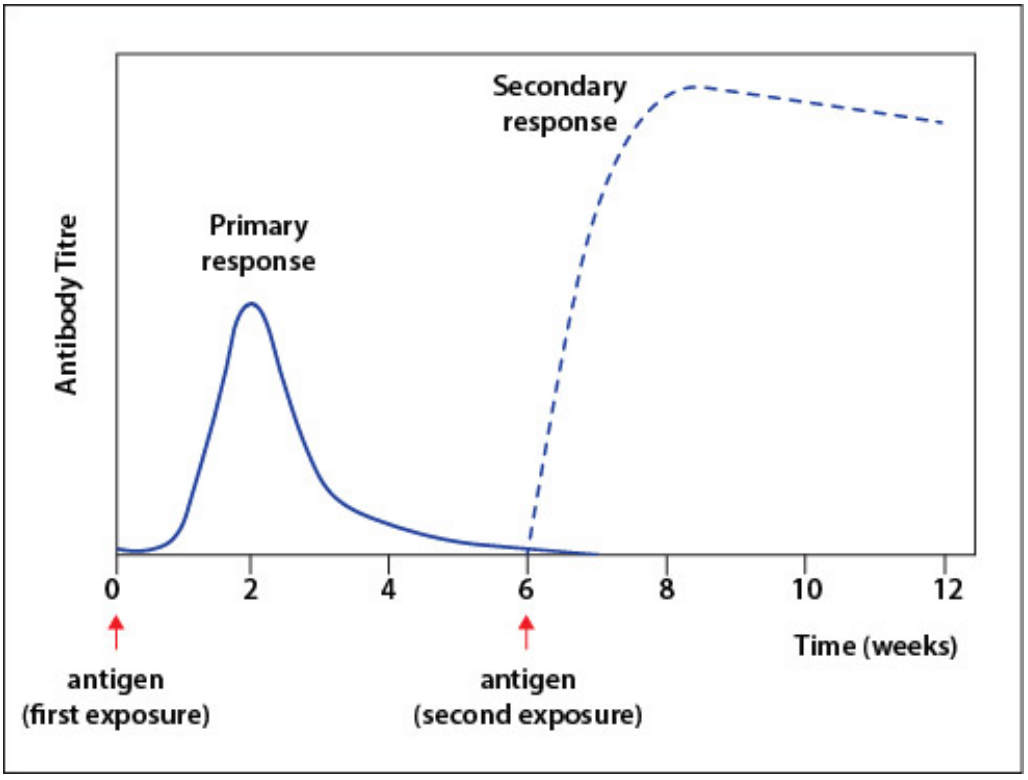
VACCINES

How do hosts survive the deprivations of the constant microbial onslaught incurred simply by living in a contaminated world? They can become more impervious to infection (resistant) or more able to tolerate or ameliorate disease (better defence or repair processes). To do so, hosts have evolved an array of immune responses to combat invading pathogens and provide protection against further infection.

Immune defences

Nonspecific defences such as the skin and inflammation provide general barriers to infection, but other immune responses are more specific, identifying and destroying particular invaders. Many consider there to be three lines of immunological defence to infection:

- The first line of defence involves nonspecific barriers to infections: both physical barriers (such as the skin and mucous membranes) and chemical barriers (such as mucus, lysozyme and gastric juices).
- The second line of defence involves nonspecific innate immunity, whereby inflammatory responses deliver cells (phagocytes and natural killer (NK) cells) and antimicrobial proteins (complement (C'), interferon (IFN)) to the site of infection to combat invading organisms. The four cardinal signs of inflammation involve rubor (redness), calor (heat), tumor (swelling), and dolor (pain) due to the increased blood flow at the site of infection.
- The third line of defence involves specific adaptive (or acquired) immunity, whereby cytotoxic cells and antibodies are produced to specifically attack the invading pathogens. These specific responses involve effector and memory cells, the latter facilitating more efficient responses when the host is exposed to secondary challenge infections. Vaccination aims to prime the adaptive immune system to antigens of a particular microbe so that a first infection induces a secondary response.

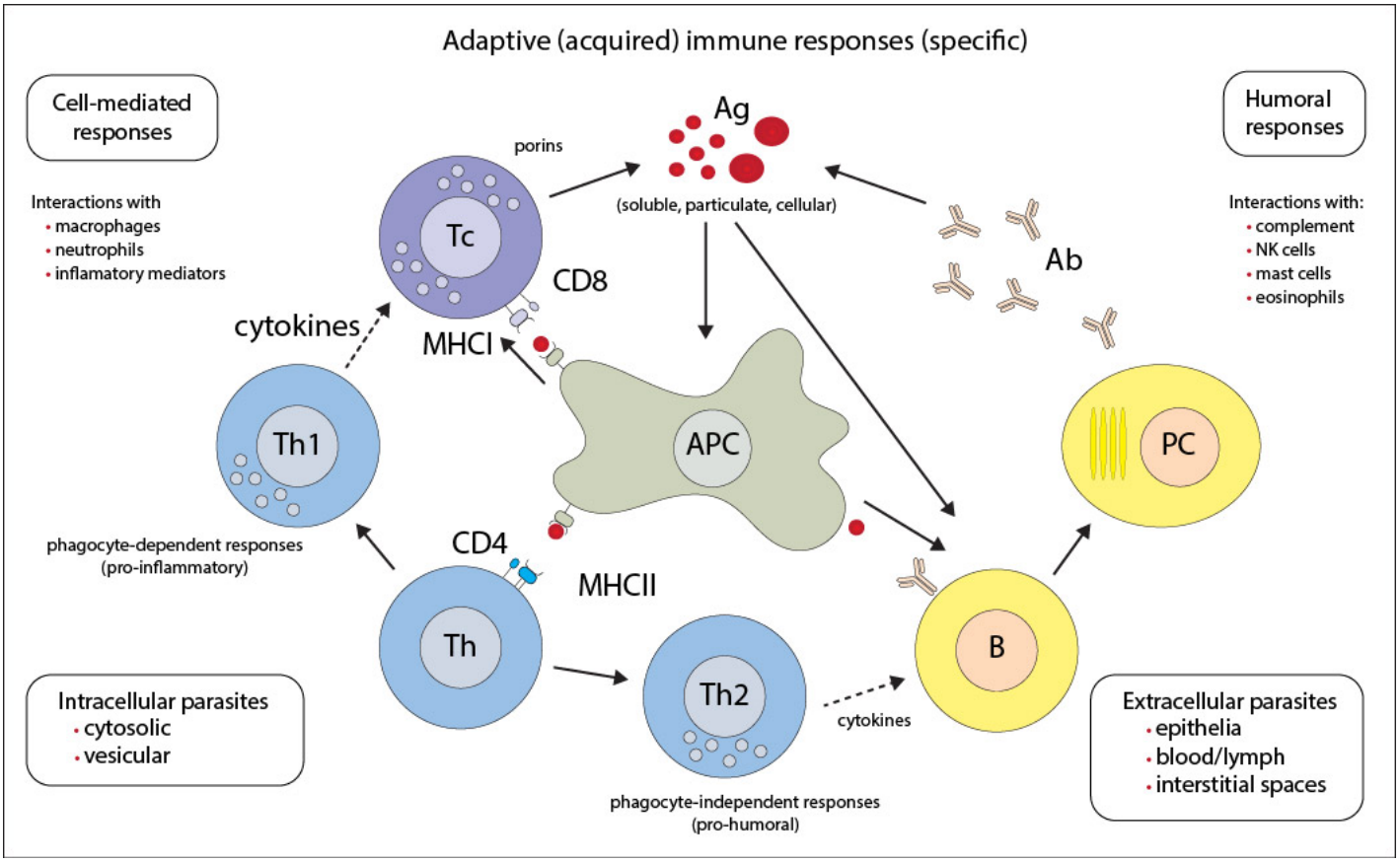


Adaptive (acquired) immunity

Adaptive immune responses are highly specific and are reliant on lymphocytes. These cells circulate throughout the blood and lymph and are found in high numbers in lymphatic tissues. They develop from pluripotent stem cells in the bone marrow; B cells mature in marrow and T cells mature in the thymus. B and T cells recognize antigens via specific surface antigen receptors; B cell membrane antibodies and T cell receptors. Self tolerance develops as cells bearing receptors for native molecules are destroyed or rendered nonresponsive. Major histocompatibility complex (MHC) molecules are crucial to antigen presentation (via antigen-presenting cells (APC)). Class I MHC molecules located on all nucleated cells present antigens to cytotoxic T cells while class II

MHC on macrophages and B cells present antigens to helper T cells. When an antigen binds to a particular lymphocyte, it is activated to produce numerous identical copies (clonal selection). The primary immune response (first exposure to an antigen) results in clones of short-lived infection-fighting effector cells as well as clones of long-lived memory cells. Subsequent exposure to the same antigen activates the memory cells and the resultant secondary immune responses are faster, stronger and often protective (providing the basis for vaccination).

Specific acquired immunity involves both cell-mediated (T-cell) and humoral (B-cell) responses. Cell-mediated responses provide excellent defence against intracellular pathogens because infected cells are identified and destroyed, while humoral responses are effective by tagging extracellular pathogens for destruction. Helper T cells (T_h) interact with antigen-class II MHC complexes on macrophages through T cell receptors and the cell surface protein CD4. Contact stimulates T_h cells to grow and divide as does the cytokine interleukin-1 (IL-1) secreted by macrophages. T_h cells secrete IL-2 which activates other cells in the immune system; including cytotoxic T cells (T_c) (stimulated to become active killer cells), B cells (stimulated to become antibody-producing plasma cells (PC)) as well as additional T_h cells (stimulated to divide more rapidly and increase cytokine production). T_h cells stimulated to proliferate first become T_h0 cells that secrete IL-2, IL-4 and interferon-gamma (IFN-γ). They then differentiate into T_h1 or T_h2 cells depending on the cytokine environment. IFN-γ drives T_h1 cell production and inhibits T_h2 cells, while IL-10 and IL-4 drive T_h2 cell production and inhibit T_h1 cells. T_h1 cells produce IFN- γ, IL-2 and tumour necrosis factor (TNF)-β, which activate macrophages and are responsible for cell-mediated immune and phagocyte-dependent protective responses. T_h2 cells produce IL-4, IL-5, IL-10 and IL-13, which are responsible for strong antibody production, eosinophil activation and inhibition of several macrophage functions, thus providing phagocyte-independent protective responses. Antigens from intracellular pathogens are also gathered in nucleated cells of the body and presented on the surface by class I MHC proteins. They are recognized by T_c cell receptors and the cell surface protein CD8. T_c cells are stimulated by contact and by IL-2 to release the protein perforin which punctures the target cell, allowing water and ions to rush in causing swelling and lysis. Humoral responses are effective against extracellular pathogens. B cells have antibody receptors in their plasma membranes specific for particular antigens. Successful binding stimulates B cell proliferation producing clones of plasma cells and memory cells. Plasma cells secrete antibodies in increasing amounts peaking 10-17 days after activation. Antibodies flow through the body's fluids and tag foreign cells and molecules for destruction via neutralization, agglutination, precipitation and complement fixation.



Immunity to parasites

The efficacies of the different types of immune responses against parasites depend largely on where the parasites are found in the hosts, and thus their accessibility to different effector systems.

- Intracellular parasites located in the host cell cytoplasm (such as coccidia, haemosporidia, piroplasms, microsporidia) or in vesicles (such as leishmanias and toxoplasms) often elicit strong protective responses afforded by cell-mediated mechanisms involving T_c and T_h cells. T_h1 cell responses are effective against intracellular bacteria and protozoa. These responses are triggered by IL-12 and IL-2, their effector cytokine is IFN-γ, and their main effector cells are macrophages as well as CD8 T cells, IgG B cells and IFN-γ CD4 T cells.

- Extracellular parasites located within interstitial spaces, blood or lymph (such as filarial worms, schistosomes and trypanosomes) or on epithelial surfaces (such as gastro-intestinal nematodes, flukes, flagellates, amoebae or ciliates) generally elicit weaker protective responses afforded by humoral immune responses involving antibody opsonization, then macrophages, natural killer cells and eosinophils. In particular, T_h2 cell responses act against extracellular helminths. The responses are triggered by IL-4, their effector cytokines are IL-4, IL-5, IL-9, IL-10 and IL-13, and their main effector cells are eosinophils, basophils and mast cells as well as B cells and IL-4/IL-5 CD4 T cells. IL-4 stimulates B-cells to produce IgE antibodies, which in turn stimulate mast cells to release histamine, serotonin, and leukotriene to cause broncho-constriction, intestinal peristalsis, gastric fluid acidification to expel helminths. IL-5 from CD4 T cells also activates eosinophils to attack helminths.

Hypersensitivity

A critical aspect in immunity is the proper regulation of host responses: hypo-responsiveness is insufficient to control the infection, while hyper-responsiveness may control the infection but go on to cause immunopathology. Excessive or exaggerated immune responses have been found to cause four types of hypersensitivity:

- Type I (immediate or anaphylactic) hypersensitivity occurs within 15-30 minutes of exposure to antigens (often allergens) and may involve the skin (urticaria, eczema), eyes (conjunctivitis), nasopharynx (rhinorrhoea, rhinitis), bronchopulmonary tissues (asthma) or gastrointestinal tract (gastroenteritis). It is mediated by IgE and the primary cellular components are mast cells and basophils. Reactions are amplified by neutrophils, eosinophils and platelets. Examples include weal and flare reactions to insect venoms and pollens, urticaria to some helminths (roundworms), and there appears to be a genetic disposition to particular atopic diseases.

- Type II (cytotoxic) hypersensitivity occurs within minutes to hours of exposure to endogenous antigens (sometimes exogenous haptens) and may affect a variety of organs and tissues (with lysis and necrosis). It is mediated by antibodies (IgG or IgM) and complement; and phagocytes and NK cells may be involved. Examples include reactions sometimes associated with haemolytic anaemia, granulocytopenia and thrombocytopenia.

- Type III (immune complex) hypersensitivity occurs within 3-8 hours and may be general (e.g. serum sickness) or involve individual organs including skin (systemic lupus erythematosus, Arthus reaction), kidneys (lupus nephritis), lungs (aspergillosis), blood vessels (polyarteritis), joints (rheumatoid arthritis) or other organs. It is mediated by soluble immune complexes comprising antibodies (mostly IgG) and antigens (exogenous microbial or endogenous non-organ-specific autoimmunity antigens) and sometimes complement. The damage is caused by platelets and neutrophils with erythema, oedema and necrosis. Immune complex disease may be seen in malarial nephritis, trypanosomiasis or schistosomiasis.

- Type IV (cell-mediated or delayed) hypersensitivity occurs within 2-3 days (sometimes up to 3 weeks) and involves the skin (eczema, erythema, induration, fibrosis) as well as a variety of organs and tissues. It has been implicated in many autoimmune and infectious diseases (tuberculosis, leprosy, blastomycosis, histoplasmosis, toxoplasmosis, leishmaniasis, filarial elephantiasis, swimmer's itch, etc.), granulomas (due to infections and foreign antigens) and contact dermatitis (poison ivy, chemicals, heavy metals, etc.). It is mediated by T cells, monocytes and/or macrophages. T_c cells cause direct damage whereas T_h1 cells secrete cytokines which activate T_c cells and recruit more monocytes and macrophages.

Specific vaccination

While adaptive/acquired immune responses may provide protection against re-infection, they only do so against the particular parasite species (or strain) that elicited the initial response. This high specificity means that no single vaccine will give broad-spectrum protection because separate vaccines will have to be developed against each individual parasite species/strain. The degree of immunity may also vary, ranging from sterile immunity (pathogens eliminated) to partial immunity (clinical disease prevented) to concomitant (premunitive) immunity (some pathogens persist but hosts are protected against super-infection). The duration of protection may also vary, with protection lasting for years or waning after months.

Many vaccination strategies have been proposed for infectious diseases, including anti-infection (prevent infection); anti-disease (prevent disease if not infection); and anti-transmission (prevent further dissemination). Most parasites have complex life-cycles involving sequential developmental stages which may be quite different from each other, may infect different tissues, and may elicit different immune responses. This complicates the process of finding parasite immunogens (antigens that also provoke protective responses). Vaccines may be developed from live organisms (drug-truncated infections, attenuated strains), whole killed organisms (fixed, frozen), subcellular fragments (excretory-secretory products, lysates, extracts, fractions), toxoids (inactivated toxins that still induce protective antibodies) or artificially synthesized antigens (recombinant proteins or DNA-encoding regions) used alone, in cocktail mixtures or with adjuvant formulations. Vaccines need to be monitored for reversion to virulence (in the case of live organisms), allergic or hypersensitivity reactions (particularly those involving adjuvants), and contamination (by non-target microbes or genes). Vaccines must also be extensively tested *in vitro* (in tissue culture) and *in vivo* (in laboratory animal models) before they undergo clinical trials (often using double-blind placebo-control protocols). The moral and ethical dilemmas involved in confirming vaccine efficacy by challenging vaccine recipients with clinical infections are numerous, particularly for virulent diseases with compromised treatment options.

Considerable work has been conducted on the development of vaccines against parasites, but with few successes. Because many infections are self-limiting and/or provoke protective responses in naturally-infected hosts, there are ample reasons to think that effective vaccines could be developed against eukaryotic parasites. However, it has proven difficult to unravel the complexities of most host-parasite immunological interactions to identify immunogens stimulating protective responses. Early studies using whole parasites (and a few fractions) elicited good protection, but the logistics involved in large scale parasite production limited their development and commercialization. Despite the promise of modern technology to produce recombinant and/or DNA vaccines, most studies on individual products have failed to provide adequate protection. There is growing evidence that cocktail vaccines are required to simultaneously stimulate different types of immune responses which collectively contribute to protection.

In addition to research designed to stimulate active immunity against parasites by natural infection or vaccination, studies have also been conducted on the acquisition of passive immunity through the transfer of effectors cells/molecules from resistant to susceptible hosts. In particular, studies have centred on the adoptive transfer of maternal antibodies from mothers to offspring by feeding natural or artificial colostrum (first few days breast milk). Colostrum is naturally enriched in antibodies and high titres against particular pathogens may be found in previously-infected mothers. High titres can also be generated in dairy cattle by experimentally inoculating cows before or during pregnancy and then harvesting the hyperimmune bovine colostrum (HIBC) post-partum. The enriched colostrum has demonstrated variable success in the treatment (immunotherapy) of gastro-intestinal infections in neonates (including rotavirus, cryptosporidiosis and giardiasis).

Commercially-available vaccines against parasites

Genus/species	Vaccine composition*	Utility
Protozoan parasites		
Leishmania major	whole mastigotes (live and killed)	two vaccines used for leishmanization in eastern Europe, largely discontinued
Leishmania infantum	recombinant fucose mannose ligand (FML) antigen	Leishmune developed for disease in dogs
Tritrichomonas foetus	killed trophozoites	TrichGuard developed to prevent reproductive failure in cattle
Giardia duodenalis	killed disrupted trophozoites	GiardiaVax developed to prevent giardiasis in dogs and cats
Eimeria spp.	live attenuated, precocious or non-attenuated heterologous strains	many (Advent, Coccivac, Eimeriavax, Embrex, Hipracox, Immucox, Inovocox,Livacox, NobilisCox, Paracaox, Viracox, etc.) developed to prevent coccidiosis in layer and broiler chickens, turkeys
Eimeria spp.	antigens from wall-forming bodies in macrogametocytes	CoxAbic developed to prevent coccidiosis in broiler chickens (via maternal immunization)
Toxoplasma gondii	live attenuated strain (S48)	Toxovax developed to prevent congenital infection in ewes
Neospora caninum	killed tachyzoites	NeoGuard developed to prevent abortion in cattle
Babesia bovis, B. bigemina	live attenuated merozoites	several (Anabasan, Combavac, Embravac, Eritrovac, Hemovac, Redwater, Trivalent, Vacuna) developed to prevent tick fever in cattle
Babesia canis, B. rossi	soluble parasite antigens (SPA)	Nobivac Piro developed to prevent babesiosis in dogs
Theileria parva, T. annulata	live wild-type parasites (infections drug-truncated), and live attenuated parasites	local stocks used to prevent theileriosis in cattle
Helminth parasites		
Dictyocaulus viviparus	irradiated larvae	Dictol and Huskvac developed to prevent parasitic bronchitis in cattle
Haemonchus contortus	proteins from worm intestines	Barbervax developed to prevent gastroenteritis in sheep
Ancylostoma caninum	irradiated larvae (L3)	irL3 vaccine developed to prevent disease in dogs (discontinued as commercial failure)
Arthropod parasites		
Rhipicephalus microplus	tick midgut membrane-bound recombinant protein (Bm86)	TickGuard and Gavac developed to reduce infestations on cattle
Caligus spp.	recombinant proteins (my32, Ls4D8)	Aquatec Sea Lice developed to reduce infestations on farmed fish (salmonids)

Experimental studies on vaccine development against protozoan parasites

Genus/species	Vaccine composition*	Vaccine efficacy
Amoebae		
Entamoeba histolytica	serine-rich protein	protective in gerbils, monkeys
Entamoeba histolytica	n-acetylgalactosamine-inhibitable lectin (GAL / GALNAC)	protective in animals
Entamoeba histolytica	cysteine-rich protein (peroxiredoxin), lipophosphoglycan, lectins	under development
Flagellates		
Histomonas meleagridis	live attenuated parasites	protective in turkeys
Trypanosoma brucei	invariant antigen in flagellar pocket (FP), invariant surface glycoproteins (ISG), membrane-associated sialidase, glycosylphosphatidylinositol (GPI) anchor	protective in mice
Trypanosoma brucei	congopain cysteine protease (CP)	protective in cattle
Trypanosoma evansi	recombinant cytoskeletal proteins (actin, tubulin)	protective in mice
Trypanosoma cruzi	live attenuated parasites	protective in dogs
Trypanosoma cruzi	recombinant proteins (Tc24, TSA-1)	under development
Trypanosoma cruzi	DNA and recombinant proteins (TcG2, TcG4)	protective in mice
Leishmania spp.	whole killed mastigotes (incl. ALM)	protective in humans
Leishmania spp.	recombinant surface-expressed glycoprotein (gp63)	protective in mice, monkeys
Leishmania spp.	hydrophilic acylated surface proteins (HASP)	protective in mice
Leishmania spp.	naked DNA (heterologous prime-boost, HPB)	protective in mice, dogs
Leishmania spp.	cysteine protease antigens	protective in mice, dogs
Leishmania spp.	live attenuated mastigotes (dihydrofolate reductase thymidylate synthase (dhfr-ts) knockout (KO))	protective in mice
Leishmania donovani	promastigote membrane antigens (LAg)	protective in mice
Leishmania donovani	recombinant fucose mannose ligand (FML) antigen	protective in mice, rabbits, dogs
Leishmania donovani	live attenuated mastigotes (centrin null (LdCEN-/-) mutants)	protection in mice
Leishmania major	*Leishmania* activated C kinase (LACK)	protective in mice
Leishmania major, L. braziliensis	*Leishmania* derived recombinant polyprotein (Leish-111f)	protection in mice, humans
Leishmania infantum	live attenuated parasites (ΔHSP70-II deletion mutant)	protective in hamsters
Apicomplexans		
Eimeria spp.	sporozoite fractions	protective in chickens
Eimeria spp.	recombinant merozoite antigens	protective in chickens, cattle
Eimeria spp.	gametocyte antigens	protective in chickens
Eimeria spp.	recombinant proteins (EtMic, GPI, LDH, SOD)	protective in chickens
Cryptosporidium parvum	irradiated oocysts	protective in calves
Cryptosporidium parvum	sporozoite surface antigens (Cp15/17, Cp23/27, Muc4/5)	protective in mice, calves
Cryptosporidium parvum	DNA encoding Cp15/60, Cp23, Cp15+Cp23	protective in mice
Sarcocystis neurona	killed merogonic stages	protective in horses
Toxoplasma gondii	DNA encoding dense granule antigens and SAG1	protective in mice
Toxoplasma gondii	bradyzoite mutant (T263) deficient in sexual reproduction	protective in cats
Neospora caninum	tachyzoites from low virulence (Nowra) strain	protective in cattle
Neospora caninum	recombinant antigens (SRS2, SAG1, DG1, DG2)	protective in rodents
Plasmodium berghei	irradiated sporozoites	protective in mice
Plasmodium falciparum, P. vivax	irradiated sporozoites	protective in humans, but discontinued (logistics)
Plasmodium falciparum, P. vivax	genetically attenuated sporozoites (PfGAP gene deletion)	protective in humans
Plasmodium falciparum	whole blood-stage parasites (low doses)	protective in animals, humans
Plasmodium falciparum	recombinant circumsporozoite protein (RTS,S)	protective in humans
Plasmodium falciparum	recombinant blood-stage antigens: apical membrane antigens (AMA), merozoite surface proteins (MSP), glutamate rich protein (GLURP), ring-infected erythrocyte surface antigens (RESA), serine repeat antigens (SERA),	some protective in mice, monkeys, humans

	erythrocyte-binding antigens (EBA), combinations (GMZ, BSAM)	
Plasmodium falciparum	surface protein antigens (Pfs25, Pvs25, Pfs28, Pvs28), some with transmission-blocking activity in mosquitoes	under development
Plasmodium falciparum	GPI toxin	protective in mice
Plasmodium falciparum	sexual stage specific antigens (Pfs48/45, Pfs230)	under development
Plasmodium falciparum	adhesion ligands, erythrocyte membrane proteins (PfEMP1), some sequestered in placenta (VAR2CSA)	protective in humans
Plasmodium falciparum	polyepitope plasmid DNA vaccine (EP1300)	protective in humans
Plasmodium falciparum	viral vectors encoding thrombospondin-related adhesion protein (TRAP) pre-erythrocytic antigen, circumsporozoite protein (CSP), AMA1, MSP, merozoite surface protein (PEV), combinations (NMRC), multi-stage, multi-antigen (NYVAC)	some protective in animals, humans
Babesia bovis, B. divergens	killed parasites	protective in cattle
Babesia bovis, B. bigemina	culture supernatant (exoantigens)	some protective in cattle
Babesia bovis, B. bigemina	parasite fractions (lipids, rhoptries, rhoptry-associated protein (RAP), GPI-anchored proteins)	protective in animals
Babesia bovis	recombinant proteins (immunodominant antigens)	protective in cattle
Babesia bigemina	recombinant proteins (RAP)	protective in cattle
Babesia divergens	live attenuated parasites (rapid passage in splenectomized calves, passage in gerbils, irradiation, low dose)	protective in cattle, mostly discontinued
Babesia divergens	recombinant protein (Bd37)	protective in animals
Babesia divergens	purified merozoite polypeptides	protective in gerbils
Theileria parva	recombinant sporozoite surface antigen (p67)	protective in cattle
Theileria annulata	attenuated live zoites	protective in cattle
Ciliates		
Ichthyophthirius multifiliis	purified cell surface immobilization antigens (I-ags)	protective in catfish
Ichthyophthirius multifiliis	DNA encoding I-ags and cysteine protease	protective in trout
Philasterides dicentrarchi	whole fixed scuticociliate trophozoites	protective in turbot

Experimental studies on vaccine development against helminth parasites

Genus/species	Vaccine composition*	Vaccine efficacy
Ascarid nematodes		
Ascaridia galli	irradiated larvae	protective in chickens
Toxocara canis	irradiated larvae; excretory-secretory (ES) proteins	protective in mice
Ascaris suum	irradiated eggs; recombinant proteins (As14, As16, As24)	protective in mice, pigs
Baylisascaris schroederi	recombinant proteins (As14 homologue)	protective in mice
Rhabditid nematodes		
Strongyloides spp.	irradiated larvae	protective in rats, sheep, chickens
Trichostrongyloid nematodes		
Nippostrongylus brasiliensis	irradiated larvae	protective in rats
Amidostomum anseris	irradiated larvae	protective in geese
Cooperia punctata	irradiated larvae	protective in cattle
Cooperia oncopora	irradiated larvae	protective in cattle
Dictyocaulus filaria	irradiated larvae	protective in sheep
Dictyocaulus viviparus	irradiated larvae; recombinant protein (paramyosin)	protective in cattle
Heligmosomoides polygyrus	irradiated larvae, ES antigens	protective in mice
Trichostrongylus vitrinus	irradiated larvae	protective in guinea pigs
Trichostrongylus tenuis	irradiated larvae	protective in grouse
Trichostrongylus colubriformis	irradiated larvae; recombinant proteins (MIF, APY, TGF, TGH, cathepsin, astacin metalloprotease, VAL/ASP protein, SSA)	protective in gerbils, guinea pigs, sheep
Haemonchus contortus	irradiated larvae; ES and hidden antigens (contortin, cysteine proteases, H11, P1, galactose-containing glycoprotein (H-gal-GP), thiol sepharose-binding protein (TSBP))	protective in sheep, goats
Ostertagia circumcincta	irradiated larvae	protective in sheep
Ostertagia ostertagi	irradiated larvae; hidden antigens (Oo-gal-GP, ES-thiol containing CP and ASP/VAL proteins, polyprotein allergen (OPA))	protective in cattle
Strongyloid nematodes		
Strongylus vulgaris	irradiated larvae	protective in horses
Oesophagostomum columbianum	irradiated larvae	protective in sheep
Syngamus trachea	irradiated larvae	protective in chickens, pheasant
Stephanurus dentatus	irradiated larvae	protective in pigs
Ancylostomatoid nematodes		
Bunostomum trigonocephalum	irradiated larvae	protective in sheep
Gaigeria pachyscelis	irradiated larvae	protective in sheep
Ancylostoma ceylanicum	irradiated larvae	protective in hamsters
Ancylostoma caninum	irradiated larvae; prominent antigen (Ac16); aspartyl haemoglobinases (Ac-APR-1)	protective in dogs
Necator americanus	larval secreted protein (Na-ASP-2); glutathione S-transferase (Na-GST-1); cysteine haemoglobinase (Ac-CP-2); aspartyl haemoglobinases (Na-APR-1)	protective in hamsters, dogs, humans
Metastrongyloid nematodes		
Metastrongylus apri	irradiated larvae	protective in guinea pigs
Filarioid nematodes		
Dirofilaria immitis	irradiated larvae	protective in dogs
Litomosoides carinii	irradiated larvae	protective in rats
Brugia pahangi	excretory-secretory (ES) larval products	protective in jirds
Brugia malayi	irradiated mosquito-borne larvae (L3); abundant larval transcripts (ALT-1, ALT-2)	protective in jirds
Onchocerca ochengi	attenuated larvae, then 8 recombinant proteins	protective in cattle
Onchocerca volvulus	microfilarial extracts, irradiated L3, recombinant proteins (ES, surface, ALT, RAL2, tropomyosin, CPI-2, FAR1)	protective in mice, jirds, cattle
Enoplid nematodes		
Capillaria obsignata	irradiated larvae	protective in chickens

Trichuris muris	ES products	protective in mice
Trichinella spiralis	irradiated larvae; ES products	protective in mice
Cyclophyllidean cestodes		
Taenia ovis	oncosphere ES material, recombinant antigen (GST-45W)	protective in sheep
Taenia saginata	recombinant oncosphere antigens (TSA9, TSA-18)	protective in cattle
Taenia solium	recombinant oncosphere antigen (TSOL18)	protective in pigs
Echinococcus granulosus	recombinant protoscolex proteins (egM4,egM9, egM123); recombinant oncosphere protein (EG95)	protective in dogs, sheep, cattle
Echinococcus multilocularis	recombinant oncosphere protein (Em95)	protective in mice
Digenean trematodes		
Schistosoma mattheei	irradiated cercariae	protective in mice
Schistosoma bovis	irradiated cercariae; GST	protective in mice, goats
Schistosoma haematobium	recombinant glutathione S-transferase (Sh-GST28); DNA encoding triose phosphate isomerase (TPI)	protective in rats, hamsters, monkeys, pigs, humans
Schistosoma mansoni	paramyosin, synthetic peptide construct with multiple antigen epitopes (MAP) from TPI, fatty acid binding protein (Sm14); GST, recombinant surface proteins (Sm23, Sm29, SmCD59-like, Sm200, SmTOR, SM-p80, Sm-TSP2)	protective in mice, rats, monkeys, humans
Schistosoma japonicum	paramyosin, recombinant protein (Sj23); GST, DNA plasmid comprising fusion of TPI, heat shock protein and IL-12	protective in mice, sheep, pigs, water buffaloes
Fasciola gigantica	fatty acid binding protein (FABP)	protective in cattle
Fasciola hepatica	leucine aminopeptidase (LAP), GST, cathepsin, FABP, hemoprotein	protective in mice, rabbits, sheep, cattle

Experimental studies on vaccine development against arthropod parasites

Genus/species	Vaccine composition*	Vaccine efficacy
Arachids (ticks)		
Rhipicephalus microplus	midgut membrane-bound recombinant protein (BA95)	protective in cattle
Rhipicephalus annulatus	midgut membrane-bound recombinant protein (BA86)	protective in cattle
Rhipicephalus microplus, Haemaphysalis longicornis	recombinant vitellin-degrading cysteine endopeptidase (VTDCE), yolk procathepsin (BYC), GST	protective in cattle
Hyalomma anatolicum	midgut membrane-bound recombinant protein (HAA86)	protective in cattle
Rhipicephalus appendiculatus	salivary cement protein (64TRP)	protective in hamsters, guinea pigs, rabbits
Rhipicephalus appendicularis	cocktail of serpins (serine protease inhibitors, RAS)	protective in cattle
Ixodes ricinus, Rhipicephalus microplus, R. annulatus	ferretin 2 recombinant protein (RmFER2)	protective in animals
Ixodes scapularis	histamine release factor (tHRF)	protective in mice
Ixodes scapularis	recombinant subolesin (SUB) protein [ortholog of insect akirins (AKR)]	protective against ticks, mosquitoes, sand flies in animals
Arachnids (mites)		
Psoroptes ovis, P. cunniculi	purified mite extracts (esp. soluble antigens)	protective in rabbits, sheep, cattle
Psoroptes ovis	recombinant scab mite allergens (Pso o I, Pso o II)	protective in sheep, cattle
Sarcoptes scabiei	recombinant paramyosin, apolipophorin-like protein (Ssag1)	recognised by immune sera, not protective in rabbits
Insects (fleas)		
Ctenocephalides spp.	hidden antigens from flea gut	protective in rabbits, dogs
Insects (flies)		
Haematobia irritans	fly tissue extracts, trypsin-like enzyme	*in vitro* anti-fly activity, protective in cattle
Hypoderma lineatum	fly larval serine proteases (hypodermins A, B, C)	protective in cattle
Lucilia cuprina	fly larval peritrophin extracts (55, 95), and recombinant homologues	*in vitro* larval growth inhibitory activity
Oestrus ovis	fly salivary gland extracts	protective in sheep
Phlebotomus spp.	sand fly salivary proteins (SGE, PpSP30)	protection against *Leishmania* in mice
Anopheles spp.	mosquito saliva	protection against malaria in mice
Culex spp.	recombinant mosquito salivary proteins (MSP)	variable success *in vitro* and in animal models

*cf. *Chaudhury A 2014 Human parasitic vaccines - an overview. J Clin Biomed Sci 4:216*
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Immuno-evasion

Hosts have evolved sophisticated immune defences to help survive parasitic infections, but how do parasites survive the immunological onslaught? Parasites have evolved a spectacular range of mechanisms to avoid host immune responses, thus taking part in the host-parasite evolutionary arms race between parasite aggressiveness (virulence) versus host defence (immunity). Theoretically, the objective would be to find a common middle ground ensuring mutual survival (= enzootic stability), but in reality, there appears to be episodic escalation by one side or the other (disease resulting from the rise of more virulent strains and/or more susceptible hosts). Parasites have adopted three basic strategies to avoid host immune mechanisms: hide, disguise, or suppress. Many parasites hide from the host immune system by developing in cryptic or immunologically inert sites, such as within cells (free in cytoplasm or membrane-bound in vesicles or parasitophorous vacuoles), within the lumen of tubular organs, behind the blood-brain barrier, or by encapsulating themselves within cysts. Other parasites disguise themselves to avoid immune surveillance by masking (coating themselves with host molecules), mimicry (copying host molecules) or changing their surface coats (antigen variation). A range of parasites have also been found to actively down-regulate or negate host immune responses by saturating effector mechanisms (antigen shedding), blocking responses (by inhibition, destruction or developing tolerance), or inducing host suppressor mechanisms (cells or cytokines). The sophistication of the immune evasion mechanisms exhibited by these eukaryotic parasites has frustrated most attempts to identify immunogens and protective responses suitable for vaccination programmes. By contrast, many vaccines have been developed against acellular pathogens (viruses) and prokaryotic organisms (bacteria). Hopefully, sustained research endeavours will one day produce effective vaccines against parasites.

MANAGEMENT

A wide range of preventive strategies have been applied to the control of parasitic diseases. Parasites move between hosts by horizontal (e.g. venereal, faecal-oral, water-borne, food-borne, predator-prey, air-borne, vector-borne) and vertical (transplacental, transmammary) routes of transmission. Infections can therefore be prevented by interrupting transmission cycles by manipulating host and environmental factors using management strategies to change:

- biotic factors (distribution and abundance of hosts, vectors, animal reservoirs);
- abiotic factors (physical and chemical environments affecting organismal survival); and
- sociological factors (cultural norms in hygiene, nutrition, housing, healthcare).

BIOTIC FACTORS

Effective control programmes rely on an intimate knowledge of the organisms involved, the environments in which they live, and their interactions. Differentiating parasites as the aetiological agents of infectious diseases from other causes (viruses, bacteria, fungi) requires considerable expertise by medical and veterinary personnel, with working experience of a range of biological entities: including parasites, hosts, and vectors.

Parasites

Many unicellular and multicellular organisms are parasitic in other animals, so clinicians and associated healthcare workers require comprehensive knowledge of many different life-forms. Recognizing patterns of infection and disease attributable to particular groups of parasites is difficult, because there are inevitably many exceptions to the rule. Generally, parasitic protozoa are associated more often with acute transient diseases as they may multiply rapidly within host tissues, while parasitic helminths and arthropods often cause persistent chronic diseases as they slowly accumulate in or on hosts. Effective management depends on reliable diagnosis, which should take into account:

- what parasite species is/are present? (biodiversity and taxonomy),
- how many and where? (distribution and abundance),
- how are they spread? (transmission), and
- how harmful are they? (pathogenicity).

Diagnosticians need to consider the often perplexing concept of parasite biodiversity, conventionally defined as species richness (how many species are there?). This requires theoretical knowledge of what constitutes a species, and practical knowledge of how to differentiate them. In biology, a species is commonly defined as an interbreeding population of individual organisms that produces fertile offspring. This biological species concept emphasizes reproductive isolation, with the existence of biological factors (pre- and post-zygotic barriers) that impede two members from producing viable fertile hybrids. Regrettably, the genetic integrity of most parasite species is not known. Many parasite life-cycles are unknown, many protistans only reproduce asexually, many platyhelminths are hermaphroditic, a few helminths and arthropods are parthenogenetic, and while most parasites cannot be cultured for experimental cross-breeding studies, some hybridization between ‘species’, strains and/or genotypes has been observed. Hopefully, molecular characterization studies will help us better define parasite species, particularly those implicated in disease outbreaks.

Parasite identity underpins their taxonomic classification, which should be phylogenetically informative and reflect kinship (evolutionary relationships). However, many of the taxonomic characters used to identify parasites (morphology, biology, biochemistry, genetics) are beyond the purview of individual workers, let alone primary producers. The differential diagnosis of diseases caused by parasites requires good cooperation between a variety of personnel (patients/owners, clinicians/nurses, laboratory/scientific staff, care-givers/farm-workers, etc.), whether it be prompted by necessity (disease occurrence requiring medical/veterinary consultation), health concerns (suboptimal growth and development requiring intervention), or risk assessment (surveillance/screening associated with preventive maintenance, research, and/or quarantine). Researchers should endeavour to develop, refine, compare and evaluate different diagnostic tests, both direct detection methods and indirect presumptive methods. Government and commercial concerns should incorporate both conventional and emergent technologies into diagnostic laboratories, ensuring tests are reliable, rapid and cheap. The consequences of testing should also be transparent, with test results influencing decisions to isolate, treat or cull infected individuals. Many parasitic diseases have been made notifiable diseases in various countries with regulations governing translocations, testing, quarantine, treatment or disposal.

The distribution and abundance of parasites is often intimately linked to parasite fecundity, which is a numbers game balancing the number of offspring with their survival. In zoology, the fitness of a species can be fundamentally enhanced by two different strategies: fast reproduction (multiplication, replication) or prolonged development (long-life, stability). This is called *r/K* selection (derived from the logistic growth model of population biology), with *r*-selected species investing in reproduction (quantity) while *K*-selected species invest in prolonged development and long-life (quality). Many parasite species have rapid life-cycles (days-weeks) and produce huge numbers of encysted offspring (ova or cysts) which are broadcast into the external

environment in the hope that some will encounter new hosts. Other parasites infecting gregarious hosts that live in close contact with each other produce fewer offspring or non-encysted stages that are more likely to encounter new hosts. Some parasites have slow maturation times, either as larvae or as developing adults, and remain in individual hosts for long periods. Other parasites are transient and only infect hosts for part of their life-cycles, with other stages living free in soil or water. Knowledge of the kinetics and dynamics of parasite reproduction helps to understand their temporal and spatial distribution, but information is also required as to their survival capabilities inside and outside of hosts.

Epidemiological studies have helped identify seasonal and/or geographic patterns to infections in domestic and wild animals, and there is much speculation about what factors affect parasite survival, longevity, dispersal, viability and infectivity. Experimental studies have tested various physico-chemical factors (esp. temperature, humidity/moisture) on the survival and infectivity of exogenous parasite stages (eggs, cysts, larvae, nymphs, or adults) to gauge the duration and degree of environmental contamination. Pathological and immunological studies on experimentally infected animals have also helped understand the course, duration and severity of infections as moderated by host defences. Field studies have shown many parasites to have aggregated (over-dispersed) distributions whereby most parasites are found only in a few hosts. This begs the question, was this coincident to exposure or due to differences in host susceptibility?

Despite centuries of observations, little is actually known about the host ranges (zoogeography) and host specificities of most parasites. Studies often indicate host preferences rather than true specificities governed by molecular, physiological, biochemical and/or behavioural compatibilities. Host species differ greatly in their innate susceptibility/resistance to particular parasites, often with variation observed between breeds, age cohorts and sometimes sexes. Transmission success between hosts often reflects the chances of parasites encountering hosts in aquatic and/or terrestrial habitats, depending on their relative densities, distributions and susceptibilities. Parasites may have direct life-cycles involving one host species or indirect life-cycles involving multiple host species. Several mathematical models have been developed for population biology, with SIR models developed for microparasites (e.g. protozoa causing acute transient multiplicative infections) and HPW models for macroparasites (e.g., helminths and arthropods resulting in chronic prolonged cumulative infections). These models may help predict transmission patterns, but they cannot presage disease severity as they do not cover variations in parasite pathogenicity.

In microbiology, it has long been known that certain criteria need to be met in order to show cause-and-effect, that is, to determine whether a particular microbe is the cause of a particular disease. These criteria are known as Koch's postulates and they state that the specific microbe must: be present in all cases of the disease; be isolated from diseased patients; cause disease when re-introduced to a healthy susceptible animal model; and then be isolated again from the new host. It is difficult to satisfy all of Koch's postulates for most parasites, as many species cannot be cultured *in vitro* or *in vivo*. In addition, multiple parasite species may occur within individual hosts, but only a few species (or strains!) may be pathogenic and cause enough cumulative damage to cause clinical disease. Parasites vary greatly in their pathogenicity (virulence) due to different invasion, feeding, migration and/or sequestration activities, and hosts vary greatly in their susceptibility to disease due to innate genetic resistance and/or acquired immunity. This has led to what has been termed an evolutionary arms race between parasite virulence and host immunity. Hosts are under pressure to evolve resistance to parasites, while parasites are under pressure to evade host immunity and achieve successful infection. It is not in the best interest of a parasite to kill its host and thus deprive itself of a home, and it is also not in the best interest of the host to expend so much energy killing parasites with potential immunopathological consequences. It appears that the best outcome involves a stable balance between the two competing strategies which leads not to the extinction of one or the other, but to their mutual co-existence (often referred to as enzootic stability).

Knowledge of all these host-parasite interactions is vital for disease control, as it helps guide which interventions may best impact on disease occurrence and spread, without upsetting any equilibria. Detailed information on parasite abundance, distribution, longevity, infectivity and pathogenicity allows decisions to be made with respect to the urgency and timing of treatments and assessing the scope of the problem for local and regional communities. Great reliance is placed on the knowledge base and experience of individual clinicians to make informed decisions for the treatment and control of infections, particularly involving episodic outbreaks. Recently, several computerized mathematical models have been developed to help schedule treatment times and other interventions (mostly for ectoparasites and gastrointestinal nematodes in ruminants), based on multiple parasite bionomic factors influenced by prevailing weather (temperature, moisture, rainfall), microclimate (photoperiod, circadian rhythms), macroclimate (seasons), vegetation (type, structure, density), geographic location (latitude, longitude, elevation), land-use (cropping, pastoral, bush) and animal husbandry (breeding/feeding history, facilities, health management). Hopefully, these aids will become more readily available in the future to assist producers and communities in designing effective intervention programs to control parasitic diseases.

Hosts

Control programmes may not be able to actively manipulate parasite stages, but they can manage host populations, mostly in farm situations (agriculture and aquaculture), zoos and fauna parks, and occasionally in free-ranging wild animals. Parasitic infections are significantly under-diagnosed because clinicians usually only see patients sick enough to have sought medical/veterinary intervention. Asymptomatic, subclinical and mild symptomatic infections may be overlooked completely because the hosts are not sick, or not sick enough to seek help. Clinical disease therefore represents the 'tip of the iceberg', with infections below the 'water-line' contributing to the long-term persistence and on-going spread of parasites. Clinicians working with sick individual patients should always consider the broader community, particularly those placed most at risk (usually by virtue of cohabitation or other forms of close contact). It is also important to determine the role the different hosts play in parasite transmission: whether they are definitive hosts producing infectious stages, intermediate hosts in which parasites develop asexually, or paratenic hosts that transport parasites without further development. The adoption of control strategies by human communities or populations depends largely on the sophistication of the health infrastructure systems in place, while the management of animal populations varies considerably depending on the type of animals involved (production, performance, companion, show, feral or wild animals).

Humans

The growth rates of human populations are closely linked to the level of economic development, with growth rates in the poorest countries being twice that of developed countries. Populations are becoming increasingly urbanized (concentrated in cities) due to the migration of people from rural areas. As of 2010, more than 50% of the global population live in urban settings, but in some areas of Asia and Africa, the majority (>60%) still live in rural environments. Urbanization appears to be a feature of strong economies (higher per capita income), facilitating access to better healthcare, education, sanitation and cleaner water. However, cities are also home to great inequities between the rich and poor, with overpopulation and socioeconomic disparities leading to urban slums with unsafe dwellings lacking utilities. Urbanization may be viewed as a 'mixing-cup' or patchwork of social behaviours, subcultures and communities, sometimes acting as 'pace-makers' for local epidemiology (providing bridges between people and ecosystems and hubs for the spread of diseases). Epidemiological studies have linked infections with particular demographic groups, according to age, gender, affluence or socioeconomic status, profession and leisure pursuits. Two factors in particular predispose for more frequent and more severe infections in human populations, those occurring in regions with warm moist climates and those in poor communities. Indeed, climate and poverty are the most significant 'drivers of disease' in human populations, followed by poor nutrition, untreated drinking water, limited sanitation, and restricted healthcare. Historically, cities were regarded as 'cess-pools of infection' leading to the emergence of many so-called 'crowd' diseases (New World communicable diseases) associated with our concentration into small contaminated environments. In contrast, rural communities continue to harbour Old World zoonotic diseases with significant animal-to-human transmission due to the greater and closer proximity to animal and vector populations. With increasing globalization and further rural and urban development, we are now encountering a new wave of 'emergent' diseases, often linked to travel, animal translocations, bushmeat or wet markets, farming exotic animals, or encroaching on new geographic regions inhabited by wildlife (particularly rats, bats, birds and insects).

In addition to conventional chemotherapeutic treatments and the promise of protective vaccines (topics covered earlier), a range of other options are available to help control parasitic infections and disease. Clinicians may sometimes resort to surgical interventions for certain conditions, where parasites occur in accessible anatomical locations and are large enough to be extracted (e.g. auguring ectoparasites from the skin) or where lesions can be excised (e.g. onchocercal nodulectomy) or drained (e.g. amoebic abscesses). A range of modern techniques have also been explored for other surgical interventions, such as cryotherapy, electro-desiccation and laser photocoagulation. Supportive therapy may also be provided to relieve dehydration, fever, diarrhoea, inflammation, pruritis, hypersensitivity and secondary bacterial infections. Alternative therapies are also available for a range of conditions, such as cooling preparations for dermatitis and various ointments and poultices for open lesions. Many alternative treatments for ectoparasitic infestations may be used to disrupt their respiratory function or structural integrity, including occlusive dressings (natural and synthetic oils and pastes), aromatic compounds, alcohols, stringent antiseptics, alkaloids, eyedrops, desiccant dusts and even raw meat poultices (the latter to entice maggots out of wounds). Much can be done to prevent parasitic diseases in humans by improving sanitation (waste management) and hygiene (personal, food and water), which often involves changing people's perspectives and behaviours.

Animals

Parasitic infections have been reported from a huge range of vertebrate animals, including farmed, companion, zoo, feral and wild species of mammals, birds, reptiles and fish. Disease control interventions that may be applied to these animals typically depend on the quantity and quality of husbandry and care provided. Obviously, more interventions can be imposed on intensively-farmed animals and pets rather than extensively-farmed animals, while interventions impacting on free-ranging wild or feral animals are more limited. In all cases, it has long been known that individual animals vary in their susceptibility to infection and disease, often related to their immunocompetence. Animals most at risk include young and old individuals, females when pregnant or lactating, immunodeficient individuals (congenital or acquired), immunosuppressed individuals (due to chemotherapy or concomitant infections) or those subject to high levels of stress (physiological, nutritional, or behavioural stress due to capture, handling, transport, crowding, breeding, weaning, poor diet, abrupt changes in environment, poor water quality, or treatment for other disorders). Every effort should be made to keep hosts well-fed, healthy and happy in stress-free conditions to bolster their defences against parasites.

Many species of animals are farmed for meat, milk, fibre, eggs and/or power, with increasing demand driven by population growth, higher incomes and urbanization. While agriculture and aquaculture are becoming more sophisticated in developed countries due to increased mechanization and technological advances, many communities in poorer developing countries still rely on subsistence farming often using traditional methods. Intensive farming practices may be economically sensible but they can lead to situations predisposing to disease outbreaks, as hosts become crowded into smaller areas which may become heavily contaminated by parasites. A variety of common-sense procedures can be used to reduce the risks of parasite transmission through good husbandry; including the provision of clean food and water sources, strategic grazing management (staggered, rotational, alternate, mixed grazing), pasture improvement (vegetation, drainage, discing), sensible stocking (cohort separation, avoid over-crowding), waste removal (organic matter, including dung, litter, bedding, carcases), improved hygiene (clean holding facilities, fomite decontamination, handwashing, footbaths, filth and wound management), regular health screening (leading to isolation, quarantine or culling infected individuals), coordinated breeding (stock and season selection), and maintaining accurate stock records (provider, purchaser, performance, contact tracing). Producers are becoming more aware that stock can be selectively bred for disease resistance without sacrificing productivity, but breeding programs should be based on more than intuitive or casual observations and include hard data on parasite burdens and host developmental traits. In the past, various surgical procedures have been used to prevent ectoparasitic infections in animals (e.g. tail docking, castration and Mules operation to combat fly strike in sheep), but some procedures have fallen into disfavour due to market pressures or ethical concerns.

The control of infectious diseases in companion and performance animals is a lucrative industry, with considerable money spent on pets and leisure, sports and show animals (including those in aviaria, terraria and aquaria). Many conventional and alternative products are available for therapeutic treatments as well as for preventive prophylaxis, with keen advertising supporting sales of parasiticides, repellents and remedies against endo- and ecto-parasitic ‘scourges’. A huge range of processed foods is available together with dietary supplements, water additives, clothing and other tack. Many devices are available to groom animal coats and/or remove ectoparasites (clippers, brushes, combs, tweezers, forceps, shampoos, conditioners). Special housing is promoted for different animal species, ranging from horse stables to dog kennels to bird cages to goldfish bowls. Behaviouralists advocate animal training to socialize pets, curb aggression and hunting, and enhance performance. Local and national governments have developed many regulations addressing such diverse issues as animal welfare, cruelty, abandonment, transportation, import/export, breeding, boarding, agistment, rescue and waste management. Despite such fanfare, parasitic diseases are still problematic in many regions due to poor compliance with chemical control protocols, the emergence of drug-resistance in parasite populations, the persistence of ectoparasites in peri-urban environments, and the indiscriminate faecal contamination of communal areas.

The management of wild animal populations is difficult but is becoming increasingly desirable mainly for conservation reasons. The impact of parasites on wildlife is hard to ascertain as sick animals may succumb to disease or predation without being observed, while animals with lighter or cryptic infections continue to be ambulatory and spread infections. Many parasite species have sylvatic cycles of infection, but a growing number of wild animal species have been found to act as reservoirs of infection for humans and domestic animals, with periodic or sporadic cross-over to rural and even urban hosts. Considerable resources have been deployed to control feral or pest animal species that are damaging ecosystems, usually by killing them (by hunting, trapping or poisoning), but sometimes by manipulating their reproduction (by sterilization or introducing sterile competitors). In areas where large herds of ungulates undertake seasonal migrations near farmlands, some measure of control has been imposed by diverting natural migration routes or providing corridors for their passage. It is prudent to use strong barriers (fences, screens) to exclude vermin and vectors from farms, fodder stores and domiciles, and to restrict the scavenging and hunting behaviours of resident carnivores. The annual migration of wild birds between feeding and breeding grounds presents an interesting paradox. It was thought that long distance migrations would be conducive to the spread of parasitic infections, particularly when animals are stressed by poor nutrition, crowding and over-exertion. However, unhealthy birds may not be able to fly long distances which prevents infections from escaping endemic regions. The culture of fish and shellfish in natural water bodies (estuaries, fjords, sea-cages, streams, dams) can be problematic when wild species (including pests and predators) infiltrate containment areas. Aquaculture enterprises should attempt to minimize incursions by intruders using barriers or other deterrents, but without compromising water quality.

Vectors

Many parasite species are transmitted between vertebrate hosts by a range of invertebrate vectors, including insects (flies/mosquitoes, fleas, lice), acari (ticks, mites), molluscs (snails) and crustaceans (copepods). These vectors act as definitive hosts if they support sexual development by the parasites, as intermediate hosts if they only support asexual development, or as paratenic hosts in which no parasite development occurs. Many arthropod vectors feed on vertebrate blood and may transmit parasites by injecting them as they bite, by contaminating wounds as they feed, or by being eaten by vertebrates. Trematodes utilize molluscs as amplification vessels which support the massive asexual reproduction of cercariae which escape into aquatic habitats to infect vertebrates. The larvae of some filarial nematodes develop in aquatic copepods and are ingested by vertebrates drinking water. While many studies have been conducted on vector biology to determine their distribution and developmental cycles, relatively few studies have compared the competence of different vectors for individual parasite species. Much of our knowledge comes from epidemiological studies in isolated regions. Clearly, further studies are required on the roles that vectors play in the transmission of parasites. Molecular biological techniques are now being used to screen vectors for specific pathogens, spawning an era of molecular epidemiology. However, the results need to be supported by experimental studies on parasites in vectors to quantify their proliferation (multiplicative potential), viability (survival, longevity, infectivity) and routes of infection (ingestion or excretion, inoculative or contaminative) to determine their relative importance in transmission cycles.

While vector populations may be huge in number and widespread in natural environments, various interventions have been applied to reduce host contact with vectors, including physical barriers, toxic chemicals or biological control strategies. Human habitations and animal holding facilities may use window and door screens to exclude arthropods and the buildings themselves should be properly maintained to eliminate entry points (holes) and hiding spaces (cracks). Bed nets have been used with great effect to protect sleeping areas from mosquito vectors in many countries with endemic malaria and viral fevers. Personnel may use protective clothing when moving around outdoors, especially with fabrics impregnated with arthropodicidal or repellent chemicals. A wide range of anti-parasitic chemicals have been developed for the therapeutic treatment of infected hosts and for prophylactic treatments to prevent infections in host at risk. Some chemicals have also been shown to work effectively against vector populations not directly associated with hosts, that is, when applied to vector habitats (such as resting or breeding sites). Insecticidal, acaricidal and molluscicidal chemicals may be used in terrestrial and/or aquatic environments in traps, baits, sprays, fogs, mists, surfactants or water additives, deliberating targeting free-living vector stages. However, considerable caution is advised when using toxic chemicals in the environment to make ensure collateral damage does not damage ecosystem health and to avoid conditions conducive to the development of drug resistance in vectors (an infamous example involves the widespread use of the insecticide DDT which has now been banned since 2004). Investigations into natural plant products with pesticidal properties led to the development of pyrethrin insecticides, and studies are examining a variety of other plants thought to have toxic or repellent activity against different vectors.

Biological control programmes show considerable promise for more environmentally-friendly and holistic approaches to reduce vector populations. Vectors usually have free-living stages that are subject to attack by predators (such as wasps, hornets, flies, ants, beetles, spiders, mosquito fish and grooming birds) as well as a range of pathogens, including entomopathogenic fungi, nematodes, microsporans, viruses and bacteria. Some bacteria have been found with natural insecticidal endotoxins (e.g. *Bacillus thuringiensis*), and others have been found to manipulate vector reproduction (e.g. *Wolbachia* spp. exhibiting selective male killing, sterilization or feminization in some insects). Over the years, many programmes have been developed to decrease vector reproduction rates by breeding and releasing sterilized or transgenically-modified males to compete for mates (strategies well investigated for the control of peri-urban mosquitoes carrying human viral diseases). Some of the greatest impacts made on vector control have involved habitat alteration or destruction, notably the draining of swamps near cities suffering from malaria (an intervention used centuries ago in Europe to reduce bad odours (‘mal-airia’), but now known to have eliminated the breeding grounds of the mosquito vectors). Many management strategies continue to be developed in rural and urban communities to reduce vector breeding sites, ranging from eliminating temporary puddles to rehabilitating waterways to strategic land clearance.

ABIOTIC FACTORS

Most parasites do not live permanently in or on their hosts or vectors, but have free-living stages in the external environment (terrestrial and/or aquatic) as non-motile encysted stages (ova, oocysts) or motile host-seeking stages (immature larvae, nymphs, swarmers or mature adults). They are therefore subject to the prevailing environmental conditions (physical and chemical factors) which can impact on their survival and dispersal. While humans may not be able to manipulate global (or large-scale) environmental conditions, recognition of the factors detrimental to parasite survival, but still favouring host survival, can facilitate subtle manipulation of local (small-scale) conditions. Considerable success has been achieved in the control of many parasitic diseases by changing abiotic (non-living) components through:

- environmental management,
- climate prediction,
- improved sanitation,
- ensuring food security, and
- countering air pollution.

Environment

Parasites and their hosts (including vectors) share the same physical environment, with many modes of transmission involving environmental contamination by infective stages (e.g. water-borne, food-borne, faecal-oral, vector-borne). To better understand parasite transmission, basic knowledge of environmental composition is required together with specific knowledge of the survival characteristics of parasites within those environments; particularly: terrestrial environments (soil and vegetation); aquatic environments (freshwater to marine); as well as on inanimate objects (fomites).

Terrestrial

Terrestrial environments involve many different types of landscapes, varying in topography, geology, hydrology, vegetation and utilization. The Earth's surface comprises 29% land and 71% ocean. Of the 141 million km^2 of land, 76% is considered habitable, with the remainder being barren (e.g. deserts) or covered by glaciers. Almost half (45%) of the habitable land is used for agriculture, with the remainder comprising forests (38%), shrublands (13%), wetlands (3%) and urban development (1%). Two-thirds of agricultural land is used for grazing livestock (meat, dairy) and one-third for cropping (food, biofuels and textiles). Parasites in these different terrestrial environments are influenced not only by their physical and chemical characteristics but also by land utilization. The most visible mark that humanity has left on the planet is the transformation of wild habitats into farmlands. Parasites often benefit from farming practices as hosts are crowded together in small contained areas subject to greater contamination. Different soil and vegetation types have been shown to affect parasite survival, or that of their vectors. For example, gastrointestinal nematode larvae are more active on moist pastures, snail vectors for trematodes are more abundant in wet soils, while *Tunga* fleas prefer warm dry sandy soils. Knowledge of parasite behaviour and survival under different conditions is vital for the alteration and implementation of farming practices that help reduce parasite contamination and transmission. For example, some parasite burdens can be reduced by draining or discing wet soils, by using rotational grazing, and by spelling pastures over hot dry summers. There are numerous anecdotal and proven farm management interventions that can be help control parasitic infections and disease, depending on our knowledge of the parasite involved.

Aquatic

Water is a vital and precious resource for life on this planet. Over 97% of water occurs in oceans as saltwater, another 2% is locked in glaciers, while only 1% is available as freshwater. Water is a perfect medium for the transmission of motile parasites as well as the carriage of non-motile developmental stages. For example, many parasites have flagellated or ciliated stages that actively swim in water seeking hosts, while others have encysted buoyant stages that serendipitously make contact with hosts or are ingested with drinking water. Other parasites utilize aquatic invertebrates as amplification hosts or as vectors for transmission, and some parasites ascend the food chain when big hosts eat small hosts. The survival of all these aquatic parasite stages depends largely on their tolerances to the chemical and physical properties of their watery habitats, particularly temperature, salinity and oxygenation. Parasites vary in their thermal ranges, some preferring colder waters than others, but they do not survive long in hot or freezing conditions. Their salt tolerances are often narrow enough that temporary freshwater baths may be used to treat some ectoparasites on marine fish, and conversely, saltwater baths may be used to treat ectoparasites on freshwater fish. Few parasite species survive in nutrient-rich eutrophic waters which often support bacterial and algal blooms robbing the water of dissolved oxygen. Invertebrate vectors also have specific requirements for their reproduction and survival; for instance, blackfly vectors breed only in flowing waters, while mosquito vectors breed mainly in stagnant waters. Knowledge of parasite biology in aquatic environments allows for various interventions to be included in environmental management programmes to modify aquatic habitats and biota to help reduce parasite transmission.

Fomites

Inanimate (non-living) objects may also carry infectious agents. These 'fomites' include a wide range of natural and artificial objects used for human habitation (buildings, fittings, furniture, clothing, utensils), farming (equipment, barns, yards, cages, nests, bedding), and transport (vehicles). People need to understand the mechanisms by which fomites become contaminated and how to decontaminate them. Contamination usually occurs via host secretions/excretions containing parasites, including faeces, urine, vomitus, sputum, phlegm and scurf. Vectors may also utilize fomites for shelter or breeding, particularly when they contain plentiful hiding places in the form of cracks, crevices or holes. Human and animal housing should be regularly maintained or repaired to eliminate sanctuaries, taking care to avoid conventional porous building materials (weathered wood, mud adobe, straw roofs, earthen floors) and using nonporous materials (hardwood sealed timber, fired bricks, ceramic tiles, plastered walls, steel tubing, roof tiles, tin roofs, concrete floors). Newer fomites are also easier to decontaminate using heat (hot washes, steam-cleaning), suction (vacuum cleaning), radiation (ultraviolet light), stringent chemicals (surfactants, solvents, bleaches), and toxic chemicals (insecticides, acaricides). Insect repellents may also be applied to absorbent materials (such as clothing, bedding, rugs, grooming equipment, harnesses, saddlery and other tack). Utilization of shared spaces should be monitored for cross-contamination, with physical and/or chemical barriers used for separation, isolation or quarantine. If required, personnel may adopt personal protection procedures, similar to those used for barrier nursing.

Climate

Many parasites exhibit temporal and spatial variations in distribution and abundance related to weather conditions. The climate of any region is generally defined as its average weather prevailing over time (at least several decades). While many physical elements contribute to the weather, the most important for parasites are temperature and moisture (as influenced by many other factors, such as sunshine, cloudiness, precipitation, humidity, air pressure, wind, evaporation). Free-living or exogenous parasite stages usually require warmth and moisture to survive, as do their hosts and vectors. Many climatic zones are recognized around the world, most exhibiting annual seasonal fluctuations in weather. Some regions also exhibit longer non-annual cycles, for example, El Nino-Southern Oscillation (ENSO) patterns across the Pacific every 5-7 years. The world is also experiencing global climate change for a variety of reasons, including greenhouse gas emissions from industry and agriculture. The impact of climate change is difficult to predict, and various models have attempted to forecast the scope of changes. In addition to overall warmer temperatures, many agree that the frequency and magnitude of extreme weather events will increase with far-reaching impacts on the environment; involving storms, floods, droughts, soil erosion, desertification, ice loss, and rising sea levels. The geographic distribution of hosts, vectors and parasites will change as regions vary in temperature and moisture levels with different seasonal patterns emerging. Human and animal populations must adapt to changing circumstances and implement different management options as appropriate, rather than rely exclusively on historical records and trends.

Sanitation

Humans and animals regularly produce large quantities of organic wastes which may transmit infectious microbial diseases. Waste products come in many forms, such as excreta (faeces and urine as sewage or manure) as well as other household, industrial and agricultural wastes (wastewater, greywater, effluents, food scraps, garbage). The effective collection, storage, treatment and disposal of waste is therefore paramount to disease control. Humans have changed their toilet habits over centuries from indiscriminate defaecation to using latrines, open cesspits, and toilets leading to closed septic tanks or sewerage collection systems. However, it has recently been estimated that 1 in 5 people still defaecate in the open, and nightsoil is still used in some areas to fertilize vegetable gardens. Sewage treatment plants have been developed to treat waste materials by filtration, sludge activation, and biocomposting, but they can become overloaded or compromised by flood events. Excrement from animals is voided into the immediate environment leading to local contamination, and while some intensive animal industries may wash out animal pens or stalls, the waste is often not collected, stored or treated but simply washed elsewhere. Animal waste, including litter from poultry sheds and straw bedding from stalls, is also often used to fertilize gardens and crops. Aquaculture ponds generally feed into local streams or estuaries without undergoing any treatment, sometimes leading to organic enrichment and microbial blooms.

One of the greatest advances made in the control of infectious diseases was the introduction of effective treatment processes to provide clean potable (drinking) water, particularly the chlorination of reticulated water systems. Water may be decontaminated by removing microbes (by sedimentation, flocculation, filtration, or adsorption) or disinfected by killing microbes (by heat, chemicals (chlorination, ozonation) or irradiation (ultraviolet light or high energy sources). Numerous engineering solutions have been applied to the collection, storage, treatment and distribution of water to urban and rural communities, but many remote and under-developed regions still rely on natural catchments, open dams and untreated water supplies. Irrigation systems are becoming more prevalent in agriculture and land-based aquaculture is proliferating in many riverine and coastal regions. Disease control through waste management should still be practised where appropriate to avoid outbreaks, particularly in intensive culture systems. Many common-sense interventions can also be applied in local situations, such as water flow regulation to cleanse waterways, clearing vegetation from irrigation channels and ponds, avoiding stagnant waters, draining ditches and swamps, maintaining reticulation systems, treating biofilm accumulations, and controlling aquatic leisure activities such as swimming or boating.

Food

Much has been said lately about food security, not only about governments securing stable supplies (sufficiency) but also ensuring food hygiene (safe and nutritious). Malnutrition encompasses both over-nutrition (more calories/protein than required) contributing to obesity, and under-nutrition (insufficient calories/protein for maintenance) manifesting in physical and intellectual growth retardation, including low weight-for-age (underweight), low weight-for-height (wasting) or low weight-for-age (stunting). Poor nutrition also impairs host innate and acquired immunity, making malnourished individuals more susceptible to disease. Many regulations have been embedded in the different food industries to check food hygiene, with industry standards applied to inspection, disinfection, preservation, distribution, storage, expiration and disposal. It is sometimes difficult for individuals within this supply chain to accept responsibility for action or inaction, particularly when faced with strong economic imperatives. Many communities now advocate holistic coverage (e.g. gate-to-plate) involving producers, processors, wholesalers, retailers and governments, with defined lines of communication and accountability. This is critically important with the growing globalization of many food markets to avoid the accidental spread of infectious diseases.

Air

Environmentalists rightly decry air pollution by human industry, with many cited examples involving toxic chemicals. While many viral and bacterial diseases may undergo air-borne transmission involving aerosols, few protozoan or metazoan parasites are transmitted via aerosols. Some infections may cause respiratory signs involving mucus production, sneezing and coughing, but any expired parasites are too heavy and do not remain as air-borne particulates. They can settle and contaminate the surrounding environment (pastures and fomites), but such stages are often fragile and do not survive for long. Nonetheless, the recent Covid epidemic has amply demonstrated the efficacy and utility of personal precautionary measures in disease control, including wearing masks, handwashing, and modifying behaviours (e.g. social distancing).

SOCIOLOGICAL BEHAVIOURS

The greatest impediment to parasite control appears to be the difficulty in changing human behaviour. Many people persist in activities/behaviours which perpetuate parasite transmission and survival. They do so for a variety of reasons: such as historical precedence, adherence to social norms, habituation, resistance to change, lack of awareness, lack of alternatives, etc. These activities are often related to socio-economic status, which can be graded by such measures as life expectancy at birth, gross domestic product per capita, and educational attainment. Poverty is the single most important global determinant for infectious disease risk, with 'poverty traps' exposing vulnerabilities involving environmental, sanitary, nutritional, behavioural and healthcare components. Health security can also be adversely affected by natural disasters, famine, social upheaval and war, due to dysfunctional infrastructure systems, poor living conditions, and rampant anxiety. The global peace index includes components categorized as societal safety and security (internal peace such as violent crime, political stability, respect of human rights, displaced persons) as well as militarization (external peace, armed conflict, war). It is predicted that climate change, population growth, resource scarcity, ideological movements and shifts in global power may degrade global peace in coming decades. Throughout this changing milieu, individuals hold onto customs and traditions, sometimes fiercely so. However, history is not always a good teacher.

Customs and traditions

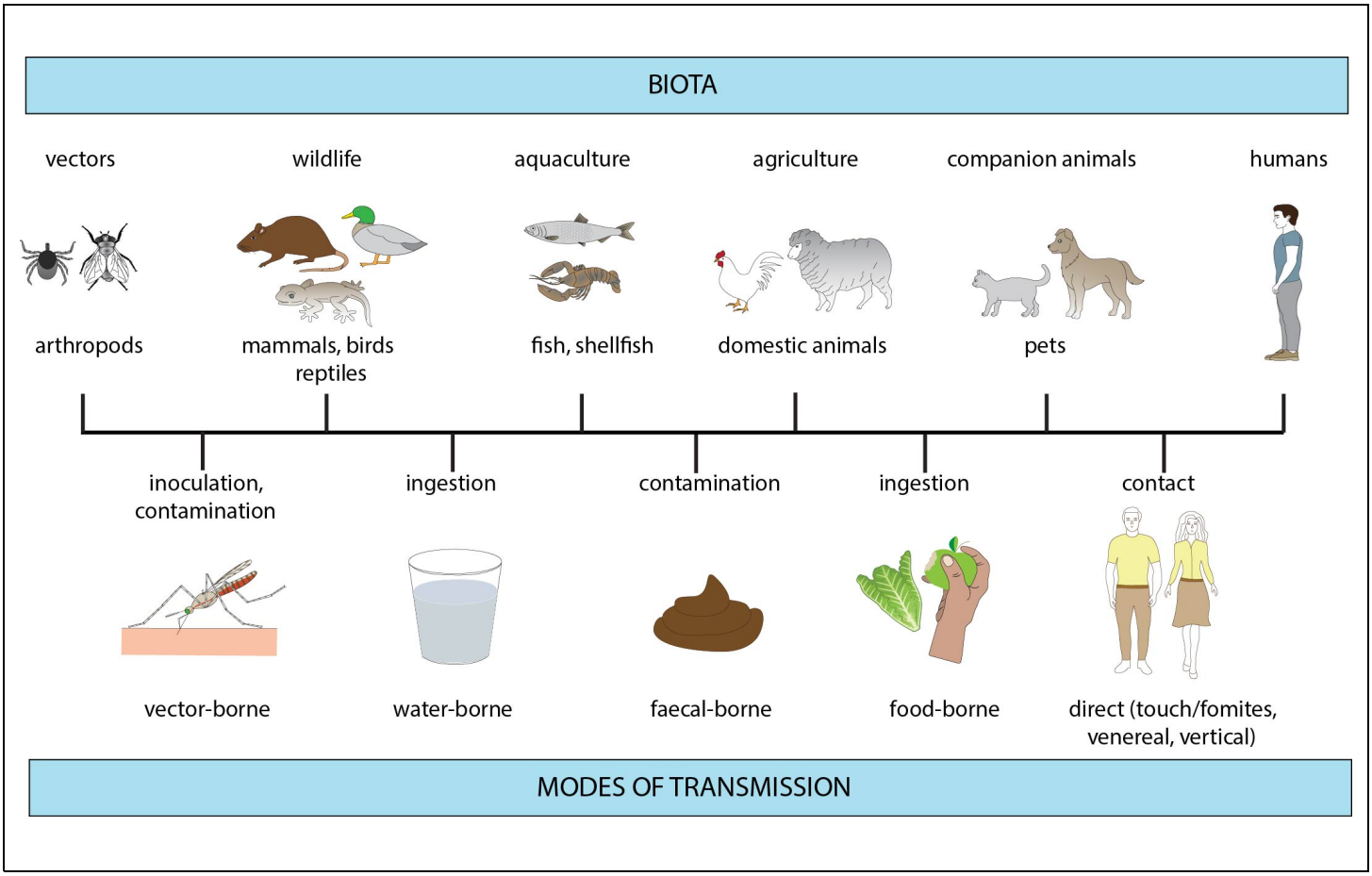
A custom is an accepted way of behaving/acting in a very specific area, society, place or time, whereas a tradition is a system of beliefs or behaviours passed down within a community or society with symbolic meaning or historical significance. Human populations frequently appreciate cultural diversity aspiring to cosmopolitanism and globalization. Some traditions, however, favour disease transmission. For example, the use of nightsoil (human faeces and urine collected overnight) to fertilize vegetable crops may enhance transmission of gastrointestinal parasites such as roundworms and amoebae. Experimental studies demonstrated that microbial biocomposting techniques could render nightsoil safe to use as a fertilizer in only a few days. Several poor communities were provided with biocomposting toilets, but subsequent studies found that parasitic infection rates did not decline. Investigation revealed that residents did not use the new toilets but continued to use nightsoil the old way because their traditions stated it must be used fresh as the vigour imparted to plants only lasted one day. Other examples involve barefoot natives being mandated to wear shoes to avoid acquiring geohelminth infections by transdermal larval penetration, and safe sex practices being advocated to pious communities to avoid sexually transmitted diseases. Many cultures have unique cuisines and cooking traditions that may facilitate food-borne transmission of parasites. The practice of eating raw or under-cooked meat can lead to the transmission of tapeworms (in pork, beef, fish and shellfish) and cyst-forming coccidia (e.g. toxoplasmosis). Many traditional methods of food preparation and preservation do not kill parasites contaminating foodstuffs, and while vegetables, salads and fruits may be cleaned by washing, the wash-water itself may be contaminated by parasites. It is therefore advisable that scientific methods be used to investigate food-borne outbreaks of disease and to identify the tolerances of different parasites to cooking and preserving processes, particularly with the globalization of many food markets.

Healthcare

Not everyone on the planet has access to modern healthcare in the form of reliable evidence-based information, diagnostic services, therapeutic treatments and ancillary care. Indeed, not everyone has the educational background to believe in the 'germ theory' that posits invisible entities cause diseases (now known to be pathogenic micro-organisms). Some degree of knowledge is required for compliance with routine personal hygiene (bathing, showering, hand washing, covering coughs and sneezes), home hygiene (cleaning fomites, vacuuming dirt, laundering clothes and bedding) and the discontinuation of other nonhygienic practices (such as spitting saliva, phlegm or sputum, and not eating soil (geophagia or pica)). Local, regional and national authorities should endeavour to provide contemporary public health amenities, including communal sanitation, water treatment, disease surveillance, epidemiological investigations, risk assessment and facilitating appropriate health treatments through clinics, animal health advisers, community nurses and clinicians. Action should be taken to remediate strange and inappropriate traditional treatments, such as discouraging the use of raw meat and frogs as poultices for open wounds. Every effort should be made to provide and promote cost-effective interventions for disease control, and to assess their acceptance and efficacy in the field. Public education campaigns should be developed to explain and implement control programs, particularly where people are required to change ingrained behaviour patterns. Education programmes are most effective when they target specific diseases rather than providing general advice. Media coverage should include conventional print (newspapers, posters, billboards, stickers, pamphlets) and modern audiovisual aids (radio, television, mobile phones, and internet sources with advertisements, commentaries and testimonials). The general public should be given specific advice with recommended courses of action and recommended timelines, preferably with incentive and reward schemes to support implementation rather than punitive schemes to punish miscreants.

INTEGRATED MANAGEMENT

Parasite control programs should adopt an integrated approach whereby multiple interventions can be practiced in attempts to reduce the incidence of parasitic diseases. The 3 main components involved are logically the parasites (P) themselves, the hosts (H) they infect, and the environments (E) in which they occur. Modelers have collated these components into a conceptual model (known as the HPE epidemiological triad) that attempts to address interactions between hosts, parasites, and their environments; quantified where possible in terms of dynamics (quantity) and kinetics (duration). For example, the thermal tolerances of protozoal cysts and worm eggs should be determined in terms of both temperature optima and exposure time. It has been said that the epidemiological triad imagines our struggle against infectious disease where significant progress can be achieved when you 'know yourself, know your enemy, and know your battleground'. Having identified potential weak spots, interventions can be planned and implemented specifically targeting those interactions to reduce disease transmission and occurrence. Great successes have been recorded by implementing small 'common-sense' interventions; e.g. sleeping under bed-nets to avoid mosquitoes carrying malarial parasites, wearing shoes to avoid transdermal infections by hookworm larvae, straining drinking water to remove copepods bearing guinea-worm larvae, etc. Above all, people should be empowered through public education campaigns to make informed choices to change behaviours and engage in sensible, reliable and cost-effective disease control procedures. Knowledge is power!



Index to parasite genera

Acanthamoeba 76.
Acanthocheilonema 1590.
Acuaria 1476.
Aedes 2278.
Aelurostrongylus 1277.
Akiba 581.
Ambiphrya 681.
Amblyomma 2678.
Amblyospora 801.
Ameson 801.
Amoebotaenia 1763.
Amyloodinium 98.
Ancylostoma 1181.
Angiostrongylus 1285.
Anisakis 1252.
Anncaliia 815.
Anopheles 2305.
Anoplocephala 1742.
Anoplocephaloides 1742.
Apiosoma 681.
Aponomma 2678.
Argas 2543.
Argulus 2965.
Armillifer 2977.
Ascaridia 1375.
Ascaris 1319.
Ascarops 1466.
Aspiculuris 1414.
Austrobilharzia 2010.
Babesia 593.
Balamuthia 83.
Balantidium 620.
Benedenia 2062.
Besnoitia 473.
Biguetiella 552.
Billbraya 557.
Bioccala 550.
Bonamia 765.
Boophilus 2618.
Bothriocephalus 1854.
Bothriocroton 2714.
Bovicola 2123.
Brugia 1571.
Bunostomum 1214.
Calliphora 2449.
Camallanus 1631.
Capillaria 1659.
Carchesium 681.
Caryospora 366.
Ceratomyxa 831.
Ceratophyllus 2253.
Chabertia 1147.
Chelopistes 2139.
Cheyletiella 2815.
Chilodonella 627.
Chirodiscoides 2914.
Chloromyxum 831.
Choanotaenia 1769.
Chorioptes 2864.
Chrysomya 2463.
Chrysops 2369.
Cimex 2178.
Clonorchis 1938.
Cochliomyia 2463.
Cochlosoma 122.
Cooperia 1084.
Cordylobia 2474.
Cosmocephalus 1476.
Costia 287.
Cothurnia 681.
Craterostomum 1126.
Crepidoodinium 98.
Cryptobia 294.
Cryptosporidium 313.
Ctenocephalides 2220.
Cuclotogaster 2139.
Culex 2278.
Culicoides 2317.
Cyathospirura 1459.
Cyathostomum 1134.
Cyclospora 374.
Cylicocyclus 1134.
Cylicodontophorus 1134.
Cylicospirura 1459.
Cylicostephanus 1134.
Cystoisospora 382.
Cytauxzoon 615.
Cytodites 2894.
Dactylogyrus 2040.
Damalinia 2123.
Davainea 1780.
Demodex 2805.
Dermacentor 2723.
Dermanyssus 2766.
Dermatobia 2506.
Dibothriocephalus 1831.
Dicrocoelium 1981.
Dictylocaulus 1229.
Dientamoeba 172.
Dionisia 553.
Dipetalonema 1590.
Diphyllobothrium 1831.
Dipylidium 1755.
Dirofilaria 1602.
Dispharynx 1476.
Dracunculus 1643.
Draschia 1421.
Echidnophaga 2211.
Echinococcus 1734.
Echinochasmus 1899.
Echinoparyphium 1902.
Echinostoma 1884.
Echinuria 1476.
Eimeria 399.
Elaphostrongylus 1269.
Encephalitozoon 815.
Entamoeba 63.
Enterobius 1390.
Enterocytozoon 815.
Epieimeria 447.
Epistylis 681.
Equinia 1742.
Ergasilus 2953.
Eucoleus 1659.
Eutrombicula 2837.
Fallisia 561.
Fasciola 1869.
Fasciolopsis 1877.
Felicola 2132.
Filaroides 1303.
Frenkelia 452.
Gaigeria 1222.
Garnia 560.
Gasterophilus 2531.
Gastrodiscoides 1921.
Giardia 189.
Globocephalus 1191.
Glossina 2400.
Glugea 785.
Gnathostoma 1527.
Gongylonema 1442.
Goniocotes 2139.
Goniodes 2139.
Goussia 440.
Gyrodactylus 2022.
Habronema 1421.
Haemaphysalis 2647.
Haematobia 2441.
Haematodinium 107.
Haematopinus 2084.
Haematopota 2369.
Haemocystidium 555.
Haemogregarina 324.
Haemohormidium 617.
Haemonchus 1047.
Haemoproteus 563.
Hammondia 498.
Haplosporidium 757.
Henneguya 831.
Hepatocystis 547.
Hepatozoon 337.
Heterakis 1365.
Heterodoxus 2170.
Heterophyes 1954.
Heterosporis 785.
Hexamita 179.
Hippobosca 2417.
Histomonas 165.
Holomenpon 2157.
Hyalomma 2739.
Hymenolepis 1807.
Hyostrongylus 1076.
Hypoderma 2522.
Ichthyobodo 287.
Ichthyodinium 107.
Ichthyophthirius 641.
Ichthyosporidium 785.
Isospora 382.
Ixodes 2577.
Johnsprentia 579.

Kabatana 785.
Klossiella 360.
Knemidokoptes 2928.
Kudoa 975.
Lagenophrys 681.
Laminosioptes 2936.
Leishmania 268.
Leporacarus 2907.
Leptotrombicula 2837.
Lernaea 2944.
Leucocytozoon 581.
Linguatula 2987.
Linognathus 2091.
Lipeurus 2139.
Loa 1614.
Loma 785.
Lucilia 2449.
Lutzomyia 2357.
Lynxacarus 2900.
Macracanthorhynchus 1696.
Mansonella 1580.
Mansonia 2278.
Marteilia 776.
Melophagus 2410.
Menacanthus 2157.
Menopon 2157.
Mesnilium 558.
Metagonimus 1962.
Metastrongylus 1237.
Metorchis 1946.
Microgemma 785.
Mikrocytos 771.
Minchinia 757.
Moniezia 1742.
Muellerius 1253.
Multiceps 1720.
Musca 2424.
Myobia 2822.
Myocoptes 2921.
Myxidium 831.
Myxobolus 831.
Naegleria 88.
Necator 1206.
Nematodirus 1093.
Neoknemidocoptes 2928.
Neoparamoeba 71.
Neospora 482.
Neotrombicula 2837.
Nippostrongylus 1109.
Nosema (arthropod) 801.
Nosema (tetrapod) 815.
Nosopsyllus 2263.
Notoedres 2880.
Nycteria 551.
Oesophagodontus 1126.
Oesophagostomum 1154.
Oestrus 2514.
Ollulanus 1102.
Onchocerca 1552.
Oncicola 1702.
Opisthorchis 1929.
Ornithodorus 2555.
Ornithonyssus 2757.
Oslerus 1312.
Ostertagia 1053.
Otobius 2570.
Otodectes 2857.
Oxyspirura 1502.
Oxyuris 1383.
Panstrongylus 2185.
Parafilaria 1538.
Paragonimus 1990
Paramoeba 71.
Paramphistomum 1907.
Parascaris 1238.
Parastrongylus 1293.
Parelaphostrongylus 1261.
Passalurus 1398.
Pediculus 2104.
Pelodera 1029.
Pentatrichomonas 145.
Perkinsus 116.
Phlebotomus 2357.
Physaloptera 1512.
Physocephalus 1466.
Piscinoodinium 98.
Plasmodium (mammal) 505.
Plasmodium (bird) 519.
Plasmodium (reptile) 535.
Pleistophora 785.
Pneumonyssoides 2774.
Pneumonyssus 2774.
Polychromophilus 549.
Polymorphus 1708.
Porocephalus 2977.
Poteriostomum 1134.
Prograniа 562.
Protostrongylus 1245.
Pseudocapillaria 1659.
Psorergates 2829.
Psorobia 2829.
Psoroptes 2850.
Pthirus 2110.
Pulex 2203.
Raillietia 2781.
Raillietina 1789.
Rayella 554.
Rhabditis 1029.
Rhipicephalus 2618.
Rhodnius 2185.
Sauroleishmania 280.
Sauroplasma 616.
Sarcocystis 452.
Sarcophaga 2482.
Sarcoptes 2871.
Schistosoma 1999.
Schyzocotyle 1854.
Scyphidia 681.
Setaria 1622.
Simulium 2335.
Solenoptes 2098.
Sphaeromyxa 831.
Spilopsyllus 2237.
Spirocerca 1451.
Spirometra 1843.
Spironucleus 179.
Sprattiella 580.
Stephanofilaria 1545.
Stephanurus 1164.
Sternosoma 2787.
Stomoxys 2433.
Streptocara 1476.
Strongyloides 1020.
Strongylus 1117.
Syngamus 1171.
Syphacia 1404.
Tabanus 2369.
Taenia 1720.
Teladorsagia 1067.
Tetrahymena 648.
Tetrameres 1430.
Tetramicra 785.
Theileria 605.
Thelazia 1494.
Thelohanellus 831.
Thelohania 801.
Thysaniezia 1742.
Toxascaris 1335.
Toxocara 1342.
Toxoplasma 490.
Trachipleistophora 815.
Triatoma 2185.
Trichinella 1685.
Trichobilharzia 2010.
Trichodectes 2116.
Trichodina 658.
Trichomonas vaginalis 128.
Trichomonas gallinae 136.
Trichomonas (misc.) 145.
Trichostrongylus 1036.
Trichuris 1650.
Triodontophorus 1126.
Tritrichomonas 156.
Trixacarus 2888.
Trombicula 2837.
Trypanoplasma 301.
Trypanosoma (fish) 197.
Trypanosoma (reptile) 210.
Trypanosoma (bird) 223.
Trypanosoma brucei 233.
Trypanosoma cruzi 242.
Trypanosoma evansi 260.
Tunga 2244.
Uncinaria 1198.
Unicapsula 975.
Uronema 634.
Urosporidium 757.
Vaginicola 681.
Varroa 2795.
Vavraia 801.
Vittaforma 815.
Vorticella 681.
Wohlfahrtia 2498.
Wuchereria 1562.
Xenopsylla 2229.
Zoothamnium 681.
Zschokkella 831.

Disclaimer

This resource was developed for professional students of parasitology, notably those at tertiary or quaternary levels of higher education where one of their first main tasks for a project or thesis is to conduct a literature review of their parasite of interest. To this end, I conducted reviews for the each of the 250+ parasite genera covered in this resource by accessing material principally through targetted library searches (including research papers, case reports and topical reviews). Any errors remaining in the foregoing reviews are my own.

While the internet provides unprecedented access to material, it can be a medium for mediocrity if one ventures away from accredited sources. There are some good credible sites managed by professional societies, health organizations and museum agencies, but there are a plethora of casual sites meaning well but often perpetuating misinformation, inaccuracies or myths. The Australian Society for Parasitology (ASP Inc.) has taken on the responsibility of maintaining the PARA-SITE web resource for future generations of parasitologists, so we would welcome any comments or suggested corrections (bear in mind that taxonomy changes over time as different characters are explored or revealed, so we do not want to enter into debate over classification - that is best left to experts specializing in particular parasite groups).

When compiling species tables (host-parasite lists), it was often difficult to reconcile information available from different data-bases for a variety of reasons (missing records, naming confusions, incomplete descriptions, etc). I have bundled this material together in holistic fashion (as would any student) but I have attempted to indicate the current status of species when known (e.g. as bonafide species, synonymized species, reassigned species or species inquirenda). Note that these species lists are not intended as definitive works cast in concrete but are merely consolidated lists with comments. It was also often difficult to review species data characteristic for the whole genus, especially for speciose genera and those exhibiting highly variable traits. Nonetheless, information given is most pertinent to exemplar species (highlighted in orange) which have been shown to be of medical or veterinary significance. Specific drug treatments and dosages are not given for any suggested chemotherapeutic interventions as treatment of afflicted individuals should be carried out under medical or verterinary supervision.

PARA-SITE is intended as an educational electronic resource avilable to any interested parties and the text and life-cycle diagrams have been provided without any copyright restrictions so they can be used in future teaching and research. Each genus is presented as a stand-alone chapter which can be accessed via the indices or by specific searches. The consolidated e-book is therefore unlike a conventional book as the background material is repeated within each chapter rather than being consigned to separate introductory chapters. This was done deliberately to make each chapter self-contained and thus more user-friendly for electronic platforms.

Enjoy!